

Forecasting the Winners and Losers of a Riparian Herpetofauna in Response to Habitat

Invasion and Xerification

by

Sidney Riddle

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Graduate Supervisory Committee:

Heather L. Bateman, Chair
Fabio Suzart de Albuquerque
Steven E. Saul

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ABSTRACT

Riparian systems in the arid southwest are heavily altered and, based on relative land-area, provision a disproportionately high number of native wildlife. Amphibians and reptiles are collectively the most threatened vertebrate taxa and, in the Sonoran Desert, are often reliant on riparian habitat. The link between amphibians and environmental water characteristics, as well as the association between lizards and habitat structure, make herpetofauna good organisms for which to examine the effects of environmental change.

My objective was to relate capture rates of a fossorial anuran and lizard abundance to aspects of native, invaded, and shrub-encroached riparian habitats in order to forecast the potential winners and losers of riparian habitat xerification and invasion.

I measured habitat and monitored herpetofauna at 18 sites near the confluence of the San Pedro River and Gila River in Pinal County, Arizona in 2016 and 2017. Sites were divided into three categories based on dominant tree genus; *Populus-Salix*, *Prosopis*, and *Tamarix*, which represented native riparia, xeric riparia, and invaded riparia, respectively.

Habitat measurements indicated that sites varied significantly in structure, and that dominant tree species was a useful descriptor of habitat physiognomy. Results from herpetofauna trapping demonstrated that *Scaphiopus couchii*, a fossorial anuran, occupy *Prosopis* sites at a much higher rate than at *Tamarix* sites, which were almost completely avoided. *S. couchii* was also found to be closely tied to xero-riparian habitat components present at *Prosopis* sites and soil analyses indicate that aspects of soil moisture and texture play an important role in the partitioning of this species across altered riparian

habitats. Lizard abundance was found to be significantly lower in *Tamarix* habitat, with the majority of captures attributed to the generalist whiptail *Aspidoscelis tigris*. Additionally, more than half of lizard species that were analyzed displayed a negative association to *Tamarix* habitat. Of the three habitat types considered, *Populus-Salix* supported the greatest abundance of lizards.

Based on this study, the deleterious effects of xerification on a riparian herpetofauna community may be lesser than those of *Tamarix* invasion. These two forms of riparian habitat shift often co-occur, with the ultimate cause being changes in hydrologic regime. This may imply that a bottom-up approach, wherein historic hydrology is restored to restore or maintain native habitats, to riverine management is appropriate for riparian herpetofauna conservation.

DEDICATION

I dedicate this work to my late uncle Dennis, who continues to inspire me to seek knowledge and adventure.

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CHAPTER 1

HABITAT AND SOIL ASSOCIATIONS OF A FOSSORIAL TOAD IN SOUTHWESTERN RIPARIA

INTRODUCTION

Riparian habitats are defined as the interface between aquatic and terrestrial systems (Gregory et al., 1991). This ecotone is generally considered to have higher levels of disturbance than adjacent uplands and, as a result, may support an elevated degree of plant compositional and structural diversity (Gregory et al., 1991). Compared to uplands, riparian areas support greater plant diversity and habitat physiognomy, which support large numbers of animal species in arid regions (Brinson et al. 1981; Kondolf et al. 1996). Variable water flow regimes and large amounts of sediment scoured from watershed areas create a dynamic land-water interface characterized by frequent river channel widening and shrinking, channel migration, and channel entrenchment (Stromberg et al. 2009).

Abiotic shifts, such as rising mean-annual temperature and declining annual precipitation levels, can have particularly dramatic effects on the arid ecosystems of the southwestern United States. Because many plants and animals in these arid systems persist at or near their physiological limits, slight changes in temperature or precipitation may result in changes in the distribution, abundance, and ultimately, the composition of these environments (Archer and Predick, 2008). The coupled effects of hydrologic change and climate change most often result in a transition toward a more arid landscape and 21st century climate models indicate that the drying of the southwestern United States (hereafter, southwest) is imminent or already underway (Seager et al. 2007).

Hydrological changes to river systems and xerification are both contributing to the change in composition and habitat physiognomy, or structure, of riparian areas (Poff et al. 2010). Human alterations to flow regimes of riparian streams are known to disconnect rivers from adjacent floodplains which can change the composition of riparian habitats and may promote the establishment of non-native plants (Merritt and Cooper, 2000). Saltcedar (*Tamarix* spp.) is a woody tree/shrub originally introduced to the southwest in the mid-1800s (Robinson 1965) and is now the third most common woody tree in riparian areas in the southwest (Friedman et al. 2005). There are eight species of the genus *Tamarix* currently found in the United States and Canada (Baum 1967), which include the most common invasive *Tamarix* species in the southwest; *T. ramosissima*, *T. chinensis*, and *T. parviflora* (Gaskin 2013). Because of the difficulty of identifying to the species level the members of the genus *Tamarix* (Gaskin 2013), as well as the potential for hybridization (Gaskin and Shafroth 2005), all *Tamarix* species will be referred to by genus. *Tamarix* tends to proliferate in areas with high water availability, like riparian zones (Brock 1994), and is facilitated by anthropogenic land-use practices such as livestock grazing, land clearing, and groundwater pumping common to the southwest (Shafroth et al., 2005). However, species belonging to the genus *Tamarix* are generally considered facultative phreatophytes, which may proliferate in areas regardless of the depth of water, despite their well-developed and relatively deep root system (Di Tomaso, 1998). Richness and abundances of many wildlife communities are shown to be lower in stands dominated by *Tamarix*. For example, Durst et al. (2008) found that arthropod diversity was lower in *Tamarix* stands compared to native forests. For avifauna, *Tamarix* may be suitable habitat (Paxton et al. 2011), but for the majority of specialists, key

habitat requirements are likely to be missing (Bateman et al. 2013). In a study along the Virgin River in Mojave Desert, Bateman and Ostoja (2012) found lizard abundance and small mammal diversity lower in monotypic *Tamarix* compared to stands mixed with native and non-native trees.

In addition to the proliferation of non-natives, Dixon et al. (2009) predicted, in a study of the Upper San Pedro River in Arizona, that within a 100 year span, *Populus fremontii* (Fremont's cottonwood) and *Salix gooddingii* (Gooding's willow) gallery-forest width would significantly decrease and give way to *Prosopis* spp. (mesquite) woodlands. The encroachment of grasslands by woody shrubs in the southwest, most notably by *Prosopis* spp. and *Larrea tridentata* (creosote bush), has been well documented in the last several decades (Mueller et al., 2009; Laliberte et al., 2004; Grover and Musick. 1990) and has been attributed to cattle grazing, fire suppression, and climate change (Grover and Musick. 1990). In a 2006 study, Scott et al. concluded that encroachment of southwestern riparian areas by the woody shrub *Prosopis velutina* fundamentally alter carbon and water cycles. *Prosopis* is a group of shrub-like tree species with a particularly broad phenotypic plasticity (Stromberg et al. 2009). Because of this, it has been historically abundant in many southwestern rivers, but more recent river entrenchment, and subsequently lowered water tables, may have created a reduced hydrologically suitable environment for areas which were historically dominated by sacaton grasslands (*Sporobolus* spp.) and are now more suitable for *Prosopis* woodland (Bryan 1928; Stromberg et al. 2009). Arid riparian areas in the southwest provision a diverse array of wildlife taxa (Hubbard 1977) and shifts in habitat, such as the proliferation of *Tamarix*

and *Prosopis* in southwestern riparian areas, are known to have deleterious effects on amphibian populations (Cushman 2006).

More than half of all amphibian and reptile species located within the Mojave, Chihuahuan, and Sonoran Deserts utilize riparian or wetland habitats (Lowe 1989), however, less than 3% of the total land area in the southwest is classified as riparian (Naiman and Decamps 1997). Collectively, amphibians and reptiles have the highest threat status of all terrestrial vertebrates (IUCN 2018). Global population declines of both amphibians and reptiles are well documented (Gibbon et al. 2000; Collins and Storfer 2003; Araujo et al. 2006; Whitfield et al. 2007) and many scientists consider the loss of suitable habitat as the single greatest cause of such declines (Mittermeier et al. 1992; Alford and Richards 1999; Gardner et al. 2007). The distribution and abundance of amphibians and reptiles have been documented to be a good indicator of habitat quality in riparian areas (Bateman and Ostoja 2012). Amphibians are especially sensitive to changes in both terrestrial and aquatic environments because of their dual life cycles, specific microhabitat requirements, and specialized physiological requirements (Welsch and Ollivier 1998, Bury and Corn 1988). As such, examining the amphibian and reptile communities that rely on riparian habitats may provide insight into how habitat shifts affect herpetofauna communities.

Because reptiles exhibit a strong dependence on habitat structure and amphibians use temporary water sources for at least part of their life cycle, herpetofauna can be model organisms to examine wildlife responses to native plant invasion (Bateman et al. 2013). Landscape-level habitat suitability models for Couch's spadefoot toad (*Scaphiopus couchii*) demonstrate a close association to clay-loam soils with moderate to

high water-retaining capabilities (Dayton and Fitzgerald 2006). *S. couchii* presents a unique opportunity to study the effects of both hydrologic change and biotic community change in a desert riparian area. *S. couchii* is a mostly fossorial toad that inhabits some of the most xeric habitats in North America (McClanahan, 1967) by avoiding activity and sub-surface exposure for the majority of the year, and in some prolonged droughts, for several years at a time (Mayhew 1965). During summer monsoon rain events, *Scaphiopus* emerge from their fossorial burrow to exploit temporary favorable foraging and breeding conditions (McClanahan 1967). Skeletochronology of this species indicates that population dynamics are heavily influenced by the duration and intensity of summer monsoon rainfall (Tinsley and Tocque 1995). The literature on *S. couchii* is replete with information on developmental plasticity, physiological adaptation, genetic variation, and endocrinology (Newman 1989; Mayhew 1965; Newman 1988; Harvey et al. 1997) but there seems to be a gap in the literature related to habitat and soil associations of this species, particularly in riparian areas.

Research Objectives

The purpose of this study is to document the effects of non-native plant invasion and shrub encroachment on a fossorial desert amphibian by comparing three riparian habitat types with different dominant tree species. My objectives are:

- 1) Quantify the difference in soil texture, soil moisture, and habitat physiognomy across three riparian habitat types.
- 2) Compare *S. couchii* abundance across three habitat types.
- 3) Relate the occupancy of *S. couchii* to habitat and soil characteristics.

METHODS

Study site

I established study sites (Appendix A) near the confluence of the San Pedro and Gila Rivers in Pinal County, Arizona, USA near Winkleman, AZ (33°00'27.2"N 110°50'36.3"W) upstream to south of Dudleyville, AZ (32°51'23.3"N 110°43'18.9"W) in a linear distance of <20km (Appendix B). Locations were chosen in three distinct habitat types located within the riparian floodplain, and based on dominant tree-canopy composition: stands of monotypic *Tamarix* spp. (saltcedar) along the Gila River, gallery forest of native *Populus fremontii* (Fremont's cottonwood) and *Salix goodingii* (Gooding's willow) along the Lower San Pedro River Preserve near Dudleyville, AZ, and xero-riparian *Prosopis velutina* (velvet mesquite) woodlands along the lower San Pedro River near Dudleyville, AZ (Appendix C).

The San Pedro River is one of the last undammed perennial rivers in the desert Southwest (Thomas and Pool 2006). It originates in Sonora, Mexico and flows north through lower Sonoran Desert subdivision of the Sonoran Desert until its confluence with the Gila River in Winkleman, AZ. The characteristic near-stream habitat type of the modern San Pedro River is the *P. fremontii* and *S. goodingii* gallery forest. This habitat type generally includes a tall (about 30m) canopy of *P. fremontii* and *S. goodingii* trees (Stromberg et al., 2009) and an understory of evergreen shrubs like *Baccharis emoryi* (Emory's baccharis), *Baccharis salicifolia* (seepwillow), and *Salix exigua* (narrowleaf willow) (Szaro 1989).

Spadefoot sampling

To investigate how habitat type influenced the capture rate of *S. couchii* (Appendix D) I sampled herpetofauna using live-trapping techniques. I employed drift-fence trapping arrays composed of four pitfall (19L) traps and six funnel traps positioned along three 6m lengths of drift fence at 0, 120, and 240 degrees from center pitfall trap (Appendix A). I established six trapping arrays in each of the three stand types based on dominant tree species; *Tamarix*, *Prosopis*, and *Populus-Salix* (n=18). Hereafter, these sites will be referred to as *Populus-Salix*, *Prosopis*, and *Tamarix* (Appendix E). Trapping arrays were spaced at least 250m apart and not within 25m of riparian forest edge. I checked traps daily from May to August 2016 and April to August 2017. Data from five of six *Populus-Salix* sites (Appendix B) were excluded after 7 July 2017 due to the Roach wildfire, which burned 136 ha (335 acres) of riparian gallery forest along the lower San Pedro River in six days before it was suppressed (InciWeb 2018). I classified herpetofauna to species, sex, and recorded snout to vent (SVL), and weight metrics. To reduce the human error involved in the transcription of data to database, all morphological measurements were recorded in an Android tablet using a mobile application designed by Bateman et al. (2013) for herpetofauna capture-mark-recapture studies.

To detect calling male *S. couchii*, I deployed two acoustic monitoring devices from July to September 2017 (Wildlife Acoustics Songmeter SM2) roughly 50m from trapping arrays and rotated them equally through three sites to maintain a similar recording effort across habitat types (Table 1.1). Acoustic monitoring devices were programmed to record the first two minutes of every hour, on a 24 h cycle, every day of

the week. Only recordings from 0600 to 1800 were evaluated because calling *S. couchii* were not assumed to actively call in the middle of the day. Presence of calling *S. couchii* was determined for each two-minute sampling period (12 per 24 h sampling period).

Vegetation measurements

I quantified characteristics of habitat physiognomy and composition along two randomly selected 20m transects and four 2x2m plots at each herpetofauna trapping site (Appendix B). Transects were located 15m from the center of each trap array at 60, 180, or 300 degrees and plots were located at 2m further from the end of each 20m transect. At 1m increments along each transect, I recorded; litter depth, ground cover type, and canopy cover type. I recorded woody debris size class and density below 0.5m at every other meter along transects. In the plots, I recorded number, size class, and species of woody stems. I estimated herbaceous ground cover, canopy cover (variable densitometer), and visible light (REED Instruments SD-1128 light meter) within each plot. Canopy cover and visible light measurements were taken from the center of each plot at each of the cardinal directions and averaged (Appendix C).

Soil measurements

Soil core samples were obtained using a (7/8in. x 12in.) AMS Soil Recovery Probe. Soil sampling sites were located at the 10m point of 20m transects where habitat was measured at trapping sites (Appendix B). Each 2x2m plot sample consisted of four (7/8in. x 12in.) soil cores, which were blended to equal one sample per site (Appendix C).

In the lab, I weighed 10g (± 0.001 g) samples of soil from each plot and dried them in a thermostatically controlled soil kiln at a constant temperature between 105 °C

and 110 °C for at least 48 hours. After drying, each sample was placed in a desiccator and allowed to cool to room temperature for at least 12 hours before weighing the dried sample. Soil moisture content was determined using the percent soil moisture formula (Formula 1).

Soil texture is either a qualitative or quantitative description of clay, silt, and sand components of a particular soil. I quantitatively determined percentages of each of these soil components at each plot by conducting particle size analyses. I began by weighing 50g (± 0.001 g) of soil and passing the contents through a 2mm sieve to remove all coarse fragments. Fragments of rock and organic matter that remained in the sieve were weighed and discarded. The proportion of coarse fragment was then determined using the percent coarse fragment formula (Formula 2).

The remaining soil was then weighed and diluted in a soil stirring cup with roughly 500mL distilled water and 10mL of a 25% sodium hexametaphosphate solution, a dispersal agent. The diluted sample was immediately transferred to a mixing machine (Hamilton beach HMD200 Series) and mixed at speed for 2 minutes. After mixing, the diluted solution was transferred to a 1L settling cylinder, further diluted to the 1L mark with distilled water, and vigorously stirred with a porous stirring rod for 10 seconds. The soil solution was allowed to settle for 40 seconds, at which point a hydrometer (Fisherbrand Specific Gravity Hydrometer) was placed in the solution and a measurement was recorded. This initial stirring and measurement procedure was repeated four times to obtain an average 40-second reading. Following the 40-second readings, water temperature was measured to obtain a temperature-corrected hydrometer reading; 0.25 units were added to the averaged hydrometer reading for each 1.0 °C above 18.0 °C and

0.25 units were subtracted for each 1.0 °C below 18.0 °C. The grams of sand in the total sample was determined with Formula 3.

The soil solution was allowed to settle for two hours after the initial 40 second measurements, and the same procedure as above was used to obtain a two-hour hydrometer reading. Grams of clay was determined by taking the average of four 2-hour temperature-corrected hydrometer readings, and the grams of silt was calculated using Formula 4. To obtain the total percentage of each soil type, I used Formula 5.

Data Analyses

Because amphibians were not given unique marks, I defined *S. couchii* abundance at trapping sites as the number of captures per 100 days of trap effort, where each “day” is considered a 24 h trapping period. I used an independent-samples Kruskal-Wallis test to determine if there was a significant effect of habitat type on capture rate of *S. couchii*. This non-parametric method was carried out using R Statistical Program (R Core Team 2018).

I used a nonmetric multidimensional scaling ordination (NMDS) in PC-ORD Version 6 (McCune and Mefford 2011) to explore the relationship between trapping site and *S. couchii* abundance. This ordination technique attempts to represent species and habitat relationships as accurately as possible in low-dimensional space (Gauch 1982). I reduced the dimensionality of interrelated habitat and soil variables using a principal components analysis (PCA) in SPSS version 24.0 (IBM Corp 2016). The objective of PCA in this study was to reduce the number of predictor variables to a smaller number of synthetic components, while retaining as much information as possible. The number of useful principal components was determined based on components with eigenvalues

greater than or equal to one (Legendre & Legendre 1998). We interpreted the biological result of each principal component based on how each environmental variable loaded on synthetic components. Those components which explain the greatest amount of variance are often the easiest to interpret and there is no reason why all components, particularly those which explain little variance, should have a simple interpretation (Jolliffe 2002).

I ranked linear regression models using an Akaike's Information Criterion, adjusted for small datasets, (AICc) to judge whether the synthetic components were useful predictors of *S. couchii* presence (R Core Team 2018). All combinations of components were regressed against *S. couchii* capture rate in a multi-model inference approach where all models with $\Delta\text{AIC} \leq 2$ were included as top models and assumed to have substantial support (Burnham & Anderson 2002).

RESULTS

Scaphiopus couchii

During the 2016 and 2017 trapping seasons (637 trap days), I captured 112 *S. couchii*. I found the capture rate of *S. couchii* to be significantly higher at *Prosopis* sites than at *Tamarix* sites ($H=10.351$, 2 d.f., $P=0.006$) and three times higher at *Prosopis* sites than both *Tamarix* and *Populus-Salix* sites (Fig. 1.1). An NMDS ordination revealed that *S. couchii* have high fidelity to *Prosopis* sites (final stress = 5.11, linear fit $R^2 = 0.98$; Appendix F). A total of 1872 minutes of audio recordings were evaluated (Table 1.1). Presence of calling males was confirmed in 38 of 696 sampling periods at *Populus-Salix* sites, three of 672 sampling periods at *Prosopis* sites, and zero of 504 sampling periods at *Tamarix* sites (Table 1.1).

Vegetation and Soil

Vegetation and soil characteristics varied significantly across habitat types in several instances (Appendix H). *Tamarix* sites had significantly higher proportion of woody ground cover ($F_{2,15} = 6.65$, $P = 0.009$) and small diameter woody debris ($F_{2,15} = 8.48$, $P = 0.003$). *Prosopis* sites had significantly lower counts of medium ($F_{2,15} = 7.84$, $P = 0.005$) and large diameter ($F_{2,15} = 5.91$, $P = 0.013$) woody debris than *Tamarix* sites. *Prosopis* sites were also significantly further from the river ($F_{2,15} = 15.4$, $P < 0.001$) than *Tamarix* sites and *Populus-Salix* sites. Although not statistically significant, I found soil moisture was tending to be higher at *Prosopis* sites than *Tamarix* and *Populus-Salix* sites ($H=5.485$, 2 d.f., $P=0.064$), which contained similar soil moisture levels (Fig. 1.2). A particle size analysis determined different texture classes at *Prosopis*, *Tamarix*, and *Populus-Salix* sites. On average, *Prosopis* sites had a higher percent clay and lower percent sand content than both monotypic *Tamarix* and *Populus-Salix* gallery forests (Fig. 1.3).

The PCA analysis reduced 25 habitat and soil variables (Appendix H) to six synthetic components which explained 83.4 percent of the total variation across trapping sites (Table 1.2). Component One (C1) was characterized by water-retaining *Prosopis* habitat. Trapping sites with high C1 scores had high *Prosopis* canopy cover and soils with moisture-retaining properties, whereas sites with low C1 scores had high *Tamarix* canopy and large amounts of woody debris. Sites with high Component Two (C2) scores were located far from river channel and have silty soils. Sites with low C2 scores were characterized by sandy soils and have open, *Populus* and *Salix* canopy. Component Three (C3) represented sites with high litter depth and visible light penetration, whereas sites

with low C3 scores were characterized by bare groundcover and little open canopy. Trapping sites with high Component Four (C4) scores corresponded to sites with high density of *Populus* and *Salix* stems and high percent herbaceous ground cover. Component Five (C5) sites have a large percentage of mid-story shrub cover. Sites with high Component Six (C6) scores had high visible light penetration and herbaceous ground cover. I interpreted and renamed the six components for reference: C1: Soil moisture, *Prosopis* or *Tamarix* cover C2: Distance from channel; C3: Litter and Canopy; C4: Native stems and herbs; C5: Shrubby mid-story; C6: Open canopy, herb cover.

Spadefoot – Habitat model

My analyses provided one conclusive species-habitat model (Table 1.3). This top-performing model described *S. couchii* abundance as positively correlated with principal components C1 and C4 and negatively correlated with principal component C3 (Table 1.2). This indicated that *S. couchii* abundance was positively associated with habitats characterized by water-retaining soils, absence of non-native canopy species, and *Prosopis* canopy, as well as components of native *Populus-Salix* habitat. Abundance of *S. couchii* was also negatively associated with sites that had high canopy cover and litter depth (Table 1.3)

DISCUSSION

This study provides insights into how habitats and soils influence the occupation of a fossorial anuran in Southwestern riparian corridors. Amphibians are among the most threatened vertebrate taxa (IUCN 2018), and understanding the effects of habitat change on amphibian abundance is an important step in keeping common species, such as *S.*

couchii, common throughout their ranges. Soils with moisture-retaining texture classes as well as high percentages of moisture are important predictors of the occupation of habitat by *S. couchii*. Above-ground habitat components, such as dominant tree species and groundcover, also play a meaningful role in the partitioning of *S. couchii* across riparian landscapes. I recognize the potential for inflated abundance estimates when not marking individuals and conforming to capture-mark-recapture protocols, but argue that short time period spent above ground (Newman and Dunham 1994), as well as the explosive breeding life history of *S. couchii* (Tinsley 1990), diminish the likelihood and effect of overinflated abundance estimates.

The positive correlation between soil moisture content and percentage of clay particulate, as well as the negative correlation between soil moisture content and percentage of sand particulate, is well illustrated (Gupta and Larson 1979; Saxton et al. 1986; Saxton and Rawls 2006). Results of my study provide further evidence for these established relationships, by showing similar patterns between percentage of clay particles and percent soil moisture. Soils with relatively high soil moisture contents are thought to reduce potential for desiccation in desert amphibians (Shoemaker 1988; Dayton et al. 2004). Walter and Whitford (1970) demonstrated the exceptional ability of *S. couchii* to osmoregulate in fossorial conditions and concluded that the ability to absorb water from the soil is a factor which contributes to the distribution of anurans.

The marked absence of *S. couchii* in *Tamarix* stands suggest that some component of *Tamarix*-invaded habitat, either above or below ground, may act as a deterrent of *S. couchii*. Although a shift in arthropod assemblage and abundance of insect prey in *Tamarix* habitat are likely (Strudley and Dalin 2013) and may affect the presence of *S.*

couchii, an alternative explanation may exist. Elevated soil and groundwater salinity in *Tamarix* stands are likely to occur in the absence of other environmental factors like overbank flooding and surface evaporation (Ohrtman and Lair 2013). Due to the high permeability of amphibian skin (Clarke 1997), and the especially high permeability *S. couchii* skin (Walter and Whitford 1970; Hillyard 1976), salinity may prohibit use of *Tamarix* habitat by *S. couchii*. To my knowledge, the direct effects of saline soils on *S. couchii* have not been investigated and the findings of this study warrant further research into the effects of soil salinization on various life stages of *S. couchii*.

My models suggest an association to xero-riparian *Prosopis* and components of *Populus- Salix* gallery forests by *S. couchii*. Dayton et al. (2004) found that, in a study in the Chihuahuan Desert ecoregion, the frequency of occurrence of *S. couchii* in *Prosopis* habitat was greatest among four co-occurring desert anurans. Despite the generalist habitat requirements of this species, we believe this study demonstrates that not all riparian stand types provide adequate habitat for *S. couchii*. Specifically, *S. couchii* exhibit an avoidance of monotypic *Tamarix* habitat and a preference for *Prosopis* habitat that is characterized by relatively clay-rich riparian soils with moisture-retaining properties.

Management implications

Riparian zones represent possibly the most disproportionately valuable habitat in the Sonoran Desert. Less than three percent of land cover in the southwest is riparian (Naiman and Decamps 1997), yet more than half of herpetofauna in the Sonoran Desert utilize riparian areas at some point in their life cycle (Lowe 1989). Streams and riparian areas also provide breeding habitat for *S. couchii* (Lazaroff et al. 2006). Because of

human water use, riparian zones in the southwest often fall victim to hydrologic changes and subsequent habitat shifts. In the southwest this generally takes two forms; invasion by *Tamarix* (Di Tomaso 1998) and shrub encroachment by *Prosopis* (Dixon et al. 2009). Invasive fishes, plants, and other amphibians are considered to have the greatest negative impact on native amphibian species (Bucciarelli et al. 2014). I argue that *S. couchii* be added to the exhaustive list of wildlife negatively affected by the invasive woody genus *Tamarix*, which often forms monotypic stands in the southwest. Unchecked *Tamarix* proliferation could have deleterious effects on populations of this species in riparian areas. Stands of monotypic *Tamarix* are likely to be unsuitable aestivation sites. Soil and water salinity levels in dense *Tamarix* stands are known to be elevated (Glenn and Nagler 2005) and *S. couchii* have a permeable skin-environment interface (Walter and Whitford 1970) which may lead to increased rates of desiccation in these habitats. Additionally, dense and expansive thickets of *Tamarix* may act as impassable barriers to river channels, where *S. couchii* are known to facultatively breed in streams and rivers (Lazaroff et al. 2006). *Scaphiopus couchii* is currently considered a species of least concern (IUCN 2018). However, current climate vulnerability models suggest that the species may be particularly vulnerable to climate change, primarily because of their close tie to water (Griffis-Kyle et al. 2018). Extreme vulnerability to climate change, coupled with large-scale habitat shifts, warrant monitoring of this species in riparian areas

TABLE 1.1. Calling *Scaphiopus couchii* detected by acoustic logger along the San Pedro River and Gila River, Pinal County, Arizona, USA. Sampling Periods are 2-minute recording intervals and Positive Vocalization periods are Sampling Periods where *S. couchii* were detected.

Habitat	Site	Days	Sampling Periods	Positive Vocalization Periods
Cottonwood-Willow	CW1-1	29	696	38
Mesquite Woodland	MQ2-2	28	672	3
Monotypic Saltcedar	SC2-2	21	504	0

TABLE 1.2. Principle components analysis (PCA) used to reduce dimensionality of soil and habitat predictor variables. The number of relevant principal components was chosen based on eigenvalues greater than one. Bold values indicate variables that load on each synthetic component.

Variable	Component					
	1	2	3	4	5	6
<i>Tamarix</i> Canopy Cover (%)	-0.896	0.254	0.006	0.013	-0.236	0.126
<i>Prosopis</i> Canopy Cover (%)	0.880	0.343	-0.025	-0.186	0.011	0.119
Woody Debris Md. diameter/ 10 meter	-0.820	0.379	0.186	0.058	0.016	-0.258
Woody Debris Lg. diameter / 10 meter	-0.796	0.376	0.074	0.299	0.128	-0.092
Clay Soil Particle (%)	0.775	0.222	-0.119	0.042	0.006	-0.216
Grass Cover (%)	0.766	-0.061	-0.196	0.213	-0.297	0.045
Woody Debris Sm. diameter / 10 meter	-0.765	0.232	0.220	-0.205	-0.191	-0.191
Soil Coarse Fragment (%)	0.724	0.206	0.203	0.378	0.333	-0.301
Woody Ground Cover (%)	-0.710	0.605	-0.187	0.054	0.108	-0.106
Litter Ground Cover (%)	0.663	-0.518	0.432	-0.111	-0.200	0.017
Soil Moisture (%)	0.586	0.505	0.150	0.168	0.308	-0.275
Density of <i>Tamarix</i> Stems / 4 sq. meter	-0.545	0.133	0.158	-0.264	0.157	-0.020
Density of <i>Prosopis</i> Stems / 4 sq. meter	0.421	0.330	0.056	-0.232	0.399	0.360
Silt Soil Particle (%)	0.329	0.794	-0.018	-0.228	0.165	-0.027
Sand Soil Particle (%)	-0.543	-0.742	0.056	0.176	-0.141	0.097
<i>Populus</i> and <i>Salix</i> Canopy Cover (%)	-0.110	-0.700	0.054	0.365	0.402	-0.227
Open Canopy (%)	-0.350	-0.634	-0.201	-0.490	0.133	0.159
Distance to river (m)	0.506	0.625	-0.003	-0.259	-0.179	0.111
Litter Depth (cm)	0.149	-0.451	0.778	0.102	-0.018	-0.236
Light Meter (lux)	0.323	-0.346	-0.703	-0.169	-0.131	-0.385
Bare Ground (%)	-0.441	0.270	-0.696	0.171	0.291	0.118
Visible Light (%)	-0.202	0.447	0.592	0.260	0.118	0.498
Density of <i>Populus</i> and <i>Salix</i> / 4 sq. meter	0.014	-0.345	-0.362	0.469	0.397	0.213
Shrub Cover (%)	0.065	-0.555	0.131	-0.433	0.582	0.258
Herb Cover (%)	0.326	0.002	-0.150	0.493	-0.370	0.519
Variance Explained (%)	32.8	20.5	10.4	7.3	6.6	5.8
Cumulative Variance Explained (%)	32.8	53.3	63.3	71.1	77.7	83.4

TABLE 1.3. Importance of soil and habitat components in predicting *S. couchii* abundance on the San Pedro River and Gila River, Pinal County, Arizona, USA using multiple-model inference. Top ten models included for visualization purposes, but only the top performing model falls within the significance level of the $\Delta AICc < 2.0$ framework.

Top Model (+/-)	AICc	$\Delta AICc$	ω	Components					
				C1	C2	C3	C4	C5	C6
C1+C3+C4	22.92	0	0.50	+		-	+		
C1+C3+C4+C6	25.53	2.6	0.14	+		-	+		+
C1+C3+C4+C5	26.45	3.5	0.09	+		-	+	+	
C1+C4	26.51	3.5	0.08	+			+		
C1+C2+C3+C4	26.72	3.8	0.08	+	-	-	+		
C1+C4+C6	29.13	6.2	0.02	+			+		+
C1+C4+C5	29.71	6.7	0.02	+			+	+	
C1+C3+C4+C5+C6	29.85	6.9	0.02	+		-	+	+	+
C1+C2+C4	29.89	6.9	0.02	+	-		+		
C1+C2+C3+C4+C6	30.16	7.2	0.01	+	-	-	+		+

*Note that AICc is Akaike's information criterion (corrected for small sample size), a metric used to judge model fit. $\Delta AICc$ is the difference in AICc from the top-performing model. Component AICc weights are the average relative weights of all combinations of models.

FIGURE 1.1. Capture rate of *Scaphiopus couchii* at three riparian habitat types; *Populus-Salix* (cw), *Prosopis* (mq), and *Tamarix* (sc) along the San Pedro River and Gila River, Arizona, USA. Boxplots symbolize median, first quartile, third quartile, minimum, and maximum. Letters symbolize independent-sample Kruskal-Wallis results; variables with different letters are significantly different.

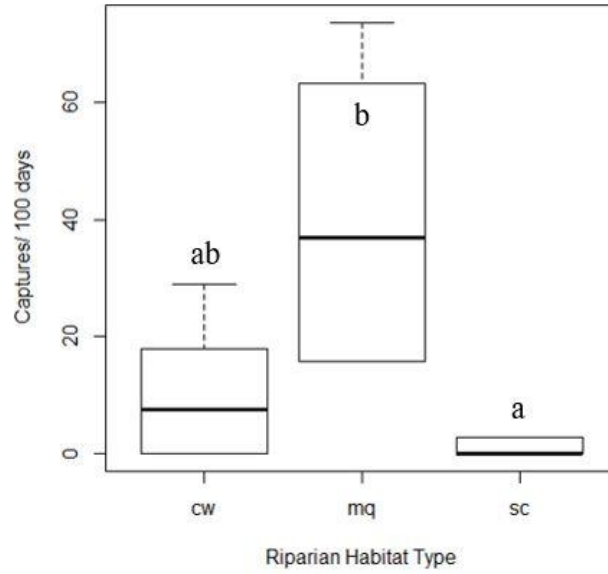


FIGURE 1.2. Percent Sand, Clay, Silt, Moisture, and Coarse Fragment of soil samples collected at three riparian habitat types along the San Pedro River and Gila River, Arizona, USA. Boxplots symbolize median, first quartile, third quartile, minimum, and maximum. Letters symbolize independent-sample Kruskal-Wallis results; variables with different letters are significantly different.

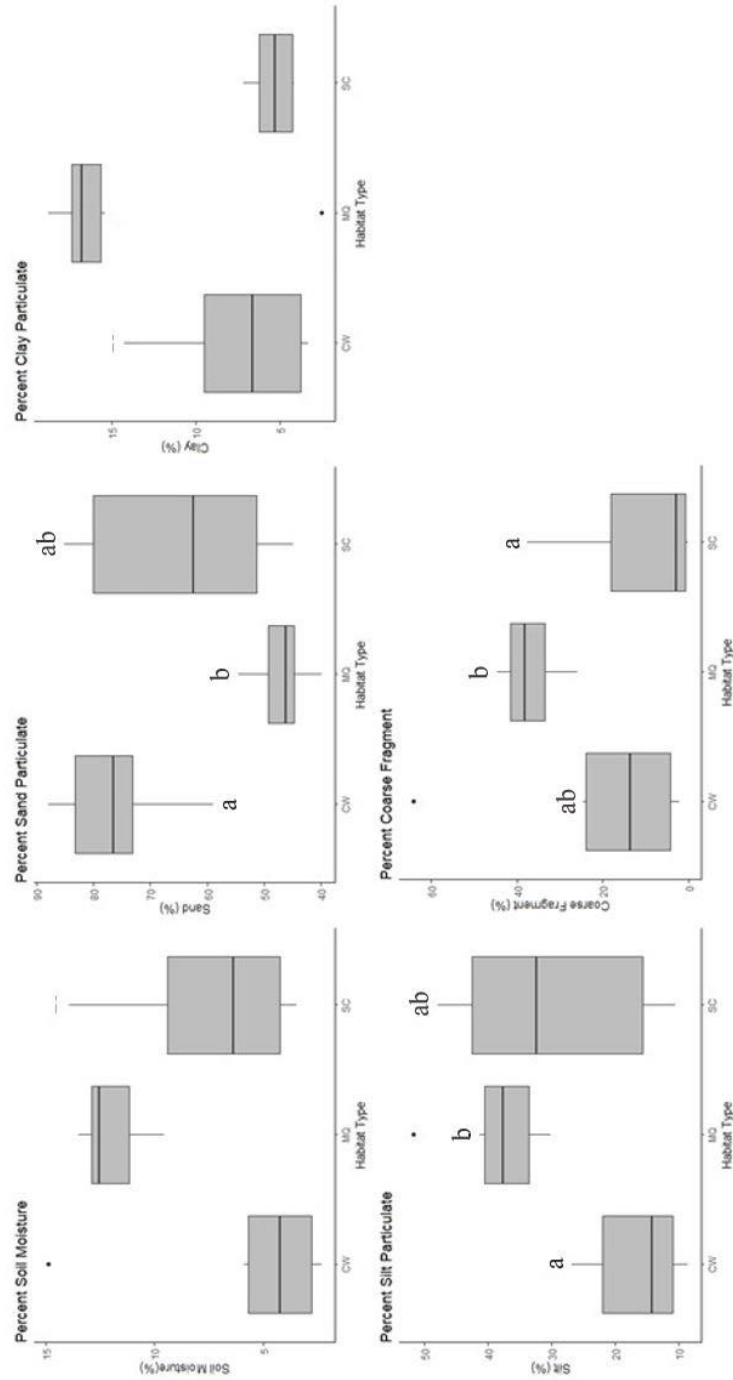


FIGURE 1.3. Soil texture classes of study sites across three riparian habitat types along the San Pedro River and Gila River, Pinal CO Arizona, USA.

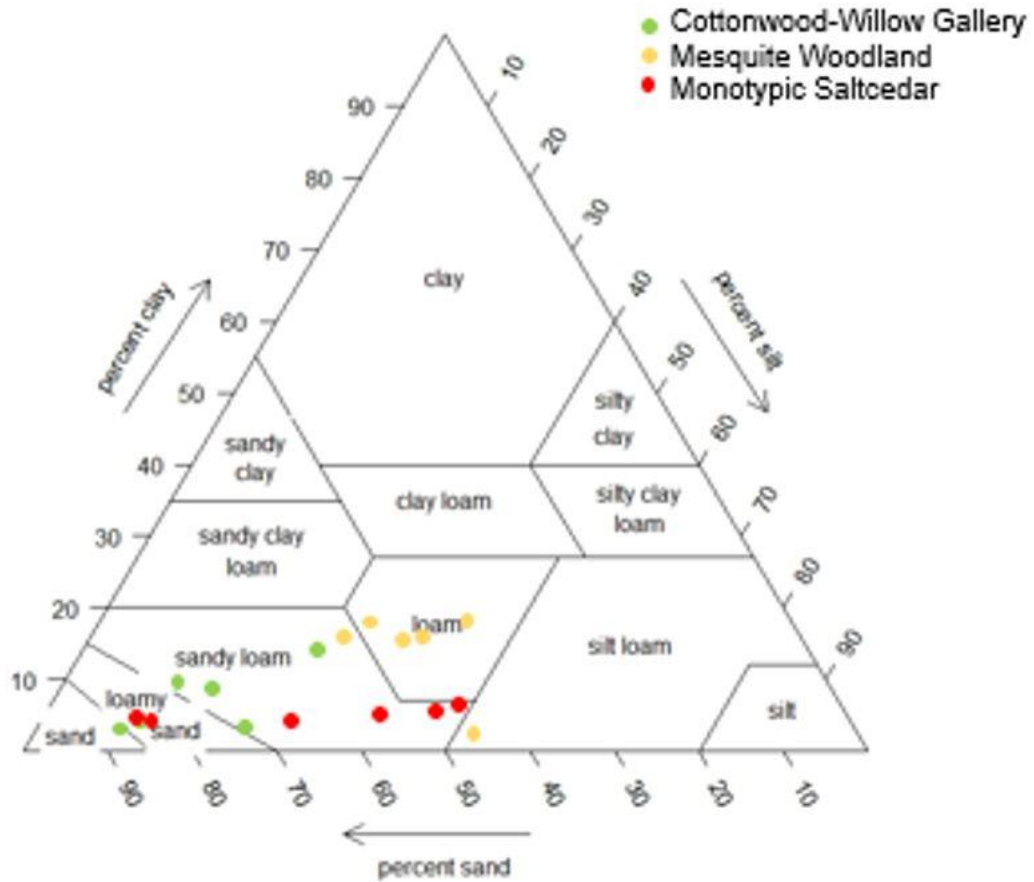
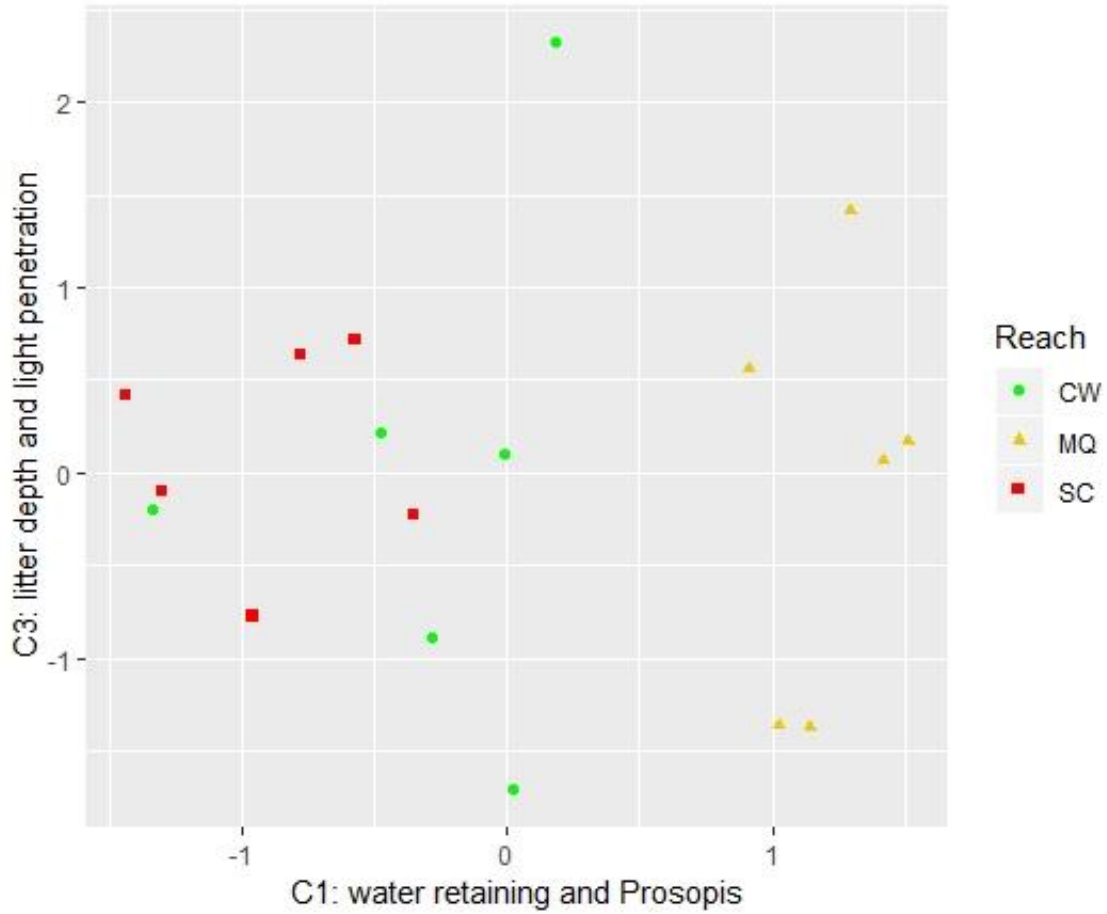


FIGURE 1.4. Vegetation and soil physiognomy values from Principal Component 1: Water Retaining and Prosopis and Principal Component 3: Litter Depth and Light Penetration (Table2) in *Populus-Salix* (CW), *Prosopis* (MQ) and *Tamarix* (SC) sites (also “Reach”) along the San Pedro River and Gila River, Pinal County, Arizona, USA.



FORMULA 1. Percentage of moisture content of soil sample.

$$MC\% = \frac{W_3 - W_2}{W_3 - W_1} \times 100$$

Where:

$MC\%$ = Percent soil moisture, W_1 = Mass of empty weighing tin (g), W_2 = Mass of moist soil + weighing tin (g), W_3 = Mass of dried soil + weighing tin (g).

FORMULA 2. Percentage of coarse fragment (<2mm) content of soil sample.

$$CF\% = \frac{W_f}{W_t} \times 100$$

Where:

$CF\%$ = Percent coarse fragment, W_f = Mass of coarse fragments from 2mm sieve, W_t = Mass of original sample

FORMULA 3. Mass (g) of sand particulate in soil sample. Determined by particle size analysis.

$$S = \frac{W_s}{H_1}$$

Where: S = Grams of sand particulate, W_s = Mass of sample (after sieving), H_1 = Average of four 40 second temperature-corrected hydrometer readings

FORMULA 4. Mass (g) of silt particulate in soil sample. Determined by particle size analysis.

$$I = W_s - (S + C)$$

Where:

I = Grams of silt particulate, W_s = Grams of sample (after sieving), S = Grams of sand particulate, C = Grams of clay particulate

Formula 5. Percentage particulate in soil sample. Determined by particle size analysis.

$$\frac{W_p}{W_s} \times 100$$

Where: W_p = Grams of particulate (sand, silt, or clay), W_s = Grams of sample (after sieving)

CHAPTER 2

HABITAT ASSOCIATIONS OF A RIPARIAN LIZARD COMMUNITY

INTRODUCTION

Loss and degradation of suitable habitat is widely recognized as the greatest threat to biodiversity and a leading cause of extinction (Gibbons et al. 2000). The ultimate cause of habitat degradation in riparian areas are numerous and include damaging patterns such as hydrologic regime changes, livestock grazing, wildfire, climate change, and direct anthropogenic consumption of water (Stromberg and Tellman 2009). In riparian areas of the southwest, shrub encroachment and *Tamarix* proliferation represent two of the most common outcomes of habitat degradation.

Tamarix spp. (saltcedar) was originally introduced to the American West in the mid-1800s (Robinson 1965) and has spread considerably in arid riparian systems (Harms and Hiebert 2006). The proliferation on *Tamarix* in the arid Southwest is largely attributed to changes in hydrologic regime (Howe and Knopf 1991; Sher et al. 2002). *Tamarix* is credited with potentially causing billions of dollars in economic damage in the coming decades (Zavaletta 2000) and is known to reduce habitat quality (Shafroth et al. 2005) and negatively impact wildlife communities (Bateman et al. 2013). In addition to the increase of *Tamarix* in arid riparian areas, Dixon et al. (2009) predicted that *Populus fremotii* (Fremont's cottonwood) and *Salix gooddingii* (Gooding's willow) gallery-forest would be replaced by patches of *Prosopis velutina* (velvet mesquite) along much of the San Pedro River in a 100-year span. *Prosopis* is considered a xero-riparian species (Grandmaison et al. 2010) and has been historically abundant in many southwestern

rivers, but lowered water tables may have created a reduced hydrologically suitable environment for *Prosopis* (Bryan 1928; Stromberg et al. 2009).

The importance of habitat physiognomy to lizard communities is well established (Pianka 1966; Taylor and Fox 2001; Bateman and Ostoja 2012). Due to the strong association to habitat structure, lizards can be model organisms to examine responses to non-native plant invasion (Bateman et al. 2013). Additionally, the encroachment of riparian areas by *Prosopis* spp. in the American Southwest are known to change habitat physiognomy (Nie et al. 2012), but the effects on wildlife, and particularly herpetofauna, are largely unknown.

Research Objectives

The purpose of this study was to document the effects of non-native plant invasion and shrub encroachment on the riparian lizard community by comparing three riparian habitat types with different dominant tree species. My objectives were to:

- 1) Quantify the difference in habitat physiognomy across three riparian habitat types.
- 2) Compare lizard abundances across three habitat types.
- 3) Relate the abundance of lizard species to habitat physiognomy measurements.

METHODS

Study Site

Study sites occurred along the San Pedro River and Gila River in Pinal County, Arizona, USA (Appendix A; Appendix B) and were the same as those described in Chapter One (*Study Site*, page 6)

Field Methods: Lizard Sampling and Vegetation Measurement

Lizard capture methods were the 18 trapping arrays as those described for *S. couchii* in Chapter One (*Spadefoot Sampling*, page 7). Each lizard was marked with a unique alphanumeric toe-clip code (Waichman 1992). This method assumes that species abundance at a site represents the minimum number of that species at the particular site. This method also relies on the assumption that animals are not moving between sites. Vegetation measurement methods (Appendix G) were the same as those used in Chapter One (*Vegetation Measurements*, page 8).

Data Analyses

I defined lizard abundance as the number of uniquely marked captures per 100 days of trap effort, where each “day” is considered a 24 h trapping period. Independent-samples Kruskal-Wallis test, nonmetric multidimensional scaling (NMDS) ordination, and principal components analysis (PCA) were used similar to Chapter One (*Data Analyses*, page 9).

I ranked linear regression models using an Akaike’s Information Criterion, adjusted for small datasets, (AICc) to judge whether the principal components were useful predictors of *S. couchii* presence (R Core Team 2018). I used multiple linear regression to model species which were ubiquitous, or present, across all sites and logistic regression, which accounts for only presence/absence, for lizard species not present across all sites. Abundance of each lizard species was $\log(x + 1)$ transformed. All combinations of principal components were regressed against lizard abundance in a multi-model inference approach that reports all models with $\Delta AIC \leq 2$ (Burnham &

Anderson 2002). I used a variable weighting and ranking scheme to determine the relative contribution of individual components to all models.

RESULTS

Lizard Abundance and Community

During the 2016 and 2017 trapping seasons (637 trap days), we captured 960 unique individuals representing nine different species (Table 2.1). Lizard capture rate differed significantly across habitat types ($H=14,342$, 2 d.f., $P=0.001$). Capture rates in *Populus-Salix* habitat was more than twice as high as the capture rate in *Tamarix* and greater than 50 percent higher than the capture rate in *Prosopis* habitat (Fig. 2.1). The most commonly captured lizard at both *Populus-Salix* and *Prosopis* sites was the Sonoran spotted whiptail (*Aspidoscelis sonorae*). The tiger whiptail (*Aspidoscelis tigris*) was the most commonly captured lizard at *Tamarix* sites. The only lizard captured at every trapping location was the Southwestern fence lizard (*Sceloporus cowlesi*).

Taken separately, the abundance of two out of six lizard species differed significantly across habitat types. *S. cowlesi* tended to be significantly lower at *Tamarix* sites than at *Populus-Salix* sites ($H=7.622$, 2 d.f., $P=0.022$). Additionally, *A. sonorae* abundance was significantly higher at *Populus-Salix* sites than at *Tamarix* sites ($H=14.176$, 2 d.f., $P=0.001$)(Fig. 2.2).

A 2-dimensional NMDS ordination (final stress = 5.11, linear fit $R^2 = 0.98$; Appendix F) provides evidence that no lizard species captured during this study exhibited fidelity to *Tamarix* habitat. The most noticeable separation occurs along NMDS Axis 1, where *Tamarix* sites are ordinated distinctly far in “species-space” from *Populus-Salix*

and *Prosopis* sites (Appendix F). This observation is further supported by the lack of a significantly higher occupation rate of *Tamarix* sites by any lizard species encountered during the study (Fig. 2.2). Three of the four notably arboreal lizard species encountered in this study (*S. cowlesi*, *S. clarkii*, and *U. ornatus*) ordinate closer to *Prosopis* and *Populus-Salix* sites than to *Tamarix* (Appendix F).

Habitat

Vegetation and soil characteristics varied significantly across habitat types in several instances (Appendix H). *Tamarix* sites had significantly higher proportion of woody ground cover ($F_{2,15} = 6.65$, $P = 0.009$) and small diameter woody debris ($F_{2,15} = 8.48$, $P = 0.003$). *Prosopis* sites had significantly lower counts of medium ($F_{2,15} = 7.84$, $P = 0.005$) and large diameter ($F_{2,15} = 5.91$, $P = 0.013$) woody debris than *Tamarix* sites. *Prosopis* sites were also significantly further from the river ($F_{2,15} = 15.4$, $P < 0.001$) than *Tamarix* sites and *Populus-Salix* sites.

The principal components analysis reduced 20 habitat variables (Appendix) into six components that explained 84.5 percent of the cumulative variance across trapping sites (Table 2.2). Sites with high component one (C1) scores were characterized by monotypic *Tamarix* canopy and ample woody debris. Sites with low C1 scores had non-woody groundcover and high woody species richness. Component two (C2) embodied native *Populus-Salix* gallery forest, with open canopies and a shrubby component. Sites with low C2 scores were found far from the river channel with *Prosopis* canopies. Component three (C3) sites were characterized by bare groundcover and high light penetration to the ground. Sites with low C3 scores had high percentage of visible light

and litter depth. Component four (C4) sites had high percent herbaceous ground cover and sites with low C4 scores had open canopies with high densities of *Populus-Salix* stems. Component five (C5) was a *Prosopis* component; sites with high C5 scores would exhibit a high proportion of visible light and shrub cover as well as high density of *Prosopis* stems. Finally, sites with high component six (C6) scores were characterized by high rates of woody species richness, and sites with low C6 scores possessed low proportion of herbaceous ground cover. I interpreted and renamed the six synthetic components for reference: C1: invasion gradient; C2: xeric to mesic; C3: litter and canopy; C4: native stems and herbs; C5: mid-story presence; C6: woody richness.

Species-habitat Relationships

Because of low abundances, only the six most common lizard species were included in species-habitat analyses. Analyses of five of the six lizard species yielded conclusive models (Table 2.3). *A. sonorae* abundance was shown to be negatively associated with sites characterized by *Tamarix* canopy and woody debris (C1) and positively associated with open canopy, shrubby, *Populus-Salix* habitat (C2) and woody species richness (C6) (Fig. 2.3). The top model for *A. tigris* included positive associations with monotypic *Tamarix* and woody debris (C1), open canopy, shrubby, *Populus-Salix* habitats (C2), and bare ground cover and high light penetration to ground (C3). Both *S. cowlesi* and *Urosaurus ornatus* produced top models that negatively associated with *Tamarix* canopy and woody debris (C1). Logistic regression models for *S. magister* indicate a negative association with woody species richness (C6) (Table 2.3).

DISCUSSION

Riparian areas represent a disproportionately important habitat for desert herpetofauna. More than half of amphibians and reptiles in the Chihuahuan, Mojave, and Sonoran Deserts use riparian habitats at some life stage (Lowe 1989), yet less than three percent of land-cover in the American Southwest is riparian (Naiman and Decamps 1997). As such, forecasting the effects of certain patterns of habitat shift on riparian reptiles can provide useful management information and aid in conserving species and their habitats. Overall, the important findings of this chapter show that habitat differs across three riparian stand types, lizards are partitioned according to elements of physical habitat, and that most species are negatively associated with *Tamarix*-dominated habitats and positively associated with aspects of native riparian habitat.

Habitat

Trapping sites differed on the basis of habitat composition and physiognomy. *Populus-Salix* and *Prosopis* sites were characterized by greater woody species richness and lacked non-native canopy when compared to *Tamarix* sites. *Tamarix* sites had high densities of woody debris, which is likely a result of the high canopy coverage also found at these sites. *Prosopis* sites were characterized by multiple aspects of xero-riparian habitat, such as the presence of a shrubby mid-story and distance from river channel.

Species-habitat relationships

This study found that, although no species of lizard outright avoided either monotypic *Tamarix* or xero-riparian *Prosopis* habitats, abundances were significantly lower than in native *Populus-Salix* gallery forest. Arboreal lizard species appeared to be most closely associated with *Prosopis* and *Populus-Salix* sites than *Tamarix* sites.

Species-habitat models for three of five lizard species indicate a negative association to *Tamarix*-invaded habitat and no lizard species appeared to select *Tamarix* dominated habitat. Similar patterns of reduced lizard abundance in *Tamarix* habitat have been reported for different systems (Bateman and Ostoja 2012) and removal of *Tamarix* has been shown to increase relative abundance of some common riparian lizards (Bateman et al. 2008).

A. tigris was the only lizard species in this study with habitat models that predict an association to monotypic *Tamarix* habitat. This could potentially be a result of the generalist natural-history of *A. tigris* (Bateman and Ostoja 2012) and/or some competitive-release interaction that occurs in *Tamarix*-dominated habitats. This competitive-release theory may be supported by the near absence of the syntopic congener *A. sonorae* in *Tamarix*-dominated habitats. In adjacent *Populus-Salix* habitats, the parthenogenic species *A. sonorae* is the most commonly-encountered lizard and co-occurs with *A. tigris*. Cuellar (1979) documented sympatry between *A. tigris* (formerly *Cnemidophorus tigris*), *A. uniparens*, and *A. tessellatus* and noted that, in this particular system at Caballo Dam State Park, *A. tigris* was found almost exclusively in a *Prosopis* dune habitat, whereas *A. uniparens* was found to inhabit a *Tamarix* edge habitat. Interestingly, Jakle and Gatz (1985), in a study of lizard communities along the Gila River in Pinal County, Arizona, found a similar reduction of overall lizard density in *Tamarix* habitat but also reported a complete absence of *A. tigris* in *Tamarix* habitat; a result which contradicts the findings of this study.

Management Implications

This study demonstrates the utility of herpetofauna, and particularly lizards, in understanding the effects of riparian habitat shifts. Lizard communities in the arid southwest are the most diverse in the United States (Schall and Pianka 1978), which allow for the ability to draw robust conclusions about community-level habitat relationships. Avifauna communities are often investigated to understand the effects of riparian habitat change (Walker 2006; Sogge et al. 2008), but lizards also make excellent model organisms because of their non-transitory use of habitat (Shafroth et al. 2005), relatively small home-ranges (i.e., generally reported at the scale of m²; Rose 1982), and correlation to habitat physiognomy (Pianka 1966).

Riparian systems in the American southwest represent areas of high potential conflict between anthropogenic uses of water and native plants and wildlife. Human land and water use in the lower San Pedro River basin include mining, agriculture, livestock grazing, and groundwater pumping, which is associated with changes in hydrology, has increased each decade from 1940 to 1990 (Katz et al. 2009). Alteration of hydrologic regime is known to lead to habitat shifts towards xeric species and invasive species. *Tamarix* is currently the third most common riparian tree in the American Southwest (Friedman et al. 2005) and continuous proliferation is expected in many riparian systems. Removal of *Tamarix* is costly (Shafroth and Briggs 2008) and may only yield successful results when coupled with other restoration measures such as reestablishing historic flow regimes (Harms and Hiebert 2006). Climate scenario models for the San Pedro River predict a dramatic reduction in the width of *Populus-Salix* patch coverage and an increase in the coverage of *Prosopis* patches (Dixon et al. 2009). This study demonstrates that

these two disparate forms of shifting riparian habitats could have very different outcomes for the riparian lizard community at the confluence of the San Pedro River and Gila River.

TABLE 2.1. Mean (\pm SE) of unique lizards captures at trapping site during 2017 and 2018 in *Populus-Salix* (cottonwood-willow), *Prosopis* (mesquite), and *Tamarix* (saltcedar) along the San Pedro River and Gila River, Pinal County, Arizona, USA. Captures are standardized as number of unique captures per 100 days. Code is the first two letter of the genus and the first two letter of the specific epithet, except in *Sceloporus cowlesi*.

Family	Species	Code	CW n=6	MQ n=6	SC n=6
Eubelpharidae					
	<i>Coleonyx variegatus</i>	COVA	0.0 (0.0)	0.4 (0.4)	0.0 (0.0)
Phrynosomatidae					
	<i>Callisaurus draconoides</i>	CADR	0.6 (0.6)	0.0 (0.0)	0.0 (0.0)
	<i>Sceloporus clarkii</i>	SCCL	10.6 (4.7)	6.6 (3.6)	6.3 (1.7)
	<i>Sceloporus cowlesi</i>	SCOW	52.5 (8.6)	40.4 (5.2)	24.3 (2.9)
	<i>Sceloporus magister</i>	SCMA	0.4 (0.4)	1.8 (1.1)	3.2 (1.6)
	<i>Urosaurus ornatus</i>	UROR	6.1 (1.5)	14.5 (3.5)	10.4 (4.8)
	<i>Uta stansburiana</i>	UTST	0.0 (0.0)	1.3 (0.9)	0.9 (0.6)
Teiidae					
	<i>Aspidoscelis sonorae</i>	ASSO	138.3 (21.5)	55.7 (8.2)	0.9 (0.6)
	<i>Aspidoscelis tigris</i>	ASTI	43.4 (9.0)	20.6 (8.1)	32.9 (5.3)
All Lizards			298.3	141.2	78.8

TABLE 2.2. Principle components analysis (PCA) used to reduce dimensionality of habitat predictor variables. The number of relevant principal components was chosen based on eigenvalues greater than one. Bold values indicate variables that load on each synthetic component.

Variable	Component					
	1	2	3	4	5	6
<i>Tamarix</i> Canopy Cover (%)	0.915	-0.025	-0.014	0.028	-0.102	-0.208
Woody Debris Md. diameter/ 10 meter	0.914	0.005	-0.142	0.033	-0.131	0.222
Woody Ground Cover (%)	0.894	-0.246	0.234	-0.047	0.023	0.085
Woody Debris Lg. diameter / 10 meter	0.881	-0.023	0.005	0.252	0.075	0.279
Litter Ground Cover (%)	-0.811	0.186	-0.484	0.021	-0.147	-0.069
Woody Debris Sm. diameter / 10 meter	0.808	0.048	-0.246	-0.184	-0.263	-0.063
Grass Cover (%)	-0.714	-0.317	0.160	0.189	-0.169	-0.248
<i>Prosopis</i> Canopy Cover (%)	-0.700	-0.607	0.013	-0.203	0.116	0.130
Woody Species Richness	-0.621	0.290	0.147	0.160	0.029	0.586
Density of <i>Tamarix</i> Stems / 4 sq. meter	0.573	0.192	-0.181	-0.191	0.092	-0.099
Distance to river (m)	-0.246	-0.812	-0.033	-0.294	0.017	0.104
<i>Populus</i> and <i>Salix</i> Canopy Cover (%)	-0.140	0.811	0.003	0.383	0.143	0.274
Open Canopy (%)	0.078	0.666	0.124	-0.499	0.124	-0.376
Shrub Cover (%)	-0.265	0.575	-0.160	-0.431	0.559	-0.093
Litter Depth (cm)	-0.260	0.356	-0.764	0.117	-0.152	0.046
Bare Ground (%)	0.501	-0.056	0.744	0.022	0.298	0.030
Light Meter (lux)	-0.460	0.260	0.674	-0.195	-0.392	0.164
Visible Light (%)	0.345	-0.381	-0.548	0.359	0.462	0.013
Herb Cover (%)	-0.321	-0.301	0.156	0.559	0.025	-0.477
Density of <i>Populus</i> and <i>Salix</i> / 4 sq. meter	-0.121	0.349	0.396	0.435	0.417	-0.196
Density of <i>Prosopis</i> Stems / 4 sq. meter	-0.273	-0.440	-0.066	-0.273	0.591	0.171
Variance Explained (%)	34.62	16.81	12.24	7.93	7.28	5.62
Cumulative Variance Explained (%)	34.62	51.43	63.67	71.60	78.88	84.50

TABLE 2.3. Importance of habitat components in predicting lizard abundance on the San Pedro River and Gila River, Pinal County, Arizona, USA using multiple-model inference of multiple linear regression and logistic regression (SCMA). Top performing models within the significance level of the $\Delta AICc < 2.0$ are included. Directionality of relationship between habitat and species indicated by (+/-). Component descriptions are given in TABLE 2.2. Species abbreviations given in TABLE 2.1.

Species	Components	AICc	$\Delta AICc$	AICw	Components					
					C1	C2	C3	C4	C5	C6
ASSO	1, 2, 6	37.83	0	0.43	-0.58	0.33				0.34
ASTI	1, 2, 3	21.99	0	0.24	0.21	0.22	0.18			
	1, 2	23.46	1.47	0.12	0.21	0.22				
SCTR	1	-5.78	0	0.12	-0.09					
	1, 6	-5.57	0.21	0.12	-0.09					0.07
	1, 2	-5.40	0.38	0.11	-0.09	0.07				
	1, 2, 6	-5.25	0.52	0.10	-0.09	0.07				0.07
	Null	-3.89	1.89	0.05						
UROR	1	16.37	0	0.30	-0.18					
SCMA	6	29.02	0	0.22						-0.22
SCMA	Null	30.02	0.99	0.13						

*Note that AICc is Akaike's information criterion (corrected for small sample size), a metric used to judge model fit. $\Delta AICc$ is the difference in AICc from the top-performing model. Component AICc weights are the average relative weights of all combinations of models.

FIGURE 2.1. Mean (\pm SE) of all lizards captured per 100 trapping days at *Populus-salix* (CW), *Prosopis* (MQ), and *Tamarix* (SC) sites along the San Pedro River and Gila River, Pinal County, Arizona, USA. Letters symbolize independent-sample Kruskal-Wallis results; variables with different letters are significantly different.

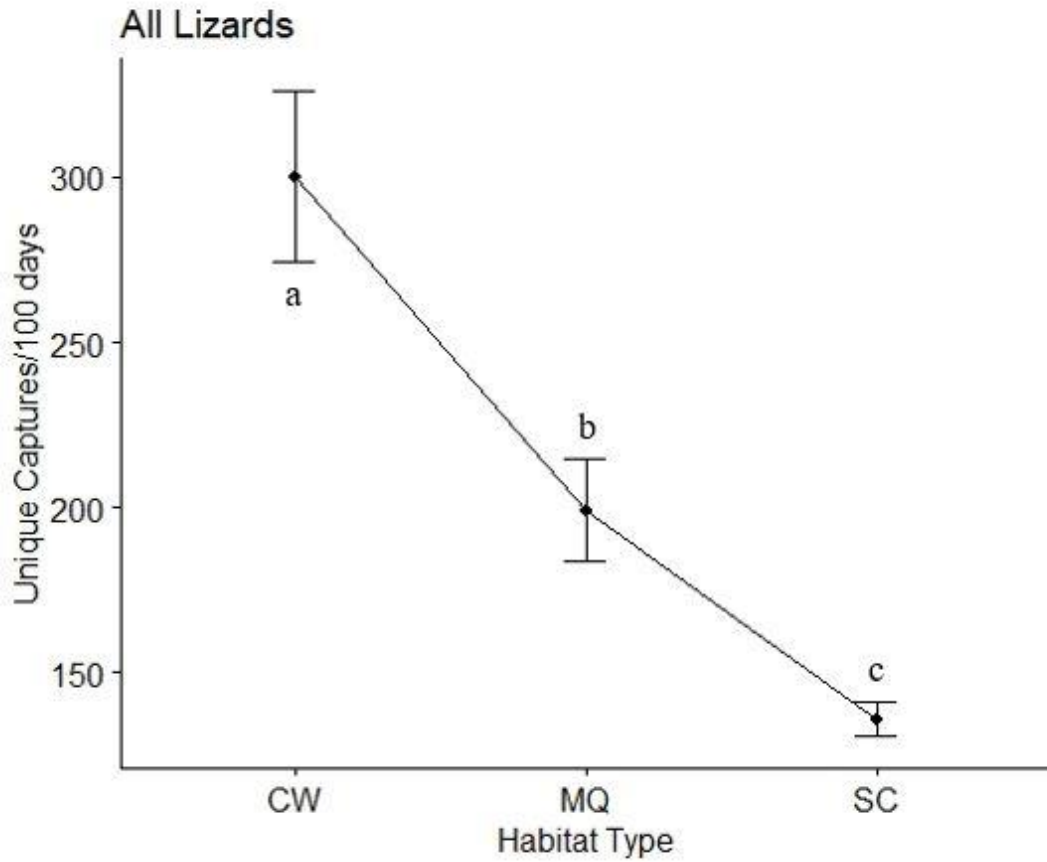


FIGURE 2.2. Mean (\pm SE) of lizards captured per 100 trapping days at *Populus-salix* (CW), *Prosopis* (MQ), and *Tamarix* (SC) sites along the San Pedro River and Gila River, Pinal County, Arizona, USA. Letters symbolize independent-sample Kruskal-Wallis results; variables with different letters are significantly different

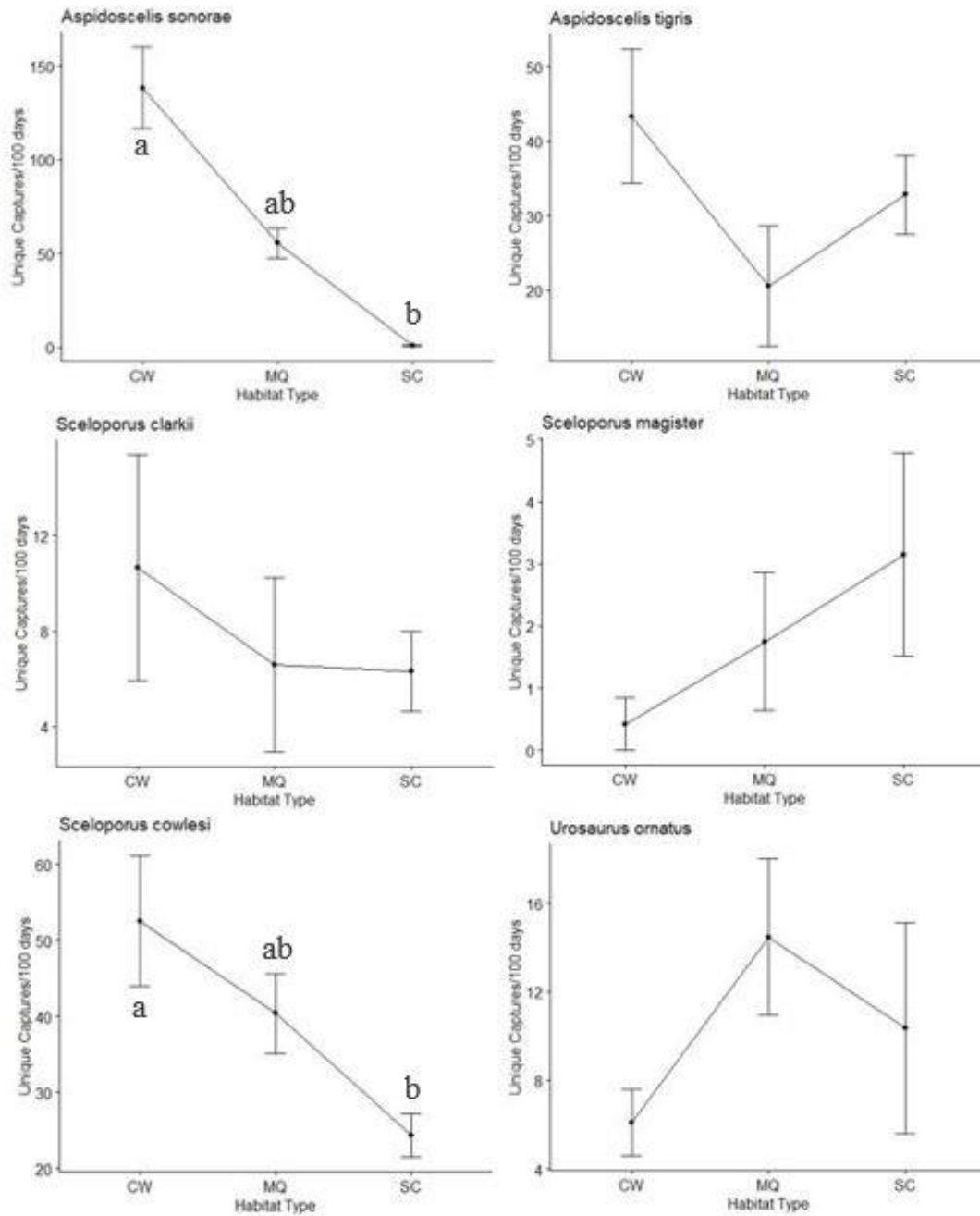
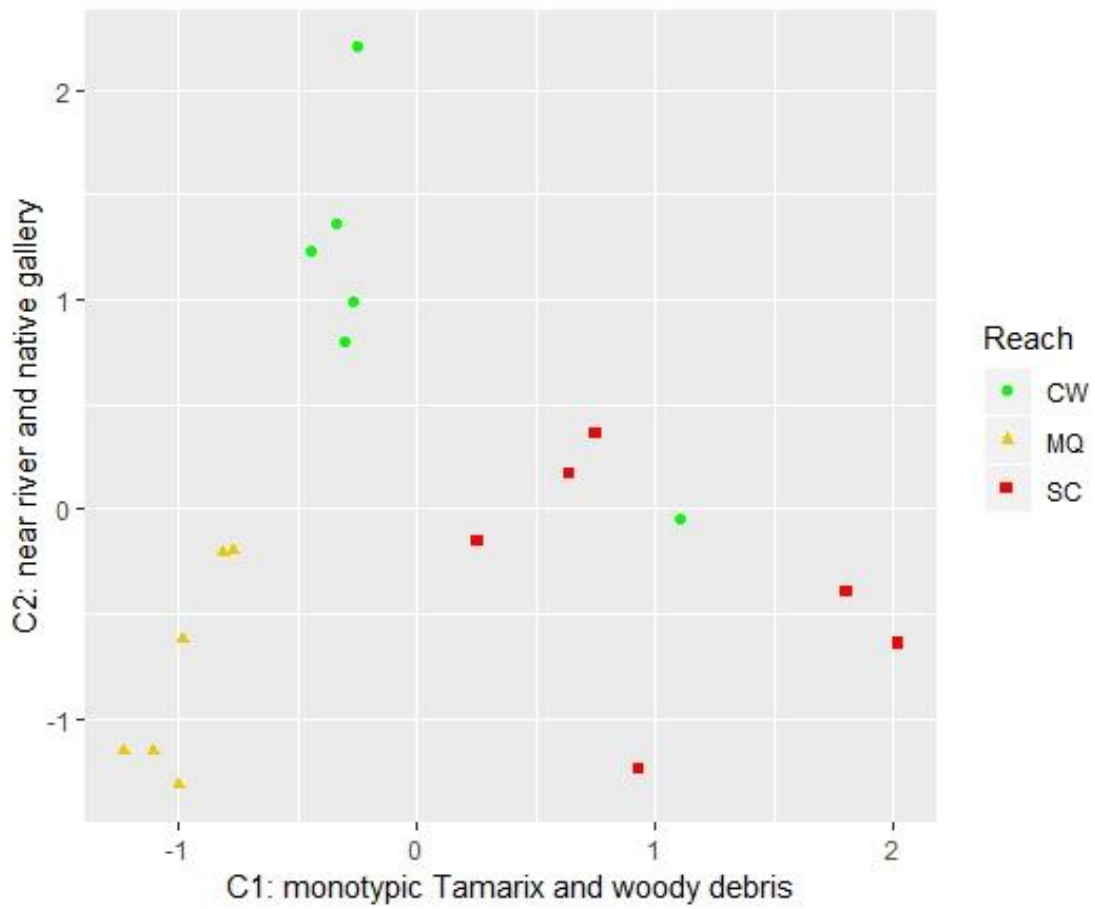


FIGURE 2.3. Vegetation physiognomy values from a PCA (TABLE 1.2) in *Populus-Salix* (CW), *Prosopis* (MQ) and *Tamarix* (SC) sites along the San Pedro River and Gila River, Pinal County, Arizona, USA.



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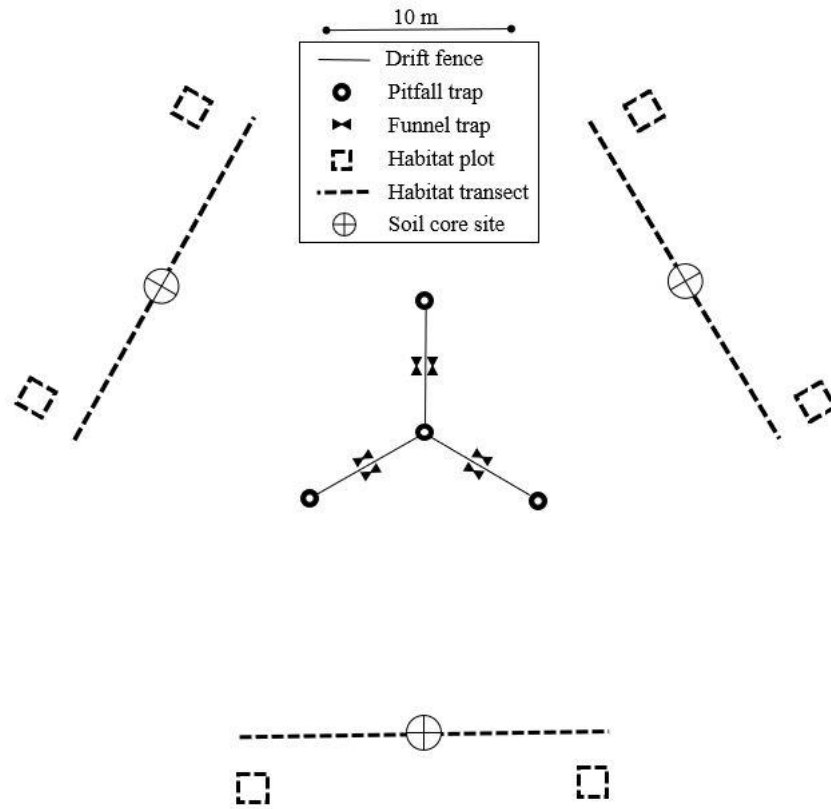
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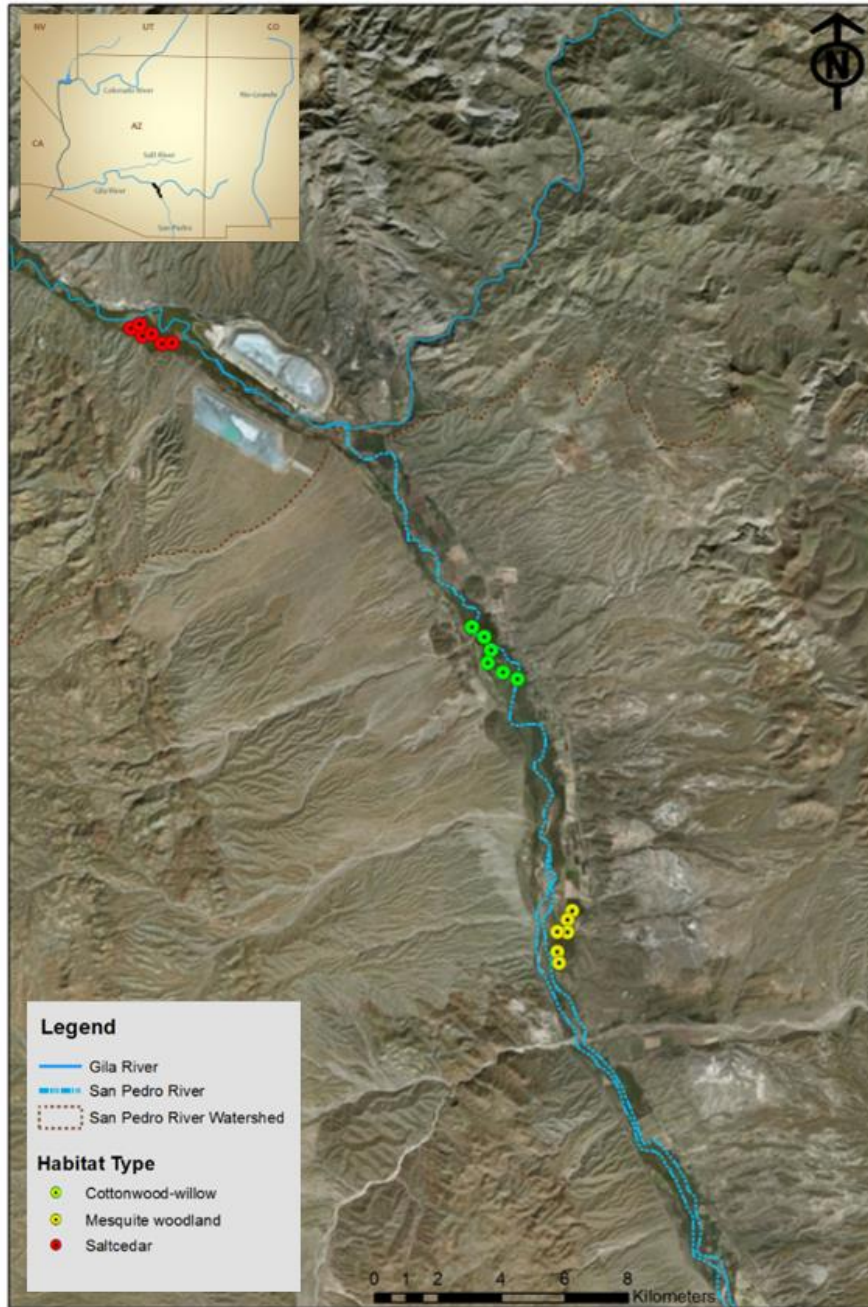
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APPENDIX A
SITE SCHEMATIC



APPENDIX A. Schematic of herpetofauna trapping and vegetation/soil measurement site along the San Pedro River and Gila River, Pinal County, Arizona, USA.

APPENDIX B
STUDY AREA MAP



APPENDIX B. Map of trapping sites along the San Pedro River and Gila River, Pinal County, Arizona, USA.

APPENDIX C
STUDY SITE LOCATIONS

APPENDIX C. Site name, habitat classification, and geographic location (Zone 12S, Datum NAD83) of herpetofauna trapping arrays/ vegetation measurement sites.

Site	Habitat Type	River System	Easting	Northing
SC1-1	Monotypic <i>Tamarix</i>	Gila River	514627	3652137
SC1-2	Monotypic <i>Tamarix</i>	Gila River	514862	3652242
SC2-1	Monotypic <i>Tamarix</i>	Gila River	514926	3651931
SC2-2	Monotypic <i>Tamarix</i>	Gila River	515181	3651987
SC3-1	Monotypic <i>Tamarix</i>	Gila River	515452	3651728
SC3-2	Monotypic <i>Tamarix</i>	Gila River	515722	3651749
CW1-1	<i>Populus-Salix</i>	San Pedro River	523517	3644435
CW1-2	<i>Populus-Salix</i>	San Pedro River	524089	3643917
CW2-1	<i>Populus-Salix</i>	San Pedro River	524203	3643661
CW2-2	<i>Populus-Salix</i>	San Pedro River	524040	3643491
CW3-1	<i>Populus-Salix</i>	San Pedro River	524518	3643083
CW3-2	<i>Populus-Salix</i>	San Pedro River	524908	3642896
MQ1-1	<i>Prosopis</i> Woodland	San Pedro River	526362	3636784
MQ1-2	<i>Prosopis</i> Woodland	San Pedro River	526242	3636550
MQ2-1	<i>Prosopis</i> Woodland	San Pedro River	526242	3636219
MQ2-2	<i>Prosopis</i> Woodland	San Pedro River	525975	3636237
MQ3-1	<i>Prosopis</i> Woodland	San Pedro River	525973	3635699
MQ3-2	<i>Prosopis</i> Woodland	San Pedro River	526018	3635412

APPENDIX D

STUDY ORGANISM: COUCH'S SPADEFOOT



APPENDIX D. Image of Couch's spadefoot (*Scaphiopus couchii*) in Fremont's cottonwood (*Populus fremontii*) litter encountered along the San Pedro River, Pinal County, Arizona, USA.

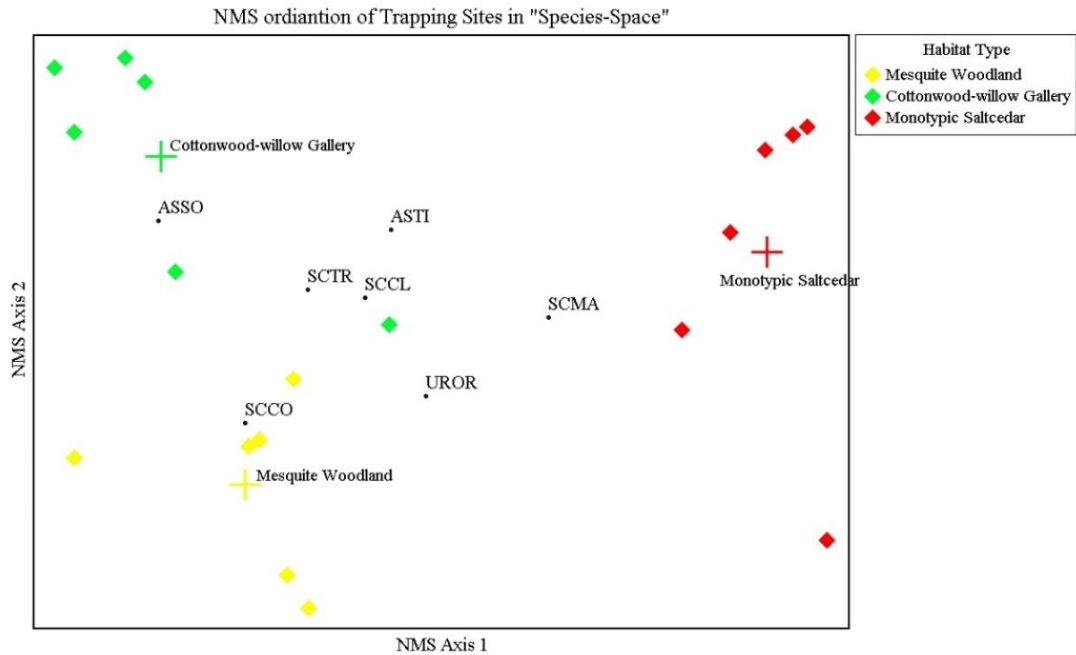
APPENDIX E
REPRESENTATIVE HABITAT TYPES



APPENDIX E. Images from three representative habitat types based on dominant canopy cover; cottonwood-willow (left), mesquite (middle), and saltcedar (right).

APPENDIX F

ORDINATION OF TRAPPING SITES IN "SPECIES-SPACE"



APPENDIX F. Nonmetric multidimensional scaling (NMDS) ordination of 18 trapping sites along the San Pedro River and Gila River, Pinal county, Arizona, USA. Circular dots symbolize herpetofauna species, diamonds symbolize trap sites, and pluses symbolize the centroid of site type. Four letter species codes are described in Table 2.1. Three lizard species were not included in the ordination due to low capture rates.

APPENDIX G

SOIL AND VEGETATION MEASUREMENT METHODS

APPENDIX G. Methods for habitat and soil variables (n=25) recorded at trapping sites along the San Pedro River and Gila River, Pinal County, Arizona, USA.

Variable	Measurement Method
Other	Core Samples for % Soil Moisture, Soil Particle Size, and % Coarse Fragment taken at 10m point of 20m transect. Measurements for %Canopy Cover and Visible Light take inside of 2x2m plot.
<i>Soil Moisture (%)</i>	Percentage of soil moisture (% volume)
<i>Soil Particle Size (%)</i>	Percent sand, silt, and clay determined by particle size analysis
<i>Canopy Cover (%)</i>	Average of four measurements taken in each cardinal direction with variable densiometer in center of plot, and divided against a control taken in open canopy
<i>Visible Light (%)</i>	Average of four measurements taken in each cardinal direction with light meter (REED instruments SD-1128) in center of plot, and divided against a control taken in open canopy
<i>Coarse Fragment (%)</i>	Determined during particle size analysis
<i>Distance to River (m)</i>	Measured from center pitfall trap of each array to center of river channel. Distance calculated in ArcGIS 10.5
Transect Point-Intercept	Recorded at 1m intervals along 20m transect
<i>Litter Depth (cm)</i>	Depth of leaf litter if present

<i>Ground Cover (%)</i>	Percentage of bare ground, woody debris, or leaf litter
<i>Tree and Shrub Cover</i>	Proportion of Open, <i>Prosopis</i> , <i>Tamarix</i> , or <i>Populus-Salix</i> canopy cover
Transect Line-Intercept	Recorded at every-other point along 20m transect
<i>Woody Debris (count)</i>	Small (1.0-2.5cm) woody debris, Medium (2.5-7.5cm) woody debris, Large (>7.5cm) woody debris
Plot Stem Counts	Woody plants rooted within 2x2m plots were recorded
<i>Woody Trees and Shrubs</i>	Count of <i>Tamarix</i> , <i>Populus</i> and <i>Salix</i> , or <i>Prosopis</i> stems
<i>Woody Richness</i>	Number of unique woody species in 2x2m plots

APPENDIX H

SOIL AND VEGETATION VARIABLES ACROSS RIPARIAN HABITATS

Variable	CW	MQ	SC	ANOVA ($\alpha = 0.05$)
	<i>n</i> = 6	<i>n</i> = 6	<i>n</i> = 6	<i>n</i> = 18
Litter Depth (cm)	2.52 (0.4)	2.14 (0.2)	1.98 (0.2)	$F_{2,15} = 0.72, P = 0.504$
Percent Bare Groundcover	19.6 (4.4)	19.6 (3.3)	20.8 (4.0)	$F_{2,15} = 0.14, P = 0.871$
Percent Litter Groundcover	70.4 (6.6)	80.4 (7.5)	50.0 (7.1)	$F_{2,15} = 3.33, P = 0.064$
Percent Woody Groundcover	10.0 (3.0) ^a	5.00 (3.5) ^a	29.2 (3.5) ^b	$F_{2,15} = 6.65, P = 0.009$
Proportion Open	0.09 (0.1)	0.01 (0.0)	0.06 (0.0)	$F_{2,15} = 1.23, P = 0.321$
Proportion of <i>Tamarix</i>	0.31 (0.1) ^a	0.00 (0.0) ^b	0.85 (0.1) ^c	$F_{2,15} = 29.9, P < 0.001$
Proportion of <i>Populus</i> and <i>Salix</i>	0.43 (0.1) ^a	0.00 (0.0) ^b	0.00 (0.0) ^b	$F_{2,15} = 11.0, P = 0.001$
Proportion of <i>Prosopis</i>	0.11 (0.0) ^a	0.87 (0.0) ^b	0.09 (0.1) ^a	$F_{2,15} = 49.4, P < 0.001$
Count of Woody Debris, small diameter (1.0-2.5 cm)/ 10 m	36.2 (7.3) ^a	20.3 (4.1) ^a	71.2 (10.3) ^b	$F_{2,15} = 8.48, P = 0.003$
Count of Woody Debris, medium diameter (2.5-7.5 cm)/ 10 m	14.7 (3.1) ^{ab}	5.25 (1.1) ^a	24.7 (3.6) ^b	$F_{2,15} = 7.84, P = 0.005$
Count of Woody Debris, large diameter (>7.5 cm)/ 10 m	4.25 (1.2) ^{ab}	0.25 (0.1) ^a	5.75 (1.3) ^b	$F_{2,15} = 5.91, P = 0.013$
Stems <i>Tamarix</i> / 2 m ²	0.68 (0.4)	0.00 (0.0)	0.46 (0.2)	$F_{2,15} = 1.32, P = 0.296$
Stem <i>Populus</i> & <i>Salix</i> / 2 m ²	0.42 (0.4)	0.00 (0.0)	0.00 (0.0)	$F_{2,15} = 1.28, P = 0.308$
Stems <i>Prosopis</i> / 2 m ²	0.54 (0.3)	2.71 (1.3)	0.96 (0.6)	$F_{2,15} = 1.26, P = 0.313$
Canopy Cover (%)	81.8 (2.9)	82.1 (4.2)	86.9 (3.1)	$F_{2,15} = 0.46, P = 0.640$
Distance to River (m)	112.0 (50.9) ^a	583.5 (78.5) ^b	294.3 (47.2) ^a	$F_{2,15} = 15.4, P < 0.001$
Percent Cover of Shrubs	9.63 (4.3)	4.52 (2.1)	0.10 (0.0)	$F_{2,15} = 1.79, P = 0.201$
Percent Herbaceous Cover	9.00 (3.1)	12.1 (5.2)	6.92 (2.9)	$F_{2,15} = 0.34, P = 0.716$
Percent Cover of Grasses	15.7 (6.2) ^{ab}	32.9 (5.4) ^a	6.19 (3.4) ^b	$F_{2,15} = 4.70, P = 0.026$
Visible Light	0.35 (0.1)	0.36 (0.1)	0.15 (0.0)	$F_{2,15} = 2.34, P = 0.131$
Percent Soil Moisture	5.68(1.9) ^a	11.9 (0.5) ^b	7.35 (1.7) ^{ab}	$F_{2,15} = 5.31, P = 0.018$
Percent Sand Particulate	76.2 (4.2) ^a	46.9 (2.5) ^b	64.7 (7.1) ^a	$F_{2,15} = 10.2, P = 0.002$
Percent Clay Particulate	7.37 (1.8)	14.6 (2.9)	5.41 (0.5)	$F_{2,15} = 3.53, P = 0.055$

Percent Silt Particulate	16.4 (3.0) ^a	38.5 (3.8) ^b	29.9 (6.6) ^{ab}	F _{2,15} = 5.57, P = 0.016 F _{2,15} = 4.83, P = 0.024
Percent Coarse Fragment	20.4 (9.6) ^{ab}	36.9 (3.3) ^a	11.2 (6.3) ^b	

APPENDIX H. Mean (\pm SE) of vegetation and soil variables quantified in riparian forest along the San Pedro River and Gila River, Pinal County, Arizona, USA. Tukey's multiple comparison of means post-hoc results of a one-factor ANOVA are denoted by superscripts (variables with different letters are significantly different).