Received: 27 January 2023 | Revised: 28 August 2023 | Accepted: 26 September 2023
DOI: 10.1002/eco.2598

RESEARCH ARTICLE

WILEY

Effects of stream drying, season, and distance to refuge on macroinvertebrate community structure in an arid intermittent stream basin

Kelsey D. Hollien | **Brian A. Gill** | **Drew E. Eppehimer** | **Michael T. Bogan**

School of Natural Resources and the Environment, University of Arizona, Tucson, Arizona, USA

Correspondence
Kelsey D. Hollien, School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, USA.
Email: hollienk@arizona.edu

Funding information
National Science Foundation, Grant/Award Number: DEB-1802766

Abstract

Intermittent streams are globally ubiquitous and represent a large percentage of stream networks. As climate change in many arid regions increases the frequency and intensity of drying disturbances, it is important to understand how aquatic biota will respond to such disturbances and how it would impact aquatic biodiversity. To address these topics, we sampled 10 stream reaches in the Sycamore Creek basin, an arid-land stream in central Arizona (USA), with reach-scale flow regimes ranging from perennial to highly intermittent. We sampled aquatic macroinvertebrates during 4 seasons to explore seasonal variability in community structure through flowing and drying phases. We also collected continuous flow data with remote data loggers to explore the impacts of intermittency and distance to perennial refuges on species richness, taxonomic composition and trait composition. Overall, richness was lower at intermittent reaches than perennial reaches, and richness values increased linearly as flow duration increased. We found no relationship between richness and distance to the nearest perennial refuge. Community assemblages differed significantly by season but were not distinct between perennial and intermittent reaches. Trait composition was also distinct between seasons and flow regimes, with traits such as a lack of diapause, longer life span and predatory feeding behaviours being indicators for perennial reaches. As climate change alters natural flow regimes, understanding the responses of macroinvertebrate community structure to drying disturbances in arid-land streams can provide insight on aquatic community responses to climate change at larger scales.

KEYWORDS
intermittency, macroinvertebrates, refuge, seasonality

1 | INTRODUCTION

Intermittent streams make up a large portion of global stream networks (>50%: Fritz et al., 2013; Messager et al., 2021). Intermittent streams occur in all biomes, and in arid regions, they account for as much as 80% of stream networks (Acuña et al., 2014). Although these streams do not flow year-round, intermittent waterways still provide valuable ecosystem services and can harbour unique faunas that contribute to basin-wide biodiversity (Koundouri et al., 2017). Even when intermittent streams are dry, they provide pathways for energy, nutrients and organisms (Acuña et al., 2017). Despite their importance, intermittent streams were historically understudied (Shanafield et al., 2020). For example, most research on aquatic ecosystems has been done in temperate perennial systems (Datry et al., 2014). Influential stream ecology concepts such as the river continuum concept, linking the biology of streams with hydrology and geography, were developed in temperate environments with no reference to stream drying (Allen et al., 2020; Vannote et al., 1980). It was believed that periodic drying was a harsh filter that acted on communities in intermittent streams, leading them to be less biodiverse than communities in perennial systems (Poff & Ward, 1989).

However, an increasing body of research on intermittent streams in recent years has shown that intermittent streams are more dynamic and hold more ecological value than previously thought. Periodic drying maintains habitat heterogeneity and influences biogeochemical processes and biodiversity in intermittent systems at a larger scale (Datry et al., 2014). Intermittent streams are now recognized as metacommunities, that is, an ensemble of communities that are not closed and isolated but whose local dynamics and structure can be linked to larger spatial scales (Datry et al., 2017; Stubbington, Bogan, et al., 2017).

In intermittent streams, the intensity, location and extent of drying events shape ecosystem processes and may strongly influence macroinvertebrate community composition (Bogan et al., 2015; Kelso & Entrekin, 2018). Flow intermittency is an environmental constraint that can determine community structure, and it may be especially influential in selecting for functional traits that taxa need to persist in drying environments (Bonada et al., 2007; Miliša et al., 2022). Resistance traits, such as desiccation resistant eggs or larvae, can allow aquatic organisms to remain in the stream bed and return to an active form after the dry period (Datry, Bonada, & Heino, 2016; Sarremejane et al., 2017). In contrast, resilience traits, such as rapid life cycles, timed breeding events and flight dispersal, can allow recolonization by individuals from perennial refuges elsewhere in the stream system (Chester & Robson, 2011; Fournier et al., 2023).

The spatial configuration of perennial and intermittent reaches within a stream network can vary across networks and regions and influence biodiversity as well (Gill et al., 2022; Sarremejane et al., 2020). In mesic regions, flow intermittency is typically found only in the headwaters (Fritz et al., 2013), whereas in arid regions, it can occur at any point within the watershed (Acuña et al., 2014). The connectivity of aquatic organisms is shaped by the precise locations of flow intermittency within a stream network: the distance to, and direction from, perennial refuges can influence community structure and impact resilience to disturbances such as drought (Bogan et al., 2015; Datry, Moya, et al., 2016). For example, highly isolated intermittent habitats may only be accessible to taxa who can remain in the streambed during drying or are highly mobile to recolonize quickly when flow returns (Crabot et al., 2020; Robson et al., 2011). Recolonization of these isolated habitats would be reliant on taxa that are strong active fliers or those that can drift from upstream refuges if flow connects for long enough (Bogan et al., 2017). Distance to the nearest perennial refuges may determine how quickly these reaches can be recolonized and whether high biodiversity can be sustained within the reach (Gill et al., 2022; Robson et al., 2011).

In addition to longitudinal changes in flow regimes, the habitat types within individual reaches also can shift seasonally and subseasonally between lotic, lentic and dry stages, with different species colonizing or utilizing each phase. This turnover through time can increase overall functional and taxonomic diversity of a given reach in an intermittent stream (Datry et al., 2014; Hill & Milner, 2018). For example, taxa with adaptations to survive stagnant water and low levels of dissolved oxygen (e.g., air-breathers) may dominate during dry season, when only isolated pools remain in the stream (Bogan & Lytle, 2007; Gray & Fisher, 1981). In fact, taxa with strong aerial dispersal abilities (e.g., beetles and dragonflies) may prefer to colonize intermittent reaches when only stagnant pools remain and complete their life cycles in these seasonal lentic habitats (Bogan & Boersma, 2012; Miliša et al., 2022). However, when flow returns to these same reaches during wetter periods, macroinvertebrates that require well-oxygenated flowing conditions may recolonize the reach by drifting down from upstream perennial refuges (Datry, Moya, et al., 2016; Vander Vorste et al., 2016), highlighting the dynamic seasonal nature of intermittent stream communities.

Even in naturally intermittent streams, where taxa have adapted to dry spells or have dispersal strategies to recolonize reaches when flow returns, the increasing intensity and severity of drying events due to climate change may outpace species survival capacity (Crabot et al., 2021). Shorter flow durations in intermittent streams could cause the loss of even the hardiest taxa from intermittent reaches, as they may need a minimum of 6–8 weeks of flow to complete their larval life cycles (Bogan, 2017; Cover et al., 2015) or return aerially from distant perennial refuges (Washko & Bogan, 2019). The losses of key taxa that support food webs or ecosystem processes could amplify the impacts of drying at the population, community and ecosystem scales (Acuña et al., 2017). A better understanding of the relationship between drying and the aquatic communities that intermittent streams support will be essential in determining the consequences of climate change on both perennial and intermittent streams (Crabot et al., 2021; Jaeger et al., 2014).

Here, we explore how flow intermittency, the distance to perennial refuges and seasonal habitat dynamics influence macroinvertebrate community structure across an arid-land stream basin. At 10 reaches within the Sycamore Creek basin in central Arizona (USA), we sampled benthic macroinvertebrates and quantified reach-scale flow metrics using remote data loggers. Using these data, we hypothesized that (1) flow intermittency is a primary driver of macroinvertebrate species richness and taxonomic and trait composition, (2) distance to perennial refuges is a secondary driver of local species richness in intermittent reaches due to species-specific variation in dispersal abilities and (3) within a reach, species richness and taxonomic and trait composition vary seasonally as fluctuating water availability influences the presence of species with adaptive traits for lotic versus lentic habitat conditions. We predicted that (1) reaches with greater intermittency would have lower species richness and distinct taxonomic communities dominated by taxa with drying resistance or resilience traits, (2) more isolated reaches (i.e., further from perennial refuges) would have lower species richness and (3) within a reach, richness will be higher during the spring high flow periods when the most habitat is available and will decrease during the summer and fall as habitat contracts. We also predicted that community structure would shift from less tolerant lotic taxa during wetter months to more tolerant and mobile taxa during the drier months.

2 | MATERIALS AND METHODS

2.1 | Study area

Sycamore Creek is a second order stream in central Arizona, USA that drains 505 km^2 (Figure 1). The basin ranges in elevation from 1700 m in its headwaters in the Mazatzal mountains to 430 m where it meets the Verde River near Fort McDowell, AZ. The headwaters descend from mixed conifer forest and pass though chaparral and desert before merging with the mainstem and passing through desert scrub on its way to its confluence with the Verde River. Most of Sycamore Creek lies within the Tonto National Forest and is largely free of urban development and associated impacts.

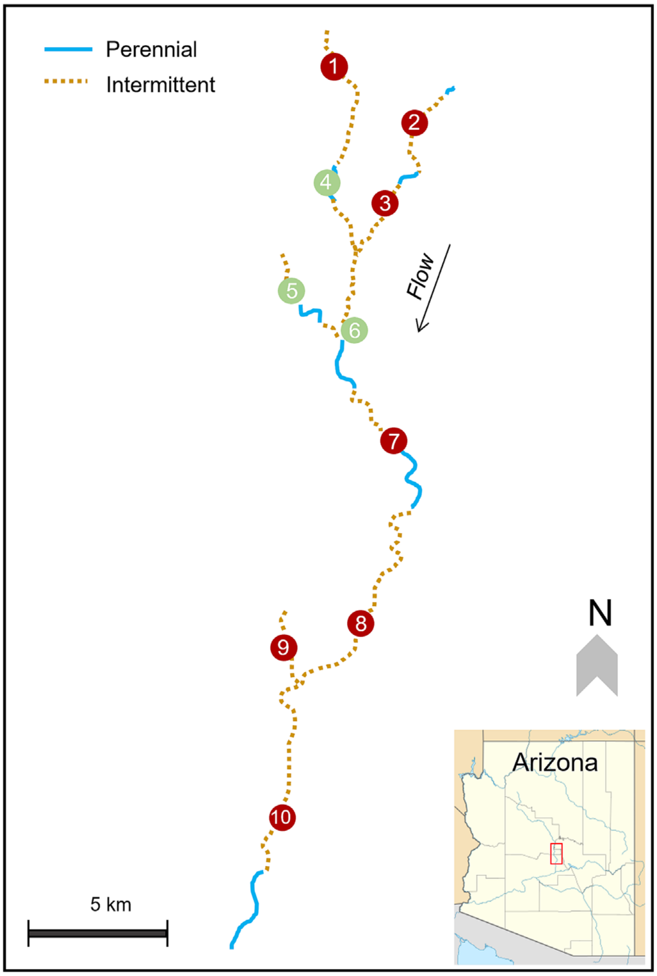


FIGURE 1 Map of Sycamore Creek study area. Solid blue sections indicate a perennial refuge, and dashed yellow lines indicate intermittent sections as determined by wet-dry mapping. Green numbered markers indicate perennial sample reaches, and red indicates intermittent sample reaches. Red numbered markers correspond to the last two digits in the reach names (e.g., 1 for SYCA-01).

Sycamore Creek receives an average of 409 mm of rainfall a year via a bimodal precipitation pattern of winter and summer rains (NEON, 2017). Summer precipitation typically presents as monsoon storms—short, locally intense thunderstorms, often affecting smaller portions of the watershed, and can result in localized or more widespread flash floods (Sponseller et al., 2010). In contrast, winter precipitation results from large frontal systems that often affect a larger area and can cause extended high flows, and sustained elevated baseflow, for longer periods of time (Stanley et al., 1997). The average annual air temperature for Sycamore Creek is 20.7°C, with summer temperatures frequently exceeding 40.5°C (NEON, 2017).

Most of Sycamore Creek is classified as intermittent and drying disturbances are common (Stanley et al., 1997). Seasonal drying and periods of low flow are typical during the summer months, with some flow returning during summer monsoon and winter rains. While these precipitation events may create flow for several months out of the year, the magnitude of drying is fairly extreme (Stanley et al., 1997). Drying events can last for several months during summer, with a historical annual average of 103 days without flow (Sponseller et al., 2010). There are a few stretches with perennial flow, and deep pools may persist through the dry seasons in intermittent reaches with bedrock stream channels.

Within the basin, 10 150-m-long study reaches were chosen that exhibit varying degrees of intermittency and distances from perennial refuges (Figure 1). Each reach was separated by a minimum of 1.5 km, and the distance from the uppermost reach to the lowest was approximately 30 km.

2.2 | Study design

2.2.1 | Characterization of flow intermittency

At each of the 10 study reaches, Hobo sensors (HOBO Pendant Temperature/Light 64K Data Logger) were deployed to quantify flow intermittency across the study period (March 2020 to March 2021). Sensors were modified to record conductivity as a proxy to detect the presence or absence of water (Chapin et al., 2014). In each of the 10 study reaches, a total of 5 sensors were evenly placed along the 150-m length of the reach in various macrohabitats (targeting pools and riffles) to capture drying dynamics as flow decreases, then ceases and then remnant pools dry (Jaeger & Olden, 2012). When one or more of the sensors in a given reach recorded dry conditions, that indicated that flow was beginning to contract laterally and/or longitudinally. When all five sensors in a given reach detected dry conditions, that indicated complete drying of the reach. To give a proxy of the general flow conditions within a given reach, sensor data were summed across all five sensors for each reach to illustrate whether that reach was flowing completely or beginning to dry (e.g., 0 = all sensors dry, 5 = all sensors wet) (Figure S2).

Flow sensors were also used to calculate reach-specific flow regime characteristics including: (1) days flowing (number of consecutive days the reach was wet from the start of the flow record or the most recent drying event to the next biological sampling event), (2) drying frequency (number of drying events longer than 48 h between one biological sampling event to the next) and (3) flow permanence (proportion of the total flow record for the study when the reach was wet). For these metrics, if at least one of the sensors within a reach indicated flow, then the entire reach was coded as at least partially wet (i.e., not experiencing complete drying). Perennial reaches were assigned a drying frequency of 0, flow permanence of 1 and days flowing was recorded arbitrarily as 1099 days for the first biological sampling event to represent multi-year flow duration and to distinguish them from long-flowing intermittent reaches.

2.2.2 | Determination of distance to perennial refuge

To determine the locations of all possible perennial refuges, wet/dry mapping (Turner & Richter, 2011) was conducted during the driest part of the study period (January 2021, Figure S1). The entire length of the basin that was included in the study, as well as any notable tributaries, was walked, and GPS coordinates were taken where any remnant pools or flow were found. Direct aerial distances and stream channel distances were then estimated from the sample reach to the nearest perennial refuge using Google Earth. This study was conducted during two of the driest and hottest years on record for Arizona (Mankin et al., 2021), so any surface water that persisted during this time was likely to be reliable across multiple years.

2.3 | Biological sampling

Biological sampling for aquatic macroinvertebrates occurred four times: early spring when winter flow was the highest (March 2020), early summer when flow was contracting (July 2020), early fall after monsoon rains (September 2020) and again in early spring (February 2021) for repeat sampling during a second winter flow season when conditions were much drier than the previous year (Figure S1).

Biological samples were collected using the reach-wide benthic and targeted edge approaches (Eppehimer et al., 2020). The reach-wide approach consisted of using a 30 × 30-cm Surber net to collect 11 ‘kicks’ of benthic macroinvertebrates, one every 15 m along the 150-m reach, which are all composited into one sample that represents the entire reach. The targeted edge approach consisted of 5 sweeps through marginal habitats (aquatic vegetation or undercut banks along the edges of the stream) with a 30 × 30-cm D-net within each 150-m transect. The placement and length of sweeps for this method were at the discretion of the collector; edge samples were only used as a qualitative method to determine the presence of margin-dwelling taxa that might not be detected in the reach-wide samples (Eppehimer et al., 2020). Samples were then processed in the field to remove large organic debris and preserved in 95% ethanol for transport back to the laboratory at the University of Arizona.

2.4 | Laboratory processing

Samples were further processed in the laboratory to separate aquatic macroinvertebrates from small debris and algae. Macroinvertebrates then were identified to the genus level whenever possible using taxonomic keys in Merritt et al. (2008) and Thorp and Rogers (2015). Early life stages of some insects and non-insect taxa were identified to family and order, respectively.

For community composition analyses (see below), macroinvertebrate densities were calculated for each taxon using quantitative reach-wide samples. For taxonomic richness analyses, however, we combined taxa lists from both the edge and reach-wide samples to determine the total number of taxa detected from a given reach and sampling date. Combining both sample types allows for a more robust estimation of the total number of macroinvertebrate taxa occurring in a reach during a sampling event (Eppehimer et al., 2020).

2.4.1 | Compilation of the trait matrix

To determine the composition of adaptive traits within the invertebrate communities, we first generated a trait matrix based on 7 broad categories of traits that may be beneficial for surviving in intermittent systems. Categories included body size, voltinism, dispersal, respiration, functional feeding group, diapause and locomotion (Poff et al., 2006; Vieira et al., 2006). These traits represent a suite of basic physiological, developmental and morphological traits that would be necessary to characterize the macroinvertebrate community (Boersma et al., 2014a; Boersma et al., 2016). After samples were identified taxonomically, taxa were assigned established categorical trait values within trait categories (Schriever et al., 2015). Definitions of traits and their assigned categorical values can be found in Table S3.

2.5 | Hypothesis testing

2.5.1 | Flow characteristics

To test our first hypothesis that flow intermittency is a primary driver of macroinvertebrate community structure, we first used a linear mixed-effects modelling approach to evaluate the relationships between richness and calculated flow regime metrics. The correlations among all of our flow metrics were assessed prior to modelling using all possible pairwise correlations of three predictors: days flowing, drying frequency and flow permanence. We found that some of these predictors had high degrees of collinearity (Dormann et al., 2013; see Table S2 for all combinations and values). Days flowing and flow permanence were highly correlated ($r = 0.83$), but days flowing and drying frequency ($r = 0.65$) were less correlated. Given these collinearities in flow metrics, only days flowing and drying frequency were retained as a flow metrics in the richness model. A linear mixed-effects model using these predictors was run with sample reach as a random effect, using the package *glmmTMB* (Brooks et al., 2017) in R

(R Core Team, 2021). A Gaussian distribution was used, and model performance was checked by visually inspecting the residual diagnostic plots for residual versus fitted values of the model. A log-likelihood ratio test was performed using *lmtest* (Zeileis & Hothorn, 2002), to test for significance of the predictors.

To determine how taxonomic and trait community composition varied by flow class (intermittent vs. perennial reaches), seasonal samples were combined for each reach for flow class analyses. We used non-metric multidimensional scaling (NMDS) to visualize communities in taxonomic and trait space with the R package *vegan* (Oksanen et al., 2020). To use traits as proxy for species, the trait matrix was multiplied by a taxonomic matrix containing abundance data relativized by sample unit from all samples to generate a sample-by-trait matrix (Boersma et al., 2016). We calculated Gower dissimilarity from this matrix and applied a square root transformation to standardize before NMDS ordination.

To test for differences in taxonomic composition between flow classes, we used permutational multivariate analyses of variance (perMANOVAs) in *vegan*. We then conducted an indicator species analysis for perennial vs intermittent samples, using the package *indicspecies* (Cáceres & Legendre, 2009). To characterize functional differences in macroinvertebrate communities between flow classes, we used traits as pseudo-species (Ricotta et al., 2015) and conducted another indicator species analysis for perennial versus intermittent samples using *indicspecies*. We corrected for multiple testing in both indicator species analyses using the false discovery rate (FDR) method (Benjamini & Hochberg, 1995).

2.5.2 | Distance to perennial refuges

To test our second hypothesis that distance to perennial refuges is a secondary driver of local species richness due to species-specific variation in dispersal abilities, we used a linear mixed-effects modelling approach. Correlations among our calculated metrics of distance-to-refuges were assessed prior to modelling using two possible pairwise correlations of stream distance to the nearest perennial refuge and aerial distance to the nearest refuge. Stream and aerial distances were highly correlated ($r = 0.92$). Because previous studies have found that movement along stream channels may be a more biologically relevant pathway for aerial dispersers in arid regions (Bogan & Boersma, 2012), aerial distance to refuge was excluded from further analysis. A linear mixed-effects model using stream distance to refuge as a predictor was run with sample reach as a random effect, using *glmmTMB* (Brooks et al., 2017). A Gaussian distribution was used, and model performance was checked by visually inspecting the residual diagnostic plots for residual versus fitted values of the model. A log-likelihood ratio test was performed using *lmtest* (Zeileis & Hothorn, 2002), to test for significance of the predictors.

2.5.3 | Seasonal dynamics

To test our third hypothesis that species richness, taxonomic composition and trait composition vary seasonally, we plotted and visualized richness values for each sampling reach between seasons. To determine how the communities varied in their taxonomic and trait composition by season, we used NMDS to visualize seasonal taxonomic and trait communities using *vegan*. To evaluate if season had a significant effect on taxonomic and trait composition, we performed perMANOVAs, followed by pairwise comparisons to determine which seasons were significantly distinct. Lastly, we conducted an indicator species analysis between sampling seasons for both taxa and traits using *indicspecies* (Cáceres & Legendre, 2009). We corrected for multiple testing in indicator species analyses using the FDR method.

3 | RESULTS

3.1 | Taxonomic data overview

We collected a total of 29 macroinvertebrate samples from the 10 study reaches across the four sampling seasons, as some reaches were dry during one or more seasons. From these samples, we identified a total of 193 macroinvertebrate taxa. The most diverse orders were Diptera (79 taxa), Coleoptera (36 taxa) and Hemiptera (17 taxa).

3.2 | Hydrological conditions

Flow sensor data revealed highly variable flow regimes in many reaches of Sycamore Creek. All 10 reaches were flowing at the start of the study, but many contracted to pools or dried completely during the summer and into the fall—responding only briefly to precipitation events, and then rewetted again in the winter and following spring (Figure S2). Overall flow permanence across our study period ranged from as little as 40% in some reaches to 100% in our perennial and near perennial reaches. The number of days that intermittent reaches had been flowing prior to biological sampling ranged from 8 to 455 days (mean: 168 ± 115 SD). Many of these reaches also experienced drying events once or twice in the sampling period (Figure S2). One intermittent reach (SYCA-07) was dry during initial scouting visits in September 2019 but began flowing again soon after and never dried during the length of the study (Figure S2). Perennial reaches did not experience complete flow cessation, but sensor data indicated that there was variation in periodic lateral or longitudinal contraction of the wetted area among them. For example, at our site named SYCA-05, alluvial parts of the reach dried during summer while bedrock-bound parts of the reach continued to flow (Figure S2). In contrast, our site SYCA-06 maintained flow across the entire reach during the study period.

3.3 | Macroinvertebrate responses to flow characteristics

Average taxonomic richness was 61% higher in perennial than intermittent reaches. Richness values ranged from 14 to 56 (mean:

35 ± 11 SD) in intermittent reaches and from 36 to 66 (mean: 55 ± 8 SD) in perennial (Figure 2). Across all samples, richness significantly increased with days flowing, with nearly 50% of the variation in richness explained by days flowing alone and only 8% additional variation explained by reach-specific factors (Marginal R^2/Conditional $R^2 = 0.50/0.58$, $p = 0.003$) (Table 1, Figure 3a). Drying frequency was not a significant predictor of richness ($p = 0.674$) (Table 1, Figure 3b).

We observed no distinct clustering of samples by flow class in multivariate species-space but found no significance in the taxonomic composition of flow classes (perMANOVA, $R^2 = 0.05$, $F_{1,27} = 1.55$, $p = 0.053$; Table 2; Figure 4a). Indicator species analysis revealed the odonate *Argia* ($p = 0.019$), the mayfly *Caenis* ($p = 0.019$), the beetle *Gyrinus* ($p = 0.029$) and the midge *Pseudochironomus* ($p = 0.026$) to be indicator species for perennial reaches (Table 3).

In contrast, intermittent and perennial reaches did cluster by flow class in multivariate trait-space (Figure 4c, stress $= 0.08$, $R^2 = 0.97$), and trait composition differences were significantly different (perMANOVA, $R^2 = 0.14$, $F_{1,27} = 4.58$, $p = 0.01$). Indicator species analysis also showed that lack of diapause (*diapause 3*, $p = 0.024$), less than 1 generation per year (*voltinism 1*, $p = 0.024$), and engulfers/predators (*functional feeding group 7*, $p = 0.024$) were indicator traits for perennial samples, but there were no significant indicator traits for intermittent reaches (Table 3).

3.4 | Effects of distance to refuge on macroinvertebrates

Linear mixed effect modelling revealed there was no significant relationship between richness and stream distance to perennial refuge ($p = 0.809$) (Table 4, Figure 3c).

TABLE 1 Summary of linear mixed effects model results explaining variation in richness with the predictors days flowing and drying frequency. Results include incidence rate ratios (estimates) with corresponding 95% confidence intervals (*CI*) and *p* values (*p*). Bold indicates significant log-likelihood ratio derived *p* values of predictors ($\alpha \le 0.05$).

	Richness		
Predictors	**Estimates**	**CI**	***p***
(Intercept)	31.30	22.35–40.26	**<0.001**
Days flowing	0.02	0.01–0.03	**0.003**
Drying frequency	1.58	−5.79 to 8.95	0.674
Random effect: reach			
σ^2	79.01		
τ_{00}	15.47		
ICC	0.16		
N_{Reach}	10		
Observations	29		
Marginal R^2/Conditional R^2	0.498/0.580		

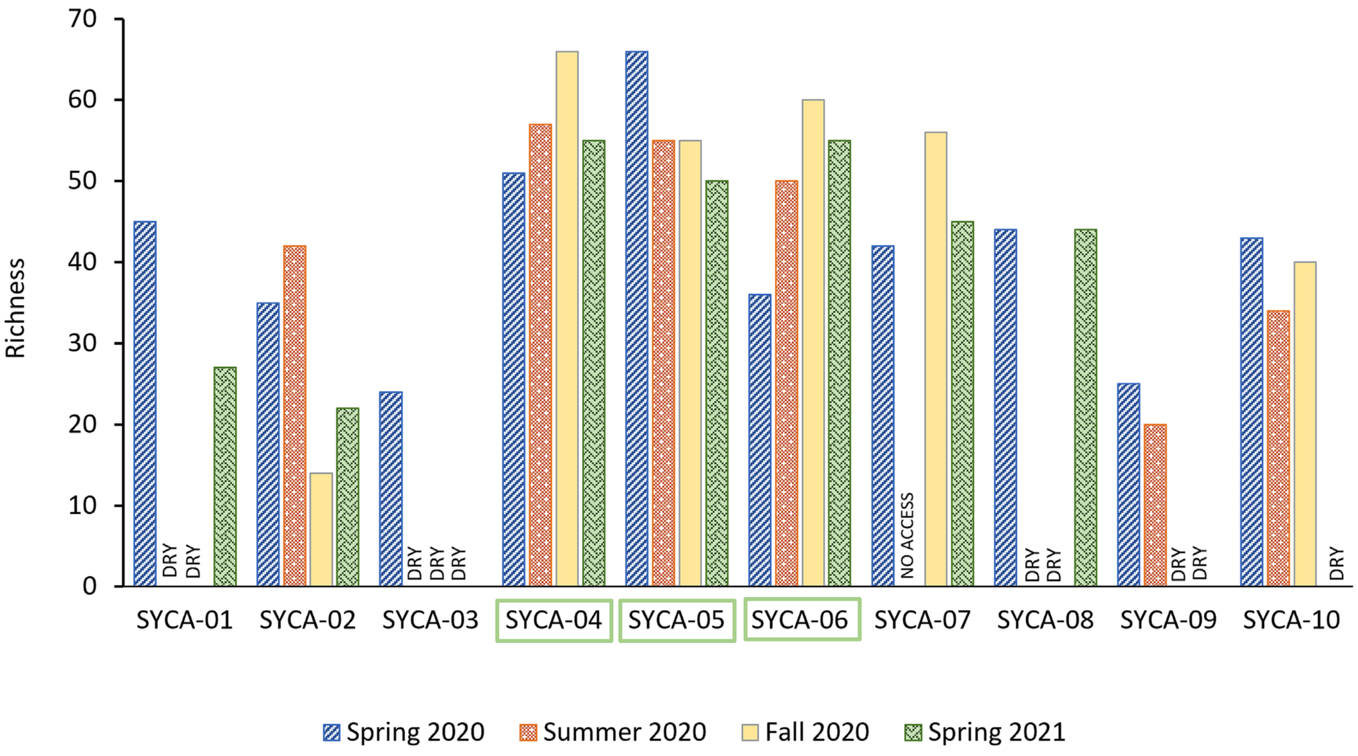


FIGURE 2 Taxonomic richness from the 10 sample reaches at Sycamore Creek by season. Reaches SYCA-04, -05 and -06 are perennial, denoted by the green boxes, while reaches SYCA-01, -02, -03, -07, -08, -09 and -10 are intermittent.

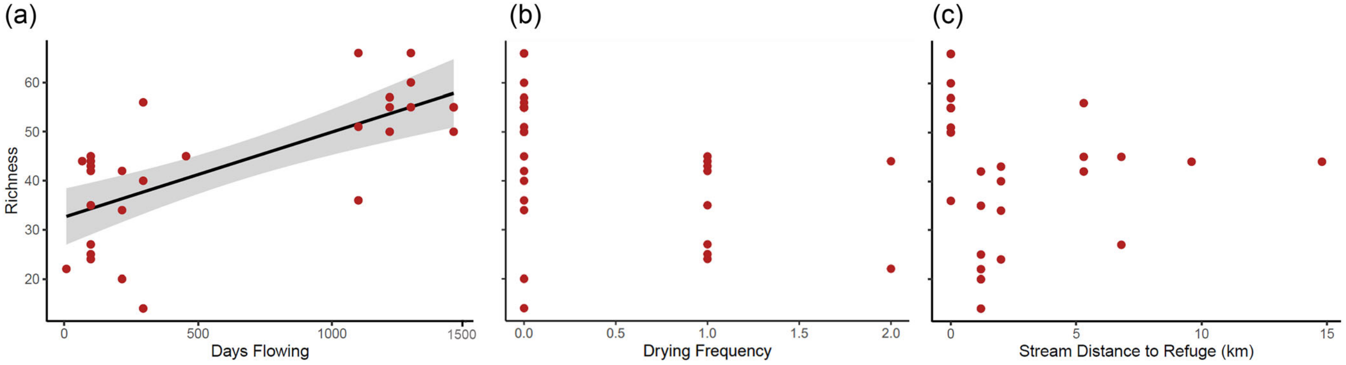
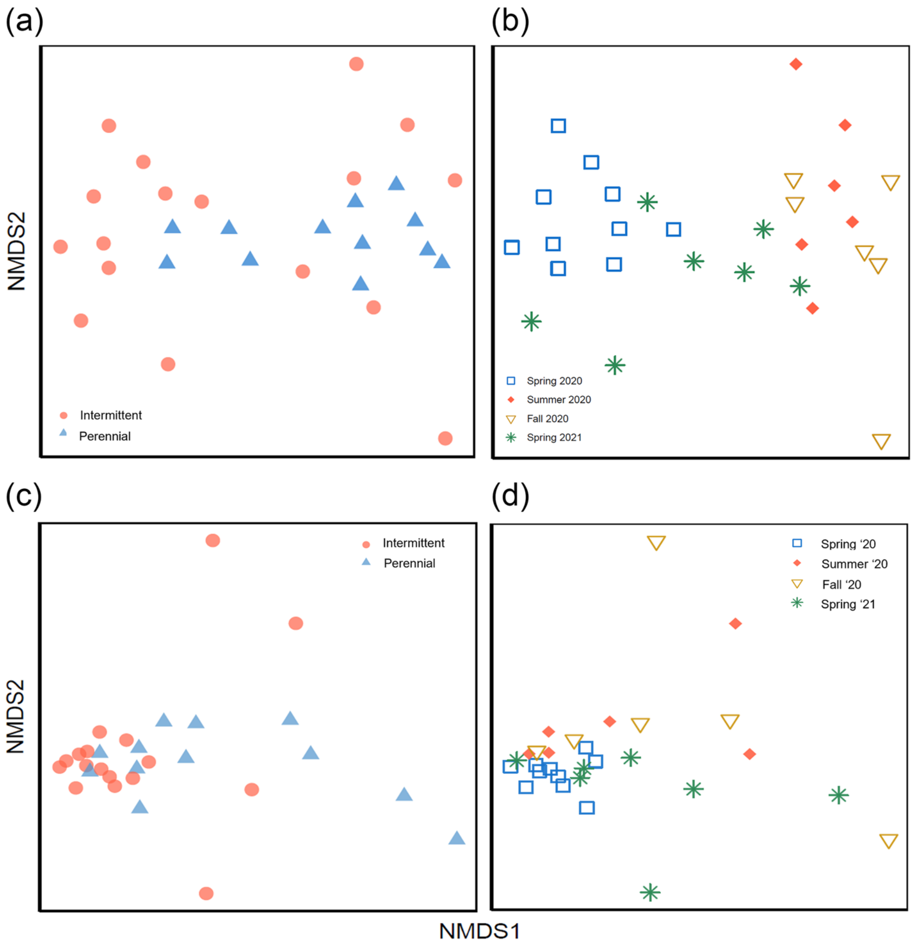


FIGURE 3 Macroinvertebrate richness was positively related to the days flowing (a). In contrast, macroinvertebrate richness was not significantly associated with drying frequency (b) or stream distance to refuge (c). The dark grey shaded area around the trend line on panel a represents a 95% confidence interval.

FIGURE 4 (a,b) Taxonomic ordination of macroinvertebrate samples from all reaches at Sycamore Creek by (a) flow class (perennial vs. intermittent) and (b) season. (c,d) Trait ordinations of macroinvertebrate samples from all reaches at Sycamore Creek by (c) flow class (perennial vs. intermittent) and (d) season.



3.5 | Seasonal dynamics of macroinvertebrate communities

Richness values varied between reaches across seasons. In some reaches, richness increased across the seasons, but in other reaches, it decreased (Figure 2).

NMDS ordination showed an overall clustering of samples by season in taxonomic-space, with the most overlap occurring between Summer and Fall samples in 2020 (Figure 4b; stress $= 0.16$, $R^2 = 0.87$). We found significant differences in the taxonomic composition between seasons (perMANOVA, $R^2 = 0.23$, $F_{3,25} = 2.50$, $p = 0.001$). Pairwise comparisons further revealed that taxonomic composition was distinct between all seasons (pairwise perMANOVA, $p = <0.05$, Table 2), except between Spring 2020 and Fall 2020. However, indicator species analysis revealed there were no strong indicator species for any of the sampling seasons.

Intermittent and perennial reaches also clustered by season in trait-space (Figure 4d, stress = 0.08, $R^2 = 0.97$), and there was significant distinction in trait composition between seasons (perMANOVA, $R^2 = 0.24$, $F_{3,25} = 2.57$, $p = 0.031$). Pairwise comparisons further revealed that the trait composition of Spring 2020 was distinct from all other seasons (perMANOVA, $p = <0.05$, Table 2), but Summer 2020, Fall 2020 and Spring 2021 were not distinct from each other. The only significant indicator traits identified were for the Fall 2020 sampling period and included plant-piercers (*functional feeding group 5*, $p = 0.033$) and skaters (*locomotion 6*, $p = 0.045$) (Table 5).

4 | ECOLOGICAL RESPONSES

Intermittent arid-land streams are highly dynamic systems in which aquatic communities respond strongly to drying disturbances but are often thought of as being low in diversity (Datry et al., 2014; Poff & Ward, 1989). In this study, however, we documented a diverse suite of 193 macroinvertebrate taxa from Sycamore Creek in central Arizona. A previous study of multiple reaches in the same basin only found 104 macroinvertebrate taxa (Gray, 1981). Our results also demonstrated that (1) flow intermittency was a primary driver of macroinvertebrate species richness; (2) season and, to a lesser degree, intermittency are primary drivers of taxonomic composition; (3) and that both intermittency and season influenced trait composition.

TABLE 2 Results of pairwise perMANOVA (999 permutations) for taxonomic (Bray–Curtis) dissimilarity and trait composition (Gower) dissimilarity for different sampling seasons.

Pairs	R^2	*F*	*p* value
Taxonomic composition pairwise perMANOVA for different seasons			
Spring 2020 vs. Summer 2020	0.201	3.515	0.001
Spring 2020 vs. Fall 2020	0.225	4.071	0.001
Spring 2020 vs. Spring 2021	0.180	3.290	0.002
Summer 2020 vs. Fall 2020	0.076	0.825	0.736
Summer 2020 vs. Spring 2021	0.122	1.526	0.044
Fall 2020 vs. Spring 2021	0.127	1.593	0.042
Trait composition pairwise perMANOVA for different seasons			
Spring 2020 vs. Summer 2020	0.213	3.778	0.034
Spring 2020 vs. Fall 2020	0.322	6.662	0.002
Spring 2020 vs. Spring 2021	0.249	4.962	0.010
Summer 2020 vs. Fall 2020	0.083	0.905	0.392
Summer 2020 vs. Spring 2021	0.071	0.846	0.440
Fall 2020 vs. Spring 2021	0.079	0.944	0.379

4.1 | Flow characteristics

Taxonomic richness at Sycamore Creek increased with the number of days of flow prior to sampling and richness was lower in intermittent reaches than perennial reaches, similar to observations from many parts of the globe (Datry et al., 2014). Although ~60% of the variation in our richness model was explained by the duration of flow, there could be other abiotic factors such as water quality, substrate and the availability of nutrients influencing the observed increase in richness in combination with flow duration (Allan, 1995; Statzner et al., 1988).

In contrast, intermittency did not appear to strongly influence macroinvertebrate taxonomic composition. Previous studies have found support for both distinct communities with unique taxa in intermittent reaches (e.g., Bogan et al., 2013; Gill et al., 2022) and intermittent communities that were merely nested subsets of those found in perennial reaches (e.g., Bonada et al., 2007; Vander Vorste et al., 2021). However, the level to which some taxa were identified in previous studies could impact the level of taxonomic distinctness that is detected between intermittent and perennial reaches. We were able to identify blackflies (Simuliidae) and midges (Chironomidae) to genus or species; these groups have high intra-family variation, with many species adapted to intermittency (Bogan et al., 2013). Datry (2012) found blackflies and midges to be among the most abundant taxa at intermittent reaches but did not identify them beyond the family level. In the current study, we failed to find taxonomic distinctness between intermittent and perennial reaches despite having fine taxonomic resolution of blackflies and midges. However, we did find the desiccation-resistant taxa *Neohermes* (Corydalidae) and *Hydrobaenus* (Chironomidae) exclusively in intermittent reaches (Bogan et al., 2013; Cover et al., 2015), but their abundances were not high

TABLE 3 Significant species and traits by flow regime class as determined by indicator species analysis. The index column lists the associated indicator value (IndVal). There were no significant indicator species or traits from intermittent reaches.

Taxon	Intermittent	Perennial	Index	stat	*p* value	*p* value (corrected)
Argia	0	1	2	0.333	<0.001	0.019
Caenis	0	1	2	0.448	<0.001	0.019
Gyrinus	0	1	2	0.272	<0.001	0.029
Pseudochironomus	0	1	2	0.405	<0.001	0.026
Trait						
Voltinism 1	0	1	2	0.397	0.004	0.044
FFG 7	0	1	2	0.526	0.001	0.024
Diapause 3	0	1	2	0.484	0.002	0.024

enough to result in overall community distinction. We also found the damselfly *Argia* to be an indicator species for perennial samples, and almost all species within this genus in Arizona are known to be restricted to perennial springs and streams and are less tolerant of drying conditions (Bailowitz et al., 2015).

The lack of strong taxonomic distinction between intermittent and perennial reaches could have resulted from unusual flow conditions during the beginning of the study period. A series of large winter storms in November 2019 caused all intermittent reaches to maintain flow until the first sampling event in March 2020 (Figure S2). This extended period of high flow conditions could have allowed specialist taxa from upstream intermittent reaches to colonize downstream perennial reaches via drift, thus creating broader taxonomic overlap between flow classes. For example, capniid stoneflies, the midge *Eukiefferiella brehmi* and the blackfly *Prosimulium*, which have been found in other studies to often be associated with intermittent streams (Bogan et al., 2013; Stubbington, Bogan, et al., 2017), were found in both intermittent and perennial reaches during March 2020. However, these taxa were restricted to intermittent reaches during the February 2021 sampling event, which was not preceded by a long period of high flow conditions (Figure S2). Other studies have shown a similar convergence of taxonomic composition in perennial and intermittent reaches if sampling is conducted after several months of continuous flow (Mathers et al., 2019).

In contrast to our taxonomic observations, flow intermittency significantly influenced macroinvertebrate trait composition. Perennial reaches of Sycamore Creek were characterized by traits that would be maladaptive in intermittent reaches (Mathers et al., 2019), including a lack of desiccation-resistant diapause stages and a longer life span (>1 year). However, intermittent reaches had no significant trait indicators. We had predicted that aerial flight dispersal may be an important trait to exhibit for taxa living in intermittent reaches (Miliša et al., 2022), but this was not the case—perhaps due to an anomalously dry monsoon season in 2020. Aerial flight dispersal in this region is often triggered by summer monsoonal rainfall (Bogan & Boersma, 2012), but monsoon rains were at record low levels in 2020 (Mankin et al., 2021). Thus, macroinvertebrates living in the basin may never have received the proper cue to disperse aerially and colonize intermittent reaches. Additionally, we hypothesized that having diapause stages to survive dry seasons would be a trait that only taxa in intermittent reaches would exhibit. However, as mentioned previously, the high flow winter season in 2020 may have facilitated drift dispersal of intermittent specialists into downstream perennial reaches, thus making diapause a trait that was not restricted to intermittent reaches. Because perennial reaches are so much rarer and smaller in Sycamore Creek (Figure 1), there may not have been as much of an opportunity for perennial specialists to colonize intermittent reaches. Recent studies from Europe have also found relatively few indicator taxa for highly intermittent reaches compared to mildly intermittent and nearly perennial reaches (Miliša et al., 2022; White et al., 2018).

TABLE 4 Summary of linear mixed effects model results explaining variation in richness with the predictor stream distance to refuge. Results include incidence rate ratios (estimates) with corresponding 95% confidence intervals (*CI*) and *p* values (*p*). Bold indicates significant log-likelihood ratio derived *p* values of predictors ($\alpha \leq 0.05$).

	Richness		
Predictors	**Estimates**	**CI**	***p***
(Intercept)	41.96	32.77–51.17	**<0.001**
Stream distance	−0.23	−2.06 to 1.60	0.809
Random effect: reach			
σ^2	73.04		
τ_{00}	112.84		
ICC	0.61		
N_{Reach}	10		
Observations	29		
Marginal R^2/Conditional R^2	0.003/0.608		

4.2 | Distance to refuge

Surprisingly, we found no relationship between taxonomic richness and distance to perennial refuges. Other researchers have found that intermittent reaches with greater connectivity to perennial reaches tend to be more species rich and have communities more similar to those of perennial refuges (Bonada et al., 2007; Datry et al., 2014; Robson et al., 2011), but this relationship may be complex and context dependent. For example, the maximum distance from an intermittent reach to a perennial refuge in the Sycamore Creek basin was nearly 15 km. Previous studies have found that most macroinvertebrates disperse less than 1 km, with only some strong fliers capable of dispersing 10 km or more (Chester et al., 2015). If most perennial refuges in Sycamore Creek are >1 km from intermittent reaches, then the influence of those refuges on the communities in distant intermittent reaches may be minimal. The lack of relationship between richness and distance to refuge may also be due to the distribution of perennial refuges the Sycamore Creek basin. Perennial reaches were generally found in the central part of the basin, with intermittent reaches in the

TABLE 5 Significant traits by season as determined by indicator species analysis. The index column indicates the associated indicator value (IndVal). There were no significant indicator traits for samples from Spring 2020, Summer 2020 or Spring 2021.

Trait	Spring 2020	Summer 2020	Fall 2020	Spring 2021	Index	stat	*p* value	*p* value (corrected)
FFG 5	0	0	1	0	1	0.584	0.001	0.033
Locomotion 6	0	0	1	0	1	0.469	0.003	0.045

headwaters and lower reaches (Figure 1). If perennial refuges were more uniformly distributed throughout the basin and located upstream of intermittent reaches (to facilitate drift dispersal), then distance to refuge might have been a more influential factor in shaping richness values (Bogan et al., 2017). Future studies in this basin should expand the number of sampling sites and locations to include a careful examination of the spatial orientation of perennial refuges (upstream vs. downstream), as that could influence the ability of taxa to recolonize intermittent reaches (Gill et al., 2022; Wilding et al., 2018).

4.3 | Seasonal dynamics

While richness responded predictably with increased number of days flowing, there was no uniform pattern in richness across seasons. Intermittent reaches did not experience a steady decline in richness as habitat contracted during the dry seasons, potentially due to reach-specific characteristics such as habitat heterogeneity and variability through the seasons (Stubbington, England, et al., 2017). For example, SYCA-02 (Figure S2) was highly intermittent but was sampled in each season. In that reach, we saw an increase from the spring high flow period to the summer dry period, followed by a dramatic decrease after that in the fall until rising again the next spring. In contrast, SYCA-05 is a perennial reach where half the reach is fed by a reliable spring flowing over bedrock, and the other half is alluvial and experienced drying during the summer and fall. At this reach, habitat contracted predictably through time and richness decreased each season as water quality conditions worsened (e.g., increasing temperature, decreasing dissolved oxygen; Boersma et al., 2014a), and microhabitats were lost to drying (Bogan et al., 2015). Finally, another reason that richness may not have changed reliably across seasons is the potential for seasonal replacement of taxa (Boulton & Lake, 1992) or a 'time-sharing' of different species through the year, where some species leave and others arrive (Bogan & Lytle, 2007). This process would result in distinct compositional or trait differences by season even when alpha richness values within a reach do not change across seasons.

In contrast to the lack of distinction by flow class, there were significant differences in macroinvertebrate taxonomic composition across seasons. Seasonality in taxonomic composition has been documented in both temperate and arid systems, though seasonal variation in arid regions tends to be stronger than in temperate regions (Bogan et al., 2015; Boulton & Lake, 1992). At Sycamore Creek, a large number of taxa that prefer lentic conditions, including snails, true flies, microcrustaceans and *Callibaetis* mayflies, were more abundant in summer and fall samples (Figure 4b, Table 4). This 'time-sharing' of reaches, where lotic taxa inhabit the reach during high flow periods, and lentic taxa colonize the reach during low flow periods, has been previously documented from streams in southeastern Arizona (Bogan & Lytle, 2007) and elsewhere (e.g., Hill & Milner, 2018).

We also found significant distinction in trait composition among seasons. This pattern may be a reflection of a gradient in changing habitat conditions (Beche et al., 2006). In intermittent reaches, flow contraction, cessation and rewetting of habitat across seasons result in greater habitat heterogeneity than in more stable reaches (Stubbington, England, et al., 2017). So, the trait shifts we observed may be in response to this seasonal heterogeneity, with traits adaptive to lentic conditions being common in the summer and traits adaptive to lotic conditions being common in the winter (Beche et al., 2006; Boulton & Lake, 1992).

Seasonal variation in trait composition has not been a consistent finding in other studies. For example, Beche et al. (2006) did not find significant trait compositional differences between seasons in California streams. However, their study took place in a more temperate environment over multiple years, where the magnitude of change in habitat between seasons was less pronounced than it is in more arid regions (Beche et al., 2006). In southeastern Arizona streams, Giam et al. (2017) did find significant trait differences between intermittent and perennial reaches but not across seasons within perennial reaches. These contrasting findings illustrate the complex, and often context-dependent, responses of trait composition to seasonal dynamics and other environmental factors (Boersma et al., 2016).

5 | CONCLUSIONS

As climate change intensifies, the frequency and intensity of drying events will increase in many streams across the region (Miller et al., 2021; Seager & Vecchi, 2010). In perennial reaches, where alpha diversity is higher and species have traits that are maladaptive to drying disturbances, these sensitive species could be lost when unprecedented drying events occur (Bogan & Lytle, 2011). The loss of key taxa in perennial reaches can lead to cascading trophic and ecosystem effects across aquatic and riparian food webs (Boersma et al., 2014b). Even in intermittent streams with highly adapted communities, current climate predictions could push these communities beyond their abilities, and species could start to disappear from these systems as well (Bogan et al., 2015).

While some components of our hypotheses were not supported, these systems do not always respond to drying disturbances the same way. Each stream may have a unique combination of factors converging to shape reach-scale hydrology and drive aquatic communities. While the body of work around intermittent streams has focused on how flow regime characteristics such as days flowing and drying duration have direct impacts on the biota, seasonal changes are important as well. Even where flow is perennial, water levels change throughout the year—potentially influencing other factors that impact biota, such as water quality, nutrients, temperature and habitat availability. Understanding these seasonal changes can allow for a more nuanced understanding of species responses to increases in the intensity and frequency of drought and stream drying across the region.

ACKNOWLEDGEMENTS

We are thankful to members of the Bogan Lab for their support and feedback, to Kate Boersma for statistical guidance and to Kelly Mott Lacroix and Alison Mettler of Tonto National Forest for permitting and logistical support. This research was funded by the USA National Science Foundation Macrosystems Biology and NEON-Enabled Science (award number: DEB-1802766). All research sites are located on the ancestral homelands of the Kewevkepaya (Southeastern Yavapai) people.

DATA AVAILABILITY STATEMENT

The document 'Supplemental Materials' containing Figures S1 and S2, Tables S1–S3, Legends for Datasets S1–S3 and Datasets S1–S3 have been uploaded as electronic supplementary material.

REFERENCES

Acuña, V., Datry, T., Marshall, J., Barcelo, D., Dahm, C. N., Ginebreda, A., McGregor, G., Sabater, S., Tockner, K., & Palmer, M. A. (2014). Why should we care about temporary waterways? *Science*, *343*, 1080–1081. https://doi.org/10.1126/science.1246666

Acuña, V., Hunter, M., & Ruhí, A. (2017). Managing temporary streams and rivers as unique rather than second-class ecosystems. *Biological Conservation*, *211*, 12–19. https://doi.org/10.1016/j.biocon.2016.12.025

Allan, J. D. (1995). *Stream ecology: Structure and function of running waters*. Chapman and Hall. https://doi.org/10.1007/978-94-011-0729-7

Allen, D. C., Datry, T., Boersma, K. S., Bogan, M. T., Boulton, A. J., Bruno, D., Busch, M. H., Costigan, K. H., Dodds, W. K., Fritz, K. M., Godsey, S. E., Jones, J. B., Kaletova, T., Kampf, S. K., Mims, M. C., Neeson, T. M., Olden, J. D., Pastor, A. V., Poff, N. L. R., … Zimmer, M. (2020). River ecosystem conceptual models and non-perennial rivers: A critical review. *Wiley Interdisciplinary Reviews Water*, *7*(5), e1473. https://doi.org/10.1002/wat2.1473

Bailowitz, R. A., Danforth, D., & Upson, S. (2015). *A field guide to the damselflies & dragonflies of Arizona and Sonora*. Nova Granada Publications.

Beche, L. A., Mcelravy, E. P., & Resh, V. H. (2006). Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean-climate streams in California, USA. *Freshwater Biology*, *51*(1), 56–75. https://doi.org/10.1111/j.1365-2427.2005.01473.x

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B: Methodological*, *57*(1), 289–300.

Boersma, K. S., Bogan, M. T., Henrichs, B. A., & Lytle, D. A. (2014a). Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. *Freshwater Biology*, *59*(3), 491–501. https://doi.org/10.1111/fwb.12280

Boersma, K. S., Bogan, M. T., Henrichs, B. A., & Lytle, D. A. (2014b). Top predator removals have consistent effects on large species despite high environmental variability. *Oikos*, *123*(7), 807–816. https://doi.org/10.1111/oik.00925

Boersma, K. S., Dee, L. E., Miller, S. J., Bogan, M. T., Lytle, D. A., & Gitelman, A. I. (2016). Linking multidimensional functional diversity to quantitative methods: A graphical hypothesis-evaluation framework. *Ecology*, *97*(3), 583–593. https://doi.org/10.1890/15-0688

Bogan, M. T. (2017). Hurry up and wait: Life cycle and distribution of an intermittent stream specialist (*Mesocapnia arizonensis*). *Freshwater Science*, *36*(4), 805–815. https://doi.org/10.1086/694746

Bogan, M. T., & Boersma, K. S. (2012). Aerial dispersal of aquatic invertebrates along and away from arid-land streams. *Freshwater Science*, *31*(4), 1131–1144. https://doi.org/10.1899/12-066.1

Bogan, M. T., Boersma, K. S., & Lytle, D. A. (2013). Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. *Freshwater Biology*, *58*(5), 1016–1028. https://doi.org/10.1111/fwb.12105

Bogan, M. T., Boersma, K. S., & Lytle, D. A. (2015). Resistance and resilience of invertebrate communities to seasonal and supraseasonal drought in arid-land headwater streams. *Freshwater Biology*, *60*(12), 2547–2558. https://doi.org/10.1111/fwb.12522

Bogan, M. T., Chester, E. T., Datry, T., Murphy, A. L., Robson, B. J., Ruhi, A., Stubbington, R., & Whitney, J. E. (2017). Resistance, resilience, and community recovery in intermittent rivers and ephemeral streams. In *Intermittent rivers and ephemeral streams* (pp. 349–376). Academic Press.

Bogan, M. T., & Lytle, D. A. (2007). Seasonal flow variation allows 'time-sharing' by disparate aquatic insect communities in montane desert streams. *Freshwater Biology*, *52*(2), 290–304. https://doi.org/10.1111/j.1365-2427.2006.01691.x

Bogan, M. T., & Lytle, D. A. (2011). Severe drought drives novel community trajectories in desert stream pools. *Freshwater Biology*, *56*(10), 2070–2081. https://doi.org/10.1111/j.1365-2427.2011.02638.x

Bonada, N., Rieradevall, M., & Prat, N. (2007). Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. *Hydrobiologia*, *589*(1), 91–106. https://doi.org/10.1007/s10750-007-0723-5

Boulton, A. J., & Lake, P. S. (1992). The ecology of two intermittent streams in Victoria, Australia: III. Temporal changes in faunal composition. *Freshwater Biology*, *27*(1), 123–138.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., … Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Cáceres, M. D., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, *90*(12), 3566–3574. https://doi.org/10.1890/08-1823.1

Chapin, T. P., Todd, A. S., & Zeigler, M. P. (2014). Robust, low-cost data loggers for stream temperature, flow intermittency, and relative conductivity monitoring. *Water Resources Research*, *50*(8), 6542–6548. https://doi.org/10.1002/2013WR015158

Chester, E. T., Miller, A. D., Valenzuela, I., Wickson, S. J., & Robson, B. J. (2015). Drought survival strategies, dispersal potential and persistence of invertebrate species in an intermittent stream landscape. *Freshwater Biology*, *60*(10), 2066–2083. https://doi.org/10.1111/fwb.12630

Chester, E. T., & Robson, B. J. (2011). Drought refuges, spatial scale and recolonisation by invertebrates in non-perennial streams. *Freshwater Biology*, *56*(10), 2094–2104. https://doi.org/10.1111/j.1365-2427.2011.02644.x

Cover, M. R., Seo, J. H., & Resh, V. H. (2015). Life history, burrowing behavior, and distribution of Neohermes filicornis (Megaloptera: Corydalidae), a long-lived aquatic insect in intermittent streams. *Western North American Naturalist*, *75*(4), 474–490. https://doi.org/10.3398/064.075.0405

Crabot, J., Heino, J., Launay, B., & Datry, T. (2020). Drying determines the temporal dynamics of stream invertebrate structural and functional beta diversity. *Ecography*, *43*(4), 620–635. https://doi.org/10.1111/ecog.04835

Crabot, J., Mondy, C. P., Usseglio-Polatera, P., Fritz, K. M., Wood, P. J., Greenwood, M. J., Bogan, M. T., Meyer, E. I., & Datry, T. (2021). A global perspective on the functional responses of stream communities to flow intermittence. *Ecography*, *44*(10), 1511–1523. https://doi.org/10.1111/ecog.05697

Datry, T. (2012). Benthic and hyporheic invertebrate assemblages along a flow intermittence gradient: Effects of duration of dry events. *Freshwater Biology*, *57*(3), 563–574. https://doi.org/10.1111/j.1365-2427.2011.02725.x

Datry, T., Bonada, N., & Heino, J. (2016). Towards understanding the organisation of metacommunities in highly dynamic ecological systems. *Oikos*, *125*(2), 149–159. https://doi.org/10.1111/oik.02922

Datry, T., Corti, R., Heino, J., Hugueny, B., Rolls, R. J., & Ruhí, A. (2017). Habitat fragmentation and metapopulation, metacommunity, and metaecosystem dynamics in intermittent rivers and ephemeral streams. In *Intermittent rivers and ephemeral streams* (pp. 377–403). Academic Press.

Datry, T., Larned, S. T., & Tockner, K. (2014). Intermittent rivers: A challenge for freshwater ecology. *Bioscience*, *64*(3), 229–235. https://doi.org/10.1093/biosci/bit027

Datry, T., Moya, N., Zubieta, J., & Oberdorff, T. (2016). Determinants of local and regional communities in intermittent and perennial headwaters of the Bolivian Amazon. *Freshwater Biology*, *61*(8), 1335–1349. https://doi.org/10.1111/fwb.12706

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Eppehimer, D. E., Hamdhani, H., Hollien, K. D., & Bogan, M. T. (2020). Evaluating the potential of treated effluent as novel habitats for aquatic invertebrates in arid regions. *Hydrobiologia*, *847*(16), 3381–3396. https://doi.org/10.1007/s10750-020-04343-6

Fournier, R. J., de Mendoza, G., Sarremejane, R., & Ruhi, A. (2023). Isolation controls reestablishment mechanisms and post-drying community structure in an intermittent stream. *Ecology*, *104*(2), e3911. https://doi.org/10.1002/ecy.3911

Fritz, K. M., Hagenbuch, E., D'Amico, E., Reif, M., Wigington, P. J. Jr., Leibowitz, S. G., Comeleo, R. L., Ebersole, J. L., & Nadeau, T. L. (2013). Comparing the extent and permanence of headwater streams from two field surveys to values from hydrographic databases and maps. *JAWRA Journal of the American Water Resources Association*, *49*(4), 867–882. https://doi.org/10.1111/jawr.12040

Giam, X., Chen, W., Schriever, T. A., van Driesche, R., Muneepeerakul, R., Lytle, D. A., & Olden, J. D. (2017). Hydrology drives seasonal variation in dryland stream macroinvertebrate communities. *Aquatic Sciences*, *79*(3), 705–717. https://doi.org/10.1007/s00027-017-0530-7

Gill, B. A., Sanabria, A., Gonzales, M., Carlson, S. M., & Bogan, M. T. (2022). Effects of drying and orientation to perennial refuges on aquatic biodiversity across two basins differing in aridity. *Ecosphere*, *13*(5), e4071. https://doi.org/10.1002/ecs2.4071

Gray, L. J. (1981). Species composition and life histories of aquatic insects in a lowland Sonoran Desert stream. *American Midland Naturalist*, *106*, 229–242. https://doi.org/10.2307/2425159

Gray, L. J., & Fisher, S. G. (1981). Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran Desert stream. *American Midland Naturalist*, *106*, 249–257. https://doi.org/10.2307/2425161

Hill, M. J., & Milner, V. S. (2018). Ponding in intermittent streams: A refuge for lotic taxa and a habitat for newly colonising taxa? *Science of the Total Environment*, *628*, 1308–1316. https://doi.org/10.1016/j.scitotenv.2018.02.162

Jaeger, K. L., & Olden, J. D. (2012). Electrical resistance sensor arrays as a means to quantify longitudinal connectivity of rivers. *River Research and Applications*, *28*(10), 1843–1852. https://doi.org/10.1002/rra.1554

Jaeger, K. L., Olden, J. D., & Pelland, N. A. (2014). Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proceedings of the National Academy of Sciences*, *111*(38), 13894–13899. https://doi.org/10.1073/pnas.1320890111

Kelso, J. E., & Entrekin, S. A. (2018). Intermittent and perennial macroinvertebrate communities had similar richness but differed in species trait composition depending on flow duration. *Hydrobiologia*, *807*(1), 189–206. https://doi.org/10.1007/s10750-017-3393-y

Koundouri, P., Boulton, A. J., Datry, T., & Souliotis, I. (2017). Ecosystem services, values, and societal perceptions of intermittent rivers and ephemeral streams. In *Intermittent rivers and ephemeral streams* (pp. 455–476). Academic Press.

Mankin, J. S., Simpson, I., Hoell, A., Fu, R., Lisonbee, J., Sheffield, A., & Barrie, D. (2021). *NOAA drought task force report on the 2020–2021 southwestern U.S. drought*. NOAA Drought Task Force, MAPP, and NIDIS.

Mathers, K. L., Stubbington, R., Leeming, D., Westwood, C., & England, J. (2019). Structural and functional responses of macroinvertebrate assemblages to long-term flow variability at perennial and nonperennial sites. *Ecohydrology*, *12*(6), e2112. https://doi.org/10.1002/eco.2112

Merritt, R., Cummins, K., & Berg, M. B. (2008). *An introduction to the aquatic insects of North America* (4th ed.). Kendall Hunt Publishing.

Messager, M. L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., Tockner, K., Trautmann, T., Watt, C., & Datry, T. (2021). Global prevalence of non-perennial rivers and streams. *Nature*, *594*(7863), 391–397. https://doi.org/10.1038/s41586-021-03565-5

Miliša, M., Stubbington, R., Datry, T., Cid, N., Bonada, N., Šumanović, M., & Milošević, D. (2022). Taxon-specific sensitivities to flow intermittence reveal macroinvertebrates as potential bioindicators of intermittent rivers and streams. *Science of the Total Environment*, *804*, 150022. https://doi.org/10.1016/j.scitotenv.2021.150022

Miller, O. L., Putman, A. L., Alder, J., Miller, M., Jones, D. K., & Wise, D. R. (2021). Changing climate drives future streamflow declines and challenges in meeting water demand across the southwestern United States. *Journal of Hydrology X*, *11*, 100074. https://doi.org/10.1016/j.hydroa.2021.100074

NEON [National Ecological Observatory Network]. (2017). *Field site: Sycamore Creek NEON/SYCA*. NEON. https://www.neonscience.org/field-sites/syca

Oksanen J., Guillaume F.B., Friendly M., Kindt R., Legendre P., McGlinn D., … James Weedon (2020). vegan: Community ecology package. *R package version 2.5-7*. https://CRAN.R-project.org/package=vegan

Poff, N. L., Olden, J. D., Vieira, N. K., Finn, D. S., Simmons, M. P., & Kondratieff, B. C. (2006). Functional trait niches of North American lotic insects: Traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, *25*(4), 730–755. https://doi.org/10.1899/0887-3593(2006)025[0730:FTNONA]2.0.CO;2

Poff, N. L., & Ward, J. V. (1989). Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, *46*(10), 1805–1818. https://doi.org/10.1139/f89-228

R Core Team. (2021). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*. https://www.R-project.org/

Ricotta, C., Carboni, M., & Acosta, A. T. (2015). Let the concept of indicator species be functional! *Journal of Vegetation Science*, *26*(5), 839–847. https://doi.org/10.1111/jvs.12291

Robson, B. J., Chester, E. T., & Austin, C. M. (2011). Why life history information matters: Drought refuges and macroinvertebrate persistence in non-perennial streams subject to a drier climate. *Marine and Freshwater Research*, *62*(7), 801–810. https://doi.org/10.1071/MF10062

Sarremejane, R., Cañedo-Argüelles, M., Prat, N., Mykrä, H., Muotka, T., & Bonada, N. (2017). Do metacommunities vary through time? Intermittent rivers as model systems. *Journal of Biogeography*, *44*(12), 2752–2763. https://doi.org/10.1111/jbi.13077

Sarremejane, R., England, J., Sefton, C. E., Parry, S., Eastman, M., & Stubbington, R. (2020). Local and regional drivers influence how aquatic community diversity, resistance and resilience vary in response to drying. *Oikos*, *129*(12), 1877–1890. https://doi.org/10.1111/oik.07645

Schriever, T. A., Bogan, M. T., Boersma, K. S., Cañedo-Argüelles, M., Jaeger, K. L., Olden, J. D., & Lytle, D. A. (2015). Hydrology shapes taxonomic and functional structure of desert stream invertebrate communities. *Freshwater Science*, *34*(2), 399–409. https://doi.org/10.1086/680518

Seager, R., & Vecchi, G. A. (2010). Greenhouse warming and the 21st century hydroclimate of southwestern North America. *Proceedings of the National Academy of Sciences*, *107*(50), 21277–21282. https://doi.org/10.1073/pnas.0910856107

Shanafield, M., Godsey, S., Datry, T., Hale, R., Zipper, S., Costigan, K., Krabbenhoft, C., Dodds, W., Zimmer, M., Allen, D., Bogan, M., Kaiser, K., Burrows, R., Hammond, J., Busch, M., Kampf, S., Mims, M., Burgin, A., & Olden, J. (2020). Science gets up to speed on dry rivers. *Eos*, *101*. https://doi.org/10.1029/2020EO139902

Sponseller, R. A., Grimm, N. B., Boulton, A. J., & Sabo, J. L. (2010). Responses of macroinvertebrate communities to long-term flow variability in a Sonoran Desert stream. *Global Change Biology*, *16*(10), 2891–2900. https://doi.org/10.1111/j.1365-2486.2010.02200.x

Stanley, E. H., Fisher, S. G., & Grimm, N. B. (1997). Ecosystem expansion and contraction in streams. *Bioscience*, *47*(7), 427–435. https://doi.org/10.2307/1313058

Statzner, B., Gore, J. A., & Resh, V. H. (1988). Hydraulic stream ecology: Observed patterns and potential applications. *Journal of the North American Benthological Society*, *7*(4), 307–360. https://doi.org/10.2307/1467296

Stubbington, R., Bogan, M. T., Bonada, N., Boulton, A. J., Datry, T., Leigh, C., & Vander Vorste, R. (2017). The biota of intermittent rivers and ephemeral streams: aquatic invertebrates. In *Intermittent rivers and ephemeral streams* (pp. 217–243). Academic Press.

Stubbington, R., England, J., Wood, P. J., & Sefton, C. E. (2017). Temporary streams in temperate zones: Recognizing, monitoring and restoring transitional aquatic-terrestrial ecosystems. *Wiley Interdisciplinary Reviews Water*, *4*(4), e1223. https://doi.org/10.1002/wat2.1223

Thorp, J. H., & Rogers, D. C. (Eds.). (2015). *Thorp and Covich's freshwater invertebrates*. Elsevier.

Turner, D. S., & Richter, H. E. (2011). Wet/dry mapping: Using citizen scientists to monitor the extent of perennial surface flow in dryland regions. *Environmental Management*, *47*(3), 497–505. https://doi.org/10.1007/s00267-010-9607-y

Vander Vorste, R., Malard, F., & Datry, T. (2016). Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river. *Freshwater Biology*, *61*(8), 1276–1292. https://doi.org/10.1111/fwb.12658

Vander Vorste, R., Stubbington, R., Acuña, V., Bogan, M. T., Bonada, N., Cid, N., Datry, T., Storey, R., Wood, P. J., & Ruhí, A. (2021). Climatic aridity increases temporal nestedness of invertebrate communities in naturally drying rivers. *Ecography*, *44*(6), 860–869. https://doi.org/10.1111/ecog.05349

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(1), 130–137. https://doi.org/10.1139/f80-017

Vieira, N. K., Poff, N. L., Carlisle, D. M., Moulton, S. R., Koski, M. L., & Kondratieff, B. C. (2006). A database of lotic invertebrate traits for North America. *US Geological Survey Data Series*, *187*, 1–15.

Washko, S., & Bogan, M. T. (2019). Global patterns of aquatic macroinvertebrate dispersal and functional feeding traits in aridland rock pools. *Frontiers in Environmental Science*, *7*, 106. https://doi.org/10.3389/fenvs.2019.00106

White, J. C., House, A., Punchard, N., Hannah, D. M., Wilding, N. A., & Wood, P. J. (2018). Macroinvertebrate community responses to hydrological controls and groundwater abstraction effects across intermittent and perennial headwater streams. *Science of the Total Environment*, *610*, 1514–1526. https://doi.org/10.1016/j.scitotenv.2017.06.081

Wilding, N. A., White, J. C., Chadd, R. P., House, A., & Wood, P. J. (2018). The influence of flow permanence and drying pattern on macroinvertebrate biomonitoring tools used in the assessment of riverine ecosystems. *Ecological Indicators*, *85*, 548–555. https://doi.org/10.1016/j.ecolind.2017.10.059

Zeileis, A., & Hothorn, T. (2002). Diagnostic checking in regression relationships. *R News*, *2*(3), 7–10.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Hollien, K. D., Gill, B. A., Eppehimer, D. E., & Bogan, M. T. (2023). Effects of stream drying, season, and distance to refuge on macroinvertebrate community structure in an arid intermittent stream basin. *Ecohydrology*, e2598. https://doi.org/10.1002/eco.2598