Responses of riparian tetragnathid spiders to wildfire in forested ecosystems of the California Mediterranean climate region, USA

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Abstract: Mediterranean ecosystems of California are characterized by high interannual variability in precipitation and susceptibility to frequent high-severity wildfires. Variability in precipitation and fire severity are likely to become more pronounced because of climate change, but their relative effects on linked aquatic–terrestrial components of Mediterranean ecosystems have received limited attention. We investigated the effects of wildfire on riparian spiders of the family Tetragnathidae, which are common shoreline consumers that can be highly reliant on aquatic food resources in stream ecosystems. From 2011–2012, we assessed stream geomorphology; density and community composition of aquatic benthic macroinvertebrates; and density, Hg body loads, trophic position (TP), and reliance on aquatically derived energy (based on naturally abundant C and N isotopes) of tetragnathid spiders in study sections of 12 paired stream reaches in Yosemite National Park. The riparian zone of one member of each pair had experienced a high-severity wildfire, whereas the riparian zone of its counterpart had experienced a low-severity fire. After the 2013 Rim Fire, we resurveyed a subset of these variables in study sections of 4 reaches by means of a paired before-after–control-impact design. We also explored how reach- and catchment-scale variability might affect spider density and trophic dynamics. Differences in spider responses between paired sections were not statistically significant, but model-selection results suggested that variability in benthic invertebrate density, catchment-scale fire frequency, and precipitation were important drivers of spider density and TP. The consistent signal of precipitation across multiple spider responses suggests that climate variability could have greater effects on aquatic–terrestrial ecological linkages than the influence of fire alone.

Key words: aquatic–terrestrial linkages, Mediterranean, riparian spiders, trophic position, wildfire, precipitation, climate

Wildfire activity is increasing globally in both scope and frequency (Westerling et al. 2006, Flannigan et al. 2009, Moritz et al. 2012). Climate-change-induced shifts in terrestrial ecosystem structure and function are implicated as significant drivers of the increased wildfire activity (Davis et al. 2013). A large portion of California, including the west slope of the Sierra Nevada mountain range from lat 28 to 44°N, has a Mediterranean-type climate (Grove and Rackham 2001). This climate type is characterized by periods of extremely wet or dry conditions and high interannual variability in precipitation (Bonada and Resh 2013). Streams in the Sierra Nevada generally have peak flows in autumn following rain and in spring following snowmelt. The magnitude of flow each year depends on the El Niño Southern Oscillation. Flows are high in El Niño years and low in La Niña years (Bonada and Resh 2013). In addition, uplands draining into Sierra Nevada streams are highly susceptible to drought and are projected to experience heightened frequency and severity of wildfire (Lenihan et al. 2003). The percentage of high-severity fire (extent) in Ponderosa pine (*Pinus ponderosa*) and mixed conifer forests of the Sierra Nevada has increased 2× in the period 1984–2010 (Miller et al. 2009). Despite broad recognition of fire as a key source of disturbance in terrestrial ecosystems (Agee 1993, Carrion et al. 2003, Stephens et al. 2007), the role of fire in stream ecosystems of Mediterranean climates has garnered relatively less attention than it has in temperate climates (Verkaik et al. 2013a).

The role of fire relative to the ecological connections between land and water has received increasing attention in recent years (Spencer et al. 2003, Malison and Baxter 2010, Jackson et al. 2012), but it has not been the focus

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of research in ecosystems influenced by Mediterranean-type climate. A growing body of literature suggests that streams and their adjacent riparian zones are tightly linked through energy exchanges, and reciprocal transfers of energy are essential to maintain ecosystem functions. Transfers of energy between terrestrial and aquatic ecosystems are important energetic pathways by which terrestrially derived organic matter, nutrients, and biota fuel aquatic consumers (Covich et al. 1999, Power et al. 2004, Romero et al. 2005). Flows of energy from aquatic to terrestrial systems also provide important nutritional subsidies to riparian and terrestrial food webs (Power and Rainey 2000, Henschel et al. 2001, Baxter et al. 2005). Aquatic insects that emerge from streams as adults (hereafter emergent insects) are an especially critical energy source for riparian consumers (Murakami and Nakano 2002, Baxter et al. 2005). For instance, spiders of the family Tetragnathidae (a widely distributed riparian consumer) can rely heavily on aquatic insects as prey (reviewed by Burdon and Harding 2008), and Sanzone et al. (2003) found that riparian orb-weaving spiders (Araneidae and Tetragnathidae) obtained 100% of their C and 39% of their N from in-stream sources. Therefore, we used riparian tetragnathid spiders as a model organism to assess the effects of wildfire on cross-boundary ecological linkages.

Background

The characteristic upslope-to-downslope (e.g., Hynes 1975) and upstream-to-downstream (e.g., Vannote et al. 1980) connectivity of stream–riparian ecosystems makes it probable that the extent, severity, and frequency of fire at both reach and catchment scales (sensu Frissell et al. 1986) have implications for cross-boundary ecological linkages (Polis et al. 1997, Gresswell 1999), but authors of studies relating wildfire effects to stream–riparian ecosystems typically consider fire severity only at the reach scale (but see Frissell et al. 1986, Arkle et al. 2010). The multiscale influence of wildfire may be pronounced in systems characterized by strong Mediterranean dry–wet seasonality, high interannual variability in precipitation and runoff, and floods that frequently occur in autumn and winter (often immediately after wildfire) rather than after spring snowmelt as in temperate ecosystems (Verkaik et al. 2013a). The strong interactions between wildfire and hydrology governing stream ecosystem processes (Arkle et al. 2010, Verkaik et al. 2013b, Rugenski and Minshall 2014) also implicate upstream wildfire characteristics as a likely driver of stream–riparian connectivity in Mediterranean climate-mediated ecosystems.

High-severity fire (i.e., involving removal of the riparian conifer canopy) affects riparian plant community structure, composition, and distribution (Davis et al. 1989, Jackson and Sullivan 2009) and other aspects of stream–riparian systems, such as large wood (Davis et al. 1989, Bendix and Cowell 2010, Vaz et al. 2011), that directly modify riparian spider habitat. Riparian plants are often highly adapted to fire disturbance (Dwire and Kauffman 2003, Jackson and Sullivan 2009) and, in some cases, can reestablish within a single growing season (Davis et al. 1989, Bêche et al. 2005). Furthermore, estimates of postfire snag fall range from 17 to 43% over 2 to 3 y in California shrublands (Davis et al. 1989, Bendix and Cowell 2010). Together, recovery of riparian vegetation and addition of large wood may result in greater postfire than prefire habitat heterogeneity and web-building structure for riparian spiders. In contrast, low-severity fire (i.e., riparian canopy remains intact and only understory vegetation is consumed) may have little to no effect on riparian vegetation and inputs of large wood (and consequently spiders) over time (Jackson and Sullivan 2009, Arkle and Pilliod 2010).

Fire severity also might influence energetic relationships in linked stream–riparian ecological networks. Trophic position (TP) is an integrative measure of food webs that reflects an organism's relative feeding relationship within a community and the complexity of the web (Post 2002). For instance, maximum TP in a food chain, or food-chain length (FCL), describes the number of transfers of energy from the bottom to the top of a food web (Sabo et al. 2009) and is one of the primary indicators of ecosystem function and stability. The dynamic constraint hypothesis (Pimm and Lawton 1977) predicts that ecosystems affected by frequent or intense (i.e., exerting significant force) disturbance should have shorter FCL because of removal of predators, decreased biodiversity, or increased omnivory. Habitat heterogeneity also has been implicated as an environmental determinant of FCL (Persson et al. 1992). The influence of disturbance on FCL in stream ecosystems typically has been framed from a hydrological perspective (e.g., variability in discharge; Poff and Ward 1990, Fausch et al. 2001, Sabo et al. 2010) and, to our knowledge, terrestrial disturbance processes (e.g., wildfire) have not been considered in this context for streams. Fish are commonly considered to be the top predators in aquatic systems and are most commonly used to estimate FCL (e.g., McHugh et al. 2010, Sabo et al. 2010), but in small tributary streams without piscivorous fish species, TP of spiders probably is similar to that of insectivorous fish and other aquatic vertebrate consumers (e.g., salamanders; Parker 1994).

Reach- and catchment-scale variability can affect the aquatic invertebrate communities (reviewed by Minshall 2003) on which tetragnathid spiders depend. Changes in channel geometry following wildfire can be variable (Verkaik et al. 2013a), but fire-induced changes in stream hydrogeomorphology (greater stream discharge, reduced sediment supply, and streambed incision; Legleiter et al. 2003, May and Gresswell 2003, Shakesby 2011) can alter benthic macroinvertebrate larval populations with concomitant effects on adult emergence. In particular, loss of riparian leaf-litter inputs (Jackson et al. 2012) and scouring flows

(Koetsier et al. 2010, Vieira et al. 2011) can decrease shredder abundance and lead to shifts in the diet of individual taxa (Mihuc and Minshall 1995, 2005, Spencer et al. 2003). In small headwater streams, higher densities of emergent insects have been associated with burned catchments (Mellon et al. 2008). Collectively, these patterns may result in greater reliance on aquatically derived energy (i.e., nutritional subsidies originating from aquatic primary productivity) and a shift in spider TP.

Concentration of heavy metals (e.g., Hg) in riparian consumers may serve as a complementary aquatic–terrestrial foodweb tracer (Walters et al. 2008, 2010, Alberts et al. 2013). Few, if any, aquatic ecosystems have escaped contamination because even remote freshwater systems receive atmospherically transported contaminants (Blais 2005). Contaminants in the tissues of aquatic insects are transported to riparian and terrestrial consumers via multiple energetic pathways (Sullivan and Rodewald 2012). For example, Walters et al. (2008) found that polychlorinated biphenyl concentrations in riparian spiders and herpetofauna were closely related to reliance on emergent aquatic prey. Therefore, Hg concentration in riparian consumers can be indicative of reliance on emergent insect prey and may help elucidate how fire affects energetic linkages between streams and their adjacent riparian zones.

Approach

Within this linked stream–riparian context, we sought to understand how wildfire severity at the reach scale (for this study, 10^2 m) and wildfire frequency and extent at the catchment scale influence local stream–riparian foodweb dynamics in a Mediterranean-climate-mediated system. We evaluated the responses of Tetragnathidae to fire severity in riparian zones of study sections of 6 pairs of stream reaches (each pair consisted of a stream reach with a riparian zone that experienced high-severity fire and one with a riparian zone that experienced low-severity fire; 12 streams total) in Yosemite National Park, California, USA (2011–2012).

We used the naturally abundant stable isotopes ^{13}C and ^{15}N to estimate realized (sensu Post 2002) tetragnathid spider TP and reliance on aquatic energy pathways (i.e., nutritional subsidies derived from benthic algae) and the concentration of Hg in spiders as a complementary tracer of aquatically derived energy. We also assessed differences in geomorphology and aquatic food resources (benthic macroinvertebrates) between treatment groups. We predicted higher tetragnathid spider density and lower reliance on aquatically-derived energy, spider TP, and Hg body loading in high- than in low-severity riparian fire sections.

To complement our categorical paired-reach design and to incorporate catchment-scale features, we assessed the potential influences of a suite of quantitative, continuous variables at both the reach (geomorphology, riparian spider habitat, and density and community composition of benthic macroinvertebrates) and catchment (fire extent, fire frequency, catchment size, and precipitation) scales on spider responses. We predicted that: 1) rapid recovery of riparian vegetation and increased streamside habitat heterogeneity related to additions of small and large wood following high-severity riparian fire would lead to increased web-building habitat structure for spiders and increases in spider density; 2) changes in channel geometry and deposition of fine sediments would decouple near-shore habitat from the stream and reduce benthic macroinvertebrate density, leading to reduced tetragnathid spider access to aquatic insect prey and decreased reliance on aquatically derived energy; 3) reductions in the diversity of benthic macroinvertebrate assemblages (used as a proxy for emergent insects; see Methods) after high-severity riparian fire and shifts toward dominance by habitat generalists would result in reduced foodweb complexity and lower tetragnathid spider TP; and 4) increases in fire frequency and extent would lead to decreased variability of tetragnathid spider TP through decreased habitat heterogeneity. The strength of evidence supporting each of these predictions was assessed using all 12 study sections in a model-selection approach (Burnham and Anderson 2004).

In late summer 2013, the Rim Fire, which burned extensively throughout the Stanislaus National Forest and Yosemite National Park (>101,000 ha) with large patches of high-severity fire, burned the riparian zones of study reaches of 2 streams used in 2011–2012. We took advantage of this situation and present a paired before–after comparison of the short-term effects of the Rim Fire on stream geomorphology, benthic macroinvertebrates, and tetragnathid spiders in study sections of 2 reaches with riparian zones burned by the Rim Fire and study sections of 2 reaches with unburned riparian zones similar in stream size, elevation, and aspect that served as controls ($n = 4$).

METHODS
Phase 1 (2011–2012)

Yosemite National Park has an excellent fire-history record. The park contains 2 large catchments in an expansive wilderness largely devoid of confounding anthropogenic effects. We selected 12 tributary stream reaches of the Tuolumne and Merced rivers based on burn characteristics including severity and time since last burn (Fig. 1). Reaches were grouped in pairs by riparian fire severity (each pair consisted of 1 reach with a low-severity and 1 with a high-severity burned riparian zone; all fires were natural wilderness, nonprescribed fires). Fire severity was assessed based on the appearance of the conifer
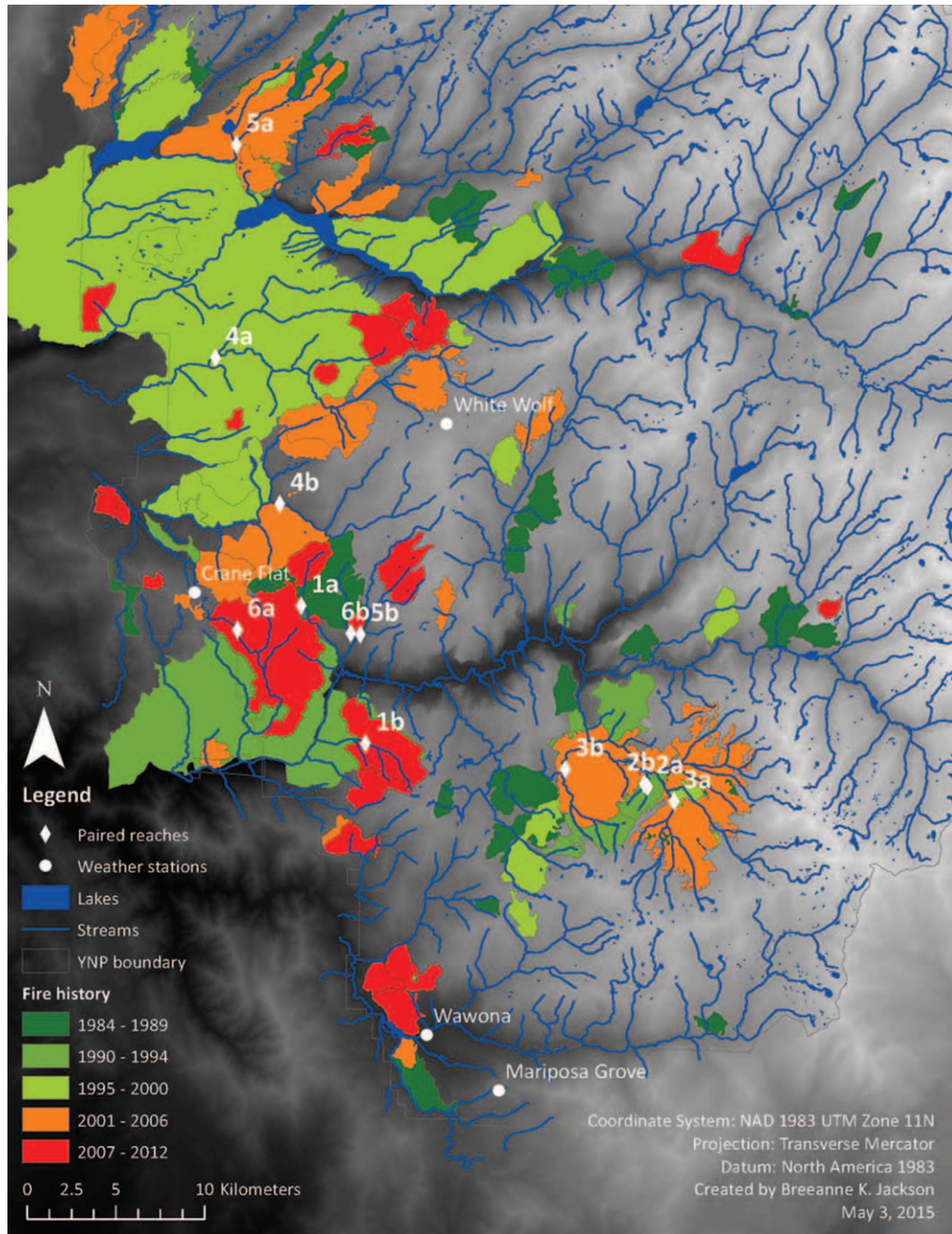
Figure 1. Fire history starting in 1984 within Yosemite National Park. Study sections within paired reaches are Tamarack (1a) and Grouse (1b), Meadow (2a) and Camp (2b), Buena Vista (3a) and Mono (3b), Middle Tuolumne (4a) and South Tuolumne (4b), Frog (5a) and Cascade (5b), and Crane (6a) and Coyote (6b). Weather stations are White Wolf, Crane Flat, Wawona, and Mariposa Grove.

canopy (low-severity: canopy intact, only riparian understory burned; high-severity: conifer canopy removed by fire over ≥75% of the study reach) (Jackson and Sullivan 2009, Malison and Baxter 2010). All riparian zones of reaches burned between 1996 and 2011 (Table 1). Within each reach, we selected a study section with length ~10 × bankfull width as our sampling unit (Cianfrani et al. 2009).

Logistical constraints related to accessibility partly determined reach selection, but we attempted to minimize variation in other variables including time since last burn, elevation, aspect, stream geomorphology, channel width, drainage area, and dominant vegetation between sections of paired reaches (Table 1). Study sections in a few pairs were spatially distant from one another (e.g., reaches 5a

Table 1. Study sections in stream reaches paired by riparian fire severity (high, low) from Yosemite National Park. Year burned refers to the last time the riparian zone of the stream reach burned. In some cases, a more recent fire occurred elsewhere in the catchment. Channel–reach morphology was classified following Montgomery and Buffington (1997). Stream order was determined based on Strahler (1957).

Study sections	Code	Fire severity	Year burned	Elevation (m)	Aspect	Order	Study-section length (m)	Channel–reach morphology	Dominant riparian vegetation	Dominant upland forest type
Tamarack	1a	High	2009	1931	S	2	43.2	Step–pool	*Salix*	Lodgepole pine and red fir
Grouse	1b	Low	2009	1574	NW	3	60.7	Step–pool	*Alnus, Cornus*	Yellow pine belt
Meadow	2a	High	2005	2127	N	1	13.1	Pool–riffle	*Salix*	Subalpine (lodgepole pine)
Camp	2b	Low	2005	2098	N	1	21.5	Pool–riffle	*Alnus, Cornus*	Subalpine (lodgepole pine)
Buena Vista	3a	High	2001	2154	NNW	3	80.3	Step–pool	*Salix, Rubus, Alnus*	Subalpine (lodgepole pine)
Mono	3b	Low	2004	2096	N	3	62.5	Pool–riffle	*Salix, Cornus, Alnus*	Subalpine (lodgepole pine)
Middle Tuolumne	4a	High	1996	1766	SW	3	125.0	Pool–riffle	*Salix, Populus, Rhododendron*	Yellow pine belt
South Tuolumne	4b	Low	2002	1716	NW	3	139.5	Step–pool	*Salix, Alnus*	Yellow pine belt
Frog	5a	High	2006	1909	S	3	95.8	Step–pool	*Salix, Cornus, Rhododendron*	Lodgepole pine and red fir
Cascade	5b	Low	2007	1864	SW	3	75.7	Step–pool	*Salix, Cornus, Rhododendron*	Lodgepole pine and red fir
Crane	6a	High	2009	1850	E	2	19.7	Step–pool	*Cornus, Rhododendron*	Lodgepole pine and red fir
Coyote	6b	Low	2007	1836	SE	2	47.8	Step–pool	*Salix, Cornus, Rhododendron*	Lodgepole pine and red fir

and 5b; Fig. 1), but we chose to focus on reducing variability in section characteristics and examined the effects of regional climate by considering precipitation in our analysis.

We established 3 cross-channel transects (upstream, midstream, downstream) in each study section. At each transect, we measured bankfull width and water depth and calculated width-to-depth ratio (Cianfrani et al. 2009). We estimated median grain size (D_{50}, mm) from Wolman (1954) pebble counts on 100 sediment clasts per transect ($n = 300$ per study section). We measured the percentage of each study section occupied by large wood (>10 cm diameter × >1.0 m length) and small wood (<10 cm diameter) and counted pieces of wood. We also recorded the percentage of the nearshore zone (<1 m from water edge) of each study section covered by understory vegetation.

We were unable to sample emergent insects directly with the use of emergence traps because of the wilderness setting. Therefore, we used rapid assessment adapted from the US Environmental Protection Agency Rapid Bioassessment Protocols (Barbour et al. 1999) to describe benthic macroinvertebrate community composition as a proxy. We collected macroinvertebrates with a Surber sampler (500-μm-mesh net) at 2 to 3 locations (depending on channel width) along each transect ($n = 6$–9 samples/study section). We used keys provided by Voshell (2002) to identify insects to order.

We surveyed tetragnathid spiders along 30-m transects running longitudinally along each bank of each study section. Transect locations were representative of the vegetation and hydrogeomorphic characteristics of each study section, based on in-stream transects and vegetation surveys (BKJ and SMPS, unpublished data). We counted spiders for 60 min/bank at night (2100–2300 h) in July and August (2011 and 2012) when spiders are at peak abundance in temperate regions (Williams et al. 1995, Meyer and Sullivan 2013). We also collected 4 to 8 spiders, 4 to 8 samples of epilithic algae from cobbles, and 3 to 5 samples of detritus from throughout the study section for stable isotope analysis (see Sample processing below).

We delineated the area draining to each study section with the watershed tool in ArcGIS (version 10.1; Environmental Systems Research Institute, Redlands, California). We estimated the proportion of each catchment that had been burned >2× since 1930 (i.e., fire frequency) and the proportion burned with moderate-to-high severity during the most recent fire >80 ha (i.e., fire extent). We estimated fire severity at the catchment scale by means of normalized burn ratios (NBRs) calculated from Landsat 7 Enhanced Thematic Mapper Satellite Imagery (Key and Benson 2006) and calculated relative differences in NBRs (RdNBRs) for each burned catchment. We estimated breakpoints in RdNBR for each pixel and assigned pixels as unburned or low-, moderate-, or high-severity fire. From

these estimates, we determined % catchment burned at each level of severity and total % catchment burned.

We obtained precipitation data (cm) from the Western Regional Climate Center and used data from the Remote Automatic Weather Station closest to each study section and situated at approximately the same elevation. We estimated precipitation based on average monthly precipitation for the water year prior to sampling (1 October of the previous year to 30 September of the sampling year; Bêche and Resh 2007).

Sample processing   In the laboratory, we rinsed spiders with distilled water and oven dried them at 60°C for 48 h. We homogenized tissue from 3 to 5 individual spiders per study section, pulverizing the tissue with a mortar and pestle, and packed it in Sn capsules. We scraped epilithic algae from cobbles, removed other materials (e.g., invertebrates and sediment), and combined algae from all cobbles into a single composite sample per study section. We sorted terrestrial detritus from other materials in grab samples and combined terrestrial detritus from all grab samples into a single composite sample per study section. Algae and detritus samples were rinsed with distilled water, oven dried, homogenized into a fine powder using a Pica Blender Mill (Cianflone Scientific Instruments Corporation, Pittsburgh, Pennsylvania) or a mortar and pestle, and packed in Sn capsules for isotopic analysis. ^{13}C and ^{15}N of all samples were analyzed by continuous flow elemental analysis isotope-ratio mass spectrometry at the Stable Isotope Core (Washington State University, Pullman, Washington). The results are reported in δ (‰) notation defined as:

$$\delta^{13}C \text{ or } \delta^{15}N = 100\left(\left[\frac{R_{\text{sample}}}{R_{\text{standard}}}\right]-1\right), \qquad \text{(Eq. 1)}$$

where R is ^{13}C/^{12}C or ^{15}N/^{14}N, respectively. Typical analytical precision was 0.08‰ for δ^{15}N and 0.19‰ for δ^{13}C.

Estimating TP and reliance on aquatically derived energy
Using a 2-source foodweb model (Post 2002), we estimated tetragnathid spider TP:

$$\text{TP} = \lambda + (\delta_c-[\delta_{b1}\alpha + \delta_{b2}\{1-\alpha\}])/\Delta_n, \qquad \text{(Eq. 2)}$$

where λ is the TP of the basal food sources (i.e., 1 for primary producers), δ_c is the δ^{15}N signature of the consumer, δ_{b1} and δ_{b2} are the signatures of the 2 basal food sources, α is the proportion of N from basal food source 1, and Δ_n is the enrichment in δ^{15}N/trophic level (3.4‰; Post 2002). We estimated α with a 2-end-member Bayesian isotopic mixing model solved with the R software package *SIAR* [Stable Isotope Analysis in R; Parnell and Jackson 2013), which is equipped to handle variability in sources, consumers, and trophic fractionation factors (Parnell et al. 2010).

For all study sections the 2 end members were the basal food sources, epilithic algae and terrestrial detritus. We used the $\delta^{13}C$ and $\delta^{15}N$ data to estimate the contribution from each basal food source to the consumer. Trophic fractionation factors for tetragnathid spiders were estimated using the per trophic step fractionation given by Post (2002) (3.4 ± 0.98‰ for $\delta^{15}N$ and 0.39 ± 1.3‰ for $\delta^{13}C$) multiplied by the estimated number of trophic transfers between the consumer and basal resources (estimated a priori as the difference between the consumer $\delta^{15}N$ and mean basal resource $\delta^{15}N$ divided by 3.4‰). In our study, adjusting for the number of trophic transfers had little effect on the mixing model results because $\delta^{15}N$ signatures of the 2 basal resources tended to be similar.

Tetragnathid spider tissue samples were analyzed for Hg concentrations (µg/kg dry mass) at the Diagnostic Center for Population and Animal Health, Toxicology Section, Michigan State University. Inductively coupled plasma atomic emission spectrometry (ICP-AES; Varian Vista, now part of Agilent, Santa Clara, California) and inductively coupled plasma mass spectrometry (ICP-MS; Agilent 7500ce) instruments were calibrated with standards derived from National Institute of Standards and Technology (NIST, Gaithersburg, Maryland) traceable stock solutions for each element (GFS Chemicals, Cincinnati, Ohio). Quality was assured in each sequence run by analyzing laboratory reagent blanks, NIST-traceable Multi-mix (Alfa Aesar Specpure, Ward Hill, Massachusetts), and digests of NIST standard reference materials, including Mussel Tissue 2976, Trace Elements in Water 1643e, or Montana II Soil 2711a, as appropriate. Hg was analyzed by cold vapor atomic absorption spectrometry (CETAC CVAA, Omaha, Nebraska) with similar calibration and quality control.

Statistical analysis   We compared density, reliance on aquatically derived energy, Hg body loading, TP, and standard deviation of TP (SD_{TP}) of tetragnathid spiders between high- and low-severity-fire study sections with paired t-tests. We used both mean and SD_{TP} to ascertain differences in magnitude and variability, respectively, of tetragnathid spider TP between treatment groups. We also used paired t-tests to evaluate potential differences in benthic macroinvertebrate density and composition (% Ephemeroptera, Plecoptera, Trichoptera [EPT]) and stream geomorphology (D_{50}, width-to-depth ratio, and entrenchment ratio) between high- and low-severity riparian fire study sections.

We compared the influence of quantitative reach- (streamside habitat and geomorphology, benthic macroinvertebrate density and composition) and catchment- (catchment fire frequency and extent, catchment size, and precipitation) scale environmental variables on tetragnathid spider responses (density, TP, reliance on aquatically derived energy, and Hg body loading) with an information theoretic model selection approach based on the Akaike Information Criterion adjusted for small sample size (AIC$_c$; Anderson and Burnham 2002, Burnham and Anderson 2004). We selected competing models per response variable based on the significance ($p < 0.05$) of the predictor variables by linear regression. For comparison, we included the null model (intercept only) in each set of competing models.

We first examined potential correlations among the predictor variables for each model set. No variables with $|r| \geq 0.80$ were included in the same model (e.g., Sullivan et al. 2007, Allen and Vaughn 2010). We ranked all candidate models according to their AIC$_c$ values. The most parsimonious model was the one with the lowest AIC$_c$ value (Anderson and Burnham 2002, Burnham and Anderson 2004). Although models within 2 AIC units of the best model are considered to have the greatest support, those within 6 units from the best model are still worth consideration (Richards 2005). For this study, we considered all models that were within 4 AIC units of the best model and calculated Akaike weights (w_i) to assess the weight of evidence in favor of each model (Anderson and Burnham 2002, Burnham and Anderson 2004).

We used subsequent linear regression to highlight key bivariate relationships between spider descriptors and environmental predictors and between tetragnathid TP and Hg body loading. Given our relatively limited sample size and high variability in responses expected among study sections, we used α = 0.05 to indicate statistical significance and α = 0.10 as a trend (e.g., Rowse et al. 2014). We performed all statistical analyses with JMP (version 10.0; SAS Institute, Cary, North Carolina).

Phase 2: Paired before-after–control-impact experiment (2014)

We used a paired before-after–control-impact design (BACIP; Stewart-Oaten et al. 1986, Downes et al. 2002) to compare study sections in 2 reaches with riparian zones that were burned by the Rim Fire with study sections in 2 reaches with riparian zones that were not burned by the Rim Fire (i.e., sections in control reaches). A high-severity fire in 1996 burned the riparian zone of the Middle Tuolumne Creek reach, and a low-severity fire burned the riparian zone of the South Tuolumne Creek reach in 2002. The riparian zone of the Middle Tuolumne reach was burned again by high-severity fire and the riparian zone of the South Tuolumne reach was burned again with low-severity fire during the Rim Fire, thereby creating 2 separate treatments (high/high- and low/low-severity riparian fire). We resampled at Frog Creek and Cascade Creek (neither of which was inside the Rim Fire perimeter) as controls because they are similar in elevation and stream size to Middle Tuolumne and South Tuolumne Creeks, respectively. Previous riparian fires in these reaches were classified as high severity (Frog Creek reach) and low severity (Cascade Creek reach).

We collected (and calculated) a subset of data (tetragnathid spider density, benthic invertebrate density, D_{50}, % large and small wood, and % overhanging vegetation) based on the protocols described above. We used paired t-tests to compare our focal measures before (in 2012) and after (in 2014) the Rim Fire for each of the 4 study sections. We calculated means and SDs for t-test analysis using intrasection subsamples as replicates, whereby we partitioned tetragnathid spider density, % overhanging vegetation, and % large and small wood by 5-m increments and by bank and calculated D_{50} for each of the 3 pebble counts/ study section. We used benthic invertebrate density in each taxonomic order to generate means and SDs for t-tests.

RESULTS
Phase 1 (2011–2013)

Average monthly precipitation for each water year ranged from 3.9 cm/mo (Crane Flat, 2012) to 13.5 cm/mo (Wawona, 2011). Most of the winter precipitation fell as snow. July and August were the driest months. Mean monthly precipitation at Crane Flat decreased throughout the study period from 8.1 cm/mo in the 2010–2011 water year to 3.5 cm/mo in the 2013–2014 water year.

Study sections were in streams that ranged from 1st- to 3rd-order and varied in size from 1.3 to 14.0 m wide at bankfull (Table 2). Mean depth varied from 0.3 to 0.9 m. The % large and small wood in high-severity riparian fire study sections was almost twice that in low-severity riparian fire study sections ($t = -2.0$, df = 5, $p = 0.103$; Fig. 2A). Percent overhanging vegetation (Fig. 2B), D_{50} (Fig. 2C), and width-to-depth ratios (Fig. 2D) did not differ between treatment groups.

Benthic macroinvertebrate density was 1.5× greater in high- than in low-severity riparian fire study sections ($t = -2.3$, df = 5, $p = 0.072$; Fig. 2E). We identified benthic invertebrates from the orders Megaloptera, Plecoptera, Trichoptera, Ephemeroptera, Coleoptera, Diptera, Trombidiformes (Hydracarina), Oligochaeta, and class Turbellaria. Most individuals belonged to EPT orders (72 ± 11% across all study sections) in both treatment groups (Fig. 2F).

Tetragnathid spider density was numerically higher in low- than in high-severity riparian fire study sections, but this difference was not statistically significant ($t = 1.5$, df = 5, $p = 0.195$; Fig. 3A). Differences between treatment groups in tetragnathid spider TP (Fig. 3B), reliance on aquatically derived energy (Fig. 3C), and body loading of Hg (Fig. 34D) also were not statistically significant. TP was a weak predictor of tetragnathid spider Hg loading across all study sections ($R^2 = 0.30$; Fig. 4), suggesting that emergent insects contributed to spider diets.

Model-selection results suggested support for 2 models explaining tetragnathid spider density (Table 3). In the model receiving the most support ($w_i = 0.58$), precipitation and benthic macroinvertebrate density explained 78% of the variation in spider density across study sections. The 2nd model ($w_i = 0.23$), with precipitation as a predictor variable, explained 53% of the variation in spider density. A bivariate model with benthic macroinvertebrate density and fire frequency as predictor variables received the greatest support for explaining tetragnathid spider TP ($w_i = 0.50$), and a univariate model with fire frequency as a predictor received the greatest support for explaining SD_{TP} ($w_i = 0.40$). The null models for spider reliance on aquatically derived energy and body loading of Hg were most strongly supported and received 78 and 68% of support in their respective model sets (Table 3). Univariate models with precipitation as a predictor also received support for these response variables ($w_i = 0.19$ for reliance on aquatically derived energy, and $w_i = 0.25$ for Hg body loading) and warranted consideration.

Phase 2: BACIP design (2014)

Two of the 4 study sections sampled in the summer after the Rim Fire exhibited a reduction in tetragnathid spider density ($p < 0.05$; Table 4), but spider density did not change at South Tuolumne (before low, after low) or Middle Tuolumne (before high, after high) (Table 4). Benthic invertebrate density, % large and small wood, and D_{50} did not change at study sections within the control or impact reaches in the first year after the Rim Fire, but overhanging vegetation increased 50% at Frog Creek (after-control for high-severity fire) ($p < 0.05$, Table 4).

DISCUSSION

We used riparian spiders of the family Tetragnathidae as a model organism to test the effects of fire on the ecological coupling between aquatic and terrestrial ecosystems because they rely on streamside habitat and aquatic food resources. Tetragnathid spiders function at the local scale, but we anticipated that they would integrate fire effects across spatial extents because local stream characteristics (e.g., stream geomorphology and aquatic food resources) can reflect catchment-level processes (Poff 1997, Polis et al. 1997, Townsend et al. 2003). In spite of pronounced differences in the conifer canopy between study sections in stream reaches paired by riparian fire severity, tetragnathid spider attributes were largely invariant. Results from our model-selection analysis suggest that local food resources (i.e., benthic macroinvertebrate density as a proxy for emergent insects), catchment-scale fire frequency, and precipitation quantitatively influenced tetragnathid spider trophic dynamics and distribution. These findings may have important implications in the context of climate change. For example, alterations in global precipitation patterns are projected to lead to increases in the duration, severity, and frequency of extreme climate events, with more severe and less predictable flooding, droughts, and fires (Arnell 2004, Milly et al. 2005, Westerling et al. 2006).

Table 2. Biological and physical data for each study section (within stream reaches paired by riparian fire severity). Fire frequency is the proportion of catchment burned >2× since 1930, and fire extent is the proportion of catchment burned with moderate-to-high severity fire at the 12 study sections surveyed in 2011 and 2012. Reliance on aquatically derived energy is expressed as a proportion. Precipitation (sampling year) is the average of monthly totals from 1 October of the previous year to 30 September of the year sampling occurred. Ind = individuals, TP = trophic position, SD = standard deviation, % EPT = % Ephemeroptera, Plecoptera, and Trichoptera, D_{50} = median sediment size, – = unable to collect tetragnathid spiders of sufficient size and number to measure variable.

| Paired sections | Fire severity | Tetragnathidae | | | | | Macro-invertebrates | | Shoreline habitat | | Stream geomorphology | | | | Catchment-scale variables | | | |
		Tetragnathid density (ind/m)	Reliance on aquatically derived energy	TP Mean	SD	Hg (µg/kg)	Density (ind/m²)	% EPT	% overhanging vegetation	% wood	Width (m)	Depth (m)	Width-to-depth ratio	D_{50} (mm)	Precipitation (cm/mo)	Catchment size (km²)	% fire frequency	% fire extent
Tamarack	High	3.8	0.47	2.71	0.62	347	30.0	58.1	95.2	138.7	4.3	0.9	4.7	2.9	8.6 (2011)	1064.9	52.6	85.4
Grouse	Low	6.2	0.46	2.59	0.60	427	24.7	82.4	85.5	62.9	6.1	0.5	11.5	11.3	13.5 (2011)	1012.6	70.8	43.4
Meadow	High	1.0	–	–	–	–	66.8	60.5	100.0	67.7	1.3	0.3	4.1	2.1	8.7 (2011)	196.3	91.3	29.0
Camp	Low	3.5	0.48	2.46	0.57	–	30.0	84.4	58.1	54.8	2.2	0.5	4.7	1.8	8.7 (2011)	141.7	99.6	35.8
Buena Vista	High	1.4	0.35	2.58	0.59	386	58.4	85.4	91.9	33.9	8.0	0.4	24.6	22.8	8.7 (2011)	3524.1	14.8	24.6
Mono	Low	3.5	0.20	3.04	0.70	604	29.6	65.4	53.2	12.9	6.3	0.5	13.3	11.4	8.7 (2011)	2076.5	29.3	21.1
Middle Tuolumne	High	1.8	0.49	2.86	0.69	447	23.6	66.0	100.0	66.7	12.5	0.7	19.1	11.3	3.9 (2012)	9429.0	11.4	42.7
South Tuolumne	Low	3.2	0.46	2.69	0.70	505	36.0	77.8	77.4	51.6	14.0	0.9	19.6	8.2	8.6 (2011)	3477.0	1.5	9.6
Frog	High	3.0	0.47	2.64	0.63	406	42.4	83.5	100.0	101.6	9.6	0.4	21.7	8.2	3.9 (2012)	4388.8	41.8	36.9
Cascade	Low	1.2	0.52	3.22	0.83	324	21.7	59.9	83.9	21.0	7.6	0.9	8.9	11.3	3.9 (2012)	2688.2	1.5	1.5
Crane	High	1.9	0.57	2.08	0.59	213	54.2	77.8	40.3	3.2	2.0	0.6	4.0	8.1	3.9 (2012)	653.4	72.8	41.0
Coyote	Low	1.7	0.46	2.44	0.59	328	35.3	61.3	100.0	21.0	4.8	0.6	9.4	16.1	3.9 (2012)	493.5	9.5	2.4
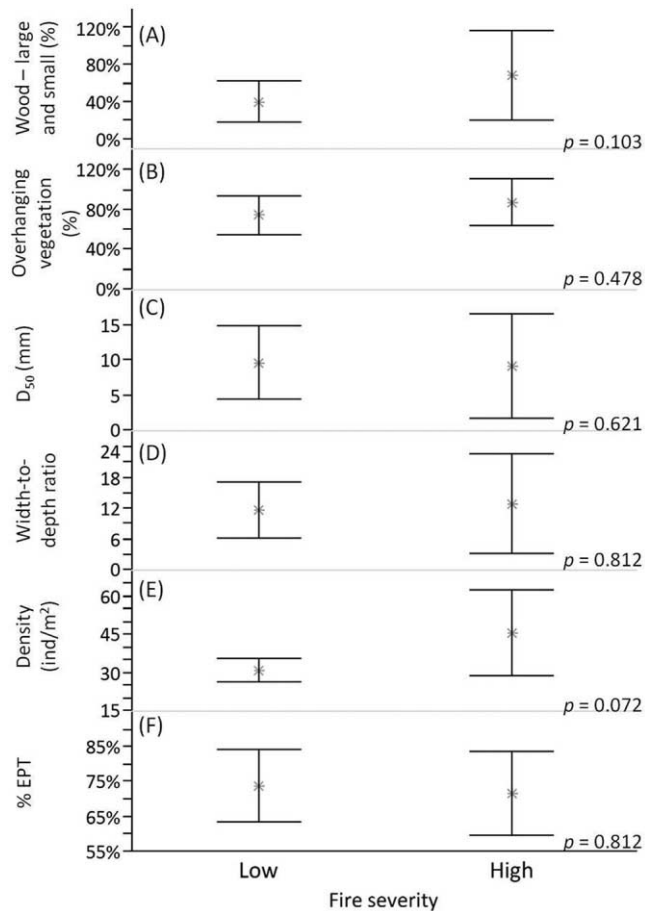
Figure 2. Mean (±1 SD) proportion of the stream bank occupied by large and small wood (A), proportion of the stream bank with overhanging vegetation (B), median substrate particle size (D_{50}) (C), stream width-to-depth ratio (D), benthic macroinvertebrate density (E), and proportion of the benthic macroinvertebrate community belonging to Ephemeroptera, Plecoptera, or Trichoptera (EPT) orders (F) at study sections of 12 paired stream reaches (low-severity fire/high-severity fire) in Yosemite National Park. n = 12 for all tests. Ind = individuals.

In temperate ecosystems, removal of the riparian canopy by fire can trigger increases in autochthonous productivity (Rugenski and Minshall 2014) and subsequent secondary productivity in the form of benthic macroinvertebrate biomass (Gresswell 1999, Malison and Baxter 2010, Rugenski and Minshall 2014). For instance, in central Idaho, riparian tetragnathid spider density was 2× greater and the flux of emergent insects into the riparian zone was 3× greater at streams reaches burned by high-severity wildfire 5 to 6 y before sampling than at reaches burned by low-severity wildfire (Malison and Baxter 2010). This pattern aligns with our finding that benthic macroinvertebrate density was 1.5× greater in high- than in low-severity riparian fire study sections. However, in our study, benthic macroinvertebrate density was negatively correlated with both tetragnathid spider density and TP. This

finding may suggest a dietary shift by tetragnathid spiders toward terrestrial prey in high-severity riparian fire study sections because terrestrial invertebrate abundance has been associated with increased shrub growth following disturbance (Romero et al. 2005); however, we did not measure terrestrial prey directly. We also observed a negative relationship between fire frequency and variability in TP (i.e., prediction 4), a result suggesting that catchment-level variability in fire frequency also may mediate spider–prey relationships.

We observed no difference in tetragnathid spider density between fire-severity treatments. Factors that influence web placement by riparian orb-web spiders include access to open water (Gillespie 1987) and web-building substrate (Tagwireyi and Sullivan 2015). Web-building substrate at our study sections included overhanging vegetation, which did not differ between fire-severity treatments, and large and small wood, which was ~30% more abundant at study sections in high- than in low-severity riparian fire reaches but was highly variable (SD = 47.9%) and not related to tetragnathid spider density in any of our models.
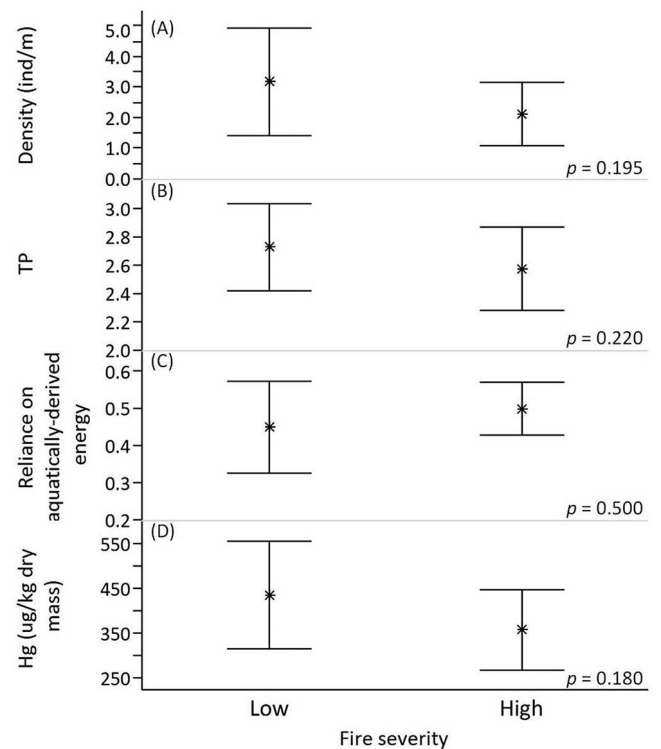

Figure 3. Mean (±1 SD) riparian tetragnathid spider density (A), trophic position (TP) (B), reliance on aquatically derived energy (C), and Hg body loading (D) at study sections of 12 paired stream reaches (low-severity riparian fire/high-severity riparian fire) in Yosemite National Park. n = 12 for panel A; for panels B (n = 11), C (n = 11), and D (n = 10), insufficient sample was available for both stable isotope and Hg analyses. Ind = individuals.
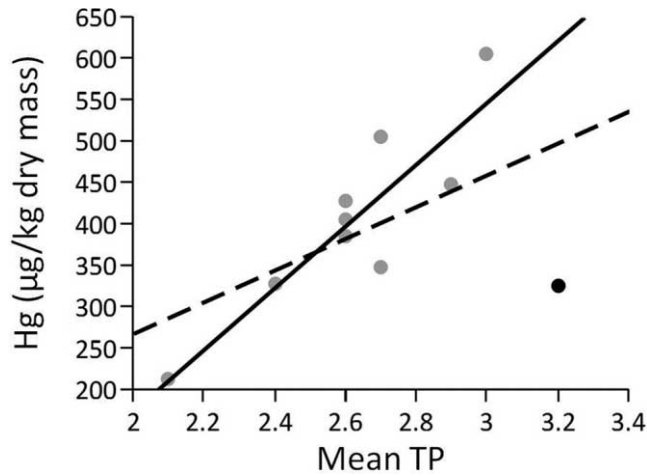
Figure 4. Relationship between body loading of Hg and mean trophic position (TP) in tetragnathid spiders across Yosemite National Park study sections. The regression slope indicated a trend using all 12 study sections (gray dots, dashed line: $p = 0.100$, $R^2 = 0.30$) and was statistically significant with data for Cascade Creek (black dot, solid line: $p = 0.0014$, $R^2 = 0.79$) removed.

Fire frequency was a supported predictor for tetragnathid spider trophic models, suggesting that the occurrence rate of fire (i.e., interval between fires) may affect subsidy dynamics between terrestrial and aquatic systems.

Fire frequency has been predicted to increase under various climate change scenarios (Westerling et al. 2006, 2011), and therefore, the potential association between fire frequency and FCL (as measured by tetragnathid spider TP in our study) may warrant further study.

The influence of precipitation on multiple characteristics of tetragnathid spiders suggests that environmental variability in climate may influence shoreline spiders more than wildfire does. Precipitation emerged as a key variable affecting tetragnathid spider density (positive relationship) and was weakly associated with spider reliance on aquatically derived energy and Hg body loading, results that provide initial evidence that climatic variability among catchments (and between years) may exert a greater effect than fire on stream biota. Precipitation is likely to have direct and indirect effects on spiders (e.g., Warren and Liss 1980). Precipitation patterns can influence benthic invertebrate density and community composition (Bêche and Resh 2007). These shifts can be driven by changes in the abundance of Chironomidae, which may be a key food source for riparian spiders (Alp et al. 2013). Extreme precipitation events can also prompt shifts in the richness and evenness of macroinvertebrate assemblages (Feio et al. 2010, Filipe et al. 2013), and extreme drought—resulting in cessation of flow—can be a primary driver of benthic macroinvertebrate community

Table 3. Retained regression models ($\Delta AIC_c \leq 4$) with corresponding Akaike Information Criterion for small sample size (AIC_c) scores, Akaike weights (w_i), and variation explained (R^2). Null models (i.e., intercept only) are also included. EPT = Ephemeroptera, Plecoptera, Trichoptera.

Tetragnathid spider response	AIC_c	ΔAIC_c	w_i	R^2
Density				
Precipitation (+), benthic macroinvertebrate density (−)	41.92	0.00	0.58	0.78
Precipitation (+)	43.73	1.81	0.23	0.53
Precipitation (+), benthic macroinvertebrate density (−), EPT (% of community composition) (+)	44.48	2.56	0.16	0.86
Null	47.75	5.83	0.03	0.00
Trophic position (mean)				
Benthic macroinvertebrate density (−), fire frequency (−)	6.30	0.00	0.50	0.66
Benthic macroinvertebrate density (−)	7.05	0.75	0.35	0.41
Null	9.00	2.70	0.13	0.00
Trophic position (SD)				
Fire frequency (−)	−24.38	0.00	0.40	0.37
Fire frequency (−) , benthic macroinvertebrate density (−)	−24.18	0.20	0.36	0.60
Null	−23.23	1.14	0.22	0.00
Reliance on aquatically derived energy				
Null	−14.79	0.00	0.78	0.00
Precipitation (−)	−11.97	2.82	0.19	0.10
Hg				
Null	126.64	0.00	0.68	0.00
Precipitation (+)	128.68	2.04	0.25	0.20

Table 4. Results of paired before-after–control-impact analysis of tetragnathid spider density, benthic macroinvertebrate density, median sediment size (D_{50}), and shoreline habitat (% wood, % overhanging vegetation) at study sections of 2 stream reaches with riparian zones burned by the Rim Fire (high or low fire severity) and 2 control reaches with riparian zones unburned by the Rim Fire. Change in means and t-test results are presented. Ind = individuals, − = data unavailable because of an error in data processing.

Study section/variable	Δ	t	p
Middle Tuolumne (before high, after high)			
Tetragnathid spider density (ind/m)	0.7	−1.16	0.282
Benthic macroinvertebrate density (ind/m^2)	34.2	−0.81	0.434
D_{50} (mm)	4.8	0.32	0.767
Wood—large and small (%)	−0.3	1.34	0.213
Overhanging vegetation (%)	0.2	0.53	0.610
Frog Creek (before high, after control)			
Tetragnathid spider density (ind/m)	−2.1	3.91	0.005
Benthic macroinvertebrate density (ind/m^2)	−12.7	0.37	0.717
D_{50} (mm)	0.0	1.44	0.286
Wood—large and small (%)	0.1	−0.45	0.667
Overhanging vegetation (%)	0.5	−4.81	0.004
South Tuolumne (before low, after low)			
Tetragnathid spider density (ind/m)	−2.1	1.42	0.118
Benthic macroinvertebrate density (ind/m^2)	36.4	−1.21	0.255
D_{50} (mm)	−0.1	0.88	0.472
Wood—large and small (%)	−0.3	1.14	0.282
Overhanging vegetation (%)	−0.2	1.34	0.226
Cascade Creek (before low, after control)			
Tetragnathid spider density (ind/m)	−2.5	5.42	0.001
Benthic macroinvertebrate density (ind/m^2)	26.8	−1.40	0.188
D_{50} (mm)	4.7	1.20	0.296
Wood—large and small (%)	−	−	−
Overhanging vegetation (%)	−0.3	1.72	0.125

composition (Verkaik et al. 2013b). Shifts in the distribution and composition of stream invertebrate food resources are expected to profoundly affect riparian consumers, including tetragnathid spiders (Kennedy and Turner 2011).

Fire and precipitation can interact to influence benthic macroinvertebrates, and many of these effects are related to stream flow (Verkaik et al. 2013b). Changes to stream flow, including altered timing and reduced magnitude of peak flows, can lead to higher concentrations of chlorophyll a and periphyton standing crop (Davis et al. 2013). For example, climate-driven shifts toward higher temperatures and an absence of scouring flows related to reduced snowpack were associated with reduced effects of wildfire on stream primary productivity and benthic macroinvertebrate community composition (Rugenski and Minshall 2014). Interannual variability in benthic macroinvertebrate community composition can be higher in streams draining catchments that have burned with greater extent of high

severity. This effect is primarily because of interannual variability in stream flow. That is, in wet years, wildfire interacts with stream flow resulting in significant shifts in benthic invertebrate community composition compared with unburned or low-severity burned catchments, but in dry years wildfire does not have a significant effect (Arkle et al. 2010).

We found preliminary evidence suggesting that fire, precipitation, and benthic macroinvertebrate density independently and jointly influenced riparian tetragnathid spider distribution and foodweb characteristics in our study system, but we did not measure stream flow directly. Our study occurred during a time of worsening drought conditions in the Sierra Nevada of California. Winter snowpack in the 2013–2014 water year was 17% of average, and annual precipitation accrual for Yosemite was 45% of the long-term average (California Data Exchange Center 2014; http://cdec.water.ca.gov/). Based on the signifi-

cant effect of precipitation across multiple spider responses observed in the pre-Rim Fire component of our study, drought may at least in part explain the decrease in spider density in 2 of the 4 sites surveyed in 2014 after the Rim Fire. Wildfires can be especially heterogeneous over space and time (Keeley et al. 2009). Thus, idiosyncratic patterns in aquatic–terrestrial responses to fire severity, frequency, and extent may be common and could contribute to the surprising lack of relationships observed in our paired analyses (both pre- and post-Rim Fire) (Gresswell 1999).

Our findings indicate that local riparian consumers may be more heavily influenced by patterns in precipitation than wildfire, but we think it likely that integrated explanations involving fire, climate, and their interactions will be most compelling (e.g., Arkle et al. 2010, Verkaik et al. 2013b, Rugenski and Minshall 2014), especially given seasonal dry–wet cycles and high interannual variability in precipitation characteristic of Mediterranean biomes. Moreover, fire can span multiple spatial extents within a catchment. Thus, explicit treatment of the relative effects of local- and landscape-scale fire characteristics will be critical, particularly in investigations of the effects of fire on stream–riparian food webs that include mobile consumers (e.g., bats, birds, lizards) that might be expected to integrate stream–riparian resources and habitats. Precipitation patterns and wildfire severity, frequency, and extent are projected to change dramatically under future climate-change scenarios (Miller and Urban 1999, Westerling et al. 2006, Miller et al. 2009), so studies examining linked fire–precipitation effects on aquatic–terrestrial responses will be of considerable conservation and management interest.

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