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Do riparian plant community characteristics differ between *Tamarix* (L.) invaded and non-invaded sites on the upper Verde River, Arizona?

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Abstract Invasion by *Tamarix* (L.) can severely alter riparian areas of the western U.S., which are globally rare ecosystems. The upper Verde River, Arizona, is a relatively free-flowing river and has abundant native riparian vegetation. *Tamarix* is present on the upper Verde but is a minor component of the vegetation (8% of stems). This study sought to determine whether riparian vegetation characteristics differed between sites where *Tamarix* was present and sites where *Tamarix* was absent during the invasion of the upper Verde. We hypothesized that herbaceous understory and woody plant communities would differ between *Tamarix* present and absent sites. Our hypothesis was generally confirmed, the two types of sites were different. *Tamarix* present sites had greater abundance of all vegetation, native understory species, graminoids, and native trees, and a positive association with perennial native wetland plant species. *Tamarix* absent sites had greater abundance of exotic plants and upland adapted plants and an association with greater abiotic cover and litter. These results are contrary to other reports of *Tamarix* association with depauperate riparian plant communities, and suggest that *Tamarix* invasion of a watershed with a relatively natural flow regime and a robust native plant community follows similar establishment patterns as the native riparian plant community.

Keywords Arizona · Community analysis · Indicator Species Analysis · Non-metric Multidimensional Scaling (NMS) · perMANOVA · Riparian · Saltcedar · *Tamarix* · Tamarisk · Verde River

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Introduction

Invasion by exotic plants may be an inevitable consequence of human influence on natural ecosystems. In riparian areas of the southwestern United States, the invasion of *Tamarix* (L.) (also called tamarisk and saltcedar) appears to be a consequence of the combination of human alterations of natural flow regimes and *Tamarix*'s inherent capability to capitalize on those alterations (Stromberg et al. 2007). Where conditions allow, *Tamarix* dominates

significant portions of river floodplains in this arid region (Friedman et al. 2005; Webb et al. 2007), and its dominance is associated with ecological changes such as increased fire frequency (Busch and Smith 1993, 1995), increased sediment retention along stream channels (Merritt and Cooper 2000), and alteration of belowground microbiota (Beauchamp et al. 2005).

Considered among the worst of invasive species (Invasive Species Specialist Group 2008), *Tamarix* has been the subject of many research projects. Previous research regarding *Tamarix* invasion has included impacts of river regulation (Merritt and Cooper 2000; Horton et al. 2001; Shafroth et al. 2002; Stromberg et al. 2007) and fluvial and alluvial dynamics (Cooper et al. 2003; Birken and Cooper 2006; Beauchamp et al. 2007) on its establishment and performance, and its effects on above- and below-ground fauna (Fleishman et al. 2003; Beauchamp et al. 2005; Moseman et al. 2008), fire (Busch and Smith 1993, 1995; Busch 1995), evapotranspiration (Moore et al. 2008; Nagler et al. 2008), and native trees (Sher et al. 2000, 2002; Sher and Marshall 2003; DeWine and Cooper 2008). The majority of these studies have reported various levels of environmental change associated with *Tamarix* invasion.

The majority of studies on *Tamarix* have focused on large and dense invasions. However, *Tamarix* invasions that occupy smaller areas and have fewer individuals may be regulated differently than their larger and denser counterparts. Information on populations of invasive species that are initially becoming established is needed to understand the invasion process, yet such information is rare (Lockwood et al. 2007).

Arid-land riparian areas of the southwestern United States, such as the Verde River in central Arizona, are dynamic and variable ecosystems. The vegetation of these areas is primarily structured by hydrologic characteristics such as surface water flow and ground water availability (Stromberg et al. 1996; Cooper et al. 2003). The hydrologic characteristics of an arid-land riparian ecosystem determine both the availability of water to plants, as well as the disturbance regime (Stromberg et al. 1996). Water stress and disturbance typically vary along gradients within riparian areas with water stress increasing and flood volume decreasing with distance perpendicular to the channel (Lite et al. 2005; Stromberg et al.

2008). Consequently, riparian vegetation forms landscape mosaics where different patch types are shaped by stress (lack of water) and disturbances such as flooding and sometimes fire (Lite et al. 2005; Bagstad et al. 2006). It is within this context of patch and gradient dynamics that plant competition occurs.

Tamarix competition with native woody vegetation has been the focus of several recent studies (Sher et al. 2000, 2002; Sher and Marshall 2003; DeWine and Cooper 2008). However, plant community characteristics associated with the onset of *Tamarix* invasion are poorly understood, especially for herbaceous plants. We used data on herbaceous plant cover and woody plant density collected on the upper Verde River from 1997 to 2007 to understand vegetative characteristics associated with *Tamarix* establishment in a relatively free flowing riparian ecosystem with a robust native plant community. Our overall hypothesis was that *Tamarix* would establish on sites that are different than sites dominated by native riparian vegetation because of negative effects (e.g., competition) of native plants on *Tamarix* establishment (Sher et al. 2000; Sher and Marshall 2003; DeWine and Cooper 2008). To inform this overall hypothesis we tested two sub-hypotheses that a) the herbaceous and b) the woody plant communities of the riparian flora of the upper Verde River would differ between *Tamarix* invaded and non-invaded sites.

Methods

Study area

The Verde River flows from Paulden, AZ approximately 125 km before being impounded by two water storage dams; the river then flows 60 km more until it converges with the Salt River outside of Phoenix, AZ (Fig. 1). The headwaters of the Verde River are at the Sullivan Dam, which separates the Verde River from the Big Chino Wash and is considered to be the river's beginning (Wirt and Hjalmarson 2000). The area for this study is in the upper 50 river kilometers and all sites are within the Prescott National Forest.

Field measurements

Riparian vegetation monitoring was initiated on the upper Verde River in 1997 by the Prescott National

Fig. 1 The Verde River and its watershed. All monitoring stations were along the upper Verde River in the Prescott National Forest
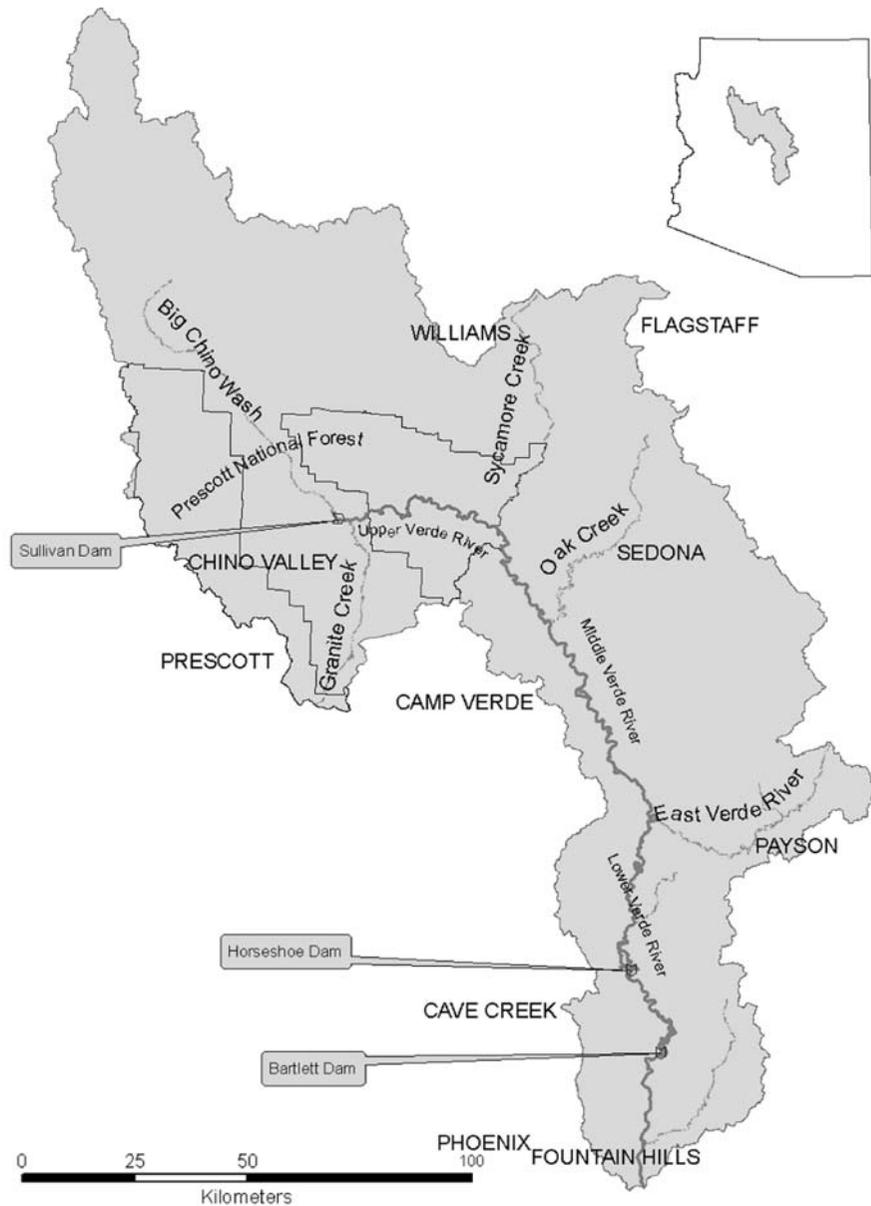
Forest in collaboration with the US Forest Service Rocky Mountain Research Station. Monitoring stations were sampled when they were established in 1997 and again six times over the next decade, during the summer growing season (June, July and August) of 1998, 2000, 2001, 2005, 2006, and 2007. Stations were established at randomly selected sites (i.e. independent of *Tamarix* presence) on the upper Verde River and each station consisted of two transects (one on each side of the river). All stations and transects were measured in the same manner each year of sampling. We assumed that transects at each station were independent for our analyses. The number of stations sampled out of the initial 42 stations varied each year depending on financial constraints. We considered for this analyses only transects that were sampled four or more times in the seven sampling periods that occurred between 1997 and 2007. To understand the differences between *Tamarix* present sites and *Tamarix* absent sites we compared a subset of transects where *Tamarix* was present during the entire study period ($n = 10$) with

Table 1 Characteristics of *Tamarix* present sites on the upper Verde River, AZ

Site	Average *Tamarix* stem density (stems m^{-2})	River distance (km)
11_R	0.10	10.70
13_R	0.10	13.10
17_L	0.11	15.80
02_R	0.31	18.50
03_R	0.23	19.00
04_R	0.12	19.10
18_R	1.23	21.40
19_R	0.25	22.20
33_L	0.10	46.00
35_L	0.10	48.70

River distance is the distance downstream from the headwaters of the Verde River at Sullivan Dam

transects where *Tamarix* was absent for the same period ($n = 10$). Transects for this analysis were not randomly selected; rather we used all transects where *Tamarix* was either present or absent for the entire study period and had been sampled four or more times. *Tamarix* present sites showed no pattern in distance downstream from the headwaters, and the density of *Tamarix* at these sites varied widely (Table 1). *Tamarix* accounted for 8% of the total woody plant stems sampled over all sites, and this percentage did not change significantly over the sampling period.

Herbaceous and woody plants were sampled in each year of assessment. Herbaceous vegetation was sampled using Daubenmire canopy coverage estimates within $40 - 1 \text{ m}^2$ microplots (Daubenmire 1959; Medina 1986). The microplots occurred each meter at the water's edge for a length of 40 m upstream and parallel to the river channel. To sample woody vegetation, the number of stems, diameter at breast height, and height were measured for each woody plant within belt transects that extended five meters from the water's edge and ran for the same 40 m as the herbaceous transects (Medina 1986). Plants were identified to species in the field. Samples of unknown plants were collected and identified using Correll and Correll (1975). Nomenclature was updated and plant characteristics were obtained for each species from the Plants National Database (www.plants.usda.gov).

Importance values

We used a percent importance value (Fierke and Kauffman 2006) for each herbaceous species as a response variable in analyses of the herbaceous plant data. Percent importance value (%IV) of each species in each transect was defined as:

$$\%\text{IV} = \frac{(\text{Fs}/\text{Ft}) + (\text{Cs}/\text{Ct})}{2} \times 100$$

where Fs is the frequency of a species, Ft is the total frequency of all species, Cs is the cover of a species, and Ct is the total cover of all species (Fierke and Kauffman 2006). This calculation of importance values combines relative cover and relative frequency (number of microplots in which a species occurs) for each species on each transect (Fierke and Kauffman 2006). This type of importance value moderates the influence of plant species with either disproportionately high cover and low frequency, or common plants with low cover. After each species' %IV was calculated, an average %IV was calculated at each transect for groups of species defined by life history and ecological characteristics (nativity, growth form, life span, and wetland indicator status). We also calculated a %IV for abiotic cover (soil, litter, gravel, and rock) for each transect. The %IV was averaged for each species across all years to yield a single %IV for each species. We used the wetland indicator status [i.e. facultative wetland, obligate wetland, etc. (www.plants.usda.gov)] of each species as an indirect measure of site wetness because hydrologic and soil variables were not measured at all sites each year over the decade of measurements.

Statistical analysis

To test our hypotheses we used several community analysis techniques to quantitatively describe differences in plant characteristics between *Tamarix* present and absent sites. Because of limited sample sizes ($n = 10$ for each type of transect) we considered p values <0.1 but >0.05 to be trending towards significance for all analyses. Woody and herbaceous plant communities were analyzed separately.

We used Non-metric Multidimensional Scaling (NMS) ordinations (PC-ORD software Version 5.12, McCune and Mefford 2006) based on Sørensen (Bray-Curtis) distance on %IV of herbaceous species

and stem density of woody species to determine if sites with or without *Tamarix* differed in plant community composition. We used NMS because of its lack of assumptions regarding multivariate normality, and its robustness to large data sets that have frequent zero values (McCune and Grace 2002). NMS is an iterative process whereby the high-dimensionality of a dataset is reduced to several ecologically meaningful axes. The best solution for NMS ordination has the lowest stress, a measure of departure from the known data structure. To find a solution with the lowest stress, we used PC-ORD to ordinate the data from different random starting locations 250 times or until an instability criterion of 0.00001 was met. Stress <10 typically indicates a solution that will not result in false or misleading structure (McCune and Grace 2002). Instability is the standard deviation of the stress over the previous ten iterations, and is an indicator that the iterations have consistently found the least stressful solution. Once the lowest stress solution was found along with the appropriate number of axes via Monte Carlo randomization, we used that configuration as the starting point for one final ordination of the original data which produced axis scores for each transect. To extract meaning from the axes produced in NMS we used Pearson and Kendall Correlations in PC-ORD to correlate environmental variables with the ordination axes. We show correlations with r^2 greater than 0.4 in our graphical results to further interpret the ordination axes.

To further understand the differences between *Tamarix* present and absent sites we used Mann–Whitney u-tests, a non-parametric analog to ANOVA (analysis of variance), to compare the average native tree stem density for woody plants and the average %IV for different herbaceous plant groups based on nativity, growth form, life span, and wetland indicator status. The resulting p-values were subjected to Bonferroni correction to account for multiple comparisons. Prior to the data analysis we decided to limit the use of u-tests to comparisons of the ten largest differences in order to control for Type II errors. The u-tests were conducted using SAS JMP v5.0.1a (SAS Institute 2002). To test for differences in average %IV for herbaceous species and average stem density for woody plant species between *Tamarix* present and absent sites we used perMANOVA (Andersen 2001). The perMANOVA (PC-ORD software Version 5.12) conducts sums of squares calculations based on the

average inter-point Sørensen (Bray-Curtis) distance of species within a group. The perMANOVA calculates an F statistic in the same manner as conventional analyses of variance by taking the ratio of among group sums of squares to within group sums of squares. Since perMANOVA does not require multivariate normality the data were not transformed. The perMANOVA calculates probabilities with Monte Carlo randomization procedures (9999 runs), where p-values are the probability of obtaining a larger F-value using random permutations of the original data.

We used Indicator Species Analysis (ISA) (Dufrene and Legendre 1997) to determine whether individual plant species were associated with *Tamarix* presence or absence. Indicator Species Analysis calculates the probability of a species being found in association with the sample units of a certain group (*Tamarix* present or absent sites). An indicator value, which is a function of a species' relative abundance and relative frequency, was calculated for each species at each transect and the group with the highest indicator value is identified for each species. The indicator value for the observed species-group combination was then compared to the indicator values for species randomly assigned to groups via Monte Carlo randomization (9999 runs). To assess whether species are significant indicators of certain groups, a p-value was calculated for each observed species-group combination. The p-value is the proportion of times that the randomized trials produce indicator values greater or equal to the observed indicator values. Because of the manner in which indicator values are calculated, species should only be considered significant indicators of groups if their indicator values are >25 and they have a significant ($p < 0.05$) or trending p value (<0.10) (McCune and Grace 2002).
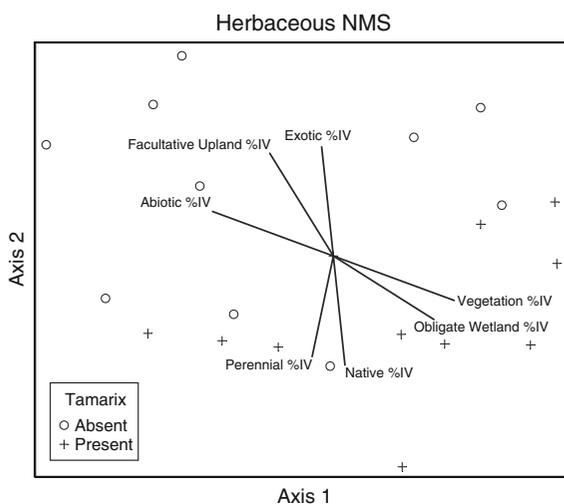
Results

NMS plant group ordinations

NMS ordinations of herbaceous and woody plant groups yielded stresses of 9.62 and 14.88 found after 96 and 72 iterations achieving instabilities of 0.00000052 and 0.00000001, respectively. The Monte Carlo method of randomization determined after 250 runs with randomized data that three axes ($p = 0.004$,

$r^2 = 0.874$) were needed to best represent the variation in the herbaceous data, and two axes ($p = 0.004$, $r^2 = 0.745$) were needed for the woody data. The low stresses, low instabilities, and significant p-values indicate that the NMS ordinations provided a reliable depiction of the plant communities.

Herbaceous plants

Ordinations of herbaceous data showed that *Tamarix* present and absent sites most clearly separated in ordination space along Axis 1 and Axis 2 (Fig. 2). Pearson and Kendall correlations showed that the lower half of Axis 2, where most *Tamarix* present sites were located in ordination space, was positively correlated with the %IV of all vegetation ($r^2 = .473$), %IV of obligate wetland plants ($r^2 = .400$), %IV of native plants ($r^2 = .427$), and %IV of perennial plants ($r^2 = .400$). *Tamarix* absent sites were scattered on the upper half of Axis 2, an area of the ordination with positive associations with %IV of abiotic (average of soil, litter, gravel, and rock $r^2 = .473$), facultative upland plant %IV ($r^2 = .403$), and exotic plant %IV ($r^2 = .427$). The u-tests (Table 2) revealed that *Tamarix* present sites had after Bonferroni correction, on average, greater native species %IV ($p = 0.0029$), greater %IV for

Table 2 u-test results comparing average importance value by species trait group (facultative upland, exotic, native, graminoid, forb, upland), ground cover types (litter, abiotic, vegetation), and average tree density (# stems ha^{-1}) between *Tamarix* present and absent sites

Variable	*Tamarix* present	*Tamarix* absent	p-value
Facultative upland	0.62%	1.15%	0.001*
Upland	0.15%	0.21%	0.042
Litter	12.39%	16.95%	0.002*
Exotic	0.53%	0.74%	0.0029*
Native	0.71%	0.63%	0.0029*
Vegetation	0.41%	0.39%	0.0049*
Abiotic	4.42%	4.81%	0.0098**
Graminoid	0.85%	0.71%	0.0049*
Forb	0.72%	0.81%	0.0098**
Native tree density	13,615.6	6996.6	0.007**

Variables with asterisk are significant after Bonferroni correction for multiple comparisons

Variables are listed by decreasing p-value

* Significance $p \leq 0.005$
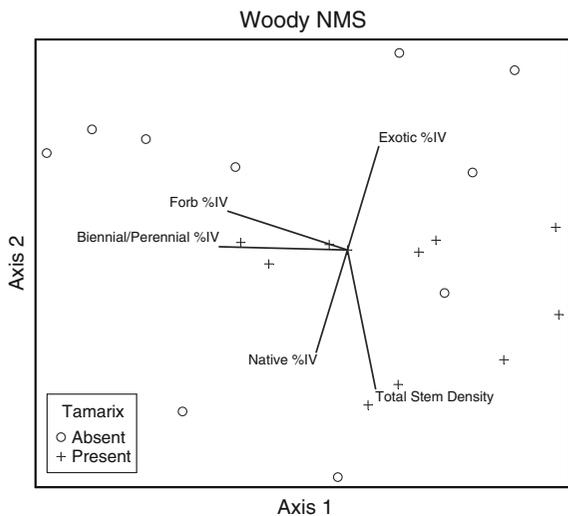
** Trending toward significance $p \leq 0.01$

all vegetation ($p = 0.0049$), and greater %IV for graminoids ($p = 0.0049$) than did *Tamarix* absent sites. *Tamarix* absent sites had greater exotic species %IV ($p = 0.0029$) and greater %IV of facultative upland species ($p = 0.001$).

Woody plants

The NMS ordination of woody plants (Fig. 3) showed no clear pattern for *Tamarix* absent sites. However, *Tamarix* present sites were clustered toward the middle of Axis 2 and the high end of Axis 1. No environmental variables were strongly correlated with this area of the ordination. The u-tests (after Bonferroni correction) showed that *Tamarix* present sites had trending significance toward greater average native tree density than *Tamarix* absent sites ($p = 0.007$, Table 2).

Abiotic variables

Some differences were found in the %IV of abiotic variables between sites with and without *Tamarix*. *Tamarix* absent sites trended towards having

Fig. 2 NMS ordinations of herbaceous plant community data for Axis 1 and 2 for *Tamarix* present (*crosses*) and absent (*circles*) sites. The length of the correlation vector indicates strength of correlation

Fig. 3 NMS ordinations of woody plant community data for Axis 1 and 2 for *Tamarix* present (*crosses*) and absent (*circles*) sites. The length of the correlation vector indicates strength of correlation

significantly higher %IV of all pooled abiotic variables ($p = 0.0098$) than *Tamarix* present sites after Bonferroni correction (Table 2). *Tamarix* absent sites also had significantly higher %IV of litter than *Tamarix* present sites ($p = 0.002$, Table 2).

Individual species components of community differences

The perMANOVA showed a significant difference in community composition based on %IV of herbaceous species ($F = 2.37$, $p = 0.013$) between *Tamarix* present and absent sites. Indicator Species Analysis (Table 3) showed that eight species were significant indicators of *Tamarix* presence. The most significant indicators of *Tamarix* presence, in both statistical ($p = 0.0005$, 0.0033 and 0.0029, indicator values = 80.5, 72.5, and 75, respectively) and ecological senses, were three members of the genus *Schoenoplectus* ((Rchb.) Palla) (formerly *Scirpus* commonly called bulrush) which are native perennial graminoids, and as obligate wetland species are associated with wetland conditions (www.plants.usda.gov). Another significant indicator species for *Tamarix* presence was cutleaf water parsnip (*Berula erecta* (Huds.) Coville) a perennial native forb that is also a wetland obligate ($p = 0.03$ indicator value = 65.7, Table 3). Two introduced species were significant indicators for

Tamarix presence as well. Dallisgrass (*Paspalum dilatatum* (Poir.)), a perennial facultative graminoid, and field bindweed (*Convolvulus arvensis* (L.)), a perennial vine, were both significant indicators of *Tamarix* presence ($p = 0.01$ and 0.03 indicator values = 56.4 and 45.9, respectively). Two other perennial native wetland plants, knotgrass (*Paspalum distichum* (L.)) and horsetail (*Equisetum laevigatum* (A. Braun)) were trending towards indicating *Tamarix* presence ($p = 0.056$ and 0.09 indicator values = 67.6 and 63.3, respectively).

Although no species were significant indicators of *Tamarix* absence, there were several trending indicator species. These species, unlike the species that indicated *Tamarix* presence, were not consistent in plant traits. For example, the closest to significance was field brome (*Bromus arvensis* (L.)), an introduced upland annual graminoid followed by sacred thorn-apple (*Datura wrightii* (Regel)) and velvetweed (*Gaura mollis* (James)), both native forbs ($p = 0.07$, 0.07 and 0.08 indicator values = 71.2, 47.2 and 38.2, respectively, Table 3).

Tamarix present and absent sites were significantly different in community composition based on woody plant stem density (perMANOVA $F = 2.7$, $p = 0.011$). Indicator Species Analysis showed that *Tamarix* present sites were significantly associated with two common native obligate-riparian woody species. The thicket forming shrub seep willow (*Baccharis salicifolia* (Ruiz and Pav.) Pers.) and small tree Bonpland willow (*Salix bonplandiana* (Kunth)) both significantly indicated *Tamarix* presence ($p = 0.0097$ and 0.0198 indicator values = 75.2 and 59.4, respectively). There were no woody plant species associated with *Tamarix* absence and none of the three most common native tree species on the upper Verde, Goodding's willow (*Salix gooddingii* (C.R. Ball)), velvet ash (*Fraxinus velutina* (Torr.)), and Fremont cottonwood (*Populus fremontii* (S. Watson)), had significant associations with *Tamarix* presence or absence ($p = 0.16$, 0.93, and 0.64 indicator values = 70.0, 45.9 and 39.3 respectively).

Discussion

Our results contribute to the understanding of vegetation characteristics associated with the onset of *Tamarix* invasion of a relatively free-flowing

Table 3 Indicator species analysis results for *Tamarix* present (group 1) and *Tamarix* absent (group 0) sites

Genus	Species	Group	*p*-value	Indicator value	FORM	LIFE	NATIVITY	WET
Schoenoplectus	*pungens var longispicatus*	1	0.0005*	80.5	G	P	N	O
Schoenoplectus	*pungens*	1	0.0033*	72.5	G	P	N	O
Paspalum	*dilatatum*	1	0.0114*	56.4	G	P	I	F
Schoenoplectus	*americanus*	1	0.0291*	75	G	P	N	O
Berula	*erecta*	1	0.0297*	65.7	F/H	P	N	O
Convolvulus	*arvensis*	1	0.0312*	45.9	V/F/H	P	I	?
VARIOUS	Algae	1	0.0464*	62.5				
Eleocharis	*quinqueflora*	1	0.0495*	66.7	G	P	N	O
Paspalum	*distichum*	1	0.0559**	67.6	G	P	N	O
Equisetum	*laevigatum*	1	0.0984**	63.3	F/H	P	N	FW
Baccharis	*salicifolia*	1	0.007*	75.2	S	P	N	FW
Salix	*bonplandiana*	1	0.0198*	59.4	T	P	N	FW
Bromus	*arvensis*	0	0.073**	71.2	G	A	I	U
Datura	*wrightii*	0	0.0739**	47.2	F/H/SS	A/P	N	?
Gaura	*mollis*	0	0.0838**	38.2	F/H	A	N	?
Cyperus	*esculentus*	0	0.0865**	40	G	P	N/I	FW
Muhlenbergia	*asperifolia*	0	0.0879**	40	G	P	N	FW
Typha	*latifolia*	0	0.0967**	71.7	F/H	P	N	O

Plant traits are coded as FORM = growth form, LIFE = life span, NATIVITY = native to the watershed, WET = wetland indicator status. Code definitions are: G = Graminoid, F = Forb, H = Herb, V = Vine, T = Tree, S = Shrub, SS = Sub-shrub, P = Perennial, A = Annual, N = Native, E = Exotic, O = Obligate Wetland, F = Facultative, FW = Facultative Wetland, U = Obligate Upland, ? = Wetland status unknown. Plant traits are from the USDA Plants National Database. Variables with asterisk are indicators of group significance

* Significance $p \leq 0.05$

** Trending toward significance $p \leq 0.1$

river in the arid Southwest. Our analysis of woody and herbaceous riparian vegetation of the upper Verde River showed that plant community composition differed between areas that had *Tamarix* between 1997 and 2007 and areas that did not. Our analysis indicated that differences occur at a community level for herbaceous plants as well as at an individual plant level for both herbaceous and woody plant species. Our data analysis revealed that sites where *Tamarix* was present supported a riparian plant community that was structured around an abundance of total vegetation (greater absolute herbaceous vegetation and native tree stem density) and that the plant species at these sites were in general native, perennial, riparian obligate plants (Fig. 2; Table 3).

The locations with *Tamarix* present had greater %IV of native plants, graminoids, and total vegetation, as well as higher stem density of native trees, compared with sites lacking *Tamarix*. This result

suggests that areas with *Tamarix* were better suited for growth of many plants and that *Tamarix* was subject to the same resource and habitat limitations as much of the rest of the riparian vegetation on the Verde River. Furthermore, sites without *Tamarix* had higher %IV of exotic species and facultative upland species, suggesting that these sites are drier and thus less hospitable to riparian plants. However, the average %IV of litter was significantly higher at *Tamarix* absent sites than *Tamarix* present sites. This finding is somewhat contrary to a previous report that *Tamarix* is a prolific litter producer (Kennedy and Hobbie 2005). Greater litter abundance at *Tamarix* absent sites is also contrary to the findings of our other analyses that suggest that areas with *Tamarix* have greater vegetative abundance than areas lacking *Tamarix*. Greater litter abundance at *Tamarix* absent sites suggests that these sites are less frequently exposed to flooding that washes away litter from the ground surface.

Previous research suggests that the vegetation of southwestern riparian systems is a function of hydrological processes (Stromberg et al. 1996), where fluvial and alluvial dynamics create habitat for species establishment (Cooper et al. 2003) and water stress and flood disturbance structure the vegetative community (Lytle and Merritt 2004; Lite et al. 2005). On unregulated or quasi-regulated rivers, such as the upper Verde River, the occurrence of *Tamarix* has been shown to fall within the continuum of patches defined by these abiotic processes (Bagstad et al. 2006). This finding suggests that *Tamarix* populations on these rivers are regulated by hydrologic conditions. It is reasonable to assume that *Tamarix* present sites on the upper Verde River likely fall within this continuum of patches created by the hydrologic environment.

While our study was not a direct test of the hypothesis that hydrologic characteristics control riparian vegetation, we found supporting evidence for this hypothesis on the upper Verde River. Our finding that *Tamarix* present sites were trending toward a higher density of native riparian trees and had a greater %IV of native plants as well as all vegetation suggests that these sites have more amiable hydrologic characteristics (e.g., water availability, flood disturbance) for riparian plants in general than sites that lack *Tamarix*. More studies are needed on the relationship between the habitat of native herbaceous riparian plant species and hydrologic conditions to further evaluate this hypothesis.

Literature on the subject of *Tamarix* interactions with understory herbaceous plants is scarce as nearly all studies of species-specific interactions with *Tamarix* focus on native trees species (Sher et al. 2000, 2002; Sher and Marshall 2003; DeWine and Cooper 2008). Few studies have described differences in herbaceous vegetation composition between *Tamarix* present and absent sites as we have. The herbaceous species that were associated with *Tamarix* presence on the upper Verde River were, for the most part, riparian obligate species, such as bulrush species and cutleaf water parsnip (Table 3). These species are perennial native plants that are commonly associated with wetlands. No species were significantly associated with *Tamarix* absence, but the several that were trending towards significance were a mixture of plants with different life strategies, growth forms, and wetland preferences (Table 3). The dichotomy of species associations we described for the two types of sites may reflect some unmeasured difference between *Tamarix* present and absent sites in plant competition, soils, or other abiotic factors on the upper Verde River.

Sites on the upper Verde River where *Tamarix* was present were trending toward a significantly higher density of native trees. This finding may seem to be inconsistent with other studies that have demonstrated *Tamarix* to be an inferior competitor to many native tree species in riparian environments with ample water supply (Sher et al. 2000, 2002; Sher and Marshall 2003). While this study was not designed to evaluate the competitive environment of the upper Verde, these results suggest that plant competition on the upper Verde is weaker in importance than the hydrologic and geomorphological environment as a control over *Tamarix* establishment.

While our hypothesis that sites with and without *Tamarix* would differ with respect to the vegetative community was supported, one of our sub-hypotheses (H_{woody}) was only slightly supported (Table 4). Our results indicate that the stem density of native trees was trending toward being significantly different between the two types of site. However, NMS ordinations did not show an interpretable pattern for *Tamarix* presence or absence based on woody plants. The perMANOVA and ISA results for individual woody plants showed that there was a difference

Table 4 Summary of hypotheses and findings regarding differences in riparian plant communities between *Tamarix* present and absent sites on the upper Verde River, AZ

Hypothesis	Prediction	Finding
$H_{Overall}$	Riparian plant communities will differ	Mostly confirmed
$H_{Herbaceous}$	Herbaceous plant community will differ	u-tests (Table 2), NMS (Fig. 2), perMANOVA, and ISA (Table 3) indicate difference
H_{Woody}	Woody plant community will differ	u-test trending difference (Table 2), perMANOVA and ISA indicate difference (Table 3), NMS unclear (Fig. 3)

between the invaded and non-invaded sites. Individual herbaceous plant species and the herbaceous plant community in general was different between *Tamarix* present and absent stations, and our results showed that *Tamarix* absent sites had a more exotic and drier plant community with greater %IV of abiotic variables.

These findings suggest that *Tamarix* invasion of watersheds that have a relatively natural flow regime and a robust native plant community follows similar establishment patterns as the native riparian plant community. *Tamarix* establishment on the upper Verde River appears to be largely influenced by the same factors that influence the micro-site occurrence of native trees and understory plants (i.e. hydrologic and geomorphic variables) since sites with *Tamarix* supported a plant community that had higher %IV of native perennial wetland plants and a trend toward higher stem densities than sites without *Tamarix*. Further studies will be needed to determine whether these findings apply to other *Tamarix* invasions of riparian ecosystems with robust native plant communities in the southwestern U.S.

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