Restoration Ecology

Rethinking Avian Response to *Tamarix* on the Lower Colorado River: A Threshold Hypothesis

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Abstract

Many of the world's large river systems have been greatly altered in the past century due to river regulation, agriculture, and invasion of introduced *Tamarix* spp. (saltcedar, tamarisk). These riverine ecosystems are known to provide important habitat for avian communities, but information on responses of birds to differing levels of *Tamarix* is not known. Past research on birds along the Colorado River has shown that avian abundance in general is greater in native than in non-native habitat. In this article, we address habitat restoration on the lower Colorado River by comparing abnndance and diversity of avian communities at a matrix of different amounts of native and non-native habitats at National Wildlife Refuges in Arizona. Two major patterns emerged from this study: (1) Not all bird species responded to *Tamarix* in a similar fashion, and for many bird species, abundance was highest at intermediate *Tamarix* levels (40–60%), suggesting a response threshold. (2) In *Tamarix*-dominated habitats, the greatest increase in bird abundance occurred when small amounts of native vegetation were present as a component of that habitat. In fact, *Tamarix* was the best vegetation predictor of avian abundance when compared to vegetation density and canopy cover. Onr results suggest that to positively benefit avian abundance and diversity, one cost-effective way to rehabilitate larger monoculture *Tamarix* stands would be to add relatively low levels of native vegetation (~20–40%) within homogenous *Tamarix* habitat. In addition, this could be mnch more cost effective and feasible than attempting to replace all *Tamarix* with native vegetation.

Key words: birds, habitat restoration, invasive species, lower Colorado River in Arizona, riparian habitat, *Tamarix*.

Introduction

Riparian ecosystems are the most heavily altered habitat type throughout the world (NRC 2002; Nilsson et al. 2005; van Andel & Aronson 2006). Many riparian habitats have been influenced by large-scale water management practices (e.g., river damming, river channelization, and flow regulation) that have resulted in a decreased frequency and intensity of natural flooding (e.g., in Asia [Mingxi et al. 2005], Australia, [Renofalt et al. 2007], Europe [Petts et al. 2006], and as Poff et al. [2007] recently demonstrated for North America). These altered flow regimes have often resulted in a loss of native vegetation that is composed primarily of species dependent upon periodic floods for establishment and regeneration (Stromberg et al. 1991; Busch & Smith 1995; Scott et al. 1997). The loss of native species is invariably followed by invasion of exotic vegetation, whether it is in Africa (Richardson et al. 2007), Australia (Bengsen & Pearson 2006), Europe (Angelstam et al. 1997), Asia (Hou et al. 2007), or even on remote islands (Scott et al. 2001). The resulting vegetation change also dramatically influences the suitability of wildlife habitat (Dean et al. 2002; Hobbs et al. 2006; van Andel & Aronson 2006).

In the western United States, riparian habitats have declined precipitously in the past century due primarily to anthropogenic perturbations such as changes in river flow regimes, agricultural conversions, urban expansion, and livestock grazing (Conine et al. 1978; Fleischner 1994; Webb et al. 2003). In the southwestern United States, the decline of riparian habitat and loss of native Cottonwood (*Populus fremontii*)–Willow (*Salix gooddingii*) gallery forests and adjacent mesquite (*Prosopis* spp.) bosques has been accompanied by the invasion of non-native *Tamarix* spp. (in this article, we use the genus name alone, *Tamarix*, to refer to the complex of tamarisk species). This change has resulted in a dramatic shift toward the dominance of *Tamarix* in riparian vegetation communities (Hunter et al. 1988; Shafroth et al. 2005). The reduction and shift in vegetation composition within riparian habitats in western North America have resulted in their classification as globally imperiled by The Nature Conservancy (Comer et al. 2003).

Although riparian habitat comprises less than 1% of the landscape in the southwestern United States, it supports more breeding bird species than all other western habitat

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types combined (Anderson & Ohmart 1977; Johnson et al. 1977; Knopf et al. 1988). Riparian areas serve as critical breeding, winter, and stopover habitat for birds, supporting 10 times greater bird numbers than the surrounding uplands (Stevens et al. 1977; Martin & Finch 1995; Skagen et al. 1998; Anderson et al. 2004). In fact, most wildlife in the xeric environments of the American Southwest depend, during some time of their annual cycle, on resources (e.g., water, cover, and food) provided by riparian areas (Grinnell 1914; Rosenberg et al. 1991).

It has been demonstrated that vegetation species composition is an important component of avian habitat selection within riparian habitats of the southwestern United States (Anderson & Ohmart 1977; Rice et al. 1984), and several studies have examined the effects of *Tamarix* on avian communities (Rice et al. 1983; Hunter et al. 1988; Kelly & Finch 1999; Finch & Yong 2000). These studies focused on comparing pure *Tamarix* to native-dominated stands and have shown that *Tamarix* monocultures contain few avian species when compared to habitat dominated by native vegetation. This has resulted in the perception that *Tamarix* provides relatively unsuitable habitat for birds and that a linear negative relationship exists between avian numbers and amounts of *Tamarix* (Kunzmann et al. 1989). This perception has helped to shape current restoration policies for riparian habitats in the southwestern United States that commonly aim to eradicate *Tamarix* (e.g., Dudley et al. 2000; Cohn 2005). The present restoration policy has evolved in spite of the fact that there is presently a lack of information on avian responses to differing levels of *Tamarix* vegetation along southwestern riparian corridors.

It is critical that we understand the dynamics and diversity of avian communities at more than just habitat extremes, especially because vegetation restoration efforts are a priority in southwestern U.S. riparian systems (http://www.mp.usbr.gov/publications/MSCPBO.pdf). In this study, we compare the response of avian communities to differing levels of native/*Tamarix* vegetation mixes at Cibola and Bill Williams River National Wildlife Refuges (NWR) on the Lower Colorado River in southwestern Arizona. We examined ways that avian communities responded to different vegetation composition along a gradient, from pure *Tamarix* to pure native habitats. We addressed these responses at the avian community, temporal guild, and individual species level. It is our hope that this information will allow land managers to reexamine present *Tamarix* restoration practices and thus be able to more precisely address avian community needs within future restoration projects.

Methods

Study Areas

Our studies were conducted at Cibola NWR (lat 33°18′N, long 114°41′W; elevation 60 m) and Bill Williams River NWR (lat 34°18′N, long 114°08′W; elevation 200 m) in La Paz County, Arizona (Fig. 1). Cibola NWR is located adjacent to the main channel of the lower Colorado River, where past intensive water management and land use practices have resulted in large expanses of the vegetation now being dominated by *Tamarix* monocultures. The large native habitat patches presently found at Cibola NWR are primarily the result of former restoration efforts (Rosenberg et al. 1991; Anderson et al. 2004). In contrast, the Bill Williams River is a perennial tributary to the lower Colorado River, and while *Tamarix* is one of the dominant tree species, the area contains some of the last remaining extensive stands of natural Cottonwood and Willow gallery forests within the lower Colorado River watershed (Busch & Smith 1995; Shafroth et al. 2002). Honey mesquite (*Prosopis glandulosa*) and to a lesser degree Screwbean mesquite (*P. pubescens*) are other native tree species found along the Bill Williams River, whereas common woody understory species include Seepwillow (*Baccharis salicifolia*), Arrow-weed (*Tessaria sericea*), and Saltbush (*Atriplex* spp.). Although Cibola NWR allowed us to examine only habitat extremes, the varied vegetation composition at Bill Williams River NWR provided an ideal location to examine the response of avian communities to differing mixes of *Tamarix* and native vegetation.

Field Methods

From 1998 to 1999, we established 16 and 14 point count stations with 100-m-radius counting areas at Cibola and Bill Williams River NWR, respectively, following the methods of Reynolds et al. (1980) and Ralph et al. (1993). Point count stations were selected based on levels of *Tamarix* and native vegetation composition (Table 1). Each

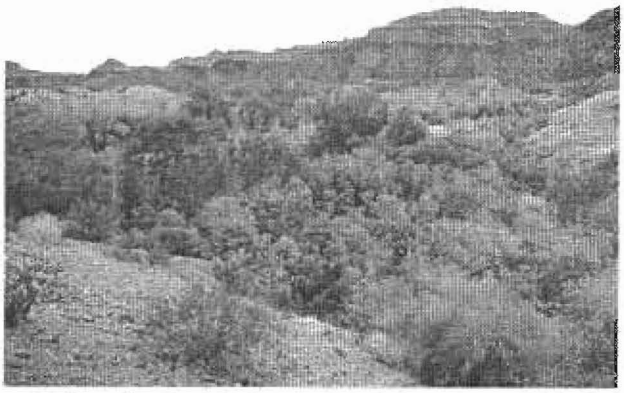

Figure 1. Photograph of one study area at Bill Williams River NWR, Arizona, U.S.A., taken in 1999. Vegetation in middle is introduced *Tamarix* vegetation surrounded by native gallery forest Cottonwood–Willow (*Populus–Salix*) habitat, with native mesquite (*Prosopis* spp.) trees along the upper edges of the drainage.

Table 1. Vegetation data collected in 1999 from bird point count stations at Cibola and Bill Williams River NWR study sites in southwestern Arizona, U.S.A.

Site	Habitat Type	Bird Point Count Number	Relative Index of Tamarisk (%)	Horizontal Cover 0–3 m (%) (SD)	Canopy Height (m) (SD)	Canopy Cover (%) (SD)	Species Richness* Trees and Shrubs
Cibola	Native	1	0.0	94.5 (10.6)	11.6 (5.3)	32.9 (25.1)	4
		2	0.0	89.1 (9.8)	10.7 (4.8)	39.8 (25.2)	5
		3	0.0	80.4 (24)	6.3 (0.1)	19.1 (13.9)	6
		4	0.0	45.5 (24.8)	11.7 (0.1)	44.4 (9)	5
		5	0.0	82.2 (25)	10.9 (6.5)	55.5 (32.4)	4
		6	0.0	49.5 (18.4)	16.9 (0.4)	43 (23.7)	4
		7	33.3	80.9 (11.5)	12.1 (—)	13.6 (16)	5
		8	32.0	100 (0)	16.6 (—)	43 (35.4)	3
	Tamarix	9	100.0	100 (0)	8.1 (—)	53.5 (26)	2*
		10	100.0	83.5 (18.4)	4.4 (—)	24.5 (31.5)	1
		11	100.0	97.2 (4.9)	5.1 (—)	56 (33.1)	2*
		12	100.0	100 (0)	6 (—)	63.6 (28)	2*
		13	87.5	63 (13.2)	8.5 (—)	43.4 (31.3)	2
		14	100.0	92.5 (15.3)	5.3 (—)	82.3 (23)	1
		15	100.0	92.6 (11.3)	8.7 (—)	47.6 (39.2)	2*
		16	100.0	99.5 (1.2)	7.5 (0.21)	31.5 (25.2)	4*
Bill Williams	Native	1	64.3	94.5 (4.8)	17.9 (4.6)	92.7 (4.7)	3
		2	47.4	84.6 (14.8)	23.3 (11.7)	88.3 (6.9)	4
		3	39.5	96.6 (4.8)	10.3 (2.5)	88.5 (7.7)	3
		4	52.2	96.4 (5.5)	27.3 (2.4)	70 (11.7)	4
		5	14.3	53.6 (26.8)	13.7 (7.8)	25.9 (25.7)	5
		6	0.0	14.5 (13.1)	10.5 (4.6)	17.7 (13.7)	4
		7	0.0	66.1 (34.7)	8.2 (7.2)	58.9 (40.2)	3
	Tamarix	8	77.8	61.1 (44.9)	7.9 (2.1)	72 (46.5)	4
		9	89.4	100 (0)	13.5 (3.6)	83.3 (9.1)	3
		10	100.0	67.3 (6.3)	10.9 (5.5)	41.2 (31.6)	2*
		11	100.0	68.1 (34.9)	12.9 (2.1)	61 (38.9)	2*
		12	100.0	100 (0)	7.2 (1.9)	84.5 (7.4)	2*
		13	100.0	80.7 (22.9)	12.0 (1.4)	83 (26.6)	2*
		14	92.5	61.4 (41.2)	10.7 (5.4)	79.2 (12.4)	2

Relative index of *Tamarix* is the total number of *Tamarix* stems divided by all stems counted at breast height. The horizontal cover is the percent of total vegetation cover counted with a density board more than a 5 m distance from 0 to 3 m aboveground (±SD). Canopy height is the mean height of the canopy overstory, averaging both vegetation plots at each station. Canopy cover is the percent total leaf cover using a densiometer and averaging both vegetation plots at that bird point count station (±SD). Species richness is the total number of different tree and shrub species counted within both vegetation plots at that bird point count station.
*Cases in which species richness is >1 for 100% tamarisk plots. Tamarisk percent was determined from only trees, while species richness was determined from both trees and shrubs.

station point was at least 300 m from adjacent stations to minimize double counting. To reduce observer variance, all people who counted birds had a hearing test, were intensively trained on aural and visual bird identification for 1 week, and then tested in the field following training. To minimize temporal bias, starting points were reversed for each survey, and point count stations were rotated among observers. Over a 5-year period (1998–2002), during March to May and August to November, we surveyed for birds every 7–10 days. Surveys were conducted between sunrise and 10:00 hours, except during rain or high winds. At each census point, observers waited 1 minute to minimize influences of any disturbance created while walking to the station, then for 5 minutes recorded all birds heard and seen within a 100-m radius of the point. Distance of each bird from the count point was recorded and birds flying overhead were excluded.

To quantify vegetation characteristics, we spun a compass to randomly select two azimuths, then located two 11.3-m-radius plots 30 m from the center of each point count station along those random directions. Vegetation parameters were measured during the spring of 1999 using a combination of vegetation sampling techniques from James and Shugart (1970), the BBIRD protocol (Martin et al. 1997), and that of Noon (1981). Vegetation measurements taken within each 11.3-m-radius plot included density of all tree and shrub stems, by species, at breast height (1.3 m aboveground); horizontal foliage density (total vegetation cover counted by measuring with a density board, over a 5 m distance from 0 to 3 m above the ground); canopy height (the mean height of the overstory); canopy cover (percent total leaf cover measured with a densiometer); and tree height (measured with a clinometer and range finder). All measurements at the two vegetation plots were combined and averaged for each bird point count station. We used a relative index of *Tamarix*, herein defined as the total number of *Tamarix* stems counted within the plot divided by the total number of all stems in

that plot, as our general measure of native/*Tamarix* vegetation composition.

Data Analyses

We used actual point count data for all analyses. To assure that the use of raw count data did not bias our findings, we used the Multiple Covariate Distance Sampling engine in the program DISTANCE (Buckland et al. 2004) to determine if detection probability varied with the relative index of *Tamarix*. We computed distance functions using the relative index of *Tamarix* as a linear covariate for groups of birds (wintering, resident, migrant, and breeding birds) and used Akaike's information criterion (AIC) to guide model selection (Buckland et al. 2001). Specifically, we first used AIC to select the best key function plus expansion term for the covariate model and then compared this best covariate model with a similar noncovariate model.

We used backward elimination, combined with partial residual plots (Ramsey & Shafer 2002), to identify vegetation parameters that were important in explaining variation in avian abundance at point count stations. First, focusing only on the Bill Williams data, we conducted backward elimination where variables with $p > 0.15$ were removed from the model and obtained a model that contained *Tamarix* and canopy height as significant predictors of avian abundance (regression model: $y = -0.02 \times$ relative index of *Tamarix* $+ 0.07 \times$ canopy height). Then, to investigate the relationship between our relative index of *Tamarix* and avian abundance, after controlling for the effects of canopy height, we created a partial residual plot in which we plotted the partial residuals of avian abundance adjusted for and as a function of canopy height. To compute the partial residual (pres), we used the formula, pres = res + $\beta \times$ pertam, where res = residual from linear fit of *Tamarix*, β = estimated slope parameter of *Tamarix* from the previous regression analysis, and pertam = value of *Tamarix* for the given observation (Ramsey & Shafer 2002, chapter 11). Because the partial residual plot showed a similar threshold pattern, in all further analyses, we focused on the relationship between the relative index of *Tamarix* and the avian guilds. We then used linear regression to explore relationships between *Tamarix* vegetation and avian abundance, species richness, and diversity (Shannon Diversity Index). Models were selected that maximized adjusted R^2, minimized pooled variance, and had residual plots that met assumptions for linear regression. The total number of detections for all visits at each point count station, adjusted for effort, was used as the response variable, whereas the relative index of *Tamarix* (total number of *Tamarix* stems/by all stems) was used as our predictor variable.

Associations of birds with vegetation parameters can vary depending upon the ecological and energetic demands associated with different stages of the avian annual cycle. Therefore, we categorized birds into temporal guilds based on the longest period of time during their annual cycle that was spent at our study areas. This categorization was based on Rosenberg et al. (1991) and Skagen et al. (2005) and was done to determine how birds in these temporal guilds responded to different relative amounts of *Tamarix*. Birds were categorized as resident (nonmigratory birds residing year round on the lower Colorado River), breeding (birds residing on the lower Colorado River only during the breeding season), neotropical migrants (migratory birds using the lower Colorado River only as stopover habitat while migrating), or wintering (birds residing on the lower Colorado River only during the winter season).

Global nonmetric multidimensional scaling (GNMDS), with the program DECODA (Minchin 1987*a*, 1987*b*), was used to examine effects of a relative index of *Tamarix* levels on the composition of avian communities at both study sites. The application of GNMDS to examine patterns of community composition has been used as an acceptable method for numerous animal (e.g., Dungey et al. 2000; Bailey & Whitham 2002) and plant (e.g., Foster & Tilman 2000) studies. This analysis considers both abundance and species richness, arranging samples in ordination space based on a dissimilarity matrix created using the Bray–Curtis dissimilarity coefficient (Faith et al. 1987). For our study, samples were point count stations and the dissimilarity matrix was based on avian species richness and abundance, where abundance was standardized to unit maxima to equalize the influence of common and rare species (McCune & Grace 2002). Point count stations were also categorized by relative amounts of *Tamarix* (0–33%, 34–67%, and 68–100%) to determine if there were potential differences in the composition of avian communities relative to different levels of *Tamarix* using an analysis of similarity (ANOSIM) test (Minchin 1987*a*, 1987*b*; Warwick et al. 1990). A vector-fitting procedure in DECODA was used to determine how the composition of avian communities at individual point count stations was structured with relation to the relative index of *Tamarix*. Vector fitting is a method that shows relationships between the environmental variables and the ordination pattern, by maximizing linear correlation between the environmental variable and the ordination axes (Kantvilas & Minchin 1989). Vector fitting in DECODA is equivalent to regressing the environmental variable against the set of ordination axes (Dickinson & Mark 1999).

Finally, to determine how individual bird species were associated with different levels of *Tamarix*, the same GNMDS vector-fitting procedure was applied only to the Bill Williams NWR data. Because the dissimilarity matrix of GNMDS is based on overall bird species richness and abundance at different point count stations, the resulting vector direction indicates how strongly that individual bird species is related to *Tamarix* abundance.

Results

We only included point count detections that were observed at less than or equal to 70 m because models generated in the program DISTANCE indicated that at

beyond 70 m, the probability of detection was less than 0.1 (Buckland et al. 2001). We also found that detection probability did not vary with the amount of *Tamarix*, as the results of our covariate analysis revealed that covariate models were not better supported than were noncovariate models for all four groups of birds (Table 2). Therefore, we used raw count data in all subsequent analyses.

During our study, we documented 85 bird species at Cibola NWR and 67 species at Bill Williams River NWR. Many species had a single detection, so to reduce variance in our community dataset and to enhance the detection of relationships between the community composition and the environmental variables (McCune & Grace 2002), we deleted rare bird species that comprised less than 1% of total observations. This resulted in the inclusion of 60 of 85 bird species detected at Cibola NWR and 47 of 67 bird species detected at Bill Williams River NWR (Table 3).

At Cibola NWR, where there are essentially only pure native and *Tamarix* habitat extremes, there was a dramatic difference in bird numbers (and species diversity) when comparing *Tamarix* with native vegetation–dominated habitats ($R^2 = 0.64$, $p = 0.0002$; Fig. 2A).

At Bill Williams River NWR, where a much wider spectrum of native/*Tamarix* habitat mixes occur, our results were quite different than at Cibola NWR. We found that overall avian abundance did not show a direct linear response relative to the relative index of *Tamarix*, but instead a quadratic relationship (Fig. 2B). There appeared to be a response threshold reached when native vegetation composed between 20 and 40% of the habitat. In fact, when all bird species were pooled, the highest bird abundance was at intermediate *Tamarix* levels ($R^2 = 0.74$, $p = 0.0007$). The same pattern also occurred with richness ($R^2 = 0.48$, $p = 0.03$) but not overall bird diversity ($R^2 = 0.05$, $p = 0.08$).

We documented variations in the patterns of response among the different avian guilds to different *Tamarix* levels indicating that birds at different stages of their annual cycle respond differently to variations in *Tamarix* abundance. At Cibola NWR, where only habitat extremes exist, there was a strong negative linear relationship of bird numbers to high *Tamarix* levels (Fig. 3). The strongest relationship was with resident birds ($R^2 = 0.82$, $p = 0.0001$; Fig. 3A), followed by breeding birds ($R^2 = 0.55$, $p = 0.001$; Fig. 3B), and then neotropical migrants ($R^2 = 0.47$, $p = 0.0036$; Fig. 3C). At Bill Williams River NWR, we found a much different pattern for overall avian abundance with resident birds ($R^2 = 0.40$, $p = 0.02$; Fig. 4A), breeding birds ($R^2 = 0.68$, $p = 0.002$; Fig. 4B), and neotropical migrant birds ($R^2 = 0.41$, $p = 0.05$; Fig. 4C) all having equal or higher abundances at intermediate *Tamarix* levels. Wintering avian abundances were not significantly related to the relative index of *Tamarix* within the habitat at either Cibola NWR ($R^2 = 0.05$, $p = 0.39$; Fig. 3 D) or Bill Williams River NWR ($R^2 = 0.05$, $p = 0.11$; Fig. 4D).

As with bottomland plant communities throughout the world, and particularly in the southwestern United States, native plant composition varies among sites and avian community composition does change with those differences. When examining the relationship of overall avian abundance to relative indices of individual tree species composition at both of our study sites, the relative index of *Tamarix* showed the strongest relationship to bird numbers. At Cibola NWR, the r^2 value for *Tamarix* was 0.64, for Cottonwood was 0.54, for Willow was 0.26, and for mesquite was 0.50. At Bill Williams River NWR, the r^2 value for *Tamarix* was 0.63, for Cottonwood was 0.23, for Willow was 0.56, and for was mesquite 0.05.

When examining the relationship between the avian species and the relative index of *Tamarix* at the community level, a two-dimensional solution was chosen as the best representation of the dissimilarity matrix between the point count stations based on the inspection of stress levels (McCune & Grace 2002). Avian community structure at Cibola and Bill Williams River NWR differed significantly at different relative indices of *Tamarix* (Fig. 5). At both sites, we found a significantly high degree of avian community structure within our GNMDS ordination indicating a strong relationship to the amount of *Tamarix* found at individual point count stations (vector results:

Table 2. Relationship between the ability to detect birds within four avian guilds and relative index of *Tamarix* at a location within Bill Williams River NWR, Arizona.

Temporal Guilds	*Key Function + Series Expansion*	*AIC*	*P*	*P LCL*	*P UCL*
Resident	Hazard + cosine no covariate	8137.68	0.45	0.40	0.50
	Hazard + cosine covariate	8139.92	0.47	0.45	0.48
Breeding	Half normal + cosine no covariate	1335.89	0.5	0.46	0.54
	Half normal + cosine covariate	1335.98	0.5	0.43	0.58
Wintering	Half normal + cosine no covariate	1894.37	0.22	0.21	0.24
	Half normal + cosine covariate	1896.06	0.22	0.21	0.24
Neotropical migrant	Hazard + cosine no covariate	770.09	0.11	0.08	0.16
	Hazard + cosine covariate	775.3	0.13	0.10	0.16

All avian censuses were conducted between 1998 and 2002 using the variable circular plot technique. Results are from analysis with the program DISTANCE, with competing models compared (covariate/no covariate) for each temporal guild. Shown are AIC values, probability of detection (*P*), along with lower (*P* LCL) and upper (*P* UCL) 95% confidence intervals for the estimate of *P*. LCL = lower confidence limits; UCL = upper confidence limits.

Table 3. Species detected at point count stations during 1998–2002 at Bill Williams River NWR.

Species	*Alpha Code*	*Number of Detections*	*Percent of Total within Temporal Guild*	*Temporal Guild*	*Vector Results*	
					r	*p*
Bell's Vireo	BEVI	226	19.0	B	0.76	0.01
Blue Grosbeak	BLGR	39	3.3	B	0.90	0.002
Bullock's Oriole	BUOR	73	6.1	B	0.68	0.05
Lucy's Warbler	LUWA	346	29.1	B	n.s.	
Summer Tanager	SUTA	108	9.1	B	0.73	0.04
Western Kingbird	WEKI	7	0.6	B	n.s.	
White-winged Dove	WWDO	164	13.8	B	n.s.	
Yellow-breasted Chat	YBCH	205	17.2	B	n.s.	
Yellow Warbler	YWAR	23	1.9	B	n.s.	
Black-throated Gray Warbler	BTYW	7	4.1	M	n.s.	
Hermit Warbler	HEWA	2	1.2	M	n.s.	
MacGillivray's Warbler	MGWA	10	5.9	M	n.s.	
Nashville Warbler	NAWA	17	10.0	M	n.s.	
Townsend's Warbler	TOWA	3	1.8	M	n.s.	
Warbling Vireo	WAVI	18	10.6	M	0.83	0.03
Western Flycatcher	WEFL	37	21.8	M	0.75	0.03
Western Tanager	WETA	24	14.1	M	n.s.	
Wilson's Warbler	WIWA	52	30.6	M	n.s.	
Abert's Towhee	ABTO	356	10.0	R	0.60	0.05
Ash-throated Flycatcher	ATFL	167	4.7	R	0.80	0.005
Bewick's Wren	BEWR	448	12.6	R	n.s.	
Black Phoebe	BLPH	70	2.0	R	n.s.	
Black-tailed Gnatcatcher	BTGN	37	1.0	R	n.s.	
Cactus Wren	CACW	17	0.5	R	n.s.	
Canyon Wren	CANW	132	3.7	R	0.65	0.03
Common Yellowthroat	COYE	236	6.6	R	0.80	0.002
Crissal Thrasher	CRTH	14	0.4	R	n.s.	
Gambel's Quail	GAQU	198	5.6	R	0.70	0.03
Gila Woodpecker	GIWO	405	11.4	R	0.70	0.03
Great-tailed Grackle	GTGR	44	1.2	R	n.s.	
House Finch	HOFI	194	5.5	R	n.s.	
Ladder-backed Woodpecker	LBWO	195	5.5	R	n.s.	
Lesser Goldfinch	LEGO	109	3.1	R	n.s.	
Mourning Dove	MODO	115	3.2	R	n.s.	
Red-shafted Flicker	RSFL	112	3.2	R	n.s.	
Say's Phoebe	SAPH	65	1.8	R	0.86	0.005
Song Sparrow	SOSP	453	12.8	R	0.82	0.005
Verdin	VERD	184	5.2	R	0.77	0.004
American Robin	AMRO	13	2.0	W	n.s.	
Audubon's Warbler	AUWA	59	9.0	W	n.s.	
Blue-gray Gnatcatcher	BGGN	42	6.4	W	n.s.	
Chipping Sparrow	CHSP	14	2.1	W	n.s.	
Orange-crowned Warbler	OCWA	91	13.9	W	n.s.	
Ruby-crowned Kinglet	RCKI	181	27.5	W	0.64	0.05
Red-naped Sapsucker	RNSA	14	2.1	W	0.90	0.01
Unknown Yellow-rumped Warbler	UYRW	167	25.4	W	n.s.	
White-crowned Sparrow	WCSP	76	11.6	W	n.s.	

Alpha codes refer to American Ornithological Union (AOU 1998) designation. Temporal guilds: R, resident; W, wintering; B, breeding; and M, neotropical migrant. Vector results are from the Figure 5 GNMDS analyses.

Cibola: $r = 0.82$, $p < 0.0001$; Bill Williams: $r = 0.88$, $p < 0.0001$). Avian community structure was significantly different between *Tamarix*- and native-dominated habitats at Cibola NWR (Fig. 5A, ANOSIM: $r = 0.51$, $p = 0.01$). However, when we examined community structure across a gradient of *Tamarix* abundance at the Bill Williams River NWR, we found that avian communities associated with low and intermediate levels of *Tamarix* did not differ, whereas both differed significantly from avian communities associated with high *Tamarix* levels (Fig. 5B, ANOSIM: $r = 0.52$, $p = 0.003$; Table 4). Thus, habitats with low and intermediate levels of *Tamarix* support similar avian communities, but contrast markedly to avian communities associated with higher *Tamarix* levels.

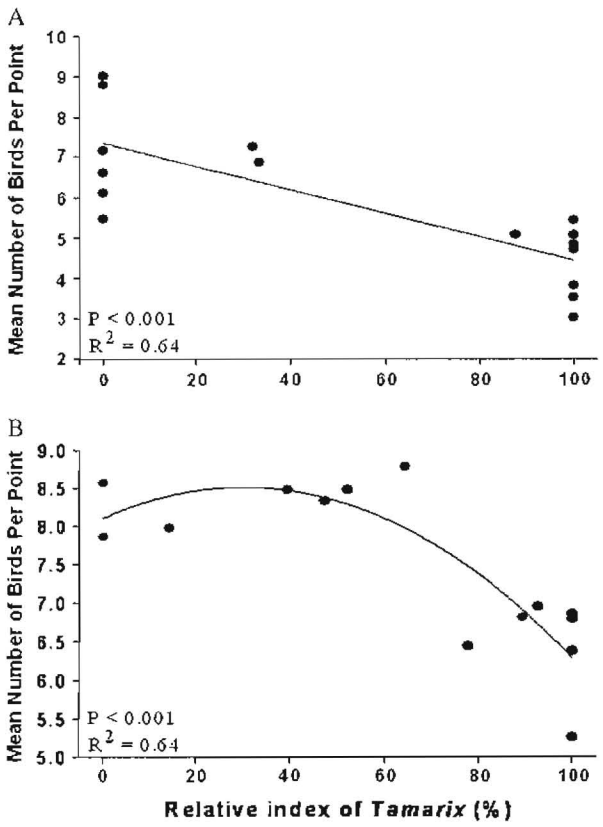

Figure 2. Relationship between mean number of birds counted per census point and vegetation composition at Cibola and Bill Williams River NWR. Birds were counted from 1998 to 2002; vegetation was measured in early 1999. The horizontal axis is a relative index (in %) of *Tamarix*, which is the total number of *Tamarix* stems divided by all stems counted at breast height at each sampling station. The vertical axis is the actual mean number of birds counted at each station (n = 3,889 at Cibola and n = 4,654 total birds counted at Bill Williams River NWR).

Of the 47 avian species vectored within the GNMDS ordination for the Bill Williams River NWR, we chose to examine the relationship of the 17 species that were significantly more abundant at different levels of *Tamarix* (Fig. 6). Most of the 17 species were negatively associated with *Tamarix*. Some, like Bullock's Oriole and Common Yellowthroat, were consistently found at highest abundances in sites with the lowest *Tamarix* levels. Other species, like the Blue Grosbeak and Say's Phoebe, were found in greater abundance at sites with increased *Tamarix*. We found no significant positive or negative *Tamarix* associations in any of the other 30 bird species.

Discussion

Our results suggest that when restoring riparian habitat for birds in southwest North America, a complete removal of *Tamarix* might not always be the most beneficial restoration technique. We found an avian response threshold in *Tamarix*-dominated habitat, characterized by a dramatic increase in bird numbers when native vegetation reached between 20 and 40%. From a restoration perspective, it is at this vegetation composition level where one can achieve the greatest benefit to avian abundance and diversity. Birds continued to respond positively with increasing amounts of native vegetation (up to about 60%) but did not increase in numbers beyond this point. Mixes of native and *Tamarix* vegetation consistently supported higher abundances of avian species. Thus, when avian abundances are viewed across habitats with different relative amounts of *Tamarix*, there was not the simple negative linear relationship that occurred at Cibola NWR, but instead nonlinearity at the species, guild, and overall avian community levels. The results from Cibola are similar to the earlier findings of Anderson and Ohmart (1977) and Kelly and Finch (1999), who demonstrated a linear relationship between bird abundance and amount of *Tamarix*, with native habitat being more beneficial to birds than was *Tamarix*.

There are two factors that we believe contribute to our observed threshold pattern. First, within habitats of intermediate *Tamarix* levels, there is a more complex vegetation structure than at habitat extremes. *Tamarix* vegetation adds complexity by providing an understory to mature native riparian areas, thus increasing plant and stem densities within the lower vegetation strata. Simply, a more complex vegetation structure increases avian species diversity (MacArthur 1964; Shugart & James 1973; Wiens 1989). This is a common pattern found throughout the world (e.g., Dean et al. 2002) and particularly in the North American Southwest (Rice et al. 1984; Anderson et al. 2004), where foliage profile characteristics are an important component of habitat selection for birds. Even in Hawaii, where native birds are quite specialized, numerous introduced plant species provide a more complex vegetation structure and contribute additional food resources (Scott et al. 2001). The second possible factor contributing to this threshold response is the enhancement of food availability, another important factor in avian habitat selection (Hutto 1985). Many studies indicate that *Tamarix*-dominated habitats overall harbor a lower arthropod abundance than native plant species but that they do support a unique arthropod community including many species in the leafhopper family (Stevens 1985; Yard et al. 2004). Yet, in the summer, insect biomass of *Tamarix* habitats is often found to be greater than any other riparian plant community due to high flower numbers and insect pollinators that they attract (Cohan et al. 1978). The incorporation of a *Tamarix* component into native habitats could thus increase the overall biomass and diversity of arthropods.

This hypothesis agrees with research in Arizona where Drost et al. (2003), Anderson et al. (2004), and McGrath and van Riper (2005) found that mixed native and *Tamarix* habitats had a higher abundance of arthropods than

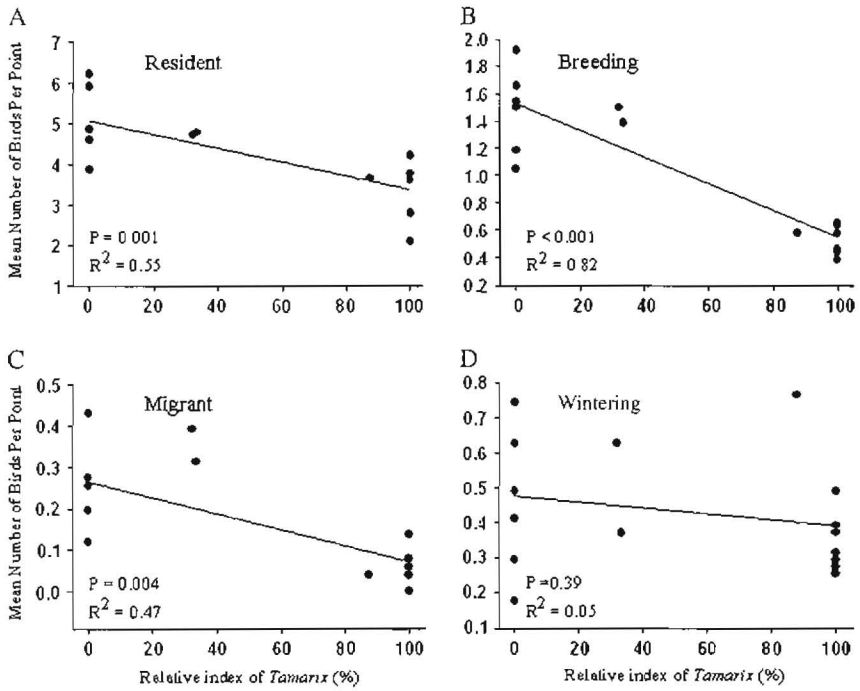

Figure 3. Relationship between mean number of birds by temporal avian guild and the relative index of *Tamarix* at Cibola NWR. Guilds include (A) resident birds, (B) breeding birds, (C) migrant birds, and (D) wintering birds.

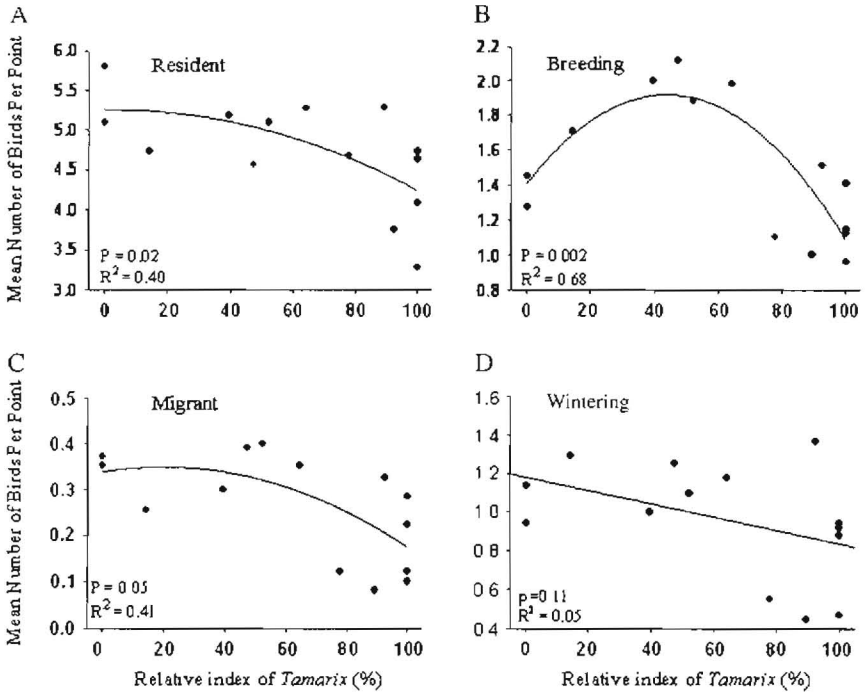

Figure 4. Relationship of mean bird numbers within different avian guilds to different *Tamarix* levels at Bill Williams River NWR. Guilds include (A) resident birds, (B) breeding birds, (C) migrant birds, and (D) wintering birds.

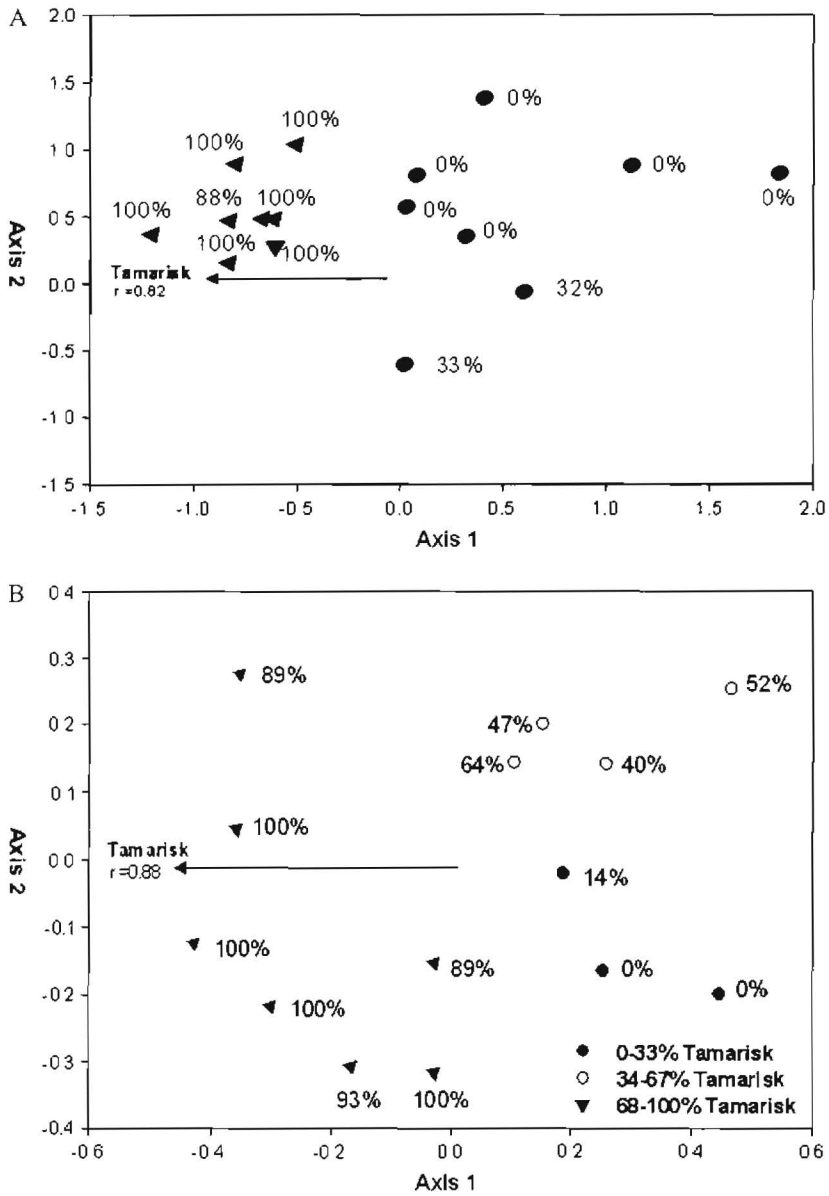

Figure 5. GNMDS showing avian community composition at (A) Cibola and (B) Bill Williams River NWR in response to *Tamarix* abundance from 1998 to 2002. The orientation of the GNMDS figure was rotated so that the *Tamarix* vector is perpendicular with the x-axis, and thus, the x-axis relates to the amount of *Tamarix*. *Tamarix* vector analysis shows that differences in avian community composition were correlated with *Tamarix* levels at point count stations. Numbers next to the point count stations indicate the relative index of *Tamarix*, which is the total number of *Tamarix* stems divided by all stems counted at breast height at each sampling station. (A) At Cibola NWR, the community composition of avian species was significantly different between the two habitat types present (ANOSIM: $p = 0.01$, $r = 0.51$). (B) At Bill Williams River, low and intermediate levels of *Tamarix* avian communities did not differ, but both communities differed significantly from those associated with high *Tamarix* levels (see Table 2 for ANOSIM results).

did homogenous native or *Tamarix*-dominated habitats. More study of arthropod communities and avian diets is needed within southwestern U.S. mixed riparian habitats to determine if this pattern is consistent throughout the region.

Habitat selection by avian species varies seasonally as energetic demands and habitat requirements change with differing phases of the annual cycle (Rice et al. 1980; Weathers 1983). When we examined temporal bird guilds, breeding, resident, and neotropical migrant birds all exhibited an overall pattern of equal or highest abundances at intermediate *Tamarix* levels. Breeding birds exhibited the strongest response toward intermediate *Tamarix* levels, with lower abundances in homogenous

Table 4. Results of ANOSIM comparing the composition of avian communities from 1998 to 2002 at Bill Williams River NWR.

	34–67% Tamarix		*68–100% Tamarix*	
Treatment	*r*	*p*	*r*	*p*
0–33% *Tamarix*	0.35	0.09	0.60	0.008
34–67% *Tamarix*			0.67	0.006
Overall ANOSIM, $r = 0.52$, $p = 0.003$				

The analysis was done by comparing all point count stations, categorized by levels of *Tamarix* (0–33%, 34–67%, and 68–100%), to determine potential differences in the composition of avian communities relative to different *Tamarix* levels

Tamarix- and native-dominated habitats. The strong predilection of breeding birds for mixed native and *Tamarix* habitats further supports the concept that habitats with intermediate levels of *Tamarix* (thus with increased vegetation structure) provides suitable habitat that meets avian breeding requirements.

Breeding and the wintering cycles strongly influence habitat selection for resident birds, and thus, overall avian habitat selection should express a compromise between the competing demands of both life stages (Greenberg & Marra 2005). This is what we found when examining resident bird abundances in relation to the amount of *Tamarix* in the habitat, where greater resident bird numbers occur with an increasing native vegetation component. Neotropical migrant birds use riparian habitat in the southwest for short periods of time to refuel, rest, and be sheltered (Skagen et al. 1998; Finch & Yong 2000; Paxton et al. 2007). Even during this short time period, we see a response to the relative amount of *Tamarix* found in the habitat, thus suggesting that there are intense selection pressures to find large quantities of food to sustain further migration.

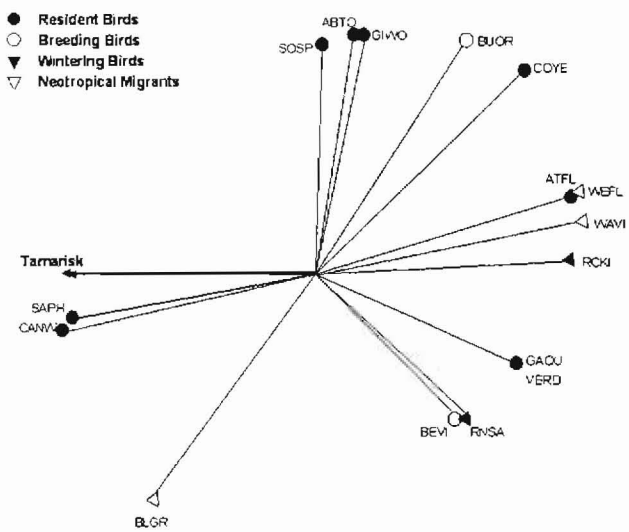

Figure 6. GNMDS vector analysis of resident, breeding, wintering, and neotropical migrant bird species in vegetation communities within Bill Williams River NWR during 1998–2002. Symbols represent the endpoint of the vector and identify particular bird species' response to *Tamarix*-dominated habitat (see Table 3 for an explanation of the bird species' four-letter alpha code).

Wintering birds on the lower Colorado River were the one group that did not show a significant relationship with the amount of *Tamarix* in the habitat. This is consistent with other studies that have shown that many wintering bird populations along the lower Colorado River are not strongly associated with vegetation structure but instead are found where habitat provides an abundant food source of fruit and seeds (Anderson & Ohmart 1977; Rice et al. 1980; Hunter et al. 1988; Anderson et al. 2004).

Finally, consistent with our threshold model, an analysis of lower Colorado River birds demonstrates a significant relationship between the avian community structure and the relative amounts of *Tamarix* found in a habitat. Three lines of evidence support this relationship. First, our vector analysis revealed a significant correlation between the amount of *Tamarix* in the habitat and the configuration of avian communities, where habitats with low and intermediate levels of *Tamarix* supported similar avian communities, but contrasted markedly with bird species associated with higher *Tamarix* levels. Second, point count stations with low and intermediate levels of *Tamarix* supported similar avian communities, although these differed significantly from point count stations with greater amounts of *Tamarix*. Third, we found that individual avian species in multiple guilds discriminated among the relative amounts of *Tamarix* in the habitat. Because our analysis treated all bird species the same (i.e., common birds were not weighted more than rare species), these patterns were not driven by a few common species but do represent overall community patterns.

In this study, our experimental design limited us to combining all native tree species when analyzing the relationship between vegetation composition and avian abundance. However, we recognize that birds probably do not respond to native trees as a group but differentially prefer specific tree species. This is especially true during times of flowering and fruiting. For example, McGrath and van Riper (2005) found that flowering Honey mesquite was a preferred foraging substrate within a matrix of native and exotic vegetation. Future studies are needed that identify avian responses to species-specific substrates in riparian habitats on the lower Colorado River.

Restoration Management Implications

Within the past century, riparian ecosystems throughout the world have been drastically reduced (van Andel & Aronson 2006). This has been particularly true in southwestern North America, where the reduction has been coupled with a shift in vegetation composition from native- to *Tamarix*-dominated habitats (Shafroth et al. 2005). As restoration policies are developed and riparian

ecosystems reclaimed, it is important that we understand how avian communities will respond to that restoration. Past research in the southwestern United States that stressed the significance of dominant vegetation (Anderson & Ohmart 1977), or that focused only on bird communities within habitat extremes (as in our Cibola study area), has greatly influenced current *Tamarix* restoration policy. This has placed a focus on large-scaled efforts that often involve completely clearing large patches of *Tamarix*, then laser leveling land for flood irrigation, with a cost from $1,400 to $1,700/ha (e.g., McDaniel & Taylor 2003). Although these restoration efforts do provide valuable habitat for wildlife, constraints such as manpower, logistics, adequate water, and financial resources often restrict the total amount of *Tamarix*-dominated habitat that can be treated and restored. On the lower Colorado River, there presently exists more than 16,000 ha of pure tamarisk habitat (Anderson et al. 2004) and throughout the West more than 600,000 ha (Shafroth et al. 2005). In the, especially, heavily managed lower Colorado River corridor, where extant riparian habitat is comprised of more than 80% *Tamarix* (Ohmart et al. 1988; Anderson et al. 2004), complete eradication of *Tamarix* would be prohibitively expensive, and as such may not be realistic. Therefore, even these large-scale projects will have minimal impact on the overall reduction of *Tamarix* within southwestern U.S. riparian systems.

Our study, which examined bird communities across gradients of *Tamarix* and native vegetation mixes, found that a relatively small amount of native vegetation within *Tamarix*-dominated sites has a disproportionately positive impact on avian abundance and diversity. We suggest that, where restoration is focused on improving habitat for avian species, by adding an additional restoration strategy of increasing native vegetation by 20–40%, land managers will be provided an option that allows for a much larger area to be treated for a reduced cost per unit of restored habitat. Our proposed restoration strategy could be used in concert with the present larger scaled *Tamarix* conversion efforts. Together, both strategies would restore the greatest amount of riparian habitat, ultimately resulting in achieving a maximum of avian abundance and diversity.

The results of our study on the lower Colorado River point out the importance of examining avian communities across the entire gradient of tree species composition to adequately assess potential impacts of invasive species and restoration practices. It is critical that research conducted within other riparian systems throughout the world, and in the southwestern United States, begins to examine avian community responses at multiple levels of introduced and native vegetation and not just habitat extremes. Additionally, many riparian areas (e.g., Australia, Asia, United States, and South Africa) have similar tree species but are individually dynamic systems that vary in species composition, environmental conditions, climate patterns, and elevation all of which ultimately affect avian community structure (Hunter et al. 1988; Dean et al. 2002; van Andel & Aronson 2006). It is important in riparian vegetation restoration efforts throughout the world that managers incorporate information from the entire vegetation gradient, so as to assure a better understanding of avian species needs within those ecosystems.

Implications for Practice

- The results of our study point out the importance of examining avian communities across the entire gradient of introduced and native vegetation species composition to adequately assess invasive plant species habitat restoration.
- On the lower Colorado River in southwestern North America, we found that relatively small amounts of native vegetation within introduced *Tamarix*-dominated sites had a disproportionately positive impact on avian abundance and diversity.
- In southwestern North America, a complete removal of *Tamarix* might not always be the most beneficial restoration technique when restoring riparian habitat for birds.
- There is an avian response threshold in *Tamarix*-dominated habitat, characterized by a dramatic increase in bird numbers when native vegetation reached between 20 and 40%.
- A restoration strategy of adding 20–40% native vegetation could be used in concert with the present larger scaled *Tamarix* conversion efforts and together both strategies would ultimately result in achieving a maximum of avian abundance and diversity in southwestern North America.
- It should be recognized that in some locations, introduced vegetation could provide increased vertical plant diversity and additional food resources that could benefit bird species.

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