

Climate-moderated responses to wildfire by macroinvertebrates and basal food resources in montane wilderness streams

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Abstract. Changes in both climate and fire frequency have been documented but the combined effects of these are poorly understood in freshwater systems, thus making it imperative for long-term studies in pristine habitats to quantify climate-mediated wildfire effects in lotic systems. We quantified the response of invertebrates and basal food resources in 6 wilderness streams in central Idaho USA for 8 years pre-fire and 5 years post-fire. We found that a shift in climate toward increased temperature and reduced peaks in snow-melt runoff moderated the effects of wildfire on basal food resources and altered invertebrate community structure and annual variation. Taxon richness significantly increased over the 13-year study period at all sites regardless of fire. Post-fire changes were accompanied by an increase in the relative abundances of chironomid midges and *Baetis* mayflies, which generally are regarded as disturbance-adapted taxa. Ordination analysis of invertebrate community biomass showed that both unburned and burned streams differed between pre- and post-fire years and combined, our results suggest that the effects of climate ameliorated the effects of fire. We found significant correlations between community structure and climatic variables of precipitation, temperature, and discharge in all streams. Our findings support previous studies that attribute a large part of negative fire effects on stream ecosystems to major increases in runoff from sparsely vegetated uplands and attendant restructuring of channels and substrata. However, we found during a period of climate warming and reduction in snow-melt runoff, these adverse effects were suppressed resulting in increases in basal food resources and invertebrate density and biomass following fire. Our results show the importance of long-term studies in quantifying community changes in responses to disturbance under a changing climate in lotic ecosystems.

Key words: benthic communities; climate change; disturbance; long-term studies; stream flow.

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INTRODUCTION

A shift to a warmer drier climate likely will increase the frequency and severity of stand-replacing wildfires altering terrestrial (Kashian et al. 2013) and aquatic (Poff et al. 2010) ecosystem structure and function. Climatic patterns are strong drivers of processes in freshwater systems

and studies have shown that increases in air temperature (Hansen et al. 2006), declines in snowpack (Hamlet et al. 2005), and associated altered variability in stream discharge, all affect freshwater ecosystem structure and function. We know very little about the combined effects of wildfire and climate on aquatic ecosystems, which may both interact to affect terrestrial and

aquatic ecosystems. A number of studies have examined the effect of uncontrolled (“wild”), intense (stand-replacing) forest fires on flowing water ecosystems in montane regions under relatively stable climatic conditions. Although many of these were short-term studies restricted to the immediate aftermath of wildfire (e.g., Rinne 1996, Mellon et al. 2008), there also were several longer-term or retrospective ones (e.g., Minshall et al. 1997, 2003, Arkle et al. 2010). Conditions during this period of climatic stability are believed to have persisted for several hundred years, resulting in characteristic stands of mature forest found in the 19th and 20th centuries (Smith and Smith 2001). Relatively stable climate conditions enabled foresters to develop predictions based on historic fire-return intervals for forest management in different recognizable geo-climatic regions (e.g., Arno et al. 1985). Predictable fire-return frequency also strongly influenced efforts to characterize the long-term fire-response patterns of lotic ecosystems (Minshall et al. 1989). The long-term response patterns of streams to wildfire in otherwise undisturbed forested lands is especially well known for the Intermountain region of the western USA. These patterns recently have been revised and summarized for lotic ecosystems in the Greater Yellowstone Ecosystem (Romme et al. 2011) but have broad application throughout the region.

Under pre-climate change conditions (i.e., relatively stable climate with little warming), fire effects on streams generally result in dramatic adverse changes that occur within the first 6 months to 3 years following a wildfire (Minshall et al. 2001a, 2004, Vieira et al. 2004, Romme et al. 2011, Verkaik et al. 2013). For example, algal biomass and leaf detritus decrease while charcoal abundance increases. Likewise, invertebrate abundance and biomass usually decline and community composition shifts toward disturbance-adapted taxa following the first major post-fire runoff event (e.g., Mihuc and Minshall 1995, Malison and Baxter 2010b). Mid-term responses in forested montane streams, starting with the cessation of major runoff events (generally within the first 3 years) and persisting over another decade, include increases in algal biomass, leaf detritus, and invertebrate abundance and biomass (Robinson et al. 1994,

Minshall et al. 2004).

There is mounting evidence that global climate has become warmer resulting in an increase in fire frequency and intensity and changes in the amount and timing of precipitation, which is quantified in altered hydrologic and thermal regimes (e. g., stream discharge, channel conditions, and temperature) (Flannigan and Van Wagner 1991, Westerling et al. 2006). For the mountainous western USA, this changing climate is predicted to result in warmer, drier conditions and a shift from a late-spring, snow-melt dominated runoff regime to one that is weeks to months earlier and more rain-influenced (Stewart et al. 2005, Westerling et al. 2006). Westerling et al. (2006) examined forests throughout the western USA, from 1970 to 2003 and found the greatest increase in wildfire frequency (accounting for 60% of the increase in large fires) occurred in the Northern Rockies. They attributed the increased wildfire activity over recent decades to sub-regional responses to climatic changes and showed an abrupt transition in the mid-1980s from a regime of infrequent large wildfires of short (average 1 week) duration to one with much more frequent and longer burning (5 weeks) fires. This transition was marked by a shift toward reduced winter precipitation, unusually warm springs and an earlier spring snowmelt, longer summer dry seasons, drier vegetation, and longer fire seasons.

Lotic invertebrate communities are controlled both directly and indirectly by climate (Poff et al. 2010), and evidence suggests that many freshwater taxa are very sensitive to climatic changes (Durance and Ormerod 2009). Direct climate effects arise from temperature and precipitation; indirect effects are especially evident through flow-regime alteration (Minshall 1988, Poff and Ward 1989, Death and Winterbourn 1995). In addition, climate may interact with non-climatic habitat factors, such as changes in substrate and current velocity (Minshall 1984). For example, climate-driven reductions in snowpack can modify the timing and duration of high and low flows, potentially affecting benthic invertebrates via indirect pathways mediated by habitat stability (Death and Winterbourn 1995, Poff et al. 2010). Due to the complexity of these interactions, the outcome of fire effects on streams under changing climate conditions is



Fig. 1. Photo points of Cliff Creek just after the fire in September 2000 (A), and in July of 2001 (B) and 2005 (C) following the fire. Photo of unburned Cougar Creek in September 2000 (D) was used for reference.

uncertain and potentially counter-intuitive.

Changes in both climate and fire frequency are revealed by recent events in the Intermountain West, which has seen progressive warming, decrease in precipitation, periods of suppressed snow-melt runoff, and several large fires since the late 1980s (Davis et al. 2013). In 2000, a particularly large, stand-replacing fire burned in this region including several tributaries that were being monitored annually as part of a long-term study examining natural variation in montane wilderness streams. Subsequent sampling of these streams immediately post-fire and continuing for an additional five years (Fig. 1) enabled us to document the effects of wildfire on long-term patterns in relation to changes in climate. Several other studies of the effects of wildfires on streams involving post-climate-change fires have been conducted, but these generally lack a sufficiently

long dataset to be able to separate the effects of climate change from those of fire or the interaction of the two (Vieira et al. 2004, Arkle et al. 2010, Malison and Baxter 2010a). The goal of this study was to examine benthic invertebrate communities and basal food resources (i.e., algae and organic matter) prior to (8 years) and after (5 years) a wildfire under changing climatic conditions (i.e., fire, temperature, precipitation, flow patterns).

METHODS

Study area

Our study area lies in the Northern Rockies zone, as defined by Westerling et al. (2006) and the “mountain humid” modified ecoregion designation of Poff et al. (2010), in the Big Creek catchment of the Frank Church River of No

Table 1. Physical variables from six Big Creek tributaries that were sampled annually from 1993 to 2005: GOA = Goat, COU = Cougar, CLI = Cliff, PIO = Pioneer, CAV = Cave, RUS = Rush. Burn designations are explained in the text. Pre-fire years are 1993–2000 and post-fire years are 2001–2005. Discharge measurements taken at baseflow during annual sampling events.

Stream	Elevation (m)	Order	Slope (%)	Discharge (baseflow) (m ³ /s)
Unburned (GOA)				
Pre-fire	1125	2	18	0.03
Post-fire				0.01
Unburned (COU)				
Pre-fire	1095	3	11	0.03
Post-fire				0.01
Burned (CLI)				
Pre-fire	1196	2	9	0.14
Post-fire				0.09
Burned (PIO)				
Pre-fire	1165	3	7	0.16
Post-fire				0.09
Burned (CAV)				
Pre-fire	1220	3	4	0.23
Post-fire				0.24
Burned (RUS)				
Pre-fire	1170	3	1.5	1.65
Post-fire				0.90

Return Wilderness Area in central Idaho, USA. In the USA, *wilderness area* refers to large, legally-designated units that are roadless, devoid of permanent inhabitants, generally pristine and, relatively unaffected by anthropogenic influence. Big Creek is a sixth-order river with a catchment area of 1540 km², a mean elevation of 2117 m, and mean precipitation of ca. 400 mm. Due to the mountainous region in which it lies, both elevation and precipitation are highly variable over the basin, ranging from about 2900 m on the highest peaks to 1031 m at its mouth and with annual precipitation ranging from ca. 450 mm in valleys to ca. 880 mm at higher elevations. The majority of the annual precipitation occurs as winter snow, resulting in peak flows from late spring through mid-summer when the snow melts. The streams generally remain near baseflow from late summer through autumn.

Primary vegetation on forested slopes is Douglas-Fir (*Pseudotsuga menziesii*), Ponderosa Pine (*Pinus ponderosa*) and aspen (*Populus tremuloides*). Open areas of grass and sagebrush (*Artemisia* spp.) are common on drier slopes, and extensive areas of bare soil and rock also are common in the region (20–30% of the surface area). Primary riparian woody vegetation consists of alder (*Alnus* sp.), dogwood (*Cornus canadensis*), chokecherry (*Prunus virginiana*), service berry (*Amelanchier alnifolia*), and willow

(*Salix* spp.). The geology of the Big Creek basin is composed of Proterozoic metasedimentary rock and intrusive diorite, plus Eocene granite and volcanic rock of the Challis Volcanic Group (Lund 2004). Soils of the well-weathered granites are easily eroded and are believed to be the main source of sediment in the area.

This study focuses on the effects of the Diamond Peak Fire in August 2000 in six study streams (Table 1), although small portions of the watersheds of some of the streams were burned by fires in 1988. Pre-fire years are 1993–2000 and post-fire years are 2001–2005. The Diamond Peak fire burned a large portion of the Big Creek catchment to varying degrees with Cave, Rush, Cliff, and Pioneer having high severity burns (burned streams) while Cougar was unburned and Goat was a low severity burn in the upper watershed (unburned streams) (Malison and Baxter 2010b). We documented pre- and post-fire changes in the six study streams through photo transects (e.g., Fig. 1) and physical and biological responses.

Climate variables

We did not have continuous water temperature data over the course of the study and used local air temperature as a proxy for water temperature in all streams. Air temperature is commonly used as a surrogate for stream

temperature in ecological studies (Kaushal et al. 2010). Although the sensitivity of stream temperature to air temperature is spatially variable (Van Vliet et al. 2010), there typically is a very high correlation between the two when they are measured within the same region (Mohseni et al. 1998), as was the case here. Fire may have altered stream water temperatures immediately following the fire and over the short-term by increasing solar radiation through the loss of canopy cover; this was not accounted for using air temperature as a proxy. We used data from the Western Regional Climate Center to analyze temperature and precipitation from 1988–2011 from the Taylor Ranch field station (109000) located in the vicinity of our study sites. Because Big Creek was not gauged at the time, we used discharge measurements from USGS South Fork Salmon River near the Krassel Ranger Station, Idaho (13310700; about 50 km west of our Big Creek study sites), as representative of flow patterns in the Big Creek watershed during 1989–2012. For each of the study streams, both annual peak flow and baseflow discharges were calculated from our field measurements within each stream using the Manning equation:

$$Q = AR^{2/3}S^{1/2}/n$$

where A is cross-sectional area, R is hydraulic radius in meters and in this situation was the same as mean depth, S is the slope, and for Manning's n we used 0.06. Peak flow values were obtained from evidence of the highest levels reached during the preceding spring runoff and baseflow was assumed for the time of actual sampling.

Biological variables

Five transects approximately 50 m apart were sampled routinely for physiochemical and biological parameters during late July from 1993 to 2005, while streams were at baseflow (two unburned streams and four burned streams). Sampling in 2000 occurred just prior to the Diamond Peak Fire and supplemental samples were collected in September and October 2000 for periphyton, benthic organic matter, and invertebrates.

Benthic algal (periphyton) samples were collected from five cobble-size rocks (Davis et al. 2001), one near each transect. A plastic cylinder,

fitted with a neoprene gasket to prevent leakage of dislodged material, was placed over the area to be sampled. The area enclosed by the cylinder (3.14 cm²) was scrubbed, using a hard bristled brush, and a syringe was used to remove the resulting slurry and deposited on a 0.45- μ m pre-ashed glass fiber filter. Samples were immediately filtered and the residue frozen and kept in the dark in a liquid nitrogen-charged container to prevent degradation. In the laboratory, algal abundance was calculated by quantifying ash-free dry mass (AFDM) and chlorophyll a using standard methods (APHA 1998, Davis et al. 2001).

Five quantitative Surber samples (0.093 m² each with a 250- μ m mesh capture net) were collected from riffle/run habitats (Davis et al. 2001) and preserved in 10% formalin. In the laboratory each benthic invertebrate sample was hand-sorted under a 10 \times magnifier lamp and identified to the lowest feasible taxonomic level, usually genus, using dissecting and compound microscopes and standard identification keys (Merritt and Cummins 1996, and regional ones). After identification, the invertebrates were dried at 60°C, cooled to room temperature in a desiccator, and weighed with a Cahn electrobalance to determine biomass. Biomass samples for July 2002 were estimated based on average weight of individual invertebrates from 2003 to 2005. Benthic invertebrate communities were examined in terms of density, biomass, and taxa richness.

The remaining organic matter from each Surber sample was dried at 60°C for 48 h and weighed to obtain dry mass. Samples were then ashed at 550°C for 3 hours and reweighed to obtain ash-free dry mass (AFDM) to determine standing stock of benthic organic matter (BOM) in the stream greater than 250 μ m in size.

Due to our unbalanced design of two unburned and four burned streams we did not compare unburned and burned against each other, but rather pre- versus post-fire years within the two burn categories. For all response variables we analyzed pre- versus post-fire years using t-tests in both unburned and burned streams. This allowed us to determine if the patterns were the same or different for pre- versus post-fire years in unburned and burned streams. When necessary, data were log trans-

Table 2. Mean values (± 1 SE) for selected environmental, basal resource, and invertebrate variables from unburned ($n = 2$) and burned ($n = 4$) Big Creek tributaries. Streams were sampled annually from 1993–2005; pre-fire years are 1993–2000 and post-fire years are 2001–2005. Alkalinity and hardness is in mgCaCO₃/L and conductance is in μ S/cm at 25°C. Substrate was measured along the longest axis (cm) from pebble counts ($n = 100$ annually). Chlorophyll *a* is in mg/m² and ash-free dry mass (AFDM) and benthic organic matter (BOM) are in g/m². Invertebrate biomass is in mg/m². Significant differences between pre- and post-fire years in unburned and burned streams were analyzed with a t-test, bold *P* values indicate significant differences between pre- and post-fire years ($\alpha = 0.05$).

Variable	Unburned		<i>p</i>	Burned		<i>p</i>
	Pre-fire years	Post-fire years		Pre-fire years	Post-fire years	
Physical and chemical						
Alkalinity (mg CaCO ₃ /L)	51 (± 4)	71 (± 3)	0.001	35 (± 2)	42 (± 2)	0.006
Hardness (mg CaCO ₃ /L)	88 (± 8)	85 (± 7)	0.08	59 (± 4)	57 (± 5)	0.80
Conductance (μ S/cm)	148 (± 9)	159 (± 6)	0.33	92 (± 5)	109 (± 5)	0.02
pH	8 (± 0)	8 (± 0)	0.88	8 (± 0.1)	8 (± 0.1)	0.07
Median substrate (cm)	17 (± 1)	13 (± 2)	0.06	18 (± 0.6)	15 (± 0.8)	0.004
Embeddedness (%)	35 (± 5)	26 (± 2)	0.14	32 (± 3)	23 (± 2)	0.003
Baseflow (m ³ /sec)	0.37 (± 0.1)	0.21 (± 0.1)	0.12	0.75 (± 0.1)	0.74 (± 0.1)	0.94
Peakflow (m ³ /sec)	3.2 (± 1.1)	3.5 (± 1.3)	0.84	4.1 (± 0.5)	4.4 (± 0.4)	0.53
Basal resources						
Chlorophyll <i>a</i> (mg/m ²)	5.0 (± 1.6)	7.4 (± 0.9)	0.03	10.6 (± 3.0)	26.3 (± 2.3)	< 0.0001
AFDM (g/m ²)	3.3 (± 1.3)	4.2 (± 1.5)	0.51	5.3 (± 0.56)	10.1 (± 2.8)	0.006
Chl <i>a</i> /AFDM	2.6 (± 0.8)	2.1 (± 0.4)	0.57	2.2 (± 0.4)	2.7 (± 0.2)	0.25
BOM (g/m ²)	49.0 (± 9.1)	86.7 (± 29.4)	0.30	23.1 (± 2.4)	40.9 (± 3.7)	< 0.0001
Invertebrate community						
Richness	19 (± 3)	28 (± 5)	0.004	22 (± 2)	30 (± 2)	< 0.0001
Density (no./m ²)	2410 (± 260)	5889 (± 718)	< 0.0001	5929 (± 1468)	15941 (± 3351)	< 0.0001
Biomass (mg/m ²)	353 (± 118)	652 (± 333)	0.02	975 (± 385)	2093 (± 681)	< 0.0001
<i>Baetis</i> (%)	13 (± 7)	14 (± 9)	0.78	18 (± 2)	21 (± 2)	0.14
Chironomidae (%)	18 (± 6)	14 (± 0.2)	0.17	18 (± 5)	31 (± 10)	0.02
<i>Baetis</i> + Chironomidae (%)	33 (± 1)	31 (± 6)	0.60	36 (± 7)	52 (± 10)	0.002

formed prior to analysis to correct for normality.

Ordination analysis

To evaluate the affects of fire versus climate we analyzed community data for benthic invertebrates using biomass and environmental variables in PRIMER-E Version 6 (Plymouth Marine Laboratory, Plymouth, UK). Non-metric multidimensional scaling (NMDS) illustrates community patterns with an iterative process that searches for an ordination of samples that best represents a similarity matrix (Clarke 1993). We analyzed for differences among the communities for 1993–2005 using NMDS for pre- and post-Diamond Peak wildfire years with the Bray-Curtis similarity index and 25 iterations (Clarke et al. 2006). All benthic invertebrate biomass data were square-root transformed prior to analysis and rare taxa (making up less than 3% frequency of occurrence) were excluded. We tested for differences in community composition pre- and post-fire using analysis of similarity (ANOSIM; 999 permutations; PRIMER 6) and similarity percentages

(SIMPER; Primer 6) to determine percentage of dissimilarity pre- and post- fire years and to identify taxa that most strongly contributed to the differences. Environmental variables were normalized (to reduce the effect of different measurement scales) and Euclidean distance was used to obtain the matrix. Pearson correlations between NMDS axes and selected environmental variables were calculated using “stats” from the R package (<http://www.r-project.org/>) to further examine the effects of climate. Each stream was analyzed separately for all analyses.

RESULTS

Physical and chemical variables

Physical and chemical properties remained relatively constant throughout the study in unburned streams (Table 2), except for alkalinity which was higher in post-fire years than pre-fire years. Burned streams had higher alkalinity, conductance, and substrate size during post-fire years relative to pre-fire; but we do not feel these

differences are biologically significant and may be driven by high variation among streams and also geologic features (Table 2).

Temperature, precipitation, and discharge

Average annual air temperature increased during the period encompassing this study ($R^2 = 0.15$, $p = 0.056$; Fig. 2A). Highest temperatures during the study period occurred in 2000, the year of the Diamond Peak wildfire, and in 2003. After our study high temperatures were recorded again in 2006 and 2007 that were higher than those recorded in 2000. Temperatures remained elevated after 2005 and above the long-term mean, except for 2008. Lowest temperatures occurred in 1993 and 1996. Mean temperature for all years was 7.1°C and all post-fire years until 2007 were above the long-term average of our study. During the same years of high temperature, annual precipitation approached drought conditions (roughly approximated as -1 SD from recorded data) and highest precipitation was during the years of 1993, 1995, and 1997–1998, all prior to the Diamond Peak wildfire. After the Diamond Peak wildfire, annual precipitation remained low with little variability, although high annual precipitation was measured in 2004 and 2010 (Fig. 2B). During the study period, hot dry years were more frequent than cool wet years (i.e., more years fell above the long-term mean for temperature and below for precipitation).

Average annual and peak discharge in the South Fork Salmon River was variable throughout 1988–2011, much like precipitation (Fig. 2C). During the study period, highest average annual discharge values were in 1995–1997 (20.0 – 25.0 m^3/s), with low discharge years in 1990–1992 (8.0 – 9.6 m^3/s), 1994 (6.9 m^3/s), and the lowest discharge (6.0 m^3/s) was recorded in 2001 just after the fire. Mean annual discharge for 1989–2011 was 14.7 m^3/s . Peak discharge values followed the same pattern as the average annual discharge (Fig. 2C). Peak discharge values were low during the years of 1989–1992, just prior to our study. However, peak discharge showed an increase through time with high peak discharges occurring in 2003, 2006, 2008, and 2010 ($R^2 = 0.21$, $p = 0.02$).

Peak discharge in unburned and burned streams was variable within and among years and there were no significant differences between

pre- and post-fire years in unburned and burned streams (Table 2, Fig. 3). In contrast, baseflow discharge for all streams remained relatively constant between 1993 and 2005, with no significant differences between pre- and post-fire years in both unburned and burned streams (Table 2). Peak discharge was high during 1995–1997 for all streams and was associated with the high average annual discharge measured in the South Fork Salmon River. In burned Cliff Creek peak discharge was higher in 2001–2005 than other years (except 1996) supporting our visual observations that some post-fire scouring occurred, but overall we did not document any major scouring events after the fire.

Periphyton

Following the fire in 2000, burned and unburned streams had higher chlorophyll *a* concentrations in post-fire than in pre-fire years (Table 2). Chlorophyll *a* ranged from 0.3 mg/m^2 in burned Cliff Creek (1997) to 78 mg/m^2 in burned Pioneer Creek in September 2000, immediately following the fire (Fig. 4). Chlorophyll *a* values were highest in all burned streams in the two years following the fire. In several streams, chlorophyll *a* values returned to near pre-fire levels by 2002 or 2003. Periphyton ash-free dry mass was significantly higher in post-fire years in burned streams, while there was no difference in unburned streams (Table 2). Periphyton AFDM ranged from 0.7 g/m^2 in unburned Cougar Creek in 1994 to 13 g/m^2 in burned Cave Creek in 1993 and followed a similar pattern as chlorophyll *a*. There also were no differences between pre- and post-fire years for chlorophyll *a*/AFDM values (autotrophic index) in both unburned and burned streams, suggesting that periphyton AFDM closely tracked chlorophyll *a* levels (Table 2).

Benthic organic matter

Mean benthic organic matter (BOM) did not differ between pre- and post-fire years in unburned streams but were significantly higher in post-fire years in burned streams (Table 2). Values ranged from 8.0 g/m^2 AFDM in burned Cliff Creek in 2003 to 339.5 g/m^2 AFDM in unburned Goat Creek in 2001 (Fig. 5). Unburned Goat Creek is an outlier, probably due to its dense riparian cover and high retention (woody

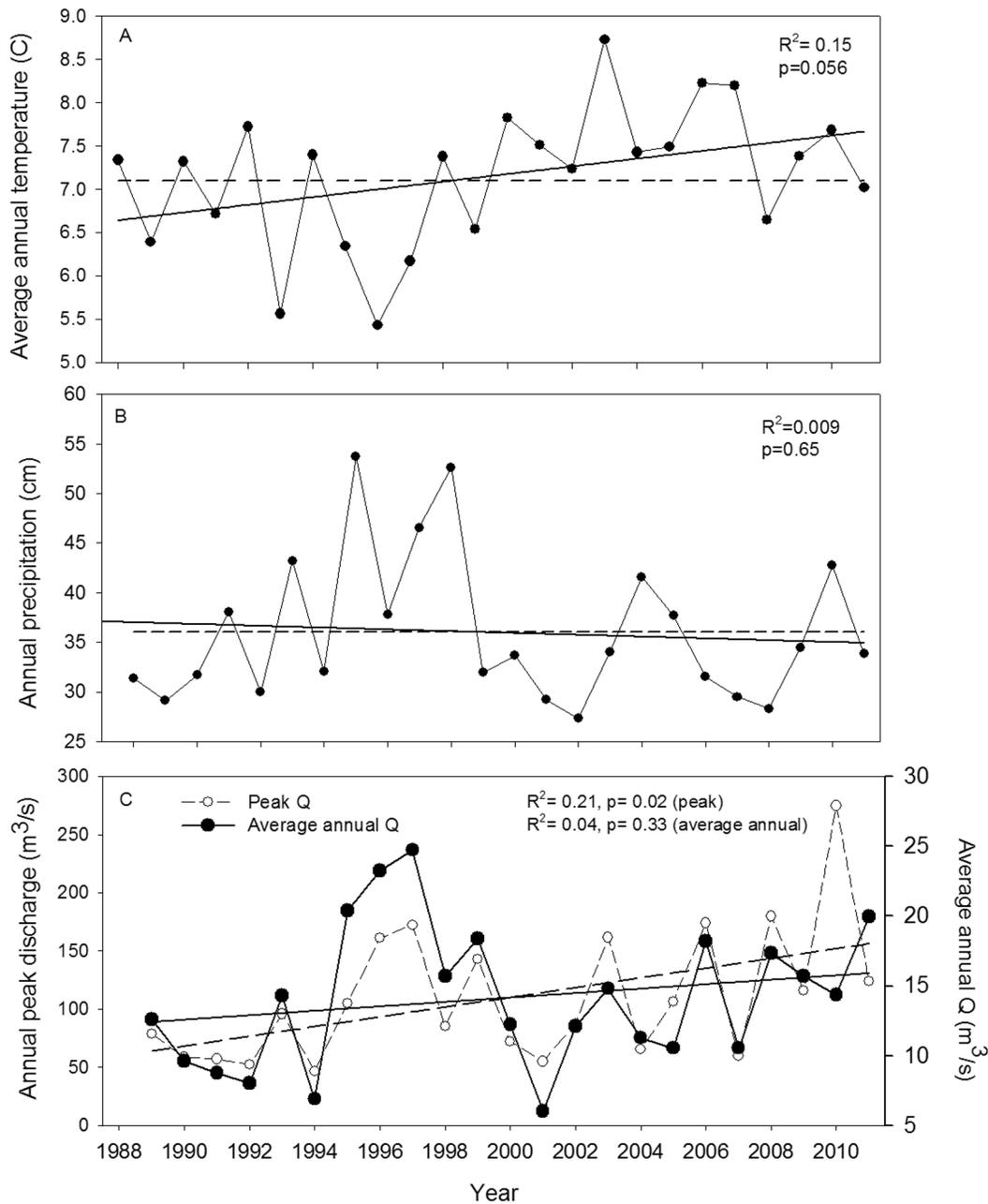


Fig. 2. Annual air temperature (°C) (A), precipitation (cm) (B), and surrogate discharge (m³/s) for the Big Creek watershed from 1988 to 2011. Dashed line for A and B is long-term average and solid line is respective linear regression. Temperature and precipitation were collected from Taylor Ranch weather station, ID (109000) and discharge from the USGS South Fork of the Salmon River gauge (13310700). Study period was from 1993 to 2005.

debris and stable substratum). Burned Pioneer and Cliff creeks had the greatest change in pre-versus post-fire BOM values (Fig. 5).

Benthic invertebrates

Mean taxon richness was higher in post-fire than in pre-fire years in both unburned and burned streams (Table 2). Mean taxon richness of

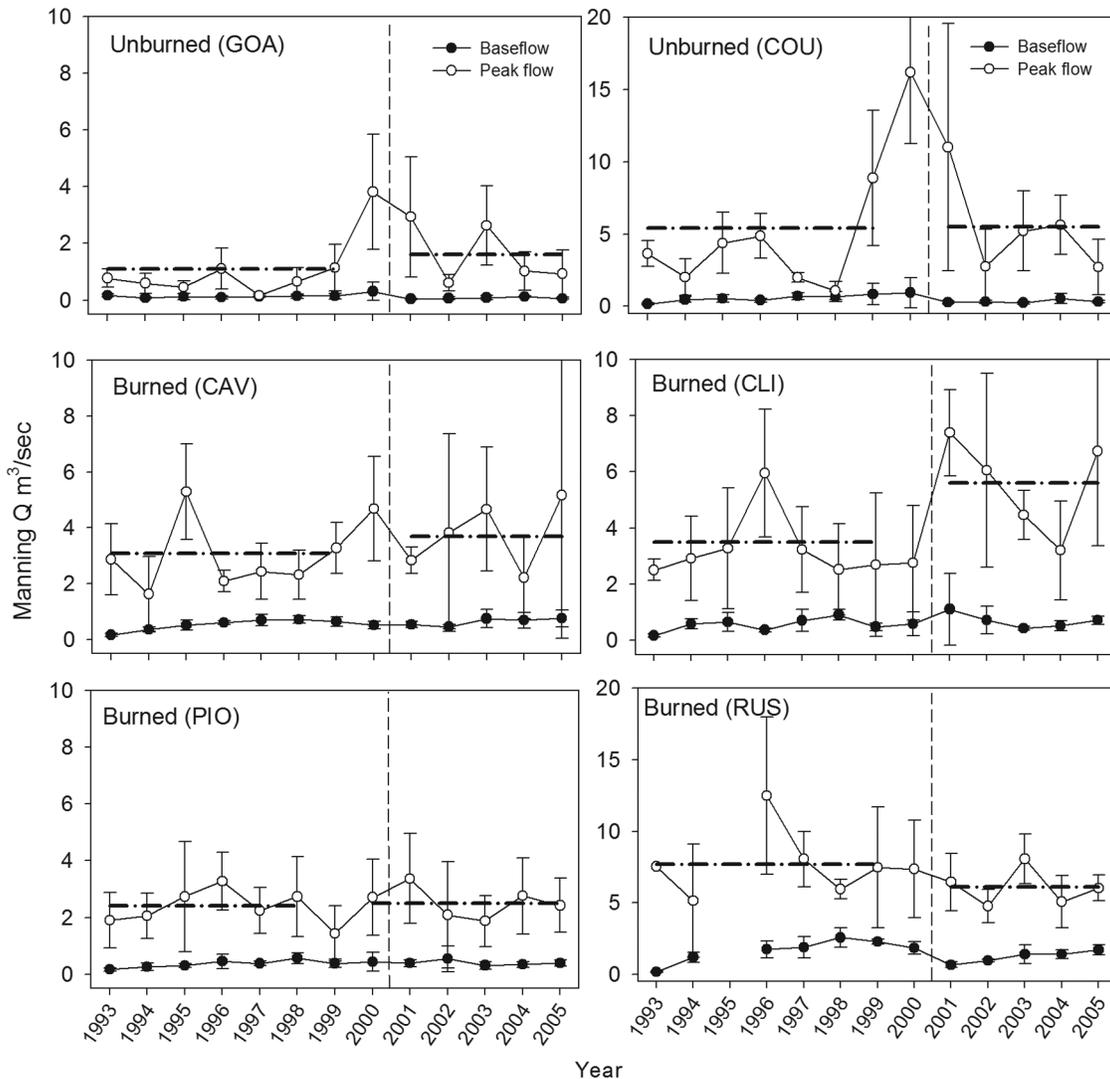


Fig. 3. Estimated peak (open symbols) and base flow (solid symbols) discharge in Big Creek unburned (GOA = Goat, COU = Cougar) and burned (CAV = Cave, CLI = Cliff, PIO = Pioneer, RUS = Rush) tributaries calculated using Manning's equation. Vertical dashed line indicates occurrence of the 2000 wildfire. Error bars are ± 1 SD, horizontal dashed line indicates pre- and post-fire means for peak flow.

benthic invertebrates was highest in burned Rush Creek in 2001 (39.0) and 2002 (38.4) following the fire, and lowest in pre-fire burned Pioneer in 1995 (10.6) and unburned Goat Creek in 1993 (10.2). Taxon richness significantly increased over the 13-year study period for all sites (Fig. 6). Taxon increases were detected at both the genus level and at the coarser family level (genus level presented in the figure). The increases in richness were due to more taxa in the Heptageniidae, Chloroperlidae, Ephemerellidae, Taeniopterygi-

diae, Hydropsychidae, Limnephilidae, and Glososomatidae families (listed in decreasing order of importance).

Mean benthic invertebrate density was significantly higher in post-fire than in pre-fire years in both unburned and burned streams (Table 2), with higher densities occurring within the first or second year post-fire (Fig. 7). Mean density ranged from 602 (± 465) invertebrates/m² in unburned Goat Creek in 1995 to 35,886 ($\pm 14,333$) invertebrates/m² post-fire in burned

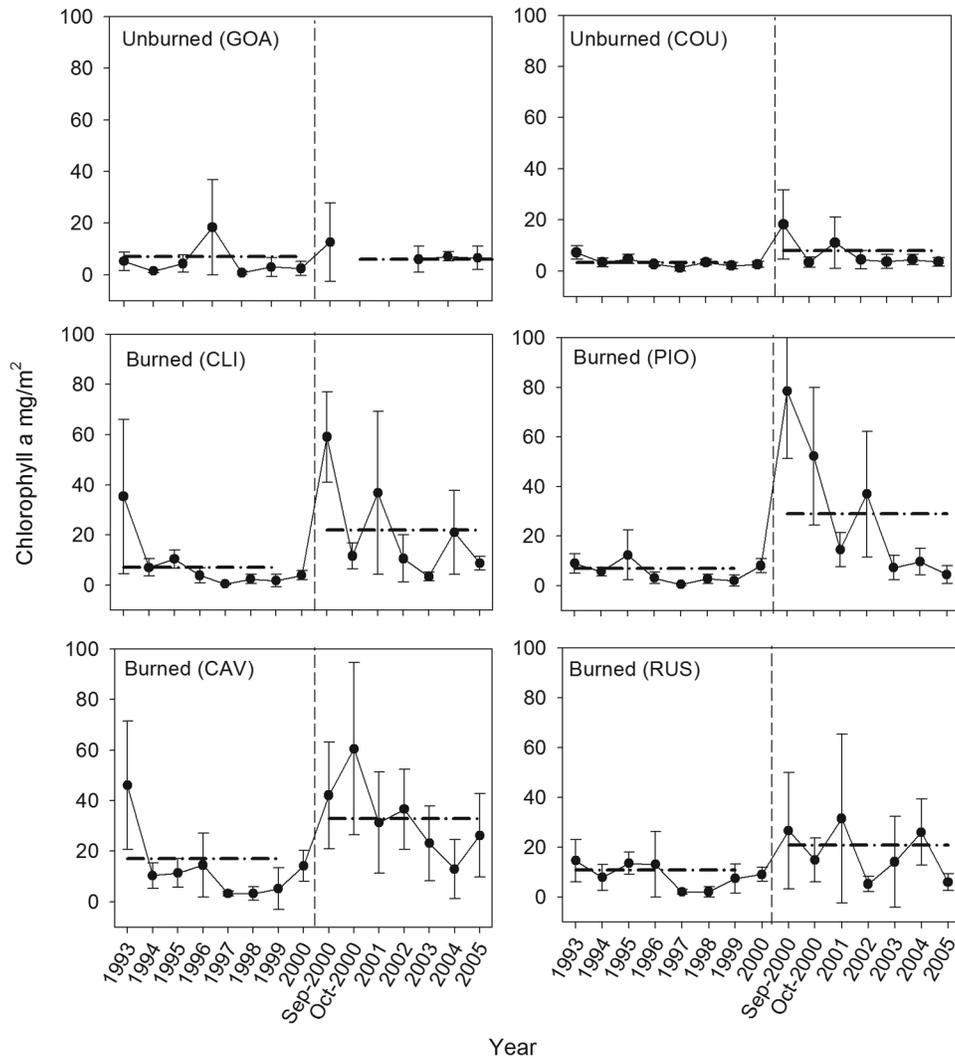


Fig. 4. Mean periphyton chlorophyll *a* (mg/m²) in Big Creek unburned (GOA = Goat, COU = Cougar) and burned (CAV = Cave, CLI = Cliff, PIO = Pioneer, RUS = Rush) tributaries 1993–2005. Error bars are ± 1 SD ($n = 5$). Vertical dashed line indicates the Diamond Peak wildfire, horizontal dashed line indicates pre- and post-fire means.

Rush Creek in 2002 (Fig. 7). Unburned Goat and Cougar Creeks remained more consistent in invertebrate density values over the post-fire years than did the remaining streams, however all densities were more variable in post-fire years (Fig. 7). Densities decreased markedly in 2003 at all sites except unburned Goat and Cougar. Mean benthic invertebrate biomass was also significantly higher in post-fire than in pre-fire years in both unburned and burned streams (Table 2). Benthic invertebrate biomass ranged from 4146

± 1830 mg/m² post-fire in burned Rush Creek in September 2000 to 75 ± 85 mg/m² in unburned Goat Creek in 1996 (Fig. 8). Biomass tended to increase prior to the Diamond Peak wildfire in all burned streams except for Pioneer and continued to increase following the wildfire in all burned streams with immediate increases in September and October 2000, except for Pioneer Creek which did not increase until 2001. However, all average biomass values were higher for post-fire years than pre-fire years and then eventually

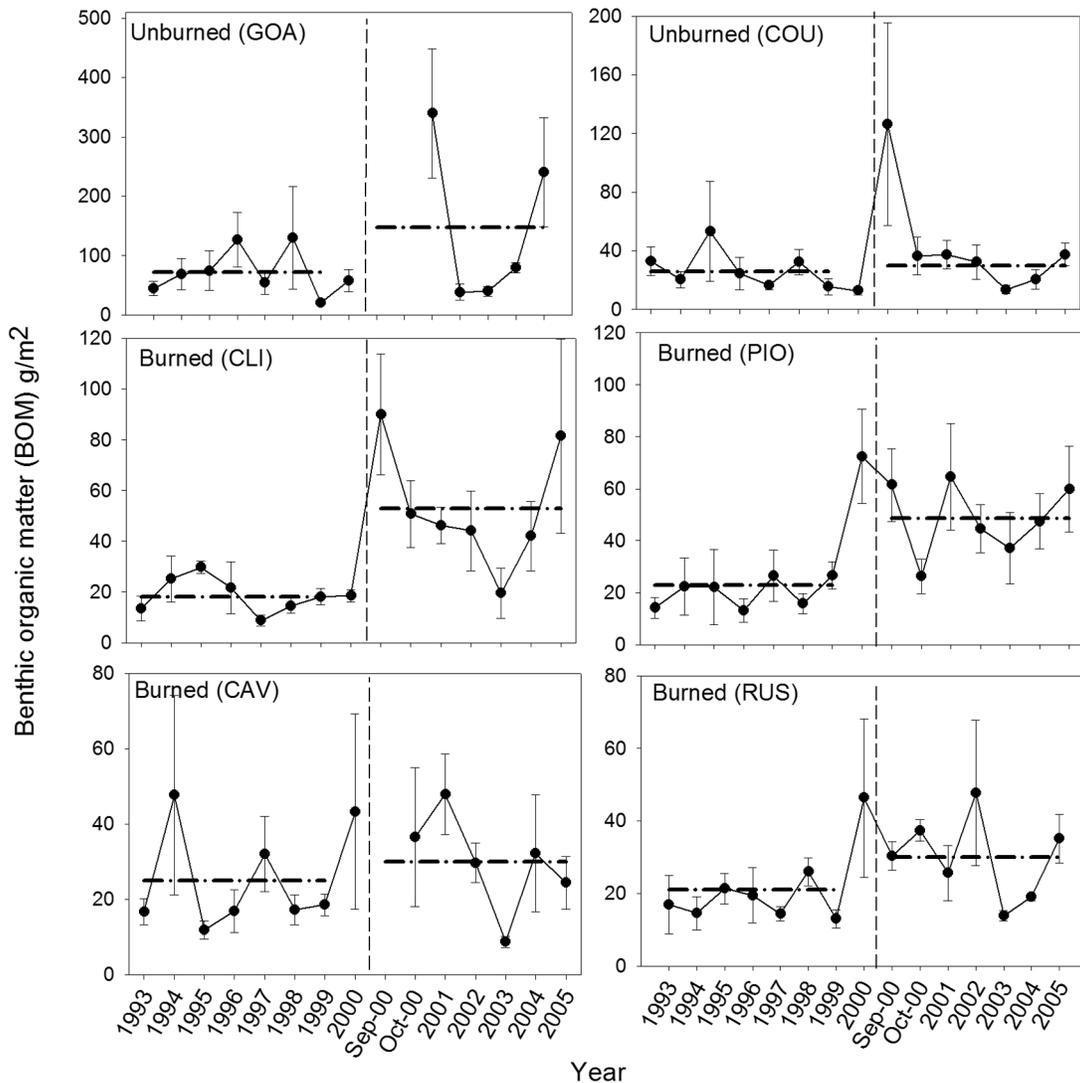


Fig. 5. Mean benthic organic matter (BOM, g/m^2) in Big Creek unburned (GOA = Goat, COU = Cougar) and burned (CAV = Cave, CLI = Cliff, PIO = Pioneer, RUS = Rush) tributaries 1993–2005. Error bars are ± 1 SD ($n = 5$). Vertical dashed line indicates the Diamond Peak wildfire, horizontal dashed line indicates pre- and post-fire means.

decreased starting in 2003 in burned streams, with the exception of Cliff Creek which remained high and variable through 2005.

The ephemeropteran *Baetis* and dipteran Chironomidae are taxa that are expected to increase in relative abundance within months after a disturbance due to the abilities for fast reproduction and growth and rapid dispersal. We found no significant difference in relative abundance of *Baetis* and Chironomidae in unburned streams between pre- and post-fire years both individu-

ally and combined together (Table 2, Fig. 9). *Baetis* and Chironomidae comprised a substantial part of the post-fire benthic invertebrate community and together were higher in burned streams in post-fire than pre-fire years (Table 2). However, individually *Baetis* did not differ between pre- and post-fire years mainly due to variation in pre-fire years that appears to be associated with a high discharge event in 1997. Chironomidae, which was the taxon having the larger influence on combined *Baetis*/Chironomidae differences,

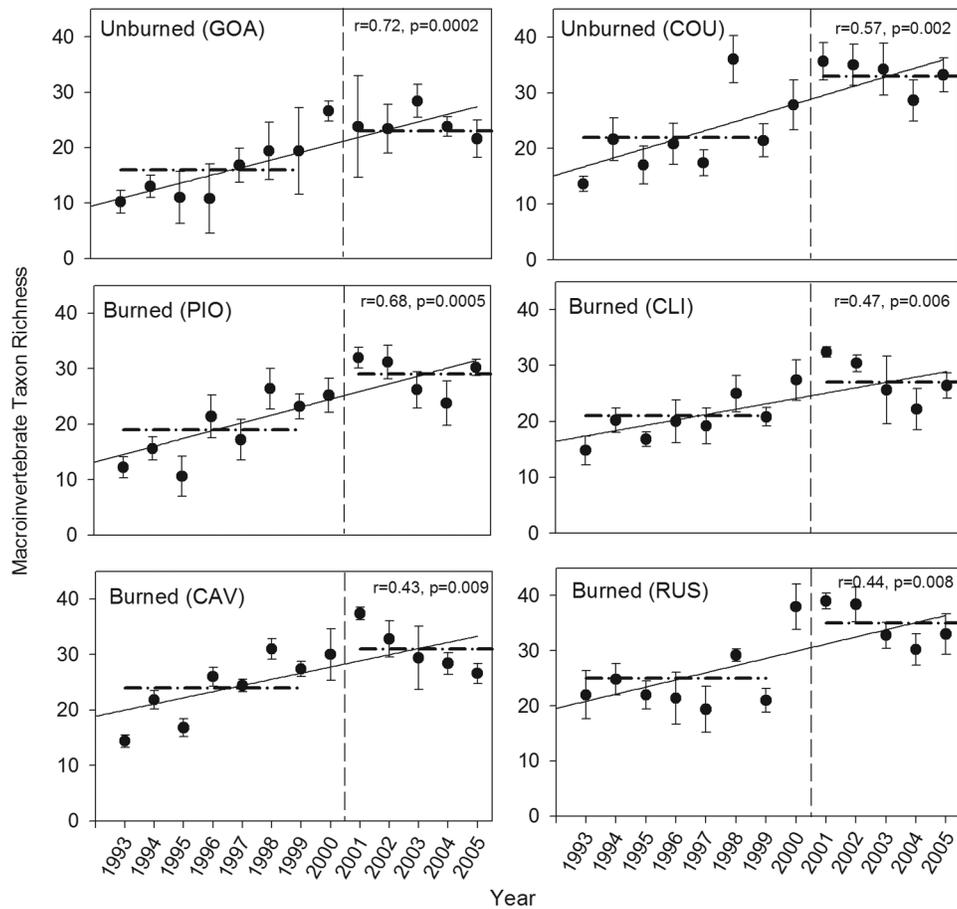


Fig. 6. Mean macroinvertebrate taxon richness in Big Creek unburned (GOA = Goat, COU = Cougar) and burned (CAV = Cave, CLI = Cliff, PIO = Pioneer, RUS = Rush) tributaries 1993–2005 and respective linear regressions. Error bars are ± 1 SD ($n = 5$). Vertical dashed line indicates the Diamond Peak wildfire, horizontal dashed line indicates pre- and post-fire means.

was higher in burned streams in post-fire than in pre-fire years (Table 2). *Baetis* ranged up to 33% post-fire in 2001 in burned Cliff Creek and Chironomidae 74% in burned Rush Creek in 2005 (Fig. 9). Burned Cliff and Rush Creeks saw the greatest increase in *Baetis* and Chironomidae following the fire, comprising up to 80% of the abundance in burned Rush Creek in 2005. Relative abundance of Chironomidae showed a sharp increase in burned Cliff in 2003 after a long period of little change but then decreased in 2004 and increased again in 2005.

Ordination analysis

Stream communities based on biomass differed among all streams among years (NMDS,

two-dimensional, stress 0.17) with Rush (largest, burned) and Goat (smallest, unburned) being the most dissimilar, followed by Cave Creek (next largest, burned) separated by Axis 1 (Fig. 10). Cougar (unburned) and Pioneer (low severity burn) communities were the most similar (Fig. 9). Axis 2 was driven on one end by burned Cave and the other end by burned Pioneer, and burned and non burned years within streams.

For all streams, pre-fire years separated from post-fire years in terms of community structure using biomass and differed significantly between pre- and post-fire years in burned Cliff (ANO-SIM, Global $R = 0.751$, $p = 0.004$), burned Pioneer (Global $R = 0.451$, $p = 0.005$), burned Rush (Global $R = 0.304$, $p = 0.02$), burned Cave (Global

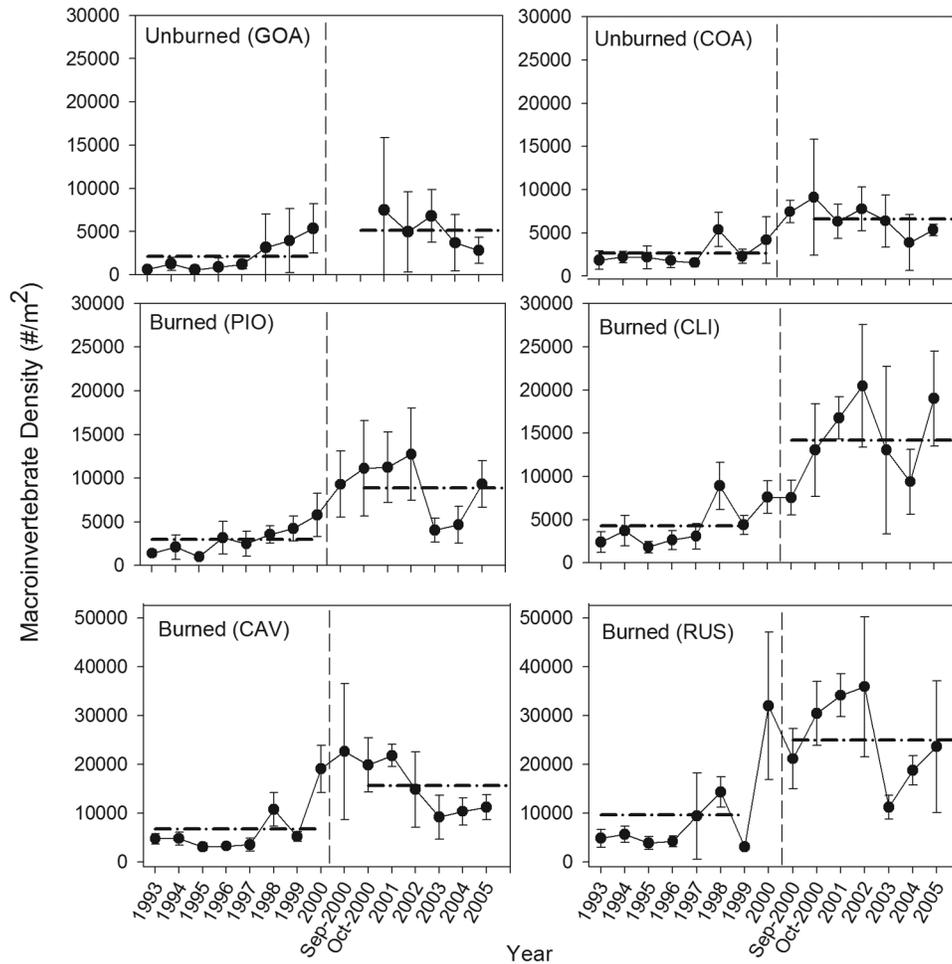


Fig. 7. Mean macroinvertebrate density in Big Creek unburned (GOA = Goat, COU = Cougar) and burned (CAV = Cave, CLI = Cliff, PIO = Pioneer, RUS = Rush) tributaries 1993–2005. Error bars are ± 1 SD, note change in y-axis scaling for Cave and Rush Creeks. Vertical dashed line indicates Diamond Peak wildfire, horizontal dashed line indicates pre- and post-fire means.

$R = 0.254$, $p = 0.04$), and unburned Goat (Global $R = 0.591$, $p = 0.005$), while unburned Cougar was marginally significant (Global $R = 0.213$, $p = 0.07$). For all streams, pre-fire years separated from post-fire years on axis 1 (Fig. 11). Post-fire benthic invertebrate communities were more similar (SIMPER, 73%) than pre-fire years (59%) for all streams averaged together. Percent dissimilarity between pre- and post-fire assemblages was highest in burned Rush Creek (53%), and lowest in unburned Cougar (33%), while burned Cave, Cliff, Pioneer, and unburned Goat had dissimilarity values of 45% between pre- and post-fire years.

Taxa that contributed the most to the dissimilarities in biomass in the unburned streams prior to the fire years were *Drunella* in unburned Goat Creek and Unionidae and *Epeorus* in unburned Cougar Creek (Table 3). Dissimilarities in post-fire years in both streams were mainly driven by *Heterlimnius* and additionally by *Zapada* in unburned Goat Creek and Perlidae and *Hexatoma* in unburned Cougar Creek. In burned streams, dissimilarities varied among streams pre- and post-fire, however biomass of Chironomidae and/or *Baetis* increased post-fire in all of these streams. Also, *Brachycentrus* and *Hexatoma* increased in burned Cave and Rush Creeks, while

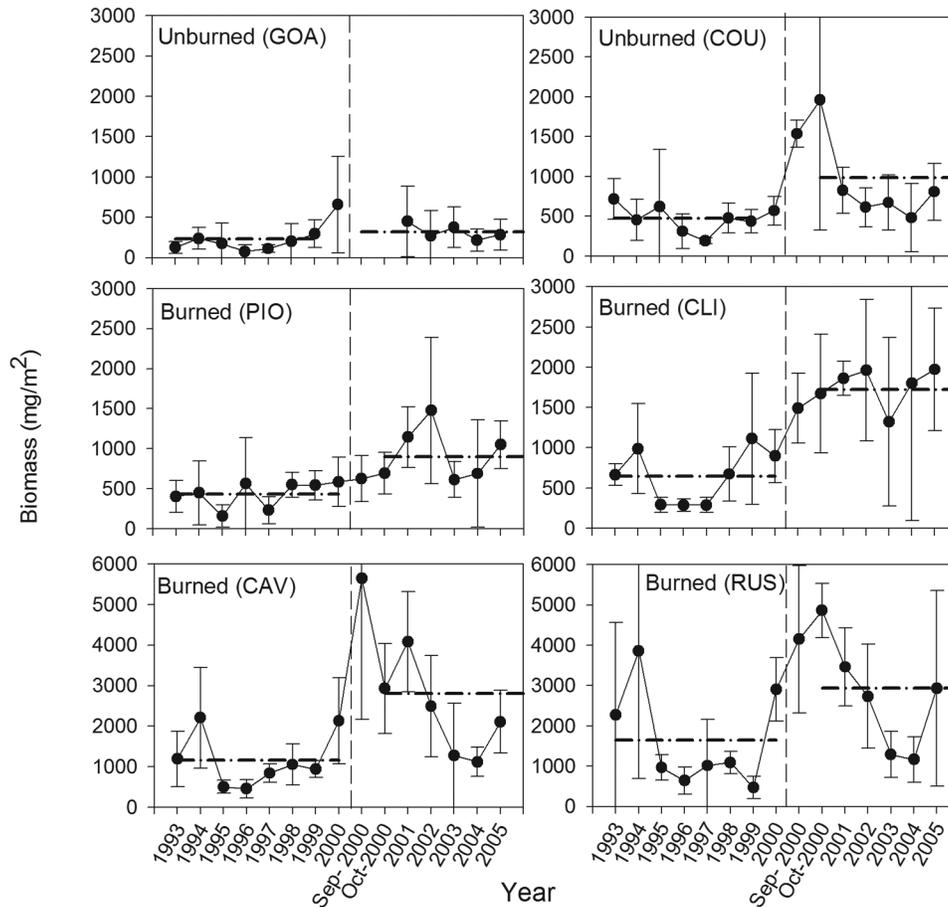


Fig. 8. Mean biomass (mg/m^2) in Big Creek unburned (GOA = Goat, COU = Cougar) and burned (CAV = Cave, CLI = Cliff, PIO = Pioneer, RUS = Rush) tributaries 1993–2005. Error bars are ± 1 SD ($n = 5$), note change in y-axis for Cave and Rush Creeks. Vertical dashed line indicates Diamond Peak wildfire, horizontal dashed line indicates pre- and post-fire means.

Heterlimnius increased in burned Cave, Cliff, and Pioneer Creeks, with increases in biomass similar to unburned streams. Limnephilidae and Perlidae increased in burned Cave and Cliff post-fire while Hydropsychidae, *Drunella*, and *Apatania* dominated pre-fire (Table 3). Additionally, in burned Rush Creek both *Pteronarcys* and *Atherix* increased post-fire, while pre-fire biomass was dominated by *Arctopsyche* and *Hesperoperla*. Conversely, burned Pioneer Creek had higher biomass of *Drunella* post-fire while *Sweltsa* was the only taxon to show higher biomass pre-fire.

We found significant correlations between invertebrate community structure and climatic variables of precipitation, temperature, and discharge in all streams (Table 4). For all streams,

low annual discharge and precipitation were associated with post-fire years and in most cases pre-fire 2000 clustered with the post-fire years (Fig. 11). Also, higher chlorophyll *a* concentrations were significantly associated with post-fire years in unburned Cougar ($r = 0.31$, $p = 0.05$) and burned Pioneer ($r = 0.45$, $p = 0.02$) and Cave Creeks ($r = 0.34$, $p = 0.04$), while high benthic organic matter standing stocks were significantly associated with post-fire years in unburned Cougar ($r = 0.3$, $p = 0.05$), and burned Cliff, and Rush Creeks, and marginally significant in Pioneer (Table 4, Fig. 11).

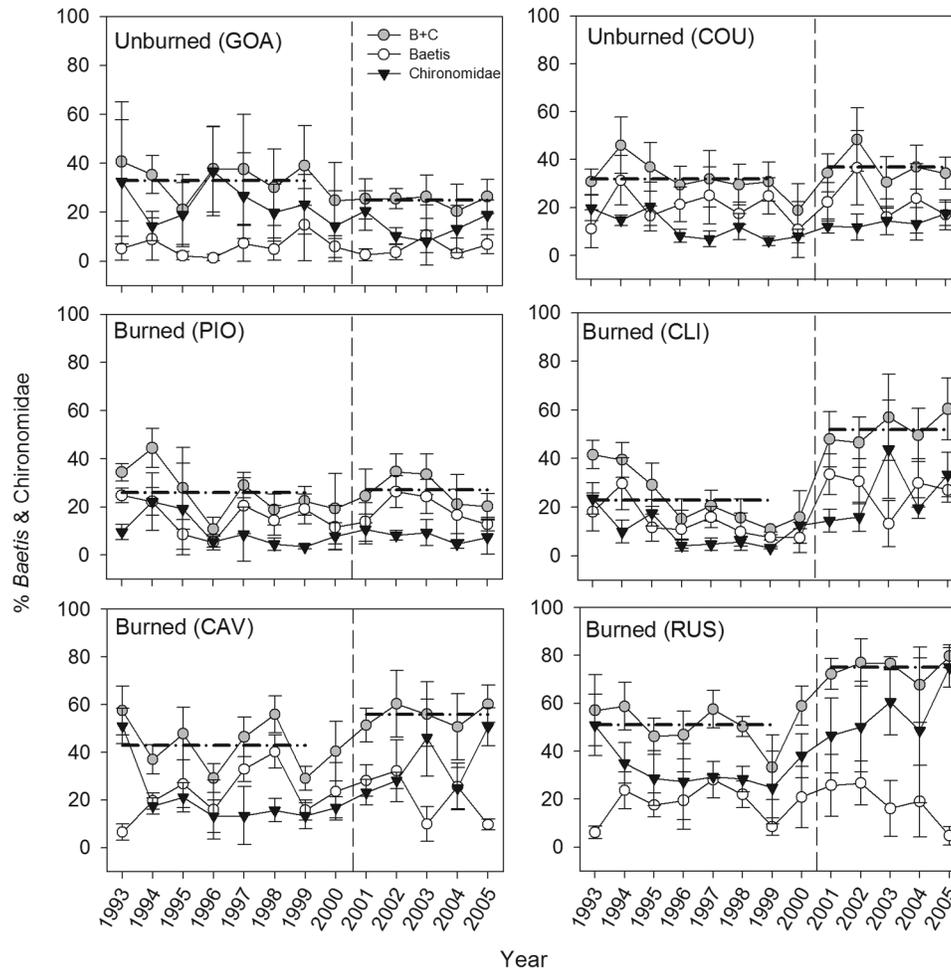


Fig. 9. Mean percent *Baetis* and Chironomidae in Big Creek unburned (GOA = Goat, COU = Cougar) and burned (CAV = Cave, CLI = Cliff, PIO = Pioneer, RUS = Rush) tributaries 1993–2005. Error bars are ± 1 SD ($n = 5$). Vertical dashed line indicates Diamond Peak wildfire, horizontal dashed line indicates pre- and post-fire means for *Baetis* + Chironomidae.

DISCUSSION

We examined the responses of benthic invertebrate community metrics and other key lotic ecosystem components to wildfire in a designated wilderness over a 13-year span of climate warming. The results provided insight into the natural range of inter-annual variability and enabled us to detect subtle effects of wildfire resulting from climate change and distinct from those found under previous climatic conditions. In general, basal food and invertebrate metrics increased post-fire in both unburned and burned streams but the increases were significantly

greater in the burned streams.

Our findings differ from previous studies of the effects of fire on stream ecosystems in western USA in which accelerated runoff from burned watersheds severely altered channel conditions (Rinne 1996, Minshall et al. 1997, 2001a, 2001b, 2003, Vieira et al. 2004, Mellon et al. 2008, Arkle et al. 2010, Romme et al. 2011). In these cases, dramatic reductions in basal food resources and consumer densities and biomass occurred within 1–3 years post-fire and persisted for several years after the initial decline. In the present study, there were no major runoff events immediately pre-fire and for several years post-

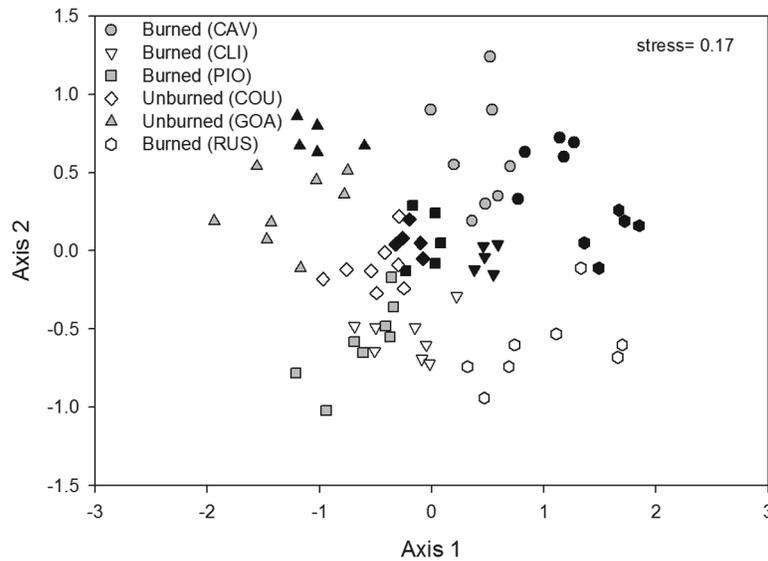


Fig. 10. Non-metric multidimensional scaling (NMDS) of macroinvertebrate assemblage based on biomass for each taxon in Big Creek tributaries from 1993 to 2005. Grey symbols represent pre-fire years (1993–2000) and black symbols represent post-fire years (2001–2005) for each unburned (GOA = Goat, COU = Cougar) and burned (CAV = Cave, CLI = Cliff, PIO = Pioneer, RUS = Rush) stream (see Fig. 11 for individual stream analysis).

fire due to reduced precipitation and suppressed and delayed spring runoff. Therefore, both climate and fire were important factors determining invertebrate community structure.

In the Big Creek watershed, air temperatures increased by 0.9°C over 22 years and 0.5°C over the study period. We do not attribute the changes we observed in basal food resources and invertebrate community metrics solely to temperature. Rather, we believe it is mainly due to a decreased snowpack and rate of snowmelt runoff that accompanied the temperature increase. In our study area, increases in spring and summer temperatures, drought, and a shift to earlier spring snowmelt have been accompanied by an increase in large wildfire activity, as has been found to be generally the case for most western USA forests (Stewart et al. 2005, Westerling et al. 2006, Davis et al. 2013). High temperatures and low precipitation occurred just prior to the 2000 fire and continued throughout the post-fire years. Precipitation was below 1 SD of the mean for 5 years of the study period indicating drought conditions during those years (1999–2003). But precipitation returned to normal in 2004 and 2005.

Wagner et al. (2000) found that lotic insects

responded strongly to climate-related factors of temperature and hydrologic regime. In our analyses, climatic factors combined with fire effects explained a greater portion of the variation among pre- versus post-fire years than fire alone, indicating that the combined effect of increasing temperatures, lower precipitation, and reduced spring runoff and annual and peak discharge had a stronger influence on invertebrate communities and their food resources than fire alone. Our results are in agreement with Poff et al. (2010) who stated that thermally driven reductions in snowpack can modify the timing and duration of high and low flows and potentially affect benthic invertebrates via indirect pathways mediated by habitat. As in many previous studies, our results show the importance of stream discharge and gradient in regulating physical disturbances usually associated with adverse intermediate-term effects (e.g., channel scouring and sediment loading) resulting from wildfire (Rinne 1996, Minshall et al. 1997, 2001a, 2004, 2003, Vieira et al. 2004, Mellon et al. 2008, Arkle et al. 2010). In the present study, we found these adverse effects following fire were minor or absent because of reduced snowpack and subsequent snowmelt runoff. In

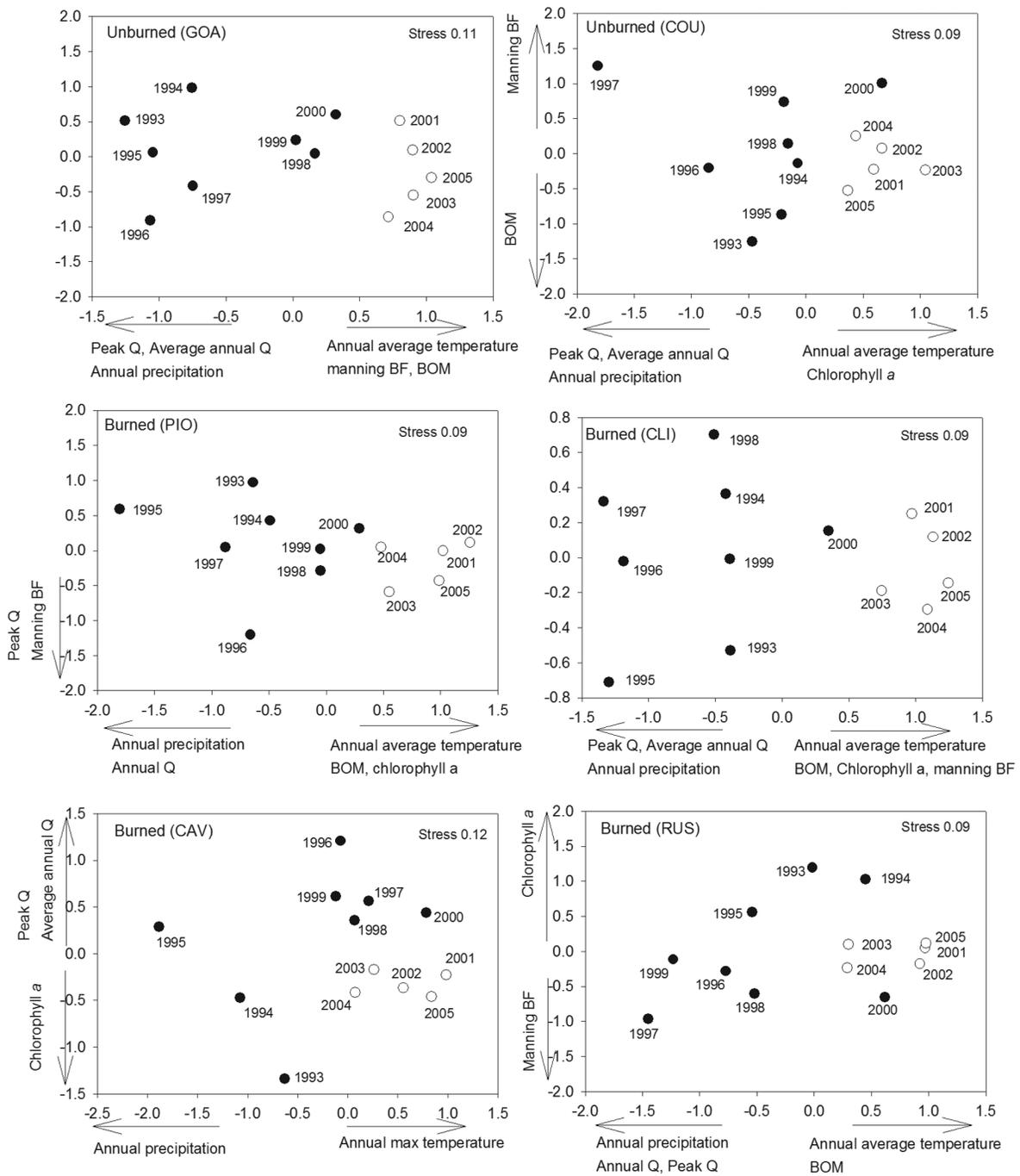


Fig. 11. Non-metric multidimensional scaling (NMDS) of macroinvertebrate assemblage based on individual taxa biomass in Big Creek unburned (GOA = Goat, COU = Cougar) and burned (CAV = Cave, CLI = Cliff, PIO = Pioneer, RUS = Rush) tributaries from 1993 to 2005 (2D stress). Each point is an average of five Surber samples. Correlated environmental variables driving differences in community biomass are shown on each axis. Goat and Cliff creeks did not have any environmental variables correlated with the y-axis.

Table 3. Mean biomass of taxa that accounted for 70% of community dissimilarity based on Bray-Curtis similarity between pre- and post-fire years for six tributaries in the Big Creek watershed. Pre-fire years are 1993–2000 and post-fire years are 2001–2005. Analysis was run on square-root transformed values, but untransformed data are presented.

Species	Unburned				Burned								
	Goat		Cougar		Cliff		Pioneer		Cave		Rush		
	pre-fire	post-fire											
<i>Brachycentrus americanus</i>										2.51	46.37	0.33	27.76
Chironomidae			1.73	1.68	1.09	16.49				8.91	31.9	12.51	44.52
<i>Arctopsyche</i>										11.96	19.11	12.41	4.05
Limnephilidae										2.61	10.64	0.11	1.78
Perlidae			2.23	4.56	4.09	17.62	0.81	0.86		3.36	11.48	0.28	1.45
<i>Hexatoma</i>			1.08	7.40						0.51	7.46	6.41	12.96
<i>Heterlimnius</i>	1.26	3.15	2.40	7.15	1.84	22.22	1.77	15.14	8.73	15.10			
<i>Doroneuria</i>							5.01	6.31	8.59	6.98			
<i>Baetis</i>			3.64	6.00	6.82	29.65	3.70	11.28	14.14	15.11	20.87	17.60	
Unionidae			1.94	0.33	1.29	4.25			1.03	3.69	0.29	1.50	
<i>Drunella</i>	4.39	0.95	4.57	3.92	18.25	13.86	4.78	21.83	7.01	2.72	2.94	1.76	
<i>Epeorus</i>	0.60	0.04	1.72	0.98			1.53	0.97	3.02	0.46			
<i>Optioservus</i>									0.1	3.54			
<i>Serratella tibialis</i>	0.42	0.64					0.18	3.82	2.18	5.98			
Hydropsychidae	0.35	0.41			5.54	1.66			0.11	1.06	0.42	1.81	
<i>Apatania</i>									3.22				
Elmidae	0.20	0.93	3.95	6.29	0.22	1.20			1.91	3.45			
<i>Rhyacophila</i>	0.05	0.45	2.63	2.19	1.65	2.76	1.58	2.10	3.47	1.98			
<i>Megarcys</i>					0.58	5.81							
<i>Chelifera</i>					0.21	3.21							
Tipulidae	3.36	2.17			0.42	3.95	0.24	1.03					
<i>Cinygmula</i>			1.89	4.51	5.84	3.40	2.06	1.99			1.65	0.17	
<i>Parapsyche</i>			9.45	9.20			5.72	4.75					
<i>Sweltsa</i>	0.29	0.97	0.50	1.78			1.47	0.90					
<i>Cleptelmis</i>	1.31	3.11											
<i>Yoraperla brevis</i>	0.48	2.05					0.36	1.11					
Hydrophilidae	0.13	1.45											
Perlodidae	1.79	1.41	0.30	1.95									
Nemouridae	0.20	0.91											
<i>Glutops</i>	0.02	0.88											
<i>Zapada</i>	0.50	1.42											
<i>Simulium</i>	0.21	0.64					0.21	0.91			0.99	1.79	
<i>Neophylax</i>							0.13	4.56					
<i>Pteronarcys</i>											1.33	28.93	
<i>Atherix</i>											5.04	20.15	
<i>Hesperoperla pacifica</i>											14.22	6.62	
Brachycentridae											23.12	0.07	
Hydroptilidae											0.05	1.28	
<i>Rhithrogena</i>											1.15	0.19	

all of our streams, baseflow conditions remained constant during the study, while peak discharge was variable with no clear pattern following the fire. Overall, the prevailing discharge conditions led to decreased scouring and runoff and to little variation in substrate embeddedness.

Our long-term dataset also revealed a progressive increase in taxon richness and supported a similar trend observed earlier in our Mortar Creek fire study (Minshall et al. 2001a), which also encompassed a drought period with lower snowmelt runoff. Most other studies of fire (and

climate change) have not found such an increase in richness over the presumed long-term pre-disturbance state and, in contrast, often have seen (or projected) a marked decrease (Rinne 1996, Vieira et al. 2004) or no change (Romme et al. 2011). With respect to drought, Durance and Ormerod (2009) observed, in contrast to our findings that in variable environments in general, richness is enhanced following resumption of wetter conditions, with recovery from drought requiring about 3 years (Boulton 2003). However, the pattern of increase in biodiversity, at a

Table 4. Pearson correlation coefficients for relationship between environmental variables and non metric multi-dimensional scaling (NMDS) axis scores. BOM = benthic organic matter, Chl *a* = chlorophyll *a*, *T* = temperature, Avg = average, PPT = precipitation. Axis used for analysis was based on NMDS vector analysis coefficients. Variables that are significantly correlated with either axis one or two are shown in bold.

Stream	Annual <i>Q</i> (m ³ s)	Peak <i>Q</i> (m ³ s)	Avg max <i>T</i> May–Aug	Avg annual <i>T</i> (°C)	Avg annual max <i>T</i> (°C)	Chl <i>a</i> (mg/m ²)	BOM (g/m ²)	Avg annual PPT (cm)	May–Aug PPT (cm)	Manning peak flow (m ³ /s)
Unburned										
Goat										
<i>r</i>	0.44	0.44	0.4	0.6	0.5	0.17	0.13	0.13	0.06	0.04
<i>p</i>	0.01	0.01	0.02	0.002	0.01	0.16	0.22	0.21	0.40	0.50
Cougar										
<i>r</i>	0.43	0.22	0.55	0.45	0.43	0.31	0.3	0.22	0.16	0.45
<i>p</i>	0.02	0.10	0.002	0.001	0.01	0.05	0.05	0.11	0.18	0.01
Burned										
Cliff										
<i>r</i>	0.55	0.18	0.14	0.49	0.35	0.2	0.37	0.23	0.04	0.15
<i>p</i>	0.004	0.14	0.20	0.01	0.03	0.12	0.03	0.09	0.50	0.19
Pioneer										
<i>r</i>	0.35	0.27	0.27	0.05	0.30	0.45	0.26	0.32	0.09	0.002
<i>p</i>	0.03	0.07	0.07	0.48	0.05	0.02	0.07	0.05	0.31	0.87
Cave										
<i>r</i>	0.46	0.26	0.36	0.17	0.13	0.34	0.10	0.28	0.22	0.00
<i>p</i>	0.01	0.07	0.03	0.16	0.22	0.04	0.28	0.06	0.11	0.82
Rush										
<i>r</i>	0.76	0.46	0.50	0.16	0.16	0.03	0.39	0.13	0.10	0.15
<i>p</i>	0.001	0.01	0.01	0.09	0.17	0.59	0.02	0.22	0.29	0.19

complex of individual sites with time, apparently is common and may occur in relatively mature or stable communities as well as in disturbed ones (Magurran et al. 2010). We believe that the increases in richness seen in the present study may be due mainly to the reduction in frequency and/or occurrence of disturbance from high flow events that allowed sparsely abundant species to increase in abundance and thereby increase the chance they would be collected in our samples. The duration of the moderated spring runoff conditions over several years may have allowed taxa to persist or become less rare which may not have done so under normal flow conditions.

Effects of wildfire and climate change on basal food resources

The dominant food resources in our study streams, as in many streams, were both periphyton and benthic organic matter (BOM) composed mainly of deciduous riparian-plant leaves and fine particulate organic matter of both terrestrial and aquatic origin. Following fire, the composition of BOM generally shifts for a time to burned matter (mainly charcoal and twigs). Both periphyton and BOM are subject to removal through scouring and suspension at elevated

flow velocities. Our results suggest that the effects of both climate and fire increased the periphyton basal food resource in burned streams. This in turn likely contributed to the higher invertebrate densities and biomasses we observed. In the burned streams, chlorophyll *a* concentrations increased following the Diamond Peak wildfire as a result of greater nutrient availability and the loss of canopy cover and subsequent increased light. The increases in chlorophyll *a* concentrations probably also were enhanced by low annual and peak discharge starting in 2000. Davis et al. (2013) found that periphyton standing crops of both chlorophyll and AFDM in Big Creek were associated with measures of streamflow, with chl *a* significantly related to the timing of median streamflow and AFDM significantly related to the timing of peak streamflow. Increases in periphyton biomass also were found immediately following 1988 Yellowstone fires, but these did not persist due to extensive scouring in subsequent years (Minshall et al. 1997, 2001b).

Our results differ from those of Malison and Baxter (2010a) five years after the Diamond Peak wildfire and Mellon et al. (2008) two years after the Togo wildfire, where no differences in

periphyton biomass between burn and reference streams were detected after fire. This could be due in part to the high variation in periphyton biomass measured across all sites and increased consumption and turnover in burned streams (Mellon et al. 2008). However, we had the advantage of pre- versus post-fire comparisons in the same streams over several years, including immediately post-fire. This likely enabled us to detect differences that many studies that substitute space for time may miss. For example, in our study the riparian vegetation recovered rapidly after fire (Fig. 1) resulting in considerable reduction in light and sequestration of nutrients and lowered periphyton biomass by year 5 or earlier.

Benthic organic matter (BOM) was highly variable across all sites; although increases in mean standing stocks were higher in Cliff, Pioneer, and Rush starting in 2000 just prior to the Diamond Peak fire. We attribute the pre-fire increases in 2000 to a reduction in the magnitude of spring runoff resulting from a lower than normal snowpack. Except for 2000, these results are similar to other studies where total benthic organic matter increased immediately following fire (McIntyre and Minshall 1996, Minshall et al. 1997, 2001b). However, those increases in quantity were accompanied by major decreases in quality as riparian deciduous leaves were initially replaced by charred sticks and particulate charcoal. In contrast to leaves and other types of riparian organic matter, charcoal is regarded as lacking in food value because it is virtually pure carbon. In subsequent post-fire years, these charred materials became markedly reduced in amount and were replaced by deciduous leaves from recovering riparian shrubs.

Effects of wildfire and climate change on invertebrate community stability

Many factors may influence the stability of lotic invertebrate communities confronted with disturbance, but on a regional basis, flow regime and geomorphology (especially as it influences channel morphology and bed composition) are of over-riding importance (Resh et al. 1988). Both climate and fire were important factors affecting flow regime and channel conditions and subsequently determining invertebrate community structure in this study. Macroinvertebrate taxo-

mic composition fluctuated across years, with communities in the post 2000 drought and fire more stable than earlier years ($\sim 70\%$ vs $<60\%$ dissimilarity) with an average of 45% dissimilarity between pre- and post- fire years. This could have influenced the increase in taxa richness in post-fire years. Also, increases in disturbance-adapted taxa seem to be driven by environmental factors (discharge and temperature) associated with both climate and fire, resulting in increased dominance by a few taxa starting in 2000. The disruptive hydrologic forces associated with increased floods generally has a strong influence on invertebrate communities under conditions following fire and may be a stronger force in the recovery and structure of these communities than fire alone (Rinne 1996, Minshall et al. 1997, 2004, Vieira et al. 2004, Arkle et al. 2010). In our study, annual separation of invertebrate community structure among years was driven mainly by reduced precipitation and discharge and associated increases in air temperature, which moderated rather than amplified the effects of fire. For example, decreased flow and physical (e.g., increased light) and chemical (e.g., increased nutrient) changes post-fire were primarily responsible for increases in channel and substrate stability and in periphyton biomass, leading to increases in invertebrate biomass and many of the associated taxonomic changes. In another fire study in this region, Arkle et al. (2010) also concluded that food sources and substrate conditions were the mechanisms driving higher inter-annual changes in invertebrate community composition in burned catchments relative to unburned ones.

Considerable inter-annual habitat and invertebrate stability in Big Creek streams before the 2000 wildfire were documented in a previous study (Robinson et al. 2000). Our more-extensive analysis supports those findings. We found much more variability in the invertebrate community composition before than after the Diamond Peak fire. Even though there were inter-annual variations in temperature, precipitation and discharge, they were not as strong as multi-year variability for invertebrates. Inter-annual variability in invertebrates was greater in pre-fire years than post-fire years, which were more similar. Although streams did cluster by pre- versus post-fire years, this was driven more by discharge

unrelated to fire but more to a shift in climate. If the effect was only due to fire, we should have seen more separation in the streams that did not burn or burned with higher or lower severity.

In the present study, fire effects were linked to flow, but the negative impacts (e.g., increased inter-annual variability and reduced abundance and biomass) were delayed for several years until more-normal spring runoff levels returned. Arkle et al. (2010) found that invertebrate communities in burned catchments did not exhibit increased similarity to communities in unburned catchments over time. Our results differ in that unburned and burned streams followed the same pattern in community structure, an indication that climate changes were having a greater impact than fire. However, burned streams saw a greater increase in percentage of *Baetis* and Chironomidae, whereas the unburned Goat and Cougar only showed increased abundance and biomass of predators with little increase in disturbance-adapted *Baetis* and Chironomidae. The increases in biomass of the rarer taxa (making up at least 3% of the biomass) in our study, that became evident during or after 2000, mainly consisted of predators including Perlidae, Perlodidae, *Megarcys*, and *Hexatoma*. These may have become more evident due to post-fire increases in potential prey, especially *Baetis* and Chironomidae as well as *Brachycentrus*, *Heterlimnius*, Heptageniidae, and *Ephemerella*. Other studies have found that *Baetis* and Chironomidae responded positively to drought versus non-drought periods in Mediterranean streams (Boix et al. 2010, Feio et al. 2010) and to fire (Minshall et al. 1997, 2001a, b, Arkle et al. 2010, Malison and Baxter 2010a). Studies of the effect of drought on stream ecosystems (Stanley et al. 1997, Lake 2000, Feio et al. 2010, Verkaik et al. 2013) rarely involve simply reduced stream flows (as opposed to total drying) or changes in the magnitude, timing, or duration of snowmelt and type of precipitation like those being encountered in Big Creek and other northern Rocky Mountains catchments in recent years.

Importance of long-term study

It is widely recognized that ecological studies at the scale of multiple years and decades have a greater likelihood of detecting rare events and subtle or complex changes in component levels of

organization and their environments than do short-term studies (Jackson and Füreder 2006, Magurran et al. 2010, Dodds et al. 2012). Monitoring the effects of climate change and fire is particularly valuable in situations where direct human disturbance remains low and constant and the effects of climate change can be decoupled from other forms of anthropogenic influence (Poff et al. 2010). Large-scale disturbances such as wildfire and climate change often alter the state and trajectory of ecosystems and have a large temporal footprint. Many studies use a space for time substitution to provide a reference for evaluating the effects of disturbances such as fire or climate shifts on streams, but in our case annual sampling extending for years before and after such events has obviated the need to rely on such surrogates. This has proven especially advantageous in the case of wildfire and gradual long-term climate shift because of their notoriously highly variable or patchy occurrence in time and, for fire at least, space. In our study, sampling only occurred annually, which may have had a small influence on our results as timing of peak flow may have varied slightly over the sampling period. However, in the Big Creek catchment, and elsewhere in the Rocky Mountains, the timing of stream discharge is reasonably predictable and its flood frequency low due to its largely snow-melt origins (Poff and Ward 1989). In another central Idaho stream, which also has a snow-melt discharge regime, monthly invertebrate population densities were found to be relatively stable following cessation of spring runoff (Robinson et al. 1993). Although our once-a-year sampling also did not reflect annual variation in temperature, the results were the product of the preceding year's temperatures and occurred near the annual peak temperature thus reflecting the impact of the long-term trend of temperature increases we observed. Except in Mediterranean-climate streams, the interaction between drought and fire on aquatic systems is poorly known, especially because of the unpredictability of such events. Long-term studies such as ours, are an important means of documenting and evaluating the effects of drought in climates where its occurrence was less frequent and its impacts were less severe and now are becoming more frequent with greater magnitude.

Finally, our long-term study has enabled us to

develop quantitative relationships between important environmental variables and the biota for use in forecasting future outcomes (Davis et al. 2013). We expect that similar efforts eventually also will be completed for the invertebrates and food-web relationships. This will enhance the capacity for predicting future effects of climate change and of climate-wildfire interactions on community structure and facilitate appropriate action by resource managers. Emphasis of future long-term studies on the effects of fire on streams should include the duration of the effect, in terms of negative or positive impacts and increased inter-annual variation, and assessment of the presence or absence of any trend toward a pre-fire state.

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