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Freshwater Biology 2011

Bogan, Michael T.
Department of Zoology, Oregon State University

Lytle, David A.
Department of Zoology, Oregon State University

Citation for official published version: Bogan, Michael T., and David A. Lytle. "Severe Drought Drives Novel Community Trajectories in Desert Stream Pools." *Freshwater Biology* 56.10 Oct. (2011): 2070-81. Web. 12 Oct. 2011. <DOI: 10.1111/j.1365-2427.2011.02638.x>.

Severe drought drives novel community trajectories in desert stream pools

Michael T. Bogan and David A. Lytle

Department of Zoology, 3029 Cordley Hall, Oregon State University, Corvallis, OR 97331

Phone: (541)-737-5536 Fax: (541) 737-0501

Corresponding author (MTB) email: boganmi@science.oregonstate.edu

Running title: Drought causes community regime shifts

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

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 loss of perennial flow due to intensified droughts and water withdrawals could lead to significant changes in community structure and species composition at local and regional scales.

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 et al., 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 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 recognized 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 et al. (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 et al., 2005).

Results from studies of lotic systems, however, are more equivocal (Dewson et al., 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: Boutlon & 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 neighboring 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 behavioral 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 yrs) 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: (1) the short-term effects of the unprecedented drying disturbance on local diversity and community composition, (2) community recovery trajectories following rewetting, and (3) the longer-term impacts of the transition to intermittent flow on local community composition. We hypothesized that the unprecedented drying disturbance would alter community composition and negatively impact diversity in the short term (<1 yr), but that communities would shift back to pre-drying conditions over longer time periods (>1 yr).

Methods

Site and climate description

French Joe Canyon is an arid-land drainage in the Whetstone Mountains of southeastern Arizona, USA. Mean annual precipitation in the region is about 35cm, but is highly variable from year to year, and strongly bimodal, with roughly half the precipitation occurring during brief, violent summer monsoon (Jul-Sep) storms and half during more prolonged, moderate intensity winter storms (Nov-Apr). 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 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 5 pools had dried, and in early 2004 only 2 perennial pools remained. These 2 remaining pools (hereafter "upper" and "lower" pools) were in the main canyon channel and were separated by approximately 100m of dry streambed. When full, the upper pool was 1m deep, with a surface area of 1.5m^2, while the lower pool was 0.3m deep, with a surface area of 2.5m^2. Outflow was negligible (< 1L min^{-1}) 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 prehistoric past. First, heavy travertine deposition throughout the reach surrounding the pools (>300m 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 harbored 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 timescales (hundreds to thousands of years) (Finn et al., 2007; Finn et al., 2009).

Though drought is a recurring phenomenon in the arid southwestern 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). Though substantial rains fell in winter 2005 and summer 2006, drought conditions returned during the last three 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, USA) and also made visual estimations of benthic substrate cover (categories: silt, sand, gravel, cobble, 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 substrates and on the surface of the water for 10 s m^{-2} of pool. This pool sampling effort was determined based on preliminary sampling of pools at 3 other local streams; an effort of 10 s m^{-2} of pool captured over 95% of the species that were detected with twice the effort (20 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 1:100000 scale map (USGS Map # 31110-E1; Fort Huachuca) and visited as many of these springs as possible to confirm their hydrologic status.

Data analyses

Univariate differences in pre- and post-drying aquatic insect density, taxon richness, water temperature, pH, and conductivity were analyzed using two-sample t-tests assuming unequal variances in Excel 2007 (Microsoft Corp., Redmond, WA, USA). Multivariate community trajectories through time were quantified using non-metric multidimensional scaling (NMS) in PC-ORD (McCune and 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: (1) pre- and (2) post-drying. We used Multi-Response Permutation Procedure (MRPP) with Sorensen distances to quantify and test within-group agreement and distinctness (Mielke and 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 and Mefford, 1999). We also used Indicator Species Analysis (ISA) to determine if particular taxa were indicative 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 and 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 three 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 events, and held that water for varying lengths of time (5 months to two 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 USGS 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 distant, one spring was completely dry (Upper Wakefield Spring), and we were unable to survey an additional 3 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. *Abedus 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 colonization from the nearest perennial springs in the Cienega Creek basin would be limited to overland- 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 Figure 3). Prior to the initial drying event there was a repeated pattern of higher richness in the low-flow season (Jun) and lower richness in the high-flow season (Mar). Post-drying, however, richness was maximized 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).

NMS ordination with the square-root transformed species matrix converged on a stable, 2-dimensional solution (stress = 12.2, final instability = 0.001, P = 0.004; see Figure 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 less than 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).

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 3 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 (Chiricahucas, Dragoons, 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 (Bogan & Lytle, in prep.).

Pre- and post-drying community samples from French Joe were completely segregated along axis 2 of the ordination (Figure 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 *Abedus 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), *R. 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 (*Abedus herberti*, *Platyvelia beameri*, and *Phylloicus 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 *Rhantus atricolor* and *R. gutticollis* were 11 times more abundant in post-drying samples compared to 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 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 & 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 (Fig. 3). Following re-wetting 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 sample densities at French Joe Canyon were nearly 9 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 due to high abundances of small-bodied mosquito larvae during 3 sampling events when pools had contracted to less than 10% of capacity. However, even excluding these 3 sampling events, densities were nearly 3 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 three years prior to the initial drying event (Fig. 4). 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 (Fig. 4; Tables 1 & 2). Additionally, community composition did not recover in the four 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 (Fig. 4). In a separate study over much of the same time period (2004-2001), 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 (Bogan & Lytle, in prep.).

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 4 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 predictable 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 three 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; Finn et al., 2009) all indicate the French Joe Canyon had perennial water in at least recent decades. Thus, the three-month complete drying of French Joe in 2005 likely represents an unprecedented disturbance. Additionally, though 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 (Fig. 2). 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 extirpated these species, and that French Joe's isolation from other perennial habitats, combined with post-disturbance abiotic filtering (in this case, an altered hydrologic regime), prevented these species from recolonizing. Two of the extirpated indicator species were the top predator *Abedus herberti* and the nuestonic predator *Platyvelia 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 streams (Lytle, 1999), it is unlikely that they could travel 10km 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 kilometers to recolonize 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 *Libellula 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 hydrologic regime. Nearly all of the species indicative of, or associated with, post-drying communities at French Joe (Tables 1 & 2) 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 reestablishment of several species at French Joe may have provided great opportunities for other species. The dytiscid beetles *Rhantus 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 in French Joe samples. Other members of our lab 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.

Though we have focused our discussion thus far on regime shifts and alternative states driven by drought and drying disturbance in lotic macroinvertebrtate 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 of 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 casacading 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 favoring 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) favored certain colonist plant species over others. Some of these initial colonists then influenced the ability of other species to colonize, 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 reestablished, 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 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 colonize 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 et al., 1996; Deacon et al., 2007; Patten et al., 2008). Additionally, climate change models for the region predict longer, more frequent, and more intense droughts in the coming century (Segear et al., 2007), surpassing the drought intensities of the past 30 years (Balling & Goodrich, 2010).

We cannot be certain if the transition to intermittent flow at French Joe Canyon was due to 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 recolonize 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).

Acknowledgements

This study was conducted under USDA Forest Service Special Use Permit #SUP0092. Kate Boersma, Laura McMullen, Colin Townsend and two anonymous reviewers provided useful criticism of earlier drafts of this manuscript. Special thanks to Claire Zugmeyer for essential logistical support during field sampling and for assistance with Figure 1. This project was supported in part by Oregon State University and National Science Foundation grant DEB-0445366 to D.A.L.

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TABLES

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

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

FIGURE LEGENDS

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 neighboring mountain ranges, 15-20km 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.

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.

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.

Fig. 4 NMS ordination plot of aquatic insect community changes in French Joe Canyon study pools between 2003 and 2009. Upper (black circles) and lower (gray circles) pool community trajectories are shown, though for clarity only the upper pool trajectory is labeled 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.

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).

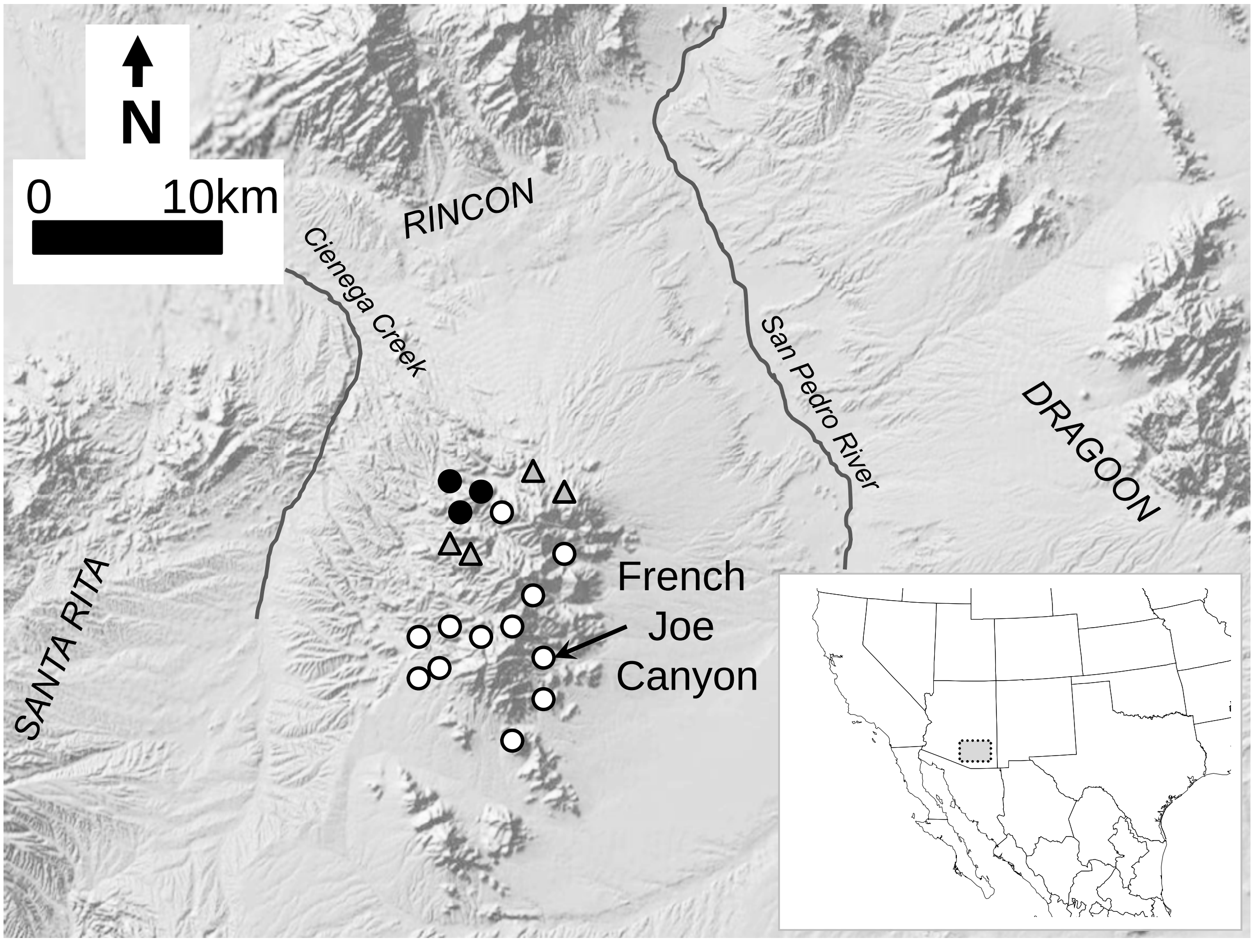

N
0
10km
RINCON
Cienega Creek
San Pedro River
DRAGOON
SANTA RITA
French
Joe
Canyon

Fig. 1

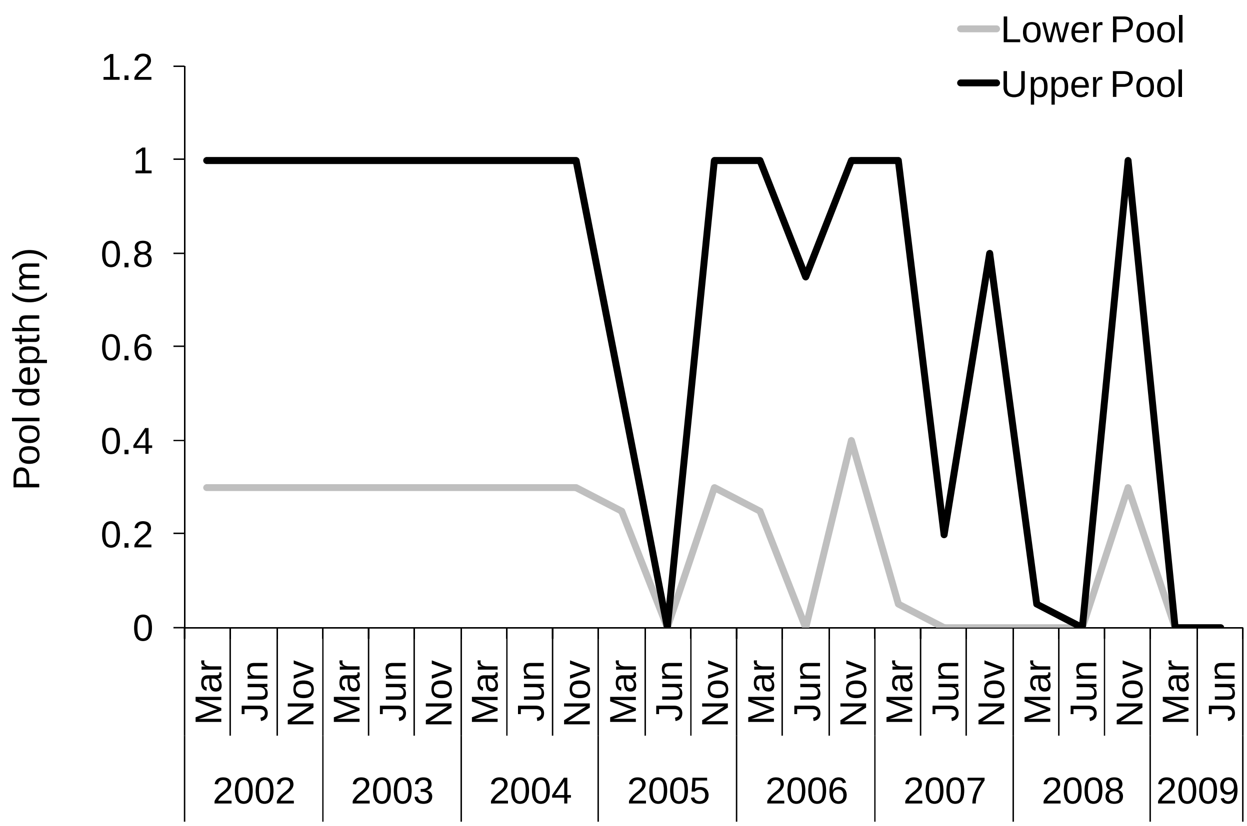

Lower Pool
Upper Pool
Pool depth (m)
1.2
1
0.8
0.6
0.4
0.2
0
Mar
Jun
Nov
Mar
Jun
Nov
Mar
Jun
Nov
Mar
Jun
Nov
Mar
Jun
Nov
Mar
Jun
Nov
Mar
Jun
Nov
Mar
Jun
2002
2003
2004
2005
2006
2007
2008
2009

Fig. 2

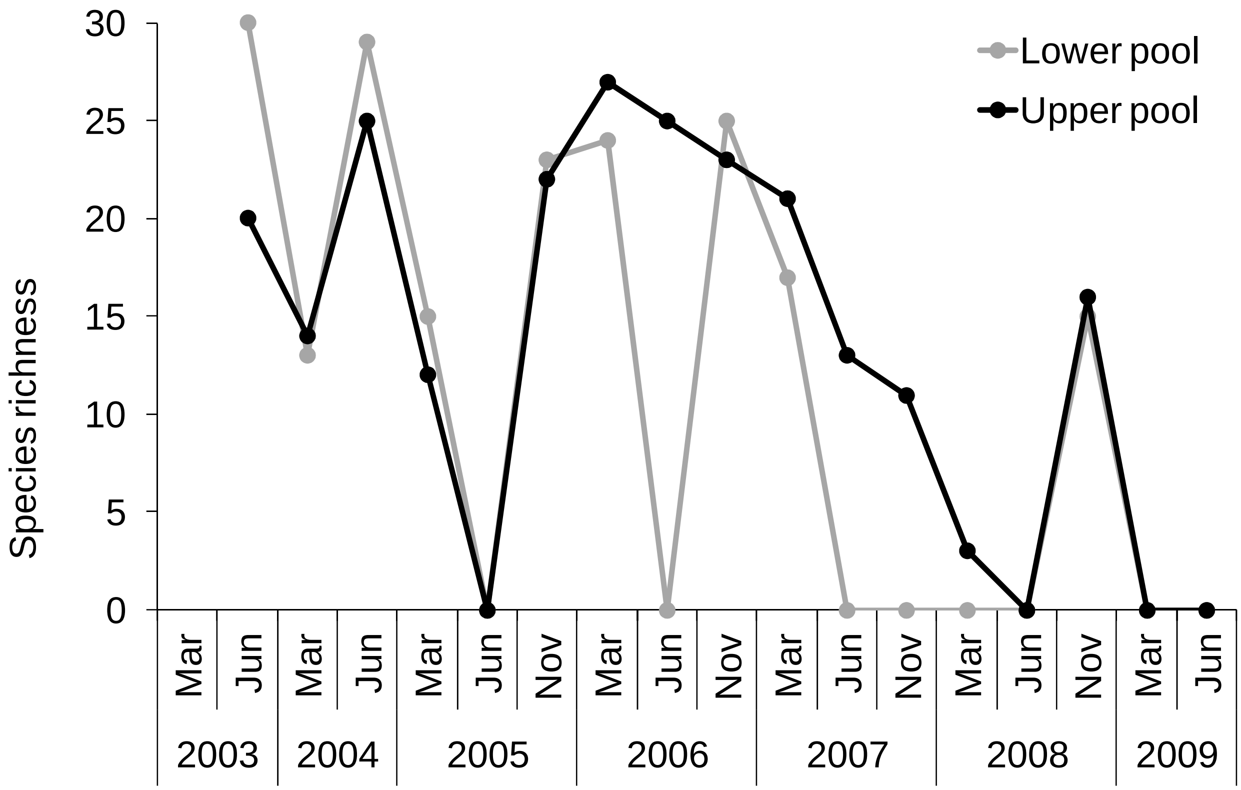
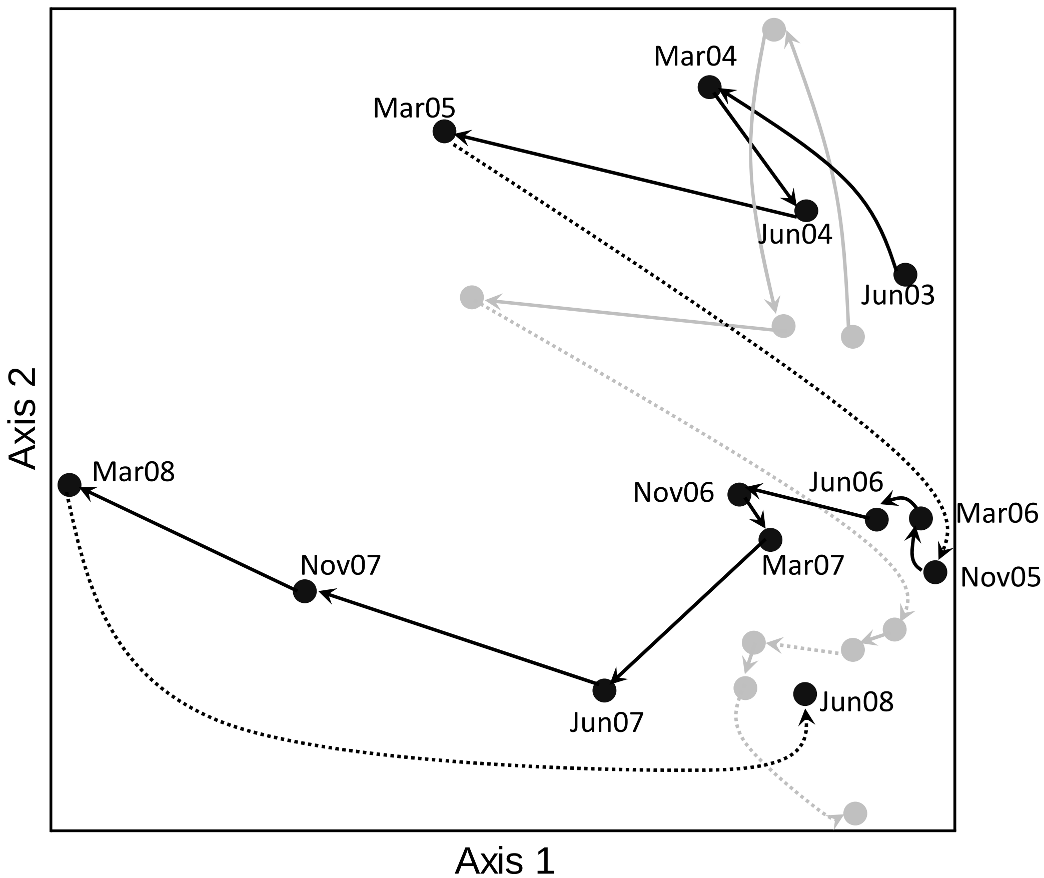

30
25
20
15
10
5
0
Species richness
Lower pool
Upper pool
Mar
Jun
Mar
Jun
Mar
Jun
Nov
Mar
Jun
Nov
Mar
Jun
Nov
Mar
Jun
Nov
Mar
Jun
2003
2004
2005
2006
2007
2008
2009

Fig. 3



Mar04
Mar05
Jun04
Jun03
Axis 2
Mar08
Nov06
Jun06
Mar06
Nov07
Mar07
Nov05
Jun08
Jun07
Axis 1

Fig. 4

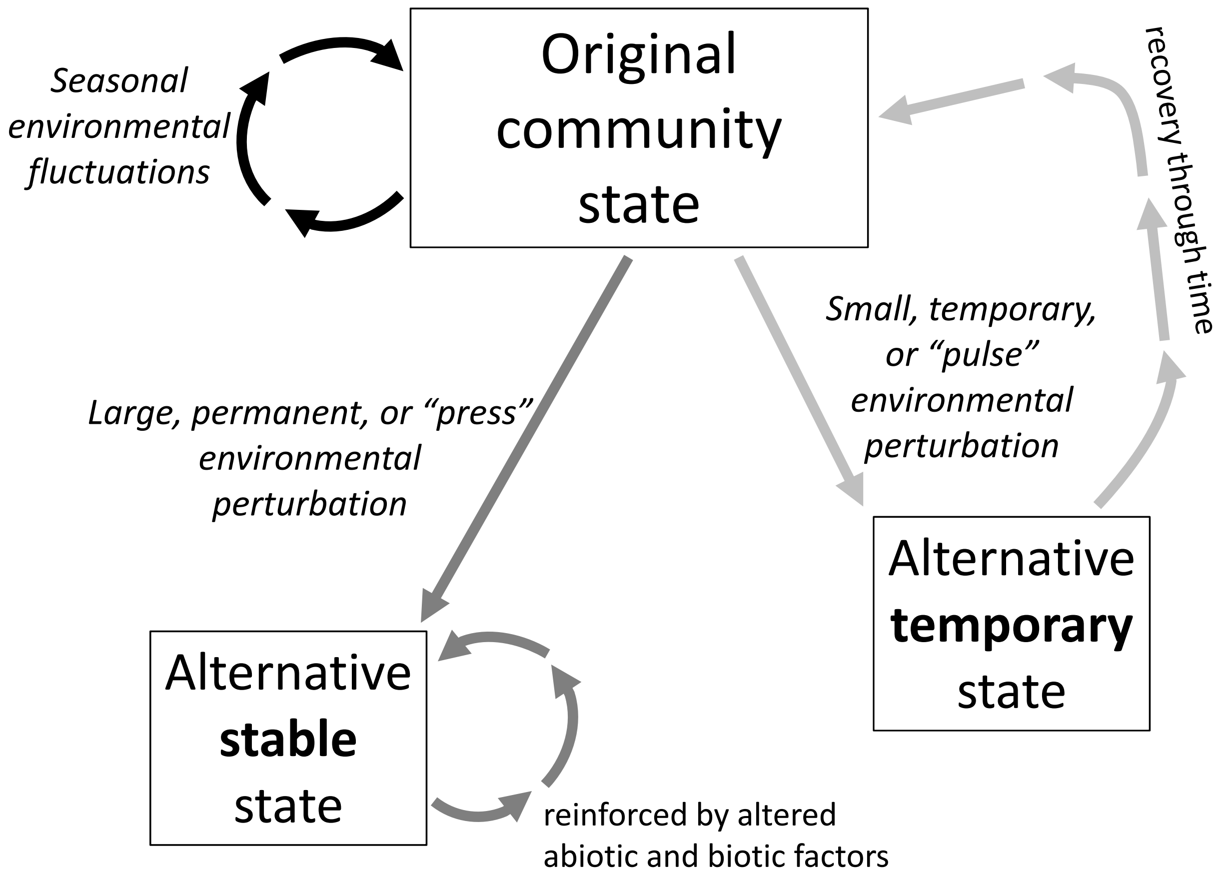

Original community state
Seasonal environmental fluctuations
Large, permanent, or "press" environmental perturbation
Small, temporary, or "pulse" environmental perturbation
recovery through time
Alternative **temporary** state
Alternative **stable** state
reinforced by altered abiotic and biotic factors

Fig. 5