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ORIGINAL PAPER

Biogeography and conservation of aquatic fauna in spring-fed tropical canyons of the southern Sonoran Desert, Mexico

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Abstract In arid regions, spring-fed habitats are frequently the only year-round source of surface water and are essential habitats for aquatic organisms and primary water sources for terrestrial animals and human settlements. While these habitats have been relatively well-studied in some regions, those of the southern Sonoran Desert have received little attention. In 2008 and 2009, we documented the biodiversity of aquatic animals at 19 sites across three arid mountain ranges in Sonora, Mexico, characterized macrohabitat types, examined seasonal variation in aquatic invertebrate communities, and explored the effects of an exotic fish (tilapia) on native communities. We documented >220 aquatic animal species, including several new species and range extensions for others. Macrohabitat type (oasis, tinaja, riffle, and seep) was more important than geographic location in structuring aquatic invertebrate communities at the scale of our study area ($\sim$9,000 km^2). We found

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little evidence of predictable seasonal variation in invertebrate communities, despite dramatic hurricane-induced flooding. Aquatic vertebrates were not diverse across the study region (4 amphibian species and 2 species each of fishes and reptiles), but were often locally abundant. Presence of non-native tilapia at one site was associated with reduced abundances of native leopard frogs and reduced richness and density of native aquatic invertebrates. The most pressing aquatic habitat conservation concerns in the region, as in other deserts, are groundwater withdrawal, unmanaged recreational visitation, and the introduction of exotic species. Spring-fed habitats around the world have been called hotspots of freshwater biodiversity, and those of the Sonoran Desert are no exception.

Keywords Arid-land springs · Biodiversity · Aquatic invertebrates · Exotic species · Oasis · Macrohabitat types

Introduction

Though freshwater habitats comprise less than 1 % of land cover on Earth, they support almost six percent of all described species (Dudgeon et al. 2006), making them much more important sources of biodiversity than their spatial extent would suggest. Despite recognition of the disproportionate role that these habitats play in supporting global biodiversity, extinction rates of freshwater fauna are up to five times higher than those of terrestrial taxa (Ricciardi and Rasmussen 1999). While lakes and rivers are the dominant freshwater habitat types, springs and small spring-fed aquatic habitats are globally-recognized biodiversity hotspots that support unique assemblages of aquatic species in Europe (Cantonati et al. 2012), Africa (Suhling et al. 2006), Australia (Fensham et al. 2011), New Zealand (Collier and Smith 2006), and North America (Stevens and Meretsky 2008).

In desert regions, spring-fed habitats are frequently the only year-round source of surface water and are essential habitats for aquatic organisms as well as primary water sources for terrestrial animals and human settlements (Shepard 1993; Unmack and Minckley 2008; Fensham et al. 2011). Anthropogenic development of desert springs can be at odds with the conservation of biodiversity, especially when desert spring species have limited distributions. For example, in North America the greatest concentration of endemic aquatic species occurs around desert springs (Stevens and Meretsky 2008) and many species living in those habitats are critically endangered by water resource development (Sada and Vinyard 2002; Deacon et al. 2007). Some species endemic to desert springs have gone extinct in the wild before being described (Hershler et al. 2011). Because of these conservation concerns, desert spring habitats have received significant study in many regions recently, including Australia (Box et al. 2008; Fensham et al. 2011), Africa (Suhling et al. 2006; Martens et al. 2010), and the Great Basin and Chihuahuan Deserts of North America (Sada and Vinyard 2002; Stevens and Meretsky 2008).

While spring-fed aquatic habitats have been relatively well-studied in most North American deserts, those of the southern Sonoran Desert have received little scientific attention. Despite having average annual rainfall totals as low as 200 mm, spring-fed aquatic habitats can be found in many canyons of southern Sonoran Desert mountain ranges (sierras). These desert- and canyon-bounded freshwater habitats are small patches of aquatic habitat, often with lush relictual tropical vegetation, isolated from one another by formidable volcanic cliffs and vast expanses of Sonoran Desert scrub vegetation (Felger 1999). These sierras act as ecological ‘islands,’ rising above dry desert lowlands and isolated from other sierras with similar freshwater habitats by 20 or more kilometers. Such a physical setting predicts that these freshwater habitats have great potential for increased endemism of the aquatic organisms they support (Cox and Moore 1993).

The isolation and small sizes of these desert-bounded tropical canyons and their aquatic habitats also make them highly vulnerable to anthropogenic disturbance. In addition to water development, desert springs face threats from unmanaged human visitation (Hadwen et al. 2012) and the introduction of exotic (non-native) species (Sada and Vinyard 2002; Fensham et al. 2011; Ruiz-Campos et al. 2014). Some spring-fed canyons in the southern Sonoran desert have become popular tourist destinations, resulting in trash, graffiti, vandalism, increased wildfires and penetration of fragile habitat by off-road vehicles (Carrizales 2007). Introduced exotic fishes can disrupt aquatic food-web dynamics and potentially alter the community structure of native vertebrates and invertebrates in both lotic and lentic ecosystems (Maezono et al. 2005; Townsend 1996). In Mexico, non-native tilapia fishes (Cichlidae) are widely used for aquaculture and have subsequently invaded or been intentionally introduced into many natural aquatic habitats, including those in the Sonoran Desert (Miller et al. 2006; Ruiz-Campos et al. 2014).

In this study, we identified spring-fed flowing and standing water habitats in canyons of the sierras El Aguaje, Santa Úrsula, and Bacatete in Sonora, Mexico, and conducted an inventory of their aquatic fauna. Our goal was to create a baseline dataset for use in biodiversity conservation planning in the southern Sonoran Desert. We conducted surveys for aquatic invertebrates and vertebrates at 19 sites during 2008 and 2009. We identified macrohabitat types and measured water quality conditions at each site and then related these measurements to aquatic animal community composition. Additionally, we surveyed one canyon over multiple seasons in 2008 and 2009 to determine if local aquatic invertebrate diversity and community composition varied seasonally. Finally, we examined the potential impacts of tilapia on native invertebrate communities by comparing invertebrate diversity, density, and community composition in pools with and without tilapia.

Methods

Physical habitat

We surveyed nearly all accessible sites with aquatic habitat in the Sierra El Aguaje, including eight sites in 2008 and seven additional sites in 2009. Additionally, we surveyed two sites each from the sierras Santa Úrsula and Bacatete in 2009 (Fig. 1; also see Table 1), representing about one-third of the known water sources in those ranges. We visited study sites in December and late-March/early-April, but biological surveys were limited to March/April to coincide with the dry season, ensuring that surveys occurred in perennial, spring-fed reaches. We classified four different types of aquatic macrohabitats from these 19 sites: (1) oasis, (2) tinaja, (3) seep, or (4) riffle (Fig. 2). Oasis macrohabitats were large, deep pools surrounded by abundant vegetation and canopy cover such as native palms and/or fig trees, often with complex underwater structure consisting of tree roots and aquatic vegetation. Tinajas, in contrast, were midsize-to-large open pools of water, often located on actively-scoured portions of stream beds, characterized by little or no riparian cover. Seeps were areas of flowing shallow (<1 cm depth) water arising from cracks in faulted bedrock. Riffles, the rarest macrohabitat type in our study, were areas of deeper (1–4 cm depth), flowing water. During site visits, we identified aquatic macrohabitat types present, estimated wetted surface area, measured water temperature, pH and conductivity, and collected the biological data described below.

Aquatic animal communities

We employed quantitative and qualitative collecting techniques in assessing aquatic invertebrate community structure. Because communities often exhibit strong compositional gradients in regard to macrohabitat, we stratified sampling techniques by macrohabitat type (oases, tinajas, riffles, and seeps). Oases and tinajas were sampled with a D-net (0.5 mm mesh) using a timed-sweep method (Bogan and Lytle 2007). Large macrohabitats (>25 m^2 surface area) were sampled by a combination of timed-sweep and searching of unique habitat features (e.g., submerged tree roots, vertical waterfalls) for target organisms (e.g., sponges, aquatic moth larvae). Riffles were too shallow to sample with a D-net or Surber sampler, we thus used a 10-cm-wide aquarium net (0.25 mm mesh). We physically disturbed a 500 cm^2 area of riffle substrate and collected dislodged invertebrates in the aquarium net placed downstream. Seeps were sampled qualitatively by collecting invertebrates in whatever manner the habitat's characteristics allowed (e.g., scraping algal films, excavating substrate). Additionally, we collected emergent adult aquatic insects at two sites using UV-light traps placed at water's edge for 30 min after dusk. All invertebrates were preserved in 95 % ethanol for transport and subsequent identification. Most of these samples were enumerated and identified at the Universidad Estatal de Sonora, Hermosillo, Mexico, with some specimens sent to experts to confirm species determinations. Representative specimens of invertebrate taxa are housed at the Universidad Estatal de Sonora, Hermosillo.

Amphibians and aquatic reptiles were sought by visual-encounter surveys during warm, daylight hours for 30 min at each site. Additionally, we searched for larval amphibians (tadpoles) during timed-sweep sampling of pools. Fishes were sought using minnow-seine nets and D-nets. Most pools were open and had relatively clear water, thus most fishes also were easily detected visually. Representative specimens of fishes are housed at DICTUS, Universidad de Sonora, Hermosillo.

Seasonal changes in invertebrate communities

Because aquatic invertebrate communities in neighboring bioregions exhibit strong seasonal variability (Bogan and Lytle 2007), we wanted to see if similar seasonal variation occurred in these spring-fed desert canyons. To explore the potential for seasonal variation, we surveyed riffle macrohabitat at one site (Nacapule) during multiple months (Apr, Jun, Aug, Nov, Dec) in 2008 and 2009, including perennial riffles in the primary study reach and intermittent riffles in three adjacent reaches that flowed only after heavy precipitation events. These intermittent reaches included one 500 m above and one 500 m below the perennial site, and one 300 m up a small tributary that joins the perennial site at its lower end.

Effects of tilapia on native species

At another site, Rancho Santa Úrsula, we used a natural break in the distribution of a non-native tilapia fish (cichliade: *Tilapia* sp.), to explore the effects of tilapia on native aquatic communities. Tilapia were historically introduced to a stream reach below a small, seasonal waterfall at the site, and probably had been reproducing in that reach for several years (L.T.F. and A.V.-R., personal observations). However, tilapia apparently have been unable to

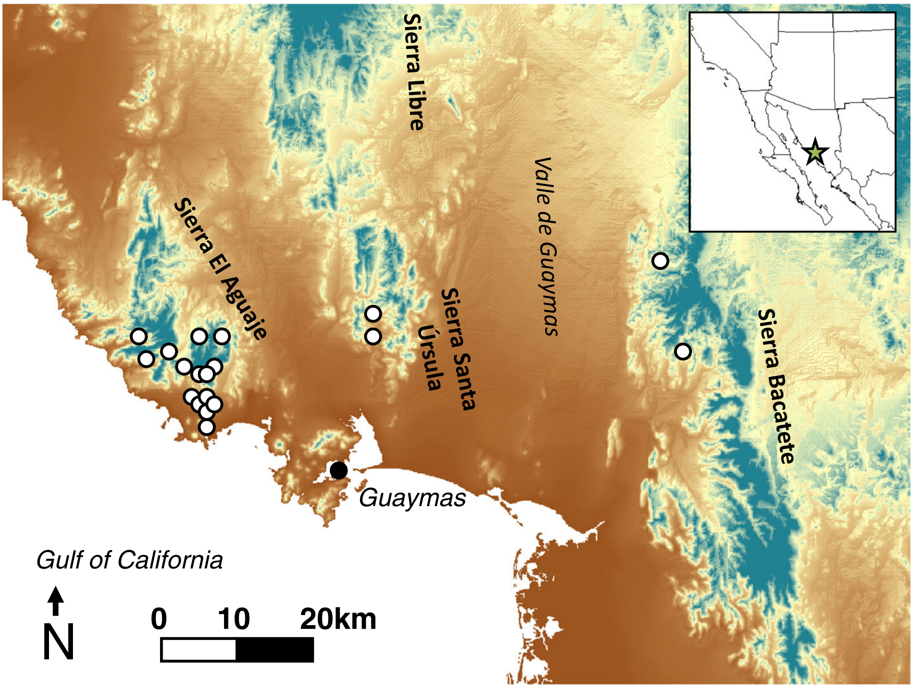


Fig. 1 Map of the study region in the southern Sonoran Desert with the 19 study sites in the sierras El Aguaje, Santa Úrsula, and Bacatete indicated by white circles (see Table 1 for place names and precise coordinates)

colonize the reach above that waterfall, thus tinajas in that reach have remained fishless. We compared aquatic invertebrate abundance, diversity, and community composition among six tinajas in a 500 m reach at Rancho Santa Úrsula, including three tinajas with tilapia below the waterfall and three tilapia-free tinajas located approximately 150 m upstream of the waterfall. Tinajas with and without tilapia had similar water quality and physical habitat characteristics [means of tilapia tinajas: 13 m^2 area, 0.7 m deep, 20 °C, 315 µS, 6.75 pH; means of tilapia-free tinajas: 18 m^2 area, 1 m deep, 23 °C, 320 µS, 7.0 pH].

Statistical analysis

Invertebrate community composition across sites and macrohabitats was examined with non-metric multidimensional scaling (NMS), with Sorensen distance as the community dissimilarity measure. Because collection techniques varied between macrohabitats, absolute numbers of individuals varied greatly between samples; thus abundance data were relativized by site prior to ordination analyses. This relativization ensured that the ordination focused on comparing relative abundances of species between sites rather than on absolute abundances (McCune and Grace 2002). We used multi-response permutation procedure (MRPP; Mielke and Berry 2001) to test for significant compositional differences among the different macrohabitat types, the three different sierras, and tinajas with and without tilapia. When significant compositional differences were found, we used indicator species analysis (ISA; Dufrêne and Legendre 1997) to identify which species were associated with each group. We performed all community analyses using the program PC-ORD (Version 5, MJM Software,

Table 1 Physical and biological characteristics of the 19 sites surveyed during 2008 and 2009 (macrohabitat codes: *O* oasis, *T* tinaja, *R* riffle, *S* seep). Place names in quotation marks are not named on regional/local maps or by local ranchers, thus we use names previously coined by one of us (LF) and other local residents or those derived from characteristics observed during site visits

Site	Invertebrate richness	Habitat area (m^2)	Macrohabitats present	Temp. (°C)	pH	Cond. (μS)	Frog(s)	Fish(es)	UTM N	UTM E
Sierra El Aguaje										
Nacapule	121	350	O, T, R, S	23	6.25	330	X		3099031	494501
La Navaja[1]	108	445	O, T, R, S	21	6.5	309	X		3099807	489726
"El Segundo"	78	120	T, S	19	6.5	431	X		3098816	492656
La Balandrona	77	340	T, R	22	6.5	322	X	X[2]	3103870	492888
Las Barajitas	63	110	O, T, R	20	6.25	310	X		3103035	484972
"Arroyo del Esterito"	63	115	T	19	6.25	580	X		3093163	494068
Las Pirinolas	59	90	O, T	24	6.75	335	X	X[2]	3104063	495241
"El Caballo"	58	180	O	18	7	828		X[3,4]	3096870	491567
"Tinajas Altas"	50	39	T	21	6.5	343			3097050	491742
"Escondido"	50	176	T	21	6.25	140	X		3095735	492737
"Las Abejas"	36	10	T	25	8	658			3095973	492015
"Keyhole"	28	36	T	24	6.5	361			3097808	491438
"Las Vacas"	15	12	S	24	6.25	342			3097771	493535
Los Anegados	13	13	S	13	6.5	830			3100786	486562
Robinson	10	8	S	25	6.5	343			3101319	489165
Sierra Bacatete										
Rancho Bacatete	82	1,200	O, T, R	21	7	584	X	X[3]	3104908	562986
Los Pilares	39	500	T	24	7.5	585		X[3]	3116437	552465
Sierra Santa Úrsula										
Rancho Santa Úrsula	93	620	O, T, R	24	7	310	X	X[2,3]	3108015	515319

Table 1 continued

Site	Invertebrate richness	Habitat area (m^2)	Macrohabitats present	Temp. (°C)	pH	Cond. (µS)	Frog(s)	Fish(es)	UTM N	UTM E
Los Pelones	36	400	T	23	7	246		X[2,3]	3109517	516099

[1] Appearing as "Alacrán" on some maps and named as such in at least one publication (Pfeiler and Markow, 2008). However, that name is in error according to long-term local ranchers (e.g., Delfino Magallanes-Molina of Rancho Palo Fierro)

[2] Native freshwater fish species

[3] Introduced exotic tilapia

[4] Tilapia not observed at this site in 2008 or 2009, but present in 2011

Fig. 2 Examples of aquatic macrohabitat types we classified in the southern Sonoran Desert: **a** oasis, **b** tinaja, **c** seep, and **d** riffle. The cliff face in (**c**) is approximately 8 m high. Note the mechanical pencil for scale in (**d**)

Gleneden Beach, Oregon).We used linear regression to examine the relationship between taxon richness and wetted habitat area across the 19 study sites and a Kruskal–Wallis test to assess differences in average taxon richness across the four macrohabitat types. Finally, we compared invertebrate taxon richness and sample density between the three tilapia-containing and three tilapia-free tinajas with standard *t* tests.

Results

Physical habitat

Tinajas were the most commonly encountered macrohabitat type across the study region, followed by oases, seeps, and riffles (Table 1). Total surface area of wetted habitat at each of the 19 sites ranged from 8 to 1,200 m^2 (Table 1). At several sites, there was evidence of seasonal expansion of wetted habitat. For example, between 2008 and 2009 total wetted habitat at Nacapule ranged from a low of 350 m^2 (Apr. 2008) to a high of 900 m^2 (Aug. 2008). Additionally, Arroyo del Esterito contained water during the rainy season and early dry season (Sep–Mar.), but was dry by mid-April in 2008 and 2009; this was the only non-perennial site we surveyed. Water temperature, conductivity, and pH were similar at most sites (temperature ~22 °C; pH 6.5; conductivity 310–350 μS; Table 1). A few sites had higher conductivity (580–830 μS) though, including those in the Sierra Bacatete, indicating either a distinct aquifer source or concentrated waters resulting from habitat contraction. One Sierra El Aguaje site (Escondido) had tinajas with low conductivities (140 μS), suggesting that surface runoff contributed more to this site than groundwater. Overall, though, the high regional similarity of water quality conditions suggests that most aquatic habitats in the region are dependent on groundwater.

Aquatic animal communities

We documented 210 invertebrate taxa across the 19 survey sites during 2008 and 2009. Taxa richness for individual sites ranged from 10 to 123 taxa (Table 1), with a mean of 58 taxa per site. We found 187 taxa at the 15 sites in the Sierra El Aguaje, 103 invertebrate taxa at the two sites in the Sierra Santa Úrsula, and 99 invertebrate taxa at the two sites in the Sierra Bacatete (see Table 4 in Appendix). These taxa included four undescribed caddisfly species collected via UV-light traps as well as several other taxa whose distributions were extended significantly northward by our surveys (Online Supplementary materials).

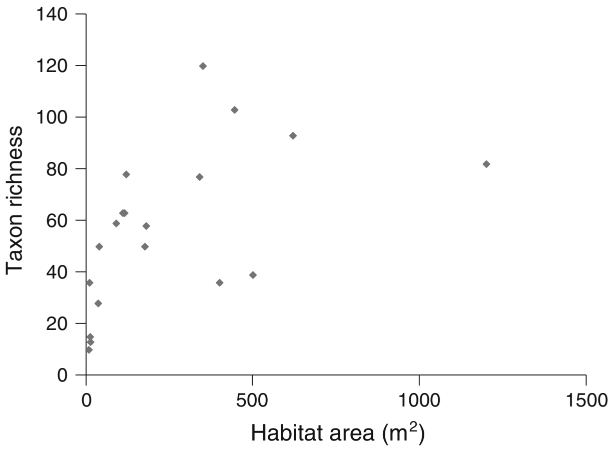
In general, invertebrate taxon richness increased with wetted habitat area (Fig. 3), though area explained less than a third of the variability in taxon richness (linear regression analysis: $F = 6.57$, $p = 0.02$, $R^2 = 0.28$). Taxon richness differed significantly across the four macrohabitat types ($H = 21.34$, $p < 0.001$). Oasis and tinaja macrohabitats supported the greatest number of taxa, while riffles supported fewer, and seeps supported the least (Fig. 4). Each macrohabitat type, however, contributed unique taxa to the regional fauna. Riffle samples supported the highest percentage of taxa that were regionally unique (22 %), and the riffle habitat at Nacapule, sampled repeatedly in 2008 and 2009, supported ten taxa that were not encountered elsewhere in our samples: *Microcylloepus inequalis, Heterelmis glabra* and *Neoelmis* sp. (Coleoptera: Elmidae); *Farrodes* sp. (Ephemeroptera: Leptophlebiidae); *Stempellina* sp. and *Stempellinella* sp. (Diptera: Chironomidae); *Pericoma* sp. (Diptera: Psychodidae); cf. *Dicranota* sp. (Diptera: Tipulidae); *Atractides* sp. and *Spechon* sp. (Hydracarina).

NMS ordination analyses of the invertebrate community data converged on a two-dimensional solution (stress = 0.21; final instability = 0.0001; $p = 0.004$; Fig. 5) that explained 56 % of the variability in the original distance matrix. None of the measured environmental variables were significantly associated with NMS axes (all r values <0.3). The ordination plot illustrates that most macrohabitat types occupied distinct regions of species-space, with only oasis and tinaja communities overlapping (Fig. 6). MRPP analysis indicated statistically significant compositional differences among macrohabitat groups ($A = 0.08$, $p < 0.00001$), but not among the three sierras (MRPP by mountain range: $A = 0.01$, $p = 0.06$). Each macrohabitat type had at least three significant ($p < 0.05$) indicator species as determined by ISA (Table 2), with oases having the greatest diversity of indicator taxa and seeps having the least.

Though oasis and tinaja samples largely overlapped in the NMS plot, results of the ISA suggest some community distinction between these two habitats. The tinaja indicator taxa are all regionally widespread and common (Bogan 2012), whereas many of the oasis indicator species are either regionally rare Neotropical species (e.g., *Beardius* sp., Diptera: Chironomidae) or potentially endemic species (e.g., *Laccophilus* sp. cf. *horni,* Coleoptera: Dytiscidae). While seeps supported relatively species-poor communities, some seep indicator species (e.g., *Culicoides* sp., Diptera: Ceratopogonidae; *Apedilum* sp., Diptera: Chironomidae) were only found in that habitat.

We found nine species of aquatic vertebrates across the 19 study sites, including four amphibians, one snake, one turtle, and three freshwater fish species, with species richness ranging from 0 to 4 species per site (see Table 5 in Appendix). Northwest Mexico leopard frog (*Lithobates magnaocularis*) was the most commonly encountered aquatic vertebrate and was often quite abundant (10 to 100 + adults observed). At Rancho Santa Úrsula, leopard frog adults and tadpoles were encountered nearly exclusively in pools without the exotic fish tilapia; only one large adult was found in a pool containing tilapia. Other amphibian species were found at four or fewer sites each (see Table 5 in Appendix) and were never abundant.

Fig. 3 Invertebrate taxon richness for each of the 19 study sites as a function of total wetted habitat area at each site (including all four macrohabitat types)



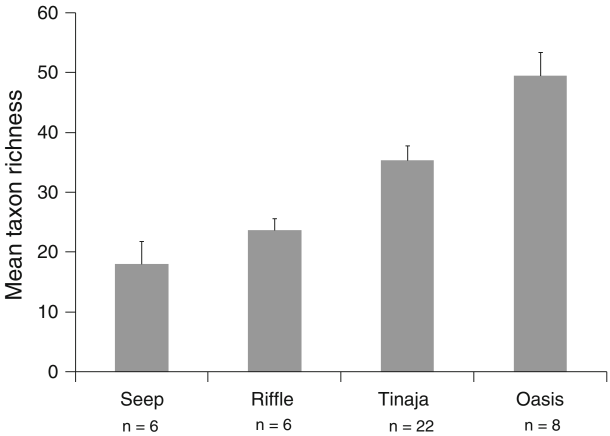


Fig. 4 Mean invertebrate taxon richness by macrohabitat type with error bars indicating one standard error

The black-necked garter snake (*Thamnophis cyrtopsis*) was found at two sites and the Sonoran mud turtle (*Kinosternon sonoriense*) was found at one site. Freshwater fishes were relatively rare across the region, but were locally abundant. Desert chub (*Gila eremica*) was abundant at two sites in the Sierra El Aguaje, but was absent elsewhere in the region. Yaqui topminnow (*Poeciliopsis occidentalis sonoriensis*) was abundant at two sites in the Sierra Santa Úrsula. Large populations of tilapia were present at all sites in the sierras Santa Úrsula and Bacatate. We did not find tilapia at any site in the Sierra El Aguaje during 2008 or 2009 surveys, but in 2011 we found a newly established population at El Caballo. On 19 February and 13 March 2011 only one or two large tilapia were seen there, but on 22 March 2011 we saw numerous individuals, both large and small, suggesting that either clandestine stocking was continuing or tilapia were already reproducing at this site.

Seasonal changes in invertebrate communities

Aquatic invertebrate taxon richness and community composition in the riffle samples from Nacapule did not vary predictably by season or sampling location (Figs. 6, 7). Despite

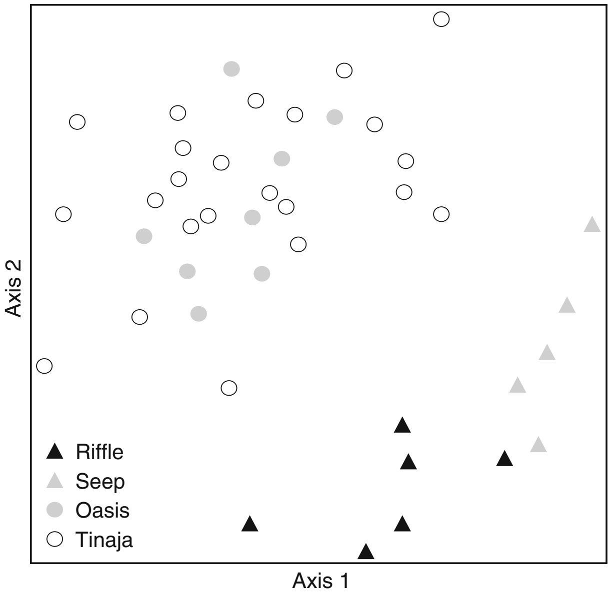


Fig. 5 Two-dimensional non-metric multidimensional ordination of all aquatic invertebrate community samples from the sierras El Aguaje, Santa Úrsula, and Bacatete. Samples are coded by macrohabitat identity

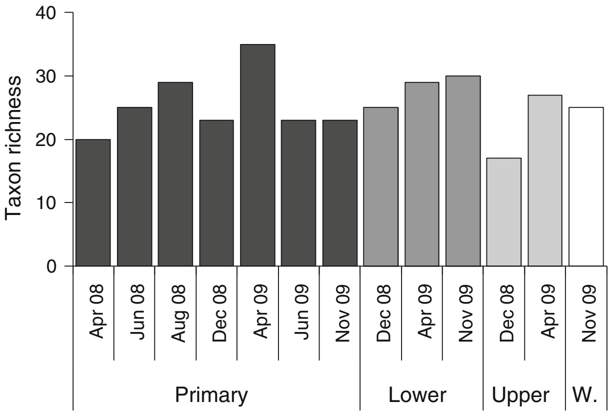


Fig. 6 Invertebrate species richness from riffles at the perennial (*primary*) and intermittent sampling reaches of Nacapule over multiple sampling periods during 2008 and 2009. *W* signifies the West branch of Nacapule. See text for precise locations of the intermittent *Lower*, *Upper* and *West branch* sites

large changes in flow, water level, and habitat structure following hurricane-induced flooding in early September 2009, Nacapule riffle communities exhibited as much variability between local sampling locations on a given date as between sampling events over two years (NMS stress = 0.14, final instability < 0.0001, $p = 0.01$, cumulative $R^2 = 0.79$; Fig. 7). Following monsoon and hurricane-edge rains in October 2008, both the lower and upper portions of Nacapule contained flowing water. The lower site was quickly colonized by species from the primary site; the NMS plot demonstrates that they initially supported similar communities. The upper site, however, was distinct from the others and

Table 2 Aquatic invertebrate indicator taxa for the four macrohabitat types including indicator values (IV) and significance (*p*)

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

was not colonized by many of the taxa for which Nacapule is unique (e.g., three genera of riffle beetles). Instead, the upper site supported widespread opportunistic species, such as the blackfly *Simulium* (Diptera: Simuliidae).

Effects of tilapia on native species

At Rancho Santa Úrsula, tilapia-free tinajas supported significantly more invertebrate taxa than tinajas with tilapia ($t = -2.55$, $p = 0.031$; Fig. 8a). Invertebrate sample densities were nearly 10 times higher in tilapia-free tinajas than in those with tilapia ($t = -2.20$, $p = 0.046$; Fig. 8b). Additionally, MRPP analysis revealed that tilapia-free tinajas supported distinct invertebrate communities from those with tilapia (A value = 0.397, $p = 0.02$). Given the small sample sizes, it was not possible to perform an ISA on these data that yielded *p* values lower than 0.098. The indicator values (IV) of this analysis, however, remain useful for looking at faithfulness and exclusivity of a species to a group. We identified nine species which were completely faithful and exclusive to tilapia-free pools (IV = 100), and an additional three taxa which had nearly perfect scores (Table 3).

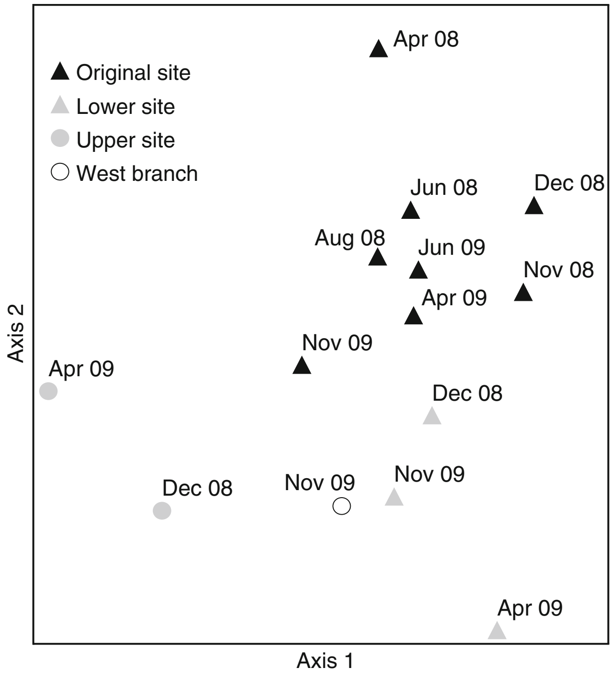


Fig. 7 Two-dimensional non-metric multidimensional ordination of samples collected from Nacapule riffles over multiple sampling periods in 2008 and 2009. See Methods text for precise locations of the four sampling sites. Point labels indicate the month (three letter abbreviation) and year ('08 and'09) of individual samples

The only indicators of tinaja with tilapia were two mayfly genera, *Tricorythodes* (Leptohyphidae) (IV = 100) and *Choroterpes* (Leptophlebiidae) (IV = 78).

Discussion

Spring-fed habitats in the sierras El Aguaje, Santa Úrsula, and Bacatete of the southern Sonoran Desert form a very small part of the landscape, but support more than 220 aquatic animal species. The aquatic fauna includes several Neotropical taxa whose known distributions were expanded into the Sonoran Desert as a result of our research. The average per-site species richness observed was two to four times higher than those reported for spring-fed habitats in the deserts of central and northeastern Australia (Box et al. 2008; Fensham et al. 2011) and the Great Basin (Rader et al. 2012), Mojave (Sada et al. 2005), and Chihuahuan (Dinger et al. 2005) deserts of North America. We also documented at least five undescribed invertebrate species from two of our study sites. Similar studies of isolated desert water bodies of central Australia have also revealed numerous undescribed species (e.g., Box et al. 2008; Murphy et al. 2013). Spring-fed habitats around the world have been called hotspots of freshwater biodiversity (Cantonati et al. 2012), and those of desert regions are no exception.

Effects of habitat characteristics and season on aquatic communities

The rich biotic diversity of these Sonoran Desert habitats is due in part to the variety of macrohabitat types that the region supports. The four macrohabitats we identified (oasis,

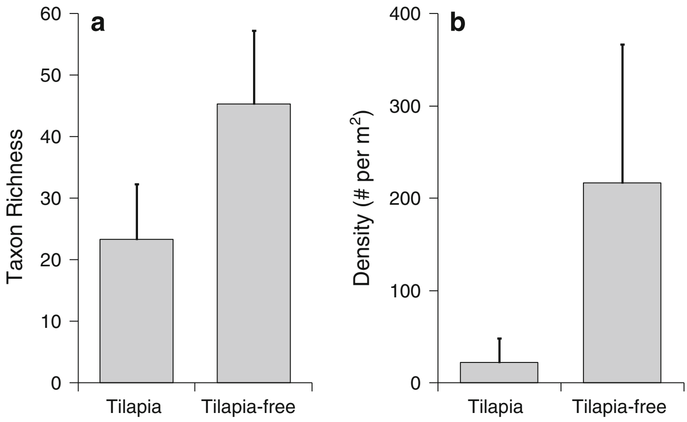


Fig. 8 Differences in taxon richness (**a**) and density (**b**) of aquatic invertebrates between pools with and without tilapia at Rancho Santa Úrsula. *Error bars* represent one standard deviation

Table 3 Aquatic invertebrate indicator taxa for tilapia-free and tilapia-containing tinajas at Rancho Santa Úrsula, including indicator values (IV) and significance (p). The limited sample size ($n = 6$ tinajas) and use of Monte Carlo randomizations for significance tests made 0.098 the lowest p value possible given the data

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

tinaja, riffle, seep) each supported a variety of species, including those unique to a given macrohabitat type. In fact, macrohabitats were more important than geographic location (i.e., mountain range) in structuring local communities at the scale of our study area ($\sim$9,000 km^2). In contrast, Rader et al. (2012) found that aquatic invertebrate communities in Great Basin Desert spring systems were more similar among sites within drainage basins than they were among three macrohabitat types (riffles, lentic wells, shallow marshes) between drainage basins. This difference in local versus regional effects on community structure may be due to the fact that different faunas occur in the Great Basin and Sonoran Deserts or because the Rader et al. (2012) study had a much larger spatial extent ($\sim$60,000 km^2). Though local water quality characteristics can strongly influence community composition in spring-fed systems (Cantonati et al. 2012), we did not find significant correlations between community composition and the physiochemical parameters we measured (e.g., pH, conductivity). Lack of strong correlation between such factors has also been noted for other desert spring systems (Sada et al. 2005; Rader et al. 2012), and may be due to the limited range of variation in water quality parameters across sites which rely on the same regional aquifer.

Total surface area of wetted habitat explained only a small percentage of the variation in invertebrate species richness in our study sites, similar to findings reported from Mojave Desert springs (Sada et al. 2005). However, oases, the largest macrohabitat we identified, did support the highest number of species overall and the highest number of unique taxa. While Sonoran Desert oases in mainland Mexico often are smaller than those typical of the Baja California peninsula (Grismer and McGuire 1993), both provide essential mesic environments in a very arid landscape. These and similar oases in other deserts are habitats for numerous aquatic species, as well as essential sources of shade, forage and drinking water for terrestrial animals such as birds (Rodríguez-Estrella et al. 2005; Jenni-Eiermann et al. 2011), reptiles (Grismer and McGuire 1993; Bogan et al. 2009), and humans (Benqlilou and Bensaid 2013). While seep macrohabitats supported the fewest number of taxa in our study, they did contribute to regional biodiversity by supporting unique taxa, as has been observed in other regions (Collier and Smith 2006). Seeps and similar aquatic macrohabitats (e.g., waterfall rock faces: Rackemann et al. 2013) often are overlooked in aquatic habitat surveys, but should be incorporated into future biodiversity studies.

The diversity and uniqueness of aquatic invertebrates occupying riffles at one of our principal sites, Nacapule, was particularly surprising. The ~ 3 m^2 of shallow riffles there supported more than 72 invertebrate taxa, 10 of which were encountered nowhere else during our study. Because flowing water habitat at Nacapule decreased significantly between the 1960s and 1990s (Felger 1999), the riffle community present there today is likely derived from a much larger historical habitat. Several Nacapule riffle taxa were rare (e.g., *Cheumatopsyche arizonensis*, only 5 individuals collected over 2 years) and are at great risk of local extinction; the wetland whisk-fern *Psilotum nudum*, unknown from elsewhere in the Sonoran Desert, has already been extirpated due to declining flows (Felger 1999). The ten invertebrate species unique to Nacapule's riffles may have once occurred at our other study sites with riffles, but perhaps were extirpated at some point in the past, as all but one of those sites currently have less riffle habitat than Nacapule.

Many lotic taxa unique to Nacapule appear to be unable to take advantage of intermittent habitats upstream from the perennial reach, though they were able to colonize intermittent riffles downstream (Fig. 8). Though these taxa may be threatened by declining flows, they appear to be very resistant to periodic flash floods. Even the extreme flooding from Hurricane Jimena in early September 2009 (730 mm of rain over 36 h) failed to alter the Nacapule riffle community any more than the previous seasonal changes we observed in 2008 and 2009. Similar resilience to extreme flooding has been observed for amphibian populations in desert oases of the Baja California peninsula (Luja and Rodríguez-Estrella 2010a). Overall, we found little evidence of predictable seasonal changes in aquatic invertebrate community composition at Nacapule, which is in sharp contrast to dramatic seasonal changes in such communities documented from the nearby Madrean Sky Islands bioregion (Bogan and Lytle, 2007).

While studies of springs in other desert regions have not statistically tested for differences among communities of distinct macrohabitats, the physical similarity of some macrohabitats among regions may allow for global quantitative comparisons in future studies. For example, the "rockholes" and "discharge springs" of Australian deserts (Box et al. 2008; Fensham et al. 2011) appear to closely resemble the tinajas and oases of the Sonoran Desert. These distant and distinct (perhaps in name only) habitat features may function similarly ecologically. For example, tinajas in our study supported mostly widespread common taxa, and rockholes in Australia similarly were found to support widespread opportunistic dispersers (Fensham et al. 2011). Future studies should explore the similarity of desert aquatic macrohabitat types across the world in order to facilitate global comparisons of the faunas and ecosystems they support.

Distribution of aquatic vertebrates and impacts of non-native tilapia

We did not find a diverse assemblage of aquatic vertebrates in the region, but vertebrates were often locally abundant. Northwest Mexico leopard frog (*Lithobates magnaocularis*), in particular, was abundant at several Sierra El Aguaje sites and at one in the Sierra Santa Úrsula. In a population genetics study, Pfeiler and Markow (2008) found that there was potentially enough genetic distinction to warrant species status for Sierra El Aguaje populations of that frog, although these populations were genetically similar to two populations of conspecifics found ~180 km east of the Sierra El Aguaje. The authors also noted that Sierra El Aguaje frogs were monomorphic in both the control region and 12S rRNA, suggesting extreme population isolation, severe population bottlenecking, or both. High levels of genetic differentiation have also been observed in amphibian populations in isolated oases of the Baja California peninsula (Recuero et al. 2006). More detailed morphological and genetic (e.g., microsatellites) studies of amphibian populations in isolated oases are needed to fully assess their taxonomic status. Additionally, genetic analyses of the two native fish taxa we found, which have even more limited dispersal potential than amphibians, would greatly advance our understanding of the biogeographic history of these isolated populations.

Introductions of tilapia have been associated with changes in native fish community structure and reduced abundances of microcrustaceans in several parts of the world (Vitule et al. 2009). Tilapia have also been widely introduced into Sonoran Desert oases of the Baja California peninsula and parts of northwestern Sonora (Ruiz-Campos et al. 2014), where they are negatively impacting native fish populations (Andreu-Soler and Ruiz-Campos 2013). We found that tilapia were associated with reduced abundances and species richness of aquatic invertebrates at one of our sites, and occurrences of tilapia and native leopard frogs in tinajas there were nearly mutually exclusive. Only two small mayfly taxa (*Tricorythodes* and *Choroterpes*) were characteristic of pools with tilapia. Both species are often found in small interstitial spaces in the substrate where tilapia may have difficulty extracting them. Also, it may be that these mayflies thrive in the absence of numerous invertebrate predator species which are reduced in abundance, or removed entirely, by tilapia (Table 3). Though Yaqui topminnow appeared to be coexisting with tilapia in the Sierra Santa Úrsula, where the chronology of tilapia introduction is unknown, careful monitoring of these populations should continue given the obvious negative impacts of tilapia locally and in other regions.

Conservation concerns

The most pressing aquatic habitat conservation concerns in the southern Sonoran Desert are related to water resource development, human visitation and resulting damage to sensitive habitats, and the misguided introduction of exotic species. Groundwater overdraft is threatening aquatic ecosystems in many parts of the world (e.g., Deacon et al. 2007; Nevill et al. 2010). In the southern Sonoran Desert, groundwater withdrawal for agricultural and municipal use in the Valle de Guaymas has already led to plummeting water tables, decreased surface flows, saltwater intrusion and abandonment of wells and settlements (Custodio 2002). The sierras Bacatete and Santa Úrsula are located immediately adjacent to that valley, and, as such, spring-fed freshwater habitats in these ranges will likely face declining water levels from local groundwater overdraft. If perennial aquatic habitat becomes lost because of this overdraft, local aquatic communities could change dramatically and long-lived and flightless taxa could face extirpation (Martens et al. 2010; Bogan and Lytle 2011). Unfortunately, the increased intensity and duration of droughts predicted by regional climate models (Seager et al. 2007) will only exacerbate water supply issues.

Unmanaged human visitation to sensitive desert spring systems has been identified as a threat to biodiversity in many parts of the world, such as Australia (Hadwen et al. 2012). As regional tourism increases and local human populations grow in the southern Sonoran Desert, recreational visits to sites such as Nacapule will increase as well. While human visitation to Nacapule has been increasing since the 1960s (Felger 1999), it has skyrocketed in recent years, leading to increased trash and vandalism (e.g., graffiti), destruction of native plants from trampling, and threats from unauthorized access by off-road vehicles (Carrizales 2007). Furthermore, the very limited $\sim 3\ m^2$ of riffle habitat at Nacapule occurs in reaches of heavy human foot traffic. This visitation, combined with the looming threat of groundwater withdrawals lowering water tables, places Nacapule's riffle habitat and its ten unique invertebrate species at great risk. These unique riffle species appear to be resistant or resilient to natural extreme flow events, but it is not known if they can persist in the face of human-induced disturbance as well.

Finally, we implore that prevention of exotic species introductions across the three sierras be an urgent conservation priority. Until 2011, tilapia had not been known from the Sierra El Aguaje. Unfortunately, they were introduced into a previously-fishless habitat there in February 2011 without permission from the communal landowner (D. Magallanes-Molina, personal communication). The spread of tilapia to other sites in the Sierra El Aguaje could be devastating to native aquatic communities and potentially lead to local extinctions of both the Northwest Mexico leopard frog and desert chub. Other exotic species, such as the American bullfrog, have not yet invaded the region, but are negatively impacting native species in the oases of Baja California Sur (Luja and Rodríguez-Estrella 2010b). Thus, preventing the spread of tilapia, and the introduction of other exotics, is essential to preserving regional aquatic biodiversity. Although part of the Sierra El Aguaje may be putatively protected in the "Cajón del Diablo" hunting preserve, its boundaries are unclear and not respected, and active protection of the landscape is far from sufficient (Gallo-Reynoso 2003). More active conservation and management activities are warranted given the increasing threats to spring-fed aquatic habitats of the Sierra El Aguaje and neighboring mountain ranges.

Acknowledgments This work was made possible in part by two grants from the non-profit group T&E Inc., and is dedicated to the memory of the group's founder, Tom Wootten. Many thanks to Enrique Castillo-Grijalva for facilitating access to several survey sites and accompanying us on several site visits, and to Doña Olga Armenta, Miguel Velázquez-Armenta, Ramón Villafraña, and Delfín Magallanes-Molina for allowing access to various study sites. Thanks to Claire Zugmeyer for providing the digital elevation map used to produce Fig. 1. Thanks to Dave Ruiter (Trichoptera), Kelly Miller (Dytiscidae), and Bill Shepard and Cheryl Barr (Elmidae) for taxonomic help with adult aquatic insects during the course of this project. Thanks to Jani Heino and two anonymous referees for their helpful comments on an earlier draft of this manuscript.

Appendix

See Tables 4 and 5.

Table 4 Aquatic invertebrate species occurrences (X) at the 19 study sites in the sierras El Aguaje, Bacatete, and Santa Úrsula (left to right) in order of species richness within each mountain range. See Table 1 for each site's habitat characteristics

Order	Family	Species	Sierra El Aguaje								
			Nacapule	La Navaja	"El Segundo"	La Balandrona	Las Barajitas	"Arroyo del Esterito"	Las Pirinolas	"El Caballo"	"Escondido"
Coleoptera	Dytiscidae	*Copelatus cheverolati renovatus*						X			
		Cybister ellipticus				X					
		Desmopachria convexa complex	X	X		X				X	X
		D. dispersa	X			X		X	X	X	X
		D. mexicana	X	X	X	X	X		X	X	X
		D. portmanni	X	X	X						
		Hydrovatus sp. cf. *davidis*									
		Hygrotus sp.									X
		Laccophilus coccinelloides						X			
		L. fasciatus		X	X	X	X	X	X	X	X
		L. sp. cf. *horni*	X	X	X	X	X		X	X	X
		L. mexicanus									
		L. pictus	X	X	X	X	X	X	X	X	X
		Liodessus obscurellus	X	X	X	X	X	X		X	X
		Macrovatellus mexicanus		X	X	X		X	X	X	X
		Neoclypeodytes amybethae		X							X
		N. fryii		X							X

Table 4 continued

Order	Family	Species	Sierra El Aguaje								
			Nacapule	La Navaja	"El Segundo"	La Balandrona	Las Barajitas	"Arroyo del Esterito"	Las Pirinolas	"El Caballo"	"Escondido"
		N. sp.	X	X	X	X				X	
		Rhantus atricolor				X					
		R. calidus	X								
		R. g. gutticollis		X	X			X			
		R. g. mexicanus									
		Stictotarsus aequinoctialis				X		X			
		Thermonectus marmoratus	X	X	X	X	X	X	X	X	X
		T. sibleyi		X		X	X		X	X	X
		T. succinctus		X		X		X		X	
	Elmidae	*Heterelmis glabra*	X								
		Microcylloepus inequalis	X								
		Neocylloepus arringtoni	X	X							
		Neoelmis sp.	X								
	Haliplidae	*Peltodytes dispersus*									
	Helophoridae	*Helophorus* sp.	X								
	Heteroceridae	Unidentified taxon					X				
	Hydraenidae	*Hydraena* sp.	X	X			X		X	X	
	Hydrophilidae	*Berosus* sp. cf. *infuscatus*									
		B. moerens	X	X	X	X	X	X	X	X	X

Table 4 continued

Order	Family	Species	Sierra El Aguaje								
			Nacapule	La Navaja	"El Segundo"	La Balandrona	Las Barajitas	"Arroyo del Esterito"	Las Pirinolas	"El Caballo"	"Escondido"
		B. notapeltatus	X					X			
		B. rugulosus	X	X	X	X	X	X	X	X	X
		B. salvini		X	X	X		X	X		
		B. sp. (larvae)	X								
		Enrochus ochraceus									
		E. sharpi	X					X		X	
		E. sp.	X		X		X		X		
		Helochares normatus	X	X	X	X		X	X	X	X
		cf. *Hydrobius* sp.									
		Hydrochus sp.	X	X	X	X	X	X	X	X	X
		Hydrophilus insularis	X	X	X		X		X	X	
		Paracymus sp. cf. *ellipsis*	X		X			X			
		Tropisternus chalybeus									
		T. ellipticus									
		T. lateralis		X	X	X		X		X	X
		T. mexicanus						X			
	Noteridae	*Suphisellus lineatus*						X	X		
	Scirtidae	*Elodes* sp.	X	X	X	X	X		X		
		Cyphon sp.						X		X	X

Table 4 continued

Order	Family	Species	Sierra El Aguaje								
			Nacapule	La Navaja	"El Segundo"	La Balandrona	Las Barajitas	"Arroyo del Esterito"	Las Pirinolas	"El Caballo"	"Escondido"
		Unidentified taxon									
Diptera (flies)	Ceratopogonidae	*Atrichopogon* sp.									
		Bezzia sp.	X	X	X	X		X			
		Ceratopogon sp.	X	X	X						
		Culicoides sp.		X	X						
		Forcipomyia sp.	X	X	X		X		X	X	
		Monohelea sp.		X		X		X			
	Chaoboridae	*Chaoborus* sp.		X	X						
	Chironomidae	*Ablabesmyia* sp.	X		X	X		X		X	
		Apedilum sp.		X	X			X			
		Apsectrotanypus sp.		X							
		Beardius sp.	X	X	X	X	X		X		X
		cf. *Lipiniella* sp.					X				
		Chironomus sp.	X			X		X			
		Coelotanypus sp.									
		Corynoneura sp.	X	X	X	X	X				X
		Cricotopus-Orthocladius	X			X	X				
		Dicrotendipes sp.	X		X						X
		Endotribelos sp.	X	X					X		
		Fittkauimyia sp.	X	X	X	X					X
		cf. *Goeldichironomus* sp.	X								

Table 4 continued

Order	Family	Species	Sierra El Aguaje								
			Nacapule	La Navaja	"El Segundo"	La Balandrona	Las Barajitas	"Arroyo del Esterito"	Las Pirinolas	"El Caballo"	"Escondido"
		Labrundinia sp.	X	X				X		X	X
		Larsia sp.	X			X					
		Lauterborniella sp.	X	X	X	X	X			X	X
		Paramerina sp.	X	X	X	X	X	X	X		X
		Parametriocnemus sp.	X	X			X				
		Paratendipes sp.	X		X	X					
		Pentaneura sp.		X							
		Polypedilum sp.	X	X			X				
		Psectrocladius psilopterus complex				X			X		
		Pseudochironomus sp.	X	X		X		X		X	
		Pseudokiefferiella sp.				X					
		Rheotanytarsus sp.	X	X							
		Stenochironomus sp.	X								
		Stempellina sp.	X								
		Stempellinella sp.	X								
		Tanypus sp.									
		Tanytarsus (*Nimbocera*) sp.	X	X	X		X				
		T. (*Tanytarsus*) sp.	X	X	X	X	X	X			
		Thienemanniella sp.	X	X				X			

Table 4 continued

Order	Family	Species	Sierra El Aguaje								
			Nacapule	La Navaja	"El Segundo"	La Balandrona	Las Barajitas	"Arroyo del Esterito"	Las Pirinolas	"El Caballo"	"Escondido"
	Culicidae	*Anopheles* sp.		X				X		X	X
		Culex sp.		X						X	X
		Unidentified taxon	X		X	X	X		X		
	Dixidae	*Dixella* sp.	X					X		X	
	Dolichopodidae	Unidentified taxon									
	Empididae	*Hemerodromia* sp.	X				X				
	Ephydridae	Unidentified taxon			X				X		
	Psychodidae	*Maruina* sp.	X		X						
		Pericoma sp.	X								
	Ptychopteridae	*Ptychoptera* sp.	X			X					
	Simuliidae	*Simulium argus*	X	X							
		S. sp. cf. *carbunculum*		X							
		S. sp.	X			X					
	Stratiomyidae	*Caloparypharus* sp.	X								
		Myxosargus sp.	X	X	X						
		Stratiomys sp.									
	Tabanidae	Unidentified taxon	X								

Table 4 continued

Order	Family	Species	Sierra El Aguaje								
			Nacapule	La Navaja	"El Segundo"	La Balandrona	Las Barajitas	"Arroyo del Esterito"	Las Pirinolas	"El Caballo"	"Escondido"
	Tipulidae	cf. *Antocha* sp.			X						
		cf. *Dicranota* sp.	X								
		Limonia sp.	X	X							
Ephemeroptera	Baetidae	*Callibaetis* sp.	X	X	X	X	X	X	X	X	X
		Fallceon sp.	X	X							
		Unidentified taxon	X			X	X				
	Caenidae	*Caenis* sp.		X					X		
	Leptohyphidae	*Tricorythodes* sp.	X		X						
	Leptophlebiidae	*Choroterpes* sp.	X		X	X	X	X	X	X	X
		Farrodes sp.	X								
Hemiptera	Belostomatidae	*Abedus vicinus sonorensis*									
		Lethocerus medius	X	X	X	X	X		X	X	
	Corixidae	*Graptocorixa abdominalis*	X	X	X	X	X	X	X	X	X
		Morphocorixa lundbladi	X	X	X	X	X		X	X	X
		Trichocorixa reticulata						X			
	Gerridae	*Limnogonus* sp.						X			
		Limnoporus sp.	X	X	X	X	X			X	X
		Rheumatobates sp.									
		Trepobates becki	X	X	X	X	X	X	X	X	X

Table 4 continued

Order	Family	Species	Sierra El Aguaje								
			Nacapule	La Navaja	"El Segundo"	La Balandrona	Las Barajitas	"Arroyo del Esterito"	Las Pirinolas	"El Caballo"	"Escondido"
	Hebridae	*Merragata* sp.							X		
	Hydrometridae	*Hydrometra* sp.	X	X							
	Mesoveliidae	*Mesovelia mulsanti*	X				X	X			
	Naucoridae	*Ambrysus melanopterus*	X	X							
		A. occidentalis	X	X		X	X				X
		A. pulchellus									
		A. sp.	X				X	X			
		Pelocoris sp.	X	X	X	X		X	X	X	X
	Nepidae	*Curicta pronotata*	X	X	X	X	X		X		
		Ranatra quadridentata	X	X	X	X	X	X	X	X	
	Notonectidae	*Buenoa albida*	X	X	X	X	X	X	X	X	X
		B. arida	X	X	X	X			X	X	X
		B. arizonis	X	X	X	X	X	X	X	X	X
		B. platycnemis	X	X	X					X	
		B. thomasi							X		
		Notonecta hoffmanni	X								
		N. lobata	X	X	X	X			X	X	X
		N. indica				X		X			
		N. sp.		X	X		X				
	Veliidae	*Microvelia sp.*	X	X	X	X	X	X	X		
		Platyvelia summersi	X	X	X	X		X		X	X

Table 4 continued

Order	Family	Species	Sierra El Aguaje								
			Nacapule	La Navaja	"El Segundo"	La Balandrona	Las Barajitas	"Arroyo del Esterito"	Las Pirinolas	"El Caballo"	"Escondido"
		Rhagovelia acapulcana									
Lepidoptera	Crambidae	*Elophila* sp.									
		Petrophila sp.		X							
Neuroptera	Sisyridae	*Climacia chapini*		X	X	X	X		X		
Odonata	Aeshnidae	*Anax walshinghami*		X			X	X	X		X
		Remartinia luteipennis									
		Rhionaeshna psilus	X		X				X	X	
	Coenagrionidae	*Argia* sp.	X	X	X		X		X	X	X
		Coenagrion / Enallagma	X	X	X			X			X
		Ischnura ramburii						X			
		Telebasis salva		X	X			X		X	
		Unidentified taxon		X					X		
	Gomphidae	*Phyllogomphoides* sp.	X	X		X					
	Lestidae	*Archilestes grandis*	X	X	X	X	X		X	X	X
	Libellulidae	*Brechmorhoga* sp.									
		Libellula saturata	X	X	X						
		Macrothemis inacuta						X			
		Miathyria sp.									

Table 4 continued

Order	Family	Species	Sierra El Aguaje								
			Nacapule	La Navaja	"El Segundo"	La Balandrona	Las Barajitas	"Arroyo del Esterito"	Las Pirinolas	"El Caballo"	"Escondido"
		Orthemis ferruginea						X			
		Paltothemis lineatipes						X		X	
		Perithemis intensa			X			X	X		
		Psuedoleon superbus	X	X		X	X	X	X	X	
		Unidentified taxon									
Trichoptera	Calamoceratidae	*Phylloicus mexicanus*	X	X	X	X	X		X		
	Helicopsychidae	*Helicopsyche* sp.				X					
	Hydropsychidae	*Cheumatopsyche arizonensis*	X	X							
		cf. *Potamyia* sp.									
	Hydroptilidae	*Leucotrichia* sp.	X								
		Neotrichia canixa	X								
		N. n. sp. 1		X							
		N. n. sp. 2		X							
		Mayatrichia n. sp.		X							
		Ochrotrichia sp.	X		X		X				
		Oxyethira sp.	X						X		
		Unidentified taxon	X	X		X					
	Leptoceridae	Unidentified taxon									
	Odontoceridae	*Marilia nobsca*	X	X	X	X	X	X	X	X	X
	Philopotamidae	*Chimarra ridleyi*		X							
		C. sp.	X	X			X				

Table 4 continued

Order	Family	Species	Sierra El Aguaje								
			Nacapule	La Navaja	"El Segundo"	La Balandrona	Las Barajitas	"Arroyo del Esterito"	Las Pirinolas	"El Caballo"	"Escondido"
		Wormaldia planae		X							
Non-insects	(Higher taxon)	(Genus or unident.)									
	Amphipoda	*Hyallela* sp.		X		X	X				
	Cladocera	Unidentified taxon	X	X	X	X			X	X	X
	Collembola	Unidentified taxon	X		X	X					
	Copepoda	Unidentified taxon	X	X	X	X		X	X	X	X
	Decapoda	*Palaemonetes* sp.						X			
	Glossiphoniidae	Unidentified taxon	X	X		X	X		X	X	
	Hydracarina	*Atractides* sp.	X								
		Hydrozetes sp.		X	X		X				
		Mucronothrus sp.					X				
		Sperchon sp.	X								
		Unidentified taxon	X	X	X	X	X		X	X	X
	Oligochaeta	Unidentified taxon	X	X	X	X	X	X		X	
	Ostracoda	Unidentified taxon	X	X				X		X	

Table 4 continued

Order	Family	Species	Sierra El Aguaje								
			Nacapule	La Navaja	"El Segundo"	La Balandrona	Las Barajitas	"Arroyo del Esterito"	Las Pirinolas	"El Caballo"	"Escondido"
	Physidae	Unidentified taxon	X	X	X	X	X		X		X
	Planorbidae	*Gyraulus* sp.									
		Planorbella sp.									
	Platyhelminthes	Unidentified taxon	X	X			X				
	Spongillidae	Unidentified taxon	X	X		X	X		X	X	

Table 4 continued

Order	Family	Species	Sierra El Aguaje						Sierra Bacatete		Sierra Santa Úrsula	
			"Tinajas Altas"	"Las Abejas"	"Keyhole"	"Las Vacas"	Los Anegados	Robinson	Rancho Bacatete	Los Pilares	R. Santa Úrsula	Los Pelones
Coleoptera	Dytiscidae	*Copelatus cheverolati renovatus*										
		Cybister ellipticus								X		
		Desmopachria convexa complex	X								X	
		D. dispersa		X						X	X	X
		D. mexicana	X		X				X		X	
		D. portmanni										
		Hydrovatus sp. cf. *davidis*		X								
		Hygrotus sp.								X		
		Laccophilus coccinelloides										
		L. fasciatus	X	X						X	X	
		L. sp. cf. *horni*	X						X		X	
		L. mexicanus		X							X	
		L. pictus	X	X	X				X	X	X	
		Liodessus obscurellus	X	X							X	
		Macrovatellus mexicanus	X						X	X	X	X
		Neoclypeodytes amybethae	X									
		N. fryii										
		N. sp.	X									

Table 4 continued

Order	Family	Species	Sierra El Aguaje						Sierra Bacatete		Sierra Santa Úrsula	
			"Tinajas Altas"	"Las Abejas"	"Keyhole"	"Las Vacas"	Los Anegados	Robinson	Rancho Bacatete	Los Pilares	R. Santa Úrsula	Los Pelones
		Rhantus atricolor										
		R. calidus										
		R. g. gutticollis	X									
		R. g. mexicanus	X									
		Stictotarsus aequinoctialis	X									
		Thermonectus marmoratus	X		X					X	X	X
		T. sibleyi	X						X		X	X
		T. succinctus		X						X		
	Elmidae	*Heterelmis glabra*										
		Microcylloepus inequalis										
		Neocylloepus arringtoni										
		Neoelmis sp.										
	Haliplidae	*Peltodytes dispersus*									X	
	Helophoridae	*Helophorus* sp.										
	Heteroceridae	Unidentified taxon										
	Hydraenidae	*Hydraena* sp.							X	X		
	Hydrophilidae	*Berosus* sp. cf. *infuscatus*										X
		B. moerens	X	X	X	X			X		X	
		B. notapeltatus										
		B. rugulosus	X	X	X				X	X	X	

Table 4 continued

Order	Family	Species	Sierra El Aguaje						Sierra Bacatete		Sierra Santa Úrsula	
			"Tinajas Altas"	"Las Abejas"	"Keyhole"	"Las Vacas"	Los Anegados	Robinson	Rancho Bacatete	Los Pilares	R. Santa Úrsula	Los Pelones
		B. salvini	X									
		B. sp. (larvae)		X							X	
		Enrochus ochraceus								X		
		E. sharpi		X						X	X	X
		E. sp.						X				
		Helochares normatus		X	X				X		X	X
		cf. *Hydrobius* sp.				X						
		Hydrochus sp.	X	X	X				X	X	X	
		Hydrophilus insularis	X						X	X	X	X
		Paracymus sp. cf. *ellipsis*									X	
		Tropisternus chalybeus							X			X
		T. ellipticus							X	X	X	
		T. lateralis	X	X	X				X	X	X	
		T. mexicanus										X
	Noteridae	*Suphisellus lineatus*								X	X	
	Scirtidae	*Elodes* sp.										
		Cyphon sp.								X	X	
		Unidentified taxon			X				X			X
Diptera (flies)	Ceratopogonidae	*Atrichopogon* sp.										
		Bezzia sp.				X	X		X			

Table 4 continued

Order	Family	Species	Sierra El Aguaje						Sierra Bacatete		Sierra Santa Úrsula	
			"Tinajas Altas"	"Las Abejas"	"Keyhole"	"Las Vacas"	Los Anegados	Robinson	Rancho Bacatete	Los Pilares	R. Santa Úrsula	Los Pelones
		Ceratopogon sp.				X	X		X		X	X
		Culicoides sp.						X			X	
		Forcipomyia sp.	X									
		Monohelea sp.					X					
	Chaoboridae	*Chaoborus* sp.	X									
	Chironomidae	*Ablabesmyia* sp.	X	X		X	X	X			X	X
		Apedilum sp.		X			X				X	
		Apsectrotanypus sp.										
		Beardius sp.	X						X		X	X
		cf. *Lipiniella* sp.										
		Chironomus sp.	X	X						X	X	X
		Coelotanypus sp.							X			
		Corynoneura sp.		X		X		X	X		X	
		Cricotopus-Orthocladius	X				X				X	
		Dicrotendipes sp.							X		X	
		Endotribelos sp.							X			
		Fittkauimyia sp.		X	X				X		X	X
		cf. *Goeldichironomus* sp.										
		Labrundinia sp.	X				X					
		Larsia sp.										
		Lauterborniella sp.		X	X			X	X		X	X

Table 4 continued

Order	Family	Species	Sierra El Aguaje						Sierra Bacatete		Sierra Santa Úrsula	
			"Tinajas Altas"	"Las Abejas"	"Keyhole"	"Las Vacas"	Los Anegados	Robinson	Rancho Bacatete	Los Pilares	R. Santa Úrsula	Los Pelones
		Paramerina sp.	X	X	X				X		X	
		Parametriocnemus sp.				X			X		X	
		Paratendipes sp.	X			X					X	
		Pentaneura sp.										
		Polypedilum sp.				X		X	X			X
		Psectrocladius psilopterus complex										
		Pseudochironomus sp.		X							X	
		Pseudokiefferiella sp.										
		Rheotanytarsus sp.							X		X	
		Stenochironomus sp.										
		Stempellina sp.										
		Stempellinella sp.										
		Tanypus sp.							X			
		Tanytarsus (Nimbocera) sp.		X		X	X	X	X		X	
		T. (*Tanytarsus*) sp.		X					X	X	X	X
		Thienemanniella sp.							X		X	
	Culicidae	*Anopheles* sp.	X		X	X			X		X	
		Culex sp.							X			
		Unidentified taxon										
	Dixidae	*Dixella* sp.							X			

Table 4 continued

Order	Family	Species	Sierra El Aguaje						Sierra Bacatete		Sierra Santa Úrsula	
			"Tinajas Altas"	"Las Abejas"	"Keyhole"	"Las Vacas"	Los Anegados	Robinson	Rancho Bacatete	Los Pilares	R. Santa Úrsula	Los Pelones
	Dolichopodidae	Unidentified taxon						X				
	Empididae	*Hemerodromia* sp.					X		X		X	
	Ephydridae	Unidentified taxon										
	Psychodidae	*Maruina* sp.										
		Pericoma sp.										
	Ptychopteridae	*Ptychoptera* sp.										
	Simuliidae	*Simulium argus*										
		S. sp. cf. *carbunculum*										
		S. sp.							X			
	Stratiomyidae	*Caloparypharus* sp.						X			X	X
		Myxosargus sp.							X		X	
		Stratiomys sp.									X	
	Tabanidae	Unidentified taxon							X			
	Tipulidae	cf. *Antocha* sp.										
		cf. *Dicranota* sp.										
		Limonia sp.							X			
Ephemeroptera	Baetidae	*Callibaetis* sp.	X	X	X				X	X	X	
		Fallceon sp.							X		X	

Table 4 continued

Order	Family	Species	Sierra El Aguaje						Sierra Bacatete		Sierra Santa Úrsula	
			"Tinajas Altas"	"Las Abejas"	"Keyhole"	"Las Vacas"	Los Anegados	Robinson	Rancho Bacatete	Los Pilares	R. Santa Úrsula	Los Pelones
		Unidentified taxon					X					
	Caenidae	*Caenis* sp.							X	X		
	Leptohyphidae	*Tricorythodes* sp.		X					X	X	X	
	Leptophlebiidae	*Choroterpes* sp.	X	X	X				X	X	X	X
		Farrodes sp.										
Hemiptera	Belostomatidae	*Abedus vicinus sonorensis*							X			
		Lethocerus medius	X		X				X	X	X	X
	Corixidae	*Graptocorixa abdominalis*	X	X	X						X	
		Morphocorixa lundbladi	X								X	
		Trichocorixa reticulata										
	Gerridae	*Limnogonus* sp.										
		Limnoporus sp.							X		X	
		Rheumatobates sp.										X
		Trepobates becki	X		X				X	X	X	X
	Hebridae	*Merragata* sp.									X	
	Hydrometridae	*Hydrometra* sp.							X	X	X	
	Mesoveliidae	*Mesovelia mulsanti*				X					X	
	Naucoridae	*Ambrysus melanopterus*										
		A. occidentalis									X	

Table 4 continued

Order	Family	Species	Sierra El Aguaje						Sierra Bacatete		Sierra Santa Úrsula	
			"Tinajas Altas"	"Las Abejas"	"Keyhole"	"Las Vacas"	Los Anegados	Robinson	Rancho Bacatete	Los Pilares	R. Santa Úrsula	Los Pelones
		A. pulchellus									X	
		A. sp.							X			
		Pelocoris sp.	X							X	X	
	Nepidae	*Curicta pronotata*								X	X	
		Ranatra quadridentata	X		X				X	X	X	X
	Notonectidae	*Buenoa albida*			X				X		X	
		B. arida	X		X						X	
		B. arizonis	X	X	X				X		X	
		B. platycnemis	X						X			
		B. thomasi										
		Notonecta hoffmanni										
		N. lobata	X		X							
		N. indica		X						X		X
		N. sp.										
	Veliidae	*Microvelia sp.*	X	X		X	X	X		X	X	
		Platyvelia summersi									X	
		Rhagovelia acapulcana							X			
Lepidoptera	Crambidae	*Elophila* sp.									X	
		Petrophila sp.										
Neuroptera	Sisyridae	*Climacia chapini*									X	X
Odonata	Aeshnidae	*Anax walshinghami*			X							

Table 4 continued

Order	Family	Species	Sierra El Aguaje						Sierra Bacatete		Sierra Santa Úrsula	
			"Tinajas Altas"	"Las Abejas"	"Keyhole"	"Las Vacas"	Los Anegados	Robinson	Rancho Bacatete	Los Pilares	R. Santa Úrsula	Los Pelones
		Remartinia luteipennis							X			
		Rhionaeshna psilus							X	X	X	
	Coenagrionidae	*Argia* sp.	X			X	X		X		X	
		Coenagrion / Enallagma		X					X	X	X	X
		Ischnura ramburii										
		Telebasis salva							X		X	
		Unidentified taxon										
	Gomphidae	*Phyllogomphoides* sp.							X			
	Lestidae	*Archilestes grandis*	X						X		X	
	Libellulidae	*Brechmorhoga* sp.							X			
		Libellula saturata							X			
		Macrothemis inacuta										
		Miathyria sp.									X	
		Orthemis ferruginea										
		Paltothemis lineatipes									X	
		Perithemis intensa							X			X
		Psuedoleon superbus		X	X					X	X	
		Unidentified taxon				X						

Table 4 continued

Order	Family	Species	Sierra El Aguaje						Sierra Bacatete		Sierra Santa Úrsula	
			"Tinajas Altas"	"Las Abejas"	"Keyhole"	"Las Vacas"	Los Anegados	Robinson	Rancho Bacatete	Los Pilares	R. Santa Úrsula	Los Pelones
Trichoptera	Calamoceratidae	*Phylloicus mexicanus*			X							
	Helicopsychidae	*Helicopsyche* sp.							X		X	X
	Hydropsychidae	*Cheumatopsyche arizonensis*										
		cf. *Potamyia* sp.							X			
	Hydroptilidae	*Leucotrichia* sp.							X			
		Neotrichia canixa							X			
		N. n. sp. 1										
		N. n. sp. 2										
		Mayatrichia n. sp.										
		Ochrotrichia sp.							X		X	
		Oxyethira sp.									X	
		Unidentified taxon							X		X	
	Leptoceridae	Unidentified taxon							X			
	Odontoceridae	*Marilia nobsca*	X	X					X		X	X
	Philopotamidae	*Chimarra ridleyi*										
		C. sp.							X		X	
		Wormaldia planae										
Non-insects	(Higher taxon)	(Genus or unident.)										
	Amphipoda	*Hyallela* sp.							X	X	X	
	Cladocera	Unidentified taxon									X	

Table 4 continued

Order	Family	Species	Sierra El Aguaje						Sierra Bacatete		Sierra Santa Úrsula	
			"Tinajas Altas"	"Las Abejas"	"Keyhole"	"Las Vacas"	Los Anegados	Robinson	Rancho Bacatete	Los Pilares	R. Santa Úrsula	Los Pelones
	Collembola	Unidentified taxon										
	Copepoda	Unidentified taxon	X						X			X
	Decapoda	*Palaemonetes* sp.										
	Glossiphoniidae	Unidentified taxon			X				X	X	X	
	Hydracarina	*Atractides* sp.										
		Hydrozetes sp.										
		Mucronothrus sp.										
		Sperchon sp.										
		Unidentified taxon							X		X	X
	Oligochaeta	Unidentified taxon	X	X	X		X		X	X	X	X
	Ostracoda	Unidentified taxon	X						X			
	Physidae	Unidentified taxon	X	X							X	
	Planorbidae	*Gyraulus* sp.							X			
		Planorbella sp.								X		X
	Platyhelminthes	Unidentified taxon										
	Spongillidae	Unidentified taxon									X	X

Table 5 Aquatic vertebrate species occurrences (X) at the 19 study sites in the sierras El Aguaje, Bacatete, and Santa Úrsula. See Table 1 for each site's habitat characteristics

Order	Family	Species	Sierra El Aguaje								
			Nacapule	La Navaja	"El Segundo"	La Balandrona	Las Barajitas	"Arroyo del Esterito"	Las Pirinolas	El Caballo"	"Escondido"
Anura	Ranidae	*Lithobates magnaocularis*	X	X	X		X				
Anura	Hylidae	*Hyla arenicolor*	X	X		X					X
Anura	Bufonidae	*Anaxyrus punctatus*		X				X			X
Anura	Leptodactylidae	*Leptodactylus melanonotus*									
Squamata	Colubridae	*Thamnophis cyrtopsis*		X					X		
Testudines	Kinosternidae	*Kinosternon sonoriense*								X	
Cypriniformes	Cyprinidae	*Gila eremica*				X			X		
Cyprinodontiformes	Poeciliidae	*Poeciliopsis occidentalis sonoriensis*									
Perciformes	Cichlidae	*Tilapia* sp.								X	

Table 5 continued

Order	Family	Species	Sierra El Aguaje						Sierra Bacatete		Sierra Santa Úrsula	
			"Tinajas Altas"	"Las Abejas"	"Keyhole"	"Las Vacas"	Los Anegados	Robinson	Rancho Bacatete	Los Pilares	R. Santa Úrsula	Los Pelones
Anura	Ranidae	*Lithobates magnaocularis*									X	
Anura	Hylidae	*Hyla arenicolor*										
Anura	Bufonidae	*Anaxyrus punctatus*										
Anura	Leptodactylidae	*Leptodactylus melanonotus*							X			
Squamata	Colubridae	*Thamnophis cyrtopsis*										
Testudines	Kinosternidae	*Kinosternon sonoriense*										
Cypriniformes	Cyprinidae	*Gila eremica*										
Cyprinodontiformes	Poeciliidae	*Poeciliopsis occidentalis sonoriensis*									X	X
Perciformes	Cichlidae	*Tilapia* sp.							X	X	X	X

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