

Invasive woody plants affect the composition of native lizard and small mammal communities in riparian woodlands

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Abstract

Nonnative *Tamarix* spp. (saltcedar) is among the most invasive and common trees along riparian habitats in the western U S, impacting native plant communities and habitat quality. *Tamarix* dominance causes a reduction in habitat physiognomic heterogeneity in riparian habitats. Animal abundance, diversity and habitat associations in monotypic stands of saltcedar remain largely unexplored for non-avian communities. We sampled small vertebrate and ground arthropod communities in monotypic *Tamarix* stands and in mixed stands of *Tamarix* and native (*Populus*, *Salix*, and *Prosopis* spp.) trees in riparian habitats along the Virgin River in the Mojave Desert. Our survey of faunal communities suggests that many species of arthropods, reptiles and small mammals utilize both *Tamarix*-dominated and mixed habitats along the Virgin River. Small mammal and lizard communities were dominated by generalist species. Mixed stands had greater arthropod abundance, lizard abundance and small mammal diversity; whereas, monotypic and mixed stands had similar lizard diversity. The habitat of mixed sites was characterized by 'nativeness' (areas with native riparian trees) and less 'shady exotic thickets' (areas with *Tamarix* and high overstory cover) compared to *Tamarix*-dominated stands. There were species-specific responses to habitat physiognomy. *Peromyscus maniculatus* (deer mouse) was associated with shady exotic thickets. *Sceloporus magister* (desert spiny lizard) and *Neotoma lepida* (desert woodrat) were associated with native trees and woody debris. Seven rodent and lizard species' abundances were explained by habitat physiognomy variables. Rare and specialist species were more impacted by nonnative vegetation. These results contribute to the body of research on animal utilization of nonnative habitats and relation to habitat physiognomy. Management of nonnative plants should consider how control activities could impact habitat physiognomy and native animal communities in riparian habitat.

Introduction

Nonnative invasive plants are considered a major conservation threat to native ecosystems (Mack *et al.*, 2000; Pimentel *et al.*, 2000). For example, invasive vegetation can impact both composition and habitat physiognomy affecting ecosystem function (D'Antonio & Vitousek, 1992; Higgins *et al.*, 1999). Although plant species identity is important to highly specialized species, animals in temperate regions are thought to respond more strongly to physical characteristics associated with the habitat rather than species composition (MacMahon, 1981). The literature is replete of examples touting the dramatic force that the physical environment has on shaping animal communities. The importance of physical characteristics such as habitat structure has been illustrated in studies involving ants (Crist & Wiens, 1994),

birds (Brownsmith, 1977; McAdoo, Longland & Evans, 1989; Fleishman *et al.*, 2003; Walker, 2008), lizards (Pianka, 1966, 1967; Castellano & Valone, 2006) and rodents (Ostoja & Schupp, 2009; Rieder, Newbold & Ostoja, 2010). Biodiversity has been linked to ecosystem function and stability (Tilman, 2000) and Diaz & Cabido (2001) have reported links between vegetation richness and animal diversity.

Consequences of nonnative invasive vegetation on native communities are illustrated throughout riparian systems of the southwestern US, where invasive *Tamarix* spp. (tamarisk or saltcedar) can alter ecosystem function (Busch & Smith, 1995). When *Tamarix* forms dense, monotypic stands, it often has detrimental effects on native plants and habitat quality (Everitt, 1980; Shafroth *et al.*, 2005). However, plant composition and physiognomy of *Tamarix*-dominated stands are variable (DeLoach *et al.*, 2000).

Critical for animal communities, *Tamarix* invasion has the potential to cause a reduction in habitat physiognomic heterogeneity and plant species diversity (Brand, White & Noon, 2008). Because *Tamarix* has a strong competitive ability, unique phenology and can increase soil salinity (Shafroth, Brown & Merritt, 2010), invaded habitats can be transformed into dense monotypic stands of exotic vegetation.

Our work relates to conserving native animal species inhabiting invasive plant habitats and possible impacts of invasive plant management on these faunal communities. However, few studies have compiled community-level analyses to document the impact of *Tamarix*-dominated systems (Bateman & Paxton, 2010). Our research is part of a long-term ecological monitoring effort to evaluate trophic-level responses to *Tamarix* and its management (i.e. biocontrol; Bateman *et al.*, 2010a). The goal of our research is to compare abundance, diversity and habitat associations of the small vertebrate community (i.e. small mammals and herpetofauna) in *Tamarix*-dominated and codominated riparian areas prior to biocontrol establishment.

Together, arthropods, herpetofauna and small mammals are consumers within a riparian food web. Monitoring these animal species can provide a tool to evaluate how the establishment and subsequent control of nonnative species can impact ecosystem-level changes. Our objectives were to (1) determine how nonnative plant habitats differ from mixed native habitats in composition and habitat structure; (2) determine animal abundance and diversity in nonnative and mixed native habitats; and (3) relate faunal community occurrence and abundance to habitat physiognomy in nonnative plant dominated systems.

Methods

Study area

We established study sites along the Virgin River in Mohave County, Arizona, near Beaver Dam Wash (36°53'N, 113°55'W) downstream 50 km to Mormon Mesa in Clark County (36°34'N, 114°20'W), Nevada (Appendix S1). The riparian area is dominated by exotic *Tamarix* spp., although some areas of native vegetation, such as cottonwood (*Populus fremontii*) and willow (*Salix gooddingii*), co-occur. Similarly, mesquite (*Prosopis* spp.) and acacia (*Acacia* spp.) are mixed with *Tamarix* in the floodplain. No areas within this reach of the Virgin River are completely free of *Tamarix*. Dominant shrub species include arrowweed (*Pluchea sericea*) and several species of saltbush (*Atriplex* spp.).

We sampled faunal communities and quantified habitat characteristics in vegetated stands at least 2 ha in size and containing monotypic stands of *Tamarix* (>90% *Tamarix* stem count, hereafter exotic sites) or mixed stands of *Tamarix* and native trees (50 to 60% *Tamarix* stem count, hereafter mixed sites). Sites occurred within the floodplain as indicated by sandy soils and below upland terraces. We used capture-mark-recapture techniques to sample verte-

brate communities at one trap location per site. Herpetofauna and arthropod trap locations were randomly established within each site using ArcGIS (9.3.1) and mammal trap locations were systematically colocated with the former to ensure trap units at least 25 m from habitat edge and at least 250 m from another site.

Lizards

We monitored lizard species at trap arrays established in 14 sites (seven exotic sites and seven mixed sites, $n = 14$) during 2009 and 16 sites (eight exotic sites and eight mixed sites, $n = 16$) in 2010 (Appendix S2). During 2010, 12 of 14 sites were resampled with two sites excluded because of defoliation caused by biocontrol. We captured lizards using drift fence arrays with pitfall traps (9 L) and funnel traps (hereafter, herpetofauna arrays; Appendix S3). Our design was adopted from pitfall designs proven useful in other habitats (Jones, 1981; Campbell & Christman, 1982; Corn & Bury, 1990). Each array was established randomly >25 m from the edge of each site and >250 m from another array. Each trapping array consisted of three 6-m long fences positioned at zero, 120 and 240° from a central trap for a total of four pitfall traps and six funnel traps. During June and July (periods of high whiptail lizard, *Aspidoscelis* sp., seasonal activity; Bateman *et al.*, 2010b), we checked traps daily in 2009 and 2010. Trapped lizards were identified to species, weighed, sexed, individually marked with a unique identifier (Waichman, 1992) and released at point of capture.

Small mammals

We monitored rodent species at 16 sites (eight exotic sites and eight mixed sites, $n = 16$) during the spring of 2010 (Appendix S2), during periods of high seasonal activity (Vamstad & Rotenberry, 2010) and periods when animals would be exposed to reasonable temperatures during trapping. We captured mammals using Sherman live traps (8 × 9 × 23 cm) baited with mixed bird seed with 10 m spacing in a 50 × 50 m trap grid (hereafter, mammal grids), resulting in 25 traps/grid. Each grid was trapped for four consecutive mornings on three occasions, between 23 March and 21 May. Where access permitted, trapping sessions were conducted 2 weeks apart to eliminate potential bias caused by concentrating sampling of a site during a narrow temporal window. Due to the remoteness of some areas, only one trapping session of four nights was conducted at the furthest downstream sites (i.e. Mormon Mesa, Nevada). Trapped animals were identified to species, weighed, sexed, individually identified with ear tags and released at point of capture.

Because shrews (*Notiosorex* spp.) are rarely captured in live traps (Brown, 1967; Bury & Corn, 1987), we sampled shrews captured in herpetofaunal pitfall traps (*sensu* Chung-MacCoubrey, Bateman & Finch, 2009) during the same time period as lizard surveys. Shrews were weighed, sexed but not given unique marks because few were captured.

Table 1 Mean (\pm SE) of habitat variables measured in *Tamarix*-dominated (exotic) and *Tamarix*-native (mixed) vegetation types along the Virgin River in Arizona and Nevada, USA at herpetofauna trap arrays ($n = 18$) and small mammal trap grids ($n = 16$)

Variables	Exotic		Mixed	
	Herp arrays	Mammal grids	Herp arrays	Mammal grids
Bare ground (%)	9.9 (3.5)	3.4 (1.2)	9.1 (5.7)	15.8 (5.4)
Woody debris ground cover (%)	13.4 (4.0)	2.7 (0.8)	32.8 (5.9)	9.1 (3.3)
Litter cover (%)	81.0 (3.5)	89.2 (2.9)	79.0 (8.3)	68.3 (6.0)
Depth of litter (cm)	2.3 (0.2)	2.2 (0.3)	3.4 (0.5)	2.1 (0.4)
Proportion of <i>Tamarix</i>	0.9 (0.0)	1.0 (0.0)	0.6 (0.1)	0.5 (0.1)
Proportion of <i>Populus</i> , <i>Salix</i>	–	–	0.2 (0.1)	0.1 (0.0)
Proportion of <i>Prosopis</i>	–	–	0.1 (0.0)	0.1 (0.0)
Number of dead branches, sm diam. (1.0–2.5 cm)	10.6 (2.0)	17.6 (2.0)	26.8 (6.5)	17.6 (3.1)
Number of dead branches, lg diam. (>2.5 cm)	2.0 (0.6)	4.4 (1.0)	7.2 (2.6)	2.9 (1.3)
Number of <i>Tamarix</i> stems, sm diam. (<2.5 cm)/10 m ²	438.0 (132.0)	121.7 (24.2)	260.6 (101.3)	75.6 (75.6)
Number of <i>Tamarix</i> stems, lg diam. (>2.5 cm)/10 m ²	63.3 (17.0)	12.0 (2.2)	18.8 (3.3)	7.6 (4.3)
Number of <i>Populus</i> , <i>Salix</i> stems/10 m ²	–	–	2.8 (1.5)	10.6 (10.2)
Number of <i>Prosopis</i> stems/10 m ²	–	0.3 (0.3)	–	1.7 (0.8)
Number of <i>Pluchea</i> shrub stems/10 m ²	34.5 (19.4)	1.3 (1.3)	578.1 (177.9)	155.9 (50.7)
Plant species richness	2.5 (0.5)	1.9 (0.6)	3.9 (0.5)	4.0 (0.5)
Canopy cover (%)	82.8 (3.2)	88.8 (4.5)	61.2 (11.8)	65.0 (9.1)

Arthropods

We sampled ground arthropods daily in herpetofaunal pitfall traps in July 2009 and June and July 2010. One pitfall trap per array was systematically selected at each site to sample arthropods (i.e. week one pitfall A sampled, week two pitfall B sampled, etc.). We identified arthropods to order-level classification, except for distinguishing ants among other Hymenoptera because of their abundance and distinguishing the suborder Auchenorrhyncha among other Heteroptera. Chilopoda were classified to the class level. We recorded simultaneous captures of reptiles and mammals in sampling pitfalls and determined arthropod abundance was similar in pitfalls with and without predators.

Habitat characterization

We measured 16 habitat variables (Table 1) during June and July 2010 at two 20 m transects and in four 2 × 2 m plots at each site at mammal grids and herpetofauna arrays (Appendix S3). At meter intervals along each transect, we noted ground cover type, depth of litter (where litter occurred) and number and size class of trees and large shrubs. *Tamarix*, mesquite and acacia size classes were: A (<1 m tall), B (>1 m tall, diameter of largest stem <2.5 cm), C (>1 m tall, diameter of largest stem = 2.5–7.5 cm) and D (>1 m tall, diameter of largest stem >7.5 cm). Cottonwood and willow size classes were: A (<1 m tall), B (>1 m tall, diameter at breast height, dbh, <5 cm), C (>1 m tall, dbh = 5–10 cm), D (>1 m tall, dbh = 10–30 cm) and E (>1 m tall, dbh >30 cm). We counted woody debris (dead branches and logs 0–0.5 m above ground) alternating meters along each transect and categorized debris as size A (1.0–2.5 cm diameter), B (2.5–7.5 cm diameter) or C (>7.5 cm diameter). Stem counts of all plant species were tallied in plots and we categorized trees by size as previously described. Percent cover was scored for each plant species using Daubenmire cover classes (Daub-

enmire, 1959). Canopy cover was estimated from four readings (facing each cardinal direction) with a spherical densiometer from the center of plots.

Data analyses

We calculated species richness as the number of species recorded in a given vegetation type (exotic vs. mixed) summed across all arrays for lizards and all grids and sessions for mammals. We calculated relative fauna abundance (hereafter, abundance) which we defined as the number of uniquely marked individuals per 100 trap days for lizards and small mammals. This conservatively estimated abundance as the minimum number of animals per site. Since arthropods were not individually marked, we calculated arthropod abundance as number of captures per 10 days per order. Because trapping occurred during 2 years for lizards and arthropods and 1 year for mammals, we combined data within each taxon to provide a more general result for diversity and habitat relations, since the temporal aspects of these parameters were not of interest in this study. Therefore, *t*-tests were used to compare the means of fauna abundances between exotic and mixed habitats, except when data did not meet assumptions of tests, we used nonparametric analyses (Zar, 1996; Mann-Whitney Rank Sum Test, SPSS Inc. version 17.0). Additionally, data were separated by year to address possible year effects on lizard abundance using a General Linear Model with years as repeated measures to compare mean lizard species abundance between vegetation types and years.

We constructed rank abundance curves by plotting species abundances (log) against species rank to determine differences between vegetation types. To determine alpha diversity (local diversity) measures for each vegetation type, we calculated Simpson's D, Brillouin evenness index and species richness. These measures frequently have been used in similar diversity studies (Hill, 1973; Solow, 1993; Whit-

ford, 1997; Magurran, 2004, 2005; Buckland *et al.*, 2005). Diversity and evenness indices were calculated for each site and the average was determined for each vegetation type (using Species Diversity & Richness 4.1.2 Software, Lymington, Hampshire, UK; Seaby & Henderson, 2006).

We summarized variation in habitat metrics throughout all sites with a principal components analysis (PCA, SPSS Inc. version 17.0, Chicago, IL, USA). The number of relevant components was determined based on scree plots, components with eigenvalues greater than one and parsimony (Legendre & Legendre, 1998). Components were interpreted based on the correlation matrix. We compared PCA component scores between exotic and mixed vegetation types with a *t*-test.

To relate lizard and mammal abundances to habitat structure and composition, we correlated species' occurrences and abundances with component scores derived from the PCA (SPSS Inc. version 17.0). For species which occurred throughout all sites, we used a backward-stepwise regression analysis to identify which component scores correlated with abundances of species. For species not ubiquitous among sites, we used a logistic regression analysis to determine which component scores best predicted species occurrence. We used a variable selection procedure that first eliminated variables with *P* greater than 0.25 (Hosmer & Lemeshow, 2000) and then computed a backward elimination logistic regression. Lizards were monitored in 18 sites (Appendix S2), and if lizards were surveyed for 2 years at one site we averaged abundance between years to regress against habitat characteristics in the multiple and logistic regression models. In this way, our sample size stayed at 18 and was not inflated by counting abundance in 2 years.

Results

Habitat

Along the Virgin River, vegetation composition and structure differed between exotic and mixed stands (Table 1, Appendices 3–6). Although *Tamarix* was ubiquitous throughout the study, mixed stands contained greater proportions of cottonwood, willow and mesquite trees and greater numbers of arrowweed compared to exotic stands (Table 1).

Four components explained 77 and 79% of the variation across all sites measured at herpetofauna arrays and mammal grids, respectively (PCA, Appendices S4 and S5). The riparian woodland was differentiated based on the following characteristics (components, C) measured at herpetofauna arrays: C1, nativeness and woody debris (i.e. areas with native trees and woody debris or logs of native trees); C2, overstory structure and shade (i.e. areas with high canopy cover and few shrubs); C3, young exotic thickets (i.e. areas with small diameter *Tamarix* and little bare ground); and C4, exotic thickets (i.e. areas with medium and large diameter *Tamarix*). Herpetofauna arrays in mixed sites had significantly greater nativeness (C1) compared to exotic sites (Appendix S6). Habitat characteristics at mammal grids were similar to herpetofauna arrays, where: C1, shady

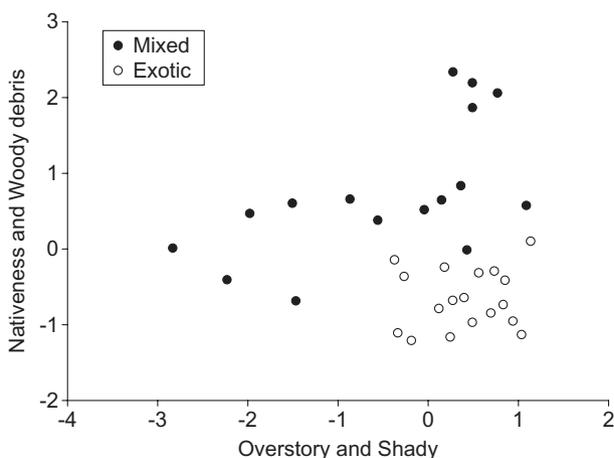


Figure 1 Habitat physiognomy values derived from a PCA (Appendix S4 and S5) in *Tamarix*-dominated (exotic) and *Tamarix*-native (mixed) vegetation types along the Virgin River in Arizona and Nevada, USA. Habitat physiognomy was measured at 16 mixed sites (at eight herpetofauna arrays and eight mammal grids) and at 18 exotic sites (at 10 herpetofauna arrays and eight mammal grids).

exotic thickets (i.e. areas with *Tamarix*, high canopy cover and leaf litter as ground cover); C2, nativeness and woody debris (i.e. areas with native trees and woody debris); C3, plant richness (i.e. areas with high native plant species richness); and C4, mixed woodland (i.e. areas with both native trees and *Tamarix*). Mammal grids in mixed sites had significantly less shady exotic thickets (C1) and significantly greater nativeness (C2; Appendix S7). Overall, mixed sites were characterized by having native trees and woody debris and more open canopies; whereas, exotic sites were characterized by fewer native trees and woody debris and a shady understory environment (Fig. 1).

Animal communities

During our 2-year study, we recorded 18 orders of arthropods captured in pitfall traps, and all orders were represented in both vegetation types. Arthropod captures were significantly greater in mixed sites with ants (Hymenoptera), pillbugs (Isopoda) and spiders (Araneae) among the most common (Table 2). Although diversity and evenness were greater in exotic sites, differences were not significant (Table 3).

We captured 665 individual lizards representing seven species during the summers of 2009 (424 trap days, $n = 14$) and 2010 (358 trap days, $n = 16$) in exotic and mixed vegetation types. All lizard species were represented when we compared relative abundances, diversity indices and rank abundance curves between vegetation types. However, only the four most common species, which represented 98% of all captures, were included in habitat analyses because rare species were too few to perform tests. As illustrated in the species rank abundance curves (Fig. 2a), total lizard abundance was greater in mixed sites, and rare species had lower abundances in exotic sites. *Aspidoscelis tigris* was the most

Table 2 Mean (\pm SE) of captures of arthropods/10 trap days during 2009 and 2010. Traps were 9 L pitfalls in *Tamarix*-dominated (exotic) and *Tamarix*-native (mixed) vegetation types along the Virgin River in Arizona and Nevada, USA. Test statistics reported for *t*-test (*t*) or Mann–Whitney Rank Sum Test (*U*) for data not meeting assumptions of normality; *n* = 18, d.f. = 16

Order	Exotic	Mixed	Statistic	<i>P</i>
Araneae	33.9 (9.4)	28.2 (3.8)	<i>U</i> = 35.0	0.689
Auchenorrhyncha	3.3 (0.8)	4.7 (0.8)	<i>U</i> = 39.5	1.00
Blattaria	0.7 (0.2)	3.1 (0.8)	<i>U</i> = 14.5	0.026
Chilopoda	0.03 (0.03)	0.04 (0.04)	<i>U</i> = 39.0	0.935
Coleoptera	24.9 (21.3)	12.9 (2.2)	<i>U</i> = 9.0	0.007
Dermaptera	0.5 (0.2)	1.1 (0.4)	<i>t</i> = 1.385	0.185
Diptera	19.4 (9.6)	55.1 (46.6)	<i>U</i> = 36.5	0.790
Heteroptera	1.6 (0.4)	0.2 (0.1)	<i>U</i> = 11.0	0.009
Hymenoptera – ants	26.0 (7.5)	72.5 (17.2)	<i>U</i> = 12.0	0.015
Hymenoptera – bees, wasps	1.1 (0.4)	1.4 (0.7)	<i>U</i> = 35.5	0.721
Isopoda	5.1 (2.3)	43.2 (24.6)	<i>U</i> = 14.0	0.023
Lepidoptera	0.3 (0.1)	0.3 (0.1)	<i>U</i> = 39.0	0.963
Mantodea	0.1 (0.1)	0.2 (0.1)	<i>U</i> = 30.5	0.272
Orthoptera	15.6 (4.7)	21.5 (7.7)	<i>U</i> = 33.0	0.564
Pseudoscorpionida	0.2 (0.1)	0.3 (0.2)	<i>U</i> = 38.0	0.887
Scorpiones	0.11 (0.08)	0.03 (0.03)	<i>U</i> = 36.0	0.632
Solifugae	0.8 (0.4)	0.2 (0.1)	<i>U</i> = 31.0	0.419
Thysanura	2.4 (1.6)	2.1 (0.7)	<i>U</i> = 28.0	0.304
Total arthropods	143.4 (42.4)	252.7 (54.6)	<i>U</i> = 16.0	0.037

Table 3 Summary values for diversity measures of small vertebrates and ground arthropods in *Tamarix*-dominated (exotic) and *Tamarix*-native (mixed) vegetation types along the Virgin River in Arizona and Nevada, USA

Taxa index	Exotic	Mixed
Lizards		
Simpson's D	2.029	2.281
Brillouin E	0.488	0.627
Richness	7	6
Small Mammals		
Simpson's D	2.104	3.538
Brillouin E	0.568	0.804
Richness	5	6
Arthropods		
Simpson's D	6.441	5.472
Brillouin E	0.720	0.672
Richness (Order)	18	18

common species in both vegetation types (Table 4). Two lizard species had greater abundances in mixed sites (*A. tigris* and *Sceloporus magister*, Table 4), and no species had greater abundances in exotic sites. Exotic and mixed vegetation types had similar measures of diversity (Table 3).

We captured 262 individual rodents representing six species (152 trap nights, *n* = 16) in exotic sites and five species in mixed sites (Table 5). We captured one insectivore species (*Notiosorex crawfordii*) in herpetofauna pitfall traps and abundance did not differ between vegetation types (*n* = 18, *U* = 39.0, *P* = 0.96). As illustrated in the rank abundance curves (Fig. 2b), rare species had lower abundances in the exotic vegetation type. *Peromyscus maniculatus* was the most common species in both vegetation types (Table 5).

Mixed sites had greater measures of diversity compared to exotic sites (Table 3).

Animal-habitat relations

Of the four species of lizards used in habitat analyses, three had conclusive habitat models (Table 6). One species of lizard was associated with habitat characteristics found in mixed sites (*S. magister*, C1; Table 6). Two species of lizards were negatively associated with shady sites (*Urosaurus graciosus*, *Uta stansburiana*, C2; Table 6).

Of the five species of rodents used in habitat analyses, four species had conclusive habitat models (Table 7). One species of rodent was associated with habitat characteristics found in mixed sites (*Neotoma lepida*, C2; Table 7). One rodent was positively associated with exotic shady thickets found in exotic sites (*P. maniculatus*, C1; Table 7); whereas, one heteromyid rodent was negatively associated with exotic shady thickets (*Dipodomys merriami*, C1; Table 7). The model predicting the presence of *N. crawfordii* was approaching significance with occurrence being positively related to nativeness and woody debris (C2; $\chi^2_{(1)} = 3.194$, *P* = 0.074, classification accuracy = 55.6%).

Discussion

Animal community composition and abundance

This study suggests that many species of arthropods, reptiles and small mammals utilize both *Tamarix*-dominated and *Tamarix*-native mixed habitats along the Virgin River in the southwestern US. Both small mammal and lizard commu-

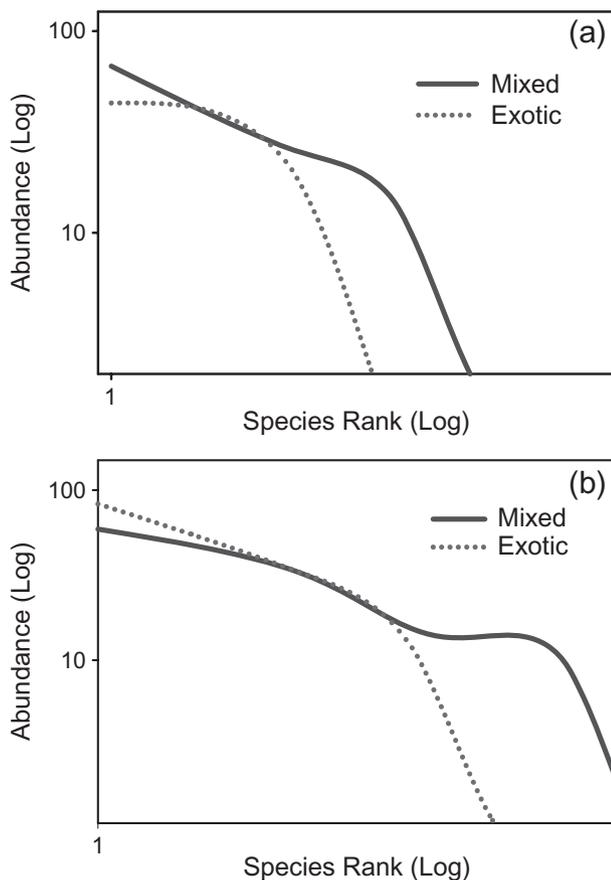


Figure 2 Lizard rank abundance curves (a) and small mammal rank abundance curves (b) for *Tamarix*-dominated (exotic) and *Tamarix*-native (mixed) vegetation types along the Virgin River in Arizona and Nevada, USA.

nities were dominated by generalist species (i.e. *P. maniculatus* and *A. tigris*); however, rare species were less abundant in the exotic vegetation type. Within the lizard community, *A. tigris* drove overall lizard abundance and was more abundant in mixed sites compared to exotic. One other species, *S. magister*, was also more abundant in mixed sites. Sabo & Power (2002) have shown that lizard species are abundant in riparian habitats due to higher levels of insect food resources, and our results showed significantly greater total arthropod abundance in mixed sites.

Most studies classify arthropods to the family level or finer; therefore, our order-level classification can only report general trends of arthropod abundance and diversity in exotic and mixed vegetation types. We found that arthropod abundance in our pitfall traps was greater in mixed sites; however, diversity was similar in mixed and exotic sites. One study on leaf-litter arthropods found that diversity in *Tamarix* litter was generally lower than in native cottonwood leaf litter (Bailey, Schweitzer & Whitham, 2001). A study in Arizona found that diversity of aerial arthropods was greatest in native plant communities compared to monotypic patches of *Tamarix*, but diversity varied by year

and season (Durst *et al.*, 2008). Our results found that Isopoda (pillbugs) were most abundant in mixed sites; similarly, a study along the middle Rio Grande in New Mexico found that isopods had highest total abundances and were more numerous in cottonwood sites than *Tamarix* sites (Ellis *et al.*, 2000). Their study also found high numbers of spiders (Araneae) and ants (Hymenoptera) in both native and exotic sites.

Although small mammal abundance was similar in *Tamarix*-invaded and mixed-riparian habitat, mixed-riparian vegetation may have been of higher quality. For example, despite the generally greater abundance of several species in *Tamarix* (Hink & Ohmart, 1984; Ellis, Crawford & Molles, 1997), the latter study reported lower overall numbers of small mammals in *Tamarix* compared to native cottonwood and willow habitats. Along the middle Rio Grande in New Mexico, Ellis *et al.* (1997) found that abundance and reproductive activity of a common rodent species (*Peromyscus leucopus*) were similar in native and *Tamarix* habitats. Contrary to previous studies, we found that species of heteromyid rodents tended to occur more commonly in mixed habitats (Hink & Ohmart, 1984; Ellis *et al.*, 1997). Ellis *et al.* (1997) reported that three species (*Reithrodontomys megalotis*, *P. maniculatus* and *Perognathus flavus*) were found almost exclusively in *Tamarix*. Similarly, our results showed that two of the previous species (*R. megalotis* and *P. maniculatus*) tended to be more abundant in exotic *Tamarix* sites. Several studies found that *N. albigula* were consistently more abundant in native habitat and avoided *Tamarix* (Anderson & Ohmart, 1984; Ellis *et al.*, 1997; Andersen & Nelson, 1999). We captured more *N. lepida*, a congener of *N. albigula*, in mixed sites. Overall, we captured few insectivores, represented by *N. crawfordi*. Hink & Ohmart (1984) reported frequent captures of *N. crawfordi* in willow stands and rarely captured them in *Tamarix*. Chung-MacCoubrey *et al.* (2009) captured more than 2000 shrews in sites with a mixture of cottonwood, willow and *Tamarix* along the middle Rio Grande. Our results did not show significant differences in abundances of *N. crawfordi* in exotic and mixed sites.

Animal-habitat associations

Although the majority of lizard and small mammal species had greater abundances in mixed sites compared to exotic sites; we did not find significant differences in abundance between the two vegetation types for many of the faunal species we monitored. However, we were able to identify habitat and physiognomic characteristics that were good predictors of animal species occurrence and abundance. For example, *S. magister* were associated with sites having native trees, woody debris and logs (Table 6). *Tamarix* stems do not grow to the diameter offered by cottonwood and willow trees, thus providing less foraging substrate for these arboreal lizards (Vitt, van Loben Sels & Ohmart, 1981). Similarly, *N. lepida* were associated with sites having native trees (Table 7). *Tamarix* stands may have provided a limited number of mesquite and other native trees for food.

Table 4 Mean (\pm SE) number of individual lizards captured/100 trap days during 2009 and 2010 in *Tamarix*-dominated (exotic) and *Tamarix*-native (mixed) vegetation types along the Virgin River in Arizona and Nevada, USA. Test statistic (F) and significance (P) for repeated-measures General Linear Model including effects of vegetation (type), year and interaction of type and year. Species abundances $\log(x+1)$ transformed (total lizard abundance not transformed) to increase data normality; d.f. = 29

Family	2009		2010		Type	Year	Interaction
	Exotic $n = 6$	Mixed $n = 8$	Exotic $n = 10$	Mixed $n = 6$			
Species					$F (P)$	$F (P)$	$F (P)$
Teiidae							
<i>Aspidoscelis tigris</i>	46.4 (9.9)	52.6 (6.2)	52.7 (12.5)	116.6 (20.8)	5.15 (0.036)	7.15 (0.023)	2.96 (0.116)
Phrynosomatidae							
<i>Callisaurus draconoides</i>	–	–	–	1.0 (1.0)	1.28 (0.274)	0.00 (1.000)	0.00 (1.000)
<i>Sceloporus magister</i>	0.6 (0.6)	10.1 (5.1)	–	13.0 (8.5)	7.56 (0.014)	0.34 (0.570)	3.43 (0.094)
<i>Urosaurus graciosus</i>	0.5 (0.5)	1.3 (1.3)	0.8 (0.6)	1.7 (1.2)	0.08 (0.775)	0.26 (0.621)	0.08 (0.784)
<i>Urosaurus ornatus</i>	1.0 (1.0)	–	–	–	1.45 (0.240)	1.00 (0.341)	1.00 (0.341)
<i>Uta stansburiana</i>	20.8 (7.4)	18.1 (6.4)	23.1 (5.7)	36.3 (15.4)	0.01 (0.912)	3.41 (0.095)	1.59 (0.237)
Gekkonidae							
<i>Coleonyx variegatus</i>	–	–	0.3 (0.3)	3.0 (2.0)	0.92 (0.347)	2.47 (0.147)	2.47 (0.147)
All lizards	69.4 (16.6)	82.0 (11.1)	78.1 (16.5)	170.7 (29.9)	8.43 (0.009)	15.06 (0.003)	4.99 (0.050)

Table 5 Mean (\pm SE) number of individual mammals captured/100 trap days during 2010 in *Tamarix*-dominated (exotic, $n = 8$) and *Tamarix*-native (mixed, $n = 8$) vegetation types along the Virgin River in Arizona and Nevada, USA. Test statistics reported for t -test (t) or Mann–Whitney Rank Sum Test (U) for data not meeting assumptions of normality; $n = 16$, d.f. = 14

Family Species	Exotic	Mixed	Statistic	P
Cricetidae				
<i>Peromyscus maniculatus</i>	4.9 (0.8)	3.5 (0.8)	$t = -1.270$	0.225
<i>Reithrodontomys megalotis</i>	1.5 (0.4)	0.7 (0.2)	$t = -1.724$	0.107
Muridae				
<i>Neotoma lepida</i>	0.1 (0.1)	0.8 (0.3)	$U = 23.0$	0.083
Geomyidae				
<i>Thomomys bottae</i>	–	0.2 (0.1)	$U = 24.0$	0.442
Heteromyidae				
<i>Chaetodipus formosus</i>	1.0 (0.6)	1.6 (0.7)	$U = 23.0$	0.382
<i>Dipodomys merriami</i>	0.04 (0.04)	0.6 (0.4)	$U = 27.0$	0.645
All rodents	7.5 (1.1)	7.3 (1.2)	$t = -1.117$	0.908

Table 6 Abundance and presence of four common species of lizards as predicted by habitat characteristics (components, C) from a multiple linear regression and logistic regression, respectively. Classification accuracies listed for logistic regression models. Lizards were monitored in *Tamarix*-dominated ($n = 10$) and *Tamarix*-native ($n = 8$) sites along the Virgin River in Arizona and Nevada, USA

Species	Pos. or Neg. correlation	Habitat characteristics	Statistic	Significance
<i>Aspidoscelis tigris</i> ^a				NS
<i>Sceloporus magister</i> ^b	+	Nativeness and woody debris (C1)	$\chi^2_{(1)} = 9.650$	$P = 0.002$ (88.9%)
<i>Urosaurus graciosus</i> ^b	–	Overstory structure and shade (C2)	$\chi^2_{(1)} = 5.052$	$P = 0.025$ (83.3%)
<i>Uta stansburiana</i> ^b	–	Overstory structure and shade (C2)	$\chi^2_{(2)} = 19.069$	$P < 0.001$ (100%)
	–	Exotic thickets (C4)		

^aMultiple linear regression.

^bLogistic regression.

Although some species had similar abundances in exotic and mixed sites, results from the habitat associations suggest that, within these vegetation types, some fauna species selected specific structural features of the habitat. For example, *U. graciosus*, *U. stansburiana* and *D. merriami* may prefer open habitats with low canopy or shrub cover (Table 6 & 7) for greater basking opportunities (for ectotherms) or openness necessary for locomotion (for Heteromyid rodents; Rieder *et al.*, 2010).

Because reptiles respond to structural changes to their habitat (Pianka, 1967), their occurrence and abundance can be good indicators of healthy riparian ecosystem structure and function. However, in contrast to studies focused on birds and mammals, comparisons of reptile communities in *Tamarix* and native or mixed riparian habitats is limited. Similar to our findings, research from mixed riparian forests along the middle Rio Grande in New Mexico found that *U. stansburiana* were also associated with such features as

Table 7 Abundance and presence of small mammal species as predicted by habitat characteristics (components, C) from a multiple linear regression and logistic regression, respectively. Adjusted r^2 is listed in parentheses for the multiple linear regression model and classification accuracies listed for logistic regression models. Small mammals were monitored in *Tamarix*-dominated ($n = 8$) and *Tamarix*-native ($n = 8$) sites along the Virgin River in Arizona and Nevada, USA

Species	Pos. or Neg. Correlation	Habitat Characteristics	Statistic	Significance
<i>Peromyscus maniculatus</i> ^a	+	Shady exotic thickets (C1)	$F_{(2,15)} = 4.467$	$P = 0.033$, $r^2 = 0.316$
	–	Mixed woodland (C4)		
<i>Chaetodipus formosus</i> ^b	–	Plant richness (C3)	$\chi^2_{(1)} = 5.390$	$P = 0.020$ (75.0%)
<i>Dipodomys merriami</i> ^b	–	Shady exotic thickets (C1)	$\chi^2_{(1)} = 3.508$	$P = 0.061$ (87.5%)
<i>Neotoma lepida</i> ^b	+	Nativeness and woody debris (C2)	$\chi^2_{(2)} = 7.459$	$P = 0.024$ (68.8%)
	–	Plant richness (C3)		
<i>Reithrodontomys megalotis</i> ^b				NS

^aMultiple linear regression.

^bLogistic regression

open understory and few thickets of *Tamarix* (Bateman, Chung-MacCoubrey & Snell, 2008). In the same study, treatments to remove exotic *Tamarix* and *Elaeagnus angustifolia* and woody fuels appeared beneficial or at least were non-damaging to species of lizards.

There are many similarities between our findings and studies focused on avian responses to nonnative *Tamarix* from the southwestern US. Research along the San Pedro River has found the highest avian diversity and species uniqueness associated with native woodlands (Brand *et al.*, 2008). On the lower Colorado River, Hunter, Ohmart & Anderson (1988) found lower bird abundance and diversity in *Tamarix* than in nearby native-dominated riparian areas and van Riper *et al.* (2008) observed a threshold response in which bird abundances were greatest in habitats characterized by moderate levels of *Tamarix* and few birds were present in dense *Tamarix* stands. Similarly, under moderate levels, *Tamarix* vegetation may resemble mixed habitats of native and nonnative riparian vegetation and support populations of common lizard and mammal species. However, when *Tamarix* density and canopy become exceedingly high, the habitat may no longer support populations of species with specific microhabitat associations, such as logs or open spaces in the understory.

Conservation implications

This work presents important findings that some species of small vertebrates are associated with specific habitat characteristics in *Tamarix* and mixed vegetation types and that rare species appear to be more adversely affected by *Tamarix*-dominated habitats. Our results provide baseline information of the fauna community composition along the Virgin River. Currently, a biological control agent (i.e. saltcedar leaf beetle, *Diorhabda carinulata*) has been introduced into *Tamarix* stands, and little is known about how the leaf beetle could impact such higher trophic levels as insectivorous reptiles, birds and mammals either by providing a novel food source or by altering the riparian habitat physiology via defoliation (Bateman *et al.*, 2010a). Following

defoliation, some plant species may become more abundant (e.g. arrowweed); therefore, it will be important to track changes in vegetation composition, structure and other potential nontarget effects (e.g. *sensu* Pearson & Callaway, 2005). Our results suggest that even partial control of *Tamarix*, whether from biocontrol or other means (i.e. herbicide, mechanical), could be beneficial to herpetofauna and small mammals if followed by restoration to promote native woody riparian species.

The pattern of rare species having lower abundances in exotic vegetation types compared to native or mixed exotic-native vegetation types has been observed in other systems (Baldi & Kisbenedek, 1997; Ostoja & Schupp, 2009; Ostoja, Schupp & Sivy, 2009). The apparent reductions in abundances of rare species may reflect a reduction in habitat suitability. Perhaps, community composition will shift from specialized species associated with native riparian trees and woody debris to species tolerant of exotic habitat, as *Tamarix* continues to invade and dominate riparian systems.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Location map of study area

Appendix S2. Site locations and fauna sampled in 2009 and 2010

Appendix S3. Herpetofauna trap array and vegetation sampling scheme

Appendix S4. Correlation matrix of component scores at herpetofauna trap arrays

Appendix S5. Correlation matrix of component scores at mammal trap grids

Appendix S6. Differences in component scores at herpetofauna trap arrays

Appendix S7. Differences in component scores at mammal trap grids

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