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Drought ecohydrology alters the structure and function of benthic invertebrate communities in mountain streams

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Abstract

1. We studied benthic macroinvertebrate communities in 12 mid-elevation mountain streams in the Sierra Nevada, California. Data were collected at nine times (seven springs and two autumns) over a 14-year period of variable hydrological conditions, including years of flood and extreme unprecedented drought.
2. The taxonomic and trait structures of communities were similar during wet and average springs but became increasingly different as drought continued and smaller streams became intermittent.
3. The density of total invertebrates, primarily chironomids, increased during the drought years, but the richness and abundance of mayfly, stonefly, and caddisfly (EPT) taxa declined during the late drought. During the late drought, the proportions of rheophilic, semivoltine taxa with clinger or swimmer behavioural habits decreased, whereas small, stress-tolerant taxa with burrower and climber habits increased. Collector-gatherers dominated in all periods, but during the severe drought the relative abundance of micropredators increased and filterers, shredders, and grazers decreased.
4. We also found greater changes in community structure between spring runoff and autumn base flow conditions in an average than a wet year. However, spring to autumn population growth rates were much greater during the wet than average year.
5. Invertebrate richness and EPT abundance decreased and community structure showed large changes when stream discharge fell below 1–10 L/s, but remained relatively constant across a range of higher flows. During the severe drought, there were significant declines in the densities of 40% of the common EPT taxa compared to average and wet years, but chironomid, mite, and other invertebrate taxa showed variable responses.
6. Invertebrate diversity, community structure, and ecosystem functions in small, headwater streams are especially vulnerable to drought conditions, which are expected to increase in frequency and intensity with climate change in the Sierra Nevada and other mountainous regions.

KEYWORDS

climate change, flow regime, headwaters, Sierra Nevada, stream biodiversity

1 | INTRODUCTION

Warming and extreme drought associated with climate change are projected to affect natural and human systems in many parts of the world (Dai, 2011). Drought may markedly affect mountain headwater streams with perennial flows, owing to their limited drainage areas and sensitivity to reduced runoff and groundwater replenishment. These considerations apply especially to streams in Mediterranean and arid climate regions of the world, such as southern Europe, the Middle East, Australia, New Zealand, South Africa, and Chile, where flow recession and drying during the summer have intensified owing to rising temperatures and/or increases in drought frequency and duration (Dai, 2013; Kundzewicz et al., 2008; Lake, 2011; Sousa et al., 2011). Areas of southwestern North America are expected to experience more frequent and extended periods of drought (Cayan et al., 2010; Null & Viers, 2013; Seager et al., 2007) with impacts on hydrological patterns related to more rain and less snow (Knowles, Dettinger, & Cayan, 2006), shifts to earlier runoff (Stewart, Cayan, & Dettinger, 2005), and diminished summer low flows (Maurer, 2007). These climate change-induced alterations of hydrological patterns drive increasing human and ecological demands for scarce water resources, exacerbating climate change impacts by increasingly altering or depleting river flows via water diversions, flow regulation, and return flows (Carlisle, Wolock, & Meador, 2010). Streams in California's Sierra Nevada may be particularly affected by drought because, at high elevations, they drain granitic basins that receive primarily snowmelt runoff with limited groundwater inflow and, at the lower elevations of the western slopes, have been altered by human activities (i.e. dams and diversions, land use changes, Zimmerman et al., 2017). Modelling exercises have indicated that the effect of climate change on Sierran hydrological patterns will vary regionally, ranging from alterations in the timing of flows to prolonged low summer flows to lower cumulative annual flows (Null, Viers, & Mount, 2010). Extremely low flows punctuated by intense floods associated with atmospheric river storm events (Dettinger, 2011), as well as human changes to the waterscape, will have probably large effects on stream and river ecosystems. As a consequence, it has become increasingly important to document the influence of extreme hydrological changes, such as severe drought, on stream and river communities, thereby providing a foundation for refining our predictions of climate change impacts and guiding future riverine research, monitoring, and management.

As a harbinger of the ecological impacts of projected climatic and hydrological change, we examined the effects of an unprecedented, prolonged drought (2012–2015) on headwater Sierran streams. These small streams have intimate connections with their catchments, recharge groundwater, moderate downstream temperatures, receive and process inputs of allochthonous organic matter, contain a variety of geomorphic habitat types, and harbour high native biological diversity (Clarke, MacNally, Bond, & Lake, 2008; Finn, Bonada, Múrria, & Hughes, 2011; Herbst, Cooper, Medhurst, Wiseman, & Hunsaker, 2018; MacDonald & Coe, 2007;

Meyer et al., 2007; Penaluna et al., 2017). Given that benthic invertebrates are a major component of overall biodiversity in these streams, form important food sources for predators, and process organic matter, we focused on stream invertebrates as indicators of the effects of hydrological change, particularly drought, on stream communities.

Although invertebrate communities and environmental conditions may change gradually during initial drought phases, conditions and invertebrate responses may deteriorate to the verge of collapse (i.e. a *ramped* or *step* response) as flows decline from continuous to spatially intermittent surface drying to isolated pools (Lake, 2003). This is because environmental tolerance thresholds for stream taxa are exceeded, and stream habitats become disconnected, producing large alterations in communities and their ecosystem functions (Boulton, 2003). These considerations apply to supra-seasonal droughts that extend over a number of years, to seasonal droughts associated with late summer and autumn base flow periods in Mediterranean climates, and to the interaction of these drought time scales. In this study, we characterise the impacts of supra-seasonal and seasonal drought on invertebrate communities in Sierran headwater streams.

Although the purpose of our studies was to document changes in invertebrate communities during a prolonged drought, we also examined expectations for how invertebrate communities respond to low or intermittent flow based on literature data and the mechanisms outlined by Rolls, Leigh, and Sheldon (2012). Rolls et al. (2012) proposed four principles for how invertebrate community structure, diversity, and production would change with diminishing flow, which we summarise as owing to: principle 1—decreases in the extent of habitat, principle 2—reduced habitat quality, principle 3—shifts in the sources and exchange of organic matter and related biological productivity, and principle 4—reductions in the connectivity and variety of habitats.

We predicted that invertebrate density would increase during the initial phases of drying owing to the concentration of invertebrates in shrinking habitat (e.g. Wright & Berrie, 1987; Stanley, Fisher, & Grimm, 1997, principle 1), succeeded by decreased densities and richness owing to diminished habitat, particularly riffle habitat, and the deterioration of environmental conditions (Rolls et al., 2012; Herbst et al., 2018, principles 1 and 2). Following principle 2, we expected that many sensitive Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies; collectively EPT) taxa would decrease and that a few tolerant taxa, such as some midges and worms (Chironomidae, Oligochaeta), would increase during prolonged droughts, leading to a net loss in diversity (Dewson, James, & Death, 2007; Lake, 2011). Concordantly, we predicted that the trait structure of invertebrate communities would be altered by drought, with selection for taxa that are more stress tolerant and able to use the food resources and habitats associated with drought (Bêche & Resh, 2007a; Griswold, Berzinis, Crisman, & Golladay, 2008). Following principle 3, we predicted that the retention of organic matter and algae would increase with decreased current velocities during drought, resulting in more grazers and deposit-feeding

collector-gatherers, with bottom-up increases in their predators, but fewer current-dependent filterers. We also expected that drying would favour fast-growing multivoltine over uni- or semi-voltine taxa, increasing overall invertebrate development rates and generational turnover. From spring to autumn, we expected population growth would be greater in a wet than an average year, owing to expanded and renewed habitat and resources in the wet year compared to the dwindling habitat in the lower base flows of the average year (Stanley et al., 1997). Finally, following principle 4, we predicted that changes in invertebrate community and trait structure and declines in richness during the drought would be greater in reaches with spatially intermittent than continuous flows, with intermittent streams being dominated by a subset of tolerant taxa as pools become the main habitat.

2 | METHODS

2.1 | Environmental Setting

Study sites were first- to third-order streams draining forested headwater catchments in the western Sierra Nevada, California, ranging from 0.8 to 6.8 km in length, 50–470 ha in area, and 1,400–2,200 m in elevation (physical features detailed in Herbst et al., 2018). These streams flow to the North Fork of the Kings River and Pine Flat Reservoir, located within the Kings River Experimental Watershed (KREW) and Teakettle Experimental Forest. These are protected research catchments in undeveloped national forest lands with few roads and conform to least disturbed reference quality conditions for California (Ode et al., 2016). Our study sites encompassed 10 first- and second-order streams draining three sub-basins (Providence, Bull, and Teakettle) and two additional third-order study sites, downstream of the confluences of the headwater tributaries draining the Bull and Providence sub-basins (see Herbst et al., 2018). Study reaches of the 10 headwater streams were located in the lower ends of their catchments, and the confluence reaches were located within 500 m below where contributing tributaries merged.

During the period of study from 2002 to 2015, flow conditions in streams varied from greater than bank-full spring floods in wet years to spatially intermittent flows in some of the smaller channels during drought years. Although discharge was gaged for portions of the study period at 10 of the 12 study sites, we used the complete long-term hydrological record available from the Pitman Creek U.S. Geological Survey (USGS) gage (20–30 km away at 2,134 m; USGS 11237500), which represented the regional hydrological regime for our study sites and times (average $R^2 = 0.81$ for regressions of Q at gaged KREW streams versus Pitman Creek), to classify periods with different flow conditions and to estimate flow metrics for KREW streams for ungaged periods. Wet, average, and dry years were designated using USGS WaterWatch definitions (dry <25%, average 25%–75%, and wet >75% of 1975–2000 long-term annual cumulative runoff, October–September water year). Based on this,

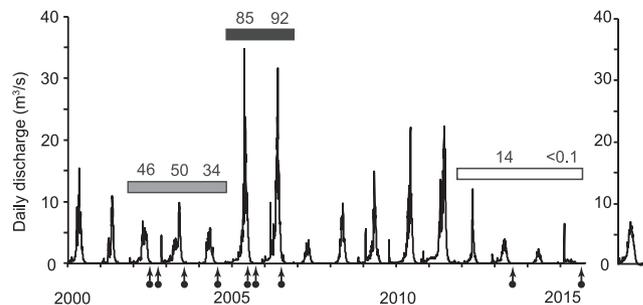


FIGURE 1 Hydrograph for Pitman Creek from 2000 to 2015. Pitman Creek is located approximately 20–30 km from the Kings River Experimental Watershed study sites and daily discharge data were taken from U.S. Geological Survey gaging station 11237500. The inset graph on the right side shows an average annual hydrograph (1975–2000) prior to the study period, extending from January to December. The dots and arrows indicate the times of sampling for this study; the bars over the hydrograph represent average (grey) and wet (black) sampling years and the duration of a prolonged drought (white) and the numbers over the bars represent the percentile for flows in that year relative to the cumulative frequency of annual flows from 1975 to 2000 (median = 50th percentile)

discharge levels at KREW sites from 2002 to 2004 were classified as average cumulative flows, followed by 2 wet years with high flows in 2005–2006 and, after a pause in sampling, 2 dry years during the increasingly severe drought of 2012–2015 (sampled in 2013 and again in 2015; Figure 1).

2.2 | Physical habitat of streams

We classified habitat into riffle, pool, and transitional zone segments for each 100-m study reach at each time, defining riffles as shallow, steeper sections with larger, sometimes emergent, substrata and fast turbulent flows and pools as deeper, flatter segments with deposits of finer sediment, calm surfaces, and slow current velocities (Herbst et al., 2018). Any segments that were not distinctly erosional riffle or depositional pool habitat types were classified as transitional. We measured stream width, bank angle, and riparian canopy cover, the latter with a concave densiometer (after U.S. Environmental Protection Agency habitat protocols, Kaufman, Levine, Robison, Seeliger, & Peck, 1999), at each of 10 cross-stream transects at 10-m intervals along each study reach. At five equal-spaced points along each transect across the wetted channel, we measured stream depth and current velocities (with a Global Water flow probe FP111) and noted substrata size classes (fines <0.1 mm, sand 0.1–2 mm, gravel 2–64 mm, cobble 64–256 mm, boulder >256 mm) and other forms of cover, such as algae, detritus (fine particulate organic matter, FPOM), leaves, wood, aquatic vegetation, and moss. We measured water temperature, conductivity and pH using an Oakton pH Con10 m at the head of each study reach. We calculated discharge as the sum of mean depth \times velocity \times width/5 over all points on each transect, then averaged these over the study reach.

2.3 | Benthic macroinvertebrates

Concurrent with the measurement of environmental variables, we collected invertebrate samples at our study sites at nine times, during or just after spring runoff (June) in 2002–2006, 2013, and 2015 and during autumn base flows in 2002 and 2005 (late September). Although some sites were subject to low intensity forest management practices in 2013 and 2015 (thinning and controlled understory burns), we found that invertebrate density and community metrics did not differ with the treated sites included or excluded from analysis of temporal patterns, so all sampled sites and times were included in analyses.

We took samples of benthic macroinvertebrates using a D-frame net (30-cm wide, 250- μ m mesh) from a defined square area above the net (0.09 m²) at each of nine riffle and three pool locations throughout each study reach at each time. Collections from riffles and, separately, collections from pools were each combined into a single riffle sample and single pool sample (see Herbst et al., 2018 for further details on sampling). We used a rotating-drum splitter in the laboratory to subsample preserved field collections and then identified sorted specimens to genus or species (except Capniidae, oligochaetes, Turbellaria, and ostracods), achieving target counts of usually >500 individuals per subsample.

2.4 | Data analysis

We concentrated on reach-scale changes in environmental conditions and invertebrate variables over time and, hence, hydrological regimes. Environmental variables, such as hydrological metrics, substrata, conductivity, and pH, were measured at the reach level, but invertebrates were sampled separately from pools and riffles. We obtained reach-wide estimates of invertebrate density for each stream and sampling date by combining the associated pool and riffle samples weighted by the proportions of stream bottom areas occurring in each habitat type. Because our designations of habitat included pool, riffle, and transitional zones, we partitioned transitional zones in proportion to the areas of riffles and pools for each reach and time to obtain total reach-wide densities for 107 total samples (12 sites by nine time periods, one missing).

We compared environmental and benthic invertebrate variable values among spring runoff hydrologic regimes. These regimes included wet (2005–2006), average (2002–2004), dry 2013 (early drought), and dry 2015 (late drought) periods. We also compared autumn samples from average 2002 with wet 2005 years. Invertebrate taxa were assigned to different trait states for voltinism, thermal tolerance, body size, behavioural habit, tolerance value, and functional feeding groups using tabulated data in Poff et al. (2006) and Barbour, Gerritsen, Snyder, and Stribling (1999, Appendix B), and to erosional riffle, depositional pool, and mixed habitat trait states using associations previously determined from studies at these same sites (Herbst et al., 2018). Community biotic (tolerance) and thermal indices for each site-time were derived 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 °C). Total and EPT richness values were determined by rarefaction to the minimum number of individuals counted in a reach-wide sample (450 fixed count) using the R function *rarefy* in *vegan* (Oksanen et al., 2015). The percent of overall invertebrate densities that were EPT taxa was also calculated. We evaluated consistent differences in response variable values across the 12 study reaches among hydrologic and seasonal groups using two-tailed site-paired *t*-tests with Benjamini–Hochberg (BH) multiple comparison adjustments for comparison-wise error (Benjamini & Hochberg, 1995; false discovery rate = 0.05). Count data were log ($x + 1$)-transformed and proportionate data were logit-transformed before analyses (Warton & Hui, 2011).

The multivariate invertebrate data consisted of a matrix of the relative abundances of all invertebrate taxa by all sites and times. Multivariate distances between all pairs of sample sites-times were calculated using the Sørensen distance metric. Non-metric multidimensional scaling (NMS) was used to display the similarity of invertebrate community structure across sites-times grouped by hydrological or seasonal category. We also examined significant correlations (Pearson's r , $p < 0.0001$) between NMS axes versus the transformed values of environmental variables and the relative abundances of common invertebrate taxa (i.e. those occurring in $\geq 25\%$ of samples). These analyses were complemented by the blocked multi-response permutation procedure (MRPP), which tested for multivariate differences in macroinvertebrate community structure among hydroperiod and seasonal categories after controlling for site-to-site variation (blocks = sites). We also conducted NMS and blocked MRPP analyses on various subsets of this dataset (e.g. pool only or riffle only data), along with correlations of trait responses with habitat and resource variables, to address specific relationships or hypotheses.

These community, trait, and taxonomic analyses were supplemented by examination of taxon-specific responses to drought. We calculated an index of the density responses of common taxa to early and late drought as: drought impact = $\ln(\text{spring density in 2013 (early drought) or 2015 (late drought) for each taxon at each site divided by the taxon's mean density at that site over wet and average springs (2002–2006)})$. Average (and associated SE) log ratio values for early (2013) and late (2015) drought impacts were thus obtained for the 12 study sites. To determine statistical consistency in the drought responses of individual taxa across sites, we compared early and late drought densities to mean wet-average year densities using paired *t*-tests, pairing by site ($n = 12$) and applying BH corrections (false discovery rate = 0.05) across the tests for 114 common taxa (occurring in $\geq 25\%$ of spring samples).

We also were interested in determining how invertebrate population growth rates from spring to autumn differed between an

average (2002) versus wet year (2005). Towards this end, we first obtained a reach-wide population size (i.e. number of individuals per reach = N) for common taxa (in this case, those occurring in >50% of the spring and autumn 2002 and 2005 samples, to minimise the number of 0s) and for higher taxonomic groups (e.g. total invertebrates, EPT, and chironomids). As an index of per capita changes in population size from spring to autumn (r) in 2002 versus 2005, we calculated r as $\ln(N_{\text{autumn}}/N_{\text{spring}})$, which assumes exponential net changes in population size and a constant per capita rate of change over the spring to autumn period. Because the minimum population size across common taxa present in the study reaches in 2002 and 2005 was 50 individuals/reach, we added 25 to N_{autumn} and N_{spring} when calculating r to deal with common taxa that were present in one season but not the other at a given site in a given year. Notice that r represents the net change resulting from all demographic and migration rates, but migration rates may be irrelevant if reach emigration = reach immigration, and that r does not include density-dependent responses (as assumed in logistic growth), which means that r will be reduced if density-dependent responses become important.

Average r values were calculated for each site in each year across all common, EPT, and chironomid taxa present at that site in that year, as well as for the total number of individuals in higher taxonomic groups for each site-time, and r values were compared between 2002 and 2005 using paired t -tests, where 2002 and 2005 r values were paired by site ($n = 12$). We also examined seasonal changes in community structure by performing an NMS on reach-wide invertebrate relative abundances in 2002 and 2005, then comparing site-specific autumn minus spring differences in NMS scores in 2002 and 2005 using paired t -tests (paired by site).

These analyses, then, indicated how environmental factors and invertebrate densities, richness, biotic and thermal indices, and community and trait structure varied across seasons and wet, average, and dry hydrological regimes, particularly focusing on the unprecedented drought from 2012 to 2015 (2013 = early drought, 2015 = late drought). As outlined in the Introduction, we examined specific hypotheses related to the Rolls et al. (2012) principles by analysing the responses of specific invertebrate variables to low or intermittent flows.

3 | RESULTS

3.1 | Physical habitat and hydrologic regime

As anticipated from the above, we found stream discharge and associated variables, such as width, depth, current velocity, habitat area, and wetted perimeter, showed the pattern, wet spring > average spring > early dry spring > late dry spring, with the average flow autumn being similar to one or both of the dry springs and the wet autumn being similar to average or early drought springs, depending on the physical variable (Table 1). As the 2012–2015 drought progressed, small, headwater streams in the Sierra became more intermittent and fragmented, with three of our study reaches becoming

intermittent in 2013 (10–20% of each reach dry) and six becoming intermittent in 2015 (10–50% of each reach dry). These intermittent stream conditions were mostly found in low elevation Providence catchments where increased evapotranspiration appears to result in reduced stream flow compared to Bull Creek (Safeeq & Hunsaker, 2016).

The percentage of reach areas in pools and detritus coverage were generally higher in the average autumn and late drought spring than at other times, and cobble was most embedded during the dry springs. Although coverages by algae and wood were greatest during late drought and the wet autumn, and by leaves was greatest during the early drought, estimates for these parameters had high variability and showed only a couple of significant differences among hydrological regimes. Conductivity and pH were lower during wet springs than at other times, and water temperatures were lower in the wet autumn than other periods and also lower in wet than average springs.

3.2 | Community structure is altered by hydrologic regime

An NMS analysis on the reach-wide relative abundances of all invertebrate taxa across all sites and times produced three axes, accounting for a cumulative 79% of the variation in the multivariate dataset (stress = 16.5). Consistent with principle 1, the first NMS axis accounted for 38% of the multivariate variation, and clearly distinguished wet and average springs (negative values) from dry springs and the average autumn (positive values, Figure 2). Positive values of NMS axis 1 (NMS 1) were characterised by low flows, and high levels of detritus and cobble embeddedness, and high relative abundances of the chironomids *Micropsectra*, *Zavrelimyia*, and *Macropelopia*, the alderfly *Sialis*, the mite *Utaxatax*, and the dipteran *Dixa*. Negative values of NMS 1 were associated with higher discharge, and larger reach and riffle areas, and the mayfly *Baetis* and chironomid *Stempellinella*. NMS 2 primarily distinguished times with greater pool areas and taxa from those with more riffle area and taxa (Herbst et al., 2018), whereas NMS 3 distinguished spring (positive values), related to algal cover, from autumn times (negative values), related to canopy cover and conductivity. Blocked MRPP results showed all hydroperiod groups differed from one another in invertebrate community structure except wet and average springs, and the average autumn and early drought spring periods ($p = 0.01$ – 0.002).

NMS analyses on the relative abundances of invertebrate taxa at the pool and riffle scales produced similar results to those produced by NMS analyses of reach-wide data, but with some refinements (Figure 3). For the pool analysis (upper plot), the first NMS axis clearly separated wet-average springs (negative values) from dry springs and average autumn (positive values). Because pools were dominated by chironomids, the pool NMS indicated associations between different chironomid taxa and hydrological regimes, with dry periods associated with *Micropsectra*, *Zavrelimyia*, *Macropelopia*, and *Polypedilum scalaenum*, and the alderfly *Sialis*, and wetter periods associated with *Stempellinella*, *Larsia*, and

TABLE 1 Mean values (with SEs underneath) for environmental variables across wet, average, early drought (Dry 13), and late drought (Dry 15) springs and average and wet autumns

	F + S (%)	G + C (%)	Algae (%)	Leaf (%)	Wood (%)	Detritus (%)	Depth (cm)	Vel (m/s)	Embed (%)	Q (m ³ /s)	Wet. Per (cm)	Area (m ²)	Pct R (%)	Pct P (%)	Temp (°C)	pH	EC (µS/cm)
Wet	34.8 4.7	52.7 4.4	3.8 ^{AB} 1.0	13.3 ^{AB} 3.1	17.1 2.6	5.2 ^B 1.1	18.2 ^A 1.4	0.27 ^A 0.04	16.0 ^{AB} 1.5	0.138 ^A 0.04	241 ^A 30	162.7 ^A 18.4	46 4	23 ^C 3	10.8 ^B 0.7	6.8 ^C 0.1	26.7 ^D 3.7
Avg	30.0 4.9	49.8 3.9	8.3 ^A 2.9	8.0 ^B 1.4	9.8 1.7	7.2 ^B 1.6	11.6 ^B 0.9	0.15 ^B 0.02	14.6 ^A 1.3	0.038 ^B 0.014	172 ^B 22	115.7 ^B 15.9	38 4	32 ^{BC} 3	12.9 ^A 0.6	7.1 ^{AB} 0.1	40.6 ^A 5.4
Dry 13	34.4 5.9	53.9 5.3	3.3 ^B 1.3	18.3 ^A 4.0	16.2 3.2	7.2 ^B 3.0	8.7 ^C 0.9	0.04 ^D 0.01	36.0 ^C 3.2	0.005 ^C 0.002	150 ^C 23	111.6 ^{BC} 21.8	46 5	24 ^C 4	12.4 ^{AB} 0.8	7.3 ^A 0.1	35.9 ^{BC} 4.8
Dry 15	31.7 7.6	54.4 6.6	17.9 ^{AB} 6.0	14.9 ^{AB} 3.8	29.6 5.6	29.2 ^A 6.5	6.9 ^D 0.8	0.01 ^E 0.00	40.5 ^C 5.3	0.001 ^D 0.0005	123 ^D 16	94.2 ^{BC} 18.1	32 6	42 ^{AB} 5	12.6 ^{AB} 0.9	6.9 ^{BC} 0.1	42.6 ^{AB} 7.1
Fall avg	32.6 5.7	52.6 4.3	5.7 ^{AB} 2.9	3.7 ^{AB} 1.0	10.4 1.4	18.2 ^A 3.5	6.8 ^D 0.7	0.04 ^D 0.01	11.3 ^{AB} 2.3	0.004 ^{CD} 0.002	123 ^D 18	103.4 ^C 16.7	42 5	41 ^A 3	11.6 ^{AB} 0.3	7.0 ^{AB} 0.1	42.2 ^A 6.1
Fall wet	36.4 5.6	51.4 4.9	7.6 ^A 1.9	14.4 ^{AB} 2.8	19.2 4.7	8.1 ^{AB} 2.3	8.8 ^C 0.6	0.09 ^C 0.02	22.3 ^B 2.5	0.013 ^B 0.004	168 ^B 22	117.6 ^{BC} 20.6	36 4	31 ^{BC} 4	8.7 ^C 0.3	7.0 ^B 0.1	34.9 ^C 4.7

Environmental variables include bottom coverage by fine and sand substrata (F + S), gravel and cobble substrata (G + C), algae, leaves, woody debris (Wood), and fine detritus (Detritus), as well as reach depths, current velocities (Vel), percentage of cobbles that were embedded (Embed), wetted perimeter (Wet.Per), overall habitat area (Area), percentage of reach area in riffles (Pct R) and pools (Pct P), water temperature (Temp), pH, and conductivity (EC). Letters next to values in each column indicate significant differences among time periods for each environmental variable, with values sharing the same letter not being significantly different ($p > 0.05$, paired t-tests, Benjamini-Hochberg corrections). Columns with no letters indicate variables with no significant differences across time periods. Percentage riffle and percentage pool do not sum to 100 because reach areas were also designated to a transitional habitat category.

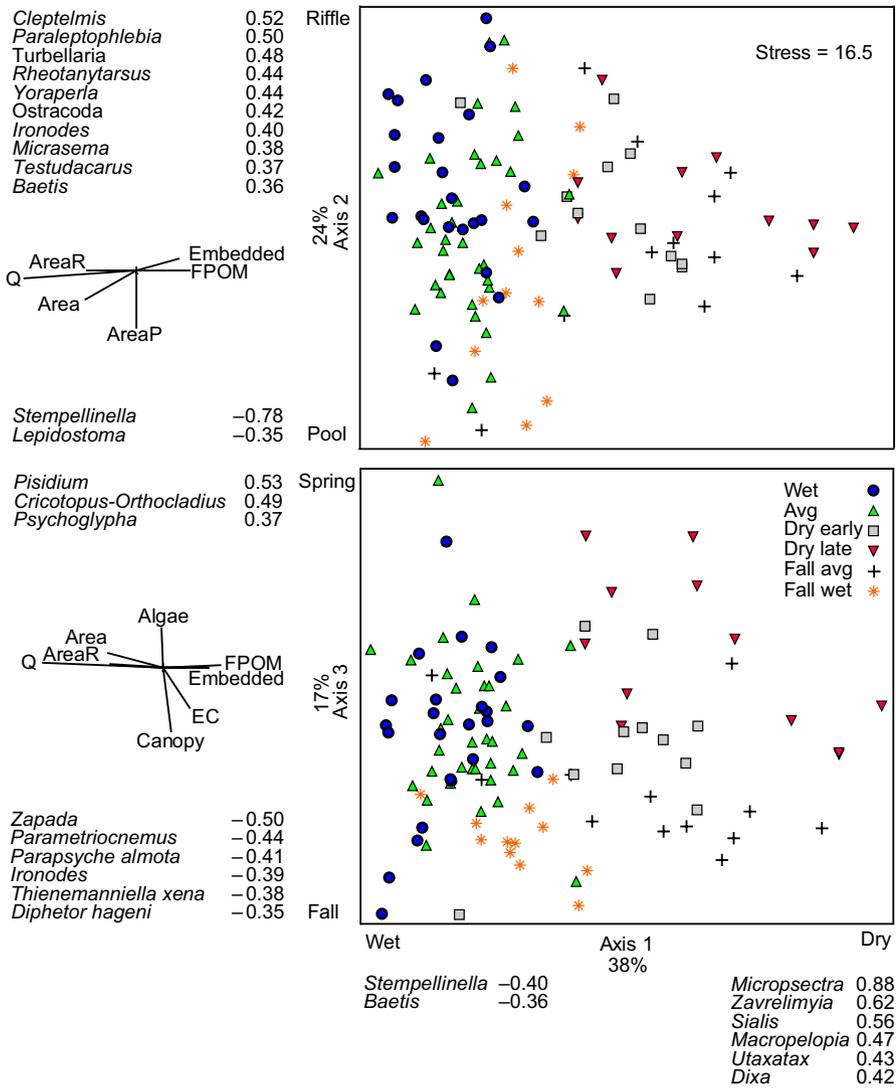


FIGURE 2 Ordination plots of nonmetric multidimensional scaling analysis (NMS) on the reach-wide relative abundances of benthic macroinvertebrate taxa across sites during wet (blue circles), average (green triangles), early drought (grey squares), and late drought springs (red triangles), and the autumns of 2002 (crosses, average year) and 2005 (yellow stars, wet year). Top: NMS axis 2 versus NMS axis 1. Bottom: NMS axis 3 versus NMS axis 1. The % variation in the multivariate data set attributable to each NMS axis is shown next to each axis label and the stress associated with the 3-axis NMS solution is shown in the top plot. The correlation coefficients (Pearson's r) of common taxa (occurring in $\geq 1/4$ of samples) significantly related ($p < 0.001$) to each axis are shown in the margins. The significant correlation vectors for environmental variables significantly ($p < 0.001$) associated with NMS axes are to the left of each plot

Tanytarsus. The second pool NMS axis was positively related to spring taxa and negatively related to autumn taxa. The first two axes produced by an NMS on riffle data both distinguished wet (negative for axis 1, positive for axis 2) from dry periods (vice versa), with the ordination plot showing bands of time points along a dry-to-wet gradient from the lower right, indicating dry conditions, to the upper left, indicating wet conditions (Figure 3, lower plot). Riffle taxa associated with wetter periods included eight EPT taxa, one chironomid, a mite, and oligochaetes, whereas taxa associated with drier times included four midges, two other dipterans, ostracods, and the fingernail clam *Pisidium*. Blocked MRPP comparisons for pool data showed all periods differed from one another except wet and average springs, and early drought spring and average autumn periods ($p = 0.02$ – 0.002), whereas blocked MRPP analysis on riffle data showed that all time periods were significantly different from one another ($p = 0.003$ – 0.0008).

Because invertebrate community structure was strongly related to flow, we examined in detail the relationships between NMS scores and discharge. To separate inter-annual from seasonal effects, we ran NMS on the relative abundances of invertebrate taxa using only

spring (June) data and only autumn (September) data, separately. Relationships between NMS 1 scores and discharge for both spring and autumn showed that NMS 1 scores increased as discharge decreased below a range of around 1–10 L/s, with more constant NMS 1 scores at discharges above this level during average and wet times (Figure 4, left side). Both spring and autumn NMS 1 scores were negatively, linearly related to log discharge, with similar slopes. NMS 1 scores were significantly higher in intermittent than continuously-flowing reaches in both 2013 (early drought, $F_{1,10} = 8.1$, $p = 0.02$) and 2015 (late drought, $F_{1,10} = 11.0$, $p = 0.01$), indicating that the greatest changes in invertebrate communities during dry years occurred in intermittent reaches.

Intermittency appeared to be driving the greatest changes in invertebrate communities as flows diminished during the drought, so we also ran NMS and MRPP using only invertebrate data from tributary headwater streams in 2013 and 2015, when some of our small, headwater study reaches became intermittent (Figure 4, right side). The ordination plot shows clear differences in the community structure of intermittent versus continuously-flowing streams during the drought. The MRPP showed that community structure

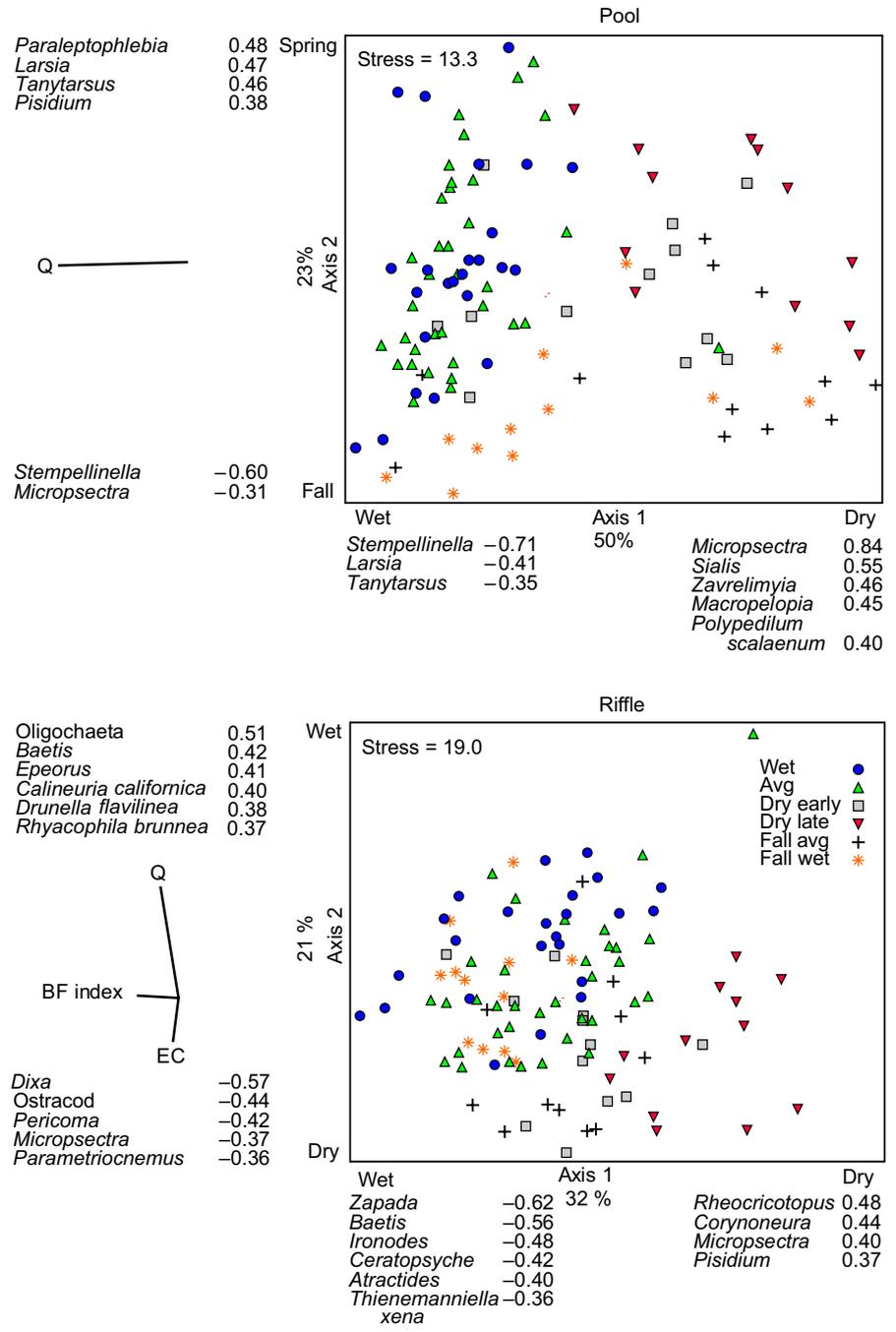


FIGURE 3 Ordination plots of non-metric multidimensional scaling analysis (NMS) on the relative abundances of benthic macroinvertebrate taxa in pools (top) and riffles (bottom) across sites during wet (blue circles), average (green triangles), early drought (grey squares), and late drought springs (red triangles), and the autumns of 2002 (crosses, average year) and 2005 (yellow stars, wet year). Other designations as in Figure 2. Code for environmental variables: Q = field-measured discharge, EC = conductivity, and BF index = baseflow index (7-day minimum divided by long-term average of actual or estimated flows for each stream for the 2001–2015 period of observations)

was significantly different for all combinations of intermittent and continuous streams in the early and late drought years, except that community structure in intermittent reaches did not differ between the 2 years. Intermittent streams also had lower total and EPT rarefied richness and a lower density of filter feeders compared to continuously-flowing streams ($p \leq 0.05$, t -tests with BH corrections).

3.3 | Taxonomic and trait structure and diversity vary with hydrologic regime

Total benthic invertebrate densities were greater during drought springs and the autumn of a wet year than in wet or average springs or the autumn of an average year (Figure 5). In general, late drought

increases in invertebrate density were comprised primarily of increases in chironomid and non-insect taxa, whereas EPT taxa also contributed to invertebrate density increases in the early drought period, but then declined later in the drought (Figure 5).

In evaluating the expectations of principle 2, we found that the biotic index, which is related to habitat degradation, was significantly higher during the late drought than in all other periods (Figure 5), involving both the loss of sensitive taxa and increased contribution of tolerant taxa. The biotic index also was greater in the average autumn than other periods except the early drought year which, in turn, had higher values than those in the wet spring and wet autumn. Thermal index patterns were different between pool and riffle habitats, with this index being lowest (= coolest) in pools in the wet autumn, but

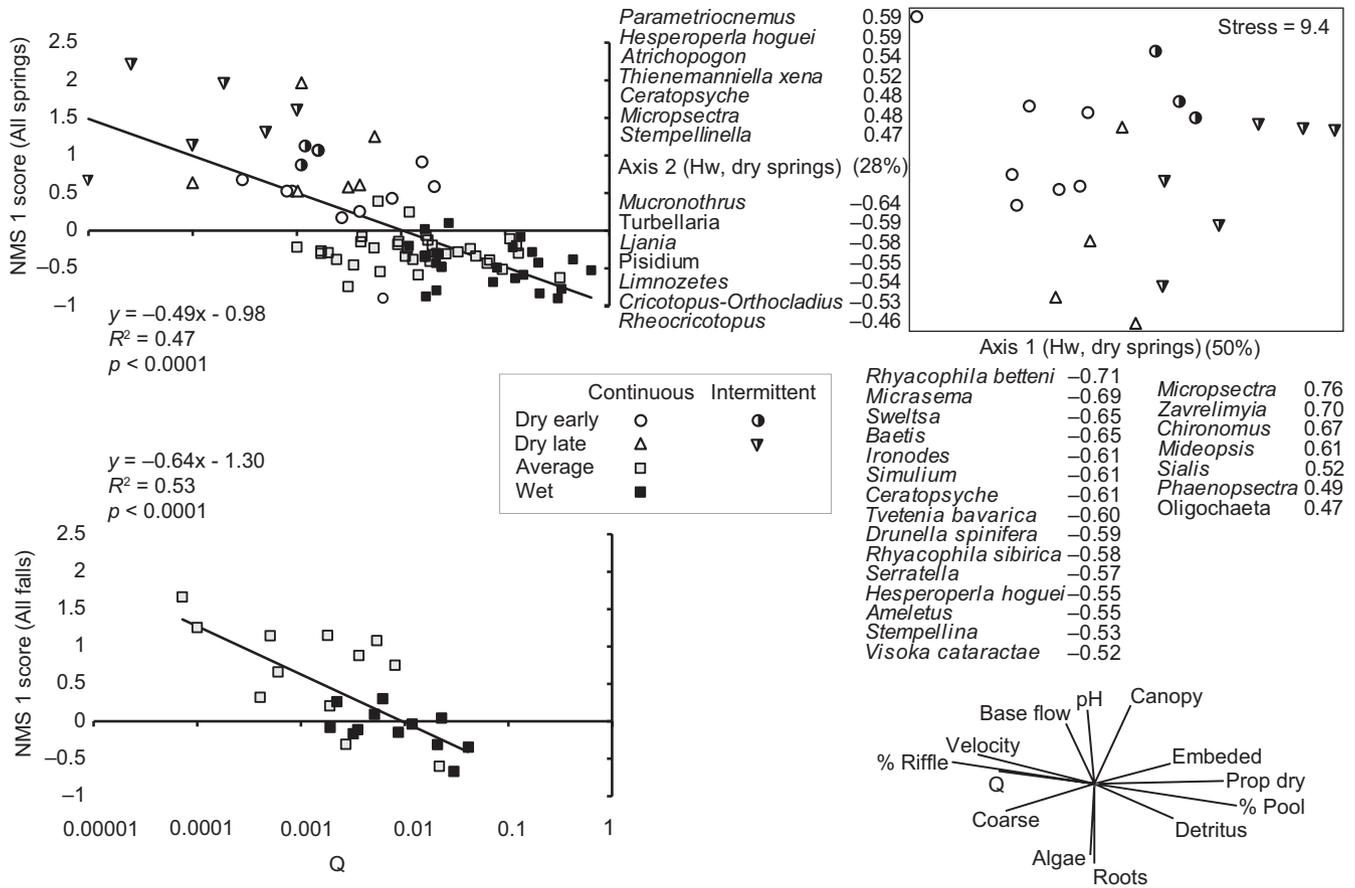


FIGURE 4 Left: Results of regression analyses showing relationships between non-metric multidimensional scaling analysis (NMS) axis 1 scores and field-measured discharge (Q, on a log 10 scale). Axis scores were derived from NMS using data on the relative abundances of invertebrate taxa in all springs (top) and all autumns (bottom) across sites and years. NMS scores were coded by wet, average, early drought (Dry early), and late drought (Dry late) years (code on figure). The results of least squares regression analyses are shown on each plot, including regression lines, equations, coefficients of determination (R^2), and p values. Right: An ordination plot of the results of NMS on the reach-wide relative abundances of benthic macroinvertebrate taxa in headwater streams during early and late drought years, distinguishing sites with intermittent versus continuous flow (code on figure). Other designations as in Figure 2, except vectors for environmental factors significantly associated with NMS axes are shown below the ordination plot (coarse = % cover of gravel and cobble substrata)

also lower in the late drought spring and average autumn than in average springs (Figure 5). In contrast, the thermal index was higher in riffles during the late drought spring than at other times, but lower in the wet autumn than in average springs. Total rarefied richness was lower in the late drought spring than wet and early drought springs. EPT rarefied richness and the proportion of invertebrates comprised of EPT taxa were lower in the late drought spring compared to all other periods, with both richness measures also being higher during wet springs than average springs and the average autumn (Table 2).

The abundances of other trait groups also differed among hydroperiods (Table 2). Burrowing taxa had higher relative abundances in the late drought spring than in wet, average and early drought springs and the wet autumn. The percent of climbers was greater during dry springs and autumns than in wet and average springs, and between the late drought and wet autumn. Sprawler proportions were greater in average springs than drought springs and in the wet autumn than the average autumn. Clinger relative abundances were lower in the average autumn and late drought spring than in other

springs, and swimmers were also lower in the late drought spring than in all other periods, reaching highest relative abundances in wet springs and the wet autumn. Among voltinism trait states, multivoltine taxa were more abundant in the autumn than spring and univoltine taxa showed the reverse pattern while also being more abundant in the late drought spring than other springs. Semivoltine taxa were less abundant in the late drought spring than other springs, associated with significant decreases in invertebrate body size during the late drought ($p < 0.05$, t -tests with BH corrections, reach-wide scale, reduced ratio of large to small taxa). Depositional taxa had highest relative abundance during the average autumn than wet spring, and mixed habitat taxa were most common in late drought ($p < 0.05$ for comparisons with early drought and average autumn). Erosional taxa had their lowest percentage representation in the late drought ($p < 0.05$ for comparisons with early drought).

In examining feeding group expectations associated with principle 3, we found that the proportions of collector-gatherers differed little among hydrologic periods but proportions of micropredators

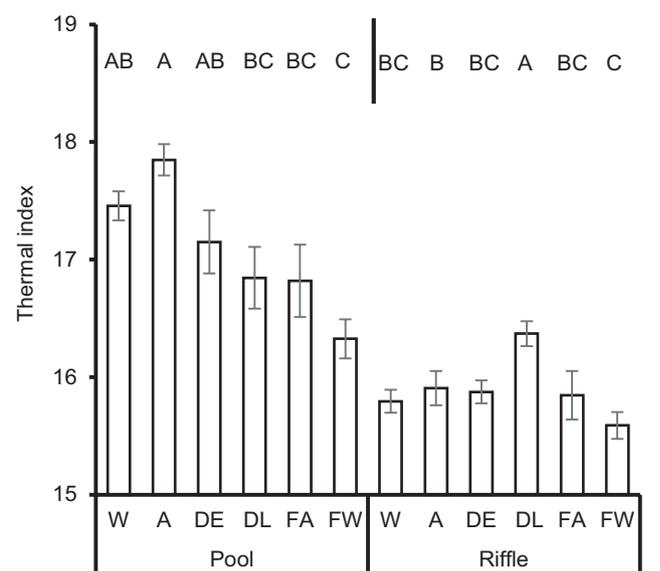
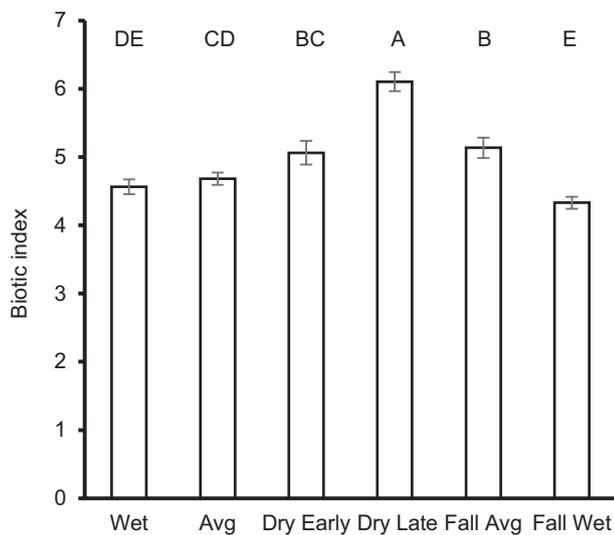
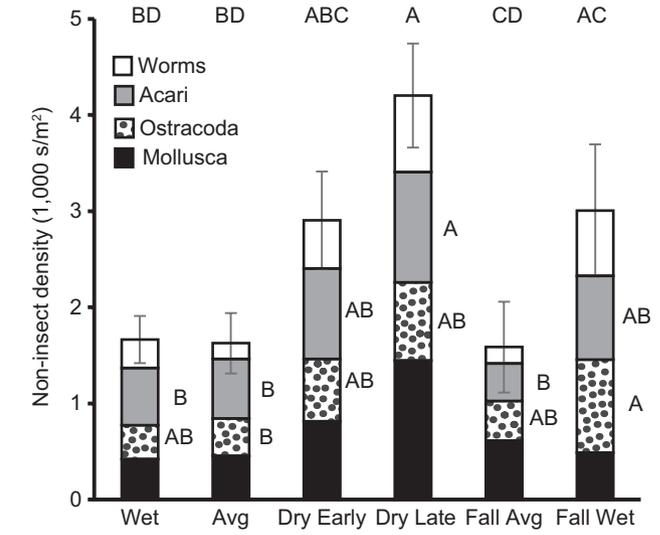
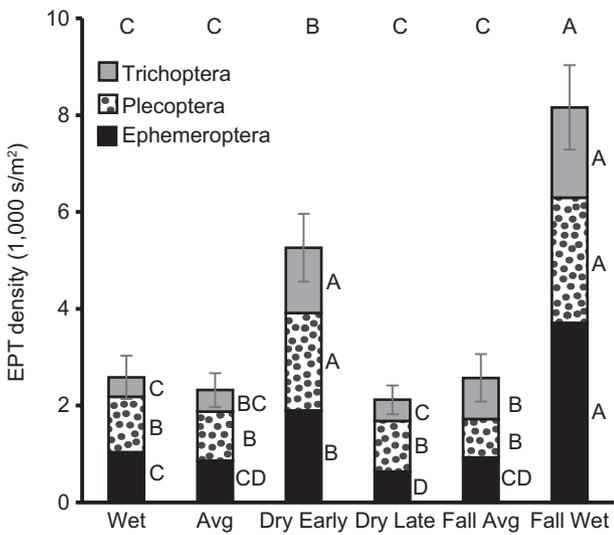
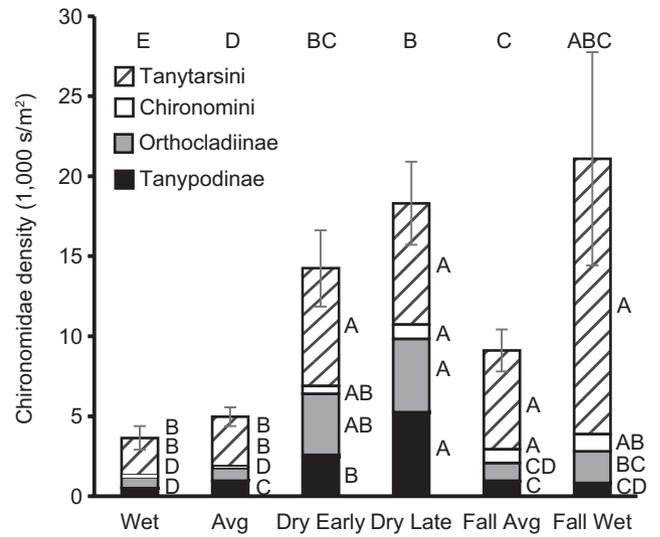
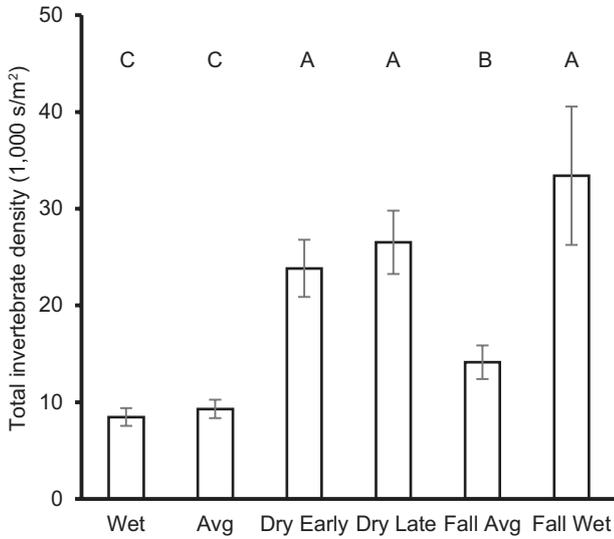


FIGURE 5 Mean values ($\pm 1SE$) for macroinvertebrate variables across time, organised by wet (2005, 2006), average (2002, 2003, 2004), early drought (dry early, 2013), and late drought (Dry late, 2015) springs and the autumns of 2002 (Fall Avg) and 2005 (Fall Wet). Reachwide data are shown for the densities of total invertebrates (upper left), chironomids (upper right), EPT taxa (middle left), and non-insects (middle right) and for reach-wide values of the biotic (tolerance) index (bottom left) and pool versus riffle values of the thermal index (bottom right). Letters above each graph indicate significant differences among time periods, with bars with the same overlying letter not being significantly different ($p > 0.05$, paired t -tests with Benjamini–Hochberg corrections applied to all comparisons across transformed invertebrate trait and taxonomic variables and untransformed indices). Stacked histograms are used to show the densities of dominant subfamilies and tribes of chironomids (upper right), different EPT orders (middle left), and non-insect groups (middle right, with worms represented primarily by oligochaetes (75%) and turbellarians (25%), molluscs represented primarily by *Pisidium*, and arachnids represented by water mites, acari). Letters to the right of different groups in the stacked histograms indicate significant differences among time periods for each group, with times with the same letter being not significantly different ($p > 0.05$, paired t -tests with Benjamini–Hochberg corrections)

(mostly tanypod midges, ceratopogonids, and mites) were greater in the late drought than at most other times (Table 2). Conversely, proportions of filter-feeders, shredders, and grazers were lower in late drought. Across all sites and times at the reach-wide level ($n = 107$), collector and shredder densities were significantly, but weakly, positively related to their resources (fine detritus and leaves, respectively) (Pearson correlation r -values = +0.20 to +0.28, p -values < 0.05 to < 0.005). Predator and micropredator densities were both strongly related to collector–gatherer densities (mostly

non-predatory midges, both r -values = +0.72, $p < 0.0001$), although predators and prey may simply be responding similarly to changing physical conditions. Although filterer densities were not related to current velocity at the reach-wide scale, they were positively related to current velocity at the unit (pool and riffle) scale ($r = +0.37$, $p < 0.0001$), reflecting higher filterer densities in riffles than pools, and for riffle data treated separately ($r = +0.23$, $p < 0.02$) (Herbst et al., 2018). In contrast, grazer densities were not related to algal coverage.

TABLE 2 Rarefied total and Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa richness, the percentage contribution of EPT taxa to total invertebrate densities, and the relative abundances of traits within each trait group across hydroclimatic periods (mean (SE))

Richness and traits	Wet	Average	Early drought	Late drought	Average autumn	Wet autumn
Total richness	67.4 (2.0) a	64.3 (1.7) ab	68.2 (3.1) a	55.5 (2.4) b	58.9 (3.0) ab	59.0 (3.2) ab
EPT richness	23.8 (0.9) a	21.4 (0.8) bc	22.7 (0.9) ab	12.0 (1.2) d	19.4 (1.0) c	22.0 (1.6) abc
Percent EPT abundance	30.5 (2.8) a	24.6 (1.7) b	23.5 (3.3) abc	8.5 (1.0) d	19.0 (2.8) c	32.8 (4.1) ab
Behavioural habit						
Burrower	21.6 (2.1) a	18.9 (2.7) ac	19.1 (2.7) ac	28.9 (3.2) b	22.0 (2.7) b	13.6 (2.4) c
Climber	5.4 (0.6) a	6.3 (1.0) a	19.2 (3.1) bc	20.8 (2.8) c	22.0 (3.9) bc	11.4 (1.4) b
Sprawler	31.3 (3.4) ac	36.6 (2.9) ad	23.2 (1.8) b	27.6 (2.4) bc	29.0 (4.2) ab	40.3 (5.0) cd
Clinger	33.6 (1.9) ac	32.6 (1.8) a	33.0 (2.6) a	20.4 (2.2) b	22.0 (3.0) b	24.8 (3.5) bc
Swimmer	8.1 (1.3) a	5.4 (0.6) b	5.4 (0.9) ab	2.2 (0.4) c	4.9 (0.9) b	9.8 (1.6) a
Life cycle						
Multivoltine	43.1 (2.8) a	41.7 (2.4) a	40.4 (3.1) a	37.0 (2.9) a	56.6 (3.9) b	56.8 (4.6) b
Univoltine	46.2 (2.6) a	47.7 (2.1) a	51.5 (3.0) a	59.1 (2.8) b	35.5 (3.0) c	33.0 (3.3) c
Semivoltine	10.5 (2.5) ab	10.4 (1.4) a	8.1 (0.7) ab	3.7 (0.7) c	7.7 (1.8) b	10.2 (1.7) ab
Habitat use						
Riffle (erosional)	39.0 (3.8) ab	32.6 (3.0) ab	37.7 (4.2) a	22.3 (3.4) b	25.9 (4.0) ab	35.5 (5.5) ab
Pool (depositional)	40.2 (4.5) b	46.8 (3.8) ab	44.1 (5.1) ab	51.4 (4.6) ab	59.2 (4.4) a	50.1 (7.0) ab
Mixed	20.8 (1.8) ab	20.6 (2.5) abc	18.2 (2.0) bc	26.4 (2.7) a	14.9 (1.1) c	14.4 (2.1) abc
Functional feeding groups						
Collector–gatherers	54.9 (3.0) a	56.6 (2.3) ab	60.3 (2.5) ab	59.9 (2.1) ab	62.4 (3.8) ab	63.2 (4.0) b
Filterers	4.5 (0.7) a	2.6 (0.5) b	3.5 (0.8) ab	1.0 (0.3) c	4.1 (1.0) ab	3.0 (1.0) ab
Grazers	4.7 (0.5) ab	3.9 (0.7) ab	3.9 (1.0) ab	2.2 (0.7) c	3.2 (0.7) bc	7.4 (1.6) a
Micro-predators	16.1 (0.9) a	19.5 (1.2) b	13.1 (1.9) ac	23.1 (2.5) b	11.3 (0.9) c	6.8 (0.5) d
Predators	5.2 (0.6) ac	5.2 (0.4) ac	8.5 (1.0) b	7.5 (1.5) ab	5.6 (0.6) a	4.3 (0.5) c
Shredders	14.5 (2.7) ab	12.2 (1.0) ab	10.8 (0.8) a	6.2 (0.9) c	13.4 (2.1) ab	15.3 (1.5) b

For each richness or trait variable, values for hydroclimatic periods with the same letter are not significantly different ($n = 12$, $p > 0.05$, paired t -tests with Benjamini–Hochberg corrections, false discovery rate = 0.05).

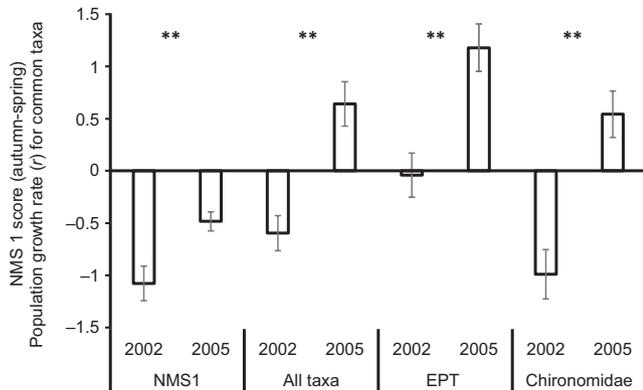


FIGURE 6 Mean autumn minus spring differences ($\pm 1SE$) in NMS axis 1 scores for 2002 and 2005 and mean per capita population growth rates (r) from spring to autumn ($\pm 1SE$) in 2002 versus 2005 for all common invertebrate, EPT, and chironomid taxa. The NMS analysis was conducted using only 2002 and 2005 autumn and spring data on the relative abundances of invertebrate taxa. Asterisks indicate significant differences between 2002 (an average year) and 2005 (a wet year; $**p < 0.01$) using paired t-tests, where values are paired by site

3.4 | Taxon-specific responses to drought

Among the 114 common taxa evaluated, the densities of 10 taxa increased and of nine taxa decreased during the early drought, whereas eight taxa increased and 31 taxa decreased during the late drought, all relative to wet-average years (paired t-tests with BH corrections, paired by site, all p values < 0.05 , Supporting information Figure S1). From wet-average springs to early drought spring, three EPT taxa increased and one declined, but by the late drought, all 17 EPT taxa showing significant changes were in decline, comprising 40% of overall EPT abundance. Chironomid taxa showed variable responses to drought with approximately equal numbers of taxa increasing or declining, including three taxa that increased and three that declined from wet-average to early and late drought periods, two that increased only in the early drought period, and two that increased and three that decreased only in the late drought period. Mite taxa also showed mixed responses to drought with two taxa increasing and five decreasing in either or both drought springs, all relative to wet-average springs. Other insect taxa showed mixed responses, with two elmid beetles, a blackfly (*Prosimulium*), and a crane fly (*Limnophila*) decreasing, and the dipteran *Dixa* and alderfly *Sialis* increasing, during the drought. Densities of the most abundant non-insect taxa, *Pisidium*, ostracods, and oligochaetes, increased >2 – 3 -fold in late drought but these responses were not significant owing to high variability. Overall, the taxa with significant responses to severe drought constituted 35% of these common taxa and 42% of the total density of the benthic invertebrate community.

3.5 | Seasonal population and community changes

In line with principle 3, we also observed lower spring to autumn population growth in a dry (2002) than wet (2005) year, with more

sustained flow, larger habitat areas, cooler temperatures, lower conductivity, and, on average, more algae, leaf, and wood cover (but less detritus) in the wet than average autumn (Figure 6, Table 1). Average net population growth rates for all common, EPT, and chironomid taxa were significantly greater in 2005 than 2002, being negative (all, chironomids) or near 0 (EPT) in 2002 but showing significant increases in 2005. Calculations of spring to autumn per capita changes in the total number of individuals per reach in each general taxonomic group produced similar patterns (mean r for total, EPT, and chironomid numbers per reach for 2002 versus 2005 = 0.10 versus 0.80, -0.06 versus 0.98, and 0.28 versus 1.06, respectively). In evaluating spring to autumn changes in habitat quality, we note that the biotic index, indicating community tolerance to degraded conditions, was higher in the average than wet autumn. Regarding resource use and availability in the wet versus average autumn, the relative abundance of grazers was higher, as were densities of collectors, grazers, and shredders, but not other functional feeding groups. Although we predicted greater population growth rates in the wet than average year, an NMS conducted on spring and autumn invertebrate data from 2002 and 2005 showed greater seasonal change in community structure in the average than wet year (Figure 6), associated with decreases in the percentage of the community comprised of EPT taxa and greater changes in community structure during drier times (Table 2).

4 | DISCUSSION

Many studies have shown that flow regime and drought have important consequences for the biological structure and function of flowing water ecosystems (reviewed in Bunn & Arthington, 2002; Dewson et al., 2007; Lake, 2011). The timing and amounts of flow across habitats, seasons, and years both provide a predictable habitat template for the stream biota but, at the extremes, may produce major disruptions in habitat conditions (Boulton, 2003; Chessman, 2015; Herbst & Cooper, 2010; Herbst et al., 2018; Yarnell, Viers, & Mount, 2010). Although floods can abruptly alter river geomorphic features, declining flows during drought often cause more gradual incremental stress as habitat contracts and lateral and longitudinal connectivity is reduced (Lake, 2003). As flows recede, riffles disappear and pools become disconnected, thereby altering invertebrate species composition and reducing richness, especially of taxa adapted to fast flows and cold waters (Bonada, Rieradevall, Prat, & Resh, 2006; Chessman, 2009; Herbst et al., 2018). As habitat extent contracts, so too may food chain length, resulting in simpler food webs in intermittent streams (McHugh, Thompson, Greig, Warburton, & McIntosh, 2015).

Our results indicate that invertebrate community structures under different hydroperiods were distinct from one another, but that low and intermittent flows during drought had a much larger effect on stream invertebrate community structure than did spring floods during wet years. The most prominent difference between hydroclimate periods was in the late drought year, which had the lowest taxonomic diversity and smallest fractions of EPT, long-lived,

erosional habit clingers and swimmers, and was dominated by small collector-gatherer and micropredator midges.

Many studies have shown rapid invertebrate recovery after floods (Giller, 1996; Lake, 2011), so flood effects may not be long-lasting and can even benefit invertebrate populations as we observed from spring to autumn in 2005. In this study, we found that wet and average spring runoff hydrologic periods had very similar invertebrate densities, richness, and community composition, but that both seasonal and interannual droughts had large effects on invertebrate communities, reducing communities during dry times to the fraction of species able to tolerate and exploit degraded conditions or refugia. Although moderate community changes were observed in the early drought year, invertebrate communities showed the greatest changes late in the drought in 2015, the driest year of the 2012–2015 drought. The impacts of low flow on invertebrate communities may accumulate over prolonged drought periods, often showing greatest changes when flows become intermittent and refuges are eliminated (Boulton, 2003; Lake, 2011; Rader & Belish, 1999).

Long-term monitoring of streams in California and nearby regions has revealed altered invertebrate density, richness, and taxonomic and trait composition during drought, particularly in small streams when drought is prolonged, intense, or frequent (Bêche & Resh, 2007a,b; Bogan, Boersma, & Lytle, 2015), possibly mediated by habitat changes as well as competitive interactions at high population densities (Resh et al., 2013). Overall, stream research has documented that declines in flow alter the structure and function of invertebrate communities owing to reductions in habitat extent, water quality, the exchange and availability of resources, and the longitudinal and lateral connectivity of habitats (Lake, 2003; Rolls et al., 2012). Below, we address how these mechanisms drive the responses of stream invertebrate communities to low or intermittent flow, as summarised by Rolls et al. (2012), then consider the implications of our results for the impacts of climate change.

4.1 | Reduced habitat area and quality with drought

In support of principle 1, habitat extent decreased and the proportion of habitat composed of pools increased during the late drought with associated changes in invertebrate community structure at all spatial scales (pool, riffle, and reach-wide). The densities of most taxa and trait groups initially increased in the early drought, becoming concentrated as stream areas contracted, then remained high for tolerant taxa, but declined for more sensitive EPT taxa, in the late drought at the lowest flows.

Sensitive taxa may decline during drought owing to habitat degradation. Organic matter can accumulate, and water quality deteriorate as flows drop, material transport conduits are eliminated, and water stagnates (Lake, 2011). As stream area and especially riffles diminished during dry periods, we also observed a deterioration of habitat quality as cobble substrata became more embedded, discharge, current velocities, and depths decreased, temperature and conductivity increased, and decomposing detritus accumulated, probably leading to reductions in dissolved oxygen levels (Dewson

et al., 2007). These stressors probably drove late drought declines in sensitive taxa and increases in tolerant forms, producing a higher community biotic (tolerance) index. Surprisingly, although the riffle thermal index was higher in late drought, this index was lower in pools in the late drought and average autumn than in average springs, suggesting an overriding influence of cool groundwater inflows in deeper pools while warming occurs in shallow riffles at low flows (consistent with Mosley, 1983 and Herbst unpublished data; see also data on unexpected stream cooling trends in the western U.S.A. in Arismendi, Johnson, Dunham, Haggerty, & Hockman-Wert, 2012). Even as pools may remain cool, and species able to inhabit mixed habitats find refuge in pools, few riffle taxa can survive without flow, so residual pools are still inadequate for the protection of riffle taxa even if temperatures are cooler.

Invertebrates with different traits also showed responses to declining habitat extent and altered habitat conditions. These traits may be useful in predicting the resistance and resilience of stream fauna to drying and use of drought refuges (Robson, Chester, & Austin, 2011). Burrowing and climbing taxa became relatively more abundant in the late drought, suggesting possible behavioural responses to increased detritus cover and more relative area in pools, whereas clinging and swimming taxa, hindered by embedded cobble and the loss of riffles, were reduced. The proportion of invertebrates with longer semivoltine life cycles also were reduced in late drought, perhaps because of lower recruitment or inability to survive deteriorating conditions. Proportions of erosional rheophilic taxa declined with drier hydroperiods while depositional taxa increased. Riffle taxa were significantly reduced from early to late drought phases as riffle habitat dwindled but mixed habitat taxa had higher relative abundances, perhaps reflecting their capabilities to tolerate, and switch between, different habitats depending on habitat extent and quality. All EPT taxa responsive to extreme drought declined to low levels, even sometimes disappearing from our collections in some streams, thereby reducing diversity as drying, fragmentation, habitat loss, and poor habitat quality (e.g. increased embeddedness) proceeded. Invertebrate body size also decreased with increasing drought severity as larger EPT taxa declined and smaller taxa, especially some midges, increased, consistent with the generalisation that climate change benefits small-bodied species (Daufresne, Lengfellner, & Sommer, 2009); however, in our case, this appears to be due more to hydrological rather than thermal alterations.

4.2 | Changes in food resources and their consumers with low flow

The mechanisms underlying principle 3 posit that changes in food resource quantity, quality, and exchange with low flow will decrease productivity and alter community structure; however, such mechanisms are difficult to evaluate with correlational data, because food quality, quantity, and spatial distributions all affect invertebrate communities, consumers can both track and depress their resources, and organic matter and algae can affect the physical environment (Marcarelli, Baxter, Mineau, & Hall, 2011). For example, fine detritus is consumed

by collector–gatherers, but varies widely in quality and, in excess, can engender low dissolved oxygen levels and bury substrata. As expected, fine detritus was higher during the late drought than at other times and, although algae, leaf, and wood coverage tended to be highest during the drought, coverage by these organic materials was not significantly different between late drought and other springs, because of variation in riparian canopy cover among streams (high canopy cover in the lower elevation Providence streams, low in the higher elevation Bull streams).

We found that trophic structure differed from early to late drought, with increased densities and proportions of micropredators, and decreased filterers, grazers and shredders. In addition, the densities of four of the five most common filterers and several key mayfly grazers (*Epeorus*, *Cinygmula*, *Ironodes*) were far lower during the late drought than wet and average years. In partial support of these results, Bogan and Lytle (2007) reported that the relative abundances of collector–gatherers and predators increased, whereas those of filterers, scrapers, and shredders declined during drought. Most functional feeding groups, except for grazers, were related to the levels of their resources, providing some support for the effects of flow conditions on food resources and, in turn, invertebrate communities. There were exceptions to these patterns, such as shredders declining in the late drought despite high leaf coverage, suggesting that other factors must be considered in explaining the abundance patterns of some feeding groups. Although shredders may have increased early in the drought owing to concentration due to habitat shrinkage and increased food resource levels, their decline in the late drought probably reflected their sensitivity to degraded habitat conditions (average tolerance value of shredders = 2.8). By contrast, collectors and micropredators probably increased in the late drought because they were comprised primarily of tolerant chironomid taxa that could take advantage of enhanced food resource conditions (average combined tolerance value of 5.0). Increased densities with drying and habitat shrinkage may have intensified predator–prey and competitive interactions for those taxa that survived stressful conditions. Consistent with the changing abundances of functional feeding groups, Ledger, Brown, Edwards, Milner, and Woodward (2013) found that food webs were drastically altered by drought in experimental stream mesocosms, losing species and links, with production shifting to small species.

Although the spring to autumn population growth rates (r) of common taxa were greater in 2005 (wet year) than 2002 (dry year), community structure, as reflected by NMS 1 scores, showed greater spring to autumn changes in 2002 than 2005, associated with a lower relative abundance of EPT taxa. Under high flow conditions, such as those in 2005, we expected increased organic matter exchange between terrestrial and stream environments and increased downstream transport, as well as enhanced habitat renewal as more habitat was submerged, lateral connectivity was increased, and deposits of refractory organic material were flushed out (Rolls et al., 2012). By contrast, poor habitat quality in autumn of 2002 associated with more detritus, lower velocities, higher temperatures and conductivity, and decreased area, inhibited or reduced invertebrate population growth. Differences in spring to autumn population growth rates, then, may be as much related to

differences in habitat quality as to altered food resource availability, so conceivably explained by either or both principles 2 and 3.

4.3 | Habitat fragmentation

Stream connectivity is disrupted and the length of flowing channels shortened when flows are reduced, as shown for Sierra Nevada streams including Bull and Providence Creeks (Godsey & Kirchner, 2014). These disruptions in flow paths are accompanied by a stepwise or ramped progression of altered community structure during the initial, late, and intermittent flow stages of drought (Boulton, 2003). As predicted, then, intermittent flow and attendant habitat fragmentation altered community structure and depleted taxonomic richness compared to continuously-flowing reaches during drought years (Figure 4). Pools do not necessarily provide refuges for riffle taxa, because many riffle taxa were generally absent or at very low densities in pools even during drought flows, indicating that pools did not meet the habitat requirements for riffle taxa (Bogan & Lytle, 2007). Although downstream drift or upstream migration may provide an escape from drying conditions for riffle taxa, these avenues are generally foreclosed for aquatic stages when stream sections dry (Bogan, Boersma, & Lytle, 2013). Early emergence may allow escape and could account for some loss of richness in drying sections. Streams with seasonal intermittent periods contain taxa that are both resistant and resilient to drying, including those that have dormant or resting stages, can breathe air, or can move from aquatic benthic to terrestrial or hyporheic habitats (Bogan et al., 2015). Because our Sierran study streams are typically perennial and have a low representation of taxa adapted to seasonal intermittency, we found losses in diversity, particularly in sensitive riffle species, and altered trophic and trait functions during prolonged, suprasedonal drought with increased stream intermittency.

The smallest streams showed the greatest changes in community structure with decreasing discharge, across both seasons and years. As stream flows declined during drought, riffles were disproportionately lost or reduced, resulting in increasing proportions of pool habitat, leading to drought assemblages dominated by tolerant, pool taxa. In general, invertebrate species richness declines as flows diminish with stream habitats receding from mixed riffles and pools, to pools with reduced hydrologic connections, to isolated pools (Bonada et al., 2006). Although levels of diversity may be similar in perennial streams and intermittent reaches after flows return, there is evidence that fewer taxa are supported among intermittent reaches at larger network scales, with rare taxa being most vulnerable to loss (Wooster & DeBano, 2018). Low or intermittent flows often are accompanied by increased conductivities and temperatures (which may differ between shallow riffles and deep pools), and the accumulation of fine sediment and organic matter, the latter stimulating microbial activity and oxygen depletion (Dewson et al., 2007). These stressors and community alterations highlight the vulnerability of invertebrate communities in headwater tributaries to changes in hydrological and thermal regimes. Further, we found congruent changes through time across all our sites showing the

strong influence of drought on community metrics and traits across regional groups of streams, similar to the observed effects of severe drought across boreal streams in Finland (Huttunen et al., 2014). Sierra Nevada headwater stream networks contain many regionally restricted or endemic species with small populations that are vulnerable to extirpation during drought (Erman & Erman, 1995).

4.4 | Hydroclimatic change

Climate models and trends suggest floods and drought may increase in frequency and intensity (Swain, Langenbrunner, Neelin, & Hall, 2018). Although invertebrate communities in headwater streams may display some resilience to floods during storm events engendered by atmospheric rivers (Herbst & Cooper, 2010), these communities may be less resilient and resistant to intensifying, long-term drought (Lake, 2003). Many arid and semi-arid regions, including parts of California, are expected to have prolonged and severe droughts with continued climate change (Cook, Ault, & Smerdon, 2015; Null & Viers, 2013). Analyses of the responses of stream invertebrates with different traits or taxonomic affiliations to climate change suggest that sensitive, rheophilic, and predominately EPT taxa may be especially vulnerable to projected alterations in runoff and warming (Poff, Pyne, Bledsoe, Cuhacyan, & Carlisle, 2010; Pyne & Poff, 2017). Our findings of an increased ratio of tolerant to sensitive taxa (biotic index) and reduced proportions of riffle taxa during late drought support the conclusion that taxa with high sensitivities to reduced flow, high temperatures, accumulations of organic matter and fine sediment, and low dissolved oxygen levels will be diminished by severe drought, whereas generalist species with broad tolerances will flourish with hydroclimatic changes, at least until dissolved oxygen levels become very low or streams dry. Although most of the responses to climate change predicted by Pyne and Poff (2017) were consistent with our observations, one notable exception was the most common mayfly *Baetis*. We saw significant late drought declines of *Baetis* mayflies, as well as of the most common large predator, the perlid stonefly *Hesperoperla*, raising the possibility of altered food webs in these mountain streams with changing climate.

Examinations of stream community responses to extreme drought may allow us to evaluate and predict the impacts of climate change, including temperature and hydrological alterations, on stream ecosystems. The high frequency and synchrony in low flow and high temperature conditions may act to both reduce invertebrate growth and survival and narrow the time available for recovery (Arismendi, Safeeq, Johnson, Dunham, & Haggerty, 2013). Knowledge of spatial and temporal variability in thermal and hydrological regimes that influence climate change impacts, however, will require long-term, regional monitoring networks covering streams varying in size, elevation, and hydrology (e.g. relative importance of groundwater versus snowmelt surface inflows).

Small, montane streams in many arid and Mediterranean climate regions may be particularly susceptible to low flows. The ecological effects of the early recession of headwater runoff due to loss of snowmelt in a rising rain-snow transition zone and variable sensitivity to changes in flow timing (Stewart, 2013) could be compounded

by expected reductions in stream flow (Ficklin, Stewart, & Maurer, 2012). As more frequent and prolonged droughts affect the Sierra Nevada and other montane systems, our results show an increased probability of alterations in stream invertebrate community structure and function and losses in species diversity.

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