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Abstract. The effects of wildfire can alter the structure of stream insect assemblages. Post-fire shifts to dominance by *r*-strategist taxa could drive increases in productivity of primary consumer and predatory insects, but this possibility has not been explicitly investigated. Likewise, the extent and duration of such effects might be mediated by fire severity, but this hypothesis also has not been evaluated. We report results from a comparative study that examined the mid-term (5–10 y post-fire) effects of wildfire of varying severity on stream insect assemblage composition and productivity measured in terms of benthic larval biomass and flux of emerging adults. We compared benthos and emergence in a suite of 2nd- to 3rd-order, unburned streams to those that had experienced low-severity and high-severity wildfire in wilderness watersheds of central Idaho. Reaches that experienced high-severity burn had the greatest biomass of *r*-strategist, generalist primary consumers that included Chironomidae, *Baetis*, and Simuliidae. The greatest biomass of predatory insects, such as *Rhyacophila*, occurred in reaches that experienced high-severity burn. Differences in composition of emerging insects were more pronounced in some time periods than others, with greatest emergence from high-severity reaches in early summer. High-severity reaches consistently had the greatest emergence flux. Reaches that experienced low-severity burn had the least emergence, and unburned reaches had intermediate emergence flux. Our results suggest that burn severity might drive differences in aquatic insect assemblages and their productivity.

Key words: wildfire, benthic insects, emergence, stream ecology, insect assemblage, disturbance.

Wildfire causes disturbance that alters stream insect assemblages (Minshall et al. 1997). Direct, immediate effects of fire on aquatic insects are often negligible, but exceptions include intense heating of water, exposure to smoke and toxins, and the replacement of food resources with ash and charcoal, any of which can lead to short-term increases in insect mortality (Minshall 2003). In the midterm (5–10 y post-fire), the greatest effects of fire on aquatic insect assemblage structure might result from disturbance by flooding or mass sediment movements during spring runoff or following periodic rains in the years after fire (Minshall 2003, Vieira et al. 2004, Arkle et al. 2010). Stream insect assemblages are changed via such disturbance as patches of the streambed are scoured, insects are removed, and recolonization proceeds (Resh et al. 1988, Townsend 1989, Lake 2000). In some cases, post-fire sedimentation can reduce the quality of habitat

available to aquatic insects. This reduction in quality could either delay recolonization or allow only a small component of the potential assemblage to be successful in the newly disturbed habitat. Successful colonizers are often highly mobile (Miyake et al. 2003) and can be trophic generalists (Mihuc and Minshall 1995). Furthermore, these disturbance-adapted species often exhibit *r*-strategist (sensu Pianka 1970) life histories, with short generation times, high fecundity, and high dispersal rates compared to other taxa. Taxa like *Baetis* (Ephemeroptera), Chironomidae, and Simuliidae exhibit these traits and might be favored over others in streams following wildfire (Mihuc et al. 1996, Vieira et al. 2004).

An assemblage shift after fire to more disturbance-adapted, *r*-strategist primary consumers could lead to increased insect production, which could be reflected in increased emergence of adult aquatic insects. Although several studies have investigated the effects of wildfire on stream insect assemblages (e.g., Mihuc et al. 1996, Minshall et al. 1997, Minshall 2003, Vieira et al. 2004, Robinson et al. 2005), few have evaluated its effects on aquatic insect productivity or patterns of

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emergence (but see Mellon et al. 2008). If fire results in increased productivity among primary consumers, this increase could propagate up the food chain to invertebrate or vertebrate predators within the stream and to terrestrial predators that feed on emerging adult insects (Baxter et al. 2005). In particular, predatory insects that prey on disturbance-adapted primary consumers might be expected to exhibit strong responses following wildfire, especially if they themselves are capable of producing multiple cohorts per year. However, the hypothesis that fire might drive increased productivity of primary and secondary insect consumers has not been fully evaluated.

Most studies of the effects of wildfire on stream ecosystems have focused on the immediate or short-term period following fire and on the effects of relatively high-severity fires. However, the effects on stream systems vary with time after fire and are likely to be mediated by severity as well. Any effects on stream insect assemblage composition and productivity might be diminished by the mid-term period after fire and might be weaker in response to lower-severity fires (Minshall 2003). In terrestrial systems, fire severity mediates plant community composition (Agee 1993, Halpern and Spies 1995, Dwire and Kauffman 2003), primary productivity, and consumer responses (e.g., Bailey and Whitham 2002). Fires of varying severity might result in similar responses in aquatic communities, but the mid-term effects of wildfires and their severity on stream insect composition and productivity are largely unknown.

The effects of disturbances like wildfire on aquatic insect assemblages and aquatic insect productivity can be evaluated by studying both the benthic larval and emergent adult life stages. A strong relationship exists between emergence of adult insects and benthic insect secondary production (measured by year-round benthic sampling of growth and cohort techniques), and repeated/time-integrated emergence samples are a good indicator of total benthic insect production (Statzner and Resh 1993, Benke and Huryn 2006). Emergence data provide a temporal perspective of the dynamics and productivity of the insect assemblage. Emergence traps also can capture insects that might be missed in benthic samples that are typically taken from riffle habitats (Malison et al. 2010). Thus, measurement of emergence provides data complementary to those derived by benthic sampling for assessing structural and functional responses to disturbances.

We report results from a comparative study that examined mid-term effects of wildfire of varying severity on aquatic insect assemblages and emergence. We hypothesized that wildfire would alter the composition of aquatic insect assemblages and cause greater production of primary consumer and predatory insects. We evaluated this hypothesis by comparing benthic and emergence data in a suite of unburned watersheds to those in watersheds that had experienced low-severity and high-severity wildfire. We tested 2 predictions: 1) reaches that experienced wildfire would have greater benthic biomass and adult emergence of aquatic insect primary consumers, primarily because of higher abundance of r-strategist taxa, and 2) greater biomass of prey would be associated with increased benthic biomass and adult emergence of insect predators at burned vs unburned reaches. In addition, we hypothesized that the effects of wildfire would be additive, such that reaches exposed to high-severity fire would have the greatest benthic biomass and emergence of primary consumers and insect predators, whereas reaches exposed to low-severity fire would fall intermediate relative to unburned reaches.

Methods

Study site

Our investigation was conducted on streams within the Payette National Forest in central Idaho. Study reaches were in tributaries of Big Creek, which flows into the Middle Fork of the Salmon River in the Frank Church 'River of No Return' Wilderness Area (Fig. 1). The streams flow through steep, narrow valleys with forested slopes of primarily Douglas Fir (*Pseudotsuga menziesii*) and Ponderosa Pine (*Pinus ponderosa*). Open areas of grass and sagebrush (*Artemisia*) are common on drier slopes. Annual precipitation generally ranges from 38 to 50 cm in the valleys and 76 to 100 cm at higher elevations. Most of the precipitation occurs as snow, resulting in peak flows from late spring through early summer (Robinson et al. 2005). The streams generally remain at baseflow conditions from late summer through winter. We chose to study the effects of wildfire in this wilderness watershed because we wanted to measure responses in stream ecosystems mostly unaltered by humans and because natural fire regimes have been minimally affected by fire suppression or land-cover change in this area.

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 upon the relative area burned upstream and condition of post-fire riparian vegetation in 2005, we classified reaches in tributaries of the lower Big Creek drainage into 3 categories (Fig. 1): 1) high-severity burn, where wildfire removed canopy
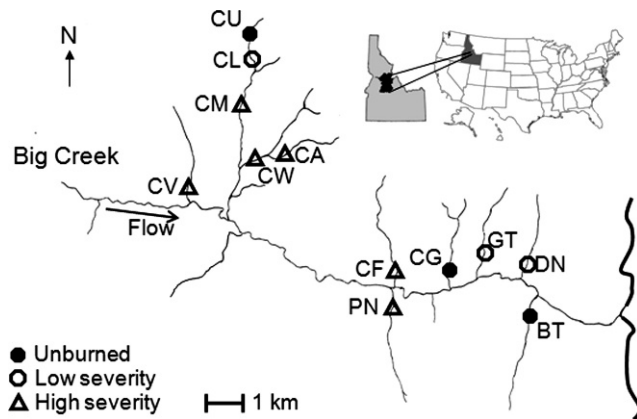
FIG. 1. Study reaches in the Big Creek Watershed in the Frank Church 'River of No Return' Wilderness Area in central Idaho. Reaches are on tributaries of Big Creek, which flows into the Middle Fork of the Salmon River. BT = Burnt, CA = Calf, CF = Cliff, CG = Cougar, CL = Cabin Lower, CM = Cabin Main, CU = Cabin Upper, CV = Cave, CW = Cow, DN = Dunce, GT = Goat, and PN = Pioneer.

from large areas of the catchment upstream and removed both riparian understory and canopy such that only the understory had returned by 2005; 2) low-severity burn, where fire burned less catchment area, and mainly removed the understory such that the understory had returned under an intact canopy; and 3) unburned, where the upstream catchment and reach were entirely unburned or burned long ago (>50 y). Because of the spatial extent and high severity of the fire, our study design was necessarily unbalanced, with 6 high-severity reaches, 3 low-severity reaches, and 3 unburned reaches. Six high-severity reaches were selected to increase statistical power, but it was impossible to find additional unburned and low-severity study reaches close enough to the study area for repeated sampling. We selected 100-m study reaches and used segment and reach classification (sensu Frissell et al. 1986, Bisson et al. 2006) to identify reaches that were similar in stream size, valley segment type, and reach type. All were 2nd- to 3rd-order streams in alluviated canyon segments and step-pool reach types. In addition, study reaches were in the lower portion of each tributary to facilitate access via hiking.

Sampling

We sampled benthic insect larvae and emerging adult aquatic insects from each study reach. We used a Surber sampler (0.093 m^2, 250-μm mesh size) to sample benthos once in July 2005 and collected 5 replicates from random locations in 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, the period of greatest emergence, with four 0.33-m^2 floating emergence traps set on the stream surface (Malison 2008, Malison et al. 2010). We placed traps over pools to create a good seal with the water surface because riffles experience more turbulence than pools and because pools might be where most emergence occurs (Iwata 2006). We used an aspirator to remove insects from the traps. From May to August, traps were deployed continuously and each set of traps accumulated insects for 4 to 5 d prior to collection. We sampled biweekly from late August through October.

We sorted, enumerated, and identified all insects to the lowest taxonomic level feasible for benthos (genus or species, except Chironomidae) and adults (family or genus). We then dried and weighed all insects (to nearest 0.001g) to obtain estimates of biomass for each taxa. Adults of bank-emerging taxa are underrepresented in floating emergence traps (Wallace and Anderson 1996, Stewart and Stark 2002). In these streams, bank-emerging taxa principally include relatively low numbers of stoneflies (Plecoptera; Malison 2008, Malison et al. 2010). These taxa were rarely captured in our traps, and we omitted these underestimated taxa from our analyses. Heavy rains washed insects out of emergence traps, so 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).

At each site, we collected data on a suite of physical factors of potential importance to the structure and productivity of aquatic insect communities. We followed methods used in other long-term studies in this region by Minshall and colleagues (see Davis et al. 2001). In addition to aspect, elevation, and gradient, we measured factors likely to be influenced by wildfire, such as solar radiation, temperature, stream width and depth, and characteristics of streambed substratum. Increases in solar energy can affect primary production and alter resources for aquatic insects. Therefore, we measured photosynthetically active radiation (PAR) just above the water surface (LI-COR, Lincoln, Nebraska). We made 20 measurements (every 2 m) along the length of the stream at cross-stream transects. Each transect measurement was made within the dominant type of lighting present (i.e., direct sunlight vs shade), taking into account the presence or absence of vegetation. We measured water temperature at each site because it affects aquatic insect species composition, life history (including timing of emergence), and production (Vannote and Sweeney 1980, Huryn and Wallace

2000). We monitored temperature year-round (Stow-Away TidbiT and HOBO data loggers; Onset, Pocasset, Massachusetts) and summarized the data by annual degree days. Channel and substrate character also influence insect assemblage structure (Minshall 1984), so we measured stream width and depth in all habitat types (i.e., pools vs riffles) present within each reach and completed substrate surveys for each reach. At 50 locations along each study reach, we randomly selected a rock (one every 2 m), measured its size, and estimated its % embeddedness.

Statistical analysis

We used multivariate techniques to identify possible patterns in insect taxonomic composition among burn categories. We analyzed aquatic insect assemblage data with nonmetric multidimensional scaling (NMDS) (Kruskal and Wish 1978) to evaluate differences among reaches visually, based on separation or overlap among reaches of different burn-severity categories in insect-assemblage space. The NMDS ordination method is well suited to ecological data that are nonnormal or discontinuous. We used biomass data in our analyses of benthos and emergence because it is more closely related than abundance to productivity and is a more relevant measure of prey availability to predators, which have requirements of prey biomass, not abundance. Furthermore, abundance data showed patterns similar to biomass (Malison et al. 2010). Relative biomass or flux (in the case of emergence) values for taxa were used for all NMDS ordinations because of high variation in raw values. We excluded rare taxa (relative values <5%) from the data set (Gauch 1982) to reduce skewness in the data. We used multiresponse permutation procedures (MRPP) to test for significant differences in community composition by burn category (Mielke and Berry 2001).

We tested the effect of burn severity on biomass of individual benthic insect taxa, including the *r*-strategist consumers *Baetis*, Chironomidae, and Simuliidae, and the predators *Rhyacophila* and predatory Tipulidae, including *Dicranota* and *Hexatoma*. We also tested the effect of burn severity on total primary consumers (biomass of all taxa minus predators) and total benthic insect predators (including genera in the following families: Ceratopogonidae, Dytiscidae, Empididae, Chloroperlidae, Perlidae, Perlodidae), with analysis of variance (ANOVA) (PROC GLM, SAS 9.1; SAS Institute, Cary, North Carolina). We chose the 3 primary consumer taxa for ANOVA because they were the dominant disturbance-adapted, *r*-strategist insects in these reaches and because results of the ordination analysis showed they were associated with differences in assemblages among burn categories. We chose *Rhyacophila*, *Hexatoma*, and *Dicranota* because they were the major predatory insects in these reaches that were present in both the benthic and emergence collections. We distinguished among tipulid genera in the benthic but not in emergence samples. Therefore, we analyzed Tipulidae emergence at the family level. We analyzed total predators in the benthic but not in emergence samples. A large component of predators (mainly dytiscid beetles and predatory stoneflies) was missing from the emergence samples because they do not emerge from the water column (Malison et al. 2010). In the analyses of benthic insects, we used Tukey's Honestly Significant Difference (HSD) to make pairwise comparisons among the least squares means by burn category. We assessed potential relationships between consumers and predators by analyzing correlations among benthic biomass of *r*-strategist consumers and benthic biomass of total predators across all reaches, regardless of burn category.

We analyzed the effect of burn severity on emergence (mg m^{-2} d^{-1}) of *Baetis*, Chironomidae, Simuliidae, *Rhyacophila*, and Tipulidae with repeated measures ANOVA (PROC MIXED). Burn severity was a fixed factor, and stream was a random factor in this analysis, and stream was nested within burn category. Sample, the unit of measurement, was repeated 22 times, but we did not begin to sample emergence at exactly the same time in all drainages. Thus, because of missing observations some weeks, we pooled every 3 to 4 samples into 6 sampling periods over the season. In the repeated measures analysis of emergence we made 1 a priori comparison (because of low power): between low- and high-severity categories. We assessed 2 post hoc pairwise comparisons among least squares means for burn category with Dunnett's test: 1) between unburned and low-severity and 2) between unburned and high-severity categories. We also conducted an analysis of correlation between emergence flux of *r*-strategist consumers and that of predators (*Rhyacophila*, Tipulidae, and Empididae) across all reaches, regardless of burn category. All biomass data were log(x)-transformed to meet the assumptions of parametric analysis. We analyzed the effect of burn severity on habitat characteristics with ANOVA (PROC GLM).

Throughout the results, all reported values are means ±1 standard error. *p*-values < 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 weak statistical power of this field study.

Results

Physical habitat factors

Physical-habitat variables for each reach are in Table 1. Differences in PAR among burn categories were marginally significant ($F_{2,8} = 4.02$, $p = 0.062$). PAR was 2× greater at the high-severity than at unburned reaches, and almost 7× higher at high-severity than at low-severity reaches (high severity vs unburned: 954 ± 211 vs 458 ± 106 µmol s^{-1} m^{-2}, Tukey HSD: $p = 0.360$; high severity vs low severity: 954 ± 211 vs 143 ± 71 µmol s^{-1} m^{-2}, Tukey HSD: $p = 0.059$). Annual degree days did not differ among burn categories ($F_{2,8} = 0.83$, $p = 0.471$). Substrate embeddedness did not differ between burn categories ($F_{2,9} = 1.66$, $p = 0.244$). Low-severity reaches tended to be slightly narrower and shallower ($F_{2,9} \geq 2.72$, $p \leq 0.119$) and to have marginally smaller median substrate size (10.5 ± 3.6 vs 20.3 ± 2.7 and 18.7 ± 2.0 cm; $F_{2,9} = 3.27$, $p = 0.086$) than the unburned and high-severity reaches.

Insect assemblage structure

Assemblage composition of benthic insects in stream reaches differed across burn categories (Table 2, Fig. 2A). The NMDS ordination of site means of benthic samples collected in 2005, based on the relative biomasses of 124 taxa, yielded a solution that represented 77% of the total variation among reaches (Fig. 2A). Reaches in different burn categories were significantly separated in community ordination space (MRPP, $A = 0.096$, $p = 0.002$), but contrary to our additive hypothesis the greatest differences in community composition were between reaches in high- and low-severity categories. Reaches were separated by burn-severity category along Axis 1, which explained 58% of the variation in assemblage structure. Differences were most strongly driven by Leptophlebiidae (Pearson's $r = 0.76$), Chloroperlidae (0.73), Leuctridae (0.59), *Dixa* (0.63), and Ceratopogonidae (0.58), which had relative biomasses that were higher in low-severity and unburned reaches than in the high-severity reaches, and *Baetis* (−0.69), *Neophylax rickeri* (−0.65), *Rhyacophila angelita* (−0.53), *Rhabdomastix* (−0.77), *Hemerodromia* (−0.58), and Chironomidae (−0.52), which had greater relative biomasses in high-severity reaches than in low-severity and unburned reaches.

The composition of insect emergence also differed by burn-severity category (Table 2, Fig. 2B), but not as distinctly as the composition of the benthos. An ordination of the mean emergence for each site from samples collected between June and October 2005, based on the relative flux of 54 taxa, yielded a solution that represented 80% of the total variation among reaches (Fig. 2B). Reaches in different burn-severity categories were not significantly separated in community ordination space (MRPP, $A = 0.036$, $p = 0.193$). Reaches were generally arrayed by burn category along Axis 1 but the axis explained only 28% of the variation in assemblage structure. Taxa most strongly associated with scores on this axis were *Rhyacophila vao* (Pearson's $r = 0.76$) and Chironomidae (−0.75) (see Fig. 2B for others).

Differences in insect emergence among burn categories were clearer when evaluated by time period, rather than when samples were combined by season. Throughout 2005, high-severity reaches had the greatest flux of emergence, low-severity reaches had the least emergence, and unburned reaches fell intermediate (Fig. 3), a pattern that was contrary to our hypothesis of an additive effect of fire severity. Total emergence (all taxa combined) varied strongly over time. The greatest differences in emergence flux among burn categories occurred between the beginning of June and mid-July when flux was highest at high-severity reaches (Fig. 3). The pulse of insect emergence at high-severity reaches during this period consisted largely of Ephemeroptera (Heptageniidae and *Baetis*), Trichoptera (Limnephilidae, Hydropsychidae, and *Rhyacophila*), and Diptera (Chironomidae, Simuliidae, and Tipulidae). Caddisflies of the family Glossosomatidae contributed to the peak of emergence from high-severity reaches but made up most of the emergence from unburned reaches. Emergence of caddisflies of the family Uenoidae was not as high, but did contribute to the observed differences during the early period. The greatest differences in emergence among burn-severity categories occurred in the early period, but the continued emergence of Chironomidae, *Rhyacophila*, and Uenoidae taxa kept emergence flux from high-severity reaches higher than fluxes from both unburned and low-severity reaches throughout summer and into autumn.

r-strategist primary consumers

Total primary consumer biomass differed significantly among burn categories (Fig. 4A). *Baetis*, Chironomidae, and Simuliidae were primarily responsible for the differences in total primary consumer biomass and assemblage composition among burn categories in the benthic and emergence data sets (see % r strategists, Table 2). Benthic biomass of these taxa was up to 18× greater in high-severity than in unburned reaches and, contrary to our expectations, up to 25×

TABLE 1. Mean (±1 SD, except depth is ±1 SE) values of physical habitat variables in study reaches of the Big Creek Watershed, Idaho, that experienced different levels of fire severity (unburned, low severity, high severity). * indicates data not collected because of logistical constraints. PAR = photosynthetically active radiation, NF = North Fork, N = north, S = south, SW = southwest.

Fire severity/reach	Width (m)	Depth (m)	Substrate size (cm)	Embeddedness (% embedded)	Aspect	Elevation (m)	Annual degree days	PAR (µmol)
Unburned								
Burnt	2.82 ± 0.38	0.13 ± 0.02	24.8 ± 20.1	47 ± 39	N	1300	1993	*
Cougar	2.14 ± 0.67	0.19 ± 0.01	20.7 ± 27.9	34 ± 28	S	1180	2126	564 ± 689
NF Cabin Upper	1.18 ± 0.40	0.11 ± 0.01	15.4 ± 23.9	46 ± 23	S	1601	1649	351 ± 545
Low severity								
Dunce	1.15 ± 0.44	0.11 ± 0.02	16.1 ± 32.3	56 ± 21	S	1165	3144	107 ± 190
Goat	0.8 ± 0.28	0.12 ± 0.01	3.9 ± 10.0	47 ± 28	S	1328	2041	42 ± 121
NF Cabin Lower	1.43 ± 0.29	0.11 ± 0.01	11.4 ± 23.8	48 ± 28	S	1584	1819	281 ± 391
High severity								
Cabin	3.74 ± 1.16	0.24 ± 0.02	20.3 ± 17.8	50 ± 36	S	1406	955[a]	1417 ± 849
Calf	0.92 ± 0.29	0.09 ± 0.01	21.1 ± 33.7	47 ± 37	SW	1394	2059	99 ± 274
Cave	4.08 ± 0.99	0.21 ± 0.01	14.0 ± 16.9	37 ± 35	S	1238	2271	1184 ± 743
Cliff	3.11 ± 0.86	0.24 ± 0.02	19.6 ± 16.5	22 ± 33	S	1213	2427	1463 ± 743
Cow	1.85 ± 0.41	0.16 ± 0.01	25.5 ± 24.4	46 ± 30	SW	1373	2241	679 ± 794
Pioneer	2.68 ± 0.56	0.20 ± 0.01	11.8 ± 20.2	26 ± 28	N	1248	1937	881 ± 716

[a] Cabin Creek degree days are based on temperatures from 20 October 2005 through 19 July 2006 (10 mo) because of a missing data logger

TABLE 2. Mean (±1 SD) abundance, biomass, and relative biomass of aquatic insect assemblages in study reaches of the Big Creek Watershed, Idaho, that experienced different levels of fire severity (unburned, low severity, high severity). Means for benthic data were from samples collected once in July 2005. Mean abundance of emergent insects is the mean number individuals caught from 4 traps in each sampling period. NF = North Fork.

Fire severity/reach	Total benthic abundance (number)	Total benthic biomass (mg)	% r-strategists in benthos	% predators in benthos	Mean abundance in emergence	% r-strategists in emergence	% predators in emergence
Unburned							
Burnt	871 ± 397	77.3 ± 25.8	5.6 ± 1.3	32.8 ± 14.2	44 ± 35	2.4	44.4
Cougar	506 ± 60	82.9 ± 30.9	7.0 ± 5.3	25.9 ± 10.8	112 ± 132	22.4	22.6
NF Cabin Upper	1030 ± 517	81.8 ± 47.9	9.7 ± 3.6	13.7 ± 3.8	84 ± 50	11.1	19.4
Low severity							
Dunce	282 ± 162	31.6 ± 22.2	2.1 ± 1.2	10.9 ± 4.8	40 ± 39	4.1	47.7
Goat	203 ± 115	14.5 ± 4.5	9.8 ± 5.3	17.7 ± 18.9	54 ± 71	15	4.8
NF Cabin Lower	778 ± 502	31.4 ± 19.6	6.2 ± 3.6	21.2 ± 13.4	81 ± 72	22.9	9
High severity							
Cabin	938 ± 301	85.9 ± 38.2	18.8 ± 9.8	16.5 ± 10.8	85 ± 66	10.6	29.4
Calf	758 ± 385	80.1 ± 53.5	50.0 ± 20.7	14.1 ± 9.8	57 ± 36	18.1	70.9
Cave	953 ± 191.4	203.2 ± 85.4	29.1 ± 5.2	19.7 ± 11.2	256 ± 234	48.1	34.3
Cliff	1761 ± 553	197.3 ± 80.8	31.7 ± 7.3	32.1 ± 10.3	208 ± 188	32.6	40.5
Cow	809 ± 407	67.6 ± 38.1	28.9 ± 11.0	32.4 ± 14.5	113 ± 126	16	49.6
Pioneer	876 ± 252	123.7 ± 28.1	12.2 ± 4.4	24.0 ± 10.3	100 ± 85	7.5	46.8

greater in high than in low-severity reaches. Patterns for each of the 3 taxa were consistent with this overall pattern, but the strength of the observed differences differed among burn category.

Of the 3 r-strategist taxa, *Baetis* in both benthic and emergence samples differed most strongly among burn categories. We observed a significant effect of burn category on benthic biomass of *Baetis* (Fig. 4B). The mean biomass of *Baetis* in the benthos was 9× greater in the high-severity than in the unburned reaches and was >25× greater in the high than in the low-severity burn reaches. Emergence of adult *Baetis* also was strongly affected by burn category ($F_{2,9} = 16.85$, $p = 0.0009$; Fig. 5A). Flux of *Baetis* was significantly greater from high-severity than from unburned and low-severity reaches throughout the study period (high severity vs unburned: 0.71 ± 0.26 vs 0.10 ± 0.05 mg m^{-2} d^{-1}, Dunnett: $p = 0.014$; high vs low severity: 0.71 ± 0.26 vs 0.04 ± 0.02 mg m^{-2} d^{-1}, Tukey HSD: $p = 0.0003$; Fig. 5A). In addition, the effect of time on emergence of *Baetis* was significant ($F_{5,28} = 6.03$, $p = 0.0007$). Greatest emergence occurred from high-severity reaches between early June and late July.

The highest biomass of Chironomidae larvae in the benthos and the greatest emergence flux of this taxon occurred in high-severity reaches, but differences among burn categories were mostly nonsignificant. No overall effect of burn category was found for larval biomass of Chironomidae (Fig. 4C), but the mean larval biomass of Chironomidae was >4× greater in high-severity than in unburned reaches (Fig. 4C). In general, a greater flux of Chironomidae emerged from high than from low-severity burn reaches, but the overall effect of burn category on emergence of Chironomidae was not significant ($F_{2,9} = 1.03$, $p = 0.397$; Fig. 5B). Time significantly affected emergence of Chironomidae ($F_{5,28} = 5.19$, $p = 0.002$). Most emergence occurred between early June and late July at unburned reaches, whereas emergence peaked at high-severity reaches between 27 June and 10 July and again in late August and throughout early September. The greatest difference in Chironomidae emergence by burn category occurred at the end of the sampling period when overall emergence was low but still elevated at high-severity reaches compared to at unburned and low-severity reaches.

The highest biomass of larval Simuliidae and the greatest emergence of adult black flies occurred at high-severity reaches, and the strength of differences across burn categories was generally intermediate to those observed for *Baetis* and Chironomidae. The overall effect of burn category on biomass of larval Simuliidae was marginally significant (Fig. 4D). Total
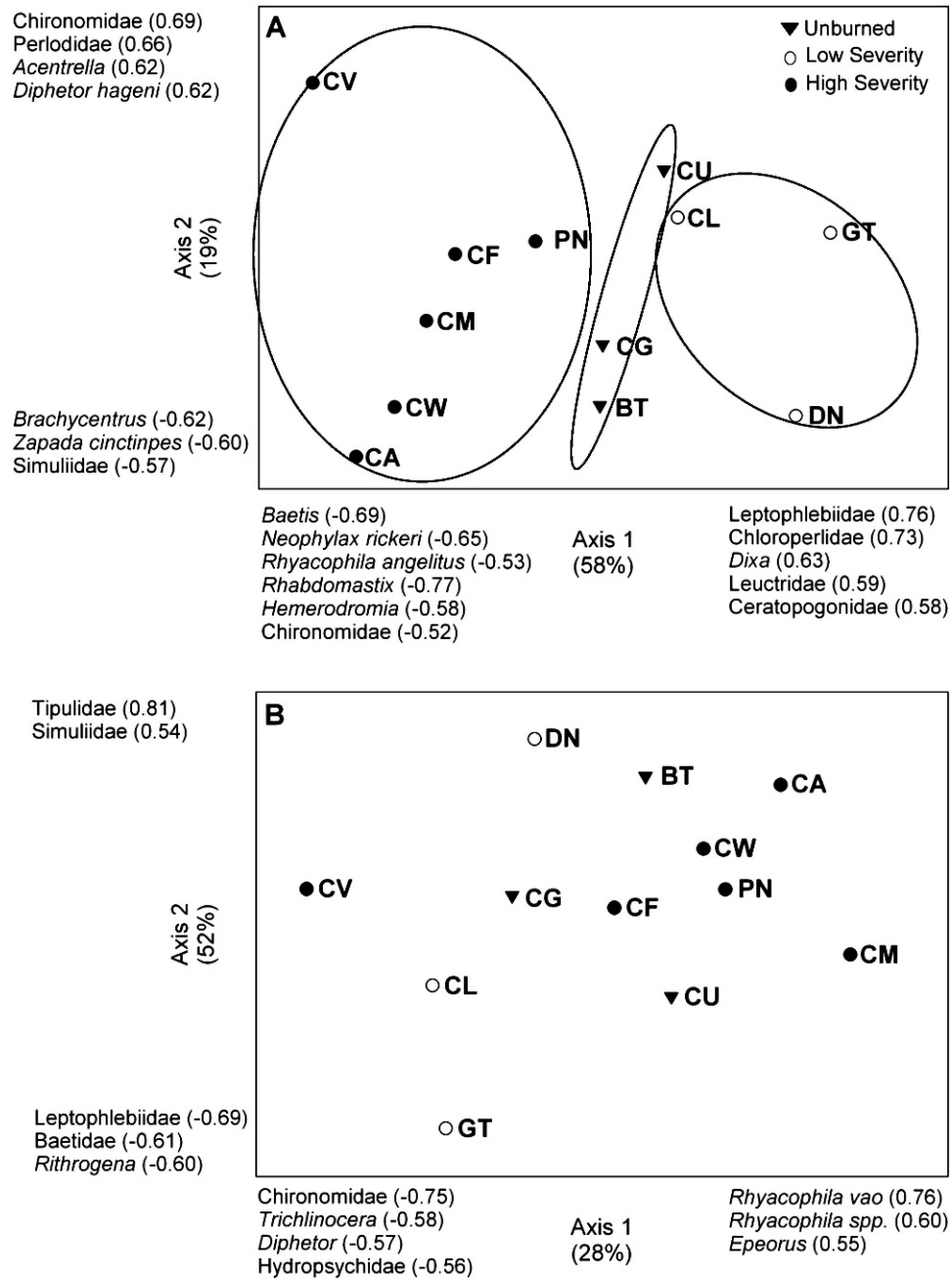
FIG. 2. Nonmetric multidimensional scaling (NMDS) ordination plot of relative biomass of insects in benthic (A) and emergence (B) samples from study reaches in the Big Creek Watershed in 2005. In panel A, points represent a mean of 5 replicate benthic samples collected from streams (see Fig. 1 for names of streams) with different burn histories. Circles enclose groups of reaches that were significantly different based on multiresponse permutation procedure analysis by burn category. In panel B, points represent means of all emergence samples collected between June and October 2005. Numbers in parentheses below axis titles represent % of variation explained by each axis. Numbers in parentheses next to taxon names are Pearson's correlation coefficients between the taxon and the axis.

biomass of larval Simuliidae was marginally higher at high-severity than at unburned reaches and low-severity reaches, but total biomass did not differ between unburned and low-severity reaches (Fig. 4D). Burn category had a marginally significant overall effect on emergence of adult Simuliidae ($F_{2,9} = 3.23$, $p = 0.088$; Fig. 5C). Significantly greater flux of Simuliidae emerged from high than from low-severity
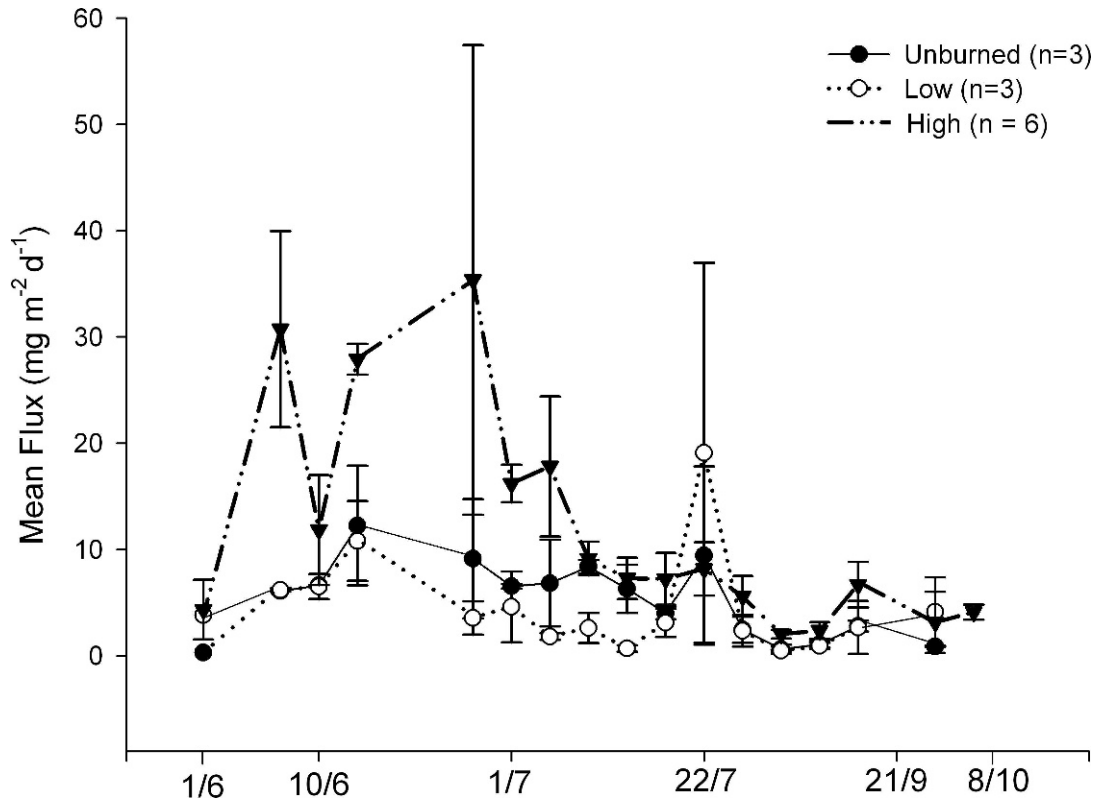
FIG. 3.   Mean (±1 SE) flux of emergence at reaches in different burn categories in the Big Creek Watershed for the period between 1 June 2005 and 8 October 2005.

reaches (0.46 ± 0.15 vs 0.31 ± 0.19 mg m^{-2} d^{-1}, respectively; Tukey HSD: p = 0.032; Fig. 5C). Time significantly affected emergence of Simuliidae ($F_{5,28}$ = 3.10, p = 0.024). Emergence from low-severity reaches peaked in September, whereas emergence from high-severity reaches generally was greater in June and July. The time × burn category interaction effect on Simuliidae emergence was significant ($F_{10,28}$ = 2.76, p = 0.017).

Predatory insects

Burn category significantly affected total benthic biomass of insect predators (Fig. 4E). High-severity and unburned reaches had significantly greater total benthic biomass of predatory insects than low-severity reaches (Table 1, Fig. 4E). In total, 25 different predatory taxa were found. Twenty-five occurred in high-severity reaches, 16 in low-severity reaches, and 21 in unburned reaches. Biomass of 13 of the 25 predatory taxa was higher in high-severity reaches than in unburned and low-severity reaches.

Rhyacophila and Tipulidae contributed to the higher biomass of predators in benthic and emergence samples at high-severity vs unburned and low-

severity reaches. Biomass of larval *Rhyacophila* was higher in high-severity and unburned reaches than at low-severity reaches (Fig. 4F). Burn category did not significantly affect overall emergence of *Rhyacophila* ($F_{2,9}$ = 1.34, p = 0.309), but biomass of emergence tended to be higher at high-severity reaches than at unburned and low-severity reaches (Dunnett: p = 0.626; Tukey HSD: p = 0.1, respectively; Fig. 5D). Time significantly affected emergence of *Rhyacophila* ($F_{5,28}$ = 12.39, p < 0.0001), with much greater emergence occurring from high-severity reaches between mid-June and the end of July than in later months. The time × burn category interaction term was marginally significant ($F_{10,28}$ = 1.79, p = 0.10). Emergence at high-severity reaches peaked in mid-June and late July, whereas emergence did not peak at low-severity reaches and peaked only once in mid-June at unburned reaches. The effect of burn category on *Rhyacophila* emergence was not significant when multiple sample periods were analyzed with repeated measures ANOVA, but *Rhyacophila* emergence did differ among burn categories when the data were analyzed by season (ANOVA, $F_{2,9}$ = 4.48, p = 0.045). The difference in total emergence was driven by marginally significant differences between high-se-
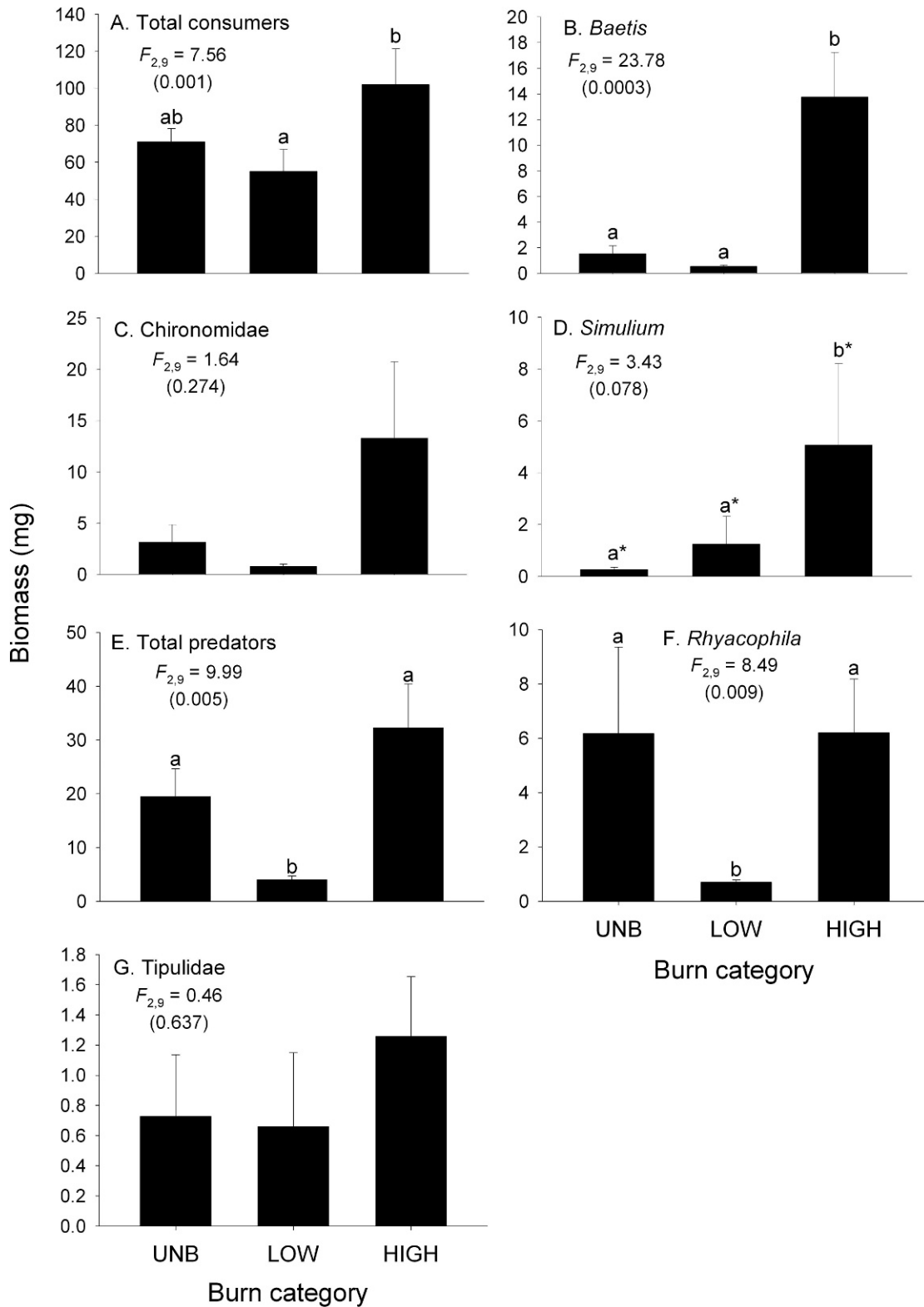
FIG. 4.   Mean (+1 SE) total biomass of the benthic total consumers (A), *Baetis* (B), Chironomidae (C), *Simulium* (D), total predators (E), *Rhyacophila* (F), and Tipulidae (G) in samples from reaches in 3 burn categories (unburned [UNB], $n = 3$; low severity [LOW], $n = 3$; high severity [HIGH], $n = 6$) collected in July 2005 from reaches in the Big Creek Watershed. Bars with different letters are significantly different ($p < 0.05$). * indicates marginally significant differences ($p < 0.1$).
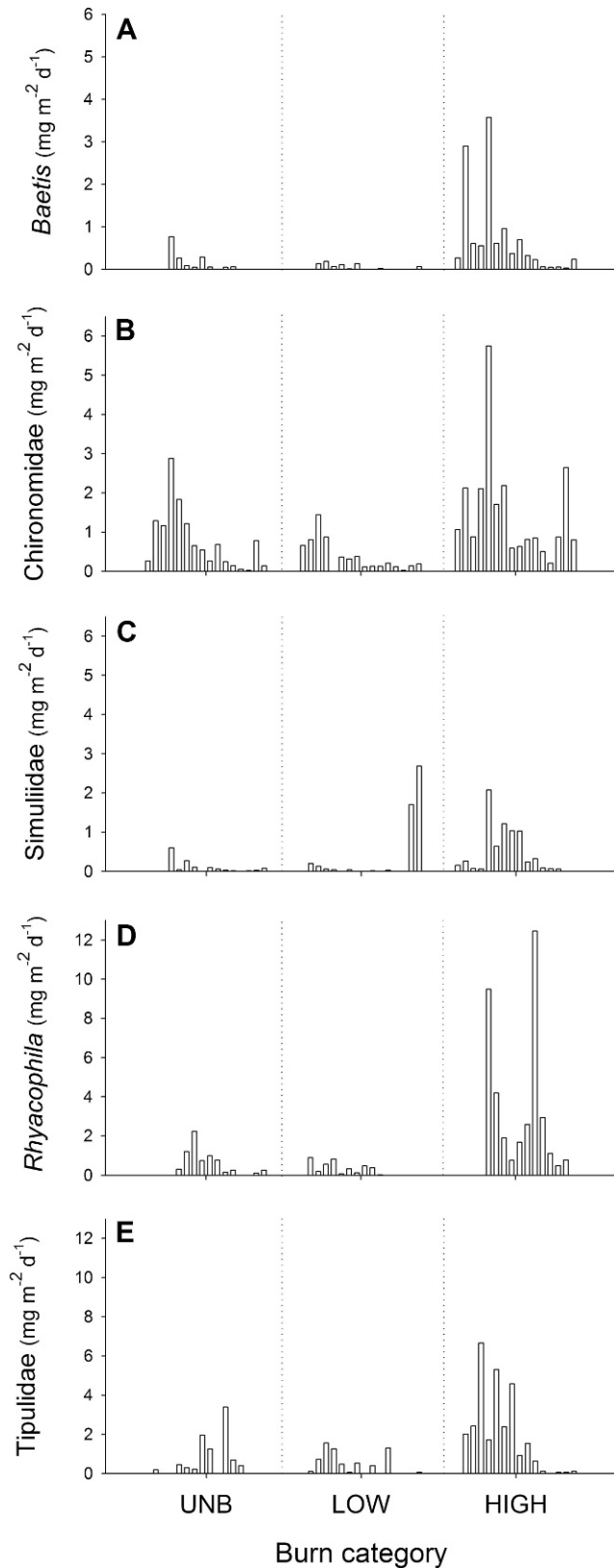
FIG. 5. Emergence flux of *Baetis* (A), Chironomidae (B), Simuliidae (C), *Rhyacophila* (D), and Tipulidae (E) collected

verity and unburned reaches (33.6 ± 13.8 vs 4.8 ± 2.7 mg m^{-2} d^{-1}, Tukey HSD: $p = 0.091$) and high- vs low-severity reaches (33.6 ± 13.8 vs 3.5 ± 1.9 mg m^{-2} d^{-1}, Tukey HSD: $p = 0.088$). A significant effect of burn category on emergence of *Rhyacophila* might not have been detected in the repeated measures analysis because peaks in *Rhyacophila* emergence were obscured when multiple sample periods were pooled for the analysis.

Benthic biomass of predatory Tipulidae (*Dicranota* and *Hexatoma*) did not differ among burn categories, although their biomass was greatest in high-severity reaches (Fig. 4G). The greatest flux of Tipulidae emergence consistently occurred at high-severity reaches, but burn category had no overall significant effect on emergence of Tipulidae ($F_{2,9} = 0.73$, $p = 0.507$; Fig. 5E). Time significantly affected emergence of Tipulidae ($F_{5,28} = 7.09$, $p = 0.0002$). The time × burn category interaction was not significant for Tipulidae ($F_{10,28} = 1.13$, $p = 0.375$), but in general, emergence was greatest at unburned reaches later in the sampling period, and at high-severity reaches earlier in the sampling period.

Across all reaches, regardless of burn category, benthic biomass of *r*-strategist consumers was positively correlated with that of predators ($r = 0.80$, $p = 0.002$), and emergence flux of *r*-strategist consumers was positively correlated with that of predators ($r = 0.63$, $p = 0.029$).

Discussion

Our results show that streams affected to varying degrees by the Diamond Peak wildfire differed in aquatic insect assemblage composition and productivity, measured by relative biomass and emergence flux, respectively. Reaches that experienced high-severity burn had the greatest biomass of *r*-strategist, primary consumers, including Chironomidae, *Baetis*, and Simuliidae, and these fast-growing taxa made up a large portion of the total emergence from these reaches. In contrast to our hypothesis that the effects

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from reaches in 3 burn categories (unburned [UNB], $n = 3$; low severity [LOW], $n = 3$; high severity [HIGH], $n = 6$) over sampling period starting 1 June 2005 and ending 8 October 2005. The vertical dotted lines separate samples collected from reaches in different burn categories. For each burn category, the sequence of bars represents a time series of emergence from 1 June 2010 (left) to 8 October 2010 with each bar representing a 4-d sampling period. Missing bars indicate that there was no emergence of the taxon during that sampling period.

of fire severity would be additive, the greatest differences were between high- and low-severity burn categories. Shifts to more *r*-strategist taxa in the years immediately following wildfire have been described previously (Mihuc et al. 1996, Minshall et al. 1997, 2001). Mellon et al. (2008) also found increased macroinvertebrate densities dominated by Chironomidae 2 y after severe forest fire in northeastern Washington. We found that compositional shifts to *r*-strategist taxa can persist for at least 5 y after high-severity fire, but these shifts did not appear to occur after low-severity fire. The differences in the dominance of *r*-strategists across levels of burn severity and in the associated productivity of these organisms were more apparent in measures of emergence over time than in 1-time samples of the benthos.

The high productivity (greater benthic biomass and emergence) of primary consumers at high-severity reaches might have propagated up a trophic level to drive greater larval biomass and adult emergence of predatory insects. This possibility seems to be supported by the consistent patterns among taxa and by strong associations between *r*-strategist consumers and predators across reaches regardless of burn category. Vieira et al. (2004) reported a similar pattern based on increases in the predators Odonata and *Isoperla* that lagged 2 to 3 y behind immediate post-fire increases in Chironomidae, Baetidae, and *Simulium*. In our study, the association was strongest for specialist predators like *Rhyacophila* that favor sessile consumers, such as larval Chironomidae and Simuliidae, but also can ambush faster moving mayflies like *Baetis* (Thut 1969, Martin and Mackay 1982, Otto 1993). Predators like *Rhyacophila* and Tipulidae might feed on other taxa, but we suspect the patterns in their benthic biomass and emergence were driven by greater availability of *r*-strategist primary consumers.

Rhyacophila emergence differed between high-severity reaches and unburned reaches, but benthic biomass did not. We see several potential explanations for this discrepancy. The complement of *Rhyacophila* species that emerged over the sampling period might have differed among reaches, or the species inhabiting high-severity reaches might have been multivoltine. Species of *Rhyacophila* exhibit a wide range of life histories, including univoltinism, bivoltinism, and multivoltinism, with emergence from spring to autumn (Ross 1956). Furthermore, insect life histories can be highly plastic (Nylin and Gotthard 1998). In high-severity reaches, species of *Rhyacophila* might have switched to a faster life-history strategy with more cohorts produced per year. We think it likely that the differences in

emergence among burn categories were caused by a combination of different species and variation in life histories.

We infer from higher emergence at high-severity reaches that the benthic assemblages were more productive there than at unburned and low-severity reaches. The mechanisms behind these differences are uncertain, but a number of possibilities exist. One possibility is that higher production of primary consumer insects at high-severity reaches was fueled by greater food resources via a bottom-up effect. However, we observed no differences in the primary factors that generally drive higher insect production (food and temperature). Inputs of terrestrial organic matter did not differ among burn categories (B. Jackson, University of Idaho, unpublished data). Both Chironomidae and *Baetis* shift to autochthonous resources after fire (Mihuc and Minshall 2005). However, mean periphyton biomass for unburned, low-severity, and high-severity reaches was 5.3, 3.6, and 5.6 mg/m^2, respectively, and did not significantly differ among burn categories (Malison and Baxter 2010). Differences in periphyton might have been undetected because periphyton productivity was measured as a snapshot of standing crop biomass. Thus, rapid turnover of periphyton or strong effects of insect grazing at high-severity reaches could have been missed. We also detected no differences in annual degree days by burn category, even though more light did enter the stream at high-severity reaches than low-severity reaches (low-severity reaches had greater shading and lower PAR than unburned reaches because of dense riparian shrubs).

We suggest that the higher productivity observed in high-severity reaches was, in large part, a consequence of the presence of greater numbers and biomass of *r*-strategist taxa. These taxa are generally small, but they have very large production to biomass (P/B) ratios that lead to high productivity (Huryn and Wallace 2000). Many taxa have P/B ratios <10 (Huryn and Wallace 2000), but Robinson and Minshall (1998) measured P/B ratios up to 20 for *Baetis tricaudatus*, 69 for Simuliidae, and 139 for Chironomidae in streams in the same region as those in our study. Thus, we reason that the shift in assemblage structure to *r*-strategist taxa that use resources more efficiently might be driving greater production of insect emergence from reaches that experienced high-severity burn.

Increased production by primary and secondary insect consumers could affect other aquatic predators, such as fish (Dunham et al. 2007, Koetsier et al. 2007), but also might propagate out of the stream (through emergence) where it could affect terrestrial insecti-

vores (Baxter et al. 2005, Paetzold et al. 2008). We found that biomass and productivity of insect predators were positively correlated with biomass and productivity of insect primary consumers in high-severity reaches. Densities of riparian spiders and incidence of bat echolocation calls were higher at high-severity reaches than at unburned reaches (Malison and Baxter 2010). In our study, aquatic insect composition differed among burn categories, and these taxonomic differences were reflected in differences in timing of emergence. Emergence differed among burn categories throughout the study period but was greatest in early summer when overall emergence was at its peak, and emergence at high-severity reaches was most elevated over unburned and low-severity reaches. High-severity reaches also had high levels of emergence later in autumn. Any of these differences in timing of emergence could have implications for the food web because the seasonality of this subsidy might be an important determinant of prey availability for both aquatic and terrestrial predators (Nakano and Murakami 2001, Baxter et al. 2005).

Insect prey might be more consistently available across the entire landscape after fire, with asynchronous peaks at streams in different burn categories. We observed taxon-specific peaks in emergence that differed by burn category. For example, peaks in emergence of *Rhyacophila* occurred at high-severity reaches in mid/late June and late July, whereas only 1 weak peak occurred at unburned reaches in late June. Moreover, emergence of Simuliidae peaked earlier in the summer at high-severity reaches, but not until later in autumn at low-severity reaches. Nakano and Murakami (2001) found that reciprocal across-habitat fluxes of prey alternately subsidized both fishes and forest birds, and these subsidies were seasonally asynchronous, with each habitat providing the other with the greatest resources when in situ prey were least available. Our results suggest that disturbance by wildfire might amplify this linkage in the mid-term period, with high-severity reaches exporting more biomass of adult insects to the adjacent terrestrial habitat later in autumn. Thus, the overall elevated emergence from high-severity reaches might be an important prey resource for insectivorous riparian consumers, but the asynchrony in emergence among reaches across the mosaic created by fire also might play a role in sustaining populations of consumers in this landscape.

Our results show that effects of wildfire can extend over time, with consequences for stream insect assemblages through the mid-term period, and that the severity of fire might have important consequenc-es for insect assemblage structure and productivity. Our observations suggest that high-severity fire might drive increased productivity through shifts in the insect assemblage to include taxa with rapid development and multivoltinism and perhaps also through particular predator–prey pathways. However, more studies are needed to determine what factors mediate the strength and nature of these responses to wildfire, and experimental studies and quantitative foodweb assessments should be conducted to determine the mechanisms behind the patterns that we have observed.

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