

# Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network

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## SUMMARY

1. Temporary streams comprise a large proportion of the total length of most stream networks, and the great majority of arid-land stream networks, so it is important to understand their contribution to biotic diversity at both local and landscape scales.

2. In late winter 2010, we sampled invertebrate assemblages in 12 reaches of a large arid-land stream network (including perennial and intermittent headwaters, intermittent middle reaches and perennial rivers) in south-east Arizona, U.S.A. Intermittent reaches had then been flowing for *c.* 60 days, following a dry period of more than 450 days. We sampled a subset of the perennial study reaches three more times between 2009 and 2011. Since intermittent reaches were dry during these additional sampling periods, we used assemblage data from two other intermittent streams in the study network (sampled in 2004–05 and 2010) to explore interannual variability in intermittent stream assemblage composition.

3. Invertebrate richness was lowest in intermittent reaches, despite their often being connected to species-rich perennial reaches. The assemblages of these intermittent reaches were not simply a subset of the species in perennial streams, but rather were dominated by a suite of stoneflies, blackflies and midges with adaptations to intermittency (e.g. egg and/or larval diapause). On average, 86% of individuals in these samples were specialists or exclusive to intermittent streams. Predators were 7–14 times more abundant in perennial than in intermittent reaches.

4. Despite being separated by long distances (12–25 km) and having very different physical characteristics, the assemblages of perennial headwaters and rivers were more similar to one another than to intervening intermittent reaches, emphasising the prime importance of local hydrology in this system.

5. The duration and recurrence intervals of dry periods, and the relative importance of dispersal from perennial refuges, probably influence the magnitude of biological differences between neighbouring perennial and temporary streams. Although perennial headwaters supported the highest diversity of invertebrates, intermittent reaches supported a number of unique or locally rare species and as such contribute to regional species diversity and should be included in conservation planning.

**Keywords:** aquatic invertebrates, diversity, flow regime, headwater streams, intermittent

## Introduction

The characteristics of flow regimes, such as the timing and magnitude of high- and low-flow events, are widely recognised as important variables in determining diversity and community composition in streams (Resh *et al.*,

1988; Poff, 1997). In recent years, drought and no-flow events have been increasingly acknowledged as important environmental drivers in many streams and as the primary environmental drivers in intermittent (seasonal flow in response to groundwater recharge) and ephemeral (short-term flow in direct response to precipitation events)

streams (Williams, 1996; Larned *et al.*, 2010a; Lake, 2011). While the number of studies of intermittent and ephemeral streams has grown greatly in the last 10 years (Datry, Arscott & Sabater, 2011), there is still much to learn about how flow intermittency drives patterns of aquatic invertebrate diversity and assemblage composition in stream networks. Given that both the extent and intensity of intermittency is expected to increase globally due to climate change and anthropogenic water withdrawals (Larned *et al.*, 2010a), further studies on the effect of flow intermittency on all aspects of stream ecology are clearly needed.

The location of intermittent reaches within stream networks, and their connectivity with perennial reaches, may influence how diverse or distinct their communities are when compared to nearby perennial reaches. If intermittent reaches occur near perennial reaches, high rates of immigration from the latter could mask the effects of even the strongest local environmental factors, including drying (Townsend, 1989). Connectivity to diverse upstream reaches can augment local diversity in downstream perennial and intermittent reaches (Muneepeerakul *et al.*, 2008; Arscott *et al.*, 2010). Indeed, upstream perennial refuges have been shown to shape communities in downstream intermittent reaches in Australia (Paltridge *et al.*, 1997), New Zealand (Storey & Quinn, 2008; Arscott *et al.*, 2010) and the United States (Fritz & Dodds, 2002). However, other studies indicate that local environmental factors can be as important as dispersal and network connectivity in shaping local stream communities (Thompson & Townsend, 2006).

Several studies have found significantly higher aquatic invertebrate diversity in perennial than in intermittent streams (e.g. Fritz & Dodds, 2002; Grubbs, 2011), while others have found little or no difference (e.g. Feminella, 1996; Chester & Robson, 2011). Some of these apparent anomalies may be explained by differences in study design and relative flow duration of intermittent reaches (Boulton & Suter, 1986; Datry, 2012). Additionally, most studies have found broad overlap between the assemblages of perennial and intermittent reaches and have identified few or no specialists of intermittent streams (Delucchi, 1988; Wood *et al.*, 2005; Banks, Li & Herlihy, 2007; Grubbs, 2011; Datry, 2012). Taxonomic resolution varies among published studies, however, with many difficult groups left at the family or order level. For example, midges (Chironomidae) and blackflies (Simuliidae) are often identified only to family (e.g. Datry, 2012) or are excluded from analyses (e.g. Santos & Stevenson, 2011), despite the fact that they are diverse groups including many species with adaptations for surviving drought (Chou *et al.*, 1999;

Adler, Currie & Wood, 2004; Cranston *et al.*, 2007). The lack of taxonomic resolution in these families is likely to have a strong impact on our ability to detect differences between invertebrate assemblages of perennial and intermittent streams in a given region.

Here, we quantified the diversity of aquatic invertebrates, as well as taxonomic and functional feeding group composition, in perennial and intermittent reaches across the upper San Pedro River basin, a large arid-land stream network (>400 km<sup>2</sup>) in Arizona, U.S.A. Most previous comparisons of temporary and perennial streams have focussed on small stream networks (<25 km<sup>2</sup>: e.g. Delucchi, 1988) or several sites along a single river (e.g. Arscott *et al.*, 2010) and have been conducted in temperate regions. In addition to quantifying differences in invertebrate taxonomic and feeding group composition between perennial and intermittent reaches, our goal was to understand whether mid-reach drying altered longitudinal patterns in invertebrate assemblages. We predicted that we would find (i) lower invertebrate richness and abundance in intermittent reaches, (ii) invertebrate assemblages in intermittent reaches that were a mix of taxa found in perennial reaches and taxa with specific adaptations to intermittency (e.g. with diapausing eggs and/or larvae) and (iii) that intermittent reaches would interrupt longitudinal compositional gradients in our focal stream network.

## Methods

### *Site and climate description*

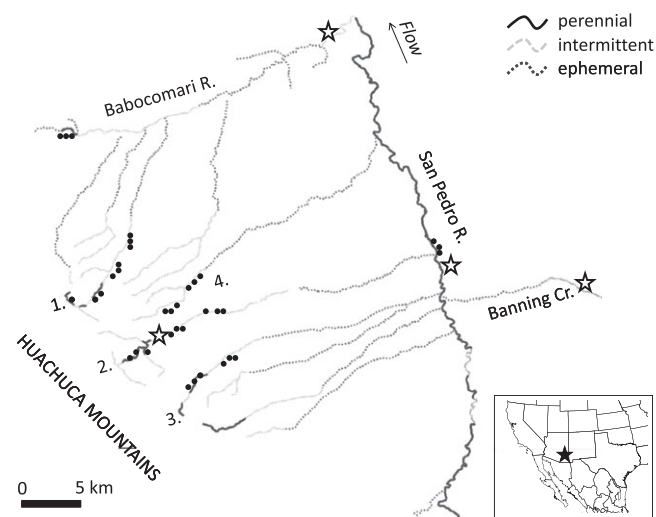
The Huachuca Mountains of south-eastern Arizona, U.S.A, rise to nearly 2800 m above the surrounding valleys (altitude *c.* 1000 m). Mean annual precipitation in the region is about 35 cm, but is highly variable from year to year and strongly bimodal, with roughly half the precipitation occurring during brief, violent summer (July–September) monsoon storms and half during more prolonged, moderate intensity winter (November–April) storms. Higher altitudes of the Huachucas receive as much as 60 cm of precipitation annually and support oak (*Quercus*) and pine (*Pinus*) forests, whereas alluvial fans and river valleys receive as little as 25 cm of rain annually and support arid grasslands and mesquite (*Prosopis*) desert scrub.

### *Stream characteristics and flow regime*

Headwater streams in the Huachuca Mountains are generally spring-fed and perennial and have substrata of

limestone bedrock or cobbles. Downstream of these perennial headwaters, streams flow across alluvial fans with a sand and gravel substratum where seepage losses are high; streams become intermittent at the canyon–alluvial fan boundaries (Fig. 1). These intermittent reaches only flow for weeks to months following extended periods of precipitation. Further downstream on the alluvial fans, the water table never rises to the level of the stream channel and flow is ephemeral and occurs only for short periods (<1 day) during extreme precipitation events. Below the alluvial fans, perennial rivers flow through incised fluvial floodplains; these systems are groundwater-fed and also have a predominantly sand and gravel substratum. All stream types are prone to violent monsoon flooding in the summer, while wet winters tend to result in prolonged increased baseflow in both perennial and intermittent reaches (see hydrographs in Fig. 2).

While there are no flow gauges in most of our intermittent study reaches, one intermittent stream sampled (Banning Creek; Figs 1 & 2) is gauged and served as a proxy for short- and long-term flow patterns in all of our intermittent study reaches. Long-term analysis of flow records at the Banning gauge identified 5 years with >30 days of winter flow between 2001 and 2011. During these wet winters, there was surface flow in Banning Creek for an average of 77 days (range: 42–103 days; Fig. 2). Concurrent with our sampling, electrical conductivity sensors were installed in many of our intermittent study reaches, and preliminary results from these sensors

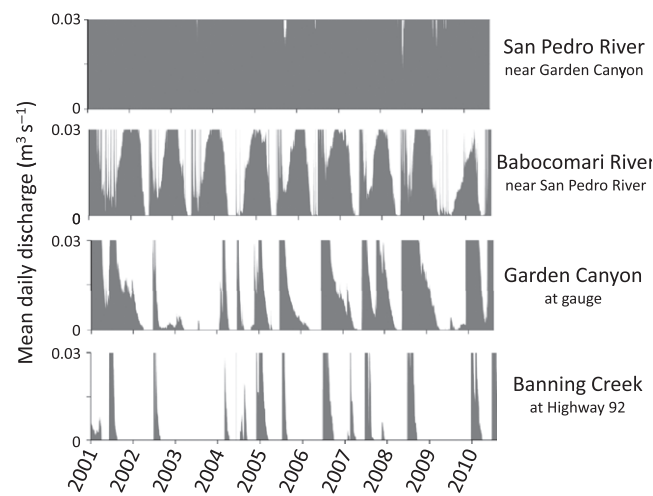


**Fig. 1** Map of the study region and locations of sampling sites (black circles) in our focal stream network (see Table 1). At each sampling site, one pool and one riffle sample were collected. The numbered study streams are (1) Huachuca Canyon, (2) Garden Canyon, (3) Ramsey Canyon and (4) Woodcutters Canyon. United States Geological Survey stream flow gauges are indicated by the stars.

indicate that flow in most of these reaches mirrors that in Banning Creek. During the initial 121-day deployment of the conductivity sensors (April–August 2010), surface flow was recorded in our intermittent study reaches from only 3 to 34% of time (Jaeger & Olden, 2012).

### Data collection

We measured habitat conditions and collected aquatic invertebrates from riffles and pools across a network of 12 reaches in six streams from 26 to 31 March 2010, near the end of the high-flow winter season (Table 1). Three of these reaches were in perennial headwaters, seven were alluvial intermittent and two were in perennial rivers. The intermittent reaches had been flowing for c. 60 days at the time, following a period without flow of over 460 days (Fig. 2). In many published studies of recovery from drying, 60 days is sufficient time for invertebrate assemblages to develop (Stanley *et al.*, 1994; Paltridge *et al.*, 1997; Fritz & Dodds, 2004). While 60 days may not always allow for a 'climax' assemblage to develop (e.g. Churchel & Batzer, 2006), our intermittent reaches began to dry after 80 days. Thus, we balanced the time needed for assemblage development with the need to take samples before streams dried. We could not sample invertebrates



**Fig. 2** Examples of differences in mean daily flow ( $\text{m}^3 \text{s}^{-1}$ ) among stream types in the study region, as illustrated by 10 years of stream flow data (2001–10) from four different flow gauges in the region (see Fig. 1 for gauge locations). Peak discharges are truncated to maximise display of dry season differences. Stream reaches in our study area range from fully perennial (San Pedro River near Garden Canyon) to nearly perennial but with occasional dry periods (Babocomari River near San Pedro River), to intermittent with dry periods of several months (Garden Canyon at gauge), to intermittent with dry periods extending over many months and/or years (Banning Creek at Highway 92).

**Table 1** Physical characteristics, flow type, number of riffle and pool samples collected, and mean water chemistry parameters across six streams and 12 study reaches in our focal arid-land stream network. Most intermittent reaches contained only riffles. See Fig. 1 for locations of each stream and positions of replicate samples within each study reach

Stream	Reach	Type	Riffles	Pools	Temperature (°C)	pH	Conductivity ( $\mu\text{S cm}^{-1}$ )	DO (ppm)	Altitude (m)	Drainage area ( $\text{km}^2$ )
Garden	Upper	Headwaters	3	3	11.5	7	448	9	1750	7
	Middle	Intermittent	3	–	11.5	7	415	8	1500	13
	Lower	Intermittent	3	–	16	7	473	7	1450	25
Huachuca	Upper	Headwaters	3	3	13.5	7.25	440	7.5	1740	9
	Middle	Intermittent	3	–	13.5	7	425	7	1560	14
	Lower	Intermittent	3	–	12.5	7	499	5.75	1490	18
Ramsey	Upper	Headwaters	3	3	8	7.5	338	7	1725	12
	Lower	Intermittent	3	–	16	7	361	7	1510	22
Woodcutters	Middle	Intermittent	3	3	12.5	6.9	410	5	1625	6
	Lower	Intermittent	3	–	13	6.75	261	5	1475	10
Babocomari	Ranch	River	3	1	14.7	7.5	597	4	1405	300
San Pedro	At garden	River	3	1	14.3	7.5	530	4.25	1230	740

from ephemeral reaches in our stream network, as these reaches supported surface water for <1 day during storm pulses (Jaeger & Olden, 2012).

At each study reach, we collected three riffle samples and three pool samples (when those microhabitat types were present). Riffles were sampled by disturbing 0.33 m<sup>2</sup> of riffle substratum to a depth of 5 cm and capturing invertebrates immediately downstream with a D-net (500- $\mu\text{m}$  mesh). When present (Table 1), pools were sampled by vigorously sweeping the D-net across all pool substrata, through the water column and at the pool surface with an effort of 10 s m<sup>-2</sup> of pool (see Bogan & Lytle, 2007, 2011). Samples were preserved in 95% ethanol and later identified as far as practical, usually to genus or species for insects and family or order for non-insects. Taxa were also assigned to functional feeding groups after Cummins, Merritt & Berg (2008).

In addition to sampling our focal stream network in March 2010, we also sampled three of the perennial reaches in November 2009 and 2010 and March 2011 to assess temporal variability in perennial headwaters and rivers. Intermittent reaches in our focal network were dry during these additional sampling periods, so we explored the temporal stability of intermittent reach assemblages by sampling two additional intermittent sites, located on the eastern and north-eastern fringe of our focal stream network. Intermittent riffles at Banning Creek (Fig. 1) were sampled in March 2010, while intermittent riffles at West Stronghold Canyon (located 30 km N of Banning Creek) were sampled during March of each of the last 3 years with abundant winter precipitation: 2004, 2005 and 2010. These two comparative sites are intermittent

headwater streams (no perennial flow located upstream or downstream of study reaches) and are isolated by >10 km of downstream ephemeral channel from the nearest perennial river reach.

At each sample location, we measured water temperature, pH (Whatman pH Indicators; Whatman International, Maidstone, U.K.), conductivity (Milwaukee waterproof EC meter C65; Milwaukee Instruments, Rocky Mount, NC, U.S.A.) and dissolved oxygen (Chemetrics K-7512; CHEMetrics Inc, Calverton, VA, U.S.A.) and also made visual estimates of riparian canopy cover and benthic substratum cover (categories with particle diameters: silt (<0.25 mm), sand (0.25–2 mm), gravel (2–64 mm), cobble (64–256 mm) and boulder/bedrock (>256 mm)). Canopy cover 5 m up- and downstream of the sampled pool or riffle was used in the canopy estimation, while substratum estimates included only the exact area that was sampled (i.e. the entire pool or the 0.33 m<sup>2</sup> area sampled for each riffle replicate).

#### Data analyses

Univariate differences in aquatic invertebrate taxon richness and abundance, the relative abundance of Chironomidae and various functional feeding groups, and measured environmental variables among perennial headwater, intermittent alluvial and perennial river reaches were analysed using mixed effects models (Bolker *et al.*, 2009). All models included stream type (headwater, intermittent, river) as a fixed effect and stream as a random effect to estimate the effect of stream type while controlling for the potential non-independence of sample



locations within streams. We used generalised linear mixed models (GLMM) with a Laplace approximation to model effects on richness and abundance, as these variables are Poisson distributed. The remaining response variables were modelled with linear mixed effects (LME) models and a maximum-likelihood approximation. We then performed linear contrasts between each stream type and corrected for multiple comparisons. All univariate analyses were conducted in R (R Development Core Team, 2011); we used the 'lme4' package (Bates & Maechler, 2010) for GLMMs and LMEs and the 'multcomp' package (Hothorn *et al.*, 2010) for multiple comparisons.

Multivariate assemblage differences among the three reach types were visualised using non-metric multidimensional scaling (NMS) in PC-ORD (McCune & Meford, 1999), with Sorensen distance as the measure of assemblage dissimilarity. Species abundances were square-root-transformed prior to ordination to reduce somewhat the influence of highly abundant species (McCune & Grace, 2002). After performing the NMS analyses, we examined linear correlations between the measured environmental variables and ordination axes. We then divided assemblage samples into three groups *a priori* (headwater, intermittent and river) and used multiresponse permutation procedure (MRPP) with Sorensen distances to quantify and test within-group agreement and distinctness (Mielke & Berry, 2001). We used indicator species analysis (Dufrene & Legendre, 1997) to determine whether particular taxa were indicative of each of the three *a priori* groups. We also conducted a higher-level MRPP with six groups distinguished by both stream type (headwater, intermittent, river) and habitat type (pool, riffle). Finally, we examined distance decay relationships (cf. Nekola & White, 1999) in riffle assemblage composition by calculating Sorensen distances between the uppermost headwater samples in Huachuca and Garden Canyons (Fig. 1) and each sample progressively further downstream. We then plotted these pairwise Sorensen distances as a function of stream network distance (km) between these uppermost headwater samples and each consecutive sample downstream.

## Results

### *Measured environmental variables*

Temperature, pH, conductivity and dissolved oxygen all varied significantly among the three stream flow types (all  $P < 0.0001$ ), but the effect sizes of most variables

were generally low, with the exception of dissolved oxygen. pH varied little between reaches, with means changing from 7.3 to 7.0 to 7.5 when moving downstream from perennial to intermittent to river reaches. Temperature-corrected (at 25 °C) mean conductivity was similar in headwater and intermittent reaches (408 versus 406  $\mu\text{S cm}^{-1}$ ), but increased significantly in river reaches (560  $\mu\text{S cm}^{-1}$ ). Mean temperature increased from 11 to 13.6 to 14.5 °C from headwater to intermittent to river reaches, while mean dissolved oxygen decreased along the same gradient (7.8 to 6.4 to 4.1  $\text{mg L}^{-1}$ ). Canopy cover was 2–3 times higher in headwater reaches (mean, 82%) than it was in intermittent (mean, 27%) and river (mean, 37%) reaches.

### *Richness and abundance*

We identified a total of 148 taxa across our stream network in March 2010. One hundred and twenty taxa were identified across all 19 headwater samples, 58 taxa from the eight river samples and only 36 taxa from the 22 intermittent samples. Seventy-two taxa were exclusive to headwater sites, 16 to river sites and 13 to intermittent sites. The remaining 47 taxa were widespread and occurred in at least two of the three stream types. Mean richness in headwater and river samples was more than twice that in intermittent samples (Table 2). Abundances were not significantly different between headwater and intermittent samples, but river samples contained more than three times as many invertebrates as either headwater or intermittent samples (Table 2).

### *Functional feeding groups*

Relative abundances of all functional feeding groups, except scrapers and collector-filterers, differed significantly among headwater, intermittent and river samples (Table 2). Collector-gatherers comprised the majority of individuals in all three stream types. Plant piercers were the least abundant group in all three stream types (<1%) and were completely absent from intermittent samples. The largest effect size by stream type was seen with predators (engulfers and piercers). The relative abundance of predators in headwater samples was nearly 14 times greater than in intermittent samples, where predators made up only 1.1% of all individuals. Over 76% of all predator individuals in intermittent samples were medium- to large-bodied larvae and adults of the dytiscid genera *Agabus* and *Stictotarsus*. Predators in perennial headwaters were diverse and included small-bodied Tanypodinae (9%), medium- to large-bodied Hemiptera

**Table 2** Mean values ( $\pm$ SE) for taxon richness, total abundance (numbers per sample) and relative abundance (%) of Chironomidae and functional feeding groups (FFG) for focal headwater, intermittent and river samples and likelihood-ratio test results for significant effects of stream type on the response

	Sample means			Likelihood-ratio test	
	Headwater ( $n = 19$ )	Intermittent ( $n = 24$ )	River ( $n = 8$ )	$P$	Pairwise
Taxon richness	32.2 $\pm$ 2.0	10.5 $\pm$ 0.4	22.8 $\pm$ 2.1	<0.0001	H versus I; H versus R; V versus I
Total abundance	453 $\pm$ 75	545 $\pm$ 81	1745 $\pm$ 350	<0.0001	H versus R; R versus I
Chironomidae % abundance	32.5 $\pm$ 3.4	79.6 $\pm$ 3.6	19.7 $\pm$ 8.0	<0.0001	H versus I; R versus I
FFG % abundance					
Collector-filterer	9.6 $\pm$ 1.6	6.5 $\pm$ 2.0	7.0 $\pm$ 2.1	0.20	
Collector-gatherer	61.2 $\pm$ 4.1	76.4 $\pm$ 3.3	80.2 $\pm$ 5.9	0.001	H versus I; R versus I
Piercer	0.6 $\pm$ 0.4	0 $\pm$ 0	0.3 $\pm$ 0.1	0.008	
Predator	15.3 $\pm$ 2.4	1.1 $\pm$ 0.3	7.9 $\pm$ 4.2	<0.0001	H versus I; H versus R
Scraper	8.1 $\pm$ 2.0	8.2 $\pm$ 1.1	4.5 $\pm$ 2.5	0.19	
Shredder	5.2 $\pm$ 1.7	7.8 $\pm$ 3.1	0.2 $\pm$ 0.2	0.001	

The pairwise column indicates significant ( $P < 0.01$ ) Bonferroni-corrected pairwise contrasts between stream types (H, headwater perennial; I, intermittent; R, river perennial).

Bonferroni-corrected pairwise contrasts between stream types for richness and abundance were derived from a penalised quasi-likelihood approximation, as this facilitated the construction of linear hypotheses for Poisson-distributed responses.

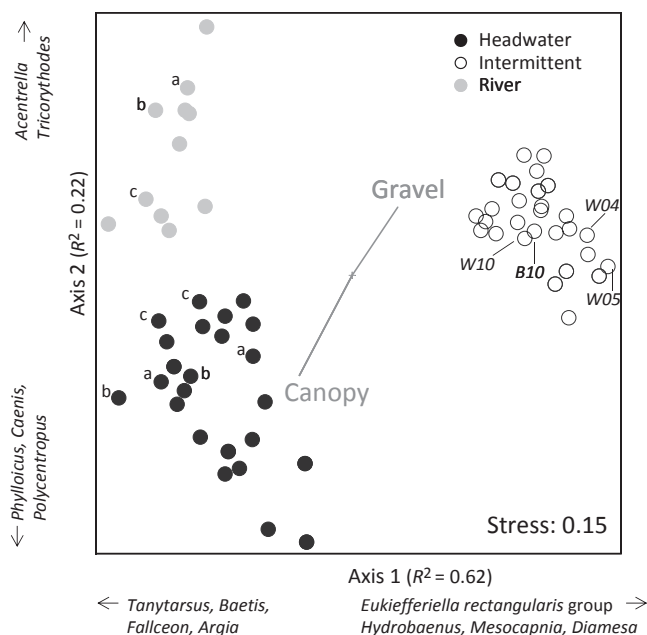
(8%) and Trichoptera (6%), and large-bodied Dytiscidae (9%) and Odonata (25%).

#### Assemblage composition

Non-metric multidimensional scaling analyses resulted in a significant two-dimensional ordination (Fig. 3; stress = 15%,  $P = 0.0196$ ) that explained 84% of variability in the distance matrix (axis 1  $R^2 = 0.62$ , axis 2  $R^2 = 0.22$ ). Of the measured environmental variables, none was strongly correlated with axis 1, and only per cent canopy cover and per cent gravel substratum were strongly correlated with axis 2 ( $r = -0.62$  and  $0.51$ , respectively). The dominant axis 1 clearly separated perennial samples from intermittent samples across streams and years for both our primary focal network sites and our comparison intermittent sites. Although there was some seasonal assemblage variation in the subset of perennial and intermittent reaches that we sampled over several years, samples from each stream type always stayed within their respective areas of species space. MRPP analysis of the focal network samples confirmed the statistical distinction among these three groups ( $A = 0.251$ ,  $P < 0.00001$ ), and all three groups were distinct from one another in Bonferroni-corrected pairwise MRPP comparisons. The higher-level MRPP comparison of the six groups delineated by stream type and microhabitat (riffle versus pool) was significant overall ( $A = 0.306$ ,  $P < 0.00001$ ), but no significant pairwise differences were found between pool and riffle samples within a given stream type.

Indicator species analysis revealed a number of significant indicators for each of the three groups (Table 3). A diverse suite of taxa was indicative of perennial headwater samples, including several caddisflies, mayflies, true flies, beetles and hydrobiid springsnails. Indicator taxa of rivers were also taxonomically diverse and included mayflies, caddisflies, true flies, crayfish, ostracods, oligochaetes and water mites. Indicators of intermittent streams, in contrast, included only a single stonefly [*Mesocapnia arizonensis* (Baumann and Gauvin)] and five midge taxa (*Eukiefferiella rectangularis* group, *Chaetocladius piger* group, *Diamesa*, *Hydrobaenus* and *Krenosmittia*). Indicator species did not change groups, nor lose significance, when analyses included the additional perennial samples (collected from 2009 to 2011) and comparison intermittent samples collected in 2004, 2005 and 2010, suggesting that indicator taxa were robust across sampling periods.

Thirteen taxa were exclusive to intermittent sites (representing 36% of all taxa found at intermittent sites), including five midge taxa (*C. piger* group, *E. rectangularis* group, *Krenosmittia*, *Mesosmittia* and *Parachaetocladius*), three blackfly taxa (*Prosimulium impostor* Peterson, *Prosimulium* sp. and *Simulium donovani* Vargus), early instars of three other Diptera families (Dolichopodidae, Ephydriidae and Muscidae), one water mite (cf. *Hydrozetes*) and one stonefly (*M. arizonensis*). These 13 taxa exclusive to intermittent sites accounted for an average of 34% of all individuals collected in such samples (range: 7–82%). When two taxa almost exclusive to intermittent sites (the midges *Diamesa* and *Hydrobaenus*) were included, the



**Fig. 3** Non-metric multidimensional scaling plot of all March 2010 samples, coded by stream type, with additional symbols designating samples from other sampling periods at our focal sites (a = November 2009, b = November 2010, c = March 2011) and comparison sites (B10 = Banning Creek, March 2010; W04, W05 and W10 = West Stronghold Canyon, March 2004, 2005 and 2010). Vectors indicate measured environmental variables with significant Pearson's correlations with axis 1 and/or axis 2. Axis 1, which explained the majority of the invertebrate assemblage variation, clearly separates perennial and intermittent assemblage samples across multiple sampling periods and streams. Eight influential taxa that contributed to the separation of intermittent and perennial sites are listed below axis 1 and five influential taxa that contributed to the separation of perennial headwater and river sites are listed below axis 2, with arrows indicating positive or negative correlations (all  $|r| \geq 0.6$ ) of those taxa with each axis.

mean percentage of all individuals in intermittent samples contributed by these 15 taxa rose to 86% (range: 56–98%).

In both Huachuca and Garden Canyons, assemblage distance was relatively high among replicate perennial headwater riffles, with nearly a 50% compositional turnover from the uppermost headwater sample to the next downstream headwater samples (Sorensen distance range: 0.44–0.51; Fig. 4). Compositional changes between the uppermost headwater samples and downstream intermittent reaches were even sharper, with Sorensen distances ranging between 0.77 and 0.93. Assemblages in the uppermost headwater samples in both drainages were more similar to the geographically distant perennial rivers (Sorensen distance range: 0.62–0.77) than they were to intervening intermittent reaches, suggesting a hump-shaped response of assemblage distance to

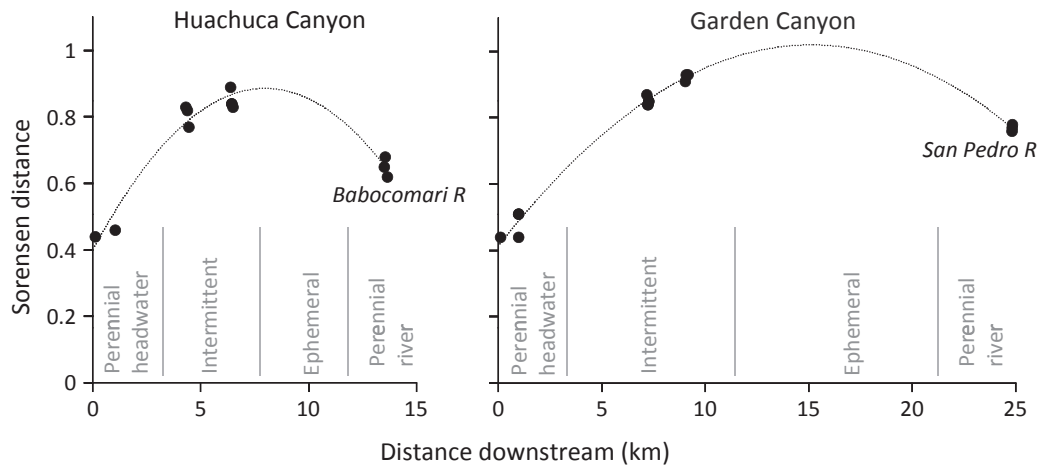
**Table 3** Indicator species analysis results for the three flow type groups with each taxon's indicator value (IV) and associated statistical significance ( $P$ ). The first IV was calculated using only March 2010 data from the focal network. The IV in parentheses was calculated using all samples, including the additional perennial samples collected in 2009–11 and the comparison intermittent samples collected in 2004, 2005 and 2011

Type	Taxon	IV	$P$
Headwater	<i>Caloparyphus</i>	80 (76)	0.000
	<i>Phylloicus</i>	78 (75)	0.000
	<i>Stempellinella</i>	72 (58)	0.000
	<i>Tvetenia bavarica</i> group	72 (75)	0.000
	<i>Caenis</i>	72 (79)	0.000
	<i>Nixe</i>	67 (63)	0.000
	<i>Polycentropus</i>	61 (58)	0.001
	<i>Nilotanytus</i>	59 (52)	0.001
	<i>Neoplasta</i>	56 (54)	0.000
	<i>Heterelmis</i>	50 (50)	0.001
	<i>Tinodes</i>	50 (58)	0.001
	<i>Pyrulopsis</i>	46 (47)	0.004
	<i>Baetis</i>	45 (61)	0.006
Intermittent	<i>Eukiefferiella rectangularis</i> group	100 (100)	0.000
	<i>Hydrobaenus</i>	98 (99)	0.000
	<i>Diamesa</i>	89 (92)	0.000
	<i>Chaetocladius piger</i> group	75 (71)	0.000
	<i>Mesocapnia arizonensis</i>	50 (57)	0.001
	<i>Krenosmitta</i>	46 (50)	0.002
River	<i>Tricorythodes</i>	96 (97)	0.000
	<i>Acentrella</i>	88 (91)	0.000
	<i>Thienemanniella</i>	84 (68)	0.000
	<i>Hydropsyche</i>	75 (82)	0.000
	Cambaridae	69 (59)	0.000
	<i>Ceratopogon</i>	68 (65)	0.000
	<i>Oxyethira</i>	63 (46)	0.000
	Ostracoda	59 (41)	0.005
	<i>Cricotopus/Orthocladius</i>	58 (56)	0.001
	<i>Atractides</i>	57 (56)	0.000
	<i>Tanytarsus</i>	56 (47)	0.001
	<i>Oligochaeta</i>	55 (55)	0.015
	<i>Homoleptohyphes</i>	50 (55)	0.001

downstream distance over the scale of this study (Fig. 4).

## Discussion

Our study of a large, arid-land stream network builds on others that have recently examined the effect of flow intermittence in streams that contain both perennial and intermittent reaches (e.g. Storey & Quinn, 2008; Arscott *et al.*, 2010; Datry, 2012). Examination of an entire stream network allowed us to examine how position within the catchment, reach-scale hydrology and proximity to other habitats all influence patterns of invertebrate diversity and assemblage composition.



**Fig. 4** Distance decay of invertebrate assemblage dissimilarity (Sorensen distance) in the Huachuca and Garden Canyon stream networks, which plots the pairwise distances between the uppermost perennial sample and each of the samples downstream as a function of geographic distance. Despite the proximity (1–5 km) of headwater and intermittent sites within a network, assemblage composition changed dramatically; assemblages in perennial headwater and river reaches were more similar to one another than to intervening intermittent reaches, despite being 12–25 km apart.

#### *Invertebrate richness and abundance*

As we predicted, there were strong differences in taxon richness between perennial and intermittent reaches in our focal stream network. Although many studies have reported little difference in richness between intermittent and perennial reaches (e.g. Feminella, 1996; Price *et al.*, 2003; Bonada, Rieradevall & Prat, 2007; Santos & Stevenson, 2011), the dry seasons in those studies tend to be very short (1–4 months), while arid-land intermittent streams may be dry for a year or longer (Fig. 2). Abell (1984) found that richness in Californian intermittent streams nearly tripled when flow lasted 4–6 months rather than 1–3 months. Examining invertebrate richness as a function of a continuous flow permanence variable, rather than an ordinal variable, may clarify some of these apparent discrepancies in previous studies. Invertebrate richness was found to decrease linearly with decreasing flow permanence in New Zealand and France when researchers used a continuous flow permanence variable derived from hydrological modelling (Larned, Datry & Robinson, 2007; Arscott *et al.*, 2010; Datry, 2012).

If at least one taxon in upstream perennial refuges is both abundant and prone to enter the drift (e.g. *Baetis*; McArthur & Barnes, 1985), then drift from upstream refuges may play an important role in supplementing abundance in downstream intermittent reaches. Invertebrates are often more abundant in intermittent reaches nearest to upstream perennial reaches than in more remote intermittent reaches (McArthur & Barnes, 1985; Paltridge *et al.*, 1997; Fritz & Dodds, 2002; Datry, 2012). In

contrast to our predictions, however, we found no differences in abundance between headwater and intermittent reaches. We cannot attribute these equal abundances to drift recolonisation alone, however, as the most abundant taxa in intermittent reaches (e.g. *Eukiefferiella rectangularis* group) were absent from upstream perennial reaches. Additionally, these same taxa were dominant in intermittent reaches with no upstream perennial refuges. Thus, some taxa of intermittent reaches apparently have the ability to rebound in numbers very quickly ( $\leq 60$  days) after extended dry periods ( $> 1$  year), without relying on drift as the primary recolonisation pathway.

#### *Functional feeding groups*

Functional feeding group composition acts as a proxy for a number of ecosystem and food-web attributes in streams and provides a manner of cross comparison between regions with different taxonomies (Cummins *et al.*, 2008). Collector-gatherers are usually the most abundant functional feeding group in low-order streams (Vannote *et al.*, 1980) and also made up the majority of individuals (61–80%) in both intermittent and perennial reaches in this study (Table 2). The relative abundance of shredders was not different between headwater and intermittent reaches, which is surprising considering that our intermittent reaches had much lower mean canopy cover (27%) than headwater reaches (81%). Perhaps, leaf litter accumulates through the long dry season to provide sufficient material for shredders when flow resumes, despite the sparse canopy cover. The relative abundance

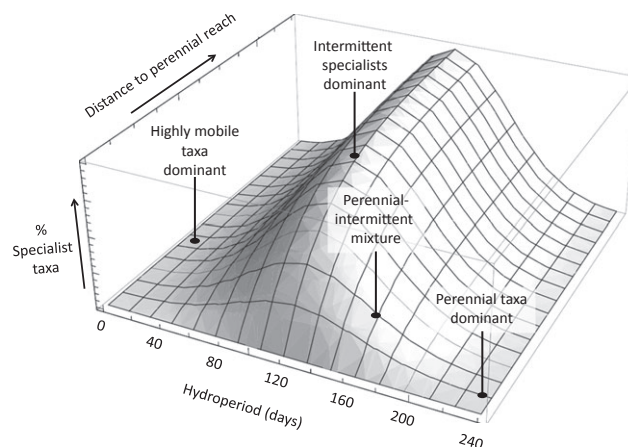


of scrapers was equal in headwater and intermittent reaches, in contrast to many studies reporting a higher abundance of scrapers in perennial streams (Progar & Moldenke, 2002; Price *et al.*, 2003; Grubbs, 2011). The more open canopy of arid-land intermittent streams may have provided for increased diatom and algal growth and thus supported more scrapers when compared to forested, temperate intermittent streams.

Temporary aquatic habitats often provide a refuge from vertebrate predation (Williams, 1996). The relative abundance of invertebrate predators in temporary waters, however, is still a matter of debate. Invertebrate predators may be more (Progar & Moldenke, 2002) or less (Price *et al.*, 2003) abundant in perennial than in intermittent streams or show no pattern with regard to flow permanence (Bonada *et al.*, 2007; Grubbs, 2011). We found invertebrate predators to be 7–14 times more abundant in perennial headwater and river reaches than in intervening intermittent reaches. While we did not estimate predator biomass, the dominant predators in intermittent reaches (Dytiscidae) were of a similar size to those in perennial reaches (Odonata and Dytiscidae). This suggests that intermittent reaches of arid-land streams may provide a significant refuge from invertebrate predation pressure.

#### Assemblage composition

Although we predicted that assemblages in intermittent reaches would be a mix of drought-adapted specialists and colonists from nearby perennial reaches, we found that intermittent reaches were dominated by specialists. This clear assemblage distinction between adjoining perennial and intermittent reaches has rarely been observed; most studies report broad assemblage overlap between neighbouring perennial and intermittent reaches (e.g. Wood *et al.*, 2005; Arscott *et al.*, 2010; Santos & Stevenson, 2011). For example, Delucchi (1988) found that riffle and pool assemblages within a flow type were more distinct than those between perennial and intermittent streams, opposite to our findings here. However, the intermittent streams in Delucchi's (1988) study flowed for 8–11 months each year, while our arid-land intermittent streams only flow for 2–4 months during wet years (five of the last 11 years). While most taxa of upstream perennial reaches rapidly (<30 days) colonised downstream intermittent reaches via drift in an Australian stream (Paltridge *et al.*, 1997), drift recolonisation from upstream perennial refuges may take 4–6 months in other streams (Abell, 1984). Thus, the very short flow durations in many arid-land intermittent streams may be insuffi-



**Fig. 5** A conceptual model illustrating potential interactive effects of hydroperiod and distance from perennial sources on the percentage of specialist or unique invertebrate taxa found in intermittent stream reaches, with four hypothetical locations. 'Highly mobile taxa dominant': a very short hydroperiod may not be sufficient time for assemblages of specialists to develop; instead, highly mobile, wide-spread taxa or dispersers from nearby perennial sites are prevalent. 'Intermittent specialists dominant': a hydroperiod of 2–5 months is sufficient for intermittent specialist taxa (those with diapause or other drought adaptations) to complete their life cycles; these will be dominant if the site is sufficiently isolated from perennial sites. 'Intermittent-perennial mixture': with close proximity to perennial sites, intermittent sites may be readily colonised by perennial taxa, thus reducing the percentage of intermittent specialist taxa. 'Perennial taxa dominant': with longer hydroperiods, taxa from perennial sites may be able to persist (via colonisation or resistance) and could outcompete or prey upon intermittent specialist taxa.

cient for taxa such as caddisflies and mayflies (Table 3) to establish populations in downstream intermittent reaches (Bonada *et al.*, 2007; also see Fig. 5).

One of our focal intermittent reaches and both of our comparison intermittent reaches were located in isolated drainages without upstream perennial reaches. Assemblages from these isolated reaches were indistinguishable from those in less-isolated intermittent reaches with upstream perennial refuges (Fig. 3). In isolated intermittent streams, aquatic invertebrates must either survive the dry season *in situ* (via a dormant stage) or arrive after flow resumption (via aerial dispersal). While many taxa in arid regions frequently disperse aerially between drainages, these tend to be beetles and true bugs (Bogan & Boersma, 2012). Even if adults of rheophilic taxa of perennial streams, like the caddisfly *Phylloicus* (Table 3), could reach isolated intermittent streams via flight, larval recruits would be unable to complete their life cycle during the short flow duration (Bogan & Lytle, 2011).

The relatively fine taxonomic resolution of midges in this study may also help to explain why our intermittent

assemblages were so distinct. Midges were 2–3 times more abundant in intermittent reaches than in perennial reaches, and all but one of the intermittent indicator taxa were midges. Many other studies comparing assemblages from sites with contrasting flow permanence identified midges only to family (e.g. Grubbs, 2011) or excluded them altogether (e.g. Santos & Stevenson, 2011). Midges can be extremely diverse in intermittent streams worldwide (e.g. Spain: Langton & Casas, 1999; United States: Chou *et al.*, 1999), so we argue that their identification is essential when comparing invertebrate assemblages of streams with contrasting flow regimes.

Several midges indicative of intermittent streams, including *Chaetocladius*, *Diamesa*, *Eukiefferiella* and *Hydrobaenus*, have previously been associated with intermittent habitats (Williams & Hynes, 1976; Towns, 1985; Chou *et al.*, 1999; Chaves *et al.*, 2008). Larvae of some of these genera have been found in intermittent streams within 5 days of flow resumption (Williams & Hynes, 1976; Abell, 1984). Chou *et al.* (1999) found that several Orthocladiinae midge taxa have dormant eggs or larvae, including *Eukiefferiella* and *Hydrobaenus*, and also found that *Chaetocladius* can persist in wet soil. Additionally, *Krenosmitta* has been documented from hyporheic habitats (Ferrington, 1984; Boulton, Valett & Fisher, 1992) and thus could potentially use the hyporheos as a refuge when surface waters dry. Larned *et al.* (2007) collected river sediments that had been dry for 200 days and found that Orthocladiinae midges readily emerged from diapause in rehydrated sediments.

Although our intermittent samples were dominated by midges, they were also characterised by high densities of the stonefly *Mesocapnia arizonensis*, which was exclusive to intermittent streams. This stonefly was first described from an intermittent stream, and the nearly all published records are from such streams (Boulton *et al.*, 1992; Jacobi & Cary, 1996). The species has an egg diapause (Gray, 1981) that may last several years; we have observed isolated populations achieve high densities within weeks of flow resumption, even after several consecutive dry years (M.T. Bogan & D.A. Lytle, unpubl. data). This ability of diapausing stonefly eggs to survive several years in dormancy has been documented for at least two other stonefly species (Sandberg & Stewart, 2004; Stewart & Anderson, 2010). Additionally, targeted collection of blackfly pupae from our intermittent streams resulted in at least eight species being identified as abundant in intermittent reaches, most of which have been previously associated with intermittent habitats and/or have desiccation-resistant eggs (Adler *et al.*, 2004). Comparable intermittent assemblages of specialised, rapidly develop-

ing (<8 weeks) stoneflies, blackflies and midges have been found in short flow-duration streams in Canada (Williams & Hynes, 1976), Australia (Towns, 1985; Boulton & Lake, 1992), the United States (Abell, 1984; Miller & Golladay, 1996) and Europe (Anna *et al.*, 2009), and as such may be useful as a global indicator assemblage for intermittent flow conditions in ungauged streams.

### Longitudinal patterns

One of the most commonly reported patterns in ecology is that community similarity between sites decreases with increasing geographic distance (i.e. distance decay; Nekola & White, 1999). Such a pattern, where neighbouring sites support more similar communities than distant sites, has also been reported in stream networks (Maloney & Munguia, 2011). Given the high connectivity provided by downstream flow in dendritic riverine networks, and the many similar assemblages in the various branches (Grant, Lowe & Fagan, 2007), recovery from drying disturbance in mid-reach intermittent streams should be facilitated by recolonisation from upstream perennial refuges. In two branches of our focal network, however, we saw substantial assemblage distances among perennial headwater samples (suggesting high beta-diversity in headwater reaches), and then a steep compositional change when moving relatively short distances downstream (1–5 km) into intermittent reaches, as predicted. Additionally, despite long distances (15–25 km) and large differences in drainage area and habitat characteristics, perennial first-order headwater and third- and fourth-order river assemblages were more similar to one another than to intervening intermittent reaches (Fig. 4). Rather than the commonly reported linear or log-linear increase in community distance with geographic distance (Nekola & White, 1999; Maloney & Munguia, 2011), our results suggest a hump-shaped response over the geographic scale of our study. While more sampling is needed to fill in gaps along the distance gradient, the observed pattern provides additional evidence that intermittent sites disrupted the usual longitudinal patterns of invertebrate assemblage composition in perennial systems.

Although the influence of flow permanence overwhelmed connectivity to upstream reaches in this study, we acknowledge that both of these factors are likely to play an important role in shaping invertebrate assemblages of intermittent streams. We present a conceptual model (Fig. 5) that explores the relative roles of these two factors in determining how many intermittent specialist taxa may be expected at a given site. Based on the data

from this and other studies, we suggest that the number of intermittent specialist taxa may be maximised at short to moderate flow durations (e.g. 80–140 days) with moderate to high isolation from perennial refuges (e.g. >1 km). For example, a hydroperiod of <30 days may be insufficient for assemblages of specialists to develop; rather, local species would largely be highly vagile taxa with rapid development times or fugitives from nearby sites (Williams, 1996; 'Highly mobile taxa' in Fig. 5). Hydroperiods of 2–5 months are long enough for most specialist taxa to complete their life cycles, but may be insufficient for taxa from perennial refuges to colonise via drift or flight, especially when intermittent reaches are distant from perennial refuges (Abell, 1984; 'Intermittent specialists' in Fig. 5). Intermittent reaches closer to perennial reaches, or with long hydroperiods, may be readily colonised by taxa from perennial refuges ('Intermittent-perennial mixture' and 'Perennial taxa dominant' in Fig. 5). These colonists may be competitively superior to or even prey upon intermittent specialist taxa (Wissinger, Brown & Jannot, 2003), thus reducing the prevalence of intermittent specialists.

While we argue that network location (i.e. proximity to perennial refuges) and flow duration are two of the primary drivers of diversity and composition in intermittent reaches, other abiotic and biotic factors probably also play a role, including the manner of flow resumption. If dry periods are broken by light or steady rains, as with the winter rains in our study, then flow resumption occurs via slow-moving groundwater fronts. However, if dry periods are broken by torrential rains, then flow resumption may occur via destructive flooding. Such catastrophic flow resumption could result in different trajectories of community recovery by scouring sediments and destroying resting stages of intermittent specialists. Additionally, some taxa from upstream perennial refuges could be transported into distant downstream intermittent reaches via catastrophic drift much faster than would occur with regular drift rates. Future studies should attempt to quantify how the manner of flow resumption affects community recovery in intermittent reaches.

In contrast to many other studies, we observed distinct invertebrate assemblages in intermittent reaches and found that mid-reach drying interrupted longitudinal patterns of richness and taxonomic and functional feeding group composition. The intense degree of intermittency in our arid-land streams probably explains why the observed differences were so pronounced among our flow permanence categories. Arscott *et al.* (2010) and Datry (2012) advocated using quantitative continuous

flow permanence variables, rather than ordinal categories of flow permanence, when examining differences between temporary and perennial streams. New flow modelling techniques (e.g. ELFMOD: Larned *et al.*, 2010b) and relatively inexpensive electrical resistance sensor arrays (Jaeger & Olden, 2012) are among the new tools that will greatly increase the understanding of relationships between flow permanence and biological communities in temporary streams. We suggest that combining numerical metrics of flow permanence and network connectivity may allow us to explain most of the current inconsistencies in the published literature (Fig. 5).

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