Debris flows amplify effects of wildfire on magnitude and composition of tributary subsidies to mainstem habitats

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Abstract: Postfire disturbances, such as debris flows, may alter the recovery of stream ecosystems from wildfire. Furthermore, changes to productivity and the dynamics of nutrients and organic matter (OM) in tributaries may affect fluxes of materials and organisms to mainstem habitats. We investigated the consequences of watershed wildfire and debris flows for exports from tributaries to mainstem habitats in the South Fork Salmon River Basin of central Idaho, USA. We compared fluxes from 15 streams ($n = 5$ unaffected [UA], $n = 5$ fire-affected [FA], and $n = 5$ fire + debris flow-affected [FDA]) in summer 2011 (4 y postfire, 3 y postdebris flow). In early June, FDA streams exported 650% higher concentrations of sediment to downstream habitats than did UA streams (mean, FDA: 18.7 g/m^3, UA: 1.9 g/m^3). Overall, concentrations of dissolved organic C were 75% greater in FDA than in UA streams (FDA: 2.8, UA: 1.6 mg/L), and the quality of OM was higher (i.e., more chlorophyll a [chl a] and higher chl a:OM) in FDA than in UA streams. Community composition of invertebrates exported from FA and FDA streams was similar and dominated by r-strategist taxa (Chironomidae, Baetidae, and Simuliidae), but FDA streams exported 470% more invertebrate biomass to downstream habitats than did FA streams (FDA: 8.6 mg/m^3, FA: 1.5 mg/m^3). Higher primary production and reduced stream retention following debris flows may have contributed to increased fluxes to mainstem habitats. Increased exports of resources from FDA tributaries to mainstem rivers may enhance productivity of the recipient habitat and benefit organisms such as drift-feeding fish.
Key words: wildfire, debris flow, invertebrate drift, organic matter, subsidies, disturbance

Wildfire is a major ecological disturbance that affects the structure and function of stream ecosystems around the world (Gresswell 1999, Verkaik et al. 2013). Effects of fire vary in space and time (Gresswell 1999, Verkaik et al. 2015), but fire has the potential to increase in-stream primary productivity (Betts and Jones 2009) and to alter invertebrate abundance and composition (Minshall 2003) and dynamics of allochthonous inputs and woody debris in streams (Gresswell 1999, Dwire and Kauffman 2003, Jackson et al. 2012). By removing vegetation and destabilizing soils, fire also can increase the likelihood of subsequent, large-scale erosional events, such as debris flows (Wondzell and King 2003). Under some circumstances, streams might be expected to return to prefire conditions within 10 y of wildfire (Romme et al. 2011), but debris flows have the potential to extend and change the trajectory of recovery of stream ecosystems (May and Gresswell 2003b). Effects of wildfire and subsequent debris flows also can propagate beyond the habitats that are directly affected (May and Gresswell 2003a), but most investigators have focused on in situ consequences rather than downstream fluxes. Ecosystems affected by dis-turbance are expected to exhibit reduced internal efficiency and, subsequently, to export more materials to adjacent habitats than undisturbed ecosystems (Bormann et al. 1974, Odum 1985). Despite this potential, few investigators have explored the combined effects of wildfire and debris flows on fluxes from headwater streams.

Upstream habitats are connected via material and energy flows to downstream habitats, so understanding rivers requires knowledge of how responses to disturbance in headwaters propagate from tributaries to mainstem rivers. Headwater exports contribute to the metabolism and productivity of organisms and ecosystems downstream, and thereby influence the integrated character of the mainstem river (Bruns et al. 1984) and create hotspots at tributary confluences (Gomi et al. 2002, Benda et al. 2004, Kiffney et al. 2006). Debris flows can alter this connectivity by removing woody debris following wildfire, subsequently reducing the ability of the stream channel to retain organic matter (OM) (May 2007). Cover et al. (2010) showed that even 100 y after debris flows, large woody debris and benthic OM were still increasing, suggesting that allochthonous

inputs can take decades to recover to predisturbance levels. Altered downstream transport can increase export of sediment, nutrients, and OM in the spring after the disturbance (Spencer et al. 2003), and nutrient levels can sometimes remain elevated for several years postfire (Mast and Clow 2008). Thus, the combination of disturbance from wildfire and debris flow may change tributary exports to mainstem rivers by altering allochthonous inputs, in situ productivity, and retention.

Disturbance by wildfire and debris flows also can alter the magnitude and composition of invertebrate subsidies from tributaries to mainstem habitats. Immediate effects of debris flows include direct mortality of macroinvertebrates, fish, and amphibians (Dunham et al. 2007), which can lead to the short-term local extirpation of some animal species and carries consequences for community composition (Gresswell 1999, Cover et al. 2010, Rieman et al. 2012). Invertebrate production in mainstem rivers and exports from affected tributaries may be influenced by a variety of pathways. First, fire and debris flows alter characteristics of riparian vegetation (Dwire and Kauffman 2003), which is a source of terrestrial invertebrate prey to headwater streams that may be exported downstream to mainstem habitats (Wipfli and Gregovich 2002). Second, by reducing canopy cover, wildfire may increase standing crops of periphyton and aquatic invertebrates (Minshall et al. 1989, Malison and Baxter 2010b, Rugenski and Minshall 2014), thereby increasing the number of aquatic invertebrates available to drift into downstream habitats. Furthermore, fire may shift the composition of aquatic invertebrates toward dominance by r-strategist taxa (Minshall 2003, Mellon et al. 2008, Malison and Baxter 2010a), which are typically characterized by high fecundity, rapid development, and small body size (Pianka 1970). Thus, watershed fire and debris flow may increase invertebrate subsidies to mainstem environments while altering the composition of such subsidies.

Invertebrates make up a relatively small portion of the total OM exported from headwater streams to mainstem rivers, but this subsidy may be critically important to certain organisms, such as drift-feeding fish. For example, Wipfli and Gregovich (2002) estimated that exports of detritus and invertebrates from fishless tributaries in southeastern Alaska supply enough energy to support 100 to 2000 young-of-year salmonids/km of fish-bearing stream. Furthermore, Torgersen et al. (2008) noted that mainstem fish abundance was highest at confluences with fishless tributaries, potentially because invertebrate prey was abundant in these locations. In general, drifting terrestrial and aquatic invertebrate prey originating from tributaries can be important to sustaining fish in mainstem rivers (Wipfli and Baxter 2010).

We investigated how wildfire and subsequent debris flows altered downstream fluxes of sediment, nutrients, OM, and invertebrates from tributaries in the South Fork Salmon River Basin of central Idaho, USA. In summer 2011, we measured fluxes from 15 tributaries draining watersheds with different disturbance histories (unaffected by fire [UA], affected by fire [FA], affected by fire + postfire debris flows [FDA]). Using this comparative study framework, we addressed the following hypotheses: 1) In the mid-term period (<10 y), wildfire leads to increased fluxes of sediment, nutrients, and OM from tributaries to mainstem habitats with attendant increases in the quality of exports (i.e., C : N). 2) Wildfire leads to increased flux of invertebrates from tributaries to mainstem habitats and a higher proportion of r-strategist taxa (i.e., of the families Baetidae, Simuliidae, and Chironomidae), and debris flows that follow wildfire amplify these changes in subsidies of 3) material and 4) organisms.

METHODS
Study area and design

We evaluated our hypotheses with a comparative study in the Salmon River Mountains (Payette National Forest; lat 44.9108°N, long 116.1031°W) of central Idaho during summer (June–August) 2011. Streams (UA: $n = 5$, FA: $n = 5$, FDA: $n = 5$) were high-gradient, low-order (1–3) tributaries to the East Fork of the South Fork Salmon River or Profile Creek, one of its major tributaries. These small tributaries (watershed area: 0.1–8.1 km^2) were characterized by erosion-prone soils derived from Idaho Batholith granite. Elevations ranged from 1140 to 1728 m asl at their confluences with the East Fork of the South Fork Salmon River or Profile Creek (Table 1). Watershed area ($F_{2,12} = 0.20$, $p = 0.82$), discharge ($F_{2,12} = 1.27$, $p = 0.32$), and wetted width ($F_{2,12} = 0.12$, $p = 0.89$) did not differ by disturbance type, but FA and FDA streams accumulated more degree days ($F_{2,8} = 51.78$, $p < 0.0001$) and had lower elevations ($F_{2,14} = 78.74$, $p < 0.0001$) than UA streams. FA and FDA streams accumulated similar degree days ($p = 0.46$), but FA streams had lower elevations than FDA streams ($p = 0.046$). Discharge did not differ among disturbance types ($F_{2,12} = 1.27$, $p = 0.32$).

Peak flows were driven by snowmelt in May and June, with base flows occurring from August to September. Mean annual precipitation ranged from 63.5 cm at the highest elevation watershed to 52.0 cm at the lowest elevation watershed. Uplands were characterized by subalpine fir (*Abies lasicarpa*), Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and ponderosa pine (*Pinus ponderosa*) mixed with grasses, forbs, and exposed rock. Riparian vegetation was composed mainly of gray alder (*Alnus incana*), red osier dogwood (*Cornus sericea*), Rocky Mountain maple (*Acer glabrum*), and water birch (*Betula occidentalis*).

The South Fork Salmon River Basin provided a unique opportunity to study the effect of disturbance on

Table 1. Characteristics of study streams in the Payette National Forest of central Idaho, USA. UA = unaffected by fire or debris flow, FDA = affected by fire and debris flow.

Stream	Watershed disturbance history	Watershed area (km²)	Mean wetted width (m)	Elevation of outlet (m)	Degree days (22 June 2011–19 May 2012)	Discharge (L/s)		
						Late June	Late July	Late August
Camp	Unburned	2.53	3.0	1728	–	–	288.4	121.3
UA 1	Unburned	0.71	1.2	1545	1531	94.6	27.8	7.0
UA 2	Unburned	0.64	1.3	1649	1312	188.8	15.5	12.7
UA 3	Unburned	0.24	0.7	1682	1294	25.0	7.7	5.4
Vibika	Unburned	0.91	1.5	1530	1270	110.0	15.5	8.2
Mean (SD)	Unburned	1.01 (0.89)	1.5 (0.9)	1627 (86)	1352 (121)	104.8 (67.2)	16.6 (121.8)	8.3 (50.6)
Dutchoven	Burned (2007)	1.00	1.0	1160	2024	9.0	4.4	2.4
Telephone	Burned (2007)	1.31	1.3	1164	–	42.6	19.1	9.0
Burned	Burned (2007)	0.22	1.0	1234	2153	2.5	0.4	2.3
Deadman	Burned (2007)	2.35	2.3	1201	1941	121.9	43.4	40.5
Williams	Burned (2007)	1.02	0.9	1140	2103	10.6	3.6	1.6
Mean (SD)	Burned (2007)	1.18 (0.77)	1.3 (0.6)	1180 (37)	2055 (93)	37.3 (49.7)	14.2 (17.9)	11.2 (16.7)
FDA 1	Burned (2007) + DF (2008)	0.34	0.7	1259	2299	2.6	1.3	0.8
Reegan	Burned (2007) + DF (2008)	8.10	4.1	1311	–	–	232.1	94.5
FDA 2	Burned (2007) + DF (2008)	0.20	1.1	1268	2009	13.5	5.6	7.2
FDA 3	Burned (2007) + DF (2008)	0.11	0.6	1335	2198	6.0	0.9	0.6
Frog Pond	Burned (2007) + DF (2008)	1.01	1.5	1237	–	89.5	19.1	11.4
Mean (SD)	Burned (2007) + DF (2008)	1.95 (3.45)	1.6 (1.4)	1282 (40)	2169 (147)	27.9 (41.3)	51.8 (101.1)	22.9 (40.3)

cross-ecosystem fluxes because of its mosaic of fire and debris-flow histories across the landscape. UA watersheds had not burned in 50 y, whereas the East Zone Complex Fire scorched substantial portions of FA watersheds in 2007. Some burned watersheds experienced subsequent debris flows that scoured riparian vegetation and reorganized stream channels in 2008 (Payette National Forest 2010).

Sampling of stream exports

To measure downstream export of OM and sediment, we placed 250-µm-mesh drift nets in the thalweg of study streams and just upstream of their confluences with the mainstem river. We collected drift samples twice monthly from June to August 2011. We deployed nets for ∼24 h during base flow in July and August or 3 times/d (dawn, midday, and dusk) when discharges were elevated in June and early July. The duration of net deployment was adjusted (1–180 min) during dawn, midday, and dusk drift sampling to allow nets to fill but not to clog. We measured water velocity through the nets with a flow meter (±0.01 m/s) (Marsh–McBirney; Hach, Loveland, Colorado) at the beginning and end of each sampling period and at any time the nets were examined for signs of clogging. We calculated the volume of water that traveled through nets during sampling periods as the mean of water velocities at the beginning and end of each sample period × the area of the net opening × the length of deployment.

We subsampled material collected in the nets to measure concentrations of chlorophyll a (chl a) in OM export. At the end of a sampling period, we rinsed each net with stream water and transferred the contents to a 1-L graduated cylinder. We brought the sample volume to 1 L, agitated the sample, and removed a 10- to 25-mL subsample, which we filtered through a precombusted (400°C for 30 min), preweighed, 0.7-µm glass-fiber filter (Millipore IRL, Tullagreen, Ireland). We wrapped filters in aluminum foil and kept them in the dark and on dry ice until processed in the laboratory. In the laboratory, we extracted pigments from filters with methanol and analyzed the extract with a spectrophotometer to calculate chl a concentrations (µg/m^3) (Steinman et al. 2011).

We collected a 2nd subsample in the field to assess C : N of OM export. We put this subsample in a scintillation vial and froze it immediately. In the laboratory, we dried C : N subsamples at 60°C and ball-milled them. The subsamples were analyzed for C and N at the CAMAS Lab at Idaho State University with an Elemental Combustion System 4010 (Costech Analytical Technologies, Santa Clarita, California) interfaced to a Delta V Advantage Mass Spectrometer through the ConFlo IV System (Thermo Scientific, Waltham, Illinois).

We passed the remaining sample through a 125-µm sieve (to ensure that sample contents >250 µm were not lost),

preserved the material on the sieve in 70% ethanol, and transported it to the laboratory. We separated material >1 mm from smaller particles by passing samples through nested sieves. Invertebrates were removed from drift samples collected on the 2nd sampling dates in June, July, and August with the aid of a dissecting microscope (≥7× magnification). For sampling periods when drift samples were taken 3 times/d, we averaged invertebrate biomass (see below) among sampling periods.

Drift-feeding fish primarily consume prey >1 mm (Rader 1997), so we identified all invertebrates >1 mm to the lowest taxonomic level, typically genus, and measured them to the nearest 1.0 mm (± 0.5 mm; Merritt et al. 2008). We separated taxa of terrestrial origin from taxa of aquatic origin for subsequent analyses. We identified Diptera of the family Chironomidae as either Tanypodinae or nonTanypodinae. We also used published length–mass regression equations (Benke et al. 1999) to calculate total exported biomass >1 mm.

We dried (60°C for >24 h), weighed, and combusted (550°C for 4 h) the remaining material. We rewetted, dried, and reweighed the material to calculate concentrations of OM (ash-free dry mass [AFDM]) and sediment (ash).

We collected water samples monthly from June to August 2011. We removed water from the thalweg with a syringe that was triple-rinsed with stream water. We filtered 30 mL of stream water through a membrane filter (0.45 µm; Millipore) into acid-washed bottles with no headspace. We kept water samples frozen until analysis (–20°C) for concentrations of dissolved organic C (DOC) and total dissolved N (TDN) with a Shimadzu Water Analyzer (Shimadzu, Kyoto, Japan) to the nearest 0.001 mg/L. We measured concentrations of orthophosphate and NO_3^-/NO_2^- with a SmartChem Water Analyzer (Mandel Scientific, Guelph, Ontario, Canada). The detection limit (DL) was 0.01 mg/L for both orthophosphate and NO_3^-/NO_2^-. When values were <DL, we assigned them a value of ½DL for statistical analyses (USEPA 1998).

Analyses

Many factors, including fluxes of materials and organisms from streams, can influence effects of wildfire on the stream ecosystem (Gresswell 1999), but we chose to use a comparative, univariate analytical framework because low replication reduced the statistical power to detect differences with a multivariate approach. The spatial scope of our study was constrained by availability of sites influenced by fire and by the temporally intensive sampling and multiple measures of stream export (materials and organisms) required to test our hypotheses. We conducted analyses in SAS (version 9.2; SAS Institute, Cary, North Carolina).

We used repeated-measures analysis of variance (rm-ANOVA) to examine the influences of disturbance type and time on chl a, C : N, AFDM, and sediment in stream ex-

port, and orthophosphate, NO_3^-/NO_2^-, DOC, and TDN in the water column. Before analysis, we used appropriate transformations ($\log[x]$ and $\sqrt{[x]}$) of the data to meet assumptions of normality. We expected that magnitude of differences associated with each category might vary throughout the summer in response to differing flows and the phenology of organisms, so we used Tukey's test to evaluate differences among tributary categories within sampling periods (times). We used a mixed-model repeated measures analysis when data sets included missing variables for 1 point in the time series (e.g., DOC and TDN).

We used nonmetric multidimensional scaling (NMDS in PC-ORD; MjM, Gleneden Beach, Oregon; Kruskal and Wish 1978) to explore patterns in the composition of drifting insects. We used relative biomass of invertebrate export because we were interested in potential consequences for mainstem fish that respond more strongly to biomass than abundance. We excluded rare taxa (relative biomass <5%) from analysis to reduce skewness of the data (Gauch 1982). We tested for significant differences in drift composition among disturbance types with multiresponse permutation procedures (MRPP). We defined *r*-strategist taxa as the families Baetidae, Chironomidae, and Simuliidae to test whether export differed by disturbance type.

We used a graded approach to describe our certainty that results differed from what would be expected by chance alone because *p*-values describe a 'continuous measure of evidence' and are influenced by small sample size (Gelman 2013). Based upon this rationale and convention in biostatistics (Gerstman 2014), for all statistical tests we considered $p < 0.05$ significant, and *p* between 0.05 and 0.1 marginally significant, but of potential ecological meaning, given the low sample size and statistical power of our study.

RESULTS
OM and sediments

Concentrations of chl *a* in stream export (>250 μm) were higher in FA than in UA streams on 3 of 6 sampling times, but differences were greater between FDA and UA streams than between FA and UA streams (FA vs UA: $F_{2,12} = 6.47$, $p = 0.012$; FDA vs UA: $F_{5,60} = 21.87$, $p < 0.001$; Fig. 1). Chl *a* peaked in early July from FDA streams but in early June from FA streams (Fig. 1). Differences in chl *a* among disturbance types decreased as concentrations declined through time, and by late July, were no longer apparent (Fig. 1).

OM (AFDM) in export decreased over the summer ($F_{2,24} = 34.56$, $p < 0.001$), but did not differ among disturbance types ($F_{2,12} = 0.51$, $p = 0.617$; Fig. 2A). Inorganic sediment (ash) in export also decreased over the summer ($F_{2,24} = 8.46$, $p = 0.002$; Fig. 2B). The mean ash concentration was 650% higher from FDA streams than from other disturbance types in late June (FDA: 18.6, FA: 3.0, UA: 1.9 g/m³). However, variability among FDA streams was high, and neither disturbance type nor the time × distur-
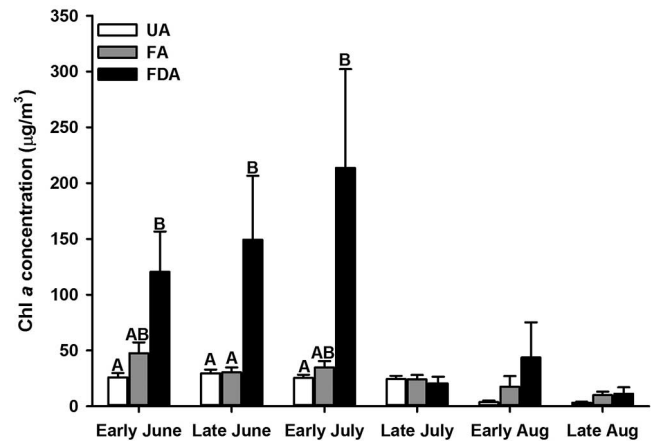

Figure 1. Mean (+1 SE; *n* = 5 for each disturbance type) chlorophyll *a* (chl *a*) in organic matter exported from streams draining watersheds with varying disturbance histories (UA = unaffected by fire, FA = affected by fire, FDA = affected by fire + debris flows) in the South Fork Salmon River Basin of central Idaho, USA, during summer 2011. Bars with the same letter within periods are not significantly different ($p < 0.05$).

bance type effects were significant (time: $F_{2,12} = 2.35$, $p = 0.138$; time × disturbance: $F_{4,24} = 1.79$, $p = 0.165$).

C:N of export differed marginally among disturbance types ($F_{2,12} = 3.25$, $p = 0.075$; Fig. 2C). C:N of export was 24% lower in FDA than in UA streams (FDA: 21.2, UA: 27.8), but the difference was marginally significant ($p = 0.062$). Exported C:N did not differ between FA and UA streams (FA: 22.1, UA: 27.8; $p = 0.429$).

The chl *a*:AFDM ratio of export was higher from FDA streams than from other disturbance types (FDA: 262 μg/g, FA: 220, UA: 112; Fig. 2D). In late June, chl *a*:AFDM was 364% higher from FDA than from UA streams (FDA: 282 μg/g, UA: 71 μg/g; $p = 0.050$) and 298% higher than from FA streams, but this difference was only marginally significant (FDA: 282, FA: 78 μg/g; $p = 0.057$). The chl *a*:AFDM ratio did not differ over time ($F_{2,24} = 1.78$, $p = 0.190$) or among disturbance type at other times in the overall model ($F_{2,12} = 1.47$, $p = 0.269$).

DOC concentrations in the water column were significantly higher in FDA than in UA streams (FDA: 2.8 mg/L, UA: 1.6 mg/L; $p = 0.039$), and marginally higher in FA than in UA streams (FA: 2.6, UA: 1.6 mg/L; $p = 0.085$) (Fig. 3A). Water-column DOC differed marginally over time, and the time × disturbance type effect was marginally significant (time: $F_{2,23} = 2.76$, $p = 0.085$; time × disturbance type: $F_{4,23} = 2.76$, $p = 0.052$). DOC was relatively constant over the summer in UA streams but variable among times in streams with other disturbance types.

Dissolved nutrients

NO_3^-/NO_2^- concentrations in the water column were higher in UA streams than in streams with other distur-
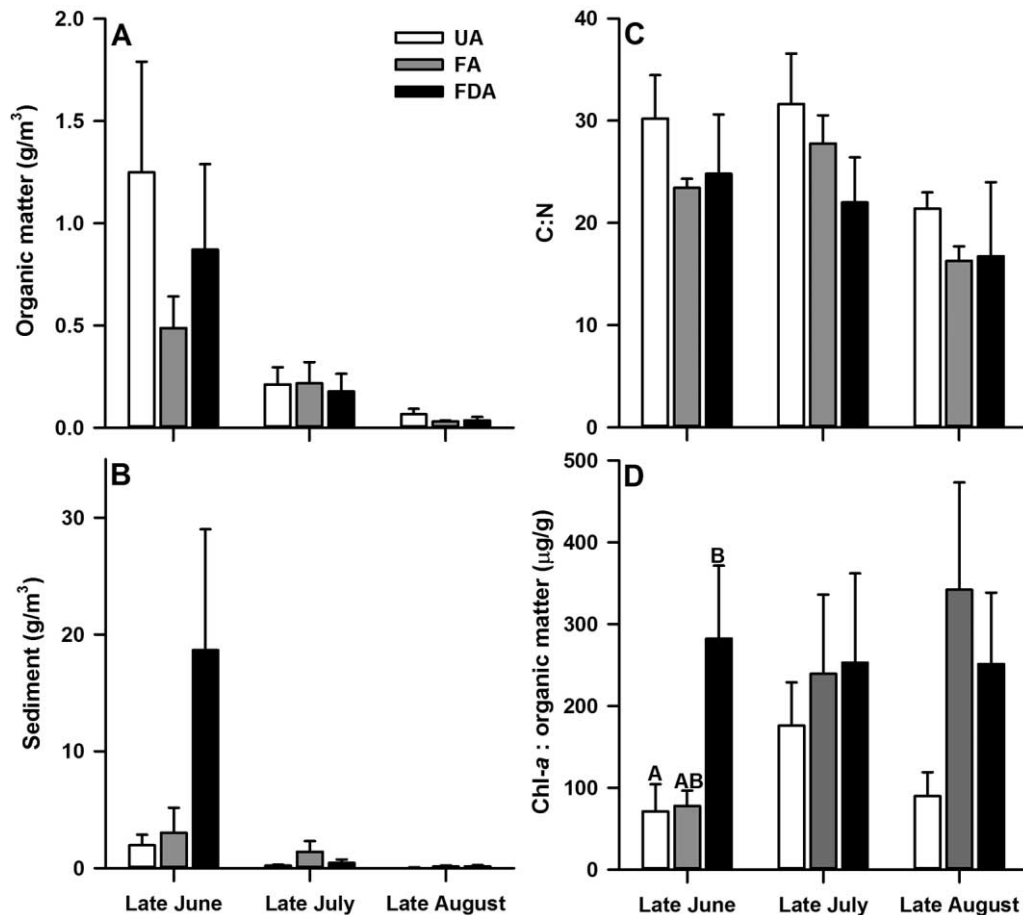
Figure 2. Mean (+1 SE; n = 5 for each disturbance type) organic matter as ash-free dry mass (AFDM) (A), sediment as ash (B), C∶N ratio (C), and chlorophyll a (chl a):AFDM (D) of material exported from streams draining watersheds with varying disturbance histories (UA = unaffected by fire, FA = affected by fire, FDA = affected by fire + debris flows) in the South Fork Salmon River Basin of central Idaho, USA, during summer 2011. Bars with the same letter within periods are not significantly different (p < 0.05).

bance types (UA: 0.06 mg/L, FA: 0.01 mg/L; FDA: 0.01 mg/L; $F_{2,12}$ = 7.64, p = 0.007; Fig. 3B). NO_3^-/NO_2^- in UA streams tended to decrease over time, but remained relatively constant in FA and FDA streams. The disturbance type × time interaction was significant ($F_{2,24}$ = 4.16, p = 0.028), but the time effect was not ($F_{2,24}$ = 2.71, p = 0.113). TDN did not differ among disturbance types ($F_{2,12}$ = 1.51, p = 0.261; Fig. 3C). Orthophosphate concentrations were highly variable and did not differ over time or among disturbance types (time: $F_{2,24}$ = 0.56, p = 0.470; disturbance type: $F_{2,12}$ = 1.27, p = 0.316; Fig. 3D).

Invertebrate exports

Total invertebrate biomass exported and the taxonomic composition of this biomass differed among disturbance types. During summer 2011, total biomass of drifting invertebrates (>1 mm) was 460% higher from FDA streams than from FA and UA streams, but the differences were only marginally significant (FDA: 8.6, FA: 2.8, UA: 1.5 mg/m³;

$F_{2,12}$ = 7.61, p = 0.052; Fig. 4). In June, exported invertebrate biomass was significantly higher (205%) from FDA streams than from FA or UA streams (FDA: 10.5, FA: 2.9, UA: 2.4 mg/m³; FDA vs FA: p = 0.020, FDA vs UA: = 0.012). Exported invertebrate biomass did not differ among disturbance types in July, but in August, export of invertebrate biomass was marginally higher from FDA than from UA streams (FDA: 6.2, UA: 0.6 mg/m³; p = 0.058; Fig. 4). Exported invertebrate biomass decreased over time in FDA and UA streams, and exported invertebrate biomass was highest in June during high stream flows. Exports decreased in July and August ($F_{2,24}$ = 4.46, p = 0.028; Fig. 4), but the time × disturbance type effect was not significant ($F_{4,24}$ = 0.52, p = 0.699).

Taxonomic composition of exported aquatic invertebrates differed significantly among disturbance types (MRPP, p < 0.001; Fig. 5). UA streams exported higher relative biomass of Heptageniidae, Limnephilidae, and Ephemerellidae than did other disturbance types, whereas FDA and FA streams exported higher relative biomass of Baetidae, Si-
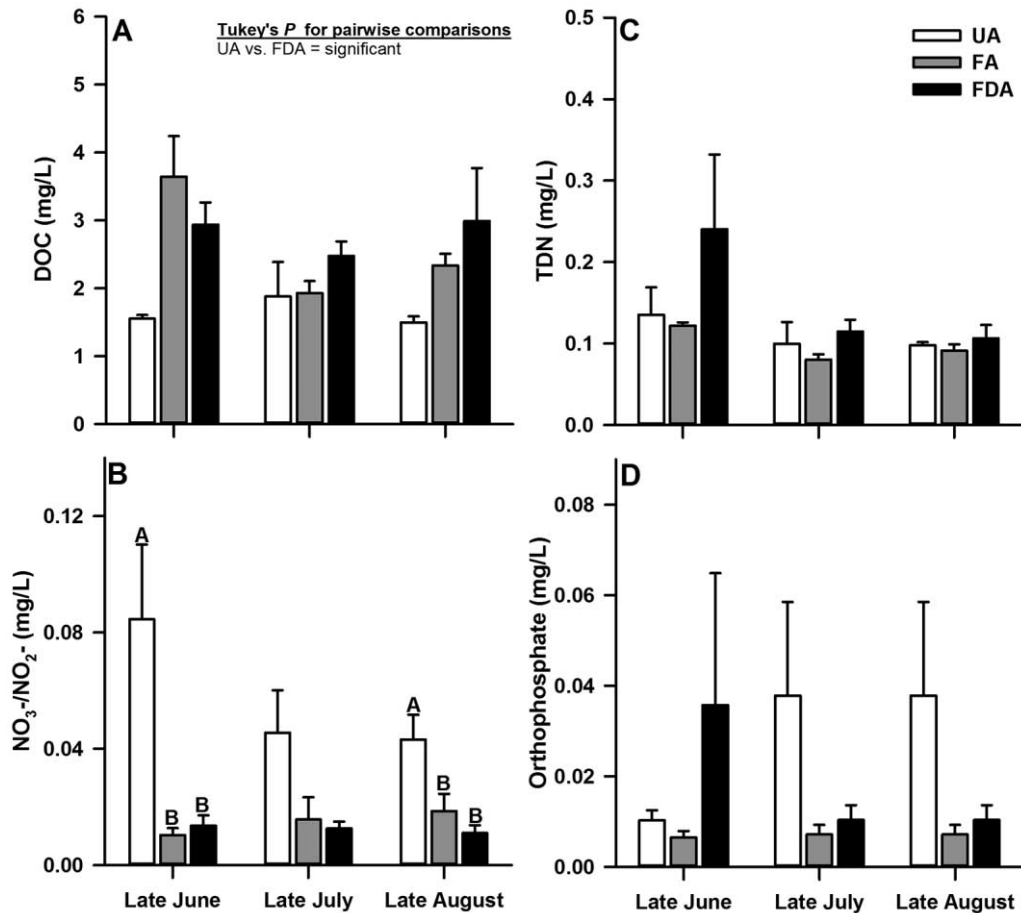
Figure 3. Mean (+1 SE; n = 5 for each disturbance type) concentrations of dissolved organic C (DOC) (A), NO_3^-/NO_2^- (B), total dissolved N (TDN) (C), and orthophosphate (D) in the water column of streams draining watersheds with varying disturbance histories (UA = unaffected by fire, FA = affected by fire, FDA = affected by fire + debris flows) in the South Fork Salmon River Basin of central Idaho, USA, during summer 2011. Significant Tukey's p-values are shown over all pairwise comparisons for an instance when Proc Mixed was used in SAS. Bars with the same letter within periods are not significantly different (p < 0.05).

muliidae, Chironomidae, and Elmidae than did UA streams. FDA streams exported significantly higher relative biomass of r-strategist taxa (Chironomidae, Simuliidae, Baetidae) than did FA or UA streams (Fig. 6A), and relative biomass of r-strategist taxa differed significantly among times (disturbance type: $F_{2,12}$= 4.62, p = 0.033; time: $F_{2,24}$ = 9.31, p = 0.003). FDA streams exported significantly higher biomass concentrations of r-strategist taxa in June than did streams of other disturbance types (FDA vs UA: p = 0.008; FDA vs UA: p = 0.020), and marginally higher concentrations of r-strategist taxa in August than did UA streams (p = 0.091).

In August, terrestrial invertebrates accounted for a large percentage (58%) of total (aquatic + terrestrial) invertebrate biomass exported from streams of all disturbance types (Fig. 4). Inclusion of terrestrial taxa in the NMDS analysis reinforced the differences in taxonomic composition of exported invertebrates among disturbance types (data not shown). Terrestrial invertebrate biomass exported was stable throughout the summer, but differed signifi-

cantly among disturbance types ($F_{2,12}$ = 5.10, p = 0.025). In June, FDA streams exported significantly (p = 0.018) and FA streams exported marginally (p = 0.056) higher terrestrial invertebrate biomass than did UA streams (Fig. 6B).

DISCUSSION

Our results suggest that the occurrence of postfire debris flows can magnify the consequences that fire has on downstream fluxes of materials and organisms. Consistent with hypotheses 3 and 4, when debris flows followed wildfire, affected streams exported OM with higher concentrations of chl a, higher chl a:AFDM (in June), lower C:N, and higher biomass of invertebrates, even though discharge did not differ among disturbance types. Debris flows can have negative effects on stream ecosystems, especially directly affected streams immediately after the disturbance. For example, researchers documented declines in invertebrate diversity (Kobayashi et al. 2010) and the loss
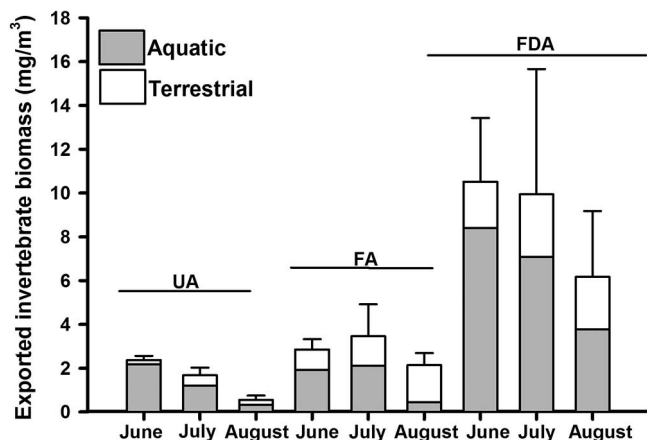
Figure 4. Mean (+1 SE; n = 5 for each disturbance type) aquatic and terrestrial invertebrate biomass exported from streams draining watersheds with varying disturbance types (UA = unaffected by fire, FA = affected by fire, FDA = affected by fire + debris flows) in the South Fork Salmon River Basin of central Idaho, USA, during summer 2011. Sampling times are late June, late July, and late August.

of certain taxa, such as amphibians (Cover et al. 2010) and fish (Lamberti et al. 1991, Sato 2006) following debris flows. However, specific effects can vary with time and among streams (Gresswell 1999). Many researchers have used the term "catastrophic" when describing debris-flow disturbance. Others have documented that delivery of sediment and wood from debris flows increases habitat heterogeneity in downstream reaches over a variety of time scales (Benda et al. 2003, 2004). Our results suggest that disturbance from postfire debris flow may increase the magnitude of invertebrate subsidies and the quality of OM delivered from tributaries to mainstem habitats.

Consistent with hypotheses 2 and 4, composition of aquatic invertebrates exported to downstream habitats by FDA streams was characterized by dominance of r-strategist taxa. Greater dominance by r-strategist taxa has been documented often after disturbance by fire or debris flow (Kiffney et al. 2004, Mellon et al. 2008, Verkaik et al. 2015) and can be associated with higher invertebrate abundance and productivity in disturbed streams (Newbold et al. 1980, Kiffney et al. 2004), possibly because disturbance opens the canopy and increases light to streams (Minshall 2003, Cover et al. 2010). However, in our study, only FDA streams exported more r-strategist taxa (Table 1). The watersheds of all streams affected by wildfire burned 4 y before our study, whereas the effect of debris flows occurred 1 y later. Reestablishment of riparian vegetation following wildfire probably had reduced incoming solar radiation to FA streams by the time we sampled them. Thus, shading from regrowth (evidenced by higher branch densities in riparian zones of FA than FDA streams; Harris 2013) may have reduced primary productivity and, conse-

quently, production of invertebrates in FA streams. In contrast, the scour of debris flow superimposed on postfire riparian vegetation may have allowed more light to reach FDA streams, stimulating primary and secondary production, which may have contributed to higher aquatic invertebrate export from FDA streams.

In our study, streams draining watersheds burned by wildfire, both with and without subsequent debris flow, exported proportionally more biomass of terrestrial invertebrates to downstream habitats than did streams draining unaffected watersheds. We infer that riparian regrowth dominated by alder and dogwood and the presence of downed, decaying wood, may have increased inputs of terrestrial insects to FA and FDA streams compared to riparian areas with mixed, deciduous–coniferous canopies along UA streams (HEH, personal observation). However, our results are in contrast with those of Jackson et al. (2012), who reported that overall inputs of terrestrial invertebrates were highest from riparian forests that remained unburned.

The combination of fire and debris flows altered exports of invertebrate subsidies and changed the quality of OM exports, supporting hypothesis 3. Many mechanisms, such as increased productivity and reduced retention, may be responsible for increased OM quality delivered from tributaries to mainstem habitats following disturbance from fire and debris flow. Reductions in canopy cover have been associated frequently with increased standing crops of
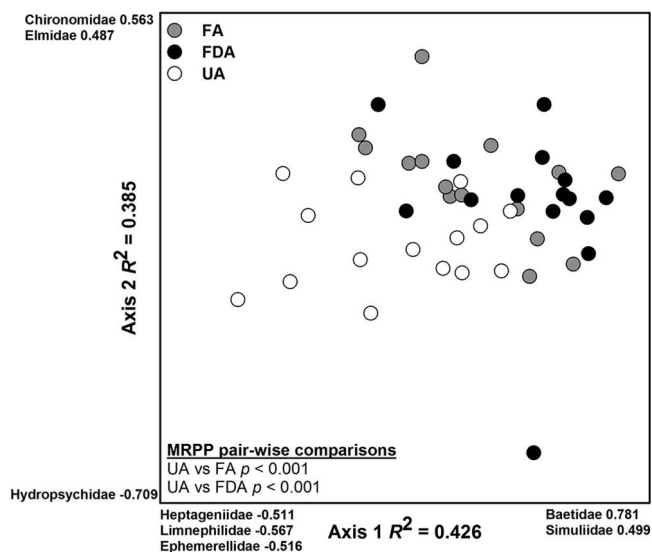

Figure 5. Nonmetric multidimensional scaling plot of relative biomass of aquatic insects >1 mm exported from streams draining watersheds with varying disturbance types (UA = unaffected by fire, FA = affected by fire, FDA = affected by fire + debris flows) in the South Fork Salmon River Basin of central Idaho, USA, during summer 2011. Pearson's correlation coefficients for taxa with strong associations with each axis and multi-response permutation procedures (MRPP) pairwise comparisons are reported.
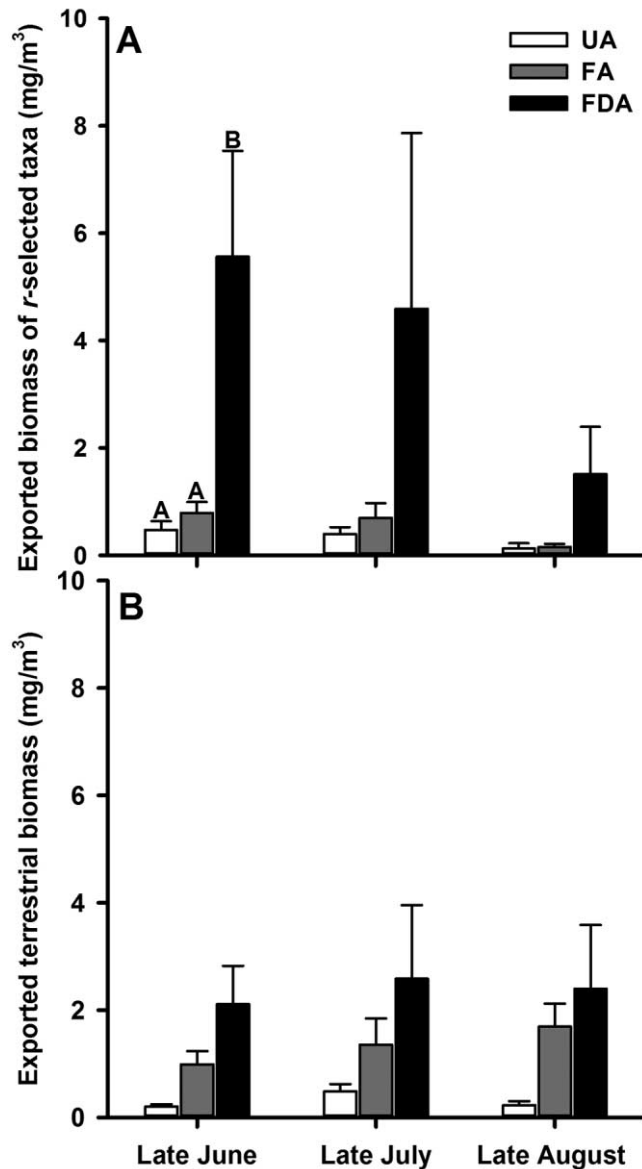
Figure 6. Mean (+1 SE; n = 5 for each disturbance type) biomass of *r*-strategist taxa of the families Chironomidae, Simuliidae, and Baetidae (A) and terrestrial invertebrates (B) exported from streams draining watersheds with varying disturbance types (UA = unaffected by fire, FA = affected by fire, FDA = affected by fire + debris flows) in the South Fork Salmon River Basin of central Idaho, USA, during summer 2011.

stream periphyton (e.g., Bilby and Bisson 1992, Hill et al. 1995), and both fire and debris flows can reduce canopy cover and increase light to streams (Minshall 2003, Cover et al. 2010). Increased periphyton biomass may stimulate uptake of N, potentially explaining why UA streams exported higher concentrations of NO_3^-/NO_2^- and OM with higher C : N than did FA or FDA streams, although a study of in-stream nutrient-spiraling dynamics would be needed to test this possibility.

Reduced retention of OM following debris flows could have contributed to elevated exports of chl *a*, especially in June and July when discharge was elevated. Debris flows reduce retention of OM via export of wood and the destruction of in-channel structures (May 2007), potentially reducing the time stream organisms have to capitalize on resources before they are exported. Furthermore, debris flows may increase DOC in stream water by mobilizing terrestrial soil. Reduction in the number of pools (Gomi et al. 2003) and debris dams (Bilby 1981) following debris flows may reduce flocculation of DOC, thereby increasing export. We think it likely that the combination of increased light and reduced retention contributed to higher-quality exports of OM (i.e., increased chl *a*, lower C : N) from FDA streams.

Changes in fluxes from tributaries may have consequences for the overall productivity of organisms in mainstem rivers. For instance, elevated inputs of DOC and increased quality of OM fluxes from FDA tributaries may stimulate microbes and invertebrates in mainstem rivers. Such disturbances can increase nutrient exports downstream (Spencer et al. 2003, Mast and Clow 2008), which may create spikes in mainstem algal biomass and abundance of primary consumers and predators (Kiffney et al. 2006). Exported sediment also can contribute to habitat diversity and affect macroinvertebrate fauna in mainstem rivers (Rice et al. 2001, 2006). Our results support previous research that underscored the importance of tributaries to the structure and function of mainstem rivers and the role of debris flows following fire in creating hotspots in mainstem productivity. This effect deserves further investigation because wildfires and debris flows are dominant processes in many montane landscapes (Montgomery 1999) that are predicted to increase in response to climate change (Goode et al. 2012), with likely consequences for stream structure and function (Davis et al. 2013).

Our findings suggest that disturbance from fire and subsequent debris flows may alter the timing of resource delivery from tributaries to mainstem habitats. For example, concentration of chl *a* exported from FDA streams increased from early June to early July, but declined in other streams during that period. Meanwhile, exports of aquatic invertebrates declined from all streams as the summer progressed, but exports of terrestrial invertebrates remained generally constant. However, our study encompassed a short time frame. Future investigations should incorporate a longer temporal context because the effect of tributary exports on mainstem habitats may be mediated by the biological and physiological state of organisms in the recipient habitat (Kiffney et al. 2006). Potential asynchronies in the timing of various exports from tributaries may contribute to overall heterogeneity in the riverscape (e.g. Uno and Power 2015) and may benefit certain mobile organisms, such as fish, that may move throughout the network to use pulses of productivity.

LITERATURE CITED

Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. The network dynamics hypothesis: how channel networks structure riverine habitats. BioScience 54: 413–427.

Benda, L., C. Veldhuisen, and J. Black. 2003. Debris flows as agents of morphological heterogeneity, Olympic Mountains, Washington. Geological Society of America Bulletin 115:1110–1121.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18:308–343.

Betts, E. F., and J. B. Jones. 2009. Impact of wildfire on stream nutrient chemistry and ecosystem metabolism in boreal forest catchments on interior Alaska. Arctic, Antarctic, and Alpine Research 41:407–417.

Bilby, R. E. 1981. Role of organic matter debris dams in regulating the export of dissolved and particulate matter from a forested watershed. Ecology 62:1234–1243.

Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540–551.

Bormann, F. H., G. E. Likens, T. G. Siccama, R. S. Pierce, and J. S. Eaton. 1974. The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. Ecological Monographs 44:255–277.

Bruns, D. A., G. W. Minshall, C. E. Cushing, K. W. Cummins, J. T. Brock and R. L. Vannote. 1984. Tributaries as modifiers of the river continuum concept: analysis by polar ordination and regression models. Archiv für Hydrobiologie 99:255–277.

Cover, M. R., J. A. de la Fuente, and V. H. Resh. 2010. Catastrophic disturbances in headwater streams: the long-term ecological effects of debris flows and debris floods in the Klamath Mountains, northern California. Canadian Journal of Fisheries and Aquatic Sciences 67:1596–1610.

Davis, J. M., C. V. Baxter, E. J. Rosi-Marshall, J. L. Pierce, and B. T. Crosby. 2013. Anticipating stream ecosystem responses to climate change: towards predictions that incorporate effects via land–water linkages. Ecosystems 16:909–922.

Dunham, J. B., A. E. Rosenberger, C. H. Luce, and R. E. Rieman. 2007. Influences of wildfire and channel reorganiza-

tion on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. Ecosystems 10:335–346.

Dwire, K. A., and J. B. Kauffman. 2003. Fire and riparian ecosystems in landscapes of the western USA. Forest Ecology and Management 178:61–74.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York.

Gelman, A. 2013. P values and statistical practice. Epidemiology 24:69–72.

Gerstman, B. B. 2014. Basic biostatistics. Jones and Bartlett Publishers, Sudbury, Massachusetts.

Gomi, T., R. C. Sidle, and J. S. Richardson. 2002. Understanding processes and downstream linkages of headwater streams. BioScience 52:905–916.

Gomi, T., R. C. Sidle, R. D. Woodsmith, and M. D. Bryant. 2003. Characteristics of channel steps and reach morphology in headwater streams, southeast Alaska. Geomorphology 51: 225–242.

Goode, J. R., C. H. Luce, and J. M. Buffington. 2012. Enhanced sediment delivery in a changing climate in semi-arid mountain basins: implications for water resource management and aquatic habitat in the northern Rocky Mountains. Geomorphology 140:1–15.

Gresswell, R. E. 1999. Fire and aquatic ecosystems in forested biomes of North America. Transactions of the American Fisheries Society 128:193–221.

Harris, H. E. 2013. Disturbance cascade: how fire and debris flow affect headwater linkages to downstream and riparian ecosystems. MS Thesis, Department of Biological Sciences, Idaho State University, Pocatello, Idaho.

Hill, W. R., M. G. Ryon, and E. M. Schillings. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. Ecology 76:1297–1309.

Jackson, B. K., S. M. P. Sullivan, and R. L. Malison. 2012. Wildfire severity mediates fluxes of plant material and terrestrial invertebrates to mountain streams. Forest Ecology and Management 278:27–34.

Kiffney, P. M., C. M. Greene, J. E. Hall, and J. R. Davies. 2006. Tributary streams create spatial discontinuities in habitat, biological productivity, and diversity in mainstem rivers. Canadian Journal of Fisheries and Aquatic Sciences 63:2518–2530.

Kiffney, P. M., C. J. Volk, T. J. Beechie, G. L. Murray, G. R. Pess, and R. L. Edmonds. 2004. A high-severity disturbance event alters community and ecosystem properties in West Twin Creek, Olympic National Park, Washington, USA. American Midland Naturalist 152:286–303.

Kobayashi, S., S. Gomi, R. C. Sidle, and Y. Takemon. 2010. Disturbances structuring macroinvertebrate communities in steep headwater streams: relative importance of forest clear-cutting and debris flow occurrence. Canadian Journal of Fisheries and Aquatic Sciences 67: 427–444.

Kruskal, J. B., and M. Wish. 1978. Multidimensional scaling. Sage Publications, Beverly Hills, California.

Lamberti, G. A., S. V. Gregory, L. A. Ashkenas, R. C. Wildman, and K. M. S. Moore. 1991. Stream ecosystem recovery following a catastrophic debris flow. Canadian Journal of Fisheries and Aquatic Sciences 48:196–208.

Malison, R. L., and C. V. Baxter. 2010a. Effects of wildfire of varying severity on benthic stream insect assemblages and emergence. Journal of the North American Benthological Society 29:1324–1338.

Malison, R. L., and C. V. Baxter. 2010b. The fire pulse: wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. Canadian Journal of Fisheries and Aquatic Sciences 67:570–579.

Mast, M. A., and D. W. Clow. 2008. Effects of 2003 wildfires on stream chemistry in Glacier National Park, Montana. Hydrologic Processes 22:5013–5023.

May, C. L. 2007. Sediment and wood routing in steep headwater streams: an overview of geomorphic processes and their topographic signatures. Forest Science 54:119–130.

May, C. L., and R. E. Gresswell. 2003a. Large wood recruitment and redistribution in headwater streams in the southern Oregon coast range, U.S.A. Canadian Journal of Forest Research 33:1352–1362.

May, C. L., and R. E. Gresswell. 2003b. Processes and rates of sediment and wood accumulation in headwater streams of the central Oregon Coast Range. Earth Surface Processes and Landforms 28:409–424.

Mellon, C. D., M. S. Wipfli, and J. L. Li. 2008. Effects of forest fire on headwater stream macroinvertebrate communities in eastern Washington, U.S.A. Freshwater Biology 53:2331–2343.

Merritt, R. K., K. W. Cummins, and M. D. Berg (editors). 2008. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing, Dubuque, Iowa.

Minshall, G. W. 2003. Responses of stream benthic macroinvertebrates to fire. Forest Ecology and Management 178:155–161.

Minshall, G. W., J. T. Brock, and J. D. Varley. 1989. Wildfires and Yellowstone stream ecosystems. BioScience 39:707–715.

Montgomery, D. R. 1999. Process domains and the river continuum. Journal of the American Water Resources Association 35:397–410.

Newbold, J. D., D. C. Erman, and K. B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Canadian Journal of Fisheries and Aquatic Sciences 37:1076–1085.

Odum, E. P. 1985. Trends expected in stressed ecosystems. BioScience 35:419–422.

Payette National Forest. 2010. Bald Hill prescribed burn project environmental assessment. Project Record 40 CFR 1502.21. US Department of Agriculture Forest Service, McCall, Idaho.

Pianka, E. R. 1970. On r- and K-selection. American Naturalist 940:592–597.

Rader, R. B. 1997. A functional classification of the drift: traits that influence availability to salmonids. Canadian Journal of Fisheries and Aquatic Sciences 54:1211–1234.

Rice, S. P., R. I. Ferguson, and T. B. Hoey. 2006. Tributary control of physical heterogeneity and biological diversity at river confluences. Canadian Journal of Fisheries and Aquatic Sciences 63:2553–2566.

Rice, S. P., M. T. Greenwood, and C. B. Joyce. 2001. Tributaries, sediment sources, and the longitudinal organization on macroinvertebrate fauna along river systems. Canadian Journal of Fisheries and Aquatic Sciences 58:824–840.

Rieman, B. E., R. E. Gresswell, and J. Rinne. 2012. Fire and fish: a synthesis of observations and experience. Pages 159–175 in C. Luce, P. Morgan, K. Dwire, D. Isaak, Z. Holden, and B. Rieman (editors). Climate change, forests, fire, water, and fish: building resilient landscapes, streams, and managers. General Technical Report RMRS-GTR-290. US Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Romme, W. H., M. S. Boyce, R. Gresswell, E. H. Merrill, G. W. Minshall, C. Whitlock, and M. G. Turner. 2011. Twenty years after the 1988 Yellowstone fires: lessons about disturbance and ecosystems. Ecosystems 14:1196–1215.

Rugenski, A. T., and G. W. Minshall. 2014. Climate-moderated responses to wildfire by macroinvertebrates and basal food resources in montane wilderness streams. Ecosphere 5(3):25.

Sato, T. 2006. Dramatic declines in population abundance of Salvelinus leucomaenis after a severe flood and debris flow in a high gradient stream. Journal of Fish Biology 69:1849–1854.

Spencer, C. N., K. O. Gabel, and F. R. Hauer. 2003. Wildfire effects on stream food webs and nutrient dynamics in Glacier National Park, USA. Forest Ecology and Management 178:141–153.

Steinman, A. D., G. A. Lamberti, and P. R. Leavitt. 2011. Biomass and pigments of benthic algae. Pages 327–356 in F. R. Hauer and G. A. Lamberti (editors). Methods in stream ecology. Academic Press, Waltham, Massachusetts.

Torgersen, C. E., R. E. Gresswell, D. S. Bateman, and K. M. Burnett. 2008. Spatial identification of tributary impacts in river networks. Pages 159–181 in S. P. Rice, A. G. Roy, and B. L. Rhoades (editors). River confluences, tributaries, and the fluvial network, John Wiley and Sons, Ltd., Hoboken, New Jersey.

Uno, H., and M. E. Power. 2015. Mainstem-tributary linkages by mayfly migration help sustain salmonids in a warming river network. Ecology Letters. doi:10.1111/ele.12483

USEPA (US Environmental Protection Agency). 1998. Guidance for data quality assessment: practical methods for data analysis. EPA/600/R-96/084. Office of Research and Development, US Environmental Protection Agency, Washington, DC.

Verkaik, I., M. Rieradevall, S. D. Cooper, J. M. Melack, T. L. Dudley, and N. Prat. 2013. Fire as a disturbance in Mediterranean climate streams. Hydrobiologia 719:353–382.

Verkaik, I., M. Vila-Escalé, M. Rieradevall, C. V. Baxter, P. S. Lake, G. W. Minshall, P. Reich, and N. Prat. 2015. Stream macroinvertebrate community responses to fire: are they the same in different fire-prone biogeographic regions? Freshwater Science 34:1527–1541.

Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries 35:373–387.

Wipfli, M. S., and D. P. Gregovich. 2002. Export of invertebrates and detritus for fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. Freshwater Biology 47:957–969.

Wondzell, S. M., and J. G. King. 2003. Postfire erosional processes in the Pacific Northwest and Rocky Mountain regions. Forest Ecology and Management 178:75–87.