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Hydrology shapes taxonomic and functional structure of desert stream invertebrate communities

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5	communities
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29 **Abstract:** Hydrology is a fundamental factor influencing ecosystem dynamics, life-history 30 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 31 systems with high spatiotemporal variability in flow. We examined invertebrate diversity from 7 32 desert streams in the Huachuca Mountains of southeastern Arizona, USA, that span a flow 33 permanence continuum from highly intermittent to perennial. We examined the relative roles of 34 flow permanence, habitat size, season, and microhabitat in determining taxonomic and functional 35 structure (according to 7 species traits compiled for 234 taxa) of these communities. We 36 predicted that both functional and taxonomic diversity would be positively related to flow 37 permanence and negatively related to the duration and number of stream drying events. As 38 predicted, increased flow permanence was associated with increased functional richness, 39 functional evenness, and taxonomic richness. Conversely, drying events reduced functional 40 diversity across all measured indices. We found a saturating relationship between functional 41 richness and taxonomic richness, indicating functional redundancy in species-rich communities, 42 which may promote resilience of ecosystem function to environmental variation. Our study adds 43 further evidence that hydrology is a key determinant of aquatic invertebrate diversity, and that 44 stream hydroperiod strongly influences both functional and taxonomic diversity in arid-land 45 streams. 46

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

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50 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 51 year-round (Poff et al. 1997). These differences in hydrology can shape patterns of species 52 diversity (Wellborn et al. 1996, Williams 1996), affect the structure of riverine and riparian food 53 webs (Sabo et al. 2010, McCluney and Sabo 2012), and drive evolutionary change in the 54 organisms themselves (Lytle and Poff 2004, Lytle et al. 2008). The strong environmental 55 gradients imposed by flow also impose a strong 'habitat filter' (sensu Southwood 1977, 1988) 56 that directly controls the taxonomic and trait composition of communities (Williams 2006, 57 Gallart et al. 2012, Mims and Olden 2012, Ledger et al. 2013b, Belmar et al. 2013). Strong 58 habitat filtering may locally favor taxa adapted to one hydrological extreme or another, as well as 59 generalists capable of persisting in a variety of habitats (Poff and Ward 1989, Williams 2006, 60 Bonada et al. 2007), but how habitat filtering affects communities along continuous gradients of 61 hydrological variability is less clear. 62

Species richness and assemblage composition are commonly used to quantify aquatic 63 communities and how they respond to perturbations (Bunn and Arthington 2002, Poff and 64 Zimmerman 2010, Carlisle et al. 2011). However, trait-based measures of diversity, or functional 65 66 diversity, may be more informative in describing ecological responses to environmental variability than taxonomy-based metrics alone (Walker 1992, Hoeinghaus et al. 2007, Cadotte et 67 al. 2011). Functional diversity can be defined as the number, type and distribution of functions 68 performed by organisms within an ecosystem (Díaz and Cabido 2001). A change in functional 69 diversity may affect ecosystem processes, whereas a change in species diversity may elicit no 70 ecosystem response at all because of functional redundancy (i.e., shared ecosystem-effect traits) 71 72 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 78 degree of functional redundancy in communities (Micheli and Halpern 2005). For instance, a 79 positive linear relationship (slope = 1) indicates that species additions to a community result in 80 new ecological functions, whereas a shallower, positive slope (<1) indicates low redundancy 81 because some species share functional traits. Curvilinear relationships between taxonomic and 82 functional diversity indicate communities rapidly acquire unique functions (associated with trait 83 values) at low diversity levels and subsequently reach an asymptote at higher levels of diversity. 84 More functionally diverse communities are thought to offer greater resilience because of greater 85 ecological redundancy (Hooper et al. 2005), as has been shown for agricultural land use 86 gradients (Fischer et al. 2007), forest-fire disturbances (Hidasi-Neto et al. 2012), and hydrologic-87 alteration gradients (Pool et al. 2010). Thus, the form of the relationship between taxonomic and 88 functional diversity can reveal much about how communities might respond to ecological 89 perturbations. 90

91 We sought to assess whether taxonomic and functional trait diversity differed across 92 aquatic habitats that span a gradient of flow dynamics ranging from highly intermittent to 93 perennial. We characterized the trait and taxonomic diversity of desert-stream invertebrate 94 communities in a stream network in southeastern Arizona and then examined the relative roles of 95 flow permanence, physical-habitat conditions, and season in determining the taxonomic and

96 functional structure of the communities. We examined the taxonomic–functional richness 97 relationship in these arid-land communities. We predicted that under more intermittent flow 98 conditions, only specialized taxa would persist locally because of habitat filtering, which would 99 lead to high similarity or compositional convergence among communities. Therefore, we 100 expected both taxonomic and functional diversity to be positively related to increasing stream 101 flow permanence and negatively related to the duration and number of stream drying events.

102

103 METHODS

104 Study area and invertebrate collection

We collected aquatic invertebrates from 28 sites distributed across 7 arid-land streams in 105 the Huachuca Mountains within the Upper San Pedro River Basin of southeastern Arizona, USA 106 107 (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 108 (November-April) from more protracted, milder frontal systems. Streams in the area consist of 109 110 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 111 our sample sites among perennial, intermittent, and ephemeral reaches (classification follows 112 (Levick et al. 2008), but we used a continuous-flow metric to quantify permanence (see below). 113 Our sampling covered nearly all available perennial habitat in the eastern Huachuca Mountains, 114 and we established additional sites to sample ephemeral and intermittent reaches when they 115 became activated with surface flows. We sampled sites multiple times between 2009 and 2011 116 with a per-stream average of 21 sampling events. However, the number of sites and samples 117 118 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 125 were sampled (primarily riffles and pools). For riffle samples (1-3/site), we disturbed 0.33 m² of 126 stream substrate to a depth of 5 cm while capturing invertebrates immediately downstream with a 127 D-net (500- μ m mesh). We sampled pools (1–3/site) by sweeping the entire pool area including 128 water column, surface, and pool benthos with a D-net at an effort of 10 s/m^2 pool habitat ((Bogan 129 130 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 131 (including Chironomidae) and family or order for non-insects. We summed abundances from 132 133 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 134 were taken from multiple locations in the same streams, so we tested for the possibility of 135 nonindependence caused by spatial autocorrelation with Mantel tests in the *ade4* package (Dray 136 and Dufour 2007) in R (version 2.15.2; R Project for Statistical Computing, Vienna, Austria). 137 Based on these results, we accepted the null hypothesis that spatial location was not related to 138 functional richness (r = -0.0175, p = 0.6) or species richness (r = 0.0437, p = 0.16). We also 139 recorded relative habitat size of the wetted reach ($<1 \text{ m}^2$, 1–10 m², 10–100 m², 100–1000 m², and 140 $>1000 \text{ m}^2$) and microhabitat type (river riffle, river pool, headwater stream riffle, headwater 141

stream pool).

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144 Hydrology and environmental variables

We measured in-stream flow variation by deploying 15 wet/dry electrical resistance (ER) 145 sensors (Jaeger and Olden 2012) to quantify timing and continuity of stream flow near 146 invertebrate sampling locations. The sensors logged relative conductivity at 15-min intervals 147 from 15 April 2010 to 31 December 2011 as a proxy for the presence of surface water (see 148 (Jaeger and Olden 2012) for in-depth description of sensor hardware, deployment, and data 149 analysis). From these conductivity data, we calculated 4 stream-flow metrics for each sampling 150 site using the nearest sensor: % flow permanence in year of sample, % flow permanence by 151 season, mean duration (number of days) of zero flow periods (ZFP) each year, and number of 152 153 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, 154 converting the time units to either days or years as appropriate for the final stream-flow metric. 155 156 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. 157 158 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 159 average how long, in days, a stream has no surface water during drying events. A site that never 160 dries will have a ZFP = 0. The number of ZFPs quantifies the number of drying events the 161 site experienced in the year. These 4 metrics were calculated from the same flow-sensor records, 162 but each was designed to characterize distinct components of the hydrologic regime that might 163 164 influence macroinvertebrate occurrence.

165

166 Functional trait data

167	We identified 234 freshwater macroinvertebrate taxa during our study. We developed a
168	trait database based on information in >80 publications from primary literature, databases, and
169	available specialist knowledge to define categorical trait states specific to the southwestern
170	region of the USA (Appendix S1). Each taxon was represented by a combination of traits, known
171	as its functional trait niche (FTN) (Poff et al. 2006). Functional trait diversity was represented by
172	a species \times trait matrix for the 225 taxa for which we found complete trait information. We used
173	7 functional traits spanning a total of 30 modalities: body size, voltinism, respiration, functional
174	feeding group (FFG), dispersal capability, diapause, and primary locomotion (Table 2).
175	We calculated taxonomic richness, Shannon diversity (H'), and evenness (Pielou index;
176	(Pielou 1969); and functional richness (FRic), functional diversity, and functional evenness
177	(FEve). FRic measures the volume of functional space occupied by a community (Cornwell et al.
178	2006, Villéger et al. 2008). FRic values are not constrained to the total number of trait modalities
179	present in the species pool because they are calculated using the minimal convex hull that
180	includes all species and quantifies the volume occupied by the community's traits (Villéger et al.
181	2008). We calculated functional diversity as H' for each community (species traits \times species
182	abundance matrix) and for individual traits (species abundances within each trait state in each
183	community sample). FEve describes the distribution of traits within a community (i.e., whether
184	they are distributed evenly within occupied trait space) (Villéger et al. 2008). FEve ranges from
185	0 to 1. Low values represent unevenly distributed species traits within trait space (e.g., high
186	density of species within a narrow range of trait space) and high values represent evenly
187	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).

190

191 Statistical analyses

All analyses were conducted in R, and significance was assigned at p < 0.05. We used 192 simple linear regression to assess the relationships between taxonomic richness and diversity vs 193 functional richness and diversity. We fitted a hyperbolic saturation curve of the form y = ax/(b + a)194 x) to the nonlinear relationship between functional richness and taxonomic richness, where a is 195 the asymptotic limit of the curve and b is the half-saturation constant. We interpreted a as the 196 limit saturation point of trait states for a given community type and b as the rate at which trait 197 saturation occurs. This type of curve arises when the number of species (x) is relatively large or 198 199 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 200 diversity because these metrics incorporate relative abundance and richness. 201

202 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 203 linear regression models could overestimate, underestimate, or fail to detect a relationship (Cade 204 et al. 1999, Cade and Noon 2003) between diversity estimates and stream-flow metrics. To 205 address this problem, we used quantile regression to estimate multiple rates of change (slopes) 206 across the distribution rather than focusing solely on the change in the center of the distribution 207 (Cade et al. 1999). In addition to detecting important relationships in different partitions of our 208 data, quantile regression is appropriate for our analyses because: 1) variances are often 209 heterogeneous across flow-permanence gradients; 2) flow permanence may be a limiting factor 210

211 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 212 diversity. The upper quantiles (ceilings) identify the constraints imposed by stream flow that 213 214 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 215 response. We followed (Rogers 1992) recommendations to select the number of quantiles 216 investigated, n > 5/q and n > 5/(1-q), where q determines the limits of reliable extreme 217 quantiles and *n* is sample size. Our analysis included 5 evenly distributed quantiles ($\tau = 0.05$, 218 219 0.25, 0.5, 0.75, 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 220 permanence by season, mean duration of ZFP, and number of ZFPs). The median quantile ($\tau =$ 221 222 (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 223 regression fit. For quantile regression tests we used the rq function in R, which uses the 224 225 Barrodale and Robert algorithm to compute model fit in the *quantreg* package (version 4.98; (Koenker 2013). 226

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.

234 2013).

235

236 **RESULTS**

237 Invertebrate assemblage structure and diversity across sampling sites

A total of 124 taxa in 43 different families or taxonomic units were identified across all 238 intermittent sites, whereas a total of 210 taxa (70 families) were found across all perennial sites. 239 Diptera were the most diverse group regardless of hydrological category (intermittent: 12 240 families, 58 species; perennial: 13 families, 85 species). Ephemeroptera and Trichoptera were 241 more diverse in perennial sites (6 families, 18 genera or species; 12 families, 12 genera or 242 species, respectively) compared to intermittent sites (3 families, 6 species; 5 families, 6 genera or 243 species). Seven major taxonomic groups of invertebrates were limited to perennial sites and were 244 245 not found in intermittent sites (e.g., Amphipoda, Procambarus crayfish, the hemipteran Abedus herberti). Invertebrate abundances did not differ significantly between perennial headwaters and 246 intermittent reaches (as seen by Bogan et al. 2013). 247 A saturation curve fit to the taxonomic-functional richness data estimated trait saturation 248 as a = 25.75 and the rate at which trait saturation occurs as b = 33.79 ($R^2 = 0.64$, p < 0.0001; Fig. 249 2A). When analyzed separately, intermittent and perennial sites showed significant saturating 250 relationships between taxonomic richness and FRic (intermittent: a = 25.66, b = 43.65, $R^2 = 0.61$, 251 p < 0.0001; perennial: a = 21.73, b = 22.05, $R^2 = 0.44$, p < 0.0001) indicating the addition of new 252 taxa beyond the asymptote did not increase FRic and that trait saturation occurred at a slightly 253 lower species richness in perennial (21.73) than at intermittent sites (25.66). The intermittent-254

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).

260 We found a strong positive relationship between taxonomic diversity (H') and functional diversity across all sites ($R^2 = 0.65$, p < 0.0001, slope = 0.31), indicating moderate levels of 261 functional-trait redundancy among coexisting species (Fig. 2B). Intermittent sites ($R^2 = 0.56$, p 262 <0.0001, slope = 0.34) and perennial sites ($R^2 = 0.58$, p < 0.0001, slope = 0.25) had similarly 263 strong positive relationships between taxonomic and functional diversity. The pattern of 264 functional redundancy was also robust for single functional traits: FFG ($R^2 = 0.67$, p < 0.0001, 265 slope = 0.44), body size ($R^2 = 0.35$, p < 0.0001, slope = 0.25), and habit/locomotion ($R^2 = 0.45$, p266 < 0.0001, slope = 0.43) (Appendix S4). 267

Taxonomic evenness was on average high (0.68), but varied across samples, indicating that some invertebrate communities were dominated by a few species. FEve and taxonomic evenness were not related ($R^2 = -0.01$, p = 0.7, n = 142).

271

272 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 S3,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 ZFP (Fig. 3B). The response

280 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, -281 0.31, respectively). This result indicates communities with low FRic respond more strongly to 282 283 ZFPs than communities with high FRic. The median quantile was not significant and, thus, the relationship between number of ZFP and FRic would not have been detected using standard 284 regression techniques (Fig. 3B). FRic and mean duration of ZFP had similar patterns, where 285 decreasing rates of change occurred at higher levels of FRic (Appendix S5). However, FRic 286 values were less certain at longer durations of ZFPs. Several quantiles were significant for the 287 relationship between functional diversity and % flow permanence and mean duration of ZFP, 288 which suggests these metrics are important predictors of functional diversity (Fig. 3C, Appendix 289 S5). The number of ZFPs and % flow permanence by season were weakly correlated with 290 291 functional diversity (Fig. 3D, Appendix S5).

292 Communities at the perennial (100% flow permanence) sites had less variable and more 293 evenly distributed traits in niche space than sites that experienced drying. FEve exhibited a 294 negative limiting relationship with the number of ZFPs and demonstrated a floor in evenness 295 with confidence bounds of FEve 0.39 to 0.68 (Appendix S6). The duration of ZFP was weakly 296 negatively related to FEve for the lowest 2 quantiles (Appendix S6). FEve declined with longer 297 dry periods. Notably, one community had a nearly-even distribution of traits in a pool that 298 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 ZPFs (Fig. 3F). 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

303 the number of ZFPs and taxonomic diversity. However the relationship also was significant for the upper extreme quantile (0.95; Fig. 3H), suggesting that the number of drying events a stream 304 experiences places a limit on the maximum diversity a community attains. We also examined the 305 306 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 307 filtering along the flow-permanence gradient was shown by a high degree of functional 308 309 dissimilarity at sites that never dry (100% flow permanence, mean duration of ZFP = 0, and number of ZFP = 0). 310

Sites had fairly low interannual variation in flow conditions (values across 16 sites, mean 311 \pm SD; % flow permanence in year of sampling: 92.10 \pm 24.39, duration of ZFP: 9.67 \pm 34.19). 312 FRic was significantly lower in intermittent samples compared to perennial communities, with 313 ~¹/₂ as much niche space occupied (Kruskal–Wallis $\chi^2 = 41.590$, p < 0.0001). Intermittent sites 314 also had lower functional diversity (Kruskal–Wallis $\chi^2 = 27.957$, p < 0.0001). FRic and 315 functional diversity typically were higher in perennial sites, but 1 intermittent site attained 316 317 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 contributed 318 to higher FRic values. Invertebrate taxonomic diversity (Kruskal–Wallis $\chi^2 = 24.419$, p < 0.0001) 319 and taxonomic richness (Kruskal–Wallis $\chi^2 = 40.809$, p < 0.0001) were highest in perennial sites. 320

321

322 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

326 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, 327 respectively. Season, although statistically significant, explained only 0.3% of the functional trait 328 329 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 330 the variation in species composition among sites was nearly equal for site microhabitat (5.9%) 331 and hydrology (5.3%) (Fig. 4B). Habitat area explained a small portion of species composition 332 (2.8%), and season was not a significant predictor (p = 0.1). These results show that microhabitat 333 and hydrology explained a larger part of variation in species composition, whereas hydrology 334 played a crucial role in explaining functional trait composition. 335

336

337 **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 saturating curve, functional richness would eventually peak at a higher taxonomic richness in intermittent (~51) than at perennial sites

 (~ 43) , although intermittent sites was still generally lower than that of perennial sites. Moreover, 349 350 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 351 likely to add new trait combinations. Only 17% of intermittent sites had species richness greater 352 than the saturation point (25) compared to 84% of perennial sites that had taxonomic richness 353 >22 species. These results partially agree with those of (Beché and Statzner 2009) showing that 354 trait saturation is rare in stream invertebrate communities. However, this was the case only at 355 intermittent streams. Differences between their findings and ours could have arisen from the use 356 of different traits (number of traits and trait states) and measures of functional richness (Petchey 357 and Gaston 2006). Beché and Statzner (2009) used number of trait categories, whereas we 358 calculated FRic using convex hull volume. 359

We found a positive relationship between taxonomic and functional diversity. This 360 relationship provides evidence for higher functional redundancy at higher levels of taxonomic 361 diversity. Functional redundancy may offer resilience to environmental changes because of niche 362 363 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 364 1992). Lower functional diversity implies lower ecological redundancy, so if stream hydrology 365 were to transition from perennial to intermittent, unique traits could be lost and that loss might 366 lead to decreased productivity and disruption of ecosystem processes. For example, a single 367 drying event could serve as a strong trait filter and cause the loss of drought-intolerant taxa (Poff 368 1997, Lamouroux et al. 2004, Cornwell et al. 2006) which might result in shorter food-chain 369 length (Sabo et al. 2010). Thus, communities with lower functional richness and diversity may 370 371 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 explaining 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. 3), 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 385 386 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, 387 whereas the number and duration of ZFPs constrained higher levels of diversity and richness. 388 These results are congruent with those of other studies of intermittent streams, but they reveal 389 new information about the relationship between stream intermittence and the functional response 390 of communities. For instance, intermittent streams are characterized by low invertebrate richness 391 (Williams 1996, Storey and Quinn 2008) and may support more specialist taxa and fewer 392 predator taxa than perennial streams (Bogan et al. 2013). In general, invertebrate species 393 394 diversity, abundance, and distribution are determined by flow (Statzner and Higler 1986,

Statzner 2008, Oldmeadow et al. 2010, Arscott 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 401 regularly distributed in trait space as sites approach perenniality. Moreover, FRic was lower at 402 403 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) 404 followed by little change across the rest of the gradient. This relationship probably represents an 405 ecological threshold (Groffman et al. 2006), where a few drying events influence all measures of 406 functional diversity (signifying a strong environmental filter to those taxa without adaptations to 407 cope with desiccation), but additional drying events have less effect on diversity measures. This 408 409 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, 410 411 this effect would be strongest for communities with lower levels of FRic. We have shown that the duration of drying events and flow permanence are key extrinsic drivers of the responses of 412 functional and taxonomic richness. Identifying ecological thresholds is imperative for making 413 water-management decisions in dryland streams, especially where groundwater extraction 414 contributes to the reduction in surface water flows. 415

416 Many authors separate aquatic habitats into discrete hydrological categories for
417 convenience. However, our study shows that responses to hydrology fall along a continuum with

418 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 419 hydrologic continuum being examined. The upper and lower quantile regression lines for most 420 421 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 422 considerable, indicating that other limiting factors influenced the diversity measures. The 423 relationship between FRic and the 2 zero-flow metrics show that quantile regression lines started 424 to converge in perennial sites, indicating that the functional niche space occupied was less 425 heterogeneous (and thus, more predictable) in perennial habitats. These results concur with the 426 habitat templet model prediction (Southwood 1977, Townsend and Hildrew 1994) that similar 427 insect communities should occur in streams with similar environmental conditions, but contradict 428 429 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 430 and, therefore, one might predict extreme communities to be most similar. In support of this, we 431 432 found strong limiting relationships between several flow permanence metrics and invertebrate diversity measures. However, intermittent sites tended to be more variable than permanent sites 433 in their physical and chemical environment and to have high species turnover. This combination 434 could lead to greater variation among and within intermittent communities, as was shown by 435 empty niche space (lower FRic) and lower FEve at intermittent sites. 436 We showed that hydrology is a stronger gradient influencing functional composition of 437

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,

441 temperature, and water quality, may play an important role. Hydrology-influenced patterns of 442 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 443 444 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 445 Williams 2013). A similar study on streams in New Zealand demonstrated that streams with 446 more variable temperature, hydrology, and geomorphology had shorter food-chain length 447 (McHugh et al. 2010). In addition, in experimental stream mesocosms, induced drought 448 conditions can cause loss of species and biomass that triggers restructuring of food webs (Ledger 449 et al. 2013a). In light of projected climate change and increased human water use in coming 450 decades (World Water Assessment Programme 2009, Marshall et al. 2010) and the importance of 451 452 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. 453 454

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641 **FIGURE CAPTIONS**

- Fig. 1. Locations of study streams and sampling sites. Dots along streams mark the specificsampling site.
- Fig. 2. Macroinvertebrate functional richness (FRic) vs taxonomic richness (y = 25.75x/[33.79 +
- 645 (A) and functional diversity vs taxonomic diversity (y = 0.31x + 2.04) (B) based on *n*
- 646 = 144 sampling events in the Huachuca Mountains, Arizona, USA. Sites are coded by
 647 whether they had flow during 100% of the sampling period (perennial) or not
- 648 (intermittent).

indicates p = 0.001.

- 649 Fig. 3. Quantile regressions of the relationships between functional richness (FRic) (A, B),
- 650 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,
- 652 H). Only significant quantiles and the median quantile (dashed line) are shown. n = 144653 for all plots.
- Fig. 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
- 657 category (Flow), their combinations, and combined effects. Fractions were tested on
- residuals (permutations = 9999). For significant combinations, * indicates p = 0.01, **
- 659
- 660
- 661

Table 1. Number of samples collected per year (after aggregation of replicate samples per

663 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.

Year				Season		Hydrological category				
	Stream	2009	2010	2011	Fall	Monsoon	Winter	Intermittent	Perennial	п
	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

665 The total number of samples collected per stream is noted by n.

Table 2. Description of the 7 traits assessed for 225 taxa of aquatic invertebrates collected from 7

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

668 streams in the Huachuca Mountains, Arizona.













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