Wildfire and drying legacies and stream invertebrate assemblages

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Abstract: Climate change is engendering droughts and wildfires in many ecosystems, especially those in Mediterranean climates. Yet, there is little information on the long-term responses of stream invertebrates in Mediterranean climates to wildfire, particularly during and after extreme drought. To examine the effects of drought and wildfire on stream invertebrate assemblages, we sampled stream reaches in southern California with surface water in 2016, at the end of a 5-y drought, and stream reaches in 2017, after flows resumed or increased, including sites within (burned), outside (unburned), and downstream of footprints for fires occurring 8 to 10 y ago. Spatial and temporal variation in invertebrate assemblages were attributed to hydrological regimes, including stream drying during the drought, but there were few fire-legacy effects. At the end of the drought, invertebrate assemblages occupying remaining standing water with high solute, temperature, and benthic organic matter levels were dominated by tolerant, lentic taxa. After flows returned in spring 2017, all sites, including those that were dry in 2016, were dominated by quick-colonizing riffle taxa. Invertebrate densities increased into the subsequent summer at the same time that flows declined and temperatures and conductivities increased; however, sensitive cool-water taxa were more abundant at perennial, shaded sites, whereas tolerant, warm-water taxa were more abundant at shallow, open sites that had dried the year before. We observed negative relationships between riparian burning extent vs canopy cover (weak) and coarse particulate organic matter levels (strong); however, invertebrate assemblage structure was similar in basins that did and did not burn. Although invertebrate populations were severely reduced at 1 site whose basin had burned the year before, invertebrate assemblages had largely recovered after 10 post-fire y, and fire-legacy effects were dwarfed by hydrological variation, particularly stream drying during the drought. Our data also suggest the importance of protecting water supplies and riparian vegetation for perennial, shaded headwater reaches, which provide refuges from drought and wildfire for native biodiversity.

Key words: wildfire, drought, streams, invertebrates, ecohydrology, riparian canopy cover

Climate change is causing the warming, drying, and burning of landscapes (Dai 2011, Williams et al. 2019, Goss et al. 2020). Fires and drought are particularly powerful and pervasive drivers of ecosystem change in Mediterranean climates because of the accumulation of fire-adapted plant biomass (fuel), often steep terrain, and large variation in precipitation, including seasonal and supraseasonal droughts and winter floods (Pausas and Fernández-Muñoz 2011, Keeley et al. 2012). Changes in the extent and severity of droughts and wildfire in Mediterranean-climate regions have the potential to alter the physical, chemical, and biological characteristics of receiving waters (Shakesby and Doerr 2006, Lake 2011, Verkaik et al. 2013a, Santos et al. 2019).

Reported responses of stream communities to fire have been variable, probably owing to variation in the timing, extent, severity, frequency, and spatial pattern of fires; the duration, frequency, and intensity of subsequent runoff events; the time since fire; the occurrence of associated post-fire

landslides; size of stream; distance from refuges; and barriers to recolonization (Gresswell 1999, Cooper et al. 2015, Tuckett and Koetsier 2018). Similarly, the effects of drought on the stream biota have varied with the predictability, intensity, frequency, and duration of drought as well as with subsequent meteorological and hydrological conditions (Lake 2011, Resh et al. 2013, Herbst et al. 2019). To understand and predict stream community responses to wildfire and drought, researchers will need to examine the context dependency of these responses across complex combinations of pre- and post-disturbance conditions and the characteristics of specific droughts and wildfires (Arkle et al. 2010, Rugenski and Minshall 2014, Robson et al. 2018). Currently, however, there are few data on the long-term (>5 y) legacy effects of wildfire on semi-arid or arid land streams under variable climatic conditions, particularly under extreme, supraseasonal drought (Verkaik et al. 2013a, Bixby et al. 2015, Monaghan et al. 2020).

In the summer of 2007, a large wildfire, the Zaca Fire, burned 972 km^2 over 3 mo in Santa Barbara and Ventura Counties, California, USA, primarily in the undeveloped United States Forest Service's Los Padres National Forest. There were numerous anecdotal reports of extensive sediment deposition in streams after this fire and subsequent rains, but it was not clear how long the effects of this fire on streams would persist. To address this question, we sampled stream reaches inside and outside the Zaca Fire footprint at the end of an unprecedented 5-y drought, 9 to 10 y after this fire occurred, and in the 1st y after the drought ended. Because some of our stream reaches dried during the drought, whereas others retained surface water during the same period, we were able to compare ecological assemblages after flows had returned or increased in reaches that had and had not dried. Stream invertebrate assemblages will differ depending on the predictability, duration, intensity, timing, and frequency of dry periods, but most of our sampled sites were typically perennial, so a subset dried only during the supraseasonal drought (Bogan et al. 2013, 2015).

The focus of this study was to evaluate associations between the short-term legacies of stream drying and the long-term legacies of wildfires on wildland stream assemblages in Southern California, while accounting for variation owing to reach longitudinal position, a more recent fire, and temporal (seasonal, interannual) changes. We concentrated on stream invertebrate assemblages because benthic invertebrates form important food sources for predators, process organic matter, are a major component of biodiversity, and are sensitive indicators of stream responses to perturbations (Allan et al. 2021).

We tested hypotheses on the possible legacy effects of stream drying and wildfire by comparing stream invertebrate assemblages in streams in Los Padres National Forest catchments that were or were not burned by wildfires in the past 10 y and that dried or did not dry during a 5-y drought. Hypothesis 1: In stream reaches still containing surface water at the end of the drought, we expected that small, tolerant, and lentic invertebrate taxa, such as some chironomids and worms, would dominate and that the richness and abundance of sensitive, rheophilic mayfly, stonefly, and caddisfly (Ephemeroptera, Plecoptera, and Trichoptera [EPT]) taxa would be low (Dewson et al. 2007, Lake 2011, Herbst et al. 2019). Hypothesis 2: In 2017, after flows resumed at sites that dried during the drought and after flows increased at sites that retained water during the drought, we predicted that dispersive taxa, such as some mayflies (Baetidae), blackflies, and chironomids, would quickly colonize and dominate all stream reaches (Griswold et al. 2008, Lake 2011, Piano et al. 2019). Hypothesis 3: Finally, after initial colonization and increases by dispersive taxa at sites that did and did not dry the year before, we hypothesized that invertebrate assemblages in reaches that did and did not dry would converge through subsequent seasons as perennial stream flows resumed (Boulton 2003, Lake 2011).

Hypothesis 4: With respect to wildfire, we predicted that the richness and abundance of invertebrate assemblages would be reduced during and immediately after post-fire floods (Vieira et al. 2004, Verkaik et al. 2015, Monaghan et al. 2019). However, dispersive taxa, such as baetid mayflies and blackflies, would quickly colonize after floods subsided, particularly where riparian vegetation had burned, sometimes exceeding densities found in streams draining unburned basins (Silins et al. 2014, Cooper et al. 2015, Verkaik et al. 2015). Hypothesis 5: After 10 post-fire y, however, we expected that there would be little difference in invertebrate assemblages in streams draining basins that did vs did not burn, owing to the rapid recovery of terrestrial vegetation, stream abiotic conditions, and invertebrate assemblages in Mediterranean climates (Verkaik et al. 2013a, b, Robson et al. 2018, Monaghan et al. 2020).

METHODS

To answer our research questions, we examined associations between stream abiotic and invertebrate variables vs past wildfire and stream drying patterns. We 1st quantified the extent and severity of vegetation burning by wildfires that had occurred within the last 10 y by using Geographical Information Systems analysis of United States Forest Service (USFS) maps. We selected study sites (reaches) that lay within, outside, or downstream of the footprints of these wildfires, then measured environmental variables and sampled invertebrate assemblages at these sites in 2016 and 2017. Among our study sites, surface water was present at the end of an unprecedented 5-y drought (in 2016) only in headwater reaches with deep pools connected by trickles, presumably fed from groundwater springs (based on cool water temperatures). Many of our study sites were completely dry in 2016. After above-average winter rains and a severe mid-February rainstorm in 2017 (21.3 cm/d), perennial flow returned to all of our sites. As a consequence, we sampled only

a subset of our sites (i.e., those with surface water) in 2016, but we then sampled all sites in 2017, after sites that were dry in 2016 began flowing again and sites that had contained water in 2016 had increased flows. We examined data from sites within, outside, or downstream of wildfire footprints and that were either dry or wet (with surface water) in 2016, allowing us to examine relationships between stream variables vs past wildfire and drying legacies (Table 1).

Study site description

The study area lies within the USFS Los Padres National Forest in southern California on the leeside of the Santa Ynez Mountains, which run east to west and rise steeply, with slopes often exceeding 35%, from the Pacific Ocean to peaks exceeding 1400 m within 3 km (Fig. 1). This steep rise strongly influences the climate of coastal areas because orographic lift causes moisture to fall at much higher quantities at higher elevations than at lower elevations on the leeside of the mountains. Streams in these drainages range from steep perennial reaches with a step-pool geomorphology in headwater areas underlain by shale and sandstone bedrock to more intermittent, wider pool–riffle reaches meandering or braiding through lower, flatter terrain underlain by alluvial deposits (Fig. 1). Drainage areas of the study sites ranged from 240 to 22,028 ha, elevations from 332 to 1407 m, and gradients from 0.6 to 8.1%, with stream water having slightly alkaline pH values (7.2–8.9), high conductivities (400–2324 µS/cm), low nutrient concentrations (NO_3^--N = 0.4 to 212 µg/L, PO_4^{-3}-P = below detection limits to 37 µg/L), and variable temperatures (7.5°C at night to 33.8°C during the day across sites in the dry season). The gamut of substrata sizes, ranging from sand to boulders and bedrock, covered stream bottoms, but fine sediments were more prominent at downstream sites and those affected by fire.

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 32 cm in the valleys on the leeside of the mountains to 86 cm on the Santa Ynez Mountain ridge. Streams in this area show high seasonal variation in discharge ranging from no or very low base flows in late summer and autumn to >900 m^3/s in the largest river (Sisquoc River) during winter floods. Rainfall and discharge in our study streams were often below average during the period from the 2007 Zaca Fire through the time of sampling in 2016 and 2017 but were particularly low during the 2012 to 2016 drought (Fig. 2A, B).

Dominant riparian trees along our study streams include white alder (*Alnus rhombifolia*), California bay laurel (*Umbellularia californica*), Fremont cottonwood (*Populus fremontii*), willow (*Salix* spp.), and western sycamore (*Platanus racemosa*), with understory shrubs such as Pacific poison oak (*Toxicodendron diversilobum*) and currant (*Ribes*

spp.). Upland areas are dominated by mixed chaparral (e.g., *Ceanothus*, *Adenostoma fasciculatum*, *Arctostaphylos*, *Salvia* spp.) with coastal sage scrub, grasslands, and oak woodlands (*Quercus* spp.) at lower elevations (Lentz 2013).

Four wildfires, the Zaca Fire (97,208 ha, July–October 2007), the La Brea Fire (36,214 ha, August 2009), the Rey Fire (13,195 ha, August–September 2016), and the Whittier Fire (7458 ha, July–October 2017), burned within our Los Padres National Forest study area between 2007 and 2017 (Fig. 1, Table 1).

Quantifying the extent and severity of vegetation burning

We determined the proportions of catchment, riparian zone, and upland zone areas draining to each study site that were burned at no, low, medium, and high vegetation burn severities using publicly available geospatial layers and ArcMap version 10.5.1 (Esri™, Redlands, California). We obtained digital elevation models (10 × 10-m resolution) from the United States Geological Survey and fire scar boundaries and fire severity burned area emergency response maps (30 × 30-m resolution) from the USFS, with all datasets downloaded using NAD_1927_California_Teale_Albers projections or transformed to fit these projections. We used digital elevation model layers to determine flow direction and flow accumulation across cells, delineate river channels, designate drainage area outlets at sampled reaches (measured in the field with GPS units), and ultimately mark the digitized boundaries of the area draining to each sampling site. Within the drainage basin for each study reach, we demarcated the riparian zone as the area lying within 30 m of a stream channel, with areas lying between the outer limits of this zone and the watershed boundaries designated as the upland zone (Sweeney and Newbold 2014).

We quantified vegetation burn severity as the relative difference normalized burn ratio between pre- and post-fire Landsat Thematic Mapper Satellite images, calibrated with the Composite Burn Index (CBI) (Miller and Thode 2007, available at VegBurnSeverityBA 2017). Each cell or pixel in the fire layer was assigned a burn severity category using the CBI field protocol developed by Key and Benson (2006), which compares spectral patterns in images to ground-truthed patterns of vegetation burn severity. The CBI protocol records fire effects in 5 strata: 1) surface fuels and soils; 2) herbs, low shrubs, and trees <1 m; 3) tall shrubs and trees 1 to 5 m; 4) intermediate trees (pole-sized trees, subcanopy); and 5) big trees (upper canopy, dominant/codominant trees). Values for all strata are averaged to create a vegetation burn severity index value for the whole plot ranging between 0 (unchanged or unburned) and 3 (highest burn severity). The CBI categories are: 1) unchanged (0–0.1, 1 y after the fire the vegetation in the area was indistinguishable from pre-fire conditions), 2) low (0.1–1.24, areas

Table 1. Physical and burn characteristics of study reaches. The time elapsed since the last fire within each basin is listed as well as the % of the upstream drainage basin lying within the fire footprint and the % of the riparian zone draining to each site that burned at moderate to high (M–H) severities for fires occurring within the last 10 y (primarily the Zaca Fire). The downstream Indian and Mono sites list 2 numbers in each cell of the last 2 columns, with the 1st representing burn extent by the 2007 Zaca Fire and the 2nd representing burn extent by the 2016 Rey Fire. *Camuesa: only upstream site affected only by the 2016 Rey Fire. **Sites sampled in both 2016 and 2017. ***Bear Creek was designated an unburned site (see text), although it was downstream of the Whittier Fire (fire data are for the Whittier Fire). # denotes the study sites shown on the map in Fig. 1. Disturbance code: Rey = burned by the Rey Fire the year before sampling, W = wet (surface water in 2016), D = dry (dry in 2016), B = within a basin burned by the 2007 Zaca and 2009 La Brea Fires, U = within a basin that was not burned within the last 10 y (Unburned), Down = downstream of fires occurring within the last 10 y.

#	Study site	Basin	Latitude	Longitude	Catchment area (ha)	Slope (%)	Elevation (m)	Disturbance code	Time since last fire (y)	% of basin in fire footprint	% riparian burned at M–H severity
1	Camuesa*	Santa Ynez	34.5669	−119.713	291	1.7	658	Rey	1	100	99.0
2	Coche	Santa Ynez	34.6788	−119.7361	475	5.4	954	DB	10	100	69.4
3	Horse	Sisquoc	34.8401	−120.0162	6455	1.4	344	DB	8	100	87.5
4	Rancho Nuevo	Santa Ynez	34.6892	−119.4114	6218	0.6	1103	DB	10	99.9	90.0
5	Santa Barbara	Cuyama	34.7635	−119.5709	3660	5.7	1034	DB	10	100	62.0
6	Abel	Sisquoc	34.8324	−119.8625	3592	3.4	574	DU	51	0.0	0.0
7	Davy Brown	Sisquoc	34.7600	−119.9537	1177	2.5	606	DU	24	0.0	0.0
8	Fir Canyon	Sisquoc	34.7682	−119.9466	2269	2.5	563	DU	24	0.0	0.0
9	Munch	Sisquoc	34.7576	−119.9538	849	4.1	619	DU	24	0.0	0.0
10	Tule	Santa Clara	34.5608	−119.2761	1884	4	1074	DU	32	0.0	0.0
11	Agua Caliente	Santa Ynez	34.5418	−119.5654	7409	2.9	730	Down	10	94.0	71.0
12	Indian Lower	Santa Ynez	34.5465	−119.642	8842	1.1	475	Down	1	78.9, 29.4	65.1, 28.8
13	Manzana - Nira	Sisquoc	34.7712	−119.9395	9085	1.5	543	Down	10	64.2	26.6
14	Manzana - Potrero	Sisquoc	34.7727	−119.9453	11,357	1.6	529	Down	10	56.8	26.1
15	Mono	Santa Ynez	34.5417	−119.6251	22,028	1.1	459	Down	1	88.1, 6.0	68.8, 7.9
16	Indian Upper	Santa Ynez	34.6599	−119.6403	1166	4.3	1121	WB	10	100	93.6
17	Manzana Narrows**	Sisquoc	34.7373	−119.8704	2044	4	913	WB	10	81.7	34.9
18	Sisquoc - Cottonwood	Sisquoc	34.7441	−119.693	5671	3	1013	WB	10	98.7	55.3
19	Sisquoc - Heath**	Sisquoc	34.7350	−119.6807	3028	2.3	1053	WB	10	100	53.4
20	Sisquoc - Lower Bear**	Sisquoc	34.7173	−119.6472	498	8.1	1407	WB	10	100	18.9
21	South Fork Sisquoc**	Sisquoc	34.7509	−119.7785	1393	6.5	865	WB	10	100	40.8
22	Alder**	Santa Ynez	34.4831	−119.4954	520	1.7	678	WU	53	0.0	0.0

Table 1. (*Continued*)

#	Study site	Basin	Latitude	Longitude	Catchment area (ha)	Slope (%)	Elevation (m)	Disturbance code	Time since last fire (y)	% of basin in fire footprint	% riparian burned at M–H severity
23	Cachuma	Santa Ynez	34.6956	−119.9105	895	1.7	632	WU	40	0.0	0.0
24	Fox**	Santa Ynez	34.4837	−119.528	240	6.3	587	WU	53	0.0	0.0
25	Lion Canyon	Santa Ynez	34.7056	−119.922	350	9	725	WU	40	0	0
26	Lion**	Santa Clara	34.5424	−119.163	2356	1.1	959	WU	85	0	0
27	Matilija	Ventura	34.5315	−119.4026	4716	4	742	WU	32	0	0
28	Reyes	Cuyama	34.6789	−119.3026	1248	NR	1223	WU	84	0.0	0.0
29	Upper North Fork Matilija	Ventura	34.5102	−119.383	3206	2.3	497	WU	32	0.0	0.0
30	Bear***	Santa Ynez	34.5295	−119.8652	428	1.7	332	WU	0.12	23.7	0.0

of surface fire occurred with little change in vegetation cover and mortality), 3) moderate (1.25–2.24, the area had a mixture of effects ranging from unchanged to high impacts on vegetation), and 4) high (2.25–3.0, vegetation had high to complete mortality). We calculated an average burn severity index for the area draining to each site by summing the products of each CBI category (1–4) weighted by the proportions of the drainage area in each category.
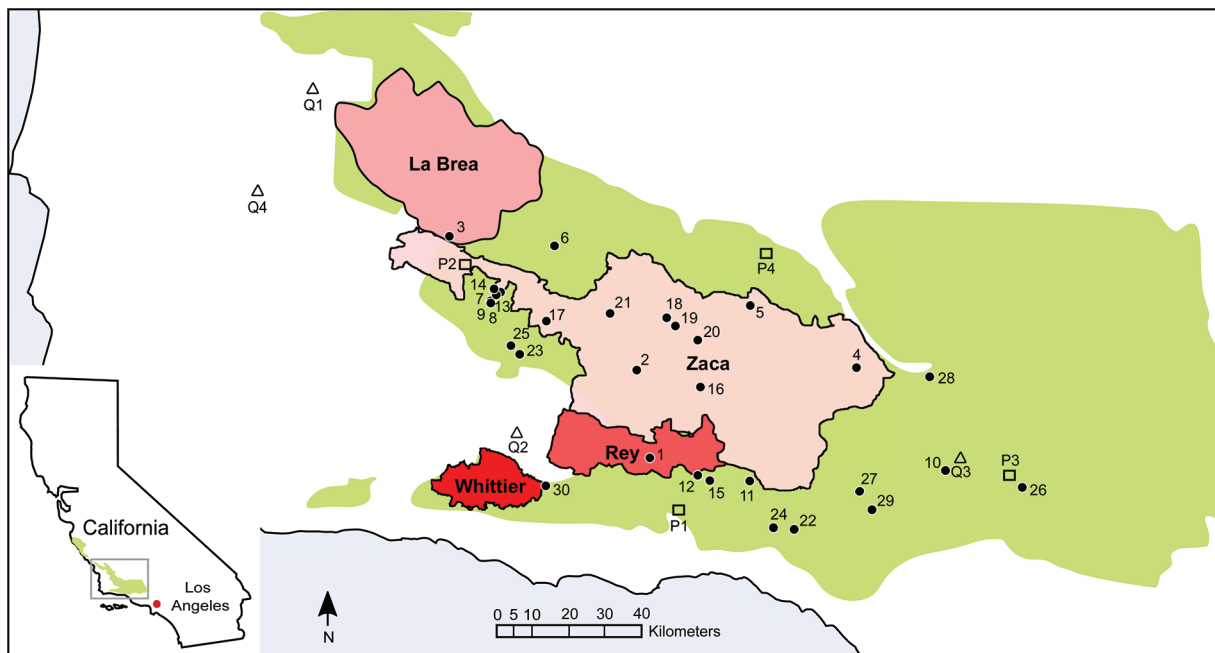

Figure 1. Map of the study area. Green areas represent the United States Forest Service (USFS) Los Padres National Forest (southern section), and red shading indicates the footprints for 4 labeled wildfires, arranged in intensity from the oldest (pink) to the most recent (dark red) fires (Zaca, La Brea, Rey, Whittier). Black circles are sampling sites (code in Table 1), open triangles represent United States Geological Survey (USGS) stream gauging sites, and open squares represent Counties of Santa Barbara and Ventura rain gauge sites (Fig. 2). Rainfall sites: Gibraltar Reservoir = P1, Manzana Schoolhouse = P2, Rose Valley (in Sespe River catchment) = P3, Santa Barbara Canyon = P4. Stream gauging sites: Cuyama River = Q1, Santa Cruz Creek = Q2, Sespe Creek = Q3, Sisquoc River = Q4. The inset shows location within California.
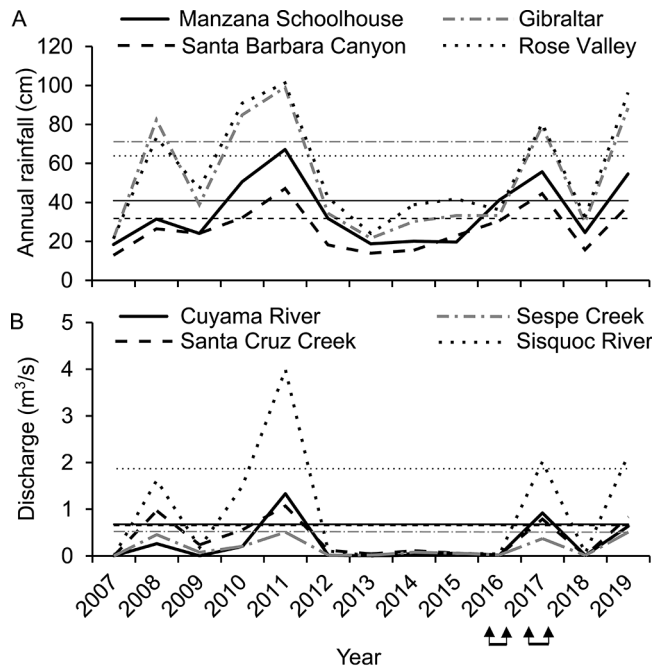
Figure 2. Annual rainfall (A) and average annual discharge (B) for gauging sites bracketing the study area in southern California (see Fig. 1). Arrows indicate the times of stream sampling for this study. Horizontal lines represent the 30-y (1990–2019 water years) averages for rainfall and discharge at each site, with some missing data for Manzana Schoolhouse, Rose Valley, Santa Barbara Canyon, and Sespe Creek.

After pre-processing the watershed, hydrological, and fire extent and severity data into compatible vector layers, we overlaid watershed and fire layers to determine overlapping areas between fire scar boundary or vegetation burn severity and watershed layers. We followed these procedures in delineating the extent of burning, overall and at different fire severities, for the Zaca, Rey, La Brea, and Whittier Fires. Our fire metrics, including the proportions of basin areas and riparian and upland zones lying within fire footprints as well as the proportions of basin, upland, and riparian areas burning at moderate to high severities, were highly intercorrelated ($r = +0.93$ to nearly 1, p all < 0.0001). We found that stream response variables showed the tightest fit with the extent of riparian burning at moderate to high severities, so we concentrated on this fire metric in analyses unless otherwise noted. For survey sites influenced by fire but not directly within the fire scar, we measured the downstream distance from the fire perimeter to the study reach by using ArcMap 10.5.1.

Sampling design

We sampled study sites (100-m reaches) that lay within, outside, or downstream of the footprints of wildfires that occurred within the last 10 y. In 2016, at the end of a 5-y

drought, some sites were dry, so our sampling in that year was limited to sites containing surface water. We refer to sites as dry sites and wet sites, respectively, reflecting their condition in 2016. We sampled all sites in 2017, when flows resumed at dry sites and flows increased at wet sites. We categorized study sites as: 1) downstream of recent (<10 y) wildfires (down, $n = 5$, all dried in 2016); 2) a site within the 2016 Rey Fire footprint (Camuesa, $n = 1$; site 1 in Fig. 1); 3) sites lying within the 2007 Zaca Fire footprint that contained surface water in both 2016 and 2017 (wet burned sites, $n = 6$) of which 4 were sampled in both 2016 and 2017 and 2 were sampled only in 2017; 4) sites lying within fire footprints that were dry in 2016 (so were sampled only in 2017) (dry burned sites, $n = 4$); 5) sites in unburned basins that contained water in both 2016 and 2017 (wet unburned sites, $n = 9$) with 3 being sampled in both 2016 and 2017, 1 being sampled in only 2016, and 5 being sampled in only 2017; and 6) sites in unburned basins that were dry in 2016, so were sampled only in 2017 (dry unburned sites, $n = 5$) (Table 1, Figs 1, 3A–F). This design produced data for 30 stream sites and 37 site-times. Other than the 5 sites that were downstream of fires, the rest of the sites were deemed upstream sites, including several that were located upstream of the sites lying downstream of fire footprints. All upstream sites within burned basins were almost completely within fire footprints (mean = 98% of basin within fire footprint, standard error = 1.6%). Our Bear Creek study site (site 30 in Fig. 1) was 0.8 km downstream from the 2017 Whittier Fire, only 24% of its drainage basin and almost none (0.3%) of its upstream riparian area burned, and this site was sampled ~6 wk after the fire had passed, before any rains had occurred. Because the riparian zone at this site was unaffected by the Whittier Fire, and no effects from upstream runoff would be expected without rains, we considered this site to be an unburned site in analyses. Our Horse Creek study site (site 3 in Fig. 1) was the only site lying within the La Brea Fire footprint. Because the 2009 La Brea Fire occurred within 2 y of the 2007 Zaca Fire, and Horse Creek had characteristics similar to those of streams affected by the Zaca Fire, we included the Horse Creek site with sites affected by the Zaca Fire in analyses.

Quantifying physical, chemical, and biological characteristics of streams influenced by wildfires and drought and testing hypotheses

We sampled physical, chemical, and biological variables at each site once in each year it was sampled. We sampled sites from June to October in 2016 and from April to October in 2017. We used standard sampling protocols for benthic macroinvertebrates, and associated physical and chemical parameters, applied to bioassessments in California (Ode et al. 2016). Ten cross-stream transects were established at 10-m intervals along each 100-m survey reach, then we measured stream wetted width and bankfull channel

Figure 3. Photographs of some study sites. A perennial (wet) site within a basin that was burned by the 2007 Zaca Fire (Manzana Narrows, site 17 on Fig. 1 and in Table 1) photographed in 2016 (at the end of a 5-y drought) (A) and in 2017 (after flows increased) (D). A wet site (Alder Creek, site 22) whose basin was not burned in the last 10 y photographed in 2016 (B) and 2017 (E). A site (Santa Barbara Canyon Creek, site 5) in a basin burned by the Zaca Fire (C); this site was dry in 2016, so was only sampled and photographed in 2017. A 2017 photo of a site (Tule Creek, site 10) in an unburned basin that was dry in 2016 (F).

width at each transect with a tape measure. We used a meter stick to measure stream depth at 3 equally spaced points along the wetted width of each transect and then determined substratum size and current speed at 60% depth at each of the 3 points via visual estimation and a Marsh–McBirney wa-

ter current meter (Model 210D; Marsh McBirney, Frederick, Maryland), respectively. Substratum sizes were converted to Krumbein phi (ϕ) values ($\phi = -\log_2 D/D_0$ where D is particle diameter (in mm), and D_0 is a reference diameter = 1 mm). We also recorded maximum depth for each study reach and

determined sediment depth at the stream center on each transect by pounding a steel rebar post into substrata with a mallet. We estimated riparian canopy cover for each transect by taking measurements with a Model-A spherical densiometer (Forest Densiometers, Barlesville, Oklahoma) in 4 directions at the stream center then facing outward at each bank (6 measurements/transect). We measured dissolved oxygen concentration (accuracy: ±0.2 mg/L or 2% of reading), water temperature (accuracy: ±0.2°C), pH (accuracy: ± 0.2 pH unit), and conductivity (accuracy: ±0.001 mS/cm) at the bottom and top of each reach with a YSI Professional Plus multimeter (Yellow Springs Instruments, Yellow Springs, Ohio) once at each site, each time the site was sampled.

We took 1 water sample from each site-time for analyses of ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-), and soluble reactive phosphorus (SRP) concentrations at the top (upstream) of each study reach. We filtered samples through 0.45-μm polycarbonate filters (Poretics Corporation, Livermore, California), then held them on ice for 1 to 8 h before freezing them at −20°C in the laboratory until analysis (up to 1 mo later) (APHA 1992). Dissolved nutrient concentrations were measured spectrophotometrically on a QuikChem 8000 flow injection analyzer (Lachat Instruments, Milwaukee, Wisconsin) using standard methods (SRP: reaction with ammonium molybdate and ascorbic acid; NO_3^-, NO_2^-: reduction of nitrate to nitrite, nitrite was diazotized with sulfanilamide and coupled with ethylenediamine dihydrochloride; NH_4^+: QuickChem Gas Diffusion Method 31-107-06-5-A).

For each site-time, we sampled benthic and floating algae at 3 equally spaced points along each cross-stream transect, primarily on hard substrata but also on soft sediments where they occurred at sampling locations (30 samples/site). To collect algae, we used a 26-mm diameter open-ended syringe with removable scouring pad attached to the bottom of the syringe plunger for hard substrata, and we used the syringe barrel as a corer for soft substrata (Davies and Gee 1993, Klose et al. 2015). Periphyton samples from each transect were combined, placed in a sealed container, and kept refrigerated in the dark until processing, at which point scouring pads (hard substrata samples) were rinsed and soft substrata core samples were agitated, mixed, and elutriated with deionized water to separate periphyton from substrata. We homogenized periphyton samples in a beaker of deionized water, stirred them thoroughly, and removed subsamples (10–200 mL), which we then filtered through GF/C glass fiber filters (Whatman, Maidstone, United Kingdom). Subsample chlorophyll a (Chl a) concentrations corrected for phaeophytin were measured using the Environmental Protection Agency rapid bioassessment protocol for streams and wadeable rivers (Rodier and Norton 1992). We determined ash-free dry mass (AFDM) for material collected on Whatman GF/C glass fiber filters by drying at 60°C for 24 h, weighing subsamples, ashing for 2 h at 500°C, then reweighing. We averaged AFDM, Chl a,

and inorganic sediment levels across the 10 transects/site to provide an estimate of algal biomass (AFDM and Chl a, separately) and sediment mass for each site.

We collected 8 macroinvertebrate samples throughout each 100-m survey reach at each site-time by using a 500-μm mesh Surber sampler (0.09 m^2), with pools and riffles being sampled in proportion to the stream lengths they occupied. We combined the samples for each reach and washed the organisms and debris in the composited sample into a bucket. Organic matter >1 mm in diameter (i.e., coarse particulate organic matter [CPOM]) was removed, washed, and placed in a plastic bag, and we elutriated bucket contents repeatedly until only inorganic matter remained in the bucket; we visually inspected the inorganic material in a pan to recover heavy organisms. Organisms and detritus collected in the net or picked from the pan were transferred to a bottle and preserved in 75% ethanol.

We subsampled invertebrates in samples by using a plankton splitter, then identified them and counted to a total target count of 600 individuals following California's Surface Water Ambient Monitoring Program protocols (Ode et al. 2016). We identified invertebrate individuals based on standard taxonomic references (e.g., Merritt et al. 2008) to obtain genus- or species-level identifications for all taxa except oligochaetes, ostracods, and flatworms as well as some insects, which were identified to family (Capniidae, Dolichopodidae, Muscidae). All Chironomidae and water mites were identified to at least genus.

To determine if the traits of collected invertebrates were related to potential driving variables of interest (e.g., previous drying, wildfire), we assigned invertebrate taxa to different trait states for pollution and thermal tolerance, functional feeding, body size, development rate, voltinism, and depositional-erosional groups based on tabulated data in Poff et al. (2006), Appendix B in Barbour et al. (1999), and Herbst et al. (2018) with erosional vs depositional designations being refined based on samples taken from streams in Santa Barbara County, California (S. Cooper and Sheila Wiseman, University of California, Santa Barbara, unpublished data). Assemblage biotic (tolerance) and thermal indices for each site-time were derived from the summed products of tolerance values and thermal associations for taxa (cumulative distribution at the 75th percentile of Yuan 2006), respectively, weighted by their relative abundances in each sample. The biotic index (0–10) indicates increasing tolerance to degraded water or habitat quality. The thermal index uses the 75th percentile of temperatures at which a taxon has been collected, weights these values by the taxon's relative abundance in a sample, then sums these weighted values to obtain a composite temperature tolerance (in °C) for the assemblage.

Because so many factors, including past wildfire, drying during the drought, longitudinal position, season, and year could affect our results, we systematically evaluated the influences of each of these factors on response variables

by culling the dataset to address the roles of specific factors and to test specific hypotheses. The 1st set of analyses used the full dataset ($n = 37$ site-times) to examine associations between environmental and invertebrate variables vs stream drying in 2016, longitudinal position (downstream vs upstream), a fire that occurred the year before (Rey Fire), and interannual variation. These analyses allowed us to examine Hypotheses 1 and 2, which deal with the structure of invertebrate assemblages in remaining standing water at the end of a drought in 2016 (Hypothesis 1) and at sites that had resumed or increased flows in 2017, after the drought ended (Hypothesis 2). In addition, we compared data from the 1 site in a basin that had burned the year before (Camuesa Creek, Rey Fire) to data from all other sites to examine short-term stream invertebrate responses to fire (Hypothesis 4). The 2nd set of analyses eliminated the downstream, Camuesa, and 2016 data ($n = 23$ remaining sites) so that we could focus on variation attributable to sites that were sampled in different seasons in 2017 (seasonal effects; Fig. S1). Because these analyses showed that invertebrate assemblages and abiotic variable values, except for riparian canopy-associated variables (see below), differed between sites sampled in spring vs summer-autumn, we did a 3rd set of analyses on 2017 data in which spring 2017 samples were eliminated ($n = 18$ sites for remaining dataset). This set of analyses allowed us to compare data from upstream sites that were burned or not by the Zaca/La Brea fires, which occurred 8 to 10 y earlier, and that did and did not dry in 2016, without the potentially confounding influences of longitudinal position, the Rey Fire, year, and season. This 3rd set of analyses allowed us to evaluate our hypotheses regarding associations between invertebrate assemblage structure vs drying legacies in the summer and autumn after a drought ended and flows increased (Hypothesis 3) and long-term (~10 y) wildfire legacies (Hypothesis 5).

For each of these 3 sets of analyses, we performed both multivariate and univariate statistical tests. The multivariate invertebrate data consisted of a matrix of the relative abundances of all invertebrate taxa by all sites and times. We calculated multivariate distances between all pairs of sampled site-times by using the Sørensen distance metric. We used non-metric multidimensional scaling (NMDS) to display how invertebrate assemblage structure varied across site-times grouped by different temporal, longitudinal, burning, and drying categories (see below). We examined correlations between NMDS axes vs the transformed values of environmental variables (see below) and the relative abundances of common invertebrate taxa (i.e., those occurring in ≥25% of samples) (threshold Pearson's $|r| \geq 0.40$). These analyses were complemented by the multi-response permutation procedure (MRPP), which tested for multivariate differences in macroinvertebrate assemblage structure between categories. We conducted indicator species analysis (ISA) to determine which invertebrate species were associ-

ated with sites assigned to different temporal (year, season), burn, and drying categories and their combinations. ISA provides a maximum indicator value (IV_{max}) for each common taxon ranging from 0 (no indication) to 100 (perfect indication, i.e., presence points only to a specific category) based on information on the average relative abundance and frequency of occurrence of a taxon in a category compared to all samples and all other categories, respectively (Dufrêne and Legendre 1997). We used the Tichý and Chytrý (2006) ϕ coefficient to determine the indicator value of each species for each category and randomization (Monte Carlo) tests to determine the p-values associated with IV_{max}. All multivariate analyses were performed with PC-ORD software (version 6; MjM Software, Gleneden Beach, Oregon).

The univariate response variables we examined included values for the environmental variables we measured, total invertebrate richness and density, and the densities of invertebrate higher taxonomic (Arachnida [Acari], other non-insects, insect orders or families, chironomid subfamilies or tribes) and trait groups (see Table S1). To meet the assumptions of parametric tests (normality, additivity of sums of squared deviations, homogeneity of variances), count data were log10($x + 1$)-transformed, variable continuous data were log10-transformed, proportionate data were logit-transformed, and other variables remained untransformed before analyses (Warton and Hui 2011; see Table S1).

To test hypotheses related to differences in invertebrate assemblage structure at upstream and downstream sites lying within and outside fire footprints at the end of the drought (2016) and after flows resumed or increased (2017) (Hypotheses 1 and 2), we performed NMDS, MRPP, and ISA on data from all sites and site-times ($n = 37$ site-times). We also conducted 1-way analyses of variance (ANOVAs) followed by Tukey's honestly significant difference multiple comparisons tests to explore variation in response variable values across different fire categories (downstream of fire, upstream sites within (burned) or outside (unburned) fire footprints). We applied 2-tailed paired t-tests to examine response variable value differences between 2016 and 2017 for sites sampled in both 2016 and 2017 (7 pairs). To examine possible short-term invertebrate responses to wildfire and post-fire floods (Hypothesis 4), we compared data from the Camuesa site to data from all other sites and categories. The Camuesa site was the only upstream site that was affected by a wildfire 1 y before sampling.

To examine the consistency of our results with Hypotheses 3 and 5, which dealt with relationships between invertebrate and environmental variables vs drying and wildfire legacies, we used only our 2017 data with data from the downstream and Camuesa sites excluded. Riparian canopy cover and some associated variables (e.g., CPOM, Chl *a*, AFDM; Table S2, Fig. S1) did not vary seasonally in 2017, but many other environmental and biological variables did. As a consequence, we examined relationships between drying and

burn patterns vs canopy cover variables using the 2017 dataset (Camuesa and downstream sites excluded, $n = 23$ sites, Table S2) and vs other variables using only summer-autumn 2017 data ($n = 18$ sites) to eliminate seasonal effects (Fig. S1). To examine associations between environmental and invertebrate variables and previous drying and wildfire patterns, we performed NMDS, MRPP, and ISA on multivariate invertebrate data from June to October 2017 (excluding data from 2016, the spring of 2017, and the downstream and Camuesa sites to mitigate the potentially confounding influences of longitudinal position, a recent fire, season, and year). To examine the separate and interactive effects of drying and wildfire legacies on univariate response variables, we performed 2-way ANOVAs (categorical independent variables: 2016 wet vs dry, burned vs unburned by the 2007 Zaca/2009 La Brea Fires) and analyses of covariance (ANCOVAs) (categorical independent variable: 2016 wet vs dry; continuous independent variable: the extent of riparian burning at moderate to high severities by the Zaca/La Brea Fire) (Table S3). More generally, we examined relationships between putative continuous dependent and independent variables by using Pearson's correlation analysis (e.g., to examine correlations among environmental and invertebrate variables to postulate possible mechanisms for fire and drying influences on invertebrate variables) (Table S2). All univariate analyses (see below) were performed with JMP (version 13 for Windows; SAS Institute, Cary, North Carolina). ANOVA, ANCOVA, regression, and t-test results across variables within each response category (abiotic factors, taxonomic and trait groups) were subjected to Benjamini–Hochberg multiple comparison adjustments for comparisonwise error (Benjamini and Hochberg 1995; false discovery rate $= 0.05$ for most analyses, 0.10 for the summer-autumn 2017 dataset, when n for wet burned sites was 2, to balance Type I and II errors).

RESULTS
Wildfire, drying, and environmental variables
For upstream sites affected by the Zaca/La Brea Fires, the extent of burning in riparian zones was lower than that in upland zones in basins draining to perennial (wet) sites, but we observed the reverse in basins draining to sites that dried in 2016 (dry sites), with average riparian fire extent and severity being greater at dry than wet sites (Table 2). Although ~70% of riparian areas at wet sites were burned by the 2007 Zaca Fire (49% at moderate–high [M–H] severity), average riparian canopy cover at these sites in 2017 was high (82%) and comparable to that at wet sites in unburned basins (89%), indicating the rapid and complete post-fire recovery of riparian vegetation at wet sites (Tables 2, 3). In contrast, >90% of the riparian zone burned at dry sites with 77% burning at M–H severity, and average canopy cover at these sites in 2017 was 35%, lower on average than that at dry sites in unburned basins (52%). Riparian canopy cover was weakly negatively related to the proportion of the riparian, but not upland, zone burned at M–H severities (multiple linear regression analysis, equation: logit canopy cover $= 0.6 - 0.56$ logit riparian M–H burn extent [$p = 0.05$] $+ 0.45$ logit upland M–H burn extent [$p = 0.11$], overall $R^2_{adjusted} = 0.12$, $F_{1,21} = 2.5$, $p = 0.10$). These legacy associations between drought and the Zaca/La Brea Fires vs riparian canopy cover may have repercussions for other stream variables because canopy cover was positively related to CPOM levels and the densities of a number of taxonomic and trait groups, such as stoneflies, alderflies, mites, caddisflies, and taxa with erosional, sensitive, and shredder traits, and negatively related to temperature, algal levels (Chl a), and invertebrate biotic (tolerance) index values (Table S2).

Other environmental variables associated with canopy cover showed relationships with drying and burning patterns. CPOM levels in 2017 were negatively related to the extent of riparian M–H burning by the Zaca/La Brea Fires but were not related to 2016 stream drying (Fig. 4B). There was a weak interactive effect of canopy cover and stream drying on Chl a concentration ($p = 0.06$), with Chl a levels being higher at dry than wet sites, presumably owing to reduced shading. Chl a levels were similar at dry sites in burned and unburned basins but increased from unburned to burned basins at wet sites (Table 3, Fig. 4C). AFDM levels were strongly related to Chl a concentrations, suggesting that AFDM was primarily derived from algae instead of detritus across these times and sites ($\log_{10}$ AFDM $= -0.58 + 0.06 \log_{10}$ CPOM [$p = 0.30$] $+ 0.70 \log_{10}$ Chl a [$p < 0.0001$], $R^2_{adjusted} = 0.52$, $F_{2,20} = 13$, $p = 0.0002$). The relationships of conductivity and inorganic sediment levels to drying and the extent of riparian M–H burning were opposite to the relationships shown by canopy cover. Among other environmental variables, depth was greater at wet sites than at dry sites, and bankfull width tended to be greater at burned than unburned dry sites but greater at unburned than burned wet sites, with the stream width to bankfull width ratio showing a pattern opposite to that of bankfull width (Table 3).

Drought and stream invertebrate assemblages
There were large differences in assemblage structure between sites containing water in both 2016 and 2017 and sites that contained water in only 2017 (dry in 2016) (MRPP on the entire 2016–2017 dataset, $A = 0.039$, $p < 0.001$). The 1st axis of an NMDS on the entire 2016 to 2017 dataset accounted for 37% of the multivariate variation and clearly distinguished sites that were dry in 2016, including the 5 downstream sites, from wet sites (those containing water throughout the drought), particularly sites in the upper Sisquoc and Manzana River basins sampled in spring 2017 (Fig. 5). Sampled sites that were dry in 2016 had low NMDS axis 1 scores and were characterized by high temperatures, conductivities, and bank widths, and high relative abundances of the mayfly *Callibaetis*, the chironomid genera *Thienemannimyia* and *Pseudochironomus*, and the dragonfly

Table 2. Mean riparian and upland burning extent and severity (and their paired-by-site differences, ±SE) for the 2007 Zaca or 2009 La Brea Fires, for areas draining to up-stream sites that dried (dry) or contained surface water (wet) in 2016 (Camuesa excluded). The last 2 columns show the results of paired t-tests (t-values [associated p-values]) comparing upland vs riparian burning extent and severity across sites within each dry-wet category, and the bottom 2 rows show the results (F values [associated p-values]) of 1-way analyses of variance (ANOVA) comparing riparian and upland burning extent and severity (and their differences paired by site) for areas draining to dry vs wet sites. One wet site (Upper Indian) had anomalous burning extent and severity values. For example, riparian (99.9%) and upland burning (95%) extents for this site were much higher than the mean values for the remaining wet sites (means ± 95% CLs: 67 ± 14, 75 ± 10). As a consequence, data and analyses for wet sites with and without this outlier are shown.

Sites	Riparian burning extent	Upland burning extent	Difference upland–riparian burning extent	Riparian burning severity	Upland burning severity	Difference upland–riparian burn severity	Upland–riparian extent, paired t-test (p)	Upland–riparian severity, paired t-test (p)
Dry ($n = 4$)	93 ± 3%	89 ± 4%	−4 ± 1%	3.00 ± 0.23	2.98 ± 0.23	−0.02 ± 0.08	−3.1 (0.05)	−0.23 (0.83)
Wet ($n = 6$)	72 ± 8%	78 ± 5%	6 ± 3%	2.40 ± 0.24	2.65 ± 0.19	0.24 ± 0.11	−0.38 (0.72)	2.26 (0.07)
Wet without outlier ($n = 5$)	67 ± 7%	75 ± 5%	8 ± 3%	2.20 ± 0.14	2.51 ± 0.15	0.31 ± 0.11	3.2 (0.03)	2.9 (0.04)
ANOVA, dry vs wet F (p)	0.74 (0.42)	2.1 (0.19)	6.2 (0.04)	3 (0.12)	1.2 (0.3)	3.1 (0.12)		
ANOVA, dry vs wet without outlier F (p)	14.3 (0.007)	6.4 (0.04)	13.2 (0.008)	9.8 (0.02)	3.1 (0.12)	5.6 (0.05)		

Table 3. Physical, nutrient, and basal resource values for sites whose basins were burned only by the Rey Fire (1 y before, Camuesa); were downstream of the Zaca Fire footprint (Downstream); or were at upstream reaches that were dry or were not dry (wet sites) in 2016 cross-classified by whether or not they lay within (burned) or outside of (un-burned) the Zaca/La Brea Fire footprints (8–10 y before). Values are means (±SE). The 2nd to the last column lists the p-values with Benjamini–Hochberg (B–H) corrections for overall 2-way analysis of variance (ANOVA) models (wet–dry × burned–unburned) and the last column lists the p-values for each main effect and their interaction. If only 2 values are shown in the last column, it means the interaction effect was insubstantial. Data analyzed for maximum depth through conductivity were from summer through autumn of 2017 (1st smaller n for wet sites), whereas data for canopy cover to inorganic sediment were from the spring through autumn of 2017 (2nd n for wet sites) (see text). SRP = soluble reactive phosphorous, CPOM = coarse particulate organic matter, Chl a = chlorophyll a (algae), AFDM = ash free dry mass, B = burned, U = unburned, W = wet, D = dry.

| Variable	Camuesa ($n = 1$)	Downstream ($n = 5$)	Dry unburned ($n = 5$)	Dry burned ($n = 4$)	Wet unburned ($n = 7$ or 8)	Wet burned ($n = 2$ or 6)	ANOVA B–H p	p's: BU, WD, BU × WD
Max depth (m)	0.42	0.49 ± 0.07	0.45 ± 0.03	0.31 ± 0.07	0.61 ± 0.06	0.84 ± 0.02	0.01	0.54, 0.0002, 0.02
Average depth (m)	0.05	0.13 ± 0.02	0.11 ± 0.01	0.08 ± 0.02	0.15 ± 0.01	0.12 ± 0	0.12	0.12, 0.05
Width (m)	1.07	3.52 ± 0.53	2.06 ± 0.38	1.95 ± 0.42	2.14 ± 0.18	3.38 ± 0.23		
Velocity (m/s)	0.03	0.13 ± 0.08	0.16 ± 0.05	0.13 ± 0.05	0.06 ± 0.02	0.18 ± 0.03		
Sediment depth (m)	0.06	0.11 ± 0.04	0.05 ± 0.02	0.04 ± 0.02	0.11 ± 0.02	0.04 ± 0.02		
Substrate size (ϕ)	−4.94	−4.44 ± 0.51	−4.25 ± 0.26	−4.78 ± 0.75	−5.42 ± 0.63	−4.32 ± 0.06		
Bank width (m)	11.00	14.25 ± 2.74	4.61 ± 1.48	8.92 ± 3.62	12.43 ± 1.22	4.55 ± 1.19	0.12	0.44, 0.46, 0.02
Stream width:bankfull width	0.10	0.32 ± 0.11	0.57 ± 0.11	0.34 ± 0.10	0.18 ± 0.02	0.78 ± 0.15	0.01	0.06, 0.74, 0.0005
Pool:Riffle	0.6	1.00 ± 0.67	1.13 ± 0.63	0.67 ± 0.33	1.84 ± 0.40	1.00 ± 0		
Average temperature (°C)	30.8	23.9 ± 1.9	19.8 ± 0.8	22.7 ± 2.9	18.7 ± 0.8	16.8 ± 1.1		
Nitrate (µg/L)	11.6	8.0 ± 3.2	10.1 ± 5.8	71.1 ± 48.3	25.9 ± 4.1	4.2 ± 3.2		
SRP (µg/L)	36.9	7.6 ± 3.4	5.0 ± 1.7	2.0 ± 0.4	5.4 ± 2.6	2.7 ± 1.0		
Conductivity (µS/cm)	1103	1453 ± 282	1045 ± 119	2065 ± 693	938 ± 124	1054 ± 135		
Canopy cover (%)	12.5	35.21 ± 9.60	52.35 ± 8.69	35.25 ± 20.06	88.60 ± 3.31	82.04 ± 6.13	0.02	0.25, 0.0004
CPOM (g/m^2)	0.19	4.95 ± 3.60	11.31 ± 7.47	0.87 ± 0.58	16.78 ± 6.42	4.46 ± 1.31	0.04	0.006, 0.10
Chl a (mg/m^2)	5.99	11.26 ± 2.76	14.91 ± 2.80	14.88 ± 9.08	3.59 ± 0.51	12.07 ± 5.09	0.08	0.85, 0.13, 0.06
AFDM (mg/cm^2)	0.65	2.00 ± 0.42	3.47 ± 0.78	1.34 ± 0.46	0.81 ± 0.23	0.85 ± 0.14	0.03	0.11, 0.016, 0.038
Inorganic sediment (mg/cm^2)	3.44	4.45 ± 0.58	12.81 ± 2.46	5.76 ± 1.83	2.98 ± 0.57	3.69 ± 1.35	0.06	0.18, 0.03, 0.18
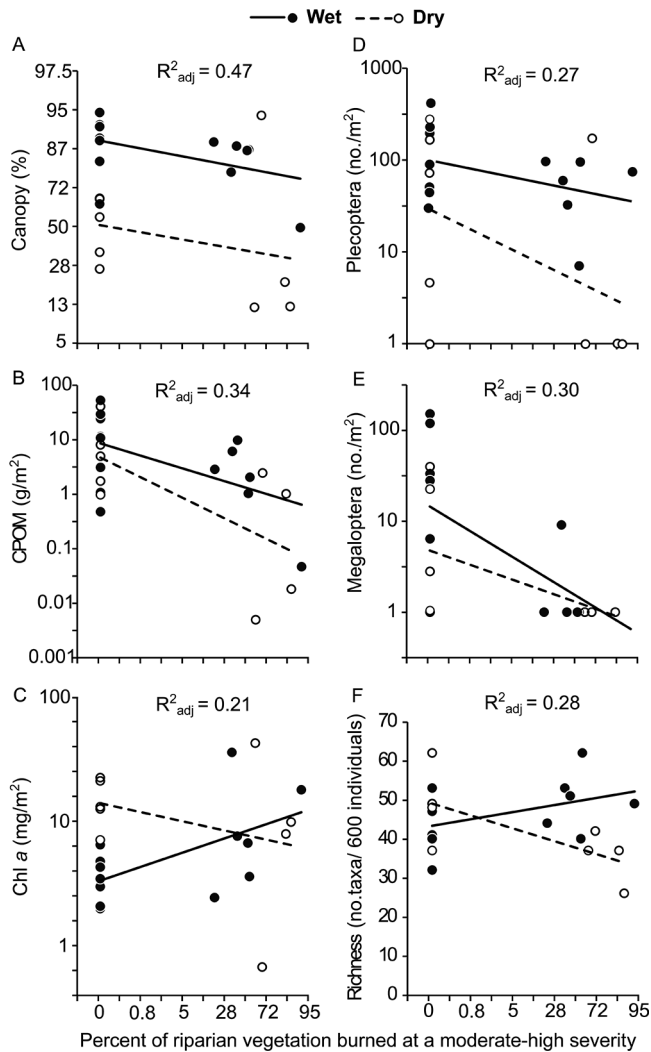
Figure 4. For the 2017 data from upstream sites excluding Camuesa Creek, relationships between canopy cover (logit proportions) (A), coarse particulate organic matter (CPOM) (B), algal (Chl a) levels (C), and the densities of stoneflies (Plecoptera) (D) and Megaloptera (*Sialis*) (E) (all log-transformed), and invertebrate richness (F) vs riparian burning at moderate to high severities by the Zaca/La Brea Fires (logit proportions) for sites that were wet (W, black circles) and dry (D, open circles) in 2016. This figure shows observed relationships between stream variables and drying-burning patterns based on inspection and statistical analyses (overall analysis of covariance [ANCOVA] model, $R^2_{adjusted}$ values shown). Canopy cover, and Arachnida (not shown) and Plecoptera densities, differed between wet and dry sites (p = 0.0004, 0.01, and 0.03, respectively); CPOM levels and Megaloptera densities declined with increasing riparian M-H burning extent (p = 0.003 and 0.006); and Chl a, invertebrate richness, and non-chironomid dipteran densities (not shown) showed wet-dry × riparian burning interactions (p = 0.04, 0.005, 0.02) (p-values from individual ANCOVAs). See also Table S3 for analyses on 2017 invertebrate data for upstream sites with data from the Camuesa site and spring samples excluded. Lines (wet sites = solid, dry sites = dashed) are best fit linear regression lines.

Paltothemis lineatipes, whereas wet sites with high NMDS axis 1 scores were associated with high canopy covers, water depths, and stream to bankfull width ratios, low temperatures and conductivities, and high relative abundances of the mayfly *Baetis* and 5 chironomid taxa (Fig. 5).

In 2017, downstream sites differed from upstream sites in drainage area, water temperature, and invertebrate assemblage structure (ANOVAs, B–H p < 0.05; MRPP A = 0.03, p = 0.001; Table S1). Further, canopy cover and stonefly (Plecoptera) density were higher at unburned upstream sites than at downstream sites, and bankfull width, Tanypodinae midge density, and the invertebrate thermal index were higher at downstream than upstream burned sites (ANOVAs, B–H p < 0.06). Four chironomid genera (*Pseudochironomus*, *Dicrotendipes*, *Thienemannimyia*, and *Labrundinia*), the caddisfly *Hydroptila*, and the dipteran *Hemerodromia* (Family Empididae) were associated with downstream sites (ISA, IV_{max} = 53–82, p = 0.03 to <0.001).

Both invertebrate assemblages and environmental variables differed between years. NMDS axis 2 primarily distinguished invertebrate assemblages collected in different years (2016 vs 2017) and accounted for 20% of the variation in the multivariate dataset (Fig. 5). The low NMDS axis 2 values for 2016 data at wet sites were associated with high pool:riffle ratios, low discharges and current velocities, and high abundances of the beetle *Eubrianax edwardsii*, the alderfly *Sialis*, the caddisfly *Gumaga*, the diperan *Neoplasta*, and 2 mite and 2 chironomid taxa (Fig. 5). The high NMDS axis 2 values for 2017, including for sites that both did and did not dry in 2016, were associated with higher velocity and discharge values and higher relative abundances of *Baetis*, the mite *Sperchon*, and the filter-feeders *Hydropsyche* (Order Trichoptera) and *Rheotanytarsus* (Order Diptera, Family Chironomidae). The invertebrate thermal index was higher in 2016 (18.1°C) than in 2017 (16.8°C) (B–H p < 0.05, paired t-test). There also were large differences in environmental variable values between 2016 and 2017 with SRP, conductivity, AFDM, CPOM, Chl a, and inorganic sediment levels being higher at the end of the drought in 2016 than in the wet year 2017, but pH being higher in 2017 than 2016 (p < 0.05 with B–H corrections, paired t-tests, 7 perennial sites sampled in both 2016 and 2017).

NMDS axis 3, which accounted for 16% of the multivariate variation in this dataset, was associated with differences in assemblage structure between the spring of 2017 and the summer of 2016 and autumn of 2017. To examine seasonal changes in response variable values more thoroughly, we analyzed only the 2017 data for upstream sites (Camuesa excluded). We found differences in invertebrate assemblage structure and many environmental variable values across seasons, with spring samples and measurements being different from those taken in summer or autumn (Fig. S1). Given these differences between spring and summer-autumn, we performed multivariate analyses (NMDS, MRPP, ISA) on
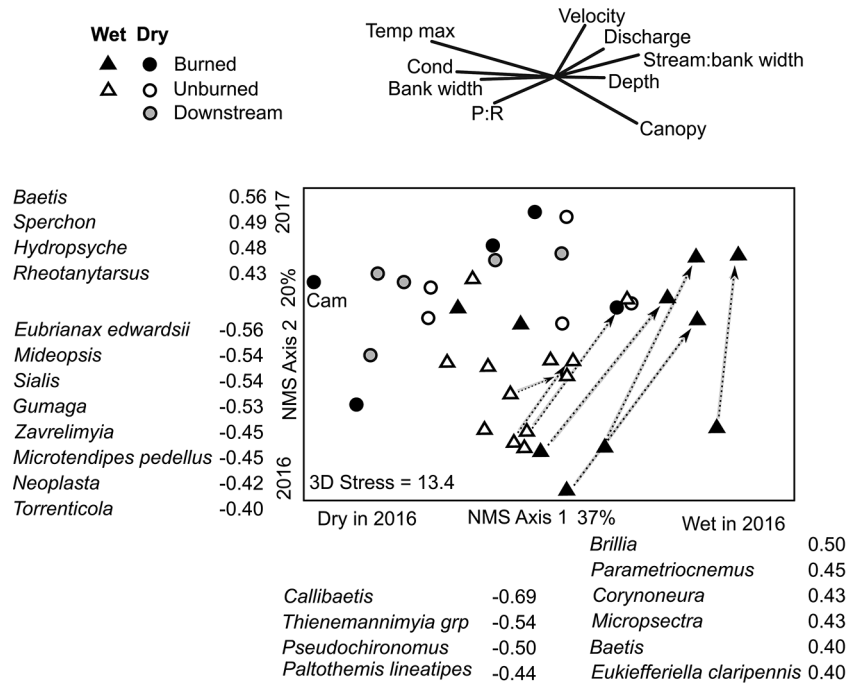
Figure 5. Nonmetric multidimensional scaling (NMDS) ordination showing the relative abundances of benthic macroinvertebrate taxa at 30 Los Padres National Forest, California, stream sites sampled in 2016, 2017, or both. Sites are coded to represent sites that were dry or wet in 2016 and that were within (Burned), outside (Unburned), or downstream (Downstream) of the footprints of fires that occurred within the last 10 y. The Camuesa site, the only upstream site affected by the Rey Fire 1 y before sampling, is designated Cam. Arrows connect sites sampled in 2016 to the same sites sampled in 2017. The stress associated with a 3-axis NMDS solution is shown in the lower left corner, and the % variation in the multivariate data set attributable to each NMDS axis is shown next to each axis label. The correlation coefficients (Pearson's r) of common taxa (occurring in ≥¼ of samples) related ($p < 0.01$) to each axis are shown in the margins. The correlation vectors for environmental variables associated with NMDS axes ($p < 0.01$) are shown above the plot. Temp max = Maximum temperature recorded; Cond = log-transformed conductivity; P:R = total pool length/total riffle length for study reaches.

only the summer-autumn 2017 data for upstream sites to eliminate any confounding effects of seasonality ($n = 18$ sites). There was still an association between assemblage structure and whether or not a site dried in 2016, indicating that drying legacy effects were apparent in the summer and autumn after the drought ended (MRPP, $A = 0.054$, $p = 0.007$). The 1st axis of an NMDS analysis on these summer-autumn 2017 data separated assemblages found in fast-flowing streams from those found in streams with wide channels and large total pool length to total riffle length ratios, whereas the 2nd axis distinguished dry from wet sites (Fig. 6). Low NMDS axis 2 values were associated with deep wet sites with high canopy cover and CPOM levels and high relative abundances of a variety of chironomid taxa, another dipteran (*Neoplasta*), 2 mites, a caddisfly (*Gumaga*), an alderfly (*Sialis*), a mayfly (*Caenis*), an elmid beetle (*Zaitzevia*), and a snail (*Physa*). High NMDS axis 2 scores were associated with shallow, dry sites with high temperatures, conductivities, and Chl *a* levels as well as high relative abundances of a mayfly (*Baetis*), several other chironomid taxa, other dipterans (*Caloparyphus, Dasyhelea*), and a caddisfly (*Hydropsyche*). At the individual taxon level, we found that all of the taxa associated with sites that were dry in 2016 were small, eurythermal dipterans or oligo-

chaetes with fast life cycles (Table S2, Fig. 6). In contrast, taxa from a wide variety of taxonomic and trait groups were associated with wet sites, with taxa indicative of wet unburned sites being found almost exclusively at those sites (Table S2, Fig. 6).

Invertebrate responses to wildfire patterns

Recent fires and invertebrate assemblages Camuesa Creek, the only upstream site affected only by the 2016 Rey Fire, had the greatest percentages of its basin, riparian, and upland areas burned at M–H severities (96, 99, and 96%, respectively) and, in 2017, the highest water temperature and SRP concentration and lowest stream width to bankfull width ratio of all study sites (Table 3). This site also was very shallow and had low canopy cover. The NMDS on the entire 2016 to 2017 invertebrate dataset showed that the Camuesa Creek site was an outlier, having the lowest scores on NMDS axis 1 (Fig. 5). This stream site had the lowest species richness and total invertebrate density of all sites, with stoneflies (Plecoptera), Megaloptera, water mites (Acari), elmid beetles (Family Elmidae), grazers, shredders, and erosional taxa being absent and chironomids, other dipterans, and
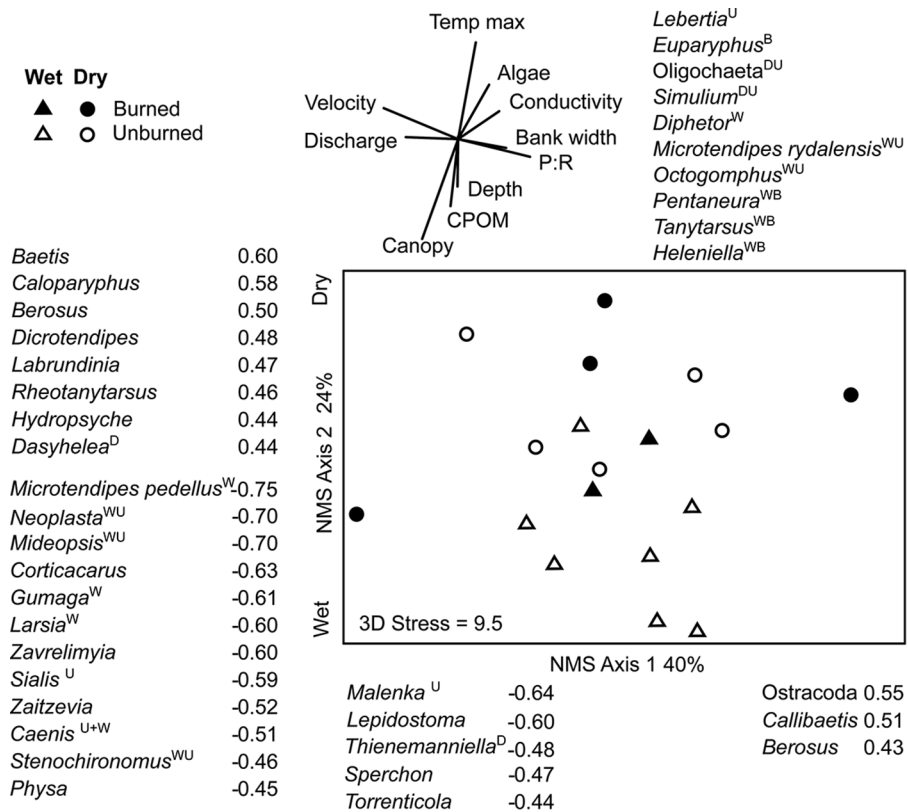
Figure 6. Ordination plot of nonmetric multidimensional scaling (NMDS) analysis on the relative abundances of benthic macro-invertebrate taxa sampled at 18 upstream sites in the summer and autumn of 2017. Sites are coded to indicate sites that were dry and wet in 2016 cross-classified by sites that were within (Burned) or outside (Unburned) the footprints for the Zaca and La Brea Fires. The stress associated with a 3-axis NMDS solution is shown in the lower left corner, and the % variation in the multivariate data set attributable to each NMDS axis is shown next to each axis label. The correlation coefficients (Pearson's r) of common taxa (occurring in ≥¼ of samples) related ($p < 0.05$) to each axis are shown in the margins. The correlation vectors for environmental variables associated with NMDS axes ($p < 0.05$) are shown above the plot. Superscripts represent indicator taxa for unburned (U), burned (B), wet (W), and dry (D) sites and combinations of these categories (Table S2). Other indicator taxa that were not correlated with NMDS axis 1 or 2 are listed at the top (indicator species analysis [ISA]). CPOM = coarse particulate organic matter; Algae = chlorophyll a (Chl a); Temp max = Maximum temperature recorded; P:R = total pool length/total riffle length for study reaches.

many trait groups having their lowest densities compared to all other sites. Camuesa Creek also had the highest invertebrate biotic (tolerance) index value.

Long-term fire legacies and invertebrate assemblages   We found no differences in invertebrate assemblage structure between burned and unburned upstream sites from analyses of the 2016 to 2017 dataset, the 2017 dataset, or the summer-autumn 2017 dataset (MRPP, $A = 0.009–0.01$, $p = 0.08–0.16$). No variation in NMDS axis scores was associated with burned vs unburned categories for any of the data sets.

Focusing on 25 trait and 15 taxonomic groups in the summer-autumn 2017 dataset, the densities of only megalopterans, elmid beetles, and taxa with slow seasonal life cycles were correlated (negatively) with the extent of riparian burning at M–H severities ($r = -0.56$ to -0.62, uncorrected

$p = 0.015–0.006$). Two-way ANOVAs and ANCOVAs (independent variables: wet-dry by burned-unburned status or transformed proportion of riparian zone burned at M–H severities) indicated that stoneflies and mites were more abundant at wet than dry sites; that megalopteran (primarily *Sialis*) densities decreased with increasing extent of past riparian burning; and that richness and non-chironomid dipterans showed wet-dry × riparian burning interaction effects (Fig. 4D–F, Table S3). In addition, Tanypodinae and Tanytarsini midges were more abundant at wet than dry sites ($p = 0.006$ and 0.02), with a weak interaction effect of wet-dry status and riparian burning extent ($p = 0.02$ and 0.04), tending to increase in abundance with riparian burning at wet sites and to decrease with burning at dry sites. Most individual taxa (*Sialis*, *Caenis*, *Malenka*) associated with unburned sites were positively correlated with CPOM levels ($r = 0.57–0.67$, uncorrected $p = 0.01–0.002$), whereas the 1 indicator taxon (*Euparyphus*) associated with burned sites

was negatively related to canopy cover ($r = -0.55$, uncorrected $p = 0.02$, associations based on ISA) (Table S2, Fig. 6).

DISCUSSION

We examined relationships between stream environmental conditions and invertebrate assemblage structure vs past wildfires and stream drying because there was little information on the long-term responses of streams in Mediterranean climates to fires occurring up to a decade ago, particularly during and after a supraseasonal drought (see Introduction). We sampled invertebrate and abiotic variables at reaches (sites) laying within, outside, or downstream of the footprints of wildfires that occurred 8 to 10 y ago, as well as at 1 site within a basin that burned the year before sampling. We collected samples at some sites containing surface water in the last year of a 5-y drought and at all sites in the year after the drought ended. Using these data, we examined the results relative to 3 hypotheses (Hypotheses 1–3) dealing with predicted invertebrate assemblage structure at the end of the drought and in different seasons after the drought ended and to 2 hypotheses dealing with stream invertebrate assemblage structure at sites within or outside of basins that had burned either 1 year before (Hypothesis 4) or 8 to 10 y ago (Hypothesis 5). Ancillary data on environmental conditions at site-times were used to explore possible reasons for relationships between invertebrate variables and drought or wildfires. In the following discussion, we examine the consistency of our results with our hypotheses, first those dealing with relationships between stream invertebrate assemblage structure and stream drying during the drought. We then compare our results to our hypotheses dealing with short-term (1 y) and long-term (8–10 y) stream responses to wildfire legacies as well as possible interaction effects of past wildfires and drying on stream assemblages. We end with a discussion of the implications of climate change for drought and wildfire with a focus on repercussions for stream communities.

Drought and stream invertebrate assemblages

Consistent with other studies, our research indicated that stream flow patterns, particularly stream drying, were strongly related to the structure of invertebrate assemblages (Sponseller et al. 2010, Bogan et al. 2015, Herbst et al. 2019), whereas fire legacies after 8 to 10 y were much less important (Verkaik et al. 2013a, b, Monaghan et al. 2020). At the end of the drought, invertebrate assemblages in pools with high conductivities and organic matter levels were dominated by depositional and mixed depositional-erosional taxa (e.g., *Sialis*, *Gumaga*, *Neoplasta*, *Zavrelimyia*) and high thermal indices, generally corroborating our 1st hypothesis (dominance by tolerant, lentic taxa; Herbst et al. 2019). When higher flows, more extensive riffles, and cooler temperatures returned in spring 2017, invertebrate assemblages were dominated by

rheophilic taxa (*Baetis*, *Hydropsyche*, *Simulium*, and *Rheotanytarsus*), corroborating our 2nd hypothesis (dominance by quick-colonizing, rheophilic taxa after flows resumed) (Lake 2011, Bogan and Lytle 2011). Mobile, rheophilic taxa increased in relative abundance in 2017 at sites that both did and did not dry in 2016, showing their abilities to quickly colonize formerly dry sites after flows returned. The return of flows also initiated a typical seasonal successional sequence with assemblage dominance by rheophilic or mixed erosional-depositional taxa in the spring followed by domination by depositional and mixed depositional-erosional taxa in the summer and autumn (Fig. S1). This seasonal sequence reflected increasing pool:riffle ratios and shifts from sensitive taxa with cooler thermal tolerances in spring to tolerant taxa with warmer thermal tolerances in summer (Bogan and Lytle 2007, Herbst et al. 2018, 2019).

Perennial (wet) sites and sites that dried in 2016 (dry) had similar invertebrate assemblages in the spring of 2017, but differences in assemblage structure between wet and dry sites were evident by summer and autumn. These results contradicted our expectation (Hypothesis 3) that invertebrate assemblage structure would converge at wet and dry sites after perennial flows resumed. Our data suggested that there were strong relationships among drying, riparian canopy cover and many related variables, and invertebrate assemblage structure. Dry sites with low canopy cover were dominated by quick-colonizing, warm-water, algivorous or filter-feeding, and rheophilic taxa (e.g., *Baetis*, *Hydropsyche*, diptera [families Stratiomyidae, Ceratopogonidae, Chironomidae], and beetles [Hydrophilidae]). On the other hand, deep, perennial sites with high canopy cover were dominated by lentic EPT and dipteran taxa, *Sialis*, elmid beetles, and snails, which either may have been intolerant of complete drying or benefited from cool temperatures and high CPOM levels (Griswold et al. 2008, Lake 2011). Although contradicting our 3rd hypothesis, our results corroborated other studies that showed longer-term effects of supraseasonal drought on invertebrate assemblage structure, owing to the extirpation of some taxa intolerant of drying and to changes in aquatic vegetation and abiotic factors that persisted after the drought (Bêche et al. 2009, Sponseller et al. 2010, Bogan and Lytle 2011).

We also suspect that there were reach-scale differences in the hydrological and thermal regimes, and riparian and environmental conditions, at our wet vs dry sites, resulting in long-term differences in invertebrate assemblages (Datry et al. 2014, Bogan et al. 2015, 2017, Piano et al. 2019). Assemblages found at deep, cool, shaded, perennial sites in 2016 and 2017, typified by Plecoptera, mites, *Baetis*, and some chironomids, differed from those found in 2017 at open, warm, wide, and shallow sites that dried in 2016, which were typified by taxa such as *Callibaetis*, *Pseudochironomus*, and *Thiennemannimyia*. Our results also suggested that species indicative of sites that dried could tolerate lower water quality

and higher temperatures than those associated with perennial sites. As is typical of southern California and many montane arid or semi-arid regions, our study streams are "upside down" with perennial dry season flows being most prevalent in headwater sections and downstream reaches overlying alluvial and floodplain deposits often drying during the dry season (Bogan et al. 2013). The invertebrate assemblages in our 5 downstream reaches were different than those in more upstream sites, particularly shaded, deep, perennial, upstream sites, even those in the same basins as the downstream sites. Although invertebrate assemblages may have differed between our upstream and downstream sites partly because of downstream reach drying, our downstream sites also were wider and had higher temperatures and lower riparian canopy cover than upstream, particularly perennial sites, consistent with the River Continuum Concept (Vannote et al. 1980).

Wildfire patterns: Recent fires and invertebrate assemblages

Our Camuesa site, which was burned by the Rey Fire ~1 y before our study, had the highest extent of upland and riparian burning at M–H severities and the lowest invertebrate densities and taxonomic richness among all of our sites. Many taxa present at other sites were absent at Camuesa. With basin vegetation diminished or destroyed, short-term invertebrate responses to wildfire are often mediated through runoff, erosion, stream discharge, sediment dynamics, and geomorphological changes (Minshall 2003, Arkle et al. 2010, Chin et al. 2019). We suspect that, consistent with our 4th hypothesis, the depauperate assemblage at this site was a product of post-fire scouring flows and high sediment loads during a large storm that occurred ~4 mo before sampling. The depauperate assemblage at this site also was consistent with the severe effects of the 1st large post-fire storms on invertebrate assemblages noted in other studies (Vieira et al. 2004, Verkaik et al. 2013a, Monaghan et al. 2019). The 1st invertebrates that re-colonize reaches exposed to severe post-fire flows, scouring, and sedimentation usually are small highly mobile species, such as baetid mayflies, blackflies, and chironomids, but insufficient time appeared to have elapsed after drying then scouring flows at our Camuesa site to allow recolonization (Minshall 2003, Vieira et al. 2004, Mellon et al. 2008).

Wildfire patterns: Long-term responses of stream ecosystems to wildfire

Fire legacies, riparian vegetation, and CPOM   Although upland vegetation destruction by fire can produce short-term inputs of sediment and solutes to streams, some of the long-term effects of wildfire appear to be mediated through fire effects on riparian vegetation (Arkle et al. 2010, Cooper et al. 2015, Musetta-Lambert et al. 2019). Our results indicated that wildfire had greater effects on riparian than on upland vegetation in basins draining to sites that dried in 2016 (dry sites), presumably because of greater fuel loads in riparian than upland zones (as in some montane forests, Van de Water and North 2011). Conversely, wildfire extent and severity were higher in upland than riparian zones draining to perennial reaches, presumably because of greater surface water and higher water tables in riparian zones, resulting in higher deciduous tree densities, shading, humidity, and foliar moisture levels at wet than dry sites (Dwire and Kauffman 2003, Pettit and Naiman 2007, Stella et al. 2013). Riparian vegetation recovery appeared to be rapid at our sites in burned basins, consistent with results from Mediterranean and other warm or semi-arid regions where deciduous trees and shrubs quickly re-sprout and grow (Dwire and Kauffman 2003, Verkaik et al. 2013a). These results contrast with those from boreal and temperate montane regions, where wildfire may engender decades-long successional sequences in riparian vegetation, leading from herbaceous vegetation and shrubs to deciduous trees to coniferous trees (Musetta-Lambert et al. 2017, 2019). We also observed that riparian vegetation recovery was faster and more complete at our wet sites compared with dry sites, consistent with studies showing that the re-establishment and growth of deciduous riparian vegetation after wildfire depends on soil moisture and subsurface water levels (Kobziar and McBride 2006, Reeves et al. 2006, Halofsky and Hibbs 2009). The relationship between riparian burning patterns and canopy cover was weak after 10 post-fire y, which was unsurprising given the complex relationships among, and variability in, geomorphology, surface flow, water table levels, and fire effects on riparian vegetation among our study sites.

Surprisingly, there was a strong negative relationship between legacy riparian burning and CPOM levels. It is possible that CPOM levels still reflected past riparian fire patterns because of the slow recovery of riparian vegetation and reduced allochthonous inputs at dry sites and, at wet sites, the re-establishment and growth of green riparian vegetation, which dropped fewer leaves than older riparian vegetation at unburned sites. Jackson et al. (2012) also reported higher inputs of allochthonous particulate organic matter at stream sites in unburned than in burned basins after 5 post-fire y.

Wildfire legacies and stream invertebrate assemblages
Although some environmental conditions, such as CPOM, still reflected past wildfire patterns, we found almost no invertebrate assemblage differences between sites in basins that did and did not burn after 8 to 10 post-fire y, consistent with our 5th hypothesis. Invertebrate assemblages in downstream sites, which all dried in 2016, were most similar to those in upstream sites that both dried and burned, suggesting that reductions in riparian vegetation at burned, headwater sites shifted longitudinal sequences upstream. The densities of the few taxa (e.g., *Sialis, Malenka, Caenis, Euparyphus*) associated with sites in unburned vs burned

basins often were related to canopy cover or CPOM levels, suggesting that some taxa still showed responses to the legacy effects of riparian burning and the loss of allochthonous inputs. Because CPOM and its major consumer group, the shredders, are often reduced by post-fire washout during storms and subsequent reductions in riparian vegetation and leaf inputs, shredders, including shredding stoneflies like *Malenka*, often are reduced by wildfire (Vieira et al. 2011, Oliver et al. 2012, Martens et al. 2019). On the other hand, other taxa (such as some Stratiomyidae) appeared to benefit from riparian burning that opened canopies, increasing algal biomass.

Comparisons and interactions of drought and wildfire legacies

In general, the short-term effects of wildfire on stream invertebrate assemblages, as evidenced by the responses of invertebrate assemblages to a fire at our Camuesa site 1 y before sampling and a flood 4 mo before sampling, overwhelmed other drivers of stream community variation (Vieira et al. 2004, Cooper et al. 2015). Variation in invertebrate assemblages attributable to the long-term (8–10 y) legacy effects of wildfire, however, were dwarfed by invertebrate responses to spatial and temporal variation in flow patterns, particularly stream drying (Verkaik et al. 2013b, Robson et al. 2018). Some of our results also indicate that there can be complex interactions between wildfire and stream drying effects. For example, taxonomic richness and the abundances of some dipteran groups (e.g., chironomid subfamilies, other dipterans) were lower in burned than in unburned basins at dry sites, perhaps because riparian burning opened the canopy and increased drying intensity. Conversely, taxonomic richness and the density of some dipterans were higher in burned than in unburned basins at wet sites, probably be-

cause shaded wet sites in burned basins were deeper and cooler than most other sites. A summary of our findings (Fig. 7) suggests that wildfire may re-inforce a-priori differences in stream assemblage structure between sites with perennial flow and sites that dry during drought.

An open question remains as to whether drought speeds or delays the recovery of stream invertebrate assemblages from wildfire. Because drought, wildfire, and hydrological conditions have interactive legacy and current effects on vegetation and, hence, on geomorphic processes, with many repercussions for stream communities at different temporal scales, ecosystem recovery after wildfire and drought is likely to be context-specific and inconsistent (Bêche et al. 2009, Resh et al. 2013, Verkaik et al. 2013a). Verkaik et al. (2015) suggested that strong post-fire effects on invertebrate assemblages in southeastern Australia were exacerbated by a 13-y drought, but Robson et al. (2018), dealing with the same region and drought, found that invertebrate assemblage structure in streams in burned and unburned basins had converged within 2 y. Rugenski and Minshall (2014) found that basal resources (periphyton) and densities of rapidly-colonizing invertebrates showed large increases after fire during years with low peak flows, contrasting with large post-fire reductions in invertebrate resources and abundance associated with strong run-off events and higher peak flows (see also Vieira et al. 2004, Arkle et al. 2010, Romme et al. 2011).

Climate change, drought, wildfire, and management recommendations

Climate change will increase temperature and alter precipitation, runoff, and flow regimes in many parts of the world. Increased stream temperatures, whether mediated through climate change, losses of riparian vegetation, or
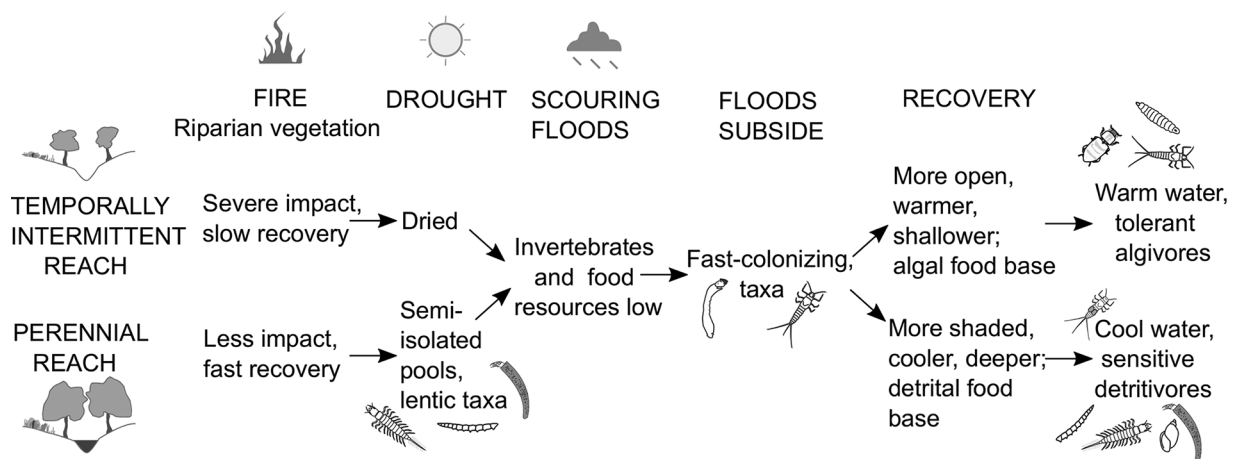

Figure 7. Conceptual diagram summarizing the physical and biological responses to fire and drought in temporally intermittent and perennial streams observed in this study.

increased surface runoff, are likely to alter stream inverte-
brate assemblages, as suggested by the responses of our
thermal index to fire and drought and by observed rela-
tionships between a variety of indicator taxa and tempera-
ture (Pyne and Poff 2017, Table S2). As in many other re-
gions, climate change in our study region also is predicted
to decrease the duration of the wet season but increase the
frequency of large storms, resulting in increased run-off,
higher peak flows, and decreased dry season flows (Feng
et al. 2019). Higher temperatures, and longer and drier sea-
sonal and supraseasonal droughts, combined with increased
human population size and intrusion into the wildland–urban
interface, also will increase the frequency and severity of
wildfires (Syphard et al. 2007, 2017, Goss et al. 2020). As
outlined above, drought and wildfires can have direct, indi-
rect, and interactive effects on stream communities via their
effects on runoff, flow, geomorphic processes, and riparian
vegetation conditions and recovery (Lake 2011, Verkaik
et al. 2013a). Fires, however, represent pulse disturbances
that engender rapid community recovery in warm regions,
provided they are not too frequent or do not permanently al-
ter riparian vegetation (Cooper et al. 2015, Bixby et al. 2015).
In contrast, supraseasonal drought represents a longer-term
ramp disturbance punctuated by steps in community effects
associated with spatial intermittence and, ultimately, drying,
leading to longer and sometimes novel post-disturbance re-
covery trajectories (Bonada et al. 2006, Bêche et al. 2009, Bo-
gan and Lytle 2011). Ultimately, both drought and wildfire
can cause a shift in stream invertebrate assemblage compo-
sition from taxa associated with wet or unburned sites with
high canopy cover and CPOM levels and low temperatures
to taxa associated with dry or burned sites characterized by
low canopy cover and high temperature and algal levels. Our
results also indicate that deep, shaded, perennial, spring-fed
pools in headwater areas can act as refuges from drought
and wildfire for the aquatic and riparian biota. Thus, where
possible, humans should sustain these refuges by protecting
or restoring riparian vegetation and preventing or decreas-
ing water abstraction (Robson et al. 2011, 2013).

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