

NOVEL TEMPORARY AQUATIC HABITATS AND DESERT INVERTEBRATE COMMUNITIES

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Abstract.—The addition of desert water developments alleviates water stress for a variety of organisms and is likely necessary for some species as water availability from other isolated water sources declines with climate change. However, constructed water catchments are different structurally and do not cycle water the same way as natural sites. We assessed whether these novel habitats, the constructed catchments of the Sonoran Desert, function as ecological equivalents of the natural waters and evaluated their effects on macroinvertebrate biodiversity, community composition, and trophic function. We documented an accumulation of ammonia and less diversity and different taxa assemblages in the novel habitat. We also documented a more heterotrophic food web in the natural water basins that are more dependent on resource pulses, and a more autotrophic food web in novel habitats that are more dependent on primary production from the open catchment basin. As natural resource managers continue to add constructed waters to mitigate for climate change induced declines in water availability, organisms are more likely to encounter these novel habitats as they disperse. Consequently, by increasing the density of these novel habitats we are having a measurable effect on the types of species and trophic groups present as well as the ecosystem cycling of energy and nutrients across the desert landscape. The consequences of these shifts in invertebrate community composition and ecosystem cycling on the larger desert ecosystem is unknown.

Keywords: ephemeral wetland, biodiversity, community ecology, tinaja, trophic function

Isolated desert wetlands that hold water ephemerally, such as the Sonoran Desert tinajas (erosional rock pools), are defined by limited water availability and resource pulses and are critical habitat for many organisms in arid systems. These water locations support concentrations of biodiversity (Bunn et al. 2006; Williams 2006) and provide habitat connectivity for species traversing the desert environment (McIntyre et al. 2016; Drake et al. 2017). These waters tend to have relatively short hydroperiods (days to months), so only quickly developing organisms can take advantage of the sites for breeding habitat and the communities tend to be simplistic (Wellborn et al. 1996; Bogan et al. 2015). The availability of this type of habitat

Recommended citation:

Griffis-Kyle, K.L., A. Eckhardt Parker & J. Goetting. 2019. Novel temporary aquatic and desert communities. *Texas J. Sci.* 71: Article 5. https://doi.org/10.32011/tjxsci_71_1_Article5.

is controlled by abiotic ephemeral pulses of rain that significantly alter resource availability in time and space (Yang et al. 2008; Tonkin et al. 2017), purging the basin of debris and providing resource subsidies that cause bottom-up trophic cascades (Nakamura et al. 2005). The pulsed nature of the disturbances and subsidies and the ephemeral character of the wetlands in the dry environment strongly influence consumer-resource interactions (Yang et al. 2010), promote diversity (Chesson et al. 2004; Bunn et al. 2006), and drive natural selection (Junk et al. 1989; Williams 2006).

Hydroperiods are declining as a result of the more variable weather caused by climate change (Seager et al. 2007; Cayan et al. 2010; IPCC 2014). Natural resource managers are taking actions to mitigate for changing weather patterns and support wildlife and livestock populations by providing reliable sources of water (e.g. constructed catchments with water storage reservoirs, AZGFD 2014) (Krausman et al. 2006). These constructed waters may function as novel isolated habitat because of differences in disturbances, resource pulses, and hydroperiod as compared to tinajas; and consequently, may support a different biological community than the similarly distributed natural habitat, tinajas (e.g. Chiroptera, Rosenstock et al. 2004; Odonata, Griffis-Kyle et al. 2014; *Ovis canadensis nelsoni*, Calvert 2015). Previous work suggests that at least some species of desert organisms do not assess habitat quality of isolated waters when selecting breeding habitat (Kiesow & Griffis-Kyle 2017), but most species have not been studied. However, if other aquatic species also select for any water available, differences in the structure and function of novel constructed habitat as compared to the natural habitat have the potential to cause population level consequences in other species dependent on these waters.

Differences in disturbances and resource pulses between natural and novel habitats can cause differences in ecosystem function and can lead to distinct biodiversity, community composition and natural selection (van Nes & Sheffer 2004). The structures of the isolated desert waters, the ephemeral tinajas and constructed catchments, likely have a large effect on the hydroperiod and chemical attributes

in the water. Structurally, tinajas are basins of various depths, often in ephemeral stream beds, that are dry for much of the year. Rainstorms create flash floods (disturbances and resource pulses) in these streams which flush decayed organic matter and sediments out of the basins and deliver resource subsidies. These subsidies arrive as vegetation, vertebrate and invertebrate carcasses, and other detritus and provide the backbone of the trophic network in these ephemeral pools. Conversely, the constructed catchments are designed to capture and store water in large covered or buried reservoirs and to minimize evaporation by using relatively small troughs that organisms can access for drinking. These constructed systems have longer hydroperiods and are not purged during rainstorms; and because they are not purged, there is an accumulation of decaying organic matter (see Lindeman's (1942) anaerobic detrital 'ooze'). The accumulation of decaying organic matter tends to support a build-up of algae (Rosenstock et al. 2004), especially as there is little disturbance to disrupt the growth.

These differences in hydroperiod and resource pulses create very different environments. Depending on species' abilities to select habitat, the addition of constructed sites may provide opportunities for novel communities to form through either differences in habitat selection or differences in evolutionary trajectories (Yeh 2004), especially for organisms like macroinvertebrates that use these sites as habitat for all or part of their life cycle. Invertebrates are excellent indicators of wetland function and give insights into the processes of ecosystem function and natural selection (Balcombe et al. 2005). Consequently, our goal was to describe and assess aspects of aquatic macroinvertebrate diversity, community assemblage, and trophic role to evaluate if the constructed desert waters function as ecological equivalents to the natural desert waters they resemble or if they provide a unique habitat type in this arid system.

MATERIALS & METHODS

To assess the ability of constructed catchments to ecologically mimic tinajas, we sampled natural and constructed water sites

managed for wildlife by Arizona Game and Fish Department during July through October of 2010 and 2012 in southwestern Arizona on the Barry M. Goldwater Range – East, managed by the U.S. Air Force. The study area was 4249 km² of Sonoran Desert characterized by a biphasic rainfall (monsoonal and winter rains). The natural sites were located in ephemeral streams receiving no spring flow, only flowing in response to heavy rainfall.

We visited 23 water sites (8 tinajas and 15 catchments; Fig. 1) on the Barry M. Goldwater Range during the summers of 2010 and 2012. We sampled open water areas of the catchments for this project. If we had a full set of invertebrate and site data for water body, that site was included in our analysis. This resulted in us analyzing the invertebrate data from 13 water sites (6 tinajas and 7 catchments) distributed across three mountain ranges (Aguila Mountains, Sand Tank Mountains, Sauceda Mountains). Sites were excluded because restricted access by the military meant we did not have the opportunity or sufficient time to collect all the data needed for the analysis, or that the site did not have enough water to sample. We conducted sampling in July and August, after the monsoonal rains began when biodiversity at those sites is expected to be greatest (Giam et al. 2017). We used aquatic D-shaped dipnets (approximately 305 mm tall by 457 mm wide by 190 mm deep), with canvas sides and bottom 500 μ m mesh, to sample for macroinvertebrates twice each sampling period and conducted between three and ten 1-m sweeps, standardized by basin volume (three sweeps in $< 2 \text{ m}^3$, five sweeps in $3\text{-}10 \text{ m}^3$, and 10 sweeps in $> 10 \text{ m}^3$), varying the depth between sweeps so the bottom, middle and surface of the water were sampled. These sweeps were conducted around the accessible portion of the perimeter of the water body. We visually estimated floating vegetation and algal cover (no emergent vegetation was present). We measured temperature, pH, and conductivity using a hand-held probe (measured both years using MP-6p Portable Meter, Hach, Loveland Colorado, USA) and total ammonia nitrogen (TAN) and nitrate+nitrite using a portable colorimeter (measured in 2012 using HachDR/890 Portable Colorimeter Hach Company, Loveland, CO). We measured basin length, and width and depth and calculated volume and surface



Figure 1. Isolated desert waters differ in their main source of food. Ephemeral tinajas (A.) are erosional pools that are flushed out after rain events dramatically reducing the algal community and subsidized with pulses of allochthonous resources. Constructed catchments (B) are not cleaned by rains and generally contain a great deal of algae providing an autochthonous basis for the trophic network. (C) Dead organic matter such as Africanized bees, carcasses, and algae decompose leading to an accumulation of mineralized nitrogen. (D) Ammonia volatilization is limited by small surface areas in relation to volume as well as physical barriers to off-gassing such as algae. (Photo Credits: A and C - K. Griffis-Kyle, B – J Goetting, D – Joseph Drake).

area, all indices of evaporation rates. We used a spherical densiometer to measure potential shading of the water surface. Site elevation came from an Arizona Game and Fish Department (D. Urquidez, pers. comm.). To evaluate temperature fluctuations, we suspended ibuttons (Maxim Integrated, San Jose, CA) just under the water surface, recording data every five minutes from July through October 2012. We calculated nearest neighbor distance to closest other water body large enough to be managed as a wildlife water (excludes shallow basins that can dry in days) as an index of isolation for each site.

We tested for differences in water chemistry (averaged between years) and structure between tinajas and catchments (SPSS version 24), first assessing data for normality (Shapiro Wilk test) and equality of error variances (Levene's test). We used surface area as one measure as the surface area of these small basins can affect oviposition of invertebrates (Griffis-Kyle unpublished data) and is significantly related to evaporation rates. Vegetation cover (algal mats and Lemnoideae) met test assumptions and was analyzed with an ANOVA. The remaining water quality parameters were extremely skewed, so we analyzed for median differences using a Fisher's Exact Test in volume, surface area, pH, conductivity, nitrate plus nitrite, TAN, shading, elevation, and nearest neighbor distance (Ott 1993).

Following established keys (Thorp & Covich 1991; Merritt et al. 2008), we identified taxa to family or lowest possible resolution above that and recorded their trophic functional role (Cummins 1973). Trophic role was defined by how the invertebrate group foraged and included: collectors and gatherers, filterers, grazers, predators, and scrapers; those groups that had variation in trophic roles were categorized as variable. Examining relationships at families or above allows us to look at general patterns in changes in taxa rather than species differences and related species tend to be ecologically and phenotypically similar (Warren et al. 2008). This analysis is focused on the flows of energy and nutrients in the system, so there are species-specific differences (e.g. dispersal) that are missed with type of analysis. We summarized taxa abundance and presence over the two years with two visits per year at each site, counting a taxon as present if we found it at least once at a site and using the maximum abundance of that taxon at a visit measured over the two years.

We analyzed a conservative measure of biodiversity between catchments and tinajas by examining taxa richness using ordinal logistic regression (SPSS version 24) and testing attributes that varied between tinajas and catchments as determined by the previously described tests. We assessed these same relationships for Shannon's Diversity Index (H') and the Berger-Parker Dominance Index (Magurran 1988) using a multivariate general linear model as our

dependent data did not violate assumptions of normality or error variances (Shapiro Wild test and Levene's test respectively, SPSS version 24).

We used non-metric multidimensional scaling to describe patterns of community assemblage and patterns in trophic structure using R 3.4.2 and the package *vegan* (R Core Team 2017; Oksanen et al. 2017). We ordinated the presence of taxa rather than measures of abundance or biomass because abundance can vary by orders of magnitude and is extremely cyclical, so our measures could have missed the peak of a particular cycle and added noise to any patterns. We ordinated the presence of taxa and then the number of taxa in each trophic group, using the Bray Curtis coefficient to quantify the dissimilarity between sites, and fit environmental variables to the data using permutation procedures (Oksanen et al. 2017).

RESULTS

The summer sampling period was drier and cooler in 2010 than in 2012. During 2010 the area received 28.2 mm of rain (17% of that year's rainfall of 162.8 mm total); over half of the rainfall that year occurred during January and over 80% of the rainfall fell before the end of March. In 2010 the average temperature was 28.7 °C (average maximum during same period 46.0 °C) . During the summer 2012 the area received 65 mm of precipitation from July through October (100% of that year's rainfall) and averaged 33.1 °C (average maximum during same period 45.6 °C) (NOAA 2012).

We identified 18 taxa of macroinvertebrates in the desert waters: 16 from tinajas and 13 from the novel constructed catchments (Table 1). Four groups were common and found in greater than ten of the waters: Corixidae, Notonectidae, Dyticidae, and Stratiomyidae. Two groups, the Oligochaeta and Physidae were unique to constructed catchments; and five groups Daphniidae, Ostrocooda, Culicidae, Hydrachnidia, and Trichoptera were unique to tinajas. Groups only detected in 2010 included Daphniidae, Oligochaeta and Trichoptera, and groups only detected in 2012 included Ostrocooda and Hydrachnidia.

Table 1. Macroinvertebrate taxa and their trophic functional groups for Sonoran desert species found primarily in tinajas and those primarily found in the novel habitat created by constructed catchments. The proportion of sites with taxa were calculated based on the number of that water site type (tinaja or catchment) with the taxon present out of the number of that water site type that we sampled. † only found in tinajas; ‡ only found in constructed catchments.

Taxon	Year(s)	Proportion of Sites with Taxa		Trophic Processing
		Tinajas	Catchments	
Anostraca	2010, 2012	0.50	0.14	Filterer + Scraper
†Ostrocooda	2012	0.17	0	Filterer
†Cladocera: Daphniidae	2010	0.33	0	Filterer
†Trombidiformes:	2012	0.17	0	Predator
Hydrachnidia				
‡Gastropoda: Physidae	2010, 2012	0	0.29	Grazer
‡Oligochaeta	2010	0	0.14	Variable
Coleoptera: Dytiscidae	2010, 2012	0.83	0.71	Predator
Coleoptera: Hydrophilidae)	2010, 2012	0.33	0.71	Collector + Gatherer
Diptera: Chironomidae)	2010, 2012	0.5	0.71	Variable
†Diptera: Culicidae	2010, 2012	0.17	0	Filterer + Collector
Diptera: Ephydriidae	2010, 2010	0.17	0.14	Herbivore (variable)
Diptera: Stratiomyidae	2010,2012	0.83	0.71	Collector + Gatherer
Ephemeroptera	2010, 2012	0.17	0.43	Variable
Hemiptera: Corixidae	2010,2012	0.83	0.86	Variable
Hemiptera: Notonectidae	2010, 2012	0.67	1.00	Predator
Hemiptera: Veliidae	2010, 2012	0.33	0.14	Predator
Odonata: Libellulidae	2010, 2012	0.33	0.14	Predator
† Trichoptera	2010	0.17	0	Variable

Our sampling was done to maximize time when sites had water; therefore, we did not test a direct measure of hydroperiod; however, the difference between volumes of tinajas, which in this study area average less than 16 m³ ($SE = 4.2$) and catchments, including their reservoirs which average at 25 m³ ($SE = 5.3$), is captured in the categorical variable of site type. Tinajas were dry at the beginning of the rainy season, whereas no catchments were dry. Tinajas and catchments only varied significantly by TAN ($P = 0.03$, Fig. 2 A), surface area ($P = 0.02$, Fig. 2 F), shading ($P = 0.02$, Fig. 2 G), and nearest neighbor distance ($P = 0.02$, Fig. 2 H). Catchments generally had greater ammonia concentrations, smaller surface areas that were less shaded and more isolated. All other attributes were not statistically different (in all other cases $p > 0.07$; Fig. 2 B-E). However, there may be biological differences between site types that are not picked up by these statistical analyses. For example, 43% (3 of

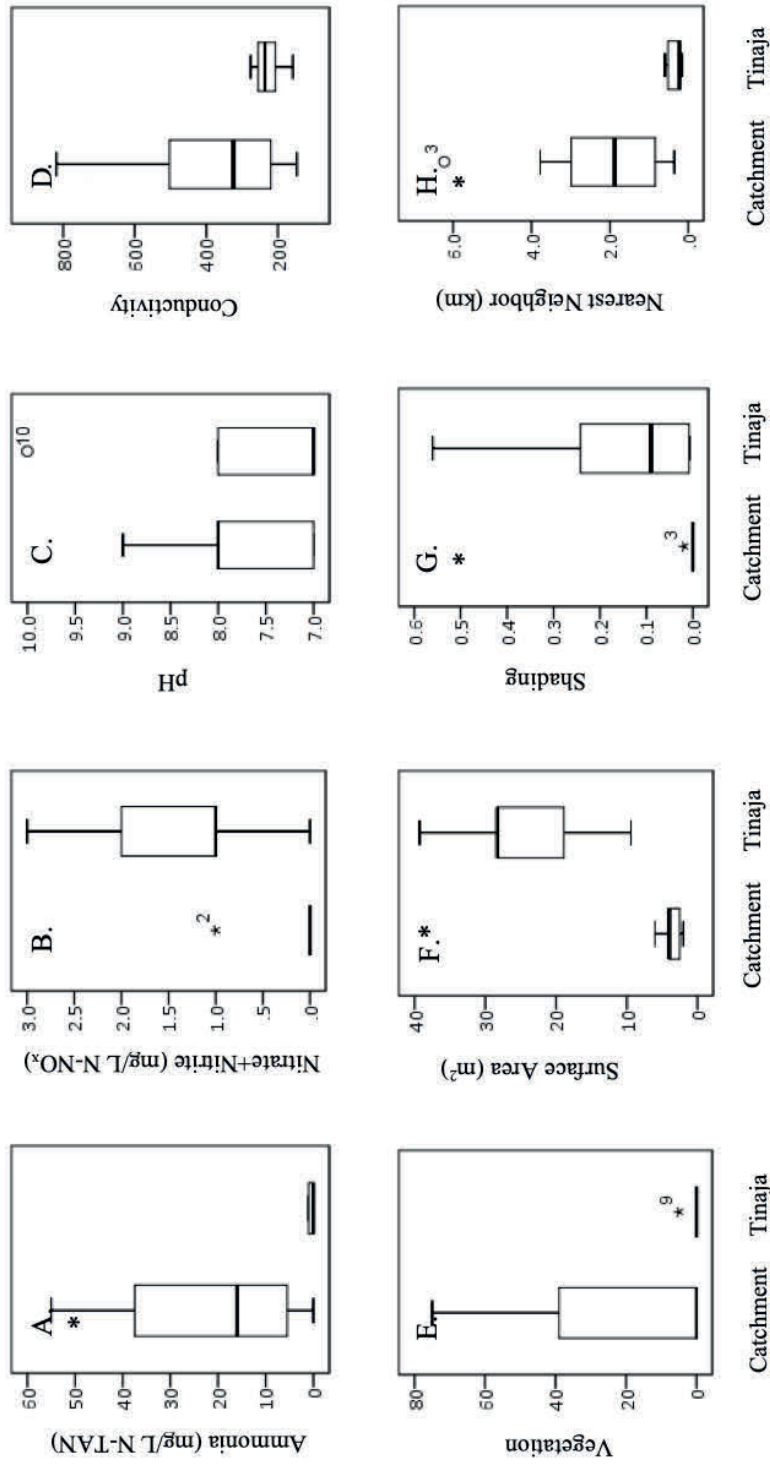


Figure 2. Comparing water site attributes. Boxes represent 1st and 3rd quartiles with the median as a line in the box. Whiskers represent largest non-outlier; outliers are represented as single points. Ammonia (A) was the only chemical parameter significantly different between the two water types. However, there may be other chemical differences not picked up through this analysis because of sample size or variability such as nitrate plus nitrite concentration (B) and conductivity (D). Tinajas had significantly more surface area (F), were more shaded (G), and less isolated than catchments (H).

7) of the catchments but only 17% (1 of 6) of the tinajas had visible vegetation (Lemnoideae) or floating mats of algae an index of primary production (Fig. 2 F), and except for one catchment at 1 mg/L N-NO₃ + NO₂ we only found detectable nitrate + nitrite concentrations in tinajas (Fig. 2 B) suggesting that nitrification (chemical cycling by bacteria changing ammonia into nitrite and then into nitrate) was functioning in the natural waters.

Temperature i-buttons disappeared from several sites, often as a result of Turkey Vultures (*Cathartes aura*) pulling them out of the water by end of the season (documented via game camera). Therefore, temperatures are based on five tinajas and three catchments (tinaja: average = 26.5°C (*SE*) = 0.8), average max 42.6°C (*SE* = 2.7); catchment average: 26.8°C (*SE* = 0.7), average max = 35.1°C (*SE* = 2.7)).

Taxa diversity did not vary by site type (Fig. 3). However, taxa richness was significantly less in sites with elevated TAN ($\chi^2 = 10.5$, *df* = 1, *P* = 0.001; Fig. 4 A), but was not significantly associated with, surface area, shading, or isolation ($\chi^2 < 0.8$, *df* = 1, *P* > 0.4; Figs. 4 and 5). The relationships were mirrored for species evenness such that Shannon's Diversity Index was also lower in sites with greater concentrations of TAN (*f* = 6.2, *df* = 1, *P* = 0.03; Fig. 4 E), but was not significantly associated with surface area, shading, or isolation (*f* < 2.0, *df* = 1, *P* > 0.2; Figs. 4 and 5). Dominance did not meet parametric assumptions because in one tinaja there were very large numbers of an order of magnitude more fairy shrimp than any other sites (visit one = 521 individuals, visit two = 784 individuals); consequently, measures of dominance, whether using parametric or non-parametric statistics show no significant relationship with TAN concentration, surface area, shading, or isolation (*P* > 0.6 in all cases; Figs. 4 and 5).

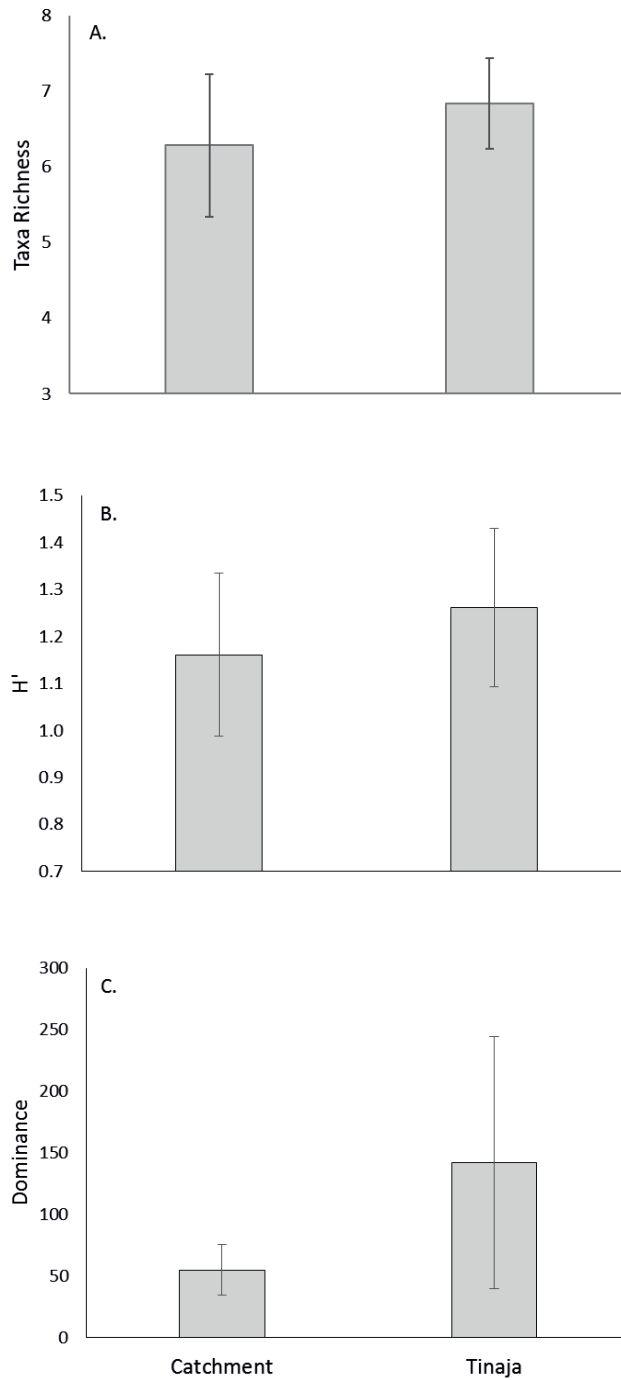


Figure 3. There was no detectable difference in invertebrate (A.) species richness, (B.) evenness (H' , Shannon's Diversity Index), or (C.) dominance (Berger-Parker Dominance Index) of taxa between the novel habitat, constructed water catchments, and tinajas in the Sonoran Desert.

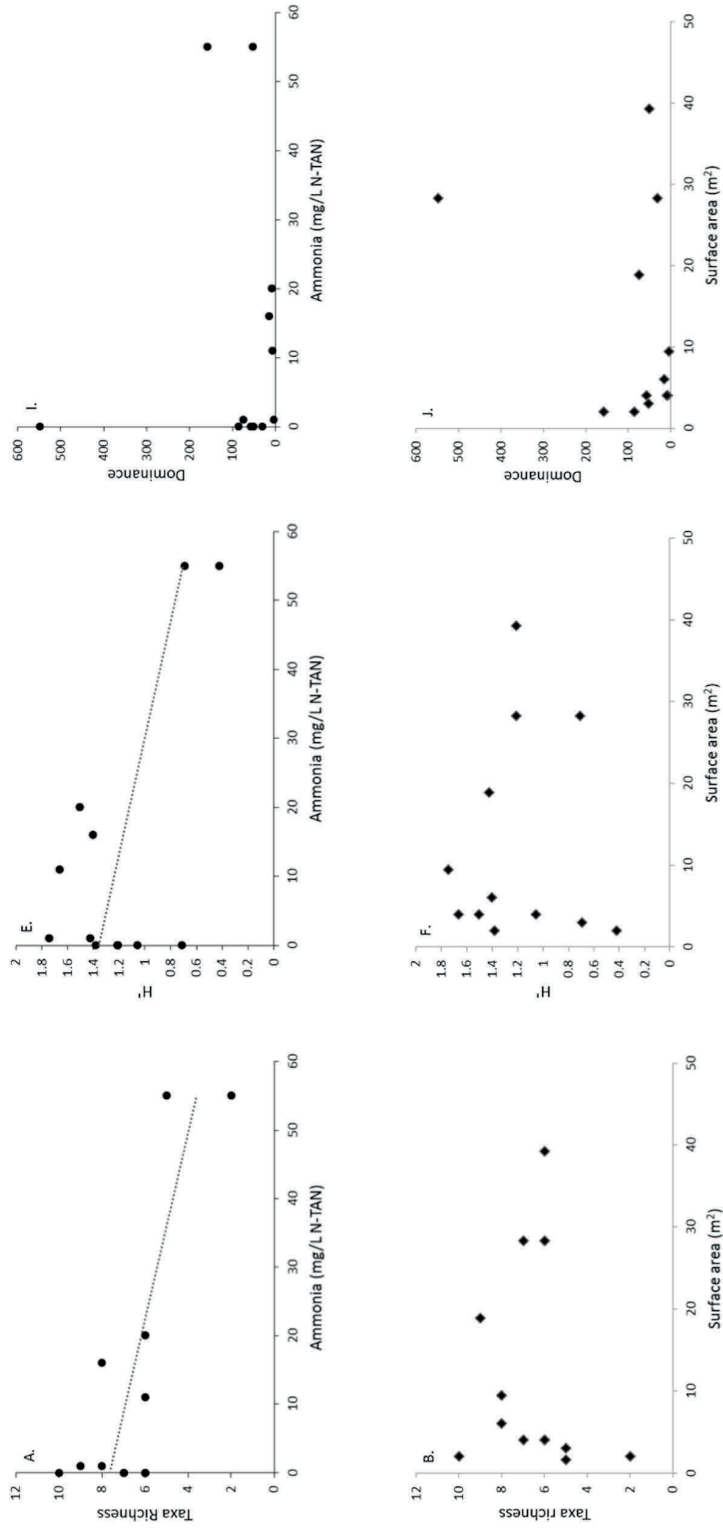


Figure 4. Effects of ammonia nitrogen (top row) and wetland surface area (bottom row) on measures of invertebrate species diversity: Taxa Richness, Shannon's Diversity Index (H'), and Berger-Parker Dominance Index (H'') in Sonoran Desert catchments and tinajas. Species Richness and Shannon's Diversity Index were both negatively correlated with ammonia. The Berger-Parker Dominance Index was not associated with either site attribute.

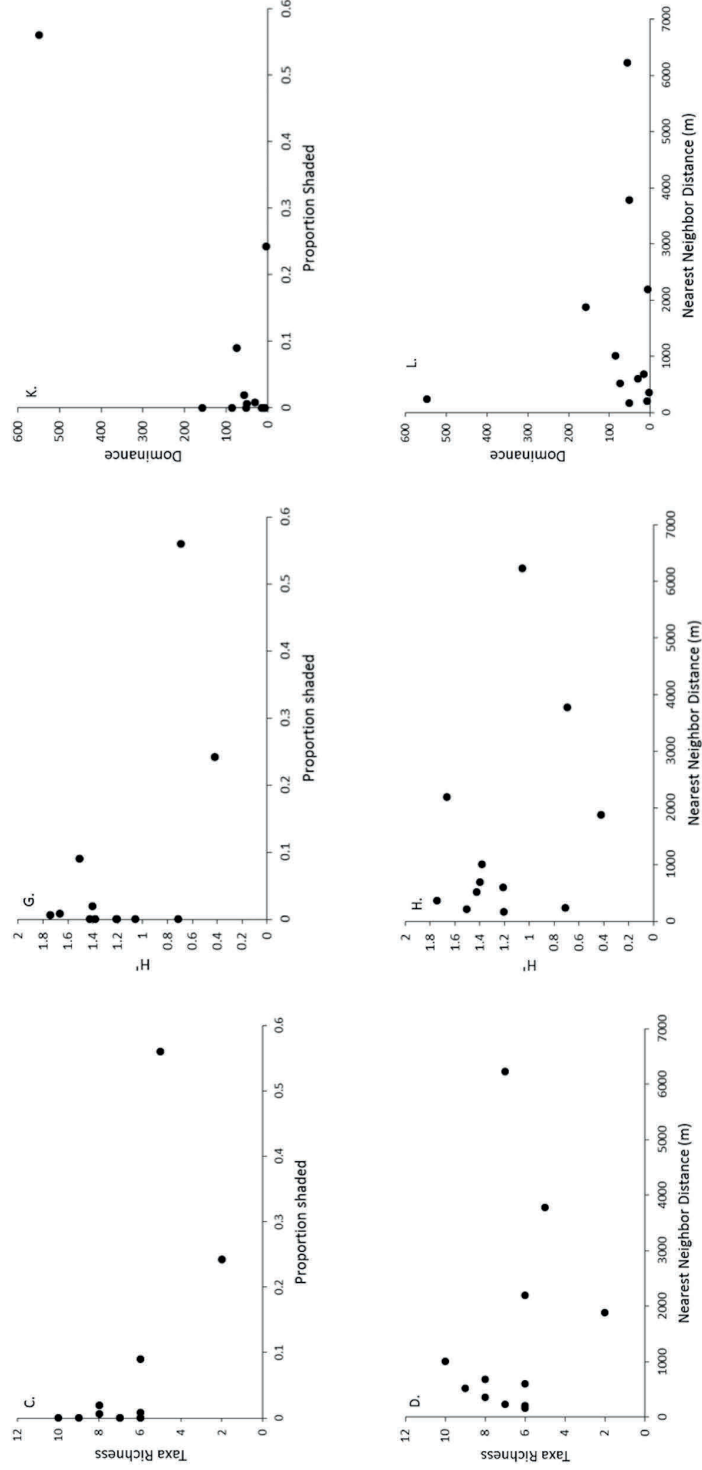


Figure 5. Effects of shading (top row) and isolation (bottom row) on measures of invertebrate species diversity: Taxa Richness, Shannon's Diversity Index (H'), and Berger-Parker Dominance Index (Dominance) in Sonoran Desert catchments and tinajas. Species Richness, Shannon's Diversity and Berger-Parker Dominance Index was not associated with either site attribute.

The non-metric multidimensional scaling identified three axes when ordinating the presence of taxa across sites (stress = 0.05, non-metric fit $R^2 = 0.99$, linear fit $R^2 = 0.99$) with 1 standard deviation (*SD*) ellipses of the tinaja sites and the novel habitat sites not overlapping (Fig. 6). Because box plots suggested biological significance in differences of water site attributes between tinajas and catchments that were not captured statistically (see Fig. 2), we used permutation tests to examine relationships between water site attributes and the distribution of species across the water sites and found taxa level associations with TAN may help control the distribution of species in the ordination (permutation test $R^2 = 0.45$, $P = 0.04$; Fig. 4). All other water site attributes were not associated with the ordination of species (in all cases $R^2 < 0.1$, $P > 0.5$).

When assessing overlap in invertebrate trophic groups in tinajas compared to catchments, the non-metric multidimensional scaling identified three axes (stress = 0.06, non-metric fit $R^2 = 0.99$, linear fit $R^2 = 0.97$) with 1 *SD* ellipses of the tinaja sites and the novel habitat sites not overlapping (Fig. 7). Total ammonia nitrogen was significantly related to the distribution of functional groups across sites (permutation test $R^2 = 0.52$, $P = 0.03$; Fig. 7). Grazers were detected more often in catchments; while filterers and scrapers were detected more often in tinajas (Table 1). Other trophic groups were found commonly in both types of waters.

DISCUSSION

Human-created novel systems, like constructed water catchments in this study, tend to differ abiotically from natural systems in ways that can lower fitness as compared to the original habitat (Shochat et al. 2006; Robertson et al. 2013; Sih et al. 2016). The constructed catchments resemble natural isolated tinajas in that they are remote relatively small pools of water but differ from the natural sites in how they catch and hold that water. These differences in processes cause

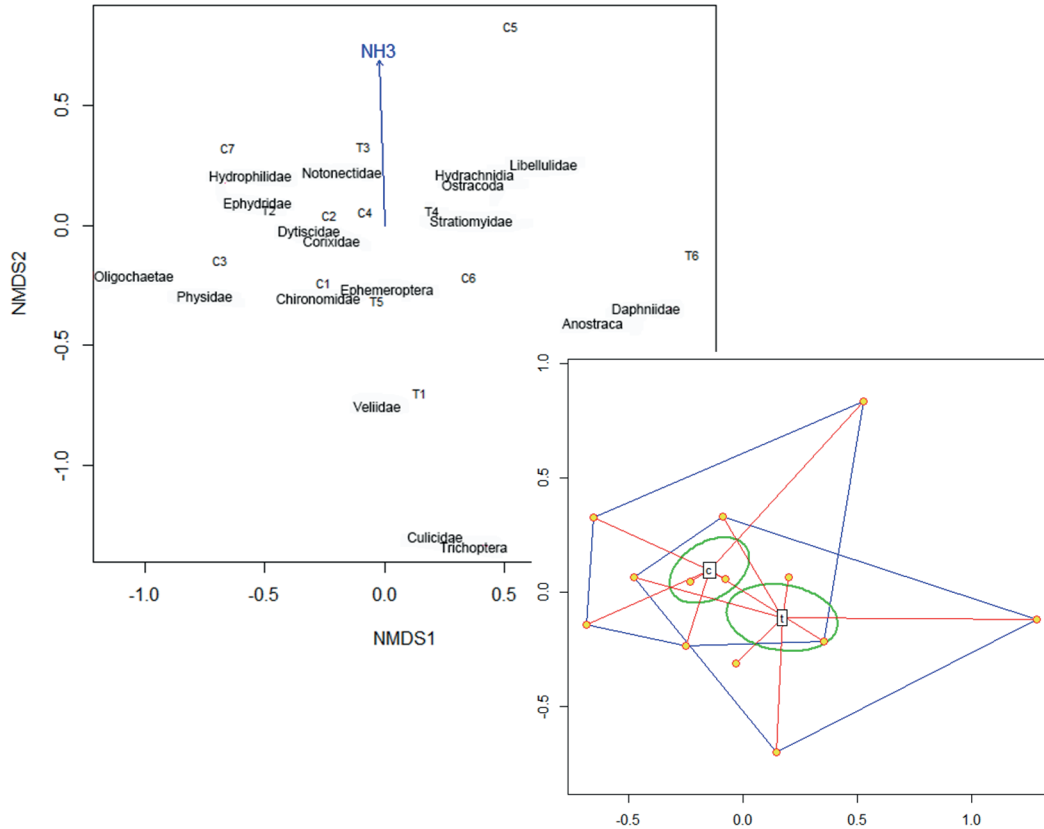


Figure 6. Presence of invertebrate taxa across catchment (C#) and tinajas (T#) water sites using non-metric multidimensional scaling. The environmental vector for total ammonia nitrogen is also plotted. Tinajas (t) and catchments (c) are shown in the inset as separate groups by green 1 SD ellipses around the mean, blue convex hulls, and red webs indicating the centroid of the group. We have also plotted ammonia, the environmental variable that influenced diversity estimates in these Sonoran Desert wildlife waters, 2012.

fundamental differences in the physical and chemical environment leading to differences in aquatic communities (Lodge et al. 1987; Wellborn et al. 1996; Stendera et al. 2012). Water catchments are designed to maximize water retention by funneling rainwater into storage reservoirs and minimizing evaporation by supplying water for terrestrial wildlife in small deep troughs. The design of these reservoirs and troughs change the nature of how rains affect the water sites. Natural sites (tinajas) generally experience flash floods during heavy rains which expel accumulated organic matter and other debris, while catchments collect and hold the rain and are not purged of the detritus. Ergo, hydroperiods are longer and there is a greater build-up

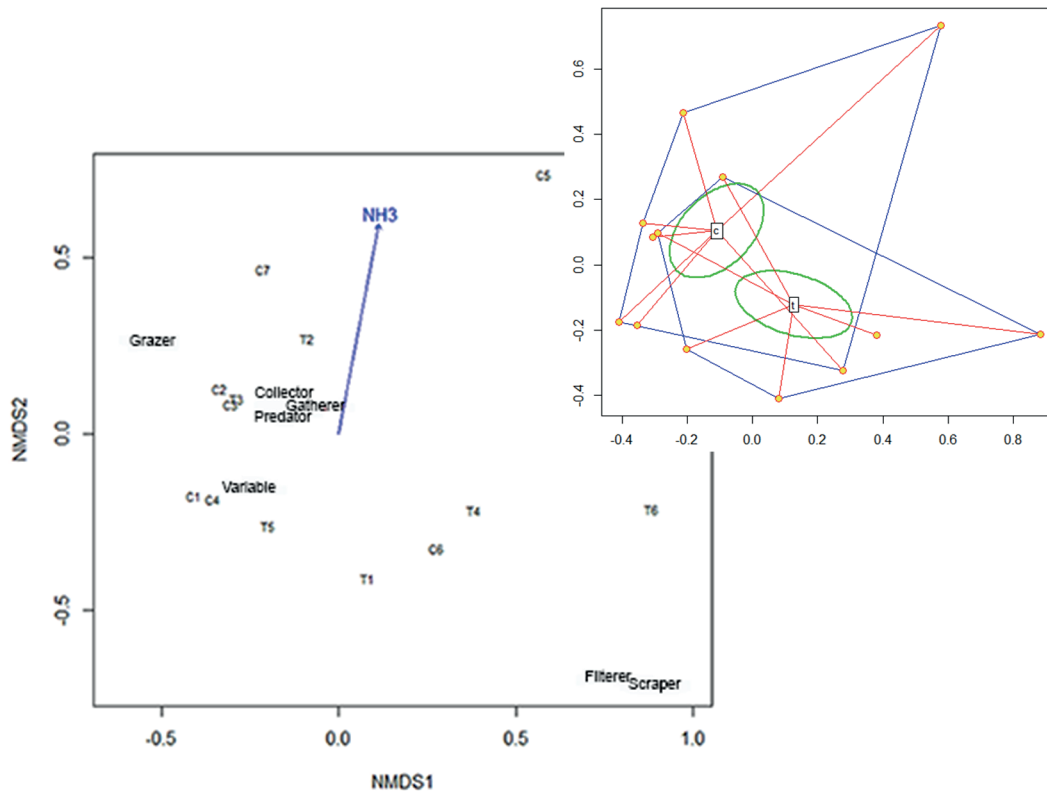


Figure 7. The number of taxa per trophic functional groups across catchments (C#) and tinajas (T#) water sites using non-metric multidimensional scaling. The environmental vector for total ammonia nitrogen is also plotted. Tinajas (t) and catchments (c) are shown in the inset as separate groups by green 1 SD ellipses around the mean, blue convex hulls, and red webs indicating the centroid of the group. We have also plotted ammonia, the environmental variable that influenced diversity estimates in these Sonoran Desert wildlife waters, 2012.

of organic matter in the constructed catchments. The decaying organic matter is mineralized into total ammonia nitrogen, and since pH averages 8.2 (and can reach over 10) and the temperatures are hot (Griffis-Kyle et al. 2014), much of this ion is present as the more toxic ammonia (Emerson et al. 1975; EPA 2013). We show this ammonia accumulates instead of volatilizing or going through nitrification, likely due in part to small trough surface areas (Fig. 1 B) and, in some cases, physical barriers to volatilization (Fig. 1 D) as well as an inhibitory feedback on mineralization (Anthonisen et al. 1976; Raszka et al. 2011). As a result, the constructed catchments accumulate ammonia at concentrations not normally seen in natural systems (Camargo & Alonso 2006), but possible in small simple waters pools

(Walker 2016). The hydrologic differences between tinajas and catchments and the resulting ammonia accumulation in the catchments create different environments for supporting aquatic biodiversity.

Aquatic organisms are susceptible to ammonia toxicity. The Environmental Protection Agency's (EPA) chronic ammonia criteria for freshwater aquatic life is listed at 1.9 mg/L TAN at pH 7.0 and 20°C. When temperatures exceed 30°C and pH is over 8.0 the criteria drop below 0.4 mg/L TAN (EPA 2013), levels much lower than those we documented in the constructed water catchments. Chronic exposure to ammonia causes a reversal in an organism's diffusion gradients and leads to a buildup of ammonia in the body's tissues (EPA 2013). This buildup of ammonia has negative consequences on fitness for both aquatic invertebrates (Goudreau et al. 1993; Hickey & Vickers 1994; Constable et al. 2003; Alonso & Camargo 2004,) and vertebrates (Alonso & Camargo 2004; Griffis-Kyle & Ritchie 2007) by interfering with respiration and feeding (Epifani & Srna 1975; Lang et al. 1987) as well as metabolism (Tomasso et al. 1980; Arillo et al. 1981; Chetty & Indira 1995; Camargo & Alonso 2006). So concentrated ammonia exposure can have large negative physiological effects on a variety of aquatic organisms.

We demonstrate that the accumulation of ammonia in the novel habitat was associated more closely with declines in biodiversity than any other site attribute. There was a decline of approximately half in taxa richness and about 40% in taxa evenness when comparing sites with no detectable ammonia and sites with the highest concentrations (Fig. 4 A and E respectively), similar to declines found in other work (Scatolini & Zedler 1996). This accumulation of ammonia is analogous to both nutrient loading that increases productivity and toxic physiological effects, both of which can lead to declines in diversity and changes in species composition as a function of changing interspecific relationships (Camargo & Alonso 2006; Shochat et al. 2006; Verhoeven et al. 2006). These changes in species relationships, in addition to the already discussed differences in environmental conditions, can lead to differences in evolutionary selective forces (Agrawal 2001).

Some of the patterns we observed in the field suggest ways to address these issues of ammonia accumulation. Several of our constructed sites (two of seven) did not have elevated ammonia which may have been a result of the state agency cleaning them out (T. Raspiller, pers. comm.); an activity suggested in an earlier state report (Rosenstock et al. 2004), but not conducted at regular or frequent intervals because of logistical issues such as time and access (T. Raspiller, pers. comm.). The removal of the detritus temporarily reduces ammonia, likely for less than one year as accumulation of ammonia is relatively quick (< 1 year, Griffis-Kyle, unpublished data); consequently, cleaning the catchments annually should reduce ammonia concentrations. However, Arizona alone has > 900 constructed catchments (AZGFD 2014), so conserving biodiversity and improving water quality by cleaning catchments may take considerable effort.

Taxa diversity did not differ between the novel habitat and the tinajas, similar to another desert study (Hale et al. 2015a). However, assemblages were different between the site types, with taxa associated with longer hydroperiods and more tolerant of poor water quality in the constructed catchments. It is worth noting that none of the waters, neither the tinajas nor the catchments, are what could be considered clean; these are differences in relative rather than absolute water quality associated with the differences in assemblages. We detected four groups (Ostracoda, Hydrachnidia, Daphniidae, Trichoptera, Culicidae) only in tinajas, whereas Oligochaeta and Physidae were only detected in catchments. The Hydrachnidia, a tinaja only group, are used as indicators of water quality in a variety of systems (Biesiadka & Kowalik 1991; Dohet et al. 2002; Więceka et al. 2013), so may be vulnerable to the accumulation of ammonia in the anthropogenic catchments. Ammonia and nutrient enrichment also cause increased mortality in Daphniidae (Gersich & Hopkins 1986) and Trichoptera (Roberts et al. 2009), also groups only detected in tinajas. Species of Culicidae (tinaja only) using simple water pools, show increased mortality in response to an accumulation of total ammonia nitrogen (Walker 2016); however, other species in this group generally respond positively to nutrient enrichment in more complex wetlands with lower concentrations of ammonia (Duguma &

Walton 2014; Lund et al. 2014). Those groups, the Oligochaeta and the Physidae that were detected only in the constructed catchments, respond positively to longer hydroperiods and tend to be more tolerant of water quality and nutrient pollution (Schubauer-Berigan et al. 1995; Arimoro & Ikomi 2008; Prendergast-Miller et al. 2009; Gingerich et al. 2015; Balcombe et al. 2005). These patterns suggest that hydroperiod and chemical cycling, in particular the accumulation of ammonia, within these waters is resulting in disparate community composition. Differences in community composition result in differences in species interactions, which in addition to dissimilar environment conditions, can lead to divergent selection and evolution (Strauss & Irwin 2004; Agrawal et al. 2006; Haloin & Strauss 2008).

The communities differ in more than just composition; there are also differences in the assemblages of trophic functional groups suggesting important differences in how food webs are structured. The structure of food webs and how energy and matter are processed in a system are determined less by species identity and more by the assemblages of trophic functional roles (Cummins 1973; HilleRisLambers et al. 2012; Lyu et al. 2016). The largest difference in trophic assemblage is that the constructed catchments had more grazers and other herbivores, and the tinajas contained more filterers and scrapers. This suggests the food web in the catchments with longer hydroperiods, more nutrients, and fewer intense disturbances, is autotrophic with many of the food sources autochthonously derived, supporting more direct consumers of primary productivity. These catchments are more likely to have large populations of primary producers such as algae, so herbivorous taxa such as Physidae and Ephydriidae have an abundant food source. Conversely, the food web in the tinajas is strongly controlled by disturbance and resource pulses that deliver allochthonous resources and consequently is more heterotrophic supporting detritivores. Both constructed catchments and tinajas are small stagnant waters; however, differences in hydroperiods and biogeochemical cycling favor different functional traits resulting in different consumer-resource dynamics. If these differences in consumer-resource dynamics and species interactions cause non-random selection between the tinajas and the novel habitat,

there should be different evolutionary trajectories in each of these two systems (e.g. Bonada et al. 2007).

We provide a conservative estimate of differences in invertebrate communities and traits. The macroinvertebrates are grouped taxonomically at the family level or higher which does not provide fine detail (Griffis et al. 2001; Cañedo-Argüelles et al. 2016), but still provides an overview of the general differences in flows of matter and energy in the systems. Additionally, seasonal tinajas in western Sonoran Desert generally have relatively depauperate communities, with only one or two species in each family, compared to perennial tinajas further east in Arizona, where numerous species within each family can be found (Bogan 2012; Bogan pers. comm.). Other aquatic desert systems show relatively consistent patterns of species succession across years and drying events such that seasonal assemblages were predictable (Boulton et al. 1992), suggesting that even though our work covers two years, it provides enough information to evaluate at least some of the differences between the constructed catchments and tinajas and provides an adequate characterization of differences in macroinvertebrate communities. Especially in a system where there are widely fluctuating weather and water availability, these large-scale patterns do not address the detailed species differences within and between systems. However, these large-scale patterns are likely to be a reasonable indicator of the system as a whole.

The system of available surface waters in arid lands is shifting with changing patterns in climate and human mitigation of those changes. As temperatures rise and patterns of precipitation change (IPCC 2014), we expect to see a change in availability of these ephemeral isolated waters and the connectivity of the waters across the desert landscape (McIntyre et al. 2016). Natural resource managers are responding to decreasing available water by constructing more catchments that have water for longer than the natural waters, making them attractive resource patches. The addition of attractive patches in patchy populations or metapopulations has a strong influence on the growth of that overall population (Hale et al. 2015b). Because these

sites provide limited resources, organisms that have evolved in a water-limited environment are taking advantage of the novel habitat (e.g. Kiesow & Griffis-Kyle 2017) which has implications as resources, disturbances and consequent interspecific relationships change.

As more constructed catchments are added to the landscape, communities of macroinvertebrates in isolated desert waters are simplified and food webs shift from hetero- to more autotrophy via changes in disturbance, hydroperiod, and nutrient cycling. Others have found differences in species composition between natural and constructed systems that resemble the natural systems but have not documented these bottom-up differences in trophic patterns and selection pressures (Williams & Zedler 1999; Shulse et al. 2010). Novel habitats create new selection pressures and can shift the trajectory of evolution (Yeh 2004). These shifts in communities as a result of changing the ecosystem dynamics in isolated waters suggest there will be selection for tolerance of nutrients, and there may be less selection for fast development and emergence because of longer hydroperiods.

The desert Southwest is projected to experience increasing temperatures and fewer, but larger rainfall events (IPCC 2014). These fewer rain events fill the isolated tinajas, which can only hold so much water before the rest runs off and evaporates, effectively reducing hydroperiods and causing further declines in water availability. Natural resource managers are mitigating some of the water limitation by constructing water catchments, and this activity is likely to continue because the water limitation will continue to get worse (Seager et al. 2007, Cayan et al. 2010), and some vertebrate wildlife populations are positively associated with these constructed desert waters (Rich et al. 2019). However, constructed catchments are not ecological equivalents of tinajas. They differ from natural isolated waters in hydroperiod, disturbance regime, and biogeochemical cycling which is leading to the creation of macroinvertebrate communities in these novel habitats that differ in composition, structure, and function from those found in tinajas. As water becomes

more limiting in this environment, and managers mitigate that limitation with additional water developments, we are likely redirecting natural selection in a segment of the invertebrate community. If water quality and overall biodiversity are a goal for desert water management, we encourage new designs for future water sources that acknowledge organismal natural history and include aspects of hydroperiod and disturbance to more closely mimic the tinaja sites. By redesigning these catchments with more realistic dynamics, we may be able to mitigate some of the biodiversity loss and support species that will still be adapted to take advantage of the natural tinajas in this extremely arid system.

ACKNOWLEDGMENTS

We acknowledge the 56th Range Management Office of Luke Air Force Base for funding and thank the entire office for support. We appreciate M Bogan's advice on the differences between complexities in tinaja invertebrate communities. We thank J Arnett for initial conversations about desert waters and logistical support throughout. J Drake, K Smith, V Marshall, T Calvert, and others participated in data collection. We thank T Raspillar and D Urquidez from the Arizona Game and Fish Department for their time and acknowledge the Department of Natural Resources Management for covering page charges for this publication. The authors report no conflict of interest.

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