Title

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 wet and dry phases, alter diversity and composition of three aquatic assemblages in non-perennial streams in southern California: benthic macroinvertebrates, soft-bodied (non-diatom) 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 preceding 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 suggests 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 with natural timing and duration of wet and dry phases that sustain refuges could support community persistence in a changing environment.

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 rivers, 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 any 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, Larned & Tockner, 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 wet and dry phases. Assemblage responses may differ 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 wet and dry 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, Olden & Pelland, 2014; Pumo *et al.*, 2016).

Benthic macroinvertebrates, soft-bodied algae, and diatoms have morphological, physiological, behavioral, 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; Wyatt *et al.*, 2014; Stubbington *et al.*, 2017). 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 (Robson, 2000; Stanley, Fisher & Jones, Jr., 2004; Calapez *et al.*, 2014). Similarly, some benthic macroinvertebrates enter desiccation-tolerant states that persist within stream sediments (Stubbington & Datry, 2013). Subsequent wetting after dry phases often breaks the dormancy of resistant life stages (Timoner *et al.*, 2014; Sabater *et al.*, 2017; Stubbington *et al.*, 2017). For example, in non-perennial streams in the arid southwestern USA, larval stoneflies (*Mesocapnia arizonensis)* can survive for several years underground and then resurface to reproduce 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), while taxa may also be well adapted to recolonize when flow resumes.

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 (Bogan & Boersma, 2012; Boersma & Lytle, 2014; Fournier *et al.*, 2022). 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 (Romaní & Sabater, 1997; Mackie *et al.* 2013; Doretto *et al.*, 2018). 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; Sabater *et al.*, 2016; Robson & Matthews, 2004). 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 onset gives organisms more time to move into refuges (Vander Vorste, Malard & Datry, 2016; Archdeacon & Reale, 2020) or make metabolic adjustments that promote desiccation tolerance (Strachan, Chester & Robson, 2015). In contrast, rapid bursts of precipitation can lead to short periods of stream wetting (<1–3 days), which could trigger the development of desiccation-sensitive organisms from dormant, desiccation-tolerant life stages. Despite evidence of resilience to these “false starts” (Strachan, Chester & Robson, 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 interseasonal variability in precipitation where non-perennial streams wet via flash flood events (Ward & Stanford, 1995; Mosisch, 2001). 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 wet and dry 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 (Zamora-Reyes, Black & Trouet, 2022; Ban, Li & Lettenmaier, 2023). Here, we characterized how novel hydrologic metrics describing wet and dry phases and their transitions influenced three aquatic assemblages: macroinvertebrates, soft-bodied algae, and diatoms in southern California, USA (Figure 1, 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 as faster rates could reduce 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 within the dry duration (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 34–32° north and 116.25–117.75° 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 (S.I.) 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 for identifying reference conditions (Ode et al. 2016) and have natural land cover (chaparral, grassland, and oak or pine forest; Figure 2; Mazor *et al.*, 2014).

From 2012–2015, California experienced one of the most severe droughts in the state's recorded history (Williams *et al.*, 2015; He, Russo & Anderson, 2017), followed by a winter (2015–2016) with below-average precipitation and then a winter (2016–2017) which was the second wettest winter 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

California 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 *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 to 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 transition point between riffles and pools at the lowest possible point within the cross-section of the stream channel. Loggers recorded water level (depth) and temperature at 6-hour 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 *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 stream bed 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, center, left) of the channel width along the longitudinal transect. 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 enumerated and 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 and microalgae) and diatoms were sampled along the same 11 transects from available substrates (e.g., cobble, silt/sand, gravel, bedrock, 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, Busse & Sheath (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 analyzed 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 analyzed 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, Bilger & Haigler, 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 drying event. Each hydrograph thus contained two wet phases and a dry phase between them (S.I.2). We identified hydrological events using the "dygraphs" R package then visually checked each hydrograph (Vanderkam *et al.*, 2018; S.I.2). We calculated the hydrologic metrics as described in Table 1. We defined a stream as "dry" when the average daily water level equaled 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, i.e. "false starts". Most false starts in this study lasted 1–3 days (S.I.2).

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, i.e., 10 hydrologic predictors (Table 1, S.I.3; 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 macroinvertebrates, soft-bodied algae, and diatom assemblages separately to novel metrics describing drying and wetting transitions as well as standard metrics describing dry and wet phases. 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, 2021). 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 (Roswell, Dushoff & Winfree, 2021; Aspin & House, 2022).

Six of the 20 sites were sampled 2-3 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, Boersma & Lytle, 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 (S.I.4). 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 (S.I.5).

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, Grace & Urban, 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, 2013). To facilitate comparison across assemblages, we rotated all ordinations to align NMDS axis 1 with the hydrologic metric Wet Duration, because Wet Duration had the largest R^2 for two 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 which hydrologic metrics predict 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 (S.I.4). 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 across years (S.I.5). Two environmental variables differed among years; the proportion of riffles (adjusted $R^2 = 0.32$, $p < 0.01$) and wetted width (adjusted $R^2 = 0.20$, $p <=0.01$; S.I.5), 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 algae were cyanobacteria from four families (Pseudanabaenaceae, Chroococcaceae, Merismopediaceae, and

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 S.I.6.

3.3 Assemblage composition and association with hydrologic metrics

Benthic macroinvertebrate assemblages varied among years (Figure 3a; MRPP: A = 0.040, p = 0.002; S.I.7). 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 = 0.94; diatoms: Figure 3c, MRPP: A = 0.019, p = 0.64). Soft-bodied algal samples were clustered more within ordination space whereas diatom samples were particularly dispersed.

All assemblages responded more strongly to hydrologic metrics than to environmental variables (Figure 3, 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 two and three, 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 S.1.7.

4. Discussion

We investigated biological responses of macroinvertebrate, soft-bodied algae, 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 three assemblages to hydrologic metrics, suggesting that the diverse morphological, physiological, behavioral, and life history adaptations to extreme hydrological variability likely determine how assemblages respond to the transitions between wet and dry 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 regional 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 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 (Robson *et al.*, 2008; Sabater *et al.*, 2017; Garg & Maldener, 2021. 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 two weeks after wetting (Dodds *et al.*, 2004). Similarly, benthic macroinvertebrate populations can recover within four weeks in small, non-perennial prairie streams (Fritz & Dodds, 2004) and in mediterranean California (Bêche & Resh, 2007) although recovery time varies 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 calendar 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 to the predictable seasonal cycles observed in non-perennial systems that allows their persistence (Bonada & Resh, 2013). In addition, diatoms have different colonization patterns, preferentially recolonizing from refuges like dried biofilms, than other types of algae, which tend to recolonize from drift (Robson et al., 2008), altering their responses to hydrological dynamics. Probable cues to initiate desiccation-tolerant behavioral 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, Chester & Robson, 2016; Tronstad, Tronstad & Benke, 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 for the richness and diversity assemblages.

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 (Sabater *et al.*, 2016; Soria *et al.*, 2017; Pineda-Morante *et al.*, 2022; Miao *et al.*, 2023). 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 favors 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 because availability and spatial distribution of refuges such as perennial pools can alter recolonization patterns across taxa (Crabot et al., 2020; Sarremejane *et al.*, 2021; Fournier *et al.*, 2022). However, our study sites were selected to avoid groundwater fed pools (S.I.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). Such 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 green and chlorophyte 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, 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; Schneider *et al.*, 2012; Nemes-Kókai *et al.*, 2023). 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, O’Dowd & Bouma-Gregson, 2020) and thus can influence macroinvertebrate food sources (Aguiar, Neres-Lima & Moulton, 2017). Canopy cover also influences carbon inputs into a stream with leaf litter while woody debris increases habitat complexity (Kaufmann *et al.*, 1999). Wetted width is positively correlated with habitat availability (Cowx, Young & Hellawell, 1984; Dewson, James & Death, 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, Thomaz & Warfe, 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; Seager *et al.*, 2013; Overpeck & Udall, 2020). 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.

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Author Contribution Statement

Conceptualization: MHB, SCC, KSB, CNJ, DCA, MZ, RStu. Developing Methods: MHB, SCC, KSB, CNJ, DCA, CL, RM, AP, MZ, RSta. Conducting the research: MHB, CNJ, CL, RM, RSta. Data Analysis: MHB, SCC, KSB, DCA, CL, RM, AP. Preparation figures & tables: MHB, KSB, DCA. Data interpretation: MHB, SCC, KSB, CNJ, DCA, CL, RM, AP, RSta, RStu, MZ. Writing: MHB, SCC, KSB, CNJ, DCA, CL, RM, AP, RSta, RStu, MZ.

Data Availability Statement

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

Conflict of Interest Statement

The authors confirm they have no conflict of interest.

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Figure Captions

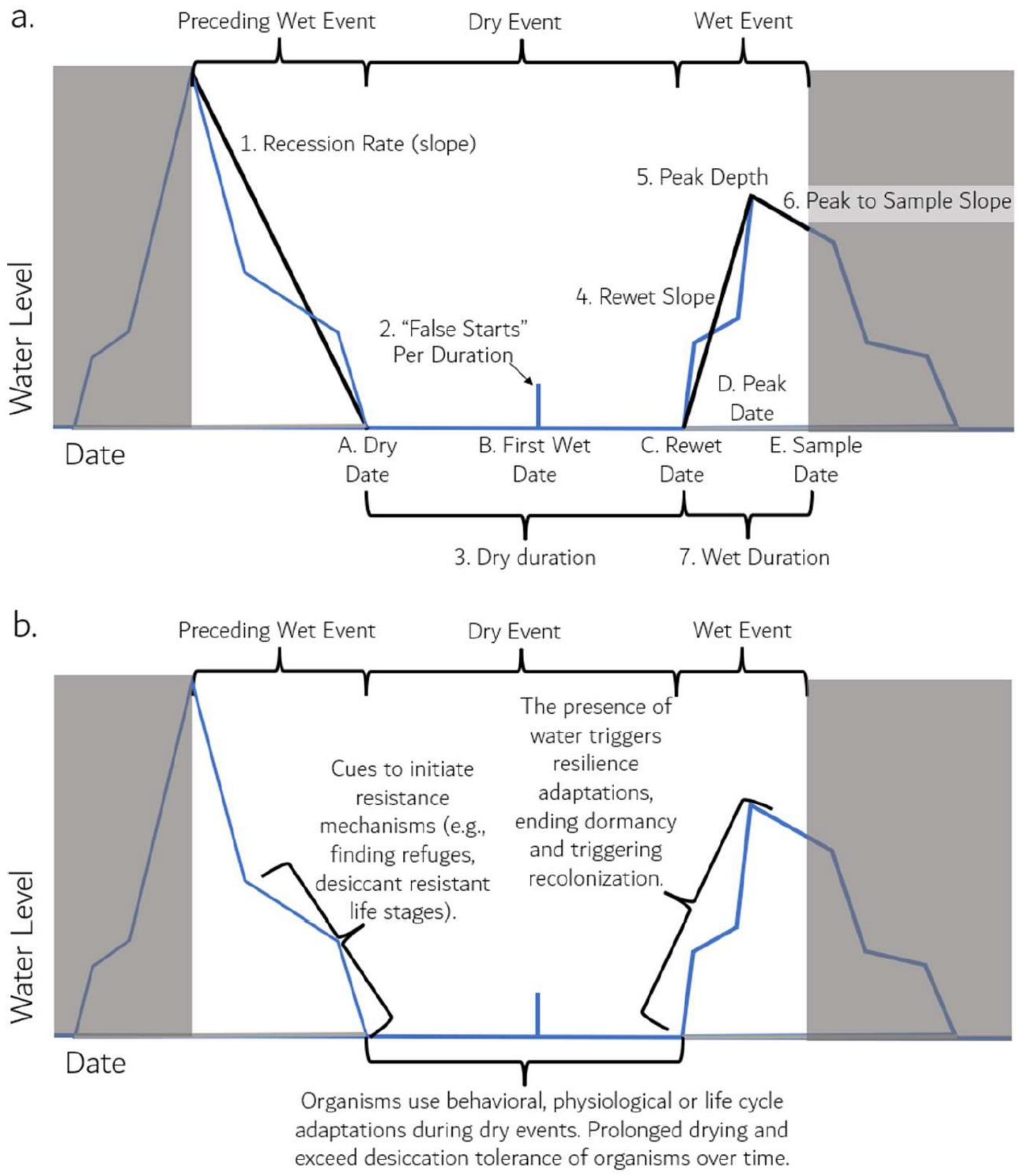

Figure 1. Conceptual hydrograph illustrating a dry event preceded and followed by wet events, as analyzed in the present study. (a) A visual representation of the various hydrologic metrics calculated and used in analyses. For detailed metric calculation descriptions, see Table 1. (b) Representations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

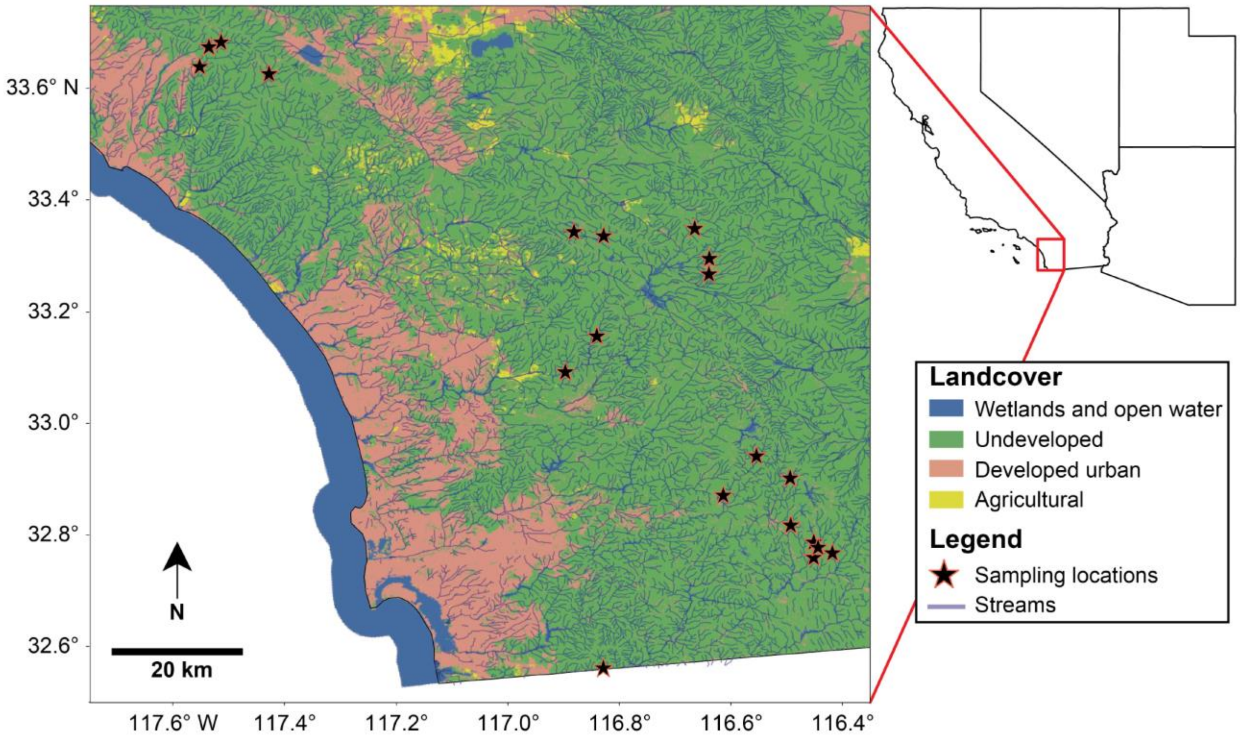

Figure 2. Study site locations in southern California with landcover in the region (16 sites in San Diego County, three in Orange County, and one in Riverside County; S.I.1).

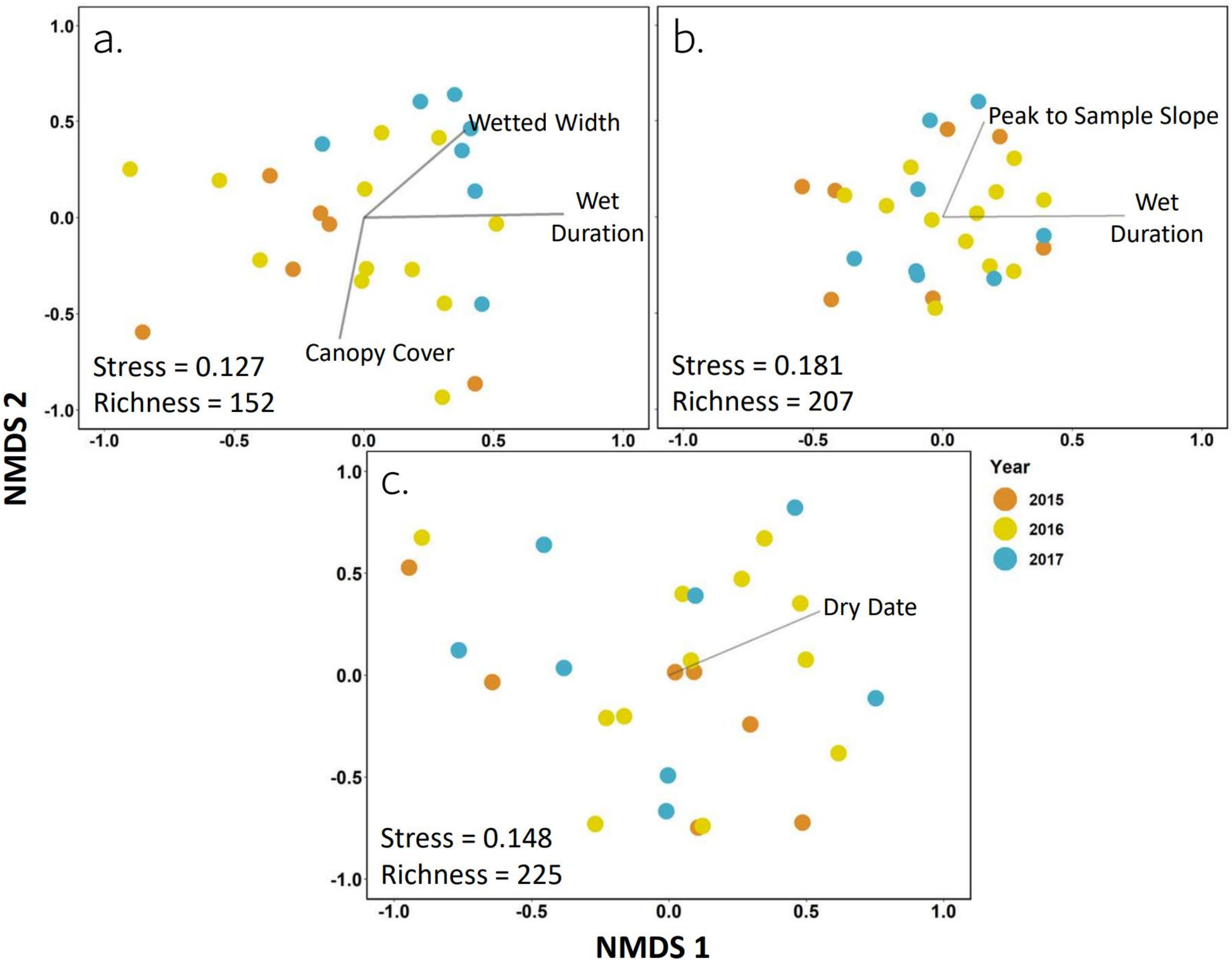

Figure 3. Two dimensional NMDS ordinations for (a) macroinvertebrate, (b) soft-bodied algal, and (c) diatom assemblages. The NMDS stress and total taxonomic richness for each assemblage are displayed. Ordinations were rotated to align the Wet Duration metric with NMDS axis 1 for clearer comparability among assemblages. Additional vectors are significant environmental variables ($p < 0.015$), with the length of the corresponding vector related to the strength of the relationship (R^2 value; Table 4).