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Fire, flow and dynamic equilibrium in stream macroinvertebrate communities

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SUMMARY

1. The complex effects of disturbances on ecological communities can be further complicated by subsequent perturbations within an ecosystem. We investigated how wildfire interacts with annual variations in peak streamflow to affect the stability of stream macroinvertebrate communities in a central Idaho wilderness, USA. We conducted a 4-year retrospective analysis of unburned (n = 7) and burned (n = 6) catchments, using changes in reflectance values (ΔNBR) from satellite imagery to quantify the percentage of each catchment's riparian and upland vegetation that burned at high and low severity.
2. For this wildland fire complex, increasing riparian burn severity and extent were associated with greater year-to-year variation, rather than a perennial increase, in sediment loads, organic debris, large woody debris (LWD) and undercut bank structure. Temporal changes in these variables were correlated with yearly peak flow in burned catchments but not in unburned reference catchments, indicating that an interaction between fire and flow can result in decreased habitat stability in burned catchments.
3. Streams in more severely burned catchments exhibited increasingly dynamic macroinvertebrate communities and did not show increased similarity to reference streams over time. Annual variability in macroinvertebrates was attributed, predominantly, to the changing influence of sediment, LWD, riparian cover and organic debris, as quantities of these habitat components fluctuated annually depending on burn severity and annual peak streamflows.
4. These analyses suggest that interactions among fire, flow and stream habitat may increase inter-annual habitat variability and macroinvertebrate community dynamics for a duration approaching the length of the historic fire return interval of the study area.

Keywords: burn severity, dynamic equilibrium, macroinvertebrate community, peak streamflow, wildfire disturbance

Introduction

According to the dynamic equilibrium view of natural systems, community structure is determined by species interactions and by disturbance frequency (Dayton, 1971; Connell & Slatyer, 1977; Menge & Sutherland, 1987). When disturbances are infrequent, biotic interactions between competitors, mutualists, predators and prey determine community structure. Conversely, when disturbances are frequent, communities tend to be dominated by colonising or pioneering species and assume new compositional states fairly continuously. Decades of investigations have found evidence for both equilibrium (i.e. deterministic biotic interaction regulation) and non-equilibrium (i.e. stochastic disturbance regulation) communities, and both mechanisms are

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likely to be regulating communities in what is often described as dynamic equilibrium (Putman, 1994).

Spates generated by rain or snow-melt have been characterised as disturbances capable of driving non-equilibrium community structure in stream macroinvertebrates (Feminella & Resh, 1990; Death & Winterbourn, 1995). Macroinvertebrate community structure and composition are influenced by the stochastic and disruptive hydrological forces that occur during spates, which are then often followed by fairly long periods of relatively stable conditions where space is limited and biotic interactions are strong (Resh *et al.*, 1988; Poff, 1992; Konrad, Brasher & May 2008). This streamflow pattern is capable of initiating and maintaining communities in dynamic equilibrium in some stream systems. However, many other factors influence the stability of communities and can contribute to increasingly dynamic macroinvertebrate assemblages.

In dry coniferous forests of the western United States, fire is a dominant disturbance influencing vegetation and ecosystem processes with historical fire return intervals estimated at 10–25 years (Agee, 1993). Riparian and upland forests burned at similar frequencies in this region (Everett *et al.*, 2003; Olson & Agee, 2005). Fires influence stream ecosystems by increasing sediment, light and large wood, thus altering habitat for stream fauna (Bisson *et al.*, 2003). Several studies have examined the effects of wildland fires on stream macroinvertebrates and found positive and negative short-term (1–10 years) responses of various taxa and long-term (≥15 years) community variability (Minshall, 2003). In a review of the effects of fire on aquatic ecosystems in forested biomes of North America, Gresswell (1999) concluded that hydrological processes are probably the primary factor influencing postfire persistence of stream fauna. However, few studies have examined how fire disturbance, in conjunction with instream hydrological disturbances, influence the dynamic equilibrium of stream communities.

The goal of this study was to examine whether fluctuations in stream macroinvertebrate communities were solely because of fire in upland and streamside forests (hereafter riparian) or were because of the interaction of fire and the annual variation in peak streamflow. We examined this relationship in the context of dynamic equilibrium theory, addressing the following hypotheses: (1) postfire habitat conditions and benthic macroinvertebrate community structure in streams are associated with the interaction of riparian burn severity and peak discharge, more so than either burn severity or discharge independently, and (2) habitat conditions and benthic macroinvertebrate community structure in streams with burned riparian forests do not follow a trend towards recovery with time (approaching unburned 'reference' streams), but instead vary from year to year depending on annual discharge patterns and burn severity of the riparian forest.

To address these hypotheses, we performed a multi-year retrospective analysis of streams flowing through catchments that burned along a gradient of extent and severity in the Big Creek (ID, USA.) drainage and examined the influence of peak streamflow in the absence of wildfire using unburned reference streams in the nearby South Fork of the Salmon River drainage.

Methods

Study area

Our study streams (n = 6 burned and 7 unburned catchments) were low-order (2–3), high-gradient streams located in the Big Creek and South Fork Salmon River (hereafter South Fork) drainages of the Salmon River in central Idaho (Fig. 1; 44°57′N, 115°41′W). Streams ranged in size from 2.15 to 9.86 m mean wetted width in burned catchments and from 2.08 to 8.96 m mean wetted width in unburned catchments (Table 1). Elevations of sampled catchments ranged from 1211 to 2711 m in the Big Creek drainage and from 1202 to 2703 m in the South Fork drainage (Table 1) and both sampling areas lay on boundaries between Hot Dry Canyons and Southern Forested Mountains of US EPA (2002) Level IV Ecoregions. In both drainages, geological parent materials were derived from the granitic Idaho Batholith and stream flows were driven by snowmelt in late spring and early summer (May and June), with base flows occurring from July to September. Plant communities in all catchments were similar, with upland vegetation dominated by subalpine fir (*Abies lasiocarpa* Hook. Nutt.), Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) at higher elevations and on north-facing slopes, and by ponderosa pine (*Pinus ponderosa* C. Lawson) and sagebrush (*Artemisia tridentata* Nutt.)-grass communities on south-facing slopes.

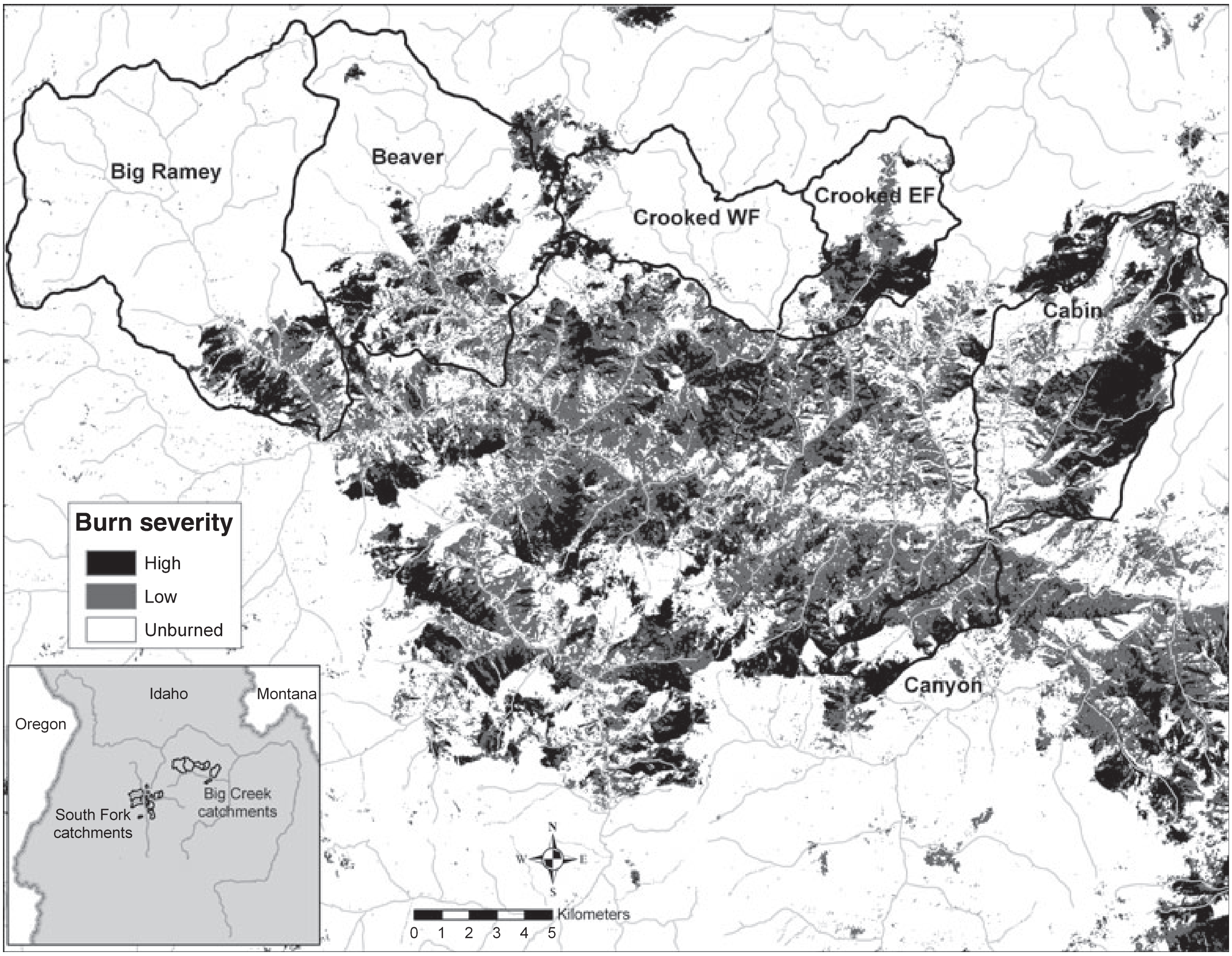

Fig. 1 Burn severity within the Diamond Peak Fire Complex. Big Creek and South Fork Salmon River drainages showing delineations of each catchment sampled for macroinvertebrates (inset).

Riparian forests were characterised by gray alder (*Alnus incana* L. Moench), red osier dogwood (*Cornus sericea* L. ssp. *sericea*), Rocky Mountain maple (*Acer glabrum* Torr.), willow (*Salix* sp. L) and water birch (*Betula occidentalis* Hook.).

In the South Fork drainage, no large stand-replacing fires had occurred within the study area in 60–75 years (Barrett, 2000), until the summers of 2006 and 2007. Thus, these catchments represent streams where variations in annual peak streamflow are probably the principle disturbance. Big Creek is largely confined to the Frank Church-River of No Return Wilderness, where, since 1985, wildland fires have been primarily managed for resource benefits (e.g. forest health). Portions of many catchments within the Big Creek drainage burned in 1988, 2000, 2005, 2006, 2007 and 2008 wildfires. Streams in these catchments are disturbed by both wildfire and variations in annual peak streamflow. The 12-year period between 1988, when small portions of some catchments burned, and 2000, represents a relatively long fire-free period in this drainage. This study was conducted following the Diamond Peak wildfire complex, which burned 606.1 km^2 of the Big Creek and Middle Fork Salmon River drainages in August and September 2000. This mixed severity wildland fire burned portions of both upland and riparian forests in many catchments.

Study design

To examine the associations between catchment-level burn severity and subsequent disturbances on stream habitat and macroinvertebrate communities,

Table 1 General site characteristics for macroinvertebrate study streams

Stream name	Mean wetted width (m)	Mean elevation (m)	Mean catchment slope (%)	Stream reach gradient (%)	Stream aspect	Mean water temp.*(C)	Catchment burned at high/low severity† (%)	Riparian zone burned at high/low severity† (%)	Total percent of catchment burned
South Fork drainage									
Blackmare	5.08	2159	24.9	13.2	East	11	–	–	–
Buckhorn	5.82	2000	20.6	5.9	Southeast	13	–	–	–
Deadman	2.15	1769	28.3	16.5	South	11	–	–	–
Fitsum	9.86	1991	23.9	5.1	East	10	–	–	–
Fourmile	6.59	2167	23.8	10.6	West	12	–	–	–
Parks	3.98	2181	21.2	15.2	South	13	–	–	–
Reegan	3.84	2092	20.6	14.3	South	12	–	–	–
Big Creek drainage									
Beaver	8.96	2228	20.1	6.3	South	10	4.1/7.6	2.7/8.8	11.7
Big Ramey	5.07	2150	18.8	13.1	South	10	7.3/17.0	2.9/18.4	24.3
Cabin	4.56	1755	8.1	5.3	South	15	25.7/30.4	23.1/56.1	56.1
Canyon	2.08	1925	26.8	14.3	North	13	23.6/48.0	18.0/52.0	71.6
East Fork Crooked	3.83	2114	19.9	1.7	Southwest	17	15.6/20.8	15.2/31.1	36.4
West Fork Crooked	3.56	2126	18.1	4.0	Southeast	14	1.4/4.9	0.1/4.2	6.3

*Water temperatures recorded at time of sampling (between 0900 and 1800 h in July and August) were averaged from 2002 to 2004.
†Percentage of each catchment or riparian forest burned in 2000 Diamond Peak Fire at high and low severity based on ΔNBR estimates.

we sampled tributaries of Big Creek for 4 years (2001–2004) after the Diamond Peak Fire of 2000. Within these catchments, we compared disturbance effects on habitat (2001–2004) and macroinvertebrate community composition (2002–2004) across increasing riparian burn severity. To determine whether variations in annual peak streamflow had similar effects on community composition and habitat in the absence of wildfire, we monitored seven unburned reference catchments in the South Fork drainage over the same time-period. Prefire data, collected in 1999 and 2000, indicated that the communities in the Big Creek and South Fork streams were not different based on macroinvertebrate total density, taxon richness and percent Ephemeroptera, Plecoptera and Trichoptera (MANOVA, Wilks' Lambda $F = 1.97$, d.f. = 7, $P = 0.209$). These data were not analysed relative to postfire data because samples were collected using D-nets with larger sized mesh than the Surber samplers used to collect postfire samples.

Because retrospective fire studies are opportunistic, there are limitations in design and inference, and potential issues with pseudoreplication exist (Van Mantgem, Schwartz & Keifer, 2001). Our study streams were not randomly selected but were chosen according to similarities in geomorphology and prefire macroinvertebrate communities in burned and in unburned catchments. Although the six burned catchments we studied were all within the same fire complex, the distance between catchments (ranging from 0.01 to 25 km), multiple ignition points, variable fuel levels and different fire weather contributed to make the disturbance conditions among catchments independent.

Burn severity modelling

Burn severity was estimated at the catchment-level within the Big Creek drainage using normalised burn ratio values (NBR) calculated from Landsat 7 Enhanced Thematic Mapper Satellite imagery (U. S. Geological Survey, Sioux Falls, SD, USA.) following Key & Benson (2006). Delta NBR (ΔNBR) was calculated as the difference in NBR between available cloud-free, pre- and postfire images taken on 18 July 1999 and 9 September 2001 respectively. We used published values (see Key & Benson, 2006) to determine breakpoints in ΔNBR and assigned each pixel in a catchment as either unburned, low severity or high severity (Fig. 1). We then calculated the percentage of pixels in each catchment that fell into the high and low burn severity categories and summed these to estimate the percentage of each catchment that burned (Table 1). Finally, using a geographic information system (ArcGis 9.0; ESRI, Redlands, CA, USA.), we selected only those pixels within 20 m of a stream to calculate the percentage of pixels in high and low burn severity classes (HIGHSEV or LOWSEV) within the complete length of the riparian forest or within our 1-km study reach to estimate the relative riparian burn severity per catchment. We used the burn severity of the complete length of each catchment's riparian forest in analyses concerning instream sediment based on our prediction that sediment, being highly mobile, would be influenced by riparian burn severity throughout a catchment, whereas other stream habitat variables would be more dependent on localised riparian burn severity within the study reach of each stream. Values of explanatory variables (e.g. HIGHSEV or LOWSEV) used in analyses are based on this rationale. We acknowledge that the severity and extent of upland vegetation burned in a catchment is important in driving changes in water infiltration rates, runoff, erosion, rill formation and stream channel sedimentation, among other factors (Wondzell & King, 2003). However, we chose to use only riparian burn severities in our analyses because of the high correlation between the percentage of each catchment's upland and riparian vegetation that burned (r^2 = 0.98, n = 16 catchments in study area) and because fire closer to stream channels is likely to result in more types of effects [e.g. changes in stream cover and large woody debris (LWD)] to the lotic system.

Benthic and riparian habitat sampling

Macroinvertebrate communities and habitat were sampled from 2002 to 2004 in five transects placed at 50-m intervals within a 200-m reach of each stream. At each macroinvertebrate sampling transect, we recorded the following habitat conditions annually: wetted width, depth, width to depth ratio (WDR), the percentage of the transect covered by silt (SILT), and the percentage riparian canopy cover (COVER). SILT and COVER were estimated by counting the number of centimeters covered on meter tapes placed across the stream width at each transect. Within each 200-m stream reach, we quantified the percentage of low gradient riffle (LGR) habitat type (number of meters of stream habitat with surface agitation, but no whitewater, out of 200 m) and the number of pieces of LWD (large end diameter ≥10 cm by length ≥1 m). We also measured V*, a unitless metric which is calculated as the ratio of the sediment volume to the total volume of a pool (Hilton & Lisle, 1993), to assess the amount of mobile sediment deposition in 10 pools in each stream annually. As pools fill to capacity with sediment, values of V* approach one. V* was estimated by averaging water depth and sediment depth at five equally-spaced locations in each pool, starting at the centre of the pool. Sediment depth was measured by pushing a metal probe into the sediment until impenetrable substrate was reached and measuring the length of the probe embedded in the sediment. Additional habitat variables were recorded as part of a concurrent stream amphibian study within the Diamond Peak Fire perimeter. These data were collected in 30 randomly placed belt transects within each stream. Each belt transect extended 1 m upstream and the width varied with the stream width at each random location. At each belt transect, we visually estimated the percentage of transect area covered by instream LWD (large end diameter >5 cm), with undercut bank morphology (UNDERCUT), and covered by organic debris (ORGANIC; litter and wood with large end diameter <5 cm). Values for each variable used in subsequent statistical analyses were derived by averaging measurments from 30 transects within each stream for each year.

Because equipping catchments with streamflow gages was prohibitively expensive, we compared the influence of annual peak streamflow magnitude (PEAKFLOW) among years and drainages using hydrological data from nearby stream gages; US Geological Survey Streamgage 13310700 was located downstream of our reference catchments and Streamgage 13310199 was located downstream of our burned catchments. Using the same PEAKFLOW metric for each burned catchment within a year probably provides a conservative estimate of flow magnitude within more severely burned catchments, which often exhibit increased runoff (Stednick, 1996; Neary, Ryan & DeBano, 2005).

Macroinvertebrate sampling

We collected benthic invertebrate samples from one location (the thalweg) along each transect (n = 5 samples per reach) using a standard Surber sampler (0.10 m^2, 500 μm mesh) during summer base flow conditions. In the laboratory, benthic macroinvertebrates were keyed to genus according to Merritt & Cummins (1996), except for Chironomidae and Oligochaeta, which were both keyed to family. We determined the density of each genus in each of five Surber samples per reach per year. Values used in calculations for macroinvertebrate metrics reflect an average density of each genus in the five samples taken from each stream annually.

Data analysis

Benthic and riparian habitat To test hypothesis (1), relationships between burn severity, annual peak streamflow and habitat variables were examined using separate regression analyses. If burn severity alone influenced habitat variables, we expected a significant relationship between HIGHSEV and a given habitat variable measured in burned catchments, when that variable was averaged across all 4 years of sampling in a given catchment (e.g. HIGHSEV versus variable averaged across years for each burned catchment; $n = 6$ burned catchments). If PEAKFLOW alone influenced habitat variables, we expected a significant relationship between average values within a year of sampling and PEAKFLOW in both burned catchments and in unburned catchments (e.g. separately for burned and unburned catchments: PEAKFLOW versus variable averaged across catchments within a given year). If an interaction between burn severity and annual peak streamflow influenced habitat variables in burned catchments, then we expected: (1) a significant relationship between HIGHSEV and the amount of year-to-year change in a habitat variable and (2) a significant relationship between PEAKFLOW and that habitat variable when averaged across all 4 year of sampling in the burned catchments, but no such relationship in the unburned catchments. For example, as PEAKFLOW increases, a habitat variable should either increase or decrease in burned catchments, but not in unburned catchments.

To determine if any habitat variables exhibited significant changes related to time since the fire (hypothesis 2), we performed regressions of habitat variables, averaged by year of sampling, against the number of years since the fire (TIME), separately for each drainage (burned or unburned). If there was no relationship between a given habitat variable and TIME in the burned catchments, we concluded that there was no significant trend towards recovery. We were able to determine temporal changes which were also occurring in unburned catchments by testing for a significant relationship between habitat variables and TIME in unburned catchments. All univariate analyses were performed using the statistical package SAS version 9.0.1; (SAS Institute Inc., Cary, NC, U. S. A.).

Macroinvertebrate communities We used generalised linear modelling to evaluate the relationship between disturbance level (riparian burn severity) and annual postfire changes in macroinvertebrate community composition in burned and unburned catchments (hypothesis 1), both of which were subject to inter-annual variations in PEAKFLOW. If both burn severity and annual peak streamflow were important in influencing macroinvertebrate communities, we expected: (1) an increasing average rate of inter-annual change in the density of genera as HIGHSEV increased and (2) a lower average rate of inter-annual change in the density of genera in unburned catchments.

In addition to quantifying burn extent and severity within each catchment, we assigned each stream to one of three burn classes (BURNCLASS) on the basis of the percentage of the riparian forest burned at high severity (HIGHSEV): unburned, <7% HIGHSEV and >7% HIGHSEV. These groups allowed us to perform multivariate analyses that required categorically defined levels of burn severity rather than a continuous measure (i.e. HIGHSEV). We obtained the 7% HIGHSEV cutoff value by regressing the total percentage of each catchment burned against HIGHSEV. We used the resulting model equation to establish a cutoff value that relates high severity fire within riparian forests of our study streams to the percentage of each catchment burned, a metric used in past research (Fig. 2). Minshall (2003) suggests that fire effects on macroinvertebrate communities initiate when 25–50% of the catchment is burned, depending on climate and topography. We chose the lower end of this range (25%) because of the steep relief, dry upland habitat, erodible soils, and the suggestion by Neary *et al.* (2005) and Stednick (1996) that removing 20–40% of vegetative cover results in alterations of hydraulic processes within a catchment.

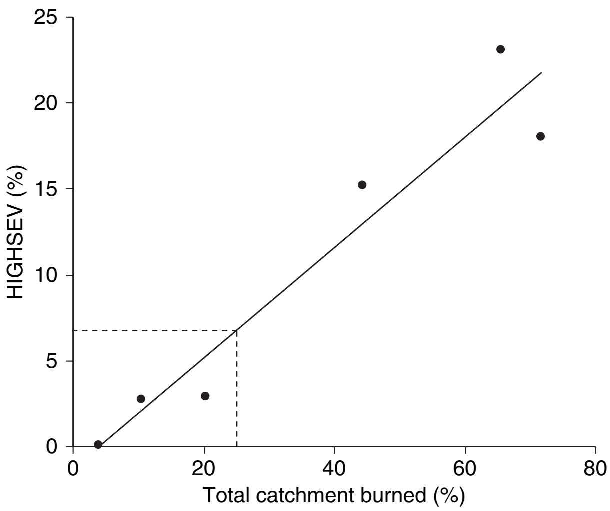

Fig. 2 The percentage of each catchment's riparian forest burned at high severity plotted against the total percentage of each catchment burned (upland plus riparian). Regression indicates that in these catchments, 25% of a catchment burned corresponds to 7% high burn severity.

To address hypothesis (2) we performed a non-metric multidimensional scaling ordination (NMS; PC-ORD 5.10 software; McCune & Mefford, 2006) on the density of individuals of each genus from all stream and year combinations. We then created a biplot relating BURNCLASS, HIGHSEV and TIME to the macroinvertebrate community composition of each stream. If macroinvertebrate communities in burned catchments exhibited increased similarity to communities in unburned catchments over time, then samples should not cluster by BURNCLASS, but TIME should be correlated with community composition. If macroinvertebrate communities in burned catchments do not become more similar to those in unburned catchments, then samples should cluster by BURNCLASS and HIGHSEV should be correlated with community composition. We used Sorenson distance to measure dissimilarity between sample units and compared 250 iterations of actual data and 250 runs of randomised data to assess the significance of each axis in representing the original community data. The final number of axes was determined by including a significant axis if it reduced the stress in the final solution by ≥5 (on a 0–100 scale). Correlation coefficients (r^2) between Sorenson distance in ordination space and original space were used to determine the proportion of variance represented by each of the final axes. Linear relationships between community composition and HIGHSEV or TIME were assessed using correlations between these variables and the ordination axes.

The relative importance of habitat variables in influencing community composition was examined with canonical correspondence analyses (CCA). We used CCA, rather than NMS, because it is a direct gradient analysis technique that provides information specifically pertaining to community structure that was related to the habitat parameters investigated, rather than overall community structure (McCune & Grace, 2002). Separate analyses were run for each year to examine temporal changes in relationships between habitat and community composition. Within these analyses, we included habitat variables known to be influenced by wildfire (SILT, COVER and nLWD) and variables that are considered to be characteristic of geomorphology differences between streams (WDR and LGR). In this way, we could compare the relative influence of fire-associated habitat variables and geomorphologic habitat variables in influencing community structure. CCA ordinations of genera in environmental space were performed using Linear Constraints scores and biplot (centred with unit variance) axis scaling. Monte Carlo tests were not performed on these ordinations because we were interested only in the relative importance of variables each year and because sample sizes were small (n = 13 streams) relative to the number of habitat variables examined (six variables) in CCA.

We performed an Indicator Species Analysis for each year to determine which macroinvertebrate taxa were significantly associated with unburned catchments or catchments with >7% HIGHSEV in a particular year of sampling. This analysis combines information on relative abundance and relative frequency of taxa occurrence within samples belonging to a predefined group (unburned or >7% HIGHSEV). Indicator values calculated for each genus range from 0 (no indication) to 100 (perfect indication of a particular group). The significance of this indication was examined using Monte Carlo tests with 4999 permutations (McCune & Grace, 2002). We then related these taxa to functional groups (from Merritt & Cummins, 1996) and sediment tolerances (from Relyea, Minshall & Danehy, 2000) to address mechanisms that could explain community changes observed in the postfire environment. The <7% HIGHSEV group was excluded from the analyses because community composition in these catchments is likely to be intermediate between the unburned and >7% HIGHSEV group, resulting in genera that are indicative of neither group alone.

Results

Riparian burn severity and extent

The catchments in the Big Creek drainage burned in a patchwork of high and low severity, while many areas were left unburned (Table 1; Fig. 1). High severity fire (HIGHSEV) burned between 0.10% and 23.1% and low severity fire (LOWSEV) burned between 4.2% and 52% of the riparian forest in each catchment. HIGHSEV was strongly correlated with the total percentage of each catchment that burned ($F = 42.3$, d.f. = 3, $r^2 = 0.96$, $P = 0.022$; Fig. 2). Within burned catchments, streams of various sizes (wetted width) spanned the range of burn severity and extent (Table 1). Thus any fire or peak streamflow effects observed should not be confounded by influences of stream or catchment size.

Benthic and riparian habitat

Annual peak flow There was a strong correlation between PEAKFLOW in the burned and unburned drainages from 2001 to 2004 ($F = 1006.17$, d.f. = 3, $r^2 = 0.998$, $P = 0.001$). The average PEAKFLOW over 40 years (with 36 years of record) was 97.1 $m^3 s^{-1}$ at the gage on the South Fork (Fig. 3). Peak flows outside (above and below) the first standard deviation occurred every 3.6 years. Ninety-one percent and 80.6% of years of record had greater peak discharge than was observed in the low-flow years of 2001 and 2004 (48.9 and 60.3 $m^3 s^{-1}$ respectively). Peak discharge in 2002 (85.2 $m^3 s^{-1}$) was similar to the long-term average peak annual flow (Fig. 3). Only six of 36 years (16.7%) of records at this gage had higher maximum discharge than the 146.7 $m^3 s^{-1}$ peak discharge in 2003, which was the highest recorded since the El Nino-influenced peak flows of 1997.

Sediment The yearly (2001–2004) average V* within each catchment was not related to either HIGHSEV or to LOWSEV (Table 2). In burned catchments, PEAKFLOW had a significant negative relationship with V*, whereas in unburned catchments, PEAKFLOW had no relationship to V* (Table 2). V* was unrelated to TIME in burned and in unburned catchments (Table 2).

The percentage of each catchment's riparian forest that had burned at high severity (HIGHSEV) was associated with significantly greater annual variation in mobile sediment (Fig. 4a), rather than perennially high sediment levels (Table 2). On a yearly basis (2001–2004), correlations between V* and HIGHSEV for each of 4 years revealed both positive and negative coefficients. When these yearly correlation coefficients (r) for the relationship between V* and HIGHSEV were plotted against PEAKFLOW (Fig. 4b), we found a significant negative correlation ($F = 51.3$, d.f. = 3, $r^2 = 0.96$, $P = 0.019$). This statistical interaction indicates that as yearly peak flow increased, sediment loads within catchments with high riparian burn severities decreased, whereas sediment loads in

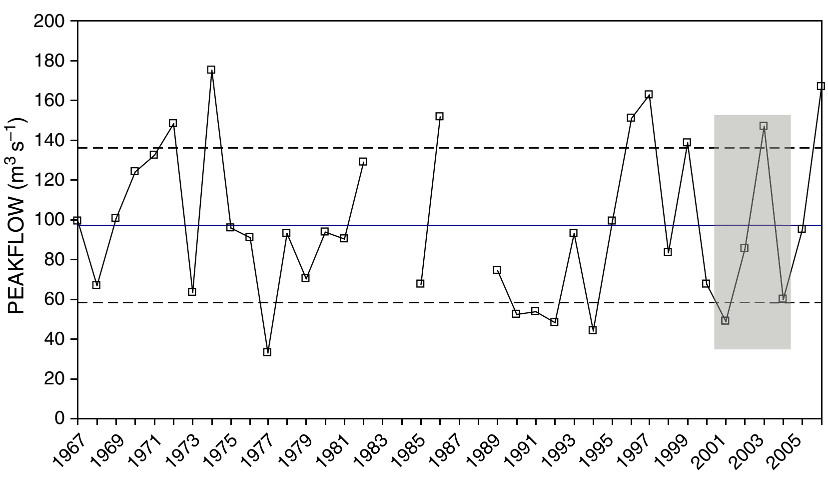

Fig. 3 Annual peak flow near reference streams on the South Fork of the Salmon River and the mean peak flow (solid line) ± 1 SD (dashed lines) of all recorded years (data were not available for 4 years). Shaded area represents study period (2001–2004).

Table 2 Correlation coefficients between instream habitat, fire, number of years postfire and annual peak flow variables for burned and unburned catchments

	Sediment (V*)		Organic debris (ORGANIC)		Large woody debris (LWD)		Undercut bank (UNDERCUT)	
	Ave. V*[1]	Ave. annual ΔV*[2]	Ave. ORGANIC[1]	Ave. annual Δ ORGANIC[2]	Ave. LWD[1]	Ave. annual Δ LWD[2]	Ave. UNDERCUT[1]	Ave. annual Δ UNDERCUT[2]
Burned								
HIGHSEV	+0.40	+0.84**	+0.47	+0.89***	+0.79**	+0.10	−0.17	+0.37
LOWSEV	+0.24	+0.10	+0.17	+0.44	+0.26	+0.81**	−0.13	+0.82**
PEAKFLOW	−0.95**	NA	−0.91**	NA	−0.89*	NA	−0.93*	NA
TIME	−0.53	NA	−0.10	NA	−0.44	NA	+0.10	NA
Unburned								
PEAKFLOW	−0.37	NA	−0.57	NA	−0.45	NA	+0.20	NA
TIME	−0.17	NA	+0.28	NA	+0.51	NA	+0.26	NA
Fire/flow interaction	As peak flow increases, V* decreases in burned catchments, but not in unburned catchments		As peak flow increases, ORGANIC decreases in burned catchments, but not in unburned catchments		As peak flow increases, LWD decreases in burned catchments, but not in unburned catchments		As peak flow increases, UNDERCUT decreases in burned catchments, but not in unburned catchments	

[1]For relationships between HIGHSEV or LOWSEV and stream habitat, each habitat variable was averaged across 4 years of record for each stream, resulting in regressions with $n = 7$ streams for burned catchments and regressions with $n = 7$ streams for unburned catchments. For relationships between PEAKFLOW or TIME and stream habitat, each habitat variable was averaged across seven burned catchments and seven unburned catchments, separately, for each year of record, resulting in regressions with $n = 4$ years for burned catchments and regressions with $n = 4$ years for unburned catchments.

[2]Habitat variable change between successive years (2001–2004) was averaged for each stream, resulting in regressions with $n = 7$ burned catchments.

*$P < 0.1$, **$P < 0.05$, ***$P < 0.01$

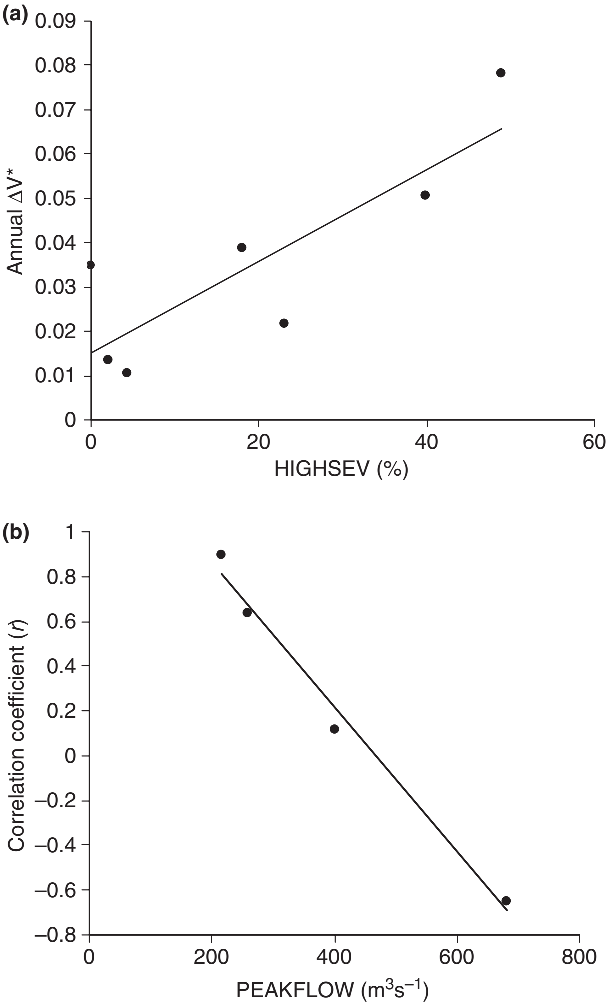

Fig. 4 (a) Average annual change in mobile sediment load (V*, a unitless metric) from 2001 to 2004 in Big Creek streams and percentage of each catchment's riparian forest that burned at high severity in 2000. Each point represents 4 years of sediment data from one catchment. (b) The annual (2001–2004) correlation coefficient for the relationship between mobile sediment load (V*) and percentage of each catchment's riparian forest burned at high severity in 2000, and annual maximum streamflow. Each point represents 1 year.

catchments with lower riparian burn severities were less affected by yearly peak flow. Correlation coefficients were unrelated to TIME ($F = 0.15$, d.f. = 3, $r^2 = 0.07$, $P = 0.74$).

Organic debris The yearly average ORGANIC, across all burned catchments, was not related to either HIGHSEV or to LOWSEV (Table 2). In burned catchments, PEAKFLOW had a significant negative relationship with ORGANIC, whereas in unburned catchments, PEAKFLOW had no relationship to ORGANIC (Table 2). ORGANIC was unrelated to TIME in burned and in unburned catchments (Table2).

Streams with greater HIGHSEV exhibited significantly greater annual variation in organic debris content ($F = 19.31$, d.f. = 6, $r^2 = 0.79$, $P = 0.007$), rather than consistently elevated or depressed debris levels (Table 2). When the yearly correlation coefficients (r) for the relationship between ORGANIC and HIGHSEV were plotted against PEAKFLOW, we found a negative correlation ($F = 69.67$, d.f. = 3, $r^2 = 0.97$, $P = 0.014$). This interaction indicates that as yearly peak flow increased, organic debris coverage within catchments having high riparian burn severities decreased, whereas organic debris in catchments with lower riparian burn severities were less affected by yearly peak flow. Correlation coefficients were unrelated to TIME ($F = 0.44$, d.f. = 3, $r^2 = 0.17$, $P = 0.57$).

Large woody debris Across all 4 years, LWD was higher in streams with increasing HIGHSEV ($F = 8.35$, d.f. = 6, $r^2 = 0.63$, $P = 0.034$), but not LOWSEV (Table 2). LWD was influenced by an interaction between fire and flow, as the yearly average LWD coverage across all burned catchments was negatively related to PEAKFLOW and LWD in unburned catchments was unrelated to PEAKFLOW (Table 2). LWD was not significantly related to TIME in burned or in unburned catchments (Table 2). Streams with more low severity fire in riparian forests (LOWSEV) experienced greater year-to-year changes in LWD ($F = 9.07$, d.f. = 6, $r^2 = 0.65$, $P = 0.029$; Table 2).

Bank morphology The yearly average UNDERCUT across all burned catchments was not related to either HIGHSEV or LOWSEV (Table 2). Instead, UNDERCUT depended on an interaction between fire and PEAKFLOW, as UNDERCUT decreased with PEAKFLOW in burned catchments but not in unburned catchments. In burned and in unburned catchments, UNDERCUT was not significantly related to TIME (Table 2). Streams with greater LOWSEV exhibited greater annual variation in the amount of bank undercutting ($F = 10.27$, d.f. = 6, $r^2 = 0.67$, $P = 0.024$; Table 2).

Macroinvertebrate communities

Despite inter-annual variations in PEAKFLOW, genera that were in unburned catchments had more stable densities across all 3 years than streams in

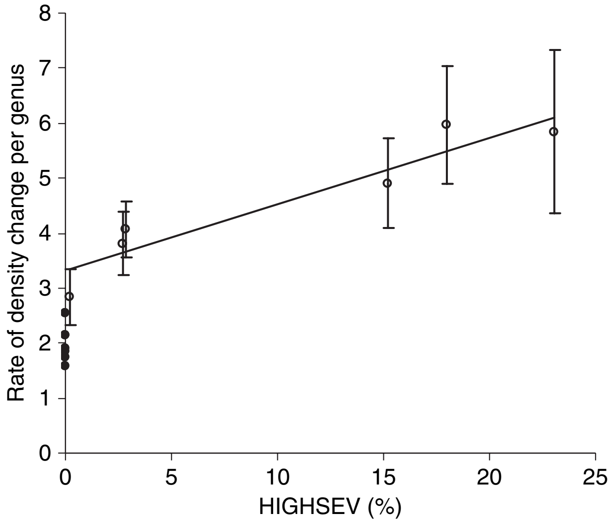

Fig. 5 The average rate of annual change in the density of each genus present in burned catchments (open circles) and in unburned catchments (filled circles) from 2002 to 2004 and the percentage of each catchment's riparian forest burned at high severity in 2000. Each point represents the number of individuals by which each genus' density fluctuates on average over 3 years for a given catchment. Error bars show the range of variability (±1 SE) in the rate of change in the density of genera in burned catchments. Error bars for unburned catchments are omitted for clarity, but range between 1.3 and 3.05 on the *y*-axis.

burned catchments (Fig. 5). Within burned catchments, the average rate of genus density change increased with HIGHSEV ($F = 34.14$, d.f. = 5, $r^2 = 0.89$, $P = 0.004$). On average, the density of each genus changed by 5.8 individuals per 0.10 m^2 $year^{-1}$ in the most severely burned catchment, but only by 2.8 individuals per 0.10 m^2 $year^{-1}$ in the least severely burned catchment. In unburned catchments, the density of each genus changed at an average rate of 1.6 (Deadman Creek) to 2.6 (Fitsum Creek) individuals per 0.10 m^2 $year^{-1}$, which was significantly lower than the burned catchment mean ($F = 29.22$, d.f. = 12, $r^2 = 0.73$, $P = 0.0002$).

Non-metric multidimensional scaling ordination of samples from each year in both drainages resulted in a three axis solution (stress = 12.43, $P = 0.0196$) representing 82.8% of the variance in the original data. This solution resulted in a final instability of 0.00001 and was reached after 75 iterations. The ordination biplot (Fig. 6) shows that samples clustered by BURNCLASS and that there was a correlation ($r^2 = 0.30$) between HIGHSEV and axis 2, which represented 28% of the variance in the original data. TIME did not correlate with any axis ($r^2 < 0.06$ with each axis).

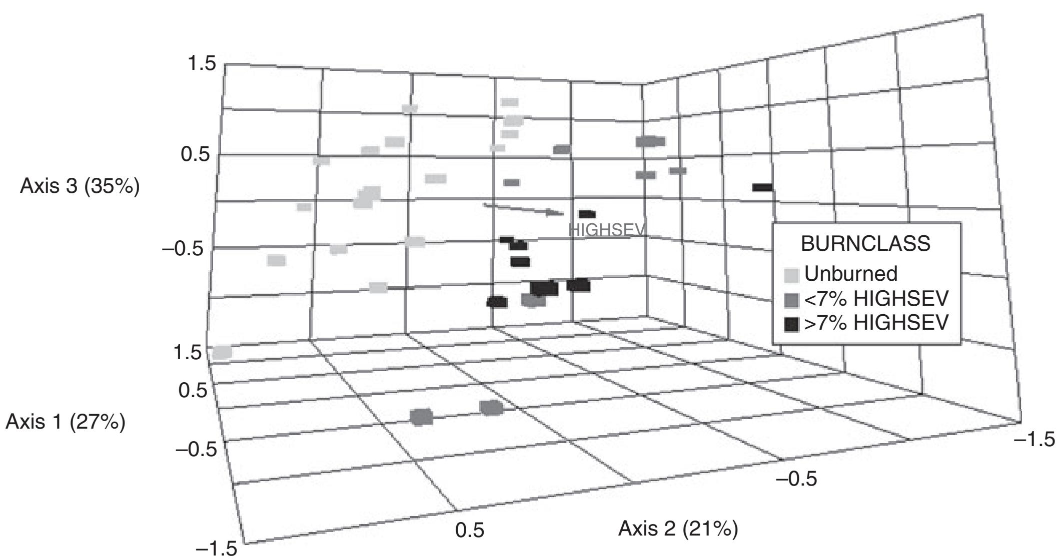

Fig. 6 Non-metric multidimensional scaling ordination biplot of macroinvertebrate samples from each stream and year plotted in three dimensional genera space. Samples plotted nearer each other are more similar based on community composition. The percentage of variance represented by each axis is included in parentheses. High burn severity is positively related to axis 2 ($r^2 = 0.30$) and TIME was not related to any axis ($r^2 < 0.06$ for all three axes).

Macroinvertebrates and habitat For 2002 data, the first two CCA axes accounted for 35.2% of the variance in the community matrix and all four canonical axes accounted for 50.5% of the variance. HIGHSEV, SILT, COVER and nLWD were the most important habitat variables influencing macroinvertebrate community composition, as they had the strongest correlations with the ordination axes (Table 3). The habitat variables WDR and LGR had a weaker relationship with these axes. There was a positive association between HIGHSEV, nLWD and SILT and a negative relationship between HIGHSEV and COVER. In 2002, an average PEAKFLOW year, catchments having a greater percentage of the riparian forest burned at high severity tended to have more silt and LWD and less vegetative stream cover.

In 2003, a year with exceptionally high peak streamflows and low sediment levels, axes one and two in the CCA ordination explained 35.9% of the variance in the species data matrix and all axes accounted for 48.7% of the variance. The first two axes were more strongly related to WDR and LGR than in the previous year, indicating that these variables became more important in influencing macroinvertebrate community composition, while nLWD, COVER and SILT became less important (Table 3). HIGHSEV, which maintained explanatory power in 2003, was negatively related to SILT and nLWD.

In 2004, a low-flow year with higher observed sediment loads in burned catchments, SILT and nLWD were again important variables in determining macroinvertebrate community composition. The first two axes accounted for 36.9% of the variability in the community matrix and all four axes accounted for 56.5% of the variance. As in 2002, the variables WDR and LGR were relatively unimportant.

Indicator Species Analysis identified 17 taxa with significant indicator values for at least one BURNCLASS in at least 1 year (Table 4). One taxon, the mayfly *Drunella*, was characteristic of streams with >7% HIGHSEV in all years. Six genera (*Acentrella*, *Serratella*, *Doroneuria*, *Skwala*, *Apatania* and *Rhyacophila*) were positively associated with these streams in all 3 years, although not significantly. *Epeorus* was the only genus significantly associated with unburned catchments. The mayflies *Ameletus* and *Rithrogena* were associated with these catchments in two of 3 years, though not significantly. In general, taxa that are collecting gatherers, scrapers and are more tolerant of fine sediment (Table 4, Relyea *et al.*, 2000) were characteristic of streams in extensively burned catchments in 2002 and 2004, while scrapers, predators and taxa with lower sediment tolerances were associated with unburned catchments in all years.

Discussion

Postfire macroinvertebrate community variability is thought to be caused by reduced stability of postfire instream habitat (O'Neill, Johnson & King, 1989; Minshall, 2003). Our analysis of the 2000 Diamond Peak Fire Complex found reduced inter-annual stability of both habitat and macroinvertebrate communities. The results of this study suggest that streams within more extensively burned riparian forests exhibit greater annual variation in mobile sediment loads, LWD, organic debris and undercut bank morphology, rather than perennially elevated or depressed levels of these variables. This important finding is further addressed in the examination of our two hypotheses.

Table 3 Interset correlation coefficients for each habitat variable in each of three separate canonical correspondence analyses

	2002		2003		2004	
Variable	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
HIGHSEV	−0.33	−0.69	0.69	−0.19	0.25	0.13
SILT	−0.03	−0.76	−0.29	−0.05	−0.06	0.80
COVER	0.09	0.61	−0.30	0.25	0.16	0.02
nLWD	−0.13	−0.61	−0.03	−0.05	−0.03	0.75
WDR	0.19	0.37	−0.65	−0.62	−0.11	−0.08
LGR	−0.48	0.34	−0.17	−0.53	−0.05	0.04

HIGHSEV, percentage of riparian forest burned at high severity; COVER, percentage riparian canopy cover; nLWD, number of pieces of large woody debris; WDR, width to depth ratio; LGR, low gradient riffle.

Table 4 Indicator values (percentage of a perfect indication) for macroinvertebrate taxa in samples grouped by BURNCLASS and year

			2002		2003		2004	
Taxon	Functional group*	Sediment tolerance†	Unburned	>7% HIGHSEV	Unburned	>7% HIGHSEV	Unburned	>7% HIGHSEV
Acentrella	CG	MI	1	63‡	0	33	1	46
Ameletus	Sc, CG (detritus)	MT	6	88‡	56	23	76	6
Drunella	Sc, P	MI	20	80‡	7	91‡	15	85‡
Epeorus	CG, Sc	MI	89‡	7	19	78	10	89
Rithrogena	CG, Sc	MI	51	33	8	81‡	67	23
Serratella	CG (detritus)	MT	0	65‡	3	27	0	98‡
Doroneuria	P (likely)	MI	10	53	0	66‡	11	83
Skwala	P	MT	8	88‡	7	83‡	20	30
Heterlimnius	CG	MT	6	94‡	57	43	21	77
Chironomidae	CG(detritus), Sc	T	22	78‡	75	25	23	77
Glutops	P, Sh	MT	3	62	17	13	0	100‡
Simulium	CF	T	61	3	8	27	1	98‡
Apatania	Sc, CG	MI	0	67‡	0	33	0	50
Arctopsyche	CF, P	I	40	35	5	87‡	14	81
Neophylax	Sc	MI	47	20	7	51	5	92‡
Rhyacophila	P, Sc, CG, Sh	MT	48	52	28	72‡	36	64

HIGHSEV, percentage of riparian forest burned at high severity.

*Functional groups based on Merritt & Cummins, 1996. Sh, Shredder; CF, collector–filterer; CG, collector–gatherer; Sc, scraper; P, predator.

†Sediment tolerance based on Relyea *et al*., 2000. I, intolerant; MI, moderately intolerant; MT, moderately tolerant; T, tolerant of fine sediment.

‡Indicator values significant ($P < 0.05$) based on Monte Carlo test of significance (4999 permutations).

In accordance with our first hypothesis (that fire and flow interact to influence streams), stream habitat parameters were found to vary inversely with annual peak streamflow in burned catchments but not in unburned catchments. Moreover, within burned catchments, as burn severity and extent increased, there was an increasing influence of peak streamflow on sediment and organic debris. These findings demonstrate that when disturbances interact, results can be somewhat non-intuitive and complex (Paine, Tegner & Johnson, 1998; Bailey & Whitman, 2002). We speculate that while high overland flows may have brought materials into the streams as expected, an intense peak in discharge in more severely burned catchments probably flushed out sediment, organic debris, LWD and any bank undercutting that had occurred from other hydraulic events. Our analysis shows that interactions between riparian burn severity and peak flow can influence annual changes in stream habitat conditions, whereas alone these explanatory variables were poor predictors of habitat conditions within any given year.

Also supporting our first hypothesis, we found that increased riparian burn severity corresponded to decreased inter-annual stability of genera densities (Fig. 5). This may be explained either by the differences in catchment burn properties directly or indirectly by increased annual changes in habitat of more severely burned catchments. Evidence supports the second alternative because communities in unburned catchments were relatively stable despite annual variations in peak streamflow (Fig. 5), communities in burned catchments were influenced by different habitat variables in different years (Table 3), and because Robinson, Minshall & Royer (2000) found considerable inter-annual habitat and macroinvertebrate community stability in neighbouring Big Creek streams before the 2000 wildfire.

Our analyses also supported our second hypothesis that changes in habitat and community structure depend more on fire and flow interactions than time since fire. In the burned catchments, habitat parameters were related to burn severity and peak streamflow, but not time since fire. These findings suggest that no significant temporal trend (either towards prefire condition or towards a stable postfire state) occurred during the study period. There was no temporal trend in habitat conditions of unburned catchments during the same time interval. Macroinvertebrate communities in burned catchments did not exhibit increased similarity to communities in unburned over time, as samples analysed with NMS clustered according to burn severity rather than year of sampling postfire (Fig. 6). Also, within 4 years postfire, genera in more severely burned catchments exhibited greater year-to-year fluctuations in density. Based on our CCA, the annual variability in macroinvertebrates can be attributed predominantly to the changing influence of sediment, LWD, riparian cover and organic debris, as quantities of these habitat components fluctuated annually depending on burn severity and stochastic patterns of precipitation and runoff. Richards & Minshall (1992) also showed that communities within burned catchments did not exhibit a recovery trend (increasing similarity to unburned reference streams with time) within the first several years of wildfire disturbance. Our findings suggest a potential mechanism explaining the lack of a recovery trend in the first few years following wildfire disturbance.

Further insight into mechanisms explaining postfire community dynamics is provided by our Indicator Species Analysis, which showed inter-annual changes in the genera associations with a particular burn class. These changes in burn class affinity appear to be related to sediment tolerance and functional group affiliation. In years where more sediment and organic debris were present in severely burned catchments (2002 and 2004), taxa associated with these streams tended to belong to groups classified as moderately tolerant, or tolerant of fine sediment. These taxa also tended to belong to collector–gatherer or predator functional groups. In 2003, when less sediment and organic debris were present in severely burned catchments, taxa associated with these streams tended to be moderately intolerant, or intolerant of fine sediment and tended to belong to scraper or predator functional groups (Merritt & Cummins, 1996; Relyea *et al*., 2000). These findings, together with those of our CCA, suggest food sources and substrate conditions as mechanisms driving higher inter-annual changes in macroinvertebrate community composition in burned catchments relative to unburned catchments.

Previous studies have related fire-associated changes in stream habitat and biota to fire extent and time since fire (Albin, 1979; Roby & Azuma, 1995; Minshall, Robinson & Lawrence, 1997; Minshall *et al*., 2001a,b; Minshall, Royer and Robinson, 2001c). Of the studies that have related wildfire and postfire streamflow to benthic communities (Rinne, 1996; Minshall *et al*., 1997; Minshall *et al*., 2001c; Vieira *et al*., 2004), none have examined the interaction of burn severity extent (as a continuum of disturbance severity) and hydrological disturbance. Here, we found that a gradient of fire disturbance severity correlated to a gradient of postfire responses in both habitat and biota. Even low severity fire in a catchment generated a response. This result is inconsistent with the supposition that fire effects on macroinvertebrates are evident beyond a threshold of catchment burn extent (Minshall, 2003), at least within these catchments.

The interaction between fire, flow and habitat conditions may drive the increased annual variations in macroinvertebrate communities observed in this study and could potentially explain the variations of up to 15 years postfire reported in other studies (Roby & Azuma, 1995; Minshall *et al*., 2001b,c). In dry ponderosa pine forests of the Pacific Northwest, historic fire return intervals as low as 10 years have been found in both upland and riparian habitat (Agee, 1993; Everett *et al*., 2003; Olson & Agee, 2005). Given that a catchment in the South Fork of the Salmon drainage was found to have a 'conservative' mean fire interval of 7 years with high continuity between upland and riparian burning (Barrett, 2000) and that high or low peak flows occur approximately every 4 years, it remains plausible that the postfire habitat variability observed here could persist until a subsequent wildfire reinitiates the fire and flow interaction. Although our study spans only 4 years, portions of several of our burned catchments reburned in 2005, 2006, 2007 and 2008 and other postfire studies have found increased community variability for 10–15 years (Roby & Azuma, 1995; Minshall *et al*., 2001b). Repetitions of this disturbance cycle could maintain the stream communities across a landscape, if not each stream's community, in a state of dynamic equilibrium (Resh *et al*., 1988; Townsend, 1989; Miller, Luce & Benda, 2003). Our findings have context within two important temporal scales: (1) the annual scale of variability in habitat conditions and dynamic equilibrium of fauna and (2) the sub-decade to decadal scale of fire return intervals in western ponderosa pine forests.

In conclusion, we suggest that when fire interacts with flow disturbances, the return to prefire conditions or to inter-annual habitat and community stability may be delayed, resulting in a community in dynamic equilibrium. If the duration of the fire-flow interaction is longer than the ecosystem's fire return interval, the system might not return to 'prefire' conditions. This amounts to an important, persistent role for fire in upland and riparian forests in structuring aquatic macroinvertebrate community composition.

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