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RESEARCH ARTICLE

The effects of riparian restoration following saltcedar (*Tamarix* spp.) biocontrol on habitat and herpetofauna along a desert stream

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Amphibians and reptiles (herpetofauna) have been linked to specific microhabitat characteristics, microclimates, and water resources in riparian forests. Our objective was to relate variation in herpetofauna abundance to changes in habitat caused by a beetle used for *Tamarix* biocontrol (*Diorhabda carinulata*; Coleoptera: Chrysomelidae) and riparian restoration. During 2013 and 2014, we measured vegetation and monitored herpetofauna via trapping and visual encounter surveys (VES) at locations affected by biocontrol along the Virgin River in the Mojave Desert of the southwestern United States. Twenty-one sites were divided into four riparian stand types based on density and percent cover of dominant trees (*Tamarix*, *Prosopis*, *Populus*, and *Salix*) and presence or absence of restoration. Restoration activities consisted of mechanically removing non-native trees, transplanting native trees, and restoring hydrologic flows. Restored sites had three times more total lizard and eight times more yellow-backed spiny lizard (*Sceloporus uniformis*) captures than other stand types. Woodhouse's toad (*Anaxyrus woodhousii*) captures were greatest in unrestored and restored *Tam-Pop/Sal* sites. Results from VES indicated that herpetofauna abundance was greatest in the restored *Tam-Pop/Sal* site compared with the adjacent unrestored *Tam-Pop/Sal* site. *Tam* sites were characterized by having high *Tamarix* cover, percent canopy cover, and shade. Restored *Tam-Pop/Sal* sites were most similar in habitat to *Tam-Pop/Sal* sites. Two species of herpetofauna (spiny lizard and toad) were found to prefer habitat components characteristic of restored *Tam-Pop/Sal* sites. Restored sites likely supported higher abundances of these species because restoration activities reduced canopy cover, increased native tree density, and restored surface water.

Key words: amphibian, cottonwood, habitat management, hydrologic flows, invasive species, lizard, Mojave Desert

Implications for Practice

- Biocontrol of non-native saltcedar (*Tamarix* spp.) may indirectly affect wildlife by reducing foliar cover and leaving voids in the riparian habitat matrix.
- Without intervention, saltcedar biocontrol does not by itself improve riparian habitat complexity and native tree recruitment; therefore, restoration of side-channel surface flows and planting native trees may be necessary.
- Restoration activities and non-native plant control methods should consider maintaining woody debris and patches of understory vegetation to maintain a sun-shade mosaic which benefits many species of lizards and other wildlife.
- Conservation projects should include monitoring following restoration or non-native plant control to assess invasion of undesirable plants that may increase with soil disturbance and canopy removal.

Introduction

Globally, researchers have monitored responses of lizards to understand how habitat restoration affects animal populations, through changes in canopy of woody vegetation, ground litter structure, and microclimate, in grasslands (Steidl et al. 2013; Stellatelli et al. 2013), agriculture areas (Jellinek et al. 2014), and riparian areas (Bateman et al. 2008*a*). About 60% of amphibian and reptile species (collectively called herpetofauna) in the Chihuahuan, Great Basin, Mojave, and Sonoran Deserts of North America utilize riparian or wetland habitats (Lowe 1989). In riparian ecosystems of the western United States, amphibians and reptiles are frequently common species but are seldom included in surveys of riparian ecosystems. Despite their abundances, there is a paucity of research on reptiles and amphibians in relation to non-native vegetation (Bateman et al. 2013).

Saltcedar (*Tamarix* spp.) is a non-native tree introduced to the United States during the nineteenth century as an ornamental species and for erosion control in the American West (Robinson 1965). Due to changes in stream hydrology (Everitt 1998; Shafroth et al. 2002) and the plant's unique tolerances

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to drought and saline conditions (Smith et al. 1998), saltcedar spread rapidly and is now the third most abundant riparian tree in the western United States (Friedman et al. 2005). Saltcedar can form dense monotypic stands, which have been linked to a decline in richness and diversity of native plants (Engel-Wilson & Ohmart 1978; Lovich et al. 1994) and wildlife (Anderson et al. 1977; Durst et al. 2008) in riparian areas. As a result, natural resource managers have invested millions of dollars to control saltcedar (Shafroth & Briggs 2008).

Saltcedar removal in riparian areas can fail or cause negative effects to habitat and wildlife if managers do not fully understand the biological history of the location, reasons behind initial colonization, and impacts resulting from control activities (Zavaleta et al. 2001; Shafroth et al. 2008). Long-term domination of saltcedar at a site may significantly alter soil chemistry (Yin et al. 2009) and microbial assemblages (Meinhardt & Gehring 2012), preventing or limiting native plant establishment (Zavaleta et al. 2001; Harms & Hiebert 2006). In addition, changes in stream hydrology that led to saltcedar domination may no longer support native vegetation (Stromberg et al. 2007). In these situations, saltcedar or other non-native plants may recolonize restored areas (Shafroth et al. 2005; Hultine et al. 2010; Ostoja et al. 2014). Even worse, large-scale removal of saltcedar may reduce the only habitat available for riparian wildlife species (Hultine et al. 2010; Paxton et al. 2011). Many saltcedar control techniques can reduce forest cover and vertical habitat structure, increase soil erosion, and facilitate invasion by other non-native plants (D'Antonio & Meyerson 2002; Shafroth et al. 2008). Although several studies have documented the effect of saltcedar biocontrol on plant and wildlife species (Sogge et al. 2008; York et al. 2011; Nagler et al. 2014; Bateman et al. 2015; Hultine et al. 2015), this study is the first to analyze plant and animal community response to biocontrol, coupled with targeted habitat restoration.

In this study, we examined the response of a local amphibian and reptile community to changes in habitat structure (including riparian plant composition and hydrologic flows) from restoration following saltcedar biocontrol. We were particularly interested in whether the addition of restoration following biocontrol benefitted wildlife habitat and species. Our objectives were to (1) determine how restored and unrestored riparian areas differ in habitat structure and physiognomy; (2) determine how restored and unrestored riparian sites differ in herpetofauna abundance and diversity; and (3) relate herpetofauna species to riparian habitat structure and physiognomy.

Methods

Study Area

We established study sites in riparian areas along the Virgin River, a tributary of the Colorado River that flows through the states of Utah, Arizona, and Nevada in the southwestern United States. Study sites were situated along the river from St. George, Utah (UTMs NAD83 274660mE 4107912mN), to Gold Butte in Clark County, Nevada (738634mE 4050113mN; Fig. 1). Study sites were divided into four stand types based on density and percent cover of dominant woody trees and presence of restoration activities: saltcedar-dominated stands (*Tam*), saltcedar-mesquite (*Prosopis* spp.) stands (*Tam-Pros*), saltcedar-cottonwood (*Populus fremontii*)/willow (*Salix* spp.) stands (*Tam-Pop/Sal*), and restored saltcedar-cottonwood/willow stands (Restored *Tam-Pop/Sal*). Saltcedar consisted of *Tamarix ramosissima* and related species and hybrids. Water flow in the Virgin River was perennial and stands varied in occurrence of side-channel surface water. Utah sites had standing surface water with marshy habitat and other sites had no surface water or marshes present.

All sites were affected by biocontrol during the period of study. In 2006, natural resource managers released an insect biocontrol agent, the northern tamarisk beetle (*Diorhabda carinulata*; see Tracy & Robbins 2009 for discussion of taxonomy and ecological background on these beetles) in the city of St. George, Utah, to control saltcedar stands (Bateman et al. 2010). Larvae and adult beetles feed exclusively on the foliage of saltcedar causing defoliation (Lewis et al. 2003). Saltcedar trees along the Virgin River have experienced several years of defoliation, canopy regrowth, and eventual canopy reduction (Hultine et al. 2015).

Restoration activities included mechanical removal of 50% of saltcedar and Russian olive (*Elaeagnus angustifolia*), stumps sprayed with herbicide (Garlon 3A), native willow and mesquite stems transplanted, and water flow introduced via trenching and redirection of irrigation/stormwater run-off. Restoration occurred during Winter/Spring of 2012 and 2013. As restored *Tam-Pop/Sal* sites were restricted to Utah and not monitored prior to restoration, we used a space-for-time substitution. We compared a restored *Tam-Pop/Sal* site to an adjacent unrestored *Tam-Pop/Sal* site in Utah of similar habitat structure and composition as a proxy to pre-restored conditions.

Herpetofauna Sampling

We monitored amphibian and reptile species ("herpetofauna") at 21 sites (eight *Tam*, five *Tam-Pros*, six *Tam-Pop/Sal*, two Restored *Tam-Pop/Sal*) using trap arrays during May through July 2013 and 2014. Trap arrays consisted of four pitfall traps (9 L buckets) and six funnel traps positioned along three 6-m-long drift fences oriented at 0°, 120°, and 240° (Bateman & Ostoja 2012; Fig. 2). Each array was randomly established using ArcGIS 9.3.1 and located at least 25 m from habitat edge. We checked traps every 24 hours (when open) and identified herpetofauna to species and released them at the point of capture. Lizards were marked with a unique toe clip (Waichman 1992). Amphibians and snakes were not marked due to low abundances.

To avoid possible confounding effects from having restored *Tam-Pop/Sal* sites located only in Utah, we established (unrestored) *Tam-Pop/Sal* sites in Utah and conducted visual encounter surveys (VES; Jaeger 1994) to supplement results from trap arrays. To ensure comparable sampling between sites, we randomized placement of three transects per site per year using ArcGIS 10.0. Transects were at least 150 m apart, except for one transect at the restored site where permanent water

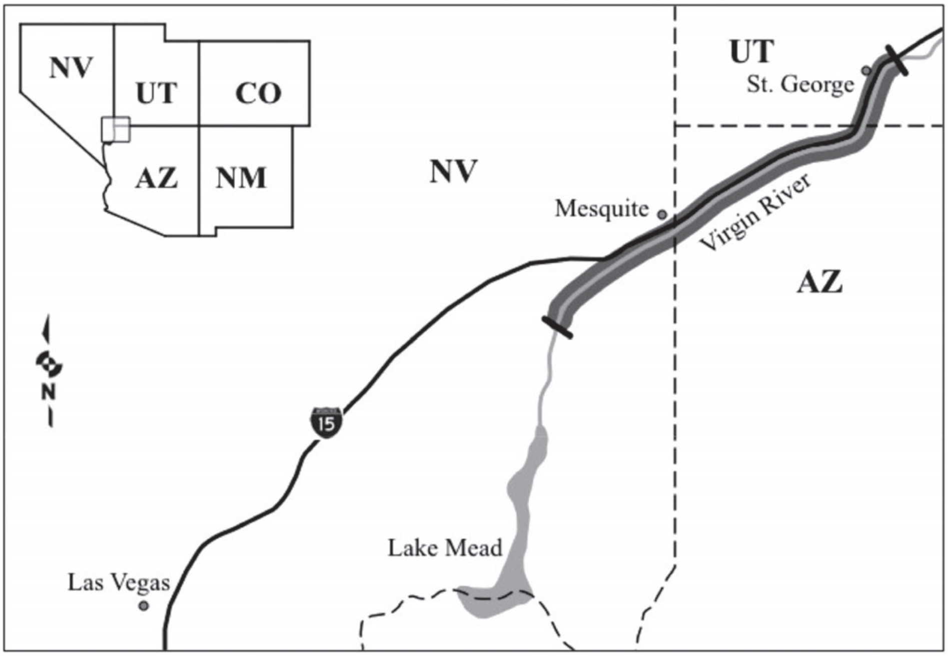

Figure 1. Map of study area along the Virgin River in Utah, Arizona, and Nevada, U.S.A. Shaded area delineates study area location.

restricted its placement to approximately 125 m to the nearest transect. Transects varied in length depending on the width of the riparian stand. We placed two 10×20−m plots along each transect as subsamples that were at least 25 m from habitat edge (Fig. 2). Two observers recorded numbers of amphibian and reptile species during four surveys per plot per year. Surveys occurred between 07:30 and 11:30 hours under similar weather conditions. The two observers walked side by side and each surveyed a 5 m width (half of the plot). Observers disturbed ground litter and debris to locate hidden animals, and searched up to 2 m above the ground to include semi-arboreal species.

Vegetation Sampling

We measured habitat structure and composition during 2013 and 2014 following Bateman and Ostoja (2012). Vegetation was measured at trapping sites using two 20-m transects and four 2×2−m plots. Transects were located 15 m from the center of trap arrays and oriented at 60°, 180°, or 300° (Fig. 2). Two of the three transects were selected by drawing lots for measurement. Plots were located 2 m away from ends of each transect. At 1 m intervals along transects, we recorded ground cover type, depth of litter, and woody tree and shrub cover. At every other meter, we recorded the number and size (between 1.0–2.5 cm and >2.5 cm) of woody debris (below 0.5 m in height) that crossed the transect. In 2014, we recorded number of stems and size class of each plant species rooted within plots. Canopy cover (measured with a spherical densiometer) and visible light (μmol, or photons m^{-2} s^{-1}; measured by LI-COR LI-250A light meter) were recorded in four cardinal directions in plots. We averaged percent visible light readings per plot and divided by a control reading (i.e. an area with no canopy cover).

We also measured habitat along transects where we conducted VES in restored and unrestored sites using methods similar to those described near trap arrays. One difference was that we measured canopy cover and visible light in the four cardinal directions at 0, 10, and 20 m along transects.

Data Analyses

We defined an index of lizard abundance at trapping arrays as the number of uniquely marked individuals captured per 100 trap days per site. As amphibians were not marked, we defined amphibian abundance as the total number of captures per 100 days. We calculated species richness as the average number of species per stand type. Simpson's Diversity and Brillouin Evenness indices were calculated for each stand type using Species Diversity & Richness 4.1.2 Software (Seaby & Henderson 2006). To determine if there was a significant effect of year and stand type on lizard abundances, we used a repeated measures general linear model (GLM; SPSS version 22.0). All abundances were $\log(x+1)$ transformed to increase data normality.

For comparisons among VES sites, we used the highest counts for each species for a given transect, over the four surveys conducted per year. We calculated species richness per transect by summing all species observed during surveys. We performed a chi-square analysis on reptile and amphibian abundance to determine if abundances differed between the restored and unrestored *Tam-Pop/Sal* sites.

We summarized variation among habitat metrics at trapping sites using a principal component analysis (PCA) with a Varimax rotation (SPSS version 22.0). Habitat metrics recorded in 2013 and 2014 were averaged prior to PCA. Components were

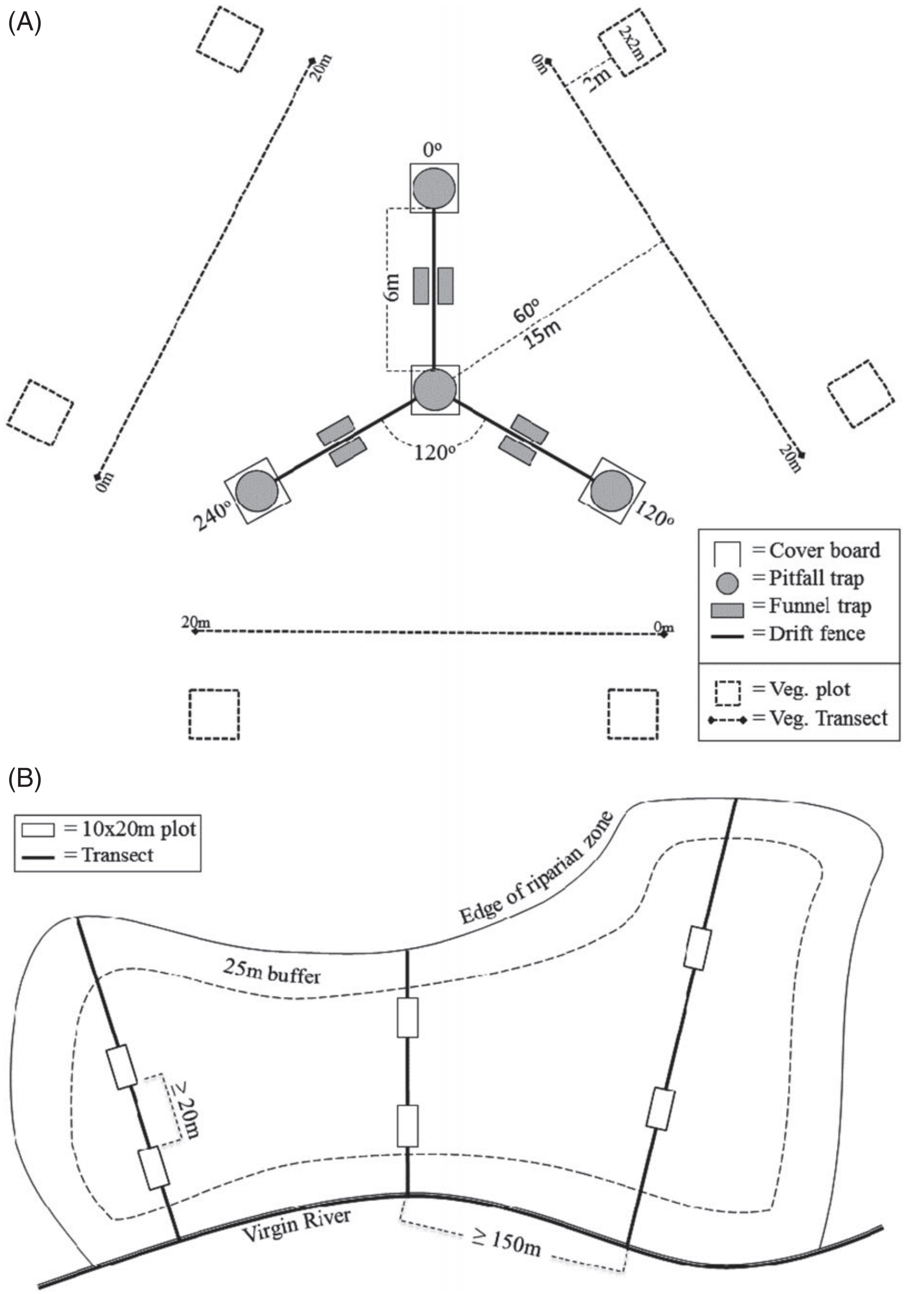

Figure 2. Diagram of trap array and vegetation transects and plots (A) and plots for VES and vegetation transects (B) used to monitor herpetofauna and habitat along the Virgin River in Utah, Arizona, and Nevada, U.S.A. Not to scale.

interpreted based on the correlation matrix. We compared components scores among stand types using a one-way analysis of variance (ANOVA) and compared restored and unrestored *Tam-Pop/Sal* sites (from VES sites) with a *t*-test.

To determine if habitat components were good predictors of herpetofauna abundance, we ranked multiple linear regression models using a multimodel inference approach Akaike information criterion (AIC) for small samples (Burnham & Anderson 2004). We considered all possible models with one and two combinations of components. The "top model" was $\Delta\text{AIC} = 0$; however, we also considered models with $\Delta\text{AIC} \leq 2$. Variable weights were calculated to determine the relative importance of each component.

Results

Herpetofauna

During 2013 and 2014 (1,060 trap days), we captured eight species of lizards (656 unique individuals), three species of

Table 1. Mean (+SE) number of lizards (unique individuals) and amphibians (total captures) captured per 100 trap days at trap arrays in four riparian stand types based on dominant trees (*Tamarix*, *Prosopis*, *Populus*, and *Salix*) along the Virgin River in Utah, Arizona, and Nevada, U.S.A. All species are native, except non-native *Pseudacris regilla* are introduced in the restored sites in Utah.

	2013				*2014*			
Family *Species*	*Tam* $n=8$	*Tam-Pros* $n=5$	*Tam-Pop/Sal* $n=6$	*Restored Tam-Pop/Sal* $n=2$	*Tam* $n=8$	*Tam-Pros* $n=5$	*Tam-Pop/Sal* $n=6$	*Restored Tam-Pop/Sal* $n=2$
Teiidae								
Aspidoscelis tigris	35.0 (7.2)	50.1 (6.2)	46.9 (13.4)	61.9 (4.8)	28.2 (3.4)	52.2 (5.6)	39.2 (7.7)	67.3 (1.9)
Aspidoscelis velox	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	4.8 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Phrynosomatidae								
Callisaurus draconoides	0.5 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Sceloporus uniformis	0.0 (0.0)	2.6 (1.7)	9.0 (3.9)	42.9 (4.8)	0.0 (0.)	2.1 (1.4)	5.8 (2.3)	36.5 (9.6)
Urosaurus graciosus	2.2 (0.9)	6.3 (5.2)	0.0 (0.0)	0.0 (0.0)	0.4 (0.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Urosaurus ornatus	0.0 (0.0)	0.8 (0.8)	0.0 (0.0)	0.0 (0.0)	1.3 (0.9)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Uta stansburiana	9.9 (5.6)	15.8 (7.7)	18.2 (13.3)	61.9 (14.3)	12.5 (4.9)	8.3 (4.4)	16.1 (6.3)	23.1 (0.0)
Eublepharidae								
Coleonyx variegatus	1.0 (1.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.4 (04)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Bufonidae								
Anaxyrus microscaphus	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.4 (2.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Anaxyrus woodhousii	11.8 (3.1)	7.2 (4.7)	43.8 (6.3)	42.9 (23.8)	3.5 (1.7)	13.1 (12.3)	8.6 (4.5)	115.4 (100.0)
Hylidae								
Pseudacris regilla	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	66.7 (42.9)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	19.2 (11.5)

snakes, and three species of amphibians at 21 trapping sites along the Virgin River (Table 1). Lizard captures were dominated (95% of marked individuals) by three species: tiger whiptails (*Aspidoscelis tigris*), common side-blotched lizards (*Uta stansburiana*), and yellow-backed spiny lizards (*Sceloporus uniformis*). Total lizard abundance differed by stand type ($F = 3.775$, degrees of freedom [df] = 3, $p = 0.030$), but did not differ across years ($F = 0.987$, $df = 1$, $p = 0.334$), and did not exhibit a year-by-stand interaction ($F = 0.242$, $df = 3$, $p = 0.866$). Total lizard abundance was three times greater at restored *Tam-Pop/Sal* sites compared with other stand types (Fig. 3). Yellow-backed spiny lizards were the only species to vary among stand types ($F = 13.068$, $df = 3$, $p < 0.001$). This species was most abundant at restored *Tam-Pop/Sal* sites (Fig. 3), and was absent from *Tam* sites. Tiger whiptails and common side-blotched lizards had highest abundances in restored *Tam-Pop/Sal* sites and tended toward significant differences among stand types ($F = 2.70$, $df = 3$, $p = 0.08$; $F = 1.07$, $df = 3$, $p = 0.39$, respectively). Abundance of these two species, added to numbers of yellow-backed spiny lizards, contributed to the overall significant difference in total lizard numbers across stand types.

Woodhouse's toads (*Anaxyrus woodhousii*) comprised 84% of amphibian captures and occurred in all stand types (Table 1). Woodhouse's toad abundance was greatest in the *Tam-Pop/Sal* and restored *Tam-Pop/Sal* sites ($F = 4.057$, $df = 3$, $p = 0.024$), but varied between years ($F = 4.436$, $df = 1$, $p = 0.050$; Fig. 3). There was no significant year-by-stand-type interaction ($F = 2.983$, $df = 3$, $p = 0.060$).

We captured the most species and lizard diversity indices were greatest at restored *Tam-Pop/Sal* sites (Tables 1 & 2). Tiger whiptails were the only species captured at every site and several species of the herpetofauna community had restricted occurrences. Plateau striped whiptails (*Aspidoscelis velox*), on the western edge of their geographic range, and non-native Pacific tree frogs (*Pseudacris regilla*) were restricted to restored *Tam-Pop/Sal* sites (Table 1). Tree frog occurrence likely represents a localized introduction of the species in Utah and only occurred in sites with standing water and marsh habitat. Other species with limited occurrences included zebra-tailed lizards (*Callisaurus draconoides*) and western banded geckos (*Coleonyx variegatus*) which we captured only in *Tam* sites and ornate tree lizards (*Urosaurus ornatus*) which we captured only in *Tam* and *Tam-Pros* sites.

Results from VES at restored and unrestored *Tam-Pop/Sal* sites indicated that reptile ($\chi^2 = 8.067$, $df = 1$, $p < 0.005$) and amphibian ($\chi^2 = 166.168$, $df = 1$, $p < 0.001$) abundance was greatest at the restored site (Table S1, Supporting Information). Abundances for individual species were too low for further analyses. Reptile and amphibian richness was similar between sites ($\chi^2 = 0.111$, $df = 1$, $p > 0.25$).

Habitat

Habitat structure and physiognomy varied among stand types (Table 3). Vegetative diversity also varied among stand types in regard to understory shrub species. For example, *Tam-Pros* sites had more arrowweed (*Pluchea sericea*) and wolfberry (*Lycium* sp.) than other site types. Baccharis (*Baccharis* sp.) and saltbush (*Atriplex* sp.) occurred at all types except were absent in *Tam* sites and absent in *Tam-Pop/Sal* sites, respectively.

Six PCA components explained 80% of the variation in habitat structure and composition among stand types (Table 4). Habitat was differentiated based on the following characteristics: (C1) overstory and mesquite/saltcedar cover, (C2)

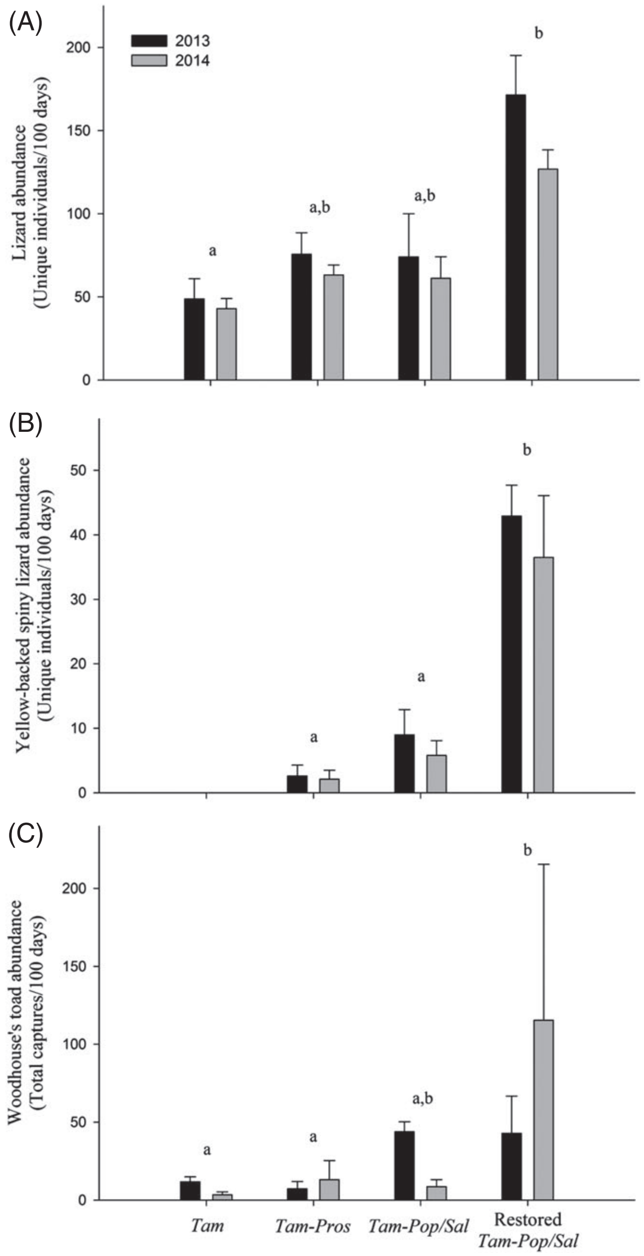

Figure 3. Mean (+SE) abundance of all lizard species (A), yellow-backed spiny lizards (*Sceloporus uniformis*; B), and Woodhouse's toads (*Anaxyrus woodhousii*; C) captured during 2013 and 2014 in four riparian stand types based on dominant trees (*Tamarix*, *Prosopis*, *Populus*, and *Salix*) along the Virgin River in Utah, Arizona, and Nevada, U.S.A. Letters represent significant difference (based on repeated measures GLM).

large woody debris and cottonwood/willow cover, (C3) cottonwood/willow density, (C4) small woody debris, (C5) small diameter saltcedar/large diameter mesquite density, and (C6) arrowweed/large diameter saltcedar density. Overall, *Tam* sites consisted of high saltcedar cover and stem density, high canopy cover, and high shade (Tables 3 & 4). *Tam-Pros* sites had high mesquite cover with open canopies and high percentage of bare ground. *Tam-Pop/Sal* sites exhibited greater variation in

Table 2. Summary values for diversity measures of lizards captured at trap arrays in four riparian stand types based on dominant trees (*Tamarix*, *Prosopis*, *Populus*, and *Salix*) along the Virgin River in Utah, Arizona, and Nevada, U.S.A.

Diversity Measure	*Tam*	*Tam-Pros*	*Tam-Pop/Sal*	*Restored Tam-Pop/Sal*
Simpson's D	1.735	1.788	1.997	3.004
Brillouin E	0.549	0.502	0.626	0.814
Richness	2.875	2.600	2.500	4.000

structure, but typically had high cottonwood/willow cover and stem density, large woody debris, and intermediate levels of canopy cover. Restored *Tam-Pop/Sal* sites were most similar to *Tam-Pop/Sal* sites but exhibited intermediate levels of habitat characteristics compared with other stand types (Table 3).

Habitat structure and physiognomy varied between restored and unrestored *Tam-Pop/Sal* sites (VES sites, Table S2). Canopy cover was significantly lower at the restored *Tam-Pop/Sal* site ($T = -2.51$, $p = 0.031$). Although not significant, the restored *Tam-Pop/Sal* site had lower saltcedar cover ($T = -1.96$, $p = 0.121$) and a higher proportion of bare ground ($T = 2.06$, $p = 0.108$) and woody debris ($T = 1.65$, $p = 0.174$) than the unrestored *Tam-Pop/Sal* site. Photographs taken at the restored site showed a large increase in abundance of secondary succession species, e.g. kochia (*Bassia scoparia*), which established in sites after disturbance caused by non-native saltcedar removal and other restoration activities.

Herpetofauna and Habitat Relationships

We included the four most common species of herpetofauna (three lizards and one amphibian) in habitat analyses. Yellow-backed spiny lizards had the only conclusive habitat model (Table 5) and were associated with areas having high densities of cottonwood/willow and large diameter mesquite; they avoided areas with high densities of small diameter saltcedar (C3 and C5). Additional models and variable weights indicated that yellow-backed spiny lizards could also be associated with high cottonwood/willow cover, large woody debris, and deep litter (C2). We observed lizards using various foraging substrate related to habitat models. We observed yellow-backed spiny lizards overhead on large trees and observed both spiny and whiptail lizards moving within leaf litter layers. Litter depth was over 50% deeper in unrestored sites with cottonwood and willow (*Tam-Pop/Sal* sites, Table 3) compared with monotypic saltcedar stands and the litter differed in structure. We observed litter in saltcedar stands to form a thick mat of debris, whereas cottonwood leaves were not as compressed and offered more air spaces, beneath which lizards were active.

Woodhouse's toads tended to be associated with ground cover of small woody debris (C4; Table 5); however, these results may be spurious associations. We did not measure surface water variables and occurrence of toads was likely linked to moist habitats and precipitation events.

Table 3. Mean (+SE) of habitat variables measured during 2013 and 2014 at trap arrays in four riparian stand types based on dominant trees (*Tamarix*, *Prosopis*, *Populus*, and *Salix*) along the Virgin River in Utah, Nevada, and Arizona, U.S.A. Density measures were recorded only in 2014.

Variable	*Tam* $n = 8$	*Tam-Pros* $n = 5$	*Tam-Pop/Sal* $n = 6$	*Restored Tam-Pop/Sal* $n = 2$
Bare ground (%)	23.4 (5.2)	46.0 (6.4)	26.5 (7.2)	25.0 (6.3)
Woody debris ground cover (%)	7.8 (2.7)	9.5 (5.3)	13.1 (2.8)	10 (3.8)
Litter ground cover (%)	68.8 (6.1)	44.5 (6.3)	60.4 (6.7)	65.0 (10.)
Litter depth (cm)	1.3 (0.1)	1.1 (0.2)	2.8 (0.7)	1.4 (0.3)
Tamarix cover (%)	90.4 (3.6)	44.4 (4.9)	51.2 (9.9)	35.6 (12.0)
Density of *Tamarix* (stems/10 m^2)	55.6 (8.0)	56.5 (23.2)	23.8 (15.3)	4.4 (4.4)
Populus/Salix cover (%)	0.0 (0.0)	0.0 (0.0)	27.0 (11.5)	14.5 (12.0)
Density of *Populus/Salix* (stems/10 m^2)	0.0 (0.0)	0.0 (0.0)	1.6 (0.7)	17.5 (7.2)
Prosopis cover (%)	0.0 (0.0)	19.6 (2.7)	4.4 (2.0)	3.9 (3.9)
Density of *Prosopis* (stems/10 m^2)	0.8 (0.8)	0.3 (0.3)	0.1 (0.1)	0.3 (0.3)
Elaeagnus cover (%)	0.0 (0.0)	0.0 (0.0)	0.7 (0.7)	8.3 (8.3)
Pluchea cover (%)	0.0 (0.0)	32.1 (13.3)	17.4 (6.4)	0.8 (0.8)
Density of *Pluchea* (stems/10 m^2)	4.4 (4.4)	110.8 (33.9)	46.5 (19.7)	0.8 (0.8)
Baccharis cover (%)	0.0 (0.0)	3.3 (3.3)	4.5 (1.5)	4.5 (2.0)
Density of *Baccharis* (stems/10 m^2)	0.0 (0.0)	0.5 (0.5)	3.8 (2.7)	14.4 (4.1)
Atriplex cover (%)	5.4 (3.5)	0.3 (0.3)	0.0 (0.0)	24.0 (22.5)
Density of *Atriplex* (stems/10 m^2)	2.0 (2.0)	0.1 (0.1)	0.0 (0.0)	3.1 (3.1)
Lycium cover (%)	0.0 (0.0)	4.8 (4.8)	0.0 (0.0)	0.0 (0.0)
Density of *Lycium* (stems/10 m^2)	0.0 (0.0)	5.0 (5.0)	0.0 (0.0)	0.0 (0.0)
Number of dead branches, Sm. Diam. (1.0–2.5 cm)/10 m	25.4 (4.2)	26.0 (6.5)	36.3 (5.7)	29.0 (1.8)
Number of dead branches, Lg. Diam. (>2.5 cm)/10 m	4.2 (0.8)	2.5 (0.9)	8.5 (3.7)	3.8 (0.5)
Canopy cover (%)	72.0 (5.3)	42.9 (10.1)	66.6 (7.0)	60.3 (12.7)
Visible light (%)	28.5 (5.5)	56.9 (8.9)	44.7 (8.3)	44.5 (9.5)

Table 4. Mean (+SE) of component scores from principal components analysis at trap arrays in four riparian stand types based on dominant trees (*Tamarix*, *Prosopis*, *Populus*, and *Salix*) along the Virgin River in Utah, Arizona, and Nevada, U.S.A. Component scores that were significantly different among stand types, based on a one-way ANOVA, are indicated in bold.

Stand Type	*C1* *Overstory Pros/ Tam Cover*	*C2* *Large Woody Debris Pop/Sal Cover*	*C3* *Pop/Sal Density*	*C4* *Small Woody Debris*	*C5* *Small Tam/Large Pros Density*	*C6* *Pluchea/Large Tam Density*
Tam	0.757 (0.208)	−0.466 (0.041)	−0.307 (0.044)	−0.096 (0.382)	0.278 (0.160)	−0.465 (0.166)
Tam-Pros	−1.159 (0.251)	−0.377 (0.160)	−0.234 (0.015)	−0.127 (0.552)	−0.132 (0.837)	0.477 (0.697)
Tam-Pop/Sal	−0.391 (0.399)	0.987 (0.605)	−0.083 (0.095)	0.235 (0.414)	−0.043 (0.281)	0.328 (0.404)
Restored *Tam-Pop/Sal*	−0.014 (0.337)	−0.155 (0.176)	2.060 (2.242)	−0.003 (0.216)	−0.653 (0.556)	−0.317 (0.268)
One-way ANOVA	$\mathbf{F = 7.368\ p = 0.002}$	$\mathbf{F = 4.056\ p = 0.024}$	$\mathbf{F = 5.187\ p = 0.010}$	$F = 0.141\ p = 0.934$	$F = 0.483\ p = 0.699$	$F = 1.292\ p = 0.309$

Discussion

Overall, this study suggests that riparian restoration in sites altered by saltcedar biocontrol positively affects abundance of lizards, particularly yellow-backed spiny lizards, and abundance of Woodhouse's toads compared with sites that experienced biocontrol without restoration. There was a trend (nonsignificant) toward higher diversity in sites with restoration treatments, compared with all other stand types. To account for possible confounding effects, we compared restored and unrestored habitats only in Utah and documented similar patterns of greater species' abundances in restored sites from VES.

Similar to other research along the Virgin River, habitat structure of riparian stands varies mostly due to dominant tree composition (Bateman & Ostoja 2012; Bateman et al. 2015). For example, sites dominated by saltcedar have the greatest amount of canopy cover and lowest solar radiation compared with sites with mesquite, cottonwood, and willow trees. Restoration activities that reduce non-native trees, maintain mature native trees, and promote native tree density create a matrix of suitable habitats to support reptiles and amphibians. Our studies (Bateman & Ostoja 2012) have linked yellow-backed spiny lizards to areas having high densities of large diameter native trees, woody debris, and deep leaf litter because spiny lizards often forage on large trees within riparian areas in the American Southwest (Vitt et al. 1981). Some elements of the habitat, such as large woody debris and deep layers of litter, are less available in saltcedar-dominated sites because these elements are typically recruited from larger diameter cottonwood and willow trees. As saltcedar has a shrub-like growth form, it may provide less suitable foraging habitat for semi-arboreal lizards and some species that forage beneath layers of litter. These findings are consistent with Bateman et al. (2008*a*), who found that lizard abundance was higher following removal of saltcedar and other non-native trees, along the Middle Rio Grande, New Mexico.

Hydrologic flows may be a possible mechanism responsible for greater toad abundance at restored sites. In this study, amphibians were linked to water availability and were typically observed in high abundances following monsoon rains.

Table 5. Abundance of the four most common species of herpetofauna (one toad and three lizards) as predicted by habitat characteristics (components) from ranked multiple linear regression models using a multimodel inference approach. Species abundances were $\log(x+1)$ transformed to increase data normality. Components with high variable weights in bold and +/− indicates the direction of correlation.

		Variable AICc Weights					
Species	*Top Model (+/−)*	*C1*	*C2*	*C3*	*C4*	*C5*	*C6*
Anaxyrus woodhousii	−C4 (small woody debris)	0.24	0.24	0.25	**0.28**	0.24	0.25
Aspidoscelis tigris	−C1 (overstory, *Pros/Tam* cover)	0.25	0.25	0.25	0.25	0.25	0.25
Sceloporus uniformis	−C5 (small *Tam*/Large *Pros* density)	0.21	**0.30**	**0.36**	0.17	**0.39**	0.17
Uta stansburiana	−C6 (*Pluchea*/Large *Tam* density)	0.25	0.22	0.25	**0.27**	0.23	**0.31**

Along the Middle Rio Grande, Bateman et al. (2008*b*) found that Woodhouse's toad and Great Plains toad (*Anaxyrus cognatus*) abundances increased during flooding as high stream flows created temporary pools in the riparian forest. Woodhouse's toad abundance along the Virgin River was likely higher at restored and unrestored sites (of saltcedar, cottonwood, and willow) due to moister soils and water enhancements during restoration.

In the short term, restored sites exhibited observable increases in non-woody vegetation since restoration efforts were implemented in 2012. Specifically, kochia, a common secondary successional plant in disturbed areas (DiTomaso et al. 2013), increased as a likely response to soil disturbance and increased solar radiation from mechanical removal of saltcedar and Russian olive. Kochia has been found to limit growth of certain crop species (Wicks et al. 1997); however, information is lacking on the effects on young riparian tree species. Arrowweed, a native woody shrub, is the main secondary succession species establishing across all stand types, with some sites exhibiting a 2.5-fold increase in arrowweed density. Unfortunately, arrowweed may not provide high-quality habitat for wildlife due to its low structural diversity (Ostoja et al. 2014). Thus, active management of these sites may be necessary if chemical and physical properties of secondary species are limiting growth and establishment of transplanted willow and mesquite stems.

Biocontrol can be an effective, although highly variable, method for controlling saltcedar with different areas seeing 0–80% saltcedar mortality after multiple defoliation events (Bean et al. 2013). However, some results of saltcedar biocontrol may indirectly affect wildlife because of how defoliation alters riparian habitats. Since biocontrol introduction along the Virgin River, we have observed a steady decline in captures of marked reptiles (Bateman et al. 2015) and decreases in canopy cover (Bateman et al. 2013). Along this reach of the Virgin River, biocontrol has caused little saltcedar mortality but has reduced foliar cover, with over 50% canopy die back during 2014 (Hultine et al. 2015) without compensatory replacement by native tree species. Reptile abundance has likely decreased following saltcedar defoliation caused by biocontrol as riparian stands have become hotter and dryer (Bateman et al. 2013). Changes in microclimate caused by defoliation have made habitats less suitable for some lizard species in this study, due to either decreased thermal variability or increased temperatures that exceed thermal maximums of some species (as in common side-blotched lizards, Goller et al. 2014).

Although biocontrol may decrease lizard abundance by altering riparian microclimate and leaving voids in the habitat matrix, incorporating restoration activities to reduce saltcedar densities and promote native tree growth can mitigate the negative effects. Restoration that attempts to fill the void created by defoliation can recreate a community that supports wildlife and wildlife habitat. However, defoliated sites will likely need to be actively managed to prevent establishment of undesirable plant species that do not provide high-quality habitat for wildlife. Also, decreased saltcedar density and canopy cover in conjunction with high water flow events would likely benefit native plant species, because cottonwoods depend on high solar radiation and flooding to germinate and grow (Braatne et al. 1996). Because of the high flammability of defoliated saltcedar (Drus et al. 2014), an additional risk to native riparian trees is an increased risk of fire. Therefore, restoration treatments that mechanically remove dead and defoliated saltcedar may prevent further loss of native riparian habitat.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Number of unique individuals observed during visual encounter surveys along transects at the restored and unrestored *Tam-Pop/Sal* site in St. George, Utah, during four sampling occasions.
Table S2. Mean (+SE) of habitat variables measured along transects at the restored and unrestored *Tam-Pop/Sal* site in St. George, Utah. To determine if there was a difference in habitat variables between sites, an independent *t*-test was conducted. Significant ($p < 0.10$) terms in bold.

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