RESEARCH ARTICLE

Effects of *Tamarix* removal on the community dynamics of riparian birds in a semiarid grassland

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Invasion of riparian habitats by non-native plants is a global problem that requires an understanding of community-level responses by native plants and animals. In the Great Plains, resource managers have initiated efforts to control the eastward incursion of *Tamarix* as a non-native bottomland plant (*Tamarix ramosissima*) along the Cimarron River in southwestern Kansas, United States. To understand how native avifauna interact with non-native plants, we studied the effects of *Tamarix* removal on riparian bird communities. We compared avian site occupancy of three foraging guilds, abundance of four nesting guilds, and assessed community dynamics with dynamic, multiseason occupancy models across three replicated treatments. Community parameters were estimated for *Tamarix*-dominated sites (untreated), *Tamarix*-removal sites (treated), and reference sites with native cottonwood sites (*Populus deltoides*). Estimates of initial occupancy (ψ_{2006}) for the ground-to-shrub foraging guild tended to be highest at *Tamarix*-dominated sites, while initial occupancy of the upper-canopy foraging and mid-canopy foraging guilds were highest in the treated and reference sites, respectively. Estimates of relative abundance for four nesting guilds indicated that the reference habitat supported the highest relative abundance of birds overall, although the untreated habitat had higher abundance of shrub-nesters than treated or reference habitats. Riparian sites where invasive *Tamarix* is dominant in the Great Plains can provide nesting habitat for some native bird species, with avian abundance and diversity that are comparable to remnant riparian sites with native vegetation. Moreover, presence of some native vegetation in *Tamarix*-dominated and *Tamarix*-removal sites may increase abundance of riparian birds such as cavity-nesters. Overall, our study demonstrates that *Tamarix* may substitute for native flora in providing nesting habitat for riparian birds at the eastern edge of its North American range.

Key words: Great Plains, invasive bottomland plants, land management, occupancy, relative abundance, salt cedar

Implications for Practice

- The invasive tree-shrub *Tamarix ramosissima* has increased in abundance along riparian corridors in the Great Plains as range expansion continues eastward.
- Specific guilds of birds varied in site occupancy and abundance among untreated sites dominated by *Tamarix*, sites where *Tamarix* was removed, and remnant riparian habitat.
- Effects of *Tamarix* removal are guild-specific and may reduce overall diversity and abundance of riparian birds.
- Sites without stands of cottonwoods had lower abundance, lower species richness of cavity-nesters, and were not near an equilibrium level of occupancy.
- Complete removal of *Tamarix* might not be the most beneficial technique of restoring habitat for some bird species, but presence of native trees can mitigate the impact of complete removal of *Tamarix* for riparian bird communities.

Introduction

Expanding populations of non-native plant species around the world are receiving increasing attention from land managers, stakeholders, and conservation organizations. In the United States, thousands of exotic plants have become established and numbers are expected to increase. When non-native plants become highly invasive and cause major ecological changes to landscapes and ecosystems, native species of wildlife can be negatively impacted (Catling 2005). Consequently, many ecological restoration programs focus efforts on elimination or control of non-native plants without knowledge of their potential impacts on native species of wildlife (Zavaleta et al. 2001; Shafroth & Briggs 2008). Postrestoration evaluations of bird communities indicate results of control efforts can range from negative to positive depending on the exotic plant, bird species, and ecosystem responses (Davis et al. 2011; Sogge et al. 2013).

In the southwestern United States, studies on the effects of introduced tamarisk (*Tamarix* spp., or salt cedar) on wildlife have highlighted how the "native good, alien bad" paradigm oversimplifies the realities and complexities of the interactions between non-native flora and native fauna (Goodenough 2010). *Tamarix* spp. are Eurasian phreatophyte tree-shrubs that can grow along rivers with regulated water flow where native riparian trees cannot persist (Shafroth & Briggs 2008). The introduced plant has an expanding distribution into riparian ecosystems east of the Rocky Mountains (Jarnevich et al. 2013), and has become the focus of concerted eradication efforts in western North America over the last several decades that have recently been questioned by many scientists, land managers, and the public (Shafroth et al. 2005; Hultine et al. 2009; Sogge et al. 2013).

As native riparian habitat declined in western North America, the spread of *Tamarix* occurred concurrently, leading to the portrayal of tamarisk as a key factor in the reduction of riparian breeding bird numbers (Kunzmann et al. 1989; DeLoach et al. 2000). Through the 1980s and 1990s, *Tamarix* habitat was viewed as undesirable, despite several studies showing extensive use of the introduced plant by native birds. Brown and Carothers (1987), Hunter et al. (1988), and Rosenberg et al. (1991) demonstrated that *Tamarix* habitat along major river systems in New Mexico, Arizona, and Colorado supported larger local and regional bird populations for some species than would have occurred if non-native vegetation was absent. In the 1990s, growing evidence suggested a positive value of *Tamarix* habitat for bird diversity and abundance in southwestern rivers of North America (Livingston & Schemnitz 1996; Sogge et al. 1997). For example, Sogge et al. (1997) found that the federally endangered Southwestern Willow Flycatcher (*Empidonax trailli extimus*) was using *Tamarix* for breeding and migration stopover habitat. Willow Flycatcher favor nesting in dense tamarisk even if native willow is available nearby (Ellis et al. 2008; Sogge et al. 2010); and nest success and survivorship of adults breeding or young fledged within tamarisk do not differ between the two habitats (Paxton et al. 2007; Ellis et al. 2008). Over the next decade, studies showed that diverse riparian bird communities exist in *Tamarix* habitat across the arid southwestern United States, where at least 49 different species of birds have been documented as breeding in tamarisk (Sogge et al. 2008; Paxton et al. 2011).

Recent studies of the responses by bird communities to tamarisk have demonstrated that negative impacts by tamarisk cannot be universally assumed; rather, evaluation of impacts should be conducted with attention to factors that vary geographically (Sogge et al. 2008, 2013). For example, when compared to native woody riparian vegetation, *Tamarix*-dominated habitat contributed few unique species to regional avian diversity along the San Pedro River in southeastern Arizona, which is one of the last free-flowing rivers in the southwestern United States (Brand et al. 2008). Moreover, Hinojosa-Huerta (2006) found that dry, native vegetation sites had greater avian abundance and species richness than dry *Tamarix* sites, while abundance and richness at wet, native versus wet, *Tamarix* sites were not different at the Colorado River delta in Mexico. Most studies on *Tamarix*-wildlife relationships in North America are conducted on river systems with an altered hydrologic regime; thus, Brand et al. (2008) and Hinojosa-Huerta (2006) revealed that surface water availability as well as size of the habitat are potentially confounding factors that add to the complexity for understanding the potential effects of non-native *Tamarix* on birds in riparian systems.

Use of *Tamarix* habitat by birds in southwestern U.S. river systems is not limited to the breeding season. Studies of enroute migrant songbird use of *Tamarix* habitat along the lower Colorado River have shown that migrants prefer mixed native and tamarisk riparian habitat over pure native or tamarisk riparian habitats (Van Riper et al. 2008). In addition, mixed tamarisk-native riparian habitat has been shown to offer superior refueling habitat for an insectivorous migrant, Wilson's Warbler (*Wilsonia pusilla*; Cerasale & Guglielmo 2010). On the other hand, Fischer et al. (2015) showed migrant use of hydrologically altered shrub-dominated habitats was minimal in pure *Tamarix* habitat but quickly increased with native shrub cover. The latter study was unique in that the survey transects were placed in hydrologically altered shrub-dominated floodplain habitat and not in cottonwood-willow [*Populus-Salix*] floodplain habitat that was historically more typical of southwestern riparian communities (Webb et al. 2007; Van Riper et al. 2008). The examples of migrant bird use of riparian habitats with established *Tamarix* indicate non-native *Tamarix*-native wildlife relationships can be site-dependent. Therefore, investigations of *Tamarix* use by riparian bird communities throughout its non-native range are important to understanding how riparian birds utilize this potential surrogate for native floodplain plants in riparian systems.

An understanding of community dynamics is critical for evaluating the effects of non-native species invasions on biodiversity, and for quantifying the effects of habitat remediation and ecological restoration (Balmford & Bond 2005). Conservation of sensitive species is often focused on habitat restoration to reverse population declines (Schrott et al. 2005). In such situations, knowledge of community responses to habitat invasions is necessary to plan and guide ecological restoration efforts (Adler & Lauenroth 2003; Hansen et al. 2005; Latta et al. 2012). For instance, changes in vegetation structure following *Tamarix* removal are predicted to benefit ground- and cavity-nesting bird species because tree removal creates more open ground for ground-nesters, whereas fewer *Tamarix* shrubs surrounding potential cavity trees could reduce predation risk for cavity-nesters (Aslan & Rejmánek 2010). Thus, additional research is needed to investigate the effects of *Tamarix* eradication on avian guild dynamics and community structure, particularly in areas outside of the American Southwest as *Tamarix* range continues to expand eastward into the Great Plains of North America (Friedman et al. 2005; Lehnhoff et al. 2011).

In this study, we evaluated the community dynamics of songbirds in riparian habitats at a xeric site in southwestern Kansas, United States. We hypothesized the occupancy rates of different foraging guilds and the relative abundance of different nesting guilds would vary by dominant plant community among three replicated treatments: *untreated* sites dominated by *Tamarix*,

treated sites where *Tamarix* was removed, and *reference* sites with intact stands of native cottonwoods. We investigated the potential benefits of passive habitat restoration for bird community dynamics at the Cimarron National Grassland in three ways: (1) we evaluated bird community dynamics in three structurally different habitat types by estimating probabilities of initial community occupancy, colonization, and local extinction, while accounting for imperfect detection; (2) we tested if songbird foraging guild assemblages at sites under different management schemes are changing or at equilibrium; and (3) we tested whether relative abundance of nesting guilds differed among habitat types. Specifically, we compared foraging guild occupancy dynamics and nesting guild abundance as a function of experimental management treatments.

Methods

Study Area

The Cimarron National Grassland (hereafter, Cimarron) is located within Morton and Stevens counties in southwest Kansas, United States (Fig. 1). Cimarron is a 43,725 ha grassland and ranges in elevation from 960 to 1,078 m. Average precipitation is less than 40 cm per year and habitats are primarily of shortgrass and sand-sage prairie. The grassland is divided by the Cimarron River, which has historically not been continuous across southwest Kansas but has typically had ephemeral water flow (Young et al. 2005). To restore the riparian habitat to a native floral condition, land managers with the U.S. Forest Service (USFS) conducted eradication of *Tamarix ramosissima*; hereafter, *Tamarix* in riparian zones at Cimarron by cutting trees at ground level, followed by application of herbicides to discourage resprouting. *Tamarix* removal was completed in May 2005 (W. Fick 2015, Kansas State University, Manhattan, KS, personal communication). Land managers identified nine sites (500×100 m) in the riparian zone with three different management schemes: three *untreated* sites that were dominated by *Tamarix*, three *treated* sites where *Tamarix* was removed, and three *reference* sites with dominant, native stands of cottonwood (Fig. 1). U.S. Forest Service records indicate treated and *Tamarix*-dominated sites historically contained woody vegetation (i.e. scattered willows (*Salix* spp.) and cottonwoods) comparable to current reference sites.

Untreated sites were composed of thick stands of *Tamarix* with an understory mosaic of alkali Sacaton (*Sporobolus airoides*), sand dropseed (*S. cryptandrus*), western ragweed (*Ambrosia psilostachya*), kochia (*Kochia scoparia*), and bare ground (Cable et al. 2015). Treated sites contained dead *Tamarix* trunks with switchgrass (*Panicum virgatum*), western wheatgrass (*Pascopyrum smithii*), tall dropseed (*S. asper*), and numerous forbs, especially sunflowers (*Helianthus* spp.). Reference sites were composed of mature stands of cottonwood, with an understory of moderate grass cover, scattered willows, willow baccharis (*Baccharis salicina*), and various forbs in the herbaceous layer, but few to no *Tamarix*.

Sampling Methods

A single observer (TTC) conducted line-transect surveys to investigate avian species richness and abundance at each of three untreated, treated, and reference sites from 2006 to 2009. Line transects ran parallel to the stream channel for 500 m and were conducted with fixed-width sampling that extended for 50 m on each side of the transect line. Transect lines were spaced at least 300 m apart to ensure independence. A relative index of abundance for each detected species was compiled from raw counts of the number of individuals recorded for each bird species seen or heard within 50 m or on either side of the transect line to limit community analyses to riparian habitat. Line transects are frequently applied in assessment of abundance, distribution patterns, and habitat preference (Bibby 2000). Studies of birds comparing fixed-width versus variable-width line transects have found little difference in results using the two techniques (Westbrooke et al. 2003). We used fixed-width line transects because the sampling method was appropriate for surveying the narrow linear habitats of the riparian zone (Taulman 2013). Transect surveys were conducted between sunrise and 10:00 hours Central Standard Time (CST) from late May to early July, and each 500-m transect took about 20 min to complete. Three transects per habitat type were visited twice throughout the season and visits were at least 2 weeks apart. Dobkin and Rich (1998) found that a single round of surveys missed many birds compared with two-visit sampling in western riparian habitats. Surveys were conducted on days without precipitation or high winds (<15 km/hour). The sequence of transects was rotated randomly by habitat type to control for time of day over the course of the study. To assess community dynamics of songbirds using riparian study sites for breeding, we included birds detected on the survey that were listed as breeding species within a five-county region of southwest Kansas or at the Cimarron National Grassland (Busby & Zimmerman 2001; Cable & Seltman 2011), and censored migratory species not known to breed locally. Survey data were used to assess the effects of habitat management on the community structure and abundance of riparian bird species.

Statistical Analysis

Community-Level Analyses. We used dynamic occupancy models to estimate initial occupancy in the first year of the study (ψ_{2006}), annual colonization (γ), and annual local extinction (ε) probabilities from 2006 to 2009 for the riparian songbird community at Cimarron (MacKenzie et al. 2003). Package "unmarked" in Program R was used to model community occupancy across multiple seasons with the function "colext" (Fiske & Chandler 2011). Most avian surveys have imperfect detection (Sliwinski et al. 2016), and we were interested in estimating the fraction of the regional species pool that was present in each management treatment (Ch. 9, MacKenzie et al. 2006). Initial occupancy (ψ_{2006}) was defined as the probability that a member of the regional species pool was present in 2006. Community colonization probability (γ_t) was the probability that a member of the regional species pool at year t enters/joins the community at year $t + 1$. Local extinction probability (ε_t) was the probability that a member of the regional species pool present at year
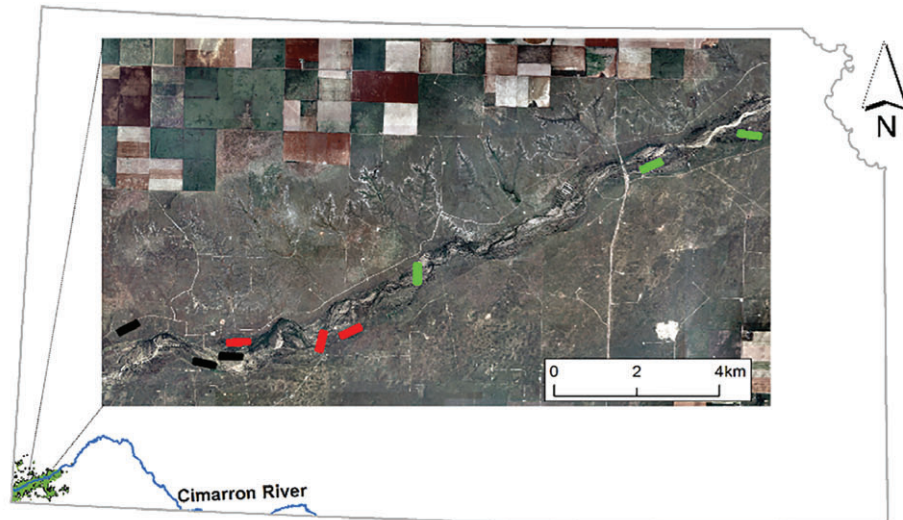
Figure 1. General outline of the Cimarron National Grassland (green), Morton and Stevens counties, Kansas, United States, with inset containing locations of untreated (red), treated (black), and reference (green) transects. Treatment types along Cimarron River included *Tamarix*-dominated, *Tamarix*-removal, and reference sites with cottonwoods at the Cimarron National Grassland in southwestern Kansas from 2006 to 2009.

t was no longer present at year *t* + 1. Our approach for unconditional modeling of dynamic processes, colonization (γ), and local extinction (ε) incorporated a mechanistic process for how the occupancy state of a community may change between seasons, whereas single-season models do not take into account dynamic processes occurring throughout the dataset (MacKenzie et al. 2006).

A detection history was constructed for each species in the regional pool and riparian site, where presence indicated detection of at least one individual of a species during any line-transect survey, and absence indicated that a species was not detected. To separate true absences due to a species not occupying a site versus false absences due to failure to detect a species that was present during a survey (Tyre et al. 2003), we conducted two rounds of surveys during each breeding season. Two rounds of surveys within a 3-week period were used to meet the assumption of population closure; that the occupancy state of a site at the species level does not change within a single season. Here, local colonization and extinctions were allowed between seasons and adjusted for false absences by using repeat surveys within a season where closure is assumed. Local colonization and extinction probabilities were determined based on between-year detection histories, estimated via

likelihood maximization, and the resulting logit-scale parameter estimates were back-transformed for inference (MacKenzie et al. 2006). Candidate models were ranked, compared, and evaluated using Akaike's information criterion with adjustments for over-dispersion and small sample size, $QAIC_c$ (Burnham & Anderson 2013). Model fit was assessed by comparing the observed Pearson χ^2 statistic for the most general model for each species with χ^2 statistics obtained from 5,000 simulated bootstrap datasets to obtain a modified over-dispersion parameter suitable for occupancy models (MacKenzie & Bailey 2004). Over-parameterized models were discarded prior to model selection.

Our approach addresses community integrity by using a model that uses repeated observations of a biological community to estimate community-level attributes constructed from occurrence data of individual species while accounting for imperfect detection (Karr 1990; Cam et al. 2000, 2002*a*, 2002*b*; Dorazio & Royle 2005; MacKenzie et al. 2006). The regional pool of species used in this analysis, *n* = 36 (see Results), were the bird species confirmed as breeding species in the study area (Cable & Seltman 2011). Therefore, our sample size for estimating initial occupancy, colonization and extinction was 36 species at each of 9 sites and over 4 years. The observational
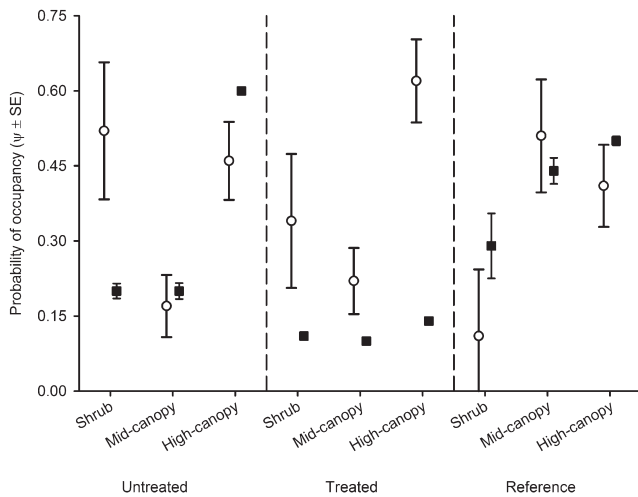
Figure 2. Initial occupancy probability (open circles) and predicted equilibrium level of occupancy (±SE, black squares) estimated from the best-fitting dynamic occupancy model for riparian bird foraging guild communities in untreated, treated, and reference treatment types at the Cimarron National Grassland in southwestern Kansas from 2006 to 2009.

unit for estimating probability of detection of the regional pool was 36 species × 9 sites × 2 visits in each season.

We developed categorical covariates to predict detection probability for each species. Visual cues for species detection including species-specific foraging tactics may affect detectability of species in sparsely vegetated habitat, whereas auditory cues are more important in highly vegetated habitats such as dense forests (Simons et al. 2009). Incorporating species-specific functional traits such as foraging behavior into occupancy models can aid in accounting for heterogeneity in detection probability (Jiguet et al. 2005; Iknayan et al. 2014). We assigned each songbird species detected in this study to one of three foraging behavior guilds based on breeding season assignments of DeGraaf et al. (1985): *Shrub* (ground-to-shrub layer foragers), *Mid-canopy* (within-canopy: on leaves, twigs, and branches of trees in main canopy), and *High-canopy* (tree-top: forages from exposed branches). Thus, we explicitly incorporated detection heterogeneity of the avian community as a function of foraging behavior. By employing models that incorporated guild dynamics for each treatment, we could estimate the relative size of each foraging guild within each treatment type, while accounting for imperfect detection of birds within each habitat treatment (MacKenzie et al. 2006; Kéry 2011; O'Brien & Kinnaird 2011).

We considered 12 candidate models to estimate community parameters. Our full candidate model included initial occupancy, colonization, extinction, and detection probability as a function of habitat and guild type and their interaction ($K = 36$). To identify the reduced model that best described the community dynamics of the study area, we tested 11 different permutations of this model. The model set included parameters testing variation in initial community occupancy, colonization, extinction, and detection probability by foraging guild (G), treatment type (*Trt*), and interaction term ($G \times Trt$), or an intercept only

model (.). Models that did not converge or that did not provide Hessian singulars (standard errors (SEs) of coefficients) were not considered further.

Community Equilibrium Dynamics. We tested whether riparian songbird communities in our study were near a state of equilibrium or in trajectories of collapse or recovery (Hanski 1994). In our approach, we compared whether the net number of sites that were colonized each season was equal, on average, to the net number of sites where the foraging guild went locally extinct. We used our estimates for the probabilities of colonization and local extinction for each foraging guild to calculate equilibrium levels of occupancy for each of the three treatment types. Equilibrium level of occupancy estimates were calculated as $\psi_{eq} = \gamma/(\gamma + \varepsilon)$ (MacKenzie et al. 2006), and compared to initial occupancy estimates (ψ_{2006}). Confidence intervals (CIs) for our derived estimates of equilibrium were calculated with the delta method (Williams et al. 2002; Powell 2007).

Population-Level Analyses. We used the SAS software (SAS Institute Inc., Cary, NC, U.S.A.) to assess the effect of treatment type on relative abundance of songbird nesting guilds at our survey transects. In the analysis of nesting guild abundance, the relative abundance of each species was an average of the number of individuals detected between the two within-season visits for each transect. The average number of individuals within each nesting guild was compared to evaluate differences in mean abundance for all nesting guilds between treatment type and to test for year by treatment-type interactions. Nesting guilds were composed of birds that were ground, cavity, canopy, and shrub-nesters based on descriptions in species accounts of the Birds of North America Online (Rodewald 2015). We excluded Brown-headed Cowbirds from the nesting-guild analysis because cowbirds are an obligate brood parasite that lay eggs in the nests of other songbird hosts. Instead, we examined changes in abundance of cowbirds among treatment types separately in a single species analysis.

We performed repeated measures analysis of variance with year as a repeated variable, nesting guild and habitat type as fixed effects, and transect within habitat type as a random effect (Bolker et al. 2009). Models were fit with PROC MIXED of Program SAS (Littell et al. 1996). We tested for year by habitat-type interactions. The covariance structure for measurements of correlation among time periods was initially unknown, and our five candidate models for covariance structure included compound symmetry, unstructured, autoregressive, Toeplitz, and heterogeneous. We compared models using Akaike's information criterion adjusted for small sample sizes, AIC_c (Brockwell & Davis 2013). Sattherwaite's approximation was used to calculate effective degrees of freedom of a linear combination of independent sample variances. Fisher's test of least significant difference (LSD) was used to make pairwise comparisons among treatments and nesting guilds. Strict inference for nesting-guild abundance was precluded due to the lack of accounting for individual bird or species detection probability with distance sampling, double-observer, or removal methods (Williams et al. 2002), which restricts our inference to data that

Table 1. Candidate models for dynamic occupancy analyses of riparian avian communities at the Cimarron National Grassland in southwestern Kansas, United States, from 2006 to 2009. Four dynamic occupancy parameters included: ψ = initial occupancy, γ = local colonization, ε = local extinction, and p = detection probability. Model structure for the four parameters included: . = constant, G = foraging guild, Trt = treatment groupings, and $\times$ = interactive models. Model fit was assessed by $QAIC_c$ values, $\Delta QAIC_c$ = $QAIC_c$ distance from top-ranked model; K = number of estimable parameters, $-2\ln L = -2 \times$ log-likelihood, and w = Akaike weight.

Model	K	$QAIC_c$	$\Delta QAIC_c$	$-2ln\,L$	w
$\psi(G \times Trt), \gamma(Trt), \varepsilon(G \times Trt), p(G \times Trt)$	30	1948.54	0	1898.54	0.47
$\psi(G \times Trt), \gamma(G), \varepsilon(G \times Trt), p(G \times Trt)$	30	1949.48	0.94	1899.49	0.30
$\psi(G), \gamma(G), \varepsilon(G), p(G)$	12	1950.62	2.08	1942.68	0.17
$\psi(G), \gamma(.), \varepsilon(.), p(G)$	8	1953.30	4.76	1954.07	0.04
$\psi(G \times Trt), \gamma(.), \varepsilon(G), p(G \times Trt)$	22	1955.01	6.47	1924.38	0.02
$\psi(G \times Trt), \gamma(.), \varepsilon(G \times Trt), p(.)$	20	1977.27	28.73	1951.53	0.00
$\psi(G), \gamma(.), \varepsilon(G \times Trt), p(.)$	14	1978.18	29.64	1966.08	0.00
$\psi(G \times Trt), \gamma(.), \varepsilon(.), p(.)$	12	1983.14	34.6	1975.53	0.00
$\psi(G), \gamma(.), \varepsilon(.), p(.)$	6	1985.93	37.39	1991.29	0.00
$\psi(Trt), \gamma(Trt), \varepsilon(Trt), p(Trt)$	12	2000.34	51.8	1992.89	0.00
$\psi(.), \gamma(.), \varepsilon(.), p(.)$	4	2000.70	52.16	2010.41	0.00

represents an unknown proportion of the sampled population (Nichols et al. 2009). Therefore, we report a relative abundance index rather than an estimate of density. Data were checked for normality and heteroscedasticity prior to statistical analysis.

Results

Species Composition. A total of 1,660 individuals of 36 species of riparian songbirds were recorded in our 4-year study. Average bird abundance per site was 25.3 ± 2.9 ($\bar{x} \pm$ SE) individuals at untreated sites, 15.5 ± 3.2 individuals at treated sites, and 32.2 ± 2.9 individuals at reference sites (Table S1, Supporting information). In total, 21, 19, and 29 bird species were detected at untreated, treated, and reference sites, respectively. Riparian bird communities at Cimarron included species from four different nesting guilds (Table S1). The canopy-nesting guild was the most diverse component of the riparian bird community, with a total of 12 species. White-winged Doves (*Zenaida asiatica*), House Wrens (*Troglodytes aedon*), Yellow-breasted Chats (*Icteria virens*), Field Sparrows (*Spizella pusilla*), and Indigo Buntings (*Passerina cyanea*) were encountered only at *Tamarix*-dominated sites, and two of these five species were in the shrub-nesting guild. On the other hand, Cassin's Sparrows (*Peucaea cassinii*) were encountered only at treated sites where *Tamarix* had been removed. The reference sites with native cottonwoods exhibited the most unique species pool with 10 species encountered only in this habitat type (Table S1).

Community-Level Analyses

The top model in the set of candidate models for dynamic occupancy had all parameters varying by treatment type and foraging guild, except the probability of colonization ($\gamma \pm$ SE) which had only a treatment effect (Trt) ($w = 0.47$, Table 1). The probability of initial occupancy (ψ_{2006}) of ground-to-shrub foragers was highest at untreated sites ($\psi \pm$ SE: 0.52 ± 0.14),

followed by treated sites (0.33 ± 0.13), and was lowest at reference sites (0.11 ± 0.13). Conversely, occupancy of mid-canopy foragers was highest at reference sites with cottonwoods (0.51 ± 0.11), followed by treated sites (0.22 ± 0.07), and was lowest at untreated sites dominated by *Tamarix* (0.17 ± 0.06). The initial occupancy state of high-canopy, open-perch foragers was highest at treated sites where *Tamarix* was removed ($\psi_{2006} = 0.61 \pm 0.08$), whereas high-canopy foraging guild occupancy tended to be similar between untreated and reference sites (0.46 ± 0.08 vs. 0.41 ± 0.08).

The probability of local colonization ($\gamma \pm$ SE) was constant among foraging guilds and was highest at reference sites (0.14 ± 0.05), followed by untreated sites (0.08 ± 0.02), and lowest at treated sites (0.02 ± 0.02, Table 2). Probability of local extinction for ground-to-shrub foragers ($\varepsilon \pm$ SE) tended to be higher at untreated (0.32 ± 0.11) and reference sites (0.35 ± 0.40) than treated sites (0.17 ± 0.16). Mid-canopy foragers had highest local extinction probability at untreated sites (0.34 ± 0.13), but relatively low probability of extinction at treated (0.18 ± 0.10) and reference sites (0.18 ± 0.10). In contrast, high-canopy foragers had lowest local extinction probability in untreated sites (0.05 ± 0.03) and relatively high probability of local extinction at treated (0.12 ± 0.05) and reference sites (0.14 ± 0.06).

Probability of detection for bird species in each foraging guild was imperfect for all treatments. Probability of detection ($p \pm$ SE) for ground-to-shrub foragers was highest at untreated sites (0.66 ± 0.08), and lower at treated (0.36 ± 0.12) and reference sites (0.18 ± 0.14). Mid-canopy foragers at untreated sites had relatively high probability of detection (0.64 ± 0.08), while detection probability of this guild was lower at treated sites (0.49 ± 0.08) and lowest at reference sites (0.35 ± 0.06). Probability of detection for high-canopy foragers was lowest at treated sites (0.60 ± 0.05), but similar between untreated (0.77 ± 0.04) and reference sites (0.74 ± 0.04).

We used our estimates of colonization (γ) and local extinction (ε) to calculate the equilibrium level of occupancy for each of the three treatment types. Reference sites tended to

Table 2. Estimates of community parameters (±95% CI) from the top dynamic occupancy model fit to encounter histories of bird species in avian communities at the Cimarron National Grassland in southwestern Kansas from 2006 to 2009.

Treatment	Foraging Guild	Initial State of Occupancy (ψ_{2006})	Colonization (γ)	Local Extinction (ε)	Detection (p)
Untreated	Shrub	0.52 (0.27, 0.76)	0.08 (0.05, 0.14)	0.32 (0.15, 0.57)	0.66 (0.48, 0.81)
	Mid-canopy	0.17 (0.08, 0.33)	—	0.34 (0.14, 0.61)	0.64 (0.47, 0.79)
	High-canopy	0.46 (0.32, 0.61)	—	0.05 (0.01, 0.17)	0.77 (0.69, 0.84)
Treated	Shrub	0.34 (0.14, 0.62)	0.02 (0.00, 0.10)	0.17 (0.02, 0.61)	0.36 (0.18, 0.60)
	Mid-canopy	0.22 (0.12, 0.38)	—	0.18 (0.05, 0.46)	0.49 (0.35, 0.64)
	High-canopy	0.61 (0.45, 0.76)	—	0.12 (0.05, 0.26)	0.60 (0.51, 0.69)
Reference	Shrub	0.11 (0.01, 0.63)	0.14 (0.08, 0.26)	0.35 (0.02, 0.94)	0.18 (0.03, 0.60)
	Mid-canopy	0.51 (0.30, 0.71)	—	0.18 (0.06, 0.45)	0.35 (0.25, 0.48)
	High-canopy	0.41 (0.27, 0.58)	—	0.14 (0.06, 0.28)	0.74 (0.64, 0.81)
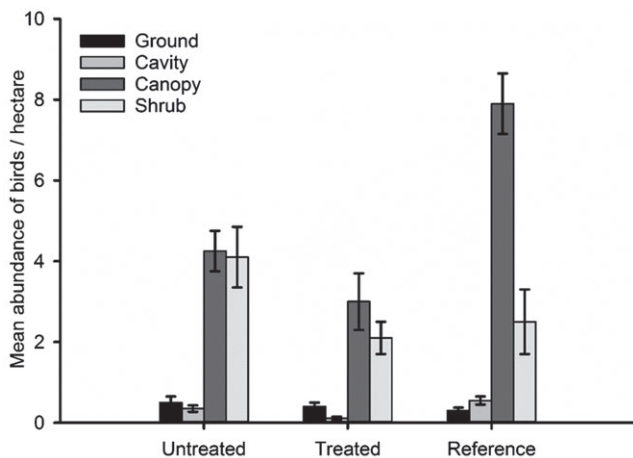
Figure 3. Mean abundance (±SE) of birds per hectare for each of four nesting guilds for each treatment type at the Cimarron National Grassland in southwestern Kansas from 2006 to 2009.

approach equilibrium for all three foraging guilds because CIs for equilibrium occupancy ($\psi_{eq} = \gamma/[\gamma + \varepsilon]$) overlapped with initial probabilities of site occupancy (ψ_{2006}; Fig. 2). Elsewhere, the mid-canopy foraging guild at untreated sites dominated by *Tamarix* was the only other treatment-foraging guild combination at or near equilibrium. At equilibrium, we calculated that treated sites would have approximately 10, 5, and 45% lower occupancy of shrub, mid-canopy, and high-canopy foragers. Thus, treated sites where *Tamarix* was experimentally removed had the most dynamic riparian bird community among the three experimental treatments in our study area.

Population-Level Analyses

We compared relative abundance of nesting guilds with a repeated measures mixed analysis of variance (ANOVA) with heterogeneous autoregressive covariance structure. Interaction terms were not significant, and we detected no significant year by habitat interactions for mean abundance within the four nesting guilds. Mean abundance of individuals per site in all nesting guilds was greater for the reference habitat than the treated habitat, but were not significantly different from the untreated habitat (F value$_{[df]}$ [$F_{[2,7.31]}$] = 10.0, $P = 0.0081$;

Fig. 3). Mean abundance of individuals per site was greatest for the canopy-nesting guild followed by the shrub-nesting guild ($F_{[3,25.1]} = 139.5$, $P < 0.0001$). Mean abundance of individuals per site did not significantly differ between the ground- and cavity-nesting guilds (Fig. 3). A significant interaction between nesting guild and habitat type indicated that nesting guild abundance varied by habitat type ($F_{[6,25.1]} = 14.4$, $P < 0.0001$). Pairwise comparisons based on LSD tests revealed that canopy-nesters at reference sites were more abundant than any other nesting-guild at the untreated or treated sites ($P < 0.001$), while marginal differences occurred in abundance of shrub-nesters between untreated versus reference ($t_{[29.6]} = -1.64$, $P = 0.11$) or treated sites ($t_{[29.6]} = -1.92$, $P = 0.07$). Abundance of ground- and cavity-nesters did not differ between treatment types ($P > 0.5$).

Abundance of Brown-headed Cowbirds at the reference (1.0 ± 0.4 birds per site) and treated sites (0.5 ± 0.3) was not different than untreated sites (1.1 ± 0.2; $F_{[2,24]} = 1.30$, $P = 0.29$). We did not detect a difference in abundance of Brown-headed Cowbird by year ($F_{[3,24]} = 0.96$, $P = 0.43$), nor was there a significant interaction between habitat type and year ($F_{[6,24]} = 1.24$, $P = 0.32$).

Discussion

Habitat type affected abundance and community structure of riparian songbirds at the Cimarron National Grassland at the foraging- and nesting-guild level. In particular, *Tamarix*-dominated habitat supported high species richness and abundance among shrub-nesting birds, and higher occupancy of shrub-foraging birds relative to remnant, reference cottonwood stands. Overall songbird abundance was highest in areas of remnant stands of native cottonwoods. The greater overall bird abundance found in reference habitats is consistent with patterns reported for other studies of riparian birds with greater bird abundance in older, generally more complex structure of remnant cottonwood forests (Warner & Hendrix 1984; Lite & Stromberg 2005). A stratified cottonwood-willow forest characteristic of riparian remnants may support high bird densities because trunk-, branch-, and foliage-foraging space are available as ecological niches (Warner & Hendrix 1984). Moreover, the apparent equilibrium state of occupancy

for each foraging guild in the reference habitat suggests that areas with native vegetation exhibited the most stable community dynamics at the Cimarron. Understanding equilibrium dynamics in degraded lands is a critical part of creating predictive tools to guide restoration (Suding et al. 2004; Suding & Leger 2012). Therefore, our results in this riparian system provide baseline information for future analyses aimed to assess recovery thresholds in systems where restoration has taken place.

Relative abundance of birds in the ground-nesting and cavity-nesting guilds as well as probability of local extinction of shrub- and mid-canopy foragers was lowest at *Tamarix*-removal sites. Low overall abundance and species composition, which reduces the likelihood of species becoming locally extinct or species immigrating to disturbed sites via conspecific attraction, may have led to low probability of songbird extinction at treated sites. Moreover, we expected lower species richness and use for removal sites compared to cottonwood and *Tamarix*-dominated sites due to lower structural diversity at removal sites. Our results also indicate that *Tamarix* removal may have negatively affected numbers of ground and arboreal species at the Cimarron grasslands. Similar results were found in an overabundant-tree/invasive shrub removal experiment in a Minnesota grassland (Thompson et al. 2016), where tree- and cavity-nesters declined post-treatment. In contrast, occupancy of high-canopy foragers including kingbirds and other open-perching species was highest in removal sites, suggesting *Tamarix* removal may open up foraging habitat for aerial insectivores, especially when snags remain in treated habitat. Our results imply that effects of *Tamarix* eradication efforts on riparian bird communities are guild-dependent, which adds complexity to the perception of this invasive tree-shrub as a nuisance species. Moreover, *Tamarix*-dominated sites supported a slightly lower number of species per site than reference habitat, including Yellow-breasted Chats as a species of local management concern. Chats are an obligate shrub-nester and were found exclusively at *Tamarix*-dominated sites. The relative abundance of shrub-nesters was greatest at the *Tamarix* habitat; thus suggesting the invasive tree-shrub can act as suitable nesting habitat for some bird species throughout its non-native range in North America.

A lack of significant changes in species relative abundance during our 4-year project limits our understanding of temporal dynamics in this system in relation to avian responses to *Tamarix*-removal. Past studies that have determined temporal patterns in avian community dynamics in response to restoration activities have lasted longer than five years after restoration (Gardali et al. 2006; Johnson et al. 2009; Thompson et al. 2016). We did not detect any substantial changes in relative abundance over our 4-year study. Thus, detecting avian responses to *Tamarix* removal in the Great Plains may require longer periods of vegetative succession. In the western United States, riparian areas treated with *Tamarix* eradication usually require substantial time to replace exotic stands with native vegetation that offer equivalent volume and structural diversity (Shafroth et al. 2005).

The three habitat types included in our field study were not homogeneous in vegetation cover. The cottonwood woodlands had open areas similar to the treated areas with *Tamarix* removal, and also had occasional *Tamarix* plants growing among the cottonwoods. Likewise, scattered cottonwood trees grew in both the treated and untreated riparian areas, providing perches and nest sites for birds not associated with live or dead *Tamarix*. No truly homogenous tracts of these woody plants exist on the study area, so the birds counted along transects represent the avian community of a mosaic of small habitat patches. The inherent patchiness of the study area at a fine spatial scale may have obscured the larger-scale habitat distinctions in the study area. However, even with overlapping vegetation types and structure, a subset of bird species were only detected in one of the three habitat categories; untreated, treated, and reference sites contributed 5, 1, and 10 unique species of birds to the regional pool of songbird species. Species uniqueness provides useful insight into the relative importance of habitat types for breeding birds along the Cimarron riparian corridor. When considering species richness and uniqueness, reference cottonwood habitat types stand out for maintaining high avian diversity. Furthermore, when considering species uniqueness across all habitat types, tamarisk contributed moderately to regional diversity, while removal habitat with only one unique species were least important for maintaining avian diversity in this riparian system.

Our research results will aid restoration professionals in determining and creating the most favorable mix of native vegetation and non-native *Tamarix* at the eastern boundary of its current range in North America. We describe the differences in riparian bird communities utilizing three habitat types with different vegetation structure along a Great Plains river with an ephemeral flow regime. Management implications for ecosystems experiencing invasion from *Tamarix* are site-dependent because the factors controlling the effects of this invasive plant species on wildlife include the structure of habitats, elevation, surface water availability, and interactions of species coexisting within such habitats; factors that are likely to vary across geographic regions (Hunter et al. 1988; Hinojosa-Huerta 2006; Brand et al. 2008; Van Riper et al. 2008). Our work did not evaluate the effects of *Tamarix* presence or absence on changes in avian guild community dynamics within our sites; however, we documented the avian species composition, foraging guild occupancy dynamics, and nesting guild abundance for each habitat type in our study area. Our results imply that the management of riparian systems for avian diversity is not a matter of the presence or absence of *Tamarix* but depends on the availability of habitat with various vertical and horizontal structural properties. Eliminating *Tamarix* is itself straightforward compared to understanding and shaping the ecological changes following removal (Shafroth et al. 2005; Sogge et al. 2013); thus, we provide new information for land managers tasked with the conservation and management of inherently complex ecosystems.

Acknowledgments

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Supporting Information

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

Table S1. Mean abundance ($\pm$SE) of individuals per nesting guild for riparian bird communities in untreated, treated, and reference treatment types at the Cimarron National Grassland in southwestern Kansas, 2006–2009.