

EFFECTS OF STREAM DRYING, SEASON, AND DISTANCE TO REFUGES ON
MACROINVERTEBRATE COMMUNITY STRUCTURE IN AN ARID INTERMITTENT
STREAM BASIN

by

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ABSTRACT

Intermittent streams are globally ubiquitous and comprise a large percentage of stream networks. As climate changes in arid regions and increases the frequency and intensity of drying disturbances, it is important to understand how aquatic biota respond to such stressors and how it would impact biodiversity. To address these topics, we sampled 10 stream reaches in the Sycamore Creek drainage, an arid-land stream in central Arizona, with reach-scale flow regimes ranging from perennial to highly intermittent. We sampled aquatic macroinvertebrates across 10 reaches during 4 seasons to explore seasonal variability in community structure as habitat transitions through flowing and drying phases. We also collected continuous flow regime data at each reach 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 however was distinct between seasons as well as flow classification, with traits such as a lack of diapause, longer life span, and predatory feeding behaviors as indicators for perennial reaches. As climate change alters natural flow regimes, understanding the response of macroinvertebrate community structure to drying disturbances in an arid-land stream can help to provide insight on aquatic community responses to a drying climate at a larger scale.

Introduction

Intermittent streams make up a large portion of global stream networks (>50%: Fritz et al., 2013; Acuña et al., 2014). 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, support important ecosystem processes, and harbor 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 the connection between aquatic ecosystems and flow regimes 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 (Vannote et al., 1980; Allen et al., 2020). It was believed that periodic drying was a harsh filter that acted on communities in intermittent streams, leading them to be less biodiverse and less dense 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 meta communities—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 et al., 2017a).

In intermittent streams, the intensity, location, and extent of drying events shape ecosystem processes and may strongly influence macroinvertebrate community composition (Bogan et al., 2013; Bogan et al., 2015, Kelso & Entekin, 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 may need to persist in drying environments (Bonada et al., 2007). Resistance traits, such as aestivation, and desiccation resistant eggs or larvae, can allow organisms to remain in the stream bed and return to an active form after the dry period. 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).

The spatial configuration of perennial and intermittent reaches within a stream network can vary across networks and regions, and influence biodiversity as well. In mesic temperate 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). Where intermittency occurs within a stream network is important to the connectivity of aquatic organisms. Distance and direction from perennial refuges in these networks can influence community structure and impact resilience to disturbances such as drought (Bogan et al., 2015; Datry 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 (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 (Robson et al., 2011; Bogan et al., 2015).

In addition to longitudinal changes in flow regimes, the habitat types within individual reaches also can shift seasonally 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 the drier summer months, when only isolated pools remain in the stream bed (Gray & Fisher, 1981; Bogan & Lytle, 2007). In fact, taxa with strong aerial dispersal abilities (e.g. beetles, dragonflies) may actively colonize intermittent reaches when only stagnant pools remain and complete their life cycles in these seasonal lentic habitats (Bogan & Boersma, 2012; Miliša et al., 2021) However, when flow returns to these same reaches during wetter periods, less tolerant macroinvertebrates that require well-oxygenated flowing conditions may recolonize the reach by drifting down from upstream perennial refuges (Vander Vorste et al., 2016; Datry et al., 2016), highlighting the dynamic seasonal nature of some 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 and water withdrawals may overwhelm these survival strategies (Bogan et al., 2015). 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 advance their larval life cycles (Cover et al., 2015; Bogan, 2017) or aeri ally recolonize 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). Forming 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 (Datry et al., 2014; Jaeger et al., 2014).

The goal of this study was to explore how flow intermittency, the distance to perennial refuges, and seasonal habitat dynamics influence macroinvertebrate community structure at intermittent and perennial reaches within an arid-land stream basin. At 10 reaches within the Sycamore Creek drainage in central Arizona (USA), we sampled benthic macroinvertebrates and quantified reach-scale flow regimes 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 from intermittent reaches is a secondary driver of local species richness due to species-specific variation in dispersal abilities, and 3) within a reach, species richness and taxonomic and trait composition varies seasonally as fluctuating water levels influence the presence of species with adaptive traits for seasonal variability in habitat conditions. We predicted that: 1) reaches with more intense intermittency would have lower species richness and have 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 drop during the summer and fall as habitat contracts. Community structure will also shift to favor tolerant, highly mobile taxa during the drier months and less tolerant lotic taxa during wetter months.

Methods

Study area

Sycamore Creek is a second order stream in central Arizona, USA that drains 505 km² (Fig. 1). It is a tributary of the Verde River that ranges from 1,700-m in elevation at its headwaters in the Mazatzal mountains, to 430-m where it meets the Verde River near Fort McDowell, AZ. The headwaters descend from coniferous forest and pass through chaparral before widening and cutting 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.

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).

A majority of Sycamore Creek is classified as intermittent and drying disturbances are common. Seasonal drying and periods of low flow are typical during the summer months, with some flow returning with monsoon precipitation 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 period in some intermittent reaches with bedrock stream channels (Fig. 2).

Within the drainage, ten 150-m long study reaches were chosen that exhibit varying degrees of intermittency and distances from perennial refuges (Fig. 1, Fig. 3). Each reach is separated by a minimum of 1.5-km, and the distance from the uppermost reach to the lowest is approximately 30-km.

Study design

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 roughly evenly placed within a 150-m transect in various macrohabitats (targeting pools and riffles) to capture drying dynamics of the entire reach as flow decreases or ceases and 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 were dry, 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 strongly or beginning to dry (Fig. 3).

Flow sensors were also used to calculate reach-specific flow regime characteristics such as: 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), drying frequency (number of drying events longer than 48 hours between one biological sampling event to the next), and 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 and distinguish them from long-flowing intermittent reaches.

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 parts of the study period (January 2021, Fig.4). The entire length of the drainage that was included in the study, as well as any notable tributaries, were 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 mapping software. This study happened to be 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.

Compilation of the trait matrix

To determine the composition of adaptive traits within the Sycamore 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 collectively represent a suite of basic physiological and morphological traits that would be necessary to characterize the macroinvertebrate community (Boersma et al., 2014a; Boersma et al., 2016). After samples were identified and a taxonomically identified matrix was compiled, the taxa were assigned a categorical value based on more descriptive levels within the broad trait categories. Definitions of the traits and their assigned categorical values can be found in Table 1.

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 any 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 (Fig. 4).

Biological samples were collected using the reach-wide benthic and targeted edge approaches. The reach-wide approach consisted of using a 30x30-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 (Epehimer et al., 2020). 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-cm x 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 (Epehimer 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 lab at the University of Arizona.

Lab processing

Samples were further processed in the lab 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 Rodgers (2015). Early life stages of some insects, and all life stages of some true flies (Diptera), such as Muscidae, were only identified to family. Taxonomically challenging non-insect taxa, such as Oligochaeta and Ostracoda, were identified to order.

For community composition analyses (see below), macroinvertebrate densities were calculated for each taxon using the quantitative reach-wide samples. For taxonomic richness analyses, however, both the reach-wide and edge samples were used 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 given reach during a given sampling event (Epehimer et al., 2020).

Data analysis

Richness

We evaluated the relationships between richness and characteristics of flow intermittency and distance to perennial refuge using a linear mixed-effects modeling approach. The correlations among all of our calculated flow regime metrics and refuge distance metrics were

assessed prior to modeling using all possible pairwise correlations of five possible predictors: days flowing, drying frequency, flow permanence, stream distance to the nearest perennial refuge, and aerial distance to the nearest refuge. We found that most of these predictors had high degrees of collinearity (see Table S2 for all combinations and values). Stream distance to refuge and aerial distance to refuge 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. Days flowing and flow permanence also were highly correlated ($r=0.83$), as were days flowing and drying frequency ($r=0.65$). Given these collinearities in flow metrics, only days flowing was retained as a flow metric in the richness model.

Days flowing and stream distance to refuge also exhibited moderate collinearity ($r=0.58$; Dormann et al., 2013). This meant that we could not include days flowing and stream distance to refuge in the same model and have high confidence in the model outcome. As such, the final model only included days flowing as a factor. However, because those two factors represent different categories of predictors (temporal vs spatial), we also assessed stream distance to refuge as a sole predictive factor of richness in a separate model. Linear mixed-effects models were run for both models with sample reach as a random effect, using the R package *glmmTMB* (Brooks et al., 2017). Model performance was checked by visually inspecting the residual diagnostic plots for residual versus fitted values of the model.

Taxonomic Composition

Non-metric multidimensional scaling (NMDS) was used to visualize taxonomic composition across all samples with the package *vegan* (Oksanen et al., 2020) in R (R Core

Team, 2020). To determine which macroinvertebrate taxa were influential in the ordination, Pearson's correlation coefficients were calculated between the abundances of each macroinvertebrate taxon and NMDS axis values. To examine relationships between taxonomic composition and flow and spatial factors, the three flow regime metrics derived from the sensors (days flowing, drying frequency, flow permanence) and the two spatial isolation metrics (stream distance to nearest perennial refuge and aerial distance to nearest refuge) were tested for significant correlations with NMDS axes. To examine differences in taxonomic composition between flow class and season, we used permutational multivariate analyses of variance (perMANOVA) in *vegan* (Oksanen et al., 2020). We tested for differences in taxonomic composition: (1) across the four sampling seasons and (2) between intermittent and perennial reaches.

Trait analysis

To determine how the community composition of Sycamore communities varied in their trait composition, we first used NMDS ordination to visualize communities in trait space. The trait matrix we generated 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. Next, we used perMANOVA in *vegan* (Oksanen et al., 2020) to test for differences: (1) across the four sampling seasons and (2) between intermittent and perennial reaches. We then used the traits as pseudo-species (Ricotta et al., 2015) to conduct an indicator species analysis for perennial vs intermittent samples using the package *indicspecies* (Cáceres & Legendre, 2009). This was done to better characterize the

functional ecology of macroinvertebrates between flow classes and look for support for our trait-based hypotheses. We corrected for multiple testing in indicator species analyses using the false discovery rate method (Benjamini & Hochberg, 1995).

Results

Flow sensor data

Flow sensor data revealed highly variable flow regimes in many reaches of Sycamore Creek. All reaches were flowing fully at the start of the study, while 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 (Fig. 3). Overall flow permanence across our study period ranged from as little as 40% in some intermittent reaches to 100% of the flow record in our perennial and near perennial reaches. The number of days the reach had been flowing prior to biological sampling in intermittent reaches ranged from 8 days to 455 days (mean: 168 ± 115 SD). Many of these reaches also experienced drying events once or twice in the period prior to sampling (Fig. 3). One intermittent reach (SYCA-07) was dry during initial reach visits (September 2019) but began flowing again soon after and never dried during the length of the study. Perennial reaches did not experience complete flow cessation, but there was within-reach variation among perennial reaches. At some of these reaches, one or more of the five flow sensors deployed indicated drying as habitat contracted laterally or longitudinally within those reaches. For example, SYCA-05 would seasonally contract, with alluvial parts of the reach ceasing to flow during summer while bedrock-bound parts of the reach continuing to flow (Fig. 2E; Fig. 3). In contrast, SYCA-06 maintained flow across the entire reach during the study period (Fig. 2A; Fig. 3).

Richness

Average taxonomic richness was 61% higher in perennial reaches than in 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 (Fig. 5). Richness values also varied within a reach across seasons, but with no discernable pattern. In some reaches, richness increased across the seasons, but in other reaches it decreased (Fig. 5). Across all samples, richness significantly increased with days flowing, with only a minor amount of variation attributed to the random reach factor (Marginal R^2 / Conditional R^2 = 0.492/0.576, $p < 0.001$) (Table 3, Fig. 6A). In contrast, there was no significant relationship between richness and stream distance to perennial refuge ($p = 0.806$) (Table 4, Fig. 6B).

Taxonomic composition

We collected a total of 29 macroinvertebrate samples across the four sampling seasons, from which we identified 193 macroinvertebrate taxa. The most diverse orders were Diptera (79 taxa), Coleoptera (36 taxa), and Hemiptera (17 taxa). NMDS ordination showed an overall clustering of samples by season in multivariate taxonomic-space, with the most overlap occurring between Summer 2020 and Fall 2020 samples (Fig. 7, Fig. 8; stress = 0.16, $R^2 = 0.87$). We found significant differences in the taxonomic composition between seasons (perMANOVA, season: $R^2 = 0.23$, $F = 2.50$, $p = 0.001$; Fig. 7) but not flow class ($R^2 = 0.054$, $F = 1.55$, $p = 0.062$; Fig. 8).

Drying frequency and days flowing were significantly correlated with NMDS taxonomic ordination axes (Fig. 8). Drying frequency was negatively correlated with axis 1 ($R^2 = 0.50$) while days flowing was positively correlated with axis 1 ($R^2 = 0.22$) (Fig. 8). Taxonomic

composition as described by the NMDS axes was not correlated with flow permanence, aerial distance to perennial refuge, or stream distance to perennial refuge.

Taxa that were positive correlated with axis 1 included several odonate (*Anax*, *Archilestes*, *Libellula*), beetle (*Boreonectes aequinoctialis*, Hydroptorinae, *Liodesus*), and non-insect taxa (Copepoda, Ostracoda, *Hyalella*, *Physa*), as well some true flies (Culicidae: *Culex*, *Aedes*; Chironomidae: *Pseudochironomus*), true bugs (Veliidae: *Microvelia*), and mayflies (Baetidae: *Callibaetis*) (Table 2). Axis 2 described, in part, a gradient from higher abundances of the dobsonfly *Neohermes* (Corydalidae) and true fly midge larvae, such as *Cricotopus/Orthocladius* and *Eukiefferiella brehmi*, to higher abundances of the beetle *Laccophilus maculosus* and the mayfly *Fallceon* (Table 2). Abundances of stoneflies in the family Capniidae, the midges *Eukiefferiella brehmi* and *Hydrobaenus*, the dobsonfly *Neohermes*, and the blackfly *Prosimulium* were negatively correlated with axis 2.

Trait composition

Intermittent and perennial reaches clustered by flow class and season in multivariate trait-space (Fig. 9, stress = 0.08, $R^2 = 0.97$). There was significant distinction in trait composition between perennial and intermittent reaches (perMANOVA, flow class: $R^2 = 0.14$, $F = 4.57$, $p = 0.023$), as well as significant distinction in trait composition between seasons ($R^2 = 0.23$, $F = 2.57$, $p = 0.03$). Multiple traits were associated with samples from perennial reaches and positively correlated with trait ordination axis 1 (Fig. 10; for a full list see Table 5). Indicator species analysis showed that *diapause 3* (no diapause, $p = 0.024$), *voltinism 1* (less than 1 generation per year, $p = 0.024$), and *functional feeding group 7* (engulfers/predators, $p = 0.024$) were indicator

traits for perennial samples, but there were no significant indicator traits for samples from intermittent reaches (Table 6).

Discussion

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

Richness

Taxonomic richness at Sycamore Creek increased with the number of days reaches had been flowing prior to sampling and richness was overall lower in intermittent reaches than in perennial reaches as predicted. While ~60% of the variation in our richness model was explained by increasing days flowing, there could be other abiotic factors such as water temperature, and the availability of nutrients influencing the observed increase in richness in combination with increasing days flowing. While richness responded predictably with days flowing, there was no uniform pattern in richness across seasons. Intermittent reaches did not predictably experience a steady decline in richness as habitat contracted during the dry seasons and the perennial reaches

did not exhibit an increase in richness values, potentially due to reach-specific characteristics such as habitat heterogeneity and variability through the seasons (Stubbington et al., 2017b). For example, SYCA 02 was highly intermittent but was able to be sampled 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) or microhabitats were lost during the contraction process (Bogan et al., 2017). 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 while 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.

We also hypothesized that that stream distance to the nearest perennial refuge would be a secondary driver of local species richness. However, we found no relationship between richness and distance to refuge. Other researchers have generally 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; Robson et al., 2011; Datry et al., 2014), but this relationship may be complex and context dependent. For example, the minimum distance from an intermittent reach to a perennial refuge in this study was roughly 1.2-km, while the maximum distance 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 hydrological characteristics and patterns across the Sycamore Creek basin. Perennial reaches were generally found in the central part of the basin, with intermittent reaches in the headwaters and lower down in the study area. If perennial refuges were more uniformly distributed throughout the basin and located upstream of intermittent reaches (to facilitate drift dispersal), then distance to refuge may be a more influential factor in shaping richness values (Bogan et al., 2017). Future studies in this basin should expand to include the spatial orientation of the perennial refuges (upstream vs downstream), as that could influence the ability of taxa to recolonize intermittent reaches.

Taxonomic composition

Intermittency did not appear to strongly influence macroinvertebrate taxonomic composition. Previous studies have found support for both distinct communities with high numbers of unique taxa in intermittent reaches (e.g., Bogan et al., 2013) and intermittent communities that were merely nested subsets of taxa found in perennial reaches (e.g., Bonada et al., 2007; Vander Vorste et al., 2021). It has also been noted that these nested subsets of taxa in intermittent reaches are often dominated by generalists that are resilient enough to colonize quickly when preferable habitats become available (i.e., lentic taxa when habitat contracts to isolated pools, lotic taxa when flow returns) (Stubbington et al., 2017b). However, the level to which some taxa were identified in some studies could impact the level of taxonomic distinctness

that is detected between intermittent and perennial reaches. We were able to identify to genus or species blackflies (Simuliidae) and midges (Chironomidae) that have high intra-family variation, with many species adapted to intermittency (Bogan & Lytle, 2007; Bogan et al., 2013). Detry (2012) found blackflies and midges to be among the most abundant taxa at intermittent reaches but did not identify them beyond the family level, while Santos et al. (2011) found them in such disproportionate densities that they were excluded entirely to avoid swamping taxonomic analyses. However, we failed to find taxonomic distinctness between intermittent and perennial reaches despite having fine taxonomic resolution of blackflies and midges in our study. We did find the desiccation-resistant taxa *Neohermes* and *Hydrobaenus* exclusively in intermittent reaches, similar to previous studies (Bogan et al., 2013; Cover et al., 2015), but their abundances were not high enough to result in overall community distinction in intermittent reaches.

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 (Figs. 3, 4). 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 broad 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 et al., 2017), were found in both intermittent and perennial reaches during the March 2020 sampling event which followed the prolonged period of high flows. However, these taxa were restricted to intermittent reaches during the February 2021 sampling event, which was not preceded by long periods of high flow conditions (Fig. 4). 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 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 (Boulton & Lake, 1992; Bogan et. al., 2015). At Sycamore Creek, a large number of taxa that prefer lentic conditions, including snails, true flies, microcrustaceans, and *Callibaetis* mayflies, were more abundant in the summer and fall samples on the right side of the NMDS ordination plot (Fig. 7, Table 2). 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).

Trait composition

In contrast to our taxonomic observations, flow intermittency significantly influenced macroinvertebrate trait composition in our study. Perennial reaches of Sycamore Creek were characterized by traits that would be maladaptive in intermittent reaches, including a lack of desiccation-resistant diapause stages and a longer life span (> 1 year) (Mathers et al., 2019). 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, but this was not the case – perhaps due to an anomalous monsoon season in 2020. Aerial flight dispersal in regional streams is often triggered by summer monsoonal rainfall (Bogan & Boersma, 2012;

Bogan, 2013) but the monsoons essentially failed during the summer of 2020 and produced very little rain (Mankin et al., 2021). Thus, macroinvertebrates living in the Sycamore Creek 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 many 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. Since perennial reaches are so much rarer and smaller in Sycamore Creek (Fig. 1), there may not have been as much opportunity for perennial specialists to colonize intermittent reaches. In a recent study from Europe, Miliša et al. (2021) also found communities in reaches with relatively high flow intermittency to have few indicative traits when compared with perennial reaches.

In addition to differences by flow class, we also found significant distinction in trait composition among seasons at Sycamore Creek. This seasonal variation in trait composition 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 results in greater habitat heterogeneity than in more stable reaches (Stubbington et al., 2017b). So the trait shifts we observed in our study may be in response to this seasonal heterogeneity, with traits that are adaptive to lentic conditions and deteriorating water quality being common in the summer and traits adaptive to lotic conditions being common in the winter (Boulton & Lake, 1992; Beche et al., 2006). This seasonal variation in trait composition has not been a consistent finding in other studies though. 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 in 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).

Conclusions

As climate change continues, the frequency and intensity of drying events will increase in many streams across the region (Seager & Vecchi, 2010; Miller et al., 2021). In perennial reaches, where biodiversity 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 also do not always respond to drying stressors the same way. Each stream may have a unique combination of factors converging to shape reach-scale hydrology and drive aquatic communities. ‘Intermittent’ as a categorical description can encompass a lot of variation, but intermittency exists on a gradient. Flow regime characteristics like days flowing and drying duration are continuous data—and their direct impacts on the biota (e.g., how quickly habitat contracts or how long an

organism must stay dormant in a dry stream bed) represent a continuum of responses. Increasing the body of work that takes a more quantitative look at intermittency—as a continuous variable and not just a categorical description—will allow for more a more nuanced understanding of species responses to drying. This more detailed ecological understanding will also allow for more informed conservation and management strategies to be deployed in response to increases in the intensity and frequency of stream drying across the region.

FIGURES

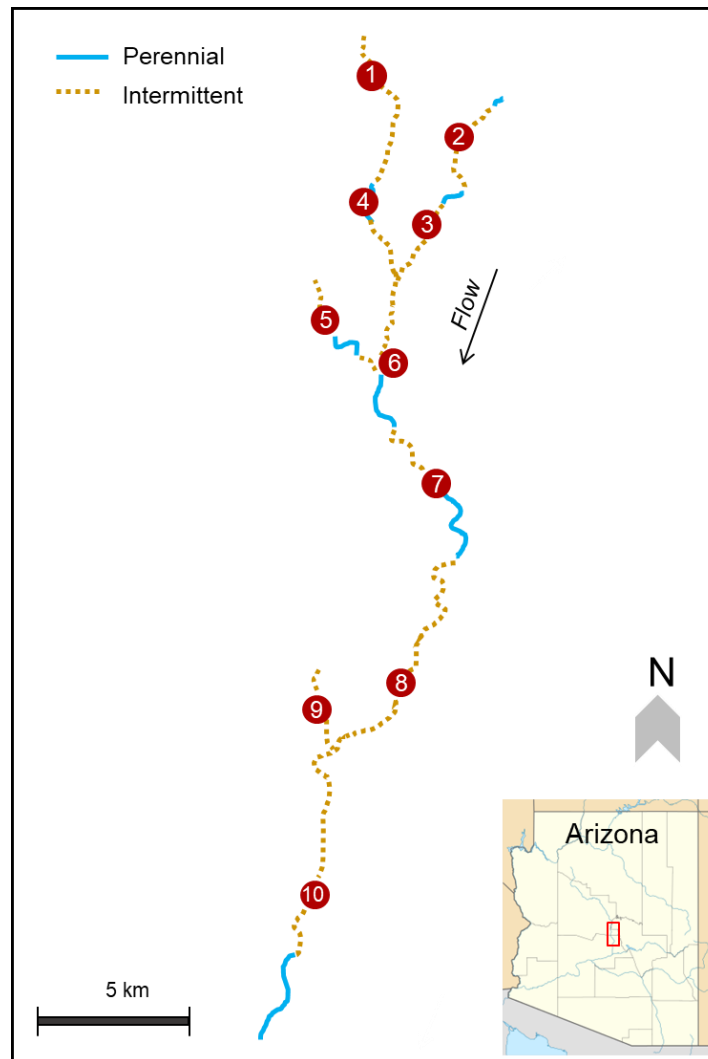


Fig. 1: Map of Sycamore Creek study area. Red numbered markers indicate sampling reaches. Solid blue sections indicate a perennial refuge found during wet-dry mapping. Dashed yellow lines indicate an intermittent reach and solid blue lines indicate a perennial reach, as determined by wet-dry mapping.



Fig. 2: Representative photos of various intermittent and perennial reaches in Sycamore Creek, AZ. Reaches shown are A) SYCA-06 (perennial), B) SYCA-02 (intermittent), C) SYCA-04 (perennial), D) SYCA-09 (intermittent), E) SYCA-05 (perennial), F) SYCA-10 (intermittent).

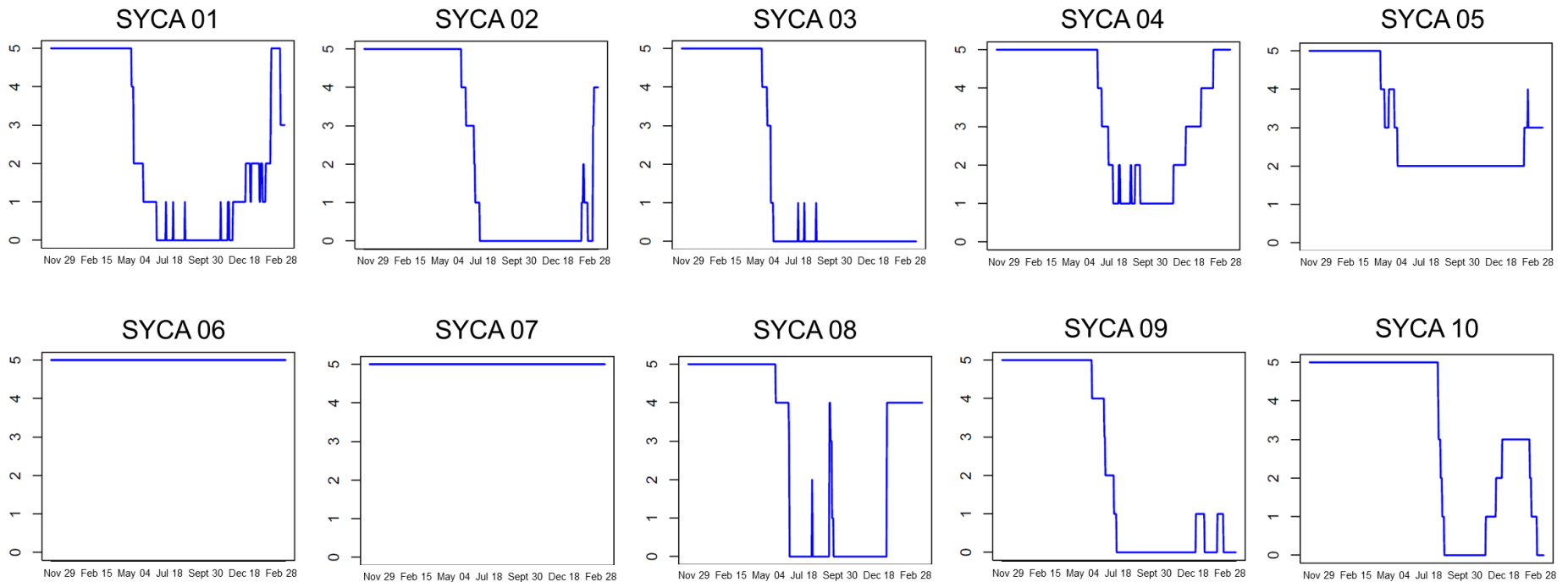


Fig. 3: Hydrographs generated from flow sensors for each of the 10 sampled reaches from November 2019 through March 2021 (x-axis). For each plot, a score of 5 on the y-axis indicates that all flow sensors in the reach were submerged. As individual flow sensors within a reach are exposed to the air, the score decreases, documenting lateral and/or longitudinal flow contraction within the reach until a reach dries completely (score = 0). Some reaches were stable across the study period (e.g., SYCA 06), while others experienced multiple drying and rewetting events (e.g., SYCA 08).

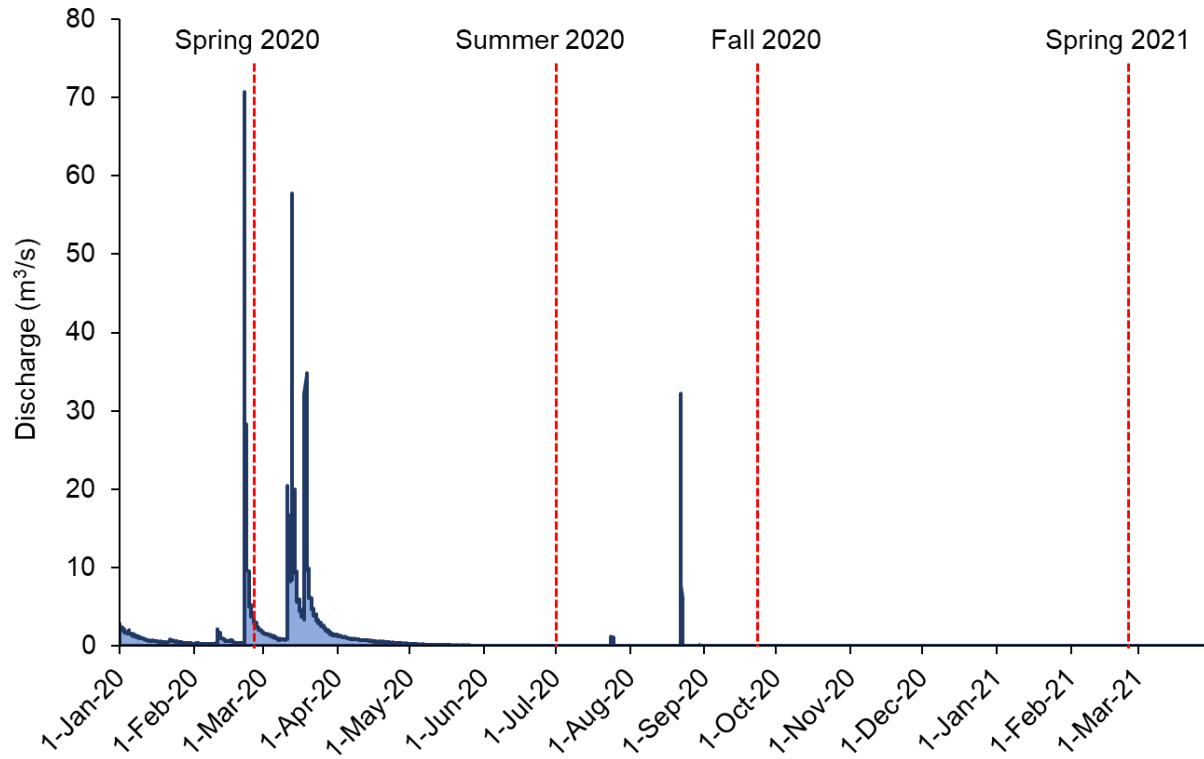


Fig. 4: Hydrograph of Sycamore Creek, AZ for the duration of the study period. Occurrence of sampling events based on flow conditions indicated by red dashed lines. Flow data provided by the nearest USGS stream gauge.

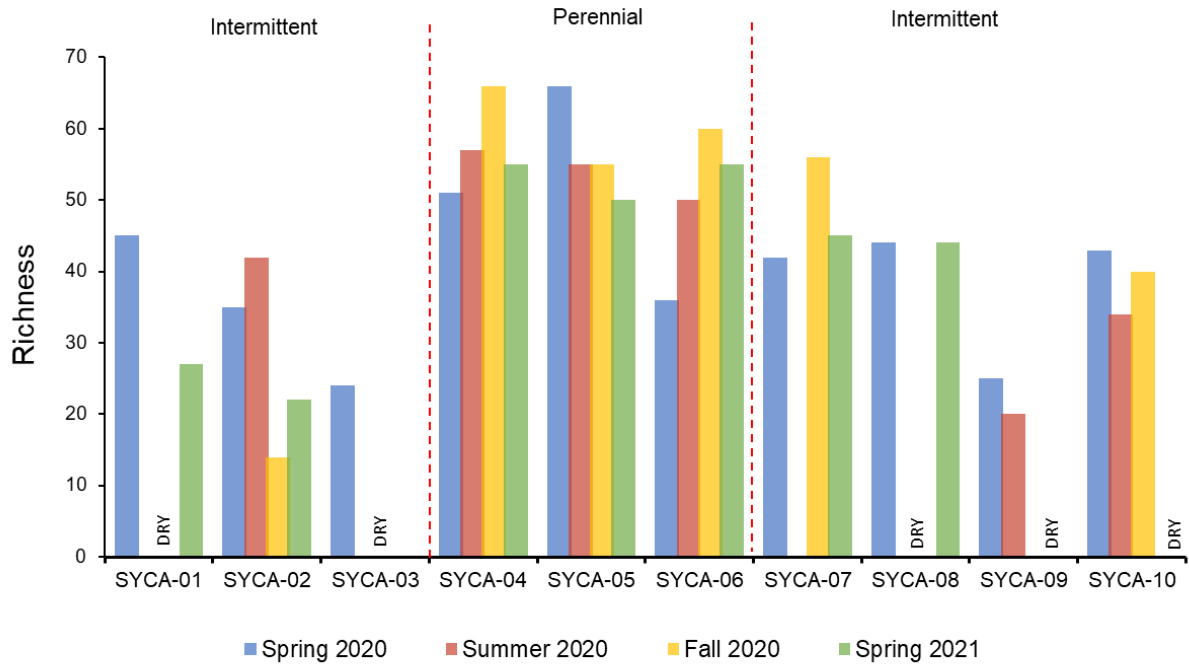


Fig 5: Taxonomic richness from the 10 sample reaches at Sycamore Creek by season. Reaches SYCA-04, 05, and 06 are perennial while reaches SYCA-01, 02, 03, 07, 08, 09, and 10 are intermittent, as labeled and denoted by the dashed lines.

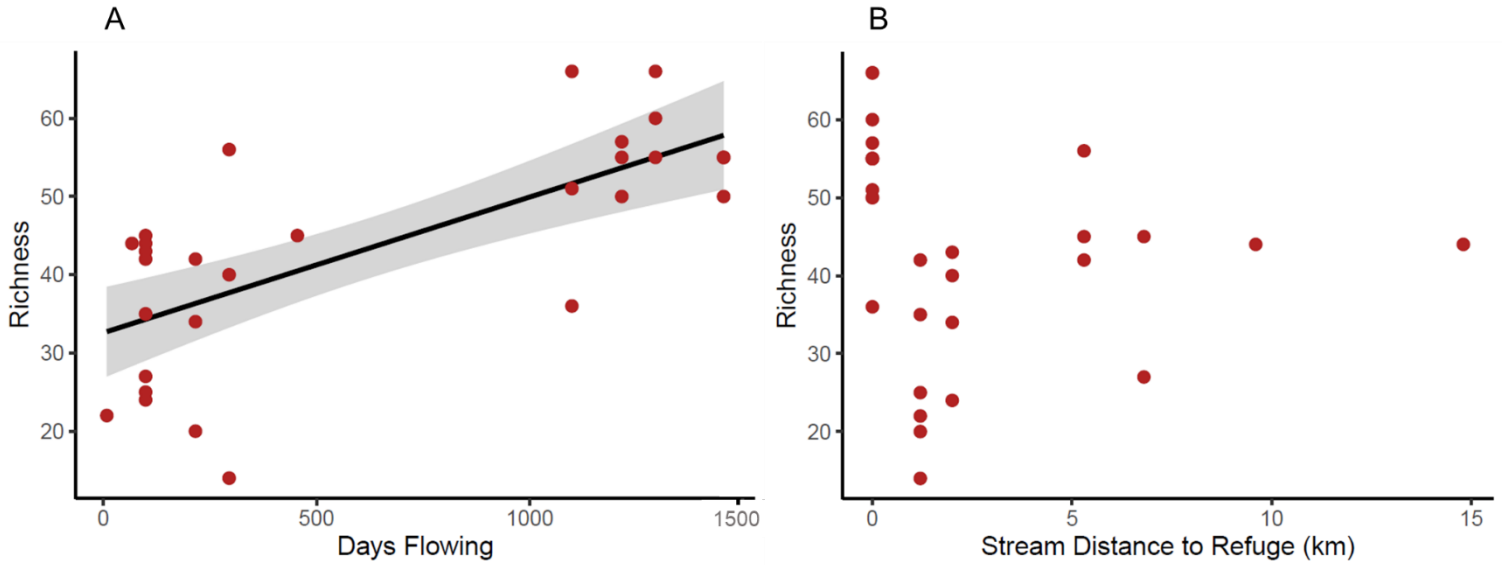


Fig. 6: Macroinvertebrate richness was positively related to the days flowing metric (A), as illustrated here in the linear mixed effects model output. In contrast, macroinvertebrate richness was not significantly predicted by stream distance to refuge (B). The dark grey shaded area represent a 95% confidence interval.

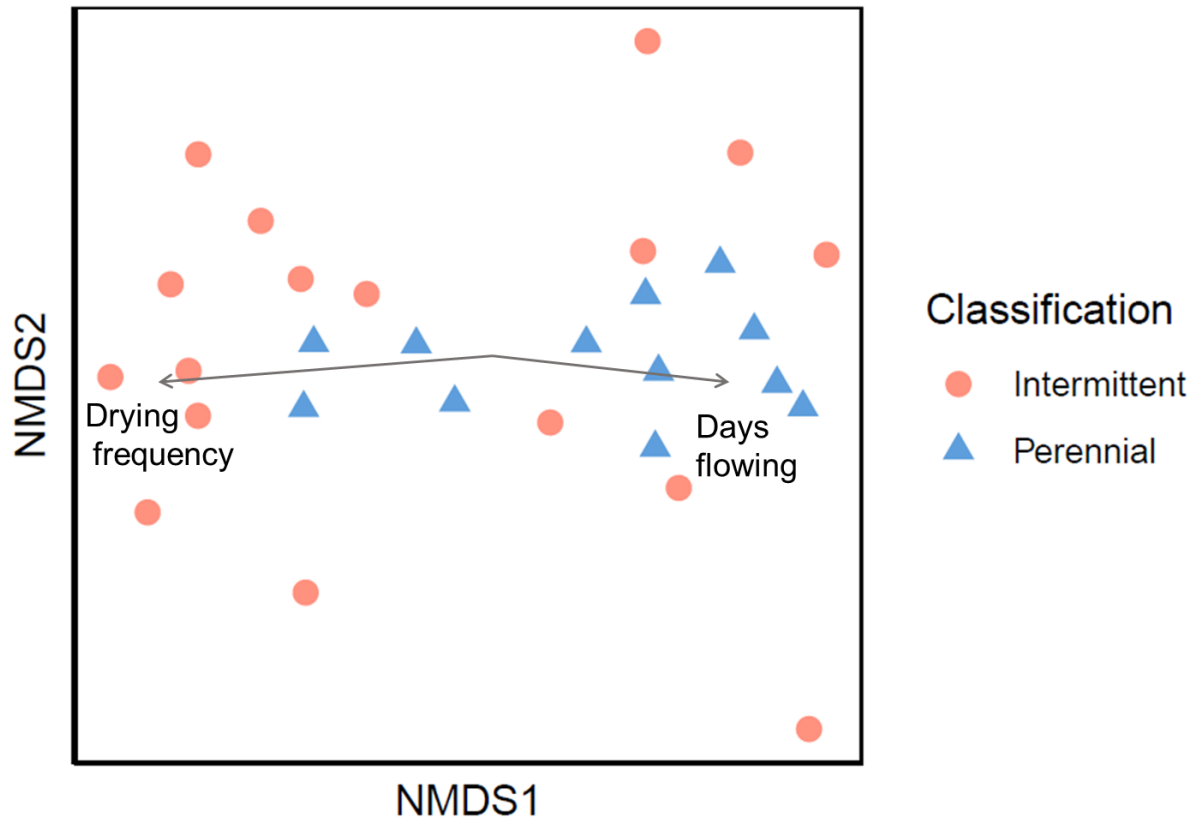


Fig 8: Taxonomic ordination (NMDS) of macroinvertebrate samples from all reaches at Sycamore Creek. The flow classification (perennial vs intermittent) of reaches are indicated by color and shape. Black arrows represent vectors of environmental factors (e.g. flow regime metrics) with significant correlations with ordination axes.

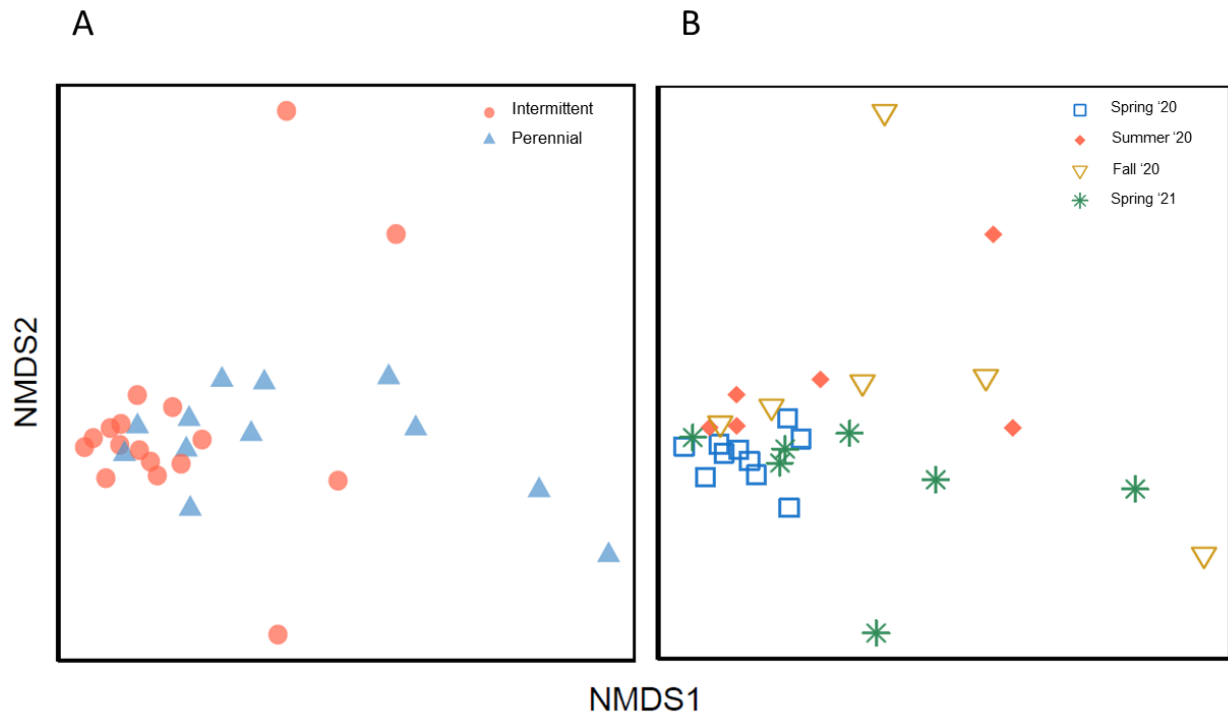


Fig. 9: Trait ordinations (non-metric multidimensional scaling) of macroinvertebrate samples from all reaches at Sycamore Creek by A) flow class (perennial vs intermittent) and B) season.

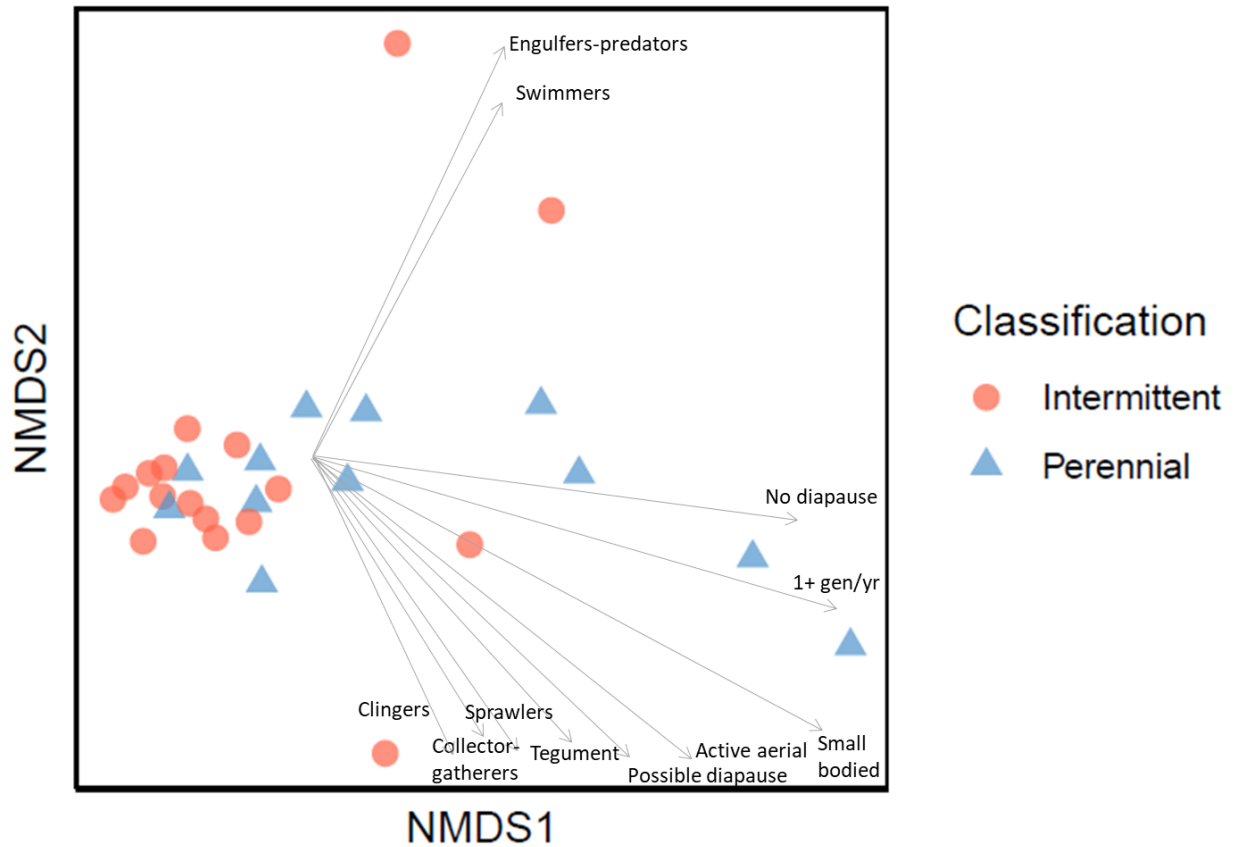


Fig. 10: Trait ordination (non-metric multidimensional scaling) of macroinvertebrate samples from all reaches in Sycamore Creek. The flow class (perennial vs intermittent) of reaches are indicated by color and shape. Grey arrows represent traits that have strong correlations ($R^2 \geq 0.70$) with ordination axes.

TABLES

Table 1: Definitions of macroinvertebrate traits and their categorical breakdown

Trait	Definition and Categories
Body size	Size of an organism; 1) <9mm, 2) 9-16mm, 3) >16mm
Voltinism	Number of generations produced per year; 1) <1gen/yr, 2) 1gen/yr, 3) >1gen/yr
Dispersal	Mobility method to colonize new habitats; 1) aquatic passive, 2) aquatic active, 3) aerial passive, 4) aerial active
Respiration	Method of breathing; 1) tegument, 2) gill, 3) plastron, spiracle, vesicle
Functional feeding group	Feeding behavior; 1) collector-gatherer, 2) shredder, 3) scraper/grazer, 4) filter-feeder, 5) piercer-plants, 6) piercer-predator, 7) engulfer-predator
Diapause	Suspended development; 1) presence of structures or diapause, 2) possible diapause or resistance (inferred in studies or found in closely related taxa), 3) no diapause or resistance known
Locomotion	Method of movement; 1) burrow, 2) interstitial, 3) sprawl, 4) attached/cling, 5) swim, 6) skate, 7) climb

Table 2: Pearson’s correlation coefficients between macroinvertebrate abundances and NMDS ordination axis 1 and 2. Macroinvertebrate taxa with strong correlations ($|r| > 0.45$) are shown.

Taxon	Axis 1 <i>r</i>	Taxon	Axis 2 <i>r</i>
<i>Boreonectes aequinoctialis</i>	0.62	<i>Laccophilus maculosus</i>	0.53
<i>Physa</i>	0.54	<i>Fallceon</i>	0.47
<i>Microvelia</i>	0.52	<i>Pentaneura</i>	0.46
Copepoda	0.50	<i>Hydrobaenus</i>	-0.45
<i>Hyaella</i>	0.50	<i>Prosimulium</i>	-0.45
<i>Libellula</i>	0.49	<i>Parametriocnemus</i>	-0.46
Ostracoda	0.49	<i>Atractides</i>	-0.48
<i>Callibaetis</i>	0.48	Capniidae	-0.48
Hydroporinae	0.48	<i>Tipula</i>	-0.49
<i>Liodessus</i>	0.48	<i>Cricotopus/Orthocladius</i>	-0.51
<i>Pseudochironomus</i>	0.48	<i>Neohermes</i>	-0.51
<i>Archilestes</i>	0.47	<i>Eukiefferiella brehmi</i>	-0.53
<i>Culex</i>	0.47		
<i>Aedes</i>	0.46		
<i>Anax</i>	0.46		

Table 3: Summary of linear mixed effects model results explaining variation in richness with the predictor days flowing. Results include incidence rate ratios (Estimates) with corresponding 95% confidence intervals (CI) and p values (p). Bold indicates significant p values of predictors ($\alpha \leq 0.05$).

Richness			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	32.74	26.75-38.73	<0.001
Days flowing	0.02	0.01-0.02	<0.001
Random Effect: Reach			
σ^2	79.42		
τ_{00}	15.66		
ICC	0.016		
N_{Reach}	10		
Observations	29		
Marginal R^2 / Conditional R^2	0.492 / 0.576		

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 p values of predictors ($\alpha \leq 0.05$).

Richness			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	41.96	32.77-51.17	<0.001
Stream distance	-0.23	-2.06-1.60	0.806
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		

Table 5: Correlation values for trait abundances and non-metric multidimensional scaling ordination axes. Traits with strong correlations ($R^2 > 0.5$) are shown, and no traits were strongly correlated with axis 2.

Taxon	Axis 1 R^2
Size 1	0.87
Dispersal 4	0.84
Locomotion 5	0.82
Voltinism 3	0.80
Diapause 2	0.79
FFG 1	0.79
Locomotion 4	0.76
FFG 6	0.73
Respiration 1	0.72
Locomotion 3	0.72
Diapause 3	0.70
FFG 7	0.67
Voltinism 2	0.67
Respiration 3	0.67
Size 3	0.65
Locomotion 1	0.65
Respiration 2	0.64
Dispersal 3	0.63
Voltinism 1	0.61
Size 2	0.59
Dispersal 1	0.54
Locomotion 7	0.52

Table 6: Significant traits by flow regime class as determined by indicator species analysis.

There were no significant indicator traits for samples from intermittent reaches.

Trait	Intermittent	Perennial	Index	stat	p value	p value (corrected)
Voltinism 1	0	1	2	0.39687	0.0044	0.044
FFG 7	0	1	2	0.52637	0.0013	0.024
Diapause 3	0	1	2	0.48438	0.0016	0.024

APPENDIX A: SUPPLEMENTAL MATERIALS

Table S1: Description of samples collected. 'X' indicates a sample was collected

Reach	Spring 2020	Summer 2020	Fall 2020	Spring 2021
SYCA-01	X			X
SYCA-02	X	X	X	X
SYCA-03	X			
SYCA-04	X	X	X	X
SYCA-05	X	X	X	X
SYCA-06	X	X	X	X
SYCA-07	X		X	X
SYCA-08	X			X
SYCA-09	X	X		
SYCA-10	X	X	X	

Table S2: Collinearity coefficients for all flow variables.

Environmental variables			r
stream distance to refuge	x	aerial distance to refuge	0.92
days flowing	x	flow permanence	0.83
days flowing	x	drying frequency	0.65
days flowing	x	stream distance to refuge	0.58
days flowing	x	aerial distance to refuge	0.59
flow permanence	x	stream distance to refuge	0.38

References

- Acuña, V., T. Datry, J. Marshall, D. Barcelo, C. N. Dahm, A. Ginebreda, G. McGregor, S. Sabater, K. Tockner, & M. A. Palmer. (2014). Conservation. Why should we care about temporary waterways? *Science* (New York, N.Y.) 343:1080-1081
- Acuña, V., Hunter, M., & Ruhí, A. (2017). Managing temporary streams and rivers as unique rather than second-class ecosystems. *Biological Conservation*, 211, 12-19.
- Allen, D. C., Datry, T., Boersma, K. S., Bogan, M. T., Boulton, A. J., Bruno, D., ... & Zimmer, M. (2020). River ecosystem conceptual models and non-perennial rivers: A critical review. *Wiley Interdisciplinary Reviews: Water*, 7(5), e1473.
- 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.
- 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.
- 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.

- 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
- Bogan, M. T. (2013). *Drought, dispersal, and community dynamics in arid-land streams*. Oregon State University.
- 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.
- 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.
- 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.
- Bogan, M. T., Boersma, K. S., & Lytle, D. A. (2015). Resistance and resilience of invertebrate communities to seasonal and suprasedasonal drought in arid-land headwater streams. *Freshwater Biology*, *60*(12), 2547-2558.
- Bogan, M. T., Chester, E. T., Datry, T., Murphy, A. L., Robson, B. J., Ruhi, A., ... & 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.
- Bogan, M. T., & Lytle, D. A. (2011). Severe drought drives novel community trajectories in desert stream pools. *Freshwater Biology*, 56(10), 2070-2081.
- 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.
- 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.
- Cáceres, M. D., & Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology*, 90(12), 3566-3574.
- 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.

- 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.
- 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.
- 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.
- 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.
- 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.
- 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.

- 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.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... & Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27-46.
- 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.
- Fritz, K. M., Hagenbuch, E., D'Amico, E., Reif, M., Wigington Jr, P. J., Leibowitz, S. G., ... & 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.
- Giam, X., Chen, W., Schriever, T. A., Van Driesche, R., Muneeppeerakul, R., Lytle, D. A., & Olden, J. D. (2017). Hydrology drives seasonal variation in dryland stream macroinvertebrate communities. *Aquatic Sciences*, *79*(3), 705-717.
- Gray, L. J. (1981). Species composition and life histories of aquatic insects in a lowland Sonoran Desert stream. *American Midland Naturalist*, 229-242.
- Gray, L. J., & Fisher, S. G. (1981). Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran Desert stream. *American Midland Naturalist*, 249-257.

- 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.
- 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.
- 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.
- Kelso, J. E., & Entekin, 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.
- 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.
- Merritt R., Cummins K. & Berg M.B. (2008). *An introduction to the aquatic insects of North America*, 4th edn. Kendall Hunt Publishing, Dubuque, Iowa.

- Miliša, M., Stubbington, R., Datry, T., Cid, N., Bonada, N., Šumanović, M., & Milošević, D. (2021). Taxon-specific sensitivities to flow intermittence reveal macroinvertebrates as potential bioindicators of intermittent rivers and streams. *Science of The Total Environment*, 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.
- NEON [National Ecological Observatory Network] (2017). *Field Site: Sycamore Creek NEON/SYCA*. <https://www.neonscience.org/field-sites/syca>
- Oksanen J., Guillaume F.B., Friendly M., Kindt R., Legendre P., McGlinn D., *et al.* (2020). *vegan: Community Ecology Package*
- 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.
- 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.
- R Core Team (2020). R: A language and environment for statistical computing
- Ricotta, C., Carboni, M., & Acosta, A. T. (2015). Let the concept of indicator species be functional!. *Journal of vegetation science*, 26(5), 839-847.

- 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.
- Santos, A. N., & Stevenson, R. D. (2011). Comparison of macroinvertebrate diversity and community structure among perennial and non-perennial headwater streams. *Northeastern Naturalist*, 18(1), 7-26.
- 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.
- Shanafield, M., Godsey, S., Datry, T., Hale, R., Zipper, S., Costigan, K., ... & Olden, J. (2020). Science gets up to speed on dry rivers. *Eos*, 101.
- 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.
- Stanley, E. H., Fisher, S. G., & Grimm, N. B. (1997). Ecosystem expansion and contraction in streams. *BioScience*, 47(7), 427-435.
- Stubbington, R., Bogan, M. T., Bonada, N., Boulton, A. J., Datry, T., Leigh, C., & Vander Vorste, R. (2017a). 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. (2017b). Temporary streams in temperate zones: recognizing, monitoring and restoring transitional aquatic-terrestrial ecosystems. *Wiley Interdisciplinary Reviews: Water*, 4(4), e1223.
- Thorp, J. H., & Rogers, D. C. (Eds.). (2015). *Thorp and Covich's Freshwater Invertebrates*. London: 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.
- 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.
- Vander Vorste, R., Stubbington, R., Acuña, V., Bogan, M. T., Bonada, N., Cid, N., ... & Ruhí, A. (2021). Climatic aridity increases temporal nestedness of invertebrate communities in naturally drying rivers. *Ecography*, 44(6), 860-869.
- 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.
- 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.