AN ABSTRACT OF THE DISSERTATION OF

Michael T. Bogan for the degree of Doctor of Philosophy in Zoology presented on July 10, 2012.

Title: Drought, Dispersal, and Community Dynamics in Arid-land Streams

Abstract approved: ______________________________________

David A. Lytle

Understanding the mechanisms that regulate local species diversity and community structure is a perennial goal of ecology. Local community structure can be viewed as the result of numerous local and regional processes; these processes act as filters that reduce the regional species pool down to the observed local community. In stream ecosystems, the natural flow regime (including the timing, magnitude, and duration of high and low flow events) is widely recognized as a primary regulator of local diversity and community composition. This is especially true in arid-land streams, where low- and zero-flow events can occur frequently and for extended periods of time (months to years). Additionally, wetted habitat patches in arid-land stream networks are often fragmented within and among stream networks. Thus dispersal between isolated aquatic patches may also play a large role in regulating local communities. In my dissertation, I explored the roles that drought, dispersal, and local habitat factors play in structuring arid-land stream communities. I examined the impact of flow permanence and seasonal variation in flow and other abiotic factors on aquatic communities at both fine spatial scales over a long time period (8 years; Chapter 2) and at a broad spatial scale over a shorter time period (1-2 years; Chapter 4). Additionally, I quantified aquatic invertebrate aerial dispersal over moderate spatial scales ($\leq$ 0.5

km) by conducting a colonization experiment using artificial stream pools placed along and inland from two arid-land streams (Chapter 4). Finally, I examined the roles of spatial isolation, microhabitat type, and local abiotic and biotic factors in structuring aquatic communities in freshwater oases scattered across one of the most arid regions of North America, the southern Sonoran Desert (Chapter 5). In Chapter 2, I found that severe drought caused an unprecedented drying event in isolated perennial stream pools, and that several additional drying events occurred over the following four years. This transition to intermittent flow caused the extirpation of several large, long-lived species with low dispersal abilities (including the top predator) and drove the local community into an alternative state. In the colonization experiment described in Chapter 3, I found that several arid-land stream invertebrate taxa disperse widely and frequently. The widespread dispersers identified by this experiment included several of the earliest colonist taxa observed following the severe drought described in Chapter 2. Other taxa, though, only dispersed overland after receiving an environmental cue (rainfall) or preferentially dispersed along stream corridors. In Chapter 4, where I examined invertebrate community structure across a large network of well-connected intermittent and perennial reaches, I found low diversity in intermittent reaches, regardless of their connectivity to diverse upstream perennial reaches. These species-poor, intermittent communities were composed of a unique suite of species with life-history adaptations that conferred desiccation resistance, including extended egg and larval diapause stages. The short flow duration of intermittent reaches (<100 days) likely precluded upstream perennial taxa from establishing populations in downstream intermittent reaches before drying occurred, while the relative predictability of flow timing (Dec-Apr) likely allowed for a small number of species to develop appropriate life-history traits (e.g., diapause stage, rapid development time) to exploit these temporally-fleeting habitats. In Chapter 5, I found over 220 species of aquatic animals (including $\geq$ 5 undescribed species) in the 19 desert oases that were

sampled across the southern Sonoran Desert. Local community composition in these oases was strongly driven by microhabitat type. Additionally, native aquatic species richness and abundance in these oases were significantly reduced by the introduction of tilapia, an exotic fish species. The threats to arid-land streams presented by increased drought severity, anthropogenic water withdrawals, and local habitat degradation (e.g., introduced species, unmanaged recreational use) are grave across the southwestern US and northwestern Mexico. I hope that in addition to furthering our understanding of ecological processes in arid-land streams, this dissertation makes a small contribution towards the efforts to preserve these habitats.

Drought, Dispersal, and Community Dynamics in Arid-land Streams

by
Michael T. Bogan

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented July 10, 2012
Commencement June 2013

Doctor of Philosophy dissertation of Michael T. Bogan presented on July 10, 2012.

APPROVED:

____

Major Professor, representing Zoology

____

Chair of the Department of Zoology

____

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

____

Michael T. Bogan, Author

ACKNOWLEDGEMENTS

Thanks to my advisor, Dave Lytle, for his enthusiasm, encouragement, and support for my dissertation research over the last 5 years. Dave also gave me an enormous amount of freedom in the last couple years of my dissertation, which made it possible for me live and conduct my research in Arizona. From jumping off cliffs into the Colorado River and roasting chiles over mesquite coals on our first field outing in 2003, to stressfully bumbling through the Spanish language on our first Sonora trip, to scrambling down limestone canyons on White Sands Missile Range on our most recent field outing, we've had a great time and done some great work. I look forward to all of our future collaborations, field outings, and adventures.

My time at Oregon State has been made enjoyable by having a great series of lab mates over my dissertation, including Asako Yamamuro, Deb Finn, Emily Hartfield, Ivan Phillipsen, Kate Boersma, and Laura McMullen. Deb has been a great postdoc and collaborator in our lab off and on since 2006, and I thank her for the opportunity to collaborate on conservation genetics projects. Laura has been my great western Arizona companion because of her field work on the Bill Williams River, near my house. Thanks to her for all the fun we've had sampling, kayaking, camping, nerding out, and eating barbeque in western Arizona. Kate has been my phenomenal office mate and partner-in-crime both in the field and at conferences. Thanks for all the time you've put into our collaborations, and the fun, laughs, birding adventures and carne asada taco dinners we've had at my house, in the field, in Mexico, and in exotic faraway cities like La Paz, Louisville, and Providence. Thanks also to Richard Van Driesche for being a great recent addition to our lab and being endlessly enthusiastic about taxonomy.

Emeritus professor Norm Anderson has been an amazing resource, fellow intermittent stream and natural history enthusiast, office neighbor, and friend over my graduate career. My split Arizona-Oregon life would not have been possible without the great help provided by the

Zoology office staff, especially Torri Givigliano, Tara Bevandich, and Traci Durrell-Khalife. Thanks so much to them for five years of scanning and faxing forms to me in Arizona that I should have filled out in person in Oregon. Thanks also to a great and supportive dissertation committee, including Bruce Menge, Doug Robinson, Gordon Grant, Judith Li, Joe Beatty, and Stan Gregory. My only regret at working remotely on my dissertation is that I didn’t get to work more closely with most of you. Stan, though, has been a great conference and Mexico travel companion (along with the always wonderful Kathryn Boyer) and has both introduced me to many great researchers at conferences and kindly given me feedback on key dissertation chapters.

Thanks to a great group of Zoology graduate students for keeping me sane during my extended stays in Corvallis, far away from my dry desert home. Among all the great friends, I’d especially like to thank Catherine Searle, Chris Friesen, Kaitlin Bonner, Margot Hessing-Lewis, Mark Christie, Paul Bradley, Rocky Parker, and Sarah Eddy. Anna Jolles, Brian Parks, Brock and Karen McLeod, Dave Paoletti, Kathyrn Boyer, Maria Kavanaugh, Rebecka Weinsteiger, and Tiffany Garcia have all been outstanding Corvallis friends. Special thanks to Alison Iles and James Feldmann for being phenomenal friends and sharing their home with me over at multiple times over the last few years.

Thanks to Dr. Dave Herbst of UC Santa Barbara’s Sierra Nevada Aquatic Research Lab for providing me with part-time remote work (and great summer field adventures) which helped to smooth my financial transition back to graduate school. Several of my old friends from the Eastern Sierra helped me out on several sampling adventures in Sonora, Chihuahua, and Sinaloa, Mexico, especially Lacey Greene and Rick Zeigler. Thanks also to the tireless and dedicated Phil Pister of the Desert Fishes Council, for providing endless encouragement and, at times, a welcome dose of reality and perspective on why I do what I do. Also, thanks to Claire Zugmeyer and Eric Wallace of Tucson, AZ: Claire provided essential logistical support (i.e., friendship and a floor to sleep on) during both of my graduate degrees and Eric accompanied me on numerous field outings hunting for intermittent stream stoneflies and is a fellow devotee of natural history.

My dissertation research has been greatly enriched by an ongoing collaboration with biologists in Sonora, Mexico including Nohemí Noriega-Felix, Sylvette Leonor Vidal-Aguilar, Lloyd T. Findley, Oscar G. Gutiérrez-Ruacho, J. Andrés Alvarado-Castro, and Alejandro Varela-Romero. Sylvette and Nohemí were incredible undergraduate field and lab companions, and we had lots of laughs over my gaffs with Spanish and theirs with English. Andrés, Oscar, and Lloyd all opened their homes to me on many occasions, so big thanks go to them and their families. And thanks to all the landowners and citizens of the properties we've worked on in Sonora for being so welcoming and friendly. The cultural and scientific experiences I've had working in Mexico are among the most influential and important I've had in my entire life.

Enormous thanks goes to my family for always encouraging me to follow my passions, even through my entirely-too-long and winding college career (which began in 1993). My parents Thomas and Bonita Bogan never once doubted my meandering pathway to this graduate degree and always encouraged me to take the path that felt right, even if it wasn't financially lucrative. My grandmothers Helen Bogan and Carrie Rozanc are continuous sources of inspiration for me, and I'm so happy they are both around to see me finish this adventure. And last, but certainly not least, thanks to my thoughtful and loving partner, Devlin Houser. His appearance in my life has probably made the last years of my dissertation less productive, but they've been the happiest by far.

CONTRIBUTION OF AUTHORS

DR. DAVID A. LYTLE gave valuable advice in the design, implementation, and editing of this dissertation, and provided financial support in the form of research assistantships during several terms between 2007 and 2012. Dr. Lytle is a co-author of Chapters 2, 4 and 5.

KATE S. BOERSMA contributed to the intellectual development of Chapter 3, and purchased field equipment and participated in both the field work and analyses described in Chapter 3. Boersma also participated in the field work and gave valuable analysis and editing input to the work described in Chapter 4. She is a co-author of both Chapters 3 and 4.

NOHEMÍ NORIEGA-FELIX and SYLVETTE VIDAL-AGUILAR both contributed to the field work, laboratory work, and editing of Chapter 5 and are both co-authors of Chapter 5.

DR. LLOYD T. FINDLEY, DR. OSCAR GUTIÉRREZ-RUACHO, DR. ANDRÉS ALVARADO-CASTRO, and DR. ALEJANDRO VARELA-ROMERO all participated in the field work described in Chapter 5 and made valuable comments on a previous draft of that chapter. All four are co-authors of Chapter 5.

TABLE OF CONTENTS

TABLE OF CONTENTS (CONTINUED)

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF APPENDIX FIGURES

LIST OF APPENDIX TABLES

DEDICATION

This dissertation is dedicated to all the wonderful wild and hidden aquatic corners of the arid West, the dripping springs, stagnant tinajas, and beautiful oases, and all of their vertebrate and invertebrate inhabitants. May you never dry up because of groundwater pumping or water diversions and may you stay free of tilapia and other invasive species. And my deepest apologies go to all of the insects that I dropped into ethanol over the course of this dissertation. I promise that I did it with the sincere intention of better understanding and conserving these special habitats.

Sky, Sand
Cottonwoods, streambank
        splashing, fording up the creekbed
black phoebe calling *pi pi pi* here, near--
Mexican blackhawk cruising -- squint at the sky,
shoes full of sand
(*Aravaipa Canyon, Arizona*)

-Gary Snyder (2005)

Drought, Dispersal, and Community Dynamics in Arid-land Streams

CHAPTER 1 - **Introduction**

Understanding the mechanisms that drive local species diversity and community structure is a perennial goal in ecology. Many of the earliest efforts to further this understanding focused on interactions between species, including between predators and prey or competing species. Later, the importance of environmental heterogeneity (e.g., Hutchinson 1961), disturbance (e.g., Connell 1978) and dispersal (e.g., MacArthur and Wilson 1967; Hanski 1998) were recognized as being perhaps equally important. Additionally, the relative importance of factors such as predation, competition, and disturbance was recognized to vary depending on recruitment rates and the harshness of the local environment (Menge and Sutherland 1987). Most recently, the metacommunity framework was developed (Leibold et al. 2004) in an attempt to encompass whole communities of species interacting with one another and dispersing among habitat patches across a landscape.

Local species diversity and community structure are clearly the result of numerous local and regional processes (Ricklefs 1987). These processes act as filters that reduce the regional species pool down to the observed local community (Poff 1997; also see Fig. 1.1); the relative importance of these different filters varies among systems and regions (Vinson & Hawkins 2003). Thus ecologists need to consider processes on multiple spatial and temporal scales in order to predict changes in diversity and community structure in the face of conservation challenges such as global climate change and anthropogenic alteration of habitat (Levin 1992).

In lotic ecosystems, natural flow regime characteristics are widely recognized as important drivers of local diversity and community composition (Resh et al. 1988; Poff 1997). Natural flow regimes encompass a wide range of environmental heterogeneity and disturbances that occur on multiple spatial and temporal scales, including flooding (which may occur on local reach or stream-level scales) and drought (which may occur at both local and regional scales).

Despite the relatively harsh and unstable habitat that many streams provide, biodiversity can be remarkably high in streams. This high diversity is due, at least in part, to a wide variety of life history, behavioral, and morphological adaptations that allow species to persist, and even thrive, through flow disturbances like flood and drought (Lytle and Poff 2004). These adaptations are to natural flow regimes, though; they may not help species persist through altered flow regimes created by human activities (e.g., dams, water withdrawals) or climate change (e.g., shrinking glaciers, longer droughts) (Brown et al. 2007; Durance and Ormerod 2007). Many freshwater species are critically endangered in altered streams and rivers around the globe. Extinction rates of North American freshwater species are five times higher than those of terrestrial species (Ricciardi & Rasmussen 1999).

In mesic regions, streams are isolated from one another by upland terrestrial areas, but the flow connectivity across a stream network can enhance the resilience of disturbed reaches (Lowe et. al. 2006). In arid regions, however, streams are often not connected to one another by continuous flow (Stanley et. al. 1997). This characteristic of arid-land streams increases their patch-like, isolated nature and potentially increases their sensitivity to disturbance. The extreme patchiness and small size of arid-land stream habitats, though, also makes them very tractable systems for examining the processes which create and sustain diverse communities. Poff and Ward (1989) noted that abiotic processes are likely the primary factors driving community structure in most arid-land streams. Arguably, abiotic factors (e.g., water temperature, drought frequencies) are easier to quantify than biotic factors. Thus, arid-land streams are ideal settings to determine how abiotic factors structure local communities. Arid-land streams are also among the most endangered freshwater habitats in North America (Briggs 1996), so understanding the factors that structure their communities at multiple spatial and temporal scales (Fig. 1.1) is essential for planning effective conservation efforts.

Arid-land streams of the southwestern United States and northwestern Mexico support extremely diverse aquatic insect communities despite dry season habitat sizes being as small as $12m^2$ (Bogan & Lytle 2007). Arguably, the defining characteristic of these streams is their extreme seasonal and interannual flow variation. In fact, extreme seasonal variation in flow appears to be in part responsible for the high diversity of their aquatic invertebrate communities (Bogan & Lytle 2007; also Appendix I). High-flow conditions in wet winters support cold-adapted Nearctic communities, while low-flow conditions the rest of the year support lentic beetle (Coleoptera) and true bug (Hemiptera) dominated communities, thus increasing the temporal beta diversity within any given stream (Bogan & Lytle 2007). In dry years with little winter precipitation, though, communities may remain dominated by lentic beetle and true bug taxa the entire year. The magnitude of flow increase between dry and wet seasons may significantly influence the degree of community change between these seasons (Appendix 1).

In this dissertation, I explore the role that drought, dispersal, and local habitat factors play in structuring arid-land stream communities (Figure A1.1). Much of my focus is on drought, and the low- or zero-flow periods it causes in streams, including both severe, multi-year droughts (Chapter 2) and more predictable, seasonal droughts (Chapter 4, Appendix I). In many types of streams, community recovery from short-term droughts is often rapid (Boulton 2003; Lake 2003). Resilience to drought is generally high in arid-land streams as well, but rates of recovery may be dependent on the specifics of drying sequences and distances to recolonization sources (Stanley et al. 1994). Drought may cause predictable shifts in community composition, but communities generally return to pre-drought configurations when surface water returns (Boulton and Lake 1992b; Acuña et al. 2005). In some cases, though, drought may eliminate sensitive taxa (Boulton and Lake 1992a) and have longer-term impacts on aquatic community composition (Bêche et al. 2009).

The predictability of drought-induced stream drying may largely determine what effects drought has on local community structure. Species that have evolved in streams regularly affected by drought have adapted to that harsh disturbance regime through a variety of mechanisms, including rapid development times and diapause stages that are synchronized with the dry season (Lytle and Poff 2004). Though seasonal drought is a recurring phenomenon in the arid southwestern United States, the last 30 years have seen a significant increase in longer-term, interannual drought severity (Balling and Goodrich 2010). In Arizona, the drought period from 1999 to 2004 equaled or exceeded any from the historic record, and in many cases resulted in the lowest recorded stream flow periods on record (Phillips and Thomas 2005). These severe, long-term droughts are resulting in unprecedented stream drying events which may exceed the ability of even drought-adapted aquatic species to persist in some streams.

In Chapter 2, I present a long-term case study from French Joe Canyon in southeastern Arizona. There are multiple lines of evidence suggesting that the stream had perennial water over the past 30 years, and likely for hundreds to thousands of years before that (Finn et al. 2007, 2009; Chapter 2). In 2005, though, the stream dried completely for several months. It was rewatered in late 2005, but from then until present it has dried several more times, essentially transitioning from a perennial stream to an intermittent stream over the course of the study. While aquatic invertebrate species richness was not affected by this transition, community composition changed dramatically. We present evidence that this dramatic change caused a regime shift to an alternative community state, one dominated by vagile, shorter-lived, smaller secondary predators after the drying disturbance caused the extirpation of the flightless top predator and other longer-lived, less vagile species.

Interspecific differences in aerial dispersal ability were likely strongly influential in the regime shift observed at French Joe Canyon. While French Joe Canyon is isolated by several kilometers from the next nearest perennial water habitat, numerous species rapidly recolonized the stream following rewetting. However, species with poor dispersal abilities, that were present in the past when French Joe supported perennial habitat, did not reappear there following rewetting. Additionally, as noted above, arid-land streams across region support high diversity of aquatic invertebrates despite recurring droughts, floods, and other disturbances. I propose that a significant proportion of this diversity is maintained by frequent aerial dispersal of many aquatic invertebrate species. Genetic and stable isotope studies, though, have indicated that while some aquatic invertebrate species disperse frequently or over long distances, dispersal abilities vary greatly among taxa (Macneale et al. 2005; Hughes et al. 2009). In order to predict community changes following severe drought in arid-land streams, we need to better understand the potential of species to reach isolated habitats.

To begin to address this challenge, I quantified colonization of aquatic invertebrates via aerial dispersal along and away from arid-land streams using replicate artificial pools placed at various distances from a perennial and an ephemeral stream (Chapter 3). Sixty-six taxa colonized the artificial pools, representing one-third of taxa documented from neighboring perennial streams. Invertebrate abundance and richness in artificial pools declined with distance inland from both the perennial and ephemeral streams. This suggests that ephemeral stream channels, even with no surface water present, may serve as important aerial dispersal corridors for aquatic invertebrates. Using spatio-temporal dispersal patterns observed in the colonization experiments, I identified five modes of aerial dispersal: (1) widespread opportunistic, (2) widespread haphazard, (3) range-restricted, (4) cue-limited, and (5) infrequent. In identifying these categories and the types of species that fall into each of them, I hope to provide a framework for spatially-explicit predictive models of invertebrate community responses to disturbance, stream restoration efforts, and climate change-induced habitat contraction or expansion.

While many arid-land streams exist as isolated patches that are never connected by surface flow to other patches, some arid-land stream networks provide a mosaic of perennial and intermittent reaches that can be connected during extended periods of precipitation, as those that occur during El Niño winters. As hinted at in Chapters 2 and 3, the location of intermittent reaches within such stream networks and their degree of connectivity with perennial reaches likely influence how distinct their communities are when compared to nearby perennial reaches. If intermittent reaches are close to perennial reaches, high rates of immigration from perennial reaches could mask the impacts of even the strongest local environmental factors, including drought (Townsend 1989).

In Chapter 4, I quantify aquatic invertebrate richness, functional feeding group composition, and community structure in multiple perennial and intermittent reaches across a large arid-land stream network ($400km^2$). The intermittent reaches in the study network only flow for an average of 80 or so days during wet winters (45% of all years). Invertebrate richness was lowest in these reaches, despite often having flow connectivity to species-rich perennial reaches. The relative predictability of the timing of the winter flow period, though, seems to have allowed for a small, but unique, group of species to evolve resistance mechanisms that confer persistence in intermittent reaches. These species-poor intermittent reach communities were dominated by stonefly, blackfly, and midge taxa with various adaptations to intermittency, such as extended egg and larval diapauses (also see Appendices II and III). Despite being separated by long distances and having very different physical attributes, disjunct perennial headwater and valley river communities were more similar to one another than to intervening intermittent reaches. In this chapter, I also present a conceptual model that explores the relative roles of flow permanence and connectivity to perennial habitats in determining how many specialist intermittent taxa may be found at a given site.

Regional climate change models predict increasing drought intensity and duration across the southwestern US and northwestern Mexico (e.g., Seager et al. 2007). Additionally, increased anthropogenic water withdrawals are predicted to significantly reduce biodiversity in isolated stream habitats (Deacon et al. 2007). These two looming threats make the need to document current levels of aquatic biodiversity in the region all the more pressing.

The negative impacts of climate change and water withdrawal will arguably be greatest in the driest portions of the region, where water resources are already incredibly scarce, including the southern Sonoran Desert. Despite their incredible aridness (mean annual precipitation ≤ 150mm), the sierras El Aguaje, Santa Úrsula, and Bacatete in southern Sonora, México contain numerous canyons supporting spring-fed aquatic habitats and relictual tropical vegetation, isolated from one another by steep cliffs and large areas of dry desert. In Chapter 5 I present the results of a series of aquatic biodiversity survey of these "oases" conducted in collaboration with a team of Mexican and American researchers. We mapped freshwater habitats in these mountain ranges, identified distinct microhabitat types at each site, and inventoried their aquatic biota. We identified more than 220 taxa of aquatic animals across 19 sites in the three sierras, including at least 5 undescribed species of caddisflies (Trichoptera) and beetles (Coleoptera). Additionally, at one site, Cañón Nacapule, we sampled aquatic invertebrate communities over multiple seasons in 2008 and 2009. Despite dramatic monsoon and hurricane-induced flooding and seasonal habitat contraction and expansion, aquatic invertebrate richness and community composition at Nacapule changed little over these two years, indicating that local species were very resilient and/or resistant to flooding disturbance. Native aquatic species richness and abundance were significantly reduced by the introduction of the exotic fish species, tilapia, at several locations. These incredible oases, and streams across the arid-lands of the southwestern US and northwestern Mexico, are in great need of coordinated conservation efforts. I hope that the results of these biodiversity surveys, and the rest of my dissertation research, provide further impetus to preserve these imperiled systems.

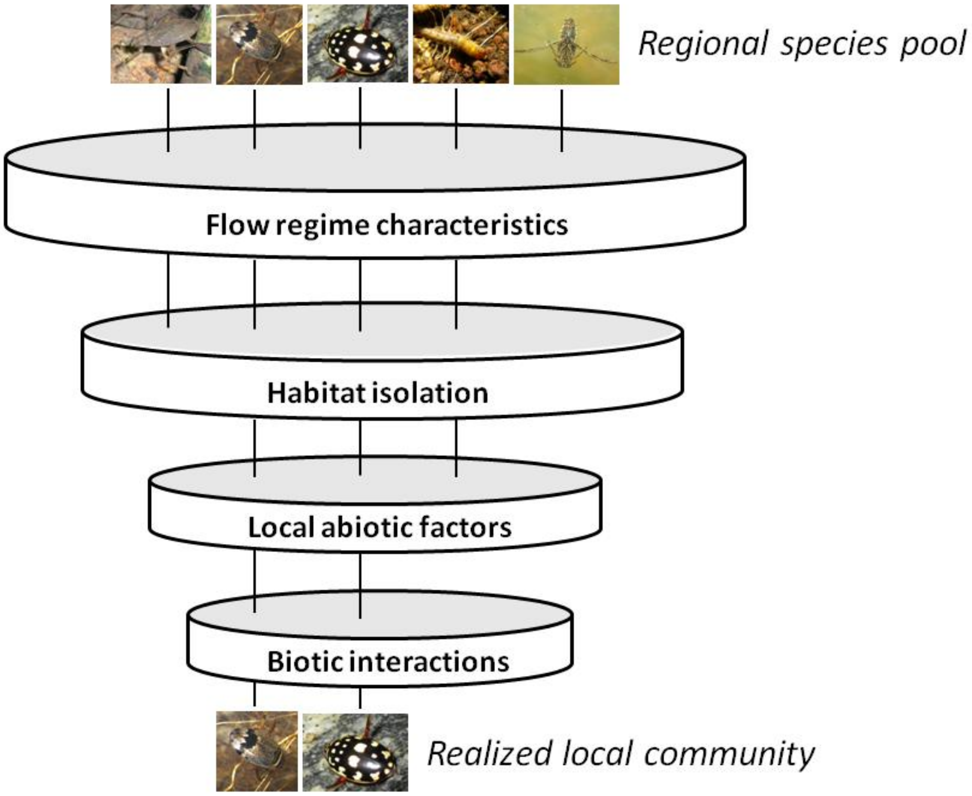

Figure 1.1. Some of the regional and local scale filters that act to produce local community structure in arid-land stream systems (modified from Poff 1997). Each of the species in the regional species pool has a combination of life history, behavioral, and morphological traits which either allow them to pass through the successive filters or not. For example, a hypothetical stream might have some small bit of perennial water which would allow the giant water bug *Abedus herberti* (on top left) to pass through the "Flow regime" filter; but if that stream is highly isolated, then the flightless *A. herberti* may not be able to recolonize it if local disturbance events cause extirpation of the local population. Alternatively, highly vagile generalist species with few microhabitat requirements (like the predaceous diving beetles in the genus *Thermonectus*) may make it through all the filters and occur in the realized local community.

CHAPTER 2- **Severe drought drives novel community trajectories in desert stream pools**

Michael T. Bogan and David A. Lytle

Published in:
Freshwater Biology
Volume 56, pages 2070-2081
Wiley-Blackwell Publishing
Hoboken, NJ

ABSTRACT

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. 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. 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. 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. 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.

2.1 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 and 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 and 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 and Lake 1992b; Acuña et al. 2005). In some cases, however, drought has been found to eliminate sensitive taxa (e.g. shrimp: Boulton and 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 and 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 and 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 (Jackson and 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).

2.2 METHODS

2.2.1. 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. 2.1). 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 and 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 and 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 and 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).

2.2.2. 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 and 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 and 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.

2.2.3. 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 and 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.

2.3. RESULTS

2.3.1. Abiotic data

Water levels in the two study pools were full and overflowing during the first three years of our observations (2002-2004; Fig. 2.2). 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. 2.2). 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 mexicanus* (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. 2.1).

2.3.2. 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. 2.3). 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; Fig. 2.4). 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 2.1).

Before the initial drying event in June 2005, both pools supported similar communities and exhibited some variation between low and high flow seasons (Fig. 2.4). 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. 2.4) 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 (see Appendix 1).

Pre- and post-drying community samples from French Joe were completely segregated along axis 2 of the ordination (Figure 2.4) 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 2.2 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.

2.4. 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.

2.4.1. 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 (Fig. 2.3). 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 and 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 and 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.

2.4.2. 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. 2.4). This pattern is consistent with what we have documented in stream communities across the region (Bogan and 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. 2.4; Tables 2.1 and 2.2). 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. 2.4). 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 (see Appendix 1).

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 and 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 and 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. 2.2). 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 and 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 and 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 2.1 and 2.2) 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 and 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 and 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 and 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 and 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. 2.5 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. 2.5). 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. 2.5). 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 and Darling 2010), further reinforcing the alternative state.

2.4.3. 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 (Seager et al. 2007), surpassing the drought intensities of the past 30 years (Balling and 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 and 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 2.1. This project was supported in part by Oregon State University and National Science Foundation grant DEB-0445366 to D.A.L.

Table 2.1 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 2.2 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

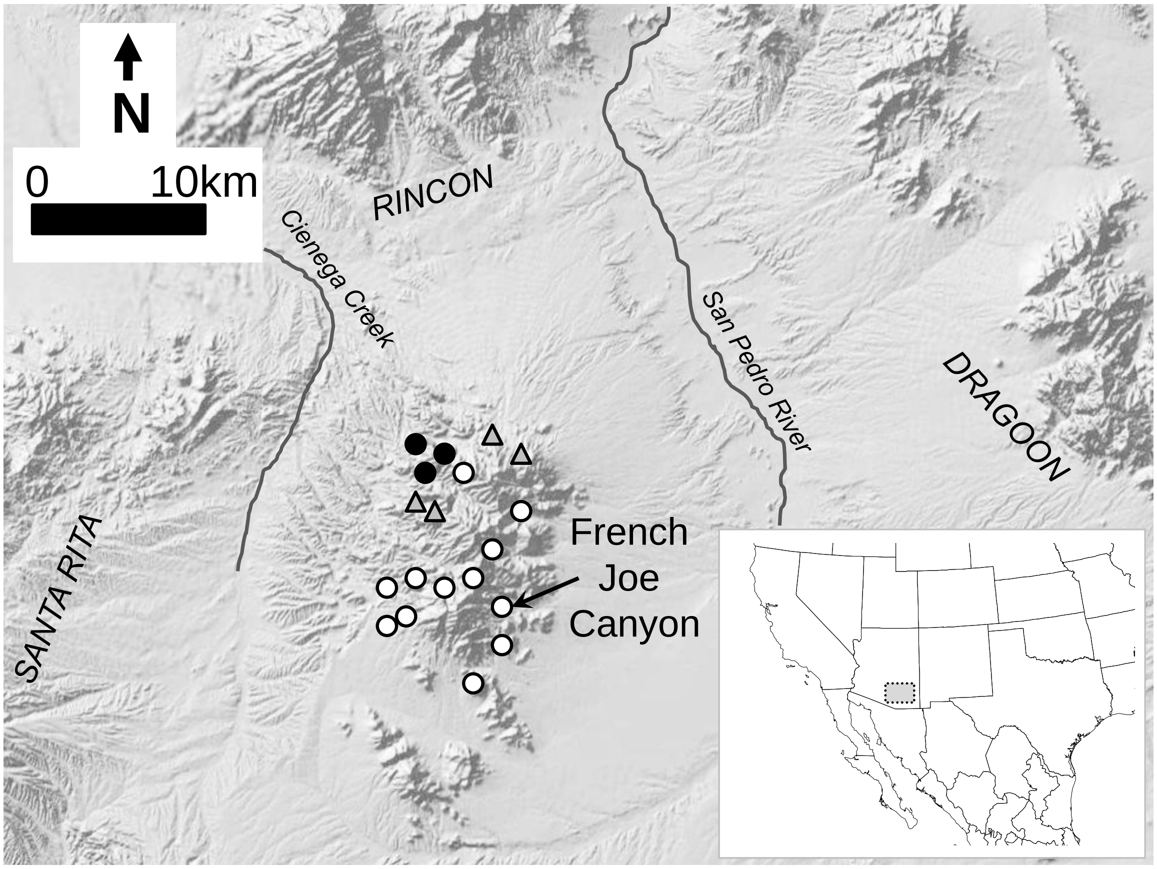

Figure 2.1 French Joe Canyon is located in the Whetstone Mountains of Arizona, one of many sky island mountain ranges in the region. French Joe Canyon supported some of the many spring-fed perennial stream reaches (indicated by circles and triangles) in the mountain range. Most of the surrounding springs 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.

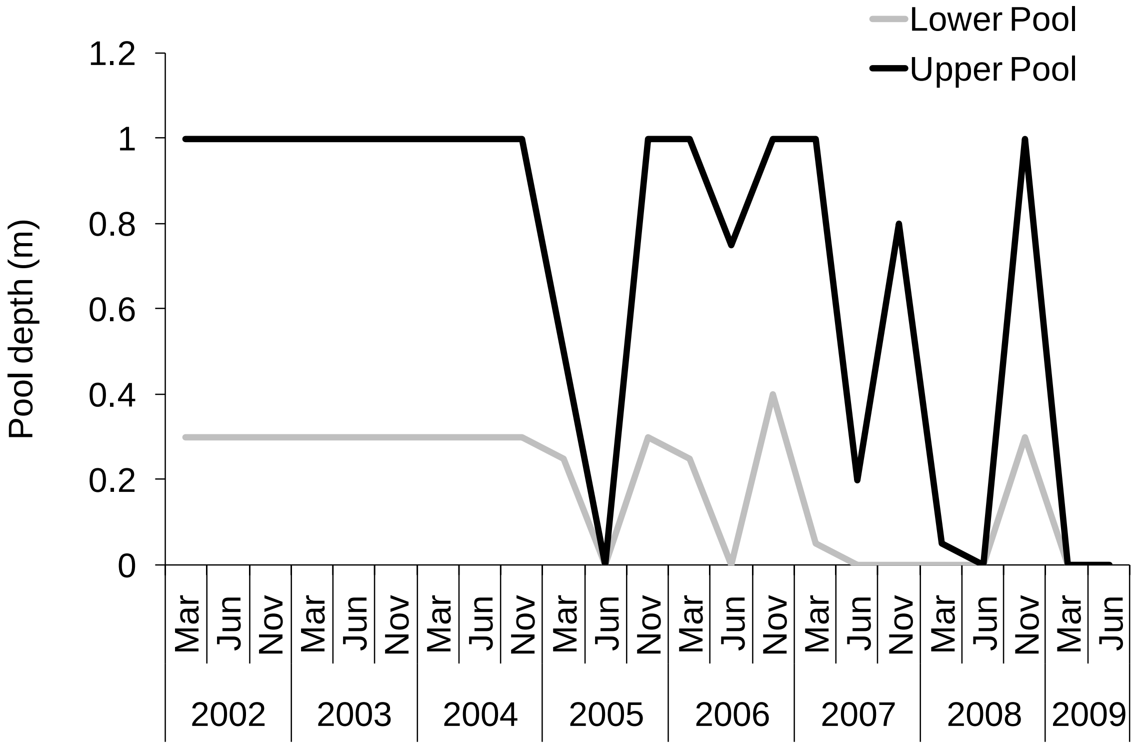

Figure 2.2 Water depths of the study pools in French Joe Canyon between 2002 and 2009. Both formerly-perennial pools dried completely in June 2005 and remained dry for several months. From late 2005 to June 2009, pool levels fluctuated greatly in response to local precipitation events.

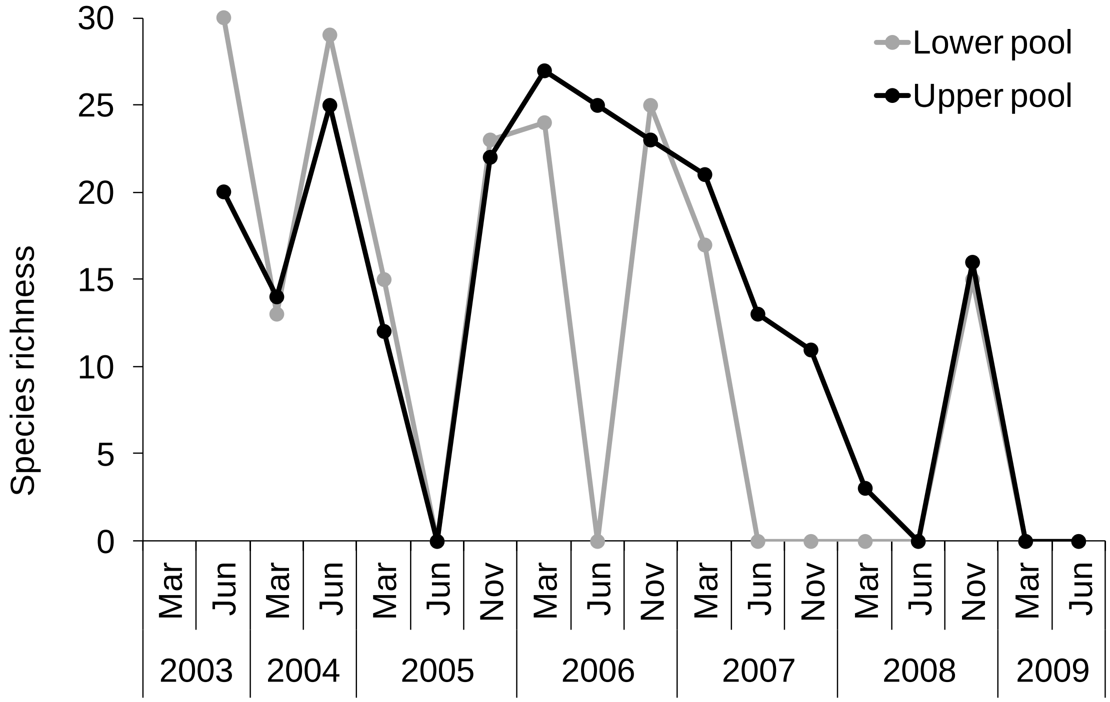

Figure 2.3 Aquatic insect taxonomic richness (number of taxa sampled from each pool at each sampling event) for the study pools at French Joe Canyon from 2003 to 2009. Richness values fell to zero only during periods of complete pool drying.

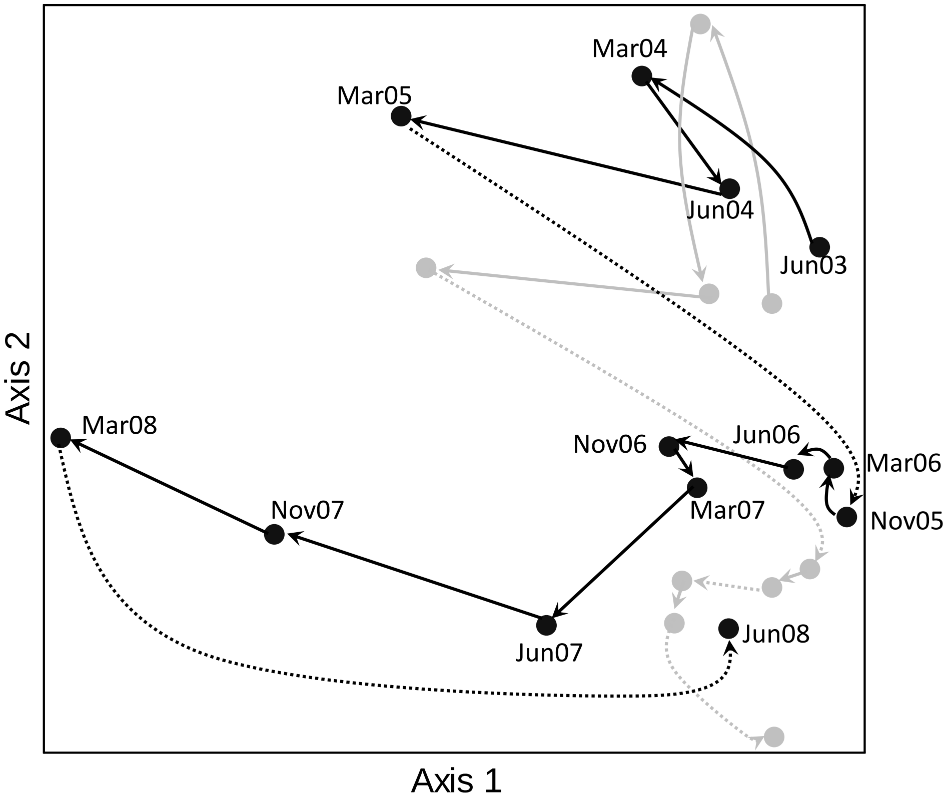

Figure 2.4 NMS ordination plot of aquatic insect community changes in French Joe Canyon study pools between 2003 and 2009. Upper (black circles) and lower (gray circles) pool community trajectories are shown, though for clarity only the upper pool trajectory is labeled with sample dates (Mar= March, 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.

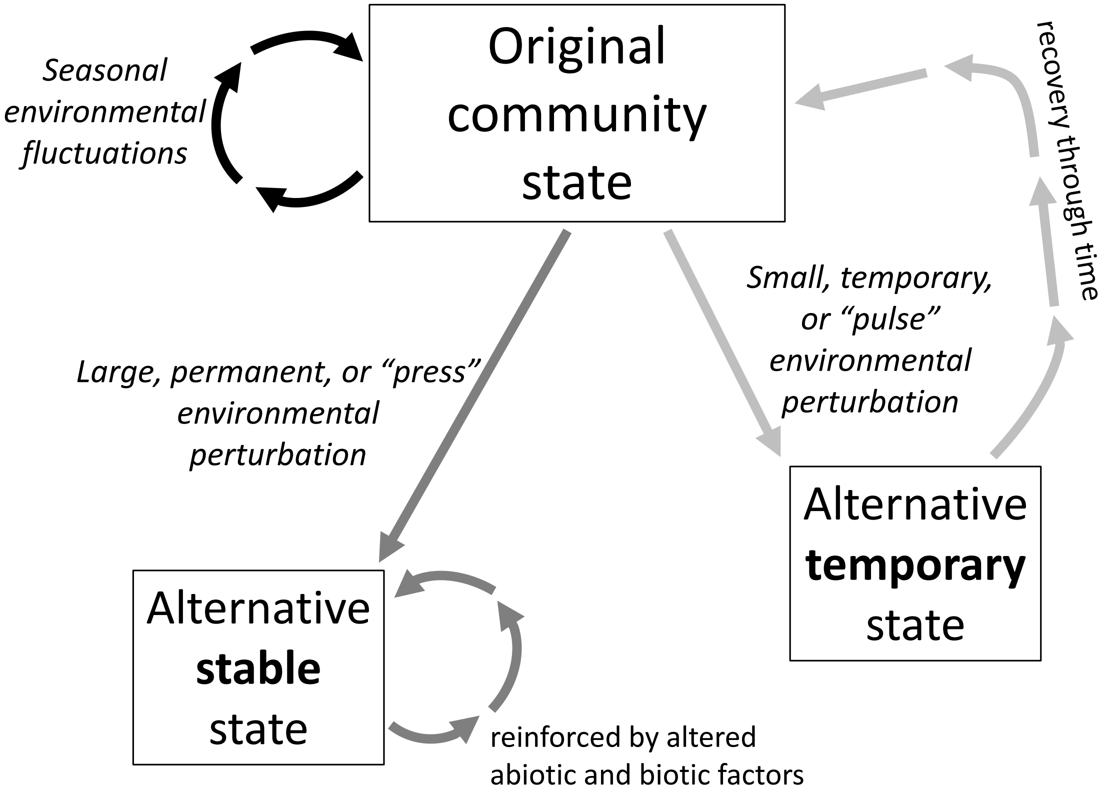

Figure 2.5 Conceptual model of community changes through time given environmental fluctuations and major or minor disturbance events. Most ecosystems exhibit some seasonal environmental fluctuations, but communities generally change in a predictable manner (black vectors). Small, temporary or "pulse" 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).

CHAPTER 3- **Aquatic invertebrate aerial dispersal along and inland from arid-land streams**

Michael T. Bogan and Kate S. Boersma

Accepted for publication, pending minor revisions in:
Freshwater Science
Allen Press
Lawrence, KS

ABSTRACT

Dispersal, the movement of individuals from one site to another, plays an essential role in metapopulation and metacommunity dynamics. Past studies of aquatic invertebrate dispersal in streams have largely focused on instream drift of larvae. Understanding aerial dispersal, though, is essential for predicting community assembly in isolated habitats following disturbance or stream restoration efforts. We examined aerial dispersal dynamics of aquatic invertebrates using artificial pools placed at three distances (5, 75 and 250 m) inland from one perennial and one ephemeral arid-land stream in Arizona over a 6-week period in summer 2009. Additionally, we conducted a shorter 2-week experiment to examine the relationship between daily rainfall and disperser abundance at the perennial site. Sixty-six aquatic invertebrate taxa colonized the artificial pools, representing one-third of taxa documented from neighboring perennial streams. On average, invertebrate abundance and species richness in artificial pools declined with distance inland from both the perennial and ephemeral streams. This suggests that ephemeral stream channels, even with no surface water present, may serve as important aerial dispersal corridors for aquatic invertebrates. Average species richness of artificial pools tripled following 58 mm of rain during the fourth week of the experiment. Data from the 2-week experiment further supported the idea that rainfall serves as either a cue to disperse or facilitates aerial dispersal in this system. Daily rainfall amount explained between 48 and 77% of the variation in disperser abundance in artificial pools at 5, 75, and 250 m inland from the perennial site. Using spatio-temporal dispersal patterns observed in our study, we identified five modes of aerial dispersal among 56 taxa: (1) widespread opportunistic, (2) widespread haphazard, (3) range-restricted, (4) cue-limited, and (5) infrequent. Classification of specific aerial dispersal traits provides a conceptual framework for spatially-explicit predictive models of benthic community responses to disturbance, stream restoration efforts, and climate change-induced habitat contraction or expansion.

3.1. INTRODUCTION

Dispersal, the movement of individuals from one site to another, is an important process in the maintenance of local populations (Hanksi 1998) and plays an essential role in determining local community composition (Palmer et al. 1996; Leibold et al. 2004). Dispersal from natal habitat can allow for inbreeding avoidance and escape from predation, competition, or deteriorating environmental conditions in local habitat patches. These benefits do not come without risks, as individual dispersers may not find suitable mates in new habitats, or may not find any appropriate habitat to colonize at all (Bilton et al. 2001). As a group, freshwater invertebrates were long believed to be frequent and/or widespread dispersers (Bohonak and Jenkins 2003). Genetic and stable isotope studies, though, have indicated that while some species disperse frequently or over long distances, dispersal abilities vary greatly among freshwater invertebrate taxa (Macneale et al. 2005; Hughes et al. 2009).

In streams, drift dispersal is often portrayed as the most important mechanism for invertebrate colonization of new or disturbed habitat patches (e.g., Williams and Hynes 1976; Gore 1982; Mackay 1992). This apparent primacy of drift (and instream movement) over aerial dispersal may reflect the bias of published studies towards wadeable, perennial temperate streams. In some studies that have examined alternate dispersal pathways, aerial dispersal has been identified as the primary colonization pathway, especially in arid-land (Gray and Fisher 1981) and equatorial (Hynes 1975) streams. Aerial dispersal likely plays a large role in the colonization of activated floodplains in large temperate rivers as well (Tronstad et al. 2007). In streams recovering from anthropogenic disturbance, aerial distance from colonist source streams can be an important predictor of local invertebrate diversity, especially during the early years of recovery (Patrick and Swan 2011). Understanding the role of aerial dispersal in streams is thus essential for predicting community assembly under changing climatic conditions and for designing and implementing stream biodiversity restoration and monitoring projects (Parkyn and Smith 2011).

To advance our understanding of aerial dispersal of stream invertebrates, two key topics deserve attention: the extent of dispersal along versus inland from stream corridors and the environmental conditions that trigger or facilitate aerial dispersal. Most studies indicate that the vast majority of adult aquatic insects disperse less than 50 m inland from stream corridors (e.g., Jackson and Resh 1989; Petersen et al. 2004; Winterbourn et al. 2007). Occasionally, though, adult aquatic insects are found from several hundred meters (Macneale et al. 2005) to several kilometers (Kovats et al. 1996) inland from their natal stream. Though difficult to observe, these occasional long-distance dispersal events may be extremely important for the maintenance of freshwater invertebrate populations (Bilton et al. 2001). In fact, genetic analyses indicate that reach-scale genetic structure in some streams may be the result of only a few matings of adult aquatic insects (Bunn and Hughes 1997).

Numerous environmental factors may trigger or facilitate aerial dispersal of stream invertebrates, both along and inland from the stream channel. Deteriorating local habitat conditions during seasonal drought, including reduced water levels and increased water temperatures, are often cited as cues to disperse overland (Kingsley 1985; Velasco and Milan 1998). Conversely, some insects (e.g. Belostomatidae) use intense rainfall as a cue to migrate from perennial stream habitats to seasonally flooded habitats (Lytle and Smith 2004). Heavy rain has also been associated with increased aerial dispersal and subsequent colonization of aquatic habitats by microcrustaceans (Caceres and Soluk 2002; Williams et al. 2007), but rainfall may be negatively correlated with aerial dispersal of macroinvertebrates in other systems (Miguelez and Valladares 2008). Additional environmental factors that facilitate aerial dispersal of aquatic invertebrates include increased air temperature (Pajunen and Jansson 1969; Ryker 1975; Briers et al. 2003; Miguelez and Valladares 2008) and decreased humidity and wind (Briers et al. 2003; Boix et al. 2011). Aerial dispersers may also be more likely to fly at times of day with maximum reflectivity of light off water bodies, which enhances the detectability of potential colonization sites (Csabai et al. 2006). Thus, in order to fully understand aerial dispersal processes, both spatial (i.e. where dispersers travel across the landscape) and temporal (i.e. when dispersers leave their habitat) aspects of dispersal need to be quantified.

In this study, we examined spatial and temporal patterns of aerial dispersal and community assembly along and inland from two arid-land streams in Arizona. Most streams in the region naturally contract to a series of small pools during the dry season; these pools may be connected by tiny trickles of flow or completely isolated from one another. Because tracking multiple species of aerial dispersers from one habitat to another is difficult to impossible, we instead quantified invertebrate arrival at novel aquatic habitats using plastic tanks to mimic isolated stream pools. We placed these artificial pools at three distances (5, 75, and 250 m) inland from the two study streams, and allowed these pools to be colonized over a 6-week period. One study stream was perennial while the other was ephemeral and contained no surface water during the experiment. We also examined the potential role of rainfall in triggering or facilitating dispersal by quantifying colonist arrivals in a separate set of artificial pools over 2 weeks (only at the perennial site) and correlating colonist abundance with rainfall. We hypothesized that species richness and abundance would decrease and community composition would change significantly with increasing distance inland from the stream at the perennial site but not at the ephemeral site because the dry stream channel would provide few, if any, dispersers. We also hypothesized that colonist abundances would be highest following rain events given that rainfall may serve as a cue to disperse in search of newly wetted habitats. Finally, we used the observed spatio-temporal dispersal patterns of individual species, including their response to rainfall, to classify species into aerial dispersal modes.

3.2. METHODS

3.2.1. Study location

Our study was conducted along two arid-land streams in the Chiricahua Mountains of southeast Arizona: the perennial Cave Creek and the ephemeral Graveyard Canyon (flows only briefly during very intense precipitation events; no flow for at least 10 months prior to start of study). The two study sites have similar elevations (1675 m) but are separated from one another by 4.5 km and a significant mountain ridge which rises to 2440 m (Fig. 3.1). There are no ponds in the Chiricahua Mountains, so streams are the only available habitat for aquatic invertebrates in the range. Upland areas of both study sites are oak (*Quercus*), pine (*Pinus*), and juniper (*Juniperus*) woodlands. Cave Creek supports a riparian forest of sycamore (*Platanus*), cottonwood (*Populus*), and willow (*Salix*), while only oak, juniper, and pine occur in the riparian area of Graveyard Canyon. The Cave Creek study site was located on the grounds of the American Museum of Natural History's Southwestern Research Station. Mean annual precipitation at the Southwestern Research Station is about 450 mm and strongly bimodal, with roughly half the precipitation occurring during brief, violent summer monsoon (Jul–Sep) storms and half during more gentle winter storms (Nov–Apr). Daily rainfall over the study period was measured at the Southwestern Research Station.

3.2.2. Six-week colonization experiment

In our first experiment, we measured colonization trends in artificial pools along and inland from our two study streams for 6 weeks, from 30 May-10 Jul 2009. This time period was selected to encompass both the peak of the spring (Apr-Jun) dry period and the beginning of the summer monsoon rains. We used 24 replicate 60-L black plastic tanks as artificial pools, with holes drilled at the top of each tank that were screened with 500-μm mesh to allow for overflow. We filled each tank with well water and then added 10g of dried oak (*Quercus*) and sycamore (*Platanus*) leaves. Twelve tanks were placed along Cave Creek and 12 tanks along Graveyard Canyon in the following arrangement: at each stream, 4 replicate tanks, spaced 100 m apart, were placed 5 m inland from the stream channel, with an additional 4 replicate tanks placed with the same 100 m spacing at both 75 m and 250 m inland from the stream channel (Fig. 3.1). Tanks were filled on 30 May and were monitored twice a week to remove any large debris and check water levels. Tank water was replenished by both rainfall and supplemental well water until 10 Jul, when the contents of each tank were filtered through a 250-μm mesh net and preserved in 95% ethanol. Aquatic invertebrates were sorted, identified to the finest taxonomic level possible (species for Coleoptera and Hemiptera, genus for all other insects, family or order for non-insects) and enumerated at Oregon State University. We used two-way ANOVA to test for differences in species richness and abundance by distance inland from channel (5 m, 75 m, 250 m), stream (Cave Creek, Graveyard Canyon), and distance X stream interactions. We analyzed differences in community composition by distance, stream, and their interaction using two-way perMANOVA, a non-parametric, permutation-based multivariate ANOVA (Anderson 2001) using PC-ORD (version 5.0, Mjm Software, Gleneden Beach, OR).

In addition to the final destructive sampling event, we conducted weekly visual surveys of species presence/absence in each tank, without removing observed individuals, starting in week 2 of the experiment. However, several genera of Chironomidae and most non-insect invertebrates (e.g., mites, springtails) were too small to be identified visually and were not included in visual surveys. To ensure that our visual surveys were reliable, we quantified similarity between community matrices arising from final visual surveys and destructive sampling of each replicate pool using Sorensen's distances. We then utilized the spatial and temporal presence/absence data from the visual surveys to place taxa into one of five aerial dispersal modes: (1) *widespread opportunistic*: found in >50% of the visual surveys over the study period, with no temporal or spatial occurrence pattern, (2) *widespread haphazard*: found in ≤50% but >5% of the visual surveys over the study period, with no temporal or spatial occurrence pattern, (3) *cue-limited*: ≥2.5 times as likely to be found after heavy monsoon rainfall began halfway through the study period than before rainfall began, (4) *range-restricted*: ≥2.5 times as likely to be found in tanks 5m from the channel than in the 75 m and 250 m tanks combined, (5) *infrequent*: found in ≤5% of visual surveys over the study period (see Fig. 3.5 for a diagrammatic representation of these 5 aerial dispersal modes). We examined community assembly in the tanks over the 6-week study period using non-metric multidimensional (NMS) ordination of a Sorensen dissimilarity matrix based on presence-absence data from the visual surveys using PC-ORD (version 5.0, MJM Software, Gleneden Beach, OR).

3.2.3. Two-week colonization rate experiment

We also conducted a shorter experiment (14 days: 22 Jun – 5 Jul 2009) to examine the relationship between aerial colonization rate and rainfall. Again, 4 replicate tanks were used at each of 3 distances inland from the stream channel (5 m, 75 m, 250 m), but for this experiment tanks were only deployed along perennial Cave Creek, no leaf litter was introduced into the tanks, and all aquatic invertebrate colonists were removed every 12 hr. Though the lack of leaf litter as a food web base and the frequent removal of all aquatic invertebrates prevented community development, we knew from preliminary observations that the mere presence of water would be enough to induce many taxa to colonize otherwise empty tanks. A 12 hr sampling interval was selected as compromise between logistical difficulties of more frequent sampling and capturing colonists before they left the resource-poor tanks. We analyzed the relationship between 24 hr rainfall totals and abundance of colonists during that same 24 hr period using simple linear regression. We analyzed rainfall-colonist relationships for each treatment distance separately (5 m, 75 m, 250 m) and for the mean of all distances.

3.3. RESULTS

3.3.1. Rainfall

Total rainfall was 105.4 mm over the 6-wk study period, with the majority (79.8 mm) occurring during a series of storms from 25-29 Jun. Weekly rainfall totals (mm) during the 6-wk colonization experiment were 0, 1.8, 0.5, 58.2, 30.7, and 14.2, respectively, for weeks 1-6. The 2-wk experiment ran during weeks 3-4 of the 6-wk experiment, capturing July storms that marked the onset of the summer monsoon season. Daily rainfall totals during the 2-wk experiment (22 Jun- 5 Jul) varied from 0 to 21.8 mm.

3.3.2. Six-week colonization experiment

Sixty-six taxa colonized the 24 artificial pools during the 6-wk colonization experiment (Table 3.2), including 38 beetle taxa, 13 dipteran taxa, 2 mayfly taxa, 7 true bug taxa, 1 dragonfly taxon, 1 caddisfly taxon, 4 non-insect taxa. The overwhelming majority of individuals collected were insects (99.8%), with the 4 non-insect taxa only accounting for 0.2% of total abundance. The 12 artificial pools along the perennial Cave Creek contained a total of 20,379 invertebrates and 47 taxa, which represents 35% of low-flow season taxa known from Cave Creek (based on June 2009 surveys; M.T. Bogan, unpublished data). The 12 artificial pools along the ephemeral Graveyard Canyon contained a total of 7861 invertebrates and 33 taxa, which represents 30% of low-flow season taxa known from the nearest perennial habitat, East Turkey Creek (based on

June surveys from 2004-2009; Bogan and Lytle 2007, M.T. Bogan, unpublished data). All taxa collected from artificial pools along Cave Creek were also found in Cave Creek, and all but 4 taxa from Graveyard Canyon artificial pools were collected from the nearest perennial source, East Turkey Creek. These 4 taxa (*Copelatus chevrolati renovatus*, *Laccophilus sonorensis*, *Berosus infuscatus*/*fraternus*, and *B. stylifer*) are known from seasonal ponds located 14 kilometers east of Graveyard Canyon (Bogan et al. *in review*).

Mean invertebrate abundances were significantly higher (2-3x) in artificial pools closest to the stream channel when compared to artificial pools at 75 and 250 m inland from both Cave Creek and Graveyard Canyon (Fig. 3.2, Table 3.1). Mean invertebrate abundances in artificial pools along the perennial Cave Creek were 2-3 times higher than abundances in artificial pools at all three distances along ephemeral Graveyard Canyon. Overall species richness was marginally higher in closer tanks at both streams, but did not differ significantly between streams. The significant interaction of distance and stream on colonist richness indicated that while richness did not significantly change with distance at Cave Creek, colonist richness significantly declined with increasing distance from the channel at Graveyard Canyon (Fig. 3.2, Table 3.1).

We found significant differences in artificial pool communities among the three distances from the stream channel and between Cave Creek and Graveyard Canyon, and we detected a different effect of distance on community structure in each of the two streams (Table 3.1). The most abundant taxa in artificial pools along both streams were *Callibaetis* (Baetidae) and *Apedilum* (Chironomidae), while *Culiseta* (Culicidae), *Liodessus* (Dytiscidae) and early instar Libellulidae were also common colonists at both sites. *Fallceon* (Baetidae), *Stempellinella*, *Paramerina*, and *Phaenopsectra* (Chironomidae) were common in Cave Creek artificial pools, but were rare or absent in Graveyard Canyon artificial pools.

Invertebrate richness in artificial pools increased slowly during the first three weeks of our visual surveys, especially in the more distant 75 m and 250 m pools (Fig. 3.3). Adult beetles and bugs arrived quickly in many tanks, often within minutes of filling the tanks with water. Mosquito and chironomid larvae and mayfly nymphs appeared in week 2, Hydroporinae beetle larvae appeared in week 3, and dragonfly nymphs appeared in week 5. Following the 58.2 mm of rain that fell during week 3, mean species richness of artificial pools more than tripled in the fourth week of the experiment (average increase in number of taxa: 6.8 ± 1.5 SD). Species richness then leveled off or declined slightly in the final two weeks of the experiment. Results from the NMS ordination (*stress*: 0.21, *final instability* = 0.0006, $p = 0.02$) of the weekly visual survey presence-absence distance matrix largely mirrored the species richness results. Artificial pool communities shifted weekly along the dominant NMS axis 2 ($R^2 = 0.42$) until the 4th week of the experiment (Fig. 3.4). In weeks 4 through 6 there was little distinction of community types along NMS axis 2 (Fig. 3.4), suggesting that the community composition described by that axis had stabilized. Mean Sorensen’s distance between the composition of final visual surveys and the destructive sampling of each artificial pool was 0.11 (± 0.2 SE), indicating nearly 90% overlap in taxa identified visually and with a microscope.

We identified spatio-temporal aerial dispersal modes for 56 of the 66 taxa identified in the 6-wk colonization experiment (Table 3.2). The remaining 10 taxa were not detected during weekly visual surveys, so we could not identify aerial dispersal modes for those taxa. Over 43% of these 56 taxa were infrequent dispersers, 34% were cue-limited, 11% were widespread haphazard, 7% were range-restricted, and 5% were widespread opportunistic. Figure 3.5 diagrammatically represents these aerial dispersal modes for 5 representative taxa. Several Coleoptera and Diptera and the hemipteran *Microvelia* were widespread dispersers, cue-limited dispersers were predominantly coleopterans, range-restricted dispersers were exclusively dipterans, and infrequent dispersers included coleopterans, hemipterans, ephemeropterans, trichopterans, odonates and non-insects.

3.3.3. Two-week colonization rate experiment

We identified 21 colonist taxa during the 2-wk colonization rate experiment, 20 coleopterans and 1 hemipteran. Despite the short time period of the experiment and the lack of leaf-litter and potential prey base, 2593 beetles and bugs colonized the 12 artificial pools. Nearly 48% of these taxa were cue-limited dispersers, 33% were infrequent, 9% were widespread opportunistic and 9% were widespread haphazard. Total abundance of colonists summed across all 12 artificial pools was closely linked to daily rainfall amount (Fig. 3.6). Daily colonization rate was strongly correlated with daily rainfall (mm) for each of the three distances separately and also when considering the mean of all distances. Rainfall amount explained 75% of the variation in colonization rate when averaged across the three treatments ($\beta = 0.83$, $p = 0.00006$; Fig. 3.7). When considered individually, regression coefficients were highest and the most variance was explained by rainfall in the 250 m artificial pools ($R^2 = 0.77$, $\beta = 1.73$, $p = 0.00004$), with decreasing but still significant regression coefficients at 75 m ($R^2 = 0.48$, $\beta = 0.41$, $p = 0.006$) and 5 m ($R^2 = 0.70$, $\beta = 0.34$, $p = 0.0002$).

3.3.4. Differences between the experiments

All 21 taxa collected during the 2-wk experiment were also collected during the 6-wk colonization experiment. Relative abundances of the 5 aerial dispersal modes for those 21 taxa largely followed the patterns from the 6-wk experiment, except for the lack of range-restricted taxa, a higher percentage of cue-limited taxa, and a lower percentage of infrequent taxa. Taxa from the 6-wk experiment that were not found in the 2-wk experiment (Table 3.3) included larvae of all chironomid and culicid taxa, larvae of mayfly, dragonfly, and beetle taxa, numerous adult-stage beetle and bug taxa and non-insect invertebrates.

3.4 DISCUSSION

Though aerial dispersal of aquatic invertebrates along and between drainages likely plays an essential role in maintaining local populations, spatial and temporal variation in aerial dispersal are rarely measured. We quantified spatio-temporal aerial dispersal patterns by measuring insect colonization of novel habitats at three distances from two arid-land stream channels through time. Though many regional aquatic beetle and bug species are capable of dispersing several kilometers (Stevens et al. 2007) and a widely-used trait matrix only quantifies potential aerial dispersal ability as greater or less than 1 km (Poff et al. 2006), we found that the spatial and temporal patterns of aerial dispersal vary significantly among species at much smaller spatial scales (<250 m). This species-specific variation in aerial dispersal mode resulted in discernible patterns in the abundance and composition of colonists in artificial pools at different distances from our arid-land study streams.

3.4.1. Spatial dispersal patterns

Aquatic invertebrate abundance decreased with increasing distance inland from the stream channel at the perennial site, Cave Creek, as we hypothesized. Declines in the abundance of dispersing aquatic invertebrates with increasing distance from potential source populations have been observed in dragonflies (McCauley 2006), midges (Delettre and Morvan 2000), predaceous diving beetles (Wilcox 2001), mayflies, stoneflies and caddisflies (Petersen et al. 2004), as well as in adult aquatic insects as a group (Jackson and Resh 1989). Contrary to our predictions, though, this effect of distance on abundance of dispersers was also significant at our ephemeral site. We had expected that because there was no local source of dispersers in the dry channel of Graveyard Canyon, invertebrates dispersing overland from other source populations would be equally likely to encounter tanks along and inland from the dry channel. Instead, artificial pools 5 m from the dry channel contained significantly more invertebrates than artificial pools at 75 and 250 m inland from the channel. This suggests that aquatic invertebrates dispersing from nearby perennial sources (e.g. East Turkey Creek; Fig. 3.1) may be preferentially following dry stream courses in search of new habitats. In New Zealand, Winterbourn et al. (2007) also found that dry streams may be important dispersal corridors for aquatic insect adults. While we only studied a single ephemeral stream and thus are limited in our ability to generalize, our findings provide further support for the possibility that ephemeral stream channels may serve as important dispersal corridors for adult aquatic insects.

In addition to reduced abundances, communities in more isolated habitats tend to have fewer species since they experience lower rates of dispersal from source habitats (Cadotte 2006). Based on this assumption, we hypothesized that species richness would decline inland from the perennial source of dispersers at Cave Creek but not at the ephemeral Graveyard Canyon. However, we found no relationship between distance and richness at Cave Creek and a strong decline in richness with distance at Graveyard Canyon. To explore what may be driving this surprising result, we examined the occurrences of common species in artificial pools at both sites. At Graveyard Canyon, all abundant taxa were more likely to be found in artificial pools adjacent to rather than inland from the stream channel. At Cave Creek, however, several taxa with high abundances were rarely or never encountered in artificial pools adjacent to the stream, but were common in the more distant 75 and 250 m artificial pools, including libellulid dragonfly nymphs, the midge *Pseudochironomus*, and the beetles *Anacaena*, *Hydraena*, and *Liodessus*. A post-hoc assessment of the contrasting effects of distance on the presence and abundance of these five taxa between the two study streams is sufficient to explain the lack of distance effect on species richness at Cave Creek (Fig. 3.2). When these five taxa were removed from analyses, invertebrate richness and abundance both declined with distance inland from Cave Creek and Graveyard Canyon.

Rather than being a violation of the long-standing idea that disperser or colonist abundance and richness decrease with increasing isolation (MacArthur and Wilson 1967), the pattern that these five taxa exhibited in Cave Creek artificial pools may be an example of a hump-shaped relationship between isolation and disperser abundance. McCauley et al. (2009) noted such a hump-shaped isolation-abundance relationship for the backswimmer *Notonecta irrorata* in artificial pools placed from 0 to 1200 m away from potential source populations. Dispersing individuals of some species may not colonize sites closest to their natal habitat, and instead colonize sites at moderate distances, presumably to avoid inbreeding or deteriorating environmental conditions associated with their natal habitat (McCauley et al. 2009). If taxa were dispersing inland from Cave Creek, they may have flown past the closest artificial pools and instead preferentially colonized the further artificial pools. In contrast, if taxa from perennial sources populations at East Turkey Creek were dispersing along or inland from the ephemeral channel of Graveyard Canyon, they would have already traveled a minimum of 900 m from the nearest perennial pools and may not have been able to risk further travel in search of aquatic habitat. Though the spatial scale of our study does not allow us to quantify the exact hump-shaped isolation-abundance relationship for these five taxa, it appears that they may increase in abundance between 0 and 250 m and then decrease in abundance by 900 m, if not closer.

3.4.2. Temporal dispersal patterns

During the dry weather period of the first three weeks of our 6-wk experiment, several beetle and true bug species arrived and a few species of dipterans oviposited and their larvae began to develop in artificial pools. Warm and dry weather conditions have been previously been associated with increased dispersal of multiple species of water beetles (Ryker 1975; Miguelez and Valladares 2008) and true bugs (Pajunen and Jansson 1973), and arid-land streams often have large swarms of midges on warm summer evenings (Jackson 1988). Midge colonization of artificial pools in the floodplain of a large Alabama river also peaked in warm summer months, and up to 14 midge taxa colonized artificial pools there in less than 3 weeks (Tronstad et al. 2007), including the genera *Apedilum*, *Larsia*, *Labrundinia*, and *Tanytarsus* which also colonized our artificial pools. Additionally, 7 of the 21 taxa detected during our 2-wk experiment arrived at artificial pools in low numbers on dry summer days, indicating a small, but measureable background rate of dispersal for multiple local aquatic invertebrate species.

This slow arrival of a limited number of species during dry weather was interrupted by the onset of monsoon rainfall when nearly 60 mm of rain fell between our visual surveys in weeks 3 and 4 of the 6-wk experiment. While heavy rainfall and high humidity have previously been associated with reduced dispersal of aquatic macroinvertebrate (Miguelez and Valladares 2008; Boix et al. 2011), species richness in our artificial pools more than doubled during that rainy week (Fig. 3.3). The results from our 2-wk experiment provide further support for the importance of rainfall in triggering or facilitating macroinvertebrate dispersal in our study system; daily rainfall amount explained up to 77% of the variation in daily abundance of artificial pool colonists (Fig. 3.6 and 3.7). Furthermore, the slope of the relationship between rainfall and number of colonists increased with distance from the stream, indicating that rainfall was more important for facilitating dispersal to distant habitats than to closer habitats. The contrast between our findings and past studies may be in part due to our study's arid location. Rainfall in arid regions may act as a signal that new, seasonal habitats are available and thus trigger dispersal to these new habitats, as it does for some giant water bugs (Lytle and Smith 2004) and spadefoot toads (Stebbins 2003). Additionally, in a hot, arid landscape, the increased humidity associated with rainfall events may facilitate successful dispersal of aquatic invertebrates by reducing the risk of desiccation while traveling through the terrestrial environment.

Though rainfall explained the majority of variation in aerial disperser abundance in our study, other environmental factors are also likely to be important triggers or facilitators of aerial dispersal. Past studies have documented that drying habitat and rising stream temperatures can trigger aerial dispersal from isolated arid-land stream pools (Velasco and Millan 1998). Indeed, the process of pool habitat contraction was occurring in our perennial study streams before monsoon rains began (Bogan and Boersma, pers. obsv.). These lowering pool levels likely provided a cue that local habitat conditions were deteriorating and may have provided additional impetus to leave the pool as soon as rainfall signaled that new habitats were potentially available. We did not measure wind direction or intensity in this study, but it is likely that calmer conditions immediately following monsoon rains would also make it easier for many species to fly, as lighter winds have been correlated with higher rates of aerial dispersal in past studies (Briers et al. 2003; Boix et al. 2011). Aerial dispersal of the smallest stream invertebrate species, though, may increase during windy conditions as these smaller taxa are carried by wind further than they would be able to disperse on their own (e.g. flightless microcrustaceans: Caceres and Soluk 2002; microcaddisflies: Jackson and Resh 1989). Small, flightless invertebrates were too rare in our study to assess the effects of environmental factors on aerial dispersal of these taxa. Future studies should incorporate measurements of wind direction and speed to disentangle the effects of wind and precipitation on aerial dispersal patterns of stream invertebrates.

3.4.3. Aerial dispersal traits

We classified taxa from our study into one of five spatio-temporal aerial dispersal categories based on the timing and extent of their colonization of artificial pools: (1) widespread abundant, (2) widespread haphazard, (3) range-restricted, (4) cue-limited, and (5) infrequent (Fig. 3.5). Compared with previously published aerial dispersal traits (e.g., Poff et al. 2006; Bonada et al. 2007), these five categories provide substantially more information about both the tendency of a given species to disperse though time and the distance inland that it may disperse. These categories also take into account the importance of precipitation as a trigger of dispersal. Though time-consuming work is required to quantify the aerial dispersal ability of individual species, we argue that the utility of this information makes the effort worthwhile.

Understanding species-specific variation in aerial dispersal ability will allow researchers and managers to develop spatially-explicit predictive models for community responses to and recovery from anthropogenic disturbance (Patrick and Swan 2011), stream restoration efforts (Parkyn and Smith 2011), and climate change (Bonada et al. 2007). In streams that experience large seasonal or interannual expansion and contraction of wetted habitat, such as arid-land streams (Stanley et al. 1997; Bogan and Lytle 2007) and large temperate rivers (Tronstad et al. 2007) among others, aerial dispersal can be the primary means of recolonizing rewetted habitats. In our study region, long-term drought is causing isolated, formerly-perennial streams to experience unprecedented drying. Following total stream drying and subsequent rewetting at one Arizona stream, French Joe Canyon, the true bug *Microvelia* and the beetle *Liodessus* were both early colonizers and dominant post-drying community members (Bogan and Lytle 2011), as would be predicted given the “widespread abundant” dispersal mode we assigned these taxa in our current study. Several taxa incapable of aerial dispersal were extirpated by the drying event at French Joe and had not recolonized the stream in the four years following the initial drying and rewetting event. Taxa classified as being "infrequent" or "range-restricted" aerial dispersers would be much less likely to recolonize isolated habitats such as French Joe following drought-induced stream drying or other disturbances.

We used invertebrate colonization of artificial pool habitats as our metric to measure aerial dispersal; however some taxa cannot be detected using this method. Though local perennial stream habitat is dominated by isolated pools during the dry season, small lotic patches remain and most of the rheophilic taxa found in these patches (e.g., Hydropsychidae, Simuliidae, Heptageniidae) did not colonize our artificial pools. To identify aerial dispersal modes for these taxa, other methods may have to be employed such as sticky or Malaise traps (Jackson and Resh 1989; Petersen et al. 2004) and pan traps (Delettre and Morvan 2000). Additionally, artificial pools could incorporate recirculating pumps and coarse mineral substrate to encourage colonization by dispersing rheophilic taxa. The relatively few "range-restricted" taxa identified in this study likely results from our failure to detect rheophilic dispersers, as it is well known that many rheophilic mayfly, stonefly, and caddisfly taxa preferentially disperse along rather than inland from streams (Petersen et al. 2004; Macneale et al. 2005; Winterbourn et al. 2007).

In addition to quantifying aerial dispersal modes of rheophilic taxa, future studies should address the seasonality of aerial dispersal of stream invertebrates. While many studies have found that aerial dispersal of aquatic insects tends to peak during summer months (e.g., Tronstad et al. 2007), numerous dragonfly, beetle, and true bug taxa undergo spring and fall migration flights as well (Corbet 1999; Stevens et al. 2007). In our study region, large mixed-species dispersal swarms of thousands of aquatic beetles and true bugs are known to occur in both spring and fall (Stevens et al. 2007) and these large flocks surely have strong ecological impacts on the pools they colonize.

Our two complementary experiments suggest that any future studies must acknowledge the different information content provided by various measures of dispersal. Artificial pools in the 2-wk experiment were destructively sampled every 12h, thereby prohibiting community development (Table 3.3). Our 6-wk experiment included a leaf litter nutrient base and was only sampled once, allowing communities to develop through time. Therefore, our 2-wk experiment is more likely to measure arrival at novel habitats than colonization per se. While both arrival and colonization are important measures of dispersal, they provide different types of information: the capacity to find novel habitats versus the decision to stay and reproduce in the novel habitat. In studies of community development, it is frequently impossible to differentiate between the two mechanisms (Vonesh et al. 2009), but our paired experiments provide a means to tease apart these different yet complementary processes and may provide a model for future studies. Our study represents an important first step in understanding spatio-temporal variability of aquatic invertebrate aerial dispersal in arid regions. These data, in addition to data from future studies, will facilitate understanding of metacommunity processes and allow predictions of community assembly in the wake of environmental disturbances like drought-induced stream fragmentation and drying.

ACKNOWLEDGEMENTS

Thanks to Dawn Wilson and the staff of the Southwestern Research Station (American Museum of Natural History) in Portal, AZ for logistical support and United States Forest Service scientific research permits issued for this study. Funding came from a Southwestern Research Station Student Support Fund grant to MTB and a World Wildlife Fund Fuller Doctoral Fellowship and an American Museum of Natural History Theodore Roosevelt Memorial Fund grant to KSB. Previous versions of this manuscript benefited from the comments of S.V. Gregory.

Table 3.1 ANOVA (for abundance and richness) and perMANOVA (for community structure) results for the effect of distance (5 m, 75 m, 250 m) and stream (perennial Cave Creek versus ephemeral Graveyard Canyon) on the abundance, richness, and community composition of replicate artificial pools at the end of the 6-week experiment.

		Abundance		Richness		Community composition	
	df	*F*	*p-value*	*F*	*p-value*	*F*	*p-value*
Distance	2	8.275	0.003	3.448	0.053	3.5651	0.0004
Stream	1	17.455	0.001	0.221	0.644	4.7283	0.0004
Interaction	2	2.511	0.109	4.823	0.021	2.8073	0.002
Residuals	18						

Table 3.2 All taxa collected from or observed in artificial pools during the 6-wk experiment listed in order of their aerial dispersal modes. Taxa only identified during final destructive sampling (i.e. not identified during visual surveys over the 6 week period) could not be associated with a dispersal mode and are listed as "Unknown".

Aerial dispersal mode	Order	Family	Genus / species
Widespread Opportunistic	Coleoptera	Dytiscidae	*Liodessus*
	Diptera	Chironomidae	*Apedilum*
	Hemiptera	Veliidae	*Microvelia*
Widespread Haphazard	Coleoptera	Dytiscidae	*Sanfilippodytes*
		Dytiscidae	*Stictotarsus aequinoctialis*
		Hydrophilidae	*Tropisternus ellipticus*
	Diptera	Chironomidae	*Chironomus*
			Paratanytarsus
			Psuedochironomus
Cue-limited	Coleoptera	Dryopidae	*Helichus suturalis*
			Helichus triangularis
			Postelichus immsi
		Dytiscidae	*Copelatus chevrolati renovatus*
			Desmopachria portmanni
			Hydroporinae (larvae)
			Laccophilus fasciatus
			Neoclypeodytes
			Rhantus atricolor
			Rhantus gutticollis gutticollis
			Rhantus gutticollis mexicanus
			Rhantus (larvae)
		Hydraenidae	*Hydraena*
		Hydrophilidae	*Berosus salvini*
			Berosus (larvae)
			Cymbiodyta
			Helophorus
	Ephemeroptera	Baetidae	*Callibaetis*
	Hemiptera	Corixidae	*Graptocorixa serrulata*
Range-restricted	Diptera	Culicidae	*Anopheles*
			Culex
			Culiseta
		Chironomidae	*Paramerina*

Infrequent	Coleoptera	Dytiscidae	*Laccophilus maculosus*
			Laccophilus pictus
			Laccophilus sonorensis
			Stictotarsus corvinus
			Stictotarsus striatellus
		Gyrinidae	*Dineutus sublineatus*
			Gyrinus plicifer
		Haliplidae	*Peltodytes dispersus*
		Hydrophilidae	*Anacaena*
			Berosus infuscatus/fraternus
			Berosus moerens
			Berosus stylifer
			Enochrus carinatus
			Helochares normatus
			Laccobius cf. *hardyi*
	Ephemeroptera	Baetidae	*Fallceon*
	Hemiptera	Gerridae	*Aquarius remigis*
		Naucoridae	*Ambrysus woodburyi*
		Nepidae	*Ranatra quadridentata*
		Notonectidae	*Notonecta lobata*
		Veliidae	*Rhagovelia varipes*
	Odonata	Libellulidae	indet.
	Trichoptera	Helicopsychidae	*Helicopsyche*
	non-insect	Hydracarina	indet.
Unknown	Coleoptera	Hydraenidae	*Octhebius* cf. *lineatus*
			Octhebius cf. *puncticollis*
	Diptera	Chironomidae	*Labrundinia*
			Larsia
			Phaenopsectra
			Stempellinella
			Tanytarsus
	non-insect	Copepoda	Copepoda
	non-insect	Hydracarina	*Mucronothrus*
	non-insect	Collembola	Sminthnuridae

Table 3.3 Taxa recorded from the 6-wk experiment (artificial pools with leaf litter that were not sampled destructively until the end of week 6) that were not recorded from the 2-wk experiment (artificial pools with no leaf litter that were sampled destructively every 12 hours), listed in columns by aerial dispersal mode.

Widespread opportunistic	Widespread haphazard	Cue-limited	Range-restricted	Infrequent	Unknown
Apedilum	*Stictotarsus aequinoctialis*	*Berosus* (larvae)	*Anopheles*	*Ambrysus woodburyi*	Copepoda
	Chironomus	*Callibaetis*	*Culex*	*Aquarius remigis*	*Labrundinia*
	Paratanytarsus	*Graptocorixa serrulata*	*Culiseta*	*Dineutus sublineatus*	*Larsia*
	Pseudochironomus	*Helichus triangularis*	*Paramerina*	*Fallceon quilleri*	*Mucronothrus*
		Hydroporinae (larvae)		*Gyrinus plicifer*	*Phaenopsectra*
		Neoclypeodytes		*Helicopsyche*	Sminthnuridae
		Postelichus immsi		*Helochares normatus*	*Stempellinella*
		Rhantus gutticollis mexicanus		Hydracarina	*Tanytarsus*
		Rhantus (larvae)		*Laccobius* cf. *hardyi*	
				Laccophilus maculosus	
				Laccophilus sonorensis	
				Libellulidae	
				Notonecta lobata	
				Peltodytes dispersus	
				Ranatra quadridentata	
				Rhagovelia varipes	
				Stictotarsus corvinus	
				Stictotarsus striatellus	

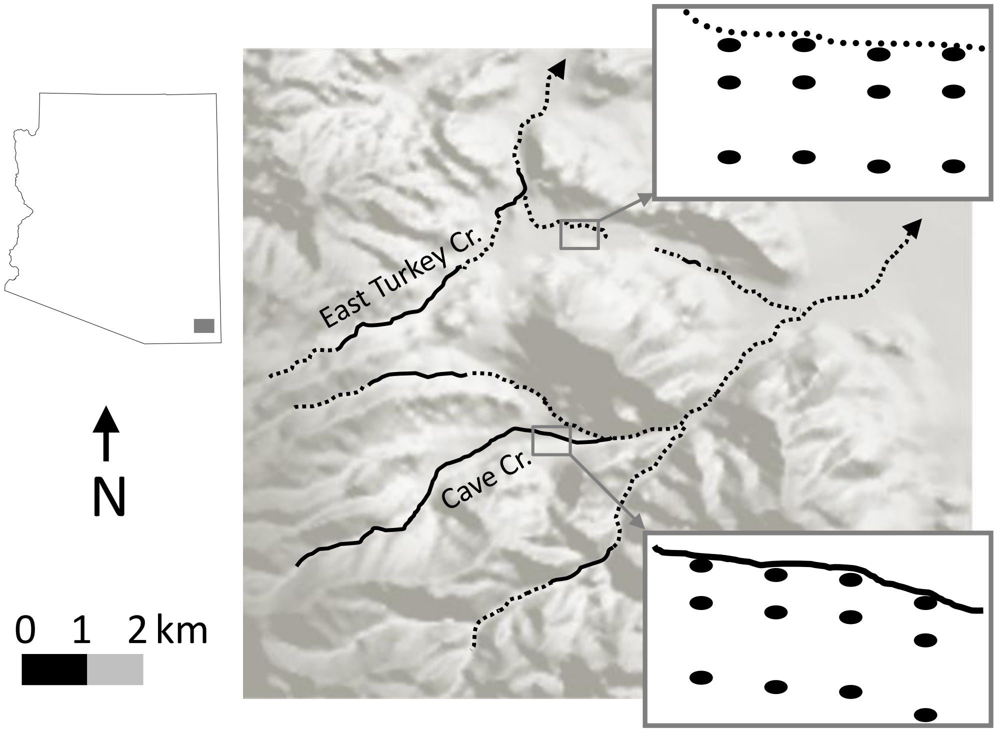

Figure 3.1 Study location and topography near the sites at Cave Creek (perennial) and Graveyard Canyon (ephemeral; tributary to East Turkey Creek), in the Chiricahua Mountains of southeast Arizona. Inset boxes show the experimental design, with four replicate artificial pools placed at each of three distances (5, 75, and 250 m) from the stream channels at Cave Creek and Graveyard Canyon.

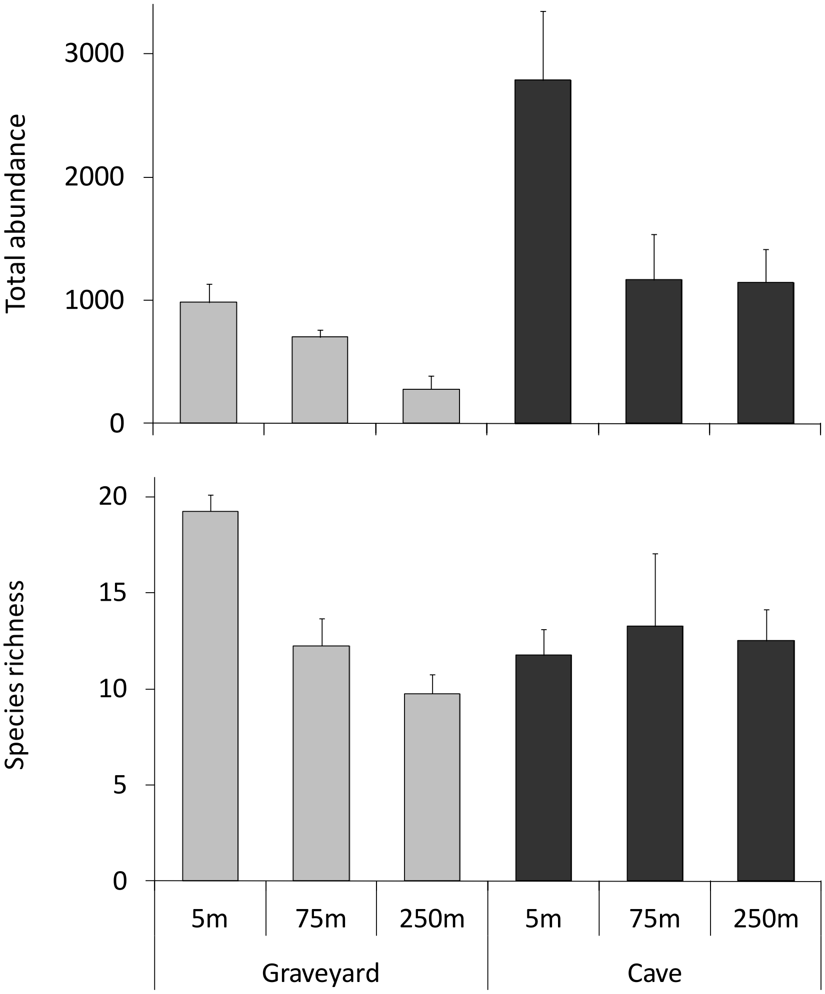

Figure 3.2 Mean total abundance (± SE) and species richness (± SE) in replicate artificial pools at three distances (5, 75, 250 m) inland from Cave Creek (perennial) and Graveyard Canyon (ephemeral) from destructive sampling of the pools at the end of the 6-week experiment.

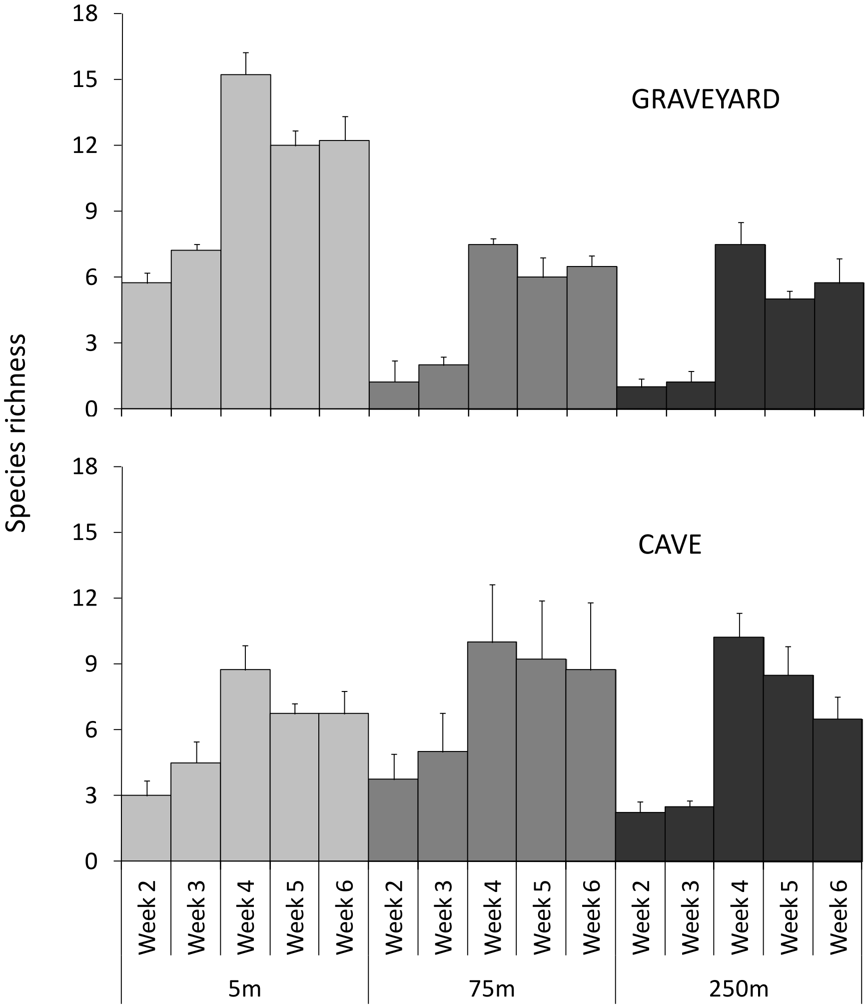

Figure 3.3 Mean species richness (± SE) from weekly visual surveys (beginning week 2) of replicate artificial pools at three distances (5, 75, 250 m) inland from Cave Creek (perennial) and Graveyard Canyon (ephemeral). There was little rain during the first 3 weeks of the experiment, but heavy monsoon rain events began occurring between weeks 3 and 4.

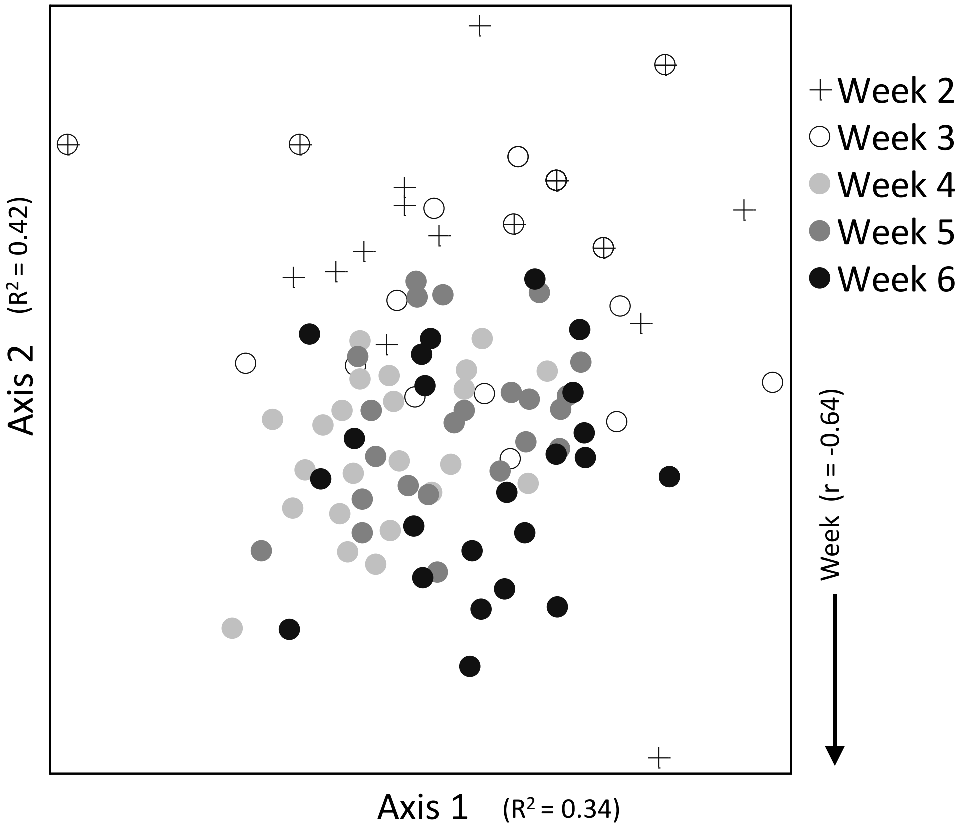

Figure 3.4 NMS ordination of community development all 24 artificial pools based on a presence/absence community matrix derived from weekly visual surveys during the 6-week experiment. Artificial pool communities changed progressively along axis 2 through week 3, but were fairly similar to one another in weeks 4 through 6.

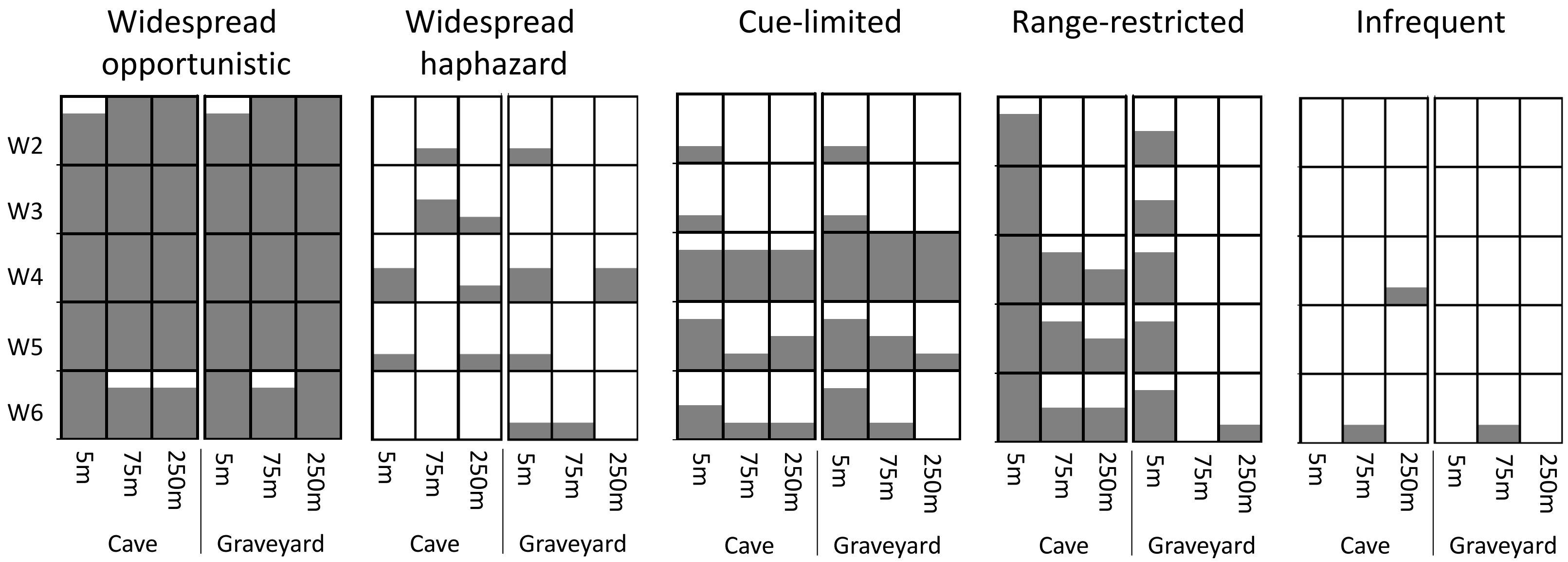

Figure 3.5 Diagrammatic representation of the 5 identified aerial dispersal modes based on weekly visual surveys during weeks 2 through 6 (W2-W6) of the 6-week experiment. A box completely shaded with dark grey indicates that a given species was found in all 4 replicate artificial pools at that distance for that site and week, while an all white box indicates that the species was not detected in any artificial pools at that site and week. Species used to illustrate the dispersal modes here include *Liodessus* (widespread opportunistic), *Sanfilippodytes* (widespread haphazard), *Rhantus gutticollis* (cue-limited), *Culex* (range-restricted), and *Berosus moerens* (infrequent).

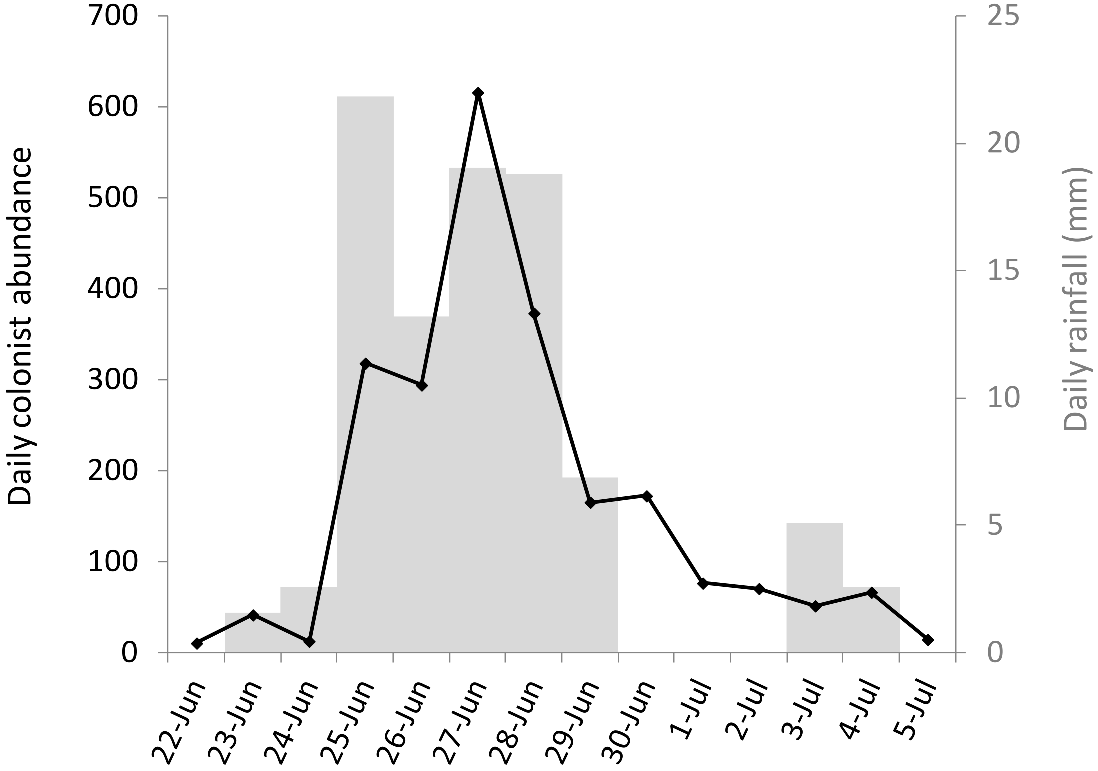

Figure 3.6 Synchronicity of daily rainfall total (mm) and the sum of colonist abundances across the 12 artificial pools during the 2-wk experiment.

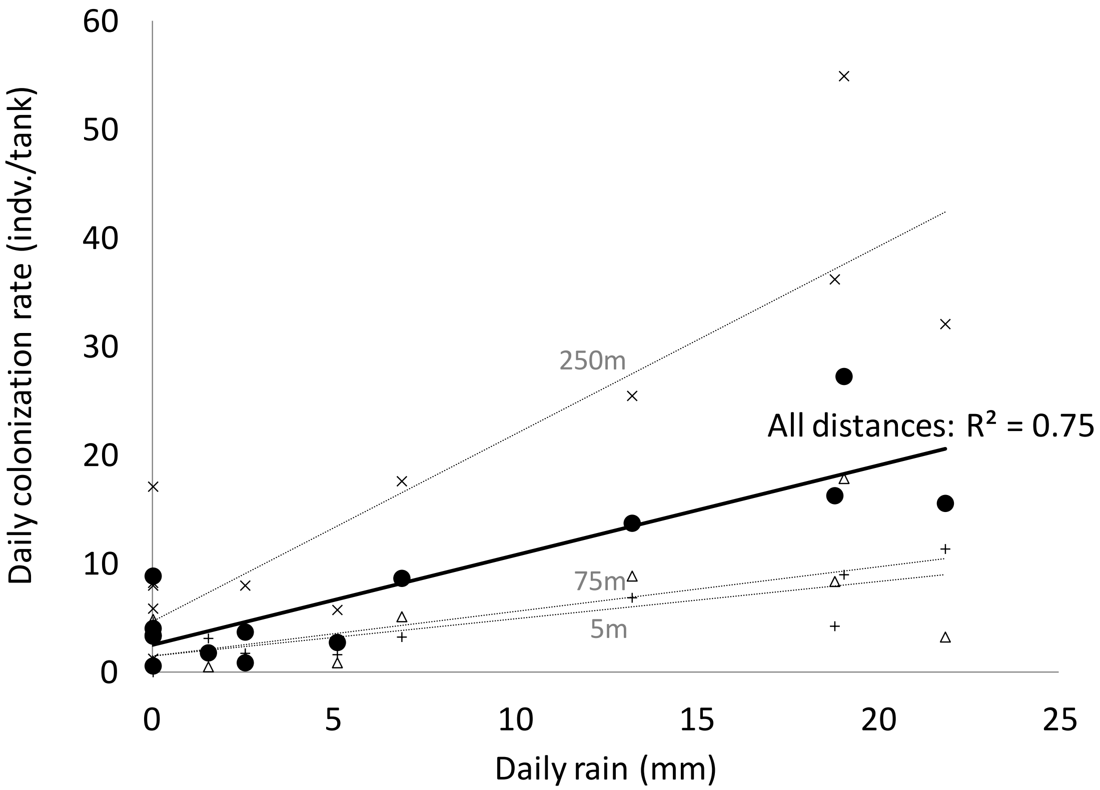

Figure 3.7 Correlation between daily rainfall and colonization rate during the 2-wk experiment. The correlation between rainfall and colonization rate was significant for each of the three treatment distances (dashed lines; 5 m, 75 m, 250 m), but the slope became steeper at greater distances from the stream. Rainfall explained 75% of the variation in the mean colonization rate of all three treatment distances (bold line).

CHAPTER 4- Distinct intermittent stream invertebrate communities alter longitudinal gradients of diversity and community structure in an arid-land stream network

Michael T. Bogan, Kate S. Boersma, and David A. Lytle

In review:
Freshwater Biology
Wiley-Blackwell Publishing
Hoboken, NJ

ABSTRACT

Temporary streams comprise a large proportion of total length in most stream networks, and the vast majority of length in arid-land stream networks, so it is important to understand their influence on biotic diversity and community structure at both local and landscape levels. We quantified patterns of invertebrate richness and community structure at 12 reaches in a large arid-land stream network (including perennial and intermittent headwaters, intermittent middle reaches, and perennial valley rivers) in southeast Arizona, USA. Sampling occurred in late winter 2010, when intermittent reaches had been flowing for approximately 60 days, following a dry period of more than 450 days. Additionally, we sampled a subset of the perennial study reaches three additional times between 2009 and 2011 and two nearby intermittent streams in 2004-2005 and 2010. Invertebrate richness was lowest in intermittent reaches, despite often having flow connectivity to species-rich upstream perennial reaches. These species-poor intermittent reach communities were not simply a subset of perennial species, but rather were numerically dominated by a suite of stonefly, blackfly, and midge genera and species with adaptations to intermittency (e.g., egg and larval diapause). On average, 86% of individuals in intermittent samples were intermittent exclusives or specialists. Perennial reaches also contained 7-14 times as many predators as intermittent reaches. Despite being separated by long distances (12-25km) and having very different physical characteristics, perennial headwater and valley river communities were more similar to one another than to intervening intermittent reaches, emphasizing the importance of local hydrology over network structure in this system. The duration and recurrence intervals of dry periods and the relative importance of dispersal from perennial refuges likely influence the magnitude of biological differences between neighboring perennial and temporary streams. Though perennial headwater reaches supported the highest diversity of invertebrates, intermittent reaches supported a number of unique species and as such

they contribute to regional species diversity and should be included in conservation planning.

4.1 INTRODUCTION

Natural flow regime characteristics, such as the timing and magnitude of high- and low-flow events, are widely recognized as “master variables” in determining diversity and community composition in streams (Resh et al. 1988; Poff 1997). In recent years, drought and no-flow events have been increasingly acknowledged as important environmental drivers in many streams and as the primary environmental drivers in intermittent (seasonal flow in response to groundwater recharge) and ephemeral (short-term flow in direct response to precipitation events) streams (Williams 1996; Boulton 2003; Lake 2003; Larned et al. 2010a). While the number of studies of intermittent and ephemeral streams has grown greatly in the last 10 years (Datry, Arscott and Sabater 2011), there is still much to learn about the role that flow intermittence plays in driving patterns of aquatic invertebrate diversity and community structure in stream networks. Given that both the extent and intensity of intermittency is expected to increase globally due to climate change and anthropogenic water withdrawals (Larned et al. 2010a), further studies on the effect of intermittence on all aspects of stream ecology are clearly needed.

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

Several studies have found higher aquatic invertebrate diversity in perennial streams than in intermittent streams (Brussock and Brown 1991; Fritz and Dodds 2002; Ruegg and Robinson 2004; Grubbs 2011), while others have found equal diversity in perennial and intermittent streams (Feminella 1996; Chester and Robson 2011). Some of these apparent differences may be explained by differences in study design and relative flow duration of intermittent reaches (Datry 2012). Additionally, most studies have found broad overlap between perennial and intermittent invertebrate communities and have indentified few to no intermittent specialist species (Delucchi 1988; Wood et al. 2005; Banks et al. 2007; Grubbs 2011; Datry 2012). Relative levels of taxonomic resolution vary among nearly all published studies, though, with many studies leaving difficult-to-identify taxa at the family or order level. For example, midges (Chironomidae) and blackflies (Simuliidae) are often left at the family level (e.g., Grubbs 2011; Datry 2012) or excluded completely from analyses (e.g., Santos and Stevenson 2011), despite the fact that they contain numerous genera and species with life history adaptations for surviving drought (Chou et al. 1999; Adler, Currie and Wood 2004; Cranston et al. 2007). The lack of taxonomic resolution in these families likely has a strong impact on researchers' ability to detect differences between perennial and intermittent invertebrate communities in a given region.

In this study, we quantified aquatic invertebrate diversity, functional feeding group composition, and community structure in multiple perennial and intermittent drainages across a large arid-land stream network ($400km^2$) in southeast Arizona, U.S.A. Most previous comparisons of temporary and perennial streams have focused on small stream networks

(<25km^2: e.g. Delucchi 1988; Santos and Stevenson 2011) or multiple sites along a single river (e.g. Arscott et al. 2010) and have been conducted in temperate regions. In addition to quantifying differences in invertebrate taxonomic and functional trait metrics between perennial and intermittent reaches, our goal was to understand whether mid-reach drying altered longitudinal patterns in these metrics across our study stream network. We predicted that we would find: (1) lower invertebrate richness and abundance in intermittent reaches, (2) invertebrate assemblages in intermittent reaches that were a mix of taxa found in perennial reaches and taxa with specific adaptations to intermittency (e.g., diapausing egg or larvae), and that (3) intermittent reaches would interrupt longitudinal gradients in community and functional feeding group composition in our focal stream network.

4.2 METHODS

4.2.1. Site and climate description

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

Stream characteristics and flow regime

Headwater streams in the Huachuca Mountains are generally spring-fed and perennial and occur in limestone bedrock- and cobble-dominated reaches. Downstream of these perennial headwaters, streams flow across alluvial fans with sand and gravel substrate where seepage losses are high; streams become intermittent at the canyon-alluvial fan boundaries (Fig. 4.1). These intermittent reaches only flow for weeks to months following extended periods of precipitation. Further downstream on the alluvial fans, the water table never rises to the level of the stream channel and flow is ephemeral, and only occurs for short periods (<1d) during extreme precipitation events. Below the alluvial fans, perennial valley rivers occur in incised fluvial floodplains; these systems are groundwater-fed and also have predominantly sand and gravel substrate. All stream types are prone to violent monsoon flooding in the summer (Jul-Sep), while wet winters (Nov-Mar) tend to result in prolonged increased baseflow in both perennial and intermittent reaches (Fig. 4.2).

While there are no flow gauges in our intermittent study reaches, a nearby intermittent alluvial stream, Banning Creek (Figs. 4.1, 4.2), is gauged and served as a proxy for short- and long-term flow patterns in our intermittent study reaches. Long-term analysis of flow records at the Banning gauge identified 5 years with >30 days of winter flow between 2001 and 2011, suggesting that intermittent reaches in the region become activated in about 45% of years. During these wet winters, surface flow occurred at Banning Creek for an average of 77 days (range: 42-103 days; Fig. 4.2). Concurrent with our sampling, electrical conductivity sensors were installed in all of our intermittent study reaches and preliminary results from these sensors (see Jaeger and Olden 2011) support the use of Banning Creek as a proxy for long-term flow patterns in our intermittent reaches.

4.2.2. Data collection

We measured habitat conditions and collected aquatic invertebrate community samples from riffles and pools across a network of 12 reaches in 6 streams during 26-31 March 2010, near the end of the high-flow winter season (Figs. 4.1, 4.2). Three of these reaches occurred in perennial headwaters, seven were alluvial intermittent, and two were perennial valley river. These intermittent reaches had been flowing for approximately 60 days, following a period of complete lack of water for over 460 days (Fig. 4.2). In many published studies of recovery from drying, 60 days is sufficient time for invertebrate communities to develop (Stanley et al. 1994; Paltridge et al. 1997; Fritz and Dodds 2004). While 60 days may not always allow for a “climax” community to develop (for example, in some Georgia intermittent streams community composition stabilized between 45 and 165 days; Churchel and Batzer 2006), our intermittent reaches began to dry after 80 days. Thus, we attempted to balance allowing time for community development with the need to sample streams before they dried. We were unable to collect invertebrate samples from ephemeral reaches in our stream network, as these reaches only supported surface water for <1 day at a time during storm pulses.

At each study reach, we collected three riffle samples and three pool samples, when those microhabitat types were present. Riffles were sampled by taking a kick sample, where 0.33 m^2 of riffle substratum was disturbed to a depth of 5 cm and invertebrates were captured downstream with a D-net (500μm mesh). Pools, when present, were sampled by vigorously sweeping a D-net (500μm mesh) above all pool substrata and on the surface of the water with an effort of 10 s per m^2 of pool (see Bogan and Lytle 2007, 2011). Samples were preserved in 95% ethanol and later identified to the finest taxonomic resolution practical, usually to genus or species for insects and family or order for non-insects.

In addition to dense sampling of our focal stream network in March 2010, we also sampled three of the perennial reaches in November 2009 and 2010, and March 2011 to document temporal variability in perennial headwaters and valley rivers. Intermittent reaches in our focal network were dry during these additional sampling periods, so we explored the consistency of the intermittent communities by sampling two additional intermittent sites, located east and northeast of our focal stream network. Intermittent riffles at Banning Creek (Fig. 4.1) were sampled in March 2010, while intermittent riffles at West Stronghold Canyon (located 30 km N of Banning Creek) were sampled during March of each of the last three years with abundant winter precipitation: 2004, 2005 and 2010. These two comparison sites are both intermittent headwater streams (no perennial flow located upstream or downstream of study reaches), and are isolated by > 10 km of downstream ephemeral channel from the nearest perennial valley river reach.

At each sample location, we measured water temperature, pH (Whatman pH Indicators, Whatman International, Maidstone, England), conductivity (Milwaukee waterproof EC meter C65; Milwaukee Instruments, Rocky Mount, NC, U.S.A.), and dissolved oxygen (Chemetrics K-7512, CHEMetrics Inc, Calverton, VA, U.S.A.) and also made visual estimations of riparian canopy cover and benthic substratum cover (categories with particle diameters: silt (<0.25mm), sand (0.25-2mm), gravel (2-64mm), cobble (64-256mm) and boulder/bedrock (>256mm)).

4.2.3. Data analyses

Univariate differences in aquatic invertebrate richness and abundance, Chironomidae relative abundances, functional feeding group relative abundances, and measured environmental variables among perennial headwater, intermittent, and valley river reaches were analyzed using Kruskal-Wallis tests. Taxa were assigned to functional feeding groups using Cummins, Merritt and Berg (2008). Bonferroni-corrected pairwise comparisons were made when significant group differences were detected. Multivariate community differences among the three reach types were visualized 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 (McCune and Grace 2002).

After performing the NMS analyses, we examined linear correlations between the measured environmental variables and ordination axes. We then divided community samples into three a priori groups (headwater, intermittent, valley river) and used multi-response permutation procedure (MRPP) with Sorensen distances to quantify and test within-group agreement and distinctness (Mielke and Berry 2001). We also conducted a higher level MRPP with 6 groups distinguished by both stream type (headwater, intermittent, and valley river) and habitat type (pool vs. riffle). We used indicator species analysis (Dufrene and Legendre 1997) to determine whether particular taxa were indicative of each of the groups. The highest possible indicator value 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). The statistical significance of each indicator value was tested using a Monte Carlo randomization with 1000 runs. Finally, we examined downstream changes in riffle community composition by calculating Sorensen distances between the uppermost headwater samples in Huachuca and Garden Canyons (Fig. 1) and samples progressively further downstream (through intermittent and perennial valley river reaches). We then plotted Sorensen distance as a function of downstream distance (km).

4.3 RESULTS

4.3.1. *Measured environmental variables*

Temperature, pH, conductivity, and dissolved oxygen all varied significantly among the three stream flow types (all $P < 0.0001$), but in general the effect sizes of most variables were low, with the exception of dissolved oxygen (Table 4.1). pH varied little between reaches, with means changing from 7.3 to 7.0 to 7.5 when moving downstream from perennial to intermittent to valley river reaches. Mean conductivity was nearly equal in headwater (408μS) and intermittent (406μS) reaches, but increased significantly in valley river reaches (560μS). Mean temperatures increased from 11°C to 13.6°C to 14.5°C from headwater to intermittent to valley river reaches, while mean dissolved oxygen decreased along the same gradient (7.8 mg/L to 6.4mg/L to 4.1mg/L). Canopy cover was 2 to 3 times higher in headwater reaches (mean: 82%) than it was in intermittent (mean: 27%) and valley river (mean: 37%) reaches.

4.3.2. *Richness and abundance*

We identified a total of 148 taxa across our stream network in March 2010. Headwater sites supported the highest macroinvertebrate diversity, with 120 taxa identified across all 19 headwater samples; 58 taxa were identified across the 8 valley river samples and only 36 taxa were identified across the 22 intermittent samples. Seventy taxa were exclusive to headwater samples, 16 taxa were exclusively found at valley river sites, and 13 taxa were exclusively found at intermittent sites. The remaining 47 taxa were widespread and occurred in at least two of the three stream types. Mean richness in headwater and valley river samples was more than twice that of intermittent samples (Table 4.2). Sample abundances were not significantly different between headwater and intermittent samples, but valley river samples contained more than three times as many invertebrates as either headwater or intermittent samples (Table 4.2).

4.3.3. Functional feeding groups

Relative abundances of all functional feeding groups except scrapers differed significantly among headwater, intermittent, and valley river samples (Table 4.2). Collector-gatherers comprised the majority of individuals in all three stream types, though they were significantly less abundant in headwater samples (61%) when compared with downstream intermittent (76%) and valley river (80%) samples. Plant piercers were the least abundant functional feeding group at all three stream types (<2%), and were completely absent from intermittent samples. The largest effect size by stream type was seen with predators (engulfers and piercers). Relative abundances of predators in headwater samples were nearly 14 times greater than in intermittent samples, where predators made up only 1.1% of all individuals.

4.3.4. Community composition

NMS analyses resulted in a significant 2-dimensional ordination (Fig. 4.3; stress = 15%, final instability < 0.0001, p = 0.0196) that explained 84% of variability in the distance matrix (axis 1 $R^2 = 0.62$, axis 2 $R^2 = 0.22$). Of the measured environmental variables, none were strongly correlated with axis 1, and only percent canopy cover and percent gravel substrate were strongly correlated with axis 2 (r = -0.62 and 0.51, respectively). The dominant axis 1 clearly separated perennial samples from intermittent samples across multiple streams and multiple years of sampling in both our focal network and comparison intermittent sites. Though there was some seasonal community variation in the subset of perennial and intermittent reaches that we sampled over multiple years, samples from each stream type always stayed within their respective areas of species-space. MRPP analysis confirmed the statistical distinction among these three groups (A = 0.251, p < 0.00001), and all three groups were distinct from one another in Bonferroni-corrected pairwise MRPP comparisons as well. The higher-level MRPP comparison of the six groups delineated by stream type and microhabitat (riffle vs. pool) was significant over all (A = 0.306, $p < 0.00001$), but no significant pairwise differences were found between pool and riffle samples within a given stream type.

Indicator species analysis revealed a number of significant indicators for each of the three groups (Table 4.3). A diverse suite of taxa were indicative of perennial headwater samples, including several caddisflies, mayflies, true flies, beetles, and spring snails. Valley river indicator taxa also were taxonomically diverse and included mayflies, caddisflies, true flies, crayfish, ostracods, oligochaetes, and water mites. Intermittent indicator species, in contrast, were comprised of a single stonefly taxon, *Mesocapnia arizonensis* (Baumann and Gaufin) and five midge taxa (*Eukiefferienlla rectangularis* group, *Chaetocladius piger* group, *Diamesa*, *Hydrobaenus*, and *Krenosmittia*). Indicator values changed little when the analysis was limited to samples from the March 2010 sampling event or also included the additional perennial samples (collected from 2009 to 2011) and comparison intermittent samples collected in 2004, 2005, and 2010; this suggests that indicator taxa were robust across multiple sampling periods.

Thirteen taxa were exclusive to intermittent sites (representing 36% of all taxa found at intermittent sites), including five chironomids (*C. piger* group., *E. rectangularis* group., *Krenosmittia*, *Mesosmittia*, *Parachaetocladius*), three blackflies (*Prosimulium impostor* Peterson, *Prosimulium* sp., *Simulium donovani* Vargus), early instars of three other Diptera families (Dolichopodidae, Ephydridae, and Muscidae), one water mite (cf. *Hydrozetes*), and one stonefly (*M. arizonensis*). These 13 exclusively intermittent taxa accounted for an average of 34% of all individuals collected in intermittent samples (range: 7 to 82%). When two nearly-exclusive intermittent indicator species, the midges *Diamesa* and *Hydrobaenus*, were included, then the average percentage of all individuals in intermittent samples contributed by these 15 taxa rose to

86% (range: 56 to 98%).

In both Huachuca and Garden Canyons, community distance was relatively high among replicate perennial headwater riffles, with nearly a 50% compositional turnover among samples (Sorensen distance range: 0.44 to 0.51; Fig. 4.4). Compositional changes between the perennial headwaters and neighboring downstream intermittent reaches were even sharper, with Sorensen distances ranging between 0.77 and 0.93. Perennial headwater communities in both drainages were more similar to the geographically distant perennial valley rivers (Sorensen distance range: 0.62 to 0.77) than they were to intervening intermittent reaches, suggesting a hump-shaped response of community distance to downstream distance over the scale of this study (Fig. 4.4).

4.4 DISCUSSION

Our study of a large, arid-land stream network builds on recent studies that examined the effect of flow intermittence in streams that contain both perennial and intermittent reaches (Storey and Quinn 2008; Arscott et al. 2010; Datry 2012). Examination of an entire stream network allowed us to examine how position within the catchment, reach-scale hydrology, and proximity to other habitats all influence patterns of invertebrate community structure. We found that invertebrate richness was highest in perennial headwater reaches, dropped dramatically in intermittent mid-reaches, and was high again in perennial valley river reaches. This finding stands in contrast with patterns seen in much larger, temperate river networks such as the Mississippi, where downstream connectivity and neutral dispersal dynamics account for the majority of variation in local species diversity (Muneepeerakul et al. 2008). Though community composition in downstream reaches should also be strongly influenced by upstream communities (Brown and Swan 2010), our species-poor intermittent study reach assemblages were not a simple subset of tolerant upstream perennial species. Instead, intermittent reaches were numerically dominated by a suite of intermittent specialist taxa with adaptations to drying disturbance (e.g., egg and larval diapause), demonstrating that the influence of flow permanence overwhelmed that of network connectivity in this network.

4.4.1. Invertebrate richness and abundance

The strong differences in taxon richness we observed between perennial and intermittent reaches in our focal stream network may be explained by the long duration of zero-flow periods in arid-land intermittent streams. Though many studies report no differences in richness between intermittent and perennial reaches (Feminella 1996; Dieterich and Anderson 2000; Price et al. 2003; Bonada et al. 2007; Chester and Robson 2011; Santos and Stevenson 2011), the dry seasons in these studies tend to be very short (1-4 months), while arid-land intermittent streams may be dry for a year or longer (Fig. 4.2). Abdell (1984) found that richness in California intermittent streams nearly tripled when flow lasted 4-6 months versus 1-3 months. Examining invertebrate richness as a function of a continuous flow permanence variable, rather than an ordinal variable, may clarify some of these apparent discrepancies in past studies. Invertebrate richness was found to decrease linearly with decreasing flow permanence in New Zealand and France when researchers used a continuous flow permanence variable derived from hydrological modeling (Datry et al. 2007; Larned et al. 2007; Arscott et al. 2010; Datry 2012).

If at least one taxon in upstream perennial refuges is both abundant and prone to enter the drift (e.g., *Baetis*; McArthur and Barnes 1985), then drift from these refuges may play an important role in bolstering abundances in downstream intermittent reaches. Intermittent reaches nearest to upstream perennial reaches often support higher abundances of invertebrates than more remote intermittent reaches (McArthur and Barnes 1985; Paltridge et al. 1997; Fritz and Dodds

2002; Datry 2012). While we found no differences in abundance between headwater and downstream intermittent reaches, we cannot attribute these equal abundances to drift recolonization alone; the most abundant taxa in intermittent reaches (e.g., *Eukiefferiella rectangularis* group, *Hydrobaenus*) were absent in upstream perennial reaches. Additionally, these same taxa were dominant in intermittent streams with no upstream perennial refuges (e.g., Banning Creek, Woodcutters Canyon). Thus, these intermittent reach taxa apparently have the ability to numerically rebound very quickly (≤60d) from extended dry periods (>1yr) without relying on drift as the primary recolonization pathway.

4.4.2. Functional feeding groups

Functional feeding group composition acts as a proxy for a number of ecosystem and food web attributes in streams and provides a manner of cross comparison between regions with different taxonomies (Cummins, Merritt and Berg 2008). Collector-gatherers are usually the most abundant functional feeding group in low-order streams (Vannote et al. 1980) and made up the majority of individuals (61-80%) in both intermittent and perennial reaches in this study (Table 2). Shredder abundances were not different between headwater and intermittent reaches which may not be surprising given the usual prominence of shredders in temperate low order streams (Vannote et al. 1980; Grubbs 2011). However, intermittent reaches had much lower mean canopy cover (27%) than headwater reaches (81%), so in that context this result is surprising. Perhaps leaf litter accumulates through the long dry season to provide ample material for shredders when flow resumes, despite the sparse canopy cover. Scraper relative abundance and taxa richness were equal in headwater and intermittent reaches, which stands in contrast to the studies of Progar and Moldenke (2002), Price et al. (2003), and Grubbs (2011) who found higher abundances of scrapers in perennial streams. The more open canopy in arid-land intermittent streams may have provided for increased diatom and algal growth, and thus supported more scrapers when compared to forested, temperate intermittent streams.

Temporary aquatic habitats often provide a refuge from vertebrate predation (Williams 1996). Relative abundances of invertebrate predators in temporary waters, though, are still a matter of debate. Predator abundances have been found to be higher (Progar and Moldenke 2002) or lower (Price et al. 2003) in perennial streams when compared with intermittent streams, or show no pattern with regard to flow permanence (Bonada et al. 2007; Grubbs 2011). We found predators to be 7-14 times more abundant in perennial headwater and valley river reaches than in intermittent reaches, suggesting that intermittent reaches of arid-land streams may provide a significant refuge from invertebrate predation pressure.

4.4.3. Community composition

The clear community distinction we found between adjoining perennial and intermittent reaches has rarely been observed, as many studies report broad community overlap between neighboring perennial and intermittent reaches (Wood et al. 2005; Arscott et al. 2010; Santos and Stevenson 2011). For example, Delucchi (1988) found that stream and pool communities within a flow type were more distinct than communities between perennial and intermittent streams, quite the opposite of our findings here. However, the intermittent streams in Delucchi’s study flowed for 8-11 months each year, while our arid-land intermittent streams only flow for 2-4 months during wet years (~45% of all years). While numerous upstream perennial taxa rapidly (<30d) colonized downstream intermittent reaches via drift in an Australian stream (Paltridge et al. 1997), drift recolonization from upstream perennial refuges can take 4-6 months in other streams (Abdell 1984). Thus, the very short flow durations in many arid-land intermittent streams may not be sufficient for upstream perennial taxa, such as caddisflies and mayflies (Table

4.3), to establish populations in downstream intermittent reaches (Bonada et al., 2007; also see Fig. 4.5).

One of our focal network intermittent reaches and both of our comparison intermittent reaches were located in isolated drainages without upstream perennial reaches. Communities from these isolated reaches were indistinguishable from those in less-isolated intermittent reaches with upstream perennial refuges (Fig. 4.3). In isolated intermittent streams, aquatic invertebrate taxa must either survive the dry season in situ (via a dormant stage) or arrive after flow resumption (via aerial dispersal). While some taxa in arid regions commonly and frequently disperse aerially between drainages, these tend to be beetle and true bug taxa (Bogan and Boersma *in review*). Even if adults of rheophilic perennial stream taxa, such as the caddisfly *Phylloicus* (see Table 4.3), could reach isolated intermittent streams via flight, larval recruits of those taxa would be unable to complete their life cycle during the short flow duration of those streams (Bogan and Lytle 2011).

The relatively high level of taxonomic resolution in identifying midges (Chironomidae) in this study may also help to explain why intermittent communities were so distinct. Midges were 2-3 times more abundant in intermittent reaches than in perennial reaches, and all but one of the intermittent indicator taxa were midges. Many other studies comparing communities in sites with contrasting flow permanence only identified midges to the family level (e.g., Grubbs 2011; Datry 2012) or have excluded them altogether (Santos and Stevenson 2011). Midges can be extremely diverse in intermittent streams worldwide (e.g., Spain: Langton and Casas 1999; United States: Chou et al. 1999), so we argue that their identification is essential when comparing streams with contrasting flow regimes.

Several of the intermittent indicator midge taxa, including *Chaetocladius*, *Diamesa*, *Eukiefferiella*, and *Hydrobaenus* have previously been associated with intermittent habitats

(Williams and Hynes 1976; Towns 1985; Chou et al. 1999; Chaves et al. 2008) and larvae of some of these genera have been found in intermittent streams within 5 days of flow resumption (Williams and Hynes 1976; Abdell 1984). Chou et al. (1999) found that several Orthocladiinae midge taxa have dormant egg or larval stages, including *Eukiefferiella* and *Hydrobaenus*, and that *Chaetocladius* can persist in wet soils. Additionally, *Krenosmitta* have been documented from hyporheic habitats in Colorado and Arizona (Ferrington 1984; Boulton et al. 1992). Larned et al. (2007) collected river sediments that had been dry for 200 days and found that Orthocladiinae midges readily emerged from diapause in rehydrated sediments.

Although our intermittent samples were dominated by midges, they were also characterized by high abundances of the intermittent exclusive stonefly *Mesocapnia arizonensis*. *M. arizonensis* was first described from an intermittent stream and has been collected from intermittent streams across the region (Boulton et al. 1992; Jacobi and Cary 1996; Bogan and Lytle unpubl. data). The species undergoes diapause as an egg (Gray 1981) and populations can recover quickly from dormant eggs, even after several consecutive dry years (Bogan and Lytle unpubl. data). This ability of diapausing stonefly eggs to survive multiple years in dormancy has been documented in at least two other stonefly species (Sandberg and Stewart 2004; Stewart and Anderson 2010). Targeted collection of blackfly pupae from our intermittent streams resulted in at least 8 species being identified as abundant in intermittent reaches, most of which have been previously associated with intermittent habitats and/or have desiccation-resistant egg stages (Adler, Currie and Wood 2004). This specialized, intermittent assemblage of rapidly developing (<8 weeks) stoneflies, blackflies, and midges has been found in short flow-duration intermittent streams in Canada (Williams and Hynes 1976), Australia (Towns 1985; Boulton and Lake 1992), the United States (Abdell 1984; Miller and Golladay 1996; Fritz and Dodds 2002), and Europe (Anna et al. 2009), and as such may be useful as a global indicator assemblage for intermittent flow conditions in ungauged streams.

4.4.4. Longitudinal patterns

One of the most commonly reported patterns in ecology is that the community similarity between sites decreases with increasing geographic distance (i.e., distance decay; Nekola and White 1999). This pattern, where neighboring sites support very similar communities and distant sites support very dissimilar communities, has also been reported in stream networks (Maloney and Munguia 2011). Given the high connectivity provided by downstream flow in dendritic riverine networks and the redundancy of having multiple replicate community types in multiple branches (Grant, Lowe and Fagan 2007), recovery from drying disturbance in mid-reach intermittent streams should be greatly facilitated by recolonization from upstream perennial refuges. In two branches of our focal network, though, we saw fairly high community distance among perennial headwater samples (suggesting high beta diversity in headwater reaches), and then a steep compositional change when moving relatively short distances downstream (1-5km) into intermittent reaches. Additionally, despite long distances (15-25km) and large differences in drainage areas and habitat characteristics, perennial 1st order headwater and 3rd-4th order valley river communities were more similar to one another than to intervening intermittent reaches (Fig. 4.4). Rather than a linear or log-linear increase in community distance with geographic distance, as are commonly reported (Nekola and White 1999; Maloney and Munguia 2011), the pattern suggests a hump-shaped response over the geographic scale of our study. While more sampling is needed to fill in gaps along the distance gradient, the observed pattern provides additional evidence that our intermittent sites disrupted longitudinal patterns of benthic community composition.

Though the influence of flow permanence overwhelmed connectivity to upstream reaches in this study, we acknowledge that both of these factors likely play an important role in structuring intermittent stream communities. In Fig. 4.5 we present a conceptual model that explores the relative roles of these two factors in determining how many specialist intermittent taxa may be found at a given site. Based on the data from this and other studies, we suggest that the number of unique intermittent taxa may be maximized at short to moderate flow durations (e.g., 80-140 days) with moderate to high isolation from perennial refuges (e.g., >1km). For example, a hydroperiod of less than 30 days may not be sufficient for specialized communities to develop; instead local species are largely short-lived, highly vagile taxa or fugitives from nearby sites (Williams 1996; “Highly mobile taxa” in Fig. 4.5). Hydroperiods of 2-5 months are long enough for many intermittent specialist taxa to complete their life cycles, but may not be long enough for taxa from perennial refuges to colonize via drift or flight, especially when intermittent reaches are far from perennial refuges (Abdell 1984; “Intermittent specialists” in Fig. 4.5). Intermittent reaches closer to perennial reaches or with long hydroperiods may be readily colonized by taxa from perennial refuges (“Intermittent-perennial mixture” and “Perennial taxa dominant” in Fig. 4.5); these colonists may be competitively superior to or even prey upon intermittent specialist taxa (Wissinger, Brown and Jannot 2003), thus reducing the prevalence of intermittent specialists.

4.4.5. Conclusions

In contrast to many other studies, we observed distinct invertebrate communities in intermittent reaches and found that mid-reach drying interrupted longitudinal patterns of richness and community structure. The intense degree of intermittency in our arid-land streams likely explains why the observed differences were so pronounced. Arscott et al. (2010) and Datry et al. (2007) advocated using quantitative continuous flow permanence variables rather than ordinal categories of flow permanence when examining differences between temporary and perennial streams. New flow modeling techniques (e.g. ELFMOD: Larned et al. 2010b) and relatively inexpensive electrical resistance sensor arrays (Jaeger and Olden 2011) are among the new tools which will greatly increase the understanding of relationships between flow permanence and biological communities in temporary streams. We suggest that combining numerical metrics of flow permanence and network connectivity may allow us to explain most of the current contradictions in the published literature (Fig. 4.5).

ACKNOWLEDGEMENTS

Thanks to Sheridan Stone for logistical and administrative support at Fort Huachuca, AZ, to Brooke Gebow and the Nature Conservancy for access to sampling sites and lodging at the Ramsey Canyon Preserve, AZ, and to Frank McChesney for access to the Babocomari River, AZ. Special thanks to Richard Van Driesche for helping to process and identify invertebrate samples. This study was supported by funding from the Department of Defense (RC-1724 and RC-2203).

Table 4.1 Physical characteristics, flow type, number of riffle and pool samples collected, and mean water chemistry parameters across six streams and twelve study reaches in our focal arid-land stream network. Most intermittent reaches did not contain pools- only riffles. See Figure 4.1 for locations of each stream and positions of replicate samples within each study reach.

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

Table 4.2 Mean values for sample richness, total abundance, and Chironomidae and functional feeding group (FFG) relative abundances (%) for focal headwater, intermittent, and valley river samples and Kruskal-Wallis test results for significant differences among the three stream type groups. The Pairwise column indicates significant ($P < 0.01$) Bonferroni-corrected pairwise contrasts between stream types (H= headwater perennial, I=intermittent, V=valley river perennial).

	Sample means			*Kruskal-Wallis Test*		
	Headwater (n = 19)	Intermittent (n = 24)	Valley river (n = 8)	K	*P*	Pairwise
Species richness	32	10.5	22.8	34.87	0.0001	H vs I; V vs I
Total abundance	453	545	1745	13.79	0.001	V vs H; V vs I
Chironomidae % abundance	32	80	20	33.99	0.0001	H vs I; V vs I
FFG Relative abundance						
Collector-Filterer	9.6	6.5	7	6.98	0.03	H vs I
Collector-Gatherer	61.2	76.4	80.2	9.57	0.008	H vs I; H vs V
Piercer	1.7	0	0.3	18.61	0.0001	H vs I; V vs I
Predator	15.2	1.1	7.9	31.39	0.0001	H vs I
Scraper	8.1	8.2	4.5	5.5	0.064	
Shredder	5.2	7.8	0.2	11.54	0.003	H vs V

Table 4.3 Indicator Species Analysis results for the three flow type groups with each taxon's Indicator Value (IV) and associated statistical significance (*P*). The first IV was calculated using only March 2010 data from the focal network. The IV in parentheses was calculated using all samples, including the additional perennial samples collected in 2009-2011 and the comparison intermittent samples collected in 2004, 2005, and 2011.

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

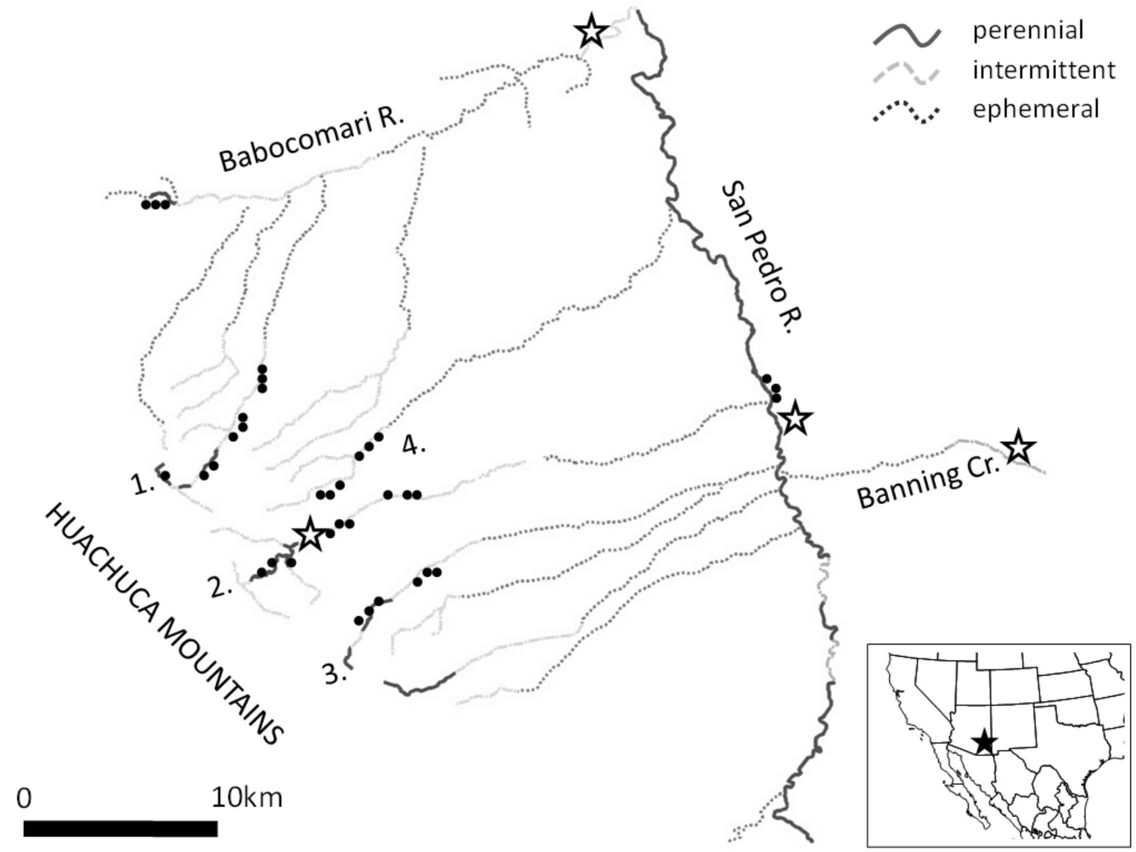

Figure 4.1 Map of the study region and locations of replicate samples in our focal stream network (see Table 1). The numbered study streams are (1) Huachuca Canyon, (2) Garden Canyon, (3) Ramsey Canyon, and (4) Woodcutters Canyon. Individual sampling locations within study reaches are indicated by black circles. United States Geological Survey stream flow gauges utilized in Figures 2 are indicated by the stars.

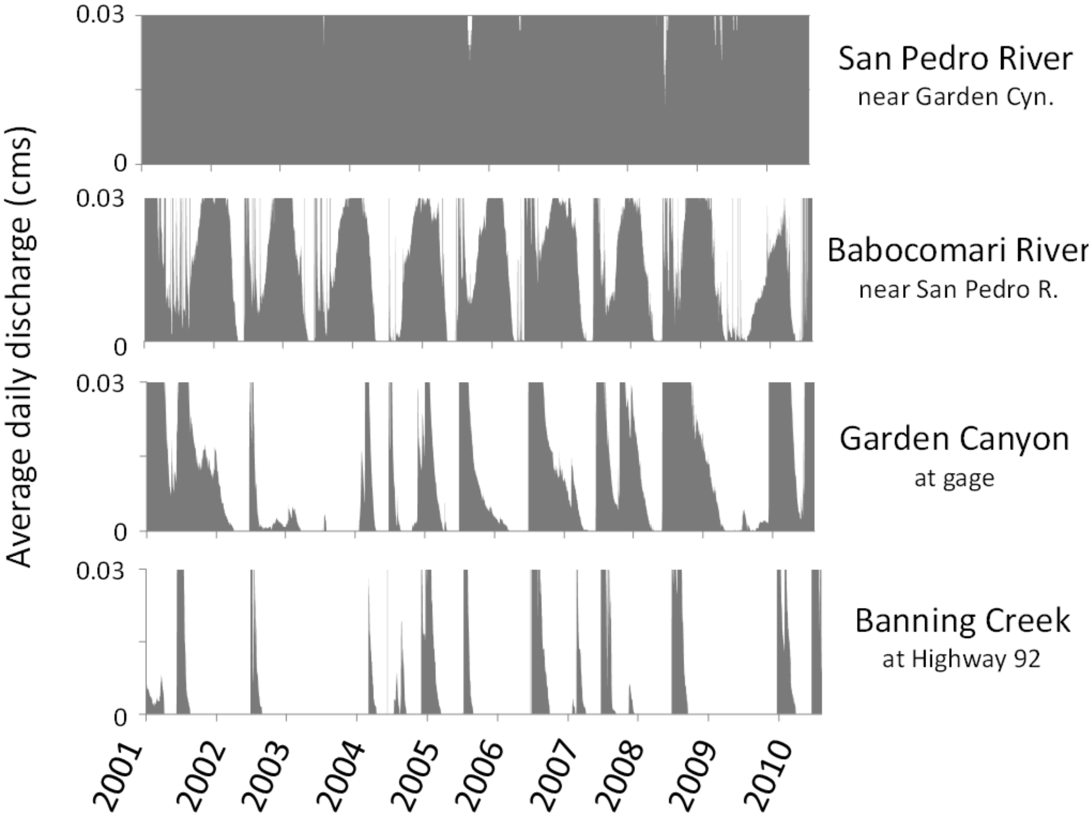

Figure 4.2 Differences in average daily flow in cubic meters per second (cms) from 2001-2010 among streams in the study region, with peak discharges truncated to maximize display of dry season differences. Stream reaches in our study area ranged from fully perennial (San Pedro River near Garden Canyon) to nearly perennial but with occasional dry periods (Babocomari River near San Pedro River), to intermittent with dry periods of several months (Garden Canyon at gauge), to intermittent with dry periods extending over many months and/or years (Banning Creek at Highway 92).

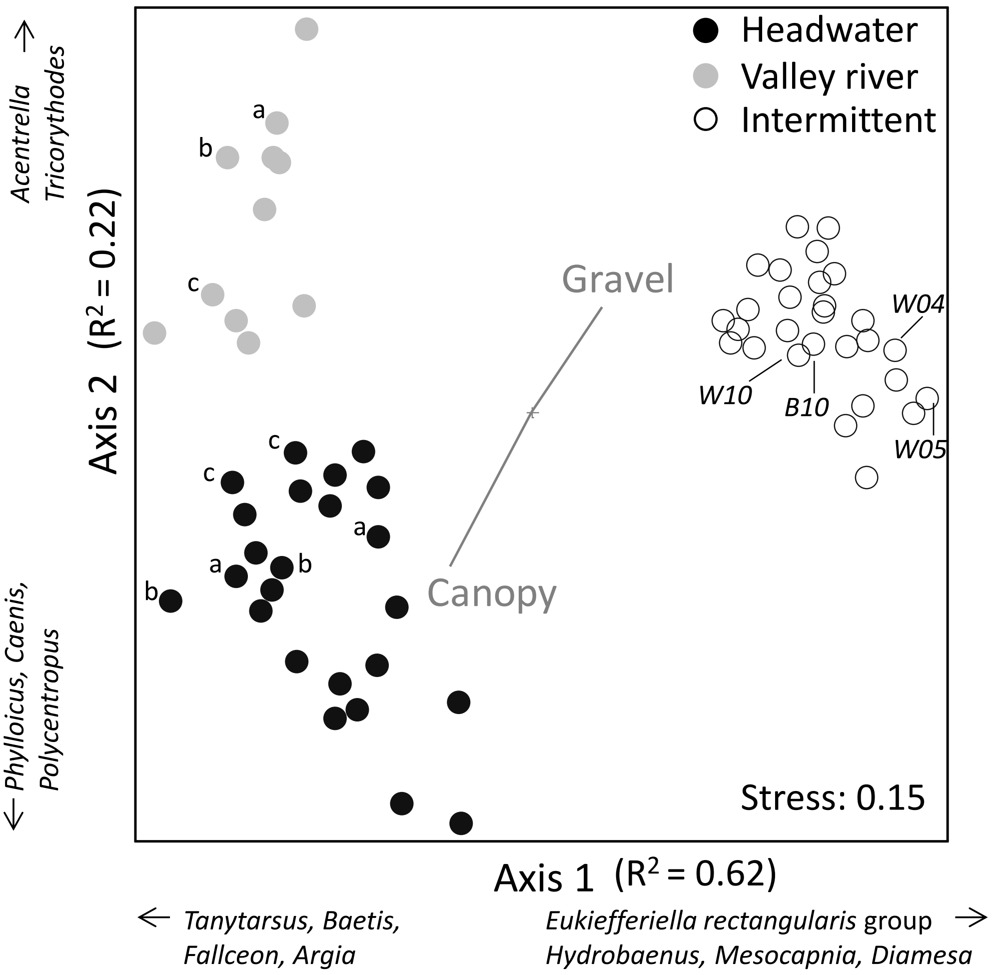

Figure 4.3 Non-metric multidimensional scaling (NMS) ordination plot of all March 2010 samples, coded by stream type, with additional symbols designating samples from other sampling periods at our focal sites (a = November 2009, b = November 2010, c = March 2011) and comparison sites (B10 = Banning Creek, March 2010; W04, W05, and W10 = West Stronghold Canyon, March 2004, 2005 and 2010). Vectors indicate measured environmental variables with significant Pearson's correlations with axis 1 and/or axis 2. Axis 1, which explained the majority of the community variation, clearly separates perennial and intermittent community samples across multiple sampling periods and streams. Eight influential taxa which contributed to the separation of intermittent and perennial sites are listed below axis 1 and five influential taxa which contributed to the separation of perennial headwater and valley river sites are listed below axis two, with arrows indicating positive or negative correlations (all $|r| \geq 0.6$) of those taxa with each axis.

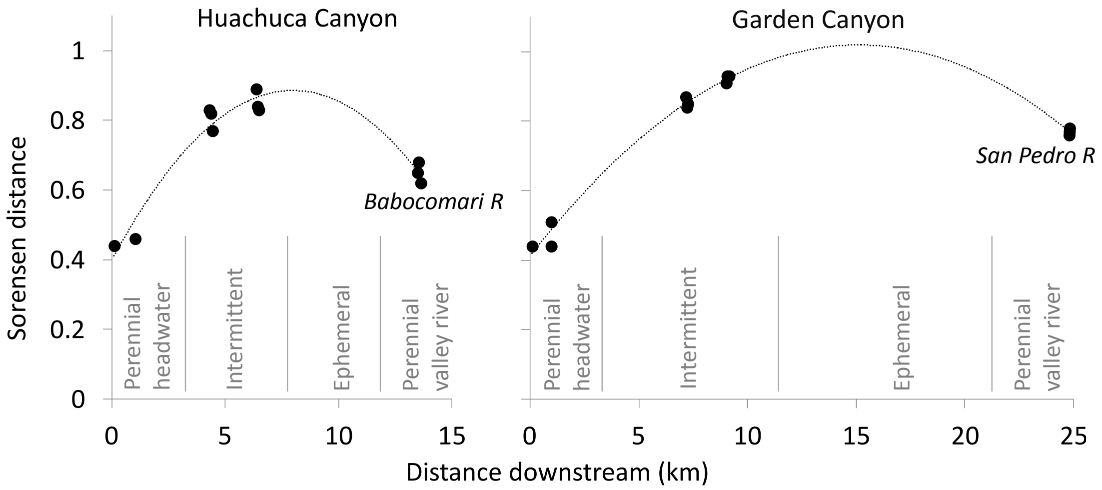

Figure 4.4 Aquatic invertebrate community dissimilarity (Sorensen distance) between uppermost headwater reaches and reaches at increasing downstream distances in the Huachuca and Garden Canyon stream networks. Despite the close distances (1-5km) between headwater and intermittent sites within a network, communities changed dramatically between these sites; communities in perennial headwater and valley river reaches were more similar to one another than to intervening intermittent reaches despite being 12-25km apart.

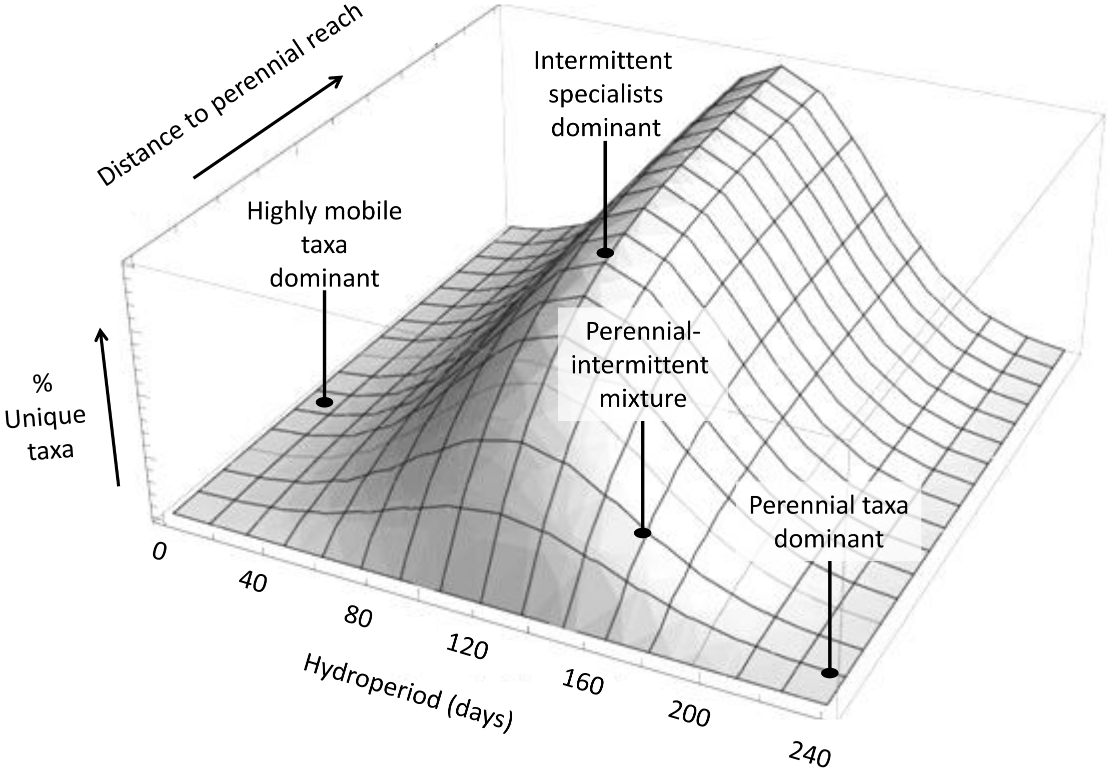

Figure 4.5 A conceptual model illustrating potential interactive effects of hydroperiod and distance from perennial sources on the percentage of specialized, unique invertebrate taxa found in intermittent stream reaches, with four hypothetical locations. “Highly mobile taxa dominant”: a very short hydroperiod may not be sufficient time for specialized communities to develop; instead, highly mobile, widespread taxa or dispersers from nearby perennial sites are prevalent. “Intermittent specialists dominant”: a hydroperiod of 2-5 months is sufficient for intermittent specialist taxa (those with diapauses or other drought adaptations) to complete their life cycles; these will be dominant if the site is sufficiently isolated from perennial sites. “Intermittent-perennial mixture”: with close proximity to perennial sites, intermittent sites may be readily colonized by perennial taxa, thus reducing the percentage of intermittent specialist taxa. “Perennial taxa dominant”: with longer hydroperiods, taxa from perennial sites may be able to persist (via colonization or resistance) and could outcompete or prey upon intermittent specialist taxa.

CHAPTER 5- **Biogeography and conservation of aquatic fauna in tropical canyons of the southern Sonoran Desert, México**

Michael T. Bogan, Nohemí Noriega-Felix, Sylvette Leonor Vidal-Aguilar,
Lloyd T. Findley, David A. Lytle, Oscar G. Gutiérrez-Ruacho,
J. Andrés Alvarado-Castro, and Alejandro Varela-Romero

In review:
Proceedings of the San Diego Society of Natural History
San Diego Natural History Museum
San Diego, CA

ABSTRACT

The arid El Aguaje, Santa Úrsula, and Bacatete mountain ranges (sierras) in southern Sonora, México contain numerous canyons supporting spring-fed aquatic habitats, isolated from one another by formidable volcanic cliffs and vast expanses of desert. While the relict tropical vegetation in such canyons has been previously studied, their aquatic life forms have received very little attention. In this study, we mapped sites in these mountain ranges that support freshwater habitat, identified distinct microhabitat types at each site, and inventoried their aquatic biota. We identified eight sites with perennial freshwater in the Sierra El Aguaje in 2008 and an additional 11 sites in the sierras El Aguaje, Santa Úrsula and Bacatete in 2009. These 19 sites supported more than 220 taxa of aquatic animals, with richness at individual sites ranging from 10 to 123 taxa. We delineated four microhabitat types (oasis, tinaja, riffle, and seep) which each supported distinct aquatic invertebrate communities. Communities were not distinct by mountain range, but rare species were occasionally found only in a single mountain range. In addition to one-time invertebrate surveys, we examined seasonal changes in aquatic invertebrate communities six additional times during 2008 and 2009 at one site, Cañón Nacapule in the southern Sierra El Aguaje. Despite monsoon and hurricane-induced flooding and seasonal habitat contraction and expansion, aquatic invertebrate species richness and composition at Nacapule changed little by season over these two years. Aquatic vertebrates were not diverse across the study area but were often locally abundant. Big-eyed leopard frog, in particular, was abundant at sites with pooled water (tinajas and oases), while canyon tree frog was less common, and sabinal frog and black-necked garter snake were rare. The native freshwater fishes desert chub and Sonoran topminnow were found at two sites each, and exotic (introduced) tilapias were found at all four sites in the sierras Santa Úrsula and Bacatete. Tilapia presence was strongly associated with a shift in aquatic invertebrate community structure and reduced invertebrate density and

species richness. The condition of these diverse aquatic habitats ranged from nearly pristine (Las Barajitas, La Balandrona) to heavily impacted (Nacapule). Groundwater withdrawal, increasing human visitation, and introduction of exotic fishes are all significant threats to the diversity of aquatic organisms in these habitats. We recommend continued monitoring of all sites, increased vigilance in protecting highly unique riffle microhabitats at sites like Nacapule, preventing further spread of exotics, and inclusion of the southern part of the Sierra El Aguaje in an actively managed protected area or biosphere reserve.

5.1 INTRODUCTION

Desert spring systems support a remarkable diversity of aquatic organisms given their arid surroundings. Many spring-fed aquatic systems in such "inhospitable" places harbor endemic aquatic invertebrates (Polhemus and Polhemus 2002; Hynes 1970), and the number of endemic species in any such community tends to increase with isolation and intensity of barriers to dispersal (Cox and Moore 1993). The spring-fed freshwater habitats in canyons of the El Aguaje, Santa Úrsula, and Bacatete mountain ranges (sierras) in southern Sonora, Mexico (Fig. 5.1) are small patches of aquatic habitat, often with lush riparian vegetation, isolated from one another by formidable volcanic cliffs and vast expanses of Sonoran desertscrub vegetation (Fig. 5.2 and 5.3). These sierras also act as ecological 'islands,' rising above dry desert lowlands and isolated from other sierras with similar freshwater habitats by 40 or more kilometers. Such physical setting predicts that these well-watered habitats have great potential for increased diversity and endemism of the aquatic organisms they support.

These freshwater habitats and lush canyons have received all too little attention from scientists. An exception to this lack of attention is the work of botanist Richard Felger. While surveying the plants of three canyons in the Sierra El Aguaje, Felger (1999) found an astounding diversity of plants, including disjunct populations of truly tropical species (e.g., *Ficus insipida*) intermixed with local Sonoran Desert species. Felger noted that riparian areas one of the three canyons, Cañón Nacapule, supported three genera of palm trees and three species of fig trees. This botanical information, along with personal observations from authors of the present study (Alvarado-Castro, Findley, Gutierrez-Ruacho, Varela-Romero), prompted us to make preliminary inventories of aquatic beetles and bugs in two Sierra El Aguaje canyons (Nacapule and La Navaja) during 2004. We found that in addition to supporting many widespread beetle and bug species, these two canyons also supported numerous tropical species and at least one undescribed water beetle (Bogan 2005). Our excitement about these findings led to our current, broader study to document the diversity of aquatic animals in freshwater habitats across the southern Sonoran Desert.

The isolation and small size of these desert-bounded, tropical canyons and their aquatic habitats not only make them interesting to study but also highly vulnerable to anthropogenic disturbance. In particular, these southern Sonoran Desert aquatic habitats face potential threats from livestock, unmanaged human visitation, increased groundwater withdrawal, changing climatic patterns, and exotic (introduced) fish species. Many of these habitats are located within a few kilometers of the growing tourist town of San Carlos. As a result of this proximity, canyons such as Nacapule have become popular tourist destinations as well as seeing increasing visitation by local families during weekends. Unfortunately, with this popularity have also come trash, graffiti, vandalism, and penetration by off-road vehicles, all of which are damaging fragile riparian habitats at Nacapule (Carrizales 2007). As the resort community of San Carlos continues to grow, visitation to this canyon and others nearby will only increase. Concordant with population growth in San Carlos is increasing demand for municipal water. Massive groundwater withdrawal projects are predicted to reduce spring discharges and thus endanger aquatic biota elsewhere in arid regions of North America (e.g., the Great Basin: Deacon et al. 2007), and similar results will likely follow excessive groundwater pumping in the southern Sonoran Desert.

Shifting precipitation and temperature regimes as a result of climate change also threaten small isolated spring systems, like those of the sierras El Aguaje, Santa Úrsula, and Bacatete. High biodiversity in nearby Madrean Sky Island stream systems is maintained in part by strong seasonality in precipitation and flow patterns (Bogan and Lytle 2007). If similar processes operate in aquatic habitats of these Sonoran sierras, slightly altered precipitation regimes could negatively impact regional aquatic species diversity. Recent droughts in Arizona and Sonora are predicted to continue and intensify, with drought conditions becoming the new climatic norm (Seager et al. 2007). This drier climate will inevitably reduce spring discharges and increase water temperatures, leading to local extinctions (Durance and Ormerod 2007), as has already been observed to the north in Madrean Sky Island streams (Bogan and Lytle 2011). At Cañón de Nacapule in the Sierra El Aguaje, Felger (1999) found that significant flow reductions between 1968 and 1999 likely resulted in the extirpation of two wetland plant species. This trend of decreasing flows is not likely to reverse.

A third major threat to aquatic biodiversity in the southern Sonoran Desert is the intentional introduction of exotic fishes, especially tilapias (Cichlidae). Exotic fish species can disrupt food-web dynamics and cause profound changes in native invertebrate and vertebrate community structure in both lotic and lentic ecosystems (Maezono et al. 2005; Townsend 1996). We knew from preliminary visits to the Aguaje Los Pilares in the Sierra Bacatete that exotics (*Tilapia* spp.) recently had been introduced into some aquatic habitats in the region. From visual surveys, it was clear that tilapia had caused major physical habitat changes (via territorial pit-building/courting by males) and invertebrates appeared scarce (Bogan and Findley, pers. obsv.). Thus, during the course of this study we looked for opportunities to compare invertebrate communities in adjacent habitats with and without tilapia.

In this paper, we present the results of two years of field work studying many of the spring-fed aquatic habitats of the sierras El Aguaje, Santa Úrsula, and Bacatete. We identified freshwater habitats across the region and created a baseline dataset for use in regional biodiversity conservation planning. We conducted surveys for aquatic invertebrates and vertebrates. We quantified microhabitat types (oasis, tinaja, seep, and riffle) and water quality conditions (pH, conductivity, temperature) at each site and then related these measurements to aquatic animal community composition. Additionally, we surveyed one canyon (Nacapule) over multiple seasons in 2008 and 2009 to determine if local aquatic invertebrate diversity and community composition varied seasonally. Finally, we examined potential impacts of exotic tilapia on invertebrate communities by comparing invertebrate diversity, density, and community composition in pools with and without tilapia at Rancho Santa Úrsula in the Sierra Santa Úrsula.

5.2 METHODS

5.2.1. Mapping of freshwater habitats – We assessed the presence of perennial waters via a four-step process. First, we consulted available maps and satellite imagery to identify montane areas that potentially contained perennial surface water. Second, we consulted with individuals at scientific institutions in the USA and Mexico who had previously visited freshwater habitat sites in the sierras El Aguaje, Santa Úrsula, and Bacatete. Third, we talked to local ejido (communal ranches) and urban residents in the region to obtain anecdotal information about water sources. Finally, we ground-truthed satellite imagery and scientific and anecdotal information by visiting all accessible potential study sites and mapping the aquatic habitat with a GPS unit. All sites were visited during the dry season (usually March and April) to determine if aquatic habitat was perennial and thus persisted through the dry season. During visits, we identified aquatic microhabitat types present, estimated wetted surface area, measured water temperature, pH and conductivity, and collected biological data described below.

5.2.2. Aquatic invertebrate sampling – We employed quantitative and qualitative collecting techniques in assessing aquatic invertebrate community structure. Because communities often exhibit strong compositional gradients in regard to microhabitat, we stratified sampling techniques by microhabitat type. Pools (oases and tinajas) were sampled with a D-net (0.5mm mesh) using a timed sweeping method. Riffles, when present, were sampled with standard 'kick' samples (Bogan and Lytle 2007). Because all riffles were too shallow to use a D-net, we used a 10-cm-wide aquarium net (0.25mm mesh) to collect riffle samples. Large pools (>25m^2 surface area) were sampled by a combination of timed sweep and the searching of unique habitat features (e.g., submerged tree roots, vertical waterfalls) for target organisms (e.g., sponges, aquatic moths). Seeps were sampled qualitatively by collecting invertebrates in whatever manner the habitat's characteristics allowed (e.g., scraping algal films; excavating substrate). Additionally, we collected emergent adult aquatic insects at three sites using UV-light traps placed at water's edge for 30 minutes at dusk. All macroinvertebrates were preserved in 95% ethanol for transport and later identification. Most samples were enumerated and identified by Bogan, Noriega-Felix, and Vidal-Aguilar at CESUES in Hermosillo, with occasional specimens sent to experts to confirm species determinations. A reference collection of aquatic invertebrates collected during this study is housed at CESUES-Hermosillo for future comparative and teaching purposes. All sampling was conducted during the dry season between late December and late April of the years covered. Easily accessible Cañón Nacapule was resampled multiple times in 2008 and 2009 to examine seasonal variation in aquatic invertebrate community structure.

5.2.3. Vertebrate surveys – Amphibians were sought with visual-encounter surveys during warm, daylight hours. We searched for larval amphibians (tadpoles) during timed sweep-sampling and during supplemental sweeping of pools. Amphibian presence and identity was confirmed with photographs of free and captured individuals. Additionally, we listened for and recorded calling amphibians. Fishes were sought using minnow-seine nets and D-nets. Most pools were open and had relatively clear water, thus most fishes also were easily detected visually. Fishes were photographed, and several voucher specimens were collected by Varela-Romero and deposited in the fish collection of the Universidad de Sonora in Hermosillo.

5.2.4. Data analysis –Community composition was examined with an ordination technique, non-metric multidimensional scaling (NMS). NMS reduces redundancy in the data matrix via a rank-based metric to reduce community data from many dimensions to a two or three dimensional ordination, and does not make distributional assumptions of the data matrix (McCune and Grace 2002). Environmental parameters were then overlain on the community composition-based ordination to elucidate relationships between measured parameters and community changes along the ordination gradients. Sorensen distances were used to calculate community dissimilarity between samples. Since collection techniques varied between habitats, absolute numbers of individuals varied greatly between samples; thus abundance data were relativized by site prior to ordination analyses. This relativization ensured that the ordination focused on comparing the relative abundances of species between sites rather than absolute abundances.

We used Multi-response Permutation Procedure (MRPP) with Sorensen distances to quantify and test within-group agreement and distinctness (see Mielke and Berry 2001) among invertebrate communities in the different microhabitat types, the three different sierras, and between pools with and without tilapia. 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. A-values of greater than 0.3 are considered large for community datasets (McCune and Grace 2002). We used Indicator Species Analysis (Dufrêne and Legendre 1997) to identify which species were associated with each group (e.g., microhabitat type, tilapia-containing vs. tilapia-free pools). Indicator Species Analysis yields an indicator value (IV) which varies between 0 (poorest indicator) and 100 (best indicator). Significance of IV values was assessed using a Monte Carlo randomization procedure. We performed all community analyses using the program PC-ORD version 5 (MJM Software, Gleneden Beach, Oregon). We compared invertebrate taxa richness and sample density between tilapia-containing and tilapia-free pools at Rancho Santa Úrsula with standard t-tests.

5.3 RESULTS AND DISCUSSION

5.3.1. Habitat assessment

We surveyed eight sites with perennial water in the Sierra El Aguaje in 2008 and later surveyed an additional seven sites there in 2009, six with perennial water and one, Arroyo El Palmar which had seasonal water (wetted in Dec., dry by April). In 2009, we also surveyed two perennial sites each from the sierras Santa Úrsula and Bacatete. We designated four different types of wetted microhabitats from these 19 sites: (1) oasis, (2) tinaja, (3) seep, or (4) riffle. Oasis microhabitats are large, deep pools surrounded by abundant vegetation and canopy cover such as native palms and/or fig trees (Figure 5.3), often with complex underwater structure consisting of tree roots and aquatic vegetation. Oasis pool substrate was generally characterized by a combination of gravels, cobbles, tree roots, and fine organic material. Tinajas, in contrast, were large open pools of water, often located on actively-scoured portions of stream beds, characterized by little or no riparian cover (Figure 5.4). Bedrock, cobbles, and gravels comprised the majority of tinaja substrate. Seeps were areas of flowing shallow (<1cm depth) water that arose from cracks in bedrock. From a distance, they often appear to simply be discolored rock, and were unconnected to any standing water but, in fact, support numerous aquatic organisms (Figure 5.5). Riffles, the rarest habitat type in our study, were areas of deeper (1-4cm depth) flowing water between pools (Figure 5.6). On average, riffles were only about 1.5cm deep. At one site in the Sierra Santa Úrsula we found "unnatural" riffles, which flowed out of a small series of artesian wells. Because the aquatic invertebrate communities of these riffles were similar to natural riffles, we did not classify artesian riffles as a distinct microhabitat type. The distribution of the four microhabitat types across the 19 sites is found in Table 5.1.

Total surface area of wetted habitat ranged from 8 to 1200 m^2 across the 19 sites (Table 5.1). At some sites, there was evidence of seasonal expansion of wetted habitat. Several of the large canyon systems in the sierras Santa Úrsula and Bacatete that we visited had extensive reaches of seasonally wetted tinajas and riffles as evidenced by dried algae and water-stained rock. During periods of intense rainfall, these large drainages collect enough water to allow significant expansion of aquatic habitats (Findley et al. 2010). Increased flow and flooding at Nacapule, in the Sierra El Aguaje, has been observed after several large monsoon rain events in close succession or in the wake of tropical eastern Pacific hurricanes (Brito-Castillo et al. 2006). Between 2008 and 2009, total wetted habitat at Nacapule ranged from a low of $220m^2$ (April 2009) to a high of $900m^2$ (Aug. 2008). This four-fold seasonal increase in habitat is much smaller than the 10- to100-fold increases in habitat size observed in streams of the nearby Madrean Sky Islands (Bogan and Lytle 2007). The Arroyo El Palmar study site was the only truly seasonal habitat during our study. This site contained water in the rainy season and early dry season (Sep.-Jan.), but was dry by April in 2008 and 2009 (Figure 5.7).

In general, water temperature, conductivity, and pH were similar at many sites (temperature ~22^{o}C; pH ~6.5; conductivity 310 to 350 μS; Table 1), which is probably indicative of regional groundwater contribution to surface flows. Several other sites, though, including those in the Sierra Bacatete, had higher conductivity (580 to 830 μS) perhaps indicating either a distinct aquifer source or concentrated waters resulting from habitat contraction. One Sierra El Aguaje site (Cañón “Escondido”) had tinajas with low conductivities (140 μS) suggesting that surface runoff contributed more to this site than groundwater. The combination of high regional similarity of water quality conditions and little-to-moderate responsiveness to precipitation events indicates that most wetted habitats in the Sierra El Aguaje are dependent on regional groundwater. The complicated and faulted geology of this volcanic range (Wilson 1978) likely provides the environment necessary for groundwater to reach the surface and create these aquatic habitats.

5.3.2. Aquatic invertebrates: species richness

We documented 210 invertebrate taxa across the 19 survey sites during 2008 and 2009. Taxa richness for individual survey sites ranged from 10 to 123 taxa (Table 5.1). We found 187 taxa at 15 sites in the Sierra El Aguaje, 103 invertebrate taxa at two sites in the Sierra Santa Úrsula, and 99 invertebrate taxa from two sites in the Sierra Bacatete (Table 5.2). Given the high diversity recorded from only two sites each in the sierras Santa Úrsula and Bacatete, it is reasonable to assume that additional surveys in these ranges would reveal range-level diversities similar to that of the Sierra El Aguaje. Oasis and tinaja microhabitats supported the greatest number of species, while riffles supported fewer, and seeps supported the least. Each habitat, however, contributed unique species to the regional species pool. These richness values represent multiple levels of taxonomic resolution. While some taxa with adult aquatic stages were identified to species (e.g., Hemiptera and Coleoptera), for many other taxa, species-level taxonomy is not yet possible for aquatic larvae (e.g., Diptera). As such, the species richness values we report are conservative. The true aquatic invertebrate species richness value across these three mountain ranges is likely much higher than the 210 taxa reported here.

The riffle habitat at Cañón Nacapule, sampled repeatedly in 2008 and 2009, produced several unique species. Ten species were recorded from that habitat which were not encountered elsewhere in the region: *Microcylloepus angustus*, *Heterelmis obscura* and *Neoelmis* sp. (Coleoptera: Elmidae); *Farrodes* sp. (Ephemeroptera: Leptophlebiidae); *Stempellina* sp. and *Stempellinella* sp. (Diptera: Chironomidae); *Pericoma* sp. (Diptera: Psychodidae); cf. *Dicranota* sp. (Diptera: Tipulidae); *Atractides* sp. and *Spechon* sp. (Hydracarina). Riffle species richness did not vary predictably by season or sampling location at Nacapule (Figures 5.7 and 5.8). Individual riffle samples contained between 17 and 35 species. The site total of 72 riffle species during the multiple 2008 and 2009 collections, however, indicates that species varied somewhat by season (see following sections).

5.3.3. Aquatic invertebrates: community composition

Non-metric multidimensional scaling (NMS) ordination analyses of the invertebrate community data matrix from all 2008 and 2009 samples converged on a stable three-dimensional solution (stress =17.5%; final instability = 0.0004; p = 0.0066; Figure 5.9). The ordination axes explained 65% of the variability in the original community matrix (axis 1 r^2 = 0.33, axis 2 r^2 = 0.12, axis 3 r^2 = 0.19). None of the measured environmental variables were significantly associated with NMS axes one, two, or three (all r values < 0.3). This lack of relationship was not surprising given the small range of values that measured environmental variables exhibited among many of the study sites.

The ordination plot illustrates that most microhabitat types occupy different regions of species-space, with only oasis and tinaja communities overlapping (Figure 5.9). As in streams of the Madrean Sky Islands to the north, running water and standing water habitats hosted different communities (Bogan and Lytle 2007). Seep samples were similar to one another, while riffle samples were more variable; the 10 species unique to Nacapule riffles contributed to this higher variability. Tinaja samples occupied a broad region of species-space, while oasis samples were mostly located within the variation of tinaja samples, though with some distinction. MRPP analysis confirmed the apparent strong distinction of these microhabitat groups, with a high A-value ($A = 0.36$, $p < 0.00001$). However, invertebrate communities did not form very distinct groups by sierra (MRPP by range: $A = 0.09$), suggesting that, at the scale of our study (~9000km^2), microhabitat type was far more influential in community composition than geographic location.

We followed up the MRPP analysis with an Indicator Species Analysis to identify which species were characteristic of each of the four microhabitat types. Each microhabitat type had at least three significant ($p < 0.05$) indicator species, with oases and riffles having the most (Table 5.3). A broad range of beetle, true bug, dragonfly, true fly, and leech taxa were indicative of oasis samples. Tinaja indicator species were fewer. A diverse group of beetles, mayflies, caddisflies, true flies, and flatworms were significant indicators of riffle habitats, while a species-poor group of true flies, along with one beetle and one true bug species, were indicators of seep habitats.

Though oasis and tinaja samples displayed overlapping community types in the NMS graph, it is clear from the Indicator Species Analysis that there are community distinctions between these two habitats. The beetle and true bug tinaja indicator taxa are all regionally widespread and common taxa (Bogan 2005), whereas some of the oasis indicator species are either regionally rare Neotropical species (e.g., *Beardius* sp., Diptera: Chironomidae) or potentially endemic species (e.g., *Laccophilus* cf. *horni,* Coleoptera: Dytiscidae). While seeps supported relatively species-poor communities, they were also the smallest in habitat area. Additionally, several seep indicator species (e.g., *Culicoides* sp., Diptera: Ceratopogonidae; *Apedilum* sp., Diptera: Chironomidae) were only found in that habitat. Thus, despite their small size and lower diversities, seeps are important contributors to regional aquatic invertebrate diversity.

The diversity and uniqueness of riffles was surprising. At Nacapule, for example, there is only about 3m^2 of shallow perennial riffle habitat, but more than 72 aquatic invertebrate species were collected there, 10 of which were encountered nowhere else in our study. Felger (1999) noted that flowing water habitat had decreased between the 1960s and 1990s, so it is probable that the riffle community present today is derived from a much larger habitat since has contracted to a small area. Several Nacapule riffle taxa were rare (e.g., *Cheumatopsyche arizonensis,* only five individuals collected during the three sampling periods). These rare taxa are likely at great risk of local extinction, as has already been noted for a wetland plant, *Psilotum nudum*, at Nacapule (Felger 1999). The ten riffle species unique to Nacapule may have once occurred at the other study sites with riffles (La Balandrona, Las Barajitas, Rancho Bacatete, and Rancho Santa Úrsula), but perhaps were extirpated at some point in the past, as all but one of those sites (Rancho Bacatete) currently have less perennial riffle area than Nacapule.

To assess seasonal variation in community composition, we surveyed riffles at our primary Nacapule survey location during multiple seasons in 2008 and 2009, as well as at an “upper” site 500m above and a “lower” site 500m below the primary site, and at one site in a smaller side canyon (“west fork”) of Nacapule. As with species richness (Figure 5.8), we did not find any predictable seasonal variation in community composition of riffles at Nacapule (Figure 5.10). This stands in contrast with streams of the more northern Madrean Sky Islands, which exhibit large and predictable seasonal changes in invertebrate community composition (Bogan and Lytle 2007). Despite large changes in flow, water level, and habitat structure following hurricane-induced flooding (Figure 5.11), Nacapule riffle communities exhibited as much variability between local sampling locations as between sampling events over the two years. Following monsoon and hurricane-edge rains in October 2008, the lower and upper portions of Nacapule contained flowing water. The lower site was quickly colonized by species from the primary site; the NMS graph demonstrates that they support similar communities (Figure 5.10). The upper site, however, was distinct from the others and was not colonized by many of the taxa for which Nacapule is unique (e.g. three genera of elmid riffle beetles). Instead, the upper site supported widespread opportunistic species, such as the black fly *Simulium*. Even the extreme flooding following Hurricane Jimena in September 2009 (550-730mm of rain in 24-36 hours recorded in nearby Guaymas and Empalme) and resultant severe channel rearrangement (Figure 5.11) failed to change the riffle community any more than the previous seasonal changes observed earlier during 2008 and 2009. Rains from that unprecedented storm also filled tinajas and formed substantial riffles in the west fork side canyon of Nacapule, and community samples collected there in November 2009 were similar to those of the nearby lower and primary sites. The riffle fauna of Nacapule thus appears to be fairly resistant or rapidly resilient to seasonal variation and extreme flow events.

5.3.4. Adult aquatic insect taxonomy

We used UV light traps to collect adult caddisflies (Trichoptera) at cañones Nacapule and La Navaja. Specimens were sent to taxonomic expert David E. Ruiter, Englewood, Colorado, for identification. As many as four undescribed species of caddisflies (families Hydroptilidae and Philopotamidae) were documented from these two sites. We are currently working on confirming that these indeed represent new species and, if so, will describe them (Ruiter, personal communication). It is interesting to note here the differences between our species lists of collected larvae versus adults (Table 5.4). Some taxa were collected as adults that were not identified in larval collections (e.g., *Wormaldia planae* [Philopotamidae] and three species of *Neotrichia* [Hydroptilidae]). Conversely, other taxa were common to abundant as larvae but were not collected in traps set for adults (e.g., *Ochrotrichia* sp. [Hydroptilidae]). Two other caddisfly genera (*Helicopsyche* and *Oxytheria*) were collected as larvae at wetted locations elsewhere in the Sierra El Aguaje, but were not documented as larvae or adults at Nacapule or La Navaja. Adult caddisflies collected from a third site, Rancho Santa Úrsula in the Sierra Santa Úrsula, are still under study.

We also had the opportunity to compare our collections of aquatic dragonfly and damselfly (Odonata) nymphs from Nacapule with a separate survey for terrestrial adult Odonata. Dennis R. Paulson, Odonata expert at the University of Puget Sound, Washington, along with D. Danforth, S. Upson, R. Behrstock, and S. Dunkle, visited Nacapule on 2 September 2006. They observed a total of 18 species of odonates, whereas we collected only seven taxa (as nymphs) during our six visits in 2008 and 2009. Paulson and associates observed five genera that we did not collect, whereas two other genera we collected were present as nymphs but were not observed as adults (Paulson, personal communication). Part of the difference in species richness between nymph and adult surveys can be explained by taxonomic resolution. For example, *Argia* (Coenagrionidae) was abundant as nymphs, but most individuals were too immature to identify to species level. During their visit, Paulson and associates identified four species of *Argia* as adults. Additionally, many dragonflies and damselflies are strong fliers and can disperse over long distances, thus species identified as adults at Nacapule are not necessarily resident there during their nymphal stage. The survey of Paulson and associates, however, underscores that the species richness values reported in our study are surely conservative, and many Odonata species remain to be documented from freshwater habitats in the region.

5.3.5. Noteworthy invertebrate species accounts

Beetles (Coleoptera) -- The dytiscid beetle *Macrovatellus mexicana* is common east of the Sierra Madre Occidental and Continental Divide (Jasper and Challet 2004), but is seldom encountered in western Mexico and has not been recorded from Arizona. We found it at most of our study sites in the sierras El Aguaje, Santa Úrsula, and Bacatete. The nearest previously known collections in Sonora are from tributaries of the Río Aros in east central Sonora (O'Brien et al. 2006), thus our collections are significant westward range extensions (~150km). At most tinaja and oasis habitats, we also collected a species of the diving beetle, *Laccophilus* (Dytiscidae), which we could not identify. It is similar to *L. horni*, but distinct in color pattern and size. A series of specimens were sent to Kelly B. Miller, a dytiscid taxonomist at the University of New Mexico, Albuquerque, and he is currently working on establishing its identity. He opines that it likely represents a new species (Miller, personal communication). We found one individual of the diving beetle *Rhantus calidus* (Dytiscidae) at Nacapule in December 2008. This Neotropical species has previously been documented from southeastern (Zimmerman and Smith 1975) and central eastern Sonora (O'Brien et al. 2006). Our collection at Nacapule represents a new western range extension for the species in mainland Mexico. In addition, the Neotropical water scavenger beetle *Tropisternus chalybeus* (Hydrophilidae) has previously been documented as far north as the state of Nayarit in western Mexico (Spangler 1960). We collected it from large pools at Rancho Bacatete (Sierra Bacatete) and Aguaje los Pelones (Sierra Santa Úrsula), indicating a significant (300km+) northward range extension.

True flies (Diptera) -- The Neotropical midge genus *Beardius* (Chironomidae) was a common inhabitant of oasis pools in our study. This genus is common in perennial waters of the tropics, but in the United States is only reported from southern Florida (Ferrington et al. 2008). *Beardius* consumes detritus (da Silva et al. 2008) and is often associated with leaf litter (Nessimian and Henriques-de-Oliveira 2005). Although we found larvae loose in leaf litter (mainly palm and fig trees), the vast majority of individuals collected had constructed silken tubes inside leaf cases of the caddisfly *Phylloicus mexicanus* (Calamoceratidae). In search of food, caddisflies drag their cases through detritus and leaf litter, thus *Beardius* larvae living in caddisfly cases likely are provided with an ample food supply. We have been unsuccessful in finding previous mention of *Beardius* larvae engaging in this phoretic trait in the scientific literature. We collected two regionally unique taxa of midges (Chironimidae: *Coelotanypus* and *Tanypus*) at Rancho Bacatete, in the Sierra Bacatete. Both genera are widespread in the Neotropics, but were not collected at any other site across the three sierras studied. Because Rancho Bacatete contains the most surface water and most lush riparian forest of all sites surveyed, it seems likely that some unique microhabitat for these two genera exists there that is lacking elsewhere in our study. The phantom midge genus *Chaoborus* (Chaboridae) is a true fly which prefers deeper lentic habitats and often undertakes daily micro-migrations, being “sprawlers” in the benthos by day and rising to become planktonic in open water by night (Courtney and Merritt 2008). We found *Chaoborus* only in two relatively deep tinajas in the Sierra El Aguaje: one 3-m-deep pool at “Tinajas Altas” and one 5-m-deep pool at Cañón “El Segundo”. The oasis at Cañón La Navaja is even deeper, but phantom midges were not found there during our study. The special habitat characteristics which these deep tinajas apparently offer phantom midges are as yet unknown to us.

Mayflies (Ephemeroptera) -- The genus *Farrodes* was only documented from larvae in riffles at

Nacapule, despite the presence of riffles at several other sites. This diverse Neotropical genus ranges from southern Texas to central South America, and likely contains many undescribed species (Dominguez 1999). The taxonomy of larvae is poorly known, making us unsure of the identity of this species. Published collection lists of this genus do not include northwestern Mexico, thus our collections from Nacapule represent a significant range extension and possibly an undescribed species.

True bugs (Hemiptera) -- Despite being common across most of Sonora, the giant water bug genus *Abedus* (Belostomatidae) is rarely encountered in the southern Sonoran Desert. We only collected one giant water bug species, *Abedus vicinus sonorensis*, during our study and it was only collected from Rancho Bacatete, which has the greatest aquatic habitat area (>1200m^2) of all surveyed sites. The Neotropical broad-shouldered water strider, *Rhagovelia acapulcana* (Veliidae), was also unique to Rancho Bacatete. It had previously been documented from Oaxaca northward to the tropical deciduous forest along the Río Mayo near San Bernardo, Sonora (Polhemus 1997). Our collection from Rancho Bacatete represents a 160-km northwestward range extension of this species into the Sonoran Desert. We collected a lentic water strider, *Limnogonus* sp. (Gerridae), at Arroyo El Palmar in December 2008. This is the only site where we found this taxon during all 2008 and 2009 surveys. This site is relatively unique in that it is located only 1km upstream from a small tidally-influenced, hypersaline estuary that borders the Gulf of California at Bahía San Carlos. Additionally, Arroyo El Palmar was the only non-perennial habitat surveyed, and, when wet, appears more like a marsh than a rocky stream (Figure 5.7). Backswimmers (Notonectidae) were also abundant at our study sites. Our collections of three Neotropical species of the backswimmer genus *Buenoa* (*B. albida, B. platycnemis, and B. thomasi*) from the Sierra El Aguaje all represent significant range extensions. The previous northwestern-most published localities for these species were from the Río Mayo, 160km southeast of the Sierra El Aguaje (Truxal 1953), though *B. albida* and *B. thomasi* were recently found in the Río Aros, 90km north of the Mayo (O'Brien et al. 2006).

Aquatic moths (Lepidoptera) -- Aquatic moth larvae were rare across the study region. We collected individuals of the genus *Petrophila* (Crambidae) by scraping surface film from the 20-m-high "trickling" waterfall that feeds the oasis at Cañón La Navaja (Figure 5.3), but nowhere else in the region. The genus *Elophila* (Crambidae) was only found at the artesian well riffles at Rancho Santa Úrsula, in the Sierra Santa Úrsula. The rarity of these taxa and the unusual habitats where they were found indicate that we have much to learn about the life history and habits of these aquatic moths.

Sponges (Porifera) and spongillaflies (Neuroptera) -- Unexpectedly, we found the spongillafly *Climacia chapini* (Sisyridae) and its obligate host and food source, an as yet unidentified freshwater sponge (Spongillidae) at six sites in the Sierra El Aguaje and at both sites in the Sierra Santa Úrsula. While freshwater sponges and their parasites, the spongillaflies, are widespread across North America, they are reported as rare in regions lacking large ponds and lakes. We collected the sponge and spongillafly in both oasis and tinaja habitats. The sponge was commonly found in encrusting form on rocks but occasionally encountered on submerged tree branches and roots (Figure 5.12). In several dry tinajas, we found large patches of dried sponge. Freshwater sponges are known to have dormant periods enabling survival through seasonal droughts (Frost et al. 2001), and presumably those of the southern Sonoran Desert have a similar adaptation.

Crustaceans -- We collected the grass shrimp, *Palaemonetes* sp. (Decapoda: Palaemonidae), at Arroyo El Palmar when it was wetted in December 2008. This family of shrimps occurs in marine and brackish waters as well as in freshwater habitats. We have yet to determine the species, but it must have colonized the seasonal freshwater portion of the arroyo from the nearby Bahía San Carlos estuary during storm surges in 2008. We have also observed *Palaemonetes* in the freshwater portion of Arroyo El Palmar during visits in several different years (2004, 2009, 2011), indicating that it frequently colonizes freshwater reaches of the arroyo when habitat becomes available.

5.3.6. Aquatic vertebrates

Big-eyed leopard frog -- *Rana magnaocularis* was the most commonly encountered aquatic vertebrate at our study sites. We found this species at six sites in the Sierra El Aguaje (cañones Nacapule, La Navaja, Pirinolas, Balandrona, Barajitas, and "El Segundo") and one site in the Sierra Santa Úrsula (Rancho Santa Úrsula). At the latter site, big-eyed leopard frog adults and tadpoles were encountered nearly exclusively in pools without the exotic fish tilapia. Only one large adult frog was observed adjacent to a pool containing tilapia. Frogs there were far more wary of humans than those observed in the Sierra El Aguaje, with adults jumping into the water before we could approach within five meters of a pool, even during night surveys.

During the course of our surveys, a population genetics study using mitochondrial DNA was published focusing on two populations of big-eyed leopard frog from the Sierra El Aguaje (Nacapule and La Navaja; Pfeiler and Markow 2008). The authors of that study determined that although Nacapule and La Navaja frogs were genetically similar to populations of *R. magnaocularis* elsewhere, there was potentially enough genetic distinction between the groups to warrant unique specific status for the Sierra El Aguaje populations. The authors also noted that, though their sample size was small (n = 15), Nacapule and La Navaja frogs were monomorphic in both the control region and 12S rRNA, suggesting extreme population isolation, severe population bottlenecking, or both.

Big-eyed leopard frog tadpoles were abundant at all sites where adults were found in the Sierra El Aguaje. Slight seasonal variation in abundance was observed at Nacapule, with many tadpoles and adults in April and June, followed by fewer tadpoles but abundant subadults in August. Adults were heard vocalizing from dusk to about an hour after dusk at Nacapule and La Navaja during visits in December, April, and August, with more frequent calls in August; these calls were recorded at Nacapule. During our August 2008 visit to Nacapule, we counted 19 adults and 80 subadults along 10m of shoreline at one large oasis pool. Frogs were present in the open, deeper water of the oasis pool, and were also abundant in most tinajas in the canyon. At dusk, many individuals were utilizing terrestrial areas up to 5m from shore for feeding on abundant adult terrestrial and adult aquatic insect prey. Frogs were nearly as active and abundant during preliminary visits to Nacapule in May and December 2004 and November 2006. Thus, at least some local big-eyed leopard frog populations are large despite limited habitat size; perhaps periods of extreme drought with resulting habitat constriction are responsible for the potential genetic bottleneck noted by Pfeiler and Markow (2008). The only obvious native aquatic predator of these frogs was the giant water bug, *Lethocerus medius* (Belostomatidae). We observed *L. medius* feeding on adult leopard frogs on several occasions (Figure 5.13).

Canyon tree frog -- We occasionally found the canyon tree frog, *Hyla arenicolor*, at Nacapule and La Navaja, but never more than two individuals during any visit. We also found this species at a large tinaja in Cañón "Escondido" in the Sierra El Aguaje, though most individuals were recently dead (Figure 5.14). Large numbers of dead individuals is not an uncommon sight in regional streams during April and May (M.T. Bogan, pers. obv.), suggesting natural predation and seasonal mortality rather than unusual circumstances or disease. We also found small tadpoles at Cañón la Balandrona and Rancho Santa Úrsula which appeared to be this species, but without adult sightings this tentative identification remains unconfirmed. It is likely that this relatively cryptic species is much more common than our surveys indicate (4 or 5 sites of 19), but perhaps peak abundances occur outside our normal survey periods.

Sabinal frog -- *Leptodactylus melanonotus* (Figure 5.15) is a common species along tropical streams throughout Central America and northward to central Sonora. The currently accepted northern-most record is from Hermosillo, Sonora (Endersen et al. 2009), so our finding of the species at Rancho Bacatete is not outside its expected range, though within 120km of its northern limit. It is fitting, however, that this typically Neotropical species was found in the most lush, tropical, and well-watered site of all locations we visited across the three mountain ranges. Rancho Bacatete represents a true tropical outpost in dry Sonoran desertscrub (Figure 5.16) and is much deserving of further study.

Black-necked garter snake -- We encountered the semi-aquatic black-necked garter snake, *Thamnophis cyrtopsis*, at one site (Las Pirinolas). However, we did not actively search for semi-aquatic reptiles at all sites and they are likely more widespread in the region. The individual captured (and released) was observed mainly due to its large size (Figure 5.17). It occupied a tinaja that contained dense populations of aquatic macroinvertebrates, including large gastropods and leeches. This species is common in mountain streams of the Mogollon Rim and Madrean Sky Islands in Arizona, and the northern Sierra Madre Occidental, and one desert outlier population occurs in the Ajo Mountains of southwest Arizona (Brennen and Holycross 2006).

We do not know if the Sierra El Aguaje population is similarly isolated (it is more than 100km to the nearest Madrean Sky Island), or if habitat preferences of the species change further south in its distribution. The wetted habitats located between the Sierra El Aguaje and the more northern Madrean Sky Islands (e.g., the Río Mátape; the Sierra Libre) have not been sufficiently surveyed to determine its presence or absence there.

<u>Desert chub</u> --We encountered relict populations of desert chub, *Gila eremica* (Cyprinidae) in two Sierra El Aguaje canyons (Pirinolas and Balandrona). This species was not found at other study sites in that sierra, nor anywhere in the sierras Santa Úrsula and Bacatete. Alejandro Varela-Romero and his students at the Universidad de Sonora in Hermosillo are currently studying the genetic and morphological variation of the specimens collected from these two sites to determine their potential uniqueness compared to other desert chub populations in Sonora (e.g., Río Mátape).

<u>Sonoran topminnow</u> --We found what appears to be Sonoran topminnow, *Poeciliopsis occidentalis sonoriensis* (Poeciliidae), at both sites visited in the Sierra Santa Úrsula (Figure 5.18). This subspecies (often recognized at specific level, *P. sonoriensis*) is known from drainages across the region, but our finding represents the first record from this mountain range (compare to Miller et al. 2006). Considerable morphologic and genetic variation often characterize species and genera in this family, and we are currently involved in analyses to determine the taxonomic status of the Sierra Santa Úrsula populations.

<u>Tilapias (Cichlidae)</u> --We found exotic (introduced) tilapia (*Tilapia* spp.: Figure 5.19) to be relatively abundant at all sites visited in the sierras Santa Úrsula and Bacatete. Tilapias, which

are largely African in origin, are widely used in aquaculture, and humans have facilitated their spread to many natural bodies of water in Mexico (Miller et al. 2006). All four sites in the sierras Santa Úrsula and Bacatete are used for cattle grazing and have easy trail or dirt road access, facilitating the introduction of exotic fishes. Courting adult males of most tilapia excavate and guard shallow spawning and nest pits, and this activity clearly disturbed benthic substrates at each site where tilapia were present (Figure 5.19). Additionally, larger invertebrate predators (e.g., giant water bugs; predaceous diving beetles) were notably scarce at all sites with tilapia. At three of the four sites they had invaded all available water. At Rancho Santa Úrsula in the Sierra Santa Úrsula, however, tilapia had invaded the lower reaches of the drainage, but failed to colonize three pools higher in the arroyo. We used this “natural” break in the distribution of tilapia there to assess their impacts on native invertebrate richness, density, and community composition (see following section).

5.3.7. Effect of tilapia on aquatic invertebrates

We sampled aquatic invertebrates from three pools containing tilapia (dates of introductions unknown) and three tilapia-free pools at Rancho Santa Úrsula to explore the effects of tilapia on native invertebrates. The tilapia versus tilapia-free reaches were separated by about 150m, and had similar water quality and physical habitat characteristics [mean of tilapia pools: 13m^2 area, 0.7m deep, 20°C, 315μS, 6.75pH; mean of tilapia-free pools: 18m^2 area, 1m deep, 23°C, 320μS, 7.0pH].

Tilapia-free pools supported significantly more invertebrate taxa than tilapia pools, with an average of 45 taxa in tilapia-free pools versus 23 taxa in tilapia pools (t = -2.55, one-sided p = 0.031; Figure 5.20). Invertebrate sample densities were nearly 10 times higher in tilapia-free pools than in tilapia pools (t = -2.20, one-sided p = 0.046; Figure 5.20). Despite the small sample sizes and large between-pool variability, the presence of tilapia is clearly associated with significant reductions in invertebrate richness and densities. Additionally, MRPP analysis revealed that tilapia versus tilapia-free pools supported distinct invertebrate communities (A-value = 0.397, p = 0.02). Unfortunately, given the small sample sizes, it was not feasible to perform Indicator Species Analysis on the tilapia versus tilapia-free pools that yielded p-values lower than 0.098. The indicator values (IV), however, remain useful for looking at faithfulness and exclusivity of a species to a group. We identified nine species which were completely faithful and exclusive to tilapia-free pools (IV = 100), and an additional three taxa which had nearly perfect scores (Table 5.5). Eight of these 12 taxa were free-swimming predatory species (e.g., predaceous diving beetles). The only indicators of tilapia pools were two mayfly taxa, the scraper *Tricorythodes* (Leptohyphidae) (IV = 100) and the grazer *Choroterpes* (Leptophlebiidae) (IV = 78) (Table 5.5). Both species have low profiles, often living in small interstitial spaces in the substrate where tilapia would have difficulty extracting them (Bogan, pers. obvs.). Also, it may be that these mayflies thrive in the absence of their invertebrate predators which become reduced in abundance, or removed entirely, by tilapia.

5.4. CONCLUSIONS

5.4.1. Overview

Freshwater habitats in the sierras El Aguaje, Santa Úrsula, and Bacatete form a small part of the landscape, but provide a wide variety of microhabitats that support more than 220 species of aquatic animals. During 2008 and 2009, we visited 19 sites with perennial water and classified four different microhabitat types (oasis, tinaja, riffle, and seep), each supporting distinct aquatic invertebrate communities. Microhabitat differences were more important than geographic location in structuring local communities at the scale of our study area (9000km^2). A few sites clearly exhibited large seasonal swings in aquatic habitat size and presence (e.g., Arroyo El Palmar), but most sites contained relatively stable perennial habitats (e.g., Cañón La Navaja). At Cañón Nacapule, we found little evidence of predictable seasonal invertebrate community variation, even though hurricane edge- or monsoon-induced flooding at times dramatically impacted microhabitats there (Figure 5.11). Many lotic taxa unique to Nacapule appear to be unable to take advantage of seasonally intermittent aquatic habitats upstream from the perennial reach, but were able to colonize downstream seasonal habitats. The aquatic vertebrates we encountered were not particularly diverse across the study region, but were often locally abundant. Big-eyed leopard frog, in particular, was abundant at many Sierra El Aguaje sites and at one in the Sierra Santa Úrsula. Two species of native freshwater fishes were found at two sites each, and exotic tilapia were found at all sites in the sierras Santa Úrsula and Bacatete. At Rancho Santa Úrsula, tilapia presence was strongly associated with a shift in aquatic invertebrate community structure and reduced invertebrate species richness and density.

5.4.2. Immediate conservation concerns

The most pressing conservation concerns in the region are related to urban and agricultural development, human visitation and resulting damage to sensitive aquatic habitats, and the misguided introduction of exotic species. Accelerating development of vacation and retirement properties in San Carlos continues, and local groundwater pumping remains the only water source for such new developments. Though the bedrock of the Sierra El Aguaje is complexly faulted (Wilson 1978), groundwater withdrawals immediately adjacent to the range will likely cause local depressional cones in the aquifer, thus reducing the outflow at spring-fed habitats. Groundwater withdrawal mainly for extensive agricultural and suburban use in the neighboring Valle de Guaymas has already led to plummeting water tables, decreased surface flows, saltwater intrusion and the abandonment of wells and settlements (Custodio 2002). The sierras Bacatete and Santa Úrsula are located immediately adjacent to that valley, and, as such, spring-fed freshwater habitats in these ranges undoubtedly will face declining water levels from this groundwater withdrawal.

As regional tourism/recreational development increases (as well as general population growth), visitation to sites such as Cañón de Nacapule will continue to increase as well. While human visitation to Nacapule has steadily increased since the 1960s (Felger 1999), it has skyrocketed in recent years, leading to increased trash and vandalism (e.g., graffiti), destruction of native plants from trampling, and threats from unauthorized access by off-road vehicles (Carrizales 2007; also see Figure 5.21). In 1998, Nacapule was named a "conservation priority" by the Wildlands Project (University of Arizona 2002) but little evidence of conservation work has been visible in the interim (Carrizales 2007). Unfortunately, the only 3m^2 of riffle habitat at Nacapule occurs in reaches of heavy human foot traffic. This trampling, combined with the looming threat of groundwater withdrawals lowering water tables, places Nacapule and its riffles at the top of our list of concerns. Ten species of aquatic invertebrates were found in the riffles of Nacapule but nowhere else in the study region; thus all ten are at high risk of local extinction. These riffle species appear to be resistant or resilient to natural extreme flow events, but it is not known if they can persist in the face of human-induced disturbance as well. We would like to see Nacapule and adjacent areas of the southern Sierra El Aguaje protected by the federal government as part of a reserva de la biosfera (biosphere reserve) system. Also, although part of the Sierra El Aguaje may be technically protected under the old "Cajón del Diablo" preserve, its boundaries are unclear and unrespected, and active protection of the landscape is woefully insufficient (Gallo-Reynoso 2003). Further protection and active management is warranted given the increasing threats to both aquatic and riparian habitats of the Sierra El Aguaje.

Other oases are also threatened as their locations are discovered by the general public and visitation increases. From 2000 to 2009, we found little evidence of visitation to the beautiful palm-ringed pool and waterfall oasis at the head of Cañón La Navaja (Figure 5.3). In 2009, video images and the exact location of this oasis were advertised on a local television program in Guaymas, Sonora. Subsequently, visitation increased and both trash and trampling became more common in this formerly seldom-visited oasis. Sadly, on 20 February 2011 the entire oasis was burned, killing most of its fig trees (*Ficus insipida*, *F. pertusa*, and *F. petiolaris palmeri*) and brushy vegetation and killing or severely damaging most of its palm trees (*Washingtonia robusta*) (Figure 5.22). Although some have opined that the fire resulted from a tourist campfire left unattended, we found evidence of numerous separated and more isolated palms which had been burned by setting their skirt of dead fronds ablaze, indicating that the fire was almost certainly the result of intentional vandalism. The local rancher who controls transit on the only road leading to the oasis trailhead reported that the perpetrators had gained unauthorized access to the oasis by skirting his ranch with all-terrain vehicles.

The introduction of exotic species also poses a grave threat to the biodiversity of these isolated freshwater habitats. The presence of exotic tilapia was associated with dramatic negative impacts on aquatic invertebrate communities, and occurrences of exotic tilapia and native big-eyed leopard frog were nearly mutually exclusive in pools at Rancho Santa Úrsula in the Sierra Santa Úrsula. We suggest that prevention of misguided tilapia introductions to other sites across the three sierras also be an urgent conservation priority. Until 19 February 2011, tilapia were absent from all sites we surveyed in the Sierra El Aguaje. Unfortunately, on that date we found tilapia in the large pool at Aguaje “El Caballo”, a site that one of us (LTF) has been visiting for the past 15 years without seeing any fishes. On 19 February and 13 March 2011 only one or two large fish were seen, but on 22 March 2011 we saw numerous individuals, both large and small.

These observations suggest that either clandestine stocking was continuing or tilapia were already reproducing in this oasis. The spread of tilapia to other sites in the Sierra El Aguaje could be devastating to invertebrate communities and potentially lead to the local extinctions of both the big-eyed leopard frog and desert chub. The native Sonoran topminnow in the Sierra Santa Úrsula appear to be persisting despite the presence of tilapia, but its two known populations there should continue to be monitored to assess whether or not they continue their coexistence with tilapia.

5.4.3. Future research directions

We strongly recommend continued biotic inventories of the three sierras' aquatic habitats, with a focus on (1) more time-intensive surveys of all sites, (2) continued seasonal monitoring at Cañón Nacapule, (3) expanding visual surveys and UV-light trapping for adult aquatic insects, and (4) gaining access to potential additional sites identified by remote sensing. At certain sites, our survey time was limited by difficulty of access, and more time-intensive surveys certainly would reveal the presence of additional aquatic species. Repeat surveys of Nacapule increased the number of aquatic invertebrate taxa detected there by more than 30% and resulted in unique collections of some regionally-rare species (e.g., the beetle *Rhantus calidus*). Further visits to the other sites we surveyed would likely result in similar increases in local and regional species diversity lists.   We also recommend conducting additional adult insect surveys at all sites in expectation of increasing species detection, and to enhance taxonomic resolution for taxa that we collected as aquatic larvae but could not identify to species. Finally, genetic studies of aquatic organisms in the region would help elucidate the level of uniqueness and isolation of the invertebrate and vertebrate populations of these sierras. The results of such studies would likely contribute greatly to local and regional conservation efforts.

ACKNOWLEDGEMENTS

This work was made possible in part by two grants from the non-profit group T&E Inc., and is dedicated to the memory of the group's founder, Tom Wootten. Many thanks to Sr. Enrique Castillo-Grijalva of Guaymas, Sonora, for (along with LTF) facilitating access to survey sites in the sierras Santa Úrsula and Bacatete, accompanying us on all visits to those ranges, and seemingly effortlessly scaling of mountains and cliff faces on often scorching hot days in that part of the Sonoran Desert. Thanks to Doña Olga Armenta and her son Miguel Velázquez Armenta of Empalme, Sonora, for allowing us to camp and work at Rancho Santa Úrsula in the Sierra Santa Úrsula. Thanks to Don Ramón Villafraña of Rancho San Antonio in Ejido Francisco Villa for allowing access to the Pirinolas and Balandrona sites in the Sierra El Aguaje. Sr. Delfín Antonio Magallanes-Molina of Rancho Palo Fierro of Ejido 13 de Julio allowed access to Cañón La Navaja and other sites nearby. Thanks to Don Armulfo of Rancho Los Anegados for allowing us to camp at the Anegados beach. Thanks to Claire Zugmeyer of the Sonoran Institute, Tucson, for providing the digital elevation map data used to produce Figure 1. Special thanks to Dave Ruiter (Trichoptera), Dennis Paulson (Odonata), Kelly Miller (Dytiscidae), Bill Shepard and Cheryl Barr (Elmidae) for taxonomic help with adult aquatic insects during the course of this project.

Table 5.1 Physical and biological characteristics of the 19 sites surveyed during 2008 and 2009 (habitat codes: O- oasis, T- tinaja, R- riffle, S- seep). Place names in quotation marks are not named on local maps or by local ranchers, thus we use names coined by L.T. Findley and other residents of San Carlos or those derived from characteristics observed during site visits.

Site	Invertebrate richness	Habitat area (m^2)	Habitat type	Temp. (°C)	pH	Cond. (μS)	Frogs	Fishes	UTM N	UTM E
SIERRA EL AGUAJE										
Cañón de Nacapule	121	350	O, T, R, S	23	6.25	330	X		3099031	494501
Cañón La Navaja	108	445	O, T, R, S	21	6.5	309	X		3099807	489726
Cañón “Segundo”	78	120	T, S	19	6.5	431	X		3098816	492656
Cañón La Balandrona	77	340	T, R	22	6.5	322	X	X	3103870	492888
Cañón Las Barajitas	63	110	O, T, R	20	6.25	310	X		3103035	484972
Arroyo El Palmar	63	115	T	19	6.25	580		X	3093163	494068
Cañón Las Pirinolas	59	90	O, T	24	6.75	335	X	X	3104063	495241
Aguaje "El Caballo"	58	180	O	18	7	828			3096870	491567
"Tinajas Altas"	50	39	T	21	6.5	343			3097050	491742
Cañón “Escondido”	50	176	T	21	6.25	140	X		3095735	492737
Aguaje "Las Abejas"	36	10	T	25	8	658			3095973	492015
Cañón "Keyhole"	28	36	T	24	6.5	361			3097808	491438
Aguaje "Las Vacas"	15	12	S	24	6.25	342			3097771	493535
Aguaje Los Anegados	13	13	S	13	6.5	830			3100786	486562
Aguaje de Robinson	10	8	S	25	6.5	343			3101319	489165
SIERRA BACATETE										
Rancho Bacatete	82	1200	O, T, R	21	7	584	X	X	3104908	562986
Aguaje Los Pilares	39	500	T	24	7.5	585		X	3116437	552465
SIERRA SANTA ÚRSULA										
Rancho Santa Úrsula	93	620	O, T, R	24	7	310	X	X	3108015	515319
Aguaje Los Pelones	36	400	T	23	7	246		X	3109517	516099

Table 5.2 Aquatic invertebrate species occurrences (X) at the 19 study sites in the sierras El Aguaje, Bacatete, and Santa Úrsula (left to right) in order of species richness within each mountain range. See Table 1 for each site's complete name and habitat characteristics (C. = Cañón; A.= Aguaje).

			Sierra El Aguaje															Sierra Bacatete		Sierra Santa Úrsula	
Order	Family	Species	C. Nacapule	C. La Navaja	C. Segundo	C. Balandrona	C. Barajitas	El Palmar	C. Pirinolas	A. El Caballo	C. Escondido	Tinajas Altas	A. Las Abejas	C. Keyhole	A. Las Vacas	A. Los Anegados	A. de Robinson	Rancho Bacatete	A. los Pilares	Santa Úrsula	Pelones
Coleoptera	Dytiscidae	*Copelatus chevrolati renovatus*						X													
		Cybister ellipticus				X													X		
		Desmopachria convexa group	X	X		X				X	X	X								X	
		D. dispersa	X			X		X	X	X	X		X						X	X	X
		D. mexicana	X	X	X	X	X		X	X	X	X		X				X		X	
		D. portmanni	X	X	X																
		Hydrovatus cf. *davidis*											X								
		Hygrotus sp.									X								X		
		Laccophilus coccinelloides						X													
		L. fasciatus		X	X	X	X	X	X	X	X	X	X						X	X	
		L. cf. *horni*	X	X	X	X	X		X	X	X	X						X		X	
		L. mexicanus											X							X	
		L. pictus	X	X	X	X	X	X	X	X	X	X	X	X				X	X	X	
		Liodessus obscurellus	X	X	X	X	X	X		X	X	X	X							X	
		Macrovatellus mexicanus		X	X	X		X	X	X	X	X						X	X	X	X
		Neoclypeodytes amybethae		X							X	X									
		N. fryii		X							X										
		N. sp.	X	X	X	X				X		X									
		Rhantus atricolor				X															
		R. calidus	X																		
		R. g. gutticollis		X	X			X				X									
		R. g. mexicanus										X									
		Stictotarsus aequinoctialis				X		X				X									

		Thermonectus marmoratus	X	X	X	X	X	X	X	X	X	X		X					X	X	X
		T. sibleyi		X		X	X		X	X	X	X						X		X	X
		T. succinctus		X		X		X		X			X						X		
	Elmidae	*Heterelmis glabra*	X																		
		Microcylloepus inequalis	X																		
		Neocylloepus arringtoni	X	X																	
		Neoelmis sp.	X																		
	Haliplidae	*Peltodytes dispersus*																		X	
	Helophoridae	*Helophorus* sp.	X																		
	Heteroceridae	Unidentified taxon					X														
	Hydraenidae	*Hydraena* sp.	X	X			X		X	X								X	X		
	Hydrophilidae	*Berosus* cf. *infuscatus*																			X
		B. moerens	X	X	X	X	X	X	X	X	X	X	X	X	X			X		X	
		B. notapeltatus	X					X													
		B. rugulosus	X	X	X	X	X	X	X	X	X	X	X	X				X	X	X	
		B. salvini		X	X	X		X	X			X									
		B. sp. (larvae)	X										X							X	
		Enochrus ochraceus																	X		
		E. sharpi	X					X		X			X						X	X	X
		E. sp.	X		X		X		X								X				
		Helochares normatus	X	X	X	X		X	X	X	X		X	X				X		X	X
		cf. *Hydrobius* sp.													X						
		Hydrochus sp.	X	X	X	X	X	X	X	X	X	X	X	X				X	X	X	
		Hydrophilus insularis	X	X	X		X		X	X		X						X	X	X	X
		Paracymus cf. ellipsis	X		X			X												X	
		Tropisternus chalybeus																X			X
		T. ellipticus																X	X	X	
		T. lateralis		X	X	X		X		X	X	X	X	X				X	X	X	
		T. mexicanus						X													X
	Noteridae	*Suphisellus lineatus*						X	X										X	X	
	Scirtidae	*Elodes* sp.	X	X	X	X	X		X												
		Cyphon sp.						X		X	X								X	X	
		Unidentified taxon												X				X			X
Diptera	Ceratopogonidae	*Atrichopogon* sp.																			
		Bezzia sp.	X	X	X	X		X							X	X		X			
		Ceratopogon sp.	X	X	X										X	X		X		X	X

	Culicoides sp.		X	X												X			X	
	Forcipomyia sp.	X	X	X		X		X	X		X									
	Monohelea sp.		X		X		X								X					
Chaoboridae	*Chaoborus* sp.		X	X							X									
Chironomidae	*Ablabesmyia* sp.	X		X	X		X		X		X	X		X	X	X			X	X
	Apedilum sp.		X	X			X					X			X				X	
	Apsectrotanypus sp.		X																	
	Beardius sp.	X	X	X	X	X		X		X	X						X		X	X
	cf. *Lipiniella* sp.					X														
	Chironomus sp.	X			X		X				X	X						X	X	X
	Coelotanypus sp.																X			
	Corynoneura sp.	X	X	X	X	X				X		X		X		X	X		X	
	Cricotopus-Orthocladius	X			X	X					X				X				X	
	Dicrotendipes sp.	X		X						X							X		X	
	Endotribelos sp.	X	X					X									X			
	Fittkauimyia sp.	X	X	X	X					X		X	X				X		X	X
	cf. *Goeldichironomus* sp.	X																		
	Labrundinia sp.	X	X				X		X	X	X				X					
	Larsia sp.	X			X															
	Lauterborniella sp.	X	X	X	X	X			X	X		X	X			X	X		X	X
	Paramerina sp.	X	X	X	X	X	X	X		X	X	X	X				X		X	
	Parametriocnemus sp.	X	X			X								X			X		X	
	Paratendipes sp.	X		X	X						X			X					X	
	Pentaneura sp.		X																	
	Polypedilum sp.	X	X			X								X		X	X			X
	Psectrocladius psilopterus group				X			X												
	Pseudochironomus sp.	X	X		X		X		X			X							X	
	Pseudokiefferiella sp.				X															
	Rheotanytarsus sp.	X	X														X		X	
	Stenochironomus sp.	X																		
	Stempellina sp.	X																		
	Stempellinella sp.	X																		
	Tanypus sp.																X			
	Tanytarsus (Nimbocera) sp.	X	X	X		X						X		X	X	X	X		X	
	T. (Tanytarsus) sp.	X	X	X	X	X	X					X					X	X	X	X
	Thienemanniella sp.	X	X				X										X		X	

	Culicidae	*Anopheles* sp.		X				X		X	X	X		X	X			X		X	
		Culex sp.		X						X	X							X			
		Unidentified taxon	X		X	X	X		X												
	Dixidae	*Dixella* sp.	X					X		X								X			
	Dolichopodidae	Unidentified taxon															X				
	Empididae	*Hemerodromia* sp.	X				X									X		X		X	
	Ephydridae	Unidentified taxon			X				X												
	Psychodiae	*Maruina* sp.	X		X																
		Pericoma sp.	X																		
	Ptychopteridae	*Ptychoptera* sp.	X			X															
	Simuliidae	*Simulium argus*	X	X																	
		S. cf. *carbunculum*		X																	
		S. sp.	X			X												X			
	Stratiomyidae	*Caloparypharus* sp.	X														X			X	X
		Myxosargus sp.	X	X	X													X		X	
		Stratiomys sp.																		X	
	Tabanidae	Unidentified taxon	X															X			
	Tipulidae	cf. *Antocha* sp.			X																
		cf. *Dicranota* sp.	X																		
		Limonia sp.	X	X														X			
Ephemeroptera	Baetidae	*Callibaetis* sp.	X	X	X	X	X	X	X	X	X	X	X	X				X	X	X	
		Fallceon sp.	X	X														X		X	
		Unidentified taxon	X			X	X									X					
	Caenidae	*Caenis* sp.		X					X									X	X		
	Leptohyphidae	*Tricorythodes* sp.	X		X								X					X	X	X	
	Leptophlebiidae	*Choroterpes* sp.	X		X	X	X	X	X	X	X	X	X	X				X	X	X	X
		Farrodes sp.	X																		
Hemiptera	Belostomatidae	*Abedus vicinus sonorensis*																X			
		Lethocerus medius	X	X	X	X	X		X	X		X		X				X	X	X	X
	Corixidae	*Graptocorixa abdominalis*	X	X	X	X	X	X	X	X	X	X	X	X						X	
		Morphocorixa lundbladi	X	X	X	X	X		X	X	X	X								X	
		Trichocorixa reticulata						X													
	Gerridae	*Limnogonus* sp.						X													
		Limnoporus sp.	X	X	X	X	X			X	X							X		X	
		Rheumatobates sp.																			X
		Trepobates becki	X	X	X	X	X	X	X	X	X	X		X				X	X	X	X

	Hebridae	*Merragata* sp.							X											X	
	Hydrometridae	*Hydrometra* sp.	X	X														X	X	X	
	Mesoveliidae	*Mesovelia mulsanti*	X				X	X							X					X	
	Naucoridae	*Ambrysus melanopterus*	X	X																	
		A. occidentalis	X	X		X	X				X									X	
		A. pulchellus																		X	
		A. sp.	X				X	X										X			
		Pelocoris sp.	X	X	X	X		X	X	X	X	X							X	X	
	Nepidae	*Curicta pronotata*	X	X	X	X	X		X										X	X	
		Ranatra quadridentata	X	X	X	X	X	X	X	X		X		X				X	X	X	X
	Notonectidae	*Buenoa albida*	X	X	X	X	X	X	X	X	X			X				X		X	
		B. arida	X	X	X	X			X	X	X	X		X						X	
		B. arizonis	X	X	X	X	X	X	X	X	X	X	X	X				X		X	
		B. platycnemis	X	X	X					X		X						X			
		B. thomasi							X												
		Notonecta hoffmanni	X																		
		N. lobata	X	X	X	X			X	X	X	X		X							
		N. indica				X		X					X						X		X
		N. sp.		X	X		X														
	Veliidae	*Microvelia sp.*	X	X	X	X	X	X	X			X	X		X	X	X		X	X	
		Platyvelia summersi	X	X	X	X		X		X	X									X	
		Rhagovelia acapulcana																X			
Lepidoptera	Crambidae	*Elophila* sp.																		X	
		Petrophila sp.		X																	
Neuroptera	Sisyridae	*Climacia chapini*		X	X	X	X		X											X	X
Odonata	Aeshnidae	*Anax walshinghami*		X			X	X	X		X			X							
		Remartinia luteipennis																X			
		Rhionaeshna psilus	X		X				X	X								X	X	X	
	Coenagrionidae	*Argia* sp.	X	X	X		X		X	X	X	X			X	X		X		X	
		Coenagrion / Enallagma	X	X	X			X			X		X					X	X	X	X
		Ischnura ramburii						X													
		Telebasis salva		X	X			X		X								X		X	
		Unidentified taxon		X					X												
	Gomphidae	*Phyllogomphoides* sp.	X	X		X												X			
	Lestidae	*Archilestes grandis*	X	X	X	X	X		X	X	X	X						X		X	
	Libellulidae	*Brechmorhoga* sp.																X			

		Libellula saturata	X	X	X											X			
		Macrothemis inacuta						X											
		Miathyria sp.																X	
		Orthemis ferruginea						X											
		Paltothemis lineatipes						X		X								X	
		Perithemis intensa			X			X	X							X			X
		Psuedoleon superbus	X	X		X	X	X	X	X			X	X			X	X	
		Unidentified taxon													X				
Trichoptera	Calamoceratidae	*Phylloicus mexicanus*	X	X	X	X	X		X					X					
(caddisflies)	Helicopsychidae	*Helicopsyche* sp.				X										X		X	X
	Hydropsychidae	*Cheumatopsyche arizonensis*	X	X															
		cf. *Potamyia* sp.														X			
	Hydroptilidae	*Leucotrichia* sp.	X													X			
		Neotrichia canixa	X													X			
		N. n. sp. 1		X															
		N. n. sp. 2		X															
		Mayatrichia n. sp.		X															
		Ochrotrichia sp.	X		X		X									X		X	
		Oxyethira sp.	X						X									X	
		Unidentified taxon	X	X		X										X		X	
	Leptoceridae	Unidentified taxon														X			
	Odontoceridae	*Marilia nobsca*	X	X	X	X	X	X	X	X	X	X	X			X		X	X
	Philopotamidae	*Chimarra ridleyi*		X															
		C. sp.	X	X			X									X		X	
		Wormaldia planae		X															
Non-insects	(Class or family)	(Genus or family)																	
	Amphipoda	*Hyallela sp.*		X		X	X									X	X	X	
	Cladocera	Unidentified taxon	X	X	X	X			X	X	X							X	
	Collembola	Unidentified taxon	X		X	X													
	Copepoda	Unidentified taxon	X	X	X	X		X	X	X	X	X				X			X
	Decapoda	*Palaemonetes* sp.						X											
	Glossiphoniidae	Unidentified taxon	X	X		X	X		X	X				X		X	X	X	
	Hydracarina	*Atractides* sp.	X																
		Hydrozetes sp.		X	X		X												
		Mucronothrus sp.					X												

	Sperchon sp.	X																	
	Unidentified taxon	X	X	X	X	X		X	X	X						X		X	X
Oligochaeta	Unidentified taxon	X	X	X	X	X	X		X		X	X	X		X	X	X	X	X
Ostracoda	Unidentified taxon	X	X				X		X		X					X			
Physidae	Unidentified taxon	X	X	X	X	X		X		X	X	X						X	
Planorbidae	*Gyraulus* sp.															X			
	Planorbella sp.																X		X
Platyhelmenthes	Unidentified taxon	X	X			X													
Porifera	Unidentified taxon	X	X		X	X		X	X									X	X

Table 5.3 Indicator taxa for the four habitat types including indicator values (IV) and significance (*p*).

Habitat	Taxon	IV	*p*
Riffles	*Corynoneura* sp.	87	0.001
	Hydroptilidae	83	0.000
	Chimarra sp.	83	0.000
	Rheotanytarsus sp.	64	0.001
	Hemerodromia sp.	58	0.000
	Fallceon sp.	50	0.003
	Parametriocnemus sp.	49	0.006
	Thienemanniella sp.	48	0.007
	Ochrotrichia sp.	47	0.005
Seeps	*Bezzia* sp.	71	0.003
	Microvelia sp.	55	0.008
	Culicoides sp.	49	0.004
	Hydrozetes sp.	39	0.021
	Apedilum sp.	36	0.040
Oasis	*Trepobates becki*	71	0.000
	Desmopachria mexicana	65	0.010
	Hydrochus sp.	65	0.013
	Macrovatellus mexicanus	64	0.005
	Laccophilus cf. *horni*	63	0.004
	Buenoa albida	62	0.007
	Beardius sp.	60	0.009
	Ranatra quadridentata	59	0.006
	Limnoporus sp.	55	0.007
	Glossosiphonidae	55	0.008
Tinaja	*Bersus rugulosus*	60	0.011
	Buenoa arizonis	48	0.038
	Tropisternus lateralis	47	0.070
	Laccophilus pictus	45	0.044

Table 5.4 Trichoptera (caddisflies) of cañones Nacapule and La Navaja, where both aquatic larvae and terrestrial adults were collected. Presence (X) or absence (-) of species noted along with life stages documented (larvae, adult, or both).

Family	Species	Nacapule Presence	Life Stage	La Navaja Presence	Life Stage
Calamoceratidae	*Phylloicus mexicanus*	X	Larvae	X	Larvae
Hydropsychidae	*Chuematopsyche arizonensis*	X	Both	X	Adult
Hydroptilidae	*Mayatrichia n. sp.*	-	-	X	Adult
	Neotrichia canixa	X	Adult	-	-
	N. new sp. 1	-	-	X	Adult
	N. new sp. 2	-	-	X	Adult
	Ochrotrichia sp.	X	Larvae	-	-
	Unidentified taxon	X	Larvae	-	-
Odontoceridae	*Marilia nobsca*	X	Larvae	X	Both
Philopotamidae	*Chimarra ridley*	-	-	X	Adult
	C. new sp.	X	Both	X	Adult
	Wormaldia planae	-	-	X	Adult

Table 5.5 Invertebrate indicator taxa for tilapia-containing and tilapia-free pools at Rancho Santa Úrsula, including indicator values (IV) and significance (*p*). The limited sample size and Monte Carlo significance tests made 0.098 the lowest *p*-value possible.

Type	Taxon	IV	*p*
Tilapia-free	*Laccophilus fasciatus*	100	0.098
	Laccophilus pictus	100	0.098
	Helochares normatus	100	0.098
	Lethocerus medius	100	0.098
	Morphocorixa lundbladi	100	0.098
	Merragata sp.	100	0.098
	Ambrysus occidentalis	100	0.098
	Buenoa arizonis	100	0.098
	Physidae	100	0.098
	Hydrochus sp.	99.2	0.098
	Pelocoris sp.	98.6	0.098
	Desmopachria dispersa	96.7	0.098
Tilapia	*Tricorythodes* sp.	100	0.098
	Choroterpes sp.	78.4	0.098

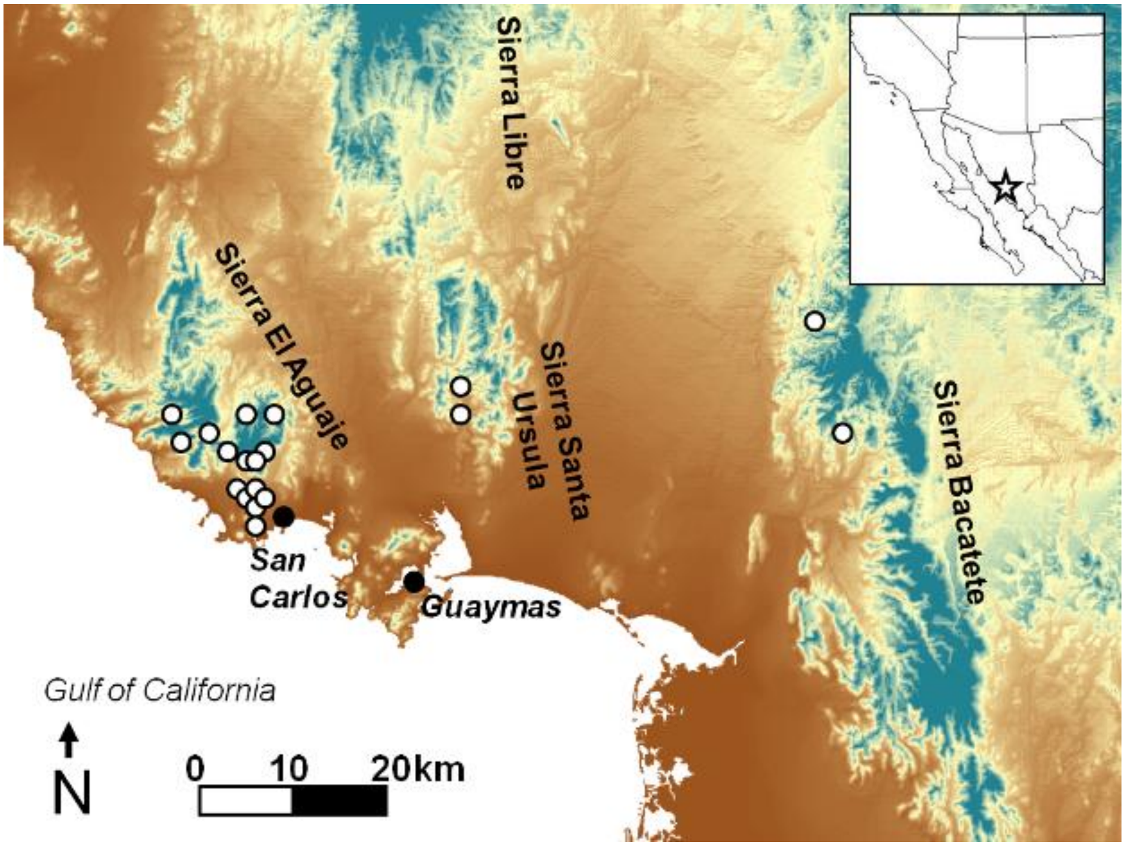

Figure 5.1 Map of the study region in southern Sonora with the 19 study sites in the sierras El Aguaje, Santa Úrsula, and Bacatete indicated by white circles (see Table 1 for place names and precise coordinates).

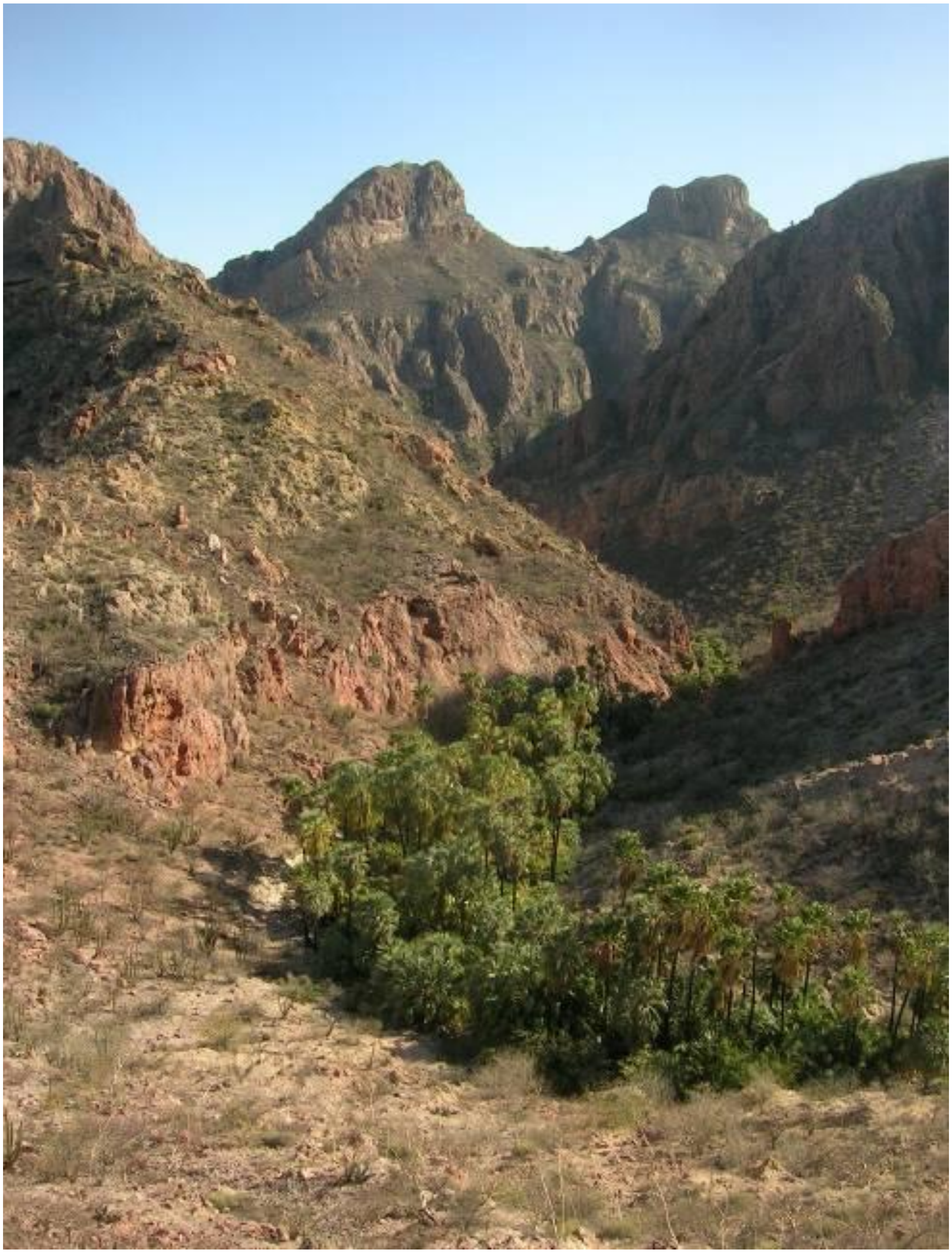

Figure 5.2 Upper part of Cañón Nacapule (looking south), illustrating how aquatic habitats (located inside the palm grove) are surrounded by vast areas of Sonoran Desert.

Figure 5.3 Palm-ringed oasis at Cañón La Navaja, Sierra El Aguaje in 2006. Palms are *Washingtonia robusta*. O. Gutierrez-Ruacho is pictured with a collecting net.

Figure 5.4 Large tinaja at Cañón La Balandrona, Sierra El Aguaje. A. Varela-Romero is pictured with a collecting net.

Figure 5.5 Seep (black stains on rock face) at Aguaje Los Anegados, Sierra El Aguaje. The cliff face supporting the seep is approximately 15 m in height.

Figure 5.6 Small, shallow riffles at Cañón Nacapule. Note the mechanical pencil for scale.

Figure 5.7 A pool at Arroyo El Palmar, Sierra El Aguaje, during the wet phase (left, in December) and dry phase (right, in April) during 2009.

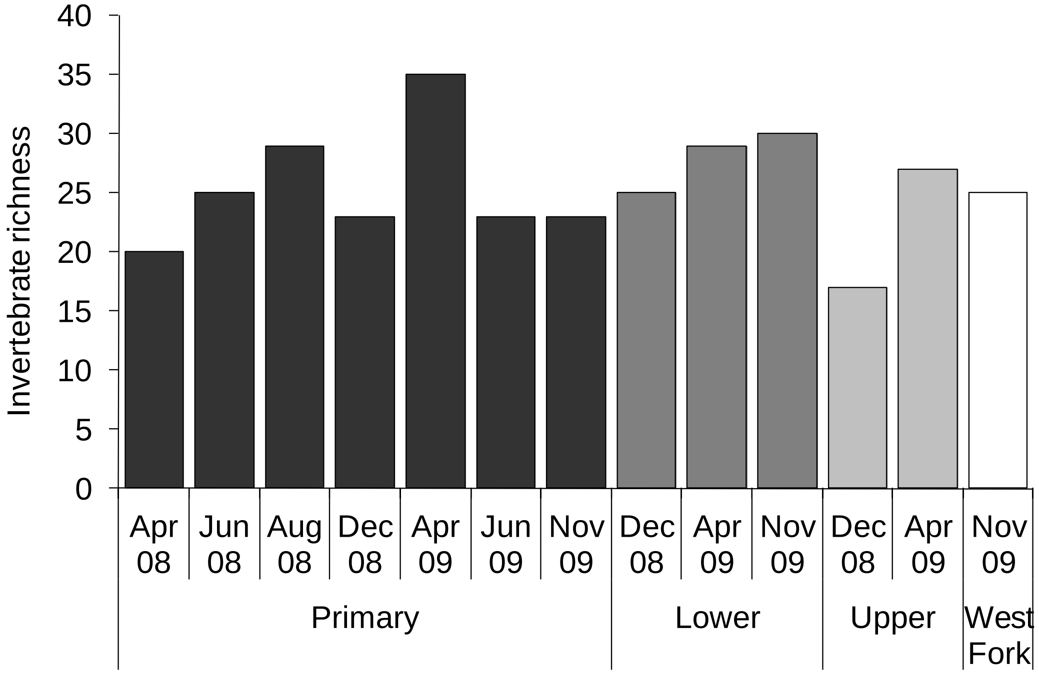

Figure 5.8 Invertebrate species richness from riffles at the primary and secondary Cañón Nacapule survey locations over multiple sampling periods during 2008 and 2009.

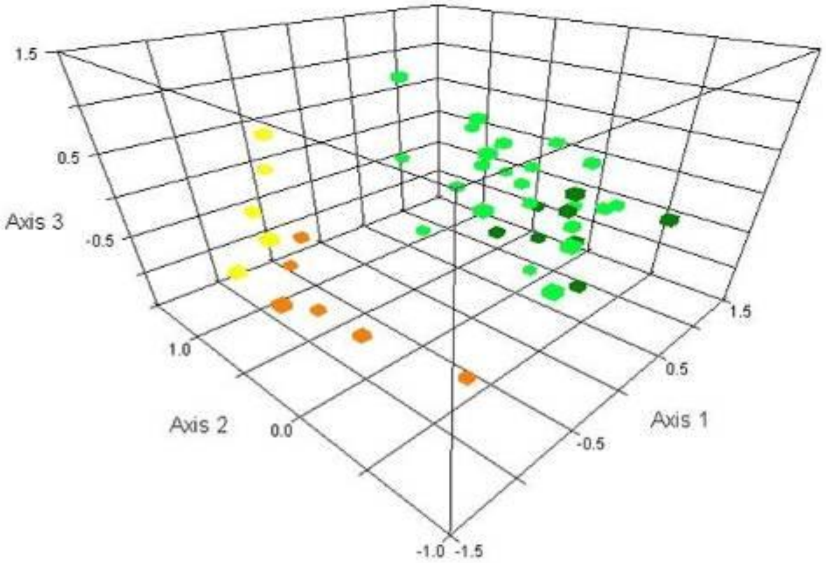

Figure 5.9 Three-dimensional non-metric multidimensional ordination of all aquatic invertebrate community samples from the sierras El Aguaje, Santa Úrsula, and Bacatete. Habitats are color-coded: tinajas (light green), oases (dark green), seeps (yellow), riffles (orange).

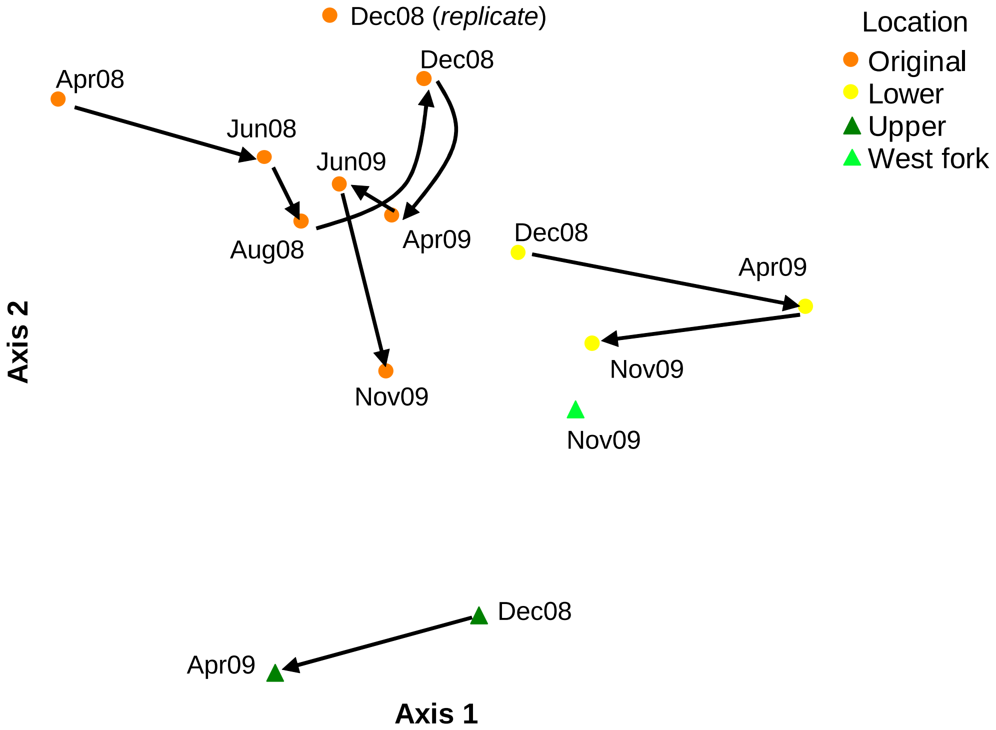

Figure 5.10 Two-dimensional non-metric multidimensional ordination of aquatic invertebrate community samples from Cañón Nacapule riffles over multiple seasons. Samples are labeled by a three-letter month code and two-digit year code (e.g., Apr08 = April 2008). “Original” = the primary site at Nacapule.

Figure 5.11 Habitat changes at the main oasis of Cañón Nacapule between May 2004 and November 2009. The star marks the same location in each photograph. Hurricane-induced flooding in 2008 reduced water levels and removed all new fig tree (*Ficus insipid*) recruits visible in August 2008, while unprecedented extreme floods from Hurricane Jimena in earliest September 2009 completely filled the oasis with course sediment and removed all riparian cover.

Figure 5.12 Spongillidae freshwater sponge growing on submerged *Washingtonia robusta* palm roots at Cañón Nacapule.

Figure 5.13 The giant water bug, *Lethocerus medius* (Belostomatidae), consuming a big-eyed leopard frog, *Rana magnaocularis*, at Cañón Nacapule.

Figure 5.14 A dead canyon tree frog, *Hyla arenicolor*, being fed upon by the water strider, *Trepobates* sp., and two species of diving beetle, the larger *Thermonectus marmoratus* and the smaller *Laccophilus pictus*, at Cañón “Escondido”. These insects likely did not kill the tree frog, but are merely making use of its remains.

Figure 5.15 Sabinal frog, *Leptodactylus melanonotus*, at Rancho Bacatete, Sierra Bacatete.

Figure 5.16 Pools and chalate fig trees, *Ficus insipida*, in the lush riparian forest at Rancho Bacatete, Sierra Bacatete.

Figure 5.17 Black-necked garter snake, *Thamnophis cyrtopsis*, found in a stream pool at Cañón Las Pirinolas, Sierra El Aguaje.

Figure 5.18 Sonoran topminnow (*Poeciliopsis occidentalis sonoriensis*) male from pools at Rancho Santa Úrsula, Sierra Santa Úrsula (specimen not vouchered).

Figure 5.19 Juvenile tilapia (Cichlidae) from pools at Rancho Santa Úrsula in the Sierra Santa Úrsula (left), and male adult tilapia guarding his courting/spawning-nest pit at Aguaje Los Pilares in the Sierra Bacatete (right).

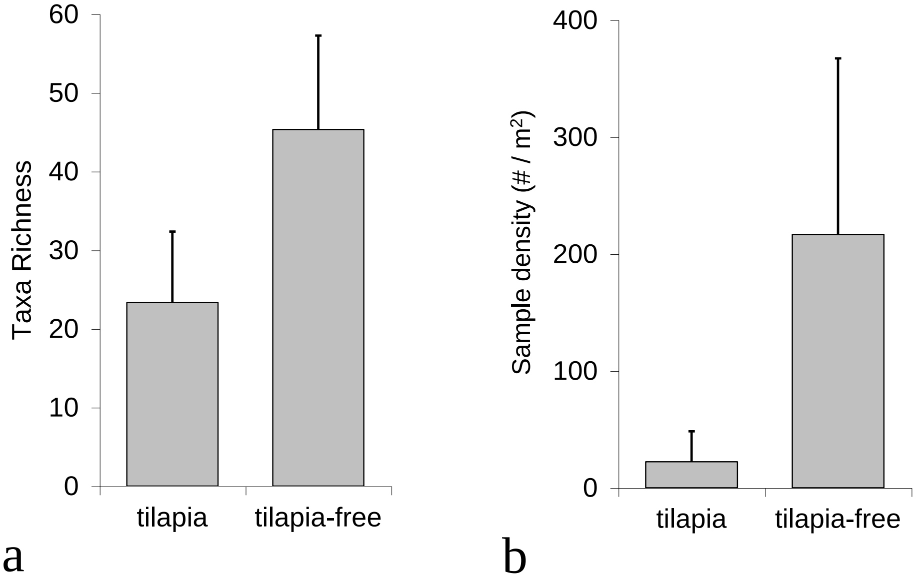

Figure 5.20 Differences between taxa richness (a) and sample density (b) of aquatic macroinvertebrates in pools with and without tilapia at Rancho Santa Úrsula, Sierra Santa Úrsula. Error bars represent one standard deviation.

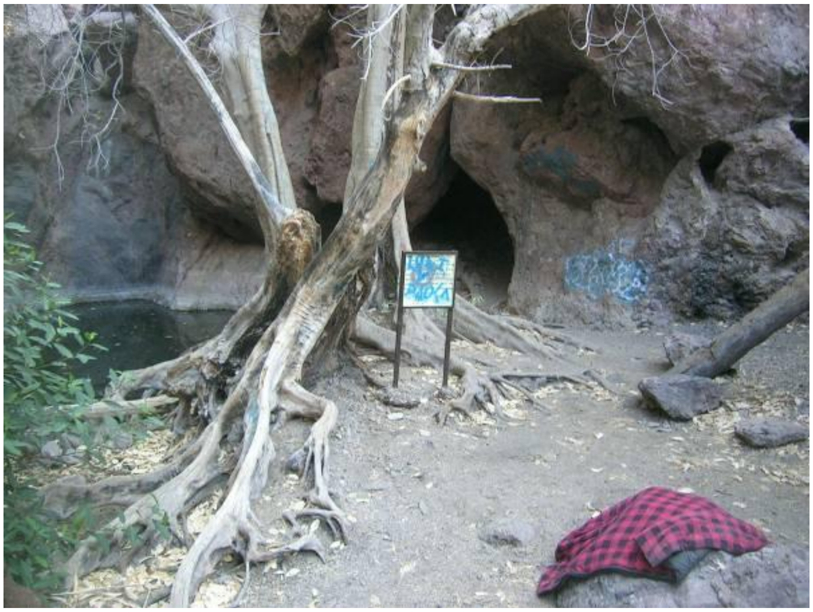

Figure 5.21 Graffiti and trash at the main oasis in Cañón Nacapule, June 2008.

Figure 5.22 Main oasis at Cañón La Navaja, 23 March 2011, one month following an intense, vandal-set fire burned its palm and fig tree groves. S. V. Gregory stands in the same place that O. Gutierrez-Ruacho was standing in Figure 5.3.

CHAPTER 7 - **Conclusion**

In this dissertation, I have demonstrated that flow regime (and particularly low- and zero-flow disturbance events), dispersal, and local habitat factors can each strongly influence local stream community structure. As these factors operate on multiple spatial and temporal scales, no single study could encompass them all. I examined the impact of flow permanence and local abiotic factors on local aquatic communities at a fine spatial scale over a long time period (Chapter 2) and at a broad spatial scale over a shorter time period (Chapter 4). Additionally, I quantified how seasonal variation in flow and abiotic factors within perennial streams affects community structure over long time periods (8 years; Appendix 1). Colonization patterns inferred from community reassembly in one isolated stream following total drying and rewetting (Chapter 2), demonstrated that overland aerial dispersal also plays a large role in structuring local arid-land stream communities. This observation led me to quantify aerial dispersal over moderate spatial scales (<0.5km) by conducting a colonization experiment using replicate artificial stream pools placed inland from two streams (Chapter 4). Finally, I examined the roles of spatial isolation, microhabitat type, and local abiotic and biotic factors in structuring aquatic communities in one of the most arid regions of North America, the southern Sonoran Desert (Chapter 5).

I found that flow regime to be the most important filter on the regional species pool in arid-land streams (Fig. 1.1), and specifically that aquatic habitat permanence (i.e., perennial vs. temporary) is the most influential aspect of flow regime in structuring local communities. Flow intermittence clearly can be a natural phenomenon, given the seasonal patterns in rainfall in temperate areas and the general paucity of rainfall in arid regions. Many aquatic species that evolved in such naturally intermittent streams have developed life history, behavioral, or morphological adaptations to avoid or resist seasonal drought (Lytle & Poff 2004). I found that a number of exclusively intermittent specialist species, even in severely intermittent streams with short winter flow durations and high year-to-year variability in the presence of flow (Chapter 4). These exclusive intermittent species formed the core of a very distinct intermittent community type. These intermittent communities remained distinct whether or not they were located downstream of perennial reaches that supported very diverse communities of invertebrates. This finding indicates that over the short time scales of intermittent reach flow (< 120 days), the influence of flow permanence trumped that of dispersal from neighboring upstream perennial refuges.

While winter flows in arid-land intermittent streams may not occur every year, they do occur at least once every few years (Figure A1.1) and during the same months (Dec-Mar) in these years. This relative predictability of winter flow is apparently enough for a small number of taxa (probably ≤ 30) to develop life-history strategies for persisting through drought. The adaptations to intermittency that these taxa have include egg and larval diapauses stages, which allow individuals (and hence populations) to persist through the dry season in situ until stream flow returns. Some of these taxa with dormant stages may employ a bet-hedging strategy, with staggered emergence from diapauses over multiple years, to maximize their fitness over longer periods of time which include both good (i.e., wet) and bad (i.e., dry) years (Appendix II). These dormant egg and larval stages must be present in stream sediments, as larvae of these taxa are abundant in rewetted streams within days of flow returning. However, I was unable to find any of these taxa in dry stream sediments that I experimentally rewetted (Appendix III). It is likely that these dormant individuals have their greatest densities in sediments that are found deeper than I was able to excavate (i.e., > 30 cm depth). By occupying greater depths in dry sediments, these dormant individuals would also be less likely to be killed by flash floods which occur nearly every summer.

While a small number of taxa have evolved persistence mechanisms in intermittent arid-land streams, the vast majority of the aquatic invertebrate diversity observed in Chapter 4 was in perennial reaches. Specifically, perennial headwater reaches supported more than four times as many exclusive taxa as downstream intermittent or perennial valley river reaches. This high diversity among headwater reaches highlights the importance of headwater streams in bolstering regional species diversity, as recently described by Finn et al. (2011). In arid-land regions, though, the water that supports these diverse perennial headwater communities is threatened by anthropogenic water withdrawal (Deacon et al. 2007) and intensifying droughts (Seager et al. 2007).

I studied one arid-land stream, French Joe Canyon, over an 8 year period when intense drought caused the stream to transition from perennial to intermittent. While species richness at French Joe was not affected by this transition, local community composition shifted to an alternative state, and did not recover to its original configuration even four years after the initial drying event. Several larger species with poor dispersal abilities were extirpated by the transition to intermittent flow, but numerous smaller, more vagile species took their place under the new intermittent flow conditions. This finding suggests that while local species richness may not be dramatically impacted by drought- or water withdrawal-induced flow failure, regional species richness may eventually decline as species with poor dispersal abilities are slowly filtered out of the regional species pool (Fig 1.1).

The likelihood that overland dispersal alone can help arid-land stream communities recover from drought disturbance depends in part upon the individual dispersal abilities of species in the regional species pool. However, the overland or aerial dispersal abilities of aquatic insect species are generally poorly known, and at best have been classified into rough categories like ‘high’ (>1km) or ‘low’ (<1km; Poff et al. 2006). Predicting spatially explicit recovery patterns following disturbances such as drought, though, will require a more detailed understanding of how frequently species disperse and what cues might prompt dispersal. In my colonization experiment (Chapter 3), I make attempted to take some of the first steps towards understanding spatio-temporal variability of aquatic invertebrate aerial dispersal in arid regions (but see Gray and Fisher 1981). I found that a few taxa disperse frequently and widely; these were also some of the taxa that were abundant at French Joe following rewetting. Many other taxa, though, require a cue to disperse in search of other habitats or are limited in either their propensity to disperse or the distance inland they are able to disperse. I determined that rainfall may be an important cue for triggering dispersal, as the diversity and abundance of colonists both increased significantly during rainfall events. Additionally, I found that dispersing aquatic invertebrates appeared to use not only perennial stream channels as dispersal corridors (as has been noted in previous studies) but also ephemeral stream channels. I hope that these data will facilitate the predication of community assembly in the wake of environmental disturbances like drought-induced stream fragmentation and drying.

The conservation concerns presented by drought and water withdrawal-induced stream drying are especially pressing in the driest parts of the West, like the southern Sonoran Desert. In this extremely arid region, hundreds of aquatic species depend on the perennial water contained in small, isolated oases (Chapter 5). As formerly perennial habitats dry and remaining habitats are degraded via exotic species introductions and recreational overuse, many species face extirpation or extinction. Meanwhile, we are still discovering and describing many new species in isolated streams across the arid West (Chapter 5; Ruiter 2011). In a sense, we are in a race against time to document and understand the drivers of aquatic biodiversity in these fragmented aquatic habitats, so that we can try to describe that diversity before it is lost. I hope that my dissertation makes at least a small contribution in that battle against extinction.

BIBLIOGRAPHY

Abell, D. L. 1984. Benthic invertebrates of some California intermittent streams. Pages 46-60 *in* S. Jain and P. B. Moyle, editors. Vernal pools and intermittent streams. University of California, Davis Institute of Ecology, Davis, CA.

Acuña, V., I. Munoz, A. Giorgi, M. Omella, F. Sabater, and S. Sabater. 2005. Drought and postdrought recovery cycles in an intermittent Mediterranean stream: structural and functional aspects. Journal of the North American Benthological Society **24**:919-933.

Adler, P. H., D. C. Currie, and D. M. Wood. 2004. The blackflies (Simuliidae) of North America. Cornell University Press, Ithaca, NY.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology **26**: 32-46.

Anna, A., C. Yorgos, P. Konstantinos, and L. Maria. 2009. Do intermittent and ephemeral Mediterranean rivers belong to the same river type? Aquatic Ecology **43**:465-476.

Arscott, D. B., S. T. Larned, M. R. Scarsbrook, and P. Lambert. 2010. Aquatic invertebrate community structure along an intermittence gradient: Selwyn River, New Zealand. Journal of the North American Benthological Society **29**:530-545.

Balling Jr., R. C., and G. B. Goodrich. 2010. Increasing drought in the American Southwest? A continental perspective using a spatial analytical evaluation of recent trends. Physical Geography **31**:293-306.

Banks, J. L., J. Li, and A. T. Herlihy. 2007. Influence of clearcut logging, flow duration, and season on emergent aquatic insects in headwater streams of the Central Oregon Coast Range. Journal of the North American Benthological Society **26**:620-632.

Baskett, M. L., and A. K. Salomon. 2010. Recruitment facilitation can drive alternative states on temperate reefs. Ecology **91**:1763-1773.

Bêche, L. A., P. G. Connors, V. H. Resh, and A. M. Merenlender. 2009. Resilience of fishes and invertebrates to prolonged drought in two California streams. Ecography **32**:778-788.

Beisner, B.E., D.T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment **1**: 376-382.

Bilton, D. T., J. R. Freeland, and B. Okamura. 2001. Dispersal in freshwater invertebrates. Annual Review of Ecological Systems **32**:159-181.

Bogan, M. T. 2005. Diversity and community structure of aquatic insect communities in montane desert streams. Master's thesis. Oregon State University, Corvallis, OR.

Bogan, M. T., and D. A. Lytle. 2007. Seasonal flow variation allows 'time-sharing' by disparate aquatic insect communities in montane desert streams. Freshwater Biology **52**:290-304.

Bogan, M. T., and D. A. Lytle. 2011. Severe drought drives novel community trajectories in desert stream pools. Freshwater Biology **56**:2070-2081.

Bohonak, A.J. and D.G. Jenkins. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. Ecology Letters **6**: 783-796.

Boix, D., A. K. Magnusson, S. Gascon, J. Sala, and D. D. Williams. 2011. Environmental influence on flight activity and arrival patterns of aerial colonizers of temporary ponds. Wetlands **31**:1227-1240.

Bonada, N., S. Doledec, and B. Statzner. 2007. Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios. Global Change Biology **13**:1658-1671.

Bonada, N., M. Rieradevall, and N. Prat. 2007. Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. Hydrobiologia **589**:91-107.

Boulton, A. J., and P. S. Lake. 1992a. The ecology of two intermittent streams in Victoria, Australia. II. Comparisons of faunal composition between habitats, rivers and years. Freshwater Biology **27**:99-121.

Boulton, A. J., and P. S. Lake. 1992b. The ecology of two intermittent streams in Victoria, Australia. III. Temporal changes in faunal composition. Freshwater Biology **27**:123-138.

Boulton, A. J., H. M. Valett, and S. G. Fisher. 1992. Spatial distribution and taxonomic composition of the hyporheos of several Sonoran Desert streams. Archiv fuer Hydrobiologie **125**:37-61.

Brennan, T. C. and A. T. Holycross. 2006. A field guide to amphibians and reptiles in Arizona. Arizona Game and Fish Department, Phoenix, AZ.

Briggs, M. K. 1996. Riparian ecosystem recovery in arid lands: strategies and references. University of Arizona Press, Tucson, AZ.

Briers, R. A., H. M. Cariss, and J. H. R. Gee. 2003. Flight activity of adult stoneflies in relation to weather. Ecological Entomology **28**:31-40.

Brito-Castillo, L., E. M. Pérez-Arvizu and O. G. Gutiérrez-Ruacho. 2006. Análisis del comportamiento de las lluvias en 2006 y el cambio de paisaje del Cañón Nacapule. Resumen, Congreso Regional de Ciencias Ambientales, Instituto Tecnológico de Sonora, Ciudad Obregón, Sonora (13-14 Nov. 2006)

Brown, B. L., and C. M. Swan. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. Journal of Animal Ecology **79**:571-581.

Brown, L. E., Hannah, D. M., and Milner, A. M. (2007) Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. Global Change Biology **13**: 1-9.

Brussock, P. P., and A. V. Brown. 1991. Riffle-pool geomorphology disrupts longitudinal patters of stream benthos. Hydrobiologia **220**:109-117.

Bunn, S. E., and J. M. Hughes. 1997. Dispersal and recruitment in streams: evidence from genetic studies. Journal of the North American Benthological Society **16**:338-346.

Caceres, C. E., and D. A. Soluk. 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. Oecologia **131**:402-408.

Cadotte, M. W. 2006. Dispersal and species diversity: a meta-analysis. The American Naturalist **167**: 913-924.

Carrizales, J. 2007. Cañón del Nacapule: Peligra paraíso ecológico. El Imparcial < http://expresionguaymas.wordpress.com/2007/01/22/canon-del-nacapule-peligra-paraiso-ecologico/> Accessed 10 Oct. 2007.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences **104**:17430-17434.

Chaves, M. L., M. Rieradevall, P. Chainho, J. L. Costa, M. J. Costa, and N. Prat. 2008. Macroinvertebrate communities of non-glacial high altitude intermittent streams. Freshwater Biology **53**:55-76.

Chester, E. T., and B. J. Robson. 2011. Drought refuges, spatial scale and recolonisation by invertebrates in non-perennial streams. Freshwater Biology **56**:2094-2104.

Chou, R. Y. M., L. C. Ferrington, B. L. Hayford, and H. M. Smith. 1999. Composition and phenology of Chironomidae (Diptera) from an intermittent stream in Kansas. Archiv fur Hydrobiologie **147**:35-64.

Churchel, M. A., and D. P. Batzer. 2006. Recovery of aquatic macroinvertebrate communities from drought in Georgia Piedmont headwater streams. American Midland Naturalist **156**:259-272.

Collier, L. C. S., and A. U. Mallik. 2010. Does post-fire abiotic habitat filtering create divergent plant communities in black spruce forests of eastern Canada? Oecologia **164**:465-477.

Corbet PS. 1999. Dragonflies: behavior and ecology of Odonata. Cornell University Press, Ithaca, NY.

Côté I.M. and E.S. Darling. 2010. Rethinking ecosystem resilience in the face of climate change. PLOS Biology **8**: 1-5.

Courtney, G. W. and R. W. Merritt. 2008. Aquatic Diptera Part 1: larvae of aquatic Diptera, pp. 687-722 in R. W. Merritt, K. W. Cummins and M. B. Berg, (eds.), An introduction to the aquatic insects of North America, 4th Edition, Kendall/Hunt, Dubuque, IA.

Cox, C. B. and P. D. Moore. 1993. Biogeography: an ecological and evolutionary approach. Blackwell Scientific, London.

Csabai, Z., P. Boda, B. Bernath, G. Kriska, and G. Horvath. 2006. A 'polarisation sun-dial' dictates optimal time of day for dispersal by flying aquatic insects. Freshwater Biology **51**:1341-1350.

Cummins K.W., Merritt R.W. and Berg M.B. 2008. Ecology and distribution of aquatic insects. pp 105-122 in: An introduction to the aquatic insects of North America. (Eds: R.W. Merritt, K.W. Cummins, M.B. Berg). Kendell/Hunt, Dubuque, IA.

Custodio, E. 2002. Aquifer overexploitation: what does it mean? Hydrogeology Journal **10**: 254-277.

da Silva, F. L., D. C. Moreira, G. L. Bochini and S. S. Ruiz. 2008. Hábitos alimentares de larvas de Chironomidae (Insecta: Diptera) do córrego Vargem Limpa, Bauru, SP, Brasil. Biotemas **21**: 155-159.

Datry, T., S. T. Larned, and M. R. Scarsbrook. 2007. Responses of hyporheic invertebrate assemblages to large-scale variation in flow permanence and surface-subsurface exchange. Freshwater Biology **52**:1452-1462.

Datry, T., D. B. Arscott, and S. Sabater. 2011. Recent perspectives on temporary river ecology. Aquatic Sciences **73**:453-457.

Datry, T. 2012. Benthic and hyporheic invertebrate assemblages along a flow intermittence gradient: effect of duration of dry events. Freshwater Biology **57**:565-574.

Deacon, J. E., A. E. Williams, C. D. Williams, and J. E. WIlliams. 2007. Fueling population growth in Las Vegas: how large-scale groundwater withdrawal could burn regional diversity. BioScience **57**:688-698.

Delettre, Y. R., and N. Morvan. 2000. Dispersal of adult aquatic Chironomidae (Diptera) in agricultural landscapes. Freshwater Biology **44**:399-411.

Delucchi, C. M. 1988. Comparison of community structure among streams with different temporal flow regimes. Canadian Journal of Zoology **66**:579-586.

Delucchi, C. M., and B. L. Peckarsky. 1989. Life history patterns of insects in an intermittent and a permanent stream. Journal of the North American Benthological Society **8**:308-321.

Dewson, Z. S., A. B. James, and R. G. Death. 2007. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. Journal of the North American Benthological Society **26**:401-415.

Didham, R. K., and C. H. Watts. 2005. Are systems with strong underlying abiotic regimes more likely to exhibit alternative stable states? Oikos **110**:409-416.

Dieterich, M., and N. H. Anderson. 2000. The invertebrate fauna of summer-dry streams in western Oregon. Archiv fur Hydrobiologie **147**:273-295.

Dominguez, E. 1999. Systematics, cladistics and biogeography of the American genus Farrodes (Ephemeroptera: Leptophlebiidae: Atalophlebiinae). Zoological Journal of the Linnean Society **126**: 155-189.

Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67**: 345-366.

Durance, I. and S. J. Ormerod. 2007. Climate change effects on upland stream macroinvertebrates over a 25-year period. Global Change Biology **13**: 942-957.

Endersen, E.F., A. Quijada-Mascareñas, D.S. Turner, P.C. Rosen and R.L. Bezy. 2009. The herpetofauna of Sonora, Mexico, with comparisons to adjoining states. Check List **5**: 632-672.

Fairchild, G. W., J. Cruz, A. M. Faulds, A. E. Short, and J. F. Matta. 2003. Microhabitat and landscape influences on aquatic beetle assemblages in a cluster of temporary and permanent ponds. Journal of the North American Benthological Society **22**:224-240.

Felger, R. S. 1999. The flora of Cañón de Nacapule: a desert-bounded tropical canyon near Guaymas, Sonora, Mexico. Proceedings of the San Diego Society of Natural History **35**: 1-42.

Feminella, J. W. 1996. Comparison of benthic macroinvertebrate assemblages in small streams along a gradient of flow permanence. Journal of the North American Benthological Society **15**:651-669.

Ferrington, L. C. 1984. Evidence for the hyporheic zone as a microhabitat of Krenosmittia spp. larvae (Diptera: Chironomidae). Journal of Freshwater Ecology **2**:353-358.

Ferrington, L. C., M. B. Berg, and W.P. Coffman. 2008. Chironomidae, pp. 847-989 in An introduction to the aquatic insects of North America (R. W. Merritt, K. W. Cummins and M. B. Berg, eds.). Kendall/Hunt, Dubuque, IA.

Findley, L. T., M. Pérez-Tello, W.L. Montgomery. 2010. A "thousand-year" flood provides long-term ephemeral habitat for "peripheral" fishes in the southern Sonoran Desert, Mexico. Abstract. Desert Fishes Council Annual Meeting, 17-20 Nov. 2010, Moab, UT. Available at: http://www.dfcstore.org/desertfishes/wp-content/uploads/2011/04/2010longprogram.pdf> Accessed 15 May 2012.

Finn, D. S., M. S. Blouin, and D. A. Lytle. 2007. Population genetic structure reveals terrestrial affinities for a headwater stream insect. Freshwater Biology **52**:1881-1897.

Finn, D. S., M. T. Bogan, and D. A. Lytle. 2009. Demographic stability metrics for conservation prioritization of isolated populations. Conservation Biology **23**:1185-1194.

Finn, D. S., N. Bonada, C. Murria, and J. M. Hughes. 2011. Small but mighty: headwaters are vital to stream network biodiversity at two levels of organization. Journal of the North American Benthological Society **30**:963-980.

Fritz, K. M., and W. K. Dodds. 2002. Macroinvertebrate assemblage structure across a tallgrass prairie stream landscape. Archiv fuer Hydrobiologie **154**:79-102.

Fritz, K. M., and W. K. Dodds. 2004. Resistance and resilience of macroinvertebrate assemblages to drying and flood in a tallgrass prairie stream system. Hydrobiologia **527**:99-112.

Frost, T. M., H. M. Reiswig and A. Ricciardi. 2001. Porifera, pp 97-133 in, Ecology and classification of North American freshwater invertebrates (J. H. Thorp and A. P. Covich, eds.). Academic Press: San Diego, CA.

Gallo-Reynoso, J. P. 2003. Estudio previo justificativo para proponer el establecimiento de la región "Sierra del Aguaje, Bahía de San Francisco e Isla San Pedro Nolasco y sus aguas aledañas" como una nueva Área Natural Protegida". <http://www.guaymas.gob.mx./ecologia/reserva.pdf> Accessed 28 Sep. 2008.

Gore, J. A. 1982. Benthic invertebrate colonization: source distance effects on community composition. Hydrobiologia **94**:183-193.

Grant, E. H. C., W. H. Lowe, and W. F. Fagan. 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. Ecology Letters **10**:165-175.

Gray, L. J. 1981. Species composition and life histories of aquatic insects in a lowland Sonoran Desert stream. American Midland Naturalist **106**:229-242.

Gray, L. J., and S. G. Fisher. 1981. Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran Desert stream. American Midland Naturalist **106**:249-257.

Grubbs, S. A. 2011. Influence of flow permanence on headwater macroinvertebrate communities in a Cumberland Plateau watershed, USA. Aquatic Ecology **45**:185-195.

Hanski, I. 1998. Metapopulation dynamics. Nature **396**: 41-49.

Hughes, J. M., D. J. Schmidt, and D. S. Finn. 2009. Genes in streams: using DNA to understand the movement of freshwater fauna and their riverine habitat. BioScience **59**:573-583.

Hutchinson, G. E. 1961. The paradox of the plankton. American Naturalist **95**:137-145.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto.

Hynes, H. B. N. 1975. Annual cycles of macro-invertebrates of a river in southern Ghana. Freshwater Biology **5**:71-83.

Jackson, J. K. 1988. Diel emergence, swarming, and longevity of selected adult aquatic insects from a Sonoran Desert stream. American Midland Naturalist **119**:344-352.

Jackson, J. K., and V. H. Resh. 1989. Distribution and abundance of adult aquatic insects in the forest adjacent to a Northern California stream. Environmental Entomology **18**:278-283.

Jackson, J. K., and L. Fureder. 2006. Long-term studies of freshwater macroinvertebrates: a review of the frequency, duration and ecological significance. Freshwater Biology **51**.

Jacobi, G. Z., and S. J. Cary. 1996. Winter stoneflies (Plecoptera) in seasonal habitats in New Mexico, USA. Journal of the North American Benthological Society **15**:690-699.

Jaeger, K. L., and J. D. Olden. 2011. Electrical resistance sensor arrays as a means to quantify longitudinal connectivity of rivers. River Research and Applications **DOI: 10.1002/rra.1554**.

Jasper, S. K. and G. L. Challet. 2004. A genus and species new to the USA, Macrovatellus mexicanus Sharp (Coleoptera: Dytiscidae), in South Texas, with habitat notes. Coleopterists Bulletin **56**:142-143.

Jeffries, M. J. 1994. Invertebrate communities and turnover in wetland ponds affected by drought. Freshwater Biology **32**:603-612.

Kingsley, K. J. 1985. *Eretes sticticus* (L.) (Coleoptera: Dytiscidae): life history observations and an account of a remarkable event of synchronous emigration from a temporary desert pond. The Coleopterists Bulletin **39**:7-10.

Kovats, Z. E., J. J. Ciborowski, and L. D. Corkum. 1996. Inland dispersal of adult aquatic insects. Freshwater Biology **36**:265-276.

Lake, P. S. 2003. Ecological effects of perturbation by drought in flowing waters. Freshwater Biology **48**:1161-1172.

Langton, P. H., and J. J. Casas. 1999. Changes in chironomid assemblage composition in two Mediterranean mountain streams over a period of extreme hydrological conditions. Hydrobiologia **390**:37-49.

Larned, S. T., T. Datry, and C. T. Robinson. 2007. Invertebrate and microbial responses to inundation in an ephemeral river reach in New Zealand: effects of preceding dry periods. Aquatic Sciences **69**:554-567.

Larned, S. T., T. Datry, D. B. Arscott, and K. Tockner. 2010a. Emerging concepts in temporary-river ecology. Freshwater Biology **55**:717-738.

Larned, S. T., D. B. Arscott, J. Schmidt, and J. C. Diettrich. 2010b. A framework for analyzing longitudinal and temporal variation in river flow and developing flow-ecology relationships. Journal of the American Water Resources Association **46**:541-553.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters **7**:601-613.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943-1967.

Lowe, W. H., Likens, G. E., and Power, M. E. (2006) Linking scales in stream ecology. BioScience **56**: 591-597.

Lytle, D. A. 1999. Use of rainfall cues by *Abedus herberti* (Hemiptera: Belostomatidae): a mechanism for avoiding flash floods. Journal of Insect Behavior **12**:1-12.

Lytle, D. A., and N. L. Poff. 2004. Adaptation to natural flow regimes. Trends in Ecology and Evolution **19**:94-100.

Lytle, D. A., and R. L. Smith. 2004. Exaptation and flash flood escape in giant water bugs. Journal of Insect Behavior **17**:169-178.

Maloney, K. O., and P. Munguia. 2011. Distance decay of similarity in temperate aquatic communities: effects of environmental transition zones, distance measure, and life histories. Ecography **34**:287-295.

Manolis T. 2003. Dragonflies and damselflies of California. University of California Press, Berkeley, CA.

Martin B. and Martin D. (1991) Arizona mountains: a hiking guide to the Grand Canyon State. Cordillera Press: Evergreen, CO.

MacArthur RH and EO Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Mackay, R. J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences **49**:617-628.

Macneale, K. H., B. L. Peckarsky, and G. E. Likens. 2005. Stable isotopes identify dispersal patterns of stonefly populations living along stream corridors. Freshwater Biology **50**:1117-1130.

Maezono, Y., R. Kobayashi, M. Kusahara, and T. Miyashita. 2005. Direct and indirect effects of exotic bass and bluegill on exotic and native organisms in farm ponds. Ecological Applications **15**: 638-650.

McArthur, J. V., and J. R. Barnes. 1985. Patterns of macroinvertebrate colonization in an intermittent Rocky Mountain stream in Utah. Great Basin Naturalist **45**:117-123.

McCauley, S. J. 2006. The effects of dispersal and recruitment limitation on community structure of odonates in artificial ponds. Ecography **29**:585-595.

McCauley, S. J., C. J. Davis, J. Nystrom, and E. E. Werner. 2009. A hump-shaped relationship between isolation and abundance of *Notonecta irrorata* colonists in aquatic mesocosms. Ecology **90**:2635-2641.

McCune B. and J.B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.

McCune B. and M.J. Mefford. 1999. PC-ORD: Multivariate Analysis of Ecological Data. Version 4.0. MjM Software, Gleneden Beach, Oregon, USA.

Menge, B. A. and J. S. Sutherland. 1987. Community regulation: variation in disturbance, competition and predation in relation to environmental stress and recruitment. American Naturalist **130**: 730-757.

Merritt, R. W., K. W. Cummins and M. B. Berg . 2008. An introduction to the aquatic insects of North America, 4th Edition. Kendall/Hunt, Dubuque, IA.

Mielke, P.W., Jr. and K.J. Berry. 2001. Permutation methods: a distance function approach. Springer, Berlin.

Miguelez, D., and L. Valladares. 2008. Seasonal dispersal of water beetles (Coleoptera) in an agriculture landscape: a study using Moericke traps in northwest Spain. Annales de la Societe entomologique de France **44**:317-326.

Miller, A. M., and S. W. Golladay. 1996. Effects of spates and drying on macroinvertebrate assemblages of an intermittent and a perennial prairie stream. Journal of the North American Benthological Society **15**:670-689.

Miller, R. R., W. L. Minckley and S. M. Norris. 2006. Freshwater fishes of Mexico. University of Chicago Press, Chicago, IL.

Muneepeerakul, R., E. Bertuzzo, H. J. Lynch, W. F. Fagan, A. Rinaldo, and I. Rodriguez-Iturbe. 2008. Neutral metacommunity models predict fish diversity patterns in Mississippi-Missouri basin. Nature **453**:220-223.

Nessimian, J. L. and A. L. Henriques-de-Oliveira. 2005. Colonização do “litter” de Elocharis sellowiana Kunth. (Cyperaceae) por larvas de Chironomidae (Diptera) em um brejo no litoral do estado do Rio de Janeiro. Entomología y Vectores **12**: 159-172.

Nekola, J. C., and P. S. White. 1999. The distance decay of similarity in biogeography and ecology. Journal of Biogeography **26**:867-878.

O’Brien, C., A. D. Flesch, E. Wallace, M. Bogan, S. E. Carrillo-Percástegui, S. Jacobs and C. van Riper III. 2006. Biological inventory of the Río Aros, Sonora, Mexico. Unpublished report to T&E Inc., Gila, NM 58 pp. < http://www.wildsonora.com/content/biological-inventory-rio-aros-sonora-mexico-river-unknown> Accessed 14 May 2012.

Östman Ö., J. M. Kneitel, and J. M. Chase. 2006. Disturbance alters habitat isolation's effect on biodiversity in aquatic microcosms. Oikos **114**:360-366.

Paine, R. T. 1966. Food web complexity and species diversity. The American Naturalist **100**:65-75.

Pajunen, V. I., and A. Jansson. 1969. Dispersal of the rock pool corixids *Arctocorisa carinata* (Sahlb.) and *Callicorixa producta* (Reut.) (Heteroptera, Corixidae). Annales Zoologici Fennici **6**:391-427.

Palmer, M. A., J. D. Allan, and C. A. Butman. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. Trends in Ecology and Evolution **11**:322-325.

Paltridge, R. M., P. L. Dostine, C. L. Humphrey, and A. J. Boulton. 1997. Macroinvertebrate recolonization after re-wetting of a tropical seasonally-flowing stream (Magela Creek, Northern Territory, Australia). Marine and Freshwater Research **48**:633-645.

Parkyn, S., and B. Smith. 2011. Dispersal constraints for stream invertebrates: setting realistic timescales for biodiversity restoration. Environmental Management **48**:602-614.

Patrick, C. J., and C. M. Swan. 2011. Reconstructing the assembly of a stream-insect metacommunity. Journal of the North American Benthological Society **30**:259-272.

Patten D.T., L. Rouse, and J.C. Stromberg. 2008. Isolated spring wetlands in the Great Basin and Mojave Deserts, USA: potential response of vegetation to groundwater withdrawal. Environmental Management **41**: 398-413.

Petersen, I., Z. Masters, A. G. Hildrew, and S. J. Ormerod. 2004. Dispersal of adult aquatic insects in catchements of differing land use. Journal of Applied Ecology **41**:934-950.

Petraitis, P. S., and C. Hoffmann. 2010. Multiple stable states and relationship between thresholds in processes and states. Marine Ecology Progress Series **413**:189-200.

Pfeiler, E. and T. A. Markow. 2008. Phylogenetic relationships of leopard frogs (Rana pipiens complex) from an isolated coastal mountain range in southern Sonora, Mexico. Molecular Phylogenies and Evolution **49**: 343-348.

Phillips, J.V. and B.R. Thomas. 2005. Hydrologic conditions in Arizona during 1999–2004: a historical perspective. United States Geological Survey Fact Sheet 2005–3081.

Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society **16**:391-409.

Poff, N. L., J. D. Olden, N. K. M. Vieira, D. S. Finn, M. P. Simmons, and B. C. Kondratieff. 2006. Functional trait niches of North American lotic insects: trait-based ecological applications in light of phylogenetic relationships. Journal of the North American Benthological Society **25**:730-755.

Polhemus, D. A. 1997. Systematics of the genus Rhagovelia Mayr (Heteroptera: Veliidae) in the Western Hemisphere (exclusive of the angustipes complex). Thomas Say Publications in Entomology, Lanham, MD.

Polhemus, D. A. and J. T. Polhemus. 2002. Basins and ranges: the biogeography of aquatic true bugs (Insecta: Heteroptera) in the Great Basin, pp 235-254 in Great Basin Aquatic Systems History (R. Hershler, D. B. Madsen and D. R. Currey, eds.), Smithsonian Contributions to the Earth Sciences **33**.

Price, K., A. Suski, J. McGarvie, B. Beasley, and J. S. Richardson. 2003. Communities of aquatic insects of old-growth and clearcut coastal headwater streams of varying flow persistence. Canadian Journal of Forestry Research **33**: 1416-1432.

Progar, R. A., and A. R. Moldenke. 2002. Insect production from temporary and perennially flowing headwater streams in western Oregon. Journal of Freshwater Ecology **17**:391-407.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, B. J. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society **7**:433-455.

Resh, V.H. 1992. Year-to-year changes in the age structure of a caddisfly population following loss and recovery of a springbrook habitat. Ecography **15**: 314-317.

Ricciardi, A., and J. B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. Conservation Biology **13**:1220-1222.

Ricklefs, R. E. 1987. Community diversity: relative role of local and regional processes. Science **235**:167-171.

Roff, D. A. 1994. Habitat persistence and the evolution of wing dimoprhism in insects. The American Naturalist **144**:772-798.

Ruegg, J., and C. T. Robinson. 2004. Comparison of macroinvertebrate assemblages of permanent and temporary streams in an Alpine flood plain, Switzerland. Archiv fur Hydrobiologie **161**:489-510.

Ruiter, D. E. 2011. Two new species of Ochrotrichia (Trichoptera: Hydroptilidae) from the southwestern United States. Zoosymposia **5**:420-424.

Ryker, L. C. 1975. Observations on the life cycle and flight dispersal of a water beetle, *Tropisternus ellipticus* LeConte, in western Oregon. The Pan-Pacific Entomologist **51**:184-194.

Sanderson, R. A., M. D. Eyre, and S. P. Rushton. 2005. Distribution of selected macroinvertebrates in a mosaic of temporary and permanent freshwater ponds as explained by autologistic models. Ecography **28**:355-362.

Sandberg, J.B. and K.W. Stewart. 2004. Capacity for extended egg diapause in six Isogenoides Klapalek species (Plecoptera: Perlodidae). Transactions of the American Entomological Society, **130**: 1-16.

Santos, A. N., and R. D. Stevenson. 2011. Comparison of macroinvertebrate diversity and community structure among perennial and non-perennial headwater streams. Northeastern Naturalist **18**:7-26.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution **18**:648-656.

Schooler, S. S., B. Salau, M. H. Julien, and A. R. Ives. 2011. Alternative stable states explain unpredictable biological control of Salvinia molesta in Kakadu. Nature **470**:86-89.

Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H.-P. Huang, N. Harnik, A. Leetmaa, N.-C. Lau, C. Li, J. Velez, and N. Naik. 2007. Model projections of an imminent transition to a more arid climate in Southwestern North America. Science **316**:1181-1184.

Shepard, W. D. 1993. Desert springs- both rare and endangered. Aquatic Conservation: Marine and Freshwater Ecosystems **3**:351-359.

Spangler, P.J. 1960. A revision of the genus Tropisternus (Coleoptera: Hydrophilidae). Ph.D. dissertation. University of Missouri.

Snyder, G. 2005. Danger on peaks: poems. Counterpoint. Berekeley, CA.

Stanley, E. H., D. L. Buschman, A. J. Boulton, N. B. Grimm, and S. G. Fisher. 1994. Invertebrate resistance and resilience to intermittency in a desert stream. American Midland Naturalist **131**:288-300.

Stanley, E. H., S. G. Fisher, and N. B. Grimm. 1997. Ecosystem expansion and contraction in streams. BioScience **47**:427-435.

Stebbins, RC. 2003. A field guide to western reptiles and amphibians, 3rd edition. Houghton Mifflin Co., New York, NY.

Stevens, L. E., J. T. Polhemus, R. S. Durfree, and C. A. Olson. 2007. Large mixed-species disperal flights of predatory and scavenging aquatic Heteroptera and Coleoptera, northern Arizona, USA. Western North American Naturalist **67**:587-592.

Stewart, K. W., and N. H. Anderson. 2010. The life history of Ostrocerca dimicki (Frison) in a short-flow, summer-dry Oregon stream. Illesia **6**:52-57.

Stromberg, J.C., R. Tiller and B. Richter. 1996. Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. Ecological Applications **6**: 113-131.

Storey, R. G., and J. M. Quinn. 2008. Composition and temporal changes in macroinvertebrate communities of intermittent streams in Hawke's Bay, New Zealand. New Zealand Journal of Marine and Freshwater Research **42**:109-125.

Thompson, R. M., and C. R. Townsend. 2006. A truce with neutral theory: local deterministic factors, species traits and dispersal limitations together determine patterns of diversity in stream invertebrates. Journal of Animal Ecology **75**:476-484.

Towns, D. R. 1985. Limnological characteristics of a South Australian intermittent stream, Brown Hill Creek. Australian Journal of Marine and Freshwater Research **36**:821-837.

Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society **8**:36-50.

Townsend, C.R. 1996. Invasion biology and ecological impacts of brown trout, Salmo trutta, in New Zealand. Biological Conservation **78**: 13-22.

Tronstad, B.P., L.M. Tronstad, and A.C. Benke. 2007. Aerial colonization and growth: rapid invertebrate response to temporary aquatic habitats in a river floodplain. Journal of the North American Benthological Society **26**: 460-471.

Truxal, F. S. 1953. A revision of the genus Buenoa (Hemiptera, Notonectidae). University of Kansas Science Bulletin **35**: 1351-1523.

University of Arizona. 2002. Deserts of the World: The Sonoran Desert. Worsening threats, vulnerable species and areas meriting protection in the subregions of the Sonoran Desert Bioregion. <http://alic.arid.arizona.edu/sonoran/documents/nabhan/ db_table13.html> Accessed 19 Oct. 2007.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**:130-137.

Velasco, J., and A. Millan. 1998. Insect dispersal in a drying desert stream: effects of temperature and water loss. The Southwestern Naturalist **43**:80-87.

Vinson, M. R., and C. P. Hawkins. 2003. Broad-scale geographical patterns in local stream insect genera richness. Ecography **26**:751-767.

Vonesh, J. R., J. M. Kraus, J. S. Rosenberg, and J. M. Chase. 2009. Predator effects on aquatic community assembly: disentangling the roles of habitat selection and post-colonization processes. Oikos **118**:1219-1229.

Wilcox, C. 2001. Habitat size and isolation affect colonization of seasonal wetlands by predatory aquatic insects. Israel Journal of Zoology **47**:459-475.

Williams, D. D. 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. Journal of the North American Benthological Society **15**:634-650.

Williams, D. D., N. Heeg, and A. K. Magnusson. 2007. Habitat background selection by colonizing intermittent pond invertebrates. Hydrobiologia **592**:487-498.

Williams, D. D., and H. B. Hynes. 1976a. The ecology of temporary streams: I. The faunas of two canadian streams. Internationale Revue der gesamten Hydrobiologie und Hydrographie **61**:761-787.

Williams, D. D., and H. B. Hynes. 1976b. The recolonization mechanisms of stream benthos. Oikos **27**:265-272.

Wilson, R. T. 1978. Reconnaissance geology and petrology of the San Carlos area, Sonora, Mexico. Master's thesis. Arizona State University, Tempe, AZ.

Winterbourn, M. J., W. L. Chadderton, S. A. Entrekin, J. L. Tank, and J. S. Harding. 2007. Distribution and dispersal of adult stream insects in a heterogenous montane environment. Fundamental and Applied Limnology **168**:127-135.

Wissinger, S. A., W. S. Brown, and J. E. Jannot. 2003. Caddisfly life histories along permanence gradients in high-altitude wetlands in Colorado (U.S.A.). Freshwater Biology **48**:255-270.

Wood, P. J., J. Gunn, H. Smith, and A. Abas-Kutty. 2005. Flow permanence and macroinvertebrate community diversity within groundwater dominated headwater streams and springs. Hydrobiologia **545**:55-64.

Zera, A. J., and R. F. Denno. 1997. Physiology and ecology of dispersal polymorphism in insects. Annual Review of Entomology **42**:207-230.

Zimmerman, J.R. and R.L. Smith. 1975. The genus Rhantus (Coleoptera: Dytiscidae) in North America, Part 1, general account of the species. Transactions of the American Entomological Society **101**: 33-93.

Zweig, C. L., and W. M. Kitchens. 2009. Multi-state succession in wetlands: a novel use of state and transition models. Ecology **90**:1900-1909.

APPENDICES

APPENDIX I

Long-term seasonal and interannual variation in arid-land stream communities

Arid-land streams are characterized by both strong season seasonal and interannual variability in precipitation (Figure A1.1) and stream flow. In this appendix, I present the results of a long-term study of three arid-land streams in southeast Arizona, East Turkey Creek (ETC), Ash Creek (AC), and West Stronghold Canyon (WSC). These three streams have small drainage areas (>15km^2) and occur in steep rugged mountain ranges between 1200 and 2600m in elevation dominated by arid woodlands (see Chapters 2, 3, and 4). ETC is the largest stream with a minimum of 571 m^2 of wetted habitat area during the summer, while WSC and AC support a minimum of 95 and 10 m^2 of wetted habitat area, respectively. In addition to perennial pools, ETC has very short reaches of mimimal perennial flow (>4L/s) during the dry summer; all three streams support expanding flowing habitat during the wet winters (see Bogan and Lytle 2007). I sampled aquatic invertebrate communities and measured physical habitat conditions in these three streams in winter (March) and summer (June) from 2004 to 2011; because of logistical difficulties, ETC and WSC were not sampled in 2007. During each visit, invertebrate community samples were collected from three pools and three riffles (see Chapters 2 and 4 for details).

Invertebrate taxon richness at each of the three streams did not differ by season (Table A1.1) or by year type (wet year vs. dry year; Figure A1.2). Richness did differ by stream though, as ETU supported twice as many species as AC or WSC. ETC was also the only stream that had any flow during the dry summer season (Table A1.1) and the surface area of dry season perennial pools at ETC was 6x and 56x greater than at WSC and AC, respectively. Richness did not differ between AC and WSC, though, despite WSC having nearly 10x the dry season perennial pool surface area of AC. Cumulative taxon richness at each of the three streams over the 8 years of the study continued to increase linearly (Figure A1.3), indicating a lack of saturation in species detection curves.

While taxon richness did not vary significantly by year or season, community composition did. Predators were 4-5 times more abundant during the summer and dry winters than they were in wet winters, while filterers and shredders nearly disappeared during dry winters and summers (Figure A1.4). Each stream supported a distinct community type, though communities in all three streams were driven strongly by flow (Figure A1.5). Individual non-metric multidimensional scaling ordinations for each stream revealed distinct seasonal and interannual patterns. The dominant axis one in each ordination (R^2 range: 0.55 to 0.78) described large seasonal shifts in composition, with summers and dry winters supporting one community type and dry winters supporting another type (Figure A1.6). Wet winter communities were dominated by stoneflies, blackflies, and dobsonflies at all three streams, though species identities within these taxonomic groups varied among streams (Table A1.2). Additionally, ETU wet winter (high flow) communities were characterized by a number of caddisflies and the coldwater true fly taxon *Philorus* / *Agathon*. During dry winters and all summers, a diverse group of beetles and true bugs dominanted communities at all three streams, including the top predator giant water bug *Abedus herberti*, and numerous species of small and medium sized secondary predators like the predaceous diving beetles *Stictotarsus* spp. and *Rhantus* spp. The smaller amount of variation explained by axis two (R^2 range: 0.18 to 0.39) was mainly driven by interannual changes, specifically a break in composition in 2007 when sampling net mesh size was changed from 1mm to 0.5mm. This change in mesh size was associated with an increased abundance of small-bodied taxa in post-2007 samples, including Chironomidae, Oligochaeta, and *Hydraena*. Finally, the magnitude of community change between seasons (as measured by Sorensen distance) was significantly predicted by the magnitude of flow difference between seasons (i.e., March flow - June flow; Figure A1.7).

Table A1.1. Mean taxon richness, flow, water temperature, conductivity and pH (± 1 SD) for the three study streams during winter (March) in wet years and dry years and summer (June) in all years.

	East Turkey	West Stronghold	Ash
Taxon richness			
Winter (Wet year)	50 ± 9	23 ± 2	21 ± 8
Winter (Dry year)	63 ± 5	32 ± 7	26 ± 10
Summer	51 ± 8	34 ± 3	21 ± 5
Flow (L s^{-1})			
Winter (Wet year)	92 ± 42	45 ± 14	39 ± 33
Winter (Dry year)	22 ± 11	0 ± 0	6 ± 8
Summer	3 ± 6	0 ± 0	0 ± 0
Temperature (°C)			
Winter (Wet year)	5.8 ± 0.8	10.3 ± 2.1	9.0 ± 1.0
Winter (Dry year)	8.8 ± 3.4	11.8 ± 2.2	9.8 ± 2.7
Summer	19.6 ± 2.1	21.0 ± 2.2	16.2 ± 2.4
Conductivity (µS)			
Winter (Wet year)	104 ± 40	178 ± 98	58 ± 8
Winter (Dry year)	193 ± 70	299 ± 164	61 ± 16
Summer	266 ± 56	434 ± 150	101 ± 31
pH			
Winter (Wet year)	6.6 ± 0.6	6.8 ± 0.3	6.7 ± 0.3
Winter (Dry year)	6.9 ± 0.7	7.5 ± 1.0	6.5 ± 0.2
Summer	7.5 ± 0.3	7.7 ± 0.3	7.2 ± 0.7

Table A1.2. Pearson’s correlation coefficients (*r*) between abundances of influential taxa and non-metric multidimensional scaling ordination axis one and two scores for each of the three stream-specific ordinations.

	East Turkey Creek		West Stronghold Canyon		Ash Canyon	
	Species	*r*	Species	*r*	Species	*r*
NMS Axis 1 (season axis)	*Abedus herberti*	-0.84	*Microvelia*	-0.89	*Stictotarsus striatellus*	-0.81
	Aquarius remigis	-0.84	*Desmopachria portmanni*	-0.80	*Agabus*	-0.80
	Stictotarsus aequinoctialis	-0.79	*Laccophilus fasciatus*	-0.79	*Sanfilippodytes*	-0.78
	Rhantus gutticollis	-0.77	*Berosus salvini*	-0.78	*Rhantus gutticollis*	-0.68
	Laccophilus fasciatus	-0.73	*Liodessus obscurellus*	-0.73	*Notonecta lobata*	-0.67
	Notonecta lobata	-0.72	*Stictotarsus aequinoctialis*	-0.71		
	Berosus salvini	-0.67	*Stictotarsus corvinus*	-0.70		
	Rhantus aticolor	-0.65	*Abedus herberti*	-0.68		
	Microvelia	-0.64	*Rhantus atricolor*	-0.66		
	Simulium	0.87	*Prosimulium*	0.92	*Neohermes filicornis*	0.88
	Baetis	0.86	*Neohermes filicornis*	0.91	*Prosimulium*	0.82
	Malenka coloradensis	0.82	*Mesocapnia arizonensis*	0.87	*Taenionema jacobii*	0.74
	Ceratopsyche venada	0.81	Hydroporinae (larvae)	0.56	*Capnia californica*	0.73
	Atopsyche	0.79	*Simulium*	0.56	Hydroporinae (larvae)	0.65
	Philorus / Agathon	0.76			Ephydridae	0.61
	Neohermes filicornis	0.70			*Simulium*	0.61
NMS Axis 2 (year axis)	Chironomidae	0.94	Chironomidae	0.84	Chironomidae	0.89
	Oligochaeta	0.89	Oligochaeta	0.80	*Aquarius remigis*	0.75
	Bezzia	0.87	Ostracoda	0.75	Oligochaeta	0.74
	Hydraena	0.82	Physidae	0.65	*Hydraena*	0.73

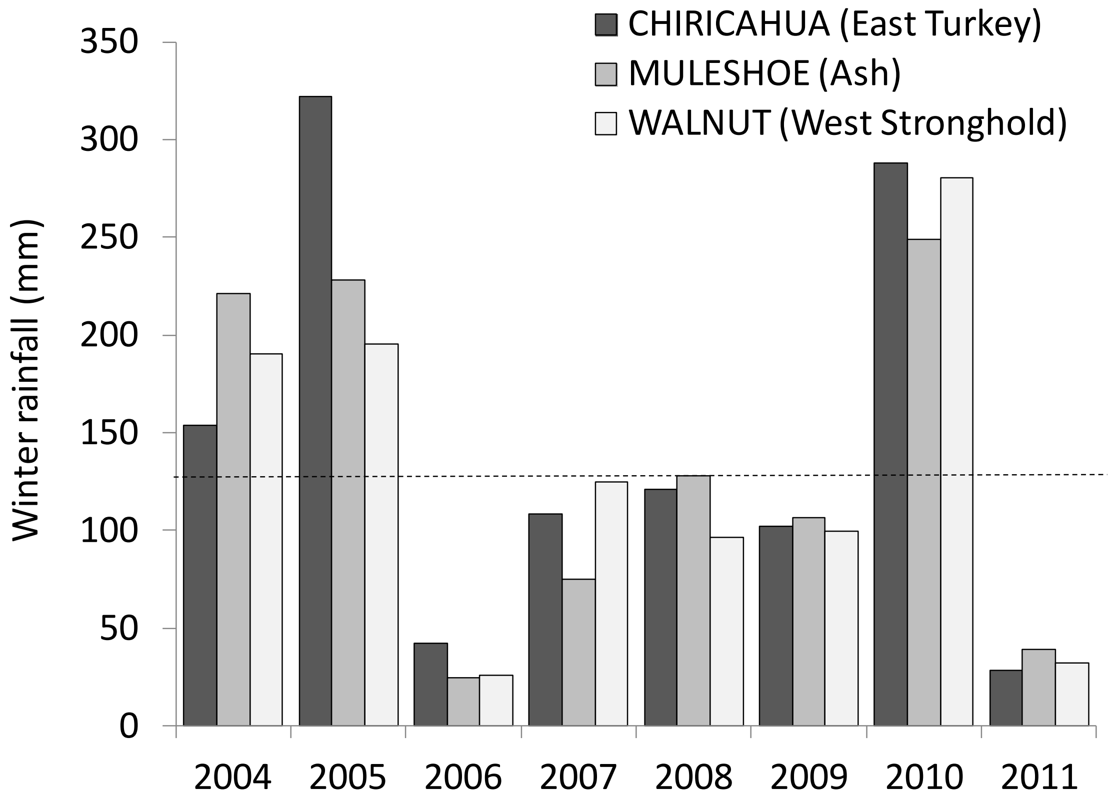

Figure A1.1. Inter-annual variability in winter (Nov-Apr) rainfall at rain gauges near the three long-term study streams (East Turkey Creek, Ash Creek, and West Stronghold Canyon) in southeast Arizona. The dashed line indicates the long-term average winter rainfall, and thus is defined as the threshold between a 'wet year' and a 'dry year'.

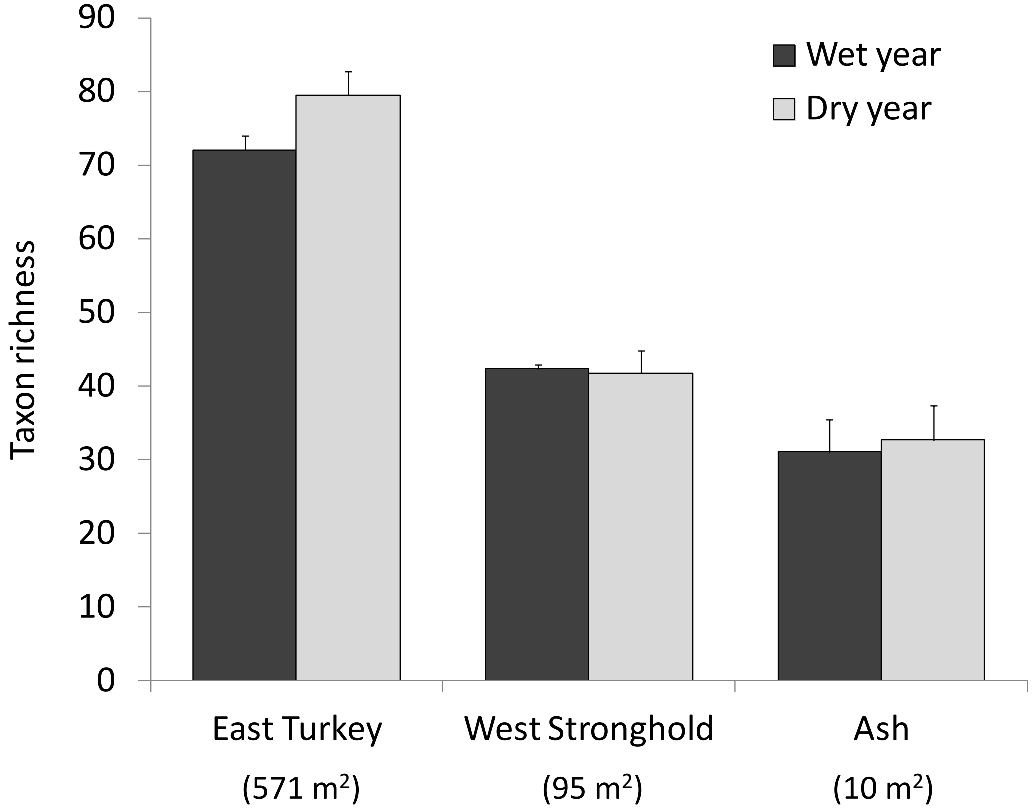

Figure A1.2. Mean number of aquatic invertebrate taxa collected during wet and dry years at each of the three sites (wet years: 2004, 2005, 2010; dry years: 2006-2009, 2011). Minimum wetted habitat area for each site is listed below the site name. Error bars represent one standard deviation.

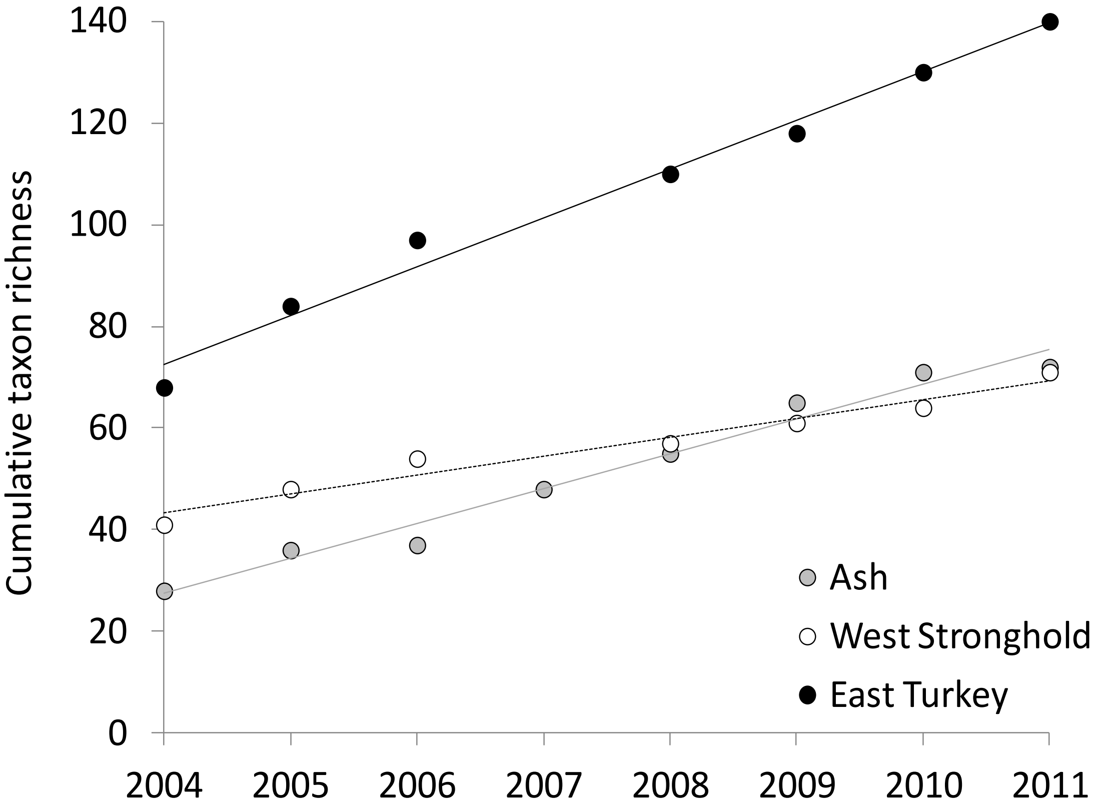

Figure A1.3. Cumulative taxon richness over the eight study years at the three streams. A positive linear relationship between year and taxon richness was the best fit for each of the three streams, indicating a lack of saturation in species detection curves. While half of all species identified from each site were collected in the first year of the study, between four and nine additional species were detected each year at each site.

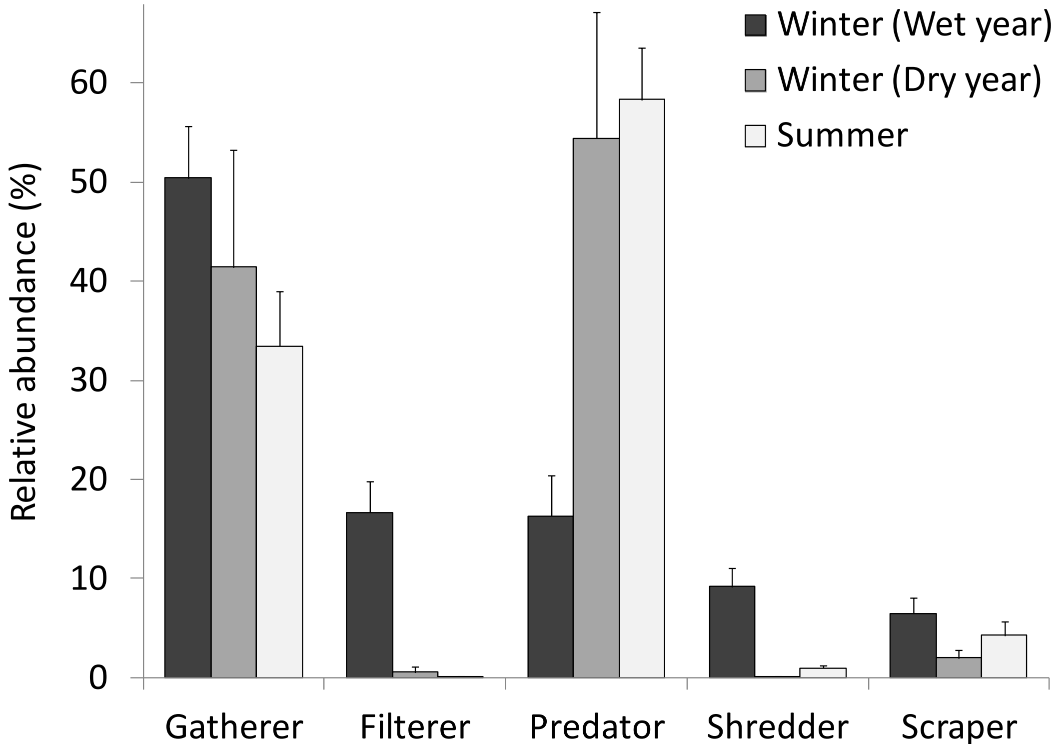

Figure A1.4. Relative abundances of functional feeding groups across samples from all three study streams, coded by sampling season and year type (the June sampling period was dry in all years). Error bars represent one standard deviation. Statistically significant Kruskal-Wallis comparisons are indicated by asterisks (*$p = 0.002$, **$p < 0.001$).

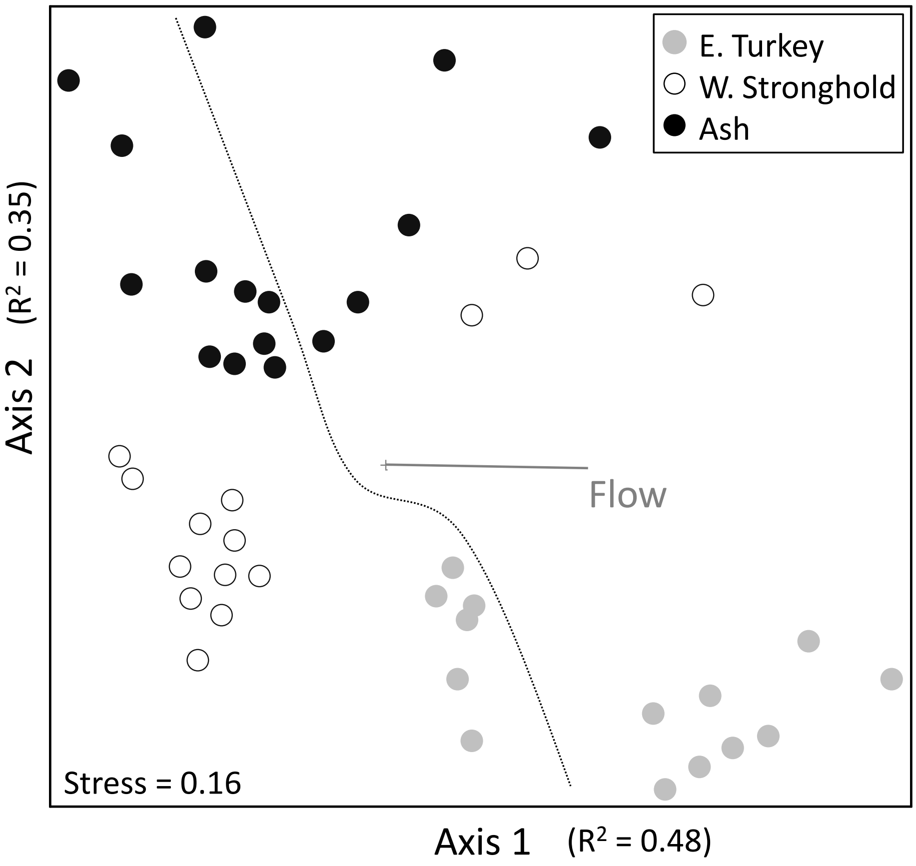

Figure A1.5. Non-metric multidimensional scaling ordination plot of seasonal community composition at the three study streams from 2004 to 2011 (individual years and seasons not coded). The dashed line separates samples collected during no flow periods (left of dashed line-- dry March samples and all but one of the June samples) from periods with flow greater than 5 L s^{-1} (right of dashed line-- wet March samples). Of all measured environmental variables, only flow was strongly correlated with an ordination axis (*r* = 0.70).

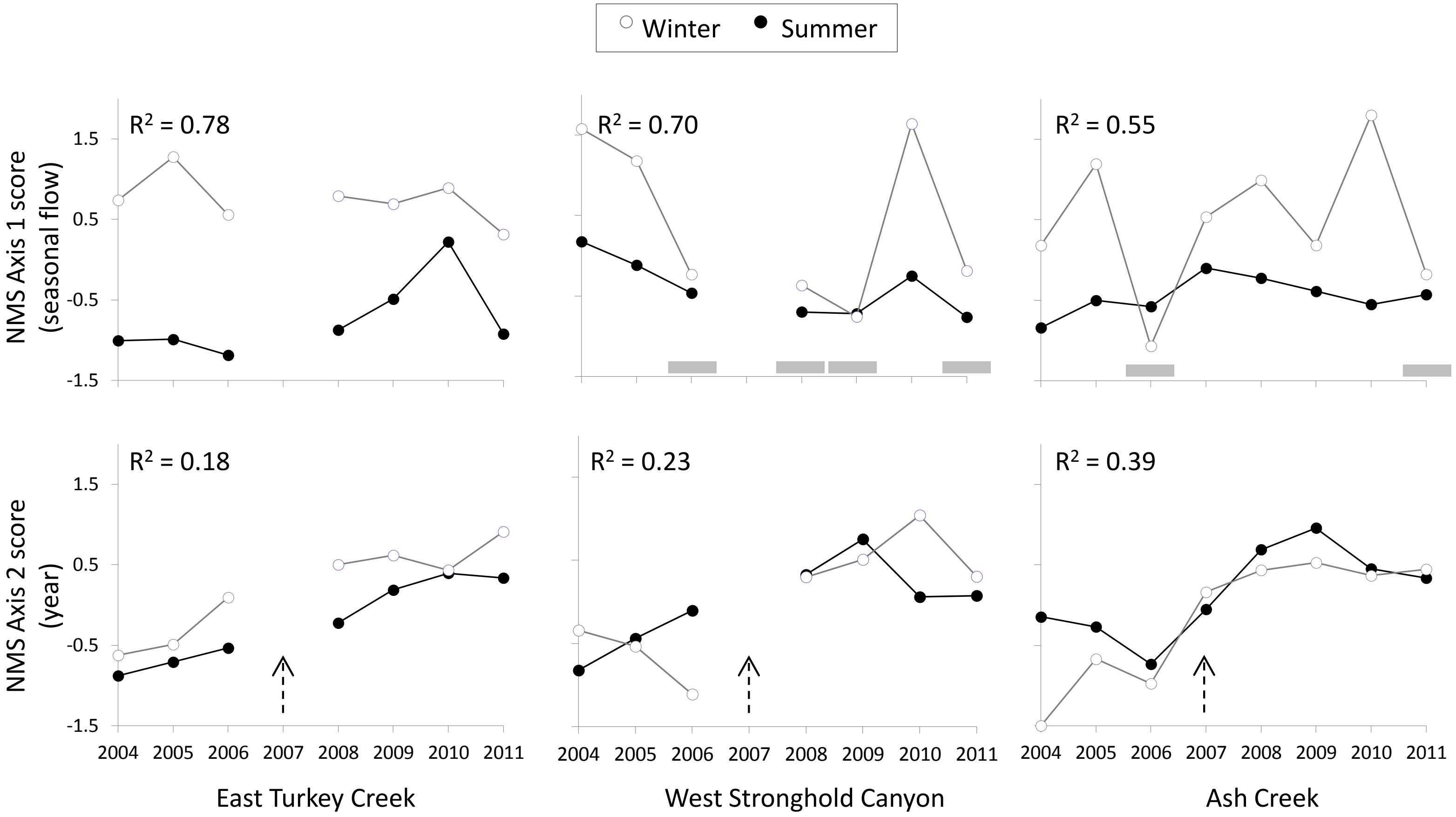

Figure A1.6. Seasonal and interannual variability in invertebrate community composition as shown by axis scores from individual NMS ordinations for each of the three study sites (each point represents the average composition of all samples collected from a given stream in a given season), with axis R^2 values given at the top of each graph. Grey bars along the x-axis of NMS axis 1 scores indicate dry years where there was zero flow during the wet season (March), and community convergence was observed between seasons. Dashed arrows along the x-axis of NMS axis 2 scores indicate the year that sampling net mesh sizes changed from 1mm to 0.5mm.

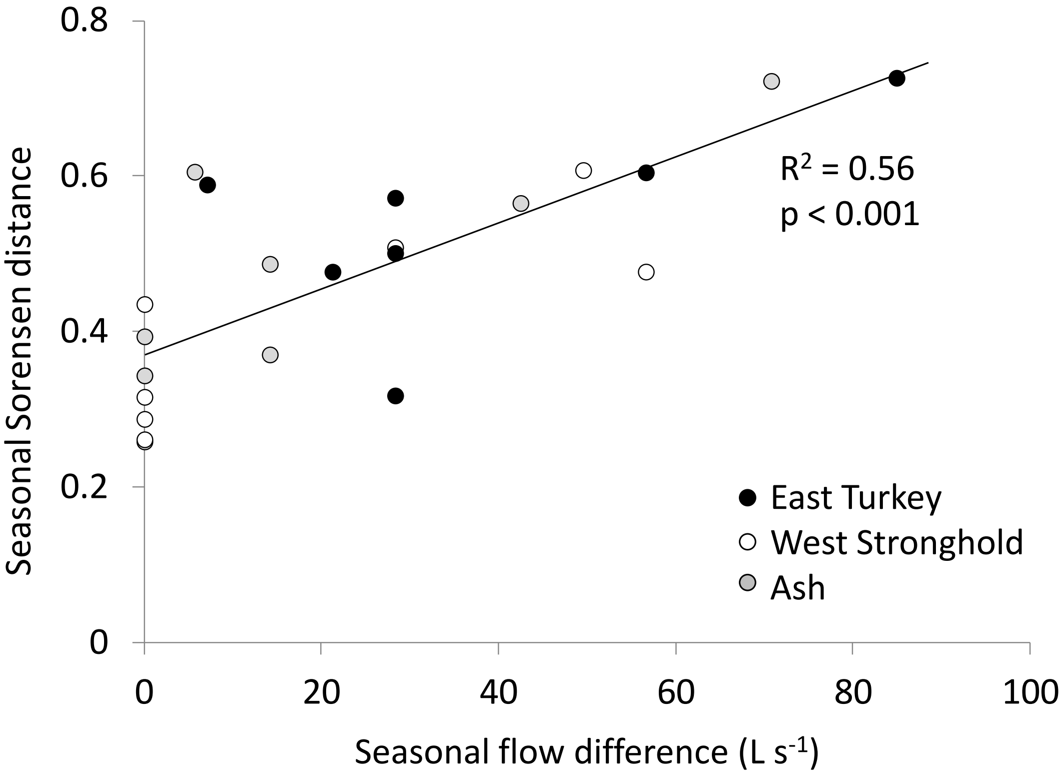

Figure A1.7. Relationship between seasonal flow difference (March discharge - June discharge) and seasonal community distance (Sorensen distance between average March and June community composition with a given stream). Points from each stream are coded by color and linear regression R2 and significance values are given. Years are not coded, but all points with zero seasonal flow difference represent dry years when there was no flow in either March or June sampling periods**.**

APPENDIX II

Potential bet-hedging strategy of a winter stonefly species in an intermittent stream

A modeling approach was used to explore potential population dynamics of the winter stonefly *Mesocapnia arizonensis* at West Stronghold Canyon (see Chapter 4 for details about the species and stream). The basic life-cycle of *M. arizonensis* is as follows: eggs hatch and pass through a brief aquatic larval stage (~12 weeks) after which they emerge as short-lived adults (~1 week) that mate and lay a number of eggs (Gray, 1981). Generally, the stream dries soon after eggs are laid. These eggs enter diapause to survive the dry season and likely remain deep in dry stream sediments (> 30 cm depth; see Appendix III). Adult males are brachypterous and cannot fly more than a meter or so, while females are fully-winged but are much more likely to crawl than fly; thus dispersal between drainages is assumed to be very low. I observed that despite this poor aerial dispersal ability the *M. arizonensis* population at West Stronghold persisted through consecutive dry years with no flow, and I hypothesized that this species uses a delayed hatch of their diapausing eggs to 'bet-hedge' across wet and dry years. Individual stoneflies are reducing their fitness in the short-term, by potentially having less offspring in the year following reproduction, but have a higher mean fitness when averaged over multiple good and bad years.

In the model (Figure A2.1), I assumed that a percentage of diapausing eggs are genetically 'programmed' to hatch the year after they were laid (% hatch one). The potential number of hatchlings in that year then depends on flow duration (whether or not flow lasts long enough for hatchlings to mature into adults) and flow magnitude (extent of flowing stream available to hatchlings). If there is zero flow in a given year, then all the eggs programmed to hatch that year would die; but a smaller percentage of the original eggs laid would be programmed to hatch in the following year (Table A2.1). This pattern continues until year five (Figure A2.1), which is the currently known survival limit for diapausing stonefly eggs (Sandberg

& Stewart, 2004). I limited stonefly densities to 80 individuals per m^2 of wetted habitat based on observed densities from other streams in the region (Bogan, unpublished data). I also assumed that, via drift of eggs and larvae, every available space would easily be occupied. This model attempts to simulate only essential abiotic factors, and as such ignores potentially important biotic factors like predation and competition.

The model was designed to track five age-classes through time: (1) reproducing adults and (2-5) eggs from those adults hatching over years two through five. Estimates of the fecundity of adults and percentage of eggs hatching in different years were drawn from a life-history study of *Isogenoides zionensis* (see Table A2.1 for values; data from Sandberg and Stewart, 2004), the only other stonefly species known to have a 5-year egg diapause period. Survivorship from egg hatchling to egg-laying adult has not been measured in published studies, but is assumed in this model to be moderately low (survivorship = 0.1). Mathematical finite difference equations for the model are as follows:

$$\text{Adults} = \text{EggY2} * \text{FD} * \text{FM} + \text{EggY3} * \text{FD} * \text{FM} + \text{EggY4} * \text{FD} * \text{FM} + \text{EggY5} * \text{FD} * \text{FM}$$
$$\text{EggY2} = \text{Adults} * \text{Sur} * \text{Fec} * \%\text{Hatch1}$$
$$\text{EggY3} = \text{EggY2} * \%\text{Hatch2}$$
$$\text{EggY4} = \text{EggY3} * \%\text{Hatch3}$$
$$\text{EggY5} = \text{EggY4} * \%\text{Hatch4}$$

[FD = flow duration, FM = flow magnitude, Sur = % survival hatch to reproducing adult, Fec = fecundity (# eggs laid)]

The presence of an adult stage and the number of recruits in any given year are limited by flow duration and flow magnitude. Flow duration was modeled as either meeting or failing to meet a time threshold (with ≥ 12 weeks of flow stoneflies can complete their life cycle, but with <12 weeks they cannot). Flow magnitude also greatly affects population dynamics. A series of years with small flow magnitudes (and smaller total stonefly abundances) would reduce the ‘seed bank’ of eggs. As West Stronghold is not gauged, I utilized 60 years of flow data from nearby stream gauges (Sabino Canyon USGS gauge # 09484000 and Rincon Creek USGS gauge # 09485000) to estimate historic flow duration and magnitude parameters for West Stronghold. In 45% of the 60 years, winter flow did not last for 12 continuous weeks. Flow magnitude (habitat size) at West Stronghold was estimated by scaling peak mean monthly flows (ft^3/s) at the gauges by estimates of stream coverage area (m^2) I made at West Stronghold Canyon from 2003 to 2005. This scalar worked well for predicting the flow magnitude observed at West Stronghold from 2005-2010 and is assumed to be acceptable for estimating past flow magnitudes at West Stronghold based on the 60 years of historic gauge data.

These flow parameters were also used in a stochastic version of the population model. The flow duration factor was modeled with a simple Bernoulli distribution with a $P(0) = 0.45$ [0 = failure, 1 = success]. Flow magnitude for the 60 years of historic gauge data roughly fit a log-normal distribution with $\alpha = 1$ (Figure A2.2). Thus, flow magnitude (habitat size) was drawn from a log-normal distribution with μ (hat) = 8.55 and δ (hat) = 0.72. An initial population size of 10,000 individuals was assumed at $t = 0$.

Historical population model results: This historical population model was implemented in Excel. For the 60 years over which the model was run (1945-2005), *M. arizonensis* abundances at West Stronghold Canyon varied wildly (see Figure A2.3), as expected given variability in flow duration and magnitude. The population crashed most severely following the intense four-year drought from 1953-1956, with only 16 eggs surviving to hatch in the year following the drought. The population peaked in 1993, following 3 good years with high flow magnitudes. Actual *M. arizonensis* population data from 2003 and 2005 matched the predicted model data well (2003- *predicted* = 0, *observed* = 0; 2005- *predicted* = 80 individuals / m^2, *observed* = 76 individuals / m^2), while model predictions from 2004 were less accurate (*predicted* = 29 individuals / m^2, observed = 13 individuals / m^2).

Stochastic population model results: The stochastic model was implemented in Excel using the “Rand()” function drawing from a Bernoulli distribution for flow duration and from a log-normal distribution for flow magnitude as described above. The 100 runs of the model were run (for 100 years each). Surprisingly, 50% of the runs resulted in the population crashing to zero and becoming extinct, even though these runs used the “real-world”, flow gauge-derived, probability of flow duration being inadequate for reproduction ($P(0) = 0.45$). These population failures occurred when the model simulated droughts greater than those of the historical record occurred (i.e., > 4 continuous years of insufficient flow duration). The 50% of runs that resulted in population persistence through 100 years (Figure A2.4) produced greatly fluctuating abundances similar to those of the historic model. Changing the Bernoulli probability of flow duration being inadequate dramatically affected the number of population replicates which persisted through 100-year simulations, especially over the range 0.3 to 0.6 (Figure A2.5).

The discrepancy between the stochastic model predictions and historical observations at West Stronghold may lie in the temporal autocorrelation of flow year types. Precipitation patterns, and the stream flows that they produce, are not truly randomly distributed; in the historic record, flow failures of greater than 4 consecutive years have not occurred. However, in the stochastic model 5 or more dry years in a row are entirely possible. Alternatively, the model may not adequately depict the limits of *M. arizonensis* diapause. If *M. arizonensis* eggs can diapause for longer periods (i.e., ≥ 5 years), then populations could persist through longer-term droughts (like those predicted in the stochastic model). Future work should include more rigorous hydrological modeling, a detailed assessment of the temporal autocorrelation of wet and dry years, and experimental rearing of *M. arizonensis* to better parameterize the model.

Table A2.1 Observed egg clutch size and hatches over multiple years for the stonefly *Isogenoides zionensis* from Sandberg and Stewart (2004). These clutch sizes and hatching percentages were used as parameters in the *Mesocapnia arizonensis* population model.

	Observed numbers of eggs and hatches in subsequent years	% hatch of total eggs
Total # eggs	733	
Year 1 hatch	230	31.4
Year 2 hatch	15	2.0
Year 3 hatch	10	1.4
Year 4 hatch	7	1.0
Year 5 hatch	3	0.4

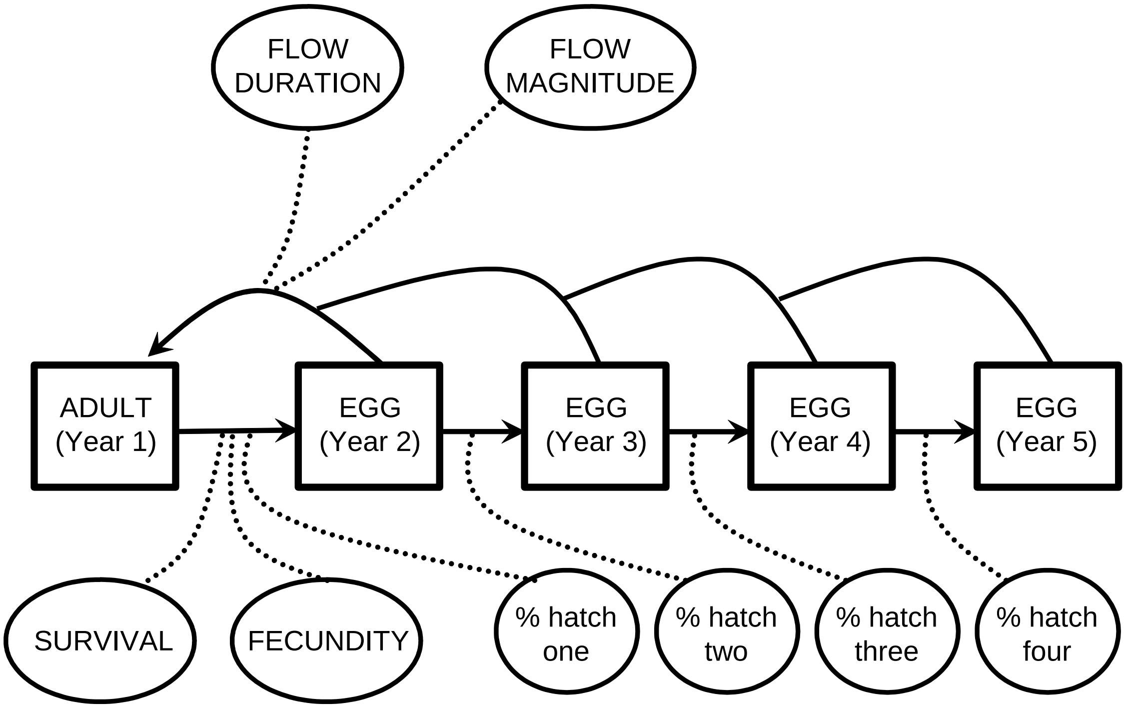

Figure A2.1. Diagrammatic representation of the stonefly population model, with solid lines as flow pathways and dashed lines as influential parameters.

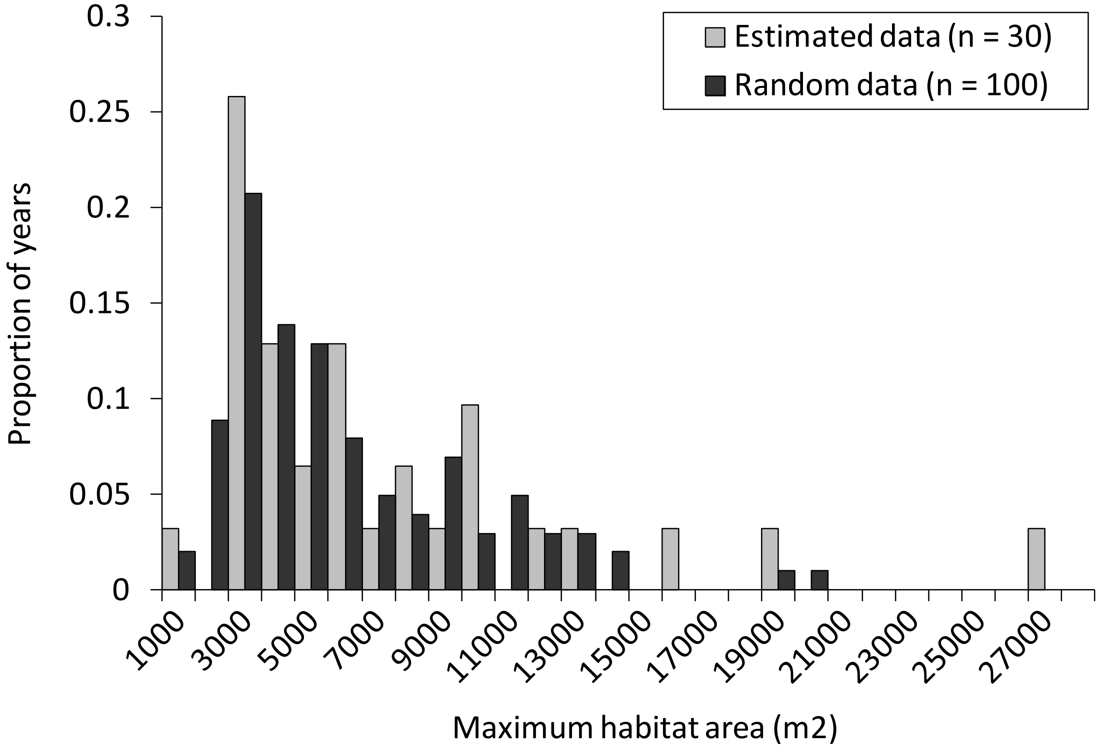

Figure A2.2. Histogram of estimated maximum winter habitat size from West Stronghold Canyon for years with sufficient flow duration (*Estimated data n = 30*) and 100 values drawn randomly from a log-normal distribution which approximated the shape of the estimated data (*Random data n = 100*).

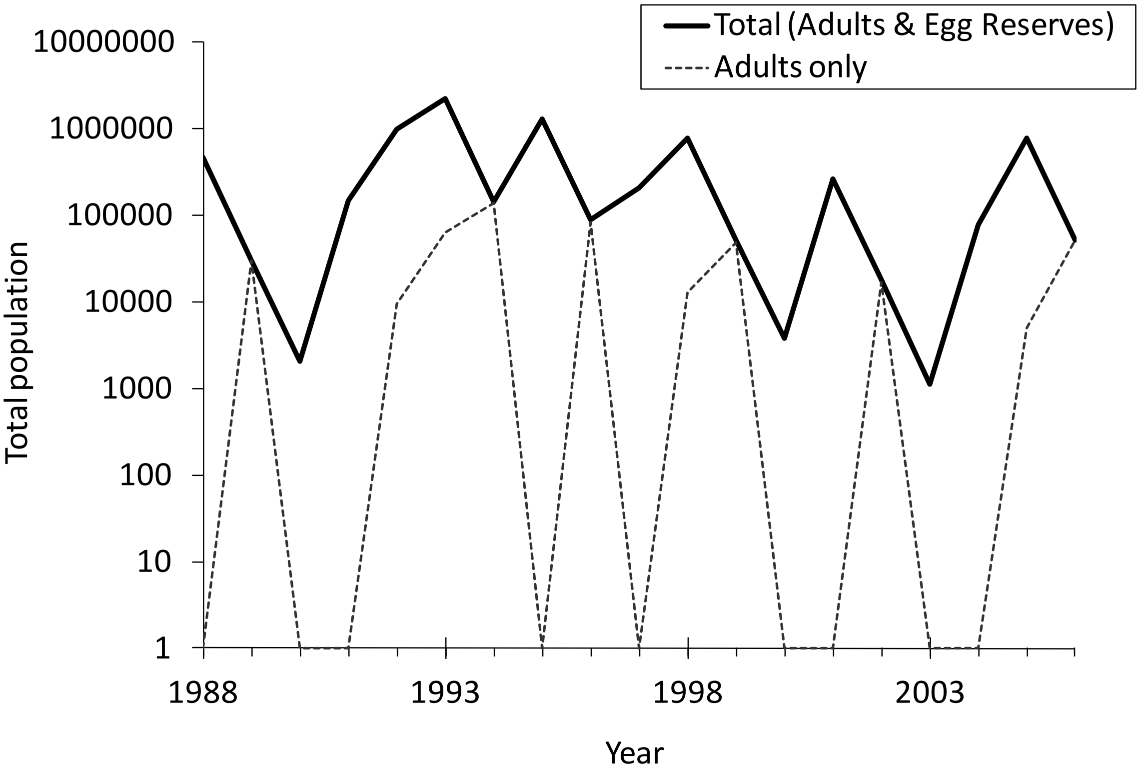

Figure A2.3. Historical model outputs for the period 1988 to 2006 with adults only (dashed line) and total population (sum of all stages).

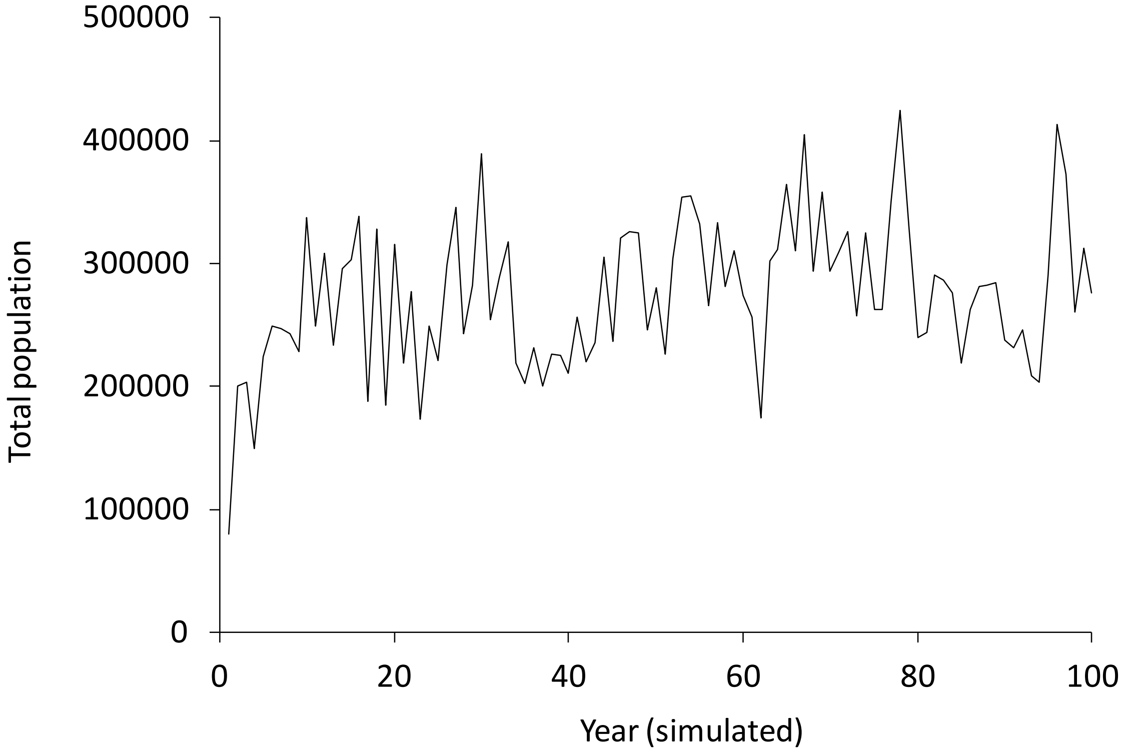

Figure A2.4. Mean *Mesocapnia* abundance (sum of all stages) from stochastic model runs which did not result in population extinction (n = 50) over a 100-year simulation.

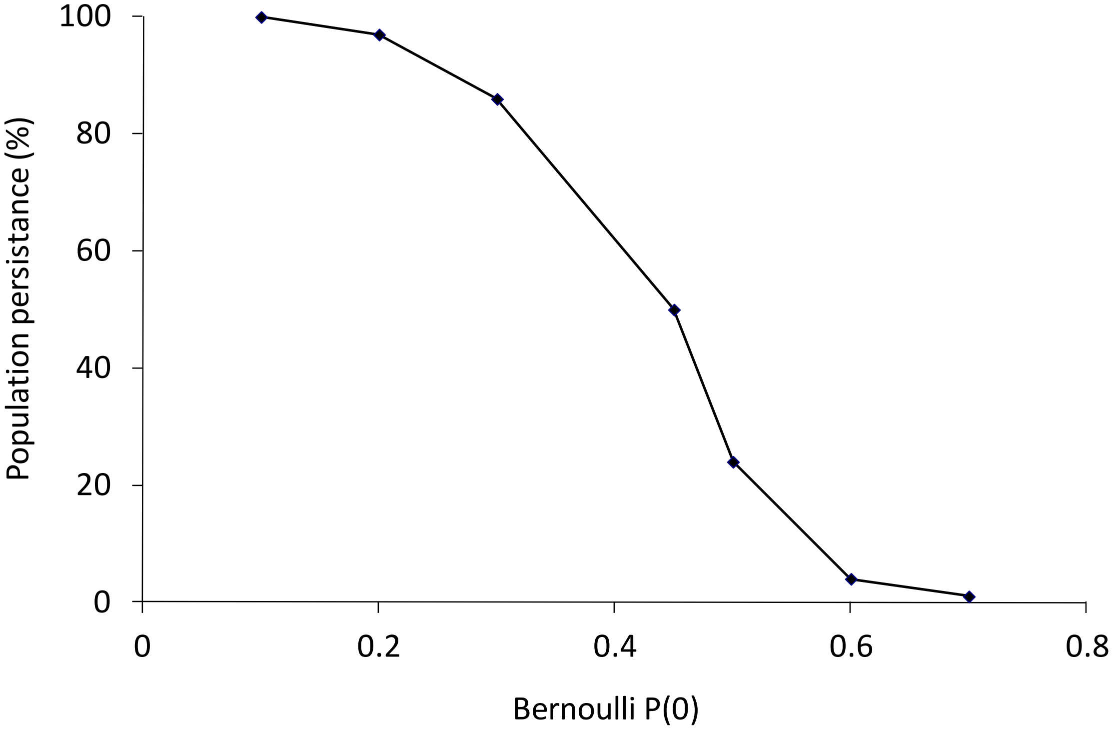

Figure A2.5. The effect of increasing the Bernoulli probability of flow duration being inadequate for reproduction in a given year [P(0)] on the percent of populations which persist through a 100-year model run (100 replications).

APPENDIX III

Experimental rewetting of dry streambed sediments

I extracted and experimentally rewetted dry sediments from West Stronghold Canyon, an intermittent stream in southeast Arizona, to explore how common the resting stages of dormant taxa (see Chapter 4) may be in dry stream sediments. I predicted that dormant invertebrates would be abundant in dry sediments and that some winter specialist species (e.g., *Mesocapnia arizonensis*; see Chapter 4) would only emerge from dormancy during cold water rewetting events, while generalist taxa (e.g., some Chironomidae) would emerge from dormancy during both cold (10°C) and warm (20°C) rewetting events.

On 4 November 2009, I extracted 15 1-L samples of dry sediment from West Stronghold Canyon by digging 30 cm into the dry stream bed (excavation area: 20 by 20 cm) using a trowel and then collecting 1-L of sand and gravel sediment from approximately 10 to 30 cm depth, retaining all organic material but discarding rocks greater than 10 cm in diameter. At most sediment extraction sites, large cobbles and boulders prevented me from digging deeper into the stream bed. Additionally, recent rehydration studies have found many dormant individuals in dry sediments in the first 20 cm channel depth (Larned et al. 2007, Datry et al. 2012). At the time of sediment extraction, the study reach had been dry for approximately 13 months.

These 15 1-L samples of dry sediment were then transported to Oregon State University where they were divided into three groups of five samples each. The first 5 1-L samples were rehydrated with filtered tap water and all sediment was examined under a dissecting microscope to look for dormant larvae or eggs. The remaining 10 samples were placed into individual 4-L trays, rewetted with 1.2 L of filtered, dechlorinated tap water (conductivity: 70 µS), and aerated with an aquarium aeration stone. Five samples were placed in a cold room (10°C) with a 10L:14D light cycle and five samples were placed in a warm room (20°C) with a 14L:10D light

cycle, meant to simulate winter (10°C) and summer (20°C) rewetting events. I inspected each of the 20 trays for aquatic invertebrates daily for 32 days and removed active individuals for identification if any were found. On day 32, I preserved all sediment and any remaining aquatic invertebrates in 95% ethanol, and then examined the preserved samples under a microscope.
I found no dormant eggs or larvae in the five dry sediment samples that were not subjected to the 32-day experimental rewetting. I also found no active invertebrates during daily visual inspection of the 10 sediment trays from the 32-day rewetting experiment. After terminating the experiment and examining preserved samples under the microscope, I found only a single individual of the mite *Hydrozetes* (Sarcoptiformes: Hydrozetidae) and 3 individual ostracods (Ostracoda) from the five replicate trays in the 10°C "winter" treatment. From the five replicate 20°C "summer" treatment trays, I found seven *Hydrozetes* individuals and one poorly-preserved specimen of the beetle *Hydraena* (Coleoptera: Hydraenidae).

Hydrozetes mites occur in a range of habitats from fully aquatic to semi-terrestrial damp soils, though are generally aquatic (Pennak 1989). Because species level identification was not possible for the immature specimens found in rewetted sediments, I could not determine whether these *Hydrozetes* represent active residents of the dry stream bed or an aquatic taxon with a dormant stage. Ostracods are aquatic and many species have a dormant egg stage which can persist in dry sediments for as long as 20 years (Pennak 1989). The ostracods I collected from rewetted sediments could either represent emergence from dormancy following rewetting or dead individuals that were washed down from upstream perennial pools during the last flow period and were well-preserved in dry stream sediments. The one *Hydraena* beetle collected was in such poor condition that it was likely dead long before sediments were rewetted. Since so few invertebrates were recovered from the rewetting experiment, it was impossible to determine whether water temperature affects emergence from dormant stages for these taxa.

None of the taxa identified from rewetted sediments were collected from the same reach when flow resumed twelve weeks after the dry sediments were collected. Benthic samples collected from the reach eight weeks after flow resumed (and twenty weeks after dry sediments were collected) supported 19 invertebrate taxa, including 10 intermittent exclusive taxa which were not found in remnant perennial pools at West Stronghold between 2004 and 2011 (Table A1.1). These 10 taxa are assumed or known to have a dormant stage to survive drought (see Chapter 4), but I was unable to find evidence of these dormant stages in the 15 L of dry near-surface (depth: 10-30 cm) sediments collected before flow resumes.

The failure to find dormant invertebrates in rewetted dry sediments could be due to, among other reasons, not enough sediment being collected or resting stages occurring at greater depths in the streambed (i.e., >30 cm). The density of invertebrates in the intermittent study reach following natural rewetting, though, was over 5200 invertebrates per m^2 (Bogan, unpublished data); thus it seems likely that at least a few individuals would have emerged from the 15 L of excavated sediments. By preferentially occupying deeper sediments (>30 cm depth), though, dormant individuals would likely experience less mortality from scouring flash floods. Winter flows only occurred in the intermittent study reach three times between 2004 and 2012, but summer monsoon flash can disturb the channel surface yearly. Despite this yearly disturbance, intermittent riffle specialist communities changed little among the wet winters of 2004, 2005, and 2010 (see Chapter 4). This finding suggests that the invertebrate specialist species that dominate these intermittent communities (Table A3.1) must not be strongly impacted by yearly monsoon flooding. Further research is needed to determine if the dormant stages of these species do indeed occupy deeper sediments in the dry stream bed (i.e., >30 cm), waiting out the years and the flash floods for winter flow to return.

Table A3.1. Taxa collected from intermittent riffles at West Stronghold Canyon eight weeks after flow resumed on 25 January 2010, and twenty weeks after dry sediments from the same reach were collected for experimental rewetting. Taxa which are only known from intermittent riffles at West Stronghold (i.e., they are not found in remnant perennial pools there) are marked with an "X". None of these taxa were found in the dry sediments that were experimentally rewetted.

Order	Family	Genus / species	Intermittent exclusive?
Coleoptera	Dytiscidae	undetermined Hydroporinae larvae	
Diptera	Ceratpogonidae	*Bezzia*	
	Chironomidae	*Diamesa*	
		Chaetocladius piger group	X
		Eukiefferiella rectangularis group	X
		Hydrobaenus	X
		Krenosmittia	X
		Parametriocnemus	
	Ephydridae	unknown species	X
	Muscidae	unknown species	X
	Simuliidae	*Prosimulum*	X
		Simulium	X
	Tipulidae	*Tipula*	X
Plecoptera	Capniidae	*Mesocapnia arizonensis*	X
Megaloptera	Corydalidae	*Neohermes filicornis*	
Trichoptera	Helicopsychidae	*Helicopsyche*	
non-insect	Oligochaeta	undetermined Oligochatea	
non-insect	Physidae	*Physa*	
non-insect	Hygrobatidae	*Atractides*	