

# Severe drought drives novel community trajectories in desert stream pools

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## SUMMARY

1. Ecological communities can be relatively stable for long periods of time, and then, often as a result of disturbance, transition rapidly to a novel state. When communities fail to recover to pre-disturbance configurations, they are said to have experienced a regime shift or to be in an alternative stable state.

2. In this 8-year study, we quantified the effects of complete water loss and subsequent altered disturbance regime on aquatic insect communities inhabiting a formerly perennial desert stream. We monitored two study pools seasonally for 4 years before and 4 years after the transition from perennial to intermittent flow to evaluate pre-drying community dynamics and post-drying recovery trajectories.

3. Mean species richness was not affected by the transition to intermittent flow, though seasonal patterns of richness did change. Sample densities were much higher in post-drying samples.

4. The stream pool communities underwent a catastrophic regime shift after transition to intermittent flow, moving to an alternative stable state with novel seasonal trajectories, and did not recover to pre-drying configurations after 4 years. Six invertebrate species were extirpated by the initial drying event, while other species were as much as 40 times more abundant in post-drying samples. In general, large-bodied top predators were extirpated from the system and replaced with high abundances of smaller-bodied mesopredators.

5. Our results suggest that the loss of perennial flow caused by intensified droughts and water withdrawals could lead to significant changes in community structure and species composition at local and regional scales.

*Keywords:* alternative stable states, drought, intermittent, long-term data, regime shift

## Introduction

Local species assemblages fluctuate on various temporal scales ranging from daily to multi-yearly. Often these fluctuations are predictable and rooted in large-scale abiotic factors (e.g. climate) and/or changes in the abundance of influential species (e.g. top predators). Occasionally, however, significant regime shifts occur in local communities with little or no prior warning, propelling the community into an alternative state (Scheffer *et al.*, 2001). While internal community factors can drive regime shifts in some

cases (predation: Paine, 1966; recruitment facilitation: Baskett & Salomon, 2010), stochastic disturbance is often the main factor triggering regime shifts (Beisner, Haydon & Cuddington, 2003). Catastrophic regime shifts occur when a community is drawn towards a new basin of attraction, wherein a return to pre-disturbance conditions in the local habitat does not result in the community returning to its previous state (Scheffer *et al.*, 2001). This fundamental alteration to local community structure may be more common in systems with strongly abiotic- or disturbance-structured communities than in systems

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weakly structured by environmental conditions (Didham & Watts, 2005).

Aquatic communities are strongly driven by disturbance and abiotic conditions (Resh *et al.*, 1988) and thus, may be inherently prone to regime shifts. In recent years, drought has been recognised as an important driver of local aquatic community composition (Boulton, 2003; Lake, 2003; Chase, 2007). Although drought disturbance has not explicitly been linked to regime shifts in aquatic systems, it has been shown to alter local and regional community dynamics. In aquatic microcosms, Östman, Kneite & Chase (2006) found that drought altered the effect of habitat isolation on local and regional diversity and community composition. In larger pond mesocosms, drought can act as a strong abiotic filter on local communities resulting in more homogenous communities in mesocosms that experience drought compared with mesocosms not experiencing drought (Chase, 2007). Observational studies of natural ponds have also shown significant effects of timing and duration of drying on aquatic community composition (Jeffries, 1994; Fairchild *et al.*, 2003; Sanderson, Eyre & Rush-ton, 2005).

Results from studies of lotic systems, however, are more equivocal (Dewson, James & Death, 2007). In many streams, community recovery from short-term droughts is rapid (Boulton, 2003; Lake, 2003). Resilience to drought is often high in arid-land streams, but rates of recovery are dependent on the specifics of drying sequences and distance to sources of recolonists (Stanley *et al.*, 1994). Drought and stream drying may cause predictable shifts in community composition, but communities generally return to pre-drought configurations with the return of surface water (Boulton & Lake, 1992b; Acuña *et al.*, 2005). In some cases, however, drought has been found to eliminate sensitive taxa (e.g. shrimp: Boulton & Lake, 1992a) and have longer-term impacts on community composition in streams (Bêche *et al.*, 2009).

Most studies examining the effects of drought disturbance on lotic community structure have focused on streams that were historically intermittent (e.g. Stanley *et al.*, 1994) or used comparisons of neighbouring perennial and intermittent streams (e.g. Delucchi & Peckarsky, 1989). Given the focus of these studies, they did not address how novel events such as severe drought could produce regime shifts in aquatic communities. Species inhabiting intermittent

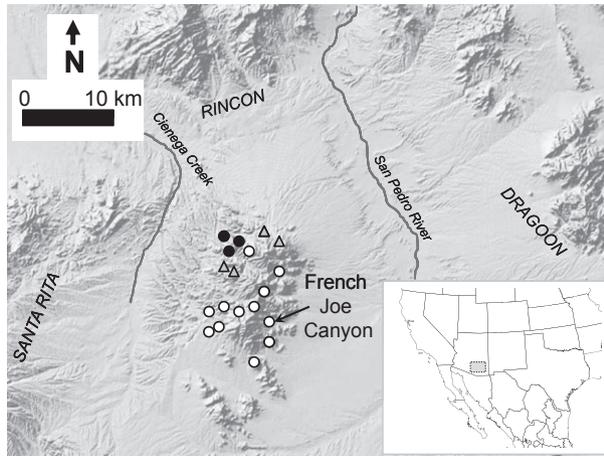
streams may have behavioural or life-history adaptations, making them resistant or resilient to drying (Lytle & Poff, 2004), and so the impacts of drying disturbance on these communities would be minor. The impact of total water loss on perennial stream communities, however, is virtually unknown (but see Resh, 1992). Furthermore, intensified droughts predicted by many regional climate-change models (e.g. Seager *et al.*, 2007) and increased anthropogenic water withdrawals (e.g. Deacon *et al.*, 2007) may deplete local aquifers and cause streams to transition from perennial to intermittent. In order to properly manage stream ecosystems in the face of such threats, long-term studies are needed to understand resilience and recovery dynamics following unprecedented drying events (e.g. Jackson & Füreder, 2006).

In this study, we used a long-term data set (8 years) to document catastrophic regime shifts in desert stream pools when severe drought caused the formerly perennial system to dry for several months and transition to an intermittent flow regime. Our goals were to understand: (i) the short-term effects of the unprecedented drying disturbance on local diversity and community composition; (ii) community recovery trajectories following rewetting and (iii) the longer-term impacts of the transition to intermittent flow on local community composition. We hypothesised that the unprecedented drying disturbance would alter community composition and negatively impact diversity in the short term (<1 year), but that communities would shift back to pre-drying conditions over longer time periods (>1 year).

## Methods

### *Site and climate description*

French Joe Canyon is an arid-land drainage in the Whetstone Mountains of south-eastern Arizona, U.S.A. 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 monsoon (July–September) storms and half during more prolonged, moderate intensity winter storms (November–April). The dominant limestone geology of the Whetstone Mountains supports an unusually dense (for the region) aggregation of springs (Fig. 1). As recently as 2002, French Joe Canyon contained a



**Fig. 1** French Joe Canyon is located in the Whetstone Mountains of Arizona, one of many sky island mountain ranges in the region. French Joe Canyon supported some of the many spring-fed perennial stream reaches (indicated by circles and triangles) in the mountain range. Most of the surrounding springs have dried since USGS mapping of the region occurred (*white circles* = dry or lacking perennial taxa; *black circles* = perennial springs; *grey triangles* = no data available). The nearest similar habitats are in the neighbouring mountain ranges, 15–20 km from the Whetstone Mountains. Most perennial habitats in the region are found in the mountain canyons like French Joe, but the San Pedro River and Cienega Creek also have some perennial reaches.

perennial reach consisting of at least 10 travertine pools located in the active stream channel and fed by subsurface springs. By early 2003, all but five pools had dried, and in early 2004, only two perennial pools remained. These two remaining pools (hereafter 'upper' and 'lower' pools) were in the main canyon channel and were separated by approximately 100 m of dry streambed. When full, the upper pool was 1 m deep, with a surface area of 1.5 m<sup>2</sup>, while the lower pool was 0.3 m deep, with a surface area of 2.5 m<sup>2</sup>. Outflow was negligible (<1 L min<sup>-1</sup>) in both pools, with inflow apparently equal to evaporation and transpiration by riparian plants. Both pools supported lush micro-riparian areas of grasses and ferns, with adjacent locust (*Robinia neomexicana* Gray) and walnut trees (*Juglans major* (Torrey), while surrounding uplands supported mesquite (*Prosopis*), agave (*Agave*), and scattered oaks (*Quercus*).

Multiple lines of evidence support the idea that French Joe Canyon had sustained perennial habitat through both the historic and pre-historic past. First, heavy travertine deposition throughout the reach surrounding the pools (>300 m of channel) indicate

that pools and flow were more extensive in the recent past. Second, a hiking description of French Joe Canyon published in 1991 warned that 'pools and waterfalls may cause you to detour out of the canyon bottom': (Martin & Martin, 1991; p.159). Finally, the presence of *Abedus herberti* Hidalgo, a flightless aquatic hemipteran that requires perennial water for survival, indicates that French Joe Canyon harboured perennial aquatic habitat until the drying events documented in this study. Genetic evidence from *A. herberti* populations throughout the region, including French Joe, suggests that the French Joe population has existed in isolation over ecological (tens to hundreds of years) and perhaps evolutionary time-scales (hundreds to thousands of years) (Finn, Blouin & Lytle, 2007; Finn, Bogan & Lytle, 2009).

Though drought is a recurring phenomenon in the arid south-western United States, the last 30 years have been marked by a significant increase in drought severity (Balling & Goodrich, 2010). A 5-year period of sustained drought (1999–2004) starting just before, and continuing into our study period, was especially intense. While most small streams in Arizona are ungaged, including French Joe Canyon, data from gaged streams across Arizona showed that this drought resulted in the lowest streamflow in 60 years and in many cases the lowest streamflow on record (Phillips & Thomas, 2005). Although substantial rains fell in winter 2005 and summer 2006, drought conditions returned during the last 3 years of our study (2007–2009).

#### Data collection

We measured habitat conditions and collected aquatic insect community samples from both pools during each visit to French Joe beginning in June 2003 (during prior visits, only selected species were collected). Initially, we sampled the pools twice a year (March and June; corresponding to high- and low-flow seasons; see Bogan & Lytle, 2007), but we later added a late autumn sampling event (November) beginning in 2005. During each visit, we measured pool depth and surface area, water temperature, pH (Whatman pH Indicators, Whatman International, Maidstone, England), and conductivity (Milwaukee waterproof EC meter C65; Milwaukee Instruments, Rocky Mount, NC, U.S.A.) and also made visual estimations of benthic substratum cover (categories: silt, sand, gravel, cobble and bedrock).

Our goal with community sampling was to detect as many species as possible during each sampling event without having a severe impact on abundance, since we were repeatedly sampling the same pools over time. During sampling, the entire pool was sampled by vigorously sweeping a D-net (0.5 mm mesh) above all pool substrata and on the surface of the water for  $10 \text{ s m}^{-2}$  of pool. This pool sampling effort was determined based on preliminary sampling of pools at three other local streams; an effort of  $10 \text{ s m}^{-2}$  of pool captured over 95% of the species that were detected with twice the effort ( $20 \text{ s m}^{-2}$ ), but without noticeably reducing the abundance of insects (Bogan & Lytle, 2007). Samples were preserved in 95% ethanol and later identified to genus for most groups, except to species for Coleoptera and Hemiptera, and to family for Chironomidae and Culicidae (Diptera).

Since local sources of colonists are essential in community recovery following disturbance such as drought, we quantified the location and extent of all other perennial springs and streams in the Whetstone Mountains. We located springs previously identified as perennial using a US Geological Survey 1 : 100 000 scale map (USGS Map # 31110-E1, United States Department of Interior, Washington DC, U.S.A.; Fort Huachuca) and visited as many of these springs as possible to confirm their hydrological status.

#### Data analyses

Univariate differences in pre- and post-drying aquatic insect density, taxon richness, water temperature, pH and conductivity were analysed using two-sample *t*-tests assuming unequal variances in Excel 2007 (Microsoft Corp., Redmond, WA, U.S.A.). Multivariate community trajectories through time were quantified using non-metric multidimensional scaling (NMS) in PC-ORD (McCune & Mefford, 1999), with Sorensen distance as the measure of community dissimilarity. Species abundances were square-root transformed prior to ordination to moderately reduce the influence of highly abundant species on the ensuing ordination (McCune & Grace, 2002). After performing the NMS analyses, we examined linear correlation coefficients between each taxon and axis of the ordination to determine which taxa were influential in the ordination. We also examined linear correlations between the measured environmental variables and ordination axes.

We then divided community samples into two groups: (i) pre- and (ii) post-drying. We used multi-response permutation procedure (MRPP) with Sorensen distances to quantify and test within-group agreement and distinctness (Mielke & Berry, 2001). This procedure yields two statistics: an *A*-statistic ( $-1 \leq A \leq 1$ ), describing the effect-size of the grouping, and a *P*-value, which evaluates the likelihood that observed differences are due to chance (McCune & Mefford, 1999). We also used indicator species analysis (ISA) to determine whether particular taxa were indicative of pre-drying or post-drying conditions. The highest possible indicator value (IV) for a taxon is 100, meaning that the taxon is always present in a particular group (faithful) and does not appear in other groups (exclusive) (McCune & Grace, 2002). The statistical significance of each IV was tested using a Monte Carlo randomization with 1000 runs.

## Results

#### Abiotic data

Water levels in the two study pools were full and overflowing during the first 3 years of our observations (2002–2004; Fig. 2). However, in March of 2005, water levels began dropping in the lower pool, and by June 2005, both pools were completely dry to bedrock, with dead aquatic invertebrates apparent in the sediment. Beginning in November 2005, the pools filled with water only following large precipitation

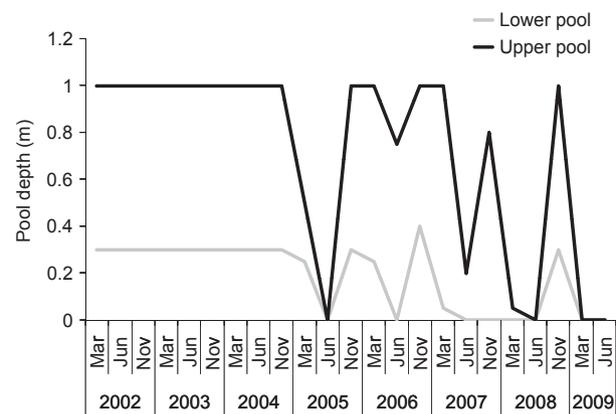


Fig. 2 Water depths of the two study pools in French Joe Canyon between 2002 and 2009. Both formerly perennial pools dried completely in June 2005 and remained dry for several months. From late 2005 to June 2009, pool levels fluctuated greatly in response to local precipitation events.

events, and held that water for varying lengths of time (5 months to 2 years; Fig. 2). From here forward, we refer to the stable, perennial conditions preceding the June 2005 drying as 'pre-drying' and the intermittent, unstable conditions beginning in June 2005 as 'post-drying'. Water temperature, pH, and conductivity were not significantly different pre- or post-drying (temperature:  $t = 0.62$ ,  $P = 0.6$ ; pH:  $t = 0.11$ ,  $P = 0.92$ ; conductivity:  $t = -1.32$ ,  $P = 0.2$ ).

We visited all springs mapped by US Geological Survey as perennial that were located within 6 km of French Joe Canyon (Simpson, Bear, Wild Cow, Death Trap, Dry Canyon, Dripping, Juniper, McGrew, Cottonwood, and Guindani Springs) at various dates between 2003 and 2007. All of these springs were either dry, or had small amounts of water that only supported taxa associated with intermittent or ephemeral habitats (e.g. Culicidae). Between 7 and 9 km distance, one spring was completely dry (Upper Wakefield Spring), and we were unable to survey an additional three springs because of private property or difficult terrain (Castanera, Bathtub, and Burro Springs). Nearly 10 km away in Wakefield Canyon, we located another group of three springs which still had flow and supported species which occur in perennial water [e.g. *A. herberti* and *Phylloicus mexicana* (Banks)]. Thus, the nearest known source of colonists from perennial water is nearly 10 km from French Joe Canyon over steep mountain terrain. All springs in canyons draining to the San Pedro River, like French Joe, were intermittent or dry, and so colonisation from the nearest perennial springs in the Cienega Creek basin would be limited to overland-dispersing species or aerially dispersing species (Fig. 1).

#### Biotic data

Fifty-four taxa were collected from the two pools across all years of community sampling. Mean taxon richness (no. taxa per pool in any given sampling event) was not significantly changed by the transition to intermittent flow (pre-drying mean: 19.8, post-drying mean: 18.8;  $t = 0.25$ ,  $P = 0.79$ ), though the seasonal dynamics of taxon richness did change (see Fig. 3). Prior to the initial drying event, there was a repeated pattern of higher richness in the low-flow season (June) and lower richness in the high-flow season (March). Post-drying, however, richness was

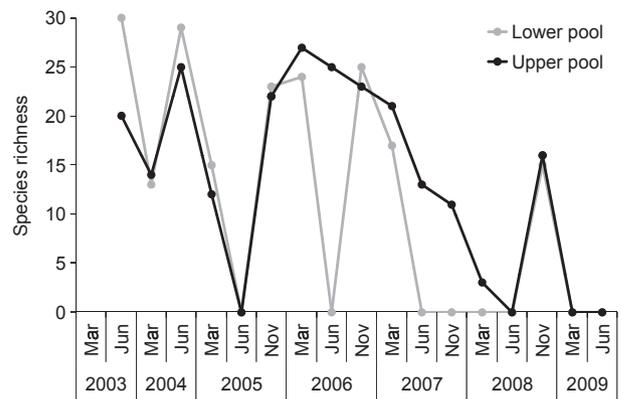
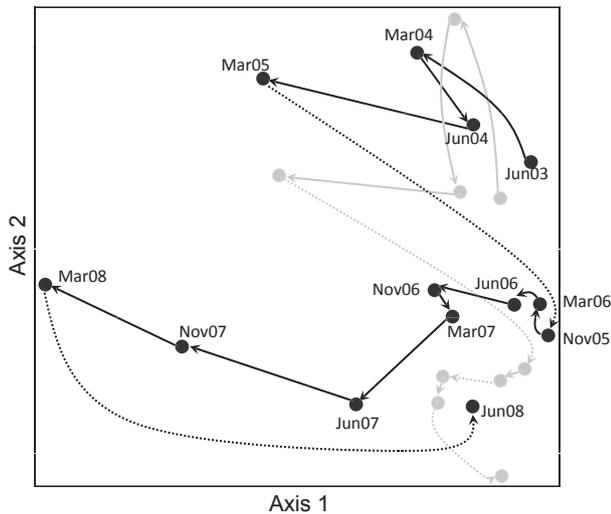


Fig. 3 Aquatic insect taxonomic richness (number of taxa sampled from each pool at each sampling event) for the two study pools at French Joe Canyon from 2003 to 2009. Richness values fell to zero only during periods of complete pool drying.

maximised upon rewatering of the dry pools and then declined as pool levels declined until the next rewatering event occurred. Aquatic insect densities (no.  $m^{-2}$  pool) were much higher in post-drying samples than in pre-drying samples (pre-drying mean: 131, post-drying mean: 1470;  $t = -2.215$ ,  $P = 0.02$ ).

Non-metric multidimensional scaling ordination with the square-root transformed species matrix converged on a stable, two-dimensional solution (stress = 12.2, final instability = 0.001,  $P = 0.004$ ; see Fig. 4). The two axes accounted for nearly 90% of the variation in community composition between sample units, and variation was split evenly between the two axes (axis 1:  $R^2 = 0.434$ ; axis 2:  $R^2 = 0.453$ ). Axis 1 was positively correlated with temperature ( $r = 0.58$ ) and pool area ( $r = 0.46$ ) and axis two was weakly negatively correlated with conductivity ( $r = -0.33$ ); all other correlations between axes and measured environmental variables were  $<0.3$ . A suite of large beetle and true bug species were positively associated with axis 1, while only mosquitoes (Culicidae) were strongly negatively associated with axis 1 (see Table 1). Thus, axis 1 describes a gradient in community composition from a rich suite of larger beetle and true bug species to a species-poor, mosquito-dominated community. A diverse group of dragonflies, beetles and true bugs were positively associated with axis 2, including many species that are longer lived and poor dispersers. An equally diverse group of mayflies, beetles and true bugs were negatively associated with axis 2, but included many highly vagile and short-lived species (Table 1).



**Fig. 4** Non-metric multidimensional scaling ordination plot of aquatic insect community changes in French Joe Canyon study pools between 2003 and 2009. Upper (black circles) and lower (grey circles) pool community trajectories are shown, though for clarity only the upper pool trajectory is labelled with sample dates (Mar, March, Jun, June, Nov, November; two-digit code indicates the year). Solid vectors indicate continuous surface water between sampling dates, while dotted vectors indicate a drying event between sampling dates. Following the March 2005 sampling period, the flow transitioned from perennial to intermittent.

Before the initial drying event in June 2005, both pools supported similar communities and exhibited some variation between low- and high-flow seasons (Fig. 4). In March 2005, however, the lower pool had already started to dry and both pool communities shifted along axis 1. When the pools were rewatered following the 3-month dry period, however, local communities shifted dramatically along both axes and occupied a new area of community space. As time progressed, communities did not recover and return to their original configuration. Instead, as the flow decreased and pool levels decreased over time, the communities shifted to the left along axis 1, moving further away from the pre-drying community type. The upper pool dried twice following the initial drying event, while the lower pool had three additional drying events. Each time rewatering occurred, communities converged to the new stable state (lower right corner of the ordination; Fig. 4) rather than returning to the original pre-drying state. As part of a separate study, we monitored aquatic macroinvertebrate communities at three perennial streams in nearby mountain ranges (Chiricahuas, Dragons,

**Table 1** Invertebrate taxa which had high Pearson's correlations ( $r > 0.5$ ) with either the non-metric multidimensional scaling (NMS) ordination axis 1 or 2

NMS axis	Taxon	$r$ -value	
Axis 1	<i>Notonecta lobata</i> Hungerford	0.69	
	<i>Stictotarsus aequinoctialis</i> (Clark)	0.69	
	<i>Berosus salvini</i> Sharp	0.69	
	<i>Rhantus atricolor</i> (Aubé)	0.56	
	<i>Aquarius remigis</i> (Say)	0.54	
	<i>Rhantus gutticollis</i> (Say)	0.53	
	<i>Laccophilus pictus</i> LaPorte	0.52	
	Culicidae	-0.85	
	Axis 2	<i>Libellula saturata</i> Uhler	0.66
		<i>Helichus triangularis</i> Musgrave	0.66
<i>Peltodytes dispersus</i> Roberts		0.63	
<i>Gyrinus plicifer</i> LeConte		0.60	
<i>Laccophilus horni</i> Branden		0.60	
<i>Abedus herberti</i> Hidalgo		0.58	
<i>Platyvelia beameri</i> (Hungerford)		0.55	
<i>Desmopachria mexicana</i> Sharp		0.54	
<i>Callibaetis</i>		-0.55	
<i>Rhantus gutticollis</i> (Say)		-0.56	
<i>Hydreana</i>		-0.59	
<i>L. pictus</i> La Porte		-0.60	
<i>R. atricolor</i> (Aubé)		-0.66	
<i>Microvelia</i> spp.		-0.70	
<i>Aquarius remigis</i> (Say)		-0.71	

and Galiuros) in March and June each year from 2004 to 2011. Community structure in these three streams varied seasonally, but predictably, as in French Joe before the initial drying event, and in these three streams, no transitions to novel community states were observed over the 8 years (M.T Bogan & D.A Lytle, in prep.).

Pre- and post-drying community samples from French Joe were completely segregated along axis 2 of the ordination (Fig. 4) and MRPP tests confirmed that pre- and post-drying communities were distinct ( $A = 0.12$ ,  $P < 0.00001$ ). Significant indicator species for pre-drying samples included large-bodied, long-lived species such as the predators *A. herberti* and *Libellula saturata* Uhler (Odonata: Libellulidae) and the shredder caddisfly *Phylloicus mexicanus* (Banks) (Trichoptera: Calamoceratidae), and mid-sized scavengers, shredders, and predators such as *Platyvelia beameri* (Hungerford) (Hemiptera: Veliidae), *Gyrinus plicifer* LeConte (Coleoptera: Gyrinidae), and *Peltodytes dispersus* Roberts (Coleoptera: Haliplidae). Indicator species for post-drying samples included a number of mesopredators (e.g. *Rhantus atricolor* (Aube), *Rhantus gutticollis* (Say), *Laccophilus pictus*

Laporte; Coleoptera: Dytiscidae) and smaller scavengers and predators (e.g. *Microvelia* spp. (Hemiptera: Veliidae) and *Liodessus obscurellus* (LeConte) (Coleoptera: Dytiscidae)). Table 2 lists all statistically significant indicator species for either pre- or post-drying samples.

As indicated from the results of the ordination and indicator species analyses, individual species varied greatly in their response to the drought-induced transition to intermittent flow. Six species were not found in post-drying samples and appear to have been extirpated from French Joe Canyon. Three of the extirpated species were formerly abundant in samples (*A. herberti*, *P. beameri*, and *P. mexicanus*), while the other three extirpated species were less common in samples prior to drying (*Berosus moerens* Sharp, *Laccophilus horni* Branden, *Neoclypeodytes cinctellus* (LeConte)). Other species appeared to succeed quite well under the new intermittent flow conditions. The mid-sized dytiscid predators *R. atricolor* and *R. gutticollis* were 11 times more abundant in post-drying samples compared with pre-drying samples and the small neustonic predator *Microvelia* was over 40 times more abundant post-drying.

## Discussion

Documenting catastrophic regime shifts in natural systems is difficult because it requires long-term studies of pre- and post-shift community dynamics

**Table 2** Significant indicator species analysis values ( $IV > 50$ ) for pre-drying (perennial conditions) and post-drying (intermittent conditions) samples at French Joe Canyon

Group	Species	IV	P
Pre-drying	<i>Helichus triangularis</i> Musgrave	88	0.000
	<i>Abedus herberti</i> Hidalgo	88	0.000
	<i>Platyvelia beameri</i> (Hungerford)	75	0.001
	<i>Libellula saturata</i> Uhler	74	0.001
	<i>Gyrinus plicifer</i> LeConte	67	0.001
	<i>Phylloicus mexicana</i> (Banks)	63	0.003
	<i>Peltodytes dispersus</i> Roberts	65	0.006
	<i>Desmopachria mexicana</i> Sharp	66	0.029
	Post-drying	<i>Microvelia</i> spp.	91
<i>Rhantus atricolor</i> (Aubé)		80	0.000
<i>Aquarius remigis</i> (Say)		76	0.001
<i>Laccophilus pictus</i> LaPorte		71	0.002
<i>Hydraena</i> spp.		69	0.007
<i>Liodessus obscurellus</i> (LeConte)		61	0.023
<i>Rhantus gutticollis</i> (Say)		61	0.050

to ensure that observed changes are not part of some natural, long-term cycle. In this 8-year study, we documented a catastrophic regime shift wherein local communities in desert stream pools shifted to an alternative state following complete water loss during a severe drought, and did not exhibit any sign of recovery more than 4 years after the initial drying event. Additionally, insect abundances were much higher in post-drying samples than in pre-drying samples, although some of this increase may be due to the replacement of large-bodied top predators with smaller-bodied mesopredators. While community and abundance responses were dramatic, owing to local extinctions of some species and greatly increased abundances of other species, changes in species richness were more equivocal. The alternative state and novel community trajectories observed at French Joe likely arose through a combination of post-drying habitat filters, habitat isolation, and altered species interactions, each of which we discuss below.

### Species richness and densities

Though mean species richness values were not significantly different pre- and post-drying, temporal patterns in species richness did change drastically after transition to intermittent flow at French Joe. Prior to the transition, richness oscillated seasonally with higher richness during the June low-flow season than during the March high-flow season. Following rewetting of the pools, however, richness values soon peaked and then declined as water levels dropped over time. This finding is consistent with other studies of drying in lotic systems, where species richness often peaks as drying begins and organisms are concentrated into small areas of habitat, and then declines as water quality conditions worsen during further habitat contraction (Boulton & Lake, 1992b; Acuña *et al.*, 2005).

Mean densities at French Joe Canyon were nearly nine times higher in post-drying samples than in pre-drying samples. As with species richness, some studies have found that abundances increase during drying events, but then plummet as physicochemical conditions worsen (Boulton & Lake, 1992b; Acuña *et al.*, 2005). In contrast, other studies have found either no consistent pattern in abundance during drying events (Stanley *et al.*, 1994) or only site-specific effects of drought on invertebrate abundance (Bêche

*et al.*, 2009). The dramatic magnitude of the post-drying increase in insect abundances at French Joe was partly because of high abundances of small-bodied mosquito larvae during three sampling events when pools had contracted to <10% of capacity. However, even excluding these three sampling events, densities were nearly three times as high in post-drying samples, indicating that the increased density was driven by real community changes and not just one influential species. At least some of these large post-drying abundances can be attributed to large-bodied predators being extirpated and replaced by smaller-bodied mesopredators.

#### *Community composition*

Similar to species richness, community composition at French Joe showed a fairly predictable seasonal oscillation between high- and low-flow (March and June, respectively) community types in the 3 years prior to the initial drying event. This pattern is consistent with what we have documented in stream communities across the region (Bogan & Lytle, 2007). After the initial drying event, however, the community composition shifted dramatically, with the loss of several long-lived, poor-dispersing beetle, true bug and caddisfly species and increased abundances of more vagile and shorter-lived beetle, true bug and mayfly species. Additionally, community composition did not recover in the 4 years following the initial drying event. Instead, new community trajectories were established, with a predictable community arising during rewatering events, and then slowly degrading through time until the next drying and rewetting sequence 'reset' the community to its new alternative stable state. In a separate study, over much of the same time period (2004–2011), macroinvertebrate communities in three streams from nearby mountain ranges exhibited the same seasonal community dynamics as French Joe before the initial drying event. These three streams, however, only contracted seasonally and never dried completely and their macroinvertebrate communities always recovered to pre-contraction states and never occupied novel community space (M. T. Bogan & D. A. Lytle, unpubl. data).

Most studies of severe drought and drying disturbance in lotic ecosystems indicate that communities recover fairly quickly (months to 2 years; reviewed in

Boulton, 2003; Lake, 2003). Often, communities will change dramatically as drying progresses during a drought but will return to pre-drought composition after water returns (Boulton & Lake, 1992b). In contrast, pool communities at French Joe Canyon changed dramatically following the initial drying event and did not recover in the four ensuing years. The length and/or predictability of the drought and subsequent stream drying events may explain these differing community impacts.

Supra-seasonal droughts are unpredictable and often last longer than seasonal droughts. Accordingly, they may also have more lasting effects on local lotic communities (Lake, 2003). Bêche *et al.* (2009) found that invertebrate communities did not return to pre-drought configurations within 6 years of the end of a severe supra-seasonal drought, though the establishment of an exotic fish species during the drought may have confounded those results. Though Resh (1992) focused on the population structure of a single caddisfly species, not community structure, he found that it took 10 years for caddisfly age structure to recovery following an unprecedented drying disturbance in a northern California spring. The 3-month drying of the formerly perennial springbrook reported in that study is very similar to what communities at French Joe Canyon experienced.

Physical habitat characteristics (e.g. extensive travertine deposits), anecdotal reports (Martin & Martin, 1991), and genetic evidence from one of the extirpated species (*A. herberti*: Finn *et al.*, 2007, 2009) all indicate the French Joe Canyon had perennial water in at least recent decades. Thus, the 3-month complete drying of French Joe in 2005 probably represents an unprecedented disturbance. Additionally, although the pools were refilled following intense rains in November 2005, perennial flow did not return to French Joe as it did in the spring described by Resh (1992). Instead, both pools became intermittent, drying multiple times between 2006 and 2009. Thus, French Joe experienced both an unprecedented supra-seasonal drought and an altered drying disturbance regime, both of which are likely factors in the lack of community recovery to a pre-drying state.

Part of the dramatic shift in community composition observed at French Joe is the result of the extirpation of three species indicative of pre-drying samples. We propose that the harsh disturbance of the initial drying event extirpated these species, and that

French Joe's isolation from other perennial habitats, combined with post-disturbance abiotic filtering (in this case, an altered hydrological regime), prevented these species from recolonizing. Two of the extirpated indicator species were the top predator *A. herberti* and the neustonic predator *P. beameri*. The population of *P. beameri* at French Joe was apterous and *A. herberti* is a flightless species, and thus, both species allocate energy to increased egg production and mating success at the expense of flight musculature for dispersal (cf. Zera & Denno, 1997). As such, these two species were inherently at higher risk for local extinction (Roff, 1994) and they could only persist in either perennial habitats or in intermittent reaches near a source of colonists. Post-drying, French Joe was no longer perennial and the nearest potential source of colonists was nearly 10 km to the northwest. While *A. herberti* may crawl overland for short distances in order to escape flash flooding (Lytle, 1999), it is unlikely that they could travel 10 km overland to French Joe. Indeed, genetic evidence suggests that although overland dispersal probably does occur, it is apparently not frequent (Finn *et al.*, 2007). Dispersal and propagule supply are known to be limiting in fragmented landscapes (Hanski, 1998), and desert springs and streams are among the most fragmented, isolated habitats in the world (Shepard, 1993).

Strong environmental adversity acting in concert with propagule limitation can have extreme consequences on local community assembly (Didham & Watts, 2005). The third formerly abundant species extirpated from French Joe, the large-bodied shredder caddisfly *P. mexicanus*, is capable of overland flight and theoretically could travel several kilometres to recolonise French Joe. However, *P. mexicanus* requires a year to pass through the larval stage, and so French Joe's transition to intermittent flow might prevent colonists from reaching adulthood, thus filtering the species from the local habitat. We observed this process with the dragonfly *L. saturata*. Pre-drying, *L. saturata* nymphs were among the largest predators in French Joe pools. Adult *L. saturata* can travel great distances overland (Manolis, 2003) and they soon repopulated French Joe following the initial drying and re-wetting event. The developing nymphs, though, never had time to grow into larger individuals and mature before subsequent drying events occurred. Thus, even species that have the ability to overcome French Joe's isolation may be prevented

from establishing reproducing populations by the new, intermittent hydrological regime. Nearly all of the species indicative of, or associated with, post-drying communities at French Joe are highly vagile (e.g. many Dytiscidae) or have short development times (e.g. *Callibaetis*, Baetidae). These traits could allow these species to persist through unpredictable variations in the presence or amount of water.

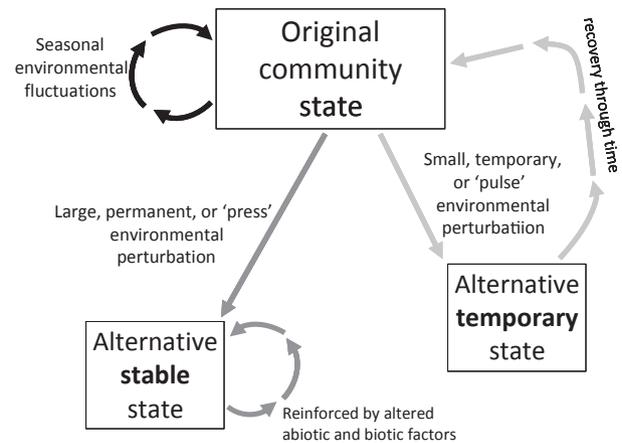
The harsh environmental filters that extirpated and prevented re-establishment of several species at French Joe may have provided great opportunities for other species. The dytiscid beetles *R. atricolor* and *R. gutticollis* were 11 times more abundant in samples after the initial drying event. These dytiscids are the system's next largest predators, after *A. herberti* and *L. saturata*, and likely experienced a competitive release following the extirpation of their larger, and less vagile, competitors. Following the extirpation of the flightless top neustonic predator *P. beameri*, the smaller, winged neustonic predator *Microvelia* (Veliidae) was 40 times more abundant. Other members of our laboratory are currently conducting mesocosm experiments of top predator removal to determine direct causal links between local extinctions and cascading effects on smaller predators and other species.

Although we have focused our discussion thus far on regime shifts and alternative states driven by drought and drying disturbance in lotic macroinvertebrate communities, similar processes and patterns have been observed for a wide variety of ecosystems. Hydrological disturbance, including cycles of flooding and drought, can drive alternative stable states in river floodplain and wetland ecosystems as well. Zweig & Kitchens (2009) identified flooding and drought as the primary mechanisms for multi-state transitions in plant communities of the Florida Everglades. Additionally, as their study occurred during a relatively wet period in Florida, Zweig & Kitchens (2009) highlighted the need for more studies on the impacts of severe drought on local ecosystems. Schooler *et al.* (2011) documented how hydrological disturbance removed certain species in Australian floodplain habitats, leading to cascading effects on other trophic levels and the rise of alternative community states. In the absence of floods, biocontrol weevils proliferated and controlled an exotic aquatic weed, but flooding removed the weevils and allowed the weed to take over, producing two alternative

states (Schooler *et al.*, 2011). Similar mechanisms may be operating at French Joe, where certain predators were eliminated by the drought (e.g. *A. herberti*) which allowed competitive release of other species and had cascading effects on lower trophic levels, thus contributing to the transition to an alternative state.

Combinations of disturbance, dispersal dynamics, and species interactions have also contributed to regime shifts and alternative stable states in marine and terrestrial ecosystems. Through experiments and observational studies, Petraitis *et al.* (2009) showed that marine intertidal patches opened via ice scour and artificial disturbance will become one of two alternative states: mussel beds or rockweed patches. Whether disturbed patches transitioned to an alternative state was dependent on the size of the disturbance, the distance to nearby colonists, and the species traits of the new colonists, some of which may create positive feedback loops favouring those early colonists (Petraitis *et al.*, 2009). In boreal forests, Collier & Mallik (2010) documented that abiotic habitat filtering following fire disturbance (e.g. variable levels of organic matter thickness) favoured certain colonist plant species over others. Some of these initial colonists then influenced the ability of other species to colonise, via competition and allelopathy, and drove further divergence of plant communities in fire-disturbed patches (Collier & Mallik, 2010). We propose that a similar combination of disturbance, post-disturbance abiotic habitat filtering, dispersal dynamics, and colonist species traits and interactions drove French Joe macroinvertebrate communities into a novel alternative state.

While we observed a catastrophic regime shift at French Joe Canyon during our study, not all drought-induced drying disturbances will necessarily result in an alternative stable state. In Fig. 5, we present a conceptual model of pathways that communities may take in response to minor and major disturbances. At French Joe, severe drought resulting in an unprecedented drying event caused a large-scale change in local community composition. Had perennial conditions been re-established, though, local communities may have eventually recovered to pre-drying conditions, if sufficient colonist sources were available (light grey vectors in Fig. 5). Instead, French Joe experienced repeated drying events following the initial event which restricted recovery and resulted in



**Fig. 5** Conceptual model of community changes through time, given environmental fluctuations and major or minor disturbance events. Most ecosystems exhibit some seasonal environmental fluctuations, but communities generally change in a predictable manner (black vectors). Small, temporary or 'pulse' environmental perturbations (i.e. minor disturbance events) may result in community regime shifts, but with time the system will recover to pre-perturbation conditions (light grey vectors). With large, permanent, or 'press' environmental perturbations, however, altered abiotic factors may effectively preclude the return of influential species, altering species interactions and resulting in a novel community regime (dark grey vectors).

an alternative stable state (dark grey vectors in Fig. 5). Following the extirpation of influential species, other species would experience competitive release and new niches could become available for novel species to colonise the site. Priority effects may then lead to these novel and/or newly dominant species precluding other species from establishing and, in concert with the altered disturbance regime, could prevent community recovery to its original state. As the new community would be composed of more tolerant and vagile species, it could be more resilient to future disturbances than the original community was (Côté & Darling, 2010), further reinforcing the alternative state.

#### Regional implications

Streams and springs in deserts are highly diverse, poorly studied, and often critically endangered habitats (Shepard, 1993). While our study focuses on a single system, the results have implications for many arid regions and may serve as a window into the future of desert aquatic habitats. In western North America, desert springs and streams are threatened

by increased pumping of aquifers for urban water use in fast-growing cities (Stromberg, Tiller & Richter, 1996; Deacon *et al.*, 2007; Patten, Rouse & Stromberg, 2008). Additionally, climate-change models for the region predict longer, more frequent, and more intense droughts in the coming century (Seager *et al.*, 2007), surpassing the drought intensities of the past 30 years (Balling & Goodrich, 2010).

We cannot be certain whether the transition to intermittent flow at French Joe Canyon was caused by drought, high rates of water withdrawal in the nearby San Pedro River aquifer, or a combination of both factors. However, as more springs and streams transition to intermittent flow across the region, remaining perennial habitats will become increasingly isolated. This isolation in turn can cause local extirpations, as stochastic events remove local populations and increased isolation precludes the ability of species to recolonise those habitats. Eventually, sensitive species such as the top predator *A. herberti* could be regionally extirpated, resulting in a simplified and depauperate regional species pool. Ironically, these new local communities may then be more resilient to climatic and anthropogenic disturbances than the original communities, as all sensitive species will have been extirpated leaving only the most tolerant and resilient species (Côté & Darling, 2010).

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