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Physicochemical and biological responses of streams to wildfire severity in riparian zones

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SUMMARY

1. We investigated the effects of a wildfire on stream physical, chemical and biological characteristics in a Mediterranean climate, comparing stream community structure and consumer resource use in burned versus unburned catchments in Santa Barbara County, CA, U.S.A.

2. Canopy cover was lower and water temperature was higher in streams draining basins where the riparian vegetation burned than in streams in unburned basins or burned basins where riparian vegetation remained intact. Stream flow and suspended sediment concentrations during large post-fire storms and wet season nutrient levels were higher in burned than unburned catchments, with increased sedimentation after flood peaks.

3. A year after fires, algal levels were highest in streams where riparian vegetation burned and lowest in streams in burned basins where the riparian canopy remained intact. In contrast, streams in burned basins had lower particulate organic matter, detritivore and predator levels than unburned basins, regardless of whether riparian vegetation burned. Where present, southern California steelhead trout (*Oncorhynchus mykiss*) were extirpated from burned basins.

4. Algivore densities were high in streams with burned riparian vegetation for two post-fire years before declining to unburned stream levels. Shredder densities rebounded in streams in burned basins with intact riparian vegetation, but remained low for 4 years where riparian vegetation burned. Predatory invertebrate densities increased at sites where trout were eliminated by wildfire.

5. Hydrogen stable isotope analysis indicated that the diets of most invertebrate taxa in streams with burned riparian vegetation a year after fires were comprised of a higher proportion of algal material than riparian detritus relative to invertebrates in streams with intact riparian vegetation.

6. Wildfire impacts on stream food webs are determined, in part, by fire severity in the riparian zone. Streams with burned riparian canopies supported algal-based food webs and streams with intact riparian canopies sustained detrital-based food webs. Fire affected basal resources (nutrients, light, allochthonous inputs) with bottom-up effects on primary producers and consumers, but top-down effects were decoupled at the trophic link between invertebrate predators and primary consumers.

Keywords: biota, disturbances, riparian, streams, wildfire

Introduction

The frequency, extent and severity of wildfire in many parts of the world are projected to increase due to changes in climate, land use and management practices (Syphard *et al.*, 2007; Bowman *et al.*, 2011; Westerling *et al.*, 2011). Climate change effects on precipitation, air temperature and wind patterns will affect fuel loads (amounts of combustible material), foliar moisture levels and humidity, influencing the ignition, spread, intensity, extent, timing and severity of wildfire (Littell *et al.*, 2009; Westerling *et al.*, 2011). Fires are particularly powerful

and pervasive drivers of ecosystem change in Mediterranean climates because of seasonal drought, the accumulation of fire-adapted plant biomass (fuel), large inter-annual variation in precipitation, winter floods and steep terrain (Keeley *et al.*, 2012; Verkaik *et al.*, 2013). In addition to effects on terrestrial ecosystems, changes in the extent and severity of wildfire in Mediterranean regions, coupled with shifts in the timing, magnitude, intensity and frequency of subsequent precipitation events have the potential to alter the physical, chemical and biological characteristics of receiving waters (Shakesby, 2011; Verkaik *et al.*, 2013). As a consequence, scientists, policy-makers and resource managers will require knowledge of the effects of wildfire on freshwater ecosystems.

By destroying catchment vegetation, altering soils and increasing run-off and erosion, wildfire can affect water quality, geomorphic processes, substrata composition, water temperature, light levels and allochthonous inputs in streams, with consequences for their ecosystems (see reviews in Gresswell, 1999; Verkaik *et al.*, 2013). Although fires have been suggested to shift the base of stream food webs from allochthonous leaf litter inputs to autochthonous algal production, predominantly by reducing riparian canopy cover (Mihuc & Minshall, 1995), reported responses of stream algae, particulate organic matter, invertebrates and fish to fire have been inconsistent (Minshall, Royer & Robinson, 2004; Bêche, Stephens & Resh, 2005; Arkle & Pilliod, 2010; Malison & Baxter, 2010; Romme *et al.*, 2011; Oliver *et al.*, 2012; Verkaik *et al.*, 2013). These variable responses of stream communities to fire have been attributed to variation in the extent, severity and spatial pattern of fires, duration and intensity of subsequent run-off events, occurrence of post-fire landslides, size of stream and time since fire (Gresswell, 1999; Minshall *et al.*, 2004; Vieira *et al.*, 2004; Robinson, Uehlinger & Minshall, 2005; Arkle, Pilliod & Strickler, 2010; Koetsier, Krause & Tuckett, 2010; Malison & Baxter, 2010; Romme *et al.*, 2011; Sestrich, McMahon & Young, 2011).

Given the past and projected importance of fire to Mediterranean landscapes and inconsistencies in reported fire impacts on stream ecosystems, we monitored stream responses to two fires that swept the coastal foothills and mountains above Santa Barbara, CA, U.S.A., in November 2008 and May 2009 (Fig. 1). Because fire effects on riparian vegetation were variable, we were able to compare ecological responses in streams draining burned basins where riparian vegetation was left intact or was destroyed by wildfire, allowing us to examine a key factor which might account for variability in stream responses to fire (Pettit & Naiman, 2007).

We focused on stream responses to wildfire after subsequent winter storms because both previous and our own observations indicated a negligible immediate effect of wildfire on stream invertebrates and fish during the dry season (Verkaik *et al.*, 2013). We made the following predictions:

(1). Increased fire-induced run-off and erosion associated with winter rains will increase stream discharge, sediment transport and deposition and nutrient concentrations, as well as remove particulate organic matter and organisms (Shakesby, 2011; Warrick *et al.*, 2012; Coombs & Melack, 2013; Verkaik *et al.*, 2013).

(2). Stream reaches where riparian vegetation burned will have decreased canopy cover and leaf litter inputs, and increased water temperature and algal biomass, resulting in increased algivore and decreased detritivore densities (Koetsier *et al.*, 2010; Malison & Baxter, 2010; Vieira, Barnes & Mitchell, 2011; Verkaik *et al.*, 2013).

(3). By extirpating trout, which consistently reduce the abundance of invertebrate predators, wildfire will increase invertebrate predator densities (Wiseman, Cooper & Dudley, 1993; Meissner & Muotka, 2006); however, invertebrate predator effects on primary consumers will be counterbalanced by bottom-up interactions stemming from wildfire effects on basal resources (algae, leaf litter).

(4). Food webs will be based on algal resources in streams where riparian vegetation burned but on detrital resources derived from riparian leaf litter in streams where riparian vegetation remained intact (Mihuc & Minshall, 1995).

Methods

Study site description

The Santa Ynez Mountains rise steeply from the Pacific Ocean to peaks exceeding 1400 m (Fig. 1). These mountains are underlain by shale and sandstone bedrock, with overlying alluvial deposits in flatter areas, such as coastal plains or terraces. This region has a Mediterranean climate, being wet and cool from November through March and dry and warm from April through October, with average annual rainfall ranging from 100 cm in the mountains to 45 cm at sea level (Keller & Keller, 2011). Streams in this area show high seasonal variation in discharge ranging from no or very low base flows (*ca.* 0.001–0.005 m^3 s^{-1}) in late summer and autumn to >15 m^3 s^{-1} during winter floods. The dominant riparian trees are alder (*Alnus rhombifolia*), California laurel (*Umbellularia californica*), willow (*Salix* spp.)
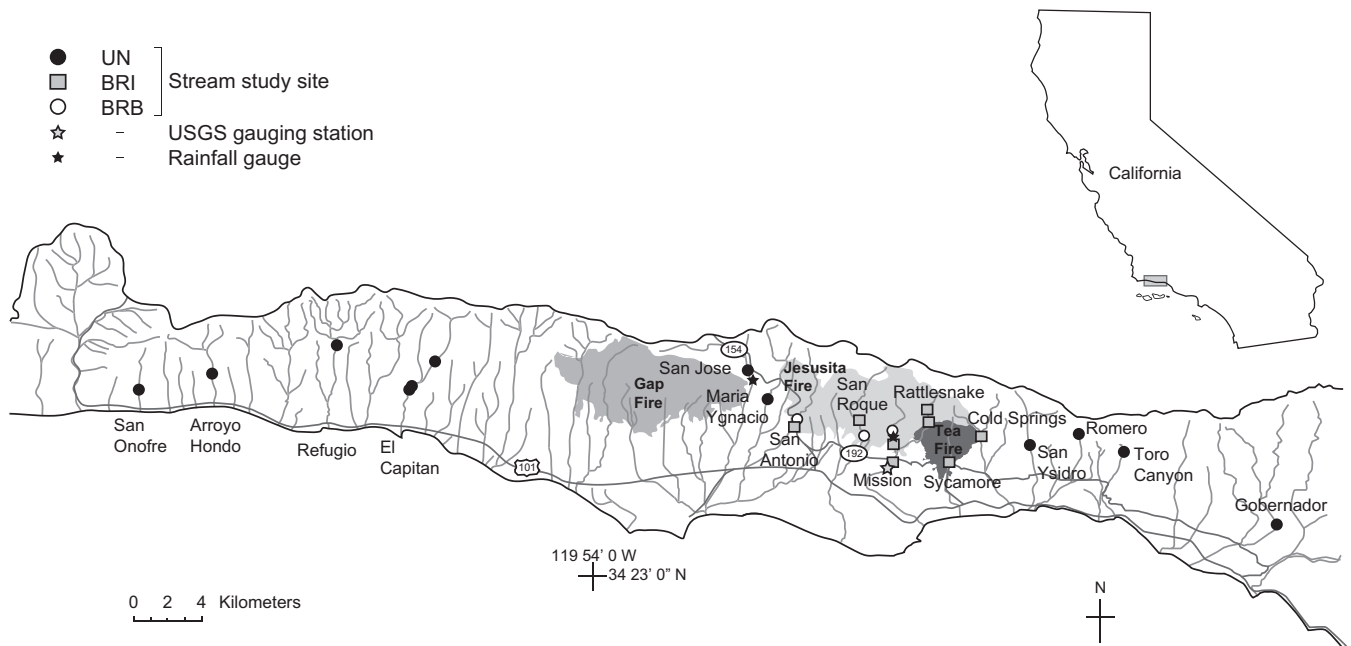
Fig. 1 Map of the study region and streams showing the locations of the hydrological gaging station, the rain gauges and the stream study sites in basins which were unburned (UN) and burned with riparian vegetation either burned (BRB) or remaining intact (BRI). Numbers with associated lines (i.e. 101, 154 and 192) represent major highways. The Jesusita, Gap and Tea Fires are shaded with light, medium and dark grey, respectively. Location within California, USA, is indicated in the inset.

and California sycamore (*Platanus racemosa*), with under-story shrubs such as Pacific poison oak (*Toxicodendron diversilobum*) and currant (*Ribes* spp.). Upland areas are dominated by mixed and *Ceanothus* chaparral, with coastal sage scrub, grasslands and oak woodland at lower elevations (Lentz, 2013).

Most chaparral in these mountains has burned in the last 50–60 years, with nearly all fires ignited by human activity (Ford, 1991). The precipitous topography and south-facing aspect of the Santa Ynez Mountains promote aggressive fires that often move rapidly, driven by hot, dry winds that blow from the mountains to the sea in the evening. The Tea Fire burned 785 ha from 13 to 17 November 2008 and the Jesusita Fire burned 3534 ha from 5 to 18 May 2009 (Fig. 1). An earlier fire, the Gap Fire, burned 3862 ha just west of the Jesusita Fire from 1 to 28 July 2008, but did not affect any of our stream study sites. We concentrate on the Jesusita Fire in this analysis because the Tea Fire burned only 1 and 11% of the drainage areas of two of three study sites influenced by the Tea Fire, and these sub-basins were subsequently burned to greater extents by the Jesusita Fire. The only study site substantially affected by the Tea Fire was Sycamore Creek (88% of the fire footprint was in its basin), but we did not start sampling this site until June 2011. From 60 to 80% of study basin areas in the Jesusita Fire's

core area were burned, with study basins on the fire's perimeter showing lower fire extents (20–50%). Soil burn severity was moderate to high in 78% of the area burned, with unburned or low burn severity areas within the fire's perimeter found primarily along stream corridors or at lower elevations (A. Janicki, US Forest Service, unpublished soils section of Burned Area Emergency Response Report). The Jesusita Fire was anomalous in occurring in spring, whereas most fires occur in summer or autumn, but it followed a dry winter (59% of the 20-year precipitation average for the City of Santa Barbara). Subsequently, the 2010 water year (WY) had average precipitation amounts (101% of 20-year average), the 2011 WY was wet (141% of average), and the 2012 and 2013 WYs were dry (57 and 44% of average) (Fig. 2).

Hydrological, precipitation and sediment analysis

To examine relationships between fire, and hydrological and sediment variables, we used US Geological Survey (USGS) hydrological gauging data and Santa Barbara Channel Long-term Ecological Research (LTER) data on suspended sediment concentrations (Fig. 2). We analysed hydrological data from USGS gauging station 11119745 on Mission Creek (elevation = 120 m,
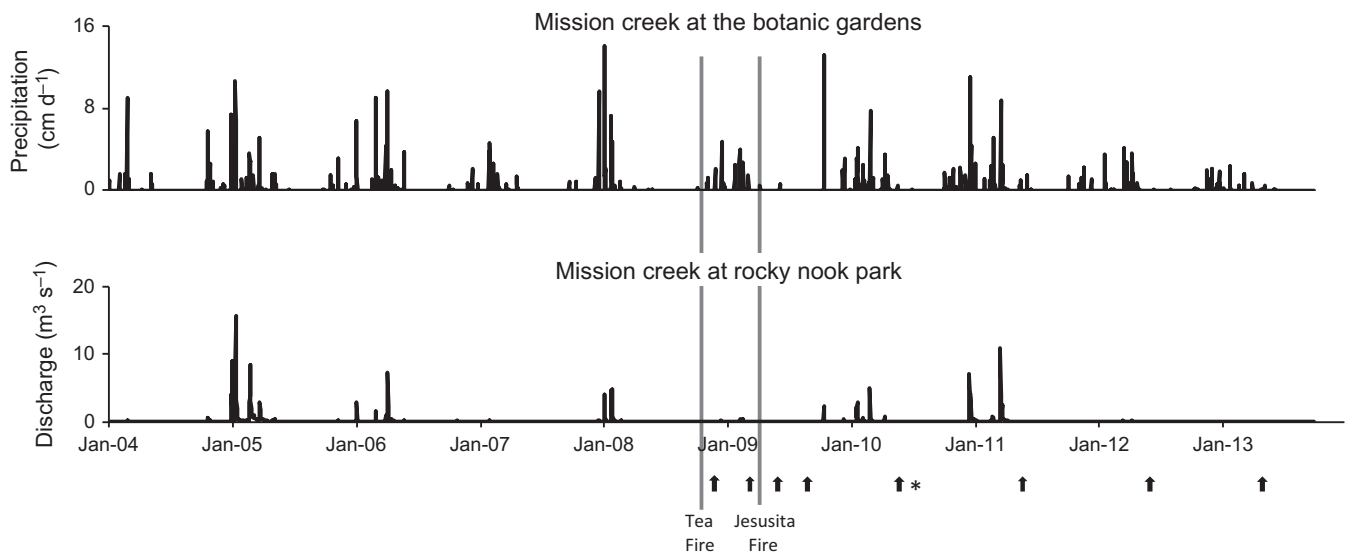
Fig. 2 Discharge and precipitation in the Mission Creek basin from 1 January 2004 to 30 September 2013. Data from USGS gaging station 11119745 and from the County of Santa Barbara's rainfall gauge at the Botanic Gardens. Arrows indicate the times of standard sweep sampling, and the arrow with an asterisk denotes the time that comprehensive sampling of all trophic levels was conducted.

drainage area = 17 km^2) from 1 October 2003 to 30 September 2013. Approximately 4% of this site's drainage area burned in the Tea Fire and >67% burned in the Jesusita Fire, with the gauging station lying <0.8 km below the Jesusita Fire perimeter. We compiled precipitation data from the County of Santa Barbara for a site near this gauging station (rain gauge elevation = 243 m) and at a high-elevation site (366 m) which received, on average, 92% of the rainfall recorded at San Marcos Pass, on the Santa Ynez Mountains ridgeline. Because high- and low-elevation stations bracketed most of the gauging station drainage area, we averaged high- and low-elevation data to obtain estimates of basin-wide rainfall amounts. Because we wanted to quantify the effects of individual storms on run-off, we first restricted the data to storm events, defined here as consecutive days of total rainfall exceeding 2 cm. To isolate the effects of individual storms on stream discharge, we subtracted daily discharge values for the day before a storm began from both the average and maximum daily discharge during the storm. We calculated individual storm precipitation and discharge amounts, run-off (discharge/drainage area) and run-off coefficients (run-off/precipitation). Nearly 60 cm of rain fell over 14 days in January and February of 2005, the wettest year of the past 15 years (182% of 20-y average), resulting in the highest run-off coefficients recorded over the analysis period. To insure that precipitation patterns were similar during pre- (WYs 2004–08) and post-fire (WYs 2010–13) periods,

these storms were not included in subsequent analyses. The final data set included run-off and rainfall data for 26 pre-fire storms (storm rainfall range = 1.9–26.2 cm) and 29 post-fire storms (2.1–33.0 cm). Suspended sediment concentrations were measured at a site on Rattlesnake Creek (elevation 300 m), a tributary of Mission Creek, during pre ($n = 11$, 2002–08) and post-fire ($n = 155$, 2010–11) storms (11% of the Rattlesnake basin burned in the Tea Fire and 67% in the Jesusita Fire, methods in Coombs & Melack, 2013).

Stream sampling design

We monitored 23 stream sites, each at least once, from December 2008 to June 2013 in the Santa Ynez Mountains and their southern foothills (Fig. 1). The number of sites varied each year depending on the sampling methods used and because some sites dried and others were added in the later years of the study (Table 1). Drainage areas of the study sites ranged from 2 to 18 km^2, elevations from 62 to 480 m and gradients from 2.5 to 13.3%, with stream water having slightly alkaline pHs (6.9–8.4), high conductivities (590–970 µs cm^{-1}) and low nutrient concentrations (NO_3^- -N = 0.1–12.1 µM, PO_4^{-3}-P = 0.2–1.2 µM). Stream substrata were dominated by gravel, cobble, boulders and bedrock, although fine sediments became prominent at sites affected by fire, and water temperatures ranged from 11 to 24 °C in the dry season and 5 to 20 °C in the wet season. Stream sites lay largely or entirely above developed areas (drainage area

Table 1 Standard sweep-sampling design. Numbers represent the number of sites sampled at each time in each fire-trout category

Category	Before Jesusita Fire		After Jesusita Fire, before rains		After Fires, after rains			
	December 2008	March 2009	June 2009	September 2009	June 2010	June 2011	June 2012	June 2013
Unburned (UN)	**9**	**11**	**7**	**6**	**7**	**8**	**11**	**9**
With trout (UNT)	4	5	3	3	3	3	5	5
Without trout (UNTL)	5	6	4	3	4	5	6	4
Burned (B)	**2**	**2**	**6**	**4**	**7**	**9**	**11**	**10**
Riparian burned (BRB)	0	0	2	1	2	3	3	3
Riparian intact (BRI)	2	2	4	3	5	6	8	7
Initially with trout	2	2	4	3	4	4	4	4
Initially without trout	0	0	0	0	1	2	4	3

The table is arranged hierarchically, so that the number of sites in burned and unburned basins (in bold) are further divided into subcategories representing sites with (UNT) and without trout (UNTL) in unburned basins and sites in burned basins where the riparian vegetation burned (BRB) and did not burn (BRI). BRI sites were further divided into those where trout were and were not originally present. The Tea Fire occurred in November 2008, and the Jesusita Fire in May 2009. Comprehensive sampling of abiotic and biotic factors for this study was carried out in June, 2010.

coverage <4% urban, <6% agricultural), with the exception of Sycamore Creek (11% urban cover).

The Jesusita Fire affected 11 of our sampling sites (Fig. 1). In our analyses, we classified our sites into four categories: two types of sites in burned (B) basins including where riparian vegetation did (BRB) and did not burn (BRI) and two types of sites in unburned (UN) basins including those with trout (UNT) and without trout (UNTL). The BRI sites monitored in the 2009 WY all contained steelhead trout, but trout disappeared from these sites during floods in the 2010 WY. From 2010 to 13, we annually monitored five to eight BRI sites, including four from which trout were extirpated and one to four which never supported trout (Table 1, Fig. 2). The BRB sites always lacked trout.

We measured physicochemical variables, benthic particulate organic matter (BOM), algae, invertebrates and fish at seven sites in unburned basins (three UNT and four UNTL) and seven sites in burned basins (two BRB and five BRI sites) in June 2010, 2 months after the last floods of the 2010 WY and 13 months after the Jesusita Fire (Fig. 2). At this time, we also collected basal resource (leaves, algae) and invertebrate samples for stable isotope analyses at 10 of these study sites (six UN (three UNT, three UNTL), two BRI and two BRB sites). In addition, we measured selected physicochemical variables and the composition and densities of large (>1 mm), epibenthic and water column invertebrates and amphibians in pools of 6–11 unburned sites (three to five UNT and three to six UNTL), one to three BRB sites, and two to eight BRI sites, twice before the Jesusita Fire, twice after the fires but before winter rains began and at annual intervals over 4 years after fires (Table 1).

Stream physical and chemical measurements

The lengths and positions of each pool and riffle along each 100-m study reach were measured in June 2010. On hard (cobbles, boulders, bedrock) versus soft (silt, sand, gravel, pebbles) substrata in each of five riffles and five pools in each reach, we measured average water depth, visually characterised substratum into the size classes noted above and measured base flow water velocity at 60% depth with a Marsh-McBirney water current metre (Model 210D, Marsh McBirney, Inc., Frederick, MD, U.S.A.). We also measured sediment and maximum water depths, wetted width and % canopy cover in four directions (upstream, downstream, facing each bank) with a Model-A spherical densiometer (Forest Densiometers, Bartlesville, OK, U.S.A.) in each of these five riffles and five pools. At the upstream end of each study reach, we measured water temperature with a YSI model 55 DO/conductivity metre (Yellow Springs Instruments, Yellow Springs, OH, U.S.A.). In June of 2011, 2012 and 2013, we measured sediment and maximum water depths and canopy cover in five pools per site, as well as water temperature at the upstream end of each site, using the methods outlined above.

In March and June, 2010, we collected water samples for inorganic nitrogen species (NO_3^-, NO_2^-, NH_4^+) and orthophosphate (PO_4^{-3}) from the upstream end of each study reach. Dissolved inorganic nutrient samples were filtered through 0.45-μm polycarbonate filters in the field, then frozen and stored at −20 °C until analysed. Nutrient concentrations were measured spectrophotometrically on a Lachat Quikchem 8000 flow injection analyzer (Lachat Instruments, Milwaukee, WI,

U.S.A.) by the UCSB Marine Science Institute Analytical Laboratory (http://analab.ucsb.edu) using standard methods (QuickChem Gas Diffusion Method 31-107-06-5-A).

Algal sampling

We sampled benthic algae from hard (cobbles, boulders, boulders, bedrock) and soft (silt, sand, gravel, pebbles) substrata at each of three random locations for each substratum type within each of five riffles and five pools over each 100-m study reach (n = 15 samples for each of four subhabitats). We took hard-substrata algal samples using the open-ended syringe sampler described by Davies & Gee (1993) and soft-substrata samples by coring the stream bottom to a depth of 0.8 cm with the syringe barrel. We rinsed hard-substrata sample pads with deionised water and agitated, mixed and elutriated soft-sediment cores, creating algal suspensions which were subsampled and filtered through GF/C filters (pore size 1.2 μm). Chl *a* filters were extracted in 90% acetone at −20 °C in the dark for 24 h with resulting solutions measured fluorometrically on a Turner 10-AU field fluorometer (Turner Designs, Inc., Sunnyvale, CA, U.S.A.). Subsamples for determination of ash-free dry mass (AFDM) were filtered through pre-combusted (at 500 °C), pre-weighed GF/C filters, which were then dried at 60 °C for 24 h, weighed, combusted at 500 °C for 2 h and reweighed (Klose *et al.*, 2012). In addition, we preserved subsamples from hard-substrata samples in 10% buffered formalin. These subsamples were settled in Sedgewick-Rafter counting chambers, then algal cells were identified to species and enumerated at 400× under a microscope. Species densities were calculated by counting all viable cells in a known subsample volume (minimum 300 cells per slide), then back-calculating to obtain estimates of areal density.

For estimates of algal % cover, we visually noted the algal type or bare substratum under each of 50 evenly spaced dots within a 28 cm × 28 cm quadrat on the clear Plexiglas bottom surface of an underwater viewing bucket (U.S. Environmental Protection Agency's rapid bioassessment protocol, Barbour *et al.*, 1999). Algal types were categorised as the genus of macroalga or as the thickness of diatom mats (thin < 0.5 mm in height, medium = 0.5–2.0 mm, thick > 2.0 mm) (Klose *et al.*, 2012). Per cent cover by algal types was determined for two hard- and two soft-substrata quadrats in each of five riffles and five pools at each site (10 quadrats for each of four subhabitats per site).

Invertebrate, particulate organic matter (POM) and macroalgal sampling

In June 2010, we collected two Surber samples (each: bottom area = 0.09 m^2, mesh size = 250 μm) from each of five riffles and from hard and soft substrata, separately, in each of five pools per site (= 10 samples for each of three subhabitats per site). Samples were composited for each subhabitat at each site, substrata were separated from organic matter via elutriation, leaves were washed and removed to labelled plastic bags and invertebrates were preserved in 70% ethanol. In the laboratory, invertebrate samples were sieved through 4-, 1-mm and 250-μm sieves. All invertebrates in the >4-mm size fraction were identified and counted, whereas invertebrates in the 1- to 4-mm and 250-μm- to 1-mm size fractions were subsampled separately using a plankton splitter and invertebrates in subsamples were identified and counted under a dissecting microscope. Macroalgae collected on the 4-mm sieve were air-dried and weighed to provide an estimate of macroalgal biomass for each subhabitat. Coarse particulate organic matter (CPOM = leaves, detritus >1 mm) washed and collected in the field, removed from the 4-mm sieve and collected in the 1–4-mm subsample after the removal of invertebrates was air-dried then weighed, separately. FPOM removed from the 250-μm to 1-mm invertebrate subsample was processed like an AFDM sample to obtain estimates of the AFDM of FPOM. Using a subset of CPOM samples and the procedures outlined for FPOM, we developed regression equations converting dry mass (air-dried) of CPOM to AFDM. We calculated the densities of invertebrate taxa in each size class and over all size classes, and the AFDM of CPOM and FPOM for each subhabitat type for each study site.

Pool epibenthic and water column macroinvertebrates and amphibians were additionally sampled by taking standard sweeps with a D-net (1-mm mesh, 30 cm lower edge, *ca.* 1 m length of each sweep). Six standard sweeps were taken along the stream bottom from each of five pools at each site on each of eight dates (30 samples per site per date) (Table 1). Invertebrates collected from each pool were identified and counted in the field where possible, otherwise under a microscope in the laboratory. Standard sweep sampling was more effective than Surber sampling at obtaining adequate numbers for statistical analyses of large, rare and/or mobile epibenthic and water column taxa (e.g. tadpoles, large predatory insects, mosquito larvae). Numbers obtained from standard sweep sampling (number per 30 standard sweeps) were positively correlated with average pool

densities of large invertebrates (>1 mm) from Surber sampling for the algivore (r = +0.84, P c. 0.0001), shredder (r = +0.82, P c. 0.0003), mosquito (r = +0.91, P < 0.0001), and, marginally, predator feeding groups (r = +0.49, P = 0.08). In June 2013, any CPOM collected in standard sweeps was washed, spun dry in a lettuce spinner then weighed on a field balance. Using a subset of CPOM samples, we developed a regression to convert CPOM wet mass to AFDM values.

Fish observations

We visually scanned study reaches for fish from vantage points as we proceeded upstream and, where the presence of fish was uncertain, additionally observed individual stream pools for 1 h to ascertain the presence or absence of fish. The only taxon present at the sites was the southern California steelhead trout, a distinct population segment of *Oncorhynchus mykiss* that has been listed as endangered under the U.S. Endangered Species Act. Our observations of trout distributions were corroborated by over 30 years of observations in study streams, by conversations with U.S. National Marine Fisheries Service (NMFS) and California Department of Fish and Wildlife (DFW) personnel, by NMFS and DFW records and by streamside and snorkelling surveys of a subset of study reaches by independent observers (Brinkman, 2007; M. Stoecker, M. Gomez, E. Brown, pers. comm.), including reaches affected by fire.

Stable isotope analyses

In June 2010, we collected qualitative samples of leaf litter, macroalgae and invertebrates from pools and riffles, separately, from 10 of our study sites (six UN, two BRB, two BRI) for stable isotope analyses. Further, additional algal and detrital samples were taken from these 10 sites and filtered through GF/C filters, as described in the algal methodology subsection above. All stable isotope samples were frozen at −20 °C prior to analyses. With the exception of chironomids, the guts of all macroinvertebrate individuals were removed prior to stable isotope analyses.

In the laboratory, leaf and macroalgae samples were thawed and rinsed in deionised water to remove adhering material. FPOM from depositional zones (soft substrata) was removed wet from GF/C filters. Samples of leaves, macroalgae, FPOM and insects were dried in glass scintillation vials without caps at 60 °C and ground to a fine powder using mortar and pestle. The ground material was divided in half with one portion

analysed for hydrogen isotopes and the other analysed for carbon and nitrogen isotopes. The number of invertebrate specimens processed varied by taxon depending on availability and individual size, with 10–100 individuals of each taxon from each site pooled to obtain sufficient material for analysis. Congruent with Doucett et al. (2007) and Finlay, Doucett & McNeely (2010), we found that hydrogen stable isotope signatures (δD) clearly separated algae from leaves and FPOM (see Results). In contrast, carbon stable isotope signatures were not consistently or substantially different between algae and leaves or FPOM; consequently, we concentrated on hydrogen stable isotope signatures in this study.

Isotopic analysis of ground subsamples (typically c. 500 mg) was conducted by the Facility for Isotope Mass Spectrometry (FIRMS) at the University of California, Riverside using a Thermo-Chemical Elemental Analyzer interfaced to a Thermo-Finnigan Delta-V Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific Corp., Breman, Germany) following procedures similar to those of Wassenaar & Hobson (2003) and Doucett et al. (2007). The natural abundance of hydrogen isotopes is expressed in standard δ notation as δD (=$\delta^2 H$) and relative to the Vienna Standard Mean Ocean Water (VSMOW). Coefficients of variation in δD values between replicate portions of the same ground sample ranged from 0.2 to 7.2% (mean = 3.3%, n = 10 replicates).

Mixing model analysis

We compared the contribution of algal versus riparian detrital sources to the diets of consumers in BRB, BRI and UN streams using a two-source mixing model (reviewed in Fry, 2006; Cheng et al., 2006). We were unable to separate microalgae cleanly from FPOM in hard-substrata samples, and microscopic examination and δD values indicated that there was substantial detrital material in microalgal samples. As a result, isotope values of known algivores (*Baetis, Callibaetis, Centroptilum, Fallceon, Eubrianax*) were used as a proxy for the algal end-member (Finlay, 2001). The assumption that the δD values of algivores reflect the algal food source seems reasonable because δD values of algivores were similar to those of macroalgae (primarily *Cladophora*) in this study and to diatoms in the study of Finlay, Doucett & McNeely (2010). Doucett et al. (2007) found that δD values for different algal groups (cyanobacteria, diatoms and filamentous green algae) did not differ consistently among sites, but Finlay et al. (2010) reported different δD values for different algal groups (e.g.

Cladophora = −225‰, diatoms = −174‰). In both studies, however, all algal δD values were much lower than δD values for leaf litter (*ca.* −100 to −110‰). Although algivores from one of the BRI sites were enriched in deuterium compared to the other sites, the δD values for *Cladophora* from this site were similar to those for our other sites, suggesting that algivores consumed more detritus at this site. As a consequence, we used the end-member values for algivores from sites in the two other basin categories as the algal end-member values for BRI sites.

For the riparian vegetation end-member, we used the δD values of either conditioned leaves obtained from each stream (for shredders) or of FPOM (for other consumers), which tended to be slightly enriched in deuterium (across all streams *c.* +15‰) relative to conditioned leaves. Because we could not obtain enough material to determine δD values of FPOM in riffles, we used δD FPOM values from pools for both pool and riffle habitats. Mixing model analyses were conducted for consumer taxa using algal and detritus end-member values for each stream, and these values were averaged for each basin category.

Recent work on shredders and algivores reported a close correspondence in δD values between body tissues and food sources (Finlay *et al.*, 2010), which was also consistent with a recent review of trophic fractionation data (Solomon *et al.*, 2009). We also have found good congruence between gut contents and δD values. The small differences in δD between these consumers and their resources suggest minor effects of trophic fractionation and isotope exchange with stream water on body δD, so we did not adjust for these effects.

Statistical analysis

We performed all statistical analyses using JMP Version 10 for Windows™ (SAS Institute, Inc., Cary, NC, U.S.A.). We analysed the hydrological data by first regressing average and maximum daily storm run-off and run-off coefficient values against average and maximum daily storm precipitation, respectively, for the pre-fire period (WYs 2004–08). We used resulting regression equations (with 95% CLs) to predict post-fire (WYs 2010–13) storm run-off and run-off coefficient values at observed rainfall levels. We calculated the differences between and ratios of observed (O) and expected (E) run-off and run-off coefficient values. O-E and O/E values were positively related to rainfall amounts with observed run-off values showing congruence with predicted values at storm rainfall amounts <9 cm, but substantially exceeding pre-

dicted values at storm rainfall >9 cm. As a consequence, we also compared pre- and post-fire data for small (<9 cm) and large (>9 cm) storms, separately. The pre-fire period had 18 small and eight large storms, whereas the post-fire period had 24 small and five large storms. Statistical significance was determined by examining whether observed post-fire run-off values for a given rainfall amount exceeded the upper 95% confidence limit for the pre-fire run-off-rainfall regression line and by comparing run-off or run-off coefficient values in pre- and post-fire periods (one-way ANOVA).

Stream physicochemical and biological data were analysed by one-way analysis of variance (ANOVA) to examine the effects of burning (BRB and BRI versus UN; unburned, including both UNT and UNTL sites), canopy openness (BRB versus BRI and UN sites), burn category (BRI versus BRB versus UN sites), and burn and trout categories (BRB versus BRI versus UNT versus UNTL sites) on response variables, depending on the contrast of interest. Where more than two independent categories were analysed, significant ANOVAs were followed by Tukey's HSD tests to examine statistical differences between all pairs of categories. We applied $\log_{10}(x)$ transformations to nutrient concentrations, current speed, CPOM, FPOM, AFDM and chlorophyll data, $\log_{10}(x + 1)$ transformations to data on invertebrate densities, and arcsine$\sqrt{(x)}$-transformations to data on proportion canopy cover, proportion macroalgal cover and the proportions of consumer tissue supported by algae.

Because different indices of macroalgal abundance, including biomass and % cover, were highly inter-correlated and because chlorophyll and AFDM concentrations were positively correlated (r = +0.55 to +0.85, P < 0.05 to <0.0001 across subhabitat types), we primarily present results for one macroalgal index (% cover) and chlorophyll concentrations here. Because we were interested in food-web interactions, we assigned macroinvertebrate taxa to feeding categories based on literature designations (Merritt, Cummins & Berg, 2008) and our own stable isotope analyses, recognising algivores (eat algae: primarily baetid mayflies, the water penny *Eubrianax* and tadpoles), deposit-feeders (eat FPOM: primarily Chironominae/Orthocladiinae, *Paraleptophlebia,* oligochaetes and various other taxa), shredders (eat CPOM: *Lepidostoma*, *Gumaga*, *Malenka*), filter-feeders (eat suspended algae and FPOM: *Simulium*, *Ceratopsyche*), predators (eat other invertebrates: odonates, hemipterans, dytiscid beetles, *Sialis*, *Rhyacophila*, *Calineuria*, *Isoperla*) and micropredators (Tanypodinae, predatory Ceratopogonidae, water mites). One exception to these designations was that the

baetid species *Diphetor hageni* was assigned to the deposit-feeder category based on its δD values. Most analyses on invertebrates concentrated on these feeding groups. We also recognised separate categories for plankton feeders (mosquito larvae), macrophyte herbivores (primarily haliplid beetles), microcrustaceans (ostracods, copepods, cladocerans) and omnivores (crayfish).

Comparisons of response variables across basin burn and trout categories were complemented by multiple regression analyses, which examined relationships between basal resources (algae, AFDM, CPOM, FPOM) and potential limiting factors (canopy cover = light, nutrients, water temperature, current velocity) and between invertebrate consumers and their resources (see Table S1). Where initial regression models contained two or more independent variables, we used a process of backward-stepwise elimination of variables to a stopping point determined by minimum-corrected Akaike information criteria (AIC) to select the most parsimonious models accounting for the greatest amount of variation in response variables.

Results

Fire effects on hydrological variables

Wildfire increased run-off in the Mission Creek basin during large (>9 cm) post-fire storms. Although run-off and run-off coefficients (RC) for the first post-fire storm on 13 October 2009, did not exceed pre-fire expectations, mean daily run-off and RCs exceeded predicted values by 2.5- to 3.7-fold for the four ensuing large storms with values significantly higher than those during the pre-fire period ($F_{1,11}$ = 11.1 and 10.4, $P < 0.01$; e.g. mean daily RC: pre-fire $\bar{x} \pm 1$ SE = 0.12 $\pm$ 0.04, post-fire = 0.25 $\pm$ 0.03) (Fig. 3). Maximum daily run-off and RCs for these four storms showed similar patterns (1.8–4.2 × predicted values), but pre- to post-fire differences were only marginally significant ($P < 0.08$). In contrast, post-fire run-off and run-off coefficients for small storms (<9 cm) did not differ substantially from predictions and there were no significant differences between pre- and post-fire periods (e.g. mean daily RC: pre-fire $\bar{x} \pm 1$ SE = 0.05 $\pm$ 0.03, post-fire = 0.03 $\pm$ 0.01).

Fire effects on stream physical–chemical variables and basal resources

Suspended sediment concentrations in Rattlesnake Creek during storms increased 36-fold after the Jesusita Fire
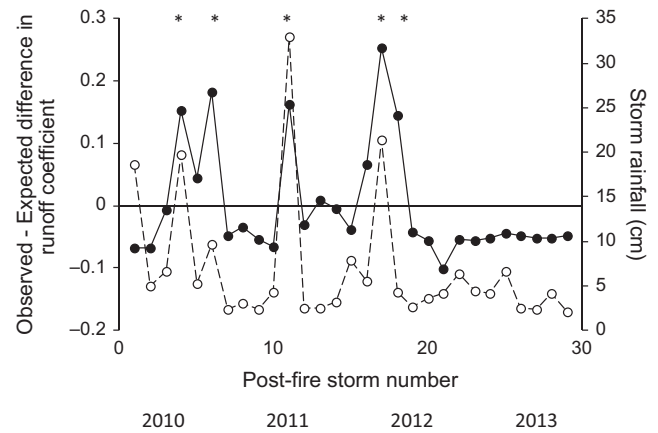

Fig. 3 Storm rainfall amounts (open circles, dashed line) and differences between observed and predicted run-off coefficients (solid circles and line) for the Mission Creek basin across the sequence of post-fire storms (>2 cm). Storm 1 occurred on October 13, 2009, during the 2010 WY. Asterisks denote run-off coefficient values significantly higher than those predicted from the pre-fire run-off coefficient–rainfall relationship.

from a pre-fire level of *c.* 60 mg L^{-1}. Also as predicted, nutrient concentrations were higher in streams in burned than unburned basins during the wet season (Fig. 4). After post-fire floods had passed, sediment depths and current velocities were greater and stream depths and BOM levels were lower at stream sites in burned than unburned basins (Figs 5 & 6). Sediment depths and nutrient concentrations were not different between BRB and BRI sites, suggesting that sediment and nutrient fluxes depended on the destruction of upland vegetation, and increased run-off and erosion, rather than local riparian conditions. In contrast, canopy cover was lower and water temperature and algal abundance were higher at sites where the riparian vegetation burned than at sites where the riparian canopy remained intact, regardless of whether upland areas burned (Figs 4, 6, 7 & 8). Our observations indicated that macroalgal biomass peaked at BRB sites in March and April, 2010, so the higher chlorophyll concentrations on soft substrata at BRB than other sites in June may represent the deposition of macroalgae that sloughed off hard substrata at BRB sites. Because nutrient concentrations were similar at BRI and BRB sites but algal abundance was higher at BRB than BRI sites, our results suggest the primacy of light levels in promoting high algal levels. Algal biomass at BRB sites, however, subsequently declined by mid-summer. In contrast, CPOM and FPOM levels were lower at sites in burned than unburned basins after fires and ensuing storms, but CPOM recovered in subsequent years at sites with an intact riparian canopy while

Fig. 4 Average values (±1 SE) of algal-associated resources and their consumers in the pools of sites in different trout and basin burn categories, including with (UNT) and without (UNTL) trout in unburned basins and with (BRI) and without (BRB) intact riparian vegetation in burned basins, June 2010. Inequalities (e.g. B > UN, UN > B) represent significant differences between sites in burned and unburned basins (ANOVA, $P < 0.05$) and burn categories overlain by the same letter are not significantly different using multiple comparisons tests ($P > 0.05$, Tukey's HSD test). Arrows point from resources to consumers and include abiotic resources (nutrients and light (as canopy cover)) on the bottom row, algal biomass (as chlorophyll concentration on hard and soft substrata) and macroalgal cover on the second row from the bottom, primary consumer densities (total algivores on soft and hard substrata, large (>1 mm) algivores on hard substrata, deposit-feeders on hard substrata) on the second row from the top and predator densities (predators and micropredators on hard substrata) on the top row. For nutrients, the results of Tukey's HSD tests are shown for March (M) and June (J), 2010. The BRIB^x designation indicates that trout and basin burn category had a marginally significant ($P < 0.10$) effect on large algivore densities.
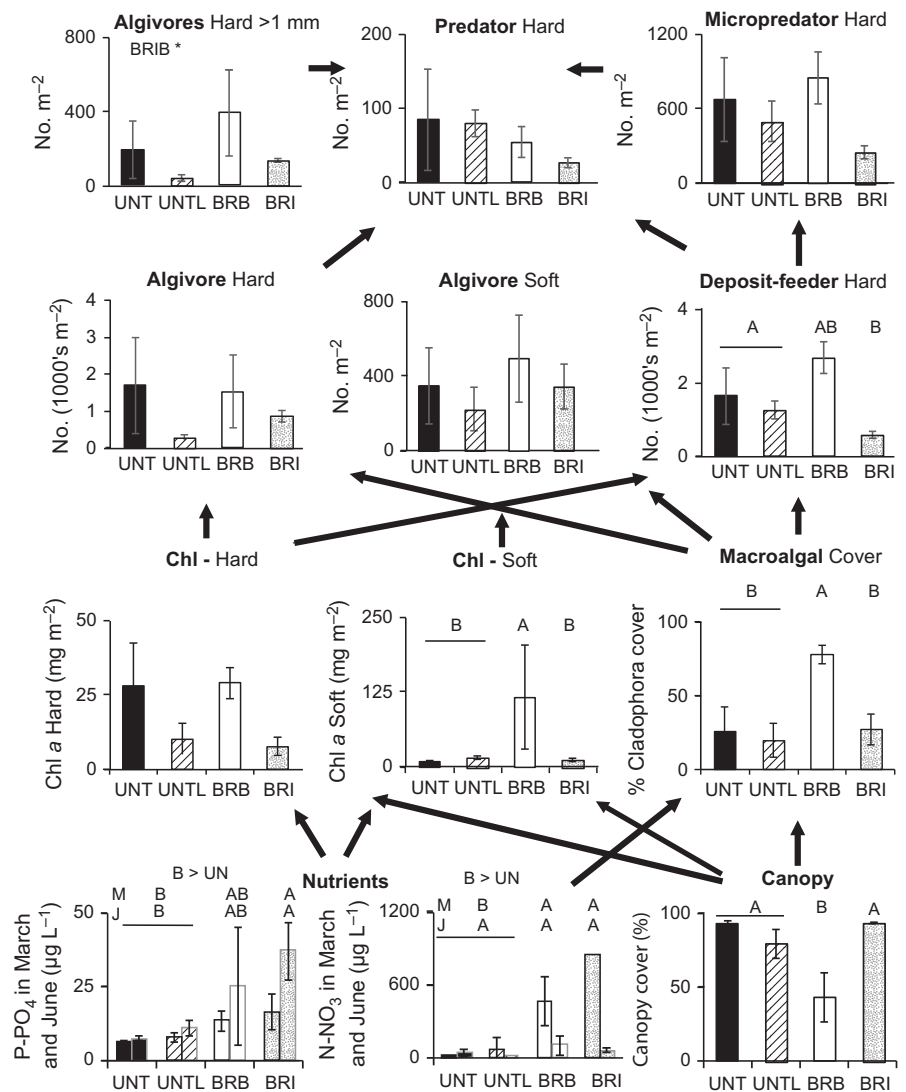
remaining low where riparian vegetation burned (Fig. 9).

Bottom-up and top-down effects of fires on stream consumers

We saw few direct, immediate effects of fire on invertebrates in the dry season (Fig. 10), but many responses after ensuing winter storms. Flood waters laden with sediment apparently scoured most organisms out of our study sites in burned basins, but organisms persisted in unburned basins with lower run-off and sediment loads, an interpretation supported by the larger size of long-lived predatory invertebrates in stream pools in unburned than burned basins (proportion of population >1 mm in length, unburned >burned, $F_{1,12} = 7.1$, $P < 0.05$). Total invertebrate densities were higher at

sites in unburned than burned basins in pool soft substrata, lower at BRI than other sites on pool hard substrata and not significantly different among burn categories in riffles (Fig. 7). In addition, there were marginally greater total large (>1 mm) invertebrate densities at BRB than other sites in riffles (ANOVA, $F_{1,12} = 4.3$, $P < 0.06$).

Analysis of algal versus detrital-based trophic pathways revealed differences in the responses of different consumers to fire (Figs 4, 6 & 8). Densities of algivores in riffles were higher in sites in burned than unburned basins whereas algivore densities averaged higher in pools at BRB than BRI or UNTL sites (Figs 4 & 8). Patterns were clearer when we focused on large algivores (>1 mm), which were more abundant at BRB than unburned sites, owing to high densities of *Callibaetis* (Figs 4, 8 & 10). Densities of deposit-feeders on hard
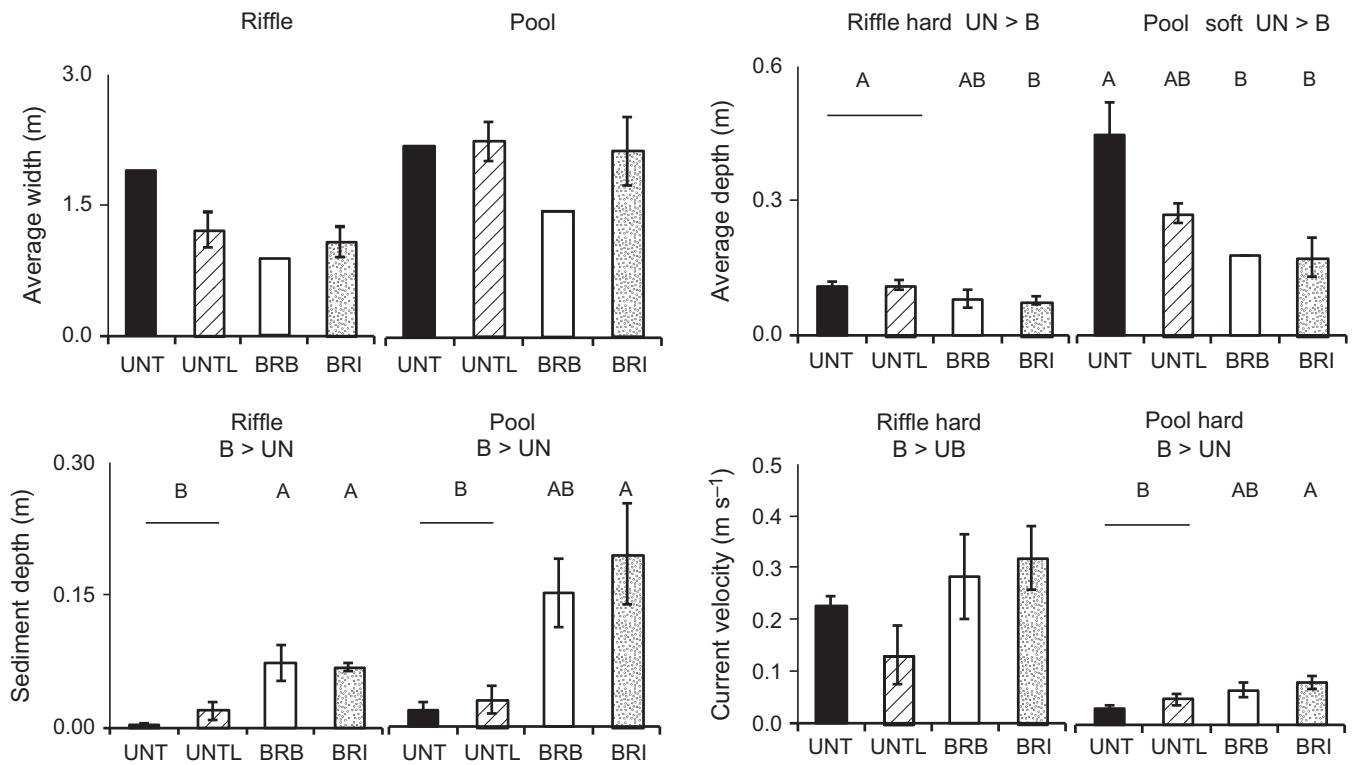
Fig. 5 Average values for physical variables (±1 SE), including stream width, depth, sediment depth and base flow current velocity, recorded in riffles and pools at stream sites in different trout and basin burn categories, June 2010. Codes and statistical designations as in Fig. 4. Hard and soft labels indicate variables were measured over hard or soft substrata.

substrata in pools tended to be higher at BRB and lower at BRI than other sites, with micropredators showing a similar, albeit non-significant, pattern (Fig. 4). In contrast, the densities of shredders and microcrustacea in all subhabitats, predators in the pool soft and riffle subhabitats and deposit feeders and micropredators in the pool soft subhabitat were significantly higher at unburned than burned sites (Figs 6 & 8).

Standard sweep data showed that large algivores (>1 mm) were significantly more abundant at BRB than other sites for up to 2 years after the Jesusita Fire (Fig. 10). In the third and fourth year after fires, densities of large algivores at BRB sites declined to levels observed at sites where riparian vegetation remained intact. Shredder densities declined at sites in burned basins after fires and rains in the first post-fire year, but rebounded at BRI sites in subsequent years while remaining at low densities at BRB sites. Although there was a statistically significant reduction in shredder density at BRB compared to other sites in June 2013, the data were not convincing (Fig. 10). Closer inspection of the data revealed that the high average shredder density recorded at BRB sites was owing to high *Gumaga* density

at one BRB site, with shredders being virtually absent at other BRB sites. Four years after the Jesusita Fire, CPOM levels were significantly lower, and the common shredder *Lepidostoma* was nearly absent, at BRB compared to other sites (Fig. 9). Throughout the sampling period, predatory invertebrate densities were significantly higher in troutless than trout streams in unburned basins (Fig. 10). Where originally present, trout were extirpated in burned basins during the first post-fire wet season. In June 2010, invertebrate predator densities were low at sites in burned basins. In the second and subsequent years after fires, invertebrate predator densities at sites in burned basins rebounded and reached densities comparable to those in unburned troutless streams, while remaining at low densities in trout streams (Fig. 10).

Regression analyses supported hypotheses regarding the effects of fire on consumers as mediated through fire impacts on consumer resources (Table S1). Among basal resources, most algal and fine detritus variables were negatively related to canopy cover or positively related to water temperature across subhabitats. FPOM was tightly, positively related to CPOM levels on pool soft
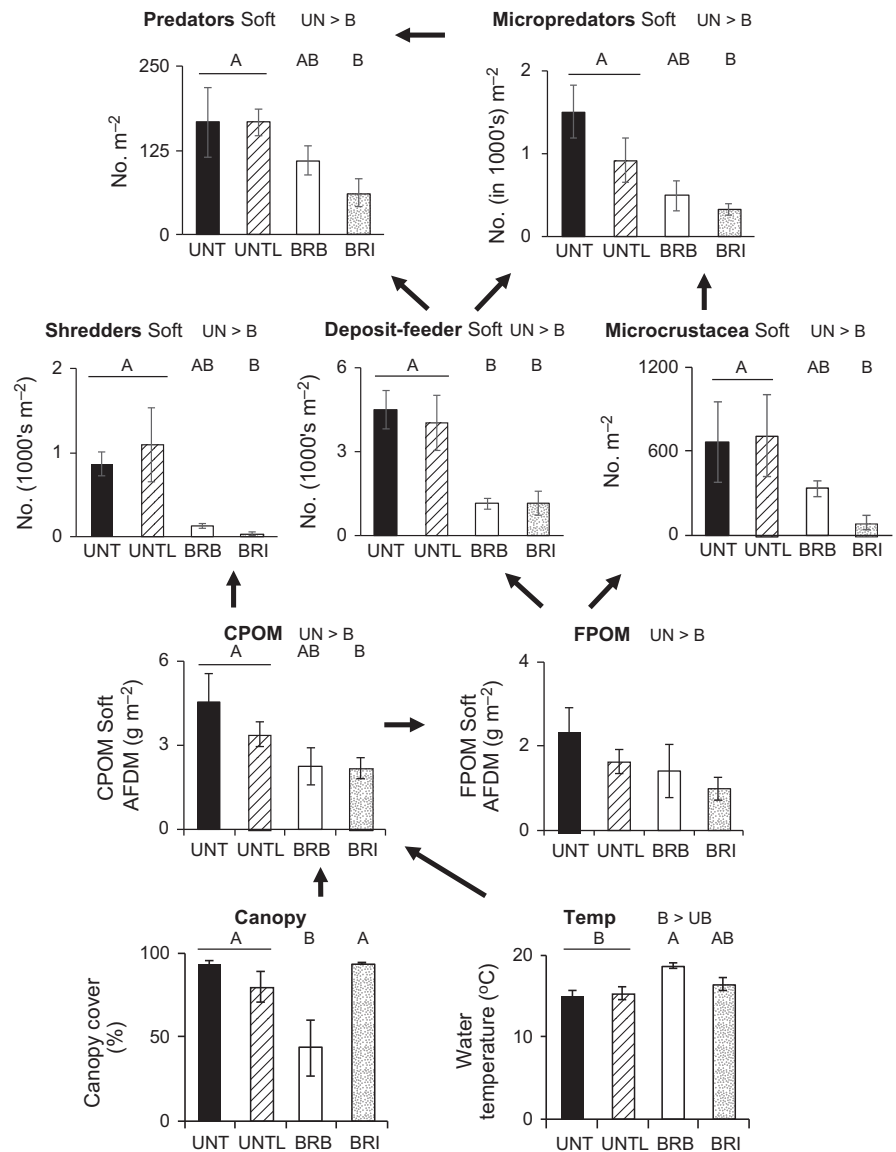
Fig. 6 Average values (±1 SE) of various detritus-associated resources and their consumers in the pools of sites in different trout and basin burn categories, June 2010. Arrows point from major sources or influences on detrital resources to those resources (connecting bottom two rows) or from resources to consumers (connecting top three rows). Riparian vegetation (represented by canopy cover) is the source of CPOM, which has water temperature-dependent (Temp) breakdown rates. Coarse and fine particulate matter (CPOM and FPOM, second row from bottom) are consumed by detritivores (second row from the top), including shredders (CPOM) and deposit-feeders and microcrustaceans (FPOM) which are, in turn, consumed by predators and micropredators (top row), which consume primarily deposit-feeders. Codes and statistical designations as in Fig. 4.

substrata and positively related to both CPOM and chlorophyll concentrations on pool hard and riffle substrata, suggesting that FPOM is primarily derived from CPOM on pool soft substrata but from both algae and CPOM in pool hard substrata and riffle subhabitats. Among primary consumers, algivore densities were positively related to macroalgal cover in pool, but not riffle, subhabitats, shredder densities were positively related to CPOM levels in the pool soft subhabitat, deposit-feeders were positively related to FPOM levels in all subhabitats and microcrustacean densities were positively related to both FPOM and chlorophyll concentrations on pool soft substrata and to FPOM on pool hard substrata. Among secondary consumers, micropredator and predator densities were positively related to deposit-feeder densities in all subhabitats and predator densities were additionally positively associated with micropredator densities in pool subhabitats (Table S1).

Stable isotope analyses

Hydrogen stable isotope signatures (δD) showed clear differences between algae (δD mean across all streams ±1 SD: −214 ± 28‰ in pools, −177 ± 33‰ in riffles) and leaves (δD = −110 ± 13‰), with FPOM showing values similar to leaves (=−95 ± 9‰) (Fig. 11). δD values for most consumers showed the pattern BRI > unburned (UN) > BRB sites. In pools, mean δD values were lower at BRB than UN and BRI sites for 14 of 17 taxa (sign test, two-tailed *P* c. 0.001) and higher at BRI than UN and BRB sites for 9 of 13 taxa (sign test, *P* c. 0.27), whereas in riffles mean δD values were lower at
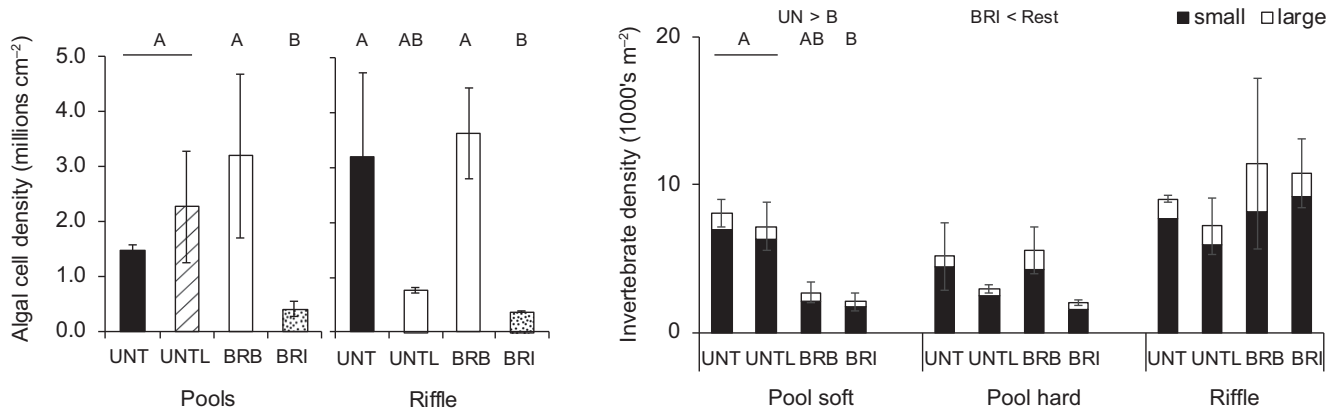
Fig. 7 Average total algal (left) and invertebrate (right) densities (±1 SE) in pools and riffles at sites in different trout and basin burn categories (as in Fig. 4) in June 2010. For the invertebrate histograms, small (black, passing a 1-mm sieve) and large (white, retained by a 1-mm sieve) invertebrate size classes are distinguished. Statistical designations as in Fig. 4.
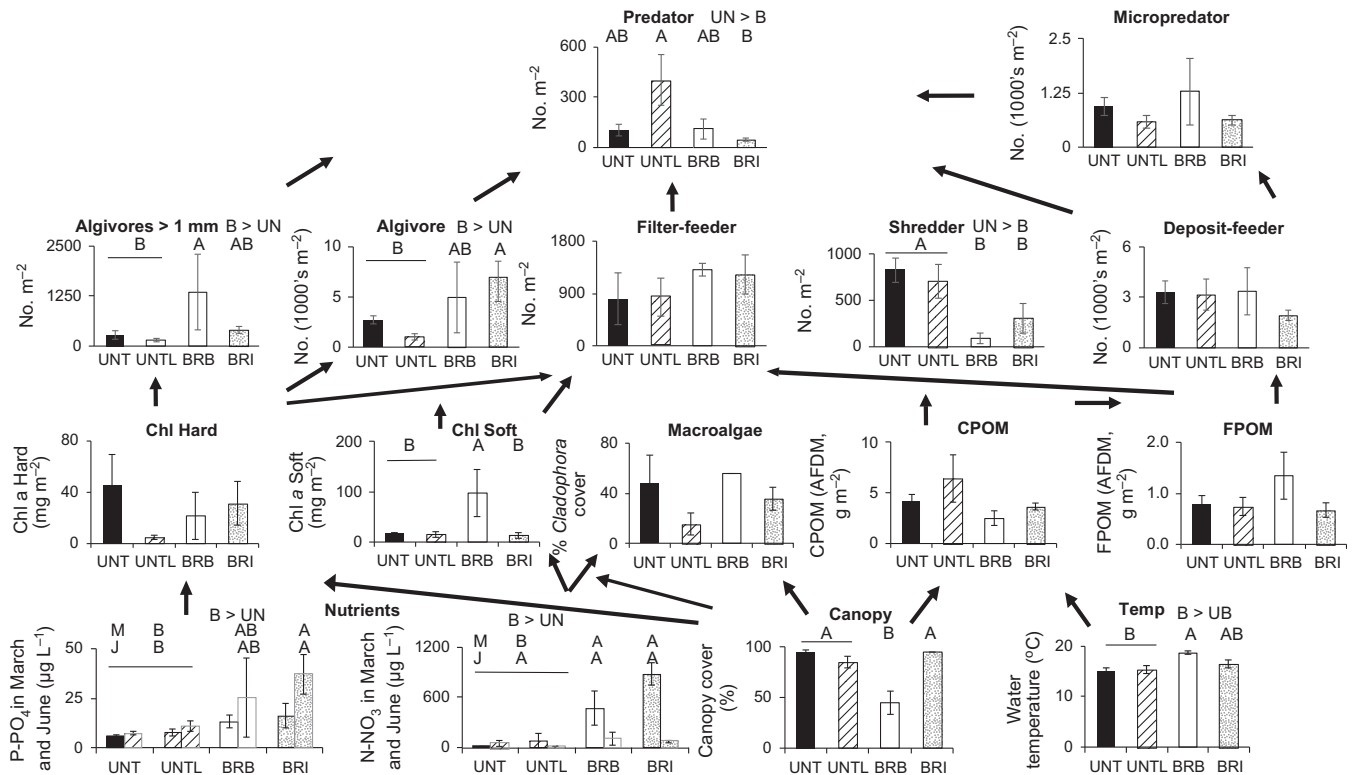

Fig. 8 Average values (±1 SE) for resources and their consumers in the riffles of sites in different trout and basin burn categories, June 2010. Arrows point from resources or influences to consumers. The bottom row represents abiotic resources or influences which affect algal or detrital levels (second row from bottom), which, in turn are consumed by primary consumers (second row from top) then, eventually, predators (top row). Basin categories and statistical designations as in Fig. 4.

BRB and higher at BRI sites than other sites for 10 of 11 taxa (sign test, two-tailed *P* c. 0.01).

In pools, δD values were significantly or marginally lower in BRB sites than sites in one or both of the UN and BRI categories for *Centroptilum*, Chironominae/Orthocladiinae, *Gumaga*, *Archilestes*, *Aeshna* and other pre-dators, whereas in riffles, δD values for the filter-feeders *Ceratopsyche* and *Simulium,* shredders (*Malenka*, *Gumaga*, *Lepidostoma*) and other predators were lower in BRB sites, and for *Baetis*, *Simulium* and Tanypodinae were greater in BRI sites, than sites in one or both of the other categories (Fig. 11, Table S2). Mixing model analyses

Fig. 9 Average values for Coarse particulate organic matter (CPOM) and densities of the common shredder *Lepidostoma* (±1 SE) for sites in different trout and basin burn categories in June, 2013, 4 years after the Jesusita Fire. Codes and statistical designations as in Fig. 4.
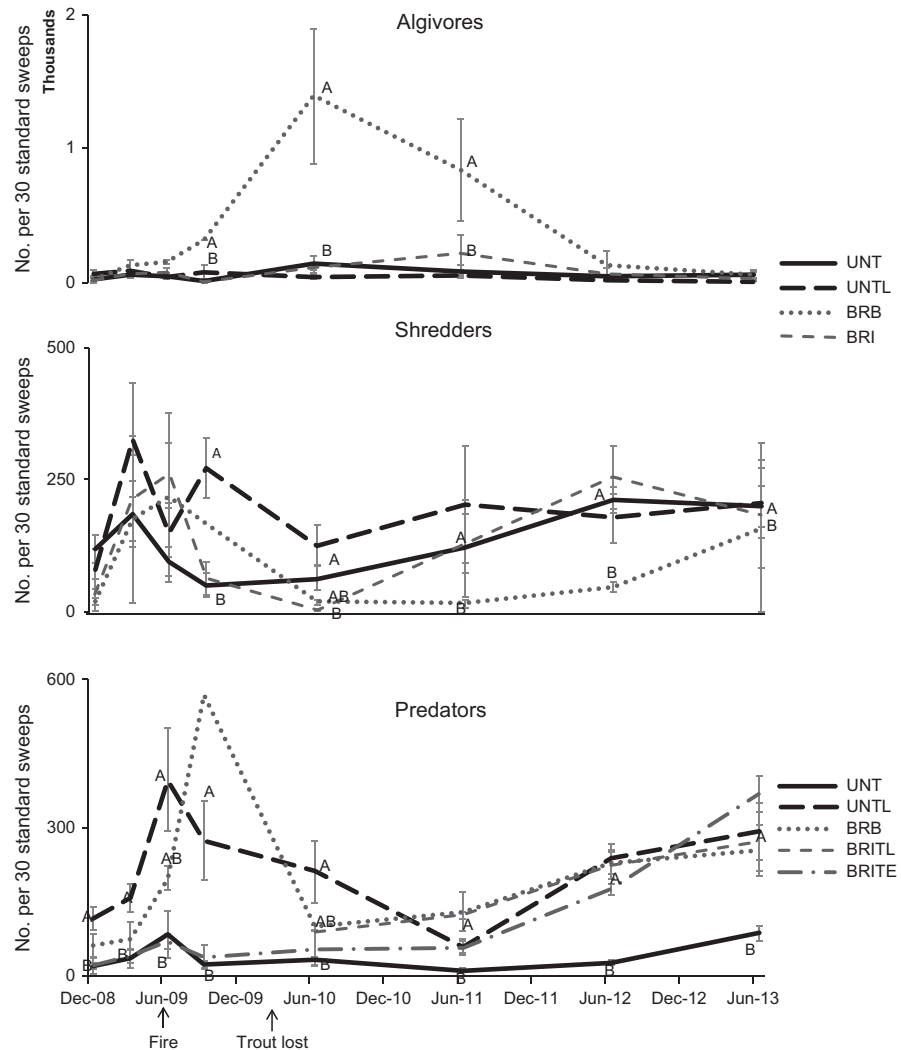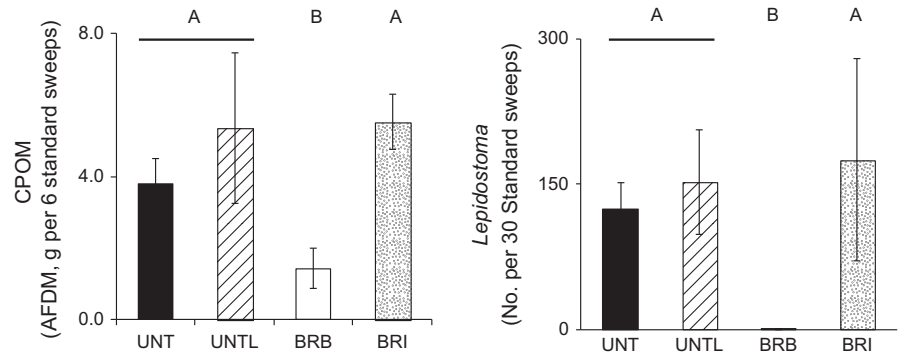

Fig. 10 Changes in the mean densities (±1 SE) of major invertebrate feeding groups at sites in different trout or basin burn categories from December, 2008, to June, 2013. Data points or groups of data points with different nearby letters on each date are significantly different (Tukey's HSD test, *P* < 0.05). Arrows at the bottom indicate the time of the Jesusita Fire and the time of ensuing winter rains when trout were lost from burned, BRI sites.

generally supported these results with algivores, *Lepidostoma*, *Archilestes* and other predators in pools and *Baetis*, *Ceratopsyche*, *Simulium*, Tanypodinae and *Rhycacophila* in riffles having significantly greater proportions of their diets based on algae than riparian detritus at BRB than BRI sites (Fig. 11, Table S2). Although filter-feeders (*Ceratopsyche*, *Simulium*) and some predators (*Archilestes* in pools, *Rhyacophila* in riffles) showed considerable variation in their reliance on algal versus detrital-based resources, other taxa showed lower dietary variation across study sites. For example, the dominant shredder, *Lepidostoma*, incorporated <16% algal resources, and

deposit-feeders (Chironominae–Orthocladiinae, *Paraleptophlebia*) and Tanypodinae micropredators <50% algal-based resources, across study sites. On the other hand, algivore tissues were supported primarily by algae (67–100%), but with one low value (33%) for *Baetis* at a BRI site, and the predatory beetle, *Stictotarsus*, appeared to select algivorous prey (73–100% of diets in pools).

Discussion

As expected, wildfire increased run-off, but only during large post-fire storms, as well as storm suspended sediment and wet season nutrient concentrations. Other studies suggest that hydrological, sediment and nutrient responses to intense fire depend on post-fire precipitation patterns, particularly the duration and intensity of storms, with results ranging from little response in dry periods to mobilisation of nutrients and sediment during small to moderate storms to extensive floods, landslides and debris flows during large, intense storms (Arkle *et al.*, 2010; Ryan, Dwire & Dixon, 2011; Warrick *et al.*, 2012; Coombs & Melack, 2013). Our results suggest that scouring floods after fire remove most particulate organic matter and organisms from streams. The recovery of stream organisms from these disturbances depends on their life cycles, with taxa with fast life cycles, such as algae and some small-bodied invertebrates, recovering quickly if limiting resources are adequate.

After the first post-fire wet season, algae in BRB streams recovered to levels higher than those found at unburned sites, apparently because of increased light and high nutrient concentrations, but remained at low levels at BRI sites where canopies remained intact. Subsequently, algal levels at BRB sites declined, despite high light levels, perhaps because nutrient concentrations had fallen or because grazer densities were high; consequently, there may be only brief periods of time when algal blooms are evident following riparian fires. Complexities in the effects of disturbance, light and nutrient levels on algal biomass and growth can account, perhaps, for some of the variable results observed in previous studies, ranging from negative to no to positive algal responses to fire (Bêche *et al.*, 2005; Koetsier *et al.*, 2010; Malison & Baxter, 2010; Oliver *et al.*, 2012; Verkaik *et al.*, 2013). In general, algal abundance after fires will depend on the intensity of scouring flood disturbances, post-flood sediment deposition, turbidity, riparian canopy cover and nutrient concentrations, which vary with the time since fire and subsequent floods (Coombs & Melack, 2013; Verkaik *et al.*, 2013). These algal responses,

in turn, can affect their consumers. Algivores with fast life cycles (primarily Baetidae) reached higher densities at sites in BRB than unburned basins within 2 months after floods had passed, but remained scarce at BRI sites, where light and algal levels were low (Verkaik *et al.*, 2013). Vagile species, such as *Baetis*, also may have been more abundant at BRB than other sites because of the dominance of macroalgae, which provide invertebrate habitat and substrata for colonisation by epiphytic diatom food resources (Dudley, Cooper & Hemphill, 1986). The decline in algivore densities in the third and fourth post-fire years could be owing to declines in algal resources at BRB sites despite low canopy covers, associated with post-fire declines in nutrient concentrations (Coombs & Melack, 2013); however, we did not measure algal biomass in those years. Alternatively, we found that baetid densities were higher in high than low flow years, so the decline in baetid densities in the third and fourth years also could be attributed to very low flows in those dry years, which might have overridden any bottom-up effects.

Levels of CPOM, FPOM and long-lived invertebrates (many shredders and predators) were lower in stream depositional habitats in burned than unburned basins a year after fire, probably because they were washed away by scouring floods and had not had time to accumulate or recover. CPOM concentrations, and shredder and predator densities, recovered within 2–4 years at sites in burned basins with intact riparian canopies, but CPOM and shredders remained at low levels where riparian vegetation burned, indicating the importance of riparian vegetation recovery for CPOM and shredder abundances (Koetsier *et al.*, 2010; Vieira *et al.*, 2011). CPOM levels appear to depend on fire-induced leaf fall, inputs of charcoal and other burned material, the density, condition and recovery of riparian vegetation, the timing, intensity and frequency of scouring floods, the occurrence of landslides and stream geomorphological and flow characteristics (Britton, 1990; Gresswell, 1999; Robinson *et al.*, 2005; Koetsier *et al.*, 2010). Further complexities arise when examining fire effects on FPOM levels, which are affected not only by the factors influencing CPOM and algal levels, but also by factors, such as water temperature and shredder densities, which affect the breakdown of CPOM and generation of FPOM (Koetsier *et al.*, 2010; Vieira *et al.*, 2011; Verkaik *et al.*, 2013). Because dominant deposit-feeders (Chironominae–Orthocladiinae) had multivoltine life cycles, their low abundance in stream depositional habitats in the first year after fires could be attributed to low FPOM levels, rather than to the direct effects of scouring floods,
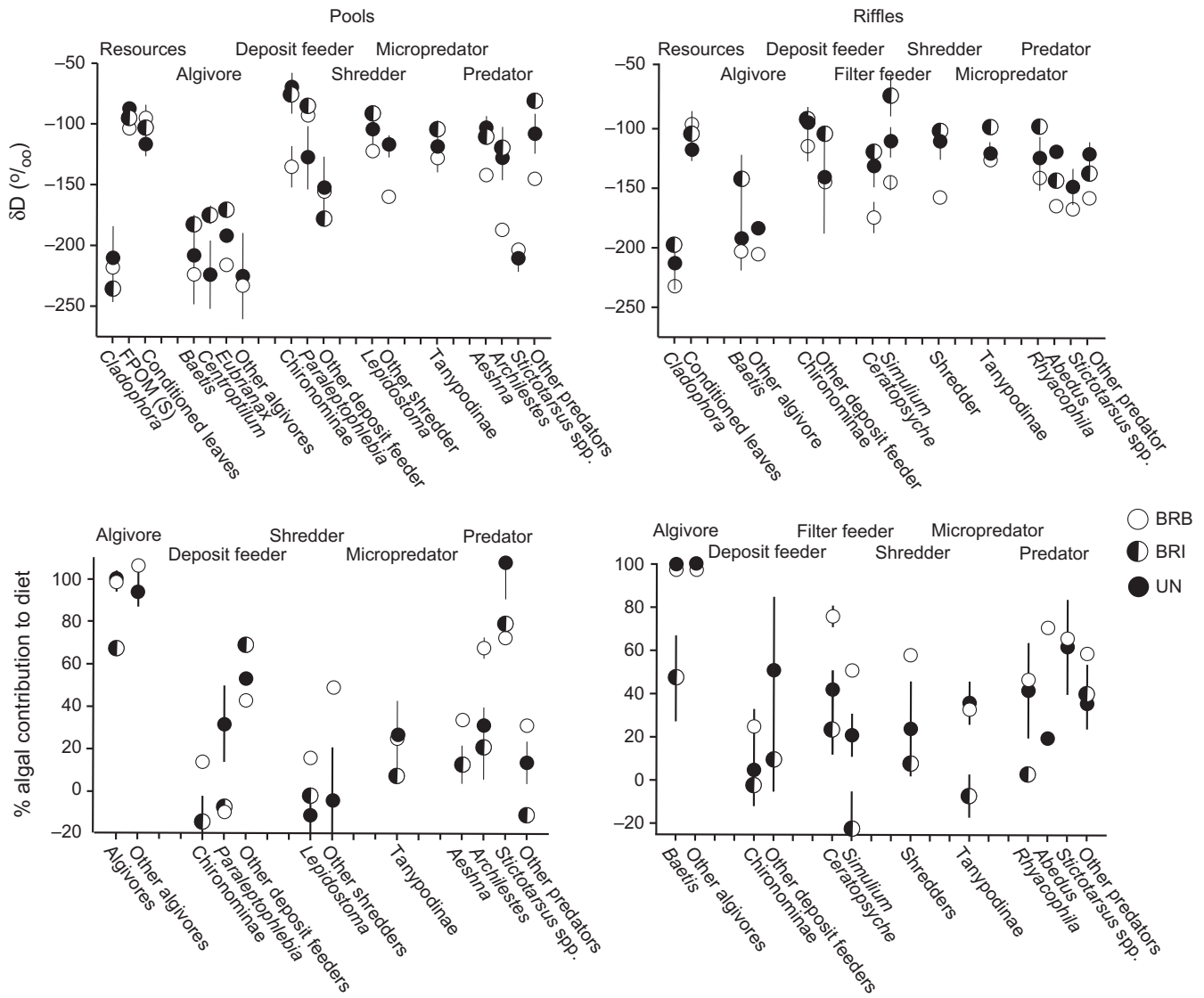
Fig. 11 The results of hydrogen isotope and mixing model analysis for resources and invertebrate consumers in pools (left) and riffles (right), June 2010. The top plots show average δD values (±1 SD) for resources (*Cladophora*, conditioned leaves, and, in pools, FPOM) and dominant consumer taxa in each feeding group at sites in different basin burn categories (unburned = UN, black dots; BRI = half black, half white dots, BRB = white dots). The bottom plots show the results of mixing model analysis, expressed as the percentage contribution of algal-based resources to dominant consumers in different feeding groups (±1 SD) at sites in different basin burn categories.

with bottom-up repercussions for multivoltine micropredators (Tanypodinae).

The effects of fire and subsequent floods on basal resources also affected consumer diets and nutrition. In general, algal resources were high but CPOM levels were low at BRB sites, both algal and POM resources were low at BRI sites and algal resources were low and POM levels high at sites in unburned basins, although variation among sites in unburned basins was high. These differences in basal resource availability among sites translated into differences in consumer diets and nutritional support among different basin burn catego-

ries. Hydrogen isotope analysis indicated that the majority of pool and riffle taxa showed higher dietary contributions of algal-based resources at BRB compared to other sites and that nearly all riffle taxa also showed lower algal contributions to their diets at BRI compared to other sites, congruent with the availability of algal resources at sites in different basin categories. The results confirm that the contribution of algal resources to consumer diets is greater in streams affected by fires that removed riparian vegetation than in streams with an intact riparian canopy, consistent with the conclusions of Mihuc & Minshall (1995). Additionally,

the results suggest that algal contributions to stream consumer diets are lower in streams where upland but not riparian vegetation burned, presumably owing to the low availability of algal resources.

This study also revealed that fire altered top-down effects of consumers on their resources. The densities of predatory invertebrates were consistently lower at sites with than without trout in unburned basins over a 5-year period. Although densities of predatory invertebrates were initially low at BRI sites, they increased after trout were extirpated by wildfire and subsequent scouring to densities similar to those at troutless sites. These results, then, indicate that predatory invertebrates are reduced by trout predators (Wiseman et al., 1993; Meissner & Muotka, 2006; Power, Parker & Dietrich, 2008). Because populations of steelhead trout in this region are near the southern range limits for this endangered race, these results predict changes in the food-web structure of southern California streams, if and when steelhead populations are extirpated by fires, or climate or land use changes (NMFS, 2012). Fires which destroyed riparian vegetation also increased summer stream temperature which, when combined with climate change, could exceed the tolerance limits of cold-water salmonids (Royer & Minshall, 1997). Whether the replacement of top trout by top invertebrate predators will affect lower trophic levels is uncertain. Although cascading effects from trout to primary consumers to algae have been reported in many studies and cascading effects from trout to small predators to primary consumers to algae in a few (e.g. Shurin et al., 2002; Power et al., 2008), the short-term effects of fire and flood disturbances on stream organisms and bottom-up interactions may have overridden any possible cascading effects to primary consumers and producers in this study.

Fire severity and frequency will likely be affected by climate change (Dwire & Kauffman, 2003; Pettit & Naiman, 2007). By increasing air temperature and altering precipitation patterns, climate change can affect fuel loads and distributions which, when combined with changes in foliar moisture, wind regimes and human land uses, will affect the frequency of ignitions and the spread, intensity, frequency and timing of fires (Lenihan et al., 2003; Moritz et al., 2004; Bowman et al., 2009; Littell et al., 2009). The Jesusita Fire occurred anomalously in spring after a dry winter, emphasising linkages between preceding climatic conditions and the timing and severity of fire (Pausas & Fernández-Muñoz, 2011). After fires, the timing, frequency, magnitude, duration and intensity of storms, which also will be affected by climate change, determine fire impacts on nutrient and sediment fluxes with ramifying effects on stream communities (Arkle et al., 2010; Warrick et al., 2012; Coombs & Melack, 2013; Verkaik et al., 2013). Fire impacts on streams, then, are probably enhanced by specific climatic sequences, including adequate rain to promote fuel build-up followed by droughts which enhance fuel ignitability and fire spread followed by sufficient precipitation to engender increased run-off and erosion. Further, the recovery of stream communities after fires is tied to the recovery of upland and riparian vegetation, which, although often rapid in Mediterranean ecosystems, is related to precipitation and discharge patterns (Keeley et al., 2012; Stella et al., 2013; Verkaik et al., 2013).

In conclusion, the abundances of algae, detritus and invertebrates can show the gamut of negative to no to positive responses to fires and subsequent floods depending on fire severity, post-fire run-off intensity, the precise time of sampling relative to fires and floods and the condition of the riparian canopy (Minshall et al., 2004; Bêche et al., 2005; Arkle & Pilliod, 2010; Arkle et al., 2010; Koetsier et al., 2010; Malison & Baxter, 2010; Romme et al., 2011; Oliver et al., 2012; Verkaik et al., 2013). Although few studies have reported fire effects on riparian vegetation, canopy cover and/or light levels, these studies emphasise the importance of fire effects on riparian cover in driving many stream community responses (this study, Sestrich et al., 2011; Malison & Baxter, 2010; Arkle et al., 2010). The return of stream communities to their original pre-disturbance condition will depend on the recovery of basin vegetation, re-establishing pre-disturbance geomorphic processes, biogeochemical cycles and the balance between allochthonous inputs and autochthonous production in streams (Pettit & Naiman, 2007; Shakesby, 2011; Verkaik et al., 2013). Linked riparian and stream communities, then, are likely to be profoundly altered by predicted increases in the synergistic actions of interrelated extreme events, such as prolonged droughts, increased wildfire and intense floods associated with climate change.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Results of multiple regression analyses examining relationships between consumers and their resources.

Table S2. Results of hydrogen stable isotope (δD values) and mixing model analyses (% of diet which was algal-based) for each major invertebrate group or taxon in pool versus riffle habitats.

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