ORIGINAL ARTICLE

Trout and invertebrate assemblages in stream pools through wildfire and drought

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Abstract

1. Climate change is increasing the frequency, severity, and extent of wildfires and drought in many parts of the world, with numerous repercussions for the physical, chemical, and biological characteristics of streams. However, information on how these perturbations affect top predators and their impacts on lower trophic levels in streams is limited.

2. The top aquatic predator in southern California streams is native *Oncorhynchus mykiss*, the endangered southern California steelhead trout (trout). To examine relationships among the distribution of trout, environmental factors, and stream invertebrate resources and assemblages, we sampled pools in 25 stream reaches that differed in the presence (nine reaches) or absence (16 reaches) of trout over 12 years, including eight reaches where trout were extirpated during the study period by drought or post-fire flood disturbances.

3. Trout were present in deep pools with high water and habitat quality. Invertebrate communities in trout pools were dominated by a variety of medium-sized collector–gatherer and shredder invertebrate taxa with non-seasonal life cycles, whereas tadpoles and large, predatory invertebrates (Odonata, Coleoptera, Hemiptera [OCH]), often with atmospheric breather traits, were more abundant in troutless than trout pools.

4. Structural equation modelling of the algal-based food web indicated a trophic cascade from trout to predatory invertebrates to collector–gatherer taxa and weaker direct negative trout effects on grazers; however, both grazers and collector–gatherers also were positively related to macroalgal biomass. Structural equation modelling also suggested that bottom-up interactions and abiotic factors drove the detritus-based food web, with shredder abundance being positively related to leaf litter (coarse particulate organic matter) levels, which, in turn, were positively related to canopy cover and negatively related to flow. These results emphasise the context dependency of trout effects on prey communities and of the relative importance of top-down versus bottom-up interactions on food webs, contingent on environmental conditions (flow, light, nutrients, disturbances) and the abundances and traits of component taxa.

5. Invertebrate assemblage structure changed from a trout to a troutless configuration within a year or two after trout were lost owing to post-fire scouring flows or drought. Increases in OCH abundance after trout were lost were much more variable after drought than after fire. The reappearance of trout in one stream resulted in quick, severe reductions in OCH abundance.

6. These results indicate that climate-change induced disturbances can result in the extirpation of a top predator, with cascading repercussions for stream communities and food webs. This study also emphasises the importance of preserving or restoring refuge habitats, such as deep, shaded, perennial, cool stream pools with high habitat and water quality, to prevent the extirpation of sensitive species and preserve native biodiversity during a time of climate change.

1 | INTRODUCTION

Climate change is increasing the incidence and duration of drought, and the frequency, extent, and severity of wildfires, in many semi-arid and arid regions of the world (Williams et al., 2019, 2020, 2022). By affecting flow conditions, sediment and solute inputs or accumulation, and riparian shading, wildfire and drought can have many impacts on stream communities and food webs (Gresswell, 1999; Lake, 2011; Verkaik et al., 2013). For example, post-fire floods and sedimentation, and drying during drought, can greatly reduce most stream organisms with subsequent initial re-colonisation by small, vagile species with short life cycles, and can increase light, nutrient, primary producer, and algivore levels and decrease coarse particulate organic matter (CPOM) and shredder levels, particularly where riparian vegetation is damaged or destroyed (Bixby et al., 2015; Cooper et al., 2015, 2021; McMahon et al., 2023; Silins et al., 2014). Although previous studies have focused on the effects of fire and drought on physical–chemical conditions in streams and, in turn, stream communities, there is less information on how these disturbances affect top predators and their impacts on the rest of the community (Ledger et al., 2013; McIntosh et al., 2018; Rodríguez-Lozano et al., 2015; Woodward et al., 2016).

Southern California has steep mountains, erodible soils, frequent wildfires, a dense and growing human population, and a Mediterranean climate increasingly typified by severe winter storms and lengthy supraseasonal droughts (Feng et al., 2019; Mooney & Zavaleta, 2016). Seasonally, stream discharge in this region peaks during the wet season (November–March), but then recedes to low levels during the dry season (April–October), producing reaches that consist of perennial, contiguous flows, isolated or semi-isolated pools, or dry stream beds depending on catchment area, longitudinal position, and antecedent rainfall. Similar to many streams draining small catchments in central and southern California, the streams in our study area, the southern Santa Barbara County, California, U.S.A., coast, are often intermittent, with low-elevation reaches flowing over alluvial fans and plains usually drying during dry periods (Boughton et al., 2009; Cooper et al., 2021). Dry season flows in some of these low gradient reaches, however, can extend to estuaries and the Pacific Ocean in very wet years. In contrast, streams flowing through the coastal foothills and mountains, the focus of this study, often constitute a mosaic of perennial and intermittent reaches during the dry season, where flows depend on the underlying lithology and, hence, the location of springs in these fractured bedrock systems, as well as on precipitation and stream geomorphological patterns through both time and space (Hwan et al., 2018). Because we initially chose flowing reaches for our investigations, approximately 60% of our study reaches were perennial throughout the study period; however, a substantial proportion (*c.* 40%) completely dried at least once, particularly during the unprecedented 2012–2016 drought. In general, then, stream flow extremes, ranging from drying to intense floods, as well as wildfire and land use changes in drainage basins, are pervasive in southern California (Underwood et al., 2019; Williams et al., 2022). These accelerating and intensifying disturbances have many effects on the abundance, diversity, trophic relationships, and biomass of the stream biota, including rare and endangered native species, such as the southern California steelhead (*Oncorhynchus mykiss*) (National Marine Fisheries Service, 2012, 2016, 2023).

Historically, the top aquatic predators in most southern California coastal streams were native *O. mykiss*, including both the endangered anadromous steelhead form and the resident rainbow trout form (Cooper et al., 1986; Dagit et al., 2020; National Marine Fisheries Service, 2012, 2016, 2023). Although steelhead or rainbow trout can move across stream reaches during the wet season when flows are adequate, they often are relegated to pools with adequate habitat, resources, and refuge space during the dry season (Cooper et al., 2015; Grantham et al., 2012; Hwan et al., 2018). Because the steelhead or rainbow trout (trout) is considered a keystone species, the loss of trout can have many repercussions for stream ecosystems (Buria et al., 2010; Power, 1990; Power et al., 2008; Shelton et al., 2015). Although it is well-known

that the survival, growth, densities, and persistence of trout populations are strongly related to flow patterns (Boughton et al., 2009; Grantham et al., 2012; Hwan et al., 2018), we currently have little information on how the loss of trout owing to catastrophic disturbances, such as wildfire, floods, or drought engendered by climate change or human activities, will affect stream communities and food webs (Cooper et al., 2015). During our study period (2008–2020), there were eight wildfires and a prolonged 5-year drought in our study region. At the outset of our study, some of our streams contained and others lacked native trout populations, but some local trout populations were extirpated during the study period during post-fire scouring floods or drought.

We were interested in three questions: (1) What disturbance events (e.g., wildfire, floods, and/or drought) and environmental conditions drive the presence or absence of trout? (2) How does the presence of trout alter invertebrate assemblage and food web structure? (3) What is the nature and rapidity of invertebrate community changes after the loss of trout owing to post-fire scouring flows and drought conditions? To answer these questions, we first characterised differences between trout and troutless stream reaches undisturbed by fire, then used this baseline to determine how and how rapidly stream assemblages changed after the loss of trout owing to wildfire or drought, thereby isolating the assemblage impacts of disturbance-mediated top predator loss. The baseline survey design compared environmental conditions, invertebrate assemblages, and food web structure at stream sites that were not affected by wildfire and that did (trout) and did not (troutless) contain trout, both to examine the environmental conditions associated with the presence of trout (Question 1) and to examine relationships among trout presence, resource (leaf litter or CPOM > 1 mm diameter, algae) levels, food web structure, and invertebrate assemblage composition and abundances (Question 2). Subsequently, we compared these baseline differences in undisturbed trout and troutless streams to changes in resource levels and invertebrate assemblages over times when trout were lost owing to wildfire (and subsequent scouring flows) or drought (drying or stagnant conditions; Question 3). Because trout in these streams are found in pools in the dry season, we concentrated on pool communities and food webs.

Based on previous research and the literature, we predicted that trout would be present primarily in cool, deep, perennial, shaded stream pools, where they would directly reduce the abundances of large, conspicuous, and predatory invertebrate taxa (e.g., Odonata, Coleoptera [primarily Dytiscidae], Hemiptera [OCH]), as well as large, algivorous amphibian larvae (primarily hylid tadpoles) (Cooper, 1988; Hemphill & Cooper, 1984; Power, 1990; Power et al., 2008; Wiseman et al., 1993). Trout also feed on algivorous invertebrates, so the indirect effects of trout on algal biomass will depend on the strength of pathways of interaction leading from trout to algae (Power et al., 2008; Rodríguez-Lozano et al., 2015). Because trout have strong impacts on predatory invertebrates in this system (Cooper, 1988; Wiseman et al., 1993), we expected a four-level trophic cascade where trout reduced invertebrate predators resulting in increased algivorous invertebrate density and decreased algal biomass, overriding the three-level trophic cascade leading from trout to algivorous tadpoles to algae (Power, 1990; Power et al., 2008; Figure 1a). In addition and as a refinement, we expected that taxa that were less vulnerable to trout predation and preferred trout habitat
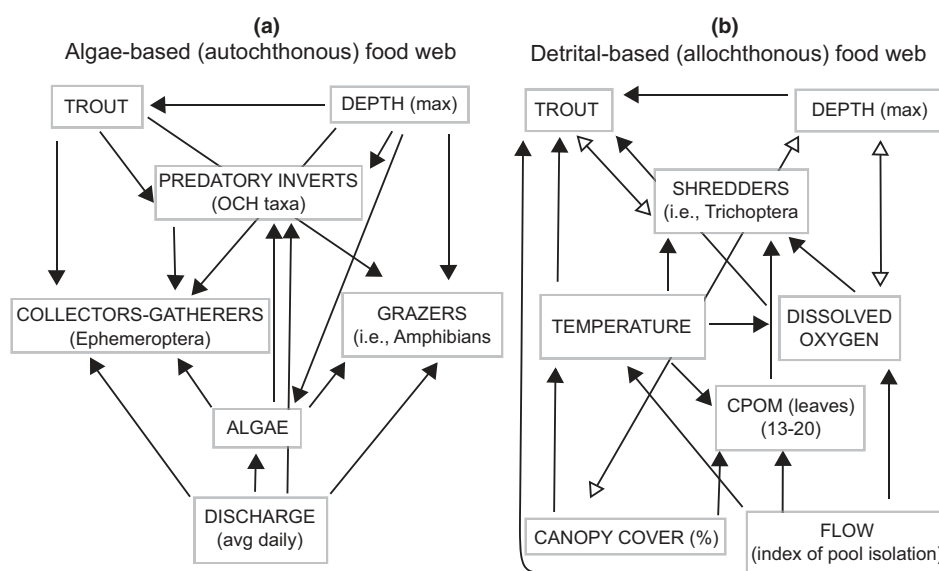

FIGURE 1 Conceptual diagram showing hypothesised relationships among components of the (a) autochthonous and (b) allochthonous food webs in study streams based on gut and stable isotope analyses and previous experimental studies and surveys (Cooper, 1984a, 1988; Cooper et al., 2015; Klose et al., 2015; Page et al., 2017). Arrows point from driver to response variables and double-headed arrows represent associations between variables. Although we have found a strong relationship between canopy cover and algal biomass in past studies (Cooper et al., 2015, 2021), those studies included sites where the canopy cover was reduced by riparian fire, whereas only shaded streams with intact riparian vegetation were examined in this study (canopy cover range: 65%–97%, mean = 89%).

conditions would be more abundant in trout than troutless streams (sensitive mayfly, caddisfly, and snail taxa with small–medium body sizes and short life cycles; Figure 1b [Hemphill & Cooper, 1984]). We expected that invertebrate assemblages in trout pools would quickly (1–2 years) shift to the community configuration found in troutless pools where trout were eliminated by wildfire or drought (Wiseman et al., 1993).

2 | METHODS

2.1 | Study sites

The Santa Ynez Mountains of southern Santa Barbara County, California, U.S.A., rise steeply from the Pacific Ocean to peaks exceeding 1400 m. 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 to March and dry and warm from April to 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 (c. 0–0.005 m³/s) in late summer and autumn to >2.6–17 m³/s during winter floods, depending on the stream. Higher flood discharge values have been recorded after wildfires (Cooper et al., 2015). The dominant riparian trees are California sycamore (*Platanus racemosa*), black cottonwood (*Populus trichocarpa*), and white alder (*Alnus rhombifolia*), with understory shrubs or vines such as willow (*Salix* sp.), toyon (*Heteromeles arbutifolia*), Pacific poison oak (*Toxicodendron diversilobum*), and blackberry (*Ribes* spp.) (McMahon et al., 2023). Upland areas are dominated by mixed and *Ceanothus* chaparral, with coastal sage scrub and grasslands at lower elevations (Lentz, 2013). Oak–bay laurel woodlands cover many moist hillslopes within canyons outside the riparian zone, and frequently grade into the riparian zone, particularly at higher elevations (McMahon et al., 2023).

Our study sites were located in the south-facing foothills and uplands of the Santa Ynez Mountains, generally above any agricultural, residential, or urban areas (Cooper et al., 2015; Klose et al., 2015; Table S1). Our streams are dominated by step-pools, forced pools, or a combination of these types (maximum depths = 0.3–1.6 m), connected in the dry season by narrow shallow riffles or waterfalls. Step-pools form in steep terrain where stream channels contain large geological elements (cobbles, boulders, bedrock) that form steps over which water plunges, creating downstream pools, whereas forced pools occur where flows converge between boulders or bedrock outcrops (Keller et al., 2015; Montgomery & Buffington, 1997). During drought and in the summer–fall, streams often are reduced to a series of semi-isolated or isolated pools or, at the extreme, dry completely. These streams, however, contain water for some portion of the wet season after rains. Drainage areas of our stream study sites ranged from 1.2 to 16.9 km², elevations from 65 to 476 m, and gradients from 2.5%

to 13.3%. Water in streams draining unburned catchments has slightly alkaline pH (6.9–8.4), high conductivity (540–970 μS/cm), and generally low nutrient concentrations ($NO_3^- $-N = 0.1–24.1 μM, PO_4^{-3}-P = 0.15–1.2 μM). Stream substrata were initially dominated by gravel, cobble, boulders, and bedrock, although sand became prominent at sites affected by the Jesusita Fire. Water temperatures ranged from 8 to 22°C, depending on the season, at sites unaffected by fire.

2.2 | The southern California steelhead trout

The only fish species found in the foothill and montane reaches of our study streams is native *O. mykiss*, which is near its southern range limits in this study region (Dressler et al., 2023). Although anadromous adult steelhead have been observed in the lower reaches of some of our study streams (Dagit et al., 2020), we believe that most *O. mykiss* in our study reaches are resident trout because the anadromous form is extremely rare in southern California (Dagit et al., 2020), barriers (dams, railroad and road crossings, bridge footings, culverts, or concrete channels) impede adult steelhead access to our montane and foothill study reaches, adult steelhead have almost never been observed recently in our study reaches, and the size, morphology, behaviour, and colour patterns of the observed fish are consonant with a resident trout classification (Moyle, 2002; Quinn, 2018). In our study reaches, trout may re-distribute themselves among pools during the wet season when water levels are high; however, most trout are trapped in home pools during the summer when flows between pools are very low or non-existent (Cooper, 1984b; Wiseman et al., 1993). Trout population sizes in our streams are highly variable through both space and time, and juvenile recruitment is sporadic (as in Bell et al., 2011; Dagit et al., 2017). The trout population in a 1.2-km reach of one of our study streams (Rattlesnake Creek) in the summers of 1982 and 1988 was composed of 0% and 11% young-of-the year (<10 cm total length), respectively, with mean trout total length being 19.7 cm (range = 10–32 cm) and 15.7 cm (range = 2–36 cm) and densities in trout pools averaging 0.1/m² and 0.23/m². Time budget analyses indicate that the majority of trout in our pools act as cruising predators in the dry season and primarily engulf prey in the surface film or on the bottom; however, a few are ambush predators that lurk near pool inlets (Cooper, 1984b; Harvey & Railsback, 2014; Rossi et al., 2021).

2.3 | Stream sampling design

We monitored 25 stream reaches once annually in summer (June–July) from 2009 to 2020, except in 2019. We also sampled stream reaches in spring (March) 2009. The number of sites sampled each time varied because some sites dried and others were added throughout the study period (Table S1). Some of our study reaches occurred in basins that were burned by wildfires (Table S1; Figure 2). We classified streams depending on the presence or absence of trout
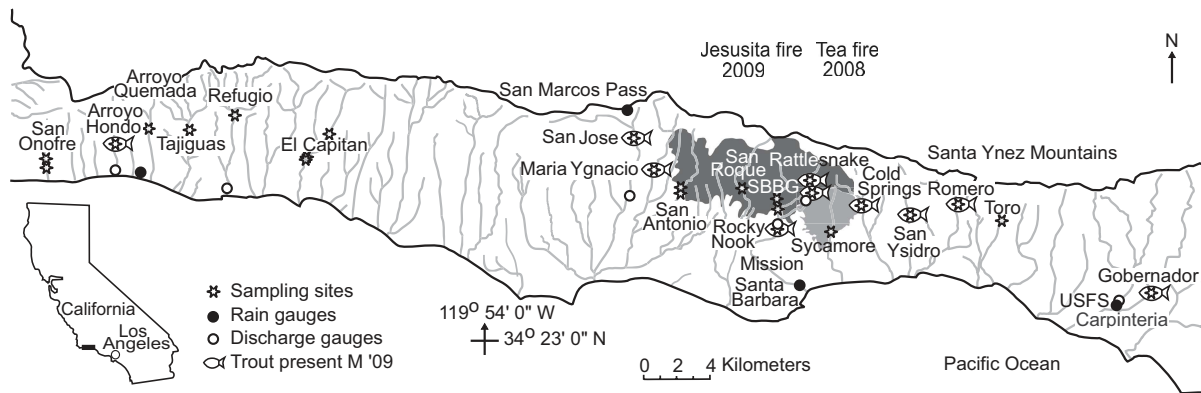
FIGURE 2 Map of the study area showing the locations of sampling sites, and rain and discharge gauges. Sites showing a fish symbol are those containing trout at the beginning of the study in spring 2009. Shaded areas show the extent of the 2008 Tea Fire and 2009 Jesusita Fire. The inset shows the location of the study area in California, U.S.A. (black bar).

in each reach in each sampling year and depending on whether a stream was exposed to wildfire disturbance. Streams drained either unburned catchments or catchments burned by wildfire but where riparian vegetation remained intact. The number of study reaches containing trout varied among years ($n = 1$–9 trout reaches), as trout were lost ($n = 8$) or regained ($n = 1$), but after a reach was affected by wildfire, it was classified as a burned riparian vegetation intact reach for the remainder of the study period. We compared environmental conditions in unburned reaches where trout were present versus absent to determine the factors driving trout distributions. To distinguish the assemblage effects of trout loss from changes in other physical, chemical, and biological variables owing to disturbance, we first compared invertebrate assemblage, trait, taxonomic, and food web structure in unburned reaches containing and lacking trout to examine trout influences on community and food web structure. Using these results as a baseline, we then followed changes in invertebrate assemblage structure in stream reaches where trout were lost owing to post-fire floods or drought compared to assemblage structure in unburned trout and troutless streams.

The major wildfire affecting our study sites containing trout was the Jesusita Fire, which burned 3,534 ha from 5 to 18 May 2009 (Cooper et al., 2015; McMahon et al., 2023), which coincidentally occurred between our March and June 2009 sampling times. The Jesusita Fire burned approximately 20%–73% of the areas draining to our sampling reaches, but the riparian vegetation at these sites remained intact. Four out of the nine stream reaches that contained trout in 2009, lost their trout by summer 2010 owing to scouring flows that occurred in the winter season following the Jesusita Fire. Although our study region was affected by subsequent wildfires, none of our study sites that contained trout following post-Jesusita fire floods were affected by later wildfires. The Jesusita Fire occurred during the 1 October 2008 to 30 September 2009 water year (2009 WY), a year at the cusp of dry to average discharge conditions (USGS WaterWatch). Subsequently, water years 2011 and 2017 were classified as wet years, 2012–2016 were the years of an unprecedented drought (2018 was also dry), and 2010, 2019, and 2020 were classified as average years (USGS WaterWatch definitions). Trout also

disappeared from four of our study reaches during the 2012–2016 drought. In analyses, we first compared environmental conditions, and food web and invertebrate assemblage structure, in trout versus troutless reaches that were unaffected by wildfire up to the time of sampling, so that baseline differences between trout and troutless reaches were not obscured by the confounding effects of wildfire (2009–2020 data). Because the Jesusita Fire occurred in May 2009 and the prolonged drought occurred from 2012 to 2016, we then separately examined invertebrate assemblage changes after the loss of trout owing to fire (2009–2014 data) or drought (2012–2020 data) compared to our baseline results that characterised differences between trout and troutless reaches in unburned streams.

2.4 | Hydrological analysis

To develop hydrographs for each of our study streams, we used or calculated daily and annual average flow (discharge, m³/s) data from three U.S. Geological Survey (USGS) gauging stations (1120500, 11119745, and 11119500) and three Santa Barbara Channel Long-Term Ecological Research (LTER) gauging stations (Arroyo Hondo, Refugio, Rattlesnake [Melack, 2019a, 2019b, 2019c]) that encompassed most of the study area. We matched each of our sampling reaches to a gauging station occurring in the same or a nearby basin with a similar drainage area. Although the USGS discharge data were continuous, there were gaps in the hydrologic record for the LTER stations. Short LTER data gaps when no precipitation occurred were filled in via interpolation, whereas long data gaps or gaps when precipitation occurred were filled in using regression equations relating discharges at the targeted station to those at a nearby station with a continuous record. For each water year (WY, 1 October of one year to 30 September of the next, designated year) we calculated the average and maximum daily discharge from the beginning of the WY to the time of sampling, as well as the discharge on the day of sampling. Because our three discharge metrics (average and maximum WY discharge, sampling day discharge) were intercorrelated (r-values $= +0.77$ to

+0.96, all p-values < 0.0001), we used average WY discharge as our discharge measure in most analyses, because it captured hydrological conditions in the water year up to and including the time of sampling.

To develop indices of drying occurrence, we first noted if a study reach was dry at the time of sampling (deemed a dry June) or had dried in the previous year. We then related the average maximum depth of the five pools in each study reach at each time to concurrent discharge at a centrally-located USGS gauging station (San Jose Creek, # 11120500) with a continuous record. For each study reach, then, we examined the USGS discharge when that reach was dry ($Q=0$), then used this discharge threshold for each study reach and the previous year's USGS hydrographic record to determine the duration of dry conditions, as well as the amount of time since dry conditions ceased and flows resumed, over the previous year. All of our study reaches had surface flow after winter rains even during the driest years. Our three drying metrics (number of dry Junes, duration of drying in the previous year, and amount of time since dry) were intercorrelated (dry Junes vs. preceding year dry duration: $r=+0.68$, $p<0.0001$; preceding year dry duration vs. time since dry: $r=-0.40$, $p=0.0008$; dry Junes vs. time since dry: $r=-0.29$, $p=0.017$), but because the time since dry metric only pertained to sites that dried in the previous year, we used the duration of drying in the previous year (0 for sites with continuous flow) as our index of drying in most analyses. Beginning in 2013, we also scored the flows into each of our study pools on a nine-point scale, with this flow index (FI) representing isolated (FI = 1–3), semi-isolated (FI = 4–6, a trickle into each pool), and well-connected pools with substantial inflow (FI = 7–9).

2.5 | Stream field methods and measurements

We measured sediment and maximum water depths using a meter stick and per cent canopy cover in four directions (upstream, downstream, facing each bank) with a Model-A spherical densiometer (Forest Densiometers, Barlesville, OK, U.S.A.) in each of five pools in each study reach at each sampling time. We measured water temperature, conductivity, and dissolved oxygen (DO) concentration with a YSI model 55 DO/conductivity meter (Yellow Springs Instruments, Yellow Springs, OH, U.S.A.) at the upstream end of each reach from 2009 to 2013, then in each of the five pools sampled in each reach on each date from 2014 to 2020. Beginning in 2013, we also measured the wet mass of macroalgae and CPOM (leaves retained by 1-mm sieve) in each pool, by spinning leaves or macroalgae collected in standard sweep samples (see below) in a lettuce spinner, then weighing these materials on a balance.

We sampled large epibenthic and water column invertebrates and amphibians in stream pools in March 2009 and from June–July of each year from 2009 to 2020, with the exception of 2019 (Table S1). We took six standard sweeps with a D net (1-mm mesh, 30-cm lower edge) from each of five pools from each study reach at each sampling time (30 standard sweeps per reach per time). All standard sweeps through the study period were taken by the senior author. Invertebrates and amphibians were identified and counted in the field, except for taxa that could not be identified to genus, which were preserved in 70% ethanol and returned to the laboratory for identification under a dissecting microscope using standard keys (Merritt et al., 2008; Thorp & Covich, 1991). Beginning in 2013, we added five taxa, including three molluscs (*Pisidium*, *Ferrissia*, *Pyrgulopsis*) and two mayflies (*Caenis*, *Tricorythodes*), to the list of taxa we counted, taxa that we originally thought were too small or interstitial to be effectively sampled using D-net standard sweeps, but were commonly observed in samples during the drought. Standard sweep sampling was more effective than Surber sampling at obtaining adequate numbers for analyses of large, rare, and/or mobile epibenthic and water column taxa (e.g., tadpoles, large predatory insects, mosquito larvae), with strong positive correlations between the numbers of large (>1 mm) invertebrates in major functional groups collected by standard sweep versus Surber sampling (Cooper et al., 2015). We also concentrated on pool epibenthic, nektonic, and neustonic taxa because our and previous research has shown that trout have much greater effects on the abundances and size structure of epibenthic and nektonic prey than on the abundances or size structure of hidden, interstitial prey (Bechara et al., 1993; Power, 1992b; Rosenfeld, 2000).

We visually scanned study reaches for trout from vantage points as we proceeded upstream and, where the presence of trout was uncertain, additionally observed individual pools for at least 15 min to ascertain the presence or absence of trout. Our observations of trout distributions were corroborated by over 40 years of observations in our study streams, by conversations with U.S. National Marine Fisheries Service and California Department of Fish and Wildlife (CDFW) personnel, by National Marine Fisheries Service and CDFW records, and by streamside and snorkelling surveys of a subset of study reaches by independent observers (Brinkman, 2007; Ecology Consultants, 2015, 2019) (M. Stoecker [Stoecker Ecological], M. Gomez and E. Brown [South Coast Habitat Restoration], M. Capelli [NOAA National Marine Fisheries Service], Dana McCanne and K. Evans [California Department of Fish and Wildlife], personal communications).

2.6 | Data analysis

2.6.1 | Wildfire, drought, and trout habitat and loss

By combining our own observations with data, reports, and information from consultants and regulatory agencies, we were able to discern when trout were lost from study reaches owing to disturbances (post-fire floods, drought). To evaluate relationships between environmental conditions and trout presence (vs. absence), we used a generalised linear logistic regression approach on data from reaches that were not affected by past fire at the time of sampling. Although we collected data on a variety of variables that may influence trout presence (e.g., average canopy cover, pool depth or size, discharge, temperature, DO concentration, conductivity), some key variables

displayed high collinearity (Table S2). Because measured temperatures did not exceed tolerance limits for juvenile and adult trout (<25°C; Myrick & Cech Jr., 2001), but oxygen fell below lethal levels (<2–3 mg/L; Carter, 2005) during the drought, we focused on DO levels and pool depth, as an index of pool size and refuge volume (McHugh et al., 2015), using a generalised linear mixed effects regression approach. Because we collected repeated observations of the same reaches through time, we included reach and year as random intercept effects. We assumed errors followed a binomial distribution, and tested for multicollinearity by estimating the variance inflation factor (Marcoulides & Raykov, 2019), using the *performance* package in R (Lüdecke et al., 2021). We assumed that collinearity would not significantly bias our inferences if the variance inflation factor was <5.

2.6.2 | Invertebrate assemblages and food web structure with versus without trout

To examine relationships between invertebrate assemblage structure and trout categories (trout present vs. absent), we used a matrix of the relative abundances of all invertebrate taxa by all sites and times. We calculated multivariate distances between all pairs of sample sites–times using the Sørensen distance metric. We used non-metric multidimensional scaling (NMS) to display the similarity of invertebrate community structure across sites–times grouped by different trout (presence vs. absence) categories. We examined correlations between NMS axes versus the values of environmental variables (logit proportionate canopy cover, log_{10} conductivity and algal and CPOM mass, rest untransformed) and the relative abundances of common invertebrate taxa (i.e., those occurring in ≥25% of samples; threshold Pearson's r's = |0.30–0.34|, $p < 0.001$, $n = 79$–93 depending on the data subset analysed). These analyses were complemented by the multi-response permutation procedure (MRPP), which tested for multivariate differences in macroinvertebrate community structure between categories. We conducted indicator species analysis (ISA) to determine which invertebrate species were associated with sites and times assigned to different trout categories (Dufrêne & Legendre, 1997). We used the Tichý and Chytrý (2006) φ coefficient to determine the indicator value of each species for each category and randomisation (Monte Carlo) tests to determine the statistical significance of maximum indicator values. All multivariate analyses were performed with PC-ORD software (versions 6 and 7; MjM Software, Gleneden Beach, OR, U.S.A.).

We determined associations between trout presence (vs. absence) and the abundances of invertebrate taxonomic and trait groups and of larval amphibians. We assigned invertebrate taxa to different trait categories for pollution and thermal tolerance, functional feeding, body size, development rate, voltinism, depositional-erosional, respiration, drift, and aerial dispersal (Barbour et al., 1999; Herbst et al., 2018; Poff et al., 2006; Vieira et al., 2006) with erosional versus depositional designations being refined based on samples taken from streams in Santa Barbara County, California, U.S.A.

(see Data Files archived in Dryad: https://doi.org/10.5061/dryad.h70rxwdqq). We chose these traits because they probably determine invertebrate responses to the direct and indirect effects of predators and disturbances (Herbst et al., 2019; Jager et al., 2021; Ware, 1972, 1973), including prey vulnerability to trout predation (e.g., body size, respiratory traits, pool affinities), trout and prey tolerances to environmental conditions (thermal and pollution indices), invertebrate roles in food webs (functional feeding groups), invertebrate recolonisation capabilities after disturbance (drift and aerial dispersal), and associated invertebrate life history characteristics (voltinism, development rates).

To test for statistical differences in the abundances of taxonomic and trait groups between trout and troutless reaches that were unaffected by wildfire, we used a mixed effects modelling approach. We hypothesised that response variables would be related to trout presence (vs. absence) after accounting for environmental variables related to stream discharge and drying. As a consequence, we included a categorical predictor variable for trout presence (vs. absence) that interacted with a categorical predictor for our taxonomic or trait group classifications. We also included log_{10} average daily discharge and the duration the stream was dry in the previous water year as fixed predictors in all models. We modelled the abundances of amphibians and of invertebrates in taxonomic and trait categories, including reach and year as random intercept effects, accounting for the structure of the data. We fit mixed effects models using the glmmTMB (Brooks et al., 2017) package in R, assuming that residual errors followed negative binomial distributions with a log-link function. Because we were interested specifically in the difference in amphibian and invertebrate abundance between stream reaches with and without trout, we estimated the marginal mean contrasts for each of our invertebrate categories in reaches with and without trout using the *emmeans* package in R (Lenth, 2023). Because our models employed a log-link function, we report the log ratio on our response scales for the abundance without trout divided by the abundance with trout. We corrected for multiple contrasts by estimating Bonferroni adjusted p-values (significance = $p \leq 0.05$).

We used a similar procedure to determine associations between trout presence (vs. absence) and aggregate stream community metrics, including total invertebrate rarified richness, evenness, and abundance. Rarefied richness was calculated for 80 individuals using the R package vegan. For the whole invertebrate assemblage we also calculated biotic (tolerance) and thermal indices for each site–time from the summed products of tolerance values and thermal associations for taxa (CD75 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 the cumulative distribution 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 for the community (in degrees Celsius). We fit separate mixed effects models to each aggregate metric, where we assumed gaussian

or Poisson distributed errors depending on if the response consisted of continuous (−Inf, Inf) or positive integers.

For ancillary, simple comparisons of response variable values among categories or with continuous predictor variables, we used standard statistical analyses, such as paired *t*-tests, ANOVAs, Tukey's HSD tests, and least squares linear regressions (specified in Section 3).

Based on previous studies in our streams (Cooper et al., 2015; Page et al., 2017), we delineated two basic food webs commonly found in most stream ecosystems: an algal-based food web fuelled by in-stream algal production and a detritus-based food web supported by allochthonous leaf litter inputs (Figure 1a,b). In this system, grazers and collector–gatherers feed primarily on algae and are eaten, in turn, by invertebrate predators (primarily OCH taxa), with trout consuming both algivores and invertebrate predators. By contrast, shredders (primarily cased caddisfly larvae) consume almost entirely leaf litter and are relatively invulnerable or unresponsive to predators (Alvarez & Peckarsky, 2005; Cooper, 1984a; McIntosh, 2022; Page et al., 2017; Power et al., 2008). Exploratory structural equation modelling revealed no connection between the biological components of our algal and detrital-based food webs. To parse the web of direct and indirect interactions among environmental and food web components in our algal and detrital-based food webs, we developed piecewise structural equation models (SEMs) based on our a priori knowledge regarding the directionality of interactions (Cooper et al., 2015; Lefcheck, 2016; Page et al., 2017). Specifically, we hypothesised relationships between exogenous environmental predictors and endogenous biological variables (e.g., trout presence, invertebrate functional feeding groups; Figure 1a,b). Our goal was to test for differences in top-down versus bottom-up control in stream communities and to delineate pathways of interaction among abiotic and biological variables. Therefore, we constructed three different hypothetical path diagrams for biological components of the algae-based food web, including purely top down, purely bottom up, and mixed top-down, bottom-up models, that differed in the directionality of links leading from trout to algal resources. We then fit SEMs for each hypothesis, and assessed global goodness-of-fit using Fisher's *C* and the chi-squared statistics. For each model we refined the paths based on tests of directed separation. We used a similar approach to fit and refine our a priori hypotheses of interaction pathways in the detrital-based food web. Because macroalgal and CPOM (leaf litter) biomass were only measured from 2013 to 2020, structural equation models (SEMs) for algae and detritus-based food webs were evaluated for this period.

2.6.3 | Invertebrate assemblage changes after trout loss

Our analyses of data from streams unaffected by wildfire allowed us to characterise differences in invertebrate community and food web structure between trout and troutless reaches. Our characterisation of invertebrate assemblage configurations in trout and troutless reaches, then, provided a baseline for comparison to reaches that lost trout owing to post-fire scouring flows and drought conditions. Because fire and drought disturbances occurred at two different times, with the Jesusita Fire occurring in 2009 and the drought occurring from 2012 to 2016, we examined invertebrate assemblage responses to trout loss owing to each type of disturbance, separately, by using different temporal subsets of the data (pre- and post-fire: 2009–2014; during and after drought: 2012–2020). Further, previous analyses showed that key functional feeding groups (primarily predatory invertebrates) had increased to abundances found in troutless reaches within a few years after trout were lost owing to post-fire floods (Cooper et al., 2015). As a consequence, we performed multivariate analyses (NMS, MRPP, ISA), as well as univariate analyses on the abundance of OCH taxa, on 2009–2014 data from reaches that lost their trout after the fire and, separately, on 2012–2020 data from reaches that lost their trout during the drought, using concurrent data from trout and troutless reaches in unburned catchments for comparisons to data from reaches that lost trout (same general statistical methods as described above). We used OCH abundance as our univariate index of invertebrate responses to trout loss because our analyses of differences in invertebrate assemblages between trout and troutless reaches unaffected by fire indicated that OCH abundance showed the most sensitive responses to trout (e.g., the results of this study comparing the abundances of invertebrate taxonomic or trait groups in unperturbed trout versus troutless reaches; Cooper, 1988; Wiseman et al., 1993; also see Power, 1990; Power et al., 2008).

3 | RESULTS

3.1 | Wildfire, drought, and trout habitat and loss

Trout were associated with deep pools (>0.75 m) and high DO levels (>6 mg/L) in streams unaffected by wildfire (Figure 3). Although trout were present in nine of our study reaches at the beginning of our study period, trout were lost from four of these reaches during winter floods after the May 2009 Jesusita Fire. Four of the five study reaches containing trout in 2012 lost their trout during the 2012–2016 drought, with one reach drying completely and two of the other three containing isolated to semi-isolated pools in 2015 and 2016 with low DO levels (<2 mg/L). One of the reaches that lost trout during the drought regained trout during high flows in 2017.

3.2 | Invertebrate assemblages and food web structure with versus without trout

Invertebrate assemblage structure differed between trout and troutless stream reaches (MRPP, $A = 0.05$, $p < 0.001$). Invertebrate assemblages in trout and troutless pools showed parallel temporal trajectories as indicated by NMS axis 1 scores, which accounted for 44% of the multivariate variation and proceeded from the
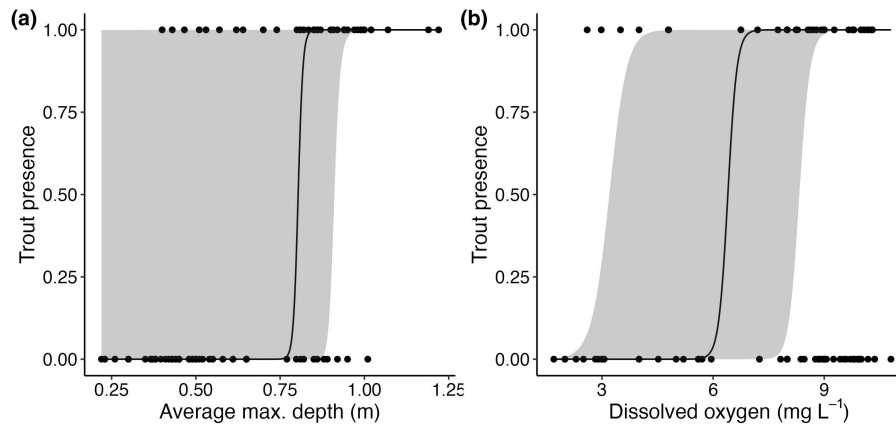
FIGURE 3 Effects of average maximum (max.) pool depth (a) and dissolved oxygen concentration (b) on the probability of trout presence. Points are the observed trout presence at each reach in each year. Lines and surrounding shading are the mean ± 95% confidence intervals for a generalised linear mixed effects model predicting trout presence. In (a) relationships between trout presence and depth are shown for average dissolved oxygen concentrations over the entire data set. In (b) relationships between trout presence and dissolved oxygen concentrations are shown with average pool depth set at the upper third quartile of pool depth across the data set.
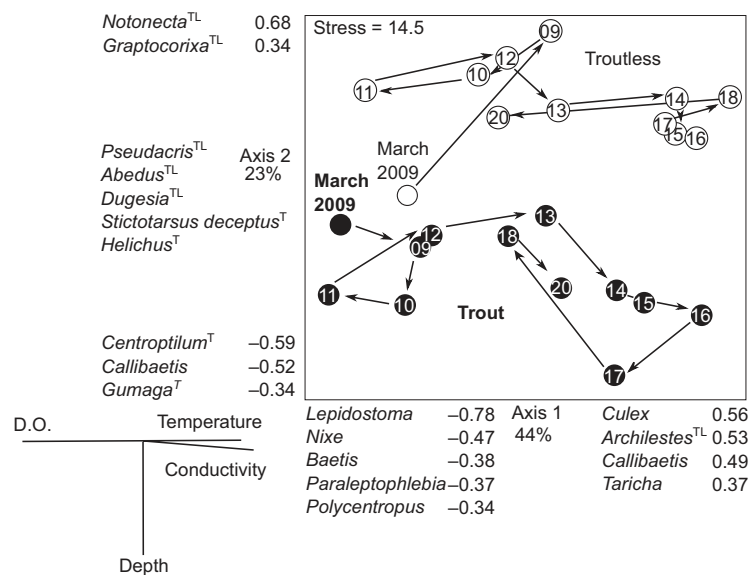

FIGURE 4 Non-metric multidimensional scaling (NMS) ordination based on the relative abundances of benthic macroinvertebrate taxa at trout versus troutless stream reaches in unburned drainage basins sampled in March 2009, and in June/July from 2009 to 2018 and in 2020. Sites are coded to represent reaches that contained (black circles) or lacked (open circles) trout. Arrows connect NMS centroids for trout versus troutless reaches between consecutive sampling times and numbers in symbols indicate years. The stress associated with a three-axis NMS solution is shown in the upper left corner, and the % variation in the multivariate data set attributable to each NMS axis is shown next to each axis label. The correlation coefficients (Pearson's r) of common taxa (occurring in ≥¼ of samples) related ($p < 0.001$) to each axis are shown in the margins at the edges of each axis. The correlation vectors for environmental variables associated with NMS axes ($p < 0.001$) are shown in the lower left-hand corner of the plot. Indicator taxa for troutless (TL) versus trout (T) reaches are indicated by superscripts and taxa listed to the left of the Axis 2 label are indicator taxa additional to those associated with the first two NMS axes.

pre-drought years with high DO concentrations on the left, associated with high relative abundances of larvae of the caddisfly *Lepidostoma* and the mayflies *Nixe*, *Baetis*, and *Paraleptophlebia*, to later drought and post-drought years on the right, which were associated with high temperatures and conductivities, and higher relative abundances of larvae of a mosquito (*Culex*), the damselfly *Archilestes*, the mayfly *Callibaetis*, and the California newt (*Taricha torosa*; Figure 4). The second axis of the NMS ordination, which

accounted for 23% of the multivariate variation in invertebrate assemblage structure, clearly separated invertebrate assemblage structure in trout versus troutless streams with deeper trout pools containing high relative abundances of the mayflies *Centroptilum* and *Callibaetis*, and the caddisfly *Gumaga*, and troutless pools containing high relative abundances of Hemiptera genera (*Notonecta hoffmanni*, *Graptocorixa* spp.; Figure 4). Indicator taxa ($p < 0.05$) for trout reaches included *Centroptilum*, *Gumaga*, and the beetles,

Stictotarsus deceptus and *Helichus*, whereas indicator taxa for troutless reaches included *Notonecta*, *Graptocorixa*, the damselfly *Archilestes*, hylid tadpoles (*Pseudacris* spp.), another hemipteran (*Abedus indentatus*), and flatworms (*Dugesia*). Invertebrate assemblages appeared to return to pre-drought configurations sooner in trout (2018) than troutless (2020) pools (Figure 4). Analyses of the additional environmental variables and taxa monitored from 2013 to 2020 corroborated these results, but also indicated that the mayflies *Caenis* and *Tricorythodes* were associated with trout pools, that the fingernail clam *Pisidium* was associated with shaded, troutless pools particularly during dry periods, and that algal biomass was strongly negatively related to canopy cover and positively related to the relative abundances of the mayfly *Callibaetis* (NMS and ISA analyses, Figure S1).

These multivariate patterns were corroborated by univariate analyses, which showed that OCH and amphibian taxa, as well as invertebrate predators with associated large body, strong flight, and atmospheric breather traits, were more abundant in troutless than trout pools (Figure 5b, Figure S2). By contrast, medium-sized caddisfly shredder and mayfly collector–gatherer taxa indicative of erosional (riffle) habitats and with non-seasonal life cycles were more abundant in trout than troutless reaches (Figure 5b, Figure S2). Although total invertebrate density, rarefied richness, evenness, and the invertebrate thermal index did not differ between trout and troutless reaches, the invertebrate biotic (tolerance) index was lower in trout than troutless reaches, indicating that trout pools had higher water or habitat quality than troutless pools (Figure 5a), reinforced by our analyses showing that trout were associated with high DO levels (Figure 3). We found that trout impacts on OCH taxa varied over time (Figure 6a), with negative trout impacts on OCH taxa increasing at higher discharges (Figure 6b). By contrast, there was a tendency for trout associations with collectors–gatherers to be neutral or positive (Figure 6a) and to decline with increasing discharge.

As predicted for the autochthonous food web, trout were associated with deep pools and were strongly, negatively related to the densities of predatory OCH taxa, which, in turn, were negatively related to collector–gatherer (primarily baetid mayfly) densities (Figure 7a). The best fit SEM also showed that there were positive relationships between macroalgal biomass and the densities of grazers (primarily hylid tadpoles and snails) and collector–gatherers (primarily baetid mayflies). In addition, densities of collector–gatherers were positively, and densities of grazers were negatively, related to maximum depth and average discharge.

SEM for the allochthonous food web suggested that shredder (primarily the caddis larvae *Lepidostoma* and *Gumaga*) densities were primarily driven by bottom-up interactions and abiotic factors. Canopy cover was positively and flow continuity negatively related to CPOM levels, which, in turn, were positively related to shredder densities, but there appeared to be no direct negative interactions between trout and shredders (Figure 7b). Further, canopy cover and flow continuity were negatively related to temperature, and temperature, in turn, was negatively related
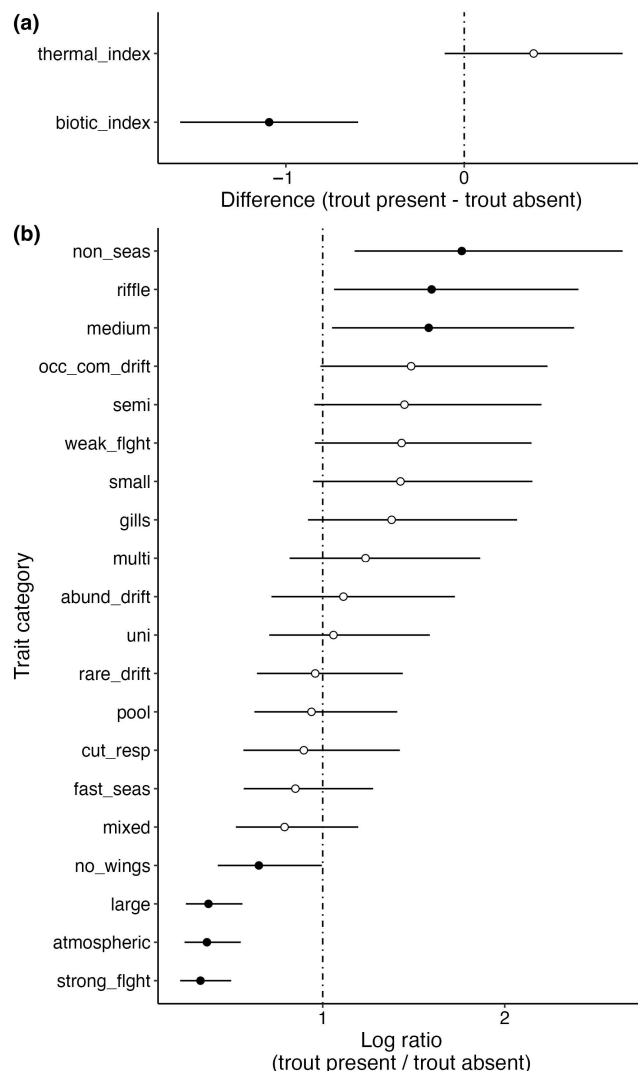

FIGURE 5 Relationships between trout presence and general invertebrate indices (a) and the abundances of invertebrates with different traits (b). Points in a represent the mean±95% confidence interval of the difference in indices when trout were present versus absent. Means (± confidence intervals) in (b) are for log response ratios (ln trout/troutless) derived from mixed effects modelling. Points to the left of the vertical dashed line indicate lower abundance in the presence of trout, whereas points to the right indicate higher abundance in the presence of trout. Points are filled if the relationship is statistically significant at *p* < 0.05, after applying Bonferroni corrections (see Section 2 for details). Code for traits: Body size: small (<9 mm), medium (9–16 mm), large (> 16 mm); Voltinism: semi = semivoltine, uni = univoltine, multi = multivoltine; Development: fast_seas = fast seasonal, non_seas = non-seasonal; Habitat: pool = depositional, mixed = both riffle and pool, riffle = erosional; Respiration: cut_resp = cutaneous, gills, atmospheric = atmospheric breather; Drift propensity: rare-drift, occ_com_drift = occasional to common in drift, abund_drift = abundant in drift; Flight: no wings, weak-flight, strong-flight.

to CPOM levels but positively related to shredder densities. DO levels were positively related to flow continuity (i.e., isolated pools had lower DO), and shredder densities were positively related
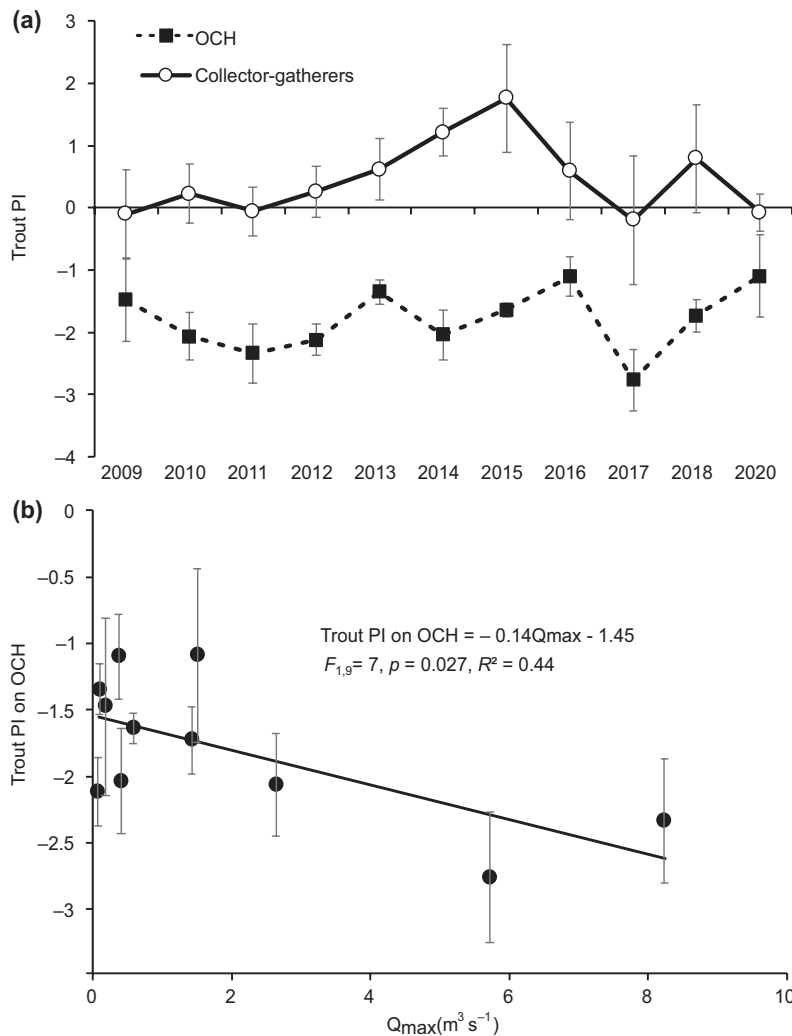
FIGURE 6 (a) Indices of trout impacts on Odonata, Coleoptera, Hemiptera (OCH) and collector–gatherer taxa (PI = ln [abundance in trout reaches/abundance in troutless reaches]) over sampling years. (b) Trout impacts on OCH taxa versus average maximum discharge in the preceding wet season. In both graphs, mean values (± 1 SD, Hedges et al., 1999) are shown. Regression line and equation, and associated statistics (F, p, and R^2 values) are shown for the bottom graph.

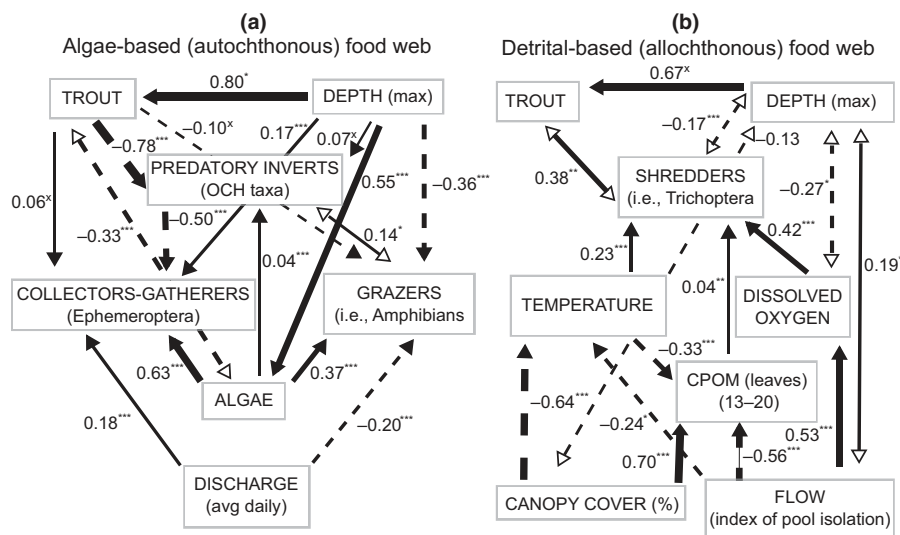In graph (b): Trout PI on OCH = $-0.14 Q_{max} - 1.45$, $F_{1,9} = 7$, $p = 0.027$, $R^2 = 0.44$

FIGURE 7 Piecewise structural equation models representing interaction pathways in the algal-based (a) and detrital-based (b) food webs. Non-significant paths at $p > 0.10$ are not displayed to improve visualisation. The path thickness reflects the magnitude of the interaction. Dashed lines reflect negative interactions, solid lines reflect positive interactions, and double headed arrows denote associations between components without a driver-response interpretation. Individual paths in each diagram are based on generalised linear mixed effects models that account for a random intercept effect of reach and year. Statistical code for coefficients: $^x p < 0.10$, $^* p < 0.05$, $^{**} p < 0.01$, $^{***} p < 0.001$.

to DO levels (Figure 7b). Shredder densities covaried with trout presence.

3.3 | Invertebrate assemblage changes after trout loss

Invertebrate assemblage structure changed within a year or two after trout were lost (Figure 8a,b). Trout persisted through the summer and autumn of 2009 in four reaches that drained basins

that burned during the May 2009 Jesusita Fire, but whose riparian vegetation remained intact. Trout were lost from these four reaches during the 2010 rainy season during floods. Pool invertebrate assemblages in these four study reaches were similar to those in other trout streams when they contained trout, but became similar to those in troutless streams by June 2010, after trout were extirpated by post-fire floods (Figure 8a). Similarly, invertebrate assemblages in the four reaches that lost trout during the 2012–2016 drought were similar to those in other trout reaches in 2012, as the drought was beginning, but became similar
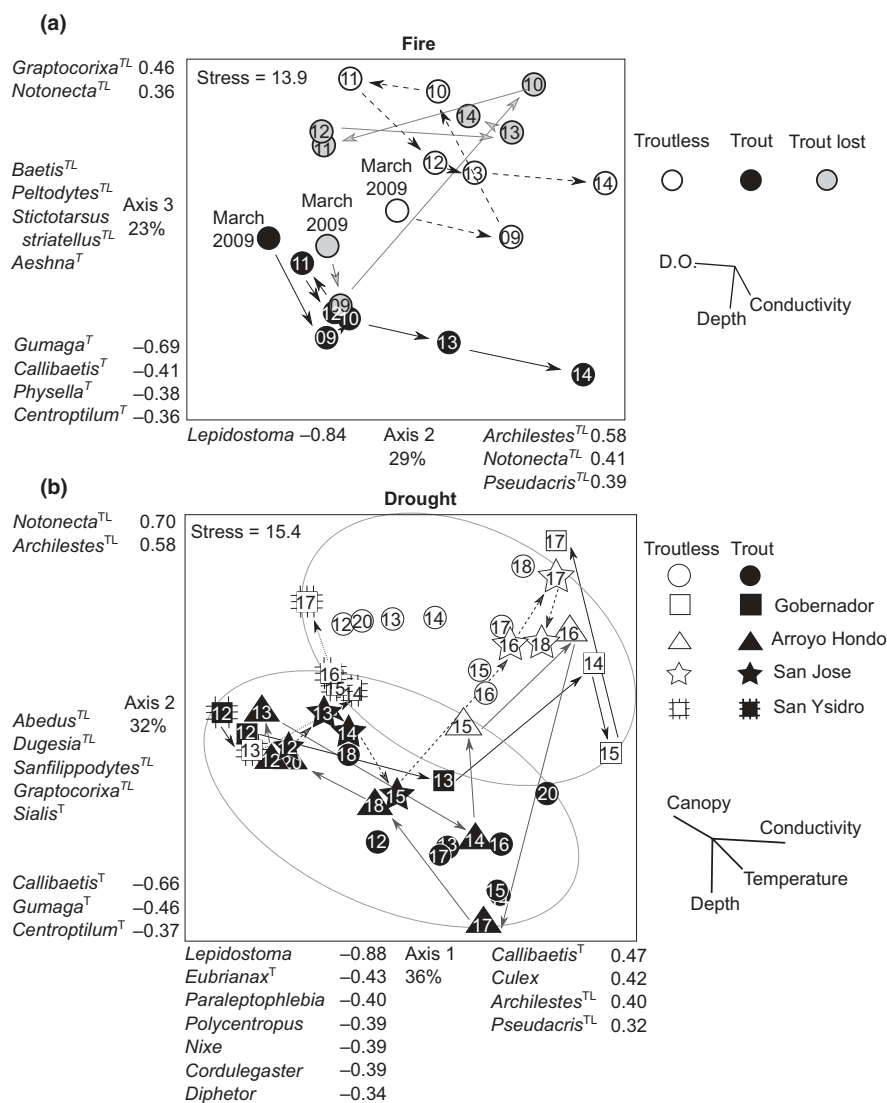

FIGURE 8 (a) Changes in invertebrate assemblages due to trout loss owing to post-fire floods. Biplot of non-metric multidimensional scaling (NMS) Axes 2 and 3 centroid scores over the 2009 through 2014 sampling years for unburned troutless and trout reaches and for reaches that lost their trout after post-fire scouring flows in winter 2010 (before 2010 sampling). Arrows connect NMS centroids for consecutive sampling times. (b) Changes in invertebrate assemblages due to trout loss owing to drought. Biplot of NMS Axes 1 and 2 scores over the 2012 through 2020 sampling years for reaches that remained troutless (troutless) or contained trout (trout) throughout this period (centroids with no connecting arrows) and for reaches in four streams (Gobernador, Arroyo Hondo, San Jose, San Ysidro) that lost trout during this period. Because these four reaches lost trout at different times during the 2012–16 drought, their trajectories are shown separately, with arrows connecting consecutive sampling times. The Arroyo Hondo reach contained trout up to 2014, lost trout in 2015 and 2016, then regained trout in 2017 and after. Times when reaches contained trout are denoted as black symbols, whereas times when reaches lacked trout are denoted as open symbols. Other designations as in Figure 3, except environmental factor vectors associated with NMS axes are shown to the right of biplots.

to those in troutless reaches after they lost their trout during the drought (Figure 8b).

We also examined how trout loss owing to drought affected the abundance of the most vulnerable group, predatory OCH taxa, and found that average OCH abundance increased to levels observed in troutless reaches in about 2 years after trout were lost to drought conditions, but that there was very high variation in OCH abundance across streams losing trout during the drought (Figure 9a). One stream reach, our Arroyo Hondo site, had lost its trout by 2015 and 2016 but trout recolonised this reach during the high flows of 2017. Invertebrate assemblages in the Arroyo Hondo reach resembled those in other troutless reaches in 2016, but changed to resemble those in another trout stream in 2017 and later (Figure 9b).

4 | DISCUSSION

4.1 | Wildfire, drought, and trout habitat and loss

At the beginning of our study, in 2009, steelhead trout were present in nine of 26 sampled reaches, but during the study, trout disappeared from four of these reaches during scouring flows after a wildfire and from an additional four reaches during the unprecedented 2012–2016 drought. Trout re-appeared in one of these study reaches (Arroyo Hondo) when flows returned in 2017, but then were extirpated during intense floods after a later fire, the 2021 Alisal Fire, that occurred after our study period (K. Evans, CDFW, S.

Cooper and S. Wiseman, personal observations). Trout re-appeared by the 2020s in a couple of the stream reaches where they were extirpated, but it is likely that they will not re-appear in many of our streams because these streams have been subjected to repeated fire, drought, debris flow, and flood disturbances with trout recolonisation often precluded by human-made barriers (National Marine Fisheries Service, 2012, 2016, 2023). Because climatic projections call for hotter and more prolonged dry conditions and intense winter rain storms in the future in this region (Feng et al., 2019), it is clear that native *O. mykiss* populations in southern California are hanging by a thread.

Nevertheless, native trout persist in this region, although at low population sizes. We found that trout were associated with deep pools and high DO levels. The association of trout with average maximum pool depth was not surprising, because this variable was an index of overall pool size, the extent of refuges from predation, perennial surface water, and water or habitat quality (as measured by the invertebrate biotic index) (Harvey & White, 2017; Lennox et al., 2019; Vander Vorste et al., 2020). Our results are concordant with other studies showing that large, deep pools constitute the major refuge for sensitive stream taxa, such as salmonids and vulnerable invertebrates, during drought (Cooper et al., 2021; Dagit et al., 2017; Elliott, 2000; Kaylor et al., 2019).

We also suspected that low DO levels played a role in the disappearance of trout from some of our study reaches during the drought, because trout disappeared from these reaches when pools became increasingly isolated and DO levels sometimes declined to lethal levels (<2–3 mg/L; this study, see also Dagit et al., 2017;
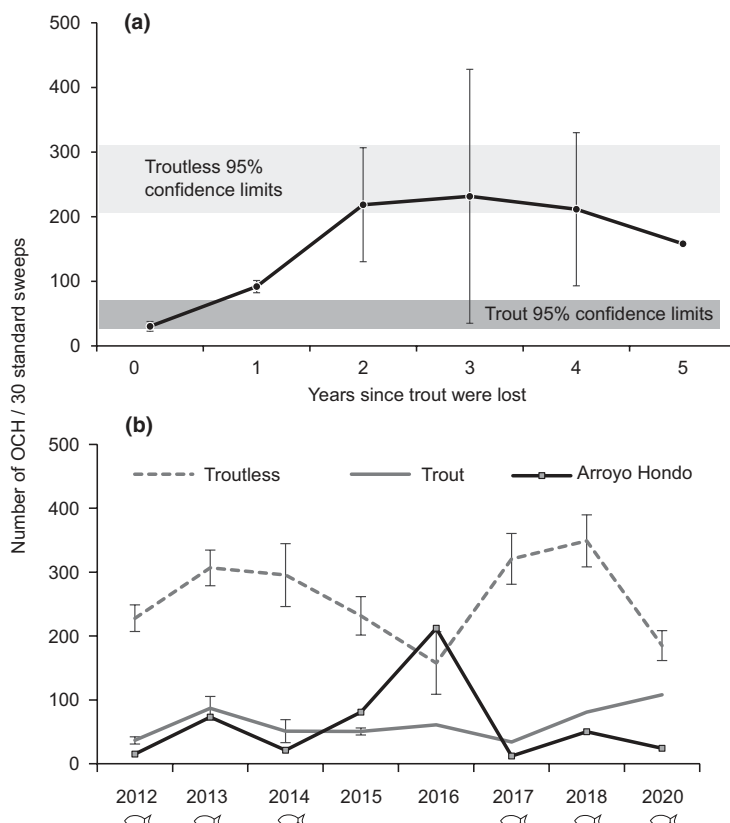

FIGURE 9 Abundance of Odonata, Coleoptera, Hemiptera (OCH) taxa (number per 30 standard sweeps; a) as a function of time since trout were lost during the drought (in years) and (b) in the Arroyo Hondo study reach compared to all other troutless and trout reaches from 2012 through 2020. Trout disappeared from the Arroyo Hondo reach in 2015 and 2016, but reappeared in 2017 and years thereafter. In (a), the 95% confidence limits for OCH abundance in unburned reaches containing trout and in troutless reaches where riparian vegetation remained intact (either because the basin was not burned or the basin was burned but riparian vegetation remained intact) throughout the 2012–20 period are shown, as well as the means ±1 SEM of abundances at sites (a) where trout were lost during the drought and (b) in trout and troutless stream reaches.

Elliott, 2000). Our analyses indicated that trout were associated with DO levels >6 mg/L, which are higher than the lethal limits for juvenile and adult trout, but are required for the development of earlier life history stages and associated with the physiological performance and growth of juveniles and adults (Carter, 2005). Plunges in stream DO concentrations and/or spikes in ash and sediment levels after wildfires have sometimes resulted in the drastic decline and even extirpation of local salmonid populations (Rust et al., 2019; Whitney et al., 2015).

Temperatures did not seem to limit the distribution of trout in our study, because maximum temperatures in the summer were within the tolerance limits for juvenile and adult *O. mykiss* (Myrick & Cech Jr., 2001; Sloat & Osterback, 2013). Our sampling was conducted during the dry season at low flows when sampled reaches consisted primarily of pools maintained by springs in this fractured bedrock groundwater system, so water temperatures remained at tolerable levels. Although we are concerned that our temperature measurements were made at only one time in each year, we also found no relationship between trout presence and the invertebrate thermal index, and long-term continuous temperature monitoring in two of our streams showed that average maximum temperatures approximated 20°C (Frazier, 2017). Although stream temperatures are often related to riparian canopy cover in this region (Cooper et al., 2015, 2021), we restricted our analyses to reaches with intact riparian vegetation. Isaak et al. (2010) reported increases in stream temperatures with increased atmospheric temperatures and wildfires and decreased flows in a mountain stream network, but projected little impact on rainbow trout populations because of minimal effects on the extent and distribution of well-connected thermal habitat suitable for this species. In addition, water temperatures in some mountain streams may decrease with lower flows induced by climate change because of an increase in the relative contribution of groundwater springs to stream water budgets (Arismendi et al., 2012; Herbst et al., 2019).

4.2 | Invertebrate assemblages and food web structure with versus without trout

Our results suggest that positive associations between trout presence and the abundances of some medium-sized collector–gatherer mayfly and shredder caddisfly taxa are owing to their common preferences for deep, cool pools with high water and habitat quality. By contrast, some of the negative relationships we observed between the abundances of large-bodied epibenthic, nektonic, or neustonic invertebrate and amphibian taxa and trout were undoubtedly owing to direct biological interactions between trout and these prey taxa (Cooper, 1988; Power, 1990; Power et al., 2008; Wiseman et al., 1993; Zamora et al., 2018). Because trout are visual, engulfing predators, invertebrate prey selection by trout is a function of prey conspicuousness, including body size, exposure, and activity (Ware, 1972, 1973). The translation of these prey vulnerability traits to the impacts of trout on prey communities depend

on environmental conditions, particularly flow regimes, with trout often having different impacts on lower trophic levels in fast-flowing versus more lentic habitats.

Most previous studies on trout impacts on stream invertebrate communities have been conducted in riffles or in fast-flowing streams (e.g., Bechara et al., 1992, 1993; McIntosh, 2022; Peckarsky et al., 2013, 2015; Vimos et al., 2015; Zimmerman & Vondracek, 2007), where trout act as ambush predators, sallying forth from resting positions to intercept prey drifting downstream in the water column (primarily midge larvae and mayfly nymphs), so prey vulnerability depends on prey size and the prey's propensity for drifting (Allan, 1978; Bechara et al., 1993; Meissner & Muotka, 2006; Newman & Waters, 1984; Rader, 1997). Under such conditions, invertebrate prey can avoid trout and respond to their exudates by hiding under rocks during the day and drifting primarily at night (Diehl et al., 2000; Douglas et al., 1994; McIntosh & Peckarsky, 1999). In contrast, trout in our streams, which are relegated to pools, generally show cruising and searching behaviours during the dry season, engulfing any conspicuous prey they encounter on the bottom, water column, or surface of pools (Cooper, 1984b; Harvey & Railsback, 2014; Rossi et al., 2021). Direct trout impacts on large, exposed prey, such as OCH predators, were corroborated by our trait analysis, which showed that large, air-breathing, epibenthic and water column taxa were associated with troutless pools, whereas smaller, more cryptic taxa were associated with trout pools (Ware, 1972, 1973).

Nevertheless, flow regimes can influence the impacts of trout on prey communities in stream pools, because prey composition, and both prey and trout behaviour, can vary with flow over inter-annual and seasonal cycles. In our study, trout impacts on vulnerable OCH taxa were higher in years with continuous rather than low or intermittent flow. We observed that trout in some isolated or semi-isolated pools with low DO levels and limited habitat space were quiescent and did not respond to the approach of observers (Lennox et al., 2019; McHugh et al., 2015; Rossi et al., 2021). The results of McHugh et al. (2015), Jellyman and McIntosh (2020), McIntosh (2022), and this study indicate that trout impacts on vulnerable prey and lower trophic levels may be a hump-shaped function of flow, ranging from low impacts in isolated pools to high impacts at intermediate flows to lower impacts during high flows, mimicking the hump-shaped relationships between trout density and discharge reported by Jellyman and McIntosh (2020).

There was little direct evidence that trout impacts on conspicuous invertebrate predators cascaded down to lower trophic levels; however, SEM indicated that there were cascading effects in the algal-based food web, proceeding from trout to OCH invertebrate predators (especially epibenthic odonates) to algivorous prey (primarily baetid mayflies). It is likely that this trophic cascade would have been undetected without SEM, because direct algivorous invertebrate losses to trout appeared to be balanced by indirect positive effects of trout on algivores as mediated through trout reductions in invertebrate predators (Harvey, 1993). Although short-term experiments have revealed cascading effects from trout

through invertebrate predators to invertebrate grazers, these trophic cascades are sometimes short-lived because fish switch to smaller, algivorous prey (mayflies, ostracods, snails) after they have reduced large, exposed predatory OCH taxa (Cooper, 1988, is a temporal analogue of the spatial system described by Pelinson et al., 2021).

The systems most similar to our system are those studied by Power et al. (2008) and Atlas et al. (2013). Power et al. (2008) reported that the strength of top-down interactions in pools in a northern California river varied from year-to-year depending on preceding hydrological regimes (flood intensity) and the traits of dominant consumers, functionally producing two to four trophic level systems. Compared to our study streams, Power et al.'s (2008) experiments were done in wider, more open, higher order river reaches with much gentler slopes that harboured seasonally luxuriant algal growth and key taxa (*Dicosmoecus*, small fish) that were not present in our system. Atlas et al. (2013) conducted an experiment to examine the impacts of steelhead (trout), Pacific giant salamanders, and terrestrial subsidies on pool communities in a small, steep stream that was tributary to the river studied by Power et al. (2008), but found little evidence for top-down impacts of trout on lower trophic levels, even though this stream had similar environmental conditions, and trout densities and size structure, as in our study streams (see also Kelson et al., 2020). Differences in the results across these and our studies, then, contrast differences in the effects of fish on the populations of prey with which they sustainably co-occur versus the effects of fish on the distributions and abundance of vulnerable prey, which can be greatly reduced or eliminated by fish (Thorp, 1986).

In our study, cascading trout effects apparently did not extend to primary producers (algae), whose biomass was primarily related to abiotic factors, such as flow or canopy cover. The primary consumer trophic level, then, appeared to occupy the fulcrum between top-down and bottom-up interactions, being reduced by invertebrate predators but increasing with algal availability. Although bottom-up and top-down interactions occur simultaneously for trophic levels below the top level, the relative magnitude and impacts of these interactions vary greatly across different ecosystems, depending on interconnected environmental conditions and the abundances, behaviour, and traits of organisms at different trophic levels (Nyström et al., 2003; Peckarsky et al., 2013, 2015; Power, 1992a), emphasising the importance of disentangling the effects of both consumers and resources on different trophic levels (Peckarsky et al., 2013, 2015; Silins et al., 2014; Wootton & Power, 1993).

In contrast to our results for the algal-based food web, we found no evidence for top-down effects in the detrital-based food web (Herbst et al., 2009; Rosenfeld, 2000; Shelton et al., 2015; Vimos et al., 2015). Although other studies have shown or suggested that trout can reduce the abundances or alter the behaviour of shredders with top-down effects on leaf litter levels and breakdown rates (Buria et al., 2010; Greig & McIntosh, 2006; Konishi et al., 2001; Ruetz III et al., 2002), the relationship

between shredder abundance and trout presence in our study was positive, suggesting that both trout and shredders preferred deep pools with high water or habitat quality. The lack of top-down interactions in the detrital food web was not surprising because invertebrate predators and trout seldom consume cased caddis larvae (*Gumaga*, *Lepidostoma*) in our and other systems (Atlas et al., 2013; Cooper, 1984a; Otto & Svensson, 1980; Power et al., 2008). Instead, the detrital food web appeared to be driven by bottom-up interactions and abiotic factors, with shredder densities being positively related to CPOM levels, which, in turn, were positively related to canopy cover, and shredder densities also being positively related to DO levels, which were positively related to flow continuity (see also Rosenfeld, 2000). These results are congruent with the results of studies showing that detrital-based ecosystems often are driven by riparian subsidies with bottom-up effects on higher trophic levels (Richardson et al., 2010; Wallace et al., 1997, 2015).

Terrestrial invertebrate prey falling into heavily-shaded streams from adjacent riparian vegetation can be a major food source for trout (Rundio & Lindley, 2008), in some cases diverting trout from stream to terrestrial prey and reducing the potential for cascading trout impacts on lower trophic levels in streams (Nakano et al., 1999). The effects of the manipulation of allochthonous inputs on trophic cascades in streams, however, has produced mixed results (Atlas et al., 2013; Baxter et al., 2004). In our study in shaded streams, trout impacts on vulnerable invertebrate predators were apparent, despite the known importance of terrestrial prey to trout diets (Marcarelli et al., 2020).

4.3 | Invertebrate assemblage changes after trout loss

Invertebrate community structure in pools switched from a trout to a troutless configuration within a couple of years after trout were extirpated by scouring flows after wildfire or by drought conditions. However, there appeared to be differences in the variability of the abundance of conspicuous prey taxa after trout were lost owing to wildfire versus drought, with uniform increases across reaches after trout were lost owing to post-fire scouring flows, but very variable responses when trout were lost during the drought. These differences in the variability of vulnerable prey responses to trout loss were probably owing to patchiness in the effects of different disturbances, and hence on refuges and colonisation pools, with scouring post-fire flows creating uniform spatial conditions in parts of the stream network within and below the fire footprint but drought resulting in a shifting mosaic of drying pools or reaches over time (Datry et al., 2014; Robson et al., 2011, 2013). As a consequence, the proximity and extent of watered refuge areas for invertebrates surviving drought changed over space and time, leading to large variation in the proximity, extent, and character of invertebrate colonisation sources (Bogan et al., 2019; Robson et al., 2011). In contrast to these spatially variable invertebrate responses to trout losses, the

re-colonisation of trout to one of our study reaches after drought resulted in the rapid, uniform loss of conspicuous taxa.

Similar results were obtained by Wiseman et al. (1993) who removed or added trout to stream pools, leaving other trout and trout-less pools as controls for trout manipulations. The addition of trout to pools resulted in the immediate reduction or loss of vulnerable taxa (see also Cooper, 1988), but the removal of trout resulted in variable, less consistent increases in vulnerable taxa, probably owing to vagaries in invertebrate colonisation dynamics. The trout removal experiment conducted by Atlas et al. (2013) produced no evidence for trout effects on invertebrate predators, probably because the colonisation pool of vulnerable prey had already been culled by trout and because the experiment was not run for long enough to allow colonisation by these vulnerable prey to pools where trout were removed.

5 | CONCLUSIONS

In some steep coastal streams in southern California, the top aquatic predators are trout, which are most frequently observed in deep pools with high water and habitat quality. Medium-sized collector–gatherer mayfly and shredder caddisfly taxa co-occur with trout, whereas large, conspicuous epibenthic and water column taxa, such as tadpoles and predatory OCH genera, are absent or very rare in pools containing trout. SEM suggested that trout greatly reduced predatory OCH taxa, which, in turn, negatively affected collector–gatherer mayfly taxa, leading to associations between some collector–gatherers and trout; however, the bottom-up effects of algal biomass on collector–gatherers and grazers overrode the reverse top-down effects. By contrast, our results suggest that bottom-up effects and relationships between abiotic and biotic variables accounted for the structure of the detrital-based food web with shredder abundance being positively related to leaf litter mass, which, in turn, was positively related to riparian canopy cover and negatively related to flow. Although there were direct effects of post-fire floods and drought on invertebrate assemblages via impacts on flow, sediment, and/or hydrochemical conditions (first axis in NMS analyses, see also Cooper et al., 2015, 2021; McMahon et al., 2023; Silins et al., 2014), changes in invertebrate and amphibian assemblages after disturbance also partly were owing to the local extirpation of trout, which led to increases in tadpoles and OCH taxa within a year or two after disturbance events, with possible repercussions for invertebrate primary consumers depending on disturbance impacts on algal resource levels (Cooper et al., 2015).

Current trends and future projections indicate that climate change will drive increased temperatures, more intensive floods, more extensive wildfires, and longer and more severe droughts in many parts of the world, including those areas with Mediterranean climates (Feng et al., 2019; Westerling, 2016; Williams et al., 2019, 2020, 2022). Our results show that post-fire scouring floods and prolonged droughts can extirpate sensitive species, such as the southern California steelhead trout, the top aquatic predator in southern California streams

(Cooper, 1988; Cooper et al., 2015; National Marine Fisheries Service, 2012, 2016). The survival of trout and other sensitive species through these disturbances depends on protecting or restoring refuge habitats at the stream network scale, such as deep, shaded, cool stream pools with high habitat and water quality or, additionally in the case of anadromous steelhead, suitable estuarine and marine habitats (Alvarez & Dagit, 2019; Bogan et al., 2019; Cooper et al., 2021; Dagit et al., 2017; Kaylor et al., 2019; Lennox et al., 2019; National Marine Fisheries Service, 2012, 2023; Robson et al., 2013). Further, the resiliency of sensitive species and stream communities to disturbances is inhibited by the construction and maintenance of barriers (e.g., dams and road crossings) that block salmonid migrations and intercept the downstream drift of stream organisms, impeding the recolonisation of disturbed habitats (Kukuła & Bylak, 2022). Human alterations of landscapes and waterscapes, then, can enhance the negative impacts of climate change on native stream species and ecosystems (Dagit et al., 2020; Monaghan et al., 2016; National Marine Fisheries Service, 2012). In the case of southern California, changes in climate, and patterns in land and water use, are combining to extirpate many native steelhead and resident trout populations (National Marine Fisheries Service, 2023). Our results suggest that these extirpations would result in the re-configuration of food webs with the replacement of trout by predatory invertebrates or, where present, small tolerant fish or newts, as the top predators in these streams with repercussions for lower trophic levels (Power et al., 2008; Rodríguez-Lozano et al., 2015; Shelton et al., 2015). Our results also suggest that the most critical factor affecting sensitive native stream species and ecosystems in this semi-arid climate is flow patterns that maintain suitable habitat and refuges, emphasising the need to manage water resources by prohibiting or limiting water abstractions (diversions, groundwater pumping) or augmenting flows during dry times (Grantham et al., 2012; National Marine Fisheries Service, 2012, 2023; Robson et al., 2013).

AUTHOR CONTRIBUTIONS

Conceptualisation: S.D.C. Developing methods: K.K., S.W.W., S.D.C. Data analysis: B.D., S.D.C. Preparation of figures and tables: S.W.W. Conducting the research, data interpretation, writing: S.D.C., S.W.W., B.D., K.K.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest and have observed all ethical guidelines.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.h70rxwdqq

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SUPPORTING INFORMATION

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