

AN ABSTRACT OF THE THESIS OF

Michael T. Bogan for the degree of Master of Science in Environmental Sciences presented on September 15, 2005.

Title: Diversity and Community Structure of Aquatic Insects in Isolated Montane Desert Streams

Abstract approved:

Redacted for Privacy

David A. Lytle

Local aquatic insect diversity and community structure is the result of multiple local and regional factors, and observed patterns depend upon the spatial and temporal scale under examination. Isolated stream systems in arid regions represent a new challenge in understanding the drivers of diversity and community structure, as most studies addressing these issues are from well-connected temperate streams. During 2004 and 2005, I quantified aquatic insect diversity and community structure at 25 small, insular streams in the Madrean Sky Islands (MSI) of the southwest US and northwest Mexico. Over 60 families of aquatic insects were identified, with over 150 species of Coleoptera and Hemiptera identified in the regional species pool. I used these data to test several hypotheses: (1) diversity and community structure are correlated with habitat size, isolation, and habitat characteristics, (2) community structure is more correlated with distance between streams than with drainage basin, and (3) seasonal abiotic variation alters community structure. Habitat area explained a significant amount of variation in local species richness (45%). Using multiple linear regression, temperature and elevation were selected as additional explanatory factors, yielding a model that explained 61% of the variation in species richness. Non-metric multidimensional scaling (NMS) analyses identified two major gradients in community structure across the MSI, one associated with temperature, elevation and latitude, and the other associated with substrate composition (% silt and bedrock). Isolation from large river systems was not an important factor in diversity or community structure, and habitat area was not associated with community structure. Communities grouped by drainage basin did not form homogenous groups, as is seen in other aquatic taxa (e.g. fish). Community distance was,

however, strongly associated with geographic distance, even after accounting for environmental variation. This indicates a strong spatial autocorrelation in MSI insect communities, and suggests that many species easily disperse across drainage divides. MSI streams are characterized by strong seasonal variation in the form of increased flow and habitat amount (2+ orders of magnitude) and decreased temperature, pH, and conductivity during the brief high flow season. This seasonal abiotic shift allows the 'time-sharing' of MSI streams by disparate aquatic insect communities (nearctic and neotropical), and increases overall site diversity. I hypothesize that high elevation headwaters, egg and larval diapause, and the hyporheos may serve as refuges for high flow-dependent species during the rest of the year. MSI streams are remarkably diverse given their small sizes, and the results of this study suggest that this diversity is supported through spatial and temporal variation in habitat size and local abiotic characteristics.

© Copyright by Michael T. Bogan
September 15, 2005
All Rights Reserved

Diversity and Community Structure of Aquatic Insects in Isolated Montane Desert Streams

by
Michael T. Bogan

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented September 15, 2005
Commencement June 2006

Master of Science thesis of Michael T. Bogan presented on September 15, 2005.

APPROVED:

Redacted for Privacy

Major Professor, representing Environmental Sciences

Redacted for Privacy

Director of the Environmental Sciences Program

Redacted for Privacy

Dean of the Graduate School

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

Redacted for Privacy

Michael T. Bogan, Author

ACKNOWLEDGEMENTS

First and foremost I'd like to thank my advisor, Dr. David A. Lytle. Lytle invited me to participate in his research based on one day we spent in the field together in Arizona, before ever seeing transcripts or qualifications. He has graciously shared 'his' streams and insects over the last two and a half years, and encouraged me to take on projects which weren't directly related to his own. The work accomplished in this thesis is in large part due to his loose but scientifically rigorous guidance and continuous enthusiasm in my projects. The great memories of climbing waterfalls in remote stream canyons, eating at roadside taco stands, soaking in hot springs, talking to *narcotraficantes*, and practicing great science with Lytle will stay with me for the rest of my life.

My labmates at OSU, Cathleen Dora, Arlo Pelegrin, and Asako Yanamuro have been essential in keeping me sane during long work days and nights. Many thanks to them for hours of comic relief and frustration venting. Thanks are due to other graduate students and post docs, including Maria Kavanaugh, M. Rockwell Parker, Elisha Wood-Charlson, Doug DeGross, and Roman Vilas, for social support and good times away from Cordley Hall. Many thanks to Frank Drake and Justin Miles, of OSU, for much needed help in sorting and preliminary identification of many community samples. My fellow OSUans Chris Stallings and M.J. Briya were ideal housemates during my time in Corvallis- thanks to them for the support and for *not* talking shop while at home. Special thanks to Rebecka Weinstein for being an outlet of sanity and keeping me aware that there is life away from work.

Many thanks to Dr. Stanley Gregory and Dr. Douglas Robinson for being supportive, helpful and resourceful committee members. It was an honor to have both of them on my committee. Dr. Norm Anderson was an invaluable resource during my time here. His incredible knowledge of aquatic insect ecology and his 30+ years of experience were essential to my success in teaching Aquatic Entomology labs and to my professional growth as a freshwater biologist. Thanks also to Dr. Arthur Boucot, both for his interesting classes and for serving as a role model for any scientist. His work ethic and dedication to science is astounding.

My work in Mexico would have been impossible without the help and cooperation of Maestro Andres Alvarado and Maestro Oscar Guitierrez of CESUES, Hermosillo, Sonora. They greatly eased the beauraucratic nightmare that envelopes any binational project, were valiant field companions, and facilitated the involvement of Mexican undergraduates in my projects. They also opened up their homes and offices to me, and for that I am grateful.

Special thanks to all those who facilitated access to private, state and federally owned field sites: Joe and Valer Austin of the Coronado Ranch; Dave Gori, Bob Rodgers, Mark Pretti

and Dale Turner of the Nature Conservancy; Larry Jones and Bonnie Stolp of the USFS Coronado National Forest; Sheridan Stone of Fort Huachuca, US Army; Jacob Malcom of the USFWS, Leslie Canyon NWR; Cathy Wertz of Bisbee, AZ; Rickard Toomey and Joanne Roberts of Arizona State Parks; Jeff Simms at BLM, Tucson Office; and Sr. Rubén Monroy Leon at Rancho Las Bellotas, Sonora, Mexico.

“Bugman” Carl Olsen graciously opened up his lab and the University of Arizona insect collections to me. Chris O’Brien, of University of Arizona, accompanied me on an especially difficult, dry, and rattlesnake-filled three day sampling expedition. I thank him sincerely for this, and for the last two years of conversation, camaraderie, and exploration of Sonoran ecology and culture. Claire Zugmeyer, of University of Arizona, graciously shared her home during my time in Tucson and I am indebted to her for that and for many great mornings at the bagel shop.

Dr. Dawn Wilson and Dr. Wade and Emily Sherbrook of the Southwestern Research Station in Portal, AZ were great hosts during the seven or so months I have spent there over the course of my thesis. Thanks to the Station ‘regulars’ Dr. Fred and Nancy Gehlbach, Lauren Chan, Ryan Martin, Dr. George Middendorf, Markus Ruger, Elliot Wilkinson (*aka* Cecil B. DeMeires), and many others, for three great summers of fun, science, and monsoons. Jacqueline Clark always served wonderful food and conversation at Station, and I’m grateful to her for hours of coffee-fueled kvetching and conversation. I’m deeply indebted to Patrick Oakes, a Station volunteer, who restored my sanity and well-being during the harried final weeks of research and writing in July 2005.

And finally, the deepest gratitude goes to my parents, Tom and Bonita Bogan, for always supporting my life endeavors and encouraging me to do what makes me happy and not what makes me money. During my journey from Starbucks Coffee manager to freshwater biologist, they have given me nothing but encouragement and emotional support. I couldn’t imagine a better pair of folks to have as parents, and this thesis is in recognition of all the support they’ve given.

CONTRIBUTION OF AUTHORS

Dr. David A. Lytle gave valuable advice in the design, implementation, and editing of this thesis, and provided financial support to Michael T. Bogan in the form of research assistantships during Summer 2003, and Spring and Summer of 2004 and 2005. Dr. Lytle is the co-author of Chapters 2 and 3.

TABLE OF CONTENTS

	<u>Page</u>
CHAPTER 1: Introduction.....	1
CHAPTER 2: Effects of regional and local processes on aquatic Coleoptera and Hemiptera diversity and community structure in isolated montane desert streams.....	5
Abstract.....	5
Introduction.....	5
Study site.....	7
Methods.....	9
Results.....	11
Discussion.....	15
CHAPTER 3: Seasonal flow variation allows 'time-sharing' by disparate aquatic insect communities in montane desert streams.....	24
Abstract.....	24
Introduction.....	24
Study site.....	26
Methods.....	29
Results.....	31
Discussion.....	37
CHAPTER 4: Summary and conclusions.....	45
Bibliography.....	49
Appendices.....	57
Appendix I: Sampling effort depletion curves.....	58
Appendix II: Species occurrence by study site.....	60
Appendix III: Coleoptera and Hemiptera species richness per unit area of habitat.....	63
Appendix IV: Comparison of stream and pond aquatic insect communities in the Madrean Sky Islands.....	64
Appendix V: Aquatic insect colonization of experimental pools near Cave Creek, Chiricahua Mountains, AZ.....	72

LIST OF FIGURES

	<u>Page</u>
1.1. The Madrean Sky Islands are the series of isolated mountain ranges in between the Mogollon Rim and the Sierra Madre Occidental.....	2
2.1. Study sites in the Madrean Sky Islands.....	8
2.2. Log species-log area relationship for 25 MSI streams.....	12
2.3. NMS ordination plots with correlated environmental factors overlain.....	13
2.4. NMS ordination with plots grouped by subbasin	14
2.5. Mantel's r and partial Mantel's r values between community, environmental and geographic distance matrices.....	15
3.1. Location of the seven study streams within Coronado National Forest, Arizona....	27
3.2. (a.) Discharge from Garden Canyon, Huachuca Mountains (b.) Stream temperature at 10cm depth from Florida Canyon, Santa Rita Mountains.....	28
3.3. Mean relative abundances of functional feeding groups by season and habitat type.....	33
3.4. NMS ordination results coded by first letters of name, habitat and season type. Environmental variables with significant correlations with axes 1 or 2 are displayed as vectors.....	34

LIST OF TABLES

	<u>Page</u>
2.1. Study sites' abbreviated codes, environmental factors.....	11
2.2. Environmental variables with strong correlations ($r^2 \geq 0.4$) to an NMS ordination axis.....	13
3.1. Seasonal differences in surface area of stream habitat at the seven study sites and presence or absence of higher elevation, permanent headwater reaches.....	32
3.2. Average densities of functional feeding groups and average taxon richness across streams and by headwater type.....	33
3.3. Correlations between aquatic insect families and NMS ordination axes.....	35
3.4. Abiotic factors averaged by season, year, and headwater type with t-test results for differences among types.....	34
3.5. Indicator values and significance from Indicator Species Analysis of aquatic insect taxa when grouped by season, habitat and headwater type.....	35

LIST OF APPENDIX FIGURES

	<u>Page</u>
A1.1. Sampling effort and cumulative species detected in 4 pools at East Turkey Creek.....	58
A4.1. Temperature recorded at 1-hr intervals at North Fork Cave Creek, located 5km above the Southwestern Research Station from 19:00 29 Jul 2005 to 21:00 2 Aug 2005.....	67
A4.2. Temperature recorded at 15-min intervals in a temporary pond located 2km north of Rodeo, NM, from 19:00 29 Jul 2005 to 21:00 2 Aug 2005.....	67
A4.3. Perennial water cattle tank in French Joe Canyon, Whetstone Mountains, AZ.....	68
A4.4. Temporary valley pond 2km north of Rodeo, NM.....	68
A4.5. NMS ordination of 26 stream and 12 pond sites, coded by habitat type.....	71
A5.1. Cumulative species richness and rainfall values for the seven survey days during July, 2004.....	75
A5.2. Cumulative number of individual colonizing insects and rainfall values for the seven survey days during July, 2004.....	75

LIST OF APPENDIX TABLES

	<u>Page</u>
A1.1. Consecutive pools sampled with a timed effort of 10sec/m ² at three streams, and the cumulative number of species detected with each additional pool.....	59
A2.1. Coleoptera species occurrences at 25 study streams.....	61
A2.2. Hemiptera species occurrences at 25 study streams.....	62
A3.1. Coleoptera and Hemiptera species richness per unit area of habitat in MSI streams.....	63
A4.1. Abiotic characteristics and locations for all sites.....	66
A4.2. Taxa found exclusively in mountain habitats.....	69
A4.3. Taxa found exclusively in valley or canyon pond habitats.....	70
A5.1. Species collected by date with their habitat affinities.....	74

DEDICATION

This work is dedicated to my undergrad thesis advisor and mentor, Dr. Robert Curry. Through his wild-eyed field lectures and enthusiastic arm-waving, I learned to see the landscape not as a static image, but as a creature of constant, and at times violent, change. Dr. Curry's teachings allowed me 'see' things in geologic time, to watch as mountains rose, eroded, lithified, and were uplifted again. He taught me to view climate as very temporary and fickle feature of our earth, and he showed me how ecosystems, past and present, are constantly adjusting to all these fluctuations in landscape and climate. He bestowed upon me a long-term perspective of our world, but without diminishing in the least the wonder and magnificence of the present moment. In fact, he encouraged an enormous love of and connection with our present landscape, from urban Los Angeles to the pristine subalpine forests of the Sierra Nevada. I will always be indebted to his time and attention, and thank him for giving me the drive to wander wildly, always asking questions about the landscape, and deeply appreciating places even when I can't answer those questions.

Old ghost ranges, sunken rivers, come again
stand by the wall and tell their tale,
walk the path, sit the rains,
grind the ink, wet the brush, unroll the
broad white space:

lead out and tip
the moist black line.

Walking on walking,
under foot earth turns.

Streams and mountains never stay the same.

-Gary Snyder (1996)

Diversity and Community Structure of Aquatic Insects in Isolated Montane Desert Streams

CHAPTER 1

Introduction

Lotic aquatic insect species form complex communities with multiple functional feeding groups that fulfill essential ecological roles at several trophic levels (Merritt and Cummins, 1996). Though some workers found aquatic insect communities to be poorly organized, stochastic assemblages of species (Winterbourne et al, 1981), most studies have identified patterns that suggest that multiple abiotic and biotic factors shape aquatic insect diversity and community structure (Downes et al, 1998; Taylor, 1997; Ward and Blaustein, 1994; Cummings et al, 1989; Allen, 1975). The relative importance of these abiotic and biotic factors is affected by flow variability and predictability (Poff and Ward, 1989). Additionally, all of these factors operate within the biogeographic and evolutionary context of the regional aquatic insect species pool (Kholin and Nilsson, 1998). Thus, local aquatic insect diversity and community structure are the intricate result of local abiotic and biotic factors acting within the hydrologic, evolutionary, and biogeographic confines of a region.

Most studies of lotic insect diversity and community structure have focused on large, well-connected stream systems in temperate and tropical regions. There are a significant number of fragmented hydrologic systems that fall outside these regions (e.g., streams of Great Basin and Sonoran Desert). These isolated stream systems represent a new challenge, as many concepts developed to explain aquatic insect species diversity and community structure in temperate systems (e.g., river continuum concept: Vannote et al., 1980) may not be as applicable to insular desert stream habitats.

The Madrean Sky Islands (MSI; Figure 1.1) consist of a series of parallel NW-SE trending mountain ranges rising above the Chihuahuan and Sonoran deserts of Arizona, New Mexico, and northwest Mexico. The MSI contain many fragmented stream habitats, isolated from one another by kilometers of dry desert both within and between mountain ranges. The continuous river system does not exist there, and instead is replaced by small patches of perennial stream habitat isolated by kilometers of ephemeral reaches which flow only under flood conditions. Thus, rather than a continuum, stream habitats exist more as islands in a dry landscape, ranging in size from a few isolated pools to several kilometers of flowing stream. The perennial reaches of MSI streams generally occur within an elevational belt between 1400 and 2200 meters, forming riparian ribbons of sycamore and maple through rocky, arid oak-pine woodlands. Riparian and upland ecosystems are comprised of a unique mixture of temperate and

neotropical species (Brown, 1994; Minckley and Brown, 1994), due to the MSI's position between the southern extensions of the Rocky Mountains (e.g., White Mountains, Mogollon Rim) and the Sierra Madre Occidental of northwest Mexico.

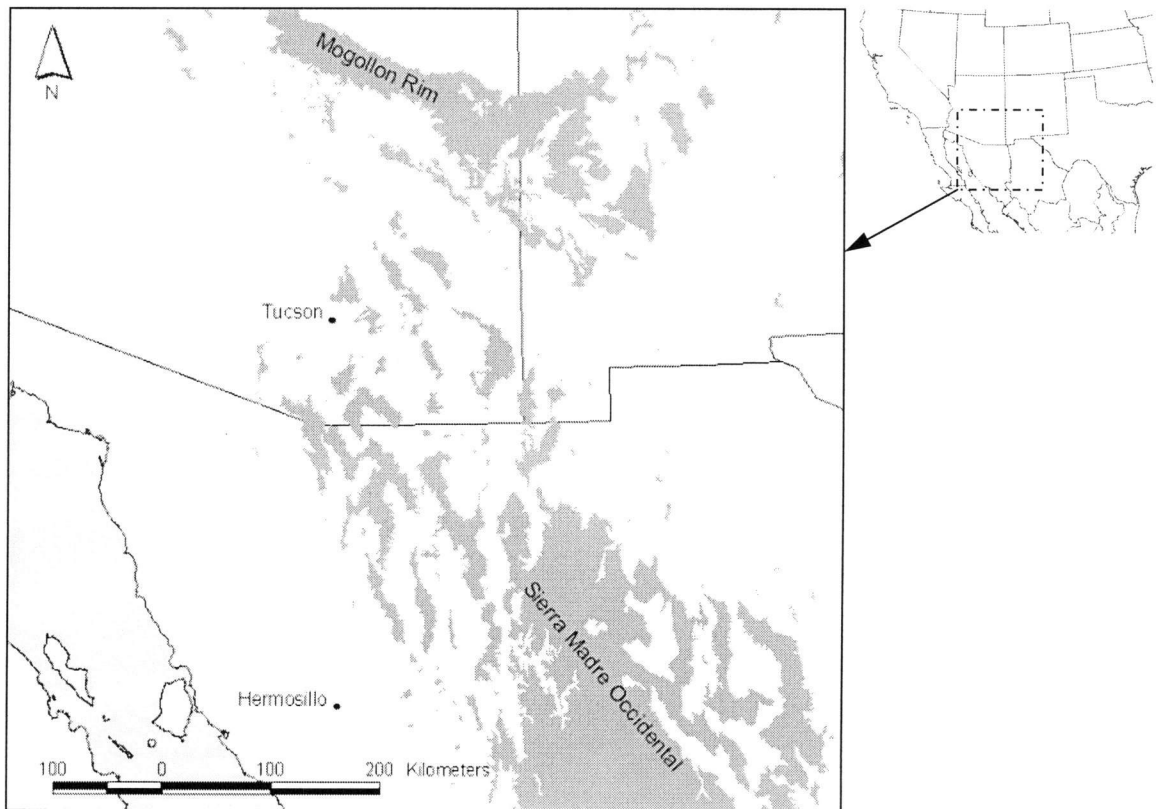


Figure 1.1. The Madrean Sky Islands are the series of isolated mountain ranges in between the Mogollon Rim and the Sierra Madre Occidental.

Aquatic insect communities of MSI streams are clearly distinct from the communities of other aquatic habitat types in the region (Appendix IV). Since they form a concise group, MSI aquatic insect communities represent an opportunity to examine the mechanisms driving diversity and community structure across an entire geographic region. Additionally, there are a large number of isolated and small streams in the MSI, which offer numerous, independent replicate sites. Since MSI streams are quite small during the low flow season (habitat area: 8 to 9000m²), species detection rates are relatively high (Appendix I) and precise biogeographic patterns can be elucidated.

The general objectives of this study were to describe patterns of aquatic insect species richness and community assembly in isolated streams of the Madrean Sky Islands, and to test if the observed patterns supported several hypotheses addressing isolated ecosystems. Specifically, I tested whether habitat size, isolation, local and regional habitat characteristics, and seasonal variation were significant factors in determining local aquatic insect diversity and community structure. In this study, species richness is defined simply as the number of species present while community structure accounts for both the identity and the abundance of all species present.

Since MSI streams exist as islands in a dry landscape, the connectivity of aquatic insect populations is limited by the overland dispersal and colonization abilities of each species. Accordingly, in the Madrean Sky Islands I hypothesized that aquatic insect diversity and community structure would be predicted by factors considered under island biogeography theory: (1) island size, (2) distance to source population, and (3) dispersal/colonization potential. Though MacArthur and Wilson's (1967) equilibrium theory of island biogeography was developed using oceanic islands, it has since been applied to both continental habitat islands and islands of aquatic habitat in a terrestrial landscape (Kiflawi et al, 2003; Nilsson et al, 1994; Dodson, 1992; Sepkoski and Rex, 1974). The theory proposes that as an island's habitat area increases, colonization rates increase and extinction rates decrease for individual species, given that larger habitats can support larger populations. Additionally, more isolated islands should have lower immigration rates (MacArthur and Wilson, 1967). Therefore, we can predict that insular habitat area is positively correlated with richness and isolation is negatively correlated with richness through their respective impacts on colonization and extinction rates of insular populations. I tested these richness-area and richness-isolation predictions by quantifying habitat area and isolation at 25 insular MSI stream habitats and using those values to model aquatic insect diversity and community structure.

In addition to area and isolation, many local habitat characteristics can affect aquatic insect communities in insular habitats. Local stream conditions like water temperature, pH, conductivity, substrate composition, and elevation can be drivers of both diversity and community structure (Clenaghan et al., 1998; Downes et al., 1998; Lancaster and Scudder, 1987; Ward and Stanford, 1982; Allen, 1975). Additional riparian factors, like canopy cover and land use type, shape local species compositions in many temperate streams (Corkum, 1990; Cummins et al., 1989). I hypothesized the above factors would be correlated with species diversity and community structure even after the effects of habitat area and isolation were considered. This hypothesis was tested using multiple regression and non-metric multidimensional scaling analyses.

While local habitat characteristics are often the primary structuring forces in aquatic insect communities, these factors operate within the context of regional processes and the biogeographic and hydrologic histories of a stream. Fish distributions often are restricted by hydrologic connectivity, historical and present (Hendrickson et al., 1980), but aquatic insects are less restricted due to their aerial adult stage (Williams et al., 2003). I tested the hypothesis that aquatic insect communities are not restricted by hydrologic history by comparing the homogeneity of communities grouped by mountain range versus grouped by drainage basin. Additionally, I examined spatial autocorrelation in MSI aquatic insect communities by testing for correlation between geographic and community distances after accounting for environmental variability.

Observed patterns of diversity and community structure in streams are dependent upon the spatial and temporal scale examined (Vinson and Hawkins, 1998; Scarsbrook and Townsend, 1993; Hawkins and Sedell, 1981). I examined MSI communities at three spatial scales (individual pool/riffle, stream, and basin scales), but I wanted to model how seasonal variability impacted diversity and community structure. MSI streams experience drastic seasonal shifts in discharge and water chemistry. During the winter high-flow season, streams have an elevated base flow and reduced temperatures, pH and conductivities for a period of several weeks to a couple of months. The rest of the year, flow is nearly zero except during monsoon induced flash floods from July through September. Temperature, pH and conductivity are all elevated during the low-flow period. I hypothesized that seasonal abiotic variation significantly alters aquatic insect communities and increases overall site beta diversity by hosting taxa with incompatible habitat requirements at different times of the year. Using a subset of 7 MSI streams sampled during both high-flow (March-April) and low-flow (late May-early July) periods, I tested this hypothesis using a combination of univariate and multivariate statistical approaches.

In addition to contributing to the understanding of biogeographic and community ecology theory, this study will aid conservation efforts in the MSI by locating areas of high diversity and/or endemism in streams, and determining what factors are associated with those areas. This study will also aid in modeling future changes in MSI streams. Aquatic insect communities are sensitive to climate-induced changes in habitat characteristics (Daufresne et al., 2003, Woodward et al., 2002). Small streams in arid areas are especially sensitive to climate change. Several formerly permanent MSI streams have recently gone ephemeral (Lytle, pers. comm.; Bogan, pers. obsv.). The greater understanding of seasonal variation in MSI streams that arose from this study will help us to model the impacts of further climatic change on MSI aquatic insect communities.

CHAPTER 2

Effects of local and regional processes on aquatic Coleoptera and Hemiptera diversity and community structure in isolated montane desert streams

Abstract

Both regional and local factors can act to filter the regional species pool and produce local species assemblages. We used aquatic insects inhabiting small isolated stream habitats to test specific hypothesis concerning the relative importance of habitat size, distance to “mainland” habitats, local abiotic conditions, and geographic isolation for determining local aquatic insect diversity and community structure. Aquatic beetle (Coleoptera) and true bug (Hemiptera) diversity and community structure were quantified at isolated 25 streams in the Madrean Sky Islands of the southwest USA and northwest Mexico. Permanent stream habitat ranged in size from 8 m² to 9000 m². Habitat area explained a significant amount of the variation (45%) in local species richness. Stepwise multiple linear regression analyses identified temperature and elevation as additional explanatory variables for species richness. Non-metric multidimensional scaling identified two major gradients in community structure: (1) a gradient strongly associated with the interrelated factors of latitude, temperature, and elevation and (2) a gradient associated with a shift from silt- to bedrock-dominated substrates. Habitat area, isolation, pH, and conductivity were not significantly associated with community structure. Sites grouped by drainage basin were not homogenous, as is common in other aquatic taxa (e.g., fish), but sites grouped by mountain range were more similar to one another. Partial Mantel tests indicated that geographic and community distances were still significantly correlated after removing the effect of measured environmental variables, suggesting that a strong spatial autoregressive component may exist in these isolated streams. For MSI streams, local abiotic factors and spatial position strongly influence aquatic insect diversity and community structure, but regional (drainage) history does not act to constrain local aquatic insect communities.

Introduction

Species diversity and community structure are the result of multiple regional and local processes which filter the regional species pool and produce the local species pool (Kiflawi et al., 2003; Malmqvist, 2002; Ricklefs, 1987). For aquatic insect species, these filters range from drainage basin geologic history (regional factor) to microhabitat availability (e.g., substrate type:

local factor). Factors at both scales may be equally important in determining local diversity and community structure (Malmqvist, 2002).

Small, isolated streams provide an ideal setting in which to determine which regional and local factors influence in local diversity and community structure. In this study, we quantified aquatic Coleoptera and Hemiptera species richness and community structure at 25 isolated streams in the Madrean Sky Islands (MSI) bioregion. The MSI contain a large number of isolated and small streams, which provide many independent, replicate study sites. Since most MSI streams are small (<1000 m² habitat area), sampling power and species detection probabilities are higher than in large rivers. Coleoptera and Hemiptera were selected for analyses since adults are fully aquatic, aiding species-level identification. The high regional diversity of these taxa also increases our ability to resolve biogeographic and ecological patterns. Additionally, aquatic Coleoptera and Hemiptera species have a wide range of dispersal abilities, from non-flying species to those capable of multiple kilometer flights (Lytle and Smith, 2004; Townsend et al., 2003; Wallace and Anderson, 1996), creating the potential for interesting geographic patterns in community structure.

We used this dataset to test four hypotheses regarding how regional and local factors affect aquatic insect diversity and community structure in isolated streams: (I) Local diversity and community structure are significantly associated with habitat area, (II) Local diversity and community structure are significantly associated with habitat isolation significantly associated with (due to selective extinctions and differing recolonization abilities), (III) Local habitat characteristics (e.g., water chemistry, substrate composition) are significant predictors of local diversity and community structure, and (IV) Mountain range affiliation is a greater determinant of community structure than drainage basin affiliation (regional factor), implying that aerial dispersal between sites is more important than hydrologic connectivity.

Habitat area and isolation were identified by the equilibrium theory of island biogeography (MacArthur and Wilson, 1967) as the primary factors driving species richness in insular habitats via their effects on immigration and extinction rates. While the effect of isolation has not been frequently demonstrated in aquatic habitats (but see Sepkoski and Rex, 1973), area is positively correlated with species richness for many lentic (e.g., invertebrates: Kiflawi et al., 2003; Odonata: Oertli et al., 2002; zooplankton: Dodson, 1992) and lotic (e.g., mussels: Sepkoski and Rex, 1973) invertebrate taxa. Additionally, elevation (Vinson and Hawkins, 2003; Oertli et al., 2002), temperature (Kholin and Nilsson, 1998), conductivity (Lancaster and Scudder, 1987), substrate diversity (Allan, 1975) and vegetation structure (Nilsson et al., 1994) are all correlated with aquatic insect diversity. Local factors tend to have more influence in determining diversity

than regional factors, although regional history may limit the total species pool available to a local site (Kholin and Nilsson, 1998).

Poff and Ward (1989) predicted that local abiotic factors would be the primary drivers of community structure in arid, intermittent streams, while others have predicted that regional factors (e.g., biome type) shape local community structure (Corkum, 1992). Many local abiotic factors which affect species diversity are also influential in lotic and lentic aquatic insect community structure (e.g., substrate diversity: Sanderson et al., 2005; area: Rundle et al., 2002; conductivity: Lancaster and Scudder, 1987; elevation: Allan, 1975). Additionally, in lotic systems, water pH (Sanderson et al., 2005; Clenaghan et al., 1998) and canopy cover (Cummins et al., 1989; Hawkins et al., 1982) can strongly shape local communities. Regional upland habitat type (e.g., biome type) may be a driver of local aquatic insect community structure, but this factor is easily overwhelmed by local human land use practices (e.g., silviculture and agriculture) (Corkum, 1990, 1992).

The spatial position of a stream relative to other streams is often an important consideration when examining aquatic insect communities (Sanderson et al., 2005). Neighboring streams may share many influential abiotic traits, as regional factors like geology and climate are highly spatially autocorrelated. Neighboring streams can also serve as important recolonization sources. Accordingly, the distributions of taxa with low dispersal abilities (e.g., Ephemeroptera: Petersen et al., 2004) exhibit high spatial autocorrelation while far-dispersing taxa (e.g., Coleoptera: Townsend et al., 2003) are less dependent on local recolonization sources. This disparity in dispersal ability and the spatial position of each stream act as significant filters for local community structure (Sanderson et al., 2005; Bohonok and Jenkins, 2003).

Study Area

The Madrean Sky Islands (MSI) are a series of parallel NW-SE trending mountain ranges located between the southern Rocky Mountains of Arizona and New Mexico and the Sierra Madre Occidental of northwest Mexico. Each mountain range is isolated from other ranges by large areas of lowland desert and grassland. Permanent streams in the MSI mainly occur in a narrow elevation band between 1200m and 2200m in the Madrean Evergreen Woodland vegetation zone, an arid oak and pine woodland. Below 1200m, stream channels are usually dry except during flash floods. Streams in this elevation band are high-gradient and contain extensive sections of permanent bedrock pools interspersed with alluvial riffles and runs which tend to dry seasonally. Streams often flow for a couple months during the winter (Dec-Apr), and then contract to a series of isolated pools during the rest of the year. Flash floods may occur during

the monsoon season (July-Sept), but are brief and generally do not result in increased baseflow (Lytle, 2003). Twenty-three study sites are distributed across the MSI, with 2 sites located in the Sierra El Aguaje, SW of the MSI (Figure 2.1); difficult stream access resulted in fewer Mexican sites.

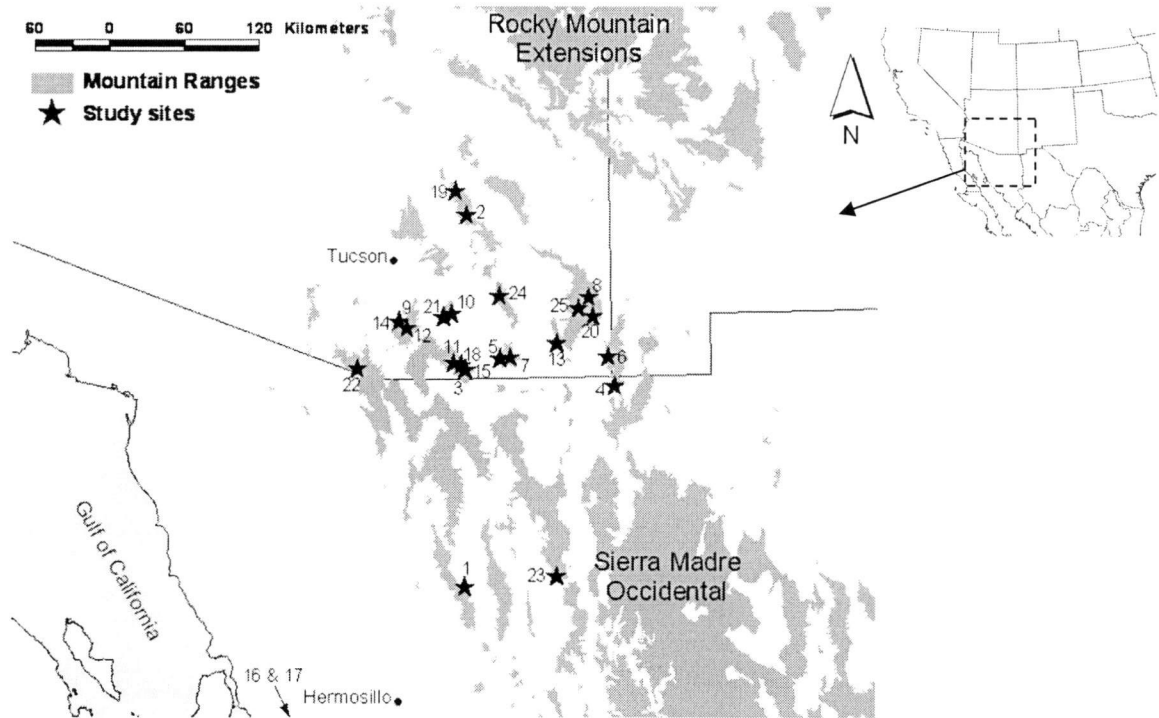


Figure 2.1. Study sites in the Madrean Sky Islands (isolated ranges in between the Rocky Mountain Extensions and Sierra Madre Occidental). 1-Aco; 2-Ash; 3-Bea; 4-CajT; 5-Chu; 6-Ctw; 7-Dix; 8-Etu; 9-Flo; 10-Frj; 11-Gdn; 12-Gnr; 13-Les; 14-Mad; 15-Mil; 16-Nac; 17-Ppo; 18-Ram; 19-Rat; 20-Ruc; 21-Sim; 22-Syc; 23-Val; 24-Wst; 25-Wtu (see Table 1 for codes). Sites 16 and 17 located approx. 100km south of Hermosillo, outside of the MSI.

Two sites were sampled approximately 125 km SW of the MSI (Nacapule Canyon and Paradise Palm Oasis) in the extremely isolated Sierra El Aguaje. These sites occur at lower elevation and latitude than MSI streams, but they contain aquatic vertebrate species typical of the MSI (e.g., *Rana yavapaiensis*, *Ambystoma rosaceum*) and have significant aquatic invertebrate faunal overlap with MSI streams. These two sites were included in the analyses to increase the range of elevation and latitude examined in study.

Methods

Field Sampling

Preliminary sampling and scouting during 2003 and early 2004 revealed that the best sampling time to maximize species detection and determine minimum habitat size was late-May to early-July, after winter high flows and before monsoon flooding. To determine sampling effort necessary to maximize species detection at a given site, effort-species detection saturation curves were created at three sites (East Turkey Creek, Rucker Canyon, Simpson Spring). Sweeping with a D-net (1 mm mesh) was performed in pools, with samples separated at regular intervals (5 s). On average, over 95% of species were detected with an effort of 10 seconds per m² of pool surface area. Several pools were then sampled at this effort level within a reach. Nearly 97% of species collected in a reach were detected after 3 pools had been sampled (see Appendix I). Since aquatic communities often have a steep compositional gradient in relation to elevation, a stratified random sampling scheme was used; 3 pools were sampled in each 300 m elevation band within which permanent water occurred. Riffles were sampled by taking a 'kick-sample', where 0.25 m² of riffle substrate was disturbed to a depth of 5cm and insects were captured downstream with a D-net (1 mm mesh). MSI streams rarely contain riffles during the low flow season (3 of 25 sites had riffles), but if riffles were encountered, 3 'kick samples' were collected in each 300 m elevational band. Accordingly, anywhere from three to twelve samples are used to describe the insect community at each site, commensurate with the range of habitats present and elevation range occupied by each stream. Pool and riffle sample locations were haphazardly selected from permanent water habitat maps created at each site before sampling. The nearest riffle to the haphazardly selected map point was sampled. Using the same selected map points, the closest pool meeting pre-defined criteria (size: >2 m², <5 m²; max. depth: >0.5 m) was sampled. All Coleoptera and Hemiptera collected were preserved in 95% ethanol and identified to species-level and counted at Oregon State University. Since area sampled in riffles was 0.25 m² and pool sizes ranged from 2 to 4 m², all abundance counts were converted to densities per meter squared to make sample unit values comparable across sites and habitat types (Merritt et al., 1996).

Temperature (°C), pH, and conductivity (µS cm⁻¹) were measured with hand-held meters at 10 cm below the surface. Substrate (bedrock, cobble, gravel, sand, silt, organic) cover and percent of canopy cover were visually estimated. Total stream surface area was calculated by mapping all wetted reaches between 1200 and 2200 m. In small streams, all pool and riffle sizes were visually estimated and tabulated. For larger streams, beginning and ending flow GPS points were recorded to calculate flowing reach lengths. Representative 100 m sub-reaches were then measured and used to extrapolate the amount of wetted habitat within the entire flowing reach.

Data Analysis

To test the hypotheses (I and II) of significant species-area and species-isolation relationships, species richness was regressed with total habitat area and isolation. Data were log-transformed when necessary to achieve normality. Isolation distances were quantified as the linear distance between a site and the nearest southern Rocky Mountain (Mogollon Rim & White Mountains) and Sierra Madre Occidental stream. These 'mainland' cordilleras contain extensive stretches of well-connected, continuously flowing streams, and thus could be seen as a potential 'mainland' source for the isolated stream 'islands' of the MSI.

Stepwise multiple regression with an AIC variable selection method was used to evaluate the hypothesis (III) that local environmental factors are significantly predictors of local diversity. Species richness was modeled using all recorded variables (area, isolation, pH, conductivity, temperature, elevation, canopy cover, and substrate composition variables). Additionally, we calculated coleopteran and hemipteran species richness per unit area values for all sites. Though this metric is not commonly reported in stream biodiversity studies, we propose that MSI streams contain high levels of diversity given their small size.

We examined the association between community structure and environmental variables (hypothesis III) with non-metric multidimensional scaling (NMS) in PC-ORD (McCune and Mefford, 1999). NMS takes advantage of redundancy in the data matrix, using a rank-based metric to reduce community data from many dimensions to a 2- or 3-D ordination (McCune and Grace, 2002). Environmental parameters can then be overlain on the community structure-based ordination to elucidate relationships between measured parameters and community shifts. Replicate community samples within streams were averaged to create a species by stream matrix for analyses. Sorensen distances were used to calculate community dissimilarity between sites. After performing the NMS analyses, we examined correlation coefficients between measured environmental variables and ordination axes to identify potential drivers of community assembly.

To test the hypothesis (IV) that community assembly is more closely correlated with a stream's drainage basin vs. mountain range, community matrix sample units were broken into *a priori* hydrological ($n = 7$) and mountain range ($n = 12$) groups. We used Multi-response Permutation Procedure (MRPP) with Sorensen distances to quantify and test within-group agreement and distinctness (see Mielke and Berry, 2001). This procedure yields two statistics: an A-statistic ($-1 \leq A \leq 1$), describing the effect-size of the grouping, and a p-value which evaluates the likelihood that observed differences are due to chance (McCune and Mefford, 1999). The effect of geographic position and environmental factors on community assembly was further

examined with a Mantel test, which yields a correlation coefficient, r , known as the standardized Mantel statistic (Sokal and Rohlf, 1995). The significance of r was evaluated with a Monte Carlo test (McCune and Mefford, 1999). The Mantel test evaluated the correlations between community, environmental and geographic distance matrices for all study streams. Community and environmental distance matrices were constructed using Sorensen distances, while the geographic distance matrix represented linear (Euclidean) distances between sites measured in kilometers. Partial Mantel tests were used to assess the correlation between community and geographic distance matrices after removing the effect of the environmental variation and between community and environmental matrices after removing the effect of geographic position.

Results

One hundred and fourteen species of aquatic coleopterans ($n = 76$) and hemipterans ($n = 38$) were collected from the 25 streams (Appendix II), with a total of 20,271 individuals identified.

Table 2.1. Study site codes, environmental factors (Elevation = m.a.s.l.; Temp = water temperature °C; Cond = $\mu\text{S cm}^{-1}$; Size = m^2) and species richness of Coleoptera and Hemiptera

Range	Site	Code	Drainage	Elevation	Temp	Cond	pH	Size	Coleoptera	Hemiptera
<i>Atascosa Mountains</i>	Sycamore Canyon	Syc	Concepcion	1250	24	270	8.0	884	25	14
<i>Chiricahua Mountains</i>	East Turkey Creek	Etu	Upper Gila	1820	18	230	7.7	571	20	10
	Leslie Canyon	Les	Yaqui	1410	18	535	7.6	235	12	6
	Rucker Canyon	Ruc	Yaqui	1843	19.5	170	7.4	1029	30	14
	West Turkey Creek	Wtu	Willcox	1860	22	110	7.3	598	28	12
<i>Dragoon Mountains</i>	West Stronghold	Wst	Upper Gila	1585	19.5	490	7.9	93.75	24	7
<i>Galiuro Mountains</i>	Ash Canyon	Ash	Upper Gila	1738	18	125	8.2	8	18	5
	Rattlesnake Creek	Rat	Upper Gila	1585	19.5	80	7.5	3128	22	7
<i>Huachuca Mountains</i>	Bear Canyon	Bea	Upper Gila	1677	22	420	7.7	380	33	13
	Garden Canyon	Gdn	Upper Gila	1750	18	395	7.8	2270	34	12
	Miller Canyon	Mil	Upper Gila	1951	11.5	210	8.0	235.5	14	4
	Ramsey Canyon	Ram	Upper Gila	1768	17	360	8.2	250	17	11
<i>Mule Mountains</i>	Chulo Canyon	Chu	Upper Gila	1768	23	95	7.6	53.25	18	9
	Dixie Canyon	Dix	Upper Gila	1622	27	470	7.8	693	28	15
<i>Santa Rita Mountains</i>	Florida Canyon	Flo	Lower Gila	1463	19.5	280	7.4	76	23	9
	Gardner Canyon	Gnr	Lower Gila	1700	21.3	150	7.9	89	23	10
	Madera Canyon	Mad	Lower Gila	1503	19.5	480	7.8	95	22	8
<i>Sierra Aconchi</i>	Aconchi Agua Caliente	Aco	Sonora	1150	21	425	7.5	1200	26	17
<i>Sierra el Aguaje</i>	Nacapule Canyon	Nac	Coastal	300	21.3	400	7.0	109	10	13
	Paradise Palm Oasis	Ppo	Coastal	400	22	400	7.3	137	13	12
<i>Sierra la Madera</i>	Vallecitos Creek	Val	Yaqui	1850	15	150	6.9	415	20	13
<i>Sierra San Luis / Peloncillo</i>	Cajon Bonito	CajT	Yaqui	1280	23	260	8.1	8895	29	18
	Cottonwood Creek	Ctw	Yaqui	1501	21.5	590	8.0	8.5	8	9
<i>Whetstone Mountains</i>	French Joe Canyon	Frj	Upper Gila	1701	18.5	630	7.7	12	20	6
	Simpson Spring	Sim	Lower Gila	1628	18.9	890	7.9	12.5	22	8

Coleopteran species richness per habitat unit area was as high as 2.3 species m^{-2} , while hemipteran values ranged from 0.01 to 0.64 species m^{-2} (Appendix III). All streams were circumneutral, with low to moderate conductivities, and ranged in size from 8 to 8895 m^2 (Table 2.1). The Lower Gila (Santa Cruz River) and Upper Gila (San Simon and San Pedro Rivers) sections are separated from one another by approximate 300km of dry, heavily modified stream channel.

Species richness models

Log habitat area alone explained 45% of the variation in site species richness ($p = 0.0002$). By contrast, linear isolation distances from the Sierra Madre or the Rocky Mountains only explained 3% and 5%, respectively, of species richness variation and were not statistically significant predictors ($p \geq 0.3$). Stepwise multiple regression selected log area ($\beta = 6.9$; $p = 0.0002$), temperature ($\beta = 1.3$; $p = 0.005$) and elevation ($\beta = 0.005$; $p = 0.10$) as the best predictors of species richness (model $r^2 = 0.63$; $p = 0.00009$). Conductivity, pH, isolation, substrate composition, and percent canopy cover were all insignificant variables. Thus, a model including temperature and elevation explains an additional 18% variation in species richness when compared with using only log area. To make our results comparable with other regions and biotas, we also modeled log species richness with log area relationship, yielding the following equation: $\log\text{Richness} = 1.2462 + 0.1035 \cdot \log\text{Area}$ (Figure 2.2).

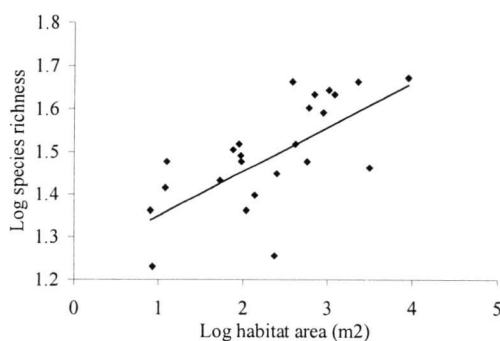


Figure 2.2. Log species-log area relationship for 25 MSI streams ($r^2 = 0.40$; $p = 0.0007$)

Community structure analyses

The NMS ordination converged on a stable, 2-dimensional solution (stress = 18.075, final instability = 0.004, $p = 0.0196$; see Figure 2.3). The two axes accounted for nearly 70% of the variation in community structure between sample units (axis 1: $r^2 = 0.35$; axis 2: $r^2 = 0.34$). Axis

one describes a shift from communities containing more southerly distributed species (i.e. *Thermonectus sibleyi*, *Buena albida*) to those with species whose centers of distribution are north of the MSI (i.e. *Stictotarsus striatellus*, *Aquarius remigis*). Many generalist species (those which are found in both stream and pond environments) are positively correlated with axis 2 (e.g., *Notonecta* spp., *Laccophilus* spp.). Conversely, many species with specific habitat requirements or preferences (e.g., flowing riffles: *Psephenus* sp.; silt or aquatic vegetation: *Peltodytes dispersus*) are negatively correlated with axis 2. Several measured environmental variables overlain on the species ordination were strongly associated with axes 1 and 2. Temperature, latitude and elevation were associated with the community gradient expressed by axis 1, while axis 2 was associated with substrate composition (Table 2.2). Though these factors are usually correlated, in this study temperature was not correlated with latitude ($r = -0.12$) and was marginally correlated with elevation ($r = -0.37$, $p = 0.07$). The two Sierra El Aguaje sites SW of the MSI (Nac, Ppo) are located on the edge of the ordination, but are not significant outliers.

Table 2.2. Environmental variables with strong correlations ($r \geq 0.5$) to an NMS ordination axis.

	Axis 1 correlation	Axis 2 correlation
Temperature	-0.56	0.20
Elevation	0.79	0.08
Latitude	0.75	-0.04
% Bedrock	-0.26	0.69
% Silt	0.08	-0.52

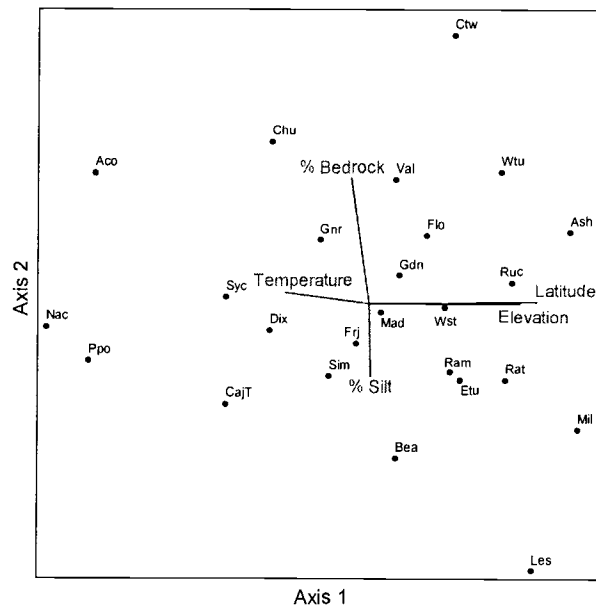


Figure 2.3. NMS ordination plots with correlated ($r > 0.5$) environmental factors overlain

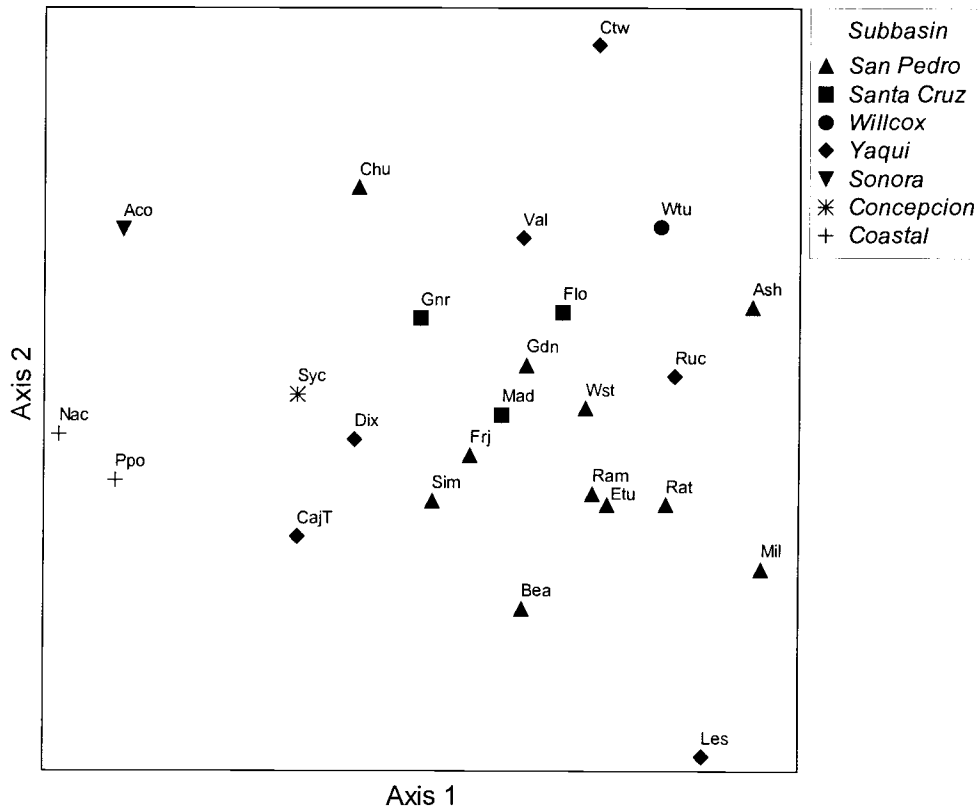


Figure 2.4. NMS ordination with plots grouped by subbasin.

When sites in the ordination were grouped by drainage basin and by mountain range, no obvious patterns emerged (see Figure 2.4). MRPP analyses confirmed the lack of community concordance when grouped by drainage basin ($A = 0.07$). Grouping by mountain range did yield a slightly larger group-effect value ($A = 0.14$, $p < 0.001$). The number of mountain range groups ($n = 12$), however, requires caution in interpreting this result, as four mountain ranges contain only one study stream. Therefore, Mantel tests were used to further examine this potential geographic pattern (Figure 2.5). Mantel tests showed that geographic distance between streams was strongly associated with community distance (Mantel's $r = 0.45$, $p = 0.001$). This result explains why communities grouped by mountain range (small geographic area) are more homogenous than communities grouped by drainage basin (large geographic area). Additionally, after accounting for measured environmental variables, community distance was still strongly correlated with geographic distance (partial Mantel's $r = 0.41$, $p = 0.001$). Community and environmental distance, however, were not significantly correlated after accounting for the effect of spatial position (Figure 2.5).

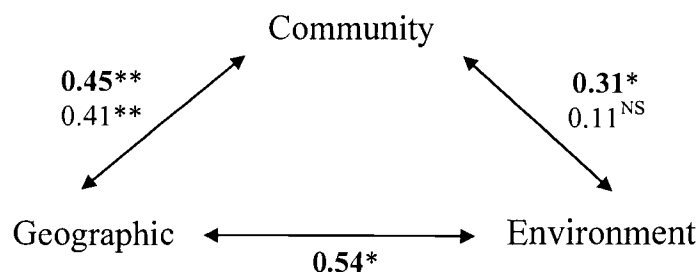


Figure 2.5. Mantel's r (in bold) and partial Mantel's r values between community, environmental and geographic distance matrices (* $p \leq 0.01$, ** $p \leq 0.001$, ^{NS} $p > 0.05$).

Discussion

Species Richness

Habitat area was clearly the most important measured factor in determining local species richness in MSI streams. Though studies of lentic aquatic insect communities have occasionally failed to identify habitat area as an important factor to local species richness (for Coleoptera: Oertli et al., 2002), the majority of studies describe significant species-area relationships (Kiflawi et al., 2003; Rundle et al., 2002; Kholin and Nilsson, 1998; Nilsson, 1984). This study is the first to demonstrate a significant species-area relationship for lotic aquatic insects at the scale of an entire stream. Isolation of MSI streams from the continuous stream networks of the Rocky Mountains and Sierra Madre Occidental was not a significant predictor of species richness. Originally, we hypothesized that the well-connected streams of these 'mainland' mountain ranges may have served as historical or current population sources for MSI aquatic insects. Since very small streams are more vulnerable to drought in arid areas, the distance to larger, well-connected and more drought-resistant habitats could be influential in recolonization potential, but this appears not to be the case in MSI streams. Alternatively, nearest-neighbor stream isolation distances within the MSI may influence local species richness, but these are difficult to quantify. The distribution of permanent streams in the MSI is not well-known and calculating distances between study sites would surely ignore many intervening streams with potential source populations. Thus, isolation is not a factor for species richness in the classic island biogeography sense, but may still play a role in within-MSI metapopulation dynamics.

In addition to area, regression analyses identified temperature and elevation as being significant predictors of species richness. While increased temperature has been linked to increased richness in aquatic insects (Kholin and Nilsson, 1998), elevation is usually inversely

related to species richness (Vinson and Hawkins, 2003; Oertli et al. 2002; Allan, 1975). The steepness of the elevation-richness curve increases above 2600m, where species richness declines precipitously for all aquatic insects including coldwater taxa such as Plecoptera (Vinson and Hawkins, 2003; Allan, 1973). Our study included only streams below 2200m, though coleopteran and hemipteran diversity is greatly decreased above 2600m in the MSI as well (Bogan, unpublished data). These data suggest that in MSI streams the elevation-richness curve is positive between 300m and 2200m (the range included in this study), but then becomes negative at higher elevations.

Species richness was not inversely related to latitude in MSI streams, even though aquatic beetle diversity increases with decreasing latitude (Vinson and Hawkins, 2003). Instead of an increasing number of species, there appeared to be species replacement with decreasing latitude, where neotropical species (e.g., *Macrovatellus mexicanus*, *Thermonectus sibleyi*) replaced more widespread temperate species (e.g., *Stictotarsus striatellus*, *Aquarius remigis*). Our study only included streams between 32.7°N and 28°N, so perhaps a wider latitudinal range is required before the inverse latitude-richness trend can be detected.

Community structure

Habitat area is important in determining lentic beetle assemblages (Rundle et al., 2002), but beetle and bug assemblages do not follow any predictable patterns with increasing habitat size in MSI streams. Some large MSI species (*Abedus herberti*, *Rhantus atricolor*) are flightless or only capable of short flights. We hypothesized that small habitats, which are more vulnerable to complete desiccation, would not contain species with poor recolonization potential. Additionally, we expected that isolated sites would be lacking species with limited dispersal abilities. NMS ordination, however, did not identify habitat area or isolation from the Rocky Mountains or Sierra Madre as being significantly associated with community structure. Thus, we reject our hypotheses that stream size and isolation from 'mainland' ranges are influential in structuring MSI aquatic insect communities.

NMS ordination identified two major gradients in MSI aquatic insect community structure: one associated with latitude and local temperature and elevation, and the second associated with local substrate composition. Though temperature generally covaries with latitude, these variables were not correlated in this study. The presence of novel neotropical taxa (e.g., those not found in the northern MSI) at the southernmost sites suggests that latitude may have an effect on community independent of temperature. Faunal composition shifts have also been associated with elevation in many studies (see Vinson and Hawkins, 2003), and these shifts

are often independent of terrestrial vegetation shifts (Allan, 1975). Local habitat structure in temperate streams can often explain much of the variation in aquatic insect communities (Sanderson et al., 2005; Petersen et al., 2004; Corkum, 1990). In MSI streams, a shift from bedrock to silt dominated streams appears to be influential for community structure. Silt and detritus levels are especially important for some species (Corkum, 1990), while bedrock-dominated streams in the MSI contain more generalist species.

Surprisingly, canopy cover, pH, and conductivity were also not associated with any shifts in community structure. In mesic temperate streams, canopy type and percent cover can be more important than substrate for explaining variation in aquatic insect community structure (Hawkins et al., 1982; Vannote et al., 1980). Many species of Ephemeroptera and Trichoptera rely on specific riparian vegetation food sources, which may control their distribution (Cummins et al., 1989). Our study, however, focused on hemipterans and coleopterans which are primarily predators and scavengers, and are less likely to be sensitive to the amount or type of riparian leaf input. This suggests that desert streams dominated by hemipterans and coleopterans, like those of the MSI, are fundamentally different from mesic temperate streams in their response to riparian vegetation. The lack of response of MSI aquatic insect communities to conductivity and pH may be explained by the range of these variables measured in our study streams. Conductivity was important for structuring lentic hemipteran and coleopteran communities over a range of 50 to 15,000 $\mu\text{S cm}^{-1}$ in Canadian lakes, with completely disjunct species distributions at 80 and 5000 $\mu\text{S cm}^{-1}$ (Lancaster and Scudder, 1987). In contrast, MSI streams only exhibited mean conductivities from 80 to 890 $\mu\text{S cm}^{-1}$, a range which may be too narrow to have an impact on community structure. Similarly, all MSI streams are circumneutral (pH: 6.9-8.2), whereas many studies identifying pH as a driver of community structure are from acidic stream systems with more spatial variability in pH (Sanderson et al., 2005). Thus, the apparent lack of community response to pH and conductivity likely is due to the narrow range these parameters exhibit in MSI streams.

Historical constraints (e.g., drainage basin history) often act to exclude aquatic species from otherwise suitable locations. Fish distribution, in particular, is 'filtered' by historical constraints (Williams et al., 2003). MSI streams drain to four different river systems (Gila, Yaqui, Sonora, Concepción) and one endorheic basin (Willcox Playa), and the distribution of fish species is limited by these basins (Hendrickson et al., 1980). We hypothesized that aquatic insect species may similarly be constrained by drainage basin, but MRPP analyses found no differences in community structure between drainage basins. In fact, communities grouped by mountain range were twice as homogenous as communities grouped by drainage basin. Clearly, MSI

aquatic insect communities respond to local environmental factors but are not constrained by drainage basin origin.

Aquatic insects are less restricted by hydrological connectivity than fish because they have an adult stage which can fly between basins and colonize new habitats (Wallace and Anderson, 1996). In the MSI, streams from completely different drainage basins are often separated by only a few kilometers. Short flights could link drainage basins that have different outlets to the sea, and thus no shared hydrologic histories or affinities. Many hemipteran and coleopteran adults are strong flyers and engage in long-distance dispersal and migrational flights (Velasco and Millan, 1998; Schlichting and Sides, 1969). Hemipteran and coleopteran flight dispersal is triggered by increased stream temperature, reduced water levels, and increased insect densities (Velasco and Millan, 1998), conditions which MSI streams regularly exhibit outside of the winter rainy season. These factors likely facilitate between basin transfers of species, and thus contribute to the lack of homogeneity of MSI aquatic insect communities when grouped by drainage basin.

Frequent dispersal events in aquatic insects can lead to non-random patterns in species distributions between streams (Rundle et al., 2002). Additionally, since the number of colonizers and proximity of sources greatly impact colonization success and site persistence times for aquatic insects (Ahlroth et al., 2003), we hypothesized that proximity of sites would be correlated with community similarity. Mantel tests indicated a significant correlation between geographic and community distances ($r=0.45$). In fact, after accounting for geographic distances there was no significant correlation between community and environmental distance matrices (partial Mantel $r=0.11$, $p=0.3$). Even after accounting for measured environmental variables, though, geographic distances were still strongly correlated with community distances (partial Mantel $r=0.41$), suggesting the presence of spatial autocorrelation in community structure that was not explained by environmental factors. This contrasts sharply with other studies which have shown moderate to strong spatial autocorrelation in Ephemeroptera, Trichoptera, and Plecoptera distribution, but low autoregressive components for coleopterans (Sanderson et al., 2005). Townsend et al. (2003) found that geographic location was not at all influential in explaining assemblages of strongly flying insects in British streams. This apparent discrepancy regarding the influence of geographic position on coleopteran and hemipteran communities may be explained by the spatial resolution of the studies. We examined the effects of geographic locations over a very large area ($\sim 150,000\text{km}^2$) with a mean nearest neighbor distance of 18km. Previous studies have focused on much smaller areas (50 to 5000km^2) with much shorter mean nearest neighbor distances (400m to 5km) (Sanderson et al., 2005; Townsend et al., 2003; Rundle

et al., 2002). Thus, spatial autocorrelation may not be apparent for strong flying taxa at small scales in mesic regions, but was observed for coleopterans and hemipterans at large spatial scales in the isolated habitats of the MSI.

Conclusions

Small, isolated desert streams, like those of the MSI, exist as insular habitats in a terrestrial landscape rather than as continuous dendritic habitats that most temperate streams offer. As such, MSI streams offer discrete, quantifiable habitat units that are well-suited to examining island biogeography principles and the effects of regional and local factors in structuring local aquatic insect communities.

Though species richness is the result of regional and local processes (Ricklefs, 1987), our study demonstrates the overwhelming importance of the species-area relationship (i.e. local habitat area) in determining local species diversity in MSI streams. The species richness per unit area in MSI streams is quite high, and the factors which support this high diversity are deserving of further study. Additionally, we found that local environmental factors are more important in shaping MSI hemipteran and coleopteran community structure than historical (i.e. regional) constraints. MSI aquatic insect communities, unlike fish communities, are not correlated with regional drainage patterns. We identified gradients in community structure within the regional vegetation type (biome: arid evergreen woodland). Community differences between streams in the MSI and outlier sites in the Sierra el Aguaje (biome: tropical thornscrub) were explained by temperature, elevation and latitude, suggesting that regional vegetation is not strongly shaping local aquatic insect communities.

Though other studies have failed to find small-scale spatial autocorrelation in the distribution of strong flying taxa, we observed spatial autocorrelation in these taxa at a larger geographic scale. Most observed species richness and spatial autocorrelation patterns are scale-dependent (Vinson and Hawkins, 1998; Weaver, 1995; Legendre, 1993; Wiens, 1989), so it is essential take scale into account when describing and interpreting these patterns.

Acknowledgements

This work was conducted under USDA Forest Service Special Uses Permit #SUP0092 (U.S.A.) and SEMERNAT Permiso #SGPA/DGVS/04147 (Mexico). Scientific collection permits (ATZS-*ISB* 200-3) for Garden Canyon (Fort Huachuca) were made possible by Sheridan Stone, US Army Wildlife Biologist. A portion of the work was conducted at the American Museum of Natural History's Southwestern Research Station. Funding came from Oregon State University

and National Science Foundation grant DEB-0445366 to D.A.L. Carl Olson graciously allowed the use of lab space and access to the aquatic insect reference collection at the University of Arizona. Thanks to Dave Gori and Dale Turner of the Tucson office of the Nature Conservancy for GIS data and access to Ramsey Canyon. Special thanks to our Mexican collaborators Maestro Andres Alvarado and Maestro Oscar Gutierrez of CESUES, Hermosillo, Sonora, without whom Mexico collection efforts would have been futile. Thanks to Joe and Valer Austin for access to their fantastic properties at Rancho San Bernadino and Rancho Los Ojos, Sonora and also to Sr. Rubén Monroy Leon for his warm hospitality and access to Vallecitos at Rancho Las Bellotas, Sonora.

Literature Cited

- Ahlroth, P., R. V. Alatalo, A. Holopainen, T. Kumpulainen, and J. Suhonen. 2003. Founder population size and number of source populations enhance colonization success in waterstriders. *Oecologia* 137:617-620.
- Allan, J. D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. *Ecology* 56:1040-1053.
- Armitage, P. D., and C. E. Cannan. 2000. Annual changes in summer patterns of mesohabitat distribution and associated macroinvertebrate assemblages. *Hydrological Processes* 14:3161-3179.
- Bohonak, A. J., and D. G. Jenkins. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters* 6:783-796.
- Clenaghan, C., P. S. Giller, J. O'Halloran, and R. Hernan. 1998. Stream macroinvertebrate communities in a conifer-afforested catchment in Ireland: relationships to physio-chemical and biotic factors. *Freshwater Biology* 40:175-193.
- Corkum, L. D. 1990. Intra-biome distributional patterns of lotic macroinvertebrate assemblages. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2147-2157.
- Corkum, L. D. 1992. Spatial distributional patterns of macroinvertebrates along rivers within and among biomes. *Hydrobiologia* 239:101-114.
- Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry, and W. B. Taliaferro. 1989. Shredders and riparian vegetation. *BioScience* 39:24-30.
- Dodson, S. 1992. Predicting crustacean zooplankton species richness. *Limnology and Oceanography* 37:848-856.
- Hawkins, C. P., M. L. Murphy, and N. H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. *Ecology* 63:1840-1856.

- Hendrickson, D. A., W. L. Minckley, R. R. Miller, D. J. Siebert, and P. H. Minckley. 1980. Fishes of the Rio Yaqui basin, Mexico and United States. *Journal of the Arizona-Nevada Academy of Science* 15:65-106.
- Kholin, S. K., and A. N. Nilsson. 1998. Regional enrichment of predacious water beetles in temporary ponds at opposite east-west ends of the Palearctic. *Journal of Biogeography* 25:47-55.
- Kiflawi, M., A. Eitam, and L. Blaustein. 2003. The relative impact of local and regional processes on macro-invertebrate species richness in temporary pools. *Journal of Animal Ecology* 72:447-452.
- Lancaster, J., and G. G. Scudder. 1987. Aquatic Coleoptera and Hemiptera in some Canadian saline lakes: patterns in community structure. *Canadian Journal of Zoology* 65:1383-1389.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659-1673.
- Lytle, D. A. 2003. Reconstructing long-term flood regimes with rainfall data: effects of flood timing on caddisfly populations. *The Southwestern Naturalist* 48:36-42.
- Lytle, D. A., and R. L. Smith. 2004. Exaptation and flash flood escape in giant water bugs. *Journal of Insect Behavior* 17:169-178.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton.
- Malmqvist, B. 2002. Aquatic invertebrates in riverine landscapes. *Freshwater Biology* 47:679-694.
- McCune, B. and J. B. Grace. 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, OR, USA.
- McCune, B. & M.J. Mefford. 1999. PC-ORD. Multivariate Analysis of Ecological Data. Version 4.0. MjM Software, Gleneden Beach, Oregon, USA.
- Merritt, R. W., V. H. Resh, and K. W. Cummings. 1996. Design of aquatic insect studies: collecting, sampling and rearing procedures. Pages 12-28 in R. W. Merritt and K. W. Cummings, editors. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque.
- Mielke, P. W., Jr, and K. J. Berry. 2001. *Permutation Methods: A distance function approach*. Springer, Berlin.
- Nilsson, A. N. 1984. Species richness and succession of aquatic beetles in some kettle-hole ponds in northern Sweden. *Holarctic Ecology* 7:149-156.
- Nilsson, A. N., J. Elmberg, and K. Sjöberg. 1994. Abundance and species richness patterns of predaceous diving beetles (Coleoptera, Dytiscidae) in Swedish lakes. *Journal of Biogeography* 21:197-206.

- Oertli, B., D. A. Joye, E. Castella, R. Juge, D. Cambin, and J.-B. Lachavanne. 2002. Does size matter? The relationship between pond area and biodiversity. *Biological Conservation* 104:59-70.
- Petersen, I., Z. Masters, A. G. Hildrew, and S. J. Ormerod. 2004. Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology* 41:934-950.
- Poff, N. L., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1805-1818.
- Ricklefs, R. E. 1987. Community diversity: relative role of local and regional processes. *Science* 235:167-171.
- Rundle, S., A. Foggo, V. Choiseul, and D. T. Bilton. 2002. Are distribution patterns linked to dispersal mechanism? An investigation using pond invertebrate assemblages. *Freshwater Biology* 47:1571-1581.
- Sanderson, R. A., M. D. Eyre, and S. P. Rushton. 2005. The influence of stream invertebrate composition at neighboring sites on local assemblage composition. *Freshwater Biology* 50:221-231.
- Schlichting Jr., H. E., and S. L. Sides. 1969. The passive transport of aquatic microorganisms by selected Hemiptera. *Journal of Ecology* 57:759-764.
- Sepkoski, J. J., and M. A. Rex. 1974. Distribution of freshwater mussels: coastal rivers as biogeographic islands. *Systematic Zoology* 23:165-188.
- Sokal, R. R. and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd edition. W. H. Freeman and Co, New York. 887 pp.
- Townsend, C. R., S. Doledec, R. Norris, K. Peacock, and C. Arbuckle. 2003. The influence of scale and geography on relationships between stream community composition and landscape variables: description and prediction. *Freshwater Biology* 48:768-785.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- Velasco, J., and A. Millan. 1998. Insect dispersal in a drying desert stream: effects of temperature and water loss. *The Southwestern Naturalist* 43:80-87.
- Vinson, M. R., and C. P. Hawkins. 1998. Biodiversity of stream insects: variation at local, basin, and regional scales. *Annual Review Entomologia* 43:271-293.
- Vinson, M. R., and C. P. Hawkins. 2003. Broad-scale geographical patterns in local stream insect genera richness. *Ecography* 26:751-767.
- Wallace, B. J., and N. H. Anderson. 1996. Habitat, life history, and behavioral adaptations of aquatic insects. Pages 41-73 in R. W. Merritt and K. W. Cummins, editors. *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt, Dubuque.

- Weaver, J. C. 1995. Indicator species and scale of observation. *Conservation Biology* 9:939-942.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Williams, L. R., C. M. Taylor, M. L. Warren, and J. A. Clingenpeel. 2003. Environmental variability, historical contingency, and the structure of regional fish and macroinvertebrate faunas in Ouachita Mountain stream systems. *Environmental Biology of Fishes* 67:203-216.

CHAPTER 3

Seasonal flow variation allows ‘time-sharing’ by disparate aquatic insect communities in montane desert streams

Abstract

We hypothesized that two disparate aquatic insect faunas (montane temperate and neotropical) could be maintained at the same sites by strong seasonal variation in abiotic conditions. Aquatic insect assemblages were sampled at 7 isolated montane desert streams in SE Arizona during 2004 and 2005. A total of 59 aquatic insect families were collected. We assessed changes in aquatic insect community and functional feeding group assemblages by habitat (riffle, pool) and season (high flow, low flow). Non-metric multidimensional scaling was used to elucidate gradients in community assemblage across season and habitat type and to determine correlations between environmental parameters and community assemblage. Taxa with strong seasonal affinities were identified with Indicator Species Analysis. Kruskal-Wallis tests were used to identify factors correlated with changes in functional feeding group assemblages. Community assemblages showed strong seasonal patterns: Rocky Mountain fauna were strongly associated with the high flow season while neotropical hemipterans and coleopterans were associated with the low flow season. Increased temperature was significantly associated with this shift from temperate to neotropical assemblages. Functional feeding group assemblages shifted dramatically by season. Predator abundance increased from 24.5% (high flow) to 75.2% (low flow) while filterer and shredder abundance declined from 38.4% (high flow) to 1.7% (low flow). We conclude that ‘time-sharing’ of disparate communities is facilitated by high elevation refuges for temperate montane taxa, egg and larval diapause to survive the dry season, and strong seasonal variation in flow and temperature.

Introduction

Lotic macroinvertebrates have evolved in very dynamic environments and exhibit strong responses to seasonal flow variability at both the species and community level (Lytle and Poff, 2004; Cowell et al., 2004; Thompson and Townsend, 1999; Matthews et al., 1991; McElravy et al., 1989; Hawkins and Sedell, 1981). Seasonal community assemblage shifts have even been noted in streams with minor seasonal variation (Scarsbrook and Townsend, 1993). Streams in

arid environments are often subject to extreme seasonal variation in flow, temperature, water chemistry and productivity (Lytle and Poff, 2004; Stanley et al., 1994; Poff and Ward, 1989; Gray, 1980). The response of arid land lotic invertebrate communities to severe floods (Lytle, 2000; Grimm and Fisher, 1989; Gray and Fisher, 1981) and droughts (Clinton, 1996; Stanley et al., 1994) has been well studied, but few studies have specifically examined community-level response to seasonal variability in these streams (but see Gray, 1980).

Shifts in community structure can be quantified taxonomically, by functional feeding groups, or by density. Clearly, each species has its own strategy for dealing with seasonal variation (Lytle and Poff, 2004), so a taxonomic evaluation is valid, but quite often species-level determinations are not possible with aquatic insect larvae. Since allochthonous and autochthonous inputs can vary dramatically with season (Cowell et al., 2004; Thompson and Townsend, 1999), functional feeding groups are useful proxies for examining community response to seasonal variation. Habitat type (e.g., riffle, pool) can also greatly affect both taxonomic and functional feeding group composition both within (Hose et al., 2005; Brown and Brussock, 1991) and between seasons (Hose et al., 2005; Arunachalam et al., 1991). In mountain streams, density and diversity of aquatic invertebrates is generally higher in riffles than pools (Brown and Brussock, 1991). Thus, a reach-level perspective based on habitat types is needed to accurately model seasonal variability in stream communities (Brussock and Brown, 1991).

The main influence of seasonal variation is often expressed as changed abundances of species rather than complete species replacement (Brooks, 2000; Thomson and Townsend, 1999). For species to be present in some seasons but not others, refuges must be available during the off-season(s). The hyporheic zone serves as an important refuge for some taxa to escape dry seasons, either as active individuals or as diapausing eggs or larvae (Hose et al., 2005; Anderson, 1997; Jacobi and Cary, 1996; Boulton, 1989; Delucchi, 1989). Neighboring streams may also serve as sources for seasonal populations in a given stream, though many taxa (e.g., Ephemeroptera) do not stray far from the stream corridor (Petersen et al., 2004; Kovats et al., 1996) and are unlikely to cross drainage divides in arid areas. Other taxa, however, may travel long distances during dispersal (e.g., Coleoptera: Sanderson et al., 2005). Upstream, headwater reaches may also serve as a source for seasonal populations (via drift: Gray and Fisher, 1981), although, significant longitudinal distances within a stream are often required to achieve species turnover (Brussock and Brown, 1991; Vannote et al., 1980). Thus, a steep stream gradient and significant elevational relief would be needed for headwater reaches to serve as a close source for seasonally-induced species turnover in lower reaches.

Streams of the Madrean Sky Island bioregion have both steep gradients and significant elevation relief within short distances. Additionally, these streams are uniquely situated between the Rocky Mountains and the Sierra Madre, which offer a large, diverse regional species pool adapted to both warm and cold water streams. To describe differences in community assembly between high and low flow periods in Madrean Sky Island streams, we surveyed seven randomly selected streams under both flow conditions. We recorded physical and water quality characteristics at each site, and sampled the aquatic insect community in each type of stream habitat present. These data were then used to describe differences in aquatic insect communities between season and habitat type. We described the association between biogeographic origin and season and/or habitat type by determining the biogeographic affiliation (Rocky Mountain or Sierra Madre) of taxa in each sample unit. We hypothesized that seasonal variation in flow and temperature allows disparate faunas (Rocky Mountain and Sierra Madre) to coexist in the same site, but during different seasons.

Study Area

The Madrean Sky Islands (MSI) consist of a series of parallel NW-SE trending mountain ranges in southeast Arizona, southwest New Mexico, and northwest Mexico. The MSI are located in between the southern Rocky Mountain and the Sierra Madre cordilleras, and share floral and faunal associations with both cordilleras. Each mountain range is isolated from other ranges by large areas of lowland desert and grassland. Permanent streams in the MSI occur mainly in a narrow elevation band between 1200 and 2200 m in the Madrean Evergreen Woodland vegetation zone, an arid oak and pine woodland. Streams in this elevation band are high-gradient and contain extensive sections of permanent bedrock pools interspersed with alluvial riffles and runs which often dry up seasonally. In lower mountain ranges (<2700 m), headwaters are seasonally dry, while higher mountain ranges (>2700 m) contain permanent headwater springs and relict Rocky Mountain conifer forests. Below 1200 m, stream channels are usually dry except during flash floods. The seven study streams are distributed across the northern MSI, with four sites in lower elevation ranges, and three sites in a higher elevation mountain range (Chiricahua). All seven sites occur in the Coronado National Forest (Figure 3.1).

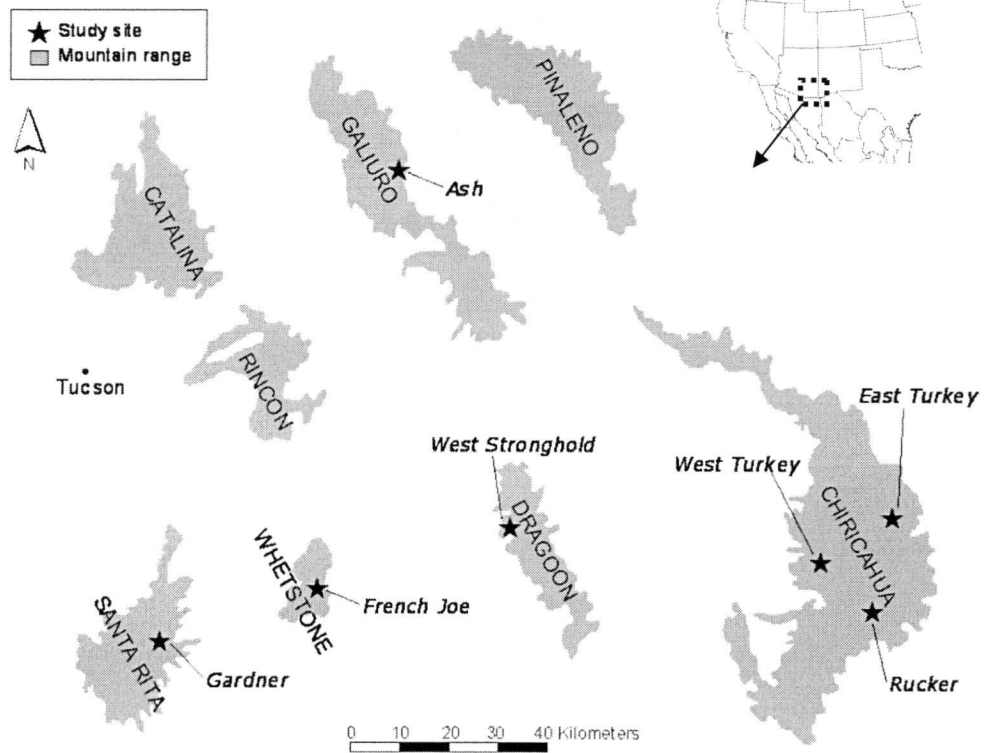
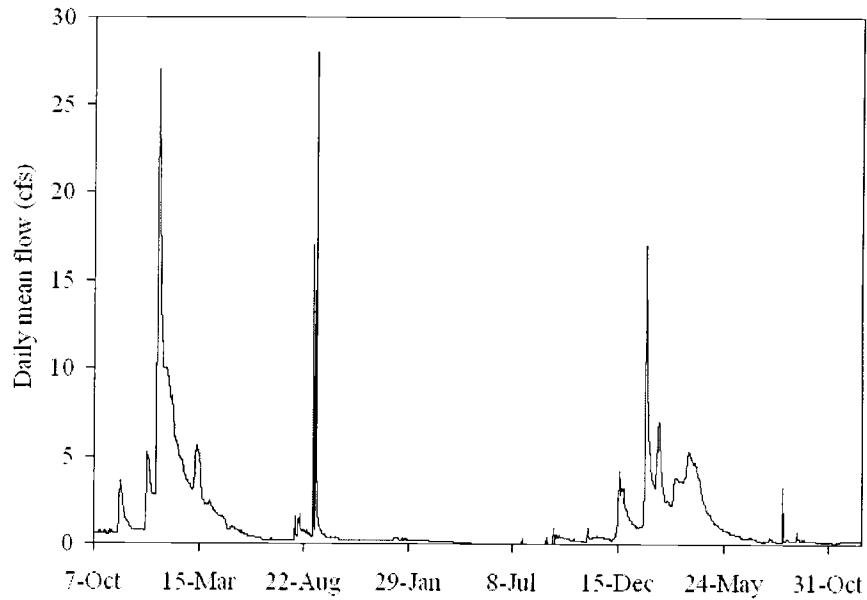
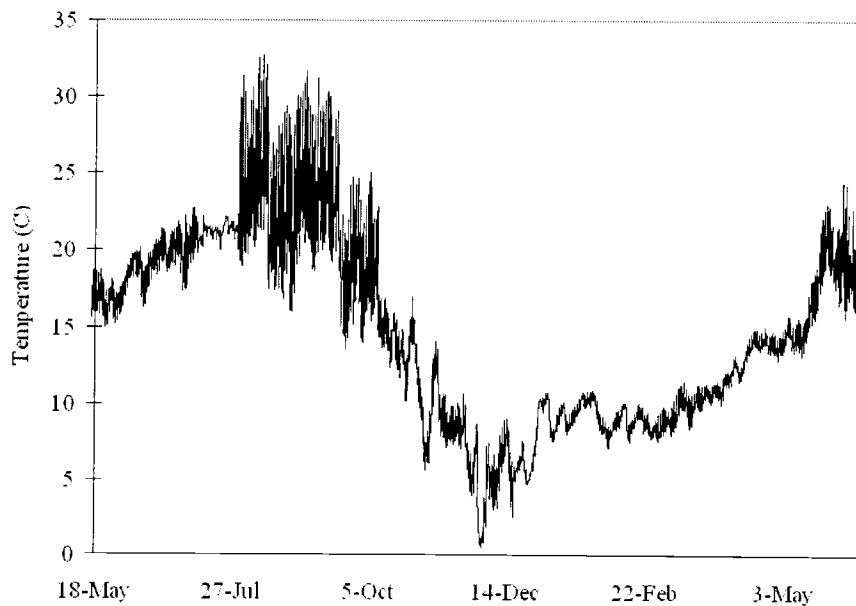


Figure 3.1. Location of the seven study streams within Coronado National Forest, Arizona.

Rainfall and stream flow in MSI streams are highly seasonal. In summer, convective monsoon storms bring torrential rains lasting from several minutes to hours and cause severe flash flood events, but do not provide for much increased baseflow. Conversely, winter storms tend to be prolonged, with rain falling over several days. Total precipitation is split fairly evenly between the two seasons. The consistency and duration of winter storms allow for a sustained increase in baseflow (high flow season), lasting from several weeks to months. During the rest of the year (low flow season), flow in most MSI streams is less than $0.005 \text{ m}^3/\text{s}$ and is often zero (Figure 3.2a). Stream temperature is also highly seasonal and variable. During the summer, diurnal fluctuations can be as great as 12°C , and during the winter temperatures can drop to near 0°C and are subject to much lower diurnal flux (Figure 3.2b).



a.)



b.)

Figure 3.2. (a.) Discharge from Garden Canyon, Huachuca Mountains at USGS Gage # 09470800, 1 Oct 1959 to 31 Oct 1962. Continuously gaged streams are non-existent in the MSI, and gages often operate over very short time periods, but this period exemplifies the seasonality of MSI streams. (b.) Stream temperature at 10 cm depth from Florida Canyon, Santa Rita Mountains, recorded with a HOBO Water Temp Pro© from 18 May 2004 to 12 June 2005. This site is 3km from the study site at Gardner Canyon, and is representative of a typical MSI stream temperature regime (Bogan and Lytle, unpublished data).

Methods

Sampling

Sampling was conducted at seven Madrean Sky Island streams in southeastern Arizona during March-April (high flow) and June (low flow) 2004 and 2005. The permanent reaches of most of these streams occupy a narrow elevational band between 1200 and 2200 meters. This elevational band has very similar climatic, biotic and abiotic characteristics across the region, but because aquatic communities often have a steep compositional gradient in relation to elevation, a stratified random sampling scheme was devised. Preliminary community samples from three streams (East Turkey Creek, Rucker Canyon and Simpson Spring) were used to create species-effort saturation curves and determine the effort necessary to maximize species detection. An effort of 10 s per m² of pool combined with sampling three pools per elevational stratum (300 m) detected approximately 95% of taxa present (Bogan, unpublished data). Thus, within each 300 m elevational band where surface water occurred, three pools and riffles were sampled when present. Accordingly, for each season (low flow and high flow) anywhere from three to twelve samples are used to describe the insect community, depending on type of habitat present and elevation range occupied by each stream. Entire pools were sampled by vigorously sweeping a D-net (1 mm mesh) above all pool substrates and on the surface of the water for 10 s per m² of pool. Riffles were sampled by taking a 'kick-sample', where 0.25 m² of riffle substrate was disturbed to a depth of 5 cm and insects were captured downstream with a D-net (1 mm mesh). Pool and riffle sample locations were haphazardly selected from permanent water habitat maps created at each site before sampling. The nearest riffle to the haphazardly selected map point was sampled. Using the same selected map points, the closest pool meeting set criteria (size: >2 m², <5 m²; max. depth: >0.5 m) was sampled. At each sample unit location, water temperature, conductivity (μS), and pH were measured at 10 cm depth.

All collected insects were preserved in 95% ethanol and identified to family-level and counted at Oregon State University. Identification to family was all that was possible for many early instar taxa (e.g., Capniidae: Plecoptera, Chironimidae: Diptera), so this level of taxonomic resolution was used for all individuals. Since area sampled in riffles was 0.25 m² and pool sizes ranged from 2 to 4 m², all abundance counts were converted to densities per meter squared to make sample unit values comparable across sites and habitat types (Merritt et al., 1996). Additionally, collected taxa were assigned to functional feeding groups to create a secondary, functional feeding group matrix.

Single samples were taken from two additional sites, Rustler Park (2560 m) and Grant Creek (2680 m). These locations were selected to describe the insect communities found at high

elevations in the Madrean Sky Islands, in relictual conifer forests. These sites are different from the seven lower elevation sites in that they have spring-fed, cold flowing water year-round and are dominated by riffles and spring-head pools, much like headwater streams in the Rocky Mountains. These sites were sampled in June 2004, when lower elevation streams had almost zero flow and were considerably warmer. Our purpose with including these 'outgroups' in the dataset was to determine if the relictual conifer stream insect communities were similar to arid evergreen woodland stream communities under high-flow conditions.

Stream surface area was assessed during the low flow season by walking along the entire stream and visually estimating pool and riffle sizes. During the high flow season, starting and ending GPS points for flow were recorded to calculate total flowing length. These lengths were then multiplied by the average ($n \geq 10$) stream width to estimate total stream surface area.

Data Analysis

Aquatic insect assemblage data matrices were analyzed using non-metric multidimensional scaling (NMS) in PC-ORD (McCune and Mefford 1999). NMS takes advantage of redundancy in the data matrix, using a rank-based metric to reduce community data from many dimensions to a 2- or 3-D ordination. Environmental parameters can then be overlain on the community structure-based ordination to elucidate relationships between measured parameters and community shifts. Sorensen distances were used to calculate community dissimilarity between samples and sites. Before ordinations were run, taxa which occurred in only one sample were removed from the matrices. These 'singleton' taxa add noise to the dataset, without revealing any information about the relatedness of sites. Several transformations were considered with the reduced (singleton-deleted) dataset, as taxa abundances were quite variable between season and site. Square-root transformations and relativization by row totals ($p=1$) did reduce the coefficient of variation among the species and/or sample unit values, but had little effect on the ensuing ordination. Sample unit outliers were sought using the distribution of Sorensen's distance measure between each sample and all other samples. No sample units were identified with mean Sorensen distance to all other sample units greater than 2.0 standard deviations from the grand mean. Additionally, the variation between low flow and high flow insect densities may reflect differential taxa responses to flow variation, and thus be biologically significant. For these reasons, we used the reduced, untransformed dataset. Replicate samples within each stream and year were averaged by habitat type and season. After performing the NMS analyses, we examined correlation coefficients between each taxon and axis of the

ordination to determine which taxa were influential in the ordination and which environmental variables those taxa are associated with.

Community matrix sample units were broken into three *a priori* groups using flow-condition and habitat type (high-flow riffle, high-flow pool, and low-flow pool). Those three groups were also subdivided further into six groups based on whether or not the streams contained permanent, high-elevation headwaters. We used Multi-response Permutation Procedure (MRPP) with Sorensen distances to quantify and test within-group agreement and distinctness (see Mielke and Berry, 2001). This procedure yields two statistics: an A-statistic ($-1 \leq A \leq 1$), describing the effect-size of the grouping, and a p-value which evaluates the likelihood that observed differences are due to chance (McCune and Mefford 1999).

Indicator Species Analysis (ISA) was used to determine if particular taxa were indicative of the groups defined by flow, habitat and headwater-type. The highest possible indicator value (IV) for a taxon is 100, meaning that the taxon is always present in a particular group (faithful) and does not appear in other groups (exclusive) (McCune and Grace 2002). The 'faithfulness' multiplier is the proportional abundance of a given species in a group relative to its abundance in all groups, while the 'exclusivity' multiplier is the percentage of plots that a given species occupies within a given group. The product of these percentages yields the IV, thus both percentages must be high for a species to gain a high IV. The statistical significance of each IV was tested using a Monte Carlo randomization method with 1000 runs.

Differences in aquatic insect densities (total and by functional feeding group) and taxon richness between season, habitat, site, year, and streams with and without permanent headwaters were analyzed using the Kruskal-Wallis test, since both sample sizes ($3 \leq n \leq 12$) and variances between sites and habitats were uneven. When testing for differences between season and habitat type, all sites in both years were combined. When testing for site differences, all habitat types' and both years' data were grouped for each site. Differences in environmental parameters (temperature, pH, and conductivity) between season, year, and streams with and without permanent headwaters were tested using two-sample t-tests.

Results

Fifty-nine aquatic insect families were recorded across the streams, seasons, and habitats, with a total of 25,960 individuals identified. Streams during low flow periods covered an average of 343 m², while during high flows coverage averaged 9934 m². The magnitude of seasonal change varied between streams with and without permanent headwaters. During the high flow

season, area increased by 2.1 orders of magnitude in streams without permanent headwaters and only 1.3 orders of magnitude in streams with permanent headwaters (Table 3.1). French Joe Canyon, a limestone spring-fed system, was atypical as habitat expansion during the high flow season did not create riffle habitat (only additional pools). Additionally, the stream dried completely after March 2005, thus could not be sampled during the low flow season of 2005.

Table 3.1. Seasonal differences in surface area of stream habitat at the seven study sites and presence or absence of higher elevation, permanent headwater reaches.

Study site	Low flow size (m ²)	High flow size (m ²)	Permanent headwaters?
Rucker Canyon	1029	18000	y
West Turkey Creek	598	14500	y
East Turkey Creek	571	9000	y
West Stronghold Canyon	94	9200	n
Gardner Canyon	89	7800	n
French Joe Canyon	12	240	n
Ash Canyon	9	10800	n

Functional feeding groups and taxon richness

Relative abundances of functional feeding groups were significantly affected by season and habitat types (Figure 3.3). Collector-filterer and predator relative abundances varied significantly by season-habitat type ($\chi^2 = 24.0$ and 22.9 respectively, $p < 0.0001$). Collector-filterers achieved greatest density in the high flow riffles (742 m^{-2}), while predator density peaked in low-flow pools (385.5 m^{-2}). Relative abundances of shredders also varied significantly by season-habitat type ($\chi^2 = 8.3$, $p = 0.004$). Shredders were most abundant in high flow riffles (130.7 m^{-2}). These functional feeding group differences contributed to a highly significant effect of season and habitat type on overall aquatic insect density ($\chi^2 = 12.2$, $p = 0.0005$). Scrapers and shredders were more abundant in 2005 than in 2004 ($\chi^2 = 4.8$, $p = 0.03$ and $\chi^2 = 6.9$, $p = 0.009$, respectively), contributing to a significant effect of year on overall density of aquatic insects ($\chi^2 = 4.5$, $p = 0.03$). Significant differences between streams were only observed with scrapers and overall taxon richness ($p < 0.001$; Table 3.2). The source of these differences was elucidated by grouping streams by headwater type. Scraper density and overall taxon richness were significantly higher in streams with permanent headwaters ($p < 0.001$; Table 3.2). Additionally, shredders were more abundant in streams with permanent headwaters ($p = 0.004$).

Taxon richness did not vary significantly by season/habitat type or by year ($p > 0.05$; Table 2), but there were differences between streams ($p < 0.001$; Table 3.2). Streams with

permanent high elevation headwaters contain higher diversity than those lacking permanent high elevation headwaters ($p < 0.001$; Table 3.2).

Table 3.2. Average densities ($\#/m^2$) of functional feeding groups and average taxon richness across streams and by headwater type. Chi-square statistics from Kruskal-Wallis tests examining variation of densities and taxon richness between streams and headwater types.

	Stream							Headwater		χ^2	
	Ash	Etu	Frj	Gnr	Ruc	Wst	Wtu	Permanent	None	Stream	Headwater
<i>Density</i>											
All taxa	531.4	683.8	243.6	624.3	525.8	505.5	941.4	717.0	508.4	2.3	0.3
Collectors-gatherers	34.1	299.0	105.9	73.7	155.1	115.2	119.6	191.2	81.1	7.8	2
Collectors-filterers	176.8	96.1	0.0	423.0	133.9	150.7	416.8	215.6	216.3	10.89	7.5**
Predators	264.8	70.3	128.1	119.6	109.4	186.9	307.1	162.2	177.4	2.9	0.6
Scrapers	0.4	83.6	0.8	1.9	112.1	10.3	70.8	88.8	3.9	22.0***	19.7***
Shredders	55.2	134.8	8.9	6.1	15.5	42.5	27.1	59.1	29.7	11.4	8.4**
Taxon Richness	7.6	23.4	18.0	15.2	21.7	12.3	20.7	21.550	12.850	24.9***	19.5***

Significance level, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

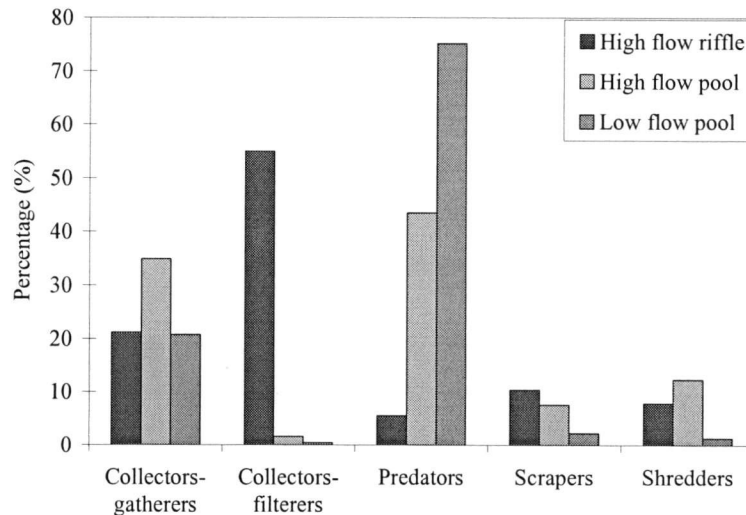


Figure 3.3. Mean relative abundances of functional feeding groups by season and habitat type.

NMS Ordination

NMS ordination with the reduced (singleton-deleted), untransformed species matrix converged on a stable, 2-dimensional solution (stress = 13.830, final instability = 0.00001, $p = 0.0196$; see Figure 3.4). The two axes accounted for nearly 73% of the variation in community structure between sample units (axis 1: $r^2 = 0.543$; axis 2: $r^2 = 0.184$). The two habitat types (pool and riffle) in the ordination clearly represent distinct communities. High pool and low flow

pools generally occupy distinct areas of species space, though with some overlap due to variability in high flow pools (Figure 3.4). The two 'outgroup' low-flow, high elevation samples (GRT366- Grant Creek; RUST- Rustler Park) occupied the high flow region of space. Thus, during the low-flow season these high elevation headwater stream communities are compositionally similar to lower elevation stream communities during the high flow season.

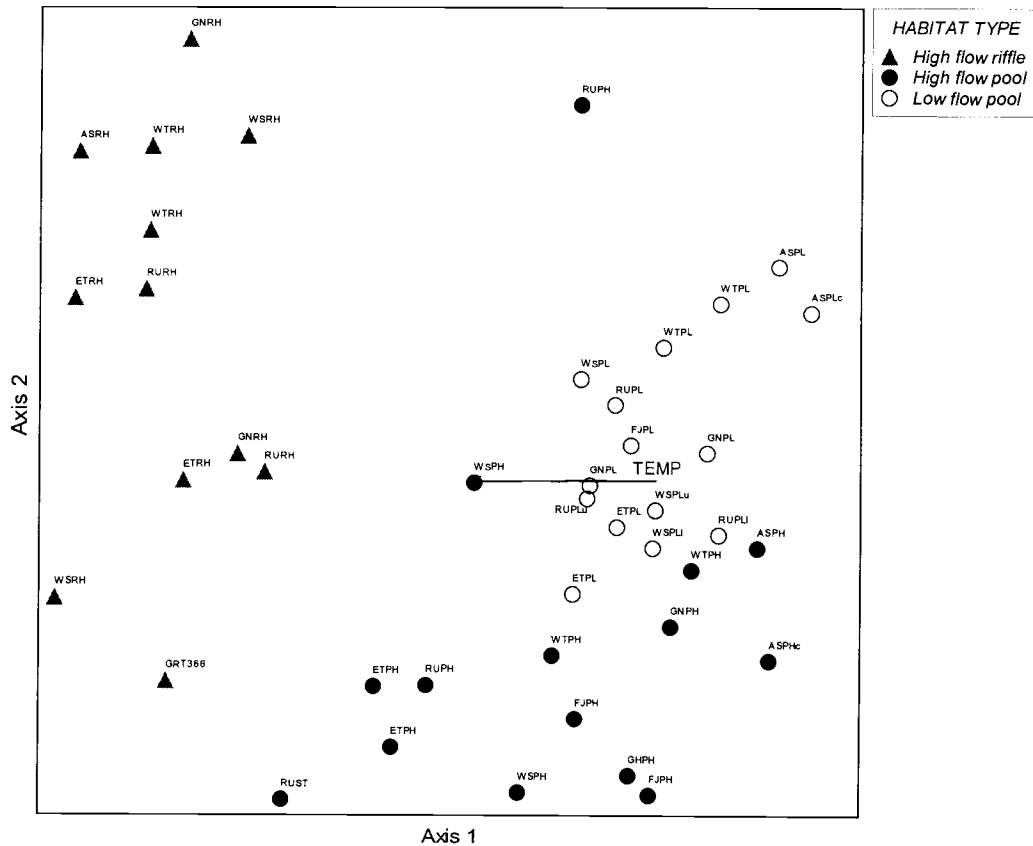


Figure 3.4. NMS ordination results coded by first letters of name, habitat (r = riffle, p = pool) and season (h = high flow, l = low flow) type. Environmental variables with significant correlations ($r > 0.5$) with axes 1 or 2 are displayed as vectors. Only temperature was strongly correlated ($r = 0.57$) with an axis.

By examining which taxa are associated with each axis, broader generalizations can be made about the gradients in community assemblage that are expressed in the ordination. Axis 1 represents a clear gradient from a community that requires cool, and sometimes flowing, water to a community dominated by lentic and warm water taxa (Table 3.3). Many of the taxa with negative relationships to axis one (i.e. Blephariceridae, Heptageniidae) are characteristic of cool, Rocky Mountain-type streams. Conversely, those with positive correlations to axis 1 (i.e.

Dytiscidae, Notonectidae) increase in diversity and dominance in warm neotropical streams. Axis 2 represents a weaker gradient in community composition, and may illustrate community response to an environmental variable not measured in this study.

Table 3.3. Correlations between aquatic insect families and NMS ordination axes.

	Axis 1	Axis 2
	r	r
Chironomidae	-0.62	0.36
Corydalidae	-0.58	0.62
Simuliidae	-0.54	0.69
Hydropsychidae	-0.49	0.30
Hydrobiosidae	-0.42	0.33
Blephariceridae	-0.37	0.26
Heptageniidae	-0.36	0.17
Hydrophilidae	0.35	-0.02
Gyrinidae	0.43	0.07
Gerridae	0.45	0.08
Notonectidae	0.46	0.06
Veliidae	0.49	0.14
Dytiscidae	0.56	0.21

Abiotic stream characteristics

Temperature was the only environmental variable to be significantly associated with an ordination axis (axis 1, $r = 0.57$), though pH and conductivity showed weak correlations with axis 1 ($r = 0.39$ and 0.25 , respectively). Stream size, percent canopy cover, and geographic location were not significantly correlated with the NMS ordination. Thus, temperature, pH, and conductivity were chosen for further examination with t-tests (Table 3.4). Season significantly affected temperature, pH, and conductivity: all were significantly lower during the high flow season. Additionally, streams without permanent headwaters had significantly higher temperature, pH, and conductivity. Both temperature and conductivity were significantly lower in 2004, which may be a result of El Niño conditions which yielded greater precipitation amounts during the 2005 high flow season.

Table 3.4. Abiotic factors averaged by season, year, and headwater type with t-test results for differences among types.

	Season		Year		Headwater		t		
	Low flow	High flow	2004	2005	Permanent	None	Season	Headwater	Year
Temperature	20.0	10.2	15.2	12.4	12.8	14.9	16.2***	2.0*	2.8**
pH	7.7	6.9	7.1	7.3	7.1	7.3	10.8***	2.1*	-1.9
Conductivity	244.3	143.3	220.6	139.5	119.7	239.7	3.6***	4.5***	2.9**

Significance level, * $P=0.05$, ** $P<0.01$, *** $P<0.001$

MRPP and Indicator Species Analysis

Three *a priori* groups (high-flow riffle, high-flow pool, and low-flow pool) were clearly distinct in community composition ($A = 0.18$, $p < 0.001$). Several taxa received very high indicator values for the low-flow pool (LFP) and high-flow riffle groups (HFR), but no taxon scored a statistically significant indicator value for the high-flow pool (HFP) group. Simuliidae ($IV = 85$, $p = 0.001$), Corydalidae ($IV = 69.7$, $p = 0.004$), and Heptageniidae ($IV = 66.7$, $p = 0.016$) were all good indicators of high-flow riffles. Notonectidae ($IV = 88.9$, $p = 0.001$), Dytiscidae ($IV = 86.9$, $p = 0.001$), and Hydrophilidae ($IV = 77.7$, $p = 0.001$) were among the best indicators of low-flow pools. Only Siphonuridae and Polycentropodidae ($IV = 22.7$ and 17.9 , respectively) were identified as indicators of high-flow pools, and these values were not significant ($p > 0.4$). The three *a priori* groups were then subdivided by headwater type (permanent or not); the resulting six groups also represent distinct community assemblages ($A = 0.21$, $p < 0.001$). Indicator species analysis of these six groups illustrates a clear split between communities in streams with and without permanent headwaters (Table 3.5).

Table 3.5. Indicator values (IV) and significance (p-value) from Indicator Species Analysis of aquatic insect taxa when grouped by season, habitat and headwater type.

Group	Taxa	IV	p-value
<i>Permanent headwaters</i>			
High Flow Riffle	Heptageniidae	90	0.001
	Blephariceridae	85	0.001
	Hydrobiosidae	71	0.002
	Hydropsychidae	65	0.002
	Tipulidae	63	0.024
High Flow Pool	Limnephilidae	38	0.093
	Nemouridae	33	0.087
Low Flow Pool	Corixidae	62	0.001
	Nepidae	54	0.001
	Naucoridae	53	0.003
	Gerridae	50	0.001
	Dryopidae	48	0.009
	Belostomatidae	39	0.015
<i>Non-permanent headwaters</i>			
High Flow Riffle	Capniidae	78	0.001
	Corydalidae	61	0.001
	Simuliidae	61	0.001
High Flow Pool	Libellulidae	30	0.338
Low Flow Pool	Hydrophilidae	65	0.003
	Notonectidae	65	0.001
	Lestidae	58	0.008
	Veliidae	46	0.014

HFR in streams with headwaters were characterized by Rocky Mountain-affiliated cold water taxa, while taxa with diapause stages (e.g., Capniidae) or hyporheos-dwelling potential (e.g., Corydalidae) were indicators of HFR in non-permanent headwater streams. Again, indicator species for HFP were not statistically significant, though the marginal significance of Limnephilidae and Nemouridae (Rocky Mountain-affiliated taxa) for HFP with permanent headwaters may be biologically significant.

Discussion

Biogeographical considerations

Madrean Sky Island streams exhibit strong community assemblage responses to seasonal flow variation and habitat type. Multi-response permutation procedure (MRPP) tests clearly distinguished between the three sample types (high flow riffle, high flow pool, low flow pool), indicating that they occupied distinct areas of taxonomic space. Non-metric multidimensional scaling (NMS) ordination showed a strong gradient from communities requiring cold, lotic conditions to those tolerant of warm, lentic conditions. Though temperature was most strongly associated with this gradient ($r=0.57$), pH and conductivity were also potentially relevant environmental factors ($r=0.39$ and 0.25 , respectively). Most aquatic insect taxa are sensitive to temperature (Wallace and Anderson, 1996; Ward and Stanford, 1982), and both pH (Sanderson et al., 2005; Woodward et al., 2002; Clenaghan et al., 1998) and conductivity (Lancaster and Scudder, 1986) can be significant drivers of aquatic insect community structure.

Essentially, the NMS ordination's gradient describes a transition from a temperate Rocky Mountain stream to a neotropical Sierra Madre stream. This transition occurs not geographically, however, but seasonally within the same stream. The environmental requirements of Rocky Mountain and Sierra Madre fauna are seemingly incompatible, but the extreme seasonal variation of flow and water chemistry (Figures 3.2a, 3.2b; Tables 3.1, 3.2) allows temporal cohabitation. In this sense MSI streams offer 'time-share' habitat, where high flow conditions are ideal for Rocky Mountain fauna, while the Sierra Madre fauna flourishes under the warm, lentic conditions of the low flow season.

Indicator species analysis (ISA) of the three sample types supports this concept. Simuliidae, Heptageniidae, Hydropsychidae, and Blephariceridae were all significant indicators of high flow riffles (HFR), and all are taxa which are abundant in Rocky Mountain streams and have nearctic origins (Hogue, 1981; McCafferty, 1981; Edmunds et al., 1976). Conversely, Dytiscidae, Belostomatidae, and Notonectidae were significant indicators of low flow pools

(LFP). While these taxa are present in temperate streams, they increase in diversity and dominance in neotropical streams (Vinson and Hawkins, 2003; Menke, 1969; Usinger, 1956) and could thus be considered characteristic of Sierra Madre streams. High flow pools did not have any significant indicator species and were differentiated from HFR and LFP mainly by significantly reduced numbers of individuals and a lack of many LFP-affiliated taxa. Since many of these indicator taxa for HFR and LFP have incompatible environmental requirements, the seasonal variation that allows site coexistence also increases overall site diversity. These results are congruent with past studies which found that streams with considerable seasonal flow variation are actually more species-rich than neighboring streams with relatively constant flow (Dietrich and Anderson, 2000).

For taxa to occur only seasonally in streams, refuges must exist to serve as a source for colonization. The most important source of colonizers in streams is via drift from upstream areas (Gray and Fisher, 1981; Williams and Hynes, 1976). MRPP analyses found significant differences between MSI aquatic insect communities with and without permanent, high elevation headwaters. Additionally, communities with permanent headwaters were significantly more taxon rich than those with ephemeral headwaters. In the NMS ordination two high-elevation, headwater 'outgroup' samples (Figure 4: GRT366 and RUST) taken during the low flow season occupied the same region of species space as low elevation samples during the high flow season. Thus, the aquatic insect communities of these headwater streams are likely the source of seasonal populations of Rocky Mountain fauna in lower elevation MSI streams.

Many streams in the MSI, however, do not have permanent, high-elevation headwaters, and yet still have distinct high flow communities composed of taxa not present in the low flow season. Most MSI streams are quite isolated (>5km) from other water bodies, so colonization from other streams is unlikely considering the short distances traveled by most aquatic insect adults (Petersen et al., 2004; Malmqvist, 2002). Many indicator taxa of high flow MSI streams with permanent headwaters (e.g., Heptageniidae) are weak fliers which do not leave the stream corridor; this pattern has led to strong spatial autocorrelation in other stream communities for these taxa (Sanderson et al., 2005). Since aerial colonization and drift are unlikely sources in these streams, the hyporheos may serve as the most important recolonization source for seasonal inhabitants. Though in some stream types the hyporheos may not be a significant refuge (del Rosario and Resh, 2000), many studies have demonstrated the use of hyporheos as a temporal refuge from drying surface conditions (Hose et al., 2005; Anderson, 1997; Clinton et al., 1996).

ISA identified three taxa as significant indicators of high flow riffles in streams without permanent headwaters: Capniidae (Plecoptera), Simuliidae (Diptera) and Corydalidae

(Megaloptera). Capniid larvae have been found in hyporheic substrates in other Arizona streams (Clinton et al., 1996) and may exhibit both egg (Gray, 1981) and larval diapause (Jacobi and Cary, 1996; Harper and Hynes, 1970). Most capniid species are restricted to streams with temporary seasonal flow in the Southwest (Jacobi and Cary, 1996). Simuliidae are also capable of egg diapause and can pass rapidly through the larval stage (≥ 4 days), a useful trait in seasonal habitats (Peterson, 1996). These diapause periods are functionally equivalent to spatial dispersal in streams with headwater source populations (Bohonak and Jenkins, 2003). Corydalid larvae are semivoltine and thus need several years to complete the larval stage, but have been observed in the substrate of dry streambeds (Evans and Neunzig, 1996) and in riparian areas (Bogan, pers. obsv.), and may survive the dry season as active larvae. Thus, taxa characteristic of high flow streams lacking permanent headwaters have adaptations to allow them to take advantage habitats that are only available for a few months out of the year.

Ecological considerations

The significant seasonal variation observed in community structure was not limited to shifts in taxonomic composition and biogeographical origin. Functional feeding groups also shifted between season and habitat, as has been observed in other temperate streams (Cummins et al., 1989; Hawkins and Sedell, 1981). MSI streams, however, undergo a much more severe seasonal shift in functional feeding group composition than other temperate streams. During the high flow season, collectors-filterers, shredders and scrapers made up a significant percentage of the community (28%, 9% and 10% respectively: pool and riffle averaged). As habitat shrinks from the high flow to low flow seasons though, predators (mainly adult Coleoptera and Hemiptera) become concentrated and increase in percentage from 24% to an astonishing 75% of individuals present. This pattern has been observed in other desert streams, but not to this extreme extent (Stanley et al., 1994). In a sense, low flow pools are 'cooked down' versions of high flow pools but lack all of the filterers, shredders and scrapers that are sensitive to high temperatures and lentic conditions. Collector-filterers, shredders, and scrapers are reduced to a cumulative 4% of total individuals during the low flow season. What remains is a dense (385 individuals/m²) brew of predators which quickly devour any available aquatic and terrestrial prey (e.g., amphibians, terrestrial moths, flies, and beetles) (Bogan, pers. obsv.). Collector-gatherers seem to be the only group immune to seasonal variation. Their abundances peak in the high flow season (28%: pool and riffle averaged), but are only slightly reduced during the low flow season (20%). Collector-gatherers are the least specialized functional feeding group (Cummins and

Merritt, 1996), which may explain their continued abundance despite the lack of flowing water and perhaps reduced allochthonous input that other groups require (e.g., filterers and shredders).

Conclusions

Madrean Sky Island streams support two types of 'time-share' communities via seasonal flow variation. In streams with permanent headwaters relictual Rocky Mountain fauna move down to lower elevations during the high flow season to take advantage of expanded suitable conditions. In streams lacking permanent headwaters, the hyporheos and/or egg and larval diapause likely serve as refuges until high flow conditions return, allowing growth and development to continue during the brief season. Both high elevation and hyporheic/diapause refuges must be stable over long time periods, as MSI streams will often endure multiple years without a significant high flow season (Figure 3.2a). During the low flow season, streams of both headwater-types are dominated by a diverse 'Madrean' fauna of hemipterans and coleopterans which prefer warmer, lentic conditions. Dramatic seasonal fluctuations were also observed with functional feeding groups. Collectors, shredders and scrapers dominate during the high flow season (75.5%), but after streams 'cook down' to remnant pools in the low flow season the vast majority of insects present are predators (75.2%).

Many recent studies have shown the sensitivity of aquatic insect communities to long-term changes in climatic patterns and stream chemistry. Cold-water taxa have been lost from streams experiencing continued warming trends (Daufresne et al., 2003), and interactions between warming summer temperatures and increased pH have significantly altered communities in naturally acidic streams (Woodward et al., 2002). We suggest that MSI streams and their seasonal 'time-share' communities are extremely sensitive to climatic changes as well. Slight changes in rainfall patterns or increased temperatures could eliminate the ability of streams to seasonally support remnant Rocky Mountain fauna, reducing overall stream diversity. Small seasonally variable streams, like those of the MSI, are often surprisingly diverse. The factors supporting high diversity in these streams and the sensitivity of MSI aquatic insect communities to changing climatic conditions are deserving of further study.

Acknowledgements

This study was conducted under USDA Forest Service Special Use Permit #SUP0092. A portion of the work was conducted at the American Museum of Natural History's Southwestern Research Station. Funding came from Oregon State University and National Science Foundation grant

DEB-0445366 to D.A.Lytle. Carl Olson graciously allowed the use of lab space and access to the aquatic insect reference collection at the University of Arizona. Thanks to Frank Drake and Justin Miles for assistance with preliminary sorting and identification of samples at Oregon State University. Special thanks to Claire Zugmeyer for logistical support during field sampling.

Literature Cited

- Anderson, N. H. 1997. Phenology of Trichoptera in summer-dry headwater streams in western Oregon, U.S.A. Pages 7-13 in R. W. Holzenthal and O. S. Flint, editors. *8th International Symposium on Trichoptera*. Ohio Biological Survey, Columbus, OH.
- Arunachalam, M., K. C. Madhusoodanan Nair, J. Vijverberg, K. Kortmulder, and H. Suriyanarayanan. 1991. Substrate selection and seasonal variation in densities of invertebrates in stream pools of a tropical river. *Hydrobiologia* 213:141-148.
- Bohonak, A. J., and D. G. Jenkins. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters* 6:783-796.
- Boulton, A. J. 1989. Oversummering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria. *Transactions of the Royal Society of South Australia* 31:23-24.
- Brooks, R. T. 2000. Annual and seasonal variation and the effects of hydroperiod on benthic macroinvertebrates of seasonal forest ("vernal") ponds in central Massachusetts, USA. *Wetlands* 20:707-715.
- Brown, A. V., and P. P. Brussock. 1991. Comparisons of benthic invertebrates between riffles and pools. *Hydrobiologia* 220:99-108.
- Brussock, P. P., and A. V. Brown. 1991. Riffle-pool geomorphology disrupts longitudinal patterns of stream benthos. *Hydrobiologia* 220:109-117.
- Clenaghan, C., P. S. Giller, J. O'Halloran, and R. Hernan. 1998. Stream macroinvertebrate communities in a conifer-afforested catchment in Ireland: relationships to physio-chemical and biotic factors. *Freshwater Biology* 40:175-193.
- Clinton, S. M. 1996. Response of a hyporheic invertebrate assemblage to drying disturbance in a desert stream. *Journal of the North American Benthological Society* 15:700-712.
- Cowell, B. C., A. H. Remley, and D. M. Lynch. 2004. Seasonal changes in the distribution and abundance of benthic invertebrates in six headwater streams in central Florida. *Hydrobiologia* 522:99-115.
- Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry, and W. B. Taliaferro. 1989. Shredders and riparian vegetation. *BioScience* 39:24-30.

- Cummins, K. W., and R. W. Merritt. 1996. Ecology and distribution of aquatic insects. Pages 74-97 in R. W. Merritt and K. W. Cummins, editors. *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt, Dubuque.
- Daufresne, M., M. C. Roger, H. Capra, and N. Lamouroux. 2003. Long-term changes within the invertebrate and fish communities of the Upper Rhone River: effects of climatic factors. *Global Change Biology* 10:124-140.
- del Rosario, R. B., and V. H. Resh. 2000. Invertebrates in intermittent and perennial streams: is the hyporheic zone a refuge from drying? *Journal of the North American Benthological Society* 19:680-696.
- Delucchi, C. M. 1989. Movement patterns of invertebrates in temporary and permanent streams. *Oecologia* 78:199-207.
- Dieterich, M., and N. H. Anderson. 2000. The invertebrate fauna of summer-dry streams in western Oregon. *Archiv fuer Hydrobiologie* 147:273-295.
- Edmunds Jr, G. F., S. L. Jensen, and L. Berner. 1976. *The Mayflies of North and Central America*. University of Minnesota Press, Minneapolis.
- Evans, E. D., and H. H. Neunzig. 1996. Megaloptera and aquatic Neuroptera. Pages 298-308 in R. W. Merritt and K. W. Cummins, editors. *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt, Dubuque.
- Gray, L. J. 1980. Species composition and life histories of aquatic insects in a lowland Sonoran Desert stream. *American Midland Naturalist* 106:229-242.
- Gray, L. J., and S. G. Fisher. 1981. Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran Desert stream. *American Midland Naturalist* 106:249-257.
- Grimm, N. B., and S. G. Fisher. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society* 8:293-307.
- Harper, P. P., and H. B. Hynes. 1970. Diapause in the nymphs of Canadian winter stoneflies. *Ecology* 51:925-927.
- Hawkins, C. P., and J. R. Sedell. 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. *Ecology* 62:387-397.
- Hogue, C. L. 1981. Blephariceridae. Pages 191-197 in *Manual of Nearctic Diptera Vol 1*. Biosystematics Research Institute, Ottawa.
- Hose, G. C., P. Jones, and R. P. Lim. 2005. Hyporheic macroinvertebrates in riffle and pool areas of temporary streams in south eastern Australia. *Hydrobiologia* 532:81-90.
- Jacobi, G. Z., and S. J. Cary. 1996. Winter stoneflies (Plecoptera) in seasonal habitats in New Mexico, USA. *Journal of the North American Benthological Society* 15:690-699.

- Kovats, Z. E., J. J. Ciborowski, and L. D. Corkum. 1996. Inland dispersal of adult aquatic insects. *Freshwater Biology* 36:265-276.
- Lancaster, J., and G. G. Scudder. 1987. Aquatic Coleoptera and Hemiptera in some Canadian saline lakes: patterns in community structure. *Canadian Journal of Zoology* 65:1383-1389.
- Lytle, D. A. 2000. Biotic and abiotic effects of flash flooding in a montane desert stream. *Archiv fuer Hydrobiologie* 150:85-100.
- Lytle, D. A., and N. L. Poff. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* 19:94-100.
- Malmqvist, B. 2002. Aquatic invertebrates in riverine landscapes. *Freshwater Biology* 47:679-694.
- Matthews, G. B., R. A. Matthews, and B. Hachmoller. 1991. Mathematical analysis of temporal and spatial trends in the benthic macroinvertebrate communities of a small stream. *Canadian Journal of Fisheries and Aquatic Sciences* 48:2184-2190.
- McCafferty, W. P. 1981. *Aquatic Entomology: The fishermen's and ecologists' illustrated guide to insects and their relatives*. Jones and Bartlett, Boston.
- McCune, B. and J. B. Grace. 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, OR, USA.
- McCune, B. & M.J. Mefford. 1999. PC-ORD. Multivariate Analysis of Ecological Data. Version 4.0. MjM Software, Gleneden Beach, Oregon, USA.
- McElravy, E. P., G. A. Lamberti, and V. H. Resh. 1989. Year-to-year variation in the aquatic macroinvertebrate fauna of a northern California stream. *Journal of the North American Benthological Society* 8:51-63.
- Menke, A. S. 1969. Introduction. Pages 1-15 in A. S. Menke, editor. The semiaquatic and aquatic Hemiptera of California. University of California Press, Berkeley.
- Merritt, R. W., V. H. Resh, and K. W. Cummings. 1996. Design of aquatic insect studies: collecting, sampling and rearing procedures. Pages 12-28 in R. W. Merritt and K. W. Cummings, editors. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque.
- Mielke, P. W., Jr, and K. J. Berry. 2001. *Permutation Methods: A distance function approach*. Springer, Berlin.
- Petersen, I., Z. Masters, A. G. Hildrew, and S. J. Ormerod. 2004. Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology* 41:934-950.
- Sanderson, R. A., M. D. Eyre, and S. P. Rushton. 2005. The influence of stream invertebrate composition at neighboring sites on local assemblage composition. *Freshwater Biology* 50:221-231.

- Scarsbrook, M. R., and C. R. Townsend. 1993. Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. *Freshwater Biology* 29.
- Stanley, E. H., D. L. Buschman, A. J. Boulton, N. B. Grimm, and S. G. Fisher. 1994. Invertebrate resistance and resilience to intermittency in a desert stream. *American Midland Naturalist* 131:288-300.
- Thompson, R. M., and C. R. Townsend. 1999. The effect of seasonal variation on the community structure and food-web attributes of two streams: implications for food-web science. *Oikos* 87:75-88.
- Usinger, R. L. 1956. Aquatic Hemiptera. Pages 182-228 in R. L. Usinger, editor. *Aquatic Insects of California*. University of California Press, Berkeley.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- Vinson, M. R., and C. P. Hawkins. 2003. Broad-scale geographical patterns in local stream insect genera richness. *Ecography* 26:751-767.
- Wallace, B. J., and N. H. Anderson. 1996. Habitat, life history, and behavioral adaptations of aquatic insects. Pages 41-73 in R. W. Merritt and K. W. Cummins, editors. *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt, Dubuque.
- Ward, J. V., and J. A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* 27:97-117.
- Williams, D. D., and H. B. Hynes. 1976. The recolonization mechanisms of stream benthos. *Oikos* 27:265-272.
- Woodward, G., J. I. Jones, and A. G. Hildrew. 2002. Community persistence in Broadstone Stream (U.K.) over three decades. *Freshwater Biology* 47:1419-1435.

CHAPTER 4

Summary and conclusions

Despite their small size and isolation, streams of the Madrean Sky Islands contain a remarkably diverse aquatic insect fauna. I identified over 60 families of aquatic insects from MSI streams and more than 150 species of Coleoptera and Hemiptera in the regional species pool. Thirty or more species of Coleoptera and Hemiptera were even found in streams as small as 12m². Habitat size was the primary predictor of this high diversity, though temperature and elevation were also identified as significant predictors. Temperature, elevation, latitude and substrate type were correlated with community structure in these streams. Stream insect communities were not significantly associated with drainage basins, as is observed with aquatic vertebrate taxa. Instead, geographic distances between streams were strongly correlated with community distances even after accounting for environmental variation. Seasonal abiotic variation was strong in MSI streams, and this temporal variation facilitates the seasonal 'time-sharing' of streams by otherwise incompatible taxa, and increases overall site species richness.

In insular ecosystems, habitat area and isolation are predicted under island biogeography theory to be the primary drivers of species richness via their effect on immigration and colonization rates (McArthur and Wilson, 1967). In MSI streams, I found that habitat area accounted for a large amount (45%) of the variability in species richness. Isolation from 'mainland' river systems explained very little variation in species richness (3-5%), and was not a statistically significant predictor. In NMS ordinations, isolation from the larger stream systems of the Sierra Madre and Rocky Mountains were not identified as correlates with community structure either. Though isolation from large river systems was associated with species richness and distribution in freshwater mussels (Sepkoski and Rex, 1974), this form of isolation had little effect on aquatic insects of the MSI. This lack of an isolation influence may be due to the aerial dispersal ability of most coleopteran and hemipteran species. Though a few species have reduced wings or are flightless (Lytle, 2000), perhaps enough species are capable of long-distance dispersal to negate a strong isolation effect on the whole community. A better metric of isolation is needed to account for presence of intermediate islands between isolated islands and the mainland (Rosenzweig, 1995). Unfortunately, our knowledge of the distribution of permanent streams in the MSI is presently unknown, making other isolation metrics (i.e. nearest neighbor) difficult to calculate.

Surprisingly, habitat area was also not associated with community structure. I expected that there may be a predictable loss of species as habitat size decreased, since many species of aquatic coleopterans and hemipterans in the MSI are large bodied and occupy a 'top predator' position in these streams. I thought that competition may become too intense as stream size decreases, thus excluding certain species from smaller sites. These large predators, however, did not follow any predictable absence pattern in progressively smaller streams. The factors affecting community structure appear to be completely independent of habitat area.

In addition to habitat area, regression analyses identified stream temperature and elevation as being positively correlated with species richness, and yielded a model that explained 63% of the variation in species richness. Though temperature is positively correlated with species richness in many temperate systems (Kholin and Nilsson, 1998; Dahlberg and Conyers, 1973), elevation is usually negatively correlated with species richness (Vinson and Hawkins, 2003; Allan, 1975). This apparent discrepancy between MSI streams and other streams is likely explained by the range of elevations under examination. Other studies examined ranges from near sea level to alpine streams (3400m), while this study only included streams between 300 and 2200 m. Diversity of coleopteran and hemipteran species appears to decline precipitously above 2400 m in MSI streams (Bogan, unpublished data), so if this study had included a wider range of elevations, the elevation-richness relationship may have been negative.

Temperature and elevation also were correlated with a community structure gradient, along with latitude. This gradient described a transition from communities with more nearctic-affiliated species (increased elevation and latitude, decreased temperature) to communities dominated by neotropically-derived species (decreased latitude and elevation, increased temperature). This gradient indicates that MSI streams contain a unique blend of temperate and neotropical species, a pattern seen with many terrestrial taxa in the MSI as well (Brown, 1994; Minckley and Brown, 1994). The second gradient in MSI aquatic insect community structure identified by NMS analyses described a shift from habitat generalist taxa to taxa with more specialized habitat requirements. This second gradient was associated with a transition from bedrock-dominated habitats to silt-dominated habitats. This association suggests that local substrate type may play an important role in structuring communities, an idea supported by studies of other stream systems (Smith et al., 2003; Downes et al., 1998).

While local abiotic and habitat conditions and latitude are clearly important in determining community structure, regional history and drainage connectivity are often significant filters for local stream communities (Williams et al., 2003). MSI aquatic insect communities, however, did not form distinct groups by drainage basin as MSI fish communities do

(Hendrickson et al., 1980). Many coleopteran and hemipteran species are strong flyers, capable of long-distance dispersal; this suggests that aerial dispersal between drainages has overwhelmed any effect of drainage connectivity on local communities. To further examine this idea, I tested the association between geographic and community distances after accounting for environmental variability. I found significant spatial autocorrelation in MSI stream communities even after accounting for environmental variables. Given that aquatic insect colonization success depends on the number of and distance to source populations (Ahloth et al., 2003), it's logical that community distance is strongly linked with geographic distance. Though smaller-scale studies have only found spatial autocorrelation in weakly flying taxa (Sanderson et al., 2005), spatial autocorrelation of strongly flying taxa is significant at larger scales in MSI streams.

While local abiotic factors and spatial distribution of streams likely shape communities during the dominant low flow season, seasonal flow variation facilitates strong temporal variability in MSI aquatic insect communities. In most years, a short winter high flow season (3-12 weeks duration) brings cold stream temperatures, reduced pH and conductivities, expanded habitat area (increases of 2+ orders of magnitude) and abundant riffle habitat. This abiotic shift allows a completely different fauna to colonize the streams, and appears to suppress the low flow, coleopteran and hemipteran dominated fauna. In streams with high elevation headwaters, the high flow fauna is composed of many Rocky Mountain-derived fauna including nemourid stoneflies, blepharicerid true flies, and heptageniid mayflies. In streams without high elevation headwaters, the winter fauna is not as diverse, and mainly consists of insects that can survive in the hyporheos, either as diapausing or active individuals (e.g., capniid stoneflies, simuliid true flies, corydalid alderflies). These hyporheic habitats and diapause periods offer temporal refuges. Accordingly, I propose that high elevation headwater springs and the hyporheos (with diapausing individuals) act as refuges for high flow taxa during the low flow season and occasionally over multiple years if winter precipitation is not sufficient to produce high flow conditions.

In addition to increasing overall site diversity by hosting otherwise incompatible taxa at different times of the year, this seasonal abiotic variability may subsidize the high diversity of MSI streams under low flow conditions. As streams expand in habitat area during the high flow season, reaches are colonized by large numbers and high densities of gatherer and filterer taxa (e.g., baetid mayfly larvae, chironomid and simuliid larvae). These taxa are able to grow without the interference of large predators, as most coleopteran and hemipteran predators are reduced in abundance or absent during the high flow period. However, as stream habitat contracts at the end of the high flow season, predatory coleopteran and hemipteran species increase in richness and density. The abundance of prey likely supports these predator taxa well

into the low flow season. Once stream habitat has maximally contracted in the low flow season, though, these winter prey taxa have either been consumed or can no longer tolerate the increased stream temperatures. At this point, cannibalism and predators eating other predators are common events in MSI stream pools, and terrestrial subsidies (e.g., terrestrial Lepidoptera, Orthoptera and Coleoptera species) likely become important in maintaining predator populations. I propose that the high abundance of prey taxa during the high flow- low flow transition period may support increased colonization success by many predator taxa, thus increasing low flow diversity. Conditions later in the low flow season (e.g., high densities, lower food resource levels) would discourage colonization and encourage dispersal away from streams (Velasco and Millan, 1998; Smith, 1973), potentially reducing site species richness. Future studies which test these hypotheses of how 'time-share' species utilize temporal refuges and how high species richness is maintained in MSI streams would contribute greatly to the understanding region-wide and general community ecology processes.

In conclusion, this study demonstrates the high aquatic insect diversity of small isolated stream habitats in the Madrean Sky Islands. Much of this diversity, however, depends on habitat size and seasonal abiotic variation. This dependency places MSI aquatic insect communities in a vulnerable position. During the Pleistocene, stream systems were larger and more connected (Betancourt et al., 1990). Since the end of the Pleistocene, the region has undergone a significant drying trend, creating many fragmented, insular stream habitats (Elias, 1997). The current climate in the MSI and surrounding Chihuahuan Desert is the driest and warmest it has been in at least 40,000 years (Van Devender, 1990). A number of formerly perennial springs and streams have become ephemeral in the last 10 years (pers. obs.; Lytle, pers. comm.; Mitchell, pers. comm), and one of my 'perennial' stream study sites desiccated during the course of this thesis (French Joe Canyon). Even if these newly ephemeral streams regain perennial reaches, many of the formerly abundant taxa with poor dispersal abilities would not be able recolonize (e.g., the giant water bug, *Abedus herberti*), thus altering local community structure. Additionally, slight variations in timing and intensity of winter rainfall could dramatically alter high flow abiotic conditions. If high flow durations were shortened or more irregular from year to year, many 'time-share' taxa would not be able to complete their life cycle, thus removing them from the stream. This removal could have negative impacts on low flow communities by reducing food resources in the early low flow season. This thesis represents a detailed snapshot of MSI aquatic insect communities under present climatic conditions and stream sizes. The data and results from this study will be essential for understanding how continuing climatic change and resultant stream habitat changes will further alter aquatic insect diversity and community structure of MSI.

BIBLIOGRAPHY

- Ahloth, P., R. V. Alatalo, A. Holopainen, T. Kumpulainen, and J. Suhonen. 2003. Founder population size and number of source populations enhance colonization success in waterstriders. *Oecologia* 137:617-620.
- Allan, J.D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. *Ecology* 56: 1040-1053.
- Anderson, N. H. 1997. Phenology of Trichoptera in summer-dry headwater streams in western Oregon, U.S.A. Pages 7-13 in R. W. Holzenthal and O. S. Flint, editors. *8th International Symposium on Trichoptera*. Columbus, OH: Ohio Biological Survey.
- Armitage, P. D., and C. E. Cannan. 2000. Annual changes in summer patterns of mesohabitat distribution and associated macroinvertebrate assemblages. *Hydrological Processes* 14:3161-3179.
- Arunachalam, M., K. C. Madhusoodanan Nair, J. Vijverberg, K. Kortmulder, and H. Suriyanarayanan. 1991. Substrate selection and seasonal variation in densities of invertebrates in stream pools of a tropical river. *Hydrobiologia* 213:141-148.
- Bass, D. 2003. A comparison of freshwater macroinvertebrate communities on small Caribbean islands. *BioScience* 53(11): 1094-1100.
- Betancourt, J.L., T.R. Van Devender, and P.S. Martin. 1990. Introduction. pp. 2-14 in Betancourt, J.L., T.R. Van Devender, and P.S. Martin eds. *Packrat middens: the last 40,000 years of biotic change*. Tucson: University of Arizona Press.
- Bohonak, A. J., and D. G. Jenkins. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters* 6:783-796.
- Boulton, A. J. 1989. Oversummering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria. *Transactions of the Royal Society of South Australia* 31:23-24.
- Briggs, M.K. 1996. *Riparian Ecosystem Recovery in Arid Lands: Strategies and References*. Tucson: University of Arizona Press.
- Brooks, R. T. 2000. Annual and seasonal variation and the effects of hydroperiod on benthic macroinvertebrates of seasonal forest ("vernal") ponds in central Massachusetts, USA. *Wetlands* 20:707-715.
- Brown, A. V., and P. P. Brussock. 1991. Comparisons of benthic invertebrates between riffles and pools. *Hydrobiologia* 220:99-108.
- Brown, D.E. 1994. Madrean evergreen woodland. pp.59-66 in Brown, D.E. ed. *Biotic Communities of the Southwestern United States and Northwestern Mexico*. Salt Lake City: University of Utah Press.

- Browne, R.A. 1981. Lakes as islands: biogeographic distribution, turnover rates, and species composition in the lakes of central New York. *Journal of Biogeography* 8: 75-83.
- Bruns, D.A. and W.L. Minckley. 1980. Distribution and abundance of benthic invertebrates in a Sonoran Desert stream. *Journal of Arid Environments* 3: 117-131.
- Brussock, P. P., and A. V. Brown. 1991. Riffle-pool geomorphology disrupts longitudinal patterns of stream benthos. *Hydrobiologia* 220:109-117.
- Clenaghan, C., P. S. Giller, J. O'Halloran, and R. Hernan. 1998. Stream macroinvertebrate communities in a conifer-afforested catchment in Ireland: relationships to physio-chemical and biotic factors. *Freshwater Biology* 40:175-193.
- Clinton, S. M. 1996. Response of a hyporheic invertebrate assemblage to drying disturbance in a desert stream. *Journal of the North American Benthological Society* 15:700-712.
- Corkum, L. D. 1990. Intra-biome distributional patterns of lotic macroinvertebrate assemblages. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2147-2157.
- Corkum, L. D. 1992. Spatial distributional patterns of macroinvertebrates along rivers within and among biomes. *Hydrobiologia* 239:101-114.
- Cowell, B. C., A. H. Remley, and D. M. Lynch. 2004. Seasonal changes in the distribution and abundance of benthic invertebrates in six headwater streams in central Florida. *Hydrobiologia* 522:99-115.
- Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry, and W. B. Taliaferro. 1989. Shredders and riparian vegetation. *BioScience* 39:24-30.
- Cummins, K. W., and R. W. Merritt. 1996. Ecology and distribution of aquatic insects. Pages 74-97 in R. W. Merritt and K. W. Cummins, editors. *An Introduction to the Aquatic Insects of North America*. Dubuque, IA: Kendall/Hunt.
- Dahlberg, M. D., and J. C. Conyers. 1973. Winter fauna in a thermal discharge with observations on a macrobenthos sampler. Pages 414-422 in J. W. Gibbons and R. R. Sharitz, editors. *Thermal Ecology*. Augusta, GA: U.S. Atomic Energy Commission.
- Daufresne, M., M. C. Roger, H. Capra, and N. Lamouroux. 2003. Long-term changes within the invertebrate and fish communities of the Upper Rhone River: effects of climatic factors. *Global Change Biology* 10:124-140.
- del Rosario, R. B., and V. H. Resh. 2000. Invertebrates in intermittent and perennial streams: is the hyporheic zone a refuge from drying? *Journal of the North American Benthological Society* 19:680-696.
- Delucchi, C. M. 1989. Movement patterns of invertebrates in temporary and permanent streams. *Oecologia* 78:199-207.
- Dieterich, M., and N. H. Anderson. 2000. The invertebrate fauna of summer-dry streams in western Oregon. *Archiv fuer Hydrobiologie* 147:273-295.

- Dodson, S. 1992. Predicting crustacean zooplankton species richness. *Limnology and Oceanography* 37(4): 848-856.
- Downes, B.J., P.S. Lake, E.S. Schreiber, and A. Glaister. 1998. Habitat structure and regulation of local species diversity in a stony, upland stream. *Ecological Monographs* 68(2): 237-257.
- Dunne, T. and L.B. Leopold. 1978. *Water in Environmental Planning*. New York: Freeman.
- Edmunds Jr, G. F., S. L. Jensen, and L. Berner. 1976. *The Mayflies of North and Central America*. University of Minnesota Press, Minneapolis.
- Elias, S.A. 1997. *The Ice-Age history of southwestern National Parks*. Washington: Smithsonian.
- Evans, E. D., and H. H. Neunzig. 1996. Megaloptera and aquatic Neuroptera. Pages 298-308 in R. W. Merritt and K. W. Cummins, editors. *An Introduction to the Aquatic Insects of North America*. Dubuque, IA: Kendall/Hunt.
- Fisher, S.G., L.J. Gray, N.B. Grimm, and D.E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 52(1): 93-110.
- Gray, L. J. 1980. Species composition and life histories of aquatic insects in a lowland Sonoran Desert stream. *American Midland Naturalist* 106:229-242.
- Gray, L. J., and S. G. Fisher. 1981. Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran Desert stream. *American Midland Naturalist* 106:249-257.
- Grimm, N. B., and S. G. Fisher. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society* 8:293-307.
- Harper, P. P., and H. B. Hynes. 1970. Diapause in the nymphs of Canadian winter stoneflies. *Ecology* 51:925-927.
- Hawkins, C. P., M. L. Murphy, and N. H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. *Ecology* 63:1840-1856.
- Hawkins, C. P., and J. R. Sedell. 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. *Ecology* 62:387-397.
- Hecnar, S. and R. M'Closkey. 1998. Species richness patterns of amphibians in southwestern Ontario ponds. *Journal of Biogeography* 25: 763-772.
- Hendrickson, D. A., W. L. Minckley, R. R. Miller, D. J. Siebert, and P. H. Minckley. 1980. Fishes of the Rio Yaqui basin, Mexico and United States. *Journal of the Arizona-Nevada Academy of Science* 15:65-106.
- Hogue, C. L. 1981. Blephariceridae. Pages 191-197 in *Manual of Nearctic Diptera Vol 1*. Ottawa: Biosystematics Research Institute.

- Hose, G. C., P. Jones, and R. P. Lim. 2005. Hyporheic macroinvertebrates in riffle and pool areas of temporary streams in south eastern Australia. *Hydrobiologia* 532:81-90.
- Jacobi, G. Z., and S. J. Cary. 1996. Winter stoneflies (Plecoptera) in seasonal habitats in New Mexico, USA. *Journal of the North American Benthological Society* 15:690-699.
- Kholin, S. and A. Nilsson. 1998. Regional enrichment of predacious water beetles in temporary ponds at opposite east-west ends of the Palearctic. *Journal of Biogeography* 25: 47-55.
- Kiflawi, M., A. Eitam, and L. Blaustein. 2003. The relative impact of local and regional processes on macroinvertebrate species richness in temporary pools. *Journal of Animal Behaviour* 72: 447-452.
- Kovats, Z. E., J. J. Ciborowski, and L. D. Corkum. 1996. Inland dispersal of adult aquatic insects. *Freshwater Biology* 36:265-276.
- Lancaster, J., and G. G. Scudder. 1987. Aquatic Coleoptera and Hemiptera in some Canadian saline lakes: patterns in community structure. *Canadian Journal of Zoology* 65:1383-1389.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659-1673.
- Lytle, D. A. 2003. Reconstructing long-term flood regimes with rainfall data: effects of flood timing on caddisfly populations. *The Southwestern Naturalist* 48:36-42.
- Lytle, D. A. 2000. Biotic and abiotic effects of flash flooding in a montane desert stream. *Archiv fuer Hydrobiologie* 150:85-100.
- Lytle, D. A., and N. L. Poff. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* 19:94-100.
- Lytle, D. A., and R. L. Smith. 2004. Exaptation and flash flood escape in giant water bugs. *Journal of Insect Behavior* 17:169-178.
- Malmqvist, B. 2002. Aquatic invertebrates in riverine landscapes. *Freshwater Biology* 47:679-694.
- Matthews, G. B., R. A. Matthews, and B. Hachmoller. 1991. Mathematical analysis of temporal and spatial trends in the benthic macroinvertebrate communities of a small stream. *Canadian Journal of Fisheries and Aquatic Sciences* 48:2184-2190.
- McArthur, R. and E.O. Wilson. 1967. *The theory of island biogeography*. Princeton: Princeton University Press.
- McCafferty, W. P. 1981. *Aquatic Entomology: The fishermen's and ecologists' illustrated guide to insects and their relatives*. Boston: Jones and Bartlett.
- McCune, B. and J. B. Grace. 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, OR, USA.
- McCune, B. & M.J. Mefford. 1999. PC-ORD. Multivariate Analysis of Ecological Data. Version 4.0. MjM Software, Gleneden Beach, Oregon, USA.

- McElravy, E. P., G. A. Lamberti, and V. H. Resh. 1989. Year-to-year variation in the aquatic macroinvertebrate fauna of a northern California stream. *Journal of the North American Benthological Society* 8:51-63.
- Meffe, G.K. and W.L. Minckley. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. *American Midland Naturalist* 117(1): 177-191.
- Menke, A. S. 1969. Introduction. Pages 1-15 in A. S. Menke, editor. *The semiaquatic and aquatic Hemiptera of California*. Berkeley: University of California Press.
- Merritt, R.W., and K.W. Cummings. 1996. *An introduction to the aquatic insects of North America 3rd Edition*. Dubuque: Kendall/Hunt.
- Merritt, R. W., V. H. Resh, and K. W. Cummings. 1996. Design of aquatic insect studies: collecting, sampling and rearing procedures. Pages 12-28 in R. W. Merritt and K. W. Cummings, editors. *An introduction to the aquatic insects of North America*. Dubuque, IA: Kendall/Hunt.
- Mielke, P. W., Jr, and K. J. Berry. 2001. *Permutation Methods: A distance function approach*. Berlin: Springer.
- Miller, M.P., D.W. Blinn, and P. Keim. 2002. Correlations between observed dispersal capabilities and patterns of genetic differentiation in populations of four aquatic insect species from the Arizona White Mountains, U.S.A. *Freshwater Biology* 47: 1660-1673.
- Minckley, W.L. and D.E. Brown. 1994. Interior and Californian Riparian Deciduous Forests and Woodlands. pp. 250-254 in Brown, D.E. ed. *Biotic Communities of the Southwestern United States and Northwestern Mexico*. Salt Lake City: University of Utah Press.
- Minshall, G.W., R.C. Petersen, and C.F. Nimz. 1985. Species richness in streams of different size from the same drainage basin. *American Naturalist* 125(1): 16-38.
- Mitchell, Don. 1/12/2004. Email communication with Don Mitchell, Fisheries Program Manager, Region V, Arizona Game and Fish Department.
- Nilsson, A. N. 1984. Species richness and succession of aquatic beetles in some kettle-hole ponds in northern Sweden. *Holarctic Ecology* 7:149-156.
- Nilsson, A. N., J. Elmberg, and K. Sjöberg. 1994. Abundance and species richness patterns of predaceous diving beetles (Coleoptera, Dytiscidae) in Swedish lakes. *Journal of Biogeography* 21:197-206.
- Oertli, B., D. A. Joye, E. Castella, R. Juge, D. Cambin, and J.-B. Lachavanne. 2002. Does size matter? The relationship between pond area and biodiversity. *Biological Conservation* 104:59-70.
- Petersen, I., Z. Masters, A. G. Hildrew, and S. J. Ormerod. 2004. Dispersal of adult aquatic insects in catchments of differing land use. *Journal of Applied Ecology* 41:934-950.

- Poff, N. L., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1805-1818.
- Ricklefs, R. E. 1987. Community diversity: relative role of local and regional processes. *Science* 235:167-171.
- Rosenzweig, M.L. 1995. *Species diversity in space and time*. Cambridge: Cambridge University Press.
- Rundle, S., A. Foggo, V. Choiseul, and D. T. Bilton. 2002. Are distribution patterns linked to dispersal mechanism? An investigation using pond invertebrate assemblages. *Freshwater Biology* 47:1571-1581.
- Sanderson, R. A., M. D. Eyre, and S. P. Rushton. 2005. The influence of stream invertebrate composition at neighboring sites on local assemblage composition. *Freshwater Biology* 50:221-231.
- Scarsbrook, M. R., and C. R. Townsend. 1993. Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. *Freshwater Biology* 29.
- Schlichting Jr., H. E., and S. L. Sides. 1969. The passive transport of aquatic microorganisms by selected Hemiptera. *Journal of Ecology* 57:759-764.
- Sepkoski, J., and M. Rex. 1974. Distribution of freshwater mussels: coastal rivers as biogeographic islands. *Systematic Zoology* 23(2): 165-188.
- Smith, H., P. J. Wood, and J. Gunn. 2003. The influence of habitat structure and flow permanence on invertebrate communities in karst spring systems. *Hydrobiologia* 510:53-66.
- Sokal, R. R. and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd edition. New York: W. H. Freeman and Co.
- Stanford, J.A., and J.V. Ward. 1983. Insect species diversity as a function of environmental variability and disturbance in stream systems. pp 265-278 in J.R. Barnes and G.W. Minshall, eds. *Stream Ecology: application and testing of general ecological theory*. New York: Plenum.
- Stanley, E. H., D. L. Buschman, A. J. Boulton, N. B. Grimm, and S. G. Fisher. 1994. Invertebrate resistance and resilience to intermittency in a desert stream. *American Midland Naturalist* 131:288-300.
- Statzner, B., J.A. Gore, and V.H. Resh. 1988. Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society* 7(4): 307-360.
- Taylor, C.M. 1997. Fish species richness and incidence patterns in isolated and connected stream pools: effects of pool volume and spatial position. *Oecologia* 110: 560-566.

- Thompson, R. M., and C. R. Townsend. 1999. The effect of seasonal variation on the community structure and food-web attributes of two streams: implications for food-web science. *Oikos* 87:75-88.
- Townsend, C. R., S. Doledéc, R. Norris, K. Peacock, and C. Arbuckle. 2003. The influence of scale and geography on relationships between stream community composition and landscape variables: description and prediction. *Freshwater Biology* 48:768-785.
- Usinger, R. L. 1956. Aquatic Hemiptera. Pages 182-228 in R. L. Usinger, editor. *Aquatic Insects of California*. Berkeley: University of California Press.
- Van Devender, T.R. 1990. Late Quaternary vegetation and climate of the Chihuahuan Desert, United States and Mexico. pp. 104-133 in Betancourt, J.L., T.R. Van Devender, and P.S. Martin eds. *Packrat middens: the last 40,000 years of biotic change*. Tucson: University of Arizona Press.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- Vinson, M. R., and C. P. Hawkins. 1998. Biodiversity of stream insects: variation at local, basin, and regional scales. *Annual Review Entomologia* 43:271-293.
- Vinson, M. R., and C. P. Hawkins. 2003. Broad-scale geographical patterns in local stream insect genera richness. *Ecography* 26:751-767.
- Velasco, J., and A. Millan. 1998. Insect dispersal in a drying desert stream: effects of temperature and water loss. *The Southwestern Naturalist* 43:80-87.
- Wallace, B. J., and N. H. Anderson. 1996. Habitat, life history, and behavioral adaptations of aquatic insects. Pages 41-73 in R. W. Merritt and K. W. Cummins, editors. *An Introduction to the Aquatic Insects of North America*. Dubuque, IA: Kendall/Hunt.
- Ward, D., and L. Blaustein. 1994. The overriding influence of flash floods on species-area curves in ephemeral Negev Desert pools: a consideration of the value of island biogeography theory. *Journal of Biogeography* 21: 595-603.
- Ward, J. V., and J. A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* 27:97-117.
- Weaver, J. C. 1995. Indicator species and scale of observation. *Conservation Biology* 9:939-942.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Williams, D. D., and H. B. Hynes. 1976. The recolonization mechanisms of stream benthos. *Oikos* 27:265-272.
- Williams, L., C. Taylor, M. Warren Jr., J. A. Clingenpeel. 2003. Environmental variability, historical contingency, and the structure of regional fish and macroinvertebrate faunas in Ouachita Mountain stream systems. *Environmental Biology of Fishes* 67: 203-216.

Winterbourne, M.J., J.S. Rounnick, and B. Cowie. 1981. Are New Zealand stream ecosystems really different? *New Zealand Journal of Freshwater Research*. 15: 321-328.

Woodward, G., J. I. Jones, and A. G. Hildrew. 2002. Community persistence in Broadstone Stream (U.K.) over three decades. *Freshwater Biology* 47:1419-1435.

APPENDICES

APPENDIX I

Sampling effort depletion curves

To determine sampling effort necessary to maximize species detection at a given site, effort-species detection saturation curves were created at three sites with varying total stream habitat area: East Turkey Creek (571 m²), Rucker Canyon (1029 m²), and Simpson Spring (12.5 m²). Vigorous sweeping with a D-frame net (1 mm mesh) was performed in pools ranging in area from 2 to 5 m², with samples separated at regular intervals (5-10 sec). On average, over 95% of species were detected with an effort about 9 sec m⁻² of pool surface area at East Turkey Creek, AZ. Based on this, I selected a sampling effort of 10 seconds per m² of pool to maximize species detection while minimizing effort (Figure A1.1). To detect the remaining 5% of species, I would have had to be nearly double my effort, thus reducing the total number of sample streams. I decided to sample at approximately a 95% efficiency rate in order to maximize the number of streams I could visit. Several pools were then sampled at this effort level within a reach at East Turkey Creek, Rucker Canyon, and Simpson Spring, AZ. Nearly 97% of species collected in a reach (defined as a 300 m elevation band of perennial water) were detected after 3 pools had been sampled (Table A1.1).

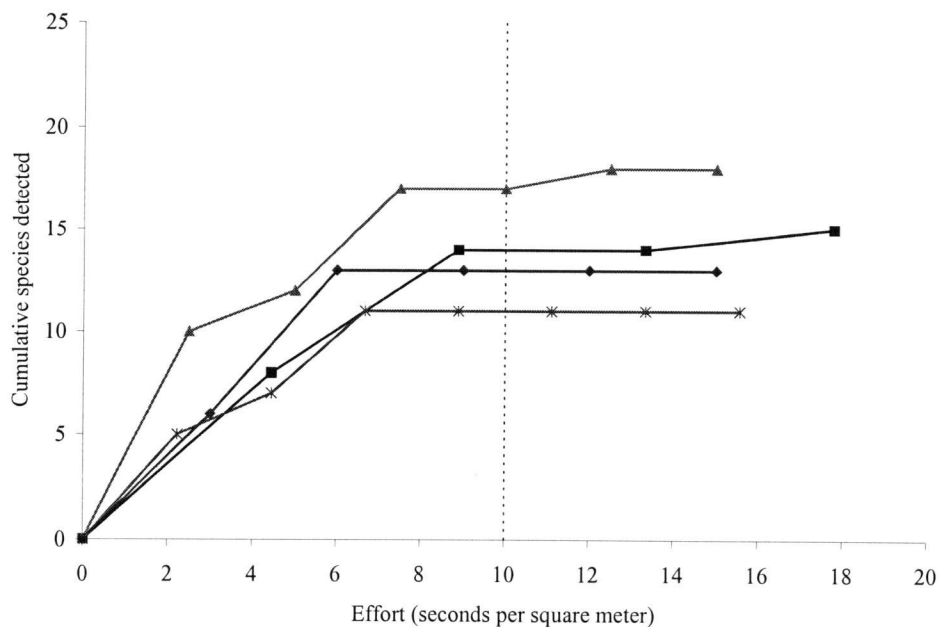


Figure A1.1. Sampling effort and cumulative species detected in 4 pools (size: 2.25-4 m²) at East Turkey Creek.

Table A1.1. Consecutive pools (1-6) sampled with a timed effort of 10 sec m⁻² at three streams, and the cumulative number of species detected with each additional pool.

<i>Cumulative species richness by pool</i>						
Site	Pool 1	Pool 2	Pool 3	Pool 4	Pool 5	Pool 6
East Turkey Creek	17	25	30	30	30	30
Rucker Canyon	26	39	44	45	45	48
Simpson Spring	19	26	30	31	*	*

* Simpson Spring only contained 4 pools which met sampling criteria

APPENDIX II

Species occurrence by study site

This appendix contains species occurrences for all 25 study sites examined in Chapter 2. Site codes are as follows: Aco- Aconchi Agua Caliente; Ash- Ash Canyon; Bea- Bear Canyon; CajT- Cajon Bonito; Chu- Chulo Canyon; Ctw- Cottonwood Creek; Dix- Dixie Canyon; Etu- East Turkey Creek; Flo- Florida Canyon; Frj- French Joe Canyon; Gdn- Garden Canyon; Gnr- Gardner Canyon; Les- Leslie Canyon; Mad- Madera Canyon; Mil- Miller Canyon; Nac- Cañon de Nacapule; Ppo- Paradise Palm Oasis; Ram- Ramsey Canyon; Rat- Rattlesnake Creek; Ruc- Rucker Canyon; Sim- Simpson Spring; Syc- Sycamore Canyon; Val- Vallecitos; Wst- West Stronghold Canyon; Wtu- West Turkey Creek (see Chapter 2 for map of sites). When taxonomic keys were not available or species determinations were impossible, individuals were identified at the generic level. When species determinations were made, but known ranges did not include the collection site or one character was ambiguous, a question mark was placed after the species name.

Table A2.2. Hemiptera species occurrences at 25 study streams.

HEMIPTERA	Aco	Ash	Bea	Caj	Chu	Ctw	Dix	Etu	Flo	Frj	Gdn	Gnr	Les	Mad	Mil	Nac	Ppo	Ram	Rat	Ruc	Sim	Syc	Val	Wst	Wtu	
BELOSTOMATIDAE																										
<i>Abedus herberti</i>	*			*	*		*	*	*	*	*	*	*	*	*	*		*	*	*		*	*	*	*	*
<i>Lethocerus medius</i>	*			*			*		*		*	*	*	*	*	*		*	*	*		*	*	*	*	*
CORIXIDAE																										
Corixidae sp.																										
<i>Graptocorixa abdominalis</i>	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Graptocorixa emburyi</i>					*																					
<i>Graptocorixa gerhardi</i>			*							*									*							
<i>Graptocorixa serrulata</i>	*		*	*	*	*	*	*	*		*								*	*	*	*	*	*	*	*
<i>Hesperocorixa laevigata</i>			*																							
<i>Morphocorixa lundbladi</i>	*							*								*	*						*			
<i>Trichocorixa arizonensis</i>				*																						
GELASTOCORIDAE																										
<i>Gelastocoris</i> sp.	*		*																							
GERRIDAE																										
<i>Aquarius amplus</i>																								*		
<i>Aquarius renigis</i>		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*	*	*	*	*
<i>Gerris</i> sp.			*																					*		
<i>Limnoporus</i> sp.																	*	*								
<i>Metrobates</i> sp.																										
<i>Trepobates hecki</i>	*		*													*	*						*			
HEBRIDAE																										
<i>Hebrus</i> sp.							*																			
HYDROMETRIDAE																										
<i>Hydrometra</i> sp.	*		*			*											*									
NAUCORIDAE																										
<i>Ambrysus</i> sp.	*		*	*			*	*									*			*			*			
<i>Pelocoris</i> sp.	*															*	*					*				
NEPIDAE																										
<i>Curicta pronotata</i>											*						*	*					*			
<i>Ranatra quadridentata</i>	*	*	*				*	*	*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
NOTONECTIDAE																										
<i>Buenoa albidia</i>												*					*	*								
<i>Buenoa arida</i>	*	*		*	*	*				*		*					*		*		*	*	*	*	*	*
<i>Buenoa arizonis</i>	*		*						*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Buenoa margaritacea</i>													*				*		*		*	*	*	*	*	*
<i>Buenoa scimitra</i>												*					*		*		*	*	*	*	*	*
<i>Martarega mexicana</i>				*																				*		
<i>Neocorixa snowi</i>							*	*													*			*		
<i>Notonecta hoffmani</i>				*	*	*	*	*						*							*			*		
<i>Notonecta kirbyi</i>		*		*	*	*	*	*			*										*			*		
<i>Notonecta lobata</i>	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
SALDIDAE																										
<i>Saldula</i> sp.	*										*															
VELIIDAE																										
<i>Microvelia hinei</i>	*																					*				
<i>Microvelia</i> sp.	*	*	*	*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Platyvelia</i> sp.				*			*			*	*					*					*	*	*	*	*	*
<i>Rhagovelia</i> sp.				*	*		*			*	*					*				*	*	*	*	*	*	*

APPENDIX III

Coleoptera and Hemiptera species richness per unit area of habitat

This appendix reports Coleoptera and Hemiptera species richness per square meter of permanent stream habitat at 25 Madrean Sky Island streams.

Table A3.1. Coleoptera and Hemiptera species richness per unit area of habitat in MSI streams.

Range	Site	Coleoptera	Hemiptera	Latitude	Longitude
<i>Atascosa Mountains</i>	Sycamore Canyon	0.03	0.02	31.4191	111.1936
<i>Chiricahua Mountains</i>	East Turkey Creek	0.04	0.02	31.9174	109.2319
	Leslie Canyon	0.05	0.03	31.5892	109.5073
	Rucker Canyon	0.03	0.01	31.7567	109.3643
	West Turkey Creek	0.05	0.02	31.8611	109.3362
<i>Dragoon Mountains</i>	West Stronghold	0.26	0.07	31.9339	109.9960
<i>Galiuro Mountains</i>	Ash Canyon	2.25	0.63	32.5068	110.2364
	Rattlesnake Creek	0.01	0.00	32.6953	110.3440
<i>Huachuca Mountains</i>	Bear Canyon	0.09	0.03	31.4106	110.2826
	Garden Canyon	0.01	0.01	31.4674	110.3585
	Miller Canyon	0.06	0.02	31.4069	110.2874
	Ramsey Canyon	0.07	0.04	31.4442	110.3171
<i>Mule Mountains</i>	Chulo Canyon	0.34	0.17	31.4855	109.9825
	Dixie Canyon	0.04	0.02	31.4955	109.8972
<i>Santa Rita Mountains</i>	Florida Canyon	0.30	0.12	31.7509	110.8432
	Gardner Canyon	0.26	0.11	31.7022	110.8005
	Madera Canyon	0.23	0.08	31.7242	110.8807
<i>Sierra Aconchi</i>	Aconchi Agua Caliente	0.02	0.01	29.8460	110.2849
<i>Sierra el Aguaje</i>	Nacapule Canyon	0.11	0.09	28.0090	111.0971
	Paradise Palm Oasis	0.12	0.11	28.0100	111.2000
<i>Sierra la Madera</i>	Vallecitos Creek	0.05	0.03	29.9216	109.5136
<i>Sierra San Luis / Peloncillo</i>	Cajon Bonito	0.00	0.00	31.2780	109.0021
	Cottonwood Creek	0.94	1.06	31.4895	109.0702
<i>Whetstone Mountains</i>	French Joe Canyon	1.67	0.50	31.8176	110.4092
	Simpson Spring	1.76	0.64	31.7893	110.4703

APPENDIX IV

Comparison of stream and pond aquatic insect communities in the Madrean Sky Islands

This appendix compares the aquatic insect communities of Madrean Sky Island (MSI) mountain streams with those from ponds and cattle tanks located in valley bottoms and lower elevation canyons. Though most MSI streams consist of isolated pools with little or no flow much of the year, approximating lentic environments, there are significant differences between stream habitats and cattle tanks and ponds. Stream pools generally occur in bedrock depressions and hold water year-round. These stream pools occur at higher elevations (1400-2200 m) and are partially shaded by riparian trees (e.g., sycamore, ash, walnut), which moderates water temperature (Figure A4.1). Constructed cattle tanks in lower elevation (1200-1600 m) canyons are often small (~1 m²) concrete tanks which are semi-permanent, but located outside of the stream channel in the arid Madrean Evergreen Woodland (Figure A4.3). Low elevation (>1300m) valley ponds usually have silt substrates, occur seasonally (duration: 1-4 months), and can be shallow and without shade, leading to very high diurnal temperature fluctuation (Figures A4.2, A4.4).

Due to their size, substrate and ephemeral nature, many ponds were difficult to sample in an effective standardized manner, so pond-stream comparisons were made using presence-absence transformed data, rather than counts or densities. Standardized collection methods (see Chapter 2) were employed at 25 stream sites from May-July 2004. One additional stream site (Mazatan) was sampled in May 2004, but there was only time for collection at two pools instead of the standard three. Twelve lentic habitats (8 valley ponds and 4 mountain canyon cattle tanks) were haphazardly selected and sampled between April and July 2004. At each site, a 1 mm mesh D-net was used to vigorously sweep substrate and vegetation in a 2 m band from the shore along the entire pond perimeter. All collected insects were placed in 95% ethanol, and later identified and enumerated at Oregon State University. Temperature, pH and conductivity were recorded at a depth of 10 cm (when possible) using hand-held meters.

Non-metric multidimensional scaling (NMS) was used to examine differences in stream and pond Hemiptera and Coleoptera communities. Replicate samples within stream sites were pooled so that one species presence-absence matrix represented each stream and pond site. Taxa occurring at only one site were removed before analysis, as they do not reveal any information about the relatedness of sites.

One-hundred and fifty species of Coleoptera and Hemiptera were identified from the 26 stream and 12 pond sites. Of the 150 species collected, 29 species were singleton taxa and were deleted before NMS analyses. Sixty-five species (43% of all species) were only found in mountain stream habitats (Table A4.2), while 15 species (10% of all species) were unique to pond community samples (Table A4.3). The remaining 47% of species were encountered in both pond and stream habitats.

The NMS ordination converged on a marginally stable, 2-dimensional solution (final stress = 18.659, final instability = 0.006; $p = 0.0196$). The slightly elevated stress and higher instability was expected due to the high variability between pond sites and the high species turnover between stream and pond communities. Most stream communities formed tightly clustered group in the ordination graph (Figure A4.5). Streams located on the extreme southwestern margin of the MSI (Mazatan) and 100km southwest of the MSI (Nacapule and Paradise) have higher axis one scores than other streams, but are within the range of axis 2 scores for all other streams. Pond communities occupy a much wider range of 'species-space' than stream communities. Canyon pond communities form a more clustered group than the widespread valley pond communities. This pattern may be associated with differences in environmental variation between valley and canyon ponds. Valley tanks offer a wide range of habitat types from very shallow (<20 cm) and warm temporary ponds (Figure A4.2) to deeper (>50 cm), vegetated permanent ponds (Table A4.1). Temporary valley ponds can reach temperatures of over 40°C and exhibit dramatic diurnal fluctuations in temperature (Figure A4.4). Canyon tanks were usually cooler, deeper (>75 cm) concrete tanks (Figure A4.3) which contain water year-round (see Table A4.1 for full comparison of measured abiotic characteristics).

Table A4.1. Water temperature, conductivity and pH, and geographic locations for all sites (Temperature= °C; Conductivity= μ S).

Site	Temperature	Conductivity	pH	Latitude	Longitude
<i>Streams</i>					
Aconchi Agua Caliente	21	425	7.5	29.8460	110.2849
Ash Canyon	18	125	8.2	32.5068	110.2364
Bear Canyon	22	420	7.7	31.4106	110.2826
Cajon Bonito	23	280	8.1	31.2780	109.0021
Caliente Cajon Bonito	21	620	8.3	31.2824	108.9963
Chulo Canyon	23	95	7.6	31.4855	109.9825
Dixie Canyon	27	470	7.8	31.4955	109.8972
East Turkey Creek	18	230	7.7	31.9174	109.2319
Florida Canyon	19.5	280	7.4	31.7509	110.8432
French Joe Canyon	18.5	630	7.7	31.8176	110.4092
Garden Canyon	18	395	7.8	31.4674	110.3585
Gardner Canyon	21.3	150	7.9	31.7022	110.8005
Leslie Canyon	18	535	7.6	31.5892	109.5073
Madera Canyon	19.5	480	7.8	31.7242	110.8807
Mazatan	24	420	8.0	29.0911	110.2209
Miller Canyon	11.5	210	8.0	31.4069	110.2874
Nacapule Canyon	21.3	400	7.0	28.0090	111.0971
Paradise Canyon	22	400	7.3	28.0100	111.2000
Ramsey Canyon	17	360	8.2	31.4442	110.3171
Rattlesnake Creek	19.5	80	7.5	32.6953	110.3440
Rucker Canyon	19.5	170	7.4	31.7567	109.3643
Simpson Spring	18.9	890	7.9	31.7893	110.4703
Sycamore Creek	24	270	8.0	31.4191	111.1936
Vallecitos	15	150	6.9	29.9216	109.5136
West Stronghold Canyon	19.5	490	7.9	31.9339	109.9960
West Turkey Creek	22	110	7.3	31.8611	109.3362
<i>Mean</i>	<i>20.1</i>	<i>349</i>	<i>7.7</i>		
<i>Standard Deviation</i>	<i>3.12</i>	<i>196</i>	<i>0.4</i>		
<i>Ponds / Tanks</i>					
Bear Spring	19.5	700	7.75	31.7752	110.4616
Boulder Tank	19.5	300	8.5	31.7613	110.4856
Cottonwood Tanks	21	590	8.1	31.4737	109.0909
East Willow Tank	25.5	40	6.85	31.8150	109.0597
Exit 292 Pond	31	150	9	31.9777	110.5087
Guindani Tank	19	380	7.3	31.8415	110.3694
Halfmoon Pond	12.2	300	6.5	31.9124	109.9779
Kartchner Caverns Tank	24	280	8.6	31.8835	110.3577
Rock Tank North	32	220	9.5	31.9449	109.1176
Rock Tank South	25	440	8.5	31.9394	109.1170
"Stuck" Tank	29	65	7	31.8647	109.0367
"The Thing" Pond	24.5	170	7.6	32.0825	110.0526
<i>Mean</i>	<i>23.5</i>	<i>303</i>	<i>7.9</i>		
<i>Standard Deviation</i>	<i>5.66</i>	<i>200</i>	<i>0.9</i>		

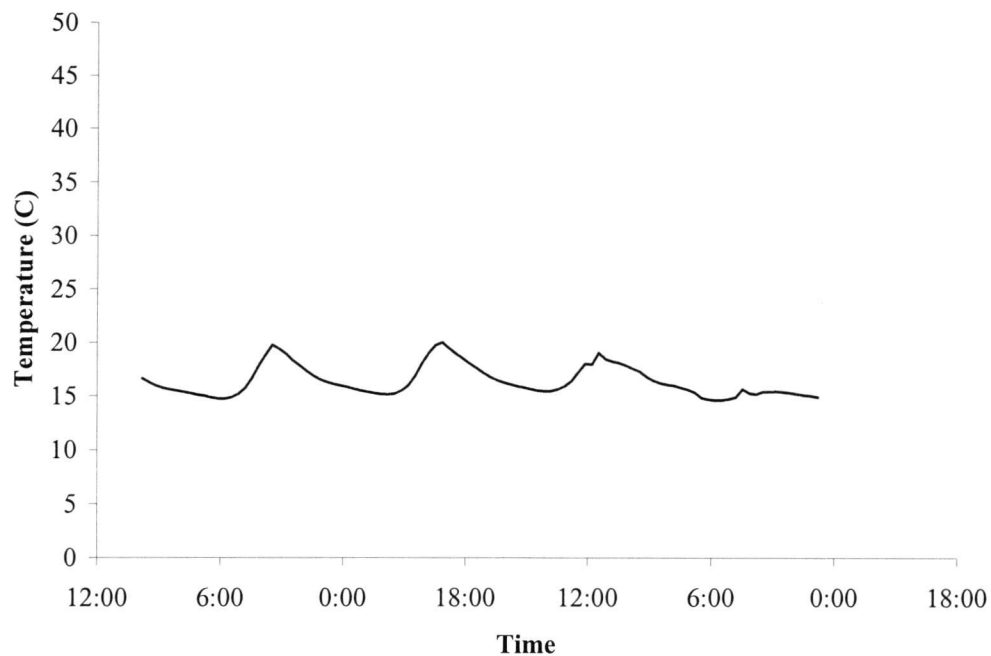


Figure A4.1. Temperature recorded at 1-hr intervals at North Fork Cave Creek (1915 m), located 5 km above the Southwestern Research Station from 19:00 29 Jul 2005 to 21:00 2 Aug 2005.

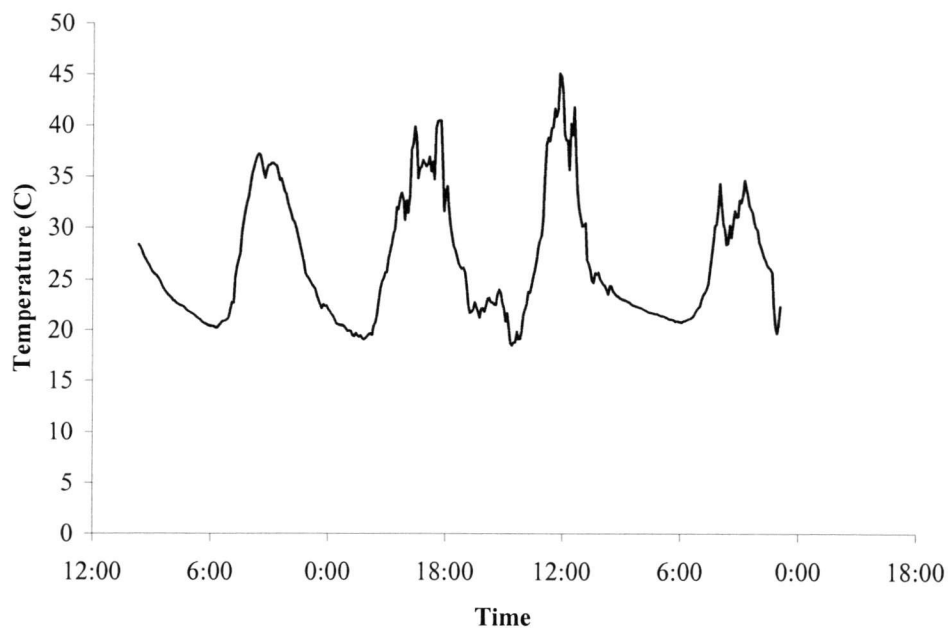


Figure A4.2. Temperature recorded at 15-min intervals in a temporary pond (1260m) located 2 km north of Rodeo, NM, from 19:00 29 Jul 2005 to 21:00 2 Aug 2005.

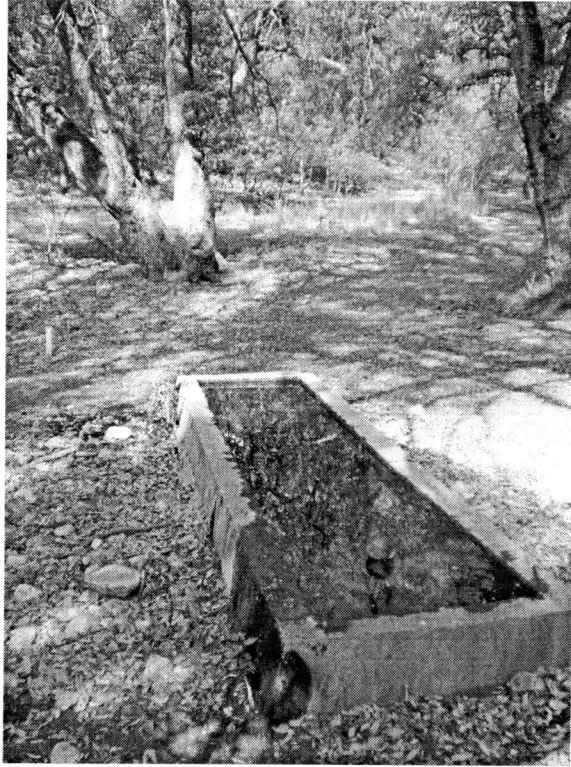


Figure A4.3. Perennial water cattle tank in French Joe Canyon, Whetstone Mountains, AZ.

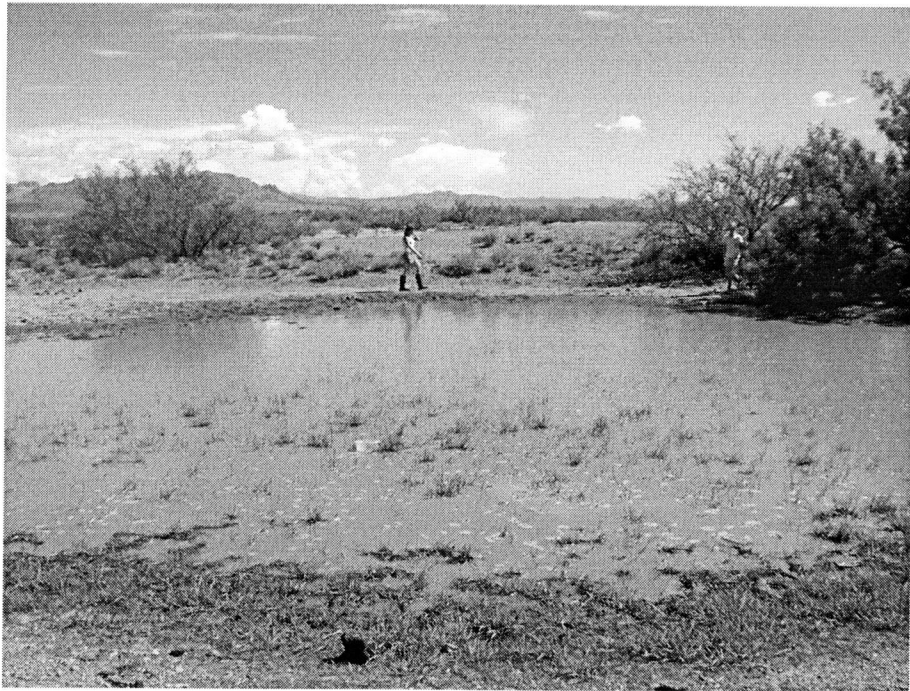


Figure A4.4. Temporary valley pond 2 km north of Rodeo, NM.

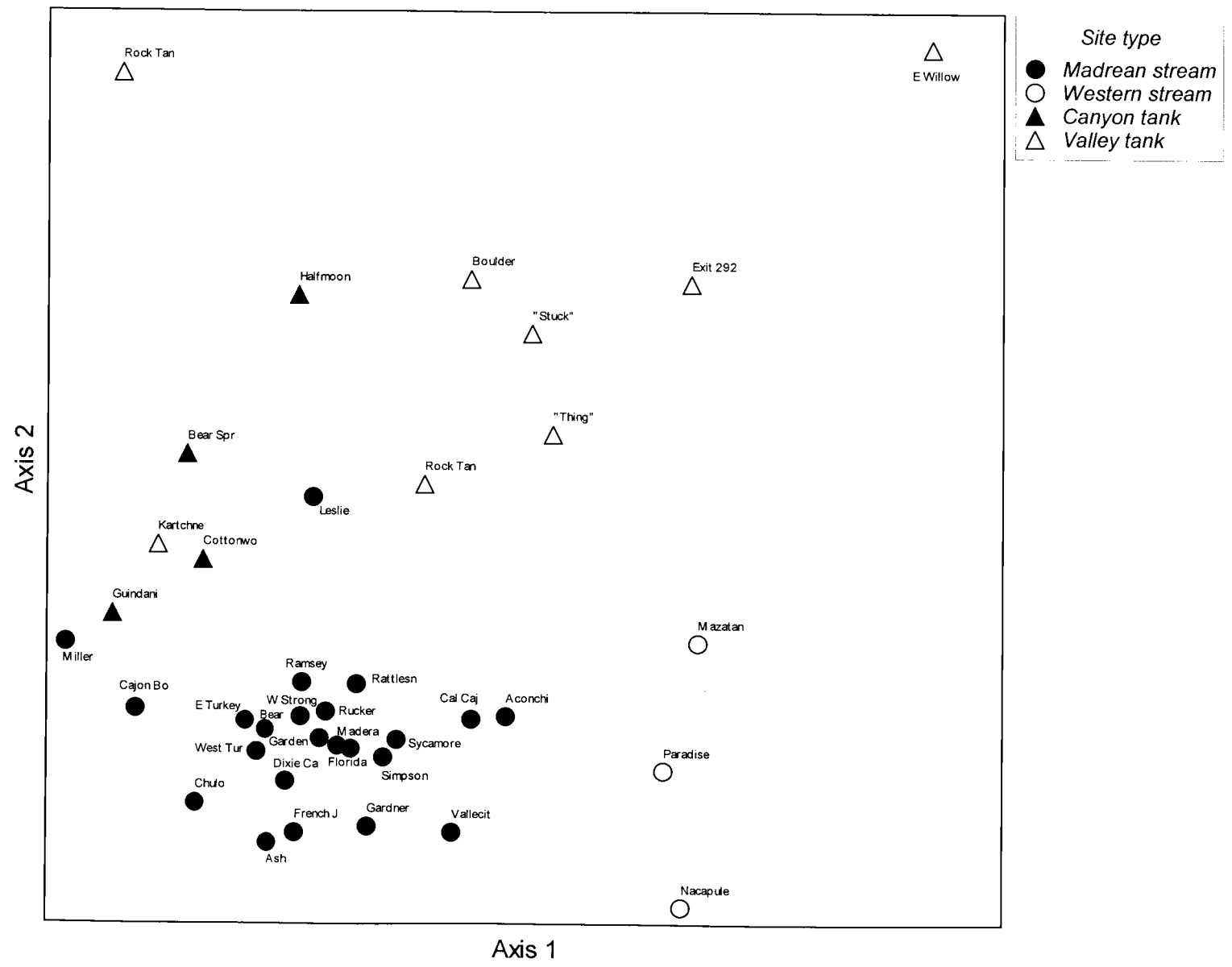
Table A4.2. Taxa found exclusively in mountain streams (%Occ = the percent of all mountain streams occupied by the species).

Mountain Exclusive		
Species	Family	% Occ
<i>Thermonectus marmoratus</i>	Dytiscidae	70
<i>Abedus herberti</i>	Belostomatidae	67
<i>Gyrinus plicifer</i>	Gyrinidae	63
<i>Dineutus sublineatus</i>	Gyrinidae	60
<i>Rhantus atricolor</i>	Dytiscidae	53
<i>Sanfilippodytes</i> sp.	Dytiscidae	53
<i>Stictotarsus corvinus</i>	Dytiscidae	53
<i>Berosus rugulosus</i>	Hydrophilidae	50
<i>Rhantus gutticollis mexicanus</i>	Dytiscidae	33
<i>Ambrysus</i> sp.	Naucoridae	30
<i>Postelichus</i> sp.	Dryopidae	30
<i>Helichus triangularis</i>	Dryopidae	27
<i>Hydraena</i> sp.	Hydraenidae	27
<i>Hydrochus</i> sp.	Hydrochidae	27
<i>Pelocoris</i> sp.	Naucoridae	27
<i>Trepobates becki</i>	Gerridae	27
<i>Stictotarsus roffi</i>	Dytiscidae	23
<i>Laccobius</i> sp.	Hydrophilidae	20
<i>Helichus suturalis</i>	Dryopidae	20
<i>Neoclypeodytes fryii</i>	Dytiscidae	20
<i>Notonecta kirbyi</i>	Notonectidae	20
<i>Platyvelia beameri</i>	Veliidae	20
<i>Rhagovelia varipes</i>	Veliidae	20
<i>Anacaena limbata</i>	Hydrophilidae	17
<i>Curicta pronotata</i>	Nepidae	17
<i>Hydrometra</i> sp.	Hydrometridae	17
<i>Dytiscus habilis</i>	Dytiscidae	13
<i>Laccophilus oscillator</i>	Dytiscidae	13
ELMIDAE sp.	Elmidae	10
<i>Graptocorixa gerhardi</i>	Corixidae	10
<i>Liodes</i> sp.	Dytiscidae	10
<i>Neocorixa snowi</i>	Corixidae	10
<i>Gelastocoris</i> sp.	Gelastocoridae	10
<i>Berosus notapeltatus</i>	Hydrophilidae	7
<i>Cymbiodyta</i> sp.	Hydrophilidae	7
<i>Cyphon</i> sp.	Scirtidae	7
<i>Heterelmis obesa</i>	Elmidae	7
<i>Hydrobius</i> sp.	Hydrophilidae	7
<i>Paracymus</i> sp.	Hydrophilidae	7
<i>Peltodytes</i> sp.	Haliplidae	7
<i>Platyvelia</i> sp.	Veliidae	7
<i>Rhagovelia</i> sp.	Veliidae	7
<i>Saldula</i> sp.	Saldidae	7
<i>Hesperocorixa laevigata</i>	Corixidae	7
<i>Microvelia hinei</i>	Veliidae	7
<i>Aquarius amplus</i>	Gerridae	3
<i>Chaetarthria</i> sp.	Hydrophilidae	3
<i>Copelatus chevrolati renovatus</i>	Dytiscidae	3
<i>Copelatus distinctus</i>	Dytiscidae	3
<i>Crenitis</i> sp.	Hydrophilidae	3
<i>Cymbiodyta fraterculus</i>	Hydrophilidae	3
<i>Dytiscus</i> sp.	Dytiscidae	3
<i>Hydrochara lineata</i>	Hydrophilidae	3
<i>Hydroporus axillaris</i>	Dytiscidae	3
<i>Gerris comatus</i>	Gerridae	3
<i>Graptocorixa emburyi</i>	Corixidae	3
<i>Hebrus</i> sp.	Hebridae	3
<i>Macronychus glabratus?</i>	Elmidae	3
<i>Neoporus arizonicus</i>	Dytiscidae	3
<i>Octhebius discretus</i>	Hydraenidae	3
<i>Paracymus subcupreus?</i>	Hydrophilidae	3
<i>Postelichus confluentus</i>	Dryopidae	3
<i>Psephenus</i> sp.	Psephenidae	3
<i>Trichocorixa arizonensis</i>	Corixidae	3
<i>Zaitzevia parvula</i>	Elmidae	3

Table A4.3. Taxa found exclusively in valley or canyon pond habitats (%Occ = the percent of all ponds occupied by the species).

Valley Exclusive		
Species	Family	% Occ
<i>Corisella edulis</i>	Corixidae	64
<i>Berosus stylifer</i>	Hydrophilidae	36
<i>Gerris</i> sp.	Gerridae	27
<i>Notonecta unifasciata</i>	Notonectidae	27
<i>Belostoma</i> sp.	Belostomatidae	18
<i>Berosus infuscatus?</i>	Hydrophilidae	18
<i>Berosus miles?</i>	Hydrophilidae	18
<i>Eretes occidentalis</i>	Dytiscidae	18
<i>Berosus peregrinus</i>	Hydrophilidae	9
<i>Corisella</i> sp.	Corixidae	9
<i>Corisella tarsalis</i>	Corixidae	9
<i>Neoclypeodytes</i> sp.	Dytiscidae	9
<i>Notonecta undulata</i>	Notonectidae	9
<i>Ramphocorixa acuminata</i>	Corixidae	9
<i>Salda</i> sp.	Saldidae	9

Figure A4.5. NMS ordination of 26 stream and 12 pond sites, coded by habitat type.



APPENDIX V

Aquatic insect colonization of experimental pools near Cave Creek, Chiricahua Mountains, AZ

This appendix presents data from a colonization experiment designed to detect which aquatic insect species are leaving the adjacent stream corridor and looking for new habitats to colonize. The experiment took advantage of four small plastic pools (children's swimming pools) that were set up 20m west of Cave Creek at the American Museum of Natural History's Southwestern Research Station, near Portal, AZ. The four pools were set up and used for 30 days by Ryan Martin of University of North Carolina at Chapel Hill for rearing spadefoot (*Spea* spp.) toad tadpoles. I used these four pools to monitor aquatic insect colonization in newly created aquatic habitats.

I monitored aquatic insect colonization in 4 plastic pools adjacent to Cave Creek every 4 days between July 1st and July 25th, 2004. Pools had a radius of approximately 0.75 m and a maximum depth of approximately 0.3 m. Total surface area of the four pools combined was approximately 7 m². Pools were located in an open, grassy meadow adjacent to Cave Creek and 15 m from any riparian vegetation. Pools were filled at 2pm on July 1st, and received a silt substrate (approx 1cm deep) and *Spea* spp. tadpoles on July 6th. No other alterations or additions were made during the time of the experiment. Aquatic insects were collected using a small aquarium net (mesh size = 0.5 mm) in the late afternoon of each collection day (July 1, 5, 9, 13, 17, 21, 25). All individuals collected were preserved in 70% ethanol and identified to the lowest taxonomic level possible (species for Coleoptera and Hemiptera, genus and family for other orders). Daily rainfall data was obtained from a NOAA weather station, located approximately 200m from the experimental pools. Since the four pools were identical in size, volume of water, and external treatments (tadpole and silt presence), samples from individual pools were combined.

Thirty-two species of aquatic insects were collected from the colonization pools between July 1st 25th (Table A5.1). Some species colonized the pools immediately and continuously through the month (*Microvelia* sp., *Stictotarsus* spp.). After 21 days, *Baetis* sp. (Ephemeroptera) larvae were present in the pool, and after 25 days Chironomidae (Diptera), Libellulidae (Odonata), *Graptocorixa serrulata* (Hemiptera), and *Baetis* sp. larvae were encountered. Half of all species and individuals collected were only recorded on the last collection day, after a significant rainfall event. In general, both cumulative species and individuals collected followed

the same increasing trend as rainfall (Figures A5.1, A5.2). Most of the species (78%) collected are found in both permanent mountain stream and ephemeral valley pond habitats (Table A5.1; also see Appendix IV). This suggests that the majority of colonizing species in this study are long distance dispersers both within and between mountain streams and ranges. One species (3% of total) with a valley pond affinity was collected (*Berosus infuscatus*) in the pools, but it was only one individual from the final collection day. It is possible that this individual was transitory, flying across the mountain ranges in search of pond habitat. Alternatively, populations of this species may exist in nearby streams, but at densities too low to be detected with the stream sampling method (see Appendix I). Of the six species collected (19% of total) with mountain stream affinities, five were collected only on the last day following significant rainfall. Increased humidity and cloud cover that occurs with rainfall may present more hospitable conditions for aquatic insects to leave the stream corridor in search of new habitats. Pre-monsoon rain conditions at mountain streams are characterized by very dry (humidity as low as 10%), hot (temperatures as high as 35°C) weather, which may inhibit the aerial dispersal of aquatic insects.

In summary, 32 species of aquatic insects colonized 4 small pools adjacent to Cave Creek which suggests a large amount of dispersal occurs adjacent to, but outside of stream corridors. Most of these dispersers are generalist species, found in both temporary and permanent stream and pond habitats, and are capable of long distance dispersal. The number of taxa and individuals dispersing were closely associated with local rainfall, suggesting that rainfall and associated weather conditions (i.e. increased humidity, cloud cover) are conducive to dispersal behavior of aquatic insects in arid streams.

Table A5.1. Species collected by date with their habitat affinities (M =mountain streams, V = valley ponds, B = both valley and mountain habitats). All individuals collected were adults unless otherwise noted (*L* = larvae collected, *A+L* = both adult and larvae collected).

Taxa	Collection date						Habitat affinity
	5-Jul	9-Jul	13-Jul	17-Jul	21-Jul	25-Jul	
COLEOPTERA							
Dryopidae							
<i>Postelichus</i> sp.			x		x	x	M
Dytiscidae							
<i>Desmopachria portmanni</i>						x	B
Dytiscidae sp.						x (<i>L</i>)	B
<i>Hygrotus</i> sp.				x		x	B
<i>Laccophilus fasciatus terminalis</i>	x		x			x	B
<i>Laccophilus maculosus shermani</i>					x	x	B
<i>Laccophilus mexicanus</i>						x	B
<i>Laccophilus pictus</i>				x		x	B
<i>Rhanus gutticollis gutticollis</i>					x	x	B
<i>Stictotarsus aequinoctialis</i>	x	x			x	x	B
<i>Stictotarsus striatellus</i>	x	x	x				B
Gyrinidae							
<i>Gyrinus plicifer</i>						x	M
Helophoridae							
<i>Helophorus</i> sp.			x	x		x	B
Hydraenidae							
<i>Ochthebius discretus</i>				x			M
Hydrophilidae							
<i>Anacaena limbata</i>						x	M
<i>Berosus infuscatus</i>						x	V
<i>Berosus salvini</i>		x					B
<i>Enochrus</i> sp. 1						x	B
<i>Enochrus</i> sp. 2						x	B
<i>Laccobius hardyi</i>						x	B
<i>Tropisternus ellipticus</i>					x	x	B
<i>Tropisternus lateralis</i>						x	B
DIPTERA							
Chironomidae							
Chironomidae sp.						x (<i>L</i>)	B
EPHEMEROPTERA							
Baetidae							
<i>Baetis</i> sp.		x			x (<i>L</i>)	x (<i>L</i>)	B
HEMIPTERA							
Corixidae							
<i>Graptocorixa abdominalis</i>						x	B
<i>Graptocorixa serrulata</i>				x	x	x (<i>A+L</i>)	B
Gerridae							
<i>Aquarius remigis</i>						x	B
Naucoridae							
<i>Ambyrsus</i> sp.						x	M
Nepidae							
<i>Ranatra quadridentata</i>					x		B
Saldidae							
<i>Saldula</i> sp.						x	M
Veliidae							
<i>Microvelia</i> sp.	x	x	x	x	x	x	B
ODONATA							
Libellulidae							
Libellulidae sp.						x (<i>L</i>)	B

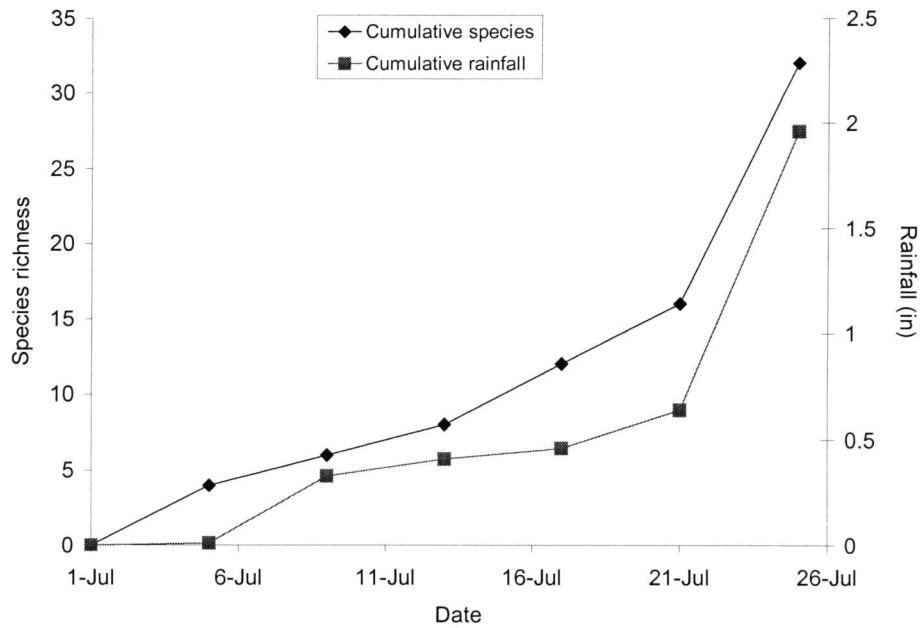


Figure A5.1. Cumulative species richness (4 colonization pools combined) and rainfall values for the seven survey days during July, 2004.

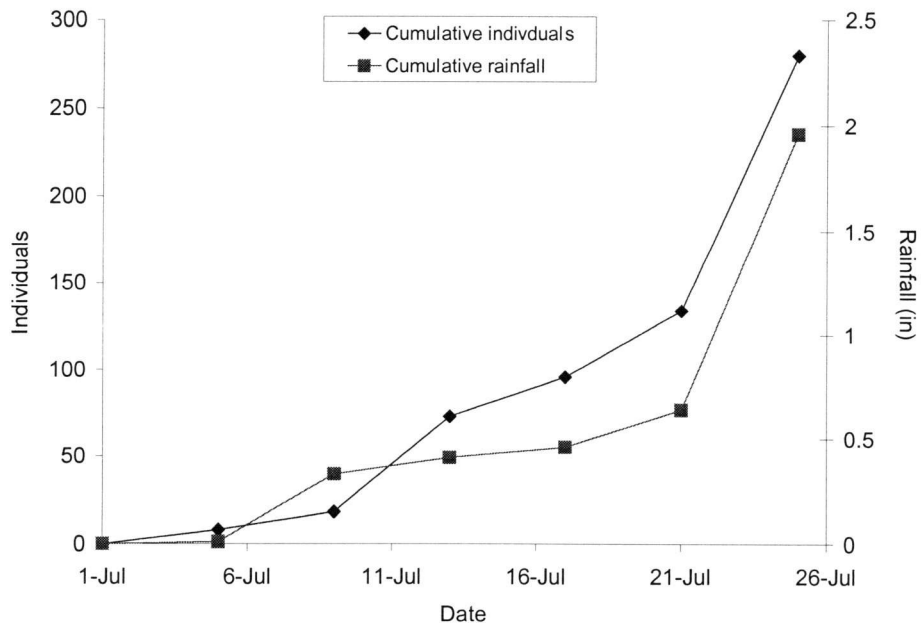


Figure A5.2. Cumulative number of individual colonizing insects (4 colonization pools combined) and rainfall values for the seven survey days during July, 2004.