

Responses of macroinvertebrate communities to long-term flow variability in a Sonoran Desert stream

RYAN A. SPONSELLER*, NANCY B. GRIMM†, ANDREW J. BOULTON‡ and JOHN L. SABO†

*Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487, USA, †School of Life Sciences, Arizona State University, Tempe, AZ 85287-3211, USA, ‡Ecosystem Management, University of New England, Armidale, New South Wales 2350, Australia

Abstract

Current global models predict a hotter and drier climate in the southwestern United States with anticipated increases in drought frequency and severity coupled with changes in flash flood regimes. Such changes would likely have important ecological consequences, particularly for stream and riparian ecosystems already subject to frequent hydrologic disturbance. This study assessed the potential response of aquatic macroinvertebrates to inter-annual variation in hydrology in a spatially intermittent desert stream (Sycamore Creek, AZ). We compiled data on the recovery of macroinvertebrate communities following spring floods, with successional sequences captured 11 times over a 16-year period (1983–1999). This period encompassed a transition from perennial to intermittent flow in this system, and included a record drought in 1989–1990. Results show that while the size of floods initiating sequences had little explanatory power, changes in macroinvertebrate community structure during postflood succession were closely associated with antecedent flooding and drought. Year-to-year differences in benthic communities integrated taxon-specific responses to antecedent disturbance, including differential resistance to channel drying, use of hyporheic refugia, and variable rates of recovery once stream flow resumed. The long-term consequences of drying on community structure were only evident during later stages of postflood succession, illustrating an interaction between flood and drought recovery processes in this system. Our observations highlight the potential for predicted climate changes in this region to have marked and long-lasting consequences for benthic communities in desert streams.

Keywords: benthic macroinvertebrates, climate change, disturbance, drought, flood, succession

Received 19 August 2009; revised version received 10 January 2010 and accepted 18 January 2010

Introduction

Current climate models predict that the southwestern United States will become progressively more arid by mid-century (IPCC, 2007; Seager *et al.*, 2007; Karl *et al.*, 2009). Forecasted increases in aridity will arise from projected temperature increases of up to 6 °C, increases in evaporative water loss at these higher temperatures, and changes in the seasonality of precipitation. As a result, annual runoff in some parts of the region is predicted to decline by as much as 45% over the next 50 years (Hoerling & Eischeid, 2007). Such an increase in aridity, coupled with already observed and projected increases in precipitation intensity (Karl *et al.*, 2009), would likely have widespread ecological consequences by altering flood and drought intensity and timing (e.g., Breshears *et al.*, 2009). Understanding how terrestrial and aquatic ecosystems in this region may respond to these changes is thus a current research priority.

Hydrologic disturbance has long been recognized as a central organizer of ecological pattern and process in running waters (reviews in Resh *et al.*, 1988; Lake, 2000, 2003). Early work on disturbance in streams emphasized the role of floods that scour and reconfigure the streambed, redistribute and remove resources, and displace or eliminate organisms (Fisher *et al.*, 1982). A more recent focus on drought has shown that drying can reduce habitat availability, intensify biotic interactions, and cause widespread mortality in organisms that lack drought-resistant stages or refugia (Stanley *et al.*, 1997; Lake, 2003; Griswold *et al.*, 2008). In fact, many streams are subject to both high- and low-flow disturbances (e.g., Dodds *et al.*, 2004; Sabo & Post, 2008) operating at different spatial and temporal scales. Both floods and droughts initiate a series of 'recovery' (i.e., successional) processes that occur at variable rates depending on the timing, magnitude, or predictability of the disturbance initiating the successional sequence (Lake, 2003). When the two disturbance types interact, ecological responses may be complex and highly scale-dependent (Stanley *et al.*, 2004; Robson *et al.*, 2008).

Correspondence: R. A. Sponseller, tel. + 1 205 348 1795, fax + 1 205 348 1403, e-mail: rasponseller@bama.ua.edu

Collectively, the number, timing, and magnitude of floods and droughts comprise a disturbance *regime* that may differ among years for any given stream ecosystem. Among streams of different regions, disturbance regimes vary as a function of climate, catchment area, geology, topography, land use, and vegetation. These factors interact to determine the input, routing, and loss of water within drainage networks (Poff, 1996). Climate plays an obvious role as a driver of hydrologic pattern, and variability in rainfall and temperature has major consequences for the disturbance regime and habitat template of aquatic ecosystems (Firth & Fisher, 1992; Heino *et al.*, 2008). Furthermore, multiyear studies in streams have shown that climate-driven changes in hydrology may substantially affect the structure of aquatic macroinvertebrate communities (Bêche & Resh, 2007; Durance & Ormerod, 2007; Magalhães *et al.*, 2007; Power *et al.*, 2008), and projected reductions in river discharge are expected to result in the widespread loss of species (Xenopoulos & Lodge, 2006). Because of this sensitivity to flow regime, aquatic ecosystems and their communities are recognized as useful sentinels for a suite of climate and land-use changes that have the potential to alter hydrologic routing in both the terrestrial and aquatic sectors of a landscape (Williamson *et al.*, 2008).

Aquatic ecosystems of arid and semiarid regions are hypothesized to be particularly sensitive to climate variability and change (Grimm *et al.*, 1997). Relative to mesic counterparts, small changes in precipitation and evaporative loss can have disproportionately large effects on stream hydrology in xeric catchments (Dahm & Molles, 1992). For desert streams, this relationship between climate variability and runoff, together with notoriously variable rainfall patterns, results in a disturbance regime characterized by intense flash flooding (Grimm & Fisher, 1989), periodic drought (Stanley *et al.*, 1997), and high stochastic and catastrophic variation in flow (Sabo & Post, 2008). Consequently, desert stream communities consist of species with a suite of unique life history characteristics aimed at avoiding, resisting, or recovering from both forms of hydrologic disturbance (Gray, 1981; Boulton *et al.*, 1992b; Lytle & Poff, 2004; Robson *et al.*, 2008). Because such streams are readily subject to both flooding and drying, they represent particularly useful systems for understanding how climate variability and change can shape the structure of lotic communities (see also Dodds *et al.*, 2004).

Here, we use long-term data from the spatially intermittent Sycamore Creek in the upper Sonoran Desert of central Arizona to evaluate associations between interannual variation in climate and hydrology and the structure of stream macroinvertebrate communities. Sycamore Creek has a long history of research examining the effects of flash floods (e.g., Grimm & Fisher,

1989; Boulton *et al.*, 1992b) and drought (Stanley *et al.*, 1997) on stream ecosystems, and has served as a model system for understanding ecological succession (Fisher *et al.*, 1982). We compiled data from short-term (2–6 months) postflood successional sequences described for benthic macroinvertebrates 11 times at a single stream reach over a 16-year period (1983–1999). Our objective was to quantify interannual changes in community structure in the context of intra-annual successional dynamics following floods. Importantly, this period of record captures a transition from an era of continuous stream flow in Sycamore Creek during the 1970s and early 1980s to one characterized by widespread drought in the late 1980s and 1990s (Fig. 1). This period also includes a record drought in 1989–1990, affording us the rare opportunity to assess the long-term ecological consequences of a large, rare hydrologic disturbance.

Methods

Site description

Sycamore Creek (33°45'N, 111°30'W) is in the upper Sonoran Desert of central Arizona, USA, ~30 km northeast of Phoenix. This stream drains a mountainous watershed that ranges in elevation from 427 to 2164 m and is composed of igneous and metamorphic rock overlain by shallow soils and unconsolidated alluvial sediments (Thomsen & Schumann, 1968). Annual rainfall in the basin varies with elevation, from 39 cm at 510 m to 51 cm at 1040 m, and is distributed bimodally, with ~35% of precipitation associated with convective summer monsoonal thunderstorms (July–September), and the remainder resulting from Pacific fronts in the winter and spring (December–March; Welter *et al.*, 2005). Sycamore Creek is spatially intermittent (Stanley *et al.*, 1997), with six recognized 'perennial' segments that often retain surface flow throughout the year (one includes the USGS station, ID: 09510200). Average annual discharge from 1960 to 2005 was $0.78 \text{ m}^3 \text{ s}^{-1}$, but was as low as $0.002 \text{ m}^3 \text{ s}^{-1}$ in 2001–2002 and as high as $4.4 \text{ m}^3 \text{ s}^{-1}$ in 1992–1993, and is closely correlated with the amount of winter precipitation (Grimm & Fisher, 1992).

Sycamore Creek has a flashy hydrograph characteristic of most arid catchments, and discharge events $> 1 \text{ m}^3 \text{ s}^{-1}$ are often sufficient to 'reset' the system by scouring the channel, mobilizing bed materials, or by depositing fine sediments (Grimm & Fisher, 1989). The average number of floods per year varies from ~8 during wet years to ~2 during dry years (Grimm, 1993). These floods represent a major ecological disturbance, often removing as much as 99% of the benthic biomass, and initiating succession by algae and aquatic macroinvertebrates (Fisher *et al.*, 1982). Rates of postflood recovery can be rapid, with peak algal and invertebrate biomass reached in as little as 30 days (Fisher *et al.*, 1982; Grimm & Fisher, 1989).

The long-term hydrologic record for Sycamore Creek shows alternating periods of perennial and intermittent flow (from 1960 to 2000; Fig. 1). During the 1960s, the stream was characterized

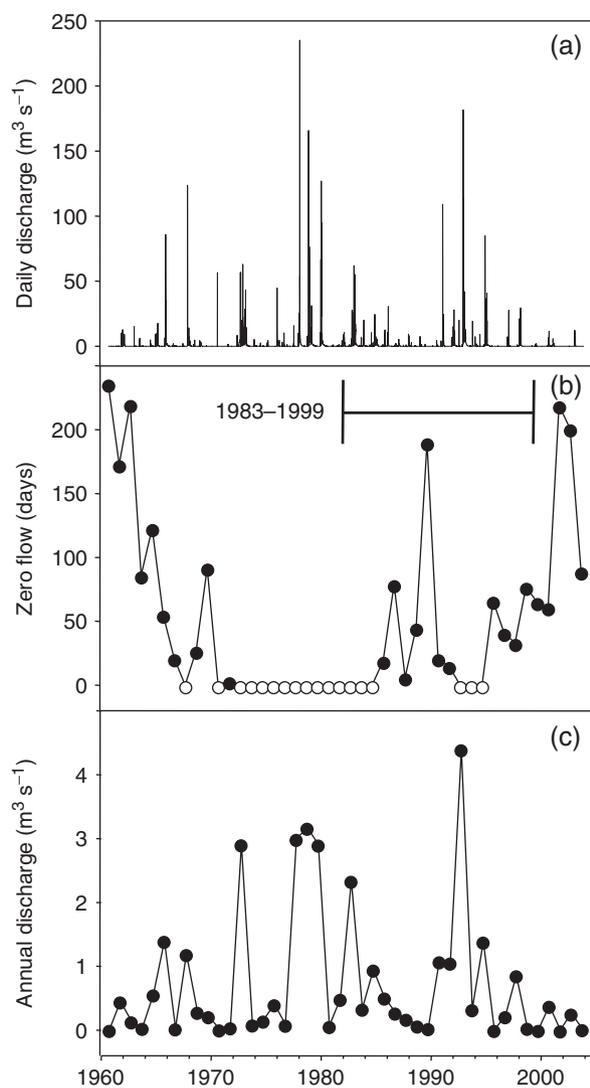


Fig. 1 Daily discharge ($\text{m}^3 \text{s}^{-1}$; panel a), annual number of days without surface discharge (b), and mean annual discharge ($\text{m}^3 \text{s}^{-1}$; c) for Sycamore Creek, Arizona, USA from 1960 to 2004. Data are from the USGS gauging station Sycamore Creek near Fort McDowell (ID: 09510200). (b) The horizontal bar represents the time period over which successional sequences were characterized, and closed symbols indicate years in the long-term record with 1 or more days without surface discharge in the stream.

by regular drying with an annual average of 103 days without flow at the USGS gage (zero flow days; ZFDs hereafter) from 1960 to 1970. An extended wet period followed, during which continuous flow was recorded from the 1970–1971 to 1984–1985 water years. A subsequent dry period from 1986 to 1992 had an average of 53 ZFDs per year, including the fifth most extensive drought during this period of record (190 ZFDs in 1989–1990; described in Stanley *et al.*, 1997). This dry period was followed by another brief phase of continuous stream flow, from the winter of 1992 to summer 1995, corresponding to two consecutive El Niño years (1992 and 1993). Stream flow during this

period was characterized by extensive flooding during the winter and spring, with maximum discharge estimated as high as $400 \text{ m}^3 \text{ s}^{-1}$ in 1992–1993. Following this wet period, the stream experienced yet another extended period of drying from 1996 to 1999, when macroinvertebrate sampling ended. During this final dry period, there was an average of 54 ZFDs per year.

Characterizing postflood succession

In this paper, we compile data on macroinvertebrate successional sequences that were initiated by the final flood of the winter–spring rain season, and terminated by the first flood of the monsoon season. These ‘spring–summer sequences’ occur during a period when flood probability is at its lowest (Gray, 1981), and rates of biological activity in the stream are high relative to other seasons (Jackson & Fisher, 1986). These sequences are also characterized by rapid postflood increases in macroinvertebrate density to a maximum value after about 2 months (range in this study: 50–92 days), followed by a decline in abundance during late successional stages, potentially related to nutrient limitation brought on by repeated coprophagy (Grimm & Fisher, 1989).

Macroinvertebrate succession was described from the same 100 m stream reach 11 times between 1983 and 1999. The size of the flood initiating sequences (estimated from maximum flow at the USGS gage) varied among years from ~ 1.0 (1999) to 67.0 (1986) $\text{m}^3 \text{ s}^{-1}$, and represented from 1.4- (1985) to ~ 200 -fold (1997) increases in mean daily flow above preflood discharge observed 1 week before events. Sequences themselves ranged in length from 71 to 189 days, with initial samples taken between 5 and 16 days postflood, and then again at weekly to monthly intervals. All sequences thus included sampling dates that covered the entire period of succession before being ‘reset’ by a summer (monsoon) flood. The exception was 1989, when the first sample was not taken until 62 days postflood, and the sequence included only four dates (data from Stanley *et al.*, 1994). In addition, data from spring 1983 were compiled for several dominant taxa (Jackson & Fisher, 1986), and are used here to evaluate interannual patterns of abundance for particular groups, but not overall community structure.

Macroinvertebrates were collected on each date from sandy run habitats, which account for 45–60% of the stream reach. Samples were taken using a 0.008 m^2 corer (10 cm depth), elutriated in the field through a $250 \mu\text{m}$ mesh net, and preserved using 10% formalin (described in Grimm & Fisher, 1989). Five individual samples were collected throughout the 100 m reach and macroinvertebrate abundance reported here represents the pooled values from among these. Concurrent to invertebrate sampling, discharge was also measured at the study reach from estimates of cross-sectional area and water velocity.

Data analysis

Our analysis of community structure was based on the 23 most common macroinvertebrate taxa found in the sandy run habitat. Taxonomic resolution for several of these groups varied over the 16 years due to personnel turnover, so we were obliged to use the most conservative level of

identification for analysis. Specifically, several groups identified to genus in the 1980s were classified to the level of family or higher in the 1990s. These included larvae of the Ceratopogonidae, Tipulidae, and Hydropsychidae, as well as physid snails. For tipulids, surveys in the 1980s indicate that this group was represented in Sycamore Creek almost entirely by *Cryptolabis* sp. Similarly, *Cheumatopsyche* sp. was the dominant hydropsychid genus observed during spring successional sequences (Boulton *et al.*, 1992a–c). Snails in Sycamore Creek are dominated by the genus *Physella*, but were classified as Gastropoda in the 1990s. Finally, both *Probezzia* sp. and *Bezzia* sp. are common ceratopogonid midges in Sycamore Creek.

We described patterns of community composition using nonmetric multidimensional scaling (NMDS) on $\log(x + 1)$ -transformed abundance data and Bray–Curtis similarity matrices (Clarke & Warwick, 2001). We carried out two analyses that were designed to: (1) characterize differences in community structure among years, integrating across the multiple sampling dates within each recovery sequence and (2) evaluate how successional trajectories themselves vary among sequences that follow wet or dry periods. We used discharge measured at the USGS gage as an estimate of flood size at the site, and to provide a coarse description of catchment-wide flood and drought regimes preceding successional sequences. Discharge measured at the site (~10 km upstream from the gage) was used to assess ecological associations with flow during postflood recovery. Both the USGS station and the study site are located within two of the six 'perennial segments', and considering all sampling dates, discharge measured at the site was significantly correlated with estimates made at the gage ($r^2 = 0.82$, $P < 0.001$). However, this relationship was less strong during periods of low flow and on several occasions there was zero flow recorded at the gage but surface water was observed at the site. Field notes and published work at Sycamore Creek document occasions of zero flow at this site in 1989, 1990, and 1997 (Stanley *et al.*, 1994, N. B. Grimm, personal observation).

Our first NMDS ordination was carried out using the average abundance for each taxonomic group calculated from pooled values across all postflood sampling dates within each sequence. We assessed the potential for these averages to be biased by extreme outliers on given dates by completing the same analysis on median abundances, and found nearly identical results. Following ordination, analysis of similarities (ANOSIM; Clarke & Warwick, 2001) was used to compare differences in community structure between 'wet' and 'dry' years, where 'dry' years were defined as those with 1 or more days of zero flow at the gage within the year before the sequence. ANOSIM computes a test statistic (Global R) based on the comparison of rank similarities among replicates within groups (hereafter referred to as 'wet' vs. 'dry') with similarities observed from all pairs of replicates between groups. Global R scores fall between 0 and 1, with higher values corresponding to greater dissimilarity between groups. Finally, the similarity percentage–species contributions (SIMPER) procedure (Clarke & Warwick, 2001) was used to identify taxa that were most responsible for dissimilarities observed between wet and dry years. Average abundances for taxa identified by SIMPER were then compared

between sequences following wet and dry years using t -tests after confirming that data met assumptions of this parametric test.

Taxa identified as important by the SIMPER procedure were used in rank-correlation analyses that assessed how peak abundance during succession for individual groups varied among years as a function of hydrologic metrics described during and before sequences. Sequence-scale metrics included the size of the flood initiating succession and median discharge measured at the site during the period of recovery. Median discharge was used because it was less sensitive to measurements made early during postflood recovery and was therefore a better representation of flow across entire sequences. Antecedent flood metrics were characterized from the beginning of the water year (1 October) to the start of each sequence and included median discharge, number of floods ($> 1.0 \text{ m}^3 \text{ s}^{-1}$), number of 2-year floods estimated via Log–Pearson III methods (Kottegoda, 1980), and median flood size. Because antecedent hydrologic variables were autocorrelated, we used a principal component analysis (PCA) to produce a smaller number of uncorrelated axes from which to generate a single score (PCA axis 1) that characterized 83% of variation in the winter flow regime among years. Finally, as described above, we used the number of ZFDs during the year preceding each sequence as a surrogate for antecedent drought in the basin.

For the second NMDS analysis, we sought to characterize recovery trajectories for each sequence and compare these among sequences that followed wet vs. dry years. Ordination was carried out on a similarity matrix derived from each individual sample ($n = 5$) collected on each postflood sampling date (i.e., not on pooled abundances). For this analysis, we omitted data from 1989 because that year did not include an entire sequence. Following ordination in two-dimensional (2D) space, we generated centroids based on median axis 1 and 2 scores derived from the five samples collected on each date. We then estimated the rate of successional change as the distance between consecutive centroids divided by the number of days between sampling (after Boulton *et al.*, 1992a). To visually assess differences in successional trajectories, we plotted taxon richness, successional rate, and NMDS axis 1 and 2 scores against days postflood for all sequences. Multivariate statistics were carried out in PRIMER V6.1.11 (PRIMER-E Ltd., Plymouth Marine Laboratory, Plymouth, UK); all other analyses were done in SYSTAT V12 (Systat Software Inc., Chicago, IL, USA).

Results

Temporal patterns of macroinvertebrate abundance during postflood succession were generally similar among years. Peak abundance during succession, however, did vary among years from 1810 individuals in 1987 to 14933 in 1997 (pooled abundance from five 0.008 m^2 samples, data not shown). These differences were heavily influenced by changes in the density of Oligochaete worms, which accounted for an average of 35% of total abundance over the long term but were particularly dominant ($> 75\%$ of total density) in 1992

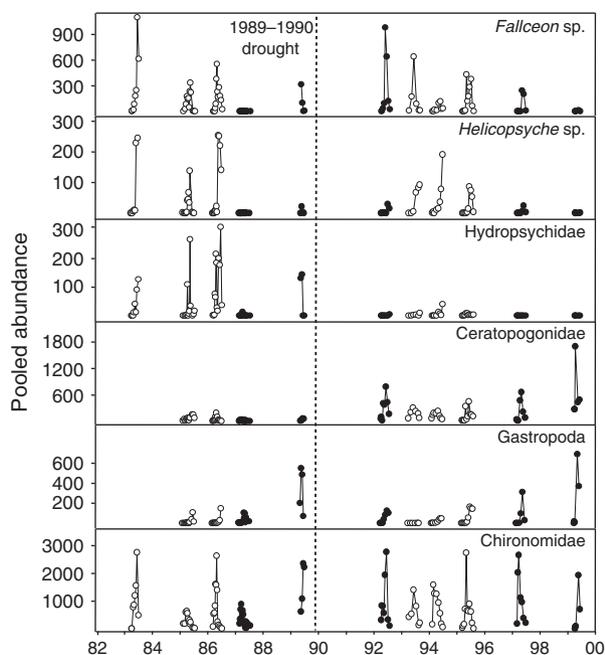


Fig. 2 Time-series data from 1983 to 1999 showing patterns of abundance for several dominant taxonomic groups in Sycamore Creek. Values represent pooled abundance values from five 0.008 m² sediment cores taken from the same stream reach over time. Open symbols indicate data from sequences following years with continuous surface flow ('wet' years); dark symbols indicate sequences that follow years with 1 or more days without surface water at the gauging station ('dry' years).

and 1994–1997. Among years, patterns of abundance varied among taxonomic groups, with four general trends apparent (Fig. 2). Some groups, like the Chironomidae and Oligochaeta, showed very little directional change throughout the period of record. A second pattern, observed for *Fallceon* sp., *Helicopsyche* sp., and Tipulidae, included a decrease in abundance following dry periods in 1986–1987 or 1989–1990, recovery during the wet phase from 1992 to 1995, and another reduction in numbers during a second dry phase (1997–1999). A third pattern was observed for the Hydropsychidae, which were abundant in sequences between 1983 and 1989, but never recovered following the major drought of 1989–1990, and in fact were entirely absent from the final sequences (1997 and 1999). Finally, both gastropods and ceratopogonid larvae were often most abundant during periods of low flow. In fact, gastropod density was greatest during sequences with the lowest flow (1989, 1999) but was notably low during the sequence that followed the winter with the most intense flooding (1992–1993). Ceratopogonids increased in abundance following the 1989–1990 drought and were particularly dominant during the second dry period from 1997 to 1999.

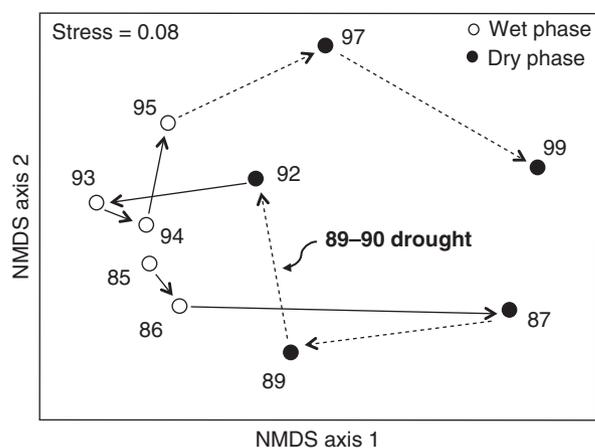


Fig. 3 Nonmetric multidimensional scaling (NMDS) plot based on log ($x + 1$)-transformed abundances averaged across sampling dates within successional sequences for each year. Symbols correspond to 'wet' and 'dry' years as in Figs 1 and 2.

Ordination of macroinvertebrate communities based on average abundance for each sequence demonstrated variation in assemblage structure over the period of record (Fig. 3; NMDS 2D stress = 0.08). In general, community structure shifted along NMDS axis 1 in association with successional sequences that followed 'wet' vs. 'dry' years. ANOSIM confirmed that assemblage composition differed statistically between these two groups (Global $R = 0.49$, $P = 0.008$). Six taxa accounted for nearly 50% of the community dissimilarity observed between sequences following wet vs. dry years: Tipulidae (12.8%), *Helicopsyche* sp. (8.1%), Hydropsychidae (7.0%), Gastropoda (6.5%), *Fallceon* sp. (6.3%), and Stratiomyidae (6.3%; Table 1). Of these, Tipulidae ($t = -4.1$, $P = 0.003$, $df = 7.9$), *Helicopsyche* sp. ($t = -5.4$, $P = 0.002$, $df = 5.9$), and Stratiomyidae ($t = -2.3$, $P = 0.05$, $df = 8.0$) were significantly more abundant during sequences that followed wet rather than dry years. Conversely, average abundance of gastropods was greater following dry compared to wet years ($t = 2.6$, $P = 0.003$, $df = 7.6$).

Among-year differences in the peak abundance for these six key taxa were correlated with different hydrologic metrics (Table 1). For example, peak density of *Fallceon* sp. larvae was positively correlated with median discharge measured at the site during sequences, and was negatively associated with PCA axis 1 scores that characterized the prior winter's flow regime. Conversely, gastropod abundance was negatively associated with discharge during succession and was positively correlated with PCA axis 1 scores. Peak abundances for Tipulidae and *Helicopsyche* sp. were negatively correlated with PCA axis 1 scores and the number of ZFDs in the prior year, but were not related to flow measured during sequences. Peak abundance of hydropsychid larvae correlated negatively with ZFDs, but was unrelated to

Table 1 Results from the SIMPER procedure, which identifies taxa that contribute most to the dissimilarity observed between wet and dry hydrologic phases from 1985 to 1999

Taxa	SIMPER results		Average abundance (\pm SE)		Spearman's rank coefficients			
	Dissimilarity	% contribution	Wet phase	Dry phase	Flood size	Sequence Q	PCA 1	ZFDs
Tipulidae	3.6	12.8	220.1 (63.4)*	8.5 (7.7)	0.34	0.58	-0.67	-0.65
<i>Helicopsyche</i> sp.	2.3	8.1	40.0 (8.6)*	3.4 (1.3)	0.58	0.45	-0.61	-0.77
Hydropsychidae	2.0	7.0	29.6 (18.8)	14.1 (13.7)	0.02	0.05	-0.23	-0.67
Gastropoda	1.9	6.5	18.9 (7.7)*	135.1 (58.6)	-0.20	-0.65	0.61	0.49
<i>Fallceon</i> sp.	1.8	6.3	119.7 (22.0)	82.7 (43.5)	0.28	0.66	-0.82	-0.37
Stratiomyidae	1.8	6.3	57.1 (30.9)*	9.3 (5.0)	0.62	0.01	-0.22	-0.38

Shown also is the average pooled abundance from wet and dry phases (\pm SE, $n = 5$) for these same taxa and years, as well as results from Spearman's rank correlation analyses between peak density during succession and different hydrologic descriptors ($n = 10$ or 11). *($P \leq 0.05$) differences in average abundance between wet and dry phases following *t*-test on transformed data; correlation coefficients (*r*) in bold represent significant relationships ($P \leq 0.05$). SIMPER, similarity percentage–species contributions; PCA, principal component analysis; ZFD, zero flow days.

all other metrics. Of these key taxa, only peak abundance of stratiomyid larvae correlated with size of the flood that initiated successional sequences.

A more explicit consideration of community change during succession illustrated generalities that were observed across all years, but also revealed patterns distinguishing sequences that followed wet or dry periods (Fig. 4a and b; NMDS 2D stress = 0.21). For example, in all sequences, species richness increased over successional time, leveling off after about 60 days (Fig. 5a). For sequences following wet periods, however, peak richness during mid- to late succession ranged from 17 taxa in 1993 to 20 in 1985. For sequences following drier periods, richness ranged from only 12 taxa in 1999 to 17 in 1992. The rate of community change was generally highest during the early stage of recovery, declining after 30–40 days postflood (Fig. 5b). This initial rate of community change (averaged over the first 30 days) was highest in 1999 (0.17) and lowest in 1993 (0.02), but was otherwise similar among the remaining sequences (range: 0.03–0.07). Community change during recovery showed little difference in NMDS axis 1 scores between wet and dry periods during early succession, but diverged during mid- to late succession (Fig. 5c). Axis 2 scores were more variable during early stages of succession for dry compared with wet periods, but in general these two groups overlapped considerably (Fig. 5d).

Discussion

Our results demonstrate a clear relationship between interannual climate variability and macroinvertebrate community structure in a desert stream. The transitions between 'wet' and 'dry' hydrologic phases observed over

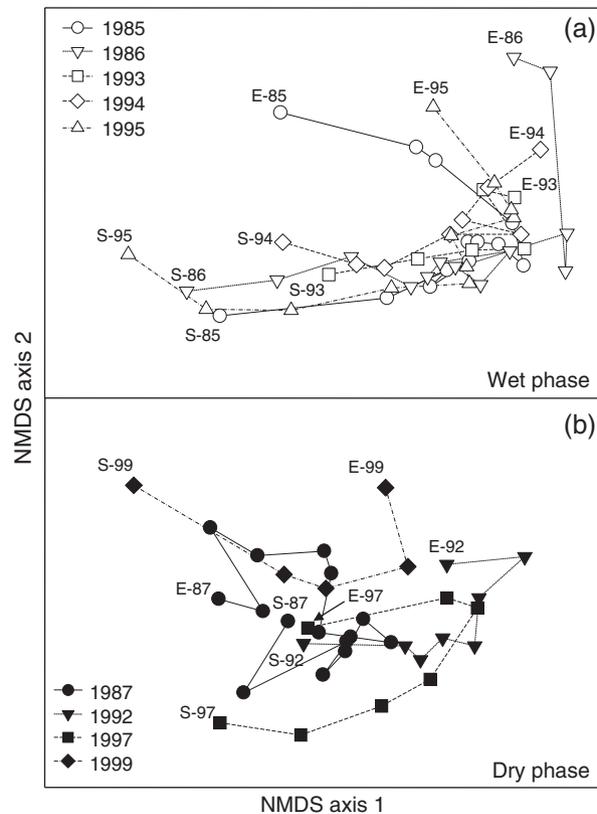


Fig. 4 Spring–summer successional trajectories of macroinvertebrate communities in dry (a) and wet (b) phases of a 16-year study period in Sycamore Creek. Trajectories are plotted as the centroid of values calculated from nonmetric multidimensional scaling (NMDS) axes 1 and 2 scores derived from five replicate samples from each date in each successional sequence. S and E denote the start and end, respectively, of each sequence (e.g., S-99 is the start of the 1999 sequence). Closed and open symbols indicate 'wet' and 'dry' years as in Figs 1–3.

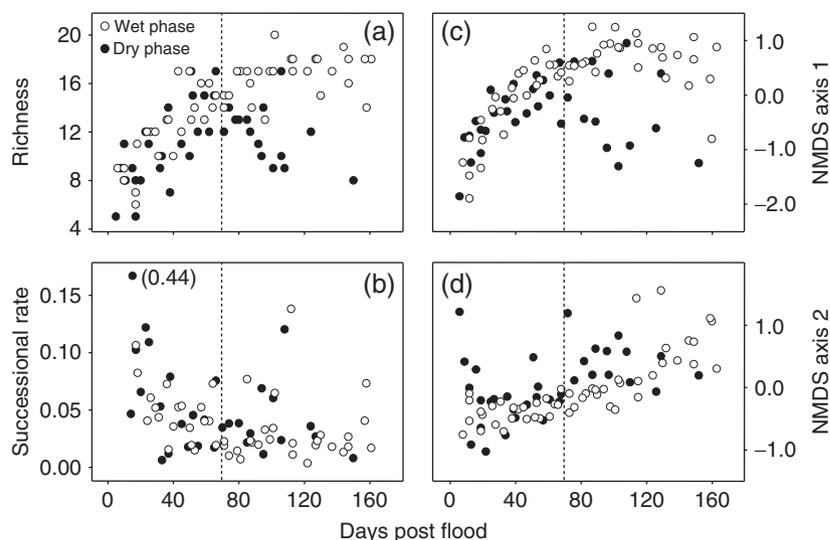


Fig. 5 Changes over successional time (days postflood) in (a) taxon richness, (b) successional rate, (c) nonmetric multidimensional scaling (NMDS) axis 1 score, and (d) NMDS axis 2 score for all sampling dates in all years. The dashed vertical line represents the average time to peak macroinvertebrate density and is used here to delimit early and mid-to-late successional stages. Closed and open symbols indicate 'wet' and 'dry' years as in Figs 1–4.

the long-term record for Sycamore Creek corresponded to marked changes in assemblage structure, including the local extinction of groups that were abundant when research was initiated in this system in the late 1970s. Overall, these results are consistent with other studies on the general effects of drought on stream communities (e.g., Boulton, 2003; Lake, 2003), and further suggest that if drought frequency and severity increase in the Southwest United States as predicted (e.g., Hoerling & Eischeid, 2007), the consequences for the structure of benthic communities in streams like Sycamore Creek are likely to be dramatic and potentially long-term. While streams that support extended periods of surface flow do not account for the majority of channel length in most arid and semiarid regions, they do represent key refugial habitat for a diverse group of aquatic macroinvertebrates, fish, anurans, and obligate wetland plants. Such habitats are thus disproportionately important from the standpoint of conserving regional flora and fauna, and appear particularly vulnerable to projected climate change in this region.

Long-term changes in community structure

The structure of benthic communities over postflood successional time varied among years, and this variation was better explained by antecedent hydrology than the characteristics of the floods that initiated recovery sequences. Previous work in this system has shown that the loss and recovery of ecosystem-level attributes (e.g., algal and macroinvertebrate biomass; Fisher & Grimm, 1988; Grimm & Fisher, 1989) vary with flood magnitude, but that benthic community structure instead appears to

follow more predictable seasonal patterns (Boulton *et al.*, 1992b). The long-term perspective of the current study is consistent with this general notion, but further highlights the role of drought disturbance as an organizer of assemblage composition in this stream over longer time scales. Other multiyear studies have implicated antecedent disturbance as a driver of benthic community and food web structure (e.g., Wood *et al.*, 2000; Power *et al.*, 2008). Moreover, long-term research in streams of northern California, where flooding and drought also co-occur, shows a similar transition between 'wet-year' and 'dry-year' communities (Bêche & Resh, 2007). Our results thus add to a growing body of long-term studies in streams and provide an example of how extreme dry periods (e.g., the 1989–1990 drought) can have long-lasting consequences for community structure.

The long-term change in community structure observed in Sycamore Creek integrates taxon-specific responses to both flooding and drought disturbance. Time-series data for individual taxa reveal four general response types, which in turn reflect differences in life-history characteristics and refuge use that have consequences for survival and recovery following disturbance. Benthic macroinvertebrates use a variety of strategies to survive dry periods, including desiccation-resistant stages and subsurface refugia (Lake, 2003). Early studies in Sycamore Creek, however, showed little evidence for either mechanism of drought resistance (Gray, 1981; Stanley *et al.*, 1994), but instead highlighted several strategies that represent apparent adaptations to a severe flood regime (e.g., rapid developmental rate, continuous reproduction). Exceptions to this are found in some benthic groups, including the

Oligochaeta, Chironomidae, and Ceratopogonidae, which are abundant in the hyporheic zone (Gray & Fisher, 1981; Clinton *et al.*, 1996), even when the surface stream is dry (Boulton *et al.*, 1992c). The long-term record shows that these same groups were either (1) resistant to drought on an interannual basis with little directional change over time (e.g., Chironomidae and Oligochaeta) or (2) found in greater relative abundance following protracted drying (Ceratopogonidae). Thus, while surface fauna may not actively enter the hyporheic zone as the channel dries (Stanley *et al.* 1994), our results suggest that, at long time scales, those groups that are able to use deeper sediments as habitat may be less affected by the onset of drought, and better poised to colonize the surface stream once flow resumes.

Two other interannual patterns observed at Sycamore Creek were linked to taxa that lack known mechanisms for resisting drought. First, several of the dominant groups (e.g., the Tipulidae, *Helicopsyche* sp., *Fallceon* sp.) demonstrated resilience to drought on an interannual basis. In such cases, abundance was greatly reduced following dry periods, but then recovered to approximately predisturbance levels during the transition back to a wet phase. A second, less common, pattern involved greater drought vulnerability, in which taxa (e.g., the Hydropsychidae) were eliminated from the stream reach following protracted drying, and were not able to recover to predrought levels during the period of record. Rather than representing discrete 'response types', these two categories likely represent a single group of taxa that reside along a continuum of post-drought recovery rates. Differences in recovery following drought are linked to the distances over which recolonization must occur (and thus refugia use), and are further influenced by a suite of life history characteristics, including developmental time, adult longevity, vagility, and mode of recolonization (Lake, 2000). Given that taxa accounting for most of the community dissimilarity between wet and dry periods came from these general response categories, the dynamics associated with postdrought recovery represent the basis for change in overall assemblage composition at long time scales, and therefore merit further study. Importantly, our results indicate that predicted increases in drought frequency and associated reductions in the duration of intervening wet periods will likely 'filter out' taxa that may require greater periods of time to recover, leaving only those groups that are either resistant to drought or able to recover most rapidly once stream flow resumes.

In addition to the effects of drought, variation in the severity of winter flooding may also have influenced interannual patterns of abundance for certain taxonomic groups. In particular, peak abundance of snails was negatively correlated with the magnitude of antecedent flooding and with discharge during the recovery

period. Indeed, this group was virtually absent in the spring of 1993, which followed a winter season characterized by intense rainfall, severe flooding, and sustained periods of high flow. This relationship between snail abundance and hydrology could reflect a relatively greater sensitivity to flooding by snails in Sycamore Creek, as is observed for other sessile grazers in California's Eel River (Power *et al.*, 2008). Alternatively, the high abundance of snails observed during sequences with lowest discharge (1989, 1999) may reflect their ability to thrive under limnological conditions that are often associated with very low flow, including elevated water temperature and reduced dissolved oxygen (Stanley *et al.*, 1997).

Interannual variability in successional dynamics

The design of this study allowed us to address how community succession as a process was influenced by antecedent hydrology. Results showed fairly consistent recovery patterns for sequences that followed wet years, but more variability in both early and late successional dynamics for sequences following dry years. Despite these year-to-year differences in successional trajectories, the rates of community change following winter/spring floods showed similar temporal patterns and were of similar magnitude among most years. There is some indication, however, that rates of change early in succession may be sensitive to the broader hydrologic regime. For example, the low rates of community change observed in 1993 may reflect the particularly severe and prolonged flooding that characterized the winter and spring season before that recovery sequence. On the other hand, the high rates of change observed during early succession in 1999 might reflect the very small flood that initiated that particular sequence ($\sim 1.0 \text{ m}^{-3} \text{ s}^{-1}$).

One important insight gained from the unique structure of this dataset was that observing long-term change in community composition associated with the onset of drought required some consideration of how assemblage structure varied over the course of postflood succession. This implies an important interaction between flooding and drought response by stream communities. Specifically, for the spring–summer sequences we considered here, the long-term effects of drying on both species richness and community composition could only be observed during later stages of postflood recovery. At the same time, differences in community trajectories during postflood succession could only be understood by considering the timing of those short-term recovery sequences within broader transitions between perennial and intermittent flow in the system.

The interaction we observed between community response to flooding and drought is based, in part, on

fundamental constraints to recovery following floods. As has been shown previously at Sycamore Creek (Grimm & Fisher, 1989), early- to mid-successional communities are composed of the fastest-growing taxa, which are able to most rapidly colonize sediments following floods. Because several of these early postflood colonizers (e.g., Chironomidae and Ceratopogonidae) appeared relatively unaffected by drought over the long term, macroinvertebrate communities of early successional stages varied little between wet and dry phases in the record. It was only during middle to late postflood succession that long-term community change could be observed. For pre-drought sequences in the 1980s, communities during these later successional stages were characterized by more slowly growing taxa (e.g., the Hydropsychidae and Helicopsychidae), or by groups that become abundant after a sufficient period of stable flow (e.g., snails). As described above, it was these groups that were often most strongly influenced, in either negative or positive ways, by the onset of drought or by interannual differences in the winter flood regime.

Understanding the interactive effects of multiple disturbances remains an important research challenge in ecology (Paine *et al.*, 1998). Meeting this challenge is critical in streams, which may experience simultaneous alterations to flooding and drying regimes, as well as a suite of additional disturbances (e.g., invasive species, sedimentation, pollutant loading, and eutrophication) associated with future climate and land-use change. In this study, we show how short-term community responses to flooding are shaped by the long-term relationships between drought disturbance and the relative abundance of dominant taxa. Similar interactions between disturbances have been documented in a study evaluating stream community responses to flooding and land-use change (Collier & Quinn, 2003), and are likely to be of widespread importance. Our results suggest that recovery dynamics following flooding and drought disturbances can operate at very different time scales (i.e., weeks vs. years), yet interact to shape the structure of stream communities at any given time.

Conclusions

Climate change predicted by current global models is likely to have widespread consequences for terrestrial and aquatic ecosystems alike. These models suggest that the Southwestern United States could experience both drying (reduced runoff) and altered timing and intensity of precipitation (Seager *et al.*, 2007; Karl *et al.*, 2009). Our results indicate that such changes in this region will alter the structure of macroinvertebrate communities in spatially intermittent streams, like Sycamore Creek, that have historically supported a rich

benthic fauna. Although results do provide evidence for multiyear recovery by some macroinvertebrate groups following drought, they also demonstrate the potential for once-dominant taxa to be essentially lost from stream reaches following severe channel drying. Under scenarios of increased drought severity and frequency (e.g., Hoerling & Eischeid, 2007), aquatic and riparian communities of arid and semiarid streams would likely become greatly simplified. The future of such systems may include assemblages characterized by a smaller subset of plant and animal species, with life-history traits that enable survival under increasingly ephemeral flow conditions. For macroinvertebrates in such streams, drought-resistant (or resilient) taxa should be favored over drought-intolerant taxa; however, this prediction hinges on any changes in the seasonal precipitation and flooding regime. Indeed, parts of the United States are also already experiencing increases in the frequency of heavy precipitation events (IPCC, 2007; Karl *et al.*, 2009). Altered timing of seasonal floods could further limit the distribution of more drought-tolerant groups, some of which (e.g., snails) may be particularly vulnerable to high-flow events, leading to even further simplification of stream communities under climate change.

Acknowledgements

Support for this work came from consecutive National Science Foundation LTREB projects (DEB-9108362 and DEB-9615358). We thank the many undergraduate and graduate students, technicians, and postdoctoral scholars over the years who participated in the baseline sampling program at Sycamore Creek, particularly Sandra Clinton, Sam Rector, Eugènia Martí, and John Schade, who were responsible for coordinating sampling campaigns at various times during the study period. Maggie Tseng processed samples and identified invertebrates from the 1990s, Julia Henry was responsible for the initial data organization, and Corinna Gries built the database for Sycamore Creek invertebrates, which is available at <http://caplter.asu.edu>. We thank Jon Benstead, Jennifer Edmonds, Steve Ormerod, and two anonymous reviewers for comments on the manuscript.

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