Habitat Type and Permanence Determine Local Aquatic Invertebrate Community Structure in the Madrean Sky Islands

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Abstract—*Aquatic environments in the Madrean Sky Islands (MSI) consist of a matrix of perennial and intermittent stream segments, seasonal ponds, and human-built cattle trough habitats that support a diverse suite of aquatic macroinvertebrates. Although environmental conditions and aquatic communities are generally distinct in lotic and lentic habitats, MSI streams are characterized by isolated perennial pools for much of the year, and thus seasonally occur as lentic environments. In this study, we compared habitat characteristics and Coleoptera and Hemiptera assemblages of stream pools with those of true lentic habitats (seasonal ponds and cattle troughs) across the MSI. We identified 150 species across the 38 sites, and despite superficial similarities in habitat characteristics, seasonal ponds and stream pools in the MSI support distinct aquatic insect communities. Stream-exclusive species included many long-lived species with poor dispersal abilities, while pond-exclusive species tended to have rapid development times and strong dispersal abilities. We suggest that, in addition to perennial streams, seasonal aquatic habitats should also be a focus of conservation planning in the MSI.*

Introduction

Abiotic factors can be highly influential in determining local aquatic invertebrate community structure, including presence or absence of flowing water (lotic vs. lentic) and hydroperiod (how long water lasts in a given habitat). Lotic and lentic environments generally support distinct aquatic insect communities (Huryn and others 2008). The physical hydraulics of flow, oxygen availability, substrate, and temperature are among the primary physical drivers of this community distinctness between lotic and lentic habitats (Vannote and Sweeney 1980; Resh and others 2008). Additionally, seasonal habitat drying can act as a strong filter on aquatic insect communities in both streams and ponds (Williams 2005). Seasonal streams and ponds (habitats that dry for extended periods of time each year) often contain species with life-history adaptations to drought (Wiggins and others 1980).

The Madrean Sky Island region (MSI) in the southwestern United States and northwestern Mexico contains a diversity of lotic and lentic habitats, including streams with perennial and intermittent surface water, seasonal ponds, and human-built cattle troughs. Perennial streams are found in the higher elevations (1200-2200 m) of most MSI mountain ranges. While wet winters and monsoon rains can result in high-flow periods where stream pools are scoured and connected to one another, many MSI streams have low to zero flow for much of the year, and the remaining isolated perennial pool habitats approximate lentic environments. Seasonal ponds form in adjacent valley bottoms; these ponds fill after summer monsoon rains or prolonged winter storms and usually contain water for fewer than 4 months. Cattle troughs also provide small lentic habitats, which often contain water year-round. All three of these environments provide lentic habitat, but whether or not they were utilized by the same taxa was previously unknown.

In this study, we surveyed stream pool, seasonal pond, and cattle trough aquatic insect assemblages across the MSI. We focused our analyses on beetles (Coleoptera) and true bugs (Hemiptera) because species-level identification is possible and they comprise over 80% of aquatic insect individuals in MSI stream pools during the dominant low-flow period (Bogan and Lytle 2007). Our objectives were to document the distribution of these taxa across the MSI and to examine assemblage differences among stream pool, seasonal pond, and cattle trough habitats. While MSI stream pools approximate lentic environments for much of the year, we hypothesized that stream pools, seasonal ponds, and cattle troughs would contain distinct beetle and true bug assemblages due to environmental differences (e.g. hydroperiod, water temperature) among these habitat types.

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Methods

Habitat Types

Perennial stream pools occur as small, fragmented habitats within MSI ranges (generally between 1200 and 2200 m), and contain water year-round. Seasonal ponds (occurring below 1200 m) that we surveyed in 2004 were dry in April and June, wetted in August, and dry again in November. Thus, these ponds contained water for no more than 4 consecutive months in 2004. Cattle troughs were found in the lower reaches of canyons (usually below 1500 m) and in valleys below 1200 m. These were small (1 to10 m2) concrete and metal tanks that were fed by spring or well water. Cattle troughs generally contain water year-round, but can dry occasionally if the pumps, hoses, or pipes that feed them break. The history of individual troughs (e.g. when they were constructed) was not available for this study. None of the streams, seasonal ponds, or cattle troughs surveyed contained exotic vertebrate predators (e.g. large-mouthed bass, bullfrogs) when they were surveyed.

Collection Methods

Aquatic beetle and true bug assemblages were sampled from pools in 25 streams, from 7 seasonal ponds, and from 5 cattle troughs between May and July 2004. Streams were the focus of a separate study (Bogan 2005), which is why more streams were surveyed than ponds or troughs. Stream pools were sampled by vigorously sweeping a D-net (1 mm mesh) above all pool substrata and on the surface of the water for 10 s m-2 of pool area, an effort that detected approximately 95% of beetle and true bug taxa in a given pool (see Bogan and Lytle 2007, 2011). Ponds, and occasionally troughs, were too large to effectively sample the entire habitat as was done for stream pools, so we focused our efforts on near-shore habitats. At each pond and trough sampling site, a 1-mm mesh D-net was used to vigorously sweep substrate and vegetation from the shore to 2 m offshore along the entire habitat perimeter. All collected insects were placed in 95% ethanol, and later identified at Oregon State University. At each sample site, temperature, pH, and conductivity were recorded at a depth of 10 cm using hand-held meters. Since sampling did not always occur at the same time of day, instantaneous water temperature values may

Table 1—Location of study sites in the Madrean Sky Islands region (SON = Sonora, Mexico; AZ = Arizona; NM = New Mexico).

Habitat type	Site	State	Latititude	Longitude
Stream pools	Agua Caliente- Aconchi	SON	29.846	110.2849
	Agua Caliente- Cajon	SON	31.2824	108.9963
	Cañon Alacrán	SON	28.01	111.2
	Ash Creek	AZ	32.50679	110.23639
	Bear Canyon	AZ	31.41056	110.2826
	Cajon Bonito	SON	31.27803	109.00212
	Chulo Canyon	AZ	31.48545	109.98251
	Dixie Canyon	AZ	31.49549	109.89718
	East Turkey Creek	AZ	31.91743	109.23194
	Florida Canyon	AZ	31.75657	110.84362
	French Joe Canyon	AZ	31.81758	110.40917
	Gardner Canyon	AZ	31.70217	110.80051
	Leslie Creek	AZ	31.58916	109.50729
	Madera Canyon	AZ	31.72416	110.88071
	Sierra Mazatán	SON	29.09106	110.22091
	Miller Canyon	AZ	31.40691	110.28742
	Cañon Nacapule	SON	28.00898	111.09712
	Ramsey Canyon	AZ	31.4442	110.3171
	Rattlesnake Creek	AZ	32.69534	110.34395
	Rucker Canyon	AZ	31.75669	109.36433
	Simpson Spring	AZ	31.78932	110.47029
	Sycamore Creek	AZ	31.41914	111.19361
	Vallecitos- La Madera	SON	29.92156	109.51361
	West Stronghold Canyon	AZ	31.93385	109.99599
	West Turkey Creek	AZ	31.86102	109.33618
Seasonal ponds	Boulder Pond	AZ	31.76126	110.4856
	East Willow Pond	AZ	31.81503	109.05965
	Exit 292 Pond	AZ	31.97767	110.50866
	Halfmoon Pond	AZ	31.91235	109.97793
	Rock Pond	AZ	31.94488	109.11757
	Stuck Pond	NM	31.86468	109.03671
	The Thing Pond	AZ	32.08254	110.05257
Cattle troughs	Bear Spring Tank	AZ	31.77523	110.4616
	Cottonwood Tanks	AZ	31.48941	109.07038
	Guindani Tank	AZ	31.84151	110.36936
	Kartchner Tank	AZ	31.8835	110.35767
	Rock Tank	AZ	31.93941	109.11703

not exhibit reliable differences between sites. To explore diurnal water temperature fluctuations, we deployed HOBO remote temperature probes (Onset Computer Corporation, Pocasset, MA) at 10 cm water depth in two ponds (East Willow and "Stuck"; table 1) and pools in two streams (one pool each in N. Fk. Cave Creek and French Joe Canyon; table 1). HOBO probes in the streams were deployed from May 2004 through June 2005, but the seasonal pond sites began to dry soon after the probes were deployed, so data are only available from 29 July-2 August 2004. Finally, we visually estimated percentages of substrate types (bedrock, cobble, gravel, sand, and fines) at each site. All insect collections and visual estimations were made by the same individual (MTB) to minimize data collector error.

Statistical Methods

Because sample sizes and variances were unequal, we used non-parametric Mann-Whitney tests to examine differences in temperature, conductivity, and pH between stream and pond sites. All tests were performed in SYSTAT v.11 (Systat Software Inc., San Jose, California). Aquatic insect assemblage variation among sites was visualized using non-metric multidimensional scaling (NMS) on Sorensen distance matrices in PC-ORD v5.0 (MjM Software, Glenden Beach, Oregon). Because pond aquatic invertebrate sampling methods were designed to maximize species detection, rather than quantifying relative abundances, all assemblage matrices were presence-absence transformed prior to statistical analyses. We used Pearson's r correlations to examine relationships between species presence, environmental factors, and axis scores. To test distinctness of stream and pond assemblages, we used Multi-Response Permutation Procedure (MRPP) tests.

Results

Pond temperatures during sampling visits (mean ± 1 SD: 23.5 °C ± 5.6) were significantly higher than stream pool temperatures (mean ± 1 SD: 20.1 °C ± 3.1; U = 225.5, p = 0.03), but conductivity and pH did not differ significantly between streams and ponds (p = 0.47 and 0.46, respectively). The HOBO temperature probes deployed from 29 July - 2 August 2004 indicated that, in addition to overall higher temperatures in ponds over those 5 days, diurnal temperature fluctuation was much higher in ponds than in stream pools (fig. 1). Mean pond temperature over those 5 days was 25.6 ± 5.1 °C, while mean stream pool temperature was 18.3 ± 2.3 °C. Pond substrate was predominately fine silt (mean ± 1SD: 80% ± 16), while stream pool substrate was variable (means ± 1SD: 38% ± 26 bedrock, 20% ± 22 fine, 16% ± 15 gravel, 16% ± 16 cobble, 10% ± 13 sand).

One-hundred and fifty species of Coleoptera and Hemiptera were identified from the 25 stream, 7 seasonal pond, and 5 cattle trough sites. Sixty-five species (43% of all species) were exclusive to stream pools, while 15 species (10% of all species) were exclusive to seasonal ponds. Forty-six species (31% of all species) were habitat generalists, encountered in both pond and stream habitats (see tables 2 and 3). No species were unique to cattle toughs. The remaining 24 species (16% of all species) were only encountered at one site so we could not confidently evaluate their habitat affinity.

The NMS ordination converged on a stable, 2-D solution (final stress = 18.7%, final instability = 0.003; p = 0.02; fig. 2). The ordination explained 81% of the variance in the original species matrix (axis 1: r2 = 0.37; axis 2: r2 = 0.44). Axis 1 was influenced by *Aquarius remigis* (r = –0.55), *Pelocoris* (r = 0.50), and *Hydrophilus insularis* (r = 0.79) among other species while axis 2 was influenced by *Notonecta lobata* (r = –0.75), *Thermonectus marmoratus* (r = –0.69),

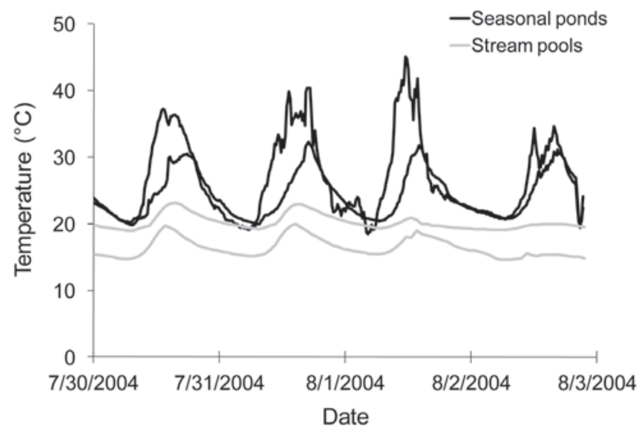

Figure 1—Diurnal water temperature fluctuations recorded at 15-minute intervals in two seasonal ponds (black lines) and two stream pools (grey lines) from 00:00h 30 July 2004 to 21:00h 2 August 2005. Each cross-hatch on the x-axis represents the beginning of that day (00:00h). The lower stream pool line is from North Fork Cave Creek and the upper is from French Joe Canyon. The lower seasonal pond line is from East Willow pond and the upper line is from "Stuck" pond (see table 1).

Desmopachria portmanni (r = –0.65), *Gyrinus plicifer* (r = –0.64), and *Corisella edulis* (r = 0.71), among others. Axis 2 values were positively associated with fine substrates (r = 0.75) and negatively associated with bedrock substrates (r = –0.53). Latitude was negatively associated with axis 1 (r = –0.45) and temperature was positively associated with axis 2 values (r = 0.42); however, both of these factors appear to be associated with assemblage gradients described in part by both axes (i.e., the vectors are diagonal to axes 1 and 2: fig. 2).

Most stream pool sites formed a tightly clustered group in the NMS graph (fig. 2). Stream pools located on the extreme southwestern margin of the MSI (Mazatán, Nacapule and Alacrán; table 1) had higher axis 1 scores than other streams pools, but were within the range of axis 2 scores for all other streams. Seasonal pond assemblages varied widely, while cattle trough assemblages showed less variability and were closer in composition to stream pool assemblages. MRPP analyses confirmed the distinctness of stream pool, seasonal pond, and cattle trough assemblages (A = 0.29, p < 0.0001).

Discussion

Despite superficial similarities in habitat characteristics, stream pools and seasonal ponds in the MSI support distinct aquatic beetle and bug assemblages. Of the 150 species identified in this study, 80 species were exclusive to either stream pools or seasonal ponds. Sixty-five of these species were only found in the perennial stream pools, while the remaining 15 were exclusively found in the environmentally variable seasonal ponds (tables 2 and 3). The relatively low number of pond exclusive species may be due to harsh environmental conditions in ponds, but could also be due to the low number of ponds sampled (n = 7) when compared with streams (n = 25). Fairy shrimp and other non-insect invertebrates are often specialists in seasonal ponds (King and others 1996), so a broader taxonomic consideration of our study ponds and pools would likely only increase the community distinction among these three habitat types.

Temperature has been identified as a major factor in aquatic insect species distributions in numerous studies (e.g. Hawkins and

Table 2— Coleoptera species identified from Madrean Sky Island region ponds and stream pools with their habitat affinities. Only common taxa (occurrences in >10% of sites) are listed in order of percentage of sites at which they were found (%). Generalist species were found in at least two of the three habitat types sampled.

Stream pool exclusive	%	Seasonal pond exclusive	%	Generalist species	%
Thermonectus marmoratus	81	*Berosus stylifer*	57	*Laccophilus fasciatus*	80
Gyrinus plicifer	73	*Eretes sticticus*	29	*Berosus salvini*	66
Dineutus sublineatus	69	*Berosus* cf. *infuscatus*	29	*Rhantus gutticollis gutticollis*	61
Rhantus atricolor	62	*Berosus* cf. *miles*	29	*Stictotarsus striatellus*	51
Sanfilippodytes	62	*Neoclypeodytes* sp.	14	*Tropisternus ellipticus*	51
Stictotarsus corvinus	62	*Berosus peregrinus*	14	*Stictotarsus aequinoctialis*	49
Berosus rugulosus	58			*Tropisternus lateralis*	49
Rhantus gutticollis mexicanus	38			*Desmopachria portmanni*	46
Postelichus immsi	35			*Thermonectus nigrofasciatus*	44
Helichus triangularis	31			*Peltodytes dispersus*	41
Hydraena sp.	31			*Berosus moerens*	41
Hydrochus sp.	31			*Hygrotus* sp.	39
Stictotarsus roffi	27			*Laccophilus horni*	39
Helichus suturalis	23			*Liodessus obscurellus*	37
Neoclypeodytes fryii	23			*Agabus* sp.	34
Laccobius sp.	23			*Desmopachria mexicana*	34
Dytiscus habilis	19			*Laccophilus maculosus*	29
Anacaena limbata	19			*Enochrus* sp.	27
Laccophilus oscillator	15			*Hydrophilus insularis*	22
Elmidae sp.	15			*Berosus punctatissimus*	17
Liodessus sp.	12			*Laccophilus mexicanus*	15
				Neoclypeodytes cinctellus	15
				Helophorus sp.	15
				Laccophilus pictus	12

Table 3—*Hemiptera* species identified from Madrean Sky Island region ponds and stream pools with their habitat affinities. Only common taxa (occurrences in >10% of habitats) are listed in order of percentage of sites at which they were found (%).Generalist species were found in at least two of the three habitat types sampled.

Stream pool exclusive	%	Seasonal pond exclusive	%	Generalist species	%
Abedus herberti	77	*Corisella edulis*	100	*Microvelia* sp.	76
Ambrysus woodburyi	35	*Gerris* sp.	43	*Graptocorixa abdominalis*	71
Trepobates becki	31	*Notonecta unifasciata*	43	*Notonecta lobata*	63
Pelocoris sp.	31	*Belostoma flumineum*	29	*Ranatra quadridentata*	59
Notonecta kirbyi	23	*Corisella tarsalis*	14	*Aquarius remigis*	54
Platyvelia beameri	23	*Corisella* sp.	14	*Buenoa arizonis*	44
Rhagovelia varipes	23	*Ramphocorixa acuminata*	14	*Graptocorixa serrulata*	39
Hydrometra sp.	19	*Notonecta undulata*	14	*Lethocerus medius*	34
Curicta pronotata	19	*Salda* sp.	14	*Buenoa arida*	32
Graptocorixa gerhardi	12			*Buenoa scimitra*	29
Neocorixa snowi	12			*Morphocorixa lundbladi*	20
Gelastocoris sp.	12			*Notonecta hoffmani*	17

others 1997). Indeed, we found that ponds had significantly higher temperatures than stream pools and also that increased temperature was associated with the shift from stream pool to seasonal pond assemblage types. Additionally, diurnal variability in temperature appears to be much higher in seasonal ponds (fig. 2), though we did not measure this factor at all sites. Temperature variability may be a more important factor than mean temperature when examining environmental drivers of observed aquatic community differences (Palmer and others 1997). High and variable temperatures can impact aquatic insect respiration and survival of early instars by changing oxygen levels and water density (Williams 2005). As seasonal ponds only occurred below 1200 m and stream pools only occurred above 1200 m, elevation is clearly a confounding factor in this study. Temperature and dissolved oxygen often co-vary with elevation, and we are unable to disentangle the effects of water quality and elevation in this study. We also did not measure nutrient levels, which may be higher in seasonal ponds visited by livestock, and recommend that such measurements be included in future studies.

Local physical habitat characteristics (e.g. substrate, channel morphology) can also strongly influence local aquatic invertebrate assemblages within a given biogeographic region. Sanderson and others (2005) determined that a gradient from silt- to boulder-dominated substrates was the most important physical factor determining stream invertebrate abundances in a northern England river system. Similarly, we identified a gradient in local beetle and true bug assemblages that was strongly associated with a shift from bedrock-dominated to

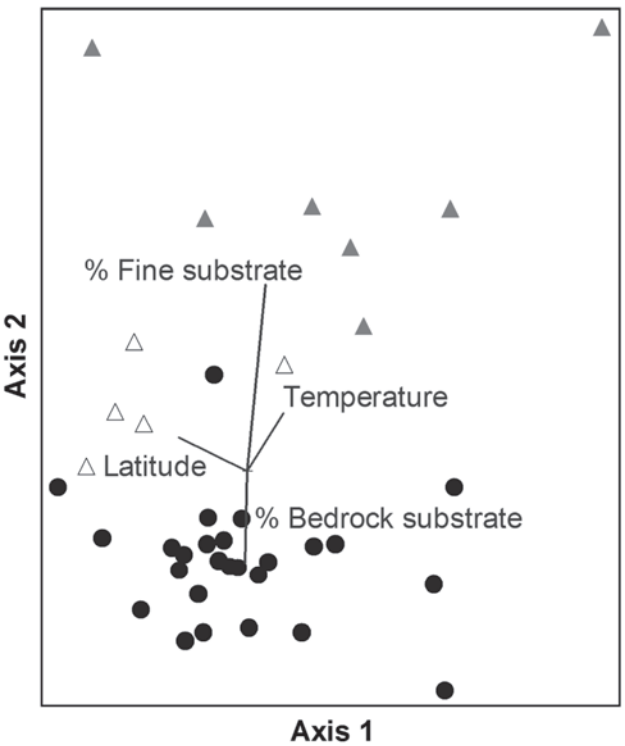

Figure 2—NMS ordination of the beetle and true bug assemblages from 26 stream pool sites (black circles), 7 seasonal valley pond sites (open triangle) and 5 constructed cattle tank sites (grey triangles). Environmental factors with Pearson's correlations greater than 0.4 with either axis are illustrated as vectors. The length of each factor's vector is proportional to that factor's correlation values with the two axes.

fines-dominated substrate across all our study sites and habitat types (NMS axis 2; fig. 2).

Williams (2005) noted that a short hydroperiod may be the most constraining environmental factor for determining the distribution of aquatic organisms. Although we did not measure exact hydroperiod at our study sites, we know that ponds held water for less than 4 months during 2004. The habitat affinities of several species in our study, however, may provide insight into how short hydroperiods (as found in seasonal ponds) could act to constrain MSI beetle and true bug assemblages. Several of the exclusively stream pool species are either flightless (e.g. *Abedus herberti*; Lytle 2000) or have weak dispersal abilities (e.g. *Rhantus atricolor*; R.L. Smith, personal communication), so it is intuitive that these species would be excluded from temporary habitats. Indeed, Zimmerman and Smith (1975) noted that *R. atricolor* collections are almost exclusively from perennial mountain streams. In contrast, many pond exclusive species are capable of far and frequent dispersal (e.g. *Corisella edulis*: Hungerford 1948) and may benefit from reduced competition and predation in harsh seasonal environments (Wellborn and others 1996). The pond exclusive dytiscid beetle *Eretes sticticus* appears to be especially well adapted to seasonal habitats. It has an extremely rapid larval development time (15 days: Kingsley 1985) and has been collected almost exclusively from temporary desert ponds (Larson and others 2000).

Beetle and true bug assemblages in cattle troughs were intermediate between those from stream pools and seasonal ponds and were more similar to one another than seasonal pond assemblages (fig. 2). Aquatic insects must colonize these habitats after the troughs are constructed, creating a strong dispersal filter that could lead to more self-similar local assemblages. Since cattle troughs are filled by spring or well water, they generally contain water year-round. This longer hydroperiod may favor a distinct group of species with longer development times but tolerant of occasional dry periods (see Williams 2005) when a pipe breaks or the trough's source fails. Despite the apparent preference for human-constructed habitats by a number of dytiscid beetle species (Larson and others 2000) we did not find any species exclusive to cattle troughs.

Though widely distributed across a large geographic area (~30,000 km2), most stream pool assemblages were more similar to one another than were seasonal pond assemblages (fig. 2). Important environmental factors, such as relatively stable temperatures (fig. 1) and reliable perennial water, may allow longer-lived predators with weak dispersal abilities (e.g. top predator *Abedus herberti*: flightless, lifespan up to 3 years; Lytle 2000; Lytle and Bogan unpublished data) to persist in perennial stream pools but not in seasonal ponds. These predators, among other species ill-suited to seasonal pond conditions but highly competitive in perennial habitats, may contribute to the uniformity of stream pool assemblages by exerting a strong biotic influence on local communities (Wellborn and others 1996).

Much of the variability among stream pool sites was represented by axis 1 in the ordination, which was associated with latitude. Indeed, there appears to be a latitudinal assemblage shift, with some widespread Neartic species (e.g. *Aquarius remigis* and *Rhantus gutticollis*) being characteristic of northern sites while taxa with Neotropical centers of distribution were characteristic of southern sites (e.g. *Pelocoris, Hydrophilus insularis*). The MSI are often described as a meeting place for Nearctic and Neotropical species, so it is not surprising that we detected a north-south gradient in assemblages while looking over a large geographic range (28°-32° latitude). We did not sample enough seasonal ponds in the southern part of the MSI (i.e. south of 31° latitude) to assess latitudinal gradients in pond assemblages.

While the results from this current study suggest that hydroperiod is an influential factor in determining lentic beetle and true bug assemblages across the MSI, hydroperiod may be even more important in lotic systems. In a recent study, we compared lotic aquatic invertebrate community structure in a network of perennial and intermittent stream reaches in the Huachuca Mountains (Bogan and others, in review). We found that intermittent reaches were species-poor when compared to perennial reaches, but that these species-poor communities were composed mostly of unique species with adaptations to life in temporary water and were not found in perennial reaches. The short flow duration of intermittent reaches (<4 months, often dry for 1 or more years at a time) strongly favors species with rapid development times and dormant egg or larval stages, such as winter stoneflies, blackflies, and non-biting midges. Thus, despite being species-poor relative to neighboring perennial reaches, intermittent stream reaches are important contributors to regional species richness.

We hope that the results of these studies will help inform aquatic conservation planning in the MSI region. Temporary waters and small perennial streams are often overlooked during conservation planning, while focus is placed on larger streams or perennial lakes. We identified a number of aquatic species in the MSI, however, that appear to prefer or be restricted to seasonal habitats. Many geographically restricted, endemic invertebrate species are found in seasonal ponds in other parts of the southwestern United States (e.g. King and others 1996). With sufficient taxonomic studies, new invertebrate species endemic to MSI intermittent streams and seasonal ponds would likely be described. Additionally, numerous other species seem to require the stable perennial conditions associated with some streams. These species are increasingly threatened by drying climate and contracting or vanishing perennial stream habitat across the MSI. We are already witnessing stream-scale extirpations of important taxa (e.g. the top predator *Abedus herberti*) due to unprecedented drying of perennial habitats and increasing isolation of remaining perennial habitats (Bogan and Lytle 2011). In order to preserve local endemic species and regional aquatic diversity, aquatic conservation planning in the MSI should include a wide range of habitat types, from perennial to ephemeral and from lotic to lentic.

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