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RESEARCH ARTICLE

Wildfire and debris flows affect prey subsidies with implications for riparian and riverine predators

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Abstract

Ecosystems are connected through fluxes of nutrients, organic matter, and organisms. Disturbances that alter structure and function of one ecosystem may have consequences for other linked ecosystems. We investigated how wildfire and subsequent debris flows altered fluxes of invertebrates from tributaries in the Salmon River Basin, Idaho, USA. We compared fluxes of invertebrates downstream through drift and laterally via insect emergence from streams with varying disturbance histories (unburned, burned, and burned + debris flow) during two summers (3–4 years post fire and 2–3 years post debris flow). We observed that the combination of wildfire and debris flow increased the biomass export of invertebrates from tributaries to main-stem ecosystems 2–3 × compared to other streams. In contrast, aquatic insect emergence did not differ in magnitude among streams of different disturbance histories, but instead diverged in timing. Underwater surveys indicated trout in the main-stem river selected confluence habitats, with a tendency for stronger selection of confluences with burned streams. In a behavioral comparison between confluence and non-confluence habitats, rates of agonistic behavior were 4–6 × higher in confluence areas, indicating that confluences may be worth defending. Abundances of web-spinning spiders that depend on emerging insects did not vary with disturbance history in early-mid summer, but tended to be highest in riparian areas along burned streams by August. Because wildfire and debris flows are predicted to increase, our results elucidate potential pathways by which altered disturbance regimes may affect coupled aquatic-terrestrial ecosystems.

Keywords Invertebrate drift · Spatial subsidies · Insect emergence · Food webs · River confluences

Introduction

Disturbance is a fundamental ecological driver that determines species distribution and alters processes in ecosystems (Turner 2010). Ecosystems are connected to one another by the movement of nutrients, organic matter, and organisms (Polis et al. 1997). Thus, disturbance that alters nutrient cycling, productivity, or species composition of one ecosystem may have consequences for others because they are interconnected (McNaughton 1992). Evidence is mounting that such effects in adjacent ecosystems may span multiple trophic levels (Spiller et al. 2010), but this has received substantially less investigation than *in situ* consequences of disturbance. Moreover, ecosystems are typically influenced not just by single natural disturbances, but by an array whose combined effects may differ from those of individual events (Hughes and Connell 1999; Franssen et al. 2006; Bixby et al. 2015). Yet, few studies have addressed such combinations, let alone their effects via changes in fluxes between habitats.

A headwater stream is a prime example of an ecosystem linked to others. From their watersheds, headwater streams receive nutrients, organic matter, and organisms that contribute to their overall metabolism (Hynes 1975). In turn, headwaters subsidize neighboring ecosystems through transport of nutrients, organic matter, and organisms to downstream environments (Vannote et al. 1980; Rice et al. 2008; Wipfli and Baxter 2010), and the emergence of adult aquatic insects to the adjacent riparian forest (Jackson and Fisher 1986). Downstream subsidies may increase productivity in the recipient, main-stem habitats (Polis et al. 1997; Gomi et al. 2002). For example, Kiffney et al. (2006) demonstrated that concentrations of nitrogen and phosphorus, algal biomass, and abundance of primary consumers and predators were

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highest at or below tributary junctions. Similarly, Wipfli and Gregovich (2002) estimated that exports of detritus and invertebrates from fishless tributaries supply enough energy to support 100–2000 young-of-the-year salmonid fish per km of fish-bearing stream. Such studies highlight the ecological importance of tributary junctions and the connectivity of headwaters to main-stem food webs.

Headwaters also subsidize riparian zones through the emergence of adult aquatic insects, which can contribute substantially (25–100%) to energy intake by riparian predators such as spiders, birds, and bats (Baxter et al. 2005; Marczak et al. 2007). For example, using a stable isotope tracer, Sanzone et al. (2003) showed that aquatic production accounted for nearly 100% of carbon and 39% of nitrogen assimilated by riparian web-spinning spiders. Similarly, Nakano and Murakami (2001) established that adult aquatic insects provided about a quarter of the annual energy budget for an assemblage of riparian birds. Because headwaters provide invertebrate prey to consumers in adjacent main-stem rivers and riparian forests, multiple disturbances that affect headwaters may also affect consumers in these linked ecosystems (e.g., Davis et al. 2013).

Wildfire and subsequent debris flows (liquefied landslides that reorganize stream channels) are major ecological disturbances that may affect headwater linkages in temperate, mountainous regions. Wildfire has the potential to increase in-stream primary productivity and insect abundance as well as alter the dynamics of allochthonous inputs and woody debris in streams (Gresswell 1999; Minshall 2003). Such increases in aquatic insects may "spill over" to adjacent ecosystems. For example, Malison and Baxter (2010) reported that biomass of emerging aquatic insects from streams with drainages that burned with high severity was 2 × higher than from unburned streams. This corresponded to higher abundances of spiders that specialize on adult aquatic insects (i.e. Tetragnathidae) and higher rates of bat calls surrounding burned vs. unburned streams. Fire also increases the likelihood of large-scale erosional events such as debris flows (Miller et al. 2003), which may modify the effects of fire on streams. For instance, debris flows further alter disturbed streams by reducing canopy cover and increasing channel scour. This can decrease retention of stream organic matter and modify species composition (Cover et al. 2010). Ecological theory predicts that stressed ecosystems exhibit reduced internal efficiency, leading to increased exports of resources to linked ecosystems (Odum 1985). Thus, wildfire and debris flows may increase spillover of resources such as invertebrates to neighboring ecosystems.

Both wildfire and debris flows alter habitat characteristics in riparian areas and tributary confluences with main-stem rivers, which indirect evidence suggests may mediate responses of invertivorous predators. Marczak et al. (2007) hypothesized that physical and biotic factors might modify retention and permeability of such ecosystem boundaries. Debris flows may simultaneously modify the retention of adult aquatic insects in the riparian area and attachment points for web-spinning spiders through scour of riparian vegetation. They may also alter retention of invertebrates in confluence areas and the profitability of such habitats for fish. For example, through export of wood, boulders, and sediment from tributaries, debris flows can increase main-stem habitat heterogeneity, potentially benefitting drift-feeding fish (Bigelow et al. 2007). Thus, the combination of wildfire and debris flow may affect riparian spiders and main-stem fishes by modifying boundary characteristics as well as changing availability of prey.

Here, we investigate how two related disturbances, wildfire and subsequent debris flows, alter the fluxes of aquatic invertebrates to bordering downstream and riparian ecosystems, and how altered fluxes of invertebrate prey may change predator abundances (i.e. fish and terrestrial spiders) in these linked environments. We address the following hypotheses through a comparative approach: (1) disturbance leads to increased fluxes of prey resources from the affected ecosystem to linked ecosystems, and (2) these elevated subsidies to adjacent ecosystems increase local abundances of predators. A component of hypothesis 1 was evaluated as part of a previous analysis (Harris et al. 2015) focusing only on longitudinal fluxes from tributaries to main-stem habitats. Here, we extend this to include lateral fluxes and investigation of potential responses by aquatic and terrestrial insectivores.

Methods

Study area and design We selected first through third order study streams ($n = 4$ unburned, $n = 4$ burned, and $n = 4$ burned + debris flow drainages in August 2010 and $n = 5$ per disturbance class in June–August 2011) in the Payette National Forest in the Salmon River Mountains of central Idaho, USA (Fig. 1; Table 1). In this study, the disturbance history across the landscape largely dictated our choice of stream replicates. Unburned drainages had not been burned substantially in the last 50 years (as classified by satellite imagery). Drainages classified as either burned or burned + debris flow were burned substantially in the East Zone Complex Fire in 2007. Burned + debris flow streams subsequently experienced liquefied landslides in 2008 that scoured riparian vegetation and reorganized channels as a result of a localized cloud burst. All debris flows studied reached the main-stem river and encompassed the entire study reach. Satellite imagery collected in July 2008 indicated that fire severity (as measured by Burned Area Reflectance Classification) ranged from low to high in burned and burned + debris flow catchments (Table 1, Payette National Forest 2010). Initial sampling occurred during 2010, 3 years

Fig. 1 Representative photographs of streams with varying disturbance classes (**a** unburned in the last 50 years, **b** burned in 2007 with subsequent debris flow in 2008, and **c** burned in 2007 with no subsequent debris flow)

post wildfire and 2 years post-debris flows. Additional sampling occurred in 2011, 4 years post wildfire and 3 years post debris flows. Effects of wildfire on stream ecosystems are usually diminished after 10 years (Minshall 2003), whereas effects of debris flows can persist for a century (Cover et al. 2010). We studied mid-term (> 2 and < 10 years post disturbance) effects of fire and debris flows.

Study streams were high gradient tributaries (mean basin slope 23°–40°) that flowed into the East Fork of the South Fork Salmon River or into Profile Creek, one of its major tributaries. These tributaries (drainage area 0.26–20.98 km^2) were characterized by steep topography and erosion-prone soils derived from Idaho Batholith granite; elevations ranged from 1140 to 1728 m at their confluences with the East Fork of the South Fork Salmon River or Profile Creek. Mean annual precipitation ranged from 63.5 cm at the highest elevation drainage to 52.0 cm at the lowest elevation drainage. Peak stream flows were driven by snowmelt in May and June, with base flows occurring from August to September. Uplands were principally characterized by subalpine

Table 1 Characteristics of study streams in the Payette National Forest of central Idaho, USA

Stream	Watershed disturbance history	Burn severity (from BARC)	Watershed area (km^2)	Mean wetted width (m)	Elevation of outlet (m)	Degree days	Branch density (no./m)	Discharge (L/s)			Mean basin slope (°)
								June	July	August	
Camp	Unburned	Unburned	6.55	3	1728	–	5.1	–	288.4	121.3	23
Unburned 1	Unburned	Unburned	1.84	1.2	1545	1531	10.5	94.6	27.8	7	29
Unburned 2	Unburned	Unburned	1.66	1.3	1649	1312	7.8	188.8	15.5	12.7	23
Unburned 3	Unburned	Unburned	0.62	0.7	1682	1294	29.8	25	7.7	5.4	26
Vibika	Unburned	Unburned	2.36	1.5	1530	1270	7.4	110.1	15.5	8.2	25
Mean (SD)	NC	NC	2.61 (2.29)	1.5 (0.9)	1627 (86)	1352 (121)	12.1 (4.5)	104.8 (67.2)	16.6 (121.8)	8.3 (50.6)	25 (2)
Dutchoven	Burned	Low	2.59	1	1160	2024	8.1	9	4.4	2.4	30
Telephone	Burned	Low	3.39	1.3	1164	–	3.9	42.6	19.1	9	31
Burned	Burned	Low–moderate	0.6	1	1234	2153	5.8	2.5	0.4	2.3	32
Deadman	Burned	Moderate–high	6.09	2.3	1201	1941	7.1	121.9	43.4	40.5	30
Williams	Burned	Low–moderate	2.64	0.9	1140	2103	6	10.6	3.6	1.6	29
Mean (SD)	NC	NC	3.06 (1.98)	1.3 (0.6)	1180 (37)	2055 (93)	6.2 (0.7)	37.3 (49.7)	14.2 (17.9)	11.2 (16.7)	30 (1)
Burned + DF 1	Burned + DF	Low–moderate	0.88	0.7	1259	2299	2.7	2.6	1.3	0.8	35
Reegan	Burned + DF	Low–moderate	20.98	4.1	1311	–	11.8	–	232.1	94.5	24
Burned + DF 2	Burned + DF	Low–moderate	0.52	1.1	1268	2009	2.3	13.5	5.6	7.2	40
Burned + DF 3	Burned + DF	Low–moderate	0.28	0.6	1335	2198	1.9	6	0.9	0.6	39
Frog Pond	Burned + DF	Low–high	2.62	1.5	1237	–	1.1	89.5	19.1	11.4	25
Mean (SD)	NC	NC	5.06 (8.95)	1.6 (1.4)	1282 (40)	2169 (147)	3.9 (2.0)	27.9 (41.3)	51.8 (101.1)	22.9 (40.3)	33 (8)

Degree days calculated based on date range of 6/22/2011 to 5/19/2012

SD standard deviation. *DF* debris flow, *BARC* burned area reflectance classification, *NC* not calculated, '–' missing data fir (*Abies lasicarpa*), Douglas-fir (*Pseudotsuga menziesii*), Engelman 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 serica*), Rocky Mountain maple (*Acer glabrum*), and water birch (*Betula occidentalis*).

Size of streams did not differ systematically with disturbance history. Burned and burned + debris flow streams accumulated more degree days than unburned streams (2055°, 2169°, and 1352° days between 22 June 2011 and 19 May 2012, respectively, Table 1), although burned and burned + debris flow streams did not differ from one another ($P = 0.46$). We chose to study tributaries that were small relative to the size of the mainstem (Table 1) because we wanted to evaluate the potential influence of prey inputs from tributaries on fishes in the mainstem independent of major thermal patches or changes in main-stem habitat morphometry typically created at confluences with relatively large tributaries (Benda et al. 2004). Although the East Fork of the South Fork Salmon River was not gaged, overall contribution of study stream flow to the main-stem flow was likely low based on a comparable nearby gage. The East Fork of the South Fork Salmon River and the South Fork Salmon River are similarly sized rivers (drainage areas of 1092 and 853 km^2, respectively); therefore, we used discharge data from a nearby (< 5 km) USGS gage (#13310700, South Fork Salmon River near Krassel Ranger Station) as a proxy. On the three sampling dates when flow was measured in our study streams (6/22/2011, 7/20/2011, and 8/27/2011), discharge from the South Fork Salmon River was 96.8 m^3/s, 20.5 m^3/s, and 5.8 m^3/s, respectively. Based on this information, tributary flows made up less than 0.5% of the flow in the main-stem river.

In late August 2010, we conducted a late summer "snapshot" of sampling on 12 streams (4 streams of each disturbance class) to explore variation in export of invertebrates and predator distribution that may occur in this time period. In 2011, we expanded our study to include an additional replicate per disturbance class (5 streams of each disturbance class) to increase our power to detect differences. In 2011, we also collected a time series of data between June and August ($n = 3$) to investigate potential patterns in export and predator responses throughout a season. The hydrologic context of sample collection differed between the two study years; 2010 was an average snow and runoff year with a pronounced peak in early June whereas in 2011, flows remained significantly elevated into July and the entire summer season was characterized by above average flows (USGS gage #13310700).

Drift sampling- In late August 2010 ($n = 1$ time period) and on a monthly basis (June–August, $n = 3$) in 2011, we measured downstream drift to test whether export of invertebrate biomass to adjacent ecosystems would be higher from burned and burned + debris flow tributaries than from unburned tributaries. We placed 250 µm mesh drift nets in riffle/run habitat of tributaries ($n = 4$ for each disturbance class in 2010 and $n = 5$ in 2011), within the thalweg and immediately upstream of their junction with the mainstem. Nets were deployed approximately 24 h during base flow in August 2010 and 2011 or for three times per day (dawn, midday, and dusk) during higher flows in June and July 2011. During the dawn, midday, and dusk drift samples, the duration of the net deployment was adjusted to allow for the nets to sufficiently fill but not clog (range 1–180 min). When nets were deployed for 24 h, they were checked every 4–8 h for signs of clogging and depth and water velocity were recorded at each check.

We standardized all drift sample measurements by the volume of water sampled, which was calculated based on measures of average velocity through the net (± 0.01 m s^{-1}) taken with a flow meter (Marsh-McBirney, The Hach Company, Loveland, CO, USA) at the beginning and end of each sample collection. Drift samples were preserved in 95% ethanol prior to taxa identification. Invertebrates were removed from samples under a dissection microscope (≥ 7 × magnification). Because fishes investigated in the main-stem river (*Oncorhynchus clarkii, O. mykiss* and *O. tshawytscha, Prosopium williamsoni*, and *Salvelinus confluentus*) primarily consume prey ≥ 1 mm (Gerking 1994; Rader 1997), we focused our subsequent analyses on invertebrates in this range. We identified all of these invertebrates (≥ 1 mm) to the lowest practical 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 analysis. Terrestrial insects and non-insects were more coarsely identified, typically to order. For each taxon, we used length-mass regression equations (from Benke et al. 1999) to calculate total exported biomass. For periods when drift samples were taken three times per day, concentrations of invertebrate biomass were averaged across sample times.

Emergence sampling On a monthly basis during summer 2011 ($n = 3$, June–August), emergence of aquatic insects was sampled with sticky traps, an established method used in various ecosystems (Baxter et al. 2017). Polyvinyl chloride posts ($n = 5$, 2.5 m length) were driven into alternating sides of the bank of each stream ($n = 5$ per disturbance class) at 20-m intervals (Fig. 1). Acetate cylinders (100 cm^2) were attached to the posts (height 1.5–2 m) and painted with a sticky substance (Tanglefoot, The Tanglefoot Company, Grand Rapids, MI, USA). Traps were deployed for ca. 2 weeks monthly from June through August 2011. Insects were identified under a dissection microscope (≥ 6.3 × magnification). We identified most adult aquatic insects to order (Ephemeroptera, Plecoptera, and Trichoptera), but identified

Diptera to family, because that resolution allowed distinction between terrestrial and aquatic taxa (Merritt et al. 2008). We measured each insect to the nearest 1.0 mm (± 0.5 mm) and calculated biomass of adult aquatic insects using length-mass regressions (from Sabo et al. 2002).

Fish sampling We conducted fish surveys to test whether higher biomass of invertebrate prey from disturbed tributaries were associated with higher abundances of fish in the confluence habitat of the recipient main-stem river. In August 2010, we conducted daytime underwater surveys (via mask and snorkel) to estimate fish relative abundances in the main-stem habitat encompassing the confluence with each tributary ($n = 4$ for each disturbance class). Surveys lasted 45–60 min and included a stream length of 75–100 m, encompassing area above and below each confluence. We drew maps of the surveyed area and estimated width, depth, and length of each habitat to calculate approximate volume available to fish within habitat units (confluence, pool, riffle, and glide). We identified fish (which included *O. clarkii, O. mykiss* and *O. tshawytscha, P. williamsoni*, and *S. confluentus)* in each habitat unit (confluence and non-confluence) to species and estimated their length to the nearest 5 cm. Habitat selection ratios (for confluence and non-confluence habitats) were calculated as the proportion of each species occupying a particular habitat/proportion of total habitat volume available.

To help identify mechanisms responsible for selection of confluence habitat by fish, we conducted paired behavioral observations of fish in confluence areas and in nearby, similar habitats that lacked inputs from a tributary. Observations of fish in confluence areas were collected in the main-stem river at the intersection of a burned tributary (confluence 1) and at the intersections of two burned + debris flow tributaries (confluences 2 and 3). Observations were recorded in August 2011, to investigate whether fish behavior may be different in confluence areas with concentrated invertebrate inputs from tributaries. Fish may preferentially use confluence habitats for many reasons, including modified temperature, habitat features (Scarnecchia and Roper 2000), position in the drainage basin (Osborne and Wiley 1992), increased benthic productivity, or increased drifting prey availability (Fausch 1984; Wipfli and Gregovich 2002). We chose confluences that were strongly selected by trout and had high invertebrate inputs from tributaries, which we documented in August 2010.

We performed underwater surveys of fish abundance and behavior (scan and focal observations) with each survey lasting approximately 1 h. Surveys were repeated 3–4 times per confluence, and the starting time of each was randomized to account for varying feeding patterns throughout the day. At the beginning of each survey, we recorded all fish species present and their sizes (± 5 cm). We observed both rainbow trout (*O. mykiss*) and juvenile Chinook salmon (*O. tshawytscha*) as focal fish, because these species were most common in these confluence areas. Each focal fish was observed for 5 min, and all feeding attempts and agonistic behaviors (both chases and fleeing) were recorded. During each survey, we conducted at least 3 focal fish observations per species ($n = 42$ juvenile Chinook and 38 rainbow trout). Concurrent observations of focal fish were conducted in nearby, non-confluence habitats that did not receive direct inputs from a tributary, but that possessed similar water depth and velocity as confluence habitats ($n = 63$ juvenile Chinook salmon and 56 rainbow trout). We predicted that rates of feeding and agonistic behavior would be higher in confluence areas than in nearby non-confluence areas because of inputs of invertebrate prey delivered from tributaries to confluences.

Spider sampling During the late August "snapshot" sampling in 2010, we conducted surveys of riparian spiders along 3, 10-m transects that were spaced every 10 m ($n = 4$ streams per disturbance class). In 2011, we included an additional replicate per disturbance class ($n = 5$ streams per disturbance class), increased total survey length per stream to 50 m (5, 10-m transects spaced every 10 m) to increase our power to detect differences, and sampled monthly throughout the summer ($n = 3$, June–August) to explore spider population dynamics. We conducted surveys after dusk using high-power flashlights (Surefire, Fountain Valley, CA, USA). During each survey event, all sites were visited within 3 days of one another. Observers walked up the stream and counted all web-spinning spiders on both banks above the active channel and within 1 m of the stream edge to a maximum height of 2.5 m. Spiders were identified to family on sight, which was accomplished based on web construction and body morphology (Ubick et al. 2005). Although we recorded all spiders, we focused analyses on web-spinning spiders (i.e., Tetragnathidae, Araneidae, Linyphiidae) because these taxa rely on and can closely track adult aquatic insects (Marczak et al. 2007).

Riparian habitat surveys To investigate factors other than prey availability that may influence riparian spiders, we conducted riparian habitat surveys. In particular, we surveyed branch density because most arboreal spiders use these for attaching their webs (Power et al. 2004). We divided each 100-m study reach into 2-m increments, and in each of these, we counted live and dead branches (> 5 cm in diameter and > 50 cm in length) within 2.5 m lateral and vertical distance of the stream margin. We classified each increment as having 0, 1–5, 6–26, 25–50, or > 50 total branches and estimated total branch density of each stream reach by summing the midpoints of the categories for each increment. We used 75 as a conservative estimate for the midpoint of the > 50 category (Benjamin et al. 2011). Because stream size may also influence insect emergence and spider abundance (Benjamin et al. 2011), we measured wetted width of streams at 10-m intervals (10 measurements per stream) in mid-August 2011.

Statistical methods The overall study design compared downstream and lateral fluxes of invertebrate prey with predator responses (spiders and fish) by disturbance class. Before analysis, data were visually assessed for normality and appropriate transformations (log and square root) were performed to meet assumptions required for ANOVA. Data that were not normally distributed (fish behavior observations) were analyzed with a Mann–Whitney rank sum test. All statistical tests were performed in SAS 9.2 (SAS Institute, Cary, NC). Downstream biomass fluxes of invertebrates in 2010 were analyzed with one-way ANOVA (following square root transformation) with a post-hoc Tukey's test. Biomass fluxes of aquatic invertebrates and insect emergence from 2011 were analyzed with repeated-measures ANOVA (square root transformed data). Predator responses were compared among streams with different disturbance classes. For data from fish surveys, we compared habitat selection ratios for confluence areas among streams of differing disturbance classes using a one-way ANOVA with a Tukey's test (natural log transformed data). For behavioral observations of fish in confluence and similar non-confluence habitats, differences in rates of feeding and agonistic behaviors between species were compared with a Mann–Whitney rank sum test. Differences in rates of feeding and agonistic behaviors between habitats by species were also compared with a Mann–Whitney rank sum test. Abundances of all web-spinning spiders in 2010 were analyzed with one-way ANOVA, whereas those from 2011 were compared using repeated-measures ANOVA (square root transformed data). Tetragnathidae spider abundance in August 2011 was regressed step-wise against factors known to influence their abundance (branch density, wetted width, flux of emerging insects). Only Tetragnathidae spiders were used in regression analysis because they were the most abundant riparian spider and because their abundance has been shown to be strongly influenced by emergence of aquatic insects (e.g., Kato et al. 2003). Values used in regression analysis were from August 2011 because factors affecting spider growth may not manifest until later stages of their development (Marczak and Richardson 2008).

We used a graded approach to describe our certainty that our 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 conventions in biostatistics (Gerstman 2014), for all statistical tests we considered P values < 0.05 significant, and those between 0.05 and 0.1 marginally significant, though of potential ecological meaning, given the low sample size and statistical power of our study.

Results

Downstream drift- During August 2010, biomass of downstream export of invertebrates > 1 mm was 3–4 × higher from both types of disturbed streams than from unburned streams (ANOVA $F_{2,11} = 8.40$ $P = 0.009$). During this time period, biomass of downstream export was 3 × higher from burned streams than from unburned streams (Tukey's $P = 0.044$) and 4 × higher from burned + debris flow streams than from unburned streams ($P = 0.008$), whereas export did not differ between burned streams and burned + debris flow streams ($P = 0.540$). In contrast to August 2010, when we sampled throughout the summer of 2011, overall we observed downstream export differed only marginally among disturbance classes (Fig. 2a; repeated measures ANOVA $F_{2,12} = 7.61$ $P = 0.052$). Averaged over sample periods, export was 2–3 × higher from burned + debris flow streams than from other streams. Biomass of invertebrate export decreased through time, with highest export coinciding with peak stream flows in June and subsequently decreasing in July and August (Fig. 2a). Differences between disturbance classes were greatest in June and declined over time. In June, burned + debris flow streams exported significantly higher biomass of invertebrates than unburned and burned streams (Tukey's $P = 0.020$ and $P = 0.012$, respectively). There were not significant overall differences among disturbance classes in July or August 2011, but exported biomass was slightly higher from burned than unburned streams in August ($P = 0.058$). Thus, though we observed considerable variation in the biomass of invertebrate export from these streams, overall exports were greatest from burned + debris flow streams, whereas elevated export from burned vs. unburned streams was weaker and mainly manifested in late summer (August).

Aquatic insect emergence to riparian areas During summer 2011, insect emergence from aquatic to riparian ecosystems decreased through time (repeated measures ANOVA $F_{2,22} = 70.80$ $P < 0.0001$), but tended to be lowest from burned + debris flow streams (Fig. 2b). Although the amount of emergence did not differ significantly (repeated measures ANOVA $F_{2,12} = 2.20$ $P = 0.154$), the timing of this peak emergence did, as indicated by the significant interaction between time and disturbance class ($F_{4,22} = 9.05$ $P = 0.0002$). For example, average flux from burned and burned + debris flow streams peaked in June and declined by August. In contrast, emergence from unburned streams remained elevated throughout the summer (Fig. 2b). Thus, though the amount of emergence did not vary consistently among disturbance classes, the timing of this emergence tended to occur earlier in burned streams.

Fish selection of confluence habitat Within the 75–100 m lengths of river surveyed, confluence volume

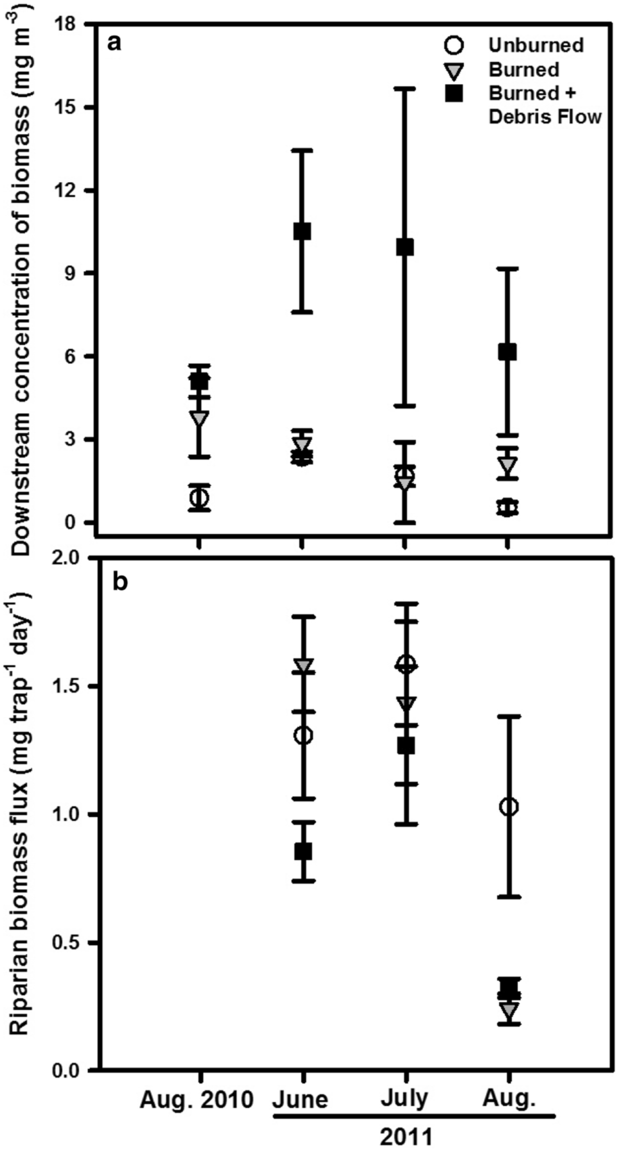

Fig. 2 Mean (±1 SE) downstream fluxes of invertebrate biomass to the main-stem river (**a**) and lateral fluxes of aquatic insects to riparian areas (**b**) from streams with varying disturbance classes in the South Fork Salmon River Basin of central Idaho, USA during summer 2010 (n = 4 for each disturbance class) and 2011 (n = 5). Emergence was not measured in August 2010

accounted for a small percent (6.5%) of the total volume available to fish (tributaries discharge was < 0.5% of main-stem discharge). Use of confluences by adult trout (*O. mykiss* and *O. clarkii*), however, exceeded what would be expected based on proportion of those habitats included in surveys. Moreover, selection ratios of confluence habitat by adult trout were, on average, more than double for disturbed streams than for unburned streams, though this difference was only marginally significant (Fig. 3; ANOVA $F_{2,9} = 1.69$ $P = 0.084$). Adult trout exhibited a marginally greater selection for confluences with burned streams relative to unburned streams (Tukey–Kramer's $P = 0.078$), but not relative to burned + debris flow streams (Tukey–Kramer's $P = 0.732$). This suggests that adult trout were selecting for confluence habitat, and this preference was strongest for confluences with burned streams.

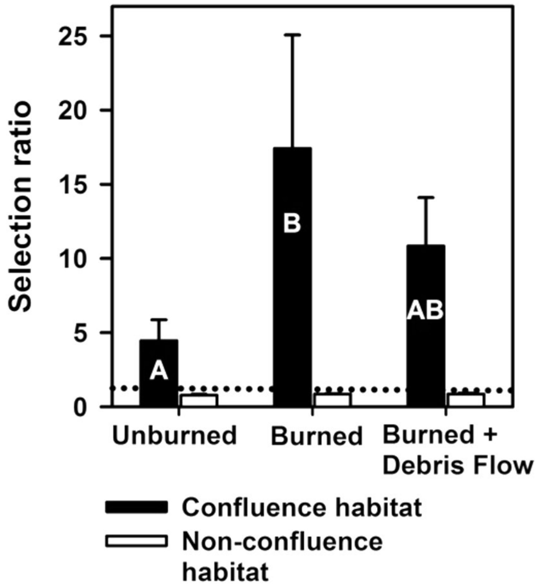

Fig. 3 Mean (±1 SE) selection ratios of confluence and non-confluence habitat by adult trout (*Oncorhynchus mykiss* and *O. clarkii*) for confluences of varying disturbance class (n = 4 for each disturbance class). Dashed line indicates no selection (a one-to-one of ratio of use to availability). Bars with different letters represent marginally significant differences according to a Tukey's test ($P < 0.10$)

Whereas *P. williamsoni*, and juvenile *O. tshawytscha* were primarily observed in lower river reaches that encompassed confluences with burned and burned + debris flow streams, *S. confluentus* was mainly observed in upper reaches that included confluences with unburned streams. Because of this systematic distribution by disturbance class, we did not conduct further analyses of habitat selection by these three species.

Fish behavior in confluence and non-confluence habitats-Fish behavior differed by species and by habitat. Overall, juvenile *O. tshawytscha* exhibited significantly higher rates of feeding than *O. mykiss* (median feeding attempts min^{-1} = 2.4 vs. 1.8, respectively, Mann–Whitney $P < 0.001$, Fig. 4a). While *O. tshawytscha* did not have higher feeding rates in confluence habitats compared to non-confluence habitats (Mann–Whitney $P = 0.595$, Fig. 5a), agonistic behaviors were 6 × higher in confluence habitats than in non-confluence habitats (median rates of agonistic behavior min^{-1} = 0.6 vs. 0.0, respectively, Mann–Whitney $P < 0.001$, Fig. 5c). In contrast, *O. mykiss* fed at marginally higher rates in confluence habitats compared with similar habitats that did not receive subsidies from a tributary (median feeding attempts min^{-1} = 2.0 vs. 1.6, respectively, Mann–Whitney $P = 0.084$,

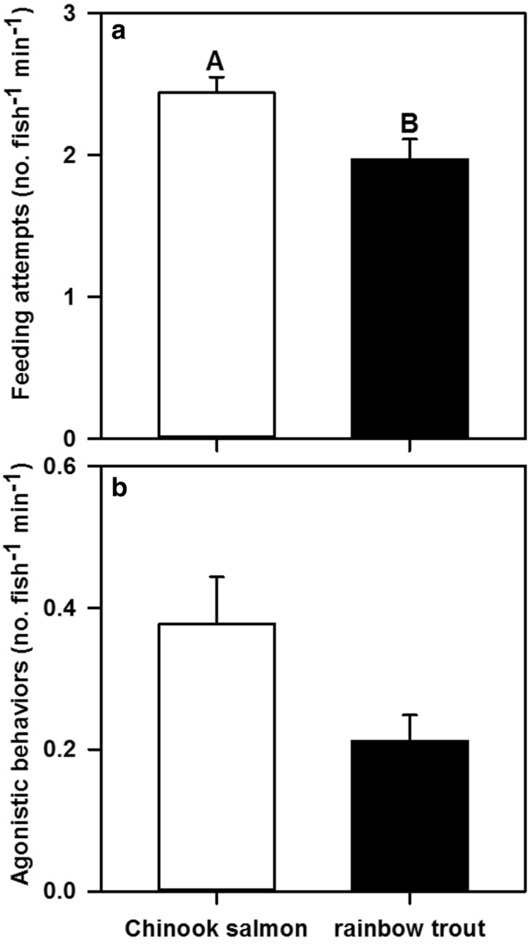

Fig. 4 Mean (±1 SE) rates of feeding (a) and agonistic behaviors (b) for juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and rainbow trout (*O. mykiss*). Bars with different letters represent significant differences according to a Mann–Whitney rank sum test ($P<0.05$)

Fig. 5b). Like juvenile *O. tshawytscha, O. mykiss* exhibited higher rates of agonistic behaviors in confluence habitats than non-confluence habitats (median rates of agonistic behavior min^{-1} = 0.4 vs. 0.0, respectively, Mann–Whitney $P<0.001$, Fig. 5d).

Spider surveys- In August 2010, abundances of web-spinning spiders were 134% higher along burned streams than along streams of other disturbance classes, though the overall effect of disturbance class was only marginally significant (ANOVA $F_{2,9}=3.93$ $P=0.059$). Burned streams had marginally higher spider abundances than unburned streams (Tukey's $P=0.077$), but did not differ significantly from abundances along burned + debris flow streams (Tukey's $P=0.102$). Owing to high variation among streams and sample periods in 2011, the abundance of web-spinning spiders did not vary among disturbance classes (repeated measures ANOVA $F_{2,12}=0.92$ $P=0.425$). However, it did increase over summer months (repeated measures ANOVA $F_{2,22}=11.15$ $P<0.001$). For instance, spider abundance was relatively similar across disturbance classes in June and July, but by August, burned streams had, on average, higher spider abundances than either unburned (ca. 2 × higher) or burned + debris flow streams (ca. 1.5 × higher) (Fig. 6). However, the interaction of disturbance class and time was not significant (repeated measures ANOVA $F_{2,12}=0.92$ $P=0.425$; $F_{4,22}=1.87$ $P=0.152$). As expected, branch density was highest along unburned streams and lowest along burned + debris flow streams. However, based on the stepwise linear regression, abundance of Tetragnathidae spiders in August was positively and significantly related to wetted width ($P<0.001$, $r^2=0.851$), but was not related to woody branch density ($P=0.450$, $r^2=0.009$) or emergence of aquatic insects ($P=0.111$, $r^2=0.029$).

Discussion

Our findings indicate that the combination of two natural disturbances (wildfire and subsequent debris flows) can have contrasting effects on lateral and downstream invertebrate fluxes, with likely consequences for predators in recipient ecosystems. For instance, the combination of wildfire and subsequent debris flow increased downstream exports of invertebrate prey from headwater streams to linked food webs of a main-stem river. This study demonstrates that, like hurricanes (that deliver pulses of resources to islands; Spiller et al. 2010) and floods (that deliver similar pulses to floodplains; Junk et al. 1989), these disturbances can increase resource transfer from one ecosystem to another. Unlike most previous studies, we investigated effects of two disturbances on fluxes in two directions. We found the combination of wildfire and debris flow apparently increased fluxes of drifting invertebrates, whereas overall insect emergence was not elevated, but instead disturbance appeared to alter its timing. Habitat context, as well as the community composition and traits of invertebrates and their predators may, in part, determine the fate (including direction of transfer) of any increased productivity that result from these disturbances. Our findings highlight the need to study effects of disturbances like wildfire on fluxes in multiple spatial dimensions to understand the dynamics of connected ecosystems.

In this study, a single disturbance, wildfire, did not consistently increase fluxes of invertebrate biomass to downstream habitats, though this appeared to vary by year. In late summer 2010, drifting invertebrate fluxes were 3 × greater from burned and 4 × higher from burned + debris flow streams, compared to those that were unburned, whereas in summer 2011 only burned + debris flow streams had elevated drifting invertebrates, and the differences were less pronounced (i.e. 2–3 × higher). It is possible that the

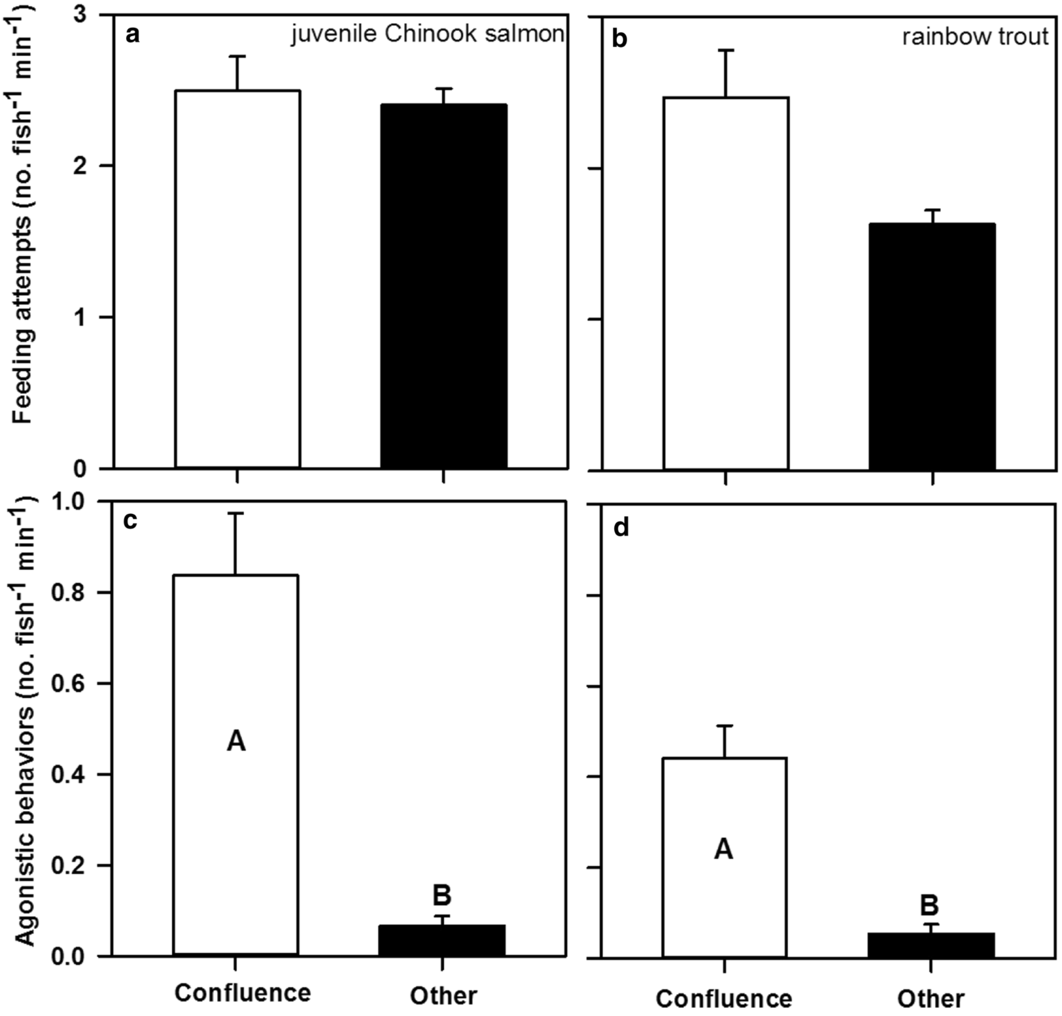

Fig. 5 Mean (±1 SE) number of feeding attempts and agonistic behaviors per minute by juvenile Chinook salmon (*Oncorhynchus tshawytscha*, **a** and **c**) and by rainbow trout (*O. mykiss*, **b** and **d**) in confluence and similar non-confluence (other) habitats. Bars with different letters represent significant differences according to a Mann–Whitney rank sum test ($P < 0.05$)

wetter spring and prolonged higher flows of 2011 altered differences among streams of different disturbance classes, perhaps disproportionately influencing those that burned and experienced a debris flow.

A range of potential mechanisms may explain the patterns of invertebrate export we observed. For example, burned and burned + debris flow streams accumulated more degree days than unburned streams (Table 1), although burned and burned + debris flow streams did not differ from one another. Burned and burned + debris flow streams experienced the most severe fire in their upper drainages (Payette National Forest 2010). In areas surrounding the confluences of burned streams with the main-stem river, however, the pine canopy was charred, but was left mostly standing and alive (H. Harris, pers. obs.). On the other hand, subsequent debris flows reduced canopy cover (branch density, Table 1), which in other regions has been found to increase light availability and boost aquatic-primary production (e.g., Cover et al. 2010). Furthermore, wildfires and debris flows can alter stream thermal regimes via this reduction in canopy cover (e.g., Gresswell 1999; Cover et al. 2010), which may have contributed to the increased number of degree days and, in turn, helped stimulate secondary production in the affected streams. Large woody debris in the stream channel can be important for retention of organic matter and invertebrates (Gurnell et al. 2002) and can decline post-debris flow (May 2007; Cover et al. 2010). Debris flows in our study streams may have similarly reduced retention of invertebrates by exporting large woody debris from tributaries to the main-stem river. Indeed, streams that experienced either fire or fire + debris flow exported more terrestrial invertebrates to downstream habitats than unburned streams (Harris et al. 2015). The lack of benthic refugia in such streams may have increased export, especially in conjunction with the

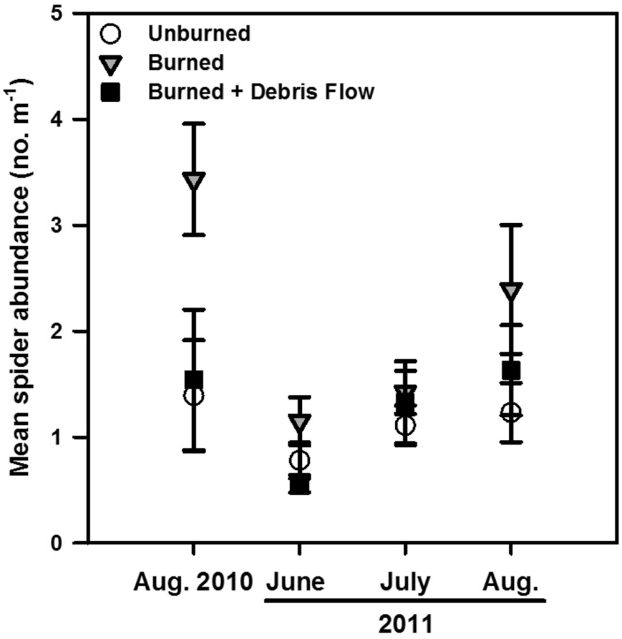

Fig. 6 Mean (±1 SE) web-spinning spider abundance (i.e. Tetragnathidae, Araneidae, Linyphiidae) along streams of varying disturbance classes in August 2010 (n = 4 per disturbance class) and summer 2011 (n = 5). Points represent mean abundance along 3 (in 2010) or 5 (in 2011) 10-m transects per stream

prolonged high flows in 2011. The combination of two disturbances also may have led to a community shift towards taxa with *r*-selected life-history strategies, and a higher propensity to drift. Indeed, export from streams that experienced fire and subsequent debris flow had higher concentrations of Baetidae mayflies (Harris et al. 2015), which have a high tendency to drift (Rader 1997). Also, export of insects of terrestrial origin was consistently higher from disturbed streams (Harris et al. 2015). Due to the comparative nature of this study, we were unable to fully assess the relative importance of these potential mechanisms for changes in stream subsidies, and could not completely eliminate the possible role of other measured (or unmeasured) watershed characteristics (e.g., slope or drainage area) on our observed results.

Disturbance did not appear to increase overall magnitude of lateral fluxes of aquatic insects to riparian areas, though emergence from burned and unburned streams did differ in timing and appeared to be protracted in unburned streams. In a nearby drainage, fluxes of emerging insect were greatest from streams with watersheds that experienced high severity fire, presumably due to less riparian canopy cover, and this difference was greatest in early summer. However, that study found that in streams that experienced low-severity fire, emergence flux was not greater than unburned streams and biomass of benthic invertebrates was lower (Malison and Baxter 2010). Annual monitoring has documented that benthic insect biomass can return to pre-fire conditions in 5–10 years in streams where canopy cover by riparian vegetation regrows quickly (Rugenski and Minshall 2014; Baxter, unpublished data). Though we observed an early-summer peak in emergence from burned streams like that observed by Malison and Baxter (2010), wildfires in the drainages studied here may not have burned with high enough severity to consistently elevate biomass of benthic or emerging insects. Further, we hypothesize that streams experiencing fire and subsequent debris flow exported insects downstream at the expense of insect emergence. Because debris flows can scour stream channels down to bedrock and reduce availability of in-stream wood (May 2007), this may lead to greater emigration through intentional downstream-drift (e.g. Siler et al. 2001) and fewer insects reaching adulthood *in situ*. Both drift and emergence can be positively related to invertebrate productivity (Huryn and Wallace 2000), but higher production may not necessarily result in simultaneous increases in both. Thus, any increase in productivity that may follow disturbance could be expected to increase export (Odum 1985) but perhaps not in all directions.

We observed that fish were more abundant at tributary confluences and that they showed selection for these habitats, a finding consistent with the observations of others (e.g., Kiffney et al. 2006; Torgerson et al. 2008) and with the idea of confluences as biological hotspots in river networks (Benda et al. 2004; Rice 2017). In this case, however, our findings point to the possibility that such effects may accrue even at confluences where tributary size is small relative to the mainstem. Fish exhibited marginally greater selection of confluences with burned streams relative to unburned streams. This mirrored the result that both types of disturbed streams exported higher concentrations of drifting invertebrates than unburned streams during the late summer when these surveys were conducted. In contrast, selection of confluences with burned + debris flow streams was not significantly stronger than for those with unburned streams, despite marginally higher levels of invertebrate drift, suggesting that additional habitat characteristics at burned + debris flow confluences may have influenced selection. We observed that rainbow trout exhibited slightly higher rates of feeding attempts in confluence habitats than in nearby locations and that rates of agonistic behavior were higher for both juvenile Chinook salmon and rainbow trout in these confluences, indicating that these habitats may be worth defending. Taken together, these observations provide some added evidence that confluences may be particularly profitable places for fish, and also suggest that certain types of disturbances (e.g. wildfire) may mediate this profitability.

Our observations of web-spinning spiders varied by year and with time during the summer season. Among the streams we surveyed in late summer 2010, there were 134% more spiders along those that had been burned vs. either unburned or burned + debris flow sites. In 2011, we did not detect strong, consistent differences in spider abundance among streams of different disturbance classes, though by late summer there was a trend of increased spider abundances along burned streams while they remained relatively constant along others. The abundance of Tetragnathidae spiders in late summer was positively associated with the wetted width of a stream, but not other habitat characters we measured. We speculate that the difference between the 2 years may have been partly driven by the wet spring and extended high flows of 2011, which may have influenced conditions for spider recruitment, including the nature of the aquatic insect emergence. We cannot speak to the latter, because we only measured emergence in 2011. Regardless, the peak of emergence we observed from burned streams in early summer may be linked to more spiders in these sites in late summer if, as is suggested by evidence from other studies, their population responses are not solely related to the total amount of insect emergence, but may be affected by its timing (Kato et al. 2003; Marczak and Richardson 2008), composition (Davis et al. 2011), or characteristics of the stream-riparian boundary (Marczak et al. 2007).

The frequency and severity of wildfire and debris flows are expected to increase with climate change (Westerling et al. 2006; Goode et al. 2012), and our findings add to growing evidence that such changes in terrestrial disturbance regimes may have additional consequences for stream ecosystems (e.g., Davis et al. 2013). For instance, other investigators have posited that climate change will increase sediment yield through changes in temperature and hydrology that stimulate vegetation disturbances (Goode et al. 2012). Others have also documented how alterations to water temperature (Isaak and Rieman 2013; Issak et al. 2017), and the combination of changing temperature, flow regime, and biotic interactions induced by climate change are expected to reduce suitable habitat for species like trout (Wenger et al. 2011). In turn, such responses may reverberate between land and water through changes in magnitude and timing of fluxes like aquatic insect emergence (Baxter et al. 2005; Malison and Baxter 2010). The findings of this study highlight the need to further explore how increases in disturbances predicted to accompany climate change may have unexpected consequences by altering fluxes of organisms and other resources among ecosystems.

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