Received: 13 March 2023 | Revised: 5 July 2024 | Accepted: 15 August 2024

DOI: 10.1111/fwb.14327

ORIGINAL ARTICLE

Freshwater Biology WILEY

Macroinvertebrate, algal and diatom assemblages respond differently to both drying and wetting transitions in non-perennial streams

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Abstract

1. Biological assemblages in streams are influenced by hydrological dynamics, particularly in non-perennial systems. Although there has been increasing attention on how drying impacts stream organisms, few studies have investigated how specific characteristics of drying and subsequent wetting transitions influence biotic responses via resistance and resilience traits.
2. Here, we characterized how hydrologic metrics, including those quantifying drying and wetting transitions as well as dry and wet phases, alter diversity and composition of three aquatic assemblages in non-perennial streams in southern California: benthic macroinvertebrates, soft-bodied algae and diatoms.
3. We found that flow duration prior to sampling was correlated with variation in macroinvertebrate and soft-bodied algal assemblage composition. The composition and richness of diatom assemblages, however, were predominantly influenced by the drying start date prior to sampling. Contrary to other studies, the duration of the dry phase prior to sampling did not influence the composition or richness of any assemblage. Although our study was conducted within a region in which each assemblage experienced comparable environmental conditions, we found no single hydrologic metric that influenced all assemblages in the same way.
4. The hot-summer Mediterranean climate of southern California likely acts as a strong environmental filter, with taxa in this region relying on resistance and resilience adaptations to survive and recolonize non-perennial streams following wetting. The different responses of algal and diatom assemblages to hydrologic metrics suggest greater resilience to drying and wetting events, particularly for primary producers.
5. As drying and wetting patterns continue to change, understanding biodiversity responses to hydrologic metrics could inform management actions that enhance the ecological resilience of communities in non-perennial streams. In particular, the creation and enhancement of flow regimes in which natural timing and

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Funding information
National Science Foundation

duration of dry and wet phases sustain refuges that support community persistence in a changing environment.

KEYWORDS
hydrologic metric, IRES, non-perennial stream, resilience, resistance

1 | INTRODUCTION

Non-perennial streams, which sometimes cease to flow and typically lose most or all surface water (Busch et al., 2020), experience hydrological transitions between dry and wet phases. The complex and variable hydrology of non-perennial streams, also commonly termed intermittent rivers and ephemeral streams, or IRES, is often simplified into two hydrological phases: a wet phase, in which surface water is connected and flowing, and a dry phase, in which surface water is absent (Busch et al., 2020). The persistence of aquatic biota in non-perennial streams is often linked to the duration of dry phases (Datry et al., 2014; Leigh & Datry, 2017; Soria et al., 2017). However, responses to drying and wetting may vary among assemblages due to the timing, rate of change and other hydrological characteristics of transitions between dry and wet phases. Assemblage responses may vary due to differences in traits conferring resistance (the ability to survive dry phases) and resilience (the ability to recover after water returns; Gasith & Resh, 1999; Fritz & Dodds, 2004; Bogan et al., 2017). This may be especially true in arid and Mediterranean-climate regions, where transitions can be rapid and differences in water availability between dry and wet phases can be extreme (Bogan & Lytle, 2007). Examining responses of diverse assemblages to drying and wetting transitions is necessary to understand biological persistence in non-perennial streams (Jaeger et al., 2014; Pumo et al., 2016).

Benthic macroinvertebrates, soft-bodied algae and diatoms have morphological, physiological, behavioural and life history traits that provide resistance to dry phases and resilience following wetting. Resistant taxa may take refuge in isolated pools that form as rivers dry (Bogan & Lytle, 2007; Robson et al., 2008; Stubbington et al., 2017). As these pools dry, taxa may also find refuge under leaf packs or in moist sediment, including benthic macroinvertebrates and diatoms that migrate vertically into the hyporheic zone (Robson et al., 2008; Stubbington et al., 2017; Wyatt et al., 2014). In addition to using refuges, many algae and diatoms have desiccation-tolerant, dormant life stages (cells or spores) that promote survival during a dry phase (Calapez et al., 2014; Robson, 2000; Stanley et al., 2004). Similarly, some benthic macroinvertebrates enter desiccation-tolerant states that persist within dry stream sediments (Stubbington & Datry, 2013). Subsequent wetting after dry phases often breaks the dormancy of resistant life stages (Sabater et al., 2017; Stubbington et al., 2017; Timoner et al., 2014). For example, in non-perennial streams in the arid southwestern USA, juvenile stoneflies (*Mesocapnia arizonensis*) can survive for several years underground and then resurface to develop rapidly during brief periods of stream flow (Bogan, 2017). Adaptations to promote drying resistance can be common in arid and Mediterranean-climate regions, where extreme drying disturbances occur regularly (Lytle & Poff, 2004).

Benthic macroinvertebrates, algae and diatoms in non-perennial streams also have resilience traits that enable recovery from refuges when surface water returns. Dispersal via flight and crawling overland may be the dominant mode of recolonization for macroinvertebrates in arid and semi-arid regions, where dispersal primarily stems from local perennial refuges (Boersma & Lytle, 2014; Bogan & Boersma, 2012). In addition, where perennial reaches occur upstream of non-perennial ones, recovery via both active and passive drift from these refuges can occur during wetting transitions (Doretto et al., 2018; Fournier et al., 2023; Romaní & Sabater, 1997). Benthic macroinvertebrates also recover by active swimming or crawling from downstream reaches once stream connectivity is restored (McArthur & Barnes, 1985).

Taxon-specific differences in traits conferring resistance and resilience combine to determine how assemblages respond to hydrological dynamics. Taxonomic richness of aquatic assemblages typically decreases with increasing dry-phase duration (Datry et al., 2014; Robson & Matthews, 2004; Sabater et al., 2016). However, less is known about biological responses to other aspects of the hydrological cycle, including the characteristics of drying and wetting transitions, such as the rate of change. For example, slower drying gives organisms more time to move into refuges (Archdeacon & Reale, 2020; Vander et al., 2016) or make metabolic adjustments that promote desiccation tolerance (Strachan et al., 2015). In contrast, rapid bursts of precipitation can lead to short periods (<1-3 days) of stream wetting, which could trigger the development of desiccation-sensitive organisms from dormant, desiccation-tolerant life stages. Despite evidence of resilience to these 'false starts' (Strachan et al., 2016; Stubbington et al., 2016), in arid, flashy streams, such events may expose sensitive individuals to desiccation once the short-term flow ends. The rate and magnitude of wetting may also alter biological diversity and composition. Wetting can mobilize substrate and displace organisms (Olsen & Townsend, 2005), particularly in regions with high seasonal variability in precipitation where non-perennial streams are weted by flash flood events (Mosisch, 2001; Ward & Stanford, 1995). Despite the importance of hydrological dynamics on biodiversity, to our knowledge, no studies have examined how quantitative measures of the timing, duration and rate of drying and wetting shape the composition of biological assemblages in non-perennial streams.

Mediterranean climate-regions with hot, dry summers are ideal locations to study relationships between hydrological transitions and aquatic assemblages because they experience extreme seasonal and interannual fluctuations in hydrology, and their aquatic species have evolved traits to persist despite high hydrological variability. The timing of annual dry and wet seasons is often predictable in such regions, allowing species to evolve synchronized life history strategies to survive stream drying (Lytle & Poff, 2004); however, arid streams are also subject to increasingly stochastic multiyear droughts and extreme precipitation events (Ban et al., 2023; Zamora-Reyes et al., 2022). Here, we characterized how novel hydrologic metrics describing dry and wet phases and their transitions influenced three aquatic assemblages: macroinvertebrates, soft-bodied algae and diatoms in southern California, USA (Figure 1 and Table 1). We made four predictions regarding how the three assemblages respond to key hydrologic metrics. We predicted that (1) the duration of the wet phase prior to sampling (Wet Duration) would influence assemblage composition and taxonomic richness, with a positive relationship between duration and richness reflecting increasing time for recolonization and recovery. We predicted that (2) faster drying rates (Recession Slope) would decrease richness by reducing the time organisms have to move to refuges or enter desiccation-tolerant states. We also predicted that (3) richness would decrease with more false starts during the dry phase (False Starts per Duration), due to the loss of desiccation-sensitive organisms. Finally, we predicted that (4) the length of the dry phase (Dry Duration) would not influence these assemblages, due to the well-adapted resistance and resilience strategies of taxa in arid and semi-arid non-perennial streams.

2 | METHODS

2.1 | Study area

This study was conducted in southern California, USA, between 34° and 32° north and 116.4° and 117.6° west in 2015–2017. Southern California has a Mediterranean climate with cool, wet winters and hot, dry summers, with almost all precipitation (dominated by rainfall) occurring between October and May (Luo et al., 2017; hot and warm-summer Mediterranean Köppen climate classes; Figure 2); (Supporting Information 1). Most streams across this region are non-perennial and typically dry completely in the summer (Mazor et al., 2014). The study sampling locations are primarily classified as unimpacted reference streams using California's minimum criteria

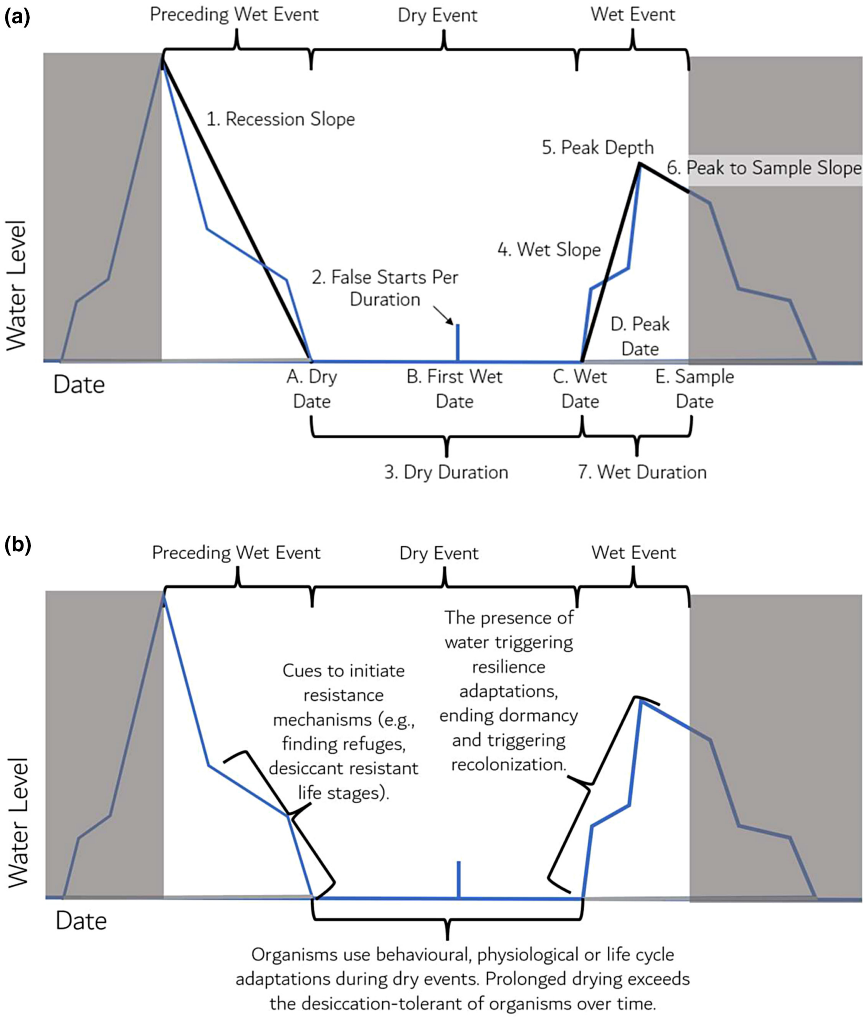

FIGURE 1 Conceptual hydrograph illustrating a dry event preceded and followed by wet events, as analysed in the present study. (a) A visual representation of the calculated hydrologic metrics. For detailed metric calculation descriptions, see Table 1. (b) Representations of resistance and resilience adaptations initiated during key periods of the hydrograph. Wide brackets indicate the variation between and within species to various cues.

TABLE 1 Description of hydrologic metrics (numbers) and important dates (letters) from Figure 1 and how each metric relates to mechanisms of resistance or resilience for the taxa included in the study.

Hydrologic metric	Calculation description	Relevance to resistance/resilience mechanisms	Citations
Recession Slope (1)	Median of the daily differences in water level between the peak from the preceding Wet Event and the Dry Date	Slopes indicate how much time organisms have to initiate behavioural, physiological, or life cycle adaptations such as moving into refuges, entering dessication-tolerant life stages. Steeper slopes indicate less time for those responses to occur	(Stanley et al., 2004; Wyatt et al., 2014; Barrios, 2015; Bogan et al., 2017; Stubbington et al., 2017)
Dry Date (A)	First Julian day followed by ≥10 consecutive days where water level = 0	Variability in the timing of Dry Date could reduce persistence of organisms with synchronized life cycles to predictable drying	(Cover, Seo & Resh, 2015; Stubbington et al., 2017; Bogan, 2017)
Dry Duration (3)	Number of days between the Dry Date and the Wet Date	As the Dry Duration increases, taxon-specific desiiccation tolerances may be exceeded	(Stanley et al., 1994; Lytle, Bogan & Finn, 2008; Acuña et al., 2015)
First Wet Date (B)	Earliest Julian day after the Dry Date when water level was >0, including false starts	Highlights when organisms potentially first receive signals to end dormancy and initiate recovery	(Chester & Robson, 2011; Timoner et al., 2014)
False Starts per Duration (2)	Number of periods between the Dry Date and the Wet Date where water level was >1	Indication of stream flashiness. False starts may trigger the end of dormancy, exposing vulnerable life stages to dry conditions	(Lytle et al., 2008; Schwalm et al., 2017)
Wet Date (C)	The first Julian day where water level was >0 in the time period including the Biological Sample Date	Similar to Dry Date, variability could desynchronize the timing of wetting and life history cycles. Due to multicollinearity, not included in models (Supporting Information 1)	(Cover et al., 2015; Stubbington et al., 2017; Bogan, 2017)
Wet Duration (7)	Number of days between the Wet Date and the Biological Sample Date	Indicates how long the site has been wet, quantifying the time resilient taxa had to recover via colonization and reproduction	(Pineda-Morante et al., 2022; Robson & Matthews, 2004)
Wet Slope (4)	Median of the daily differences in water level between the Wet Date and the Peak Date	Steeper slopes indicate greater mobilization of sediments and displacement of organisms downstream	(Fisher et al., 1982; Corti & Datry, 2012)
Peak Date (D)	The Julian day after the Wet Date with the maximum water level	No specific resistance or resilience mechanism predicted, used to calculate other metrics. Not included in models	N/A
Peak Depth (5)	Maximum water depth during the time period containing the Biological Sample Date	Given the similar size of the streams in this study, a proxy for the amount of the maximum amount of wetted habitat available upon wetting, with more habitat hypothetically leading to more habitat heterogeneity (Supporting Information 1)	(Gostner et al., 2013)
Peak to Sample Slope (6)	Median of the daily differences in water level between the Peak Date and the Biological Sample Date	Indicatation of how flow is sustained over time. For example, shallow slopes may indicate less flashy and more predictable systems	(Lytle et al., 2008)
Biological Sample Date (E)	The Julian day each site was sampled	May influence the occurrence of species with seasonal life cycle stages. Not included in models	(Gasith & Resh, 1999; Verberk, Siepel & Esselink, 2008)

for identifying reference conditions (Ode, Fetscher, & Busse, 2016) and have natural land cover (chaparral, grassland and oak or pine forest; Figure 2; Mazor et al., 2014).

From 2012 to 2015, California experienced one of the most severe droughts in the state's recorded history (He et al., 2017; Williams et al., 2015), followed by a winter (2015–2016) with below-average precipitation and then a winter (2016–2017) which was the second wettest on record (Singh et al., 2018). Our study spans 2015–2017, encompassing a wide range of hydrological patterns. It is likely that assemblages were influenced by the legacy effects of this severe drought, with such events reducing the abundance and richness of assemblages, including macroinvertebrates (Bêche et al., 2009).

2.2 | Data collection

Californian agencies (including the California Environmental Protection Agency: San Diego Regional Water Quality Control Board and the California Department of Fish and Wildlife) collected hydrological and biological data following standardized procedures, as part of long-term reference stream monitoring programs (Ode, 2007; Ode, Rehn, et al., 2016). One Onset HOBO® U20 pressure transducer logger (Cape Cod, MA, USA) was installed at each site during the autumn dry season (September–November) to record average reach-scale flow conditions. Pressure transducer loggers provide a good proxy for discharge in small, dryland intermittent streams (Caldwell et al., 2018; Lasater et al., 2022). Loggers were deployed at the

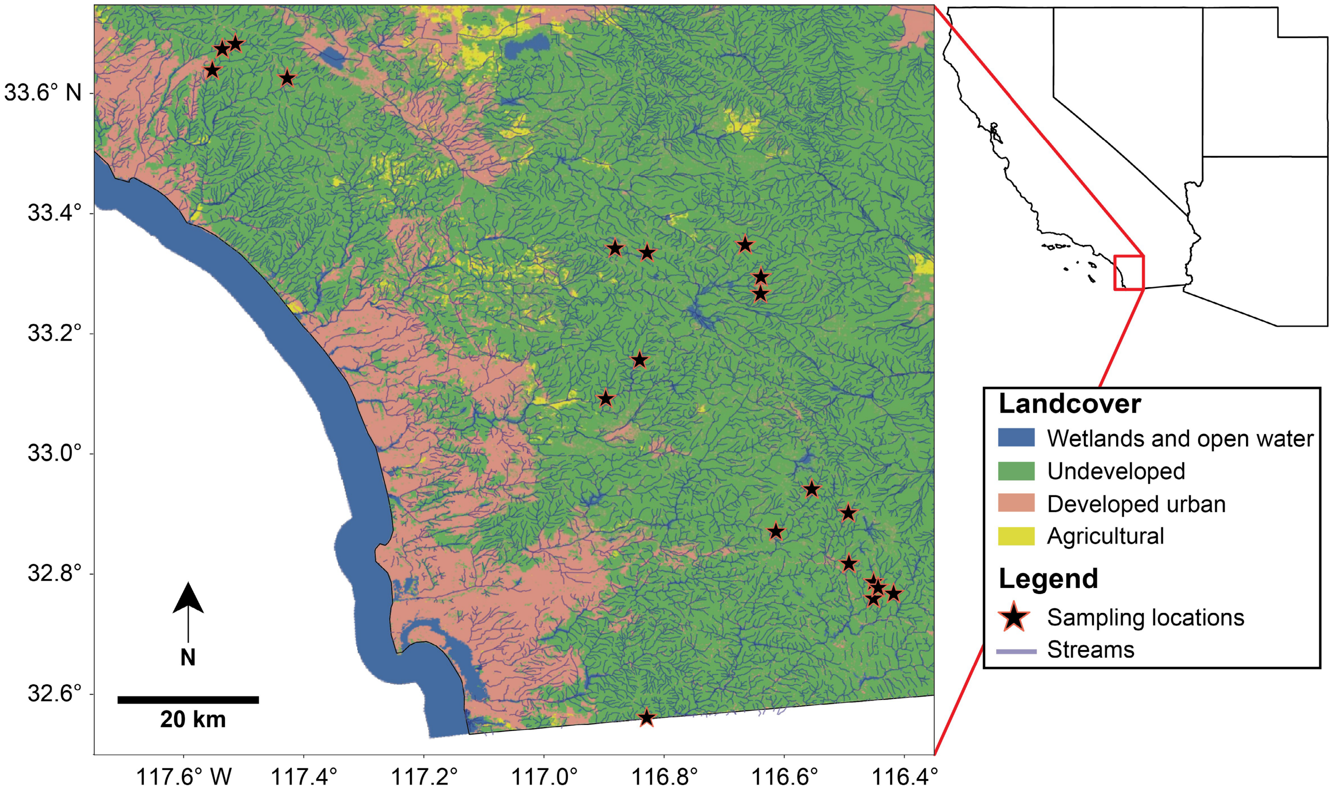

FIGURE 2 Study site locations in Southern California with landcover in the region (Supporting Information 1).

transition point between riffles and pools at the lowest point within the cross-section of the stream channel. Loggers recorded water level (depth) and temperature at 6-h intervals. Sites were visited annually to validate readings and retrieve data. In addition, conductivity loggers were deployed to assess the accuracy of loggers in detecting dry days.

Benthic macroinvertebrates, soft-bodied algae and diatoms are ubiquitous in freshwater and commonly used in stream biomonitoring (e.g. Rosenberg & Resh, 1993; Stancheva & Sheath, 2016). Each assemblage was sampled between March and May, typically at least 4–6 weeks after the most recent wetting event (Ode, 2007; Ode, Rehn, et al., 2016). During each sampling event, environmental variables were measured: water depth, wetted width, percent canopy cover, temperature, conductivity, pH, alkalinity (as $CaCO_3$) and the proportion of the reach that was riffle, pool or run (as described in Ode, 2007; Ode, Fetscher, & Busse, 2016). To collect macroinvertebrates, 150-m stream reaches were divided into 11 lateral transects. At each transect, a 500-μm D-frame kick net was used to sample 0.09 m^2 of streambed by kicking and scrubbing substrate to dislodge benthic macroinvertebrates from representative habitat types (riffles, pools, runs). Macroinvertebrates were sampled from alternating points at 25%, 50% and 75% (right, centre and left) of the channel width along the stream reach. The resulting 11 samples (0.99 m^2 total) were combined into a single composite sample, which was then preserved in ethanol. Benthic macroinvertebrates were identified to the highest taxonomic resolution feasible (species for most insects, sub-family for Chironomidae, genera for mites and snails and class for oligochaetes, flatworms and nematodes; Richards & Rogers, 2011) and each taxon enumerated.

Benthic soft-bodied algae (including macroalgae, microalgae and cyanobacteria) and diatoms were sampled along the same 11 transects from available substrates (e.g. bedrock, cobble, gravel, sand, silt and wood; Ode, 2007; Ode, Fetscher, & Busse, 2016). Soft-bodied algae and diatoms were removed from substrates by manual brushing or scraping and rinsing. Diatom samples and soft-bodied algae samples were fixed using formalin and glutaraldehyde, respectively. Soft-bodied algal samples were processed following Stancheva et al. (2015). At least 600 diatom valves from each sample were identified to the lowest taxonomic level possible (mostly to genus and morphological species) and counted on permanent slides prepared from cleaned material. We calculated relative abundances for both soft-bodied algae and diatoms. In addition to quantitative soft-bodied algae samples, qualitative samples were collected by hand-picking or scraping organisms observed within the 150-m reach. These samples were collected to record taxa growing on other surfaces, including non-mineral substrates such as vegetation, which were not included in quantitative sampling. These algae were identified and included in calculations of taxonomic richness, but not relative abundance. Due to fundamental differences in morphology, development and functional roles, we analysed soft-bodied algae separately from diatoms.

We selected sampling events at which macroinvertebrate, soft-bodied algae and diatoms were collected during a period that included a preceding wet phase, a dry phase and a wet phase that included the sampling event. In total, we analysed 27 sampling events (including all three assemblages) across 20 sites (Figure 2). For each biological sample, we resolved the final taxon list for each assemblage to avoid overestimating richness (e.g. in the family Baetidae, researchers identified most organisms to genus, thus we excluded those identified to family; Cuffney et al., 2007).

2.3 | Hydrologic metrics and other environmental predictors

We used mean daily water level data to estimate hydrologic metrics (Figure 1). To define the start date, we identified the beginning of the wet event preceding a dry event. Each hydrograph thus contained a dry phase between two wet phases (Supporting Information 1). We identified hydrological events using the 'dygraphs' R package and then visually checked each hydrograph (Vanderkam et al., 2018; Supporting Information 1). We calculated the hydrologic metrics as described in Table 1. We defined a stream as 'dry' when the average daily water level equalled zero for ≥10 consecutive days. This definition is important in this region because short, often sudden-onset heavy rainfall events may lead to stream wetting events that persist for hours to a few days, that is, 'false starts'. Most false starts in this study lasted 1–3 days (Supporting Information 1).

We used Pearson correlations to assess multicollinearity among predictor variables using the 'performance' R package (Lüdecke et al., 2022). We removed multicollinear variables with an absolute correlation coefficient >0.70, retaining variables that were most relevant to our predictions, that is, 10 hydrologic predictors (Table 1, Supporting Information 1; Hammond et al., 2021; Price et al., 2021; Zipper et al., 2021). Final models included all environmental variables except for water depth, which was correlated with the proportion of pool habitat ($r = 0.79$).

2.4 | Data analysis

To test our predictions, we related macroinvertebrate, soft-bodied algal and diatom assemblages separately to metrics describing drying and wetting transitions as well as standard metrics describing dry and wet phases (Table 1). We calculated relative abundances and two alpha diversity metrics, taxonomic richness and Hill-Shannon diversity, for each assemblage in the R packages 'vegan' (Oksanen et al., 2011) and 'hillR' (Li, 2018). We chose Hill-Shannon as a measure of alpha diversity because Hill numbers vary proportionally with taxon gains and losses, and Hill-Shannon diversity is more sensitive to rare taxa than other Hill numbers (Aspin & House, 2022; Roswell et al., 2021).

Six of the 20 sites were sampled two to three times over the 3 years of our study, resulting in 14 out of 27 samples with a temporal component. Although temporal replicates are often removed from analyses to avoid pseudoreplication, the extent of stream fragmentation and extreme environmental filtering in our study region means that aquatic communities are often more correlated spatially across streams than temporally within the same stream (Bogan et al., 2013). To test sample independence and to quantify the potential effect of year on the assemblage data, we ran linear mixed effect models in the 'lme4' package (Bates et al., 2022) on the 14 repeated samples. We included the alpha diversity metrics as response variables, all the hydrologic and other environmental variables as predictors, year as a fixed effect and site as a random effect. Year did not significantly influence any assemblage, except for Hill-Shannon diversity of algae (Supporting Information 1). We thus included all 27 samples in further analyses and did not include year in models. Thus, while our study includes both spatial and temporal components, most of the variation explained here is spatial. We also ran linear models for each hydrologic metric and environmental variable with year as the predictor to investigate potential effects of the 2012–2015 drought (Supporting Information 1).

2.4.1 | Assemblage composition and association with hydrologic metrics

To identify hydrologic metrics associated with the composition of each assemblage, we created a non-metric multidimensional scaling (NMDS) ordination with a Bray-Curtis distance matrix of log-transformed relative abundance in vegan (Oksanen et al., 2011). Due to the low stress (<0.20) and stable two-dimensional solutions for each NMDS, we retained all taxa in our analysis (McCune et al., 2002). We used the vegan 'envfit' function to fit linear correlations of hydrologic metrics and environmental variables ($p < 0.015$) to the NMDS ordinations with 999 permutations (Oksanen, 2011). To facilitate comparison across assemblages, we rotated all ordinations to align NMDS axis 1 with the hydrologic metric Wet Duration, because Wet Duration explained the most variance in of the three ordinations. We tested the effects of the sampling year with multi-response permutation procedures (MRPP) in vegan.

2.4.2 | Diversity responses to hydrologic metrics

To identify hydrologic metrics that predicted richness and Hill-Shannon diversity, we ran general linear models. For each assemblage and diversity metric, we ran a global model that included all 10 hydrologic metrics and year as predictors and the diversity metric as the response variable. We also ran univariate models for each individual hydrologic metric and compared these with a null model without any hydrologic metrics (predictor = 1), which enabled us to directly test the impacts of Wet Duration, Recession Slope, False Starts per Duration and Dry Duration on assemblage richness, thus testing our four predictions. Due to the relatively small number of sites relative to predictors, we did not include the environmental variables or include site as a random effect. Site had a negligible effect on our results when included as a random effect, suggesting some level of sample independence (Supporting Information 1). We compared models using Akaike information criteria values corrected for small sample sizes (AICc; Warren & Seifert, 2011; Galante et al., 2018), calculated in the 'MuMIn' package (Bartoń, 2022). To determine if models differed from the baseline null models, we set an absolute AICc difference of 3 (Lu et al., 2016).

Models of algal richness included qualitative and quantitative samples, while models of algal Hill-Shannon only included quantitative samples. We used *R* for all analyses (R Core Team, 2020).

3 | RESULTS

3.1 | Hydrologic metrics and environmental variables

As expected for streams in arid regions, hydrologic metrics and some environmental variables were highly variable across the 27 hydrological events. Across the 10 hydrologic metrics, only Peak Depth (adjusted $R^2=0.55$, $p<0.01$) and Wet Duration (adjusted $R^2=0.33$, $p<0.01$) varied among years (Supporting Information 1). Two environmental variables differed among years, the proportion of riffles (adjusted $R^2=0.32$, $p<0.01$) and wetted width (adjusted $R^2=0.20$, $p<=0.01$; Supporting Information 1); each was larger in non-drought years.

3.2 | Biological diversity summary

Across the 27 samples, 152 macroinvertebrate, 207 soft-bodied algae and 225 diatom taxa were identified, with mean richness of 13, 5 and 16 taxa per sample, respectively (Table 2). An additional 11 soft-bodied algae taxa were collected with qualitative sampling. Eleven of the most common macroinvertebrate taxa, present in ≥70% of samples, were either Diptera or Ephemeroptera, including nine from the Chironomidae. The four most common soft-bodied 'algae' were cyanobacteria from four families (Pseudanabaenaceae, Chroococcaceae, cand Aphanothecaceae). Nine diatom taxa were present in ≥70% of samples, including three taxa from the Achnanthidiaceae and two from Bacillariaceae. For more information on common and rare taxa, see Supporting Information 1.

TABLE 2 Summary statistics of taxonomic richness (a) and Hill-Shannon values (b) for macroinvertebrates, soft-bodied algae and diatoms. Algal richness includes quantitative and qualitative algal samples while soft-bodied algae Hill-Shannon values only include quantitative samples to account for relative abundances.

	Macroinvertebrates	Soft-bodied algae	Diatoms
(a) Richness			
Minimum	13.0	5.0	16.0
Mean	33.4	28.9	36.9
Maximum	52.0	72.0	69.0
SD	8.8	14.7	16.1
(b) Hill-Shannon Diversity			
Minimum	1.7	1.1	3.8
Mean	13.4	5.8	15.8
Maximum	29.5	18.2	35.3
SD	6.1	4.5	9.6

Abbreviation: SD = Standard deviation.

3.3 | Assemblage composition and association with hydrologic metrics

Benthic macroinvertebrate assemblages varied among years (Figure 3a, MRPP: A = 0.040, $p=0.002$; Supporting Information 1). Samples from 2017 clustered in the upper right of the ordination while samples from 2015 and 2016 overlapped and were widely distributed. The assemblage composition of soft-bodied algae and diatoms from all years overlapped (soft-bodied algae: Figure 3b, MRPP: A = 0.0006, $p=0.940$; diatoms: Figure 3c, MRPP: A = 0.019, $p=0.640$). Soft-bodied algal samples were more clustered within the ordination space whereas diatom samples were particularly dispersed.

All assemblages responded more strongly to hydrologic metrics than to environmental variables (Figure 3 and Table 3). Macroinvertebrates and soft-bodied algae had the strongest correlation with Wet Duration, supporting our first prediction ($R^2=0.59$; $R^2=0.49$, respectively). Diatoms had the strongest correlation with Dry Date ($R^2=0.40$, $p=0.005$). Contrary to predictions 2 and 3, Recession Slope and False Starts per Duration were not associated with the composition of any assemblage. As per our fourth prediction, no assemblage was correlated to Dry Duration. Algal assemblages were also correlated with the Peak to Sample Slope ($R^2=0.27$, $p=0.012$). Only benthic macroinvertebrates were correlated with any environmental variables, namely canopy cover ($R^2=0.407$, $p=0.005$) and the proportion of riffle habitat ($R^2=0.357$, $p=0.012$).

3.4 | Diversity responses to hydrologic metrics

Contrary to our first prediction, Wet Duration did not influence diversity metrics. All hydrologic metrics explained negligible variance in metrics representing both macroinvertebrate and algal assemblages: False Starts per Duration explained the most variance in macroinvertebrate assemblages ($R^2=0.06$), partially supporting our third prediction, while Peak Depth explained the most variance for algal assemblages ($R^2=0.04$). Models including Recession Slope consistently performed better than null models (AICc difference >3), although they explained virtually no variance in any assemblage ($R^2<0.01$). Models including only Recession Slope performed the best for macroinvertebrates (AICc = 192.81) and algae (AICc = 218.64), despite little variance explained, partially supporting our second prediction. Richness was not predicted by Dry Duration, supporting our final prediction. Dry Date best predicted diatom assemblage richness ($R^2=0.26$) and performed better than the null model (AICc = 223.8), although the global model explained the most variance for diatom assemblages ($R^2=0.27$; Table 4). Results for Hill-Shannon diversity were largely redundant and are presented in Supporting Information 7.

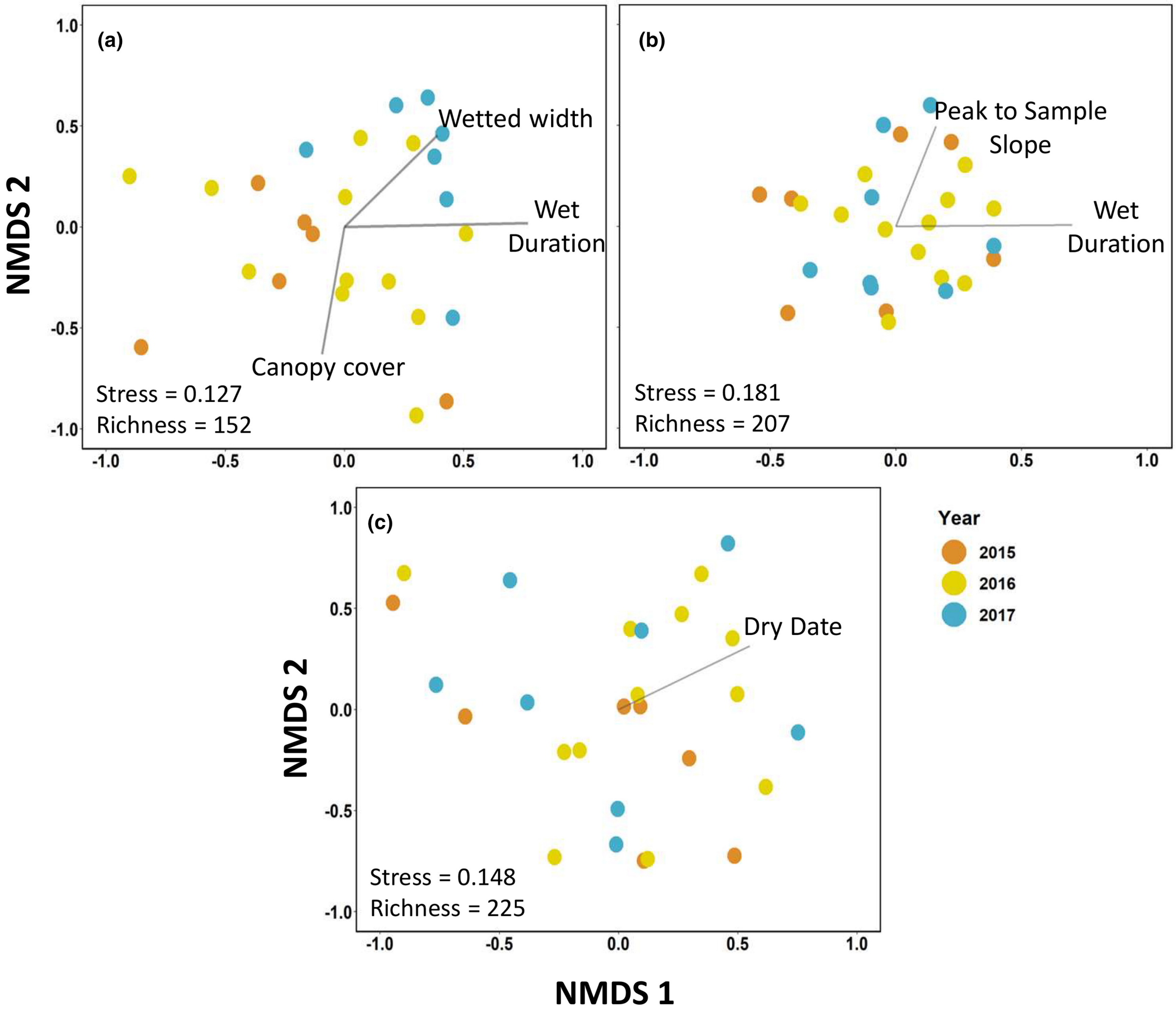

FIGURE 3 Two-dimensional NMDS ordinations for (a) macroinvertebrate, (b) soft-bodied algal and (c) diatom assemblages. The NMDS stress and total taxonomic richness for each assemblage are displayed. Ordinations were rotated to align the Wet Duration metric with NMDS axis 1 to facilitate comparison among assemblages. Additional vectors are significant hydrologic metrics and environmental variables ($p < 0.015$), with the length of the corresponding vector related to the strength of the relationship (R^2 value; Table 3).

4 | DISCUSSION

We investigated responses of macroinvertebrate, soft-bodied algal and diatom assemblages to novel drying and wetting transitions as well as dry and wet phase characteristics in non-perennial streams in Mediterranean southern California. We found contrasting responses of the three assemblages to hydrologic metrics, suggesting that their diverse morphological, physiological, behavioural and life history adaptations to extreme hydrological variability likely determine how assemblages respond to the transitions between dry and wet phases. We found partial support for our first prediction: Wet Duration influenced macroinvertebrate and algal assemblage compositions while an unpredicted hydrologic metric, Dry Date, had the largest impact on diatom composition and richness. We also found partial support for our second prediction: Recession Slope appeared to influence macroinvertebrate and algal richness, despite explaining little variance. The number of Fase Starts per Duration did not influence assemblage composition or diversity, contrary to our third hypothesis. Finally, our fourth prediction, that Dry Duration would not influence assemblage diversity or composition, was supported across the three assemblages. Collectively, these results demonstrate how the extreme aridity of southern California likely acts as a strong regional filter that limits the species pool to taxa with specialized resistance and resilience traits.

4.1 | Prediction 1: Influence of Wet Duration

Our first prediction, that the duration of the wet phase prior to sampling would explain spatial variation in assemblage composition and richness, was partially supported. Wet Duration was significantly associated with the composition of both macroinvertebrate and soft-bodied algal assemblages, reflecting the

TABLE 3 Correlations between hydrologic metrics (a) and environmental variables (b) and the NMDS ordinations for each assemblage.

	Benthic macroinvertebrates		Soft-bodied algae		Diatoms	
	R^2	*p*-value	R^2	*p*-value	R^2	*p*-value
(a) Hydrologic metric						
Dry Date	0.103	0.264	0.303	0.017	**0.402**	**0.005**
Dry Duration	0.003	0.965	0.013	0.887	0.076	0.420
False Starts per Duration	0.003	0.968	0.114	0.230	0.001	0.984
First Wet Date	0.054	0.518	0.125	0.207	0.015	0.836
Peak Date	0.156	0.155	0.257	0.025	0.008	0.925
Peak Depth	0.320	0.017	0.116	0.241	0.031	0.695
Peak-to-Sample Slope	0.071	0.415	**0.270**	**0.012**	0.180	0.094
Recession Slope	0.038	0.640	0.042	0.589	0.138	0.188
Wet Slope	0.207	0.060	0.138	0.192	0.256	0.031
Wet Duration	**0.594**	**0.001**	**0.493**	**0.001**	0.148	0.158
(b) Environmental variable						
Alkalinity	0.257	0.035	0.186	0.108	0.056	0.518
Canopy cover	**0.407**	**0.005**	0.046	0.589	0.142	0.173
pH	0.133	0.184	0.199	0.072	0.036	0.666
Pool	0.013	0.867	0.120	0.219	0.095	0.319
Riffle	**0.357**	**0.012**	0.032	0.687	0.037	0.668
Run	0.060	0.507	0.000	0.998	0.023	0.788
Conductivity	0.079	0.379	0.025	0.748	0.180	0.111
Temperature	0.239	0.054	0.249	0.048	0.029	0.714
Wetted width	0.285	0.021	0.083	0.353	0.175	0.122

Note: Metrics with $p < 0.015$ are bolded.

TABLE 4 Linear model results describing assemblage richness to hydrologic metrics.

	Benthic macroinvertebrates		Soft-bodied algae		Diatoms	
Hydrologic predictor	R^2	AICc	R^2	AICc	R^2	AICc
Dry Date	0.00	198.99	−0.02	227.14	**0.26**	**223.77**
Dry Duration	0.02	198.23	−0.04	227.72	0.01	231.59
False Starts Per Duration	0.06	197.31	−0.04	227.64	−0.02	232.42
First Wet Date	−0.03	199.64	−0.01	227.05	−0.02	232.24
Peak Date	0.05	197.41	0.01	226.46	−0.03	232.53
Peak Depth	−0.02	199.30	0.04	225.44	0.04	230.60
Peak-to-Sample Slope	−0.04	199.82	−0.03	227.50	0.05	230.38
Recession Slope	**−0.04**	**192.81**	**0.00**	**218.64**	−0.03	225.02
Wet Slope	0.02	199.36	−0.02	227.19	−0.02	232.32
Wet Duration	0.01	198.70	−0.04	227.63	−0.03	232.67
Global	−0.10	222.99	−0.22	252.27	0.27	244.82
Null		**197.39**		**225.20**		**230.30**

Note: Columns indicate R^2 and AICc values. AICc values at least three lower than null models are bolded.

importance of flow duration for recovery after wetting; in general, the longer streams flow, the greater the opportunity for taxa to recover (Mackie et al., 2013). Aerial colonization is typically the principal method by which macroinvertebrates recolonize arid and semi-arid streams, with some taxa capable of flying long distances (Bogan & Boersma, 2012; May, 2019). In contrast, soft-bodied algae can recolonize via drift from upstream refuges and/or repopulate from the sediment upon wetting (Garg & Maldener, 2021; Robson et al., 2008; Sabater et al., 2017). For example, *Zygnema*, a soft-bodied charophyte alga from non-perennial streams in southern California, can recover upon wetting due to quick germination of desiccation-tolerant spore-like cells (Fuller, 2013). Such resistant life stages allow algal assemblages to recover within as little as 2 weeks after wetting (Dodds et al., 2004). Similarly, benthic macroinvertebrate populations can recover within 4 weeks in small, non-perennial prairie streams (Fritz & Dodds, 2004) and in Mediterranean California (Bêche & Resh, 2007) although recovery times vary widely across families (Fowler, 2004; Sarremejane et al., 2019).

Unlike macroinvertebrates and algae, we found no relationship between Wet Duration and spatial variation in diatom assemblages. Rather, diatom assemblage composition and diversity were most influenced by the Julian date on which the preceding dry event began, highlighting the importance of dry-phase timing for this taxonomic group. Many diatoms identified in this study produce resting spores, likely an adaptation that allows their persistence in non-perennial streams with predictable seasonal cycles (Bonada & Resh, 2013). In addition, diatoms have different colonization patterns than other types of algae, tending to persist in situ in dried biofims rather than recolonizing from refuges by drift (Robson et al., 2008), altering their responses to hydrological dynamics. Probable cues to initiate desiccation-tolerant behavioural or morphological adaptations include seasonal water limitation, nutrient limitation and changes in temperature, further indicating the influence of Dry Date on diatom assemblages.

4.2 | Predictions 2 and 3: Influence of Recession Slope and False Starts per Duration

The richness of benthic macroinvertebrates and algae were related to the Recession Slope of the previous dry phase, partially supporting our second prediction. We also predicted that short-duration flow events could expose emerging organisms to dry conditions ultimately influencing diversity, but False Starts per Duration was not a significant predictor of diversity metrics for any assemblage. While some algae and diatoms can repopulate within minutes of wetting (Timoner et al., 2014), they may be able to shift back to desiccation-tolerant forms just as quickly, making them unaffected by false starts. Similarly, invertebrates can survive and develop in damp sediment without surface flow (Strachan et al., 2016; Tronstad et al., 2005). Equally, flows of only 1–3 days may be too short to break the dormancy of many macroinvertebrates. However, given the low variance in diversity metrics explained by the hydrologic metrics, we hesitate to make strong inferences about biological community dynamics based on these results. Therefore, we suspect that environmental variables not included in the models may be more important influences on assemblage diversity.

4.3 | Prediction 4: Influence of Dry Duration

Following our fourth prediction, the length of the previous dry phase did not influence the composition or richness of any assemblage, in contrast to prior research (Miao et al., 2023; Pineda-Morante et al., 2022; Sabater et al., 2016; Soria et al., 2017). Their lack of response to Dry Duration suggests that the taxa in this region are well adapted to dry phases (Bogan et al., 2017). Southern California is an arid region dominated by non-perennial streams (Mazor et al., 2014), and its aridity acts as a selective regional filter on species distributions that favours organisms with adaptations which facilitate survival during dry phases (Weiher & Keddy, 1995). In addition, this region has high interannual climatic variability, leading to variable hydrological patterns and biological communities (Bêche & Resh, 2007).

While our results suggest a lack of response to the duration of the dry phase, logger placement in pool-riffle transitions could have led to misleading ecohydrological relationships if pools persisted during dry phases; the availability and spatial distribution of refuges such as perennial pools can alter recolonization patterns across taxa (Crabot et al., 2020; Fournier et al., 2023; Sarremejane et al., 2021). However, our study sites were selected to avoid groundwater-fed pools (Supporting Information 1), which are found within the region and typically dry 8–12 weeks after dry-phase onset (U.S. Fish and Wildlife Service Ventura Office, 2023). Nonetheless, some pools may have been present during the drying transition and into the dry phase. Regardless, our results suggest the arid environment of southern California limits the regional species pool to taxa able to persist during seasonal dry phases.

4.4 | Variable responses and environmental predictors

The lack of consistency in predictive metrics across assemblages could reflect different traits influencing biological responses to drying, such as differences in life cycle duration and dispersal distance. Many macroinvertebrates exhibit a slower response to environmental stressors than primary producers (Dodds et al., 2004; Johnson & Hering, 2009). However, diatoms and soft-bodied algae share many broad traits, such as desiccation-resistant forms and fast reactivation upon wetting (Sabater et al., 2017). In our study, these taxa responded to different aspects of the hydrological regime: Wet Duration for soft-bodied algae and Dry Date for diatoms. Soft-bodied algae often have larger multicellular thalli which are covered by extracellular layers of mucilage. Additionally, thick cellulose walls in chlorophyte and other green filamentous algae are sometimes calcified or iron-impregnated, which may support their long-term survival during dry phases (Scarsbrook & Townsend, 1993). The thick-walled resting spores and zygotes formed by many filamentous cyanobacteria and algae provide long-term protection from dry phases. In addition, soft-bodied algae proliferate quickly upon wetting due to the fast germination of their resting stages (e.g. spores, akinetes and zygospores) that persist in situ, and thus show stronger response to Wet Duration.

In contrast, diatoms are unicellular organisms with desiccation-tolerance strategies limited mainly to formation of resting spores and resting cells by some species, which may make diatom assemblages more vulnerable to dry phases (Tornés et al., 2021). Diatoms tend to have higher dispersal rates and shorter generation times compared to soft-bodied algae, allowing for quick recovery and exploitation of epilithic space (Ledger et al., 2008; Nemes-Kókai et al., 2023; Schneider et al., 2012). Our research suggests that some diatoms may be resistant to changes in the duration of dry and wet phases, potentially providing functional redundancy in aquatic food webs during future climatic changes. Overall, these different responses to drying and wetting could increase the persistence of primary producers in non-perennial streams in this region.

Our multivariate analysis suggests that drying and wetting are not the only variables driving assemblage composition. We detected significant associations between macroinvertebrate assemblage composition and two non-hydrologic environmental variables: canopy cover and wetted width. Canopy cover determines how much sunlight reaches the streambed (Jansen et al., 2020) and thus can influence macroinvertebrate food sources (Aguiar et al., 2017). Canopy cover also influences carbon inputs into a stream as leaf litter while woody material increases habitat complexity (Kaufmann et al., 1999). Wetted width is positively correlated with habitat availability (Cowx et al., 1984; Dewson et al., 2007) and complexity (Cazaubon & Giudicelli, 1999), mediating the effects of predation and resource competition (Diehl, 1992). Further, increased habitat size and complexity often increase macroinvertebrate community diversity and abundance (Kovalenko et al., 2012) and lead to higher community stability through time (Mykrä & Heino, 2017). Thus, while we excluded environmental predictors from our linear models due to statistical power, variables such as canopy cover and wetted width may be important determinants of richness and may have shaped the effects of hydrologic metrics.

5 | CONCLUSIONS

Freshwater taxa are increasingly threatened as human water use and global climate change reduce surface water availability (Bogardi et al., 2012; Overpeck & Udall, 2020; Seager et al., 2013). Many previously perennial streams are becoming non-perennial (Jaeger et al., 2014; Pumo et al., 2016), leading to unprecedented shifts in drying and wetting patterns (Tramblay et al., 2021; Zipper et al., 2021). Here we demonstrate that assemblages vary in their responses to drying and wetting, highlighting a need for further studies exploring how characteristics of wetting and drying transitions alter the persistence of adapted resistant and resilient taxa. In addition, life history studies are required to better understand the consequences of changing wetting and drying characteristics for aquatic taxa. As drying and wetting patterns change (Tramblay et al., 2021; Zipper et al., 2021), understanding how assemblages respond to the multiple components of both flowing and drying is vital to stream management and conservation (Leone et al., 2023; Messager et al., 2023). Our study highlights differing biological responses to drying and wetting regimes that will become increasingly important for stream management in a drier future.

AUTHOR CONTRIBUTIONS

Conceptualization: M.H.B., S.C.C., K.S.B., C.N.J., D.C.A., M.Z., R.Stu. Developing Methods: M.H.B., S.C.C., K.S.B., C.N.J., D.C.A., C.L., R.M., A.P., M.Z., R.S. Conducting the research: M.H.B., C.N.J., C.L., R.M., R.S. Data Analysis: M.H.B., S.C.C., K.S.B., D.C.A., C.L., R.M., A.P. Preparation figures & tables: M.H.B, K.S.B, D.C.A. Data interpretation: M.H.B., S.C.C., K.S.B., C.N.J., D.C.A., C.L., R.M., A.P., R.S., R.S., M.Z. Writing: M.H.B., S.C.C., K.S.B., C.N.J., D.C.A., C.L., R.M., A.P., R.S., R.S., M.Z.

ACKNOWLEDGEMENTS

We thank Samuel Zipper, Joanna Blaszczak and Marion Chavarria Rivera for their initial contributions to this project. We also thank the researchers who collected the data used in this publication, in particular Andy Rehn, Shawn McBride and Nathan Mack from the California Department of Fish and Wildlife and Deborah Woodward and Carey Kowalski from the California Water Board. We thank the State of California's Surface Water Ambient Monitoring Program, which funded most of the data collection along with Jeff Geraci, who funded the collection of data from desert streams. We also thank the California Department of Fish and Wildlife Aquatic Bioassessment Lab at the California State University at Chico for identification of benthic macroinvertebrates. We thank Caryn Vaughn, Lawrence Weider, Katharine Marske and Thomas Neeson for their helpful comments and edits on the manuscript. This project is a product of the Dry Rivers Research Coordination Network, which is supported by funding from the USA National Science Foundation (NSF; 2207232). Additional personnel support was provided by the Aquatic Intermittency effects on Microbiomes in Streams (AIMS; NSF OIA 2019603). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the USA Government.

CONFLICT OF INTEREST STATEMENT

The authors confirm they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available through the California Environmental Data Exchange Network (CEDEN, www.ceden.org/about_us.shtml). Data also available through GitHub, along with code used in analyses (https://github.com/shelleydunkey/drying_wetting_regimes_assemblages).

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How to cite this article: Busch, M. H., Boersma, K. S., Cook, S. C., Jones, C. N., Loflen, C., Mazor, R. D., Stancheva, R., Price, A. N., Stubbington, R., Zimmer, M. A., & Allen, D. C. (2024). Macroinvertebrate, algal and diatom assemblages respond differently to both drying and wetting transitions in non-perennial streams. *Freshwater Biology*, *69*, 1568–1582. https://doi.org/10.1111/fwb.14327