AN ABSTRACT OF THE DISSERTATION OF

Kate S. Boersma for the degree of Doctor of Philosophy in Zoology presented on October 10th, 2013.

Title: Aquatic community responses to drought disturbance: Experimental manipulations of top predator extinctions and stream drying

Abstract approved:

David A. Lytle

Although it is generally assumed that the intensifying abiotic environment is the primary effect of drought on aquatic organisms, drought-induced top predator extinctions may be an important underlying mechanism. I used manipulative experiments to disentangle the impacts of drying and top predator extinctions on arid-land aquatic invertebrate communities. I then created a general conceptual framework that specifies how biotic and abiotic disturbances affect the composition of biological traits of species in a community (functional trait composition) and tested the framework with data from the manipulative experiments and a field study. Finally, I proposed a new metric to calculate the difference in functional trait composition between undisturbed and disturbed communities (called "functional distance") and used it to understand trait turnover between undisturbed and disturbed arid-land stream communities.

In Chapter 2, I describe two manipulative experiments in which I removed an invertebrate top predator from mesocosms containing arid-land stream invertebrates and recorded changes in the aquatic community. I found that top predator removal

consistently decreased the abundance of detritivores and increased the abundance of mesopredators, even under different background environmental conditions.

Chapter 3 describes a second mesocosm study in which I manipulated drying severity and measured aquatic community responses. My severe drying treatment allowed mesocosms to desiccate to a depth of ~1cm, yet I still I found that taxonomic and functional trait composition did not vary between treatments. The only discernable effect of drying was a decrease in abundance and increase in density of invertebrates. This result suggests that arid-land aquatic communities are highly resistant to drying disturbance that falls within the range of natural seasonal and interannual droughts but not resistant to the novel disturbance of top predator extinctions.

In Chapter 4 I describe a conceptual framework that uses functional trait diversity to understand the mechanisms behind community responses to disturbances. I applied the framework to datasets from Chapters 2 and 3 and an observational field study during severe drought. While the biotic disturbance of top predator removal did not affect species diversity in the taxonomic analysis, it increased the overall functional trait diversity and favored trait combinations associated with aerial dispersal and predatory feeding modes. Interestingly, although natural stream drying occurred concurrently with the local extinction of the invertebrate top predator in the field, this extreme abiotic disturbance was associated with a *reduction* in functional trait diversity. The contradictory effects of these two novel disturbance types highlight the importance of colonization and spatial context in the resilience of arid-land aquatic communities to future disturbances; differences between disturbed and undisturbed communities in both top predator removal and catastrophic stream drying studies were associated with aerially dispersing invertebrates. My work suggests that combining taxonomic and functional trait analyses in a rigorous hypothesis-testing framework can reveal hidden mechanisms behind the effects of drought on aquatic communities. Ultimately, I hope that this framework can be applied to other disturbed systems to better understand the effects of human actions on ecological communities.

Aquatic community responses to drought disturbance: Experimental manipulations of top predator extinctions and stream drying

by
Kate S. Boersma

A DISSERTATION

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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.

Kate S. Boersma, Author

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Dr. Michael T. Bogan contributed to the design, execution, analysis and writing of Chapters 2 and 3, and he contributed data and ongoing advice to Chapter 4. Brian A. Henrichs provided valuable assistance in the field for Chapters 2 and 3. Laura E. Dee worked with K.S.B. to develop the theoretical framework in Chapter 4. Steve Miller provided necessary quantitative and programming skills that contributed to Chapters 3 and 4.

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DEDICATION

This dissertation is dedicated to the natural historians, whose observational skills and eloquent voices remind me why I do what I do. May there always be passionate people to see the beauty in the world and inquisitive minds to ask why.

Aquatic community responses to drought disturbance: Experimental manipulations of top predator extinctions and stream drying

1 – General Introduction

Climate variability is increasing (Beniston et al. 2007, IPCC 2012), generating higher frequency and magnitude of droughts. Aquatic ecosystems are particularly vulnerable to changing drought regimes, and growing human demands on hydrologic resources further intensify extreme conditions. In some regions, the frequency and intensity of droughts has already increased (Balling and Goodrich 2010, Hoerling et al. 2011), especially during the last decade (Lehner et al. 2006).

Extreme events like severe drought are difficult to study in natural systems because they are, by definition, rare and unpredictable. Existing research on droughts in aquatic habitats is largely opportunistic and thus unable to disentangle the interacting factors that drive biological responses to drought (Boulton 2003, James et al. 2008). Manipulative experiments are necessary to develop a mechanistic understanding of drought effects on aquatic systems (Jentsch et al. 2007, Beier et al. 2012, Thompson et al. 2013), and studies are beginning to emerge that address the direct effects of individual abiotic drivers such as temperature and precipitation on biological processes in aquatic systems (e.g. Kratina et al. 2012).

However, drought is a complex phenomenon that involves more than direct abiotic effects. Research in terrestrial systems suggests that indirect biotic factors can mediate ecological responses to climate change (Gilman et al. 2010). Examples include insect-host interactions that mediate how insect species distributions respond to climate (Araújo and Luoto 2007) and climate-induced phenological shifts that affect plant-pollinator interactions (Memmott et al. 2007). Aquatic ecologists must embrace a more holistic view of environmental change that examines both direct and indirect mediators in order to understand the mechanistic relationships between climate and aquatic communities.

Drought-induced extinction of aquatic top predators is an increasingly common occurrence and warrants both concern and attention from the scientific community. Aquatic predators are disproportionately vulnerable to changing hydrology (Ledger et al. 2013). The number of aquatic predator extinctions is rising (Petchey et al. 2004, Bogan and Lytle 2011). The elimination of top predators can restructure food webs and lead to catastrophic changes in ecosystem functioning (Paine 1966, Menge 1976, Thebault et al. 2007) and therefore predator extinctions must be considered as a possible factor mediating the effects of climate change on aquatic ecosystems. Given predicted increases in drought frequency and severity, it is important to understand how aquatic biodiversity responds directly to drying processes and indirectly to drought-induced top predator extinctions.

Arid-land streams of the American Southwest make an ideal system to study the effects of drought on aquatic communities. Drought severity is increasing rapidly in arid regions (Beniston et al. 2007, Seager et al. 2007, Barnett et al. 2008, Cayan et al. 2010), and water scarcity has been associated with local extinctions of the invertebrate top predator *Abedus herberti* (Hemiptera: Belostomatidae) over the past ten years (Bogan and Lytle 2011, Bogan 2012). This aquatic insect is flightless and requires water for all phases of its life cycle, making it highly vulnerable to hydrologic changes (Finn et al. 2007). Future extinctions are expected as the region becomes more arid. Aquatic invertebrates inhabiting fragmented streams, including *A. herberti*, offer the opportunity to examine the effects of drought on ecological communities at a small and experimentally tractable scale. Growing human populations in arid regions and the subsequent demands on hydrologic resources make drought research in arid-land aquatic systems a relevant and timely ecological issue (Deacon et al. 2007, Gleick 2010, MacDonald 2010).

In this dissertation I used arid-land stream aquatic macroinvertebrates as a study system to examine the effects of drought on aquatic communities. I conducted manipulative experiments to disentangle the indirect biotic effects of drought-induced top predator extinctions (Chapter 2) from the direct abiotic effects of drying (Chapter 3) on aquatic communities. I then created a conceptual framework to predict the impacts of disturbance on community structure and used it to link drought disturbance mechanisms to aquatic invertebrate functional traits (Chapter 4).

In Chapter 2 I tested classic ecological predictions of the effects of top predator extinctions using aquatic mesocosms to replicate fragmented stream communities. Despite increasing clarity regarding the roles predators play in determining community structure and function, little is know about the consistency of these patterns against a backdrop of high variability in local environmental conditions. Arid-land streams are characterized by their high interannual and seasonal environmental variability, and I took advantage of these extremes to test the consistency of top predator effects in two years with very different background environmental conditions. I inoculated mesocosms with aquatic invertebrates, removed the top predator from half of the mesocosms as a treatment, and sampled the aquatic community at the end of the summer dry season. I repeated the experiment in two consecutive years, which represented two very different biotic and abiotic environments.

I found that many classic ecological predictions of the consequences of top predator loss were consistent between years, especially for large taxa. Top predator removal decreased the abundance of large detritivores, increased the abundance of mesopredators, and generated different colonization patterns between treatments in both years. In one of the foundational studies that inspired my research, Bogan and Lytle (2011) sampled aquatic invertebrates in an arid-land stream for 3 years before and 4 years after a severe drying event and observed dramatic community changes that included the local extinctions of top predator *A. herberti* and dominant detritivore *Phylloicus mexicanus* and a greatly increased abundance of mesopredators. The results of my manipulative experiment suggest that top predator extinctions may mediate the effects of drought on aquatic communities and be partially responsible for the changes observed in natural streams.

While my second chapter documents the potential role of biotic factors in propagating the effects of drought on aquatic communities, my third chapter explored the direct abiotic impacts of drying. It seems intuitive that drying would negatively impact aquatic communities; however, the invertebrates inhabiting fragmented arid-land streams during the summer months are adapted to their harsh abiotic environment and thus may be resistant to gradual stream drying. I manipulated drying severity in aquatic mesocosms and sampled the invertebrate community at the end of the summer dry season. I observed no differences in taxonomic or functional community structure among drying treatments, even though the most severe treatment allowed mesocosms to dry to a depth of ~1cm of water. This suggests that dry-season aquatic invertebrate communities in this region are highly resistant to pool drying, so long as some aquatic refuges remain.

In my fourth chapter I created a conceptual framework that uses animals' functional traits to understand the effects of disturbance on fragmented communities and applied it to three studies in arid-land streams: Chapter 2, Chapter 3, and the observational drought field study mentioned above (Bogan and Lytle 2011). In this framework, researchers form explicit ecologically-informed hypotheses, select functional diversity metrics to test the hypotheses, and apply them to understand mechanisms behind community responses to disturbance. While the framework is intuitive, to date functional diversity is rarely applied in a hypothesis-testing context. Additionally, I described a new approach to calculate differences between disturbed and undisturbed communities' mean trait values that accounts for the non-independence of pairwise distances. When applied to arid-land streams, I revealed mechanisms behind aquatic community responses to disturbance that were not apparent from taxonomic analyses alone. I hope that this dissertation advances our understanding of community dynamics in fragmented aquatic habitats and inspires further research on imperiled arid-land stream fauna.

2 – Top predator removals have consistent effects on large species despite high environmental variability

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Oikos
In revision

ABSTRACT

Top predator losses affect a wide array of ecological processes, and there is growing evidence that top predators are disproportionately vulnerable to environmental changes. Despite increasing recognition of the fundamental role that top predators play in structuring communities and ecosystems, it remains challenging to predict the consequences of predator extinctions in highly variable environments. Both biotic and abiotic drivers determine community structure, and manipulative experiments are necessary to disentangle the effects of predator loss from other co-occurring environmental changes. To explore the consistency of top predator effects in ecological communities that experience high local environmental variability, we experimentally removed top predators from arid-land stream pool mesocosms in southeastern Arizona, USA, and measured natural background environmental conditions. We inoculated mesocosms with aquatic invertebrates from local streams, removed the top predator *Abedus herberti* (Hemiptera: Belostomatidae) from half of the mesocosms as a treatment, and measured community divergence at the end of the summer dry season. We repeated the experiment in two consecutive years, which represented two very different biotic and abiotic environments. We found that some of the effects of top predator removal were consistent despite significant differences in environmental conditions, community composition, and colonist sources between years. As in other studies, top predator removal did not affect overall species richness or abundance in either year, and we observed inconsistent effects on community and

trophic structure. However, top predator removal consistently affected large-bodied species (those in the top 1% of the community body size distribution) in both years, increasing the abundance of mesopredators and decreasing the abundance of detritivores, even though the identity of these species varied between years. Our findings highlight the vulnerability of large taxa to top predator extirpations and suggest that the consistency of observed ecological patterns may be as important as their magnitude.

2.1 Introduction

The importance of top predators in structuring ecological communities is widely appreciated (Terborgh et al. 2001, Duffy 2003, Estes et al. 2011). Their importance, however, does not make them immune to environmental perturbations; there is growing evidence that organisms at higher trophic levels are disproportionately vulnerable to disturbance (e.g., Ledger et al. 2013). The combined influences of anthropogenic stressors such as habitat degradation and climate change have negatively impacted top predator populations worldwide (Duffy 2003). Thanks to a rich history of field observations and predator manipulation experiments, we can identify many pathways by which top predator extinctions may impact fundamental community processes such as food web dynamics (Hairston et al. 1960, Thebault et al. 2007) and community assembly (Chase et al. 2009, Vonesh et al. 2009, Wesner et al. 2012). Most top predators are large-bodied relative to the rest of the food web and have correspondingly high resource requirements (Woodward and Hildrew 2002). Small reductions in top predator abundance can, trigger secondary extinctions and modify biotic interactions at lower trophic levels (Borrvall and Ebenman 2006, Säterberg et al. 2013). Reductions in top predator populations are frequently associated with increases in the diversity and abundance of secondary predators (Soulé et al. 1988). This “mesopredator release” has been documented in terrestrial, freshwater, and marine ecosystems (e.g., Baum and Worm 2009, Elmhagen et al. 2010, Ritchie et al. 2012) and is a likely mechanism by which top predator extinctions generate trophic cascades (Prugh et al. 2009).

While the role of predators in community structure and food web dynamics is well-studied, little is known about the consistency of these patterns against a backdrop of high variability in local environmental conditions. It is widely accepted that community structure is determined by a combination of biotic and abiotic factors (Menge and Sutherland 1987, Wellborn et al. 1996). Manipulative experiments have demonstrated that both top predators and environmental extremes can effectively “filter” species from the regional species pool into a smaller subset that can survive local conditions (Chase 2007, Chase et al. 2009), thus modifying trophic dynamics (Greig et al. 2012, Ledger et al. 2013). Due to these concurrent biotic and abiotic influences, the effects of top predator extirpations are difficult to predict and become even more obscure when local environments oscillate between environmental extremes. Predation is generally assumed to exert a stronger influence on ecological communities in benign environments than in extreme environments (Peckarsky 1983, Callaway et al. 2002), and the effects of an extreme abiotic environment may obscure patterns generated by top predator extinctions (Wellborn et al. 1996).

Given predictions of increasing environmental variability (Christensen et al. 2007) and anthropogenically-induced predator extinctions (Duffy 2003) in the near future, it is imperative that we understand the effects of top predator extinctions on ecological communities across a range of environmental conditions. Studies examining the relationship between top down effects and environmental conditions demonstrate little consistency in the sign and strength of community responses to predator loss (Borer et al. 2005, Kurle and Cardinale 2011). Ecosystems that exhibit high seasonal and interannual environmental variability can be useful models for examining the consistency of the effects of top predator extirpations, because the regional species pool may remain relatively constant while background conditions naturally vary at a single location.

Arid-land streams are ideal systems to examine the ecological consequences of top predator loss under variable environmental conditions because they occur in regions with naturally high environmental variability (Grimm et al. 1997) and are currently experiencing top predator extinctions due to extreme climatic events (Bogan and Lytle 2011). Climate variability is predicted to increase in North America over the next century, including the frequency, severity and duration of extreme weather events (Christensen et al. 2007). In particular, there is wide consensus among climate change models that drought severity and duration will increase in the southwestern United States (Seager et al. 2007, Balling and Goodrich 2010). These changing drought patterns will intensify the fragmentation of aquatic habitats and degradation of abiotic conditions (e.g., increased water temperature, decreased dissolved oxygen levels) that already occur in these streams on a seasonal basis (Boulton 2003, Bogan and Lytle 2007).

The top predator in most arid-land headwater streams in the southwestern United States is *Abedus herberti* (Hemiptera: Belostomatidae), a large, flightless aquatic insect that is well-adapted to seasonal habitat fragmentation and extreme environmental conditions but cannot survive complete stream drying and has limited dispersal capacity. As a result, *A. herberti* is vulnerable to climate-induced extinction, and local extinctions have recently been recorded in two southeastern Arizona streams, along with widespread changes to local aquatic communities (Bogan and Lytle 2011). To explore the consistency of the effects of top predator extinctions on arid-land stream communities, we experimentally manipulated *A. herberti* presence/absence in replicate mesocosm communities in two years with very different background environmental conditions. Both manipulations were conducted during the harsh dry season, however the two years represented two environmental extremes as reflected by differences in stream flow, canopy cover, and the composition of the aquatic community. We used these manipulative experiments to test the classic ecological hypotheses that top predator extinctions (1) generate cascading effects on lower trophic levels and (2) increase the richness and abundance of mesopredators (mesopredator release). We predicted that these patterns would be consistent despite strong environmental differences between the two years.

2.2 METHODS

Study area and species

Our study was conducted in the Chiricahua Mountains of southeastern Arizona, USA, during the dry seasons (May-July) of 2010 and 2011. During these months, streams naturally fragment to a series of small bedrock pools, often separated from one other by dry reaches, and abiotic conditions intensify. The food web in these fragmented pools is numerically dominated by a diverse collection of beetle, dragonfly, damselfly, dobsonfly, and true bug predators, and cannibalism rates are high (Bogan and Lytle 2007). A less diverse group of grazing caddisflies and mayflies make up the herbivore community, and the detritivore class is mostly comprised of small fly larvae, with a few large-bodied taxa consuming leaf litter and other coarse particulate organic matter (Bogan and Lytle 2007). The top predator in these pools, *A. herberti*, is a flightless, long-lived (up to 3y), and large (~3cm length) true bug that can reach densities of up to 50 ind/m^2 in stream pools. Raptorial forelimbs and piercing mouthparts make *A. herberti* a voracious top predator, capable of consuming both invertebrates and vertebrates (Velasco and Millan 1998a; Appendix A, Figure A.1). Recent studies suggest *A. herberti* in adjacent streams are genetically segregated, exhibiting high site fidelity and severe dispersal limitation (Finn et al. 2007, Phillipsen and Lytle 2012).

Mesocosm experiments

We conducted predator manipulation mesocosm experiments in 2010 and 2011 at the American Museum of Natural History's Southwestern Research Station in Portal, AZ, USA. We used 60L plastic tanks (hereafter referred to as "mesocosms") to experimentally replicate fragmented bedrock stream pools. We fitted each mesocosm with aluminum flashing to prevent the escape of *A. herberti* and added two cinder blocks per mesocosm to provide aquatic invertebrates with a perch and site for emergence. Mesocosms were filled with well water and arranged in a grid, 25cm apart (Appendix A, Figure A.2), approximately 100m from Cave Creek.

One week prior to the beginning of the experiment in each year, we sampled aquatic invertebrates from Cave Creek, East Turkey Creek, and North Fork Cave Creek using a 500 μm mesh D-frame net, taking care to sample representative microhabitats (see Bogan and Lytle 2007 for full sampling description) and collect sediment and detritus in each stream. We combined these samples in a 200L tank to create a diverse inoculum with which to seed the mesocosm communities. In 2010, the inoculum was distributed across 19 containers – 16 were added to the mesocosms and 3 were preserved in 70% ethanol as initial samples. In 2011, the inoculum was distributed across 24 containers – 20 added to mesocosms and 4 initial samples. After a one-week acclimation period, we randomly applied control and *A. herberti* removal treatments to half of the mesocosms in each year, yielding eight mesocosms per treatment group in 2010 and ten in 2011. *A. herberti* were removed by hand with small aquarium nets, as they are large and easily targeted. We ensured the effectiveness of our removals by repeating the removal procedure on three consecutive days, although all *A. herberti* were successfully removed with the first attempt. Control mesocosms were standardized to contain 12 adult *A. herberti* each, which mimicked the typical dry season in-stream densities (K.S.B. unpublished). The experiments were conducted for the duration of the summer dry season (from stream fragmentation to first monsoon storm), June 1 - July 14, 2010 (6wks) and June 6 – July 8, 2011 (4wks). The start of the 2011 experiment was delayed due to a large wildfire in the Chiricahua Mountains, but results from this study and a previous mesocosm study in the same location (Bogan and Boersma 2012) suggest that 4 weeks was a sufficient duration to allow dry season community composition to stabilize. At the conclusion of each experiment, the contents of each mesocosm were preserved in 70% ethanol and identified to the lowest practical taxonomic level given available keys (e.g. Merritt et al. 2008). We measured temperature, dissolved oxygen, and pH for each mesocosm at the end of each experiment.

Environmental conditions

The winter seasons preceding each experiment created very different background stream conditions in 2010 and 2011. In 2010, total Jan-Apr precipitation at the Southwestern Research Station was 114.9mm (29.4%) above the long-term (1990-

2011) Jan-Apr mean, while in 2011 precipitation was 54.4mm (38.7%) below the mean (long-term mean = 88.8 ± 66.3mm; Figure 2.1). As a result, the source streams had over 10 times greater stream flow in 2010 than in 2011 (e.g. East Turkey Creek: June 2010 = 11L/s, June 2011 <1L/s). Despite the dramatic difference in winter precipitation preceding the two experiments and subsequent changes to stream drying trajectories, mean daily rainfall during the experiments did not differ between years (Total precipitation: 2010 = 0.58mm, 2011 = 1.14mm; Welch's t-test, $t = -0.825$, $df = 38.356$, $p = 0.415$).

All mesocosms were covered by 60-100% canopy, although the nature of this canopy differed between years. In 2010 mesocosms were located under a natural oak canopy, while in 2011 we constructed artificial shade structures to standardize the canopy across all mesocosms. The artificial canopy consisted of 12*0.9m strips of opaque shade cloth suspended 1m above each row of mesocosms. Each strip was separated by 0.3m to block direct sunlight but allow indirect light to reach the surface of the water. Shade cloths extended beyond the mesocosm array on all sides to ensure that both edge and interior mesocosms received approximately 85% canopy cover.

Analysis

<u>Univariate analyses</u>

We compared abiotic conditions (e.g., temperature, dissolved oxygen) between years or treatments using t-tests or their non-parametric equivalents. We compared species richness and abundance between treatments using a Hotelling's T^2 test to correct for the potential for Type 1 error associated with multiple tests. Variables were transformed prior to comparison when required to meet statistical assumptions. Appendix A, Table A.1 provides details on transformations and tests. We used generalized linear models (GLMs) with a Poisson distribution to compare mesopredator species richness between treatments and years because low richness values are Poisson-distributed (Bolker et al. 2009, Zuur et al. 2009), although in all cases GLM inferences were the same as those obtained from Welch's t-tests. Due to the strong environmental differences between years, we compared treatment effects within years only.

Multivariate analyses

We used multi-response permutation procedures (MRPP) to test for differences in community composition and nonmetric multidimensional scaling (NMDS) ordinations to visualize these differences (McCune and Grace 2002). Except where noted, we applied a Wisconsin transformation to the species matrices before ordinating, which first relativizes by species maxima (dividing the abundance of each species in a mesocosm by that species' total abundance across all mesocosms) and then applies a square root transformation to reduce the influence of highly abundant taxa (Legendre and Gallagher 2001). We present results from both two and three-dimensional ordinations, determined to be the best fit in each case based on stress values and convergence. Both MRPP and NMDS employed the Sørensen distance measure (Sørensen 1948). We used indicator species analysis (ISA; Dufrene and

Legendre 1997) to identify representative species for control and top predator removal treatments. Species were considered significant indicators if they had indicator values >60 and ISA permutation test $p < 0.05$.

Analyses of initial communities

To quantify initial community composition, we destructively sampled several mesocosms at the beginning of each experiment (2010: $n = 3$; 2011: $n = 4$). We used two-sample tests and GLMs to compare initial species richness between years and MRPP to compare initial community composition between years. Small sample sizes limited our power to detect differences between initial communities.

Analyses of colonization patterns

Colonization by aerially dispersing insects is an important driver of community structure in fragmented arid-land streams during the dry season (Bogan and Boersma 2012). One way to identify taxa that colonized mesocosms during the course of the experiment is to compare initial and final invertebrate communities within each year. However, this method cannot differentiate between colonizing taxa and those developing from egg masses present in the initial inoculations (i.e. selective oviposition vs. species sorting). We used information from a separate mesocosm study that restricted dispersal and colonization (Boersma et al. in press) and another that recorded colonization of un-inoculated mesocosms (Bogan and Boersma 2012) to create a list of likely colonists for use in this analysis. An additional challenge was that our small number of initial communities limited our ability to detect colonists to only abundant taxa. We defined colonist taxa as those that had abundances of 0 in initial samples and >10 in final samples, and have been observed as dry-season colonists in other studies (Bogan and Boersma 2012, Boersma et al. in press). Because of our low power to detect differences, we avoided the use of inferential statistics to compare colonists between years and instead examined the identity of colonist taxa. We used NMDS to visualize coarse differences in the composition of colonist taxa between years and treatments.

Effects of top predator removal

To test our hypothesis that top predator removal would generate cascading effects on lower trophic levels, we compared aquatic invertebrate community composition between control and removal treatments within each year using MRPP. We also examined the relationship between experimental treatment and trophic trait composition of mesocosm communities. We created a functional feeding group (FFG) matrix that placed each taxon in a trophic category based on a combination of diet and primary feeding mode (Merritt et al. 2008). FFGs are commonly used to describe aquatic insect trophic niches and facilitate comparisons of community composition among sites with different species (Hauer and Lamberti 1996). We multiplied the transposed FFG matrix (FFG categories * species) by each species matrix (species * mesocosms) to generate abundance-weighted trophic trait matrices (mesocosms * trophic trait prevalence). We used NMDS to visualize the effects of predator removals on community and trophic trait composition and ISA to determine which species or trophic traits were representative of the treatments.

To test our hypothesis that top predator removal would increase the diversity and abundance of mesopredators, we created a subset of the full species matrix that contained only medium- and large-bodied secondary predators ("mesopredators": all non-*A. herberti* predators >5mm length, a total of 17 taxa; Appendix A, Table A.2). We used this matrix to compare mesopredator richness and abundance between treatments and examine treatment differences in mesopredator assemblage composition using MRPP and NMDS.

To examine consistency in top predator removal effects between the two years, we first compared abiotic conditions, initial samples and colonization between years. Dramatic differences in year and background conditions led us to analyze treatment effects within each year separately; interannual comparisons of coarse patterns are presented alongside each year's results below. All statistical analyses were conducted in R (R Development Core Team 2011) with the perm (Fay and Shaw 2010), ICSNP (Nordhausen et al. 2012) and vegan (Oksanen et al. 2012) packages.

2.3 RESULTS

Mesocosm water quality

Mesocosm dissolved oxygen and pH at the conclusion of the experiments did not differ between treatments, but mean mesocosm water temperature was significantly higher in 2011 than in 2010 (two-sample permutation test, $p < 0.001$, Appendix A, Table A.3).

Initial inoculations

Mean species richness in the initial samples did not differ between years (Welch's t-test, $t = 1.315$, $df = 3.732$, $p = 0.264$). Taxonomic composition in these initial samples varied significantly between years (MRPP; $A=0.703$, $p = 0.030$), with twenty taxa unique to 2010 initial samples and nineteen taxa unique to 2011. The 2010 specialists were mostly cold-water, lotic taxa, while the 2011 specialists were warm-water, lentic taxa (Appendix A, Table A.4).

Colonization

We found 22 taxa with abundances >10 in our final samples that were absent from initial samples and determined to be likely colonists from previous studies (Bogan and Boersma 2012, Boersma et al. in press), suggesting that they colonized mesocosms during the course of the experiments. Of these, only 2 colonist taxa overlapped between 2010 and 2011. The 14 colonist taxa exclusive to 2010 were a diverse mix of larval dragonflies, mayflies, caddisflies and true flies, and small adult beetles, while the 6 colonists exclusive to 2011 included only adult beetle and true bug species (Appendix A, Table A.5). Mesopredators (Appendix A, Table A.2) comprised 41% of the colonizing taxa (as compared to 25% of the overall taxonomic pool) and the identities of these mesopredators also differed between years. The three mesopredator colonists unique to 2010 were soft-bodied dobsonfly and dragonfly predator-engulfers, while the four unique to 2011 were all hard-bodied adult beetle and true bug predator-piercers (Appendix A, Table A.2). Despite the small initial sample sizes, MRPP and ordinations confirm that there was little overlap in colonist community composition between years (MRPP: A = 0.113, p = 0.001; NMDS: k = 3 axes, R^2 = 0.872, Stress = 0.134, p =0.039; Figure 2.2A).

Final community samples

We identified 91 invertebrate taxa overall, including initial samples: 74 in 2010 and 57 in 2011. We identified a total of 64 taxa in the final samples taken at the end of the experiments (53 in 2010 and 39 in 2011). On average, final mesocosm samples in 2011 contained fewer species (mean richness: 2010 = 20.84, 2011 = 13.21; Welch's t-test, t = 10.203, df = 26.924, p < 0.001) than mesocosms in 2010. Final mesocosm community composition also differed between years (MRPP: A = 0.181, p = 0.001; NMDS: R^2 = 0.837, Stress = 0.183, p = 0.020; Figure 2.2B). The significant differences between 2010 and 2011 led us to conduct the analyses of top predator removal effects on each year separately.

Due to our small number of initial samples, we consider our estimates of species loss through time to be conservative. Overall species richness did not significantly differ between initial and final samples in 2010 (Initial = 24.33, Final = 20.125; Welch's t-test, t = -2.205, df = 2.999, p = 0.115; Appendix A, Figure A.3), nor did the species richness of mesopredators (Initial = 1.33, Final = 2.19; GLM Poisson: z = -0.938, p = 0.348). In contrast, in 2011 we observed significant declines in species richness (Initial = 21.5, Final = 11.55; Welch's t-test, $t = -8.973$, $df = 4.418$, $p < 0.001$; Appendix A, Figure A.3) and mesopredator species richness (Initial = 3.5, Final = 1; GLM Poisson, $z = 3.595$, $p < 0.001$) between initial and final samples, despite the small number of initial samples. Species that disappeared during the course of the experiments in both years were mostly cold-water, lotic taxa including black flies, stoneflies, mayflies, and caddisflies, however we did not record emergence/consumption so cannot speculate on the mechanism behind their disappearance.

Hypothesis 1: Top predator removal generates cascading effects on lower trophic levels

We found no effect of top predator removal on the univariate metrics of species richness and abundance in either year (Table 2.1). In 2010 there were no significant differences between control and removal treatments in the composite richness/abundance variable (Hotelling's T^2, $T^2 = 0.9255$, df 1 = 2, df 2 = 13, p-value = 0.421). Similarly, there were no significant differences between treatments in 2011 (Hotelling's T^2, $T^2 = 0.366$, df 1 = 2, df 2 = 17, p-value = 0.699).

Despite the lack of a pattern in richness and abundance, top predator removal affected invertebrate community composition, especially for large taxa. Top predator removal caused a statistically significant difference in overall community composition in 2010 (MRPP: A = 0.063, p = 0.020; NMDS: k = 3, Stress = 0.13, p = 0.020, R^2 = 0.835; Figure 2.3A) but clustering was only marginally significant in 2011 (MRPP: A = 0.038, p = 0.060; NMDS: k = 3, Stress = 0.148, p = 0.020, R^2 = 0.775; Figure 2.3B).

The large (>10mm) detritivore shredder caddisfly *Phylloicus mexicanus* was an indicator species for the control treatment in both years (2010: I.V. = 73, p = 0.037; 2011: I.V. = 73, p = 0.029), and in 2010 the control treatment was also represented by another shredder *Helichus triangularis* (I.V. = 75, p = 0.043). Two taxa were indicators of the top predator removal treatment in 2010: the large herbivorous collector-gatherer mayfly *Callibaetis* (I.V. = 77, p = 0.017) and predaceous diving beetle *Rhantus atricolor* (I.V. = 63, p = 0.026). There were no significant indicators of the removal treatment in 2011 (Appendix A, Table A.6). All of these indicator taxa were larger than 5mm, suggesting a potential selective impact of top predator removal on large taxa. Interestingly, all of the 16 insect taxa exclusive to the predator removal treatment were also >5mm, with the exception of two species of flies (Appendix A, Table A.4).

Top predator removal caused communities to significantly differ in their trophic trait composition in 2010 (MRPP: A = 0.131, p = 0.005; NMDS: k = 3, Stress = 0.060, p = 0.020, R^2 = 0.972; Figure 2.3C) but not in 2011 (MRPP: A: 0.025, p = 0.104; NMDS, k = 3, Stress = 0.089, p = 0.020, R^2 = 0.939; Figure 2.3D). ISA of trophic traits revealed that shredders were associated with the control treatment in both 2010 and 2011 (Appendix A, Table A.6). Collector-gatherers, including many of the soft-bodied prey species like mayflies, were associated with top predator removal in 2010 (I.V. = 76.4, p = 0.009), and predators with piercing mouthparts were associated with top predator removal in 2011 (I.V. = 70.5, p = 0.010).

Hypothesis 2: Top predator removal increases the richness and abundance of mesopredators

Top predator removal increased mesopredator abundance in 2010 (Welch's t-test, t = -2.887, df = 13.763, p = 0.012) and 2011 (Welch's t-test, t = -2.231, df = 17.686, p = 0.039; Figure 2.4B). In 2010, top predator removal increased mesopredator richness (GLM Poisson: z = 2.743, p = 0.006), but in 2011 there was not a statistically significantly difference in treatment means (GLM Poisson: z = 1.736, p = 0.082; Figure 2.4A). Mesopredator colonization of the removal treatment mesocosms in 2010 may explain the significant increase in mesopredator richness in that treatment (Figure 2.4A).

Notably, the largest mesopredators (diving beetles and dobsonflies ≥10mm in length) were only found in the removal treatments in both years. In 2010, these were diving beetles *Dytiscus*, *Rhantus atricolor* and *R. gutticollis gutticollis,* and dobsonfly *Neohermes*, while in 2011 these were diving beetles *R. atricolor* and *Dytiscus*, and the dobsonfly *Corydalus*. Two large dragonfly taxa were also present only in top predator removal mesocosms (Appendix A, Table A.4). These species-specific responses to predator removal between years contributed to significant differences in overall mesopredator assemblage composition between years (MRPP: A = 0.044, p = 0.001). Of the 17 mesopredator species identified, only six species were present in both years while the remaining 11 mesopredator species were unique to one year or the other (Appendix A, Table A.2).

2.4 DISCUSSION

We measured the effects of top predator removal on aquatic community structure in two years with very different background environmental conditions. We found consistent top down effects of top predator loss in both years, especially for large taxa. Top predator removal decreased the abundance of large detritivores, increased the abundance of mesopredators, and generated different colonization patterns between treatments in both years. Trophic cascades vary in strength across studies, scales, and ecosystems (Borer et al. 2005), and the top-down effects of predators on ecological communities are highly context dependent (Pace et al. 1999, Holt 2000, Chase et al. 2010, Kurle and Cardinale 2011, Coll and Hargadon 2012). Our results suggest that the effects of top predator extinctions on communities may remain consistent despite significant environmentally-driven variability community composition, and that body size may be an important determinant of the strength of top-down effects on communities.

H1: Top predator removal generates cascading effects on lower trophic levels

We found consistent effects of top predator removals on large taxa in both years, even though the treatment effect on overall community composition was not consistently strong between years. Body size correlates with many important physiological, behavioral, and life history traits (Woodward et al. 2005) and is known to influence the vulnerability of organisms to disturbances and the stability of food webs (Emmerson and Raffaelli 2004). Large-bodied species exert powerful influences on ecosystem processes in streams (Lecerf and Richardson 2011), and droughts and warming have been documented to disproportionately impact large taxa in aquatic systems (Daufresne et al. 2009, Woodward et al. 2012). Thus it is notable that an effect of top predator removal on large taxa was consistently strong in this arid-land aquatic system in both years despite high environmental variability. In our mesocosms, 99.2% of the individuals were less than 9mm total body length, yet the indicator species and all of the 16 insect taxa exclusive to the predator removal treatment were >5mm, with the exception of two species of flies (Appendix A, Table A.4). Two detritivores were indicators of the control treatment, and two mesopredators and one herbivore were indicators of the removal treatment; all species >5mm.

While the two treatments contained different large species, they did not differ in overall species richness or abundance in either year. Researchers have documented both homogenizing and diversifying effects of top predator removal on community structure, depending on the context and the system (Paine 1966, Creed 2006, Chase et al. 2009, Sieben et al. 2011). Our finding of no top predator effect on overall diversity is consistent with observations from nearby fragmented streams with similar community composition. In a study examining the effects of stream drying on aquatic invertebrate community structure, Bogan and Lytle (2011) sampled before and after the local extinction of *A. herberti* and found no change in species richness, although they did observe shifts in community composition similar to those seen in our manipulative experiments: they recorded an increase in the abundance of mesopredators and the disappearance of the detritivore caddisfly *P. mexicanus* (Bogan and Lytle 2011).

One of the consistent effects of top predator removal was a reduction in the abundance of large-bodied detritivores (>10mm). Removal of *A. herberti* caused significant decreases in the abundance of the caddisfly *P. mexicanus* and the long-toed water beetle *H. triangularis*, two important consumers of coarse particulate organic matter (Merritt et al. 2008). Similar cascading effects of top predator loss on detritivores have been observed in other systems (Ruetz et al. 2002, Wu et al. 2011); these "apparent trophic cascades" are still relatively understudied despite their importance for food webs (Moore et al. 2004). Reduced abundances of large detritivores may slow decomposition rates and limit the conversion of coarse particulate organic matter into fine particulate organic matter for consumption by lower trophic levels (Ruetz et al. 2002) and ultimately affect food web stability (Moore et al. 2004).

H2: Top predator removal increases the richness and abundance of mesopredators

Mesopredators were more abundant in removal treatments than control treatments in both years, lending support to the hypothesis of mesopredator release (an increase in the density or abundance of secondary predators caused by the removal of apex predators; Prugh et al. 2009, Ritchie and Johnson 2009). Theoretically, mesopredators could fill a trophic niche left vacant by generalist top predators and dampen the effects of top predator removal, however this is rarely seen in natural systems (Chalcraft and Resetarits 2003, Prugh et al. 2009). We observed effects of top predator removal on community structure despite mesopredator release, suggesting that mesopredators and top predators are not functionally equivalent in our system.

Mesopredator abundance reflects only one aspect of mesopredator influence on communities (Byrnes and Stachowicz 2009). Research suggests that predator identity, feeding behavior and assemblage composition may be more important determinants of how predator impact will be transferred through food webs than abundance alone (Schmitz and Suttle 2001, Chalcraft and Resetarits 2003). The significant differences between treatments we observed in the mesopredator community suggest that taxon-specific mesopredator responses to top predator removal may also be important components of the overall community responses. Top predator removal increased the abundance of large, active hunting predators (diving beetles and dobsonflies) in both years, although we only detected increases in numbers of sit-and-wait predators (dragonflies, damselflies, and true bugs) in the 2010 removal treatment. The distinct feeding behaviors of these two groups suggest that they may affect community and trophic structure differently (Schmitz and Suttle 2001). Most large diving beetles and dobsonflies are mobile predators that can hunt in pelagic or benthic habitats and consume both live and dead prey, while dragonflies and damselflies are sit-and-wait predators that capture live prey (Turner and Chislock 2007). The palatability of these two colonist groups to *A. herberti* also differed. In a series of feeding trials, we observed *A. herberti* feeding on the softer-bodied dragonflies in >50% of trials but never feeding on the harder-bodied diving beetles (n = 24 feeding trials; Boersma unpublished). These highly edible dragonflies were the primary mesopredator colonists of top predator removal mesocosms in 2010 but were nearly absent in 2011. Other studies have demonstrated that predator feeding behavior determines how predator impacts are transmitted through food webs (e.g., Klecka and Boukal 2013). The importance of mesopredator identity in our study suggests that feeding mode may in part determine the strength of trophic cascades and explain the weaker overall community divergence observed in 2011 when compared with 2010. The piercing-and-sucking feeding mode of the top predator may also be an important factor in the strength of top-down effects. This feeding mode allows *A. herberti* to consume prey that are larger than itself and releases it from gape size limitations typical of many predatory species. Similar effects of feeding behavior on trophic cascade strength have been observed in terrestrial and marine systems as well (Schmitz et al. 2004, Bruno and O'Connor 2005).

Mesopredator release and predator feeding behavior are also likely mechanisms behind the reduced abundance of large detritivores in our top predator removal mesocosms. The detritivorous caddisfly *P. mexicanus* is a long-lived univoltine species with a reproductive cycle much longer than the duration of our experiments (Wiggins 1977). Therefore, the treatment differences we observed were due to loss of individuals from the top predator removal mesocosms (via emergence or predation) and not to gain of individuals (via colonization or reproduction) in the control mesocosms. Nislow and Molles (1993) demonstrated that larval caddisflies with cases made of organic matter are regularly consumed by large dragonfly nymphs. Presence of the top predator *A. herberti* may have inhibited dragonfly colonization in our control mesocosms and released *P. mexicanus* from predation. Therefore, local direct and indirect relationships between top predators, mesopredators and detritivores may determine the sign of the effect of top predator removal on detritivores (Wu et al. 2011).

Aquatic invertebrate dispersal abilities vary greatly among arid-land stream species (Bogan and Boersma 2012), and it is likely that this variability also contributed to the differences in mesocosm colonization between years. Mean canopy cover was similar in both years, but the artificial canopy used in 2011 was positioned 1m above the water surface and the natural canopy in 2010 was 2-3m above the water surface. Many aerially-dispersing aquatic invertebrates use polarized light reflected off of water to find suitable colonization sites (e.g., Csabai et al. 2006); this reflective cue may have been visible to dispersing dragonflies when mesocosm canopy was relatively high (2-3m) in 2010 but not when it was low (1m) in 2011.

Despite the potentially confounding effect of canopy on colonization and the low power to detect differences in colonizing insects, top predator removal affected mesocosm colonist identity in both years, particularly that of large mesopredators (>10mm). Large predators can affect prey species both directly (i.e., consumption) and indirectly (i.e., antipredator behavioral changes: Dill 1987, Schmitz and Suttle 2001, Boersma et al. 2008). Several studies have demonstrated that aquatic invertebrates perceive predator cues and can select oviposition sites to minimize predation risk (Vonesh et al. 2009, Wesner et al. 2012), and it is likely that selective oviposition played a role in colonization processes in our experiments as well. In fact, three species of dragonfly and damselfly larvae and two species of dobsonfly larvae colonized only top predator removal mesocosms, suggesting that they either did not disperse to or could not establish populations in control mesocosms. Our experimental design did not allow us to differentiate between selective oviposition and predation, and further experiments are needed to elucidate the relative influence of these mechanisms on aquatic community structure and ecosystem functioning (Vonesh et al. 2009).

While other aquatic ecologists have replicated top predator removal experiments across environmental gradients (Greig et al. 2012) and examined the effects of extreme abiotic environments on aquatic top predators (Woodward et al. 2012, Ledger et al. 2013), to our knowledge our study is the first to examine the consistency of the effects of top predator removals in the context of extreme natural interannual variability. We demonstrated that top predator removals consistently affected large aquatic taxa of multiple trophic groups despite marked differences in initial community composition and background environmental conditions. Large taxa have strong and often complex influences on ecosystem functioning (Lecerf and Richardson 2011) and are disproportionately susceptible to abiotic changes (Daufresne et al. 2009, Woodward et al. 2012). Our findings highlight the vulnerability of large taxa to biotic changes as well. Finally, we suggest that if global environmental variability increases as climate predictions suggest, the consistency of observed ecological patterns may be equally important to the magnitude of their effects.

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Table 2.1 Species richness and abundance for mesocosm communities subject to experimental top predator removal.

Year	Total species richness	Mean mesocosm species richness	Mean mesocosm abundance
2010	53	20.13	4564
Control		19.13	4957
Removal		21.13	4170
2011	39	11.55	2368
Control		11.2	2392
Removal		11.9	2343

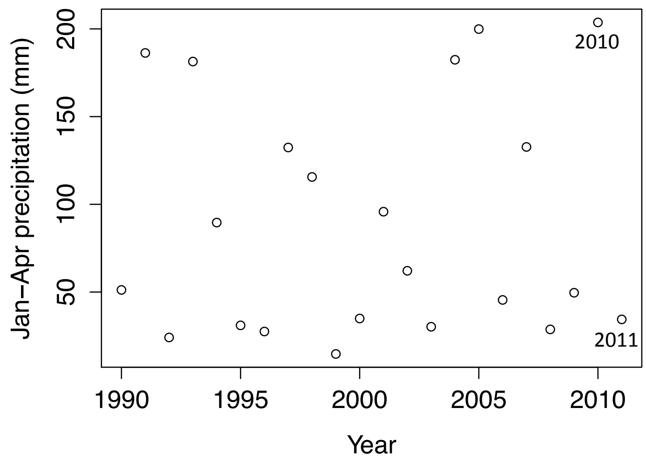

Figure 2.1 Jan-Apr precipitation from 1990-2011. The two years of this study are labeled.

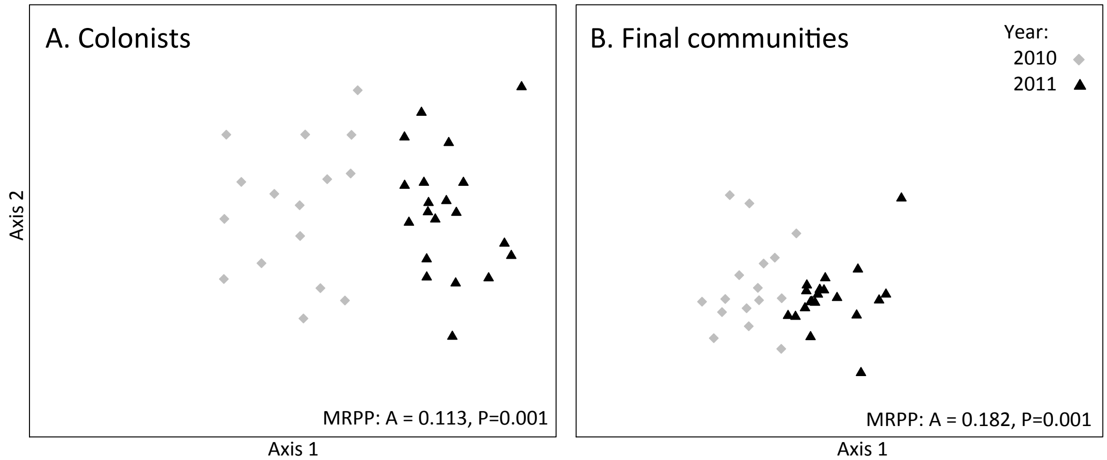

Figure 2.2 Nonmetric multidimensional scaling ordinations of interannual differences in (A) taxa colonizing during the experiments (Square-root transformation, k = 2, Stress = 0.154, p =0.020, R^2 = 0.877), and (B) overall community composition (Singleton taxa removed, k = 2, Stress = 0.186, p = 0.02, R^2 = 0.829). MRPP tests for interannual differences in community composition.

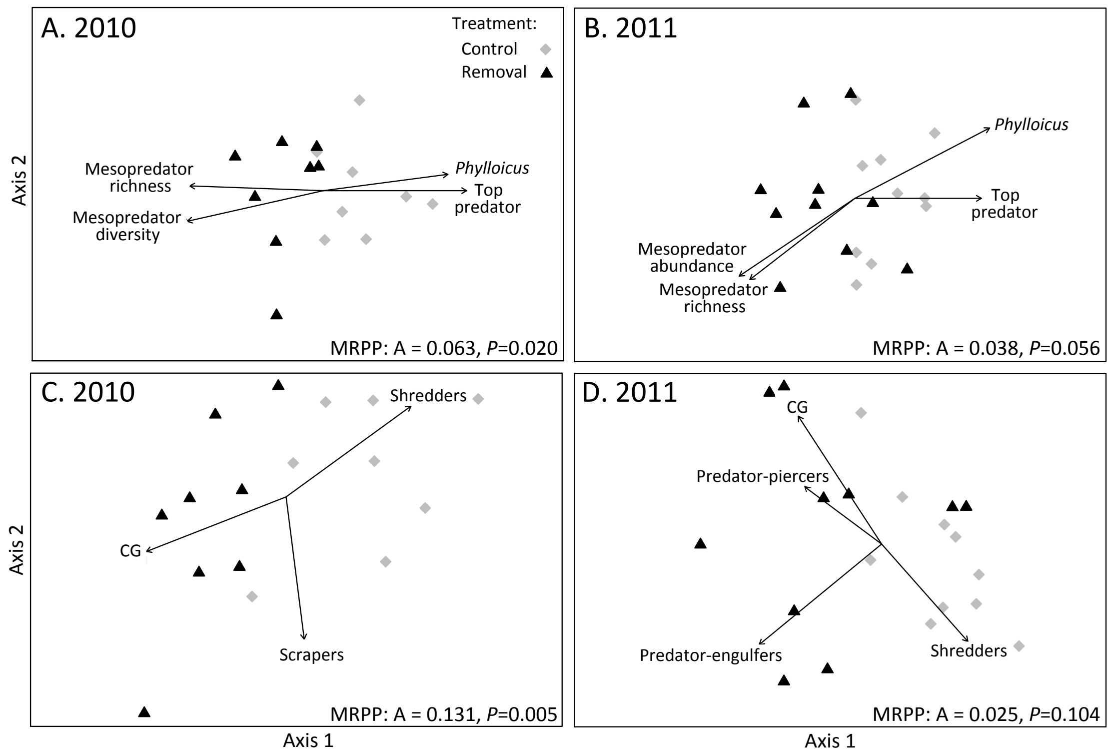

Figure 2.3 Nonmetric multidimensional scaling ordinations of the effects of experimental top predator removal on: (A) community composition in 2010 (k = 3, Stress = 0.13, p = 0.020, R^2 = 0.835), (B) community composition in 2011 (k = 3, Stress = 0.148, p= 0.020, R^2 = 0.775), (C) trophic composition in 2010 (k = 3, Stress = 0.0598, p = 0.020, R^2 = 0.972), and (D) trophic composition in 2011 (k = 3, Stress = 0.089, p = 0.020, R^2 = 0.939). We facilitated interannual comparisons of community composition by rotating each NMDS ordination to align with a vector representing the abundance of *A. herberti* in the final mesocosm samples, as reproduction and natural mortality generated some variability in predator counts. For each three-dimensional ordination, we present the two axes that captured the most variability along the *A. herberti* abundance axis. In panels (A) and (B), vectors represent correlations between axis scores and community statistics ($p < 0.05$), where "Mesopredator richness" = # of predator taxa >5mm, "Mesopredator diversity" = Shannon diversity of predators >5mm, "*Phylloicus*" = abundance of *P. mexicanus*, and "Top predator" = abundance of *A. herberti*. In panels (C) and (D), vectors represent correlations between axis scores and abundance-weighted trophic groups ($p < 0.05$). The predator groups in panels (C) and (D) represent all predators >5mm. Each three-dimensional ordination was rotated so that its first axis was parallel to the top predator abundance vector, and only axes 1 and 2 are presented here. MRPP tests for treatment differences in community composition.

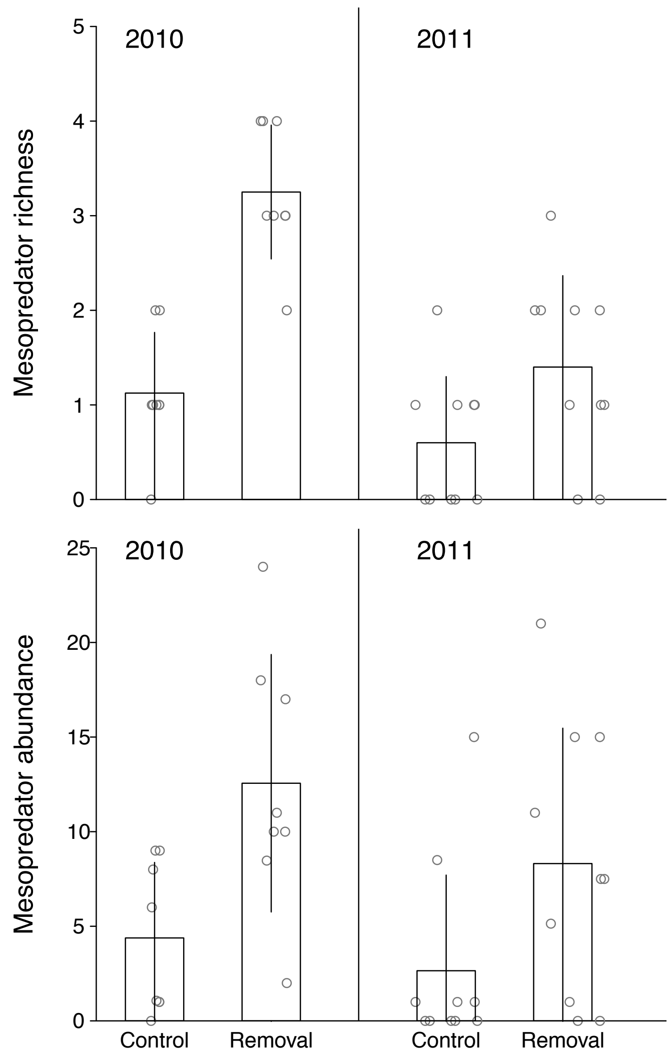

Figure 2.4 Mesopredator richness and abundance in control and top predator removal treatments in 2010 (left) and 2011 (right). (A) Mesopredator richness in final samples. (B) Mesopredator abundance in final samples. Mesopredators = all predatory taxa >5mm with the exclusion of the top predator (Appendix A, Table A.2). The grey circles represent the jittered values for each mesocosm.

3 – Arid-land stream pool invertebrate communities demonstrate high resistance and functional redundancy to severe drying

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ABSTRACT

Seasonal droughts are predictable components of arid-land stream hydrology, and many arid-land aquatic taxa have adapted to their extreme environment. However, climate change is altering this predictable hydrology, producing longer and more severe droughts and creating novel disturbance regimes for resident organisms. The hydrologic transitions from flowing stream to fragmented pools to dry stream bed are frequently associated with steep decreases in taxonomic and functional diversity, referred to as thresholds of biodiversity loss. Less is known about how taxa respond between these thresholds, as fragmented pools gradually dry and abiotic conditions intensify. While an increasingly extreme environment may be expected to reduce taxonomic and trait richness, species adapted to predictable seasonal fragmentation may be resistant to declining water levels until all surface water is lost. We used aquatic mesocosms to test two competing hypotheses of the relationship between richness and pool drying for arid-land stream invertebrates: (1) the Drought Vulnerability Hypothesis (richness gradually decreases with drying) and (2) the Drought Resistance Hypothesis (richness remains constant until complete drying occurs). We inoculated replicate mesocosms with aquatic invertebrates from arid-land streams in Arizona, USA, and applied three drying treatments representing a continuum of drying stress commonly observed in local streams during the summer dry season (water depths: 10cm, 7cm, and 1cm). Mesocosms were covered to restrict dispersal and colonization processes and isolate resistance (*in situ* survival of species)

from resilience (community recovery following disturbance). After 45 days, we destructively sampled all invertebrates in the mesocosms and calculated various taxonomic and functional trait metrics. Taxonomic richness and composition did not differ among drying treatments, providing strong support for the Drought Resistance Hypothesis. Severe drying was associated with lower invertebrate abundances and higher densities than the moderate and control treatments. This finding suggests that density-dependent processes generated by decreased available habitat may be more important determinants of community composition during droughts than abiotic stress in this system. We observed near complete overlap of trophic traits (body size and functional feeding group) and resistance traits (respiration mode and diapause) among the three treatments. This high functional redundancy may provide a buffer against changes to ecosystem functioning, even in cases of severe drying-induced habitat contraction and fragmentation.

3.1 Introduction

Droughts are predicted to increase in frequency and severity in many arid regions (Hoerling and Eischeid 2007, Seager et al. 2007, Balling and Goodrich 2010), and it is imperative that we understand how aquatic communities will respond to these events. Arid-land streams are characterized by predictable cycles of severe floods and droughts (Lake 2003), and most resident taxa have developed adaptations to this extreme environment (Lytle and Poff 2004). However, drought-induced changes in seasonal hydrology may present aquatic taxa with novel disturbance regimes to which they are not adapted (Lake 2003, Lytle and Poff 2004), making it difficult to predict the responses of biological communities to these altered flow regimes.

Boulton (2003) proposed a useful framework to describe the relationship between aquatic biodiversity and stream drying through time (Figure 3.1). He envisioned a stepped response, with gradual species losses punctuated by thresholds of high diversity loss as streams pass though important hydrologic transitions. These thresholds mark (1) the loss of lateral connectivity, when a flowing stream recedes away from the riparian zone (Figure 3.1A), (2) the cessation of flow, when a stream contracts into stagnant pools (Figure 3.1B), (3) the loss of surface water (Figure 3.1C), and (4) eventual loss of hyporheic refuges (Figure 3.1D). Since the publication of Boulton's framework, multiple studies have provided empirical evidence of the existence of thresholds of biodiversity loss during drying of aquatic habitats (Acuña et al. 2005, Dewson et al. 2007a, Walters and Post 2010). However, the relationship between drying and biological diversity during the periods between these thresholds has received much less attention, despite its importance in understanding the overall community response to drying.

The period between flow cessation (Figure 3.1B) and complete water loss (Figure 3.1C) represents gradual drying of fragmented pools and is accompanied by concurrent changes in abiotic conditions. As stagnant pools dry, temperature and conductivity increase and dissolved oxygen decreases (Everard 1996, Lake 2000).

Evaporation of water causes total habitat area to shrink and the remaining aquatic fauna may reach high densities (Lake 2003), increasing both the intensity of interactions among species (Power et al. 1985) and the likelihood that species could be eliminated via predation or competitive exclusion. These harsh abiotic conditions may act as a habitat filter that limits surviving species to those with traits conferring resistance to extreme environmental conditions (Chase 2007). Under this premise, we may expect gradual losses in taxonomic and trait diversity as abiotic conditions in pools worsen and the slope of the line between thresholds B and C to be negative (Figure 3.1, dotted line).

However, antecedent flow conditions and the natural periodicity of drought will affect species-specific responses to drying, potentially minimizing the decline in diversity between drying thresholds. The local history of drought severity, frequency, and duration likely determines whether aquatic organisms at a given site possess traits that allow them to withstand drought disturbances (Lake 2003, Lytle and Poff 2004). If local taxa are highly adapted to droughts and the biotic and abiotic changes that accompany them, then drying may not trigger a decrease in taxonomic or trait diversity until all surface water is lost, and the inter-threshold slope may be zero (Figure 3.1, dashed line). Predictable background cycles of severe floods and droughts in arid regions may mean that some droughts do not function as disturbances at all (Resh et al. 1988).

In this study, we examined the relationships between severe pool drying and taxonomic and trait diversity in an arid-land stream system with a history of extreme yet predictable seasonal droughts. We tested two alternate hypotheses regarding the relationship between drying and diversity, which we have called the Drought Vulnerability Hypothesis (negative inter-threshold slope; Figure 3.1, dotted line) and the Drought Resistance Hypothesis (flat inter-threshold slope; Figure 3.1, dashed line). We expected taxonomic and trait diversity to respond similarly to drying since any given species' survival under harsh conditions should be determined by its biological traits. We inoculated aquatic mesocosms with arid-land stream invertebrates, applied three drying treatments representing a continuum of drying stress, and then calculated taxonomic and trait diversity of the resulting communities. An observation of decreasing diversity with increasing severity of drying would support the vulnerability hypothesis, whereas the lack of a treatment effect would support the resistance hypothesis. We believe that understanding how arid-land stream biodiversity responds during this inter-threshold period will inform our ability to manage these vulnerable ecosystems as drying regimes intensify in the future.

3.2 METHODS

System

This study was conducted in the Chiricahua Mountains of southeastern Arizona, U.S.A., an arid-land mountain range that receives an average of 46 cm of rainfall annually (range: 18-65 cm, based on 1995-2011 records). Streams in this range generally contain reaches with perennial water between 1500 and 2200m and become intermittent or ephemeral downstream. The extent and duration of flow is determined by bimodal annual precipitation patterns that consist of intense, localized monsoon rains during late summer (Jul-Sep), moderate but more widespread winter rains (Nov-Mar), and a late spring and early summer dry season (Apr-Jun). On average, only 6% (2.8 cm) of the annual rainfall occurs during this 3-month dry season. During the dry season, many streams naturally fragment to a series of small bedrock pools, often separated from one another by dry reaches (Bogan and Lytle 2007).

Mesocosms

We simulated replicate fragmented pools with 40L plastic tanks (hereafter "mesocosms") filled with well water. We sampled aquatic invertebrates from three streams in the Chiricahua Mountains: Cave Creek, East Turkey Creek, and North Fork Cave Creek, using a 500 μm mesh D-frame net, taking care to sample representative microhabitats (see Bogan and Lytle 2007 for full sampling description) and collect sediment and detritus in each stream. We combined these samples in a 200L tank to create a diverse inoculum with which to seed the mesocosm communities (Boersma et al. in revision). The inoculum was distributed across 24 containers – 21 were added to the mesocosms and 3 were preserved in 70% ethanol as initial samples. Mesocosms were arranged in a grid, 25cm apart and ~500m from the nearest intermittent stream, and each contained a single cinderblock as habitat structure. We added well water to mesocosms twice weekly to maintain three drying treatments: control – constant water level at 10cm depth; moderate drying – water level was allowed to decrease to 7cm; and severe drying – water level was allowed to decrease to 1cm. Moderate and severe mesocosms reached target water levels after weeks 1 and 3 of the 6 week experiment, respectively. We randomly applied treatments to 21 mesocosms, producing 7 mesocosms per treatment. Wildlife consumed the water in one mesocosm, reducing the sample size to 6 for the moderate treatment.

Several studies have documented the importance of aerial colonization in driving community structure in streams in this region (Velasco and Millan 1998b, Bogan and Boersma 2012, Boersma et al. in revision). In this study, however, we were interested in the in-situ community responses to drying and subsequent loss of taxa, not the recovery of extirpated populations (e.g. resistance, not resilience, sensu Lake 2013), so we restricted aerial colonization by installing a shade cloth over each mesocosm. We compared taxa present in our three initial samples with those at the end of the experiment and found that the cover effectively prohibited most aerially-dispersing taxa from colonizing the mesocosms. Because of the small number of initial samples, we consider our inference of limited colonization to be conservative. Despite the shade cloth, water temperature and conductivity in mesocosms equaled or exceeded typical in-stream measurements during the summer dry season (Bogan et al. 2013b).

The experiment was conducted during the peak of the summer dry season, from 19 May to 3 July 2011. At the conclusion of the experiment the contents of each mesocosm were preserved in 70% ethanol and identified to the lowest practical taxonomic level given available keys (Merritt et al. 2008). We measured temperature, dissolved oxygen, conductivity and pH in each mesocosm at the end of the experiment. We installed six iButton temperature loggers (Maxim Integrated, San Jose, CA, U.S.A.) to record temperature every 6h in the mesocosms. Only two loggers survived the harsh mesocosm conditions, in control and moderate treatments. These loggers reported a mean diurnal temperature fluctuation of 13.3ºC and an overall mean of 27.5ºC and will not be discussed further. All references to temperature are from measurements taken by hand.

Analysis

Abiotic variables

After examining statistical distributions for each variable and verifying that parametric assumptions were met, we compared environmental variables among treatments at the end of the experiment using analysis of variance (ANOVA).

Community turnover

The small number of initial samples (3) prohibited direct multivariate comparisons between initial and final samples; however we did examine the identities and abundances of taxa that were exclusive to either initial or final samples. We considered a taxon to have been eliminated by the drying treatments if initial samples contained >5 individuals and it was absent from final samples. We considered a taxon to have colonized despite the shade cloth if it was absent from initial samples and final samples contained >5 individuals.

Taxonomic and functional diversity

We calculated species richness, Shannon diversity, and abundance for each mesocosm and compared them among treatments using analysis of variance (ANOVA), as richness values were large enough to meet parametric assumptions. To account for habitat loss during drying, we also calculated densities of individuals per unit volume of water and compared them using the Kruskal-Wallis test (unequal variance among treatments prohibited the use of parametric tests). We used permutation-based ANOVA (PERMANOVA) to test for treatment differences in community composition. We calculated community dispersion with a Sørensen distance measure (Sørensen 1948) and compared dispersions among treatments using a permutation test with 999 permutations (Anderson 2006).

According to the habitat filter framework (Townsend and Hildrew 1994, Poff 1997), an extreme environment may eliminate species with maladaptive trait combinations and permit those with favorable trait combinations to survive. We used *a priori* knowledge from other studies conducted in the region (Bogan and Lytle 2011, Bogan et al. 2013a, Boersma et al. in revision) to select four traits that we believed would be associated with organismal responses to drying disturbance: two resistance traits (respiration mode, diapause capacity) and two trophic traits (body size, functional feeding group). Trait values for each taxon were treated as exclusive categories, producing a total of 17 modalities, 15 of which were represented in species collected in our experiment. Reliable trait information was not available for four taxa of non-insects (copepods, ostracods, aquatic mites, and oligochaetes). These taxa were rare in mesocosm samples and were eliminated from our calculations. Trait modalities, values and references are provided in Appendices S1 and S2 in Supporting Information.

We calculated two functional diversity metrics to quantify differences in trait composition among treatments: functional richness and Rao's quadratic entropy. Functional richness is the volume of trait space occupied by a set of species and is determined by the presence or absence of individual trait combinations (Villéger et al. 2008). Rao's quadratic entropy (Q) is an abundance-weighted metric that measures the mean pairwise distances of randomly selected individuals in the community (Rao 1982, Botta-Dukát 2005). Both metrics require *a priori* identification of traits that can be measured or specified from the literature for every species. Combined, these two metrics provide information on the overall range of trait combinations and how these combinations are distributed across species. We compared functional richness among treatments with a Kruskal-Wallis test and Rao's quadratic entropy with ANOVA.

We used nonmetric multidimensional scaling ordination (NMDS) with a Sørensen distance measure to visualize compositional patterns in species traits for species with >5 individuals in the final samples. After considering NMDS stress and interpretability, we present two-dimensional ordinations of the untransformed trait matrix here. In addition to quantitatively comparing the functional diversity metrics among treatments, we visually examined patterns in functional redundancy by plotting resistance and trophic traits by treatment.

Previous research has documented a high proportion of invertebrate predators in drying streams (Stanley et al. 1994, Acuña et al. 2005, Bogan and Lytle 2007, 2011). To examine differences in predator proportions across a drying intensity gradient, we compared the prevalence of predators among treatments using predator-prey ratios, defined as the abundance of predatory taxa >10mm divided by the abundance of all remaining taxa. We tested for differences in predator-prey ratios using ANOVA.

All analyses were conducted in R Version 2.14.1 (R Development Core Team) with the vegan (Oksanen et al. 2012) and FD (Laliberté and Legendre 2010, Laliberté and Shipley 2011) packages.

3.3 RESULTS

Abiotic variables

Mean water levels were 10.7cm, 7cm, and 1.1cm for control, moderate and severe treatments respectively (Table 3.1). Steep mesocosm walls caused the surface area of benthic habitat to vary little among treatments, although the level of inundation above the substrate was more variable within severe treatment mesocosms than in the other treatments. Substrate in control and moderate mesocosms was inundated by a minimum of 9cm and 5 cm of water, respectively. The severe treatment mesocosms were characterized by ~20% wet, exposed substrate and ~80% shallow puddles of 2cm depth or less (Table 3.1). On average, conductivity was nearly three times higher in the severe treatment than in the control (Means: control = 1064 $\mu S\ cm^{-1}$, moderate = 1269 $\mu S\ cm^{-1}$, severe = 2907 $\mu S\ cm^{-1}$, Table 3.1), and temperature was higher in the severe treatment for both control/severe and moderate/severe comparisons (Means: control = 29.0°C, moderate = 29.7°C, severe = 30.5°C, Table 3.1). We observed no differences among treatments in pH or dissolved oxygen (Table 3.1) at the end of the experiment.

Community turnover

Sixty-three taxa were present in our three initial samples. Twenty taxa were eliminated during the course of the experiment (provided in Appendix B, Table B.3), including 14 true fly taxa (10 midges and 4 other Diptera taxa) and two taxa each of caddisflies, mayflies, and true bugs. Most of these 20 drying-eliminated taxa are normally found in cooler, flowing water (Merritt et al. 2008) rather than warm, still pools like those simulated by our mesocosms. An examination of coarse trait patterns for surviving and eliminated taxa revealed no apparent patterns in body size, diapause or respiration. We found that taxa classified as collector-gathers showed a higher rate of extirpation than other functional feeding groups (40% of disappearing taxa vs. 24% of surviving taxa), although formal statistical analyses were not applied so we cannot draw inferences from this pattern.

Sixteen insect taxa in the final samples were not present in the initial samples (provided in Appendix B, Table B.4), representing either rare taxa that were not detected due to the small number of initial samples or taxa that colonized despite the colonization barrier. Of these, 12 had abundances ≤5 individuals and were likely not detected in the initial samples due to sampling effects. The remaining three taxa were the mosquito *Anopheles*, the beetle *Berosus punctatissimus,* the true bug *Ambrysus woodburyi*, with 30, 23, and 7 individuals in final samples, respectively. All of the *Anopheles* and nearly all of the *Berosus* were larvae found in a single mesocosm, suggesting that these individuals developed from a single egg mass during the course of the study. *A. woodburyi* are capable of dispersing over land as adults and colonizing isolated mesocosms (Bogan and Boersma 2012), and the most parsimonious explanation for their presence in final mesocosm samples is that they landed on shade cloths and entered through small gaps at the edges of the mesocosms.

Taxonomic diversity

Fifty-two taxa were identified in our final mesocosm samples. We found no significant differences among treatments in species richness (ANOVA, $F_{2,17} = 2.111$, $P = 0.152$; Figure 3.2A) or Shannon diversity (ANOVA, $F_{2,17} = 0.4923$, $P = 0.620$; Figure 3.2B). Total mesocosm abundance was significantly higher in control and moderate treatments than in the severe treatment (ANOVA, $F_{2,17} = 11.367$, $P = 0.0007$; Bonferroni-corrected multiple comparisons: control/moderate, $P = 0.580$; control/severe, $P = 0.0007$; moderate/severe = 0.0186), although density increased with drying severity (Kruskal-Wallis, $\chi^2_2 = 13.895$, $P = 0.001$; Multiple comparisons: control/moderate, $P > 0.580$; control/severe, $P < 0.001$; moderate/severe , $P < 0.05$).

We found significant differences in community composition among the treatment groups based on species abundances (PERMANOVA, $F_{2,17} = 2.070$, $P = 0.018$) and species densities (PERMANOVA, $F_{2,17} = 6.382$, $P = 0.001$). However, this pattern disappeared when we analyzed the presence-absence (species richness) matrix (PERMANOVA: $F_{2,17} = 0.818$, $P = 0.695$), suggesting high overlap of species composition among treatments. Multivariate dispersion did not differ among treatments for abundance, density or presence-absence matrices (Permutation test: Species abundances, $P = 0.735$; species densities, $P = 0.391$, presence-absence, $P = 0.18$).

Functional diversity

We found no treatment effects on either functional richness (Kruskal-Wallis, $\chi^2_2 = 0.4918$, $P = 0.782$; Figure 3.2C) or Rao's quadratic entropy (ANOVA, $F_{2,17} = 0.062$, $P = 0.940$; Figure 3.2D), although the range of functional richness decreased along a gradient of increasing drought severity (Range: control = 11.380, moderate = 9.485, severe = 4.559). We also did not detect differences in predator/prey ratios among treatments (ANOVA, $F_{2,17} = 0.052$, $P = 0.950$). NMDS ordinations of species in trait space reflect the relationship among traits of taxa that were present in both control and moderate mesocosms but not severe mesocosms (NMDS, $k = 2$, stress = 0.0683, $R^2 = 0.979$, Figure 3.3). These "filtered-out" trait combinations were distributed across all trait modalities, demonstrating that there were no apparent patterns in the traits of species eliminated by the severe drying treatment. Separate plots of trophic and resistance traits highlight the complete redundancy of trophic traits (Figure 3.4) and near complete redundancy of resistance traits (not shown).

3.4 Discussion

We experimentally manipulated drying severity in mesocosms containing arid-land aquatic invertebrate taxa to test two competing hypotheses about how aquatic organisms respond to pool drying during the summer dry season. We found that taxonomic and functional richness of invertebrate communities did not differ among drying treatments despite dramatic differences in water quality and habitat availability. This lack of treatment effect supports the Drought Resistance Hypothesis, under which taxonomic and trait diversity remains constant as water levels decline in fragmented pools. We did observe significant differences among drying treatments in the density of individuals, suggesting that decreasing water volume is an important factor in aquatic community responses to drought.

Resistance of taxonomic diversity

Our results corroborate other research documenting high tolerance of aquatic invertebrates to short-term drying stress, even in temperate streams without a history of severe drying. Dewson and colleagues (2007a) conducted experimental water diversions in small streams in New Zealand and observed little change in species richness, which they credited to the presence of aquatic refuges during drying. As in our experiment, they saw a marked increase in the density of invertebrates in remaining aquatic habitat. Walters and Post (2010) similarly found no effect of water diversion on species richness in small streams in the northeastern USA, and saw significant increases in invertebrate density and decreases in biomass as water receded. Habitat contraction and loss have been identified as drivers of aquatic community responses to drought in many other stream studies (Stanley et al. 1997, Bunn and Arthington 2002, Acuña et al. 2005), and the most commonly observed result is an increased density of invertebrates (e.g. Walters and Post 2010).

While habitat contraction and decreasing water volume are likely drivers of invertebrate density, factors determining invertebrate abundances may be more complex. Intuitively, an increasingly extreme abiotic environment can decrease invertebrate abundances (Chase 2007). However, the lack of a significant treatment effect on species richness suggests that biotic drivers may be more important in this experiment and that the abundance response may involve density-dependent processes occurring at individual, population and species levels. High densities of invertebrates are known to limit resource availability and increase the intensity of biotic interactions (Power et al. 1985, Malmqvist and Sackmann 1996). Further experiments manipulating both invertebrate density and environmental variables are necessary to disentangle the biotic and abiotic drivers of our observed abundance patterns.

While similar results have been obtained in other systems, our study is unique in that it isolated the *in situ* tolerance of organisms to deteriorating conditions from the movement of organisms between aquatic habitats (community resistance from resilience). Environmental stress, such as drying, heat, or flooding, can trigger dispersal in many stream systems (Smith 1973, Velasco and Millan 1998b, Lytle et al. 2008), and Bogan and Boersma (2012) demonstrated that aerial dispersal occurs frequently in fragmented arid-land streams during the dry season. It is plausible that the drying/diversity relationship observed in many other studies could be due to the movement of individuals into and out of drying habitats instead of the survival or mortality of local individuals, as is frequently assumed. We minimized the confounding influences of dispersal and colonization with a shade cloth installed just above the water's surface in each mesocosm. Thus we can say with confidence that many arid-land stream pool taxa have high resistance to drying – with few exceptions the only organisms in our mesocosms were ones that we inoculated or larvae that developed during the experiment.

Our dispersal-restriction canopy allowed us to isolate *in situ* resistance from dispersal/colonization processes, however, it came with the cost of some ecological realism. The canopy limited light penetration, likely impacting primary productivity and diel temperature fluctuations. It prevented allochthonous inputs and the arrival of additional prey taxa, thereby restricting the availability of resources to resident taxa. All organic material in mesocosms arrived during the initial inoculations. The canopy also prevented insects from emerging from the mesocosms. We found few carcasses in our samples, suggesting that insects that were unable to emerge were consumed. The only dead or decaying organisms present in our samples belonged to three genera of caddisfly larvae that build protective cases out of small rocks and twigs (*Helicopsyche*, *Hesperophylax*, and *Oecetis*) and were probably inedible to most predators (Nislow and Molles 1993).

Resistance of functional diversity

High resistance of taxonomic diversity is one way that arid-land stream communities are buffered against environmental extremes; a redundancy of functional traits is another. Functional redundancy is the degree to which taxonomically distinct species fulfill similar ecological roles in an ecosystem or possess similar traits (Rosenfeld 2002) and it may provide ecosystems with a level of insurance against the loss of ecosystem functioning that accompanies species extinctions (Petchey et al. 2007, Philpott et al. 2012). We observed complete redundancy of trophic traits (Figure 3.4) and near complete redundancy of resistance traits (not shown) among treatments. High functional redundancy may explain the lack of a treatment effect on our two functional diversity metrics.

As many recent trait studies have demonstrated, our ability to observe patterns in functional diversity depends upon trait choice (e.g. Petchey and Gaston 2006). With only four traits we are more likely to observe redundancy and less likely to observe treatment effects than with a larger trait set. However, we selected these traits using extensive knowledge from studies on species responses to drought both from this and other arid-land aquatic systems, and we believe that our trait analysis is robust. It is well-documented that aquatic invertebrate trophic structure is vulnerable to drying stress in our system (Bogan and Lytle 2007, 2011), and both body size (Daufresne et al. 2009, Walters and Post 2010) and trophic level (Woodward et al. 2012, Ledger et al. 2013) are strongly affected by drying. Additionally, taxa that are adapted to intermittency are more likely to possess traits conferring desiccation-resistance (Bonada et al. 2007, Bogan et al. 2013a).

Conservation implications

While we found no effect of drying severity on taxonomic or functional diversity, our severe drying treatment maintained water depth at 1-2cm so that sediment and detritus remained wet and small aquatic refuges were present. We did not apply a complete drying treatment in this study and therefore do not have direct evidence of the existence of a complete drying threshold (Figure 3.1C). However, ample evidence for this threshold and the resulting biological responses comes from field observations of catastrophic drying events (e.g. Boulton and Lake 1992, Acuña et al. 2005, Bêche et al. 2009, Bogan and Lytle 2011). These field studies suggest that taxonomic richness is resilient to moderate and severe drying, but community composition and food web structure can change dramatically following complete drying events, when all aquatic refuges are lost. Bêche and colleagues (2009) found that recovery from supraseasonal drought was taxon-specific, and that large, dispersal-limited taxa never recolonized following drying disturbance. Bogan and Lytle (2011) observed no change in species richness post-drying but found similar selective recolonization capacity, which led to the elimination of the top predator and a sharp increase in the abundance of mesopredators.

Understanding how aquatic communities respond to drying disturbances may allow us to manage aquatic resources to minimize catastrophic biodiversity loss during severe drought. Our research demonstrates that our dry season arid-land aquatic communities have high resistance and thus high buffering capacity against drought. For streams subject to both seasonal droughts and anthropogenic water use, water resource managers may be able to avoid catastrophic biodiversity losses during droughts by maintaining small aquatic refuges along the stream channel until water demands subside or drought ends (Magoulick and Kobza 2003, Chester and Robson 2011). Studies on resistance and resilience to drought are useful concepts to guide this research (Lake 2013), however it is important to understand how local background disturbance rates affect community responses to current and future disturbances (Lake 2003, Lytle and Poff 2004). Predictable seasonal droughts should be associated with pre-adapted communities that demonstrate high resistance and resilience to seasonal drying, whereas supraseasonal droughts are unpredictable and may act as catastrophic disturbances. The situation becomes grave when droughts are supraseasonal and water demands are not likely to subside. Given that arid-lands are considered especially vulnerable to increased supraseasonal warming and drying in a changing climate, research on both biological and societal drivers of arid-land stream community structure will become increasingly important.

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Table 3.1 Abiotic measurements, taken at the end of the ~45-day experiment.

	Treatment	Maximum	Mean	Minimum	Standard deviation	Significant pairwise comparisons
Depth (cm)	Control	11	10.7	10	0.49	
	Moderate	8	7	6	0.89	All***
	Severe	2	1.1	0	0.69	
Conductivity ($\mu S\ cm^{-1}$)	Control	1211	1064	998	83.5	
	Moderate	1352	1269	1160	87.8	Control vs. Moderate***
	Severe	3270	2907	2180	385.4	Control vs. Severe***
Dissolved oxygen (ppm)	Control	12	8.2	5	2.8	
	Moderate	11	8.2	6	2.2	None
	Severe	12	10	7	2	
Temperature (ºC)	Control	29.9	29.0	28.3	0.53	
	Moderate	30.6	29.7	29	0.59	Control vs. Severe*
	Severe	31.9	30.5	28.7	1.21	
pH	Control	8	7.3	7	0.45	
	Moderate	7.5	7.2	7	0.27	None
	Severe	8	7.6	7	0.42	

Statistical significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

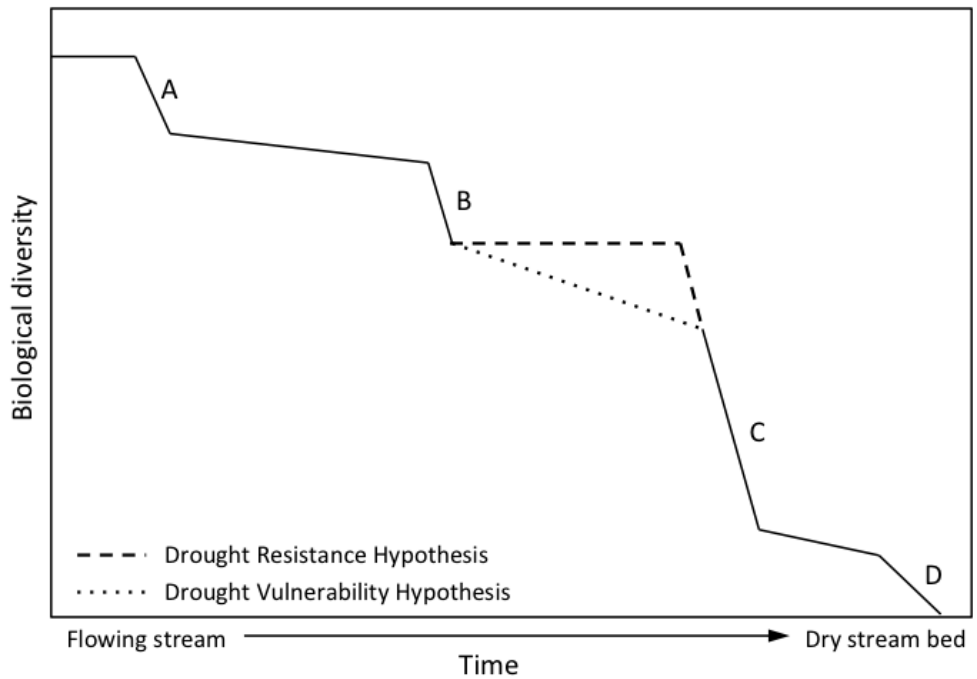

Figure 3.1 Changes in biological diversity associated with major hydrologic transitions during stream drying, modified from Boulton 2003 Figure 1. (A) Loss of lateral connectivity to the riparian zone, (B) loss of longitudinal connectivity and cessation of flow, (C) loss of surface water, and (D) loss of hyporheic refuges. The period of this study is between thresholds B and C. The Drought Resistance Hypothesis and Drought Vulnerability Hypothesis are represented by the dashed and dotted lines, respectively.

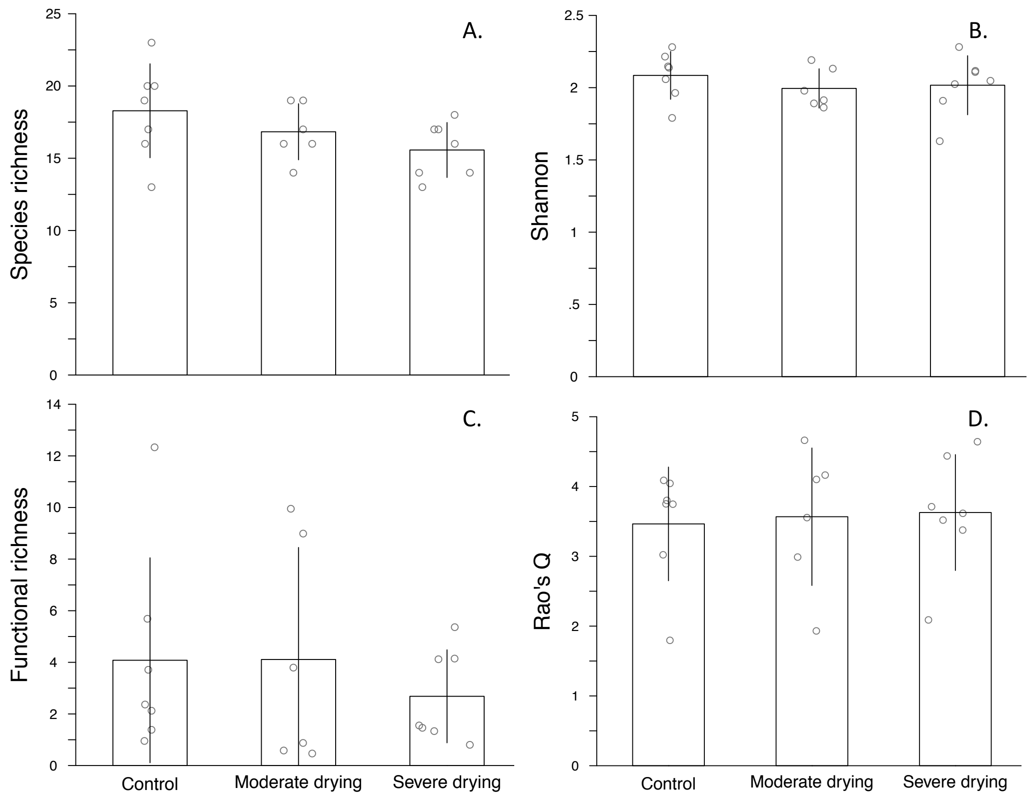

Figure 3.2 Taxonomic and functional diversity metrics by drying treatment. (A) Species richness, (B) Shannon diversity, (C) functional richness, and (D) Rao's quadratic entropy. Points are jittered along the x-axis to facilitate interpretation of variability in the response. There are no significant differences between any treatment combinations for any panel.

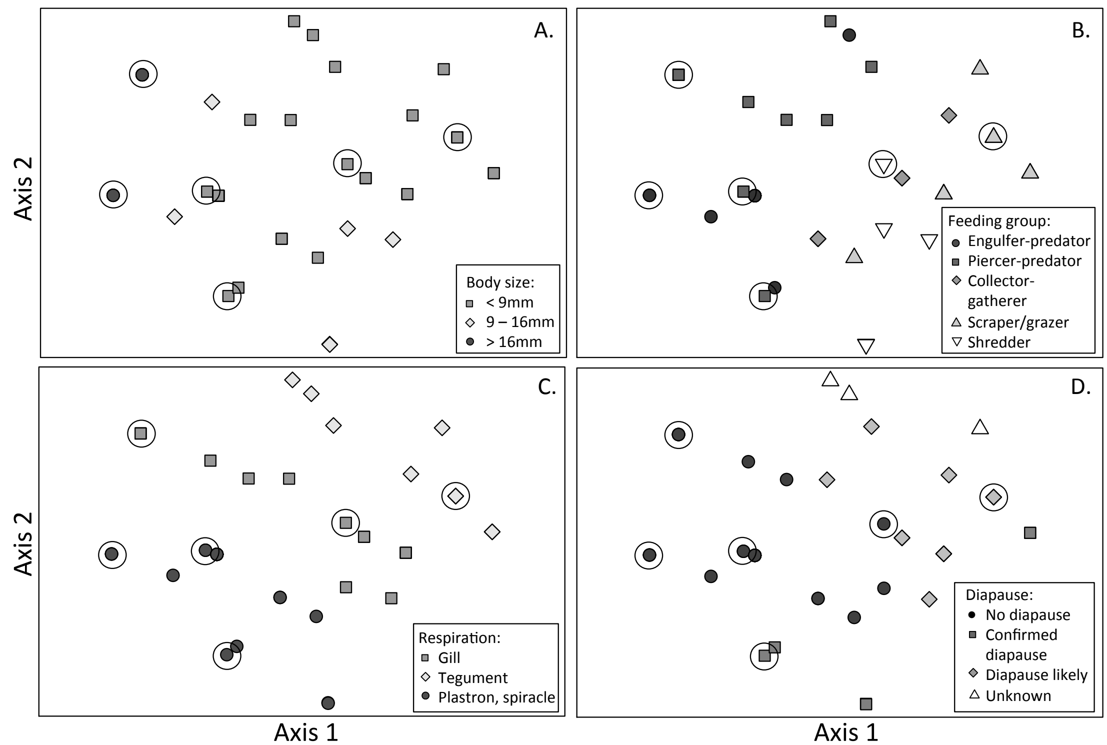

Figure 3.3 Nonmetric multidimensional scaling ordinations of species in trait space (NMDS, k = 2, stress = 0.0683, $R^2 = 0.979$). Each point is a species with abundance >5, and points are shaded by trait modality within each trait category: (A) body size, (B) functional feeding group, (C) respiration, and (D) diapause. Species that were present in the control and moderate drying treatments but absent from the severe drying treatment are indicated by grey circles. Note: species with overlapping trait combinations appear as a single point on each plot.

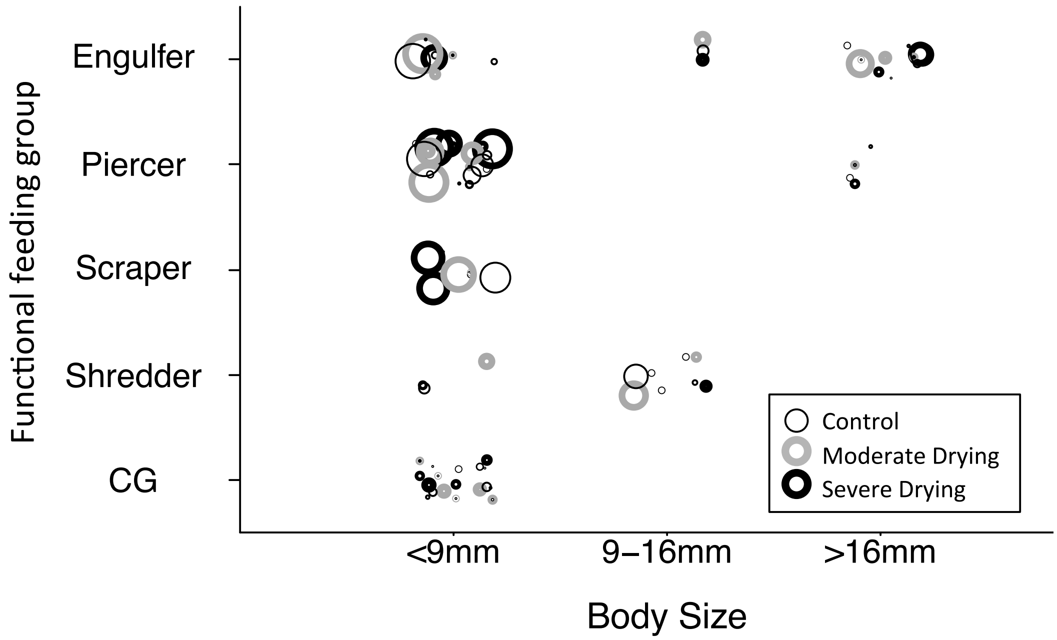

Figure 3.4 Functional redundancy in trophic traits. Each circle represents a species, where circle size reflects its relative abundance and circle shading/weight reflects treatment: thin black = control, thick grey = moderate drying, and thick black = severe drying. Circles within each trait combination are jittered so the overlap among treatments is visible; blank spaces mark trait combinations that were not represented in our samples. All represented trait combinations contain circles of all three colors, indicating complete functional redundancy.

4 – A hypothesis-driven functional trait framework reveals unexpected relationships between disturbance and functional diversity

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In preparation

ABSTRACT

Because the frequency and magnitude of extreme climatic events are increasing, it is imperative that we understand how changing disturbance regimes affect biological communities. Functional trait diversity provides an appealing means to study the impact of disturbances because species responses to disturbance are determined by their traits. However, trait-based approaches are rarely applied in a rigorous hypothesis-testing framework. In order for functional diversity to be useful in a predictive context, researchers must first pose ecologically-informed hypotheses and then select appropriate analytical methods to test their predictions. Here we use community assembly and disturbance theory to generate six hypotheses of community responses to disturbance in fragmented habitats, and apply three functional diversity metrics to test the hypotheses: functional richness, functional dispersion, and a novel modification of functional distance. We then apply this conceptual framework to three studies of fragmented stream invertebrate communities: a simulated drought experiment, a simulated top predator extinction experiment, and an 8-year field survey before and after a severe drought. We predicted that the effects of these biotic and abiotic disturbances on functional community structure would depend upon the magnitude of the disturbance relative to historic disturbance regimes. Indeed, communities exposed to the novel disturbances of predator extinctions and complete natural stream drying exhibited significant changes in functional diversity, while functional diversity did not differ when the disturbance consisted of manipulated

drying that fell within the range of natural interannual environmental variability. Disturbance only caused significant trait turnover in the top predator removal study, indicating that realistic disturbance scenarios may not yield turnover in functional traits as is frequently assumed. Our approach also suggests that different combination of functional diversity metrics may be required depending on whether disturbance acts as a threshold or as an incremental change. We submit that functional diversity can be useful to test ecologically-informed hypotheses of community responses to intensifying disturbance regimes and that our novel application of functional distance may be useful to detect disturbance-induced functional turnover.

4.1 INTRODUCTION

Climate variability is increasing (Beniston et al. 2007, IPCC 2012), as evidenced by increasingly-severe and unpredictable climatic events. Given predictions of future changes in the magnitude, duration, and frequency of environmental disturbances, it is imperative that we understand the mechanisms driving biological community responses to intensifying disturbance regimes. Because organismal responses to disturbance are determined by functional traits that affect their vulnerability (e.g. temperature tolerance, life span), species traits may be used to predict community responses to future environmental change (Suding et al. 2008, Mouillot et al. 2013, Verberk et al. 2013).

A functional diversity framework provides a much needed approach to understand community responses to disturbance because functional traits provide a mechanistic link between species and their environment. However, species traits do not act in isolation (Mouillot et al. 2013). Because correlated traits (e.g. body size and fecundity) are the norm, not the exception, it is essential to consider groups of traits that co-occur within species at a single location if we are to use traits in a predictive context (Verberk et al. 2013). The growing field of quantitative functional ecology can account for suites of non-independent traits responding in concert to their environment and holds promise as a means to include the role of non-additivity in trait effects (Mouchet et al. 2010).

Rosenfeld (2002) suggested that the functional trait composition of a community can be visualized with species as points in a Euclidean functional trait space whose axes are determined by species unique trait combinations; species that are closer together in trait space share similar functional trait combinations. Mouillot et al. (2013) added abundances to this model and applied it to examine how the abundance and distribution of trait combinations change following disturbance. These authors suggest that changes in abundance may be early indicators of future impacts because disturbance affects the abundance of trait combinations before species are lost altogether (Mouillot et al. 2013) and allow researchers to detect functional extinctions that precede taxonomic extinctions (Säterberg et al. 2013).

Functional ecology has developed rapidly over the past ten years, and ecologists now have an extensive quantitative toolbox of over a dozen functional diversity metrics to quantify and compare various aspects of functional trait space (Petchey and Gaston 2006, Mouchet et al. 2010, Schleuter et al. 2011). We can use these metrics to compare functional trait structure between disturbed and undisturbed communities and test hypotheses of community responses to change (Mouchet et al. 2010, Mouillot et al. 2013). However, empirical application of these methods in a rigorous hypothesis-testing context is still rare (Cadotte 2011, Mason and de Bello 2013). In order for a functional diversity framework to increase our understanding of how biological communities will respond to changing disturbance regimes, we must use quantitative approaches that test specific ecologically-informed hypotheses.

Here we present a hypothesis-driven conceptual framework to examine how the functional composition of biological communities in fragmented habitat patches respond to disturbances. We describe three functional diversity metrics that measure changes in community functional trait space and can be used to test our hypotheses. We then apply this framework to three studies from arid-land aquatic habitats in Arizona, US, that measure the biological consequences of three different disturbance types.

4.2 CONCEPTUAL FRAMEWORK

We propose six non-mutually exclusive hypotheses of how fragmented communities may respond to disturbances and provide a novel application of functional diversity metrics to distinguish among these hypotheses by comparing functional trait composition between disturbed and undisturbed communities. We define disturbance as an infrequent or unpredictable environmental or biological event that modifies ecological community composition. Functional traits are characteristics of the biology of an organism that can be measured at the individual level. A community functional trait responses to disturbance will depend on many factors, including community composition, background disturbance rates, and habitat connectivity, among others, and it is important for ecologists to consider the local ecological context when forming hypotheses and selecting functional diversity metrics to test them. In our case, hypothesis construction was informed by 10 years of research in an arid-land stream system (Bogan and Lytle 2007, 2011, Bogan 2012, Bogan and Boersma 2012, Bogan et al. 2013a) and work in the fields of community assembly theory (Samuels and Drake 1997, Leibold et al. 2004, Leibold and McPeek 2006), restoration ecology (Matthews and Spyreas 2010, Ruhí et al. 2012), disturbance ecology (Houseman et al. 2008, Mouillot et al. 2013), and functional ecology (Mouchet et al. 2010, Mason and de Bello 2013, Mason et al. 2013, Mouillot et al. 2013). As suggested by Rosenberg (2002) and Mouillot et al. (2013), we visualize differences in functional trait composition between disturbed and undisturbed communities using a multidimensional functional trait space with species as points and species abundances indicated by point size (Figure 4.1). Points that overlap represent functionally redundant species.

H1: No Change Hypothesis (Figure 4.1A). In communities with high background disturbance rates, species may have evolved trait combinations that make them resistant to future disturbances. In this case we expect species abundances and trait combinations to be similar in disturbed and undisturbed communities.

H2: Directional Change Hypothesis (Figure 4.1B). Alternately, communities comprised of highly vulnerable species may exhibit dramatic changes in both taxonomic and functional composition, including high turnover of trait combinations and changes in abundance for the few taxa that exist in both disturbed and undisturbed states. In this case, we would expect the abundance-weighted mean trait values (functional centroids) of the disturbed and undisturbed communities to be far from one another in trait space.

H3: Convergence Hypothesis (Figure 4.1C). Instead of eliciting complete turnover, disturbance may act as an environmental filter (Poff 1997, Leibold et al. 2004, Grime 2006) and reduce the trait combinations in disturbed communities to a subset of those existing in undisturbed communities (Leibold et al. 2004, Webb et al. 2010). Environmental filtering results in functional convergence, so that species in disturbed communities occupy less functional volume than those of undisturbed communities even though the location of each community's mean trait value (functional centroid) may be the same.

H4: Divergence Hypothesis (Figure 4.1D). In contrast, disturbance may create functional niches for colonization by species that were previously excluded from the community (e.g. Cadotte 2007). Such colonization may occur if disturbance causes the local extinction of a competitively-dominant species or facilitates the establishment of invasive species without supplanting native taxa (e.g. Hejda and de Bello 2013). Both events could lead to a community in which species in the disturbed state possess trait combinations that occupy a greater volume of trait space than in undisturbed communities, yielding functional divergence.

H5: Equal Impact Hypothesis (Figure 4.1E). In some situations, such as after habitat loss, disturbance may reduce the abundance of all trait combinations equally. In this case, neither the centroid location nor functional volume will change even though ecosystem processes may be fundamentally altered. These abundance differences will be represented by the contraction of point size in disturbed community ordinations (Figure 4.1E).

H6. Skewed Effect Hypothesis (Figure 4.1F). Disturbance could favor certain trait combinations over others without causing the addition or loss of species (Mouillot et al. 2013). Invasions by superior competitors may suppress the abundance of weak competitors, or changes in the structure of the predator community may rearrange food webs without causing species extinctions. These subtle shifts in the abundance of trait combinations may precede the complete turnover observed under the Directional Change Hypothesis. Traits that are favorable in undisturbed communities may be unfavorable in disturbed communities or vice versa. In this case species abundances in undisturbed and disturbed communities will be skewed toward favorable regions of trait space but the overall volume of trait space occupied by disturbed and undisturbed communities will be equal.

4.3 METHODS

We applied three functional diversity metrics that quantify aspects of the multidimensional functional space necessary to distinguish among the six hypotheses (Figure 4.1): functional distance (described below), functional richness (Villéger et al. 2008), and functional dispersion (Laliberté and Legendre 2010). All three metrics are derived from pairwise distances between species in trait composition. In this manuscript we use Gower dissimilarity (Gower 1971) because it can accommodate the categorical trait matrix for our case studies; however, any distance measure may be selected.

One of our goals is to determine whether disturbance affects the location of a community's abundance-weighted mean trait value, or functional centroid (as in Figure 4.1B), and we will do so using functional distances. A community's functional centroid is a composite mean trait value for all species in a community that is weighted by species abundances and is calculated using ordination methods as described below. We define functional distance as the distance between the functional centroids of two communities in trait space (as in Figure 4.1B). While it is straightforward to use ordination methods to calculate the functional distance between two communities, calculating distances between multiple communities that have been grouped, as in our case, is problematic. We wish to determine if the functional distances between disturbed and undisturbed communities are greater than distances between randomly selected pairs of communities. Biologists have long struggled to make inferences based on distance matrices because the pairwise distances associated with a single site, community, or individual (values within a row or column in the matrix) are non-independent. This non-independence creates a correlated error structure that prohibits calculation of meaningful confidence intervals or standard errors (Clarke et al. 2002). We address this problem using mixed effects models with disturbed/undisturbed as a fixed effect and community as a random effect. A similar method has been applied with genetic distances (Van Strien et al. 2012) and landscape distances (Bellamy et al. 2003), but to our knowledge this is its first application to measure functional distance.

First, we created a distance matrix of the Gower dissimilarities between communities. We then calculated an abundance-weighted centroid (hereafter "functional centroid") for each community from the distance matrix using a modification of function fdisp() in R package FD (Laliberté and Legendre 2010, Laliberté and Shipley 2011). This function applies principal coordinates analysis to the distance matrix to generate centroid coordinates for each community and correct for negative eigenvalues as described by Anderson (2006). Euclidean distances between points in principal coordinate space reflect the original Gower distances (Gower 1966). We calculated pairwise Euclidean distances between the centroids of all disturbed and undisturbed communities ("functional distances") and examined the effect of disturbance on these distances using a mixed-effects model as follows:

$$Y_{ijk} = \mu_k + \alpha_{ik} + \beta_{jk} + \varepsilon_{ijk}$$

Where Y_{ijk} is the functional distance between the centroids of communities i and j, μ_k is the fixed effect of disturbed/undisturbed (0/1), α_{ik} and β_{jk} are random effects to account for correlations between pairwise distances that have a community in common, and ε_{ijk} is the error term. Following the suggestion of Van Strien et al. (2012) and Rafael Wüest (personal communication), who addressed this issue with genetic distances, we used Markov chain Monte Carlo simulation to repeatedly resample distances from the distance matrix and compare models with and without the disturbance term. We examined posterior means and the 95% credible interval to determine model performance. When the superior model included the disturbance term and the credible interval for the disturbance term did not overlap zero, we considered communities i and j to have demonstrated a disturbance-induced shift in the functional space.

Functional distance can reflect changes in functional structure resulting from species turnover or large shifts in the abundance weighting of species in trait space, in accordance with the Directional Change and Skewed Effect hypotheses (Figure 4.1B&F). Yet, communities with no significant difference in the location of functional centroids may still exhibit important functional responses to disturbance (Figure 4.1C-E) and require metrics that are not dependent upon communities' mean trait values. Functional richness is one such metric that measures the overall volume of trait space (convex hull) that is occupied by species in a community, irrespective of abundance (Cornwell et al. 2006, Villéger et al. 2008). This metric describes the overall range of trait combinations and can detect disturbance-induced convergence or divergence in functional composition (Convergence Hypothesis and Divergence Hypothesis, Figure 4.1C&D).

Functional richness is determined by the presence or absence of species trait combinations in a community and does not take species abundances into account. Therefore functional richness is highly influenced by extreme or rare trait values and may fail to detect changes in the distribution of abundances in trait space that may forewarn local extinctions. Functional dispersion is an alternative metric that quantifies the mean of the abundance-weighted distances of each species to a community functional centroid (Laliberté and Legendre 2010). It measures how community species abundances are distributed in the functional space. Differences in dispersion between disturbed and undisturbed communities may indicate subtle sub-threshold changes in functional composition that precede changes in functional distance (Mouillot et al. 2013), as in Figure 4.1F.

We visualized the relationships between species in trait space using non-metric multidimensional scaling ordinations. We square-root transformed each community's species-by-community matrix to minimize the influence of highly abundant taxa, constrained ordinations to two dimensions, and reported stress and R^2 values for each (McCune and Grace 2002). All ordinations converged on stable solutions. For illustration purposes in our case studies, we summed species abundances within the undisturbed and disturbed communities and scaled the size of each point on an ordination by total disturbed and undisturbed abundance of that species. It is important to note, however, that functional centroids, functional richness and functional dispersion were calculated for each replicate community sample, allowing us to estimate means and variance. After examining the distributions of the response variables (functional richness and functional dispersion), we compared richness and dispersion between disturbed and undisturbed treatments using Welch's t-tests. All analyses were conducted in R version 2.14.1 (R Development Core Team 2011) using packages MCMCglmm, lme4, FD, and vegan (Hadfield 2010, Bates et al. 2011, Laliberté and Shipley 2011, Oksanen et al. 2012).

4.4 THREE CASE STUDIES

The system:

Fragmented arid-land streams of southeastern Arizona represent an ideal system to study community responses to disturbance (Bogan and Lytle 2007). Seasonal cycles of flood and drought cause small headwater streams to contract to a series of isolated pools during the early summer dry season (May-June) and streams remain fragmented until the late summer monsoons (July-September) when connectivity is restored. Aquatic invertebrate taxa inhabiting arid-land streams are adapted to high seasonal environmental variability, yet climate change and growing human demands on hydrologic resources present aquatic taxa with novel disturbance regimes, both biotic and abiotic in nature.

A decade of aquatic studies in fragmented headwater streams in southeastern Arizona has yielded a thorough understanding of seasonal and interannual dynamics in stream-dwelling invertebrate communities and recorded ongoing changes in stream hydrology and community composition (Bogan and Lytle 2007, 2011, Bogan and Boersma 2012, Bogan et al. 2013a). Our three datasets address two concurrent climate-induced threats to arid-land aquatic taxa: intensification of seasonal droughts and top predator extinctions. Observational studies show that streams that were once perennial are drying completely for the first time, leading to local extinctions of aquatic top predators and the replacement of aquatic obligate taxa by those with drought resistant traits (Bogan 2012). Stream drying and predator extinctions occur concurrently in natural streams, inspiring manipulative experiments to disentangle biotic and abiotic drivers of aquatic community responses to climate change. The following three studies use experimental and observational methods to understand invertebrate community responses to biotic and abiotic disturbances: a simulated drying experiment (Boersma et al. in review), a simulated top predator extinction experiment (Boersma et al. in revision), and a field study during severe drought (Bogan and Lytle 2011).

Trait choice:

We used a functional trait database of morphological, behavioral, and life history characteristics for nearly all aquatic insect genera in southeastern Arizona (Schriever et al. in prep, Boersma et al. in press). From this database we chose seven categorical invertebrate traits that are associated with disturbances in arid-land streams: body size, voltinism, dispersal, respiration, functional feeding group, diapause, and locomotion (Table 4.1). As with all studies involving functional traits, trait choice is a subjective process and researchers must carefully select traits based on prior knowledge of ecological processes. We chose these seven traits based on 1) our knowledge of disturbances in arid-land stream invertebrate communities, and 2) the availability of trait information for our taxa. Before study outcomes are applied to real-world management scenarios, we recommend that researchers conduct a sensitivity analysis to assess the robustness of their inferences to randomly-selected subsets of traits.

Study 1: Drying manipulation experiment

Research question: How does drying severity affect aquatic invertebrate taxonomic and functional composition?

Methods: Boersma et al. (Boersma et al. in press) manipulated drying magnitude in experimental mesocosms and measured the responses of the aquatic invertebrate community. They inoculated aquatic mesocosms with invertebrates collected from three fragmented streams in southeastern Arizona and applied two drying treatments: control ("undisturbed", water level maintained at 10cm) and severe ("disturbed", allowed to dry to 1cm, wet sediment with small pools). A moderate drying treatment was also applied that will not be discussed here. Tanks were covered with shade cloth to limit dispersal and colonization and isolate species loss via mortality from community recovery via colonization. They sampled mesocosms at the end of the 6wk dry season, identified the invertebrates, and recorded 41 taxa in control mesocosms and 35 in top predator removal mesocosms (Boersma et al. in review).

Prediction: Severe drying and limited recolonization will create a strong environmental filter on resident taxa and support the Convergence Hypothesis (Figure 4.1B) as indicated by higher functional richness in control communities than in disturbed communities.

Results: Despite a significantly more extreme abiotic environment in the severe drying treatment than in the control treatment (Boersma et al. in review), we observed no differences between treatments in the any of the functional diversity metrics (Tables 4.2, 4.3). However, abundances of most taxa were lower in the severe treatment than in the controls (Boersma et al. in review), and the effects of drying on abundance were evenly distributed across the functional space (Figure 4.2A).

Interpretation: Taxa were equally vulnerable to simulated drying disturbance, best supporting the Equal Change Hypothesis (Figure 4.1E). Notably, the severe drying treatment in this experiment maintained water depth at ~1cm so that sediment and detritus remained wet and small aquatic refuges were present for the duration of the experiment. A complete drying treatment was not applied in this study. Research in other aquatic systems suggests that aquatic invertebrates are highly resistant to drought disturbances as long as aquatic refuges remain (Dewson et al. 2007b, Walters and Post 2010) and that one of the primary effects of drying is habitat contraction, resulting in lower abundances of aquatic organisms (Stanley et al. 1997, Bunn and Arthington 2002, Acuña et al. 2005).

Study 2: Top predator removal experiment

Research question: How do simulated top predator extinctions affect aquatic invertebrate taxonomic and functional composition?

Methods: The hemipteran *Abedus herberti* is a flightless top predator that is vulnerable to changing drought disturbance regimes. Catastrophic stream drying has been associated with local extinctions of *A. herberti* in two southeastern Arizona streams in the past decade (Bogan 2012). Boersma et al. (*in revision*) simulated top predator extinctions in mesocosms containing dry-season aquatic invertebrates and sampled invertebrate communities at the end of a 6wk dry season. They removed all *A. herberti* individuals in a predator extinction treatment ("disturbed") and left the aquatic community intact in control treatments ("undisturbed"). There were 38 taxa in control mesocosms and 45 in predator removal mesocosms at the end of the six-week experiment.

Prediction: Cascading effects of top predator removal will generate high turnover in functional trait structure, supporting the Directional Change Hypothesis (Figure 4.1B). Disturbance will cause a shift in functional centroid location in trait space and be detected by a significant effect of disturbance on functional distance.

Results: We detected an effect of disturbance on functional distance (Table 4.3), and both functional richness and dispersion were significantly greater in predator removal treatments than in control treatments (Table 4.2, Figure 4.2B).

Interpretation: Community functional diversity in the top predator removal experiment supported the Directional Change Hypothesis (Figure 4.1B), Divergence Hypothesis (Figure 4.1D) and Skewed Effects Hypothesis (Figure 4.1F). Top predator removal caused functional trait composition to diverge because new taxa that colonized mesocosms following top predator removal possessed trait combinations that were not represented in the control communities, resulting in higher functional richness (Figure 4.2B). While abundances in the control treatment were fairly regularly distributed in trait space, the most abundant trait combinations in the top predator removal treatment were located at the extremes of the trait space, which generated higher functional dispersion following predator removal. Additionally, functional divergence and functional distance detected the arrival of unique species in the top predator removal treatment. Many of the colonizing taxa were secondary predators, suggesting that top predator removal created niches that were previously unavailable to colonists.

Study 3: Drought field study

Research question: How will natural aquatic invertebrate communities change following catastrophic stream drying?

Methods: Bogan and Lytle (2011) sampled aquatic invertebrates seasonally in a fragmented arid-land stream in French Joe Canyon, Whetstone Mountains, Cochise Co., Arizona, US, for 3y before and 4y after a severe drought and catastrophic stream drying. Their samples document aquatic community changes as the stream transitioned from one with permanent pools as dry-season refuges for aquatic biota to one that dries completely during extreme years. We compared 8 samples taken in the years preceding the drying event ("undisturbed") with 12 taken after the stream became intermittent ("disturbed"). There were 28 taxa in the undisturbed samples and 36 in disturbed samples.

Prediction: Complete stream drying will limit the diversity of trait combinations and produce lower functional richness in disturbed than undisturbed communities, lending support to the Convergence Hypothesis (Figure 4.1C). Additionally, recolonization by disturbance-tolerant taxa will shift the functional centroids in the disturbed communities and be reflected in the functional distances between pre- and post-drying samples, supporting the Directional Change Hypothesis (Figure 4.1B).

Results: Neither functional dispersion nor functional distance differed before and after stream drying, but functional richness was significantly higher in undisturbed pre-drying communities than in the disturbed post-drying communities (Table 4.1, Figure 4.2C).

Interpretation: The change in functional community structure following stream drying supports the Convergence Hypothesis (Figure 4.1C). There were no significant differences in species richness in the pre- and post-drying communities (Bogan and Lytle 2011). Instead, several large dispersal-limited taxa, including the top predator *A. herberti*, were locally extirpated and replaced by smaller, more vagile taxa with trait combinations that were previously excluded from the community, with no recovery during the four years following drying. Studies conducted in other systems have recorded similar community changes in response to catastrophic drying events (e.g. Boulton and Lake 1992, Acuña et al. 2005, Bêche et al. 2009).

4.5 DISCUSSION

We created a conceptual framework that consists of six non-mutually exclusive hypotheses of the effects of disturbance on functional trait structure in fragmented communities and selected three functional diversity metrics to discern among the hypotheses. We tested the framework with three studies from fragmented arid-land streams that involved biotic and abiotic disturbances. Our hypotheses effectively captured the processes observed in the studies, but not always in the manner we predicted. The mismatches between predicted and observed outcomes revealed important drivers of functional trait structure and led us to question our assumptions about disturbances in fragmented arid-land streams. We also developed a new method for estimating the effects of disturbance on the distance between functional centroids ("functional distance") that accounts for the non-independence of pairwise distances. Our framework and novel metric can be applied in other systems to generate a greater general understanding of how ecological communities respond to disturbances

Our functional distance method detected a disturbance-induced shift in centroid in the top predator manipulation (Study 2) but not in the drying manipulation (Study 1) or drought field study (Study 3). Therefore, we can conclude that functional turnover played a minimal role in the community responses to drought disturbance in this arid-land stream system. Species turnover is a classic prediction of community responses to environmental disturbances (Albouy et al. 2012, Mason et al. 2013); however, turnover in species composition may not result in equivalent turnover in functional composition if extirpated species are replaced by species with similar trait combinations (Carmona et al. 2012). In natural habitats complete turnover may be rare, and minor changes in species composition may not result in parallel shifts in the location of the functional centroid if the taxa that are eliminated possess rare or extreme trait values that fall at the edges of the functional trait space. The expectation of dramatic shifts in functional space may be misguided and may place too much emphasis on a community's mean trait value and not enough on changes in extreme or rare trait values that may play important functional roles, such as large body size or high trophic level (Säterberg et al. 2013).

Extreme and rare trait values were particularly important to the functional response in the drought field study and would be undetectable from measurements of species richness alone (Study 3). Complete stream drying acted as a strong environmental filter, decreasing the functional richness, or volume of trait space occupied, when compared with the pre-drying communities. In this study, species richness and functional richness exhibited different patterns. Species richness increased following drying while functional richness decreased. A mismatch between species richness and functional richness is informative (Micheli and Halpern 2005) and can be explained when this functional analysis is combined with the published taxonomic analysis (Bogan and Lytle 2011): the members of the community that disappeared following drying were large-bodied and poor dispersing taxa with unique trait combinations, including the top predator *A. herberti* and dominant detritivore *Phylloicus mexicanus*. Following drying, pools were colonized by multiple functionally redundant beetle species with identical trait combinations that included aerial dispersal, rapid reproduction, and air-breathing. Trait convergence is a prediction of the effects of extreme environmental filtering (Mason et al. 2013), as some traits are eliminated and only species possessing disturbance-resistant traits remain (Leibold et al. 2004). Environmental filtering is well-documented in stream invertebrate communities in temperate systems (Townsend and Hildrew 1994, Poff 1997).

Functional richness responded significantly to top predator manipulation in Study 2 as well, although the sign of the response was opposite that in the drought field study; top predator removal increased functional richness whereas stream drying decreased functional richness. We believe that the regional pool of available colonists generated these contradictory patterns. The drought field study took place in in the Whetstones Mountains, AZ, in which French Joe Canyon contained the only remaining perennial aquatic habitat within a 10km radius, whereas the top predator manipulation experiment was conducted adjacent to a perennial stream in the Chiricahua Mountains, AZ, a range replete with perennial water. These different degrees of isolation produced two different pools of available colonists. In both studies, taxa unique to the disturbed treatments were active dispersers, but taxa that were able to recolonize the very isolated habitats in the drought field study were those with a narrow set of traits that facilitate long-distance dispersal and colonization of novel habitats, including air-breathing, strong flight, and rapid reproduction (Bogan and Lytle 2011). Conversely, taxa that colonized mesocosms following top predator removal were a diverse mix of beetles, dragonflies, and alderflies with equally diverse trait combinations (Boersma et al. in revision), explaining the observed expansion of trait space in the manipulation that was not recorded in the field study. Aerial dispersal has been documented to be an important driver of community dynamics in fragmented arid-land streams during the dry season (Bogan and Boersma 2012), and the differences in functional richness between these two studies reinforced the importance of dispersal in community recovery following disturbance (resilience, sensu Lake 2013).

Dispersal and colonization likely generated the functional dispersion patterns as well. In the top predator removal treatment in Study 2, colonist species abundances were distributed at the edges of the trait space, whereas the control abundances were more central to the trait distribution (Figure 4.2B). The opposite is true in the drought field study, where the highly abundant colonists in the disturbed samples shared similar trait combinations and clustered in the center of the ordination (Figure 4.2C), although with only moderate evidence for a difference in treatment means ($p = 0.07$, Table 4.2). The top predator manipulation demonstrates the benefits of combining multiple functional diversity metrics. When used in combination, functional dispersion and functional richness highlighted both the arrival of new trait combinations as taxa colonized the top predator removal mesocosms and also more subtle shifts in the distribution of abundances in trait space (Figure 4.1D&F).

Mouillot and coauthors (2013) suggest that abundance-weighted functional diversity metrics may provide early indications of threats to ecosystem functioning before the functions themselves are lost, however we did not see evidence of this utility with our case studies. Complete stream drying as observed in the drought field study is a catastrophic disturbance for aquatic taxa that results in immediate changes to community composition, and the drying manipulation demonstrates that aquatic functional structure remains intact until all water disappears. Therefore, we would not expect abundance-weighted metrics to provide additional information on functional responses to drying since the community responds to drying as a threshold, not a gradual change (Boulton 2003).

Our analysis suggests that abundance-weighted metrics may indeed be useful in this system when the disturbance is biological in nature. The treatments in the top predator manipulation were binary, designed to mimic a dramatic extinction event akin to that observed in the drought field study (Bogan and Lytle 2011) and to compare the impacts of top predator extinction with healthy stream communities. In some arid-land streams, *A. herberti* populations are steadily declining in response to their intensifying abiotic environment instead of exhibiting a threshold effect as in the drought field study (Bogan 2012). In these instances, abundance-weighted functional diversity metrics may be valuable to detect sub-threshold changes in functional composition. Säterberg and coauthors (2013) demonstrated that large-bodied predators can only withstand small changes in mortality before they become functionally extinct, whereby a further reduction in population size leads to the extinction of another species in the community. By this definition, the functional extinction of a top predator will be preceded by changes in the abundances of other community members – changes that can be detected with abundance-weighted metrics like functional dispersion. Janeček and colleagues (2013) combined abundance-weighted and non-abundance-weighted functional diversity metrics to make recommendations on how to mitigate the effects of human actions on biodiversity in meadow plant communities, and similar applications may be possible in managing water abstractions in arid-land streams to conserve aquatic biodiversity.

In the drying manipulation experiment (Study 1), the severe drying treatment allowed mesocosms to dry to a depth of ~1cm. While this degree of drying appeared severe to the researchers, the highly adapted fauna of dry-season arid-land streams did not respond accordingly, suggesting that this “severe disturbance” did not function as a disturbance at all (Resh et al. 1988). The species that were eliminated by the drying treatment were randomly distributed across the functional space (Boersma et al. in press) and may have been eliminated by neutral extinction processes and not environmental filtering as we had predicted (Hubbell 2001). Because this experiment limited recolonization with a canopy installed above the mesocosms, these patterns reflect high resistance of functional structure. The gradual habitat loss that accompanied drying can account for the lower invertebrate abundances in the drying treatment than in the controls (Boersma et al. in press), supporting the Equal Impact Hypothesis (Figure 4.1E).

In all three studies, researchers have previously analyzed the effects of disturbance on aquatic invertebrate taxonomic composition, yet our hypothesis-driven disturbance traits framework still revealed unexpected relationships and can be used to generate new hypotheses. The framework suggests that the three studies exist along a continuum of climate change threat, from Studies 1 through 3: 1) the drying manipulation revealed the high resistance of functional composition to severe habitat loss, 2) the top predator removal manipulation demonstrated functional divergence when a nearby colonist source was available, and 3) the drought field study documented functional convergence when a nearby colonist source was absent. This analysis led us to create a new hypothesis of the importance of colonists in mitigating the effects of top predator extinctions.

As in any study of functional diversity, the quality of our inferences depends on the quality of functional trait information (Petchey and Gaston 2006). In this study we chose seven traits that we believed would be important in determining invertebrate responses to disturbance. It would be beneficial to repeat our analyses using a different selection of traits. For example, physiological traits such as temperature tolerance and metabolic rate may be important indicators of species performance under extreme conditions. Because of limited information on arid-land aquatic taxa, we relied on trait measurements from a database that provided a single categorical value for each species (Schriever et al. in prep, Boersma et al. in press). Ideally, we would measure continuous traits on all taxa to be able to estimate intraspecific variability around mean trait values (Cianciaruso et al. 2009, Violle et al. 2012). While this level of resolution is not feasible in many systems, it may be realistic for researchers to record simple continuous traits such as body size or biomass, and increase the resolution of the trait matrix without significantly increasing the amount of time spent processing samples.

4.6 CONCLUSIONS

Our hypothesis-driven functional analysis led us to challenge our assumptions of how biological and environmental disturbances fit into the region's disturbance history and consequently how future disturbances may affect the resistance and resilience of aquatic communities. Top predator extinctions (Study 2) and complete stream drying (Study 3) are novel disturbances and were accompanied by significant changes in functional diversity. In contrast, the near-complete drying simulated in Study 1 fell within background disturbance levels and functional diversity was not affected. Taxa that are exposed to predictable disturbance patterns will evolve traits to withstand future events that match the historic pattern (Lytle and Poff 2004), however, global climate change brings novel disturbance regimes and unpredictable responses by ecological communities. We suggest that functional diversity metrics, when linked to specific ecologically-informed hypotheses as in our framework, may provide a mechanistic understanding of community-environment interactions in a future characterized by greater magnitude and frequency of disturbances.

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Table 4.1. Functional trait categories. Seven traits: body size, functional feeding group, respiration, diapause, dispersal, locomotion, and voltinism.

Trait	Modalities
Body size	< 9mm, 9 - 16mm, > 16mm
Functional feeding group	Collector-gatherer, Shredder, Scraper/grazer, Filter-feeder, Plant piercer, Predator-piercer, Predator-engulfer
Respiration	Integument, Gill, Plastron/spiracle/vesicle
Diapause	Certain, Likely, Possible, Unknown
Dispersal	Aquatic passive, Aquatic active, Aerial passive, Aerial active
Locomotion	Burrowing, Interstitial, Sprawling, Attached, Swimming, Skating, Climbing
Voltinism	<1 generation/year, 1 generation/year, >1 generation/year

Table 4.2. Functional richness and functional dispersion for the three case studies. Values were compared between undisturbed and disturbed communities using Welch's t-tests.

Case study	Functional metric	Undisturbed	Disturbed	t	d.f.	p-value
Drying manipulation	Richness	0.277	0.167	1.425	9.326	0.187
	Dispersion	0.311	0.308	0.099	11.767	0.923
Top predator manipulation	Richness	0.193	0.312	3.932	12.781	0.002
	Dispersion	0.151	0.234	4.131	13.683	0.001
Drought field study	Richness	0.352	0.261	2.541	14.447	0.023
	Dispersion	0.897	0.664	1.920	17.959	0.071

Table 4.3. Results of Markov chain Monte Carlo (MCMC) generalized linear mixed-effects models with disturbed/undisturbed as a fixed effect and invertebrate community sample as a random effect. Support for models that include the fixed effect indicates an effect of disturbance on functional distance. Deviance information criteria (DICs), MCMC p-values (pMCMCs), posterior means, and credible intervals (CIs) are provided for the disturbance term in the models that include the fixed effect.

Study	Model	DIC	pMCMC	Mean functional distance	Lower CI	Upper CI
Drying manipulation	Random effect only	-204.1544				
	Random + fixed effect	-203.3527	0.434	0.01387	-0.04758	0.01908
Top predator manipulation	Random effect only	-255.5569				
	Random + fixed effect	-262.6815	0.00167	0.04412	0.01759	0.07632
French Joe field study	Random effect only	-368.9781				
	Random + fixed effect	-369.6501	0.148	0.020373	-0.005615	0.047391

Figure 4.1. Predicted community functional trait responses to disturbance. These panels show six non-mutually exclusive hypotheses for how trait distributions may respond to disturbance. Each panel is an ordination of species in multidimensional trait space, where each point represents a species and its location is determined by its combination of traits. Blue circles represent species in an undisturbed community, and red circles represent species in a disturbed community. Circle size is determined by each species' abundance. A) **Null Hypothesis:** Undisturbed and disturbed communities have identical trait distributions. This may result if communities are highly resistant to disturbance. B) **Directional Change Hypothesis**: While some trait combinations (or species) are present in both communities, undisturbed and disturbed communities occupy distinct regions of trait space, as reflected by distinct functional centroids (Xs). This may occur if some species are eliminated by disturbance and replaced by new species that possess disturbance-resistance traits. C) **Convergence Hypothesis:** Disturbed communities occupy less area in trait space than undisturbed communities. Convergence could result if disturbance acts as an environmental filter, restricting the trait combinations that can persist in disturbed communities. D) **Divergence Hypothesis**: Disturbed communities occupy more area in trait space than undisturbed communities. Convex hulls are outlined to highlight the distinct trait distributions of disturbed/undisturbed communities. Divergence could result if disturbance causes the extinction of a competitive dominant species and opens previously-unavailable niches. E) **Equal Impact Hypothesis**: Species abundances differ between disturbed and undisturbed communities, but these effects are regularly distributed through trait space. Equal Impact may occur in communities in which all trait combinations are equally impacted by disturbance. F) **Skewed Impact Hypothesis**: Abundances in the undisturbed community are regularly distributed through trait space, while abundances in the disturbed community are greater in the lower left quadrant of the ordination. Skewed Impact may occur if disturbance favors some trait combinations over others but does not eliminate any species entirely.

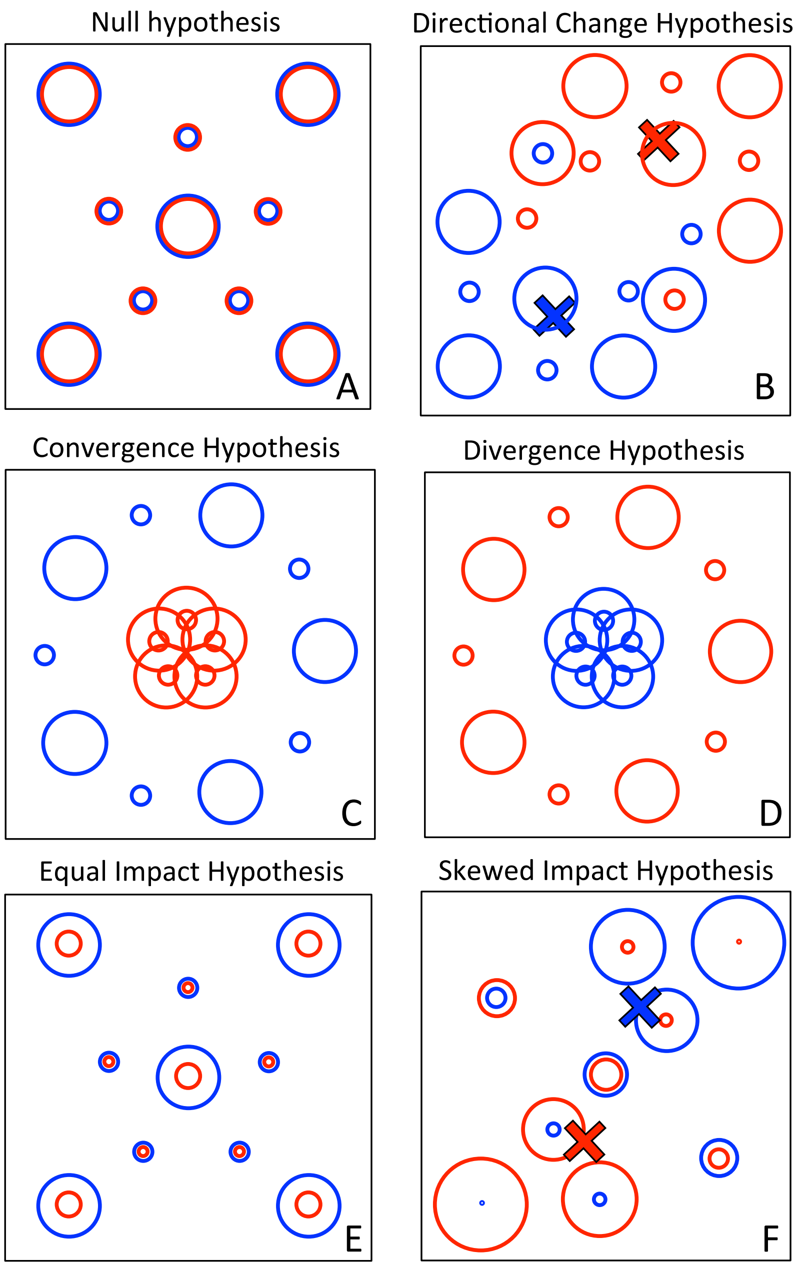
Null hypothesis
A
Directional Change Hypothesis
B
Convergence Hypothesis
C
Divergence Hypothesis
D
Equal Impact Hypothesis
E
Skewed Impact Hypothesis
F

Figure 4.1.

Figure 4.2. Visualization of community functional trait responses to disturbance for three case studies. Each panel is a nonmetric multidimensional scaling (NMDS) ordination of species in multidimensional trait space, where each point represents a species and its location is determined by its combination of traits. Blue circles represent species in the undisturbed community and red circles represent species in the disturbed community, and the convex hulls (functional richness) for each treatment are outlined with the same colors. Circle size is determined by each species' abundance. Multiple concentric circles of the same color reflect functionally redundant species. A) Study 1 - Drying manipulation (NMDS: 2 Dimensions, Stress = 0.102, R^2 = 0.949): There were no differences in trait composition between treatments, although species abundances were lower in the severe drying treatments than in the controls, as reflected by concentric blue points within red points. Study 1 supports the Equal Impact Hypothesis. B) Study 2 - Top predator manipulation (NMDS: 2 Dimensions, Stress = 0.107, R^2 = 0.947): The top predator removal (disturbed) treatment had significantly higher functional dispersion and functional richness than the control treatment, and top predator removal caused a shift in the location of the functional centroid. These differences are apparent on the ordination in the larger convex hull size of the disturbed treatment than the undisturbed treatment and the location of highly abundant species at the edges of the trait space for the disturbed treatment. Study 2 supports the Directional Change Hypothesis, Divergence Hypothesis, and Skewed Impact Hypothesis. C) Study 3 - drought field study (NMDS: 2 Dimensions, Stress = 0.0835, R^2 = 0.975): Functional richness significantly decreased following catastrophic stream drying, as reflected by the change in convex hull volume, however there were no differences in functional dispersion or functional distances. Study 3 supports the Convergence Hypothesis.

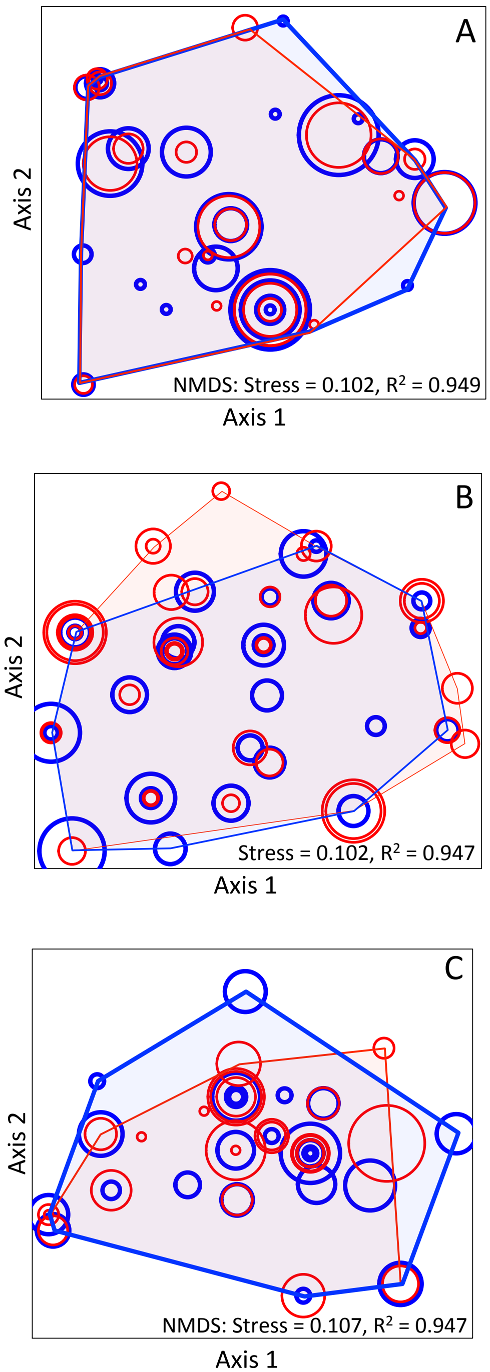
A
Axis 2
NMDS: Stress = 0.102, R² = 0.949
Axis 1
B
Axis 2
Stress = 0.102, R² = 0.947
Axis 1
C
Axis 2
NMDS: Stress = 0.107, R² = 0.947
Axis 1

Figure 4.2.

5 – Conclusion

Human-induced global climate change is dramatically modifying aquatic ecosystems, and these changes will intensify over the next century (Jackson et al. 2001, Seager et al. 2007, Barnett et al. 2008). While much is known about the direct abiotic effects of climate change on aquatic systems, understanding the indirect effects of climate projections on aquatic community structure will be essential in order to understand extinction dynamics and maintain ecosystem functioning in sensitive areas (Lake 2003). Mechanistic research on climate impacts on aquatic communities is facilitated by tractable systems with well-resolved local and regional species pools, in which dominant biotic and abiotic drivers have already been identified. This dissertation built on over ten years of research on population and community dynamics in the fragmented arid-land streams of southeastern Arizona, US (Lytle 1999, 2000, 2003, Lytle and Smith 2004, Bogan and Lytle 2007, Finn et al. 2007, Finn et al. 2009, Bogan and Lytle 2011, Bogan 2012, Bogan and Boersma 2012, Bogan et al. 2013a). These previous studies documented the limited dispersal capacity of the top predator *Abedus herberti* (Finn et al. 2007), the seasonal and interannual variation in aquatic invertebrate community composition in the region (Bogan and Lytle 2007), and the dramatic consequences of catastrophic stream drying (Bogan and Lytle 2011).

In this dissertation I conducted manipulative experiments to disentangle the indirect biotic effects of top predator extinctions from the direct abiotic effects of drying on aquatic communities. I applied a disturbance traits framework to assess how these different disturbance types influence functional trait composition. This research highlights the importance of disturbance history in predicting aquatic community responses to climate change. I observed consistent effects of top predator removal on aquatic communities in two years of experiments (Chapter 2), but predator extinctions in the field only generated some of these effects (Bogan and Lytle 2011). Top predator losses in experiments and in the field were accompanied by dramatic increases in the abundance of mesopredators and decreases in the abundance of decomposer *Phylloicus mexicanus*. However, while experimental predator removals caused an overall increase in functional trait diversity, the opposite pattern was evident in field samples (Chapter 4). I hypothesize that this discrepancy emerged because of differences in the availability of colonists. The importance of aerial dispersal in this system has been documented in other studies (Bogan and Boersma 2012).

I observed no response of aquatic invertebrate communities to drying manipulation (Chapter 3) despite clear evidence of the effects of drought in the field (Bogan and Lytle 2011). The aquatic invertebrates inhabiting dry-season pools are highly resistant to gradual seasonal drying as replicated in my experiment, but I hypothesize that dramatic community consequences would accompany the complete loss of surface water. It may be worthwhile to repeat the drought manipulation experiment with the addition of a complete drying treatment to test the effects of the complete drying threshold in an experimental setting (Boulton 2003).

It may also be fruitful to quantify the effects of colonist source on aquatic community recovery from disturbances. All three dissertation studies suggest a fundamental role of colonization in disturbance responses, but aerial dispersal and colonization are notoriously difficult to study. Repeating the top predator removal experiment (Chapter 2) and drying manipulation experiment (Chapter 3) with both open and restricted colonization would be a powerful way to quantify the effects of dispersal and tease apart in situ resistance to disturbance from resilience following disturbance (Lake 2013).

Field manipulations in fragmented arid-land streams would allow for a greater degree of realism than could be obtained with mesocosm experiments, and naturally fragmented habitats seem ideal for field experiments. However, my attempts to conduct field experiments were unsuccessful. I attempted to conduct a predator removal experiment in natural streams in 2009 using mesh exclosures to prohibit overland dispersal of the invertebrate top predator *A. herberti*. I was able to achieve reduced top predator abundances in most stream pools, but even with repeated removals I could never eliminate *A. herberti* altogether. The experiment ended abruptly when an unseasonably early flash flood washed the exclosures downstream.

Environmental variability also interfered with the top predator removal experiments (Chapter 2). In 2011 the Horseshoe II fire forced the evacuation of the Southwestern Research Station, Portal, AZ, during the first two weeks of the dry season, delaying the start of the predator removal experiment. In addition to the experiments at the research station, in 2011 I conducted a replicate predator removal experiment on the west side of the Chiricahua Mountains, in Chiricahua National Monument. I established mesocosm invertebrate communities along a small perennial reach of Bonita Creek and removed predators as described in Chapter 2. Firefighters actively contained the fire on the east side to protect landowners' property – and consequently my experiment – but the fire was allowed to burn naturally in the Monument, melting mesocosms and filling the creek with ash. This 82m stream reach was the only remaining perennial water in the monument, and I fear that *A. herberti* populations may have been extirpated by the fire. I returned to survey Bonita Creek in 2012 and found no *A. herberti*. I intend to work with National Park Service staff to monitor aquatic community recovery and census *A. herberti* in the coming years.

The effects of climate change will be amplified in arid regions, where hydrologic resources are naturally highly seasonal, fragmented, and prone to disturbance (Grimm et al. 1997). During the course of my doctorate I have witnessed the effects of changing climate on aquatic ecosystems first-hand, including one confirmed local extinction (Bogan 2012) and one potential extinction in Bonita Creek. The rate of change is astounding and I feel fortunate to have had the opportunity to work in these vulnerable habitats while there are still perennial aquatic communities to study. While it would take dramatic changes in public policy and human water consumption to halt stream drying in the American Southwest, I hope that the conceptual framework and lessons learned from my research will inform management of other aquatic ecosystems that are exposed to similar threats.

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APPENDICES

APPENDIX A. SUPPLEMENTAL MATERIALS FOR CHAPTER 2.

Figure A.1. Adult *Abedus herberti* consuming dragonfly nymph *Oplonaeschna*.

Figure A.2. 2010 mesocosm array.

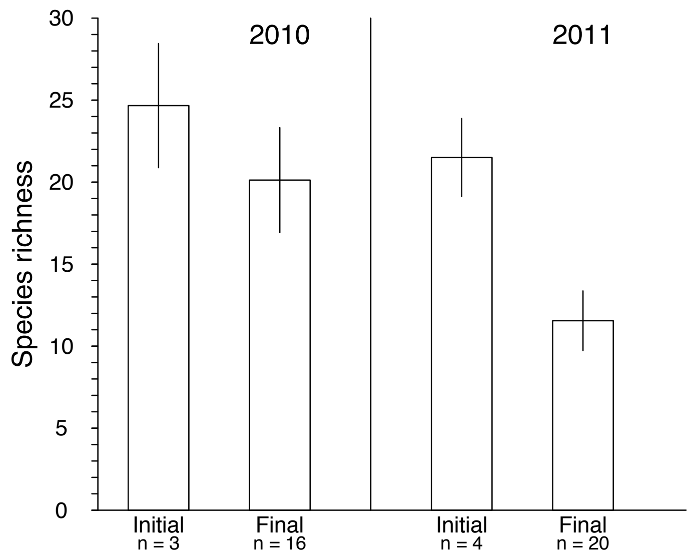

Figure A.3. Change in species richness between initial and final community samples in 2010 and 2011. 2010: Welch's t-test, t = -2.205, df = 2.999, p = 0.115; 2011: Welch's t-test, t = -8.973, df = 4.418, p = <0.001.

Table A.1. Variable transformations and two-sample comparisons.

Variable	Transformation	Statistical test
Species richness	Square root	Welch's *t*-tests
SW diversity	Untransformed	Wilcoxon rank-sum tests
Abundance	Untransformed	Welch's *t*-tests
Mesopredator richness	Untransformed	Generalized linear models
Mesopredator diversity	Untransformed	Monte-Carlo permutation tests
Mesopredator abundance	Natural log	Welch's *t*-tests

Table A.2. Mesopredators. All predatory taxa greater than 5mm in body length.

Order	Family	Genus/species
Coleoptera	Dytiscidae	*Agabus*
		Berosus puncatissimus
		Dytiscus
		Rhantus atricolor
		Rhantus gutticollis guticollis
		Thermonectus nigrofasciatus
		Tropisternus ellipticus
Hemiptera	Naucoridae	*Ambrysus woodburyi*
	Nepidae	*Ranatra*
Megaloptera	Corydalidae	*Corydalus*
		Neohermes
Odonata	Aeschnidae	*Oplonaeschna*
	Calopterygidae	*Hetaerina*
	Coenagrionidae	*Argia*
	Libellulidae	*Libellula saturata*
		Paltothemis lineatipes
Trichoptera	Polycentropodidae	*Polycentropus*

Table A.3. Abiotic characteristics of final mesocosms

Variable	2010 Mean	2010 SD	2011 Mean	2011 SD
pH	7.469	0.125	7.594	0.186
Dissolved oxygen (mg L^{-1})	4.500	0.000	4.688	0.458
Canopy cover (%)	89.36	7.216	0.838	0.000
Temperature (°C)	18.41	1.674	25.66	1.009

Table A.4. Invertebrate taxa. Category indicates treatments, years, or samples to which a taxon is unique: "Initial" = taxa present in initial samples in one year and absent from the other, "Removal" = taxa that were present in top predator removal mesocosms and not in controls within a given year, and "Control" = taxa that were present in control mesocosms and not in top predator removal mesocosms within a given year.

Order	Family	Genus/Species	Category
Coleoptera			
Hydroporinae larvae			Removal 2010
	Dryopidae	*Helichus lithophilus*	Removal 2010
		Helichus striatus	Control 2010
		Helichus triangularis	
		Posthelichus	Initial 2010
	Dytiscidae	*Agabus*	Removal 2011
		Dytiscus	Removal 2010, Removal 2011
		Hygrotus	Initial 2011, Control 2011
		Laccophilus fasciatus	
		Laccophilus maculosus	Control 2011
		Laccophilus pictus	
		Liodessus obscurellus	Initial 2011
		Rhantus atricolor	Removal 2010, Removal 2011
		Rhantus gutticollis gutticollis	Removal 2010
		Stictotarsus aequinoctialis	Initial 2011
		Stictotarsus corvinus	Initial 2010
		Stictotarsus roffi	
		Stictotarsus striatellus	Initial 2011
	Elmidae	*Microcylloepus*	
	Haliplidae	*Peltodytes*	
	Hydraenidae	*Hydraena*	
	Hydrophilidae	*Tropisternus ellipticus*	Removal 2011
		Berosus punctatissimus	
Diptera	Ceratopogonidae	*Atrichopogon*	Removal 2010
		Ceratopogon	Removal 2011
	Chironomidae		
	Culicidae	*Anopheles*	Initial 2011
		Culiseta	
		Culex	
	Dixidae	*Dixella*	Initial 2010
	Empididae		
	Ephydridae		
	Psychodidae	*Pericoma*	
	Simuliidae	*Simulium*	Initial 2010
	Stratiomyidae	*Caloparyphus*	Removal 2010
		Euparyphus	
	Tabanidae	*Tabanus*	

	Tipulidae	*Antocha*	Initial 2010
		Hexatoma	
		Limnophila	Initial 2010
		Limonia	Initial 2010
		Tipula	Initial 2011
Ephemeroptera	Baetidae	*Acentrella*	Initial 2010
		Baetis	Initial 2010
		Callibaetis	
		Fallceon	
	Heptageniidae	*Ecdyonurus*	Initial 2010
	Leptohyphidae	*Homoleptohyphes*	
	Leptophlebiidae	*Choroterpes*	Initial 2010
		Thraulodes	
	Siphlonuridae	*Siphlonurus*	Initial 2010
Hemiptera	Belostomatidae	*Abedus herberti*	
		Lethocerus	
	Corixidae	*Graptocorixa*	
	Naucoridae	*Ambrysus woodbury*	Initial 2011, Removal 2010, Removal 2011
	Nepidae	*Ranatra*	
	Veliidae	*Microvelia*	Initial 2011
Megaloptera	Corydalidae	*Corydalus*	Initial 2011, Removal 2011
		Neohermes concolor	Removal 2010
Odonata	Aeshnidae	*Oplonaeshna*	Initial 2010
	Calopterygidae	*Hetaerina*	Initial 2011, Control 2010
	Coenagrionidae	*Argia*	Initial 2011, Removal 2011
	Gomphidae	*Erpetogomphus*	Removal 2010
	Libellulidae	*Libellula saturata*	
		Paltothemis lineatipes	Removal 2010
Plecoptera	Capniidae		Initial 2010
	Nemouridae	*Malenka/Amphinemura*	Initial 2010
Trichoptera	Calamoceratidae	*Phylloicus mexicanus*	
	Helicopsychidae	*Helicopsyche*	
	Hydropsychidae	*Cheumatopsyche*	Initial 2011
		Hydropsyche/Ceratopsyche	Initial 2011
	Hydroptilidae	*Culoptila*	Initial 2010
		Hydroptila	Initial 2011, Control 2010
		Ochrotrichia	Control 2010, Control 2011
	Lepidostomatidae	*Lepidostoma*	Initial 2011
	Leptoceridae	*Oecetis*	Removal 2011
	Limnephilidae	*Hesperophylax*	Initial 2010
	Odontoceridae	*Marilia*	Initial 2011
	Philopotamidae	*Wormaldia*	Initial 2011
	Polycentropodidae	*Polycentropus*	

Non-insects		
Copepoda		Initial 2011
Mite		Removal 2011
Oligochaeta		
Ostracoda		Initial 2011
Gastropoda	Physidae	Initial 2011
Nematoda		Initial 2010
Planaria		
Platyhelmenthes		

Table A.5. Colonist taxa. Colonists were defined as taxa with >10 individuals in final mesocosm samples and 0 in initial samples. Category indicates the experiments during which each taxon colonized.

Order	Family	Genus/Species	Category
Coleoptera			
Hydroporinae larvae			2010, 2011
	Dytiscidae	*Berosus punctatissimus*	2011
		Liodessus obscurellus	2011
		Rhantus gutticollis gutticollis	2011
		Thermonectus nigrofasciatus	2011
		Stictotarsus corvinus	2011
	Elmidae	*Microcylloepus*	2010
Diptera	Culicidae	*Anopheles*	2010
		Culiseta	2010
		Culex	2010, 2011
	Ephydridae		2010
Ephemeroptera	Baetidae	*Fallceon*	2010
Hemiptera	Corixidae	*Graptocorixa*	2010
	Nepidae	*Ranatra*	2011
Megaloptera	Corydalidae	*Corydalus*	2010
Odonata	Aeschnidae	*Oplonaeschna*	2010
	Coenagrionidae	*Argia*	2010
	Libellulidae	*Libellula saturata*	2010
Trichoptera	Lepidostomatidae	*Lepidostoma*	2010
Non-insects			
Copepoda			2010
Ostracoda			2010
Gastropoda	Physidae		2010

Table A.6. Indicator species analysis of taxa significantly associated with control or top predator removal treatments based on community structure and trophic position.

	Year	Treatment	Taxon/Trophic group	I.V.	p
Community	2010	Control	*Phylloicus mexicanus*	69.7	0.037
			Helichus triangularis	75.3	0.043
		Removal	*Callibaetis*	76.9	0.017
			Rhantus atricolor	62.5	0.026
	2011	Control	*Phylloicus mexicanus*	72.7	0.029
		Removal	-	-	-
Trophic groups	2010	Control	Shredders	74.9	0.016
		Removal	Collector-gatherers	76.4	0.009
	2011	Control	Shredders	72.7	0.033
		Removal	Piercers	70.5	0.010

Notes: The indicator values (I.V.) range from 0 to 1, with 1 being complete faithfulness to a treatment group. Only indicators with I.V. > 60 and p < 0.05 are shown.

Appendix B. Supplemental materials for Chapter 3.

Table B.1. Functional trait modalities. Information was gathered on four traits: body size, respiration, functional feeding group, and diapause. See Appendix B, Table B.2 for trait values for each taxon.

Trait	Modality	Definition
Body size	1	< 9mm
	2	9 - 16mm
	3	> 16mm
Functional feeding group	1	Collector-gatherer
	2	Shredder
	3	Scraper/grazer
	4	Filter-feeder
	5	Plant piercer
	6	Predator-piercer
	7	Predator-engulfer
Respiration	1	Integument
	2	Gill
	3	Plastron, spiracle or vesicle
Diapause	1	Certain
	2	Likely
	3	Possible
	4	Unknown

Table B.2. Trait values for aquatic insect taxa. Information was gathered on four traits: body size, respiration (“Resp”), functional feeding group (“FFG”), and diapause. See Appendix B, Table B.1 for modality definitions.

Order	Family	Genus/species	Body size	Resp	FFG	Diapause	References
Coleoptera	Dryopidae	*Helichus triangularis*	1	3	3	3	Brown 1972
	Dytiscidae	*Dytiscus habilis/ marginicollis*	3	3	6	3	Larson et al. 2000
		Hydroporinae (larvae)	1	3	6	3	Arnett & Thomas 2000, Tachet et al. 2002
		Hygrotus	1	3	6	3	Larson et al. 2000
		Laccophilus fasciatus	1	3	6	3	Larson et al. 2000, Zimmerma 1970
		Liodessus obscurellus	1	3	6	3	Larson et al. 2000
		Rhantus gutticollis guticollis	2	3	6	3	Zimmerman & Smith 1975
		Sanfilippodytes	1	3	6	3	Larson et al. 2000
		Stictotarsus aequinoctialis	1	3	6	3	Zimmerman & Smith 1975a,t
		Stictotarsus corvinus	1	3	6	3	Zimmerman & Smith 1975a,t
		Stictotarsus roffi	1	3	6	3	Zimmerman & Smith 1975a,t
		Stictotarsus striatellus	1	3	6	3	Zimmerman & Smith 1975a,t
	Elmidae	*Microcylloepus pusillus*	1	3	1	3	Shepard (Bogan pers comm 2013), Brown 1972
	Gyrinidae	*Gyrinus plicifer*	1	2	7	3	Arnett & Thomas 2000, Merr et al. 2008, Usinger 1956
	Hydraenidae	*Hydraena*	1	3	3	3	Usinger 1956
	Hydrophilidae	*Berosus punctatissimus*	1	3	7	3	Usinger 1956, Van Tassel 19
		Berosus salvini	1	3	7	3	Usinger 1956, Van Tassel 19
Diptera	Ceratopogonidae	*Ceratopogon*	1	2	7	2	Tachet et al. 2002, US EPA
	Chironomidae	*Apsectroptanypus*	1	1	7	4	Wiederholm 1983
		Chironomus	1	1	1	1	Williams and Hynes 1976
		Cryptochironomus	1	1	6	4	Wiederholm 1983, Epler 199
		Dicrotendipes	1	1	1	2	Gray 1981, Wiederholm 198 Paltridge et al. 1997, Epler 2001
		Lauterborniella	1	1	1	1	Pinder & Reiss 1983
		Phaenopsectra	1	1	3	2	Grodhaus 1980
		Polypedilum	1	1	1	2	Hinton 1951
		Pseudochironomus	1	1	1	4	Wiederholm 1983, Epler 200 Thomas & Ferrington 1997

		Thienemannimyia grp.	1	1	7	2	Langton and Casas 1999
	Culicidae	*Anopheles*	1	3	7	1	Tachet et al. 2002, US EPA
	Stratiomyidae	*Caloparyphus*	2	3	2	1	Tachet et al. 2002, US EPA
		Euparyphus	2	3	2	1	Tachet et al. 2002, US EPA
Ephemeroptera	Baetidae	*Baetis*	1	2	3	2	Tachet et al. 2002
	Baetidae	*Callibaetis*	1	2	3	2	Poff et al. 2006, US EPA
	Caenidae	*Caenis*	1	2	1	2	Tachet et al. 2002
	Leptophlebiidae	*Choroterpes*	1	2	1	2	Tachet et al. 2002
		Thraulodes	1	2	1	2	Traver & Edmunds 1967, Merritt et al. 2008
Hemiptera	Belostomatidae	*Abedus herberti*	3	3	6	3	Poff et al. 2006
	Naucoridae	*Ambrysus woodburyi*	1	3	6	3	La Rivers 1951
	Nepidae	*Ranatra quadridentata*	3	3	6	3	Tachet et al. 2002
	Veliidae	*Microvelia*	1	3	6	1	Smith 1980
Odonata	Aeshnidae	*Oplonaeschna armata*	3	2	7	3	Needham et al. 2000
	Coenagrionidae	*Argia*	2	2	7	3	Westfall & May 1996
	Cordulegastridae	*Cordulegaster diadema*	3	2	7	3	Tachet et al. 2002, US EPA
	Libellulidae	*Libellula saturata*	3	2	7	3	Needham et al. 2000
		Paltothemis lineatipes	3	2	7	3	Needham et al. 2000
Trichoptera	Calamoceratidae	*Phylloicus mexicana*	2	2	2	3	Prather 2003
	Helicopsychidae	*Helicophyche*	1	1	1	2	Wiggins 1996, Jackson & Re 1989
	Leptoceridae	*Oecetis*	1	2	2	3	Wiggins 1996
	Odontoceridae	*Marilia*	2	2	2	2	Merritt et al. 2008, Wiggins 1996

Appendix B, Table B.2 References.

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Table B.3. Taxa that were eliminated by the drying treatments, defined as taxa with >5 individuals in initial samples and zero individuals in final samples.

Order	Family	Genus/species
Diptera	Chironomidae	*Ablabesmyia*
		Brillia
		Corynoneura
		Cricotopus/ Orthocladius
		Micropsectra
		Microtendipes pedellus grp.
		Paramerina
		Stempellinella
		Tanytarsus
		Tvetenia bavarica grp.
	Dixidae	*Dixa*
		Dixella
	Simuliidae	*Simulium*
	Tipulidae	*Limnophila*
Ephemeroptera	Heptageniidae	*Ecdyonurus*
	Homoleptohyphidae	*Homoleptohyphes*
Hemiptera	Gerridae	*Aquarius remigis*
	Veliidae	*Rhagovelia*
Trichoptera	Limnephilidae	*Hesperophylax*
	Polycentropodidae	*Polycentropus*

Table B.4. Taxa absent from initial samples and present in final samples.

Order	Family	Genus/species	Abundance
Coleoptera	Dytiscidae	*Dytiscus*	1
		Hygrotus	2
		Laccophilus fasciatus	3
		Rhantus gutticollis guticollis	2
		Stictotarsus roffi	3
	Hydraenidae	*Hydraena*	2
	Hydrophilidae	*Berosus punctatissimus*	23
		Berosus salvini	1
Diptera	Chironomidae	*Lauterborniella*	2
	Stratiomyidae	*Euparyphus*	5
	Simuliidae	*Anopheles*	30
Ephemeroptera	Caenidae	*Caenis*	2
	Leptophlebiidae	*Choroterpes*	2
Hemiptera	Naucoridae	*Ambrysus woodburyi*	7
	Nepidae	*Ranatra quadridentata*	3
Trichoptera	Odontoceridae	*Marilia*	1

APPENDIX C. MANUSCRIPT IN REVIEW.

OVERLAND DISPERSAL AND DROUGHT ESCAPE BEHAVIOR IN A FLIGHTLESS AQUATIC INSECT, *ABEDUS HERBERTI* (HEMIPTERA: BELOSTOMATIDAE).

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Southwestern Naturalist
In review

ABSTRACT

We report an observation of overland dispersal in a flightless aquatic insect during a period of drought-induced stream drying. We observed an adult giant water bug *Abedus herberti* (Hemiptera: Belostomatidae) crawling at 4.6 m/min along a dry stream channel in the Galiuro Mountains, Arizona, USA. We tracked the individual for 130 m and estimate that it moved 240 m from the nearest remaining aquatic habitat. Additionally, we conducted behavioral experiments that confirm that *A. herberti* can use drying as a cue to initiate movement.

MANUSCRIPT BODY

Aquatic communities in aridland streams are often separated by harsh intervening terrain that can act as a dispersal barrier. However, genetic evidence suggests that populations of several obligatory aquatic taxa exhibit some genetic connectivity, indicating that at least a few individuals move between locations, however infrequently (Finn et al., 2007). Long-distance dispersal events can be essential for the persistence of highly isolated populations because they provide genetic connectivity and can serve as mechanisms for recolonization following local extinctions, but they are rare due to the high risks incurred by dispersing individuals (Lowe, 2010). Rapid changes in the suitability of the local aquatic environment – such as stream drying – might trigger such rare dispersal events in aquatic taxa. Here we report a direct observation of what we believe to be the first documented case of overland drought escape behavior in a flightless aquatic insect.

In the early afternoon of 8 April 2009, we observed a giant water bug, *Abedus herberti* (Hemiptera: Belostomatidae) crawling along a dry stream reach in High Creek, Galiuro Mountains, Arizona, USA (UTM 12S 569134, 3603989; elevation 622 m). High Creek is a spring-fed stream that runs through Madrean evergreen woodland and fragments annually to a series of pools separated by dry reaches lined with cobble and boulders. The dispersing giant water bug was an adult male (ca. 3 cm length) moving downslope (15-20° incline) in the dry stream channel and climbing over cobbles >10 cm diameter as it went. We followed it for 130 m and estimated its movement rate at 4.6 m/min (see video at http://hdl.handle.net/1957/28659). The nearest wetted aquatic habitat was 110 m upstream; therefore this individual travelled at least 240 m over dry land. Interestingly, the insect's startle response was completely stifled and it continued its pace despite the observation and excitement of the authors. While remaining habitat was upstream, it moved down the canyon in a positively geotactic manner and remained oriented in the stream channel even when climbing over and around obstructions such as cobbles and woody debris. This unique behavior is analogous to the rainfall response behavior that is well documented for *A. herberti* and other belostomatids, where individuals use heavy rainfall as a cue to escape flash floods by moving uphill and away from the active stream channel (Lytle and Smith, 2004). Unlike rainfall response behavior, however, the dispersal behavior we observed was uniformly downhill rather than uphill, consistently within the stream channel rather than perpendicular to it, and required no rainfall cue to initiate.

Although adult and juvenile *A. herberti* were abundant during a previous visit to High Creek on 9 June 2008, *A. herberti* were scarce on our 8 April 2009 visit and the wetted stream habitat had fragmented to a series of small pools due to below-average winter precipitation (January-March rainfall was only 55% of the 30 yr mean; NOAA weather station, Willcox, Arizona). A few pools (15.8 m2 total surface area) remained 110 m upstream of the observation site, with another suitable reach 750 m further upstream. We extensively sampled the limited upstream aquatic habitat and found only five adult females, four of which were gravid, and no males or juveniles. Upon a return visit in March 2010, we found more pool habitat but only three giant water bugs, this time all adult males. Thorough sampling of all pool habitats on 3 April 2011 yielded only a single gravid female. These observations suggest that the High Creek population is highly vulnerable to local extinction, especially given that this species has already been extirpated from other streams in the region by similar drying events (Bogan and Lytle, 2011).

To explore a possible mechanism behind our fortuitous observation, we conducted laboratory experiments to determine if *A. herberti* can use stream pool drying as a cue to initiate movement. We collected *A. herberti* from East Turkey Creek, Chiricahua Mountains, Arizona, and acclimated them to tanks in the laboratory at the Southwestern Research Station, Portal, Arizona. Each experimental unit consisted of a small opaque inner tank (10.9 L) nested within a larger outer tank (29.1 L). The outer tanks contained water, and the inner tanks were either wet or dry, representing our two treatments. Inner tanks were lined with screen to allow individuals to crawl from inner to outer tanks, whereas the outer tanks' high, smooth walls prevented the insects from moving back to the inner tanks or escaping the experiment altogether. Inner tanks contained cobbles (8-20 cm mean diameter) to provide substrate similar to that found in the insects' natural habitat. To begin each trial, a single adult giant water bug was placed in each of 12 inner tanks. We returned after 12 and 24 h and recorded the movement of individuals from inner to outer tanks. We found that dryness was a strong predictor of movement in this species. In fact, insects were 10 times more likely to leave a dry tank than a wet one (Fisher's exact test, one-sided $P < 0.0001$). This simple experiment supports stream drying as a possible mechanism behind our field observation of overland dispersal.

While *A. herberti* is an air-breathing aquatic insect and is known to move distances of a few meters along fragmented streams, overland dispersal in response to drought had not previously been observed in this species. We suggest that drought escape behavior might occasionally result in long-distance dispersal of *A. herberti* and thus might allow for recolonization of areas where populations have been extirpated, or provide the genetic diversity necessary for small extant populations to avoid extinction altogether. The surprising distance and speed of the observed individual makes dispersal between aquatic habitats in the Galiuro Mountains a possibility: if an individual giant water bug were to continue for 24 h at the rate we recorded, it would travel over 6.5 km, which would put it within several days' reach of perennial habitats in adjacent stream basins. Although this scale of movement is unlikely, our observation provides some evidence that *A. herberti* populations could persist despite projected stream drying in the southwestern United States (Seager et al., 2007).

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