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APPLIED ISSUES

Effects of forest fire on headwater stream macroinvertebrate communities in eastern Washington, U.S.A.

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SUMMARY

1. Recent increases in fire frequency in North America have focused interest on potential effects on adjacent ecosystems, including streams. Headwaters could be particularly affected because of their high connectivity to riparian and downstream aquatic ecosystems through aquatic invertebrate drift and emergence.
2. Headwater streams from replicated burned and control catchments were sampled in 2 years following an intense forest fire in northeastern Washington (U.S.A.). We compared differences in benthic, drift and emergent macroinvertebrate density, biomass and community composition between five burned and five unburned catchments (14–135 ha).
3. There were significantly higher macroinvertebrate densities in burned than control sites for all sample types. Macroinvertebrate biomass was greater at burned sites only from emergence samples; in benthic and drift samples there was no significant difference between burn and control sites.
4. For all sample types, diversity was lower in the burned catchments, and the macroinvertebrate community was dominated by chironomid midges.
5. Compared to the effects of fire in less disturbed ecosystems, this study illustrated that forest fire in a managed forest may have greater effects on headwater macroinvertebrate communities, influencing prey flow to adjacent terrestrial and downstream aquatic habitats for at least the first 2 years post-fire.

Keywords: forest management, headwater stream, macroinvertebrate, prey subsidy, wildfire

Introduction

Fire is a natural disturbance process that can often shape ecosystems and influence habitat diversity and productivity, especially in the western U.S. (Bisson *et al.*, 2003; Minshall, 2003). Though aquatic ecosystems have mechanisms of resistance or resilience to recover from natural disturbances such as fire, where there has been a history of anthropogenic disturbance fire may have a greater effect (Bisson *et al.*, 2003; Minshall, 2003; Beschta *et al.*, 2004). Like other disturbances, fire has the potential to affect a stream's network, exacerbated by the high connectivity between terrestrial and aquatic habitats. While we have a general understanding of how forest fire affects benthic macroinvertebrate communities in relatively undisturbed ecosystems (Minshall, 2003), we have little knowledge of fire effects in managed forests, or how fire affects connections between headwater

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streams and downstream or adjacent terrestrial ecosystems.

Forest fire effects on aquatic communities vary greatly by location and severity (Minshall, 2003), but are greatest in small headwater streams, with measurable effects decreasing as stream size increases (Minshall, Brock & Varley, 1989). Fire has a stronger influence on headwater streams than on large rivers because a greater proportion of the adjacent catchment is likely to be burned (Minshall, Robinson & Lawrence, 1997), and the ratio between stream margin and water volume is high. As catchment area increases, there will be a higher percent of unburned forest, and the riparian area is more likely to retain its function (Bisson *et al.*, 2003; Dwire & Kauffman, 2003; Minshall, 2003), providing the stream with shade, bank stability, habitat structure and nutrients. The high level of connectivity between forest and aquatic systems is apparent in the foodweb of these headwater streams. Fishless headwater streams provide both detritus and macroinvertebrates via drift to downstream, fish-bearing systems (Wipfli & Gregovich, 2002). Emerging aquatic insects can be an important source of food to riparian area wildlife (e.g. birds, bats, amphibians and other insects) as well as fish (Jackson & Fisher, 1986; Power, 2001; Sabo & Power, 2002; Baxter, Fausch & Saunders, 2005). Macroinvertebrate contribution to drift varies by species and may increase in response to stresses such as predation, lack of food or habitat, high sediment loads or high temperature (Collier & Quinn, 2003; Wipfli & Musslewhite, 2004). The transfer of food and energy as macroinvertebrates drift and emerge into new habitats can subsidise the foodwebs of adjacent systems (Baxter *et al.*, 2005). With changes in vegetation cover, sediment and water temperature following fire, there is likely to be a change in this connectivity between aquatic and terrestrial systems and between headwater and downstream reaches.

Loss of vegetation cover from fire or other disturbance can have a profound effect on aquatic resources (Piccolo & Wipfli, 2002; Dwire & Kauffman, 2003). Typically headwater streams in temperate climates are heterotrophic (Vannote *et al.*, 1980). Following fire, streams are hypothesized to become autotrophic as increased sunlight increases primary production (Minshall *et al.*, 1989). This shift from heterotrophy to autotrophy will likely cause a shift in dominant aquatic macroinvertebrate functional feeding groups, from shredders that typically dominate headwater streams to filter feeders or collector-gatherers (Minshall *et al.*, 1989). Additionally, there may be a shift from specialist to generalist feeders (Mihuc & Minshall, 1995). Increased algal production may result in a trophic cascade of more grazing aquatic macroinvertebrates, resulting in greater food availability to predators (Hawkins, Murphy & Anderson, 1982). However, loss of allochthonous inputs could result in a decrease of detritivorous macroinvertebrates, resulting in a decrease in the food available to predators. Biogechemical changes, sediment loading, high temperatures, channel scouring or other post-fire disturbance could also greatly influence recovery time for macroinvertebrate communities (Bayley *et al.*, 1992; Minshall, 2003).

Effects of fire on aquatic ecosystems in the Rocky Mountain region have been studied in areas with minimal human influence. Following the Yellowstone fires of 1988 there was little change in macroinvertebrate density or biomass (Minshall *et al.*, 1997), but there were shifts in functional feeding groups and an increase in Chironomidae and *Baetis* (Baetidae). In the Frank Church Wilderness of Idaho (Minshall *et al.*, 2001a) macroinvertebrate biomass increased 10 years post-fire with no change in density. Given these studies, effects of fire on streams could be greater in areas with more human activities such as logging, road building and grazing (Minshall, 2003). For example, immediately following fire in a managed forest in Arizona, macroinvertebrate densities sharply declined and remained reduced 3 years post-fire (Rinne, 1996).

The majority of stream studies examining the effects of fire have focused on benthic macroinvertebrate communities, with little work on macroinvertebrate drift or emergence following fire. By considering the latter, we can examine how fire influences movement of energy downstream and exchanges between freshwater and terrestrial systems. We expected fire effects as measured by movement of aquatic macroinvertebrates from headwater streams to adjacent systems to differ from effects shown by benthic communities in other studies.

The objectives of this study were to determine how benthic macroinvertebrate communities, macroinvertebrate drift and emergence from headwater streams changed 1 and 2 years following an intense forest fire. This was accomplished by comparing

macroinvertebrate density, biomass, community structure and composition between streams in catchments with and without recent fires. The patchy and unpredictable nature of wildfires makes a study design with catchment replication difficult. The timing and spatial extent of the Togo fire, which burned 2000 ha of managed forests in Washington in 2003, allowed us to select (post-fire) five replicate burned and five replicate control (unburned) catchments of similar size and logging history, which provided reasonable statistical power to test hypotheses.

Methods

Site description

This study took place in the Kettle Mountain Range of the Colville National Forest in northeastern Washington, U.S.A. (Fig. 1). The forest receives both maritime and continental weather systems; the east side of the Kettle Mountain Range receives 64–76 cm of precipitation annually and the west side 51–64 cm (Williams *et al.*, 1995). The Togo Fire was an intense lightning-ignited fire, which burned 2000 hectares in August–September 2003 through mixed conifer forest of western larch (*Larix occidentalis* Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], lodgepole pine (*Pinus contorta* Dougl.), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) and western red cedar (*Thuja plicata* Donn ex D. Don). This fire occurred in a managed forest that was historically and is currently used for logging, grazing and recreation interests.

Extensive exploration of the landscape was conducted by pre-visit mapping, consultation with forest managers and several scouting trips the spring after the fire. Although we were unable to eliminate potential confounding factors between burned and control sites that were present pre-fire, care was taken for choosing unburned and burned sites comparable in catchment drainage, slope, aspect and discharge (Table 1). Study sites were chosen in ten small first and second order fishless headwater streams ranging 1000 to 1500 m a.s.l. in altitude (Fig. 1). The number of sites was constrained by the availability and the practicality of enumerating diverse kinds of macroinvertebrate samples. Sampling occurred in the summers of 2004 and 2005 and began 1–2 weeks after snowmelt, mid-June in 2004 and late May in 2005.

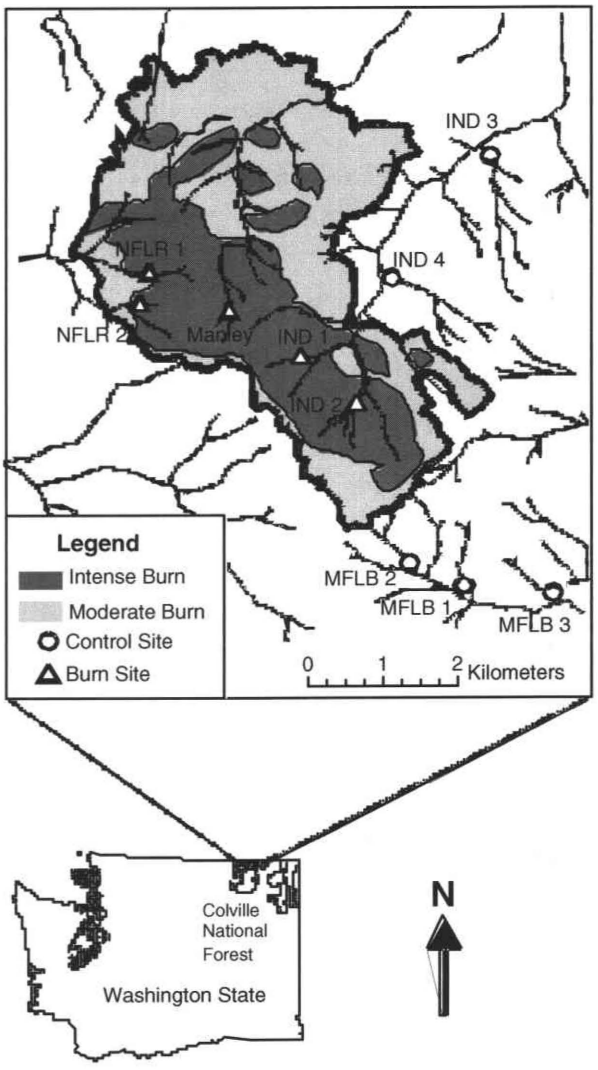

Fig. 1 Location of the Togo Fire within the Colville National Forest, Washington. Fire boundary, area of intense burn and location of study sites in the Togo Fire area. IND (Independent Creek), NFLR (North Fork Lone Ranch Creek), MFLB (Middle Fork Little Boulder Creek), Manley (Manley Creek).

Study sites were located in tributaries of four streams; Independent (IND), Manley, Middle Fork Little Boulder (MFLB) and North Fork Lone Ranch (NFLR) Creeks. Burned sites were located within two tributaries of North Fork Lone Ranch, two tributaries of Independent and one tributary of Manley; these subcatchments ranged in size between 0.14 and 0.87 km^2 and were entirely within the severe burn area (Fig. 1, Table 1). In this severe burn area, both canopy vegetation and understory plants and shrubs were completely burned to the stream. Control sites

Table 1 Average (± 1 standard deviation) catchment and site characteristics for burn and control sites

Type	Altitude (m a.sl.)	Catchment area (km^2)	Slope (%)	Year	Discharge (L/s)	Mean temperature (°C)	Maximum temperature (°C)	Algae: chlorophyll *a* ($mg\ m^{-2}$)	Algae: AFDM ($mg\ m^{-2}$)	Canopy cover (%)
Burn	1370 (70)	0.39 (0.28)	11 (7)	2004	1.0 (0.5)	13.1 (0.3)	21.6 (3.3)	N/A	N/A	41 (9)
				2005	2.2 (0.6)	11.3 (0.9)	18.6 (2.8)	33.5 (18.5)	7780 (1140)	31 (4)
Control	1280 (170)	0.79 (0.46)	10 (2)	2004	0.8 (0.5)	11.2 (0.5)	15.3 (4.1)	N/A	N/A	83 (11)
				2005	4.2 (2.7)	9.9 (0.8)	13.7 (4.0)	57.1 (46.0)	7020 (1530)	80 (10)

*Discharge was measured during drift sampling events.

were located within three tributaries of Middle Fork Little Boulder Creek and two tributaries of Independent Creek; these subcatchments ranged in size between 0.40 and 1.35 km^2 and were entirely outside of the burned area (Fig. 1, Table 1). Fifty-metre reaches of each study stream were selected based on similarities among sites such as stream size, slope and aspect (Table 1). Sites that appeared to be perennial were selected; although one control site (MFLB 1) dried completely late in the summer of both years and one burned site (IND 2) dried in July 2004. The burned site was moved upstream to where flow was perennial. The control site was not sampled the months it was dry but data from other months were used. No metrics calculated from this intermittent site were significantly different from other perennial control sites sampled.

In the 1920s–30s there were a number of large stand-replacing fires in the Colville National Forest. In these previously burned areas, tree densities are very high with small diameter mixed conifers. Since 1995, management practices on the Colville National Forest have followed Inland Native Fish Strategy (INFISH) guidelines that require a minimum 45-m riparian buffer on perennial, fishless streams (Inland Native Fish Strategy Environmental Assessment, 1995). Salvage logging occurred following the fire in 2003 and 2004 through much of the burned area, and this minimum 45-m riparian buffer was maintained at salvage logging sites. All sites were located in either mature live or burned forest and were selected to have at least a minimum 45-m buffer.

Sampling

Stream gradient, canopy cover and temperature were measured for each 50-m study reach. Gradient was measured with a handheld clinometer throughout the study reach, and canopy cover was measured from the centre of the stream at 1 m above the stream with a densiometer at four evenly spaced locations in each stream reach once each year after leafout. TidBit® (Onset Computer Corp., Pocasset, MA, U.S.A.) temperature loggers (accuracy ± 0.2 °C, resolution 0.02 °C at 25 °C) were placed in streams in July 2004 and recorded temperature every hour through August 2005; only summer months were used in calculating mean and maximum temperatures. Due to the small size of these headwater streams, limited macroinvertebrate samples could be taken (i.e. more frequent sampling would have negatively impacted the macroinvertebrate community).

To measure macroinvertebrate transport to reaches further down the drainage, macroinvertebrate drift was sampled at the downstream-most point in each study reach. Drift was collected continuously for 48 h once per month during the summers of 2004 and 2005 following methods from Wipfli & Gregovich (2002). A 10-cm wide, thin-walled (1–2 mm thickness), PVC pipe approximately 1-m long was placed at the bottom of each reach with a 250-μm mesh net attached. Sandbags were placed in the stream to secure the pipes and to channel the bulk of streamflow through each pipe without otherwise affecting natural streamflow, and therefore macroinvertebrate drift (Wipfli & Gregovich, 2002). Pipes were placed on the stream bed and extended above the surface of the stream so macroinvertebrates drifting at any position in the water column were captured. When nets were set out and collected, discharge through each pipe was estimated by measuring the time required to fill a container of known volume. During high flows in May and June 2005, discharge at some sites exceeded pipe capacity. Because all ten sites could not be sampled concurrently, nets were placed at five sites 1 day and five the following day, then collected the following 2 days to

provide 1 day of overlap when nets were out at all sites. This minimized potential differences in drift due to short term changes in discharge.

Four randomly placed emergence traps were set in the stream once per month for 3 months of the summer for 48–72 h at each site. Traps were 0.6-m × 0.3-m × 0.5-m wooden A-frames that covered 0.2 m^2 of stream bottom. Fine mesh (*c.* 500 μm) netting covered the traps and was held to the stream bottom with rocks. Insects were collected in plastic containers with approximately 5 cm of water and a drop of soap to break surface tension, set 20 cm down from the top of the netting. After 48–72 h, all insects in the wells and flying inside the net were collected and preserved in 85% ethanol. During strong summer thunderstorms in August 2004, high discharge disturbed traps at four of five burned sites and two of five control sites. This month was excluded from analysis of emergence samples.

A Surber sampler with 500-μm netting was used to collect benthic macroinvertebrates from five randomly selected locations in each reach. In 2004 a standard size sampler that collected from an area of 0.46 m^2 was used. Small stream size made it difficult to find a suitable location for this larger sampler, and in 2005, a smaller Surber sampler with an area of 0.12 m^2 was used resulting in less total area sampled in 2005. Samples were collected from riffles whenever possible, but in some locations it was only possible to sample pools or very slowly flowing water. Benthic samples were analysed from June and August of both years.

Algal samples were collected in each month of summer 2005 from six rocks randomly chosen from each site. Samples from an area of 0.09 cm^2 per rock were scrubbed, stored in the dark and frozen until analysis. Chlorophyll *a* was extracted from one half of each algal sample 3 weeks after collection using hot ethanol extraction as described in Sartory & Grobbelaar (1984). The other half of the sample was used to calculate algal dry mass (DM) and ash free dry mass (AFDM).

Sample processing

Replicate benthic and emergence samples were combined into one composite sample for each site, date and sample type. Due to the large volume of macroinvertebrates and detritus in drift and benthic samples, subsamples were taken with either a Caton Tray or a Folsom Plankton Splitter, then enumerated and identified to a minimum of 300 individuals for each composite sample (Caton, 1991; Carter & Resh, 2001). Aquatic macroinvertebrates were identified to family or genus level (Merritt & Cummins, 1996) and terrestrial macroinvertebrates to order under a dissecting microscope. Macroinvertebrates were measured to the nearest millimetre to determine biomass using length–weight regression equations (Meyer, 1989; Burgherr & Meyer, 1997; Sabo, Bastow & Power, 2002). Functional feeding groups were assigned according to Merritt & Cummins (1996).

Statistical analyses

Our study design provided a strong temporal signal (multiple samples for two sampling seasons) within the spatial constraints of five burned compared to five unburned sites. Compositing multiple samples produced an averaged assessment for each site per date that were used to detect seasonal trends. Analyses of variance (ANOVA R version 2.1.1; www.r-project.org) tested for differences in macroinvertebrate biomass, density, community composition and community structure metrics for sites grouped by type. Site type (burn or control), month (random factor), year and an interaction between year and site type were the main factors ($\alpha < 0.05$, $n = 38$ benthic, $n = 59$ drift, $n = 55$ emergence). The interaction term determined if burned sites were more similar to control in 2005 than 2004. When non-significant it was omitted, and analyses were rerun. Biomass and density measures were standardized by discharge and time or area sampled and log transformed to meet normality assumptions. Macroinvertebrate proportions were arcsine transformed prior to analysis. Measures of Shannon–Weiner diversity (Magurran, 2004), which were normally distributed, were untransformed.

Non-metric multidimensional scaling (NMS) on PC-ORD version 4 software (MjM Software, Glenden Beach, OR, U.S.A.) was used to look at differences in community composition by density at sites along environmental gradients. Taxa that were present at <5% of sites were grouped with the next higher level taxa (McCune & Grace, 2002). Macroinvertebrate abundance was standardized by discharge and time or area sampled and was square root transformed to normalize distributions. Bray-Curtis distance measures were used to calculate the distance matrix.

Stress, which is a measure of the distortion in the arrangement of sites and increases with fewer dimensions, was considered acceptable when less than 20. Number of dimensions were determined by choosing the number beyond which there was little decrease in stress (McCune & Grace, 2002). Linear correlations between taxa and axes were determined using Pearson's r values.

Results

Site characteristics

At burned sites the range of stream discharge was more narrow (from 4.3 to 8.3 $m^3\ h^{-1}$) than at control sites, where stream discharge was 2.8 to 15.2 $m^3\ h^{-1}$ (Table 1). Summer temperatures also were warmer on average (by 1.4 °C) and mean maximum temperatures were 5.3 °C warmer at burned sites. Though average canopy cover at burned sites, including overstory canopy, live or burned trees and understory vegetation, was half that of control sites (36% compared to 81%) (Table 1), there was no detectable difference in algal biomass or chlorophyll *a* between treatments ($P > 0.05$) (Table 1). Both algal ash-free dry mass (AFDM) and chlorophyll *a* were highly variable (Table 1); in particular, AFDM at burned site NFLR 1 (19 100 mg m^{-2}) was twofold higher than at any other site and chlorophyll *a* at control site MFLB 2 (134.0 mg m^{-2}) was twice as high as all other sites. Chlorophyll *a* increased during the summer at both burned and control sites ($P = 0.03$). There was no detectable difference in average canopy cover at burned sites from 2004 to 2005 ($P > 0.05$).

Macroinvertebrate patterns

We observed significantly higher macroinvertebrate drifting and benthic densities ($P < 0.05$) (Fig. 2a,b), but not biomass differences ($P > 0.05$) (Fig. 3a,b), in burned compared to control streams. Whereas total seasonal drifting export of macroinvertebrates was numerically greater from burned sites (averaging 85.6 individuals $stream^{-1}\ h^{-1}$ at burned sites and 26.4 individuals $stream^{-1}\ h^{-1}$ at control sites), total flux in biomass was similar (mean of 26.5 mg $stream^{-1}\ h^{-1}$ at burned sites and 30.0 mg $stream^{-1}\ h^{-1}$ at control sites). Benthic macroinvertebrate patterns, taken twice each summer, reflected the same patterns.

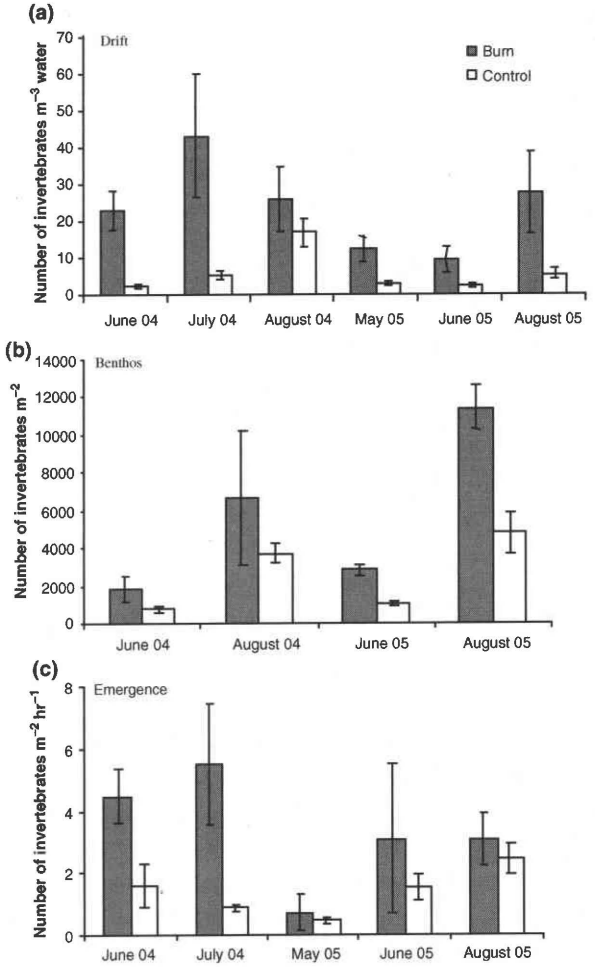

Fig. 2 Macroinvertebrate density in drift (a), benthic (b) and emergence (c) samples from burned (shaded bars) and control (open bars) sites. Each bar represents the mean with standard error of five replicate streams in each sampling period.

We did not detect difference between years for either drifting or benthic macroinvertebrates because higher abundances of benthic and drifting macroinvertebrates at burned sites persisted for both years (Fig. 2), and patterns in biomass revealed no seasonal or annual trends (Fig. 3).

Unlike drifting and benthic macroinvertebrates, emerging macroinvertebrates showed significant responses to the fire with detectable differences between years (Fig. 2c). Emergent densities were significantly higher in burned than control sites in 2004 ($P = 0.012$), but there was no difference in 2005 (Fig. 3c). For both years combined, biomass of adult emergence was significantly greater in burned than control sites ($P = 0.03$) (Fig. 3c). However, in compar-

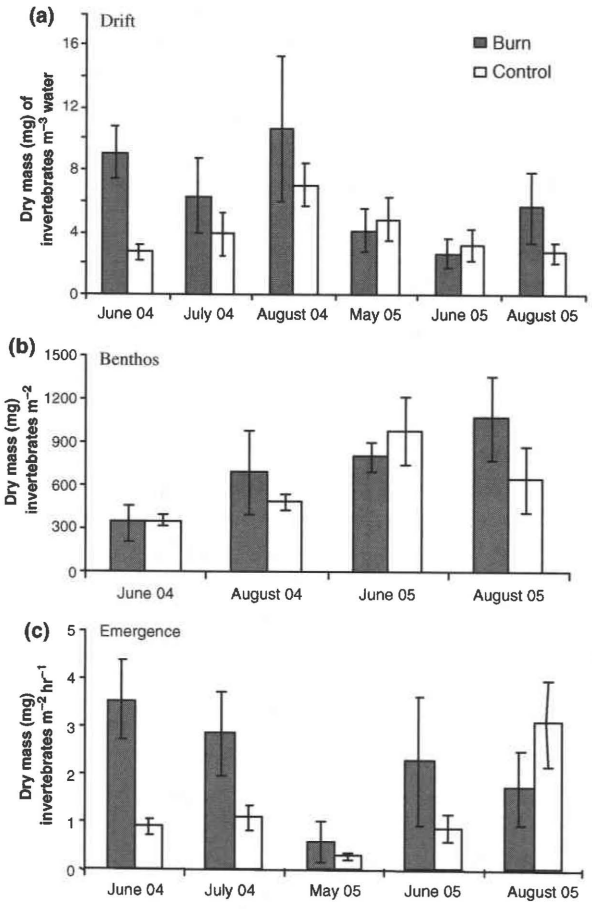

Fig. 3 Macroinvertebrate biomass in drift (a), benthic (b) and emergence (c) samples from burned (shaded bars) and control (open bars) sites. Each bar represents the mean with standard error of five replicate streams in each sampling period.

isons within each season, biomass emerging from burned sites in 2004 was much greater than from control sites. In 2005, there was little to no difference between sites resulting in a significant interaction between treatment and year ($P = 0.04$) (Fig. 3c).

Chironomidae dominated macroinvertebrate assemblages. They were significantly greater in burned sites, comprising 71% of abundance in drift and 56% in benthic samples over the study period; in control sites they comprised 21% drift, 29% benthic ($P = 0.001$ drift, $P = 0.008$ benthic) (Table 2). Though overall densities were much lower, proportions of Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa were lower in burned sites and reflected significant differences in benthic ($P = 0.031$) and noticeable but non-significant differences in drift ($P = 0.090$). EPT averaged 12% of drift in burned sites, 38% in control sites; and 26% of benthic samples in burned sites and 39% in control sites. Only in 2004 did we detect a significant difference between treatments in the composition of emergence ($P = 0.009$), associated with relatively higher proportions of Diptera and lower proportions of EPT taxa at burned sites (Table 2). The most likely signal for successional change was an increased proportion of emergent EPT taxa at burned sites in 2005 (1.2% 2004, 8.5% 2005) and increased 'other' taxa (primarily Collembola and other terrestrial insects) resulting in a non-significant difference in community composition between treatments in 2005. In combination with reduced proportion of chironomids at burned sites (Table 2), these changes in 2005 resulted in a significant interaction between site type and year sampled ($P = 0.003$). However, differences between burned and control sites in drift and benthic EPT composition persisted between years (Table 2).

Shannon–Weiner diversity, calculated using the lowest taxonomic level identified, was consistently

Table 2 Macroinvertebrate composition by percent in each order at burned and control sites in 2004 and 2005 for each sample type. 'Other' includes primarily: Coleoptera, Ostracoda, Copepoda, Oligochaeta, Gordioidea, Arachnid and Hymenoptera

		Community composition					
		Drift		Benthic		Emergence	
	Order	Burn	Control	Burn	Control	Burn	Control
2004	Diptera: non-Chironomid	3.1	2.4	8.1	6.5	17.0	6.9
	Diptera: Chironomid	74.2	21.7	57.1	29.0	73.8	15.8
	EPT	10.4	29.7	24.5	38.1	1.2	7.1
	Other	12.5	46.3	10.2	26.3	7.9	70.3
2005	Diptera: non-Chironomid	9.3	11.3	8.0	9.1	22.5	32.3
	Diptera: Chironomid	66.2	20.6	54.8	30.6	46.2	17.3
	EPT	13.0	46.6	28.1	39.1	6.4	8.5
	Other	11.6	21.6	9.1	20.8	24.9	42.0

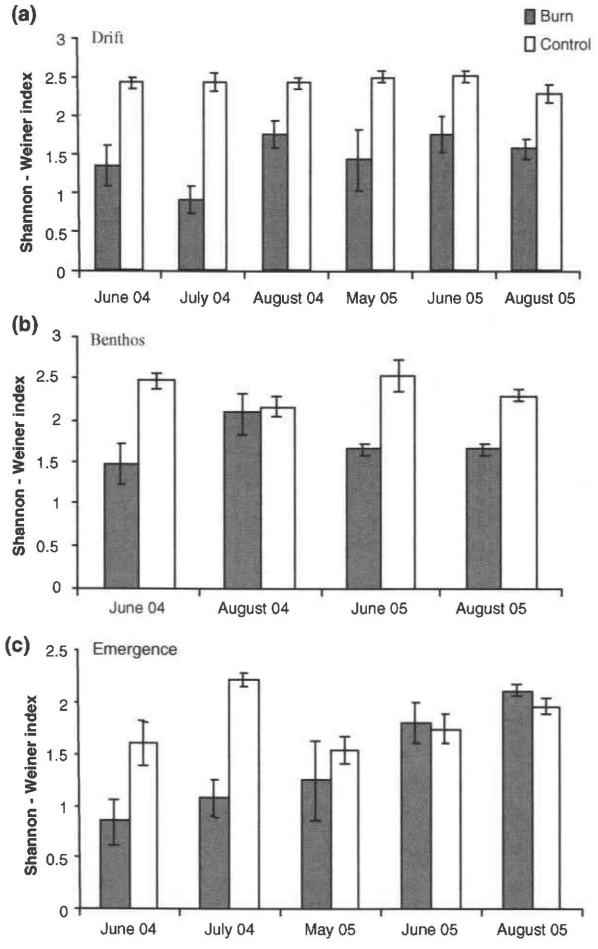

Fig. 4 Mean Shannon–Weiner diversity of drift (a), benthic (b) and emergence (c) samples from burned (shaded bars) and control (open bars) sites. Each bar represents the mean with standard error of five replicate streams in each sampling period.

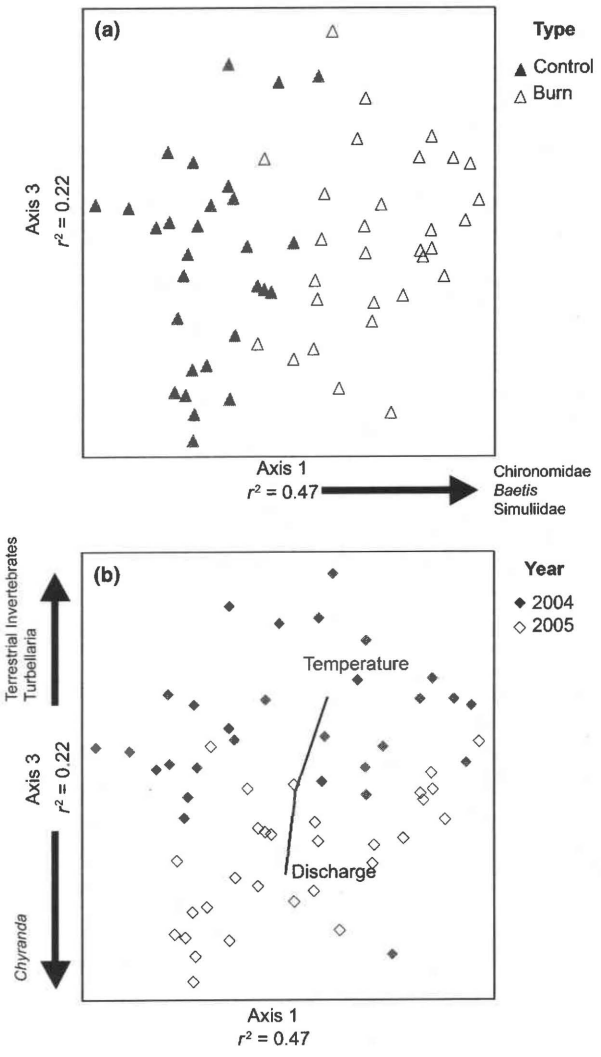

Fig. 5 Three dimensional Non-metric multidimensional scaling ordination of macroinvertebrate composition by abundance from drift samples. Each point represents one drift sample from one site and sample period. Samples coded by treatment type burn (shaded triangles) or control (open triangles) (a) Samples coded by year 2004 (shaded squares) or 2005 (open squares) (b) Taxa that were highly correlated with an axis are listed adjacent to it.

lower at burned (mean = 1.8) than control sites (mean = 2.9) overall ($P < 0.001$) (Fig. 4); however, Shannon–Weiner diversities in 2005 emergence samples were noticeably higher and more similar. As this index reflects both richness and evenness, the low values likely reflected dominance by Chironomidae as well as low representation by non-dipteran taxa; changes in summer 2005 emergence reflect changes in EPT taxa and greater evenness among taxa.

Non-metric multidimensional scaling analysis

Distinct separations between burned and control sites were also differentiated by NMS ordination of drift, benthic and emergent assemblages (Figs 5 & 6). The analyses identified gradients associated with 2004 as warmer temperatures (mean = 12.1 °C in 2004 compared to 10.6 °C in 2005) and lower discharge (5.6 $m^3\ h^{-1}$ in contrast to 9.3 $m^3\ h^{-1}$ in 2005), particularly in ordinations of drift and emergence. A few taxa characteristic of sampling seasons and streams that had been burned were also revealed.

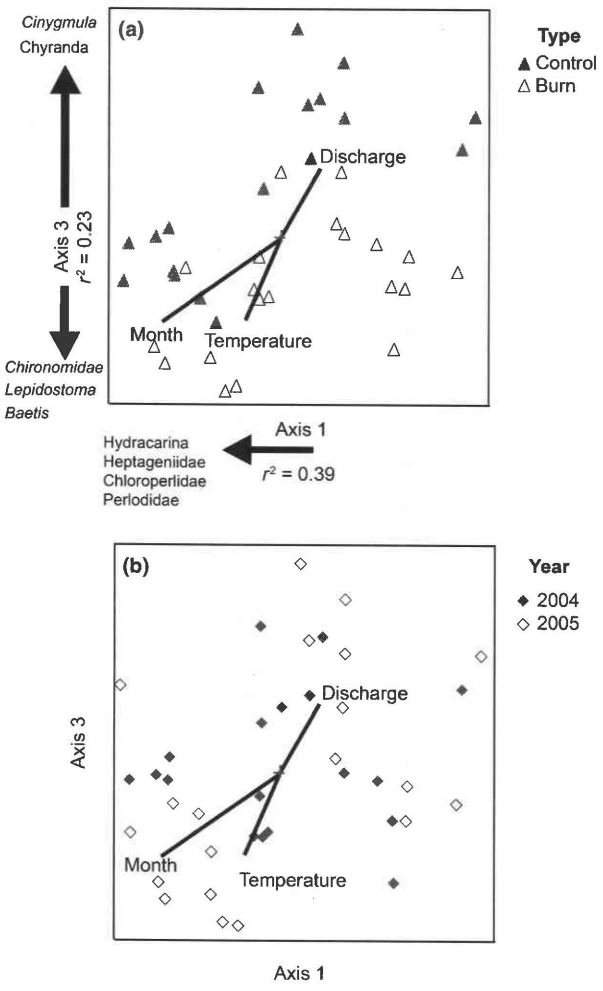

Fig. 6 Three dimensional Non-metric multidimensional scaling ordination of macroinvertebrate composition by abundance in benthic samples. Each point represents one composite benthic sample from one site and sample period. Samples coded by treatment type burn (shaded triangles) or control (open triangles) (a) Samples coded by year 2004 (shaded squares) or 2005 (open squares) (b) Taxa that were highly correlated with an axis are listed adjacent to it.

Ordination of benthic samples produced the greatest explanation of variation (r^2 = 0.91, stress = 10.0) (Fig. 6); this three dimensional solution of 38 benthic samples separated along the first and third axes by a gradient of water temperature, discharge and month sampled (June or August). There was no clear separation between 2004 and 2005, but axis 1, which explained the most variation (r^2 = 0.39), revealed a gradient based primarily on monthly differences. Heptageniidae, Chloroperlidae, Perlodidae and Hydracarina taxa that negatively correlated with the first axis, were more abundant in August of both years at burned and control sites. June samples at control sites, (upper right, axis 2), were characterized by scrapers *Cinygmula* (Heptageniidae) and *Chyranda* (Limnephilidae), though these taxa were not abundant at any site. Later in the year, Chironomidae, *Lepidostoma* (Lepidostomatidae) and *Baetis* were more abundant at burned sites. There was also some separation between burned and control sites along the second axis (not shown) indicating again that Chironomidae, collector-gatherer *Baetis* and also filter-gatherer Simuliidae, were more abundant at burned sites. A three dimensional solution of 59 drift samples clearly differentiated between control and burned sites as well as separating between year (r^2 = 0.83, stress = 13.7) (Fig. 5). As in the benthic assemblages, drifting Chironomidae, *Baetis* and Simuliidae were more abundant at burned than control sites. Whereas warmer temperatures and lower flows of 2004 were associated with abundance of Turbellaria and terrestrial macroinvertebrates (primarily Hymenoptera) in the drift, case building *Chyranda* were correlated with higher flows and cooler temperatures found at control sites in May and June, 2005 (Fig. 5b). Seasonal differences were also detected along axis 2 (not shown, r^2 = 0.14), with greater abundances of collector true flies *Dixa* (Dixidae) and shredder stoneflies *Yoraperla* (Peltoperlidae) at the end of the summer.

As in the ordination of drift and benthic samples, site type (burned or control) and year sampled were separated in NMS ordination of 55 emergence samples; however, fewer emergent taxa were associated with the gradients identified. This analysis produced a three dimensional solution (r^2 = 0.81, stress = 15.3), detected the same trends as the other ordination in correlating temperature and discharge with sampling years, and revealed no other distinctive representative taxa; therefore we note the results as corroborative evidence without graphical representation. As with the ordination on drift samples, variability in water temperature and discharge was highly correlated with year sampled but not correlated with either burned or control sites. More Chironomidae emerged in higher numbers in 2004 than 2005, and like Baetidae and other dipterans, more emerged from burned sites.

Discussion

Over the 2 years immediately following forest fire, headwater streams from burned catchments on the Colville National Forest contained four times more macroinvertebrates in drift and over two times more macroinvertebrates in the benthos than unburned sites. During the same time interval differences between burned and control sites also persisted in stream discharge, stream temperature and overstory canopy. However, we did not detect a difference in drifting or benthic biomass between burned and control conditions. Previous studies reported mixed and usually non-significant responses in both macroinvertebrate density and biomass in the first years after fire (Minshall *et al.*, 1995, 1997, 2001a; Minshall, Royer & Robinson, 2001b; Minshall, 2003). As sample variation in biomass was high, our detection of patterns in drifting and benthic macroinvertebrates might have been sharper if more study sites had been possible. Despite the potential limitation in site replication we observed a change in emergence biomass between 2004 and 2005; differences in insects emerging from burned streams were twice those at unburned sites the first year, but those differences disappeared coincident with small, but noticeably higher proportion of Ephemeroptera, Plecoptera and Trichoptera at burned sites in the second year.

Because our study sites were small order streams, persisting elevated abundances at burned sites in the Colville National Forest were likely related to the resilience of the surrounding landscape (Minshall *et al.*, 1997; Bisson *et al.*, 2003). Unlike Yellowstone National Park or the Frank Church Wilderness where many of the previous stream studies of macroinvertebrate response to fire were conducted, the Colville National Forest has a long history of anthropogenic disturbances, particularly timber harvest and cattle grazing. Return to pre-fire conditions would depend in part on sources of colonizers and favourability of local reach conditions for colonizers to succeed. Drift from undisturbed upstream sources may typically be a source of colonizing invertebrates, but in this study drift was not a likely contributor to increasing diversity as upstream reaches were as severely burned as the study sites. Ordination analyses indicated that composition of drift assemblages, indicators of upstream colonizers, remained distinctive between burned and unburned sites in 2004 and 2005, and there was no detectable difference in drifting EPT composition over the same time interval.

High environmental variability between years was the consequence of a late season snowfall resulting in higher discharges and lower water temperatures in 2005 compared to 2004. These differences in temperature and discharge may have had a greater influence on the aquatic community than any recovery process. Flooding and increased inorganic or organic loads following the fire may have more dramatic effects in managed landscapes. After a fire and subsequent flood in a southwestern U.S.A. ponderosa pine forest, invertebrate and fish densities were nearly totally depleted (Rinne, 1996). We had the opportunity to observe a similar event at one of our study sites in August 2004 when heavy thunderstorms flooded, scoured and reorganized the channel. Benthic macroinvertebrate densities from samples taken 3 days later were slightly higher than those from samples taken in June 2004, but much lower than benthic densities in 2005. Though we recorded the most obvious physical effects of flash flooding at one location, more subtle effects for slowing the recovery rate of macroinvertebrate numbers and composition in this catchment would have been likely. Nevertheless, the general response was much less than the decline observed in the arid southwest.

Because canopy cover changes dramatically after fire, we expected increased primary production in the stream, cascading to greater densities of grazing macroinvertebrates (Minshall *et al.*, 1989). Increased algal growth can support more scrapers, who graze periphytic and epiphytic algae. However, we did not observe increased algal biomass, as either AFDM or chlorophyll *a*, following fire. These patterns may be due to increased consumption and turnover at burned sites. Though higher densities of collector-gatherers such as *Baetis* or chironomids may have accounted for some of the algal production, we did not detect a dramatic increase in aquatic scrapers. Given the lack of strong response by herbivorous macroinvertebrates, disturbance from decreased bed stability, as in the flood of August 2004, and increased fine sediments may have had a significant effect on algal abundance.

In the second year of our study, herbaceous riparian vegetation, primarily fireweed (*Epilobium angustifolium* L.), shaded streams in subcachments that had burned.

Subsequent reduced light levels were another constraint of algal growth in burned sites making them more similar to control sites. Moreover, these plants probably contributed leaf litter into the streams; they could have provided food resources for shredders such as *Lepidostoma*, and collector-gatherers *Baetis* and abundant chironomids associated primarily with burned sites (Fig. 6).

Chironomids and *Baetis*, both early colonizing taxa with short life cycles and high reproductive rates, are frequently more abundant following fire and other disturbances (Anderson, 1992; Minshall, 2003). Similar to findings from other studies (Anderson, 1992; Minshall, 2003), chironomids in the Colville National Forest increased in all sample types during the 2 years following fire, however *Baetis* increased in drift but not in the benthos at burned sites in August of both years. These are tolerant, rapidly reproducing taxa that could quickly contribute to high densities. Especially when collected early in their life cycle, chironomids and baetid mayflies are smaller than many longer lived taxa, particularly EPTs. Because EPT taxa were more abundant in the benthos at unburned sites, their larger sizes may have accounted for similarities in macroinvertebrate biomass between sites despite higher overall numbers at burned sites.

The higher abundance and dominance of chironomids were reflected in lower diversity at burned sites. Gradients in the macroinvertebrate community composition as detected in benthic, drift and emergence collections may suggest potential directions in the gradual recovery from fire in this managed landscape. Though most EPT taxa were few in number, their increased appearance, particularly in late summer, provided the strongest indicators for succession. Several EPT taxa appeared in both drift and benthic samples at control and burned sites: stoneflies *Yoraperla* (in drift), Chloroperlidae and Perlodidae (benthics); benthic Heptageniidae mayflies; and drifting *Chyranda* caddisflies. Only the shredding caddisfly, *Lepidostoma*, and collector-gatherer *Baetis* mayflies were clearly identified with increasing benthic numbers at burned sites in late summer. Baetidae mayflies were the only EPT group identified with burned sites in the ordination of emergence assemblages, but the relative change in proportion of emerging EPT taxa between years was an important indicator of change.

Multiple measures of macroinvertebrate response, in the benthos, drift and as emergence, were important for assessing the potential of colonization. Within-season trends were strongest in the benthic samples, potential connectivity with upstream sites detected in the drift, and emergence was most robust in examining the re-entry of EPT taxa. Despite the variation among sites, all measures of macroinvertebrate communities show strong differences persisting between burned and unburned sites. Trends in assemblage composition, algal responses and field observations suggest that macroinvertebrates in these steep headwater streams will be particularly sensitive to changes in discharge (in storm events or occurrence of intermittency), temperature and riparian regrowth.

It has been predicted that recovery from fire would be slower in areas with previous and post-fire anthropogenic disturbances (Bisson *et al.*, 2003; Minshall, 2003; Beschta *et al.*, 2004; Karr *et al.*, 2004; Reeves *et al.*, 2006). Though the forest type and fire regime of the Togo fire was similar to that of Yellowstone and Idaho studied by Minshall *et al.* (1989, 2001b), our study found persistent, higher macroinvertebrate densities at burned sites but no differences in biomass; these results were not outside the range of variation of previous findings, and changes in community composition are very similar to other post-fire studies. We expected macroinvertebrate responses to be affected not only by fire severity and forest type, but also by management activities. In the Colville National Forest, the persistent differences in macroinvertebrate densities and very gradual rates of colonization by non-chironomid taxa, particularly EPTs, may be associated with recurring flood events that reset stream conditions. While these hydrologic disturbances tend to slow instream recovery, regrowth of streamside grasses and herbaceous plants mediated effects of canopy loss, potentially encouraging colonization by more diverse macroinvertebrate taxa. Landscape patterns were established to some extent by previous management history, but the streams post-fire can also be affected by management decisions that optimize for recovery, such as minimizing the probabilities of mass failure or flash flooding, and maximizing opportunities for riparian regrowth.

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