Indirect Effects of Omnivorous Crayfish on Semiarid Stream Macroinvertebrate Communities Mediated by Novel Riparian Vegetation

by

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ABSTRACT

Novel resource inputs represent an increasingly common phenomenon in ecological systems as global change alters environmental factors and species distributions. In semiarid riparian areas, hydric pioneer tree species are being replaced by drought-tolerant species as water availability decreases. Additionally, introduced omnivorous crayfish, which feed upon primary producers, allochthonous detritus, and benthic invertebrates, can impact communities at multiple levels through both direct and indirect effects. In arid and semiarid systems of the American Southwest, crayfish may be especially important as detrital processors due to the lack of specialized detritivores. I tested the impact of virile crayfish (*Orconectes virilis*) on benthic invertebrates and detrital resources across a gradient of riparian vegetation drought-tolerance using field cages with leaf litter bags in the San Pedro River in Southeastern Arizona. Virile crayfish increased breakdown rate of drought-tolerant saltcedar (*Tamarix ramosissima*), but did not impact breakdown of Fremont cottonwood (*Populus fremontii*), Gooding's willow (*Salix goodingii*), or seepwillow (*Baccharis salicifolia*). The density and composition of the invertebrate community colonizing leaf litter bags were both heavily influenced by litter species but not directly by crayfish presence. As drought-tolerant species become more abundant in riparian zones, their litter will become a larger component of the organic matter budget of desert streams. By increasing breakdown rates of saltcedar, crayfish shift the composition of leaf litter in streams, which in turn may affect the composition and biomass of colonizing invertebrate communities. More research is needed to determine the full extent to which these alterations change community composition over time.

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INTRODUCTION

The discipline of ecology has historically operated under the assumption that pristine complex communities exist (Collins et al., 2000). Over the past few decades, it has become clear however that pristine ecosystems that remain untouched by anthropogenic influences are rare (Vitousek, 1994). Natural systems are dynamic (Lindeman, 1942), and humans are rapidly altering the forces that underpin these dynamics. Humans both directly spread species into previously unoccupied areas and also indirectly cause species range expansions and colonization of novel habitats through global change (Webber and Scott, 2012). In most ecological communities there are now multiple, interacting sources of novel species. This novelty is worthy of study because the reaction of the historical community is transient, and these transient dynamics may allow the formation of novel ecosystems (Hastings, 2001; Hobbs et al., 2006). Novel ecosystems consist of new combinations or relative abundances of species within a biome that had not occurred prior to some form of human disturbance (Hobbs et al., 2006). In this sense, a system may still be considered novel even if the disturbance leading to its formation occurred decades or centuries ago, e.g., forests that have developed on abandoned agricultural fields in New England and Europe (Vellend et al., 2007). Further, the course of these transient dynamics may be determined not just by the direct effects of all novel species in the system, but also by interactions between different novel species.

As ecosystems face multiple disturbances, surprising ecological consequences are more likely to occur (Paine et al., 1998). These compounded effects are most visible in systems that face multiple anthropogenic stressors. Arid and semiarid streams are impacted by introduced aquatic and riparian species (e.g., Kennedy et al., 2005) as well as declining precipitation and water tables (Sabo et al., 2010b; Seager et al., 2007; Serrat-Capdevila et al., 2007). Flow regime is an extremely important driver of community structure in arid and semiarid streams (Carlisle et al., 2011; Lytle and Poff, 2004; Sabo et al., 2010a; Sabo et al., 2012; Stanley et al., 1994), and streams are more heavily impacted by flow alterations in arid regions than their temperate counterparts (Carlisle et al., 2011). Water availability in some desert streams has already become increasingly variable over the past century, with extensive community changes resulting from this transition. Severe droughts have the potential to eliminate certain macroinvertebrate taxa that depend on perennial surface water (Bogan and Lytle, 2011; Sponseller et al., 2010). Changes to flow regime threaten freshwater biodiversity worldwide (Vörösmarty et al., 2010) and can be particularly important in altering competition between native and introduced species (e.g. Seegrist and Gard, 1972).

Due to changes in flood intensity, base flows, and groundwater depth, riparian vegetation communities shift from hydric species to mesic drought-tolerant species as variation in water availability increases (Stromberg et al., 2005; Stromberg et al., 2010). These community shifts have impacts on riparian systems (Brand et al., 2011; Stromberg et al., 2010), yet little is known about how they impact stream ecosystems. Allochthonous detrital inputs can form the base of the food web in some stream systems and represent an important flow of energy between aquatic and riparian systems (Fisher and Likens, 1973; Wallace et al., 1997). Alterations to riparian systems are increasingly creating novel ecosystems (Richardson et al., 2007), and these shifts in riparian organic matter inputs associated with global change impact aquatic ecosystems worldwide (Ball et al., 2010). Introduction of novel litter from drought-tolerant plants is likely to have some impact on benthic organisms. These contrasting hydric and drought-tolerant plants may have differing effects on stream consumers because their leaves differ in quality (Kennedy and Hobbie, 2004; Tibbets and Molles, 2005). In semiarid riparian zones both native (e.g. *Baccharis* and *Prosopis*) and introduced (e.g. *Elaeagnus* and *Tamarix*) species establish populations along stream reaches with altered flow regimes (Stromberg et al., 2007; Stromberg et al., 2010), providing a mixture of novel and historically present organic matter sources for detritivores.

Omnivorous crayfish are known to directly and indirectly impact primary producers (Charlebois and Lamberti, 1996; Lodge et al., 1994), allochthonous detritus availability (Bobeldyk and Lamberti, 2010; Larned et al., 2003; Usio et al., 2000), and invertebrate communities (Bobeldyk and Lamberti, 2010; Charlebois and Lamberti, 1996; Lodge et al., 1994; McCarthy et al., 2006). Introduced crayfish threaten aquatic biodiversity worldwide (Lodge et al., 2000), but are likely to have the greatest impacts in systems such as the Colorado River basin where there were no native omnivorous analogs. While desert streams have historically hosted native omnivorous fishes such as *Agosia chrysogaster* and *Catostomus clarki*, these fishes do not feed on coarse particulate detritus (Fisher et al., 1982). Detritivorous insect larvae have exhibited higher growth rates on drought-tolerant saltcedar (*Tamarix)* than cottonwood (*Populus*) and willow (*Salix*) in laboratory experiments (Going and Dudley, 2008; Moline and Poff, 2008), and there is also evidence that saltcedar removal leads to declines in crayfish populations (Kennedy et al., 2005). Novel consumers often show a tendency to prefer novel resources to which the native species are not adapted (e.g., Ermgassen and Aldridge, 2011; Helms and Vinson, 2002), thus crayfish may heavily benefit from novel detrital inputs.

Omnivorous macroconsumers can be highly important in the breakdown of leaf litter in a diverse array of aquatic systems, even when specialized shredders are present (Coughlan et al., 2010). However, lowland desert streams in the American Southwest often lack shredders that feed on leaf material (Schade and Fisher, 1997), thus crayfish may be especially important in the processing of detritus in these systems. Through selective feeding on leaf litter, crayfish have the potential to impose indirect effects on macroinvertebrate consumers. In tropical streams detritivorous and grazing fish can have greater indirect impacts on benthic community composition than the direct impacts of predators (e.g., Flecker, 1992), thus crayfish may have similar impacts in semiarid streams if they act primarily as primary consumers rather than as predators.

In this paper I ask how a combination of novel riparian vegetation (an allochthonous resource to the food web) and novel omnivores alter community structure and ecosystem function in a desert river. My thesis is that omnivores (the crayfish *Orconectes virilis*) alter community structure primarily by hastening decomposition and relative abundance of novel litter inputs. I test two specific hypotheses. First, that crayfish increase leaf litter decomposition by efficient shredding of allochthonous plant resources. I predict that decomposition of all litter species will be faster in the presence of crayfish, but in the San Pedro River in Southeast Arizona this effect will be strongest for saltcedar due to evidence of its high food quality and its novelty in the system. Second, I hypothesize that invertebrates respond indirectly to crayfish presence via changes in resource availability caused by crayfish feeding on leaf litter as opposed to direct predation by crayfish. I predict that community composition will shift from dominance by generalists that feed on saltcedar to dominance by specialists in crayfish treatments, especially drought-tolerant litter treatments where crayfish may cause the greatest decline in resource availability for other shredders and omnivores.

METHODS

Study Sites. This research was conducted in the San Pedro River, a semiarid river draining northeastern Sonora and southeastern Arizona in the Colorado River basin. Similar to many rivers draining arid and semiarid catchments, the San Pedro is spatially and temporally intermittent, with alternating perennial and intermittent reaches (Turner and Richter, 2011). This study incorporated one perennial reach, Grayhawk Ranch (31.604°N, 110.153°W), and one reach that is intermittent in very dry years, Charleston (31.630°N, 110.178°W). Approximately 4 km separates these reaches (Figure 1). Neither reach dried completely during the study period, but Charleston (mean±SE=23.5°C±0.291) was warmer than Grayhawk Ranch (mean±SE=23.0°C±0.327) throughout the study (Appendix 1). Grayhawk Ranch features a broad gallery forest dominated by Fremont cottonwood (*Populus fremontii*) and Gooding's willow (*Salix goodingii*)), whereas Charleston has a narrow riparian forest with higher dominance of seepwillow (*Baccharis salicifolia*) as well as some cottonwood, willow, and saltcedar (*Tamarix ramosissima*). Despite these vegetation differences, canopy cover did not differ significantly above cages between sites (Charleston=37±6%, Grayhawk Ranch=38±5%). Riparian vegetation along the river can be classified along a gradient of drought tolerance (Vandersande et al., 2001; Figure 2), with declining streamflows causing shifts to drought-tolerant species such as saltcedar (Stromberg et al., 2010).

Despite the large number of studies on the riparian zone of the San Pedro, little is known about its aquatic ecology. The river is inhabited by non-native virile crayfish and red swamp crawfish (*Procambarus clarkii*), but virile crayfish numerically dominate the study reaches (Appendix 2). Additionally, the river hosts a diverse benthic invertebrate community of insects, crustaceans, and gastropods.

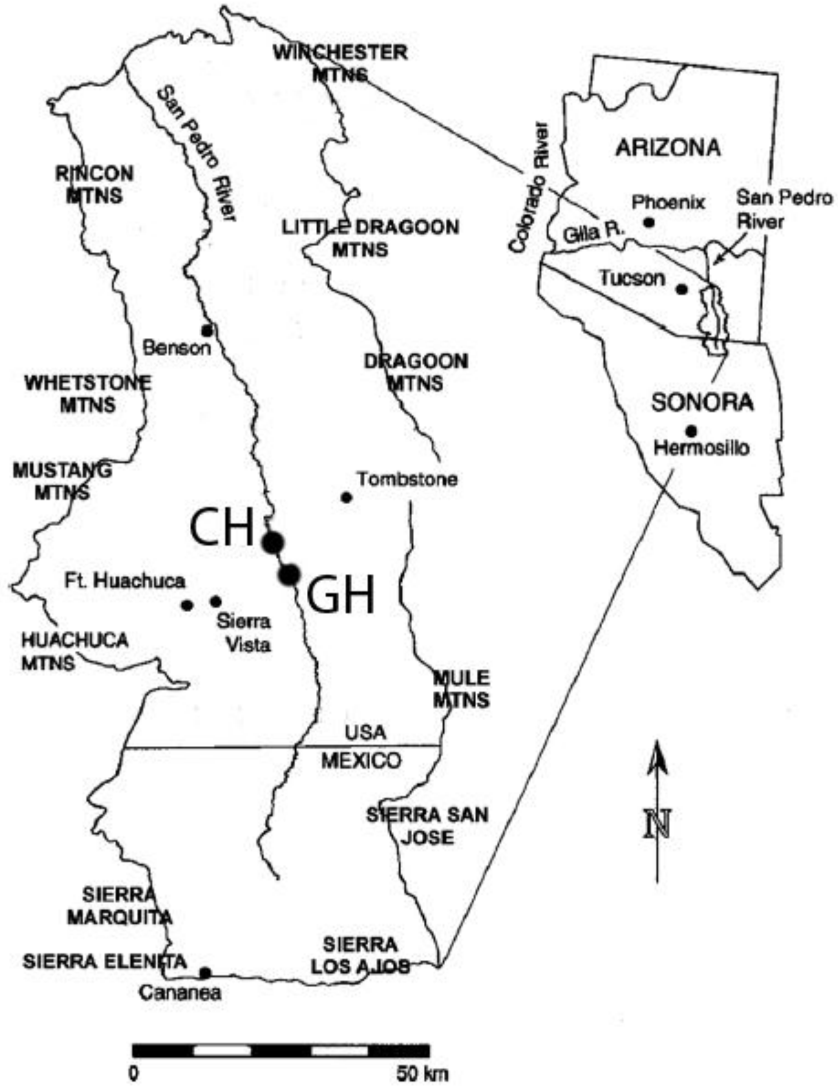

Figure 1. Map of the upper San Pedro River watershed (modified from Serrat-Capdevila et al. 2007). Large points mark the approximate locations of the study reaches (CH=Charleston, GH=Grayhawk Ranch).

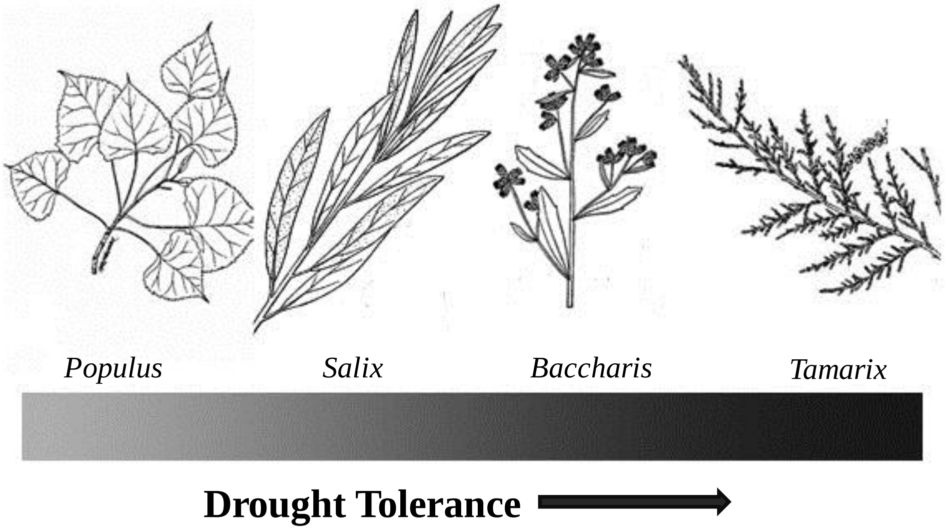

Figure 2. Generalized drought tolerance of riparian vegetation of semiarid streams (*sensu* Vandersande et al. 2001). Plant images courtesy of USDA Agricultural Research Service and University of Arizona.

Experimental Design. I deployed sixteen cages in a generalized randomized block design at each reach during the dry season on May 24, 2011 and removed them immediately preceding the first monsoonal flood on June 24, 2011. The experiment was conducted during the warm, dry season because crayfish are active in processing leaf litter during warmer months (Huryn and Wallace, 1987) and because arid riparian plants often drop leaves in response to water stress during the dry season (Horton et al., 2001). Cages measured approximately 0.2 m^2 in area and were covered with 8 mm^2 mesh on the upstream and downstream ends as well as 48 mm^2 mesh above the water to prevent interference from birds and mammals. This mesh size excluded movement by large crayfish and fish such as largemouth bass (*Micropterus salmoides*), common carp (*Cyprinus carpio*), and black bullhead catfish (*Ameiurus melas*) but allowed passage by small fish such as mosquitofish (*Gambusia affinis*) and most insects, gastropods, and small crustaceans including young-of-year (YOY) virile crayfish, which were present at Charleston but not Grayhawk Ranch. YOY crayfish are primarily predatory in comparison to larger, omnivorous juveniles and adults (Bondar and Richardson, 2009); hence, I treated them as colonizing predators in my analysis and interpretation of the results. Cages were filled with natural periphyton-covered stream sediments and set in the stream for forty-eight hours to settle before I added treatments.

Each cage received one level of a virile crayfish treatment (present/absent) and one of two levels of a leaf litter treatment. Crayfish treatment levels consisted of either one mature juvenile (mean initial carapace length=21 mm) virile crayfish representing a reasonable density for this age class (5/m^2) or a control of no crayfish. Leaf litter treatments consisted of litter bags (pecan bags; Gulf Coast Bag and Bagging Co., Houston, TX) containing 3.5 g of either hydric species (Fremont cottonwood and Gooding's willow) or more drought-tolerant species (saltcedar and seepwillow). All litter bags consisted of a single species, with separate bags of each species per treatment level in all cages receiving that level. I chose to deploy litter bags in this way because it captures two essential elements of riparian vegetation along desert rivers such as the San Pedro: 1) stands of woody riparian vegetation (and the litter they contribute to streams) consist of multiple species, thus monocultures of litter present unrealistic scenarios for detritivores and microbes, and 2) the species-pairs chosen represent communities that dominate perennial (hydric) and intermittent (drought-tolerant) reaches of these rivers, replicating co-occurring litter conditions experienced by stream detritivores across these differing hydrologic regimes. As there are generally non-additive effects of litter species mixing (Kominoski et al., 2007), it is important to consider these species-pairs together to capture dynamics at the ecosystem scale.

Senescent leaves of all species were collected from the study reaches of the San Pedro in 2010, except saltcedar which was collected from the Salt River above Granite Reef Dam. Saltcedar is not abundant along the upper San Pedro River due to long stretches of perennial flow and an active saltcedar removal program. Although litter quality may differ between Salt River and San Pedro

River populations, this was the best source of abundant saltcedar litter and further highlights its novelty to the system. Litter bags of cottonwood and saltcedar were retrieved weekly, while bags of willow and seepwillow were retrieved biweekly. This arrangement provided differing initial standing stocks of litter for each species per treatment which reflected general patterns of abundance of these riparian species at perennial and intermittent sites along streams in Arizona (Stromberg et al., 2010). Breakdown rate (*k*) was calculated for each species/crayfish treatment combination following Hauer and Lamberti (2006). All invertebrates were rinsed from leaf litter bags before processing and identified to genus or species except physid snails and chironomid midge larvae. Chironomids were separated into two groups: the predatory subfamily Tanypodinae and other non-predatory subfamilies (collectively referred to as non-Tanypodinae hereafter). Virile crayfish were measured and weighed at the beginning and end of the experimental period. All crayfish were held for a 24-hour period with no food before being weighed each time to ensure that gut contents did not factor into weight measurements. Additionally, a 0.01 m^2 unglazed ceramic tile (United States Ceramic Tile Co., Miami, FL) was placed in each cage to measure periphyton growth following Hauer and Lamberti (2006). Water temperature was measured every thirty minutes from June 10 through June 24 at both sites with a HOBO Water Temp Pro v2 temperature logger (Onset Computer Corporation, Pocasset, MA) and canopy density was measured above each cage using a densiometer (Forest Densiometers, Bartlesville, OK) on June 2, 2011.

Statistical Analysis. I performed two primary sets of analyses. To test my first hypothesis, I tested if litter treatment or crayfish treatment impacted periphyton growth and leaf litter breakdown rate. Additionally, I tested if virile crayfish growth differed across litter treatments and sites. To test my second hypothesis, I tested if the invertebrate community differed across treatments, sites, and time.

I tested assumptions of normality and equal variance of residuals of all models using Shapiro-Wilk and Levene's test, respectively. I tested virile crayfish growth as a function of leaf litter treatment using a two-factor ANOVA with interactions. I tested changes in periphyton growth across sites and treatments using a linear mixed-effects model with site as a random effect. I tested differences in log-transformed breakdown rate of leaf litter species using a generalized mixed effects model with site (Charleston vs. Grayhawk Ranch) as a random block effect, and I performed Tukey-Kramer post-hoc tests to test specific comparisons.

I tested differences in the invertebrate community (as density per gram ash-free dry mass (AFDM) leaf litter) across treatments and sites using a non-metric multidimensional scaling (NMDS) ordination with zero-adjusted Bray-Curtis distance matrices (Clarke et al., 2006). NMDS tested drivers of community composition at the finest practical taxonomic scale for each group. I excluded several invertebrate taxa that were present in very low abundance from NMDS analysis or grouped them together at higher taxonomic levels (e.g., dytiscid beetles). To avoid violations of independence, NMDS was performed only on data from the fourth and final week of the experiment and samples from both litter types per cage were pooled. I tested significance of predictor variables using a random permutations test on r^2 with 4999 permutations (using the *envfit* command in the vegan package of R). I also tested if beta diversity (measured as the slope of the species-area curve (*sensu* Lennon et al., 2001)) of invertebrates colonizing leaf litter varied between treatments using multivariate ANOVA (MANOVA) with Bray-Curtis distance matrices and 4999 permutations (using the *adonis* command in the vegan package of R). Beta diversity, i.e., the dissimilarity of benthic communities between treatments, depends on both species shared between treatments and species unique to each treatment. MANOVA included litter treatment and crayfish as predictors with site as a random effect. I tested contributions of individual taxa to the NMDS axes by calculating linear correlation coefficients between density and the axes. I also categorized macroinvertebrates into functional feeding groups (FFGs) according to Merritt and Cummins (1996) for broad-scale analysis of colonization patterns. Due to over-dispersion of the count data, I tested variation in invertebrate density using mixed-effects zero-inflated Poisson generalized linear models with site as a random effect and time as a repeated measure. There are a number of modeling approaches available to correct for over-dispersion, but I selected the zero-inflated Poisson distribution because it specifically accounts for over-dispersion caused by processes producing excess zeros (Potts and Elith, 2006). Densities were rounded to the nearest integer to satisfy the discrete nature of the Poisson distribution. I performed all statistical analyses with the statistical software R version 2.14 with the packages car, glmmADMB, lme4, sfsmisc, and vegan.

RESULTS

Leaf litter breakdown rate differed among leaf species (ANOVA, F=31.7, df=3), crayfish presence (ANOVA, F=13.9, df=1), and the interaction between species and crayfish presence (ANOVA, F=5.1, df=3) (Table 1). Results of mixed-effects models do not include p-values due to uncertainty in residual degrees of freedom (Pinheiro and Bates, 2000). Seepwillow leaves decomposed faster than cottonwood, willow, and saltcedar (Tukey-Kramer post-hoc test: $p<0.01$ for all three), but there were no significant differences between the other three species (Table 2). Breakdown rates of all species were higher at the warmer Charleston than at Grayhawk Ranch (Tukey-Kramer post-hoc test, $p<0.01$). Virile crayfish presence did have a significant effect on breakdown rates across species (Tukey-Kramer post-hoc test, $p<0.01$); however, direct comparisons revealed that virile crayfish significantly increased the breakdown rate only of saltcedar (Tukey-Kramer post-hoc test, $p<0.01$) (Figure 3). Crayfish caused saltcedar breakdown rate to differ from willow (Tukey-Kramer post-hoc test: p=0.04), but not from seepwillow (Tukey-Kramer post-hoc test: p=0.07) or cottonwood (Tukey-Kramer post-hoc test: p=0.42) (Figure 4).

Periphyton AFDM was not significantly different between crayfish and non-crayfish cages (t=-1.1, df=27, p=0.27) or between leaf litter treatments (t=-1.3, df=27, p=0.20). Growth of virile crayfish in cages did not differ significantly across sites (ANOVA: F=3.0, df=1,10, p=0.11), leaf litter treatments (ANOVA: F=3.0, df=1,10, p=0.12), or the interaction between the two variables

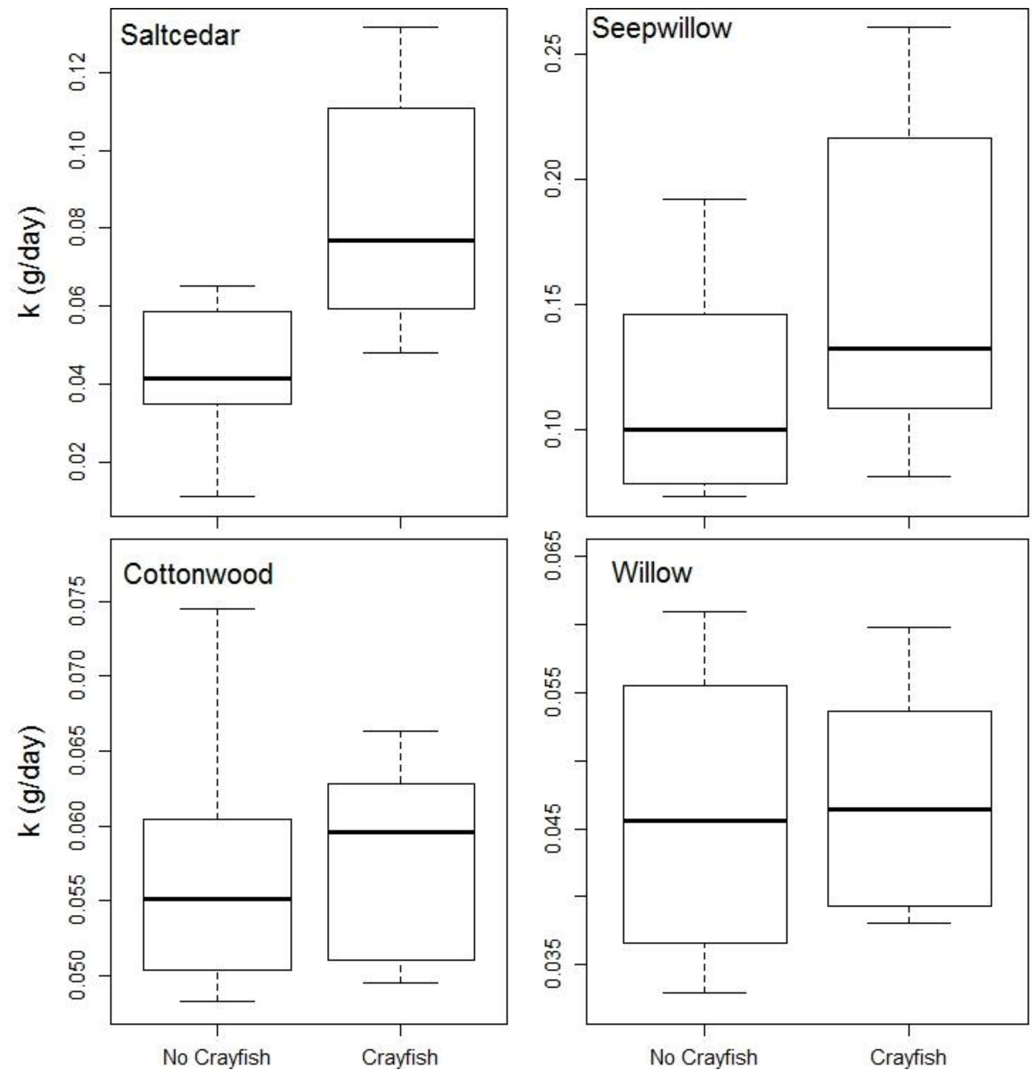

Figure 3. Effect of virile crayfish presence on breakdown rate (k) of four species of leaf litter. Crayfish significantly increased breakdown rate of saltcedar (Tukey-Kramer post-hoc test, p<0.01), but did not impact breakdown of seepwillow (Tukey-Kramer post-hoc test, p=0.59), cottonwood (Tukey-Kramer post-hoc test, p=1.00), or willow (Tukey-Kramer post-hoc test p=1.00).

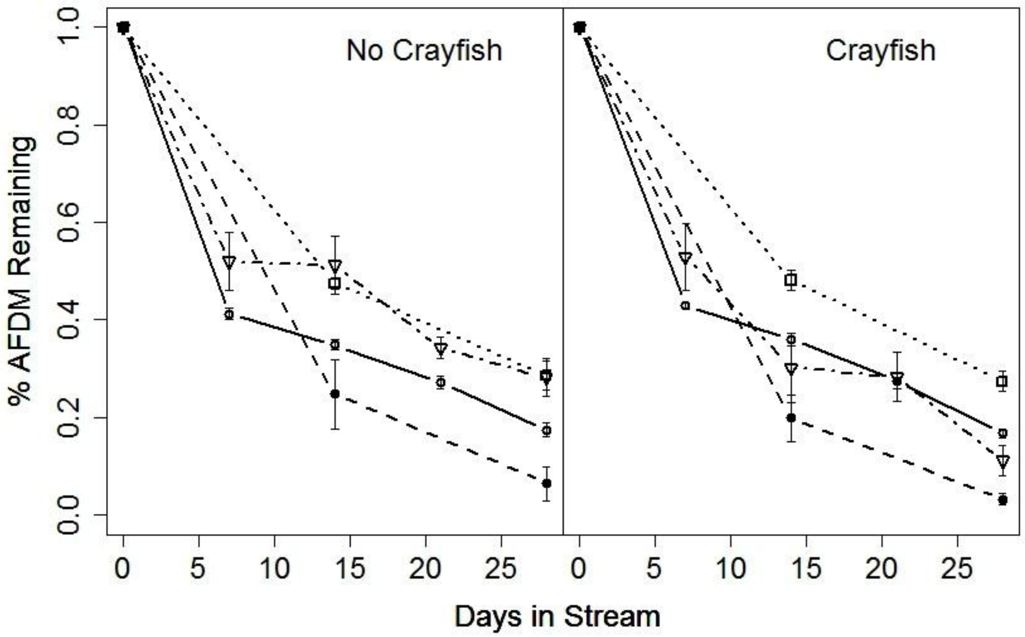

Figure 4. Mean percentage ash-free dry mass (AFDM) of leaves (±SE) from four different riparian species remaining over time in the presence and absence of virile crayfish. ○=Cottonwood, □=Willow, ●=Seepwillow, ▼=Saltcedar.

Table 1.

ANOVA table for breakdown rate of leaf litter by species and virile crayfish presence. P values are not presented due to uncertainty in calculating the denominator degrees of freedom (Pinheiro and Bates, 2000).

Factor	Df	SS	MS	F
Leaf Species	3	9.906	3.302	31.674
Crayfish Presence	1	1.446	1.446	13.874
Leaf Species*Crayfish	3	1.605	0.535	5.131

Table 2.

Tukey-Kramer post-hoc test results for the generalized mixed model of leaf litter breakdown.

Comparison	Difference	p
Crayfish-No Crayfish	0.301	**0.003**
Saltcedar-Cottonwood	0.016	0.999
Saltcedar-Willow	0.235	0.315
Seepwillow-Cottonwood	0.816	**<0.001**
Seepwillow-Willow	1.034	**<0.001**
Seepwillow-Saltcedar	0.800	**<0.001**
Willow-Cottonwood	0.218	0.378

(ANOVA: F=1.9, df=1,10, p=0.20). There was a trend of higher growth in drought-tolerant litter cages (mean±SE: 1.4%±0.32) than hydric litter cages (mean±SE: 0.78%±0.29) (Appendix 3) and at the warmer Charleston site.

No predictor vectors were significantly correlated with the ordination (Table 3). Virile crayfish presence was not a significant predictor of beta diversity of invertebrates (MANOVA: F=1.3, df=1,29, p=0.30), but litter treatment was a significant predictor (MANOVA: F=2.6, df=1,29, p=0.04) (Table 4). Examining trends in particular taxa reveals taxon-specific responses to changes in litter and virile crayfish presence (Figure 5). The mayfly *Leptohyphes* (r=0.56), physid snails (r=0.55), tabanid larvae (r=0.34), and coenagrionid damselfly naiads (r=0.34) all exhibited strong positive correlations with NMDS Axis 2 (Table 5), which most closely corresponded with drought-tolerant litter and crayfish absence. On the other hand, non-predatory midge larvae (r=-0.49), predatory midge larvae (r=-0.44), and the amphipod *Hyalella* (r=-0.41) exhibited strong negative correlations with NMDS Axis 1 (Table 5), which corresponded most closely with hydric leaf litter.

Although it is clear that there were taxon-specific responses, examining impacts of treatments on functional groups can provide insight into how ecosystem function may be affected by the treatments. No treatments significantly predicted collector-gatherer densities in the generalized mixed model (Table 6). On the other hand, virile crayfish had a significant positive impact on predator

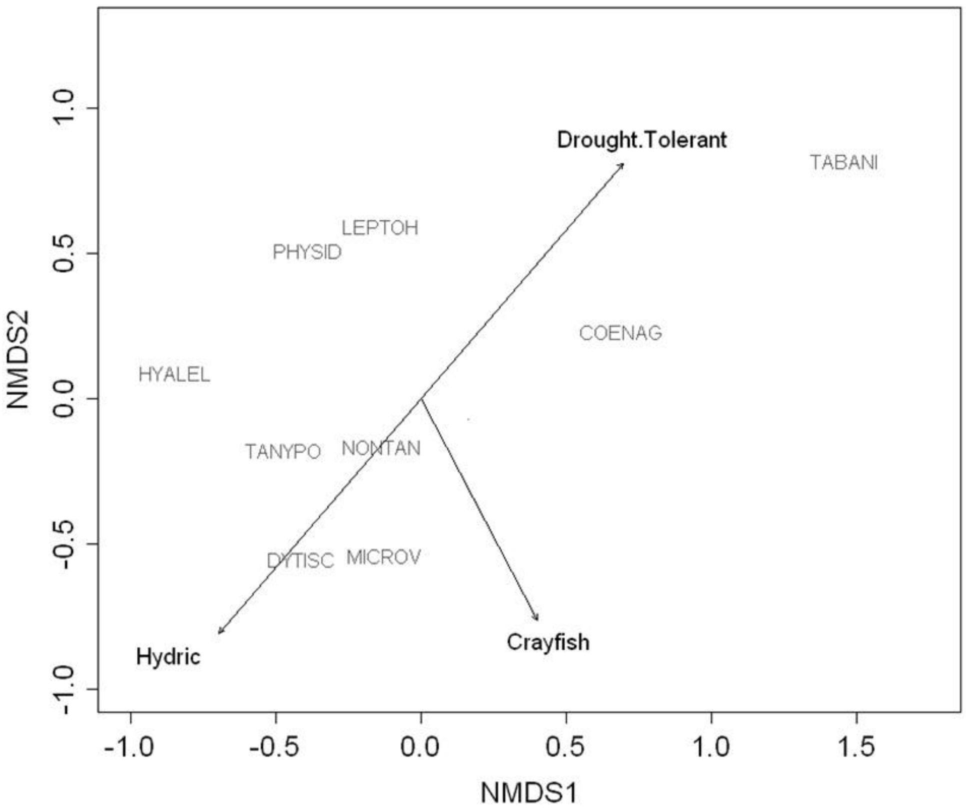

Figure 5. Non-metric multidimensional scaling (NMDS) of invertebrate density from leaf litter bags. Gray names represent distinct taxonomic groups (Appendix 5), and black names and vectors represent environmental predictors Length of arrows for predictors indicates significance and direction represents correlation with NMDS axes according to a random permutations test with 4999 permutations. Abbreviations are as follows: COENAG – Coenagrionidae, DYTISC – Dytiscidae, HYALEL – *Hyalella*, LEPTOH – *Leptohyphes*, MICROV- *Microvelia*, NONTAN – Non-Tanypodine Chironomidae, PHYSID – Physidae, TABANI – Tabanidae, TANYPO – Tanypodine Chironomidae.

Table 3.

Significance of predictor variables in the non-metric multidimensional scaling (NMDS) ordination of invertebrate densities from leaf litter bags. P values are based on a random permutations test using 4999 permutations.

Predictor	NMDS1	NMDS2	p
Hydric Litter	-0.652	-0.758	0.242
Drought-Tolerant Litter	0.652	0.758	0.242
Crayfish	0.466	-0.885	0.390

Table 4.

ANOVA table for multivariate ANOVA with Bray-Curtis distance matrices for beta diversity of arthropod communities colonizing leaf litter bags on the fourth and final week of incubation. ANOVA was run over 4999 permutations. Site was included as a random effect.

Predictor	**Df**	**SS**	**MS**	**F**	**p**
Crayfish	1	0.134	0.134	1.278	0.298
Litter	1	0.278	0.278	2.649	**0.043**
Residual	29	3.041	0.105		

Table 5.

Pearson's correlation coefficients (r) between density of taxa and NMDS axes. All taxa/axis correlations with r>0.3 or <-0.3 are shown.

NMDS Axis	**Taxon**	**r**
Axis 1	Coenagrionidae	0.490
	Tabanidae	0.470
	Physidae	-0.315
	Hyalella	-0.407
	Tanypodinae	-0.437
	Non-Tanypod Chironomidae	-0.488
Axis 2	*Leptohyphes*	0.557
	Physidae	0.553
	Tabanidae	0.341
	Coenagrionidae	0.339
	Dytiscidae	-0.309

Table 6.

Significant predictors for zero-inflated Poisson mixed models of invertebrate density (per gram AFDM leaf litter) from litter bags. Coefficients and z values represent change relative to drought-tolerant litter without virile crayfish present.

Collector-Gatherers

Predictor	**Coefficient Estimate**	**SE**	**z**	**p**
Hydric Litter	0.134	0.416	0.32	0.75
Crayfish	-0.127	0.345	-0.37	0.71
Crayfish*Hydric	-0.093	0.461	-0.20	0.84

Predators

Predictor	**Coefficient Estimate**	**SE**	**z**	**p**
Hydric Litter	-0.508	0.267	-1.91	0.06
Crayfish	0.339	0.135	2.51	**0.01**
Crayfish*Hydric	-0.406	0.230	-1.76	0.08

Scrapers

Predictor	**Coefficient Estimate**	**SE**	**z**	**p**
Hydric Litter	-0.593	0.290	-2.05	**0.04**
Crayfish	0.229	0.250	0.92	0.36
Crayfish*Hydric	-0.688	0.420	-1.64	0.10

density (z=2.5, p=0.01). Hydric litter had a significant negative impact on scraper density (z=-2.05, p=0.04). There was also a trend towards a negative impact on predator density (z=-1.9, p=0.06) (Table 6). There were insufficient *Hyalella*, the only shredders present, to fit a model.

DISCUSSION

As global change shifts species distributions, novel predators, competitors, and resources will increasingly dominate aquatic communities leading to interactions between novel species and historical communities. A primary driver of novel vegetation community establishment along desert rivers is the alteration of native flow regimes (Stromberg et al., 2007). The impacts of these changes will become increasingly important as streamflow declines due to increased human water use and projected warming and drying in the Southwestern United States (Sabo et al., 2010b; Seager et al., 2007; Serrat-Capdevila et al., 2007). Novel consumers, such as omnivorous crayfish, may be poised to capitalize on novel resource inputs which in turn may directly and indirectly affect other invertebrate consumers. In this experiment virile crayfish increased the breakdown rate of saltcedar leaves but did not impact breakdown of the other three species studied. While virile crayfish did not directly alter macroinvertebrate density or community composition through predation, they caused changes in community structure by altering organic matter resources (Figure 6). Since the leaf litter treatment was a significant predictor of invertebrate beta diversity, changes in leaf litter composition can have noteworthy effects on the composition of semiarid stream benthic communities.

Contrary to predictions, virile crayfish did not increase the breakdown rate of all species; only saltcedar decayed faster in the presence of crayfish. These

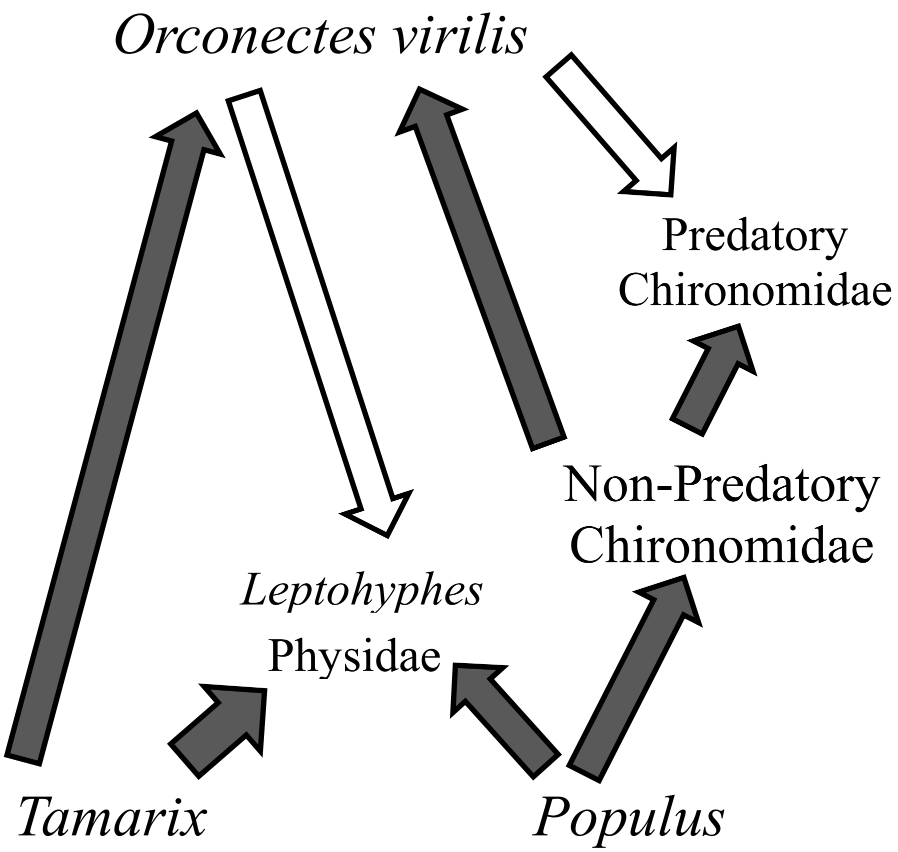

Figure 6. A hypothetical benthic food web for the San Pedro River based on results of this experiment. Dark arrows show the direction of direct energy flow and light arrows show the direction of indirect impacts via shared resources.

findings suggest that virile crayfish may not function as detritivores in semiarid streams to the same extent that was originally hypothesized (per Larned et al., 2003; Bobeldyk et al., 2010), but clearly indicate their potential to use novel resources, perhaps compensating for novel organic matter inputs into these systems. Virile crayfish are native to the upper Midwestern United States and Canada, where riparian vegetation varies but includes species of willow (*Salix*) and poplar (*Populus*), but not saltcedar (*Tamarix*) or seepwillow (*Baccharis*) (Charlebois and Lamberti, 1996, Predick and Stanley, 2010). Despite the fact that virile crayfish co-evolved with species closely related to native hydric species along the San Pedro River, they had the greatest impact on saltcedar with which their native range does not overlap. In tests with live aquatic macrophytes, crayfish foraging decisions were based on a number of factors including plant structure, nutrient contents, and secondary metabolites (Cronin et al., 2002). While this study used senescent leaves rather than live plant material, these factors were likely all important in determining crayfish feeding preferences.

As shredders were rare, crayfish themselves were the primary factors influencing change in breakdown rates between treatments. While omnivorous macroconsumers do not always increase litter breakdown rates in the absence of shredders (e.g. Rosemond et al., 1998), exclusion experiments in Hawaiian streams where native shredders are absent revealed introduced red swamp crawfish as the only invertebrates feeding on leaf litter (Larned et al., 2003).

However, omnivorous macroconsumers can be important drivers of leaf litter breakdown even when shredders are abundant (Coughlan et al., 2010).

As predicted, crayfish also had strong indirect impacts on macroinvertebrate community composition through their effects on organic matter. The leaf litter treatment was a significant predictor of beta diversity at the finest taxonomic resolution as well as for the FFG scrapers (physid snails). Examining crayfish and litter effects at fine taxonomic scales (i.e., below family level) provides the clearest insight into how these factors affect community structure. The invertebrate community colonizing litter bags was dominated by groups feeding on fine detritus and algae, but there were distinct responses from different taxa within these groups. *Leptohyphes* mayflies and physid snails both exhibited strong positive correlations with NMDS Axis 2 in the direction of drought-tolerant litter and to a lesser extent negative correlations with NMDS Axis 1 in the direction opposite crayfish presence. Surprisingly, virile crayfish did not have a significant impact on scrapers (physid snails) in the mixed model or the NMDS despite the fact that gastropods often decline in temperate systems invaded by crayfish (Lodge et al., 1994; McCarthy et al., 2006). On the other hand, non-predatory midge larvae correlated more closely with NMDS Axis 1 in the direction opposite crayfish presence.

In a litter breakdown comparison that did not test crayfish impacts, Bailey et al. (2001) found no difference in density of leptohyphid mayflies, baetid mayflies, or amphipods between cottonwood and saltcedar litter bags incubated for three weeks providing further support that these groups can readily use both species as habitat and/or food resources. Generalist collector-gatherers and shredders such as *Leptohyphes* and *Hyalella* often respond indirectly to changes in total resource availability (e.g., Flecker, 1992). In contrast, Bailey et al. (2001) found chironomids, which were not divided into subfamilies, to be less abundant in saltcedar bags than cottonwood bags after three weeks. My results corroborate those of Bailey et al. (2001) in that novel resources in desert streams (i.e., saltcedar and seepwillow) are readily colonized by generalist consumers but certain specialists will be negatively affected by their establishment.

These results provide a preliminary sketch of the impact of the interactions between novel consumers and novel resources in semiarid stream ecosystems. However, several caveats are worth discussion. The timing of this study corresponded with the presence of small YOY virile crayfish at one of our study sites, which were able to pass through cages. Studies of ontogeny of other crayfish species have indicated YOYs to be primarily predatory in contrast to omnivorous, large crayfish (Bondar and Richardson, 2009). While these YOY crayfish likely had some effect on experimental results, they did not appear to significantly influence the primary questions tested and thus were treated as colonizing predators rather than additional omnivorous crayfish. Although virile crayfish appear to have strong effects on the decomposition of some species of litter, these effects may be overshadowed by downstream export in floods. Specifically, monsoonal flooding may export a large fraction of coarse particulate organic matter downstream (Schade and Fisher, 1997) subsequent to the dynamics observed in this experiment. Future work should integrate flood disturbance and the effect of floods on OM budgets in this context.

My research provides insight into differences in breakdown rate between species along this gradient of drought tolerance. In this study seepwillow leaves decomposed faster than leaves of any other species. Seepwillow is not generally considered in studies of litter breakdown in arid and semiarid streams (e.g., Bailey et al., 2001; Pomeroy et al., 2000; Schade and Fisher, 1997), yet it is a relatively abundant riparian plant in these systems (Stromberg et al., 2010; Vandersande et al., 2001). While most authors focus on the contrast between cottonwood and saltcedar (e.g., Bailey et al., 2001; Moline and Poff, 2008), seepwillow may also become a more abundant resource as it is also more tolerant of drought than cottonwood and willow (Vandersande et al., 2001). In the absence of virile crayfish, there was no difference in breakdown rate between the remaining three species of leaves. This finding contrasts with previous reports that saltcedar decomposes more slowly (Pomeroy et al., 2000) or rapidly (Bailey et al., 2001) than cottonwood in aquatic systems. These results highlight the fact that differences in breakdown rate between these two species are context-dependent. As was evidenced by this study, the presence of generalist consumers that can use novel saltcedar inputs can significantly alter the rate at which those resources break down in the system.

My study highlights the importance of interactions between novel resources and novel consumers. The presence of these types of interactions in the system supports the idea that management approaches to introduced populations should consider the whole ecosystem rather than a singular species in isolation (Zavaleta et al., 2001). While native species do sometimes outcompete introduced competitors for novel resources (e.g., Olden et al., 2009), new species in systems without native analogs are highly likely to use novel resources successfully. Historically, there were no native omnivorous decapods in streams of the Colorado River basin, thus introduced crayfish fill this role. These novel consumers may rely on novel resource inputs. Kennedy et al. (2005) found that introduced crayfish abundance declined significantly after saltcedar was cleared from a desert spring. While saltcedar was the dominant litter input into that system and was not replaced by any litter inputs following clearing, this finding still indicates the strong potential for introduced crayfish to benefit from novel drought-tolerant litter resources in desert streams. As surface water flow becomes increasingly variable, novel communities based on drought-tolerant litter and organisms like crayfish that consume it may also increase in abundance. Long-term studies of the entire community must be conducted to understand fully the impacts of introduced crayfish and riparian vegetation changes in semiarid streams.

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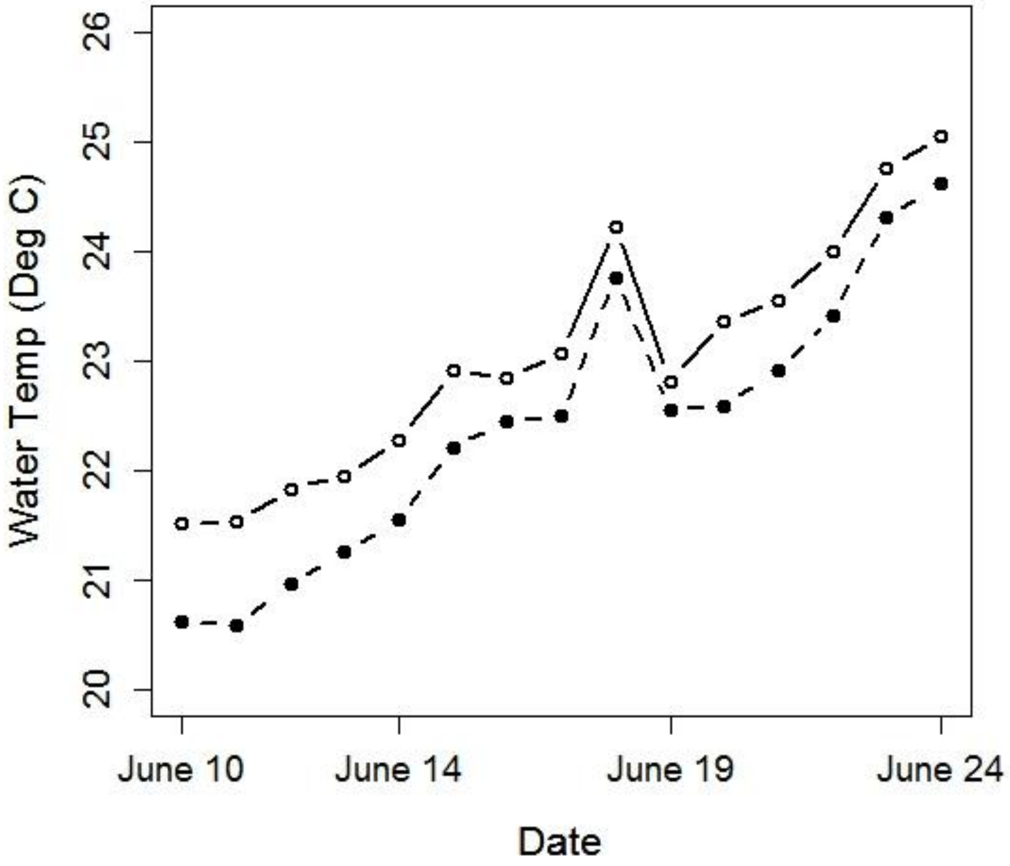
APPENDIX A

WATER TEMPERATURES AT THE STUDY SITES THROUGHOUT THE STUDY PERIOD



Water temperatures taken by a HOBO Water Temp Pro v2 temperature logger at Charleston (open circles) and Grayhawk Ranch (closed circles). Temperatures were recorded between June 10 and June 24, 2011.

APPENDIX B

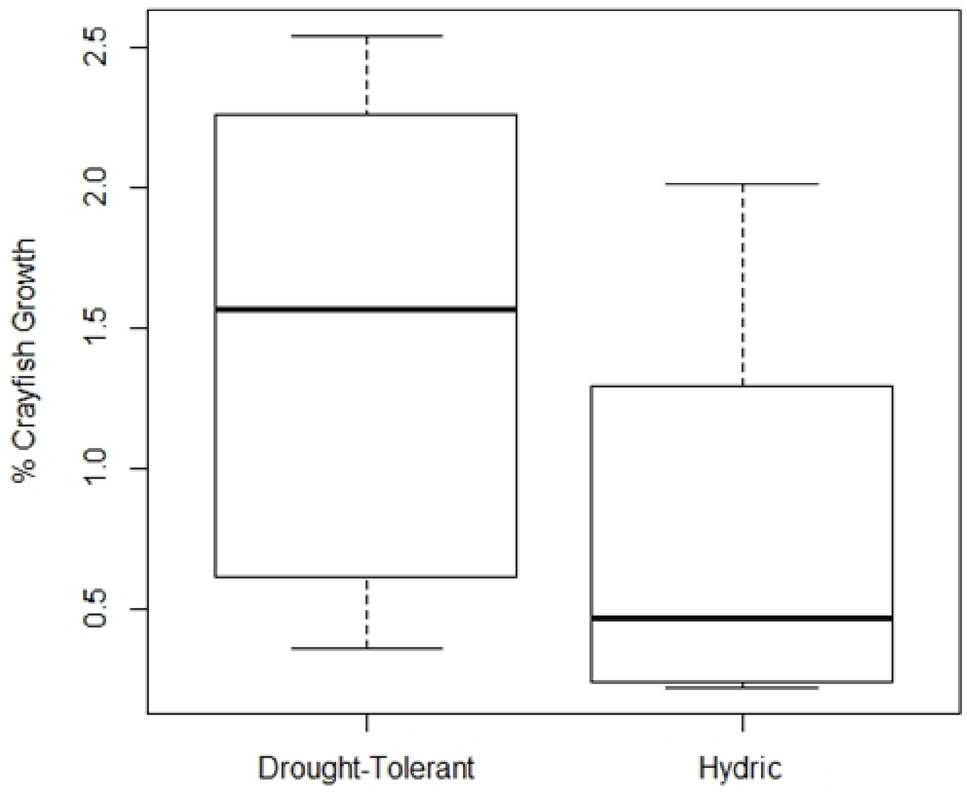
CATCH PER UNIT EFFORT OF TWO CRAYFISH SPECIES FROM THE SAN PEDRO RIVER

Species	**Backwater**	**Pool**	**Riffle**	**Run**
Orconectes virilis	4.6	3.9	0.8	6.9
Procambarus clarkii	0.2	0	0	0

Catch per unit effort (CPUE) of two species of crayfish from four different habitats in a study reach (Grayhawk Ranch) of the San Pedro River. CPUE reflects catch of ten traps set overnight in each habitat baited with canned cat food between June 20-30 of both 2010 and 2011.

APPENDIX C

VIRILE CRAYFISH GROWTH IN CAGES WITH DIFFERING LITTER TREATMENTS



Percent growth of crayfish after four weeks in cages with drought-tolerant and hydric leaf litter bags. There was no significant difference in percent growth between treatments (Two-factor ANOVA: F=2.962, df=1,10, p=0.116).