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The fire pulse: wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers

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Abstract: We investigated the midterm effects of wildfire (in this case, five years after the fire) of varying severity on periphyton, benthic invertebrates, emerging adult aquatic insects, spiders, and bats by comparing unburned sites with those exposed to low severity (riparian vegetation burned but canopy intact) and high severity (canopy completely removed) wildfire. We observed no difference in periphyton chlorophyll *a* or ash-free dry mass among different burn categories but did observe significantly greater biomass of benthic invertebrates in both high severity burned and unburned reaches versus low severity burned reaches. Moreover, a significantly greater flux of adult aquatic insect emergence occurred at sites that experienced high severity fire versus low severity burned and unburned sites. The greatest number of spiders and bat echolocation calls were also observed at sites of high severity fire. Our results suggest that fires of different severity may have very different affects on stream-riparian food webs and that high severity wildfire may lead to an extended "fire pulse" that stimulates aquatic productivity and flux of prey to terrestrial habitats, driving local increases in riparian consumers.

Résumé : Nous examinons les effets à moyen terme de feux de friches (dans ce cas-ci, cinq années après le feu) d'intensités diverses sur le périphyton, les invertébrés benthiques, l'émergence des insectes aquatiques, les araignées et les chauves-souris en comparant des sites intacts à d'autres exposés à des feux de friches de faible intensité (végétation ripicole brûlée, mais canopée intacte) et de forte intensité (couvert végétal complètement disparu). Il n'existe pas de différence dans la chlorophylle *a* ou la masse sèche sans les cendres du périphyton entre les trois catégories d'exposition au feu, mais il y a une biomasse significativement plus importante d'invertébrés benthiques dans les sections sévèrement incendiées et les sections intactes que dans les sections légèrement brûlées. De plus, une émergence significativement plus importante d'insectes aquatiques adultes se produit aux sites qui ont connu un fort incendie par comparaison aux sites peu brûlés ou intacts. Le plus grand nombre d'araignées a aussi été observé dans les sites fortement brûlés et c'est là qu'on a enregistré le plus d'appels d'écholocation. Nos résultats laissent croire que les feux d'intensités diverses ont des effets très différents sur les réseaux alimentaires des rives des cours d'eau et que les feux de forte intensité peuvent produire une « impulsion » prolongée reliée au feu qui stimule la productivité aquatique et un flux de proies vers les habitats terrestres, ce qui explique les augmentations locales de consommateurs sur les rives.

[Traduit par la Rédaction]

Introduction

Wildfire affects a variety of ecosystems, from grasslands to forests, worldwide (Whelan 2007) and is among the most important natural disturbances. In the past several decades, the importance of fire as a significant agent in driving ecosystem structure and function has been increasingly recognized. Furthermore, the effects of wildfire may continue to grow as climate change drives increases in large wildfire frequency and longer fire seasons (Westerling et al. 2006). Many studies have investigated the role of wildfire in terrestrial systems (Agee 1993; Blair 1997; Bailey and Whitham 2002), and its effects on aquatic organisms and ecosystem processes has received some attention (Minshall et al. 1989; Gresswell 1999; Bisson et al. 2003). However, fewer studies have addressed the effects of wildfire on ecological linkages and the flow of resources from water to land.

Fire has the potential to alter water–land linkages, yet relatively few studies have addressed its influences on stream systems and the vectors of aquatic–terrestrial connectivity (Bisson et al. 2003; Dwire and Kauffman 2003). Streams and rivers are closely linked to their adjacent riparian zones and upland habitats by flows of material and organisms. Land-to-water fluxes including nutrients, leaves, and woody debris are well documented (Allan and Castillo 2007), and new work has highlighted the role of terrestrial invertebrates as prey for fish (Wipfli 1997; Nakano et al. 1999; Baxter et al. 2007). Recently, it has been demonstrated that flows of

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resources from water to land can fuel terrestrial food webs (Polis et al. 2004). In particular, the emergence of adult insects from streams constitutes a substantial export of energy to terrestrial consumers such as birds, bats, lizards, and spiders (Power and Rainey 2000; Nakano and Murakami 2001; Sabo and Power 2002). As a result of such connectivity, streams and their adjacent riparian zones are coupled in their responses to natural disturbances, including wildfire.

The effects of wildfire on stream-riparian ecosystems are thought to vary with time after a fire. Minshall et al. (2004) categorized the four stages of response and recovery following fire in watersheds in the western US as (*i*) immediate (the time of active burning to a few days after), (*ii*) short-term (a few days to the beginning of spring runoff), (*iii*) midterm (usually from spring runoff of the first postfire year to sometime beyond the 10th year), and (*iv*) long-term (occurring decades or centuries later). Most studies of effects of wildfire on stream-riparian ecosystems have focused on immediate and short-term time period responses. Understanding the role of wildfire in watersheds also requires investigation of mid- to long-term responses to this natural disturbance.

In the midterm time frame, wildfire has the potential to stimulate aquatic productivity. In contrast to immediate and short-term effects, in the midterm, wildfire may contribute to greater biomass and production of stream insect larvae (Minshall et al. 1989). The basis for this increase in production may be faster algal growth in streams as a result of canopy removal, higher temperatures, or increased delivery of inorganic nutrients such as nitrogen and phosphorus (Spencer and Hauer 1991; Robinson et al. 1994; Minshall et al. 1997). An increase in stream primary production may drive increases in secondary production of herbivorous stream insect larvae (Minshall 2003). On the other hand, effects of fire might diminish zoobenthos via habitat disturbance (e.g., debris flows, increased sedimentation). If the production of benthic insect larvae were stimulated, this should translate into more adult insects emerging from streams in burned vs. unburned sites.

Consumers specializing on riparian insects may also benefit from a pulse in aquatic productivity following wildfire. A large portion of emerging insects do not return to streams (Jackson and Fisher 1986) and can contribute from 25% to 100% of the energy or carbon required by many riparian consumers (Baxter et al. 2005). For example, some guilds of spiders derive the majority of their carbon from emerging stream insects (Power and Rainey 2000; Collier et al. 2002; Paetzold et al. 2005). In particular, spiders of the family Tetragnathidae build horizontal webs in riparian zones and are dependent on emerging insects for a large portion of their diet (Williams et al. 1995; Kato et al. 2004), and their abundance tracks spatial variation in insect emergence (Kato et al. 2003; Iwata 2007; Marczak and Richardson 2007). Similarly, bats that forage on emerging insects have also been shown to track changes in the availability of this resource (Power and Rainey 2000; Fukui et al. 2006). Therefore, if wildfire drives increases in prey availability, this may lead to local increases of these terrestrial insectivores.

If wildfire affects the flux of aquatic prey to terrestrial consumers, the severity of fire may mediate the strength of such a response. For example, in terrestrial systems, more severe fires have stronger effects on forest and grassland structure and composition (Agee 1993; Halpern and Spies 1995; Dwire and Kauffman 2003). Furthermore, the response to fire severity can be incremental, with high severity fires having the greatest effects and those of low severity fire falling intermediate (see Halpern and Spies 1995). In some cases, severe fires may be more likely than mild fires to increase both primary and secondary productivity and affect higher trophic levels (see Bailey and Whitham 2002). Furthermore, pulses in productivity are common following infrequent fires in tallgrass prairie systems (Seastedt et al. 1991; Blair 1997). Just as fire severity has consequences for terrestrial ecosystems, it may also affect responses at the aquatic–terrestrial interface. Thus, there is a need for studies that explicitly investigate the effects of fire severity on linkages between stream and riparian ecosystems.

In this study, we sought to examine the midterm (5–10 years after the fire) effects of wildfire on algae, the production of stream insects, and consequences for riparian predators of these insects. We hypothesized that wildfire results in an extended “fire pulse” by stimulating aquatic production and the flux of aquatic prey to terrestrial habitats, driving an increase in riparian consumers in the midterm period. To test this hypothesis, we compared various food web components in a suite of unburned watersheds with those that had experienced low severity and high severity wildfire. We measured responses across three trophic levels: biomass of periphyton (attached stream algae), benthic insects and emergence of adult aquatic insects, and occurrence of spiders and bats. We tested four predictions: (*i*) biomass of periphyton would be greater in burned vs. unburned sites, (*ii*) biomass of benthic insects would be greater in burned vs. unburned sites, (*iii*) the flux of emerging adult aquatic insects would be greater in burned vs. unburned sites, and (*iv*) the frequency of occurrence of spiders and bats would be greater at burned vs. unburned sites. In addition, we hypothesized that the effects of wildfire would be additive such that sites exposed to high severity fire would have the highest periphyton biomass, stream insect productivity, and occurrence of riparian consumers, whereas low severity burned sites would fall intermediate relative to unburned sites. Thus, in this field study, we examined the effects of fire and fire severity on both aquatic and terrestrial organisms. Most studies of wildfire effects have tended to measure either one factor among sites or many factors at one site, whereas this investigation addressed effects on multiple trophic levels across 16 sites.

Materials and methods

Study site

Study streams were located within the Payette National Forest in central Idaho, USA, on tributaries of Big Creek, which flows into the Middle Fork of the Salmon River in the Frank Church “River of No Return” Wilderness Area. We chose to study the effects of wildfire in this wilderness watershed because we wanted to measure responses by stream ecosystems mostly unaltered by humans and also because here natural fire regimes have been minimally affected by fire suppression or land cover change. The streams flow through steep, narrow valleys with forested slopes, a mixture of primarily Douglas-Fir (*Pseudotsuga menziesii*) and Ponderosa Pine (*Pinus ponderosa*). Additionally, bare and sparsely vegetated areas of grass and sagebrush (*Artemisia*) are common. The dominant riparian vegetation includes Red Osier Dogwood (*Cornus sericea*), Rocky Mountain Maple (*Acer glabrum*), and Alder (*Alnus viridis*). The region receives an average of 40 cm of precipitation annually, the majority falling as snow, resulting in peak flows from late spring through midsummer. The streams generally remain at baseflow conditions from late summer through winter.

We selected study streams that were affected by the extensive Diamond Peak wildfire, which burned most of the lower portion of the Big Creek drainage (including upland and riparian zones) to varying degrees in 2000. Based on the relative area burned upstream and the condition of postfire riparian vegetation in 2005, we categorized reaches in tributaries of the lower Big Creek drainage into three classes (Fig. 1): (*i*) high severity burned, where wildfire removed canopy from large areas of the catchment upstream and removed both riparian understory and canopy such that only the understory had returned by 2005; (*ii*) low severity burned, where fire burned less catchment area and mainly removed the understory such that the understory had returned under an intact canopy; and (*iii*) unburned, where the upstream catchment and reach were entirely unburned or burned long ago (>50 years). Because of the spatial extent and high severity of the fire, our study design was necessarily unbalanced, with six high severity burned reaches, three low severity burned reaches, and three unburned reaches. Six high severity burned sites were selected to increase statistical power, but it was impossible to find additional unburned and low severity burned study reaches close enough to the study area for repeated sampling. For the field season of 2006, four more reaches, two unburned (second and third order) and two high severity burned (third and fifth) (Supplemental Table S1, available from the NRC Data Depository[3]), were included in the study to make additional measurements of periphyton and spider abundance. Within the three types, we selected 100 m study reaches and used segment and reach classification (sensu Frissell et al. 1986; Bisson et al. 2006) to identify sites that were similar in stream size, valley segment type, and reach type. All were second- to third-order streams in alluviated canyon segments with step-pool reach types. In addition, sites were located in the lower portion of each tributary to facilitate access via hiking.

Sampling

We sampled 12 reaches from May through October 2005, with additional samples collected on four more reaches for a total of 16 reaches in June and July 2006. At each site, we collected data on a suite of physical and biological parameters as described below following the methods of long-term monitoring studies conducted in this area (see Davis et al. 2001).

We collected data on a range of physical factors that we anticipated might affect production within the linked aquatic–terrestrial food web. These habitat variables included solar radiation, aspect, temperature, stream width and depth, streambed substrate conditions, and available structure for spider web attachment. Influx of solar energy can be an important factor in determining the productivity of a stream. We estimated solar input at each site between 1200 and 1400 on cloudless days during July 2006. Potential solar input was measured at four locations along each reach, every 25 m, using a Solar Pathfinder, which measures the available annual solar radiation as constrained by topographic features (Solar Pathfinder, Linden, Tennessee; www.solarpathfinder.com). In addition, we took 20 measurements of photosynthetically active radiation (PAR; model LI-1000, LI-COR, Lincoln, Nebraska) every 2 m just above the water surface beginning at the downstream end of each 100 m reach. We took the measurement within the dominant type of lighting present (i.e., direct sunlight vs. shade) along the width of the stream at each transect, taking into account the presence or absence of vegetation. We monitored water temperature at each site year-round using StowAway Tidbit and HOBO data loggers (Onset, Pocasset, Massachusetts) as it is known to affect aquatic invertebrate species composition, life history (including timing of emergence), and production (Huryn and Wallace 2000). We also monitored water temperature during the summer of 2006 at the additional four sites. Because the condition of the stream bed can influence the production of algae and invertebrates (Allan and Castillo 2007), we measured depths and widths of the stream channels and completed substrate surveys for each reach. At 50 locations (every 2 m) along each 100 m study reach, a rock was randomly selected, its size was measured, and percent embeddedness was estimated (Davis et al. 2001). To survey potential habitat for attachment of spider webs, we measured stream distance between vegetation over the channel and counted availability of wood (Laeser et al. 2005).

We measured stream periphyton from five rocks haphazardly selected from within riffles distributed systematically (approximately every 25 m) throughout each study reach. We scraped an area of 2.96 cm^2 of each rock and analyzed biomass as chlorophyll *a* and ash-free dry mass. We extracted chlorophyll *a* following standard methods (in 10 mL of methanol, filtered through Watman GF/F 4.7 cm filters), and estimated biomass using a spectrophotometer (model ThermoSpectronic Genesys 5, Thermo Fisher Scientific Inc., Waltham, Mass.) (American Public Health Association (APHA) 1995). Following extraction, periphyton samples were ashed at 550 °C, rewetted, dried at 105 °C, and weighed for ash-free dry mass (APHA 1995). We substituted 2005 data for two unburned and two low severity burned reaches in the analysis of periphyton samples because a wildfire in July 2006 burned study sites before sampling could be completed. Periphyton data from 2005 and 2006 were compared for all sites from which data were col-

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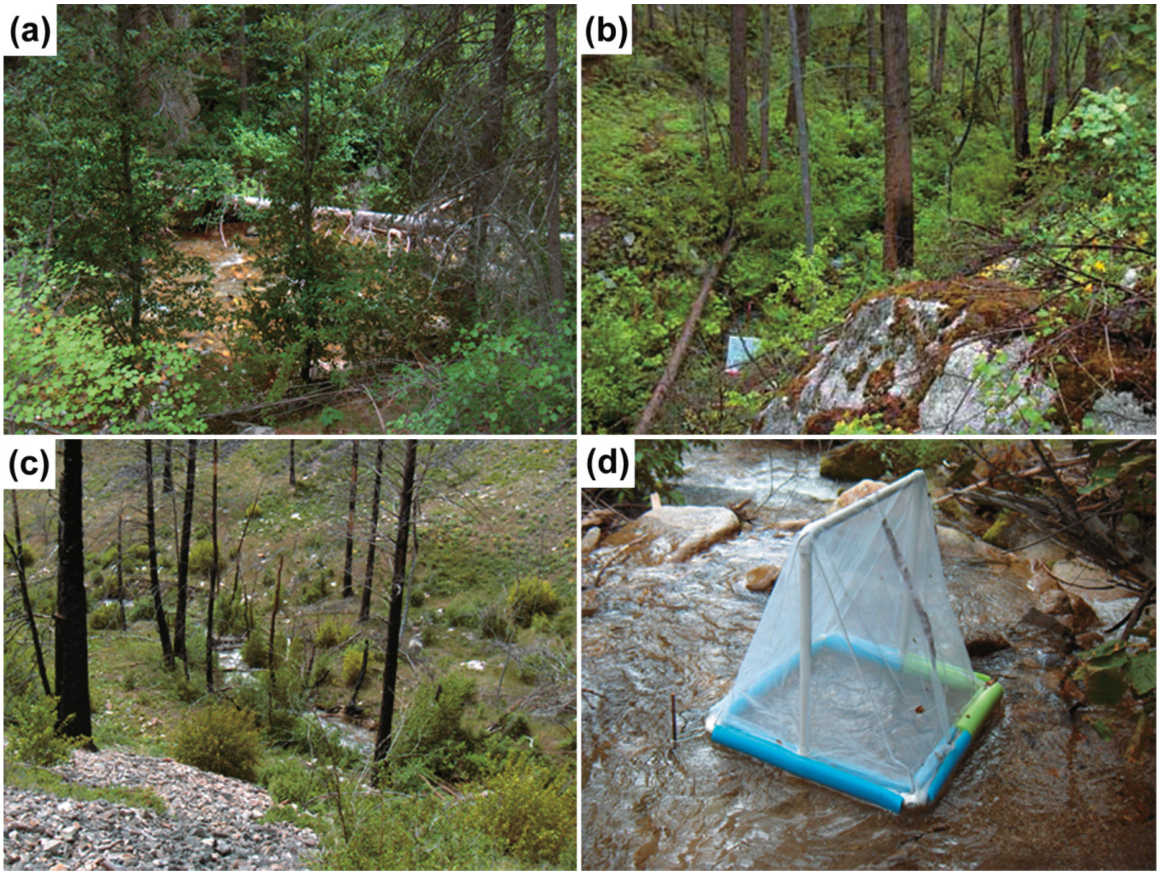
[3] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5357. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html.

Fig. 1. (*a–c*) Pictures of the three fire classes determined based on existing postfire vegetation in 2005: (*a*) unburned, within the last 50 years; (*b*) low severity burned, where fire burned riparian vegetation (as evidenced by the fire scar on the base of the tree located at the center of the image) but the canopy remained intact; and (*c*) high severity burned, with both riparian vegetation burned and canopy removed by wildfire. (*d*) Example of floating emergence trap used to collect emerging aquatic insects.



lected in both years, and no difference in periphyton biomass between years was detected.

We used a Surber sampler (0.093 m^2; Aquatic Research Instruments, Hope, Idaho) to sample zoobenthos once in July 2005 by collecting five replicates from random locations within riffles every ~20 m in each study reach. We measured the flux of adult aquatic insects emerging from each reach from May through October 2005 using four 0.33 m^2 floating emergence traps (Fig. 1) set on the stream surface. Traps were placed in pools to create a solid seal with the water surface as riffles experience more turbulence and, additionally, because pools may be where most emergence occurs (Iwata 2007). Each set of traps accumulated insects continuously for 4–5 days prior to collection from May through August and were sampled on a biweekly basis from late August through October. We removed insects from the traps using an aspirator.

We sorted all benthic and adult insects and identified them to the lowest level required to classify them into trophic guilds and major life history types (usually family or genus). The latter was done mainly to address potential responses of community composition to wildfire (Malison 2008). We dried (105 °C ≥ 24 h) and weighed all insects (to the nearest 0.001 g) to obtain estimates of biomass for each taxon. Floating emergence traps underestimate the number of adults of bank-emerging taxa (Wallace and Anderson 1996; Stewart and Stark 2002), which in these streams principally include relatively low numbers of stoneflies (Plecoptera; Malison 2008). These were rarely captured in our traps, and we omitted these underestimated taxa from our analyses. As insects were washed out of emergence traps during heavy rain, we considered the sample collection time to be the total days during the sampling period without rain, excluding brief rain showers (which were insufficient to remove insects from netting).

With respect to predators of aquatic insects, we surveyed both spiders and bats. We surveyed web-weaving riparian spiders along 30 m transects encompassing both banks of each study reach during July when spiders were at peak abundance. We surveyed spiders by walking streambeds at night (2200–0000) when spiders were most active and visible. Spider abundance was recorded by family, which is easily distinguishable in the field. More than 90% of spiders belonged to the families Tetragnathidae and Araneidae, and the former were dominant. We conducted surveys of bats at night at three unburned and three high severity burned sites, once in June, July, and August 2005, in conjunction with the moon phase (not during full moon). We used passive acoustic monitoring to record the frequency of bat echolocation calls (AnaBat Bat Detector; Titley Electronics, New South Wales, Australia). We did not survey low severity burned sites for bats because of the proximity of several of these sites to caves. Furthermore, because bats are highly mobile, we could not be sure that the distance between some low severity and high severity burned habitats was great enough that bats would not forage in both habitats during a short time period. Surveys started just after dusk and were at least 2 h in duration. We estimated bat foraging by counting the number of search and feeding buzz calls. We defined a call as the start to the end of sequential pulses ending in a silent period. Because buzz calls (characterized by an increased frequency and emitted during the terminal phase of preying on an insect) were not recorded frequently, we used the combined number of buzz and search calls to estimate foraging activity, as there is a strong association between the number of search and buzz calls (Fukui et al. 2006). The silver-haired bat (*Lasionycteris noctivagans*) was the dominant bat species in June, whereas several species of *Myotis* were more common in July and August (Jason Beck, Idaho State University, Department of Biological Sciences, 921 S. 8th Avenue, Pocatello, ID 83209, USA, unpublished data).

Statistical analysis

The effect of burn severity on all habitat characteristics was analyzed using one-way analysis of variance (ANOVA) (PROC GLM, SAS 9.1; SAS Institute Inc., Cary, North Carolina). We tested the effect of burn severity on periphyton (chlorophyll *a* and ash-free dry mass), biomass of benthic insects, and spider abundance using ANOVA (PROC GLM, SAS 9.1). In the analyses of benthic insects and spider occurrence, pairwise comparisons among the least squares means for burn type were assessed using Tukey's honestly significant difference (HSD). The effect of burn severity on flux of insect emergence ($mg \cdot m^{-2} \cdot day^{-1}$) was analyzed using repeated-measures ANOVA (PROC MIXED, SAS 9.1), using burn severity as a fixed factor and stream as a random factor (stream nested within burn type).

Sample periods, the unit of measurement, were repeated 22 times, but not all emergence traps started running at the same time in all drainages. Hence, because of missed observations in some weeks, we pooled every three to four samples into six sampling periods. In the repeated-measures analysis of emergence, we made two a priori comparisons (because of low power): between unburned and high severity burn categories and between unburned and low severity burn categories. These comparisons were assessed using Dunnett's test. A pairwise comparison among the least squares means using Tukey's HSD was used to compare emergence between low and high severity burn categories. We analyzed the bat echolocation response data using a *t* test because we had only two reach types — high severity burned and unburned. All biomass and count data were log-transformed to meet the assumptions of parametric analysis. P values below 0.05 were considered significant, and P values between 0.05 and 0.1 were considered marginally significant, though of potential biological meaning, given the low sample size and weaker statistical power of this field study.

Results

In general, habitat characteristics did not vary significantly among stream reaches in different burn severity categories (see Supplemental Tables S1 and S2[3]). Potential solar insolation (from Solar Pathfinder), stream substrate embeddedness, distance between overhanging vegetation, and amount of wood did not differ among burn severity categories ($F_{[2,8]} \leq 1.98$, $P \geq 0.200$; Supplemental Table S1[3]). Despite no statistical differences in measured potential solar insolation (shading not incorporated), there was a marginally significant difference in photosynthetically active radiation (PAR) readings at stream surfaces by burn category ($F_{[2,8]} = 4.02$, $P = 0.062$). Twofold greater PAR reached the stream surfaces at high severity burned vs. unburned sites (Supplemental Table S2[3]; 954 ± 211 vs. 458 ± 106 μmol; Tukey's HSD, $P = 0.360$), and almost seven times more reached the surface of high severity burned streams than low severity burned streams (Supplemental Table S2[3]; 954 ± 211 vs. 143 ± 71 μmol; Tukey's HSD, $P = 0.059$). Although there were differences in light, there were no differences in water temperature, as annual degree days did not differ by burn category (Supplemental Table S2[3]; 1923 ± 142 (unburned), 2335 ± 410 (low), and 2187 ± 86 (high); $F_{[2,9]} = 0.83$, $P = 0.471$). Low severity burned reaches had somewhat smaller widths and depths ($F_{[2,9]} \geq 2.72$, $P \leq 0.119$) and somewhat smaller median substrate size (Supplemental Table S1[3]; 10.5 ± 3.6 vs. 20.3 ± 2.7 and 18.7 ± 2.0 cm; $F_{[2,9]} = 3.27$, $P = 0.086$) than both the unburned and high severity burned reaches, though differences were only marginally significant.

Contrary to our hypothesis, we observed no difference in periphyton chlorophyll *a* ($F_{[2,13]} = 1.20$, $P = 0.308$) or ash-free dry mass ($F_{[2,13]} = 1.17$, $P = 0.316$) among burn categories (Fig. 2*a*). Both the unburned and high severity burned sites were similar in chlorophyll *a* (Fig. 2*a*), but the low severity burn category had a slightly lower chlorophyll *a*. Both the unburned and high severity burned sites also had similar ash-free dry mass of periphyton (6.9 ± 1.2 vs. 7.5 ± 0.8 $g \cdot m^{-2}$), and the low severity burn category had a slightly lower ash-free dry mass (5.8 ± 1.2 $g \cdot m^{-2}$).

Although we did not observe a difference in periphyton biomass, there was a strong overall effect of burn type on benthic insect biomass ($F_{[2,9]} = 41.04$, $P < 0.0001$). In contrast to our incremental hypothesis, the greatest difference that we observed was actually between high and low severity burn categories, with high severity burned sites having almost fivefold the biomass of benthic insects of low severity burned sites (Tukey's HSD, $P < 0.0001$) versus 1.6 times the biomass of benthic insects of unburned reaches (Tukey's HSD, $P = 0.100$). The latter comparison was not significant because of the high variability in burned versus unburned reaches (Fig. 2*b*).

The ordinal magnitude of emerging insect flux in the three reach types was similar to that for zoobenthos, with high severity burned reaches having the greatest emergence, unburned reaches falling intermediate, and low severity burned reaches the lowest (Fig. 2*c*). There was a marginally significant overall effect of burn severity on aquatic insect emergence (ANOVA, $F_{[2,9]} = 4.03$, $P = 0.056$). This analysis was based on over 700 samples collected from 22 different sample periods and 12 streams during June through October 2005. The difference between unburned and low severity burned reaches was small (Dunnett, $P = 0.985$), whereas the flux of emerging insects was marginally significant and more than twofold greater in the high severity burn category than in the unburned category (Dunnett, $P = 0.093$). The

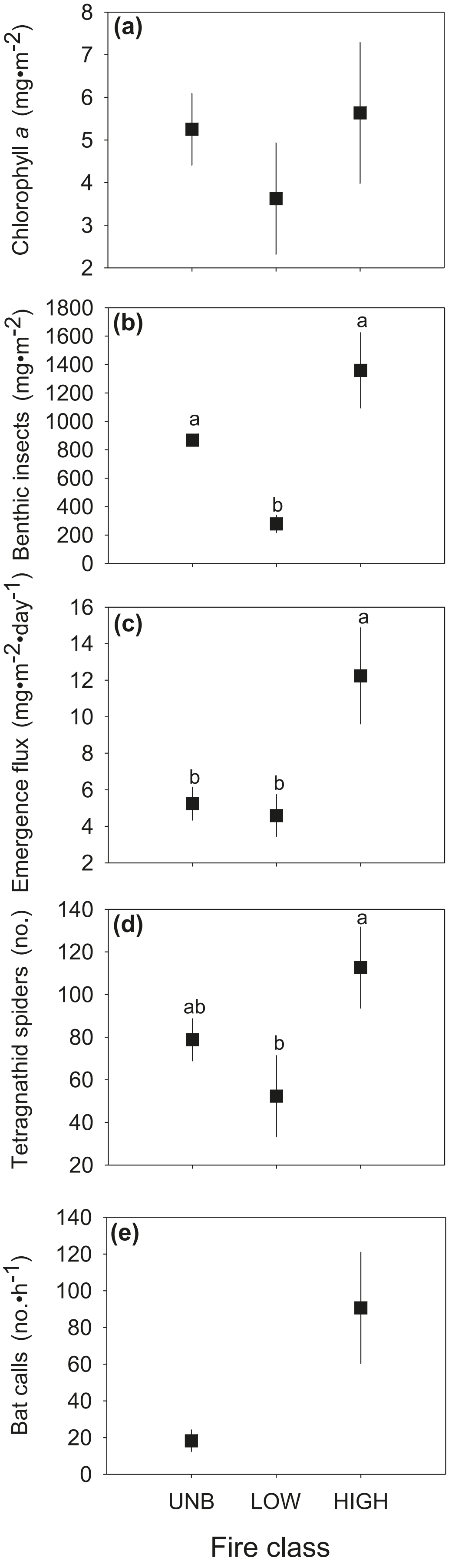


Fig. 2. Results of five food web components sampled from 16 streams between May and October 2005 in reaches of three fire classes: (*a*) periphyton chlorophyll *a*; (*b*) biomass of benthic insects; (*c*) emergence flux; (*d*) number of tetragnathid spiders; and (*e*) number of bat echolocation calls. Fire classes: UNB, unburned ($n = 5$ for chlorophyll *a* and spiders, $n = 3$ for benthic invertebrates, emergence, and bats); LOW, low severity burned ($n = 3$ for chlorophyll *a*, benthic invertebrates, emergence, and spiders); HIGH, high severity burned ($n = 8$ for chlorophyll *a* and spiders, $n = 6$ for benthic invertebrates and emergence, $n = 3$ for bats). Different letters indicate significant differences ($P < 0.1$) among burn types based on least significant difference (LSD) comparisons after analysis of variance (ANOVA) of log-transformed data. However, differences indicated in number of Tetragnathid spiders and between high severity burned and unburned emergence were marginally significant ($P = 0.07$ and 0.09, respectively).

flux of emerging insects was almost threefold greater in the high severity burn category than in the low severity burn category (Tukey's HSD, $P = 0.036$). We also observed a significant effect of time on emergence ($F_{[5,28]} = 6.74$, $P = 0.0003$), with the greatest flux difference between burn categories occurring early in the summer during peak emergence. For example, emergence was up to fivefold greater in high severity burned sites than in both unburned and low severity burned sites during the month of June. Though the flux of emergence became more similar among burn categories by late July, this same pattern held throughout August, September, and October when total emergence was lower. There was no significant interaction between time and burn type ($F_{[10,28]} = 1.26$, $P = 0.301$), indicating similar patterns of emergence in all streams.

We also observed effects of wildfire on insectivorous predators. The density of tetragnathid spiders differed by burn category, though the overall effect was only marginally significant ($F_{[2,13]} = 3.22$, $P = 0.073$). The ordinal magnitude of the three burn categories was again the same as that for benthic invertebrates and emerging insects, but the difference was only marginally significant between high and low severity burned reaches (Fig. 2*d*; Tukey's HSD, $P = 0.062$). No significant differences were observed between unburned and high severity burn categories (Tukey's HSD, $P = 0.55$) or between unburned and low severity burn categories (Tukey's HSD, $P = 0.32$). In terms of vertebrate predators, the frequency of bat echolocation calls was greater in high severity burned reaches than in unburned reaches (Fig. 2*e*; *t* test, $P = 0.04$).

Discussion

The findings of this study suggest that high severity wildfire may drive a pulse in aquatic productivity detectable at multiple trophic levels, including the riparian consumers of aquatic insects. We observed the greatest biomass of benthic insects and emerging adult aquatic insects, occurrence of tetragnathid spiders, and frequency of bat echolocation calls in reaches that had been severely burned (forest canopy removed) 5 years prior to our study. Our results further indicate that fire severity may mediate such responses because the greatest differences that we observed were between high and low severity burned sites rather than between burned and unburned sites as we had predicted. Several studies have documented short-term responses to fires, including pulses of nutrients into streams directly following fire (Tiedemann et al. 1978; Schindler et al. 1980; Spencer and Hauer 1991). However, we observed that the effects of high severity wildfire could last longer, continuing at least 5 years after the fire with an extended pulse of stream insect productivity, as indicated by adult insect emergence. Rather than a flux from land to water, characteristic of short-term fire effects on nutrients, this midterm increase in productivity was dominated by an increase in aquatic insects emerging into riparian areas. Just as the input of wood from land into streams continues for many years after a fire (Minshall et al. 1989), providing important habitat for stream organisms (Gregory et al. 2003), this midterm pulse from water to land may serve to extend the temporal effects of wildfire, with potential consequences for terrestrial predators.

The greater emergence of adult stream insects from sites that experienced high severity wildfire appeared to be associated with higher local abundance of Tetragnathid spiders and bats. Factors other than aquatic insect prey such as fire-induced changes in habitat (e.g., more open foraging habitat for bats) or increases in terrestrial insect prey may have contributed to the patterns that we observed for spiders and bats. However, the latter is not likely, as a parallel study found terrestrial insects to be least abundant at high severity burned sites compared with those in the unburned and low severity burn categories (measured by pan traps; Breanne Jackson and Jeff Braatne, University of Idaho, College of Natural Resources, P.O. Box 441142, Moscow, ID 83844, USA, unpublished data). Experimental work has shown that these insectivores can track variation in emergence (Kato et al. 2003; Fukui et al. 2006), and we expect that the same may occur following severe wildfire. As observed by Nakano and Murakami (2001), such a subsidy can be especially important in periods when terrestrial food resources are less available for riparian insectivores. Though the magnitude of organic matter flux via emerging insects is small compared with that of inputs from land to water (Fisher and Likens 1973; Webster and Patten 1979), a large portion of this high quality prey does not return to streams (Jackson and Fisher 1986) and may be of disproportionate importance to terrestrial predators, including others that we did not investigate (e.g., birds, reptiles, and amphibians) (Baxter et al. 2005).

Just as the flood pulse (Junk et al. 1989) delivers terrestrial carbon to rivers while the land is subsidized by water and other materials, wildfire also results in amplified reciprocal fluxes between the land and water and its effects can extend many years after the event. Increased postfire productivity within streams also has the potential to fuel additional aquatic consumers such as predacious aquatic insects (Malison 2008) and fish (Dunham et al. 2007; Koetsier et al. 2007). In fact, we have observed (P. Della Croce and C. Baxter, unpublished data) greater export of drifting insects and aggregation of trout at confluences of high severity burned versus unburned tributaries, suggesting that fire-induced increases in insect productivity of tributaries might have important consequences for downstream fisheries.

The mechanisms responsible for the greater benthic invertebrate biomass and emerging insect flux in sites that experienced high severity wildfire are not clear. We initially hypothesized a bottom-up effect, i.e., an increase in consumers driven by an increase in primary producers. However, we observed no significant differences in periphyton biomass by burn severity category, despite the fact that there was a greater amount of light available at high severity burned sites. There may be a number of reasons why we did not observe these differences. First, the logistics of conducting this work in the wilderness precluded measurement of actual primary productivity, though this would have been a more sensitive measure than one snapshot of standing crop biomass. Though some studies have described increases in periphyton biomass in the short and intermediate time frames following fire (e.g., Minshall et al. 1997), less detectable effects in the midterm may require more sensitive measures of production and turnover rates, which have not yet been accomplished as part of wildfire studies. Though similar biomass was present in our study, it does seem likely that production of algae may have varied by burn severity category as a result of more rapid turnover of algae at high severity burned sites. Second, there may have been greater production of algae at high severity burned sites, but also greater insect grazing effects that may have resulted in similar biomass of periphyton in different burn categories. Third, there may have been differences among categories but our sampling method did not have sufficient power or precision to detect them. Lastly, there may not have been a difference in biomass or production of algae in the midterm period following wildfire in these streams because they were limited by something other than sunlight such as nutrients (Marcarelli and Wurtsbaugh 2007). Given the patchiness of periphyton growth in both space and time and that the pattern was similar to those that we observed for higher trophic levels (just not significant), it seems likely that we did not observe a pattern in periphyton biomass because of a combination of the first three reasons.

Another possible mechanism contributing to greater aquatic insect production at sites exposed to high severity wildfire may be that these sites receive increased inputs of allochthonous carbon in the midterm period. Allochthonous carbon is known to be a key resource for headwater stream invertebrates (Allan and Castillo 2007), and the regrowth of riparian vegetation following a fire is likely to include proportionately more herbaceous plants and deciduous shrubs and trees than might have been present before a fire (Dwire and Kauffman 2003). Consequently, there may be greater delivery of more labile (edible) plant material to streams at burned versus unburned sites, and this material (combined with in-stream sources of detritus) may drive increased production among detritivorous stream insect larvae (Minshall 2003). However, a parallel study to this one, located on the same study streams, compared flux of allochthonous inputs between unburned and high severity burn categories and found that the high severity burn category had lower inputs of both deciduous and coniferous litter (B. Jackson and J. Braatne, College of Natural Resources, P.O. Box 441142, Moscow, ID 83844, USA, unpublished data). It is possible that there may be a difference in the nutrient quality of those allochthonous inputs, but this has not been investigated.

One further mechanism could be that rather than being caused by a change in basal resources, the observed differences in insect emergence may have been driven by disturbance-induced compositional differences in the invertebrate communities among sites. Previous studies have shown that benthic invertebrate communities can change in composition following wildfire (Minshall et al. 1997; Minshall et al. 2001). Generalist herbivore–detritivore taxa, e.g., *Baetis* (Baetidae) and Chironomidae, have fast life histories and seem to be well adapted for the variable physical conditions found in many postfire streams (Mihuc and Minshall 1995). As these *r* strategists (sensu Pianka 1970) produce more generations per year, a greater flux of emergence could be produced from sites that experienced high severity fire because of the faster turnover of these taxa. In fact, we did observe a greater flux of both Chironomidae and *Baetis* emerging from high severity burned sites than from either unburned or low severity burned sites (Malison 2008). Thus, the difference in emergence could have been driven by a shift in community composition to include more productive taxa following wildfire, serving to stimulate the flux of adult insect emergence to terrestrial habitats. Because of logistical and even ethical constraints, studies of wildfire effects are often based on comparative designs like this one, but determining the strength of effects and isolating mechanisms may require the control and replication of ambitious, large-scale field experimentation.

In addition to describing a midterm response to high severity fire, our results also suggest that different types of fire may have different impacts on stream-riparian ecosystems. Some of the strongest differences that we observed were between the high severity and low severity burned reaches. High severity fire appeared to stimulate the production of more benthic invertebrates, greater emergence, and more spiders and bats, whereas low severity fire seemed to have no effect on, or possibly even inhibited, these responses (low severity burned reaches had slightly lower values for some response variables than unburned reaches). Thus, it may be that the wildfire severity determines both the strength and direction of biotic responses. However, we do not know the mechanisms behind the differences that we observed between sites that experienced high versus low severity fire. The differences might simply have been the result of more sunlight entering the sites that experienced high severity versus low severity fire. Additionally, the sites that experienced low severity fire had a dense growth of riparian shrubs (reflected in greater shading and lower PAR than at unburned sites), even though their upper canopies were slightly more open than unburned reaches. Yet, if differences in insect productivity were only the indirect result of increased sunlight, we might have expected to detect differences in periphyton biomass. It is also possible that the differences between the high and low severity burn categories were, in part, due to an effect of stream size, as the low severity burn category included slightly smaller streams. Alternatively, it is possible that sites burned with high severity experienced hydrologic changes and associated streambed disturbance sufficient to shift the stream insect community to dominance by *r*-strategist taxa that resulted in greater emergence, whereas low severity fire did not trigger enough streambed disturbance to create such a community shift. Monitoring of some sites in the Big Creek watershed shows that a major scouring event had not occurred between the 2000 fire and the year of this study (G.W. Minshall, Idaho State University, Department of Biological Sciences, Pocatello, ID 83201, USA, unpublished data). Thus, there may be a threshold of disturbance frequency or intensity (Townsend 1989) that may explain differences between sites experiencing high versus low severity fire. To address this possibility, more studies comparing the effects of wildfire of varying severity on stream-riparian ecosystems are necessary, as are investigations that address the roles of climate, geomorphology, and hydrology as potential mediators of watershed responses to fire.

Inference and application of the results of this study may depend on both scale and land use context, the effects of which are unknown. Our results suggest that high severity fires do not play the same ecological role as low severity fires and allowing high severity fires to burn (rather than suppressing them) in certain forest types could be important in maintaining ecosystem function (Hutto 2008). We observed these patterns as a local effect at the scale of stream reaches, but responses to wildfire may differ at larger scales. For instance, in the western United States, wildfires are now occurring at higher magnitude and frequency (Westerling et al. 2006) such that entire river basins (e.g., Salmon River, Idaho) have been dominated by stand-replacing fires over the past 20 years. In such cases, effects at large spatial and longer time scales might include overall drying, with consequences for stream-riparian ecosystems that may contrast with those reported here. In addition, we conducted this study in a wilderness area where streams have been less impacted by humans and the linkages between streams and their surrounding riparian zones are essentially intact. The effects of wildfire might be much different for stream-riparian areas that have been altered or where linkages have been disconnected. The results of this study support the idea that high severity wildfire may amplify reciprocal fluxes between water and land for many years after the event, but future investigations are needed to address the effects in a land use context and through questions of scaling to build a deeper understanding of the role of wildfire in watershed ecosystems.

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