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Abstract

Wildfire and debris flows are important physical and ecological drivers in headwater streams of western North America. Past research has primarily examined short-term effects of these disturbances; less is known about longer-term impacts. We investigated wildfire effects on the invertebrate prey base for drift-feeding rainbow trout (*Oncorhynchus mykiss*, Walbaum) in Idaho headwater streams a decade after wildfire. Three stream types with different disturbance histories were examined: 1) unburned, 2) burned, and 3) burned followed by debris flows that reset channel morphology and riparian vegetation. The quantity of macroinvertebrate drift (biomass density) was more variable within than among disturbance categories. Average body weight and taxonomic richness of drift were significantly related to water temperature and influenced by disturbance history. During the autumn sampling period, the amount of terrestrial insects in rainbow trout diets varied with disturbance history and the amount of overhead canopy along the stream banks. Results indicate that there are detectable changes to macroinvertebrate drift and trout diet a decade after wildfire, and that these responses are better correlated with specific characteristics of the stream (water temperature, canopy cover) than with broad disturbance classes.

Introduction

Natural disturbances such as wildfire can play a key role in aquatic ecosystems, altering physical conditions that drive habitat availability and species productivity (Reeves et al. 1995, Gresswell 1999). In the short-term, wildfire can alter basin hydrology and hill slope erosional thresholds, increasing the probability of severe erosional events (postfire floods and debris flows; e.g., Benda et al. 2003) that result in extensive loss of streamside vegetation, channel reorganization (change in channel form and habitat availability), and local extirpation of

aquatic species (e.g., Pilliod et al. 2003). Most studies of wildfire and aquatic ecosystems focus on the short-term impacts of wildfire on stream ecosystems (e.g., Minshall et al. 1989, Minshall 2003); less is known about longer-term effects (Bisson et al. 2003).

A decade after wildfire, the condition of streamside vegetation and its effects on the prey of drift-feeding rainbow trout may vary depending on the severity of the disturbance. Deciduous streamside vegetation immediately adjacent to the stream can recover rapidly (5 yr; e.g., willows [*Salix* spp.] and alders [*Alnus* spp.]); whereas forest trees (e.g., Douglas fir [*Pseudotsuga menziesii*, Mirbel]) recover over decades (Taylor and Skinner 1998, Dwire and Kauffman 2003). Further, postfire debris flows can reset successional dynamics of streamside vegetation and slow riparian recovery (Dwire and Kauffman 2003). The quantity of terrestrial macroinvertebrates falling into streams—an important energy source for trout (Kawaguchi et al. 2003)—could decrease with changes in the abundance and

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composition of streamside vegetation (Wipfli 1997, Kawaguchi and Nakano 2001, Koetsier et al. 2007, McCarthy et al. 2009). The effects of altered streamside vegetation on drifting aquatic macroinvertebrates are less straightforward, but changes in riparian cover can dramatically change drift composition and density (Piccolo and Wipfli 2002). Loss of riparian vegetation reduces the amount of allochthonous energy sources for the stream (e.g., terrestrial plant material; Cummins et al. 1989), while the increase in sunlight boosts available autochthonous energy sources (e.g., algae; Hawkins et al. 1982, Hill et al. 1995, Fuller et al. 2004, Mihuc and Minshall 2005). An increase in either of these energy sources could translate into increased productivity of invertebrate prey for rainbow trout. Further, aquatic macroinvertebrates that enter the drift may benefit from the combined input of autochthonous and allochthonous energy sources in streams that have burned in the past, but have retained their streamside deciduous vegetation (Mihuc and Minshall 1995, 2005 but see Perry et al. 2003).

Increased solar radiation and warmer stream temperatures after wildfire may also affect the aquatic component of the macroinvertebrate drift (Minshall et al. 1989, Dunham et al. 2007). Some taxa may disappear entirely, either through loss of intolerant species (Vannote and Sweeney 1980) or earlier onset of adult insect emergence (Frutiger and Imhof 1997). Taxa that remain may be smaller in size if their metabolism has increased with temperature at a rate disproportionate to assimilation (Vannote and Sweeney 1980). These effects on the macroinvertebrate community could translate to lower quality and reliability of the aquatic component of the drifting invertebrate prey base for rainbow trout.

Based on the above considerations, we compared the following features of aquatic drifting prey: 1) density; 2) taxonomic richness; and 3) body weight among headwater streams contrasting in disturbance histories and habitat characteristics (canopy cover, stream temperature) in selected Idaho headwater streams. We also compared the diet of rainbow trout to investigate patterns in the predominance of terrestrial prey and the average size and taxonomic richness of aquatic macroinvertebrates. We investigated both summer and autumn characteristics of the trout prey base, with the autumn feeding season particularly

important for overwintering survival of rainbow trout. Autumnal shifts in both streamside vegetation (deciduous leaf drop) and aquatic macroinvertebrate composition and density (e.g., through larval insect emergence) could exacerbate or eliminate differences in the prey base among streams with different disturbance histories.

Study Area

We selected study streams in the Boise River basin, central Idaho, which has experienced extensive wildfire since 1992 (Dunham et al. 2007). The study area, underlain by granitic rocks of the Idaho Batholith, is characterized by steep and rugged terrain, with a snowmelt-dominated hydrology that is modulated by periodic, intense summer thunderstorms that generate local peak-flow events and postfire debris flows. As part of a larger investigation of the effects of wildfire on aquatic ecosystems, we examined characteristics of macroinvertebrate drift and diets of rainbow trout for nine streams, three in each of the following disturbance categories: 1) unburned, 2) burned, and 3) burned and debris flow, where the latter sites experienced one or more postfire debris flows within 1 month of the wildfire (Table 1). Sites were 1-km long reaches located near the outlet of each sub-basin, characterized by pool-riffle, step-pool, and cascade morphologies (Montgomery and Buffington 1997).

Our investigation is similar to work published by Koetsier et al. (2007), which was conducted at the same sites (Dunham et al. 2007), but after our fieldwork took place (2003 vs. 2005). They found greater amounts of aquatic invertebrates and inorganic material in the burned streams and, similar to our results, lower amounts of terrestrial invertebrates. However, we collected additional information on macroinvertebrate drift and conducted additional analyses on macroinvertebrate size and community composition.

Methods

Sampling and Analysis of Drift and Fish Diets

Aquatic macroinvertebrate drift was sampled in summer (July 21–25) and autumn (October 4–7) of 2003, following procedures described by Wipfli and Gregovich (2002). Drift nets were placed near the lower end of each study reach and secured with sandbags in swiftly flowing areas (riffles/

cascades). Drift nets captured aquatic macroinvertebrates continuously for a 48-hr period for each sampling occasion (nets were checked after 24 hr for clogging). Following collection, discharge was measured from the pipe and the net contents, including detritus and macroinvertebrates were preserved in 95% ethanol. Drift samples with large numbers of individuals (> 500) necessitated Caton (1991) subsampling. With the aid of a dissecting scope, macroinvertebrates were sorted, identified to the lowest reliable taxon (most to the family level), measured to the nearest millimeter (length excluding antennae and cerci), and enumerated. We then estimated individual biomass (mg dry mass) using published taxon-specific length-weight regression equations (Rogers et al. 1977, Smock 1980, Sample et al. 1993, Burgherr and Meyer 1997).

We used the following variables to describe sampled aquatic macroinvertebrate drift for each stream: (1) biomass density (mg dry mass per m³ of water), (2) average body weight of individual macroinvertebrates (mg dry mass), and (3) standardized taxonomic richness. Different numbers of macroinvertebrates processed for each sample could bias taxonomic richness measures (Bunge and Fitzpatrick 1993, Gotelli and Colwell 2001). We used rarefaction (Gotelli and Colwell 2001) to avoid this pitfall, standardizing taxonomic richness based on sample size (standard n: summer = 110, autumn = 180). The analysis was performed using the EcoSim program (Gotelli and Entsminger 2009).

Within two weeks of drift sampling, rainbow trout > 60 mm in length were captured upstream of the drift net locations (August 4–12 and October 7–8, 2003). Sampling took place during daylight hours between 11 am and 6 pm, staggered among disturbance types to avoid confounding associations with diel patterns of fish feeding. Fish stomach contents were obtained using a gastric lavage or by sacrificial sampling. We sacrificed a subset of the lavage fish (n = 10) to ensure adequate evacuation of stomach contents. Stomach content data were combined for individual trout for each stream and summarized in terms of the following variables: (1) percent biomass of terrestrial origin (mg dry mass), (2) rarefied taxonomic richness of aquatic macroinvertebrates (standard n, summer and autumn = 85), and (3) average body weight of aquatic macroinvertebrates (mg dry mass).

Habitat Measurements

We measured substrate size and channel dimensions (wetted width, depth) over the 1-km length of each study reach in cross sections placed every 5 m. The dominant grain size at seven points along the wetted width of each cross section was classified into size classes (silt, sand, gravel, cobble, boulder; e.g., Buffington and Montgomery 1999). Reach slope was measured with a hand level. From these data, we calculated reach-averaged indices of substrate diversity and mobility. Relative substrate diversity (evenness) was calculated from the normalized Shannon index (Zar 1999), while substrate mobility was determined from the excess Shields (1936) stress (τ^*/τ^*_{c50} , ratio of the applied Shields stress to the critical value for mobilizing the median grain size, 0.03; Buffington and Montgomery 1997). Mobility calculations were performed for summer low flow.

We classified riparian vegetation and canopy as open versus closed based on LANDSAT imagery acquired on July 10, 2002. Studies in neighboring basins show that vegetation types determined from this technique correlate strongly with ground-based measures of canopy shading obtained from hemispherical photographs and provide useful surrogates for riparian vegetation cover (Isaak et al. 2010). Cover was measured in terms of the proportion of stream length with open canopy over the 1-km length of each study reach (Table 1). Temperature loggers deployed within the study reaches recorded maximum summer temperatures (Dunham et al. 2007), which provide good single measures of relative temperature differences among sites and strongly correlate with other measures of stream temperature (Dunham et al. 2005). Stream temperatures were measured from 1 July to 15 September 2003. We used the ensemble data set (n = 9 study sites) for evaluating Pearson correlations between measures of macroinvertebrate drift and fish diet and habitat features. We emphasize significant relationships; null results were considered inconclusive due to the low power of this exploratory study.

Results and Discussion

Aquatic Macroinvertebrate Drift Prey Base

Prior examinations of stream ecosystems influenced by wildfire indicate that macroinvertebrate communities return to pre-impact conditions

Table 1. Characteristics of streams sampled for macroinvertebrate drift and rainbow trout sampled for stomach content analysis.

Site Features	Unburned ¹			Burned			Burned and debris flow		
	BV	LM	TL	CW	HU	LO	SFS	TR	WR
Watershed area (ha)	1451	4550	1954	3872	1142	1544	3178	1000	1022
Elevation at sampling location (m)	1341	1398	1488	1139	1357	1415	1172	1450	1489
Proportion of channel moderately to severely burned ²	0	0	0	0	1.00	0.87	0.78	0.62	0.97
Channel gradient (m/m) ³	0.040	0.037	0.035	0.056	0.046	0.061	0.061	0.054	0.069
Wetted width (m) ³	1.7	2.7	2.0	2.0	3.2	2.9	3.0	2.4	2.1
Wetted depth (m) ³	0.07	0.07	0.11	0.07	0.10	0.12	0.09	0.05	0.06
Median grain size (mm) ³	32	45	68	80	26	104	75	74	137
Percent fines (< 2 mm) ³	11	9	13	9	17	11	6	9	5
Bed mobility (excess Shields stress, $\tau^*/\tau_{*c,50}^3$) ³	2.19	1.48	1.35	0.92	2.68	1.32	1.42	0.85	0.50
Relative substrate diversity (evenness) ³	0.69	0.73	0.74	0.79	0.79	0.78	0.74	0.76	0.75
Proportion of stream length with open canopy (1 km) ⁴	0.15	0.10	0.50	0.53	0.67	0.67	0.82	0.91	0.87
Maximum summer temperature (°C) ⁴	14.4	0.25 (0.22)	20.3	22.6	0.62 (0.08)	19.9	23.8	0.87 (0.05)	24.4
		18.7 (3.1)			16.4			26.3	
		17.8 (3.1)			19.6 (3.1)			24.8 (1.3)	
Rainbow trout sampled for stomach contents ⁵									
	9	10	11	9	9	6	11	10	10
Summer <i>n</i>									
Size range (mm)	72–118	77–144	72–157	138–175	62–146	128–165	60–154	69–154	102–153
Autumn <i>n</i>	8	10	10	12	8	11	8	10	10
Size range (mm)	76–143	88–142	82–144	90–163	89–119	82–149	76–130	82–144	69–154

¹ Unburned streams: Beaver (BV), Lost Man (LM), and Trail (TL) creeks; burned streams: Cottonwood (CW), Hungarian (HU), and Lost (LO) creeks (all burned by the Rabbit Creek Fire, 1994); burned and debris flow streams: South Fork Sheep Creek (SFS), Foothills Fire, 1992) and Trapper (TR), and Wren (WR) creeks (Rabbit Creek Fire, 1994).

² Burn severity mapped by Boise National Forest: high severity—stand replacing fires; (2) moderate severity—fires that burn understory vegetation with occasional burning of individual or small groups of trees; Burton 2005).

³ Reach-average values.

⁴ Average values for each disturbance category are reported below site values followed by the standard deviation in parentheses.

⁵ Reported numbers are for full stomachs only. Incidents of empty stomachs were rare (Summer 6.5%; Autumn 5.6% of trout captured)

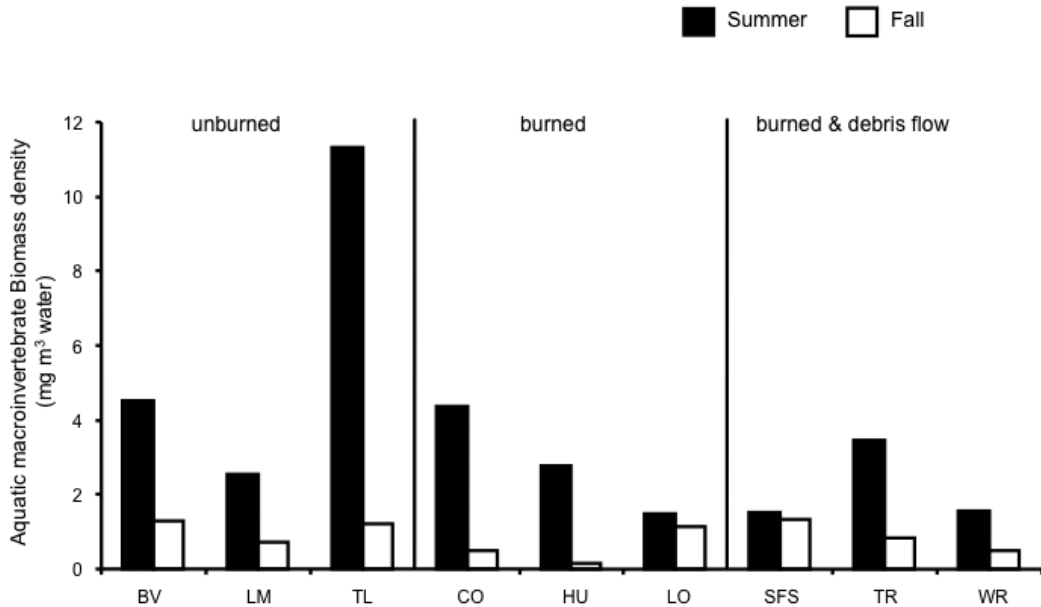


Figure 1. Aquatic macroinvertebrate biomass density in the drift of nine streams with different wildfire and disturbance histories for summer (July) and fall (October) based on sampling over a 48 hour sampling period. Stream abbreviations are given in Table 1.

within a decade (Minshall 2003). Over longer time scales (10-100 years), effects of wildfire on macroinvertebrate prey and predator dynamics are likely to be subtle and indirect, relating more directly to stream habitat characteristics affected by wildfire, such as stream temperature (Minshall 2003). Although maximum summer temperatures overlapped among sites in unburned and burned streams, the warmest temperatures occurred in the burned and debris flow sites. Overall characteristics of the aquatic macroinvertebrate drift were variable among streams and did not markedly differ among disturbance types (Figure 1). We observed the highest drift biomass density in Trail Creek, an unburned stream with canopy openness comparable to that of the burned streams (Figure 1). For all disturbance types combined, drift biomass density decreased in the autumn months (Figure 1).

Average individual body weight of aquatic macroinvertebrate drift and standardized measures of taxonomic richness during the summer overlapped between unburned and burned streams, but were lowest in burned and debris flow streams.

Across the combined data set, maximum summer temperatures negatively correlated with summer measures of average individual body weight (Pearson $r = -0.77$, $P = 0.02$) and rarefied taxonomic richness (Pearson $r = -0.76$, $P = 0.02$) of drifting aquatic macroinvertebrates (Figure 2). Burned and debris flow streams had less mobile beds (Table 1), with smaller percentages of fine material, but substrate mobility and evenness did not correlate with rarefied summer taxa richness (Pearson $r = 0.43$, $P = 0.74$ and $r = -0.25$, $P = 0.85$, respectively). For the fall samples, we observed minimal differences between disturbance types in individual body weight of aquatic macroinvertebrates; however, the pattern of lowest taxonomic richness in burned and debris flow sites continued.

In summer, variability in the proportion of terrestrial insects in diets was more apparent within than among disturbances categories. However, for the fall sample, only fish in unburned streams had a dominance of terrestrial insects in the diet. This may be related to differences in canopy cover among disturbance types; in fall, canopy cover corresponded with the proportion of terrestrial

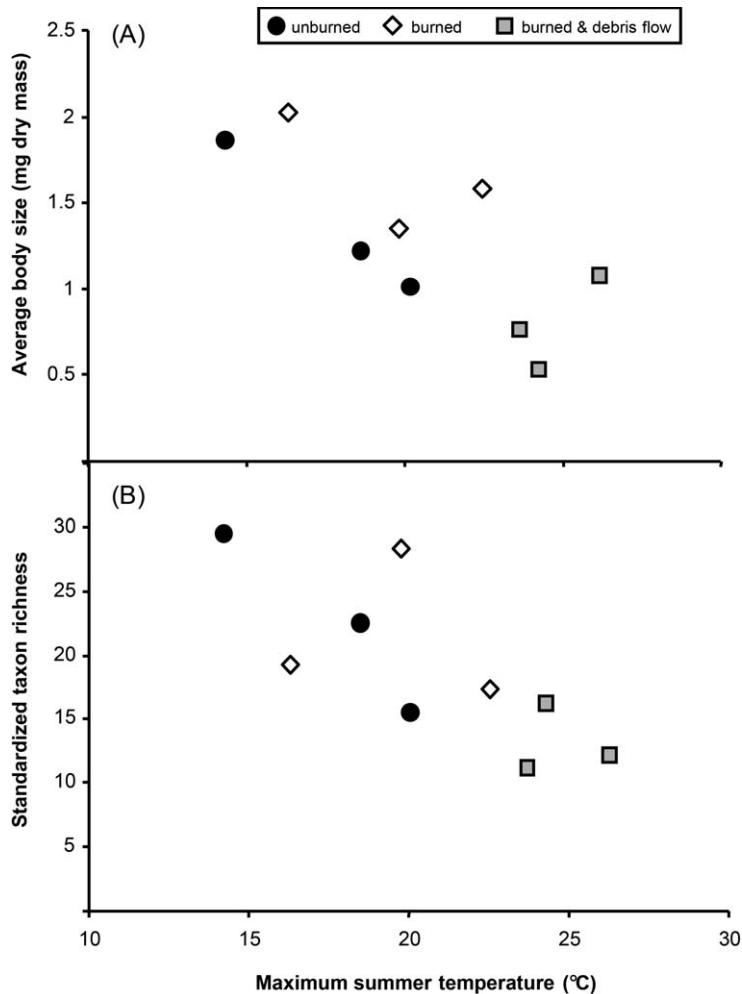


Figure 2. Correspondence of maximum summer temperature with (A) average aquatic macroinvertebrate body size and (B) standardized taxonomic richness in streams with different disturbance histories.

insects in rainbow trout diets (Pearson $r = 0.72$, $P = 0.03$) due to the dominance of terrestrial insects in the diets of rainbow trout in unburned streams (Figure 3). Some patterns observed in drift data were also observed in stomach content analysis, including smaller average body weight and richness of summer aquatic macroinvertebrates in burned and debris flow streams. Aquatic taxonomic richness in trout stomach contents negatively correlated with maximum summer temperature (Pearson $r = -0.73$, $P = 0.03$).

Loss of overhead riparian vegetation is typically associated with increased light, and increased

primary and secondary productivity in small streams (Fuller et al. 1986, Hill et al. 1995, Mihuc and Minshall 2005). We did not observe this pattern in our study, at least in terms of standing stocks of drifting aquatic macroinvertebrates. This may be attributed to limited duration of observations and our small sample size, or limited power to detect patterns in the face of multiple factors that influence aquatic drift (Minshall et al. 1985, Nakano and Murakami 2001, Kawaguchi et al. 2003). However, other plausible mechanisms could account for the lack of a strong effect of channel disturbance history on drift biomass density. Increased algal productivity from increased sunlight may be consumed by juvenile tailed frogs (*Ascaphus montanus*) abundant in these streams (Dunham et al. 2007) before entering the macroinvertebrate food web (Kiffney and Richardson 2001). An increase in nutrients in streams immediately after wildfire (Spencer et al. 2003) may be followed by a long-term decrease if nutrients in the watershed are sequestered by recovering upland vegetation before reaching the stream channel (Bormann and Likens 1994), thereby limiting instream productivity (Fuller et al. 2004).

Finally, earlier emergence in warmer systems could result in loss of aquatic macroinvertebrates that would otherwise occur in the drift during the summer months (Vannote and Sweeney 1980, Hogg and Williams 1996).

Our results underscore the importance of relating observed biotic patterns to channel features (in this case, canopy cover and stream temperature) for understanding ecosystem response to disturbance, rather than relying on disturbance classes as surrogates for those factors. The effects of temperature and canopy on macroinvertebrate drift and trout diet suggest that warmer streams, with a history of wildfire and debris flows, may

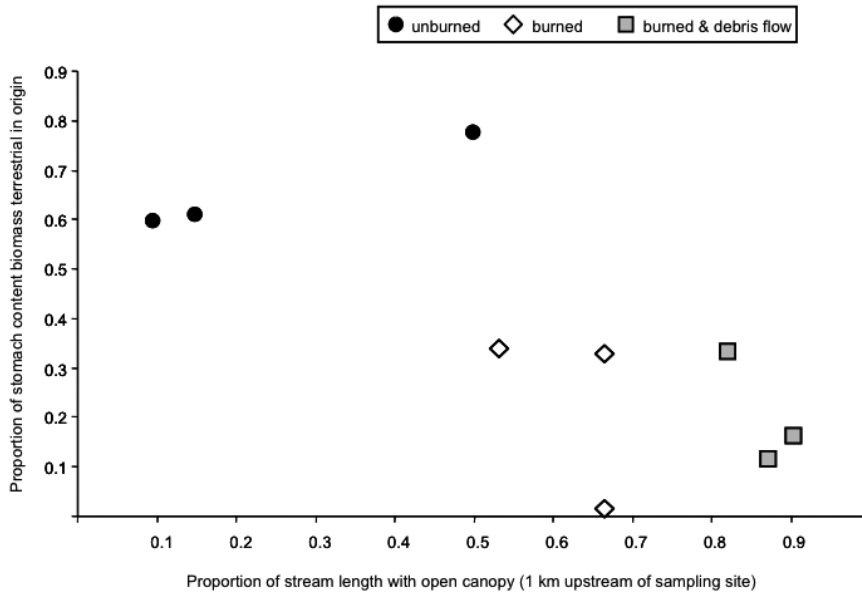


Figure 3. Terrestrial content of rainbow trout diet as a function of autumn canopy cover in streams with different disturbance histories.

present greater costs for trout in terms of food quality (prey size, Ware 1972), reliability (related to drift diversity, Brown 2003), and terrestrial input (McCarthy et al. 2009). It is in warmer streams that fish most require an abundant, consistent, and high quality food supply; water temperatures associated with positive growth under full rations may become more harmful to individuals facing smaller rations (Grove et al. 1978, McCarthy et al. 2009). In addition, in autumn, when aquatic macroinvertebrate drift is reduced (Figure 1) and trout are storing fat for winter, terrestrial input to fish diets is important (Allan et al. 2003, Nakano and Murakami 2001, but see Romero 2004); the loss of which in burned streams may be particularly important.

Results of our study reveal that, after a decade, wildfire can indirectly influence prey taxonomic composition, predator-prey interactions, and perhaps other associated ecosystem processes (e.g., Wootton et al. 1996, Baxter et al. 2005). Limited understanding of the effects of wildfire and postfire debris flows on stream ecosystem processes results from the fact that few studies have examined how wildfire influences energy input, energy flow, species interactions, or food webs in streams, particularly over longer time scales (Minshall 2003, Mihuc and Minshall 2005). Yet

these processes drive aggregate responses, such as species occurrence, abundance, and population productivity (Evans et al. 2005, Mihuc and Minshall 2005). Our study suggests that broader characteristics of stream ecosystems may recover more quickly than the underlying processes from which they are derived. Hence, detecting long-term ecosystem impacts from wildfire disturbance and assessing condition of fish populations may require more in-depth analyses than broad measures of species distribution and abundance typically used by land managers. This is particularly important considering increased water temperatures, wildfire occurrence, and accompanying shifts in ecosystem function could be exacerbated by ongoing climate warming.

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