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Hydrology shapes taxonomic and functional structure of desert stream invertebrate communities

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Abstract: Hydrology is a fundamental factor influencing ecosystem dynamics, life-history strategies, and diversity patterns in running-water habitats. However, it remains unclear how hydrology may structure the taxonomic and functional composition of communities, especially in systems with high spatiotemporal variability in flow. We examined invertebrate diversity from 7 desert streams in the Huachuca Mountains of southeastern Arizona, USA, that span a flow permanence continuum from highly intermittent to perennial. We examined the relative roles of flow permanence, habitat size, season, and microhabitat in determining taxonomic and functional structure (according to 7 species traits compiled for 234 taxa) of these communities. We predicted that both functional and taxonomic diversity would be positively related to flow permanence and negatively related to the duration and number of stream drying events. As predicted, increased flow permanence was associated with increased functional richness, functional evenness, and taxonomic richness. Conversely, drying events reduced functional diversity across all measured indices. We found a saturating relationship between functional richness and taxonomic richness, indicating functional redundancy in species-rich communities, which may promote resilience of ecosystem function to environmental variation. Our study adds further evidence that hydrology is a key determinant of aquatic invertebrate diversity, and that stream hydroperiod strongly influences both functional and taxonomic diversity in arid-land streams.

Key words: ecological filter, species traits, temporary streams, disturbance, quantile regression, American Southwest

Streams and rivers lie along a hydrologic continuum that ranges from highly intermittent flow, where surface water is present only occasionally, to perennial, where surface water occurs year-round (Poff et al. 1997). These differences in hydrology can shape patterns of species diversity (Wellborn et al. 1996, Williams 1996), affect the structure of riverine and riparian food webs (Sabo et al. 2010, McCluney and Sabo 2012), and drive evolutionary change in the organisms themselves (Lytle and Poff 2004, Lytle et al. 2008). The strong environmental gradients imposed by flow also impose a strong 'habitat filter' (sensu Southwood 1977, 1988) that directly controls the taxonomic and trait composition of communities (Williams 2006, Gallart et al. 2012, Mims and Olden 2012, Belmar et al. 2013, Ledger

et al. 2013b). Strong habitat filtering may locally favor taxa adapted to one hydrological extreme or another, as well as generalists capable of persisting in a variety of habitats (Poff and Ward 1989, Williams 2006, Bonada et al. 2007), but how habitat filtering affects communities along continuous gradients of hydrological variability is less clear.

Species richness and assemblage composition are commonly used to quantify aquatic communities and how they respond to perturbations (Bunn and Arthington 2002, Poff and Zimmerman 2010, Carlisle et al. 2011). However, trait-based measures of diversity, or functional diversity, may be more informative in describing ecological responses to environmental variability than taxonomy-based metrics alone (Walker 1992, Hoenighaus et al. 2007, Cadotte et al. 2011).

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Functional diversity can be defined as the number, type, and distribution of functions performed by organisms within an ecosystem (Díaz and Cabido 2001). A change in functional diversity may affect ecosystem processes, whereas a change in species diversity may elicit no ecosystem response at all because of functional redundancy (i.e., shared ecosystem-effect traits) among species. For example, Bonada et al. (2007) found no difference in macroinvertebrate species richness between permanent and intermittent rivers but did find significant among-site trait differences attributable to hydrology. Thus, a trait-based approach may identify consistent responses to disturbances or environmental gradients that are not revealed by taxonomic analyses alone. Functional diversity has important implications for the ability of communities to withstand and recover from disturbance and to respond to environmental change (Poff et al. 2006).

The form of the relationship between taxonomic and functional diversity determines the degree of functional redundancy in communities (Micheli and Halpern 2005). For instance, a positive linear relationship (slope = 1) indicates that species additions to a community result in new ecological functions, whereas a shallower, positive slope (<1) indicates low redundancy because some species share functional traits. Curvilinear relationships between taxonomic and functional diversity indicate communities rapidly acquire unique functions (associated with trait values) at low diversity levels and subsequently reach an asymptote at higher levels of diversity. More functionally diverse communities are thought to offer greater resilience because of greater ecological redundancy (Hooper et al. 2005), as has been shown for agricultural landuse gradients (Fischer et al. 2007), forest-fire disturbances (Hidasi-Neto et al. 2012), and hydrologic-alteration gradients (Pool et al. 2010). Thus, the form of the relationship between taxonomic and functional diversity can reveal much about how communities might respond to ecological perturbations.

We sought to assess whether taxonomic and functional trait diversity differed across aquatic habitats that span a gradient of flow dynamics ranging from highly intermittent to perennial. We characterized the trait and taxonomic diversity of desert-stream invertebrate communities in a stream network in southeastern Arizona and then examined the relative roles of flow permanence, physical-habitat conditions, and season in determining the taxonomic and functional structure of the communities. We examined the taxonomic–functional richness relationship in these arid-land communities. We predicted that under more intermittent flow conditions, only specialized taxa would persist locally because of habitat filtering, which would lead to high similarity or compositional convergence among communities. Therefore, we expected both taxonomic and functional diversity to be positively related to increasing stream flow permanence and negatively related to the duration and number of stream drying events.

METHODS

Study area and invertebrate collection

We collected aquatic invertebrates from 28 sites distributed across 7 arid-land streams in the Huachuca Mountains within the Upper San Pedro River Basin of southeastern Arizona, USA (Fig. 1). The area receives $\frac{1}{2}$ of its total yearly precipitation during the summer monsoon season (July–September) during short, intense thunderstorms and $\frac{1}{2}$ during the winter season (November–April) from more protracted, milder frontal systems. Streams in the area consist of perennial headwaters that flow into intermittent sections as streams cross alluvial fans at canyon mouths. Further downstream, flows transition to ephemeral (Bogan et al. 2013). We distributed our sampling sites among perennial, intermittent, and ephemeral reaches (classification follows Levick et al. 2008), but we used a continuous-flow metric to quantify permanence (see below). Our sampling covered nearly all available perennial habitat in the eastern Huachuca Mountains, and we established additional sites to sample ephemeral and intermittent reaches when they became activated with surface flows. We sampled sites multiple times between 2009 and 2011 with a per-stream average of 21 sampling events. However, the number of sites and samples collected differed among streams because not all sites had flow or all microhabitats during each sampling event (Table 1) and were not sampled when dry. The period of our study spanned 5 dry seasons, 3 periods of ephemeral flows from summer monsoon rains, and 1 period of intermittent flows resulting from above-average winter precipitation. Most sampling occurred during autumn and winter (November and December, March and April, respectively) for a total of 144 site \times sampling-event combinations (Table 1). More perennial ($n = 113$) than intermittent ($n = 31$) samples were collected because of the rarity of intermittent flow events.

Each site consisted of a 100-m-long stream reach in which all available microhabitats were sampled (primarily riffles and pools). For riffle samples (1–3/site), we disturbed 0.33 m² of stream substrate to a depth of 5 cm while capturing invertebrates immediately downstream with a D-net (500- μ m mesh). We sampled pools (1–3/site) by sweeping the entire pool area including water column, surface, and pool benthos with a D-net at an effort of 10 s/m² pool habitat (Bogan and Lytle 2007). We preserved samples in 95% ethanol and identified invertebrates in the laboratory to the finest taxonomic level possible, usually to genus or species for insects (including Chironomidae) and family or order for noninsects. We summed abundances from microhabitat samples collected from the same site during the same sampling event (e.g., 3 riffles) for each taxon and divided by the number of replicates to acquire relative abundances. Samples were taken from multiple locations in the same streams, so we tested for the possibility of nonindependence caused by spatial autocorrelation with Mantel tests in the *ade4* package (Dray and Dufour 2007)

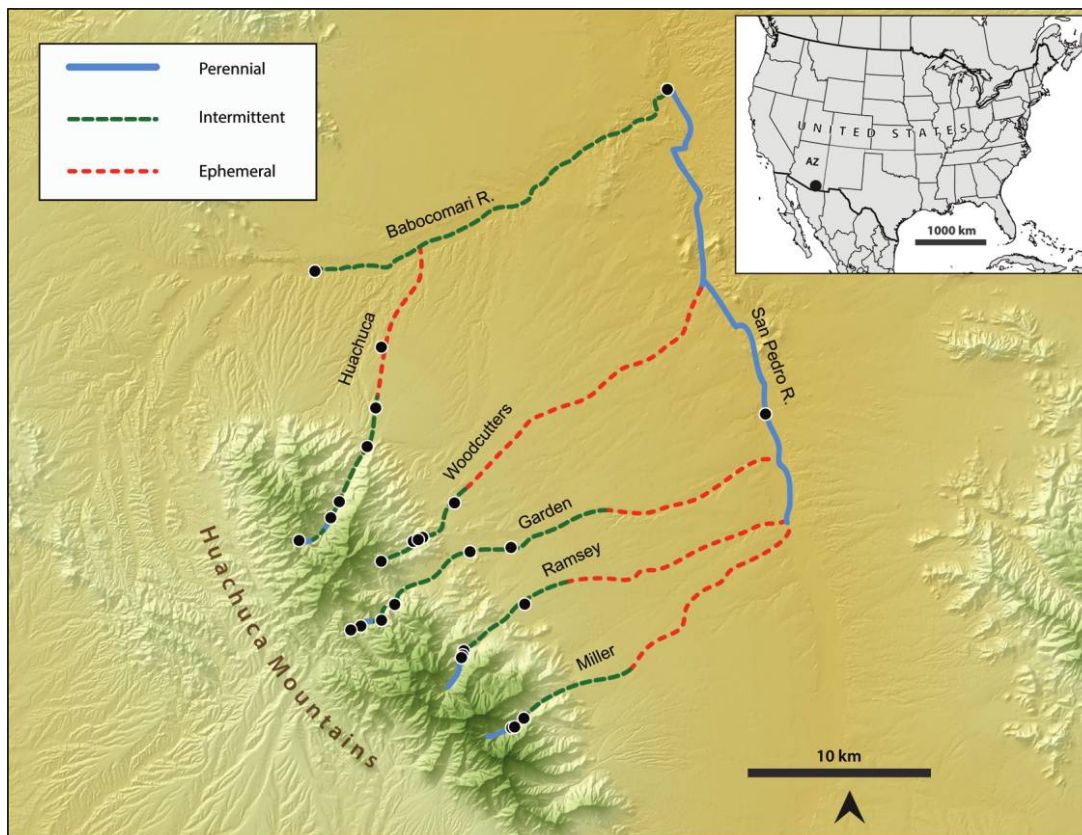


Figure 1. Locations of study streams and sampling sites. Dots along streams mark the specific sampling sites.

in R (version 2.15.2; R Project for Statistical Computing, Vienna, Austria). Based on these results, we accepted the null hypothesis that spatial location was not related to functional richness ($r = -0.0175$, $p = 0.6$) or species richness ($r = 0.0437$, $p = 0.16$). We also recorded relative habitat size of the wetted reach (<1 m², 1–10 m², 10–100 m², 100–1000 m², and >1000 m²) and microhabitat type (river riffle, river pool, headwater stream riffle, headwater stream pool).

Hydrology and environmental variables

We measured in-stream flow variation by deploying 15 wet/dry electrical resistance (ER) sensors (Jaeger and Olden 2012) to quantify timing and continuity of stream flow near invertebrate sampling locations. The sensors logged relative conductivity at 15-min intervals from 15 April 2010 to 31 December 2011 as a proxy for the presence of surface water (see Jaeger and Olden 2012 for in-depth description of sensor hardware, deployment, and data analysis). From these conductivity data, we calculated 4 stream-flow metrics for each sampling site using the nearest sensor: % flow permanence in year of sample, % flow permanence by season, mean duration (number of days) of zero flow periods (ZFP) each year, and number of ZFP each year. For the 2 flow-permanence metrics and

duration of ZFP, we summed 15-min periods of both wet and dry conditions for the sampling period and individual zero flow periods, converting the time units to either days or years as appropriate for the final stream-flow metric. We used an average of 2010 and 2011 flow data to estimate flow conditions for the November 2009 invertebrate sampling period (16 samples), which occurred prior to deployment of sensors. The flow-permanence variables measured the percentage of time a reach had water in the sampling year and the proportion of days with flow in each season. Duration of ZFP indicates on average how long, in days, a stream has no surface water during drying events. A site that never dries will have a ZFP = 0. The number of ZFPs quantifies the number of drying events the site experienced in the year. These 4 metrics were calculated from the same flow-sensor records, but each was designed to characterize distinct components of the hydrologic regime that might influence macroinvertebrate occurrence.

Functional trait data

We identified 234 freshwater macroinvertebrate taxa during our study. We developed a trait database based on information in >80 publications from primary literature, databases, and available specialist knowledge to define categorical trait states specific to the southwestern region of

Table 1. Number of samples collected per year (after aggregation of replicate samples per microhabitat), season, and hydrological category from each of the 7 streams. The number of samples varied depending on whether intermittent sites had surface water during a given season. The total number of samples collected per stream is noted by *n*.

Stream	Year			Season			Hydrological category		<i>n</i>
	2009	2010	2011	Fall	Monsoon	Winter	Intermittent	Perennial	
Babocomari	0	3	3	3	0	3	2	4	6
Garden	7	16	16	18	7	14	6	33	39
Huachuca	4	14	14	12	9	11	8	24	32
Miller	6	0	0	6	0	0	0	6	6
Ramsey	6	13	14	18	4	11	2	31	33
San Pedro	2	6	7	6	4	5	0	15	15
Woodcutters	0	11	2	1	4	8	13	0	13

the USA (Appendix S1). Each taxon was represented by a combination of traits, known as its functional trait niche (FTN) (Poff et al. 2006). Functional trait diversity was represented by a species \times trait matrix for the 225 taxa for which we found complete trait information. We used 7 functional traits spanning a total of 30 modalities: body size, voltinism, dispersal capability, respiration, functional feeding group (FFG), diapause, and primary locomotion (Table 2).

We calculated taxonomic richness, Shannon diversity (H'), and evenness (Pielou index; Pielou 1969); and functional richness (FRic), functional diversity, and functional evenness (FEve). FRic measures the volume of functional space occupied by a community (Cornwell et al. 2006,

Villéger et al. 2008). FRic values are not constrained to the total number of trait modalities present in the species pool because they are calculated using the minimal convex hull that includes all species and quantifies the volume occupied by the community's traits (Villéger et al. 2008). We calculated functional diversity as H' for each community (species traits \times species abundance matrix) and for individual traits (species abundances within each trait state in each community sample). FEve describes the distribution of traits within a community (i.e., whether they are distributed evenly within occupied trait space) (Villéger et al. 2008). FEve ranges from 0 to 1. Low values represent unevenly distributed species traits within trait space (e.g., high density of species within a narrow range of trait space) and high values represent evenly distributed species traits throughout the functional trait space. FEve incorporates species abundances in calculation of the metric. FRic and FEve were calculated using the R-based *FD* package and the function *dbFD* (Laliberté and Legendre 2010, Laliberté and Shipley 2011).

Table 2. Description of the 7 traits assessed for 225 taxa of aquatic invertebrates collected from 7 streams in the Huachuca Mountains, Arizona.

Trait	Trait state
Body size	<9 mm, 9–16 mm, >16 mm
Voltinism	Semivoltine: <1 generation/y, univoltine: 1 generation/y, multivoltine: >1 generation/y
Dispersal	Aquatic passive, aquatic active, aerial passive, aerial active
Respiration	Integument, gill, plastron, spiracle, vesicle
Functional feeding group	Collector–gatherer, shredder, scraper/grazer, filter-feeder, piercer-plants, piercer-predator, engulfer-predator
Diapause	Presence of structures for diapause or known diapause, possible diapause or resistance (inferred in studies or found in closely related taxa), no diapause or resistance known
Locomotion or habit	Burrow, interstitial, sprawl (crawl), attached (clingers), full water swimmer, surface swimmer (skater), climber

Statistical analyses

All analyses were conducted in R, and significance was assigned at $p < 0.05$. We used simple linear regression to assess the relationships between taxonomic richness and diversity vs functional richness and diversity. We fitted a hyperbolic saturation curve of the form $y = ax/(b + x)$ to the nonlinear relationship between functional richness and taxonomic richness, where a is the asymptotic limit of the curve and b is the half-saturation constant. We interpreted a as the limit saturation point of trait states for a given community type and b as the rate at which trait saturation occurs. This type of curve arises when the number of species (x) is relatively large or unbounded, but the number of trait states (y) is finite. In our case, the total number of trait states was 30. We used linear regression for relationships involving taxonomic and functional trait

diversity because these metrics incorporate relative abundance and richness.

Invertebrates often do not show a mean linear response to stream flow, but their responses may be strong at very high or low flows (Konrad et al. 2008). Therefore, traditional linear regression models could overestimate, underestimate, or fail to detect a relationship (Cade et al. 1999, Cade and Noon 2003) between diversity estimates and stream-flow metrics. To address this problem, we used quantile regression to estimate multiple rates of change (slopes) across the distribution rather than focusing solely on the change in the center of the distribution (Cade et al. 1999). In addition to detecting important relationships in different partitions of our data, quantile regression is appropriate for our analyses because: 1) variances are often heterogeneous across flow-permanence gradients; 2) flow permanence may be a limiting factor on invertebrate community composition, richness, and diversity; 3) the data might not always meet parametric assumptions, and 4) multiple interacting factors may contribute to invertebrate diversity. The upper quantiles (ceilings) identify the constraints imposed by stream flow that limit the maximum response. Cases where only the upper- or lower-most quantiles are significant indicate limiting relationships. The lowest quantile ($\tau = 0.05$) describes the minimum limit of response. We followed Rogers' (1992) recommendations to select the number of quantiles investigated, $n > 5/q$ and $n > 5/(1 - q)$, where q determines the limits of reliable extreme quantiles and n is sample size. Our analysis included 5 evenly distributed quantiles ($\tau = 0.05, 0.25, 0.5, 0.75, \text{ and } 0.95$) to test the bivariate relationships among 4 diversity measures (FRic, FEve, taxonomic richness, and diversity) and a set of 4 predictors (% flow permanence, % flow permanence by season, mean duration of ZFP, and number of ZFPs). The median quantile ($\tau = 0.5$) estimates the center of the distribution, where 50% of the data lie above and 50% lie below the estimate (Cade et al. 1999), and provides an estimate of central tendency similar to a linear regression fit. For quantile regression tests we used the *rq* function in R, which uses the Barrodale and Roberts algorithm to compute model fit in the *quantreg* package (version 4.98; Koenker 2013).

We used variance partitioning analysis (*varpart* function in the *vegan* package, version 2.0–6 in R) to isolate the variance explained by each set of abiotic variables and their combined effects: season (monsoon, autumn, and winter), flow (perennial, intermittent), microhabitat type (river riffle, river pool, stream riffle, stream pool, seep, and pond), and habitat size (<1 m², 1–10 m², 10–100 m², 100–1000 m², and >1000 m²). The function uses adjusted R^2 to assess the partitions explained by the explanatory variables and their combinations (Peres-Neto et al. 2006). We ran permutation tests to test the significance of all constraints simultaneously (Oksanen et al. 2013).

RESULTS

Invertebrate assemblage structure and diversity across sampling sites

A total of 124 taxa in 43 different families or taxonomic units were identified across all intermittent sites, whereas a total of 210 taxa (70 families) were found across all perennial sites. Diptera were the most diverse group regardless of hydrological category (intermittent: 12 families, 58 species; perennial: 13 families, 85 species). Ephemeroptera and Trichoptera were more diverse in perennial sites (6 families, 18 genera or species; 12 families, 12 genera or species, respectively) compared to intermittent sites (3 families, 6 species; 5 families, 6 genera or species, respectively). Seven major taxonomic groups of invertebrates were limited to perennial sites and were not found in intermittent sites (e.g., Amphipoda, *Procambarus* crayfish, the hemipteran *Abedus herberti*). Invertebrate abundances did not differ significantly between perennial headwaters and intermittent reaches (as seen by Bogan et al. 2013).

A saturation curve fit to the taxonomic–functional richness data estimated trait saturation as $a = 25.75$ and the rate at which trait saturation occurs as $b = 33.79$ ($R^2 = 0.64, p < 0.0001$; Fig. 2A). When analyzed separately, intermittent and perennial sites showed significant saturating relationships between taxonomic richness and FRic (intermittent: $a = 25.66, b = 43.65, R^2 = 0.61, p < 0.0001$; perennial: $a = 21.73, b = 22.05, R^2 = 0.44, p < 0.0001$) indicating the addition of new taxa beyond the asymptote did not increase FRic and that trait saturation occurred at a slightly lower species richness in perennial (21.73) than at intermittent sites (25.66). The intermittent-only curve was potentially affected by a single site with high species richness. Reanalysis without this single point suggested a linear rather than a saturating form to the curve. FEve was weakly associated with both taxonomic richness ($R^2 = 0.05, p = 0.005$) and taxonomic diversity ($R^2 = 0.07, p = 0.001$) because the distribution of traits within communities (FEve) had more variation at species-poor than at species-rich sites (Appendix S2).

We found a strong positive relationship between taxonomic diversity (H') and functional diversity across all sites ($R^2 = 0.65, p < 0.0001, \text{ slope} = 0.31$), indicating moderate levels of functional-trait redundancy among coexisting species (Fig. 2B). Intermittent sites ($R^2 = 0.56, p < 0.0001, \text{ slope} = 0.34$) and perennial sites ($R^2 = 0.58, p < 0.0001, \text{ slope} = 0.25$) had similarly strong positive relationships between taxonomic and functional diversity. The pattern of functional redundancy was also robust for single functional traits: body size ($R^2 = 0.35, p < 0.0001, \text{ slope} = 0.25$), FFG ($R^2 = 0.67, p < 0.0001, \text{ slope} = 0.44$), and habit/locomotion ($R^2 = 0.45, p < 0.0001, \text{ slope} = 0.43$) (Appendix S3).

Taxonomic evenness was on average high (0.68), but varied across samples, indicating that some invertebrate

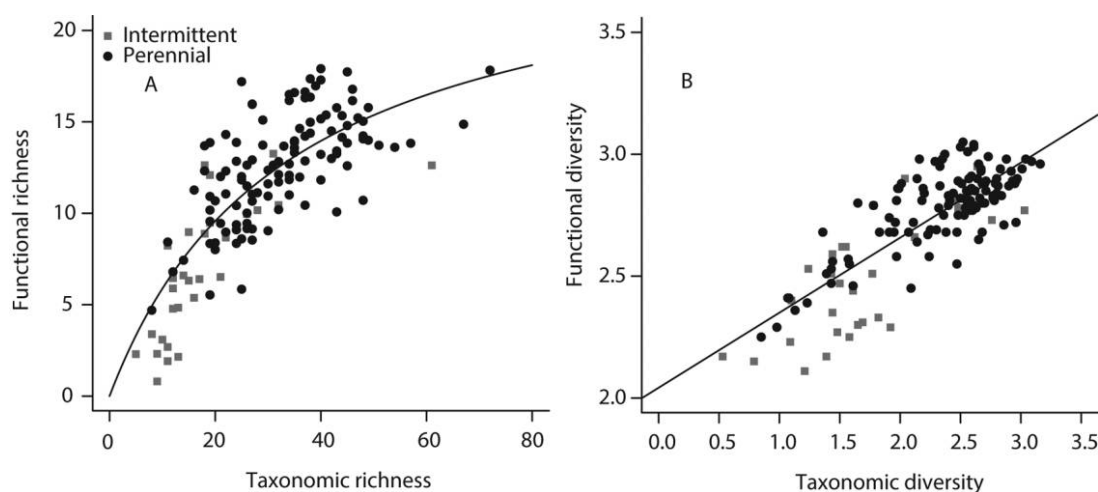


Figure 2. Macroinvertebrate functional richness (FRic) vs taxonomic richness ($y = 25.75x/[33.79 + x]$) (A) and functional diversity vs taxonomic diversity ($y = 0.31x + 2.04$) (B) based on $n = 144$ sampling events in the Huachuca Mountains, Arizona, USA. Sites are coded by whether they had flow during 100% of the sampling period (perennial) or not (intermittent).

communities were dominated by a few species. FEve and taxonomic evenness were not related ($R^2 = -0.01$, $p = 0.7$, $n = 142$).

Stream flow permanence as a driver of invertebrate diversity

As predicted, FRic was positively related to % flow permanence and negatively related to the duration and number of ZFPs (Fig. 3A, B, Appendix S4, S5). All flow metrics showed strong relationships across multiple quantiles for FRic (95% of quantiles tested were significant). Maximum FRic occurred at perennial, continuously flowing stream sites (Fig. 3A). FRic increased with % flow permanence and had uniform variance across the flow permanence gradient (lines parallel), but variances were heteroscedastic across flow increments (Fig. 3A). FRic did not respond homogeneously to changes in the number of ZFPs (Fig. 3B). The response of FRic was steep for the lower quantiles ($\tau = 0.05$ and 0.25 , slope = -1.35 , -1.38 , respectively) and different from the rates of change for the upper quantiles (0.75 and 0.95 , slope = -0.46 , -0.31 , respectively). This result indicates communities with low FRic respond more strongly to ZFPs than communities with high FRic. The median quantile was not significant, and thus, the relationship between number of ZFPs and FRic would not have been detected using standard regression techniques (Fig. 3B). FRic and mean duration of ZFP had similar patterns, where decreasing rates of change occurred at higher levels of FRic (Appendix S5). However, FRic values were less certain at longer durations of ZFPs. Several quantiles were significant for the relationship between functional diversity and % flow permanence and mean duration of ZFP, which suggests these metrics are important predictors of functional diversity (Fig. 3C, Ap-

pendix S5). The number of ZFPs and % flow permanence by season were weakly correlated with functional diversity (Fig. 3D, Appendix S5).

Communities at the perennial (100% flow permanence) sites had less variable and more evenly distributed traits in niche space than sites that experienced drying (Fig. 3E, Appendix S5). FEve exhibited a negative limiting relationship with the number of ZFPs and demonstrated a floor in evenness with confidence bounds of FEve 0.39 to 0.68 (Appendix S6). The duration of ZFP was weakly negatively related to FEve for the lowest 2 quantiles (Appendix S6). FEve declined with longer dry periods. Notably, one community had a nearly even distribution of traits in a pool that experienced the longest observed dry period (231 d) between flow events.

As predicted, taxonomic richness increased with flow permanence and declined with increasing number of drying events and longer duration of ZFPs (Fig. 3E, Appendix S5). Taxonomic diversity increased significantly at a relatively constant rate with the 2 metrics of flow permanence (Fig. 3G, Appendix S5). The median response was informative for estimating the relationship between the number of ZFPs and taxonomic diversity. However the relationship also was significant for the upper extreme quantile (0.95 ; Fig. 3H, Appendix S5), suggesting that the number of drying events a stream experiences places a limit on the maximum diversity a community attains. We also examined the relationships between flow metrics and Rao's Q and found similar positive relationships with flow permanence and negative relationships with zero flow metrics. Evidence of strong niche filtering along the flow-permanence gradient was shown by a high degree of functional dissimilarity at sites that never dry (100% flow permanence, mean duration of ZFP = 0, and number of ZFP = 0).

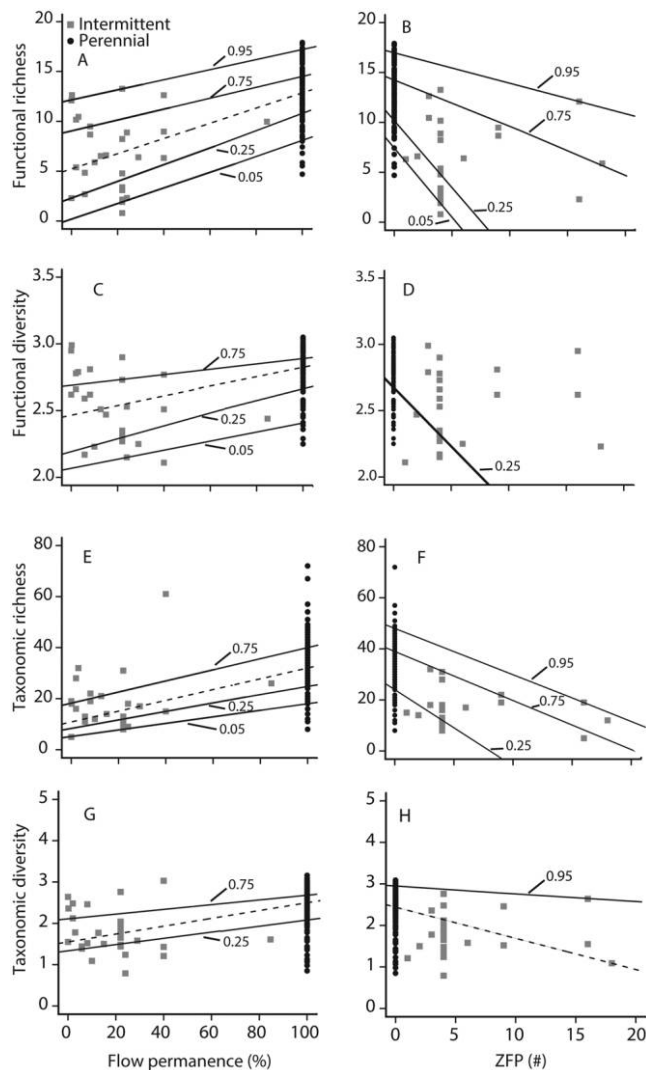


Figure 3. Quantile regressions of the relationships between functional richness (FRic) (A, B), functional diversity (C, D), taxonomic richness (E, F), and taxonomic diversity (G, H) and % flow permanence (A, C, E, G) and number of zero flow periods (ZFP) (B, D, F, H). Only significant quantiles and the median quantile (dashed line) are shown. $n = 144$ for all plots.

Sites had fairly low interannual variation in flow conditions (values across 16 sites, mean \pm SD; % flow permanence in year of sampling: 92.10 ± 24.39 , duration of ZFP: 9.67 ± 34.19). FRic was significantly lower in intermittent samples compared to perennial communities, with $\sim 1/2$ as much niche space occupied (Kruskal–Wallis $\chi^2 = 41.590$, $p < 0.0001$). Intermittent sites also had lower functional diversity (Kruskal–Wallis $\chi^2 = 27.957$, $p < 0.0001$). FRic and functional diversity typically were higher in perennial sites, but 1 intermittent site attained taxonomic and functional diversity values similar to those in perennial sites. During September 2011 this site was connected by flow to upstream perennial reaches, which possibly contrib-

uted to higher FRic values. Invertebrate taxonomic diversity (Kruskal–Wallis $\chi^2 = 24.419$, $p < 0.0001$) and taxonomic richness (Kruskal–Wallis $\chi^2 = 40.809$, $p < 0.0001$) were highest in perennial sites.

Relative roles of habitat, hydrology, and season in shaping invertebrate communities

The main gradient in functional community composition was hydrology (flow: $R^2 = 0.075$; $F = 5.44$, $p = 0.005$) after controlling for the other environmental variables (Fig. 4A). This result is congruent with the quantile regression analysis on flow metrics, indicating that functional composition and diversity indices respond strongly to hydrology. Microhabitat and total wetted area followed, explaining 3.2 and 1.7% of functional trait variation among sites, respectively. Season, although statistically significant, explained only 0.3% of the functional-trait composition. The common variation explained in functional-trait composition contributed by all factors was 14.7% of the total variation explained (68.6%). On the other hand, the percentage of the variation in species composition among sites was nearly equal for site microhabitat (5.9%) and hydrology (5.3%) (Fig. 4B). Habitat area explained a small portion of species composition (2.8%), and season was not a significant predictor ($p = 0.1$). These results show that microhabitat and hydrology explained a larger part of variation in species composition, whereas hydrology played a crucial role in explaining functional-trait composition.

DISCUSSION

We used continuous stream-flow data to examine the relationship between taxonomic and functional measures of both richness and diversity and to test for changes in diversity patterns in macroinvertebrate communities. Increased flow permanence was associated with increases in both taxonomic and functional richness of aquatic invertebrate communities. Diversity was lower in sites with more intermittent hydrological conditions, and hydrology explained more variation in trait and species composition than other environmental variables.

Functional richness was strongly related to taxonomic richness and diversity of stream invertebrates. The initial slope of this saturating relationship was steep, suggesting that at lower levels of taxonomic richness, communities have lower functional redundancy and less occupied niche space than at high taxonomic richness. Based on the saturation curve, functional richness would eventually peak at a higher taxonomic richness in intermittent (~ 51) than at perennial sites (~ 43), although intermittent sites were still generally lower than that of perennial sites. Moreover, the taxonomic and functional richness curve suggests that functional richness reached a saturation point (lower for intermittent sites) at which adding species to the community was not likely to add new trait combinations. Only

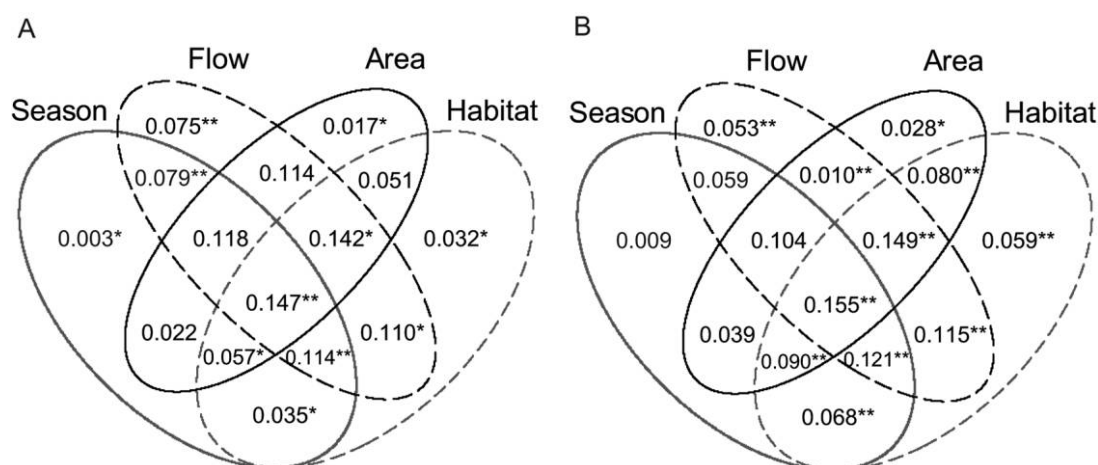


Figure 4. Variance partitioning (R^2) for trait composition (A) and taxonomic composition (B) of the matrix of environmental variables showing the respective contributions of the season, habitat area (Area), microhabitat type (Habitat), and the dominant hydrological flow category (Flow), their combinations, and combined effects. Fractions were tested on residuals (permutations = 9999). For significant combinations, * indicates $p = 0.01$, ** indicates $p = 0.001$.

17% of intermittent sites had species richness greater than the saturation point (25) compared to 84% of perennial sites that had taxonomic richness >22 species. These results partially agree with those of Bêche and Statzner (2009) showing that trait saturation is rare in stream invertebrate communities. However, this was the case only at intermittent streams. Differences between their findings and ours could have arisen from the use of different traits (number of traits and trait states) and measures of functional richness (Petchey and Gaston 2006). Bêche and Statzner (2009) used number of trait categories, whereas we calculated FRic using convex hull volume.

We found a positive relationship between taxonomic and functional diversity. This relationship provides evidence for higher functional redundancy at higher levels of taxonomic diversity. Functional redundancy may offer resilience to environmental changes because of niche complementarity. A greater range of traits available could allow more efficient resource use (Loreau et al. 2001) and could provide insurance against changes in ecosystem function (Walker 1992). Lower functional diversity implies lower ecological redundancy, so if stream hydrology were to transition from perennial to intermittent, unique traits could be lost and that loss might lead to decreased productivity and disruption of ecosystem processes. For example, a single drying event could serve as a strong trait filter and cause the loss of drought-intolerant taxa (Poff 1997, Lamouroux et al. 2004, Cornwell et al. 2006) which might result in shorter food-chain length (Sabo et al. 2010). Thus, communities with lower functional richness and diversity may be susceptible to decreases in flow permanence because their communities have less redundancy and unused niche space. The communities that contained taxa with drought-adapted life histories showed levels of diversity similar to communities in perennial sites, thereby explain-

ing the shallow slopes associated with diversity indices and flow metrics at the upper quantiles. Climate change is expected to increase drought conditions (Seager et al. 2007) by creating longer periods of low-flow conditions, resulting in intermittency of stream flow (Larned et al. 2010). We have shown that stream sites that experience more episodes and longer durations of no flow also have lower functional and taxonomic diversity.

If hydrology acts as a strong environmental filter, species should tend to occur at sites for which they are evolutionarily suited (Poff 1997, Lytle and Poff 2004), thereby resulting in lower functional richness and diversity in stream reaches with intermittent flow. Our results show that intermittent streams contained taxa with a higher degree of niche specialization (less trait volume occupied) than perennial streams (Fig. 3A–H), and that these taxa tended to be more functionally similar (as indicated by Rao's Q).

Only by evaluating multiple quantiles could we show that different aspects of stream hydrology differentially influenced multiple facets of functional and taxonomic diversity. Yearly flow permanence had a strong influence at low levels of diversity, richness, and evenness, whereas the number and duration of ZFPs constrained higher levels of diversity and richness. These results are congruent with those of other studies of intermittent streams, but they reveal new information about the relationship between stream intermittence and the functional response of communities. For instance, intermittent streams are characterized by low invertebrate richness (Williams 1996, Storey and Quinn 2008) and may support more specialist taxa and fewer predator taxa than perennial streams (Bogan et al. 2013). In general, invertebrate species' diversity, abundance, and distribution are determined by flow (Statzner and Higler 1986, Statzner 2008, Arscott et al. 2010, Old-

meadow et al. 2010) and the length of the dry season (Williams and Hynes 1976), which is congruent with our observed pattern of lower FRic and FEve in intermittent sites. Bogan and Lytle (2011) found that altered stream flow (perennial to intermittent) after a severe drought changed species composition and extirpated top predators from stream reaches, but that species richness did not change. Our results provide evidence that species richness, FRic, and FEve are also reduced by declines in stream flow duration.

Functional evenness increased with flow permanence, signifying that traits became more regularly distributed in trait space as sites approach perenniality. Moreover, FRic was lower at intermittent than at perennial sites. Functional richness and FEve declined steeply across the less extreme numbers and durations of drying events (<10 events and 100 d dry, lower quantiles) followed by little change across the rest of the gradient. This relationship probably represents an ecological threshold (Groffman et al. 2006), where a few drying events influence all measures of functional diversity (signifying a strong environmental filter to those taxa without adaptations to cope with desiccation), but additional drying events have less effect on diversity measures. This result suggests that a single drying event would reduce species richness, functional richness, and the prevalence of drought-intolerant taxa in streams that rarely experience drought. Moreover, this effect would be strongest for communities with lower levels of functional richness. We have shown that the duration of drying events and flow permanence are key extrinsic drivers of the responses of functional and taxonomic richness. Identifying ecological thresholds is imperative for making water-management decisions in dryland streams, especially where groundwater extraction contributes to the reduction in surface-water flows.

Many authors separate aquatic habitats into discrete hydrological categories for convenience. However, our study shows that responses to hydrology fall along a continuum with high variance within hydrological groups. Thus, the responses of multiple measures of functional and taxonomic diversity to stream hydrology will vary depending on the region and length of the hydrologic continuum being examined. The upper and lower quantile regression lines for most diversity measures were farther apart at the more extreme end of the hydrologic continuum (intermittent flow, more ZFPs), and scatter between the upper and lower limit lines was considerable, indicating that other limiting factors influenced the diversity measures. The relationship between FRic and the 2 zero flow metrics show that quantile regression lines started to converge in perennial sites, indicating that the functional niche space occupied was less heterogeneous (and thus, more predictable) in perennial habitats. These results concur with the habitat template model prediction (Southwood 1977, Townsend and Hildrew 1994) that similar insect communities should occur in streams with similar environmental conditions, but

contradict the prediction by Poff et al. (2006) that infrequent low-flow disturbances should lead to high community similarity. Presumably, more extreme habitats have the harshest environmental filter, and therefore, one might predict extreme communities to be most similar. In support of this, we found strong limiting relationships between several flow permanence metrics and invertebrate diversity measures. However, intermittent sites tended to be more variable than permanent sites in their physical and chemical environment and to have high species turnover. This combination could lead to greater variation among and within intermittent communities, as was shown by empty niche space (lower FRic) and lower FEve at intermittent sites.

We showed that hydrology is a stronger gradient influencing functional composition of invertebrate communities than microhabitat, habitat size, and season (Fig. 4A). However, in stream systems that exhibit less hydrologic variability, other factors, such as distance to perennial water, connectivity among habitats, or local variables, such as canopy cover, temperature, and water quality, may play an important role. Hydrology-influenced patterns of species diversity and community composition may scale up to important differences in ecosystem-level processes and foodweb dynamics. In a study on ponds, habitats with shorter hydroperiod had shorter food-chain length and fewer species at the intermediate-consumer and predator trophic levels compared to permanent ponds with longer hydroperiods (Schriever and Williams 2013). A similar study on streams in New Zealand demonstrated that streams with more variable temperature, hydrology, and geomorphology had shorter food-chain length (McHugh et al. 2010). In addition, in experimental stream mesocosms, induced drought conditions can cause loss of species and biomass that triggers restructuring of food webs (Ledger et al. 2013a). In light of projected climate change and increased human water use in coming decades (World Water Assessment Programme 2009, Marshall et al. 2010) and the importance of flow permanence for shaping the structure and function of invertebrate communities, it is imperative that arid and semi-arid streams receive additional research and management attention.

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