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RESEARCH ARTICLE

Restoration Practices Have Positive Effects on Breeding Bird Species of Concern in the Chihuahuan Desert

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Abstract

Woody plant encroachment into grasslands is a global concern. Efforts to restore grasslands often assume that removal of woody plants benefits biodiversity but assumptions are rarely tested. In the Chihuahuan Desert of the Southwestern United States, we tested whether abundances of grassland specialist bird species would be greater in plant communities resulting from treatment with herbicides to remove encroaching shrubs compared with untreated shrub-dominated areas that represented pretreatment conditions. In 2010, we surveyed breeding birds and vegetation at 16 treated–untreated pairs. In 2011, we expanded the survey effort to 21 treated–untreated pairs, seven unpaired treatment areas, and five reference grassland areas. Vegetation in treatment areas had higher perennial grass foliar and basal cover and lower shrub foliar cover compared with untreated areas. Several regionally declining grassland specialists exhibited higher occurrence and relative abundance in treated areas. A shrubland specialist, however, was associated with untreated areas and may be negatively impacted by shrub removal. Bird community composition differed between treated and untreated areas in both years. Our results indicate that shrub removal can have positive effects on grassland specialist bird species, but that a mosaic of treated and untreated areas might be most beneficial for regional biodiversity.

Key words: avian community analysis, grassland restoration, *Peucaea cassinii*, *Polioptila melanura*, rangeland management, shrub encroachment.

Introduction

Woody plant encroachment affects grassland and savanna ecosystems worldwide, producing important changes to ecosystem structure, processes, and biodiversity (Archer 2010; Eldridge et al. 2011). Consequently, restoration strategies employ woody plant removal as a means to recover historical conditions (Whitford 2002; Archer et al. 2011). The assumption that woody plant removal has positive effects on biodiversity, however, typically goes untested. The lack of quantitative information about the effects of woody plant removal has engendered controversy regarding the value of this restoration approach, particularly when reference conditions are uncertain or when restoration of historical conditions is incomplete (Fensham 2008; Archer et al. 2011). Furthermore, existing studies suggest that species of interest can respond positively (Coppedge et al. 2004; Smyth & Haukos 2010) or negatively (Martin & McIntyre 2007; Kutt & Martin 2010; Isaacs et al. 2013) to woody plant removal, depending on species' habitat requirements and the nature of habitat change induced by woody plant removal. The varying impacts of woody plant removal on species of conservation concern underscore the need for quantitative evaluations of woody plant removal effects in different ecosystems.

The Restore New Mexico program is one of the most intensive collaborative efforts to restore grasslands in the United States. The program has united government agencies, livestock producers, and conservation groups seeking to increase the pace and scale of grassland restoration within portions of the Southwestern United States that have experienced shrub and tree encroachment over the past century. Restoration efforts within much of the Chihuahuan Desert of southwestern New Mexico employ herbicides as the primary tool for removing woody plants because current grass cover is too sparse to support the use of fire (R. Lister, personal communication).

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On the basis of regional scale mapping of ecological states (Yanoff et al. 2008), we estimate that 20% of mixed shrub, shrub-dominated and shrub-invaded states within the Chihuahuan Desert of New Mexico has already been treated. While the positive effects of shrub removal on biodiversity are generally assumed (U.S. Department of Interior, BLM 2008), there have been few systematic attempts to evaluate the effects of shrub removal on animal communities (e.g. Cosentino et al. 2013).

Our evaluations focused on breeding birds, which are sensitive biodiversity elements within grasslands and savannas (Browder et al. 2002) and of primary interest to stakeholders. Grassland specialist birds are especially vulnerable to shrub encroachment and have exhibited steep regional declines in the United States (Knopf 1994; Sauer et al. 2012) as they have in other parts of the world (Sirami & Monadjem 2012). Consequently, the restoration of historical grassland or savanna vegetation structure from dense shrubland is expected to result in population increases of grassland specialists. Alternatively, if restoration treatments are incapable of restoring habitat structures and elements used by grassland specialists, their populations may not increase and the loss of shrubland specialists could lead to overall declines in biodiversity (Whitford 1997).

We conducted three analyses to examine the effects of shrub removal treatments of various ages on species representing three avian functional groups: grassland specialists (entirely dependent on grassland habitats), shrubland specialists (dependent on shrubs), and grassland facultative (use grassland but not entirely dependent on it) species (cf Raitt & Pimm 1976; Vickery et al. 1999; Agudelo et al. 2008; see species assignments to groups in Table S1, Supporting Information). First, we compared vegetation structure in three general areas: treated but formerly shrub-dominated areas, untreated shrub-dominated areas, and remnant grassland reference areas. Most shrub removal treatment areas were paired with untreated shrub-dominated areas based on soil and landscape position. Grassland reference areas were within the study region, comparable in size and site characteristics to treatment areas, but dominated by perennial grasses. We expected treatment areas would have higher perennial grass cover and lower shrub cover than untreated areas (Perkins et al. 2006). Restoration trajectories in arid grasslands may unfold over decades (Whitford 2002), so we reasoned that older treatment areas would have higher grass cover than younger treatment areas and exhibit environmental characteristics most similar to reference grasslands. Alternatively, shrubs might reinvade old treatment areas and differences from nearby untreated, shrub-dominated areas would diminish compared with young treatment areas.

Second, we directly examined relationships between occurrence and abundance of bird species and environmental factors. Treatment areas with the greatest shrub mortality and grass cover increases were expected to be occupied by grassland specialist species including horned larks (*Eremophila alpestris*) and eastern meadowlarks (*Sturnella magna*). Grassland facultative species were expected to respond positively to treatment areas featuring moderate shrub cover, but would not occur in dense shrublands or reference grasslands without shrubs (Merola-Zwartjes 2005). Shrublands specialists were predicted to respond negatively to the loss of shrubs.

Third, we examined the effect of shrub removal on community structure of breeding birds. We expected that shrub removal treatments yielding a savanna-like vegetation structure would feature a higher diversity and abundance of birds than either untreated areas or reference grasslands due to representation of all three bird functional groups (Whitford 1997; Pidgeon et al. 2001).

Methods

Study Area

The study was conducted in the Chihuahuan Desert region of Southwestern New Mexico (Fig. 1). Study areas were located on federal and state managed lands at elevations ranging from 1,260 to 1,756 m a.s.l. The region receives a mean annual rainfall of 200–250 mm. Shrub-dominated states targeted for treatment are dominated by encroaching shrub species (Gibbens et al. 2005) including creosotebush (*Larrea tridentata*) and tarbush (*Flourensia cernua*). Common grasses are dropseeds (*Sporobolus* spp.), tobosa (*Pleuraphis mutica*), black grama (*Bouteloua eriopoda*), bush muhly (*Muhlenbergia porteri*), threeawns (*Aristida* spp.), and burrograss (*Scleropogon brevifolius*) (USDA-NRCS 2012). Soils are generally gravelly sandy loams, including the Nickel, Upton, Tres Hermanos, and Del Norte soil series (Web Soil Survey 2012).

Study Design

In 2010, we sampled 16 treated–untreated pairs. The untreated areas were shrub-dominated and spatially matched to treated areas based on landform, soil type, and elevation. Untreated areas are assumed to reflect vegetation that would currently occur in adjacent treated areas had they not been subject to herbicide application (Fig. 2). In 2011, the sampling effort was expanded to include five additional pairs ($n = 21$ total pairs), seven unpaired treatment areas, and five reference grassland areas. To select treatment areas, we compiled a database of shrub removal treatments (185 treatment areas) and randomly selected treatment areas that were $\geq$300 ha (ranged from 354 to 2,845 ha, $\overline{x} = 1087$ ha), were treated once with tebuthiuron (N-[5-(1,1-dimethylethyl)-1,3,4thiadiazol-2-yl]-N,N′-dimethylurea) at an application rate of 0.56 kg/ha and occurred within 1 km of roads for accessibility. Paired treated–untreated areas were considered as blocks in most analyses.

We stratified paired areas into two groups based on treatment age. Old treatment areas were from 1981 to 1989 (n [2010] = 8; n [2011] = 10), and young treatment areas were from 1995 to 2004 (n [2010] = 8; n [2011] = 11). These two age groups represent the earliest treatment areas and the most recent treatment areas in which effects of site fidelity by birds (Knick & Rotenberry 2000) would be minimized by the short life span (<5 years) of most species of interest. Elevation, slope, and aspect did not differ between age groups in 2010

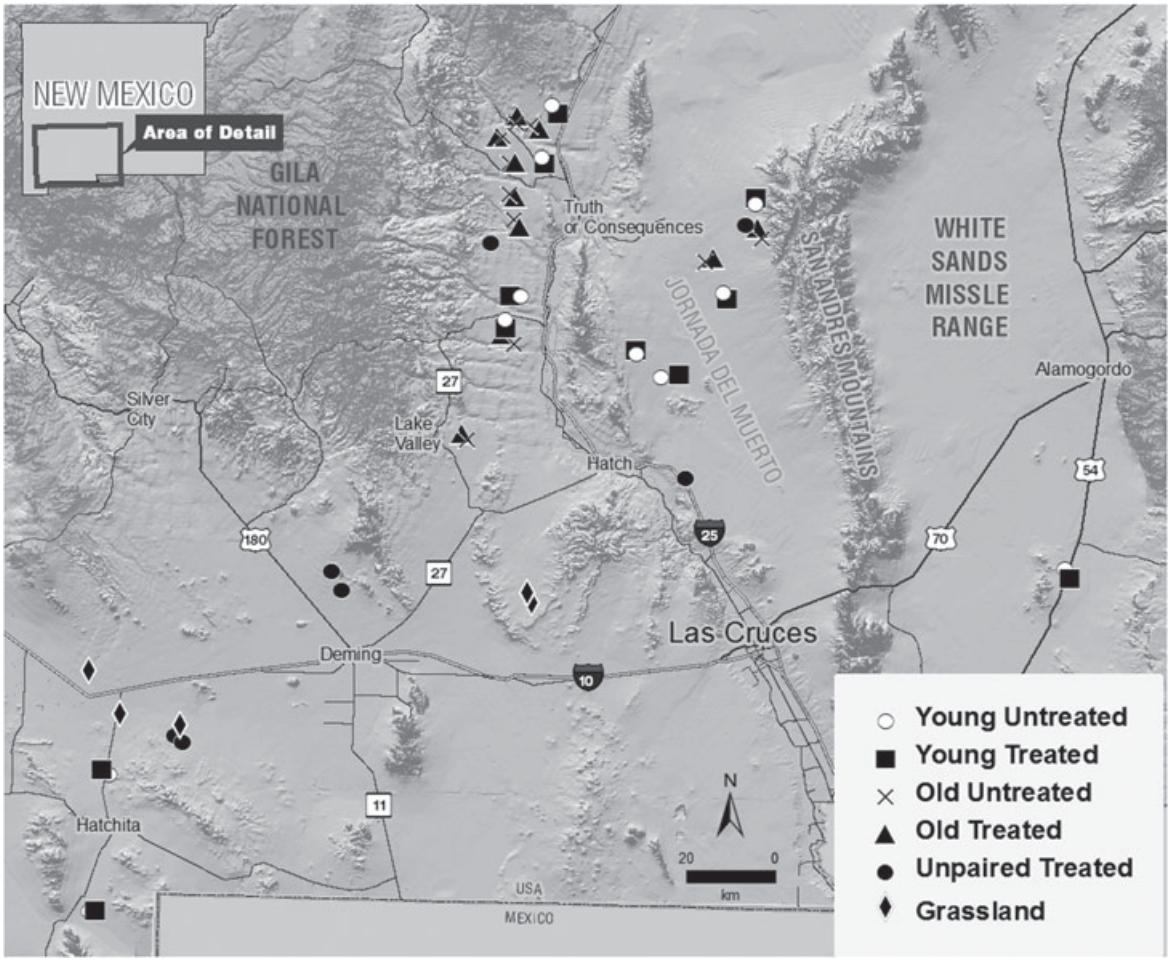

Figure 1. A map of the study region showing locations of areas including old and young paired treated and untreated areas, unpaired shrubland treatment areas, and remnant grasslands.

($n = 16$ pairs), but for the expanded data set in 2011 ($n = 21$ pairs), old treatment areas were at a higher mean elevation (old $\overline{x} = 1{,}565$ m; young $\overline{x} = 1{,}458$ m; $F = 9.52$, degrees of freedom $[df] = 1$, $p = 0.004$)

Sampling Methods

For bird surveys, we established three, 1-km sampling transects for each area. Transects were selected from a pool of randomly generated transects constrained within a discrete treatment polygon or within matched soil map units (http://soils.usda.gov/survey/geography/ssurgo) in untreated areas. All transects were greater than 300 m apart and greater than 100 m from major roads. For survey efficiency, transects were less than 1.5 km apart. Herbicides were not applied to drainages, so we excluded transects that fell in or crossed drainages.

Bird surveys were conducted between May and August in 2010 and 2011. We recorded all birds seen or heard while walking along each 1-km transect with the exception of birds that flew over without using the area. Most encounters (99%) were less than 175 m from observers. All surveys began within 20 minutes of sunrise and ended no later than 4 hours after sunrise. We surveyed one treated–untreated pair in a single morning. We sampled each pair three times in 2010 and two times in 2011. One observer J. Coffman conducted surveys in 2010. In 2011, J. Coffman plus two additional, experienced observers conducted surveys and we randomized pairs among observers such that the same observer always sampled treated and untreated areas within a pair. In both years, we mixed the sampling order of treated and untreated areas and their transects within pairs.

We established two 50-m environmental transects separated by 450 m along each of the three 1-km bird transects, but offset by 30 m and parallel to the bird transect. Data were pooled across all six environmental transects within an area. We used the line-point intercept method (Herrick et al. 2005) to estimate foliar and total basal cover of plant species or functional groups and open ground. Grass cover was divided into three groups distinguished by their responses to grazing and disturbance. Group 1 included perennials that are common in grassland reference states of the study region including tobosa,

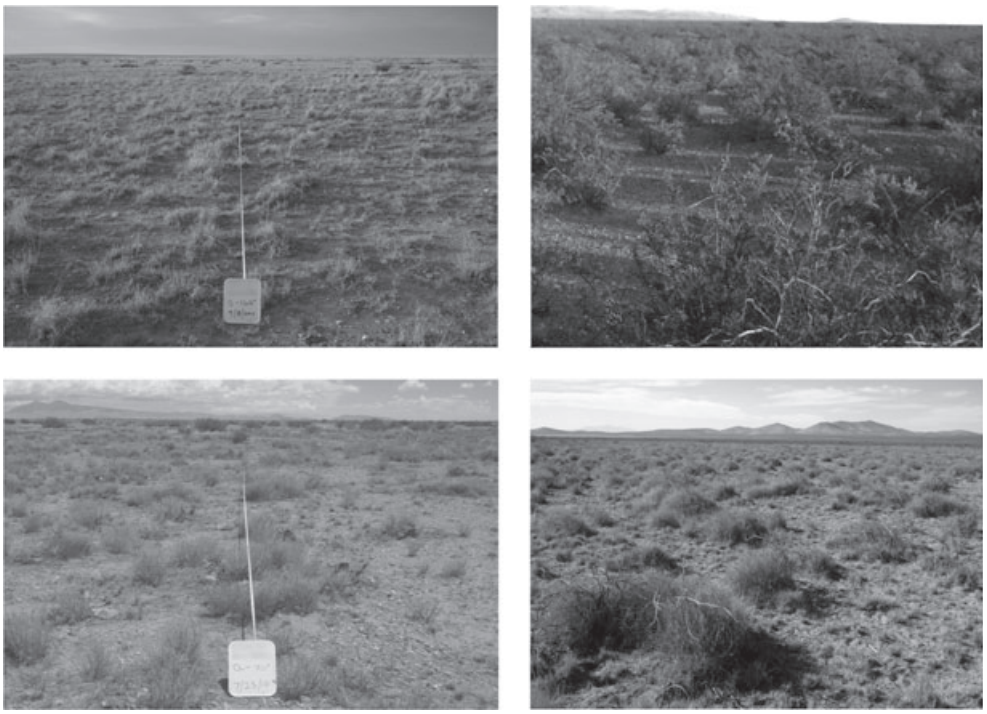

Figure 2. Photographs of representative study areas: remnant grassland (upper left), untreated (upper right), an old treatment applied in 1988 (lower left), and a young treatment applied in 2002 (lower right).

black grama, bush muhly, blue grama (*Bouteloua gracilis*), side-oats grama (*Bouteloua curtipendula*), and burrograss. Group 2 included perennial grasses that may increase as group 1 species decline with heavy grazing, including *Sporobolus* spp., *Aristida* spp., and purple three-awn (*Aristida purpurea*). Group 3 consisted of grasses that are associated with high disturbance and low site productivity including fluffgrass (*Dasyochloa pulchella*) and annual grasses (Bestelmeyer et al. 2004, USDA-NRCS 2012). Shrub density was calculated by counting the number of dead and live shrubs within 1.5 m of each side of the 50-m environmental transect and dividing the count by the area sampled (150 m^2).

All environmental sampling was conducted by one observer (JMC) during July to September in both years. Because our focus was on perennial vegetation cover, which does not change dramatically over 1 year (B. Bestelmeyer, unpublished data), we sampled each area only once for environmental variables. Mixed effects models revealed no effect of year of sampling on treated–untreated differences for environmental variables.

Data Analysis

Environmental Responses. We used a mixed effects linear model to test the effect of treatment on environmental variables in which block effects were considered random (lmer4 package; R version 2.15.0; R Development Core Team 2012). A Student's *t*-test was used to test for differences in grass cover, shrub cover, basal cover, and open ground between old ($n = 10$) and young ($n = 11$) treatment areas. A Wilcoxon ranked sum test was used to test for environmental differences between treatment areas ($n = 28$) and grassland areas ($n = 5$).

Bird Species Responses. We used blocked indicator species analysis (Blocked Indicator Species Analysis [BISA]; PC-ORD version 6; McCune & Mefford 2011*a*) to evaluate the association of different species with treated and untreated areas set in a blocked design. BISA is able to integrate the concentration of abundance (exclusivity) and frequency of occurrence (fidelity) to produce a robust measure of habitat associations of species that does not depend on normality assumptions (Dufrêne & Legendre 1997). A subset of 26 common species for the 16 pairs sampled in 2010 and 30 common species detected on the 21 pairs sampled in 2011 were used for BISA. We also used a traditional indicator species analysis designed for unpaired grouping (Indicator Species Analysis [ISA]; PC-ORD version 6; McCune & Mefford 2011*a*) for all areas sampled in 2011, including unpaired treated and grassland areas.

To explore responses of bird species in grassland associated functional groups to environmental variables, we used nonparametric multiplicative regression (NPMR) using HyperNiche (McCune & Mefford 2011*b*; Appendix S1). This analytical technique has the advantage of modeling nonlinear species responses to multiple, interacting environmental factors. Response variables were probability of occurrence for three grassland specialist species: Cassin's sparrows (*Peucaea cassinii*), horned larks, and eastern meadowlarks; one grassland facultative species: scaled quail (*Callipepla squamata*),

and two shrubland specialists: mourning dove (*Zenaida aurita*) and loggerhead shrikes (*Lanius ludovicianus*). A final NPMR model evaluated the influence of four environmental gradients: grass, shrub, basal cover, and open ground.

Bird Community Responses. We examined community patterns and species–environment relationships for the 16 pairs sampled in 2010 and used the same procedures separately for 21 pairs sampled in 2011. Abundances for each bird species were averaged across multiple visits to areas (three in 2010 and two in 2011). Average abundance, the metric used for analysis, was only considered for all breeding species with five or more encounters across all visits. Because overall abundances were low and detection rates were high (owing to short, sparse vegetation), we analyzed the relative abundance of species rather than attempting to estimate densities.

Differences in average abundance, richness, and Fisher's diversity between paired treated and untreated areas were examined using mixed effects models (lmer4 package; R version 2.15.0; R Development Core Team 2012). We tested for differences in the magnitude of treated–untreated contrasts of abundance, richness, and diversity between old and young treatment areas using a Student's t test in which we compared the mean Δ for each metric (Δ = treated − untreated). Because we had moderate and uneven sample sizes, differences in abundance, richness, and diversity between treated and grassland areas were tested using the nonparametric Mann–Whitney–Wilcoxon test (R version 2.15.0; R Development Core Team 2012).

We evaluated differences in bird community composition between treated and untreated areas using PERMANOVA (Bray–Curtis distance; McArdle & Anderson 2001; Anderson 2001). We applied a balanced, blocked design by grouping paired treated–untreated areas within blocks. No transformation or standardization of the species matrix was applied. The p-values are based on an unrestricted permutation of the raw data 9,999 times. We also tested the effect of treatment age (young vs. old treatment) using a separate PERMANOVA. A multi-response permutation procedure (MRPP; PC-ORD version 6; McCune & Mefford 2011*a*) without the paired design was used to test for community differences across all areas in 2011 including unpaired treated areas and reference grasslands.

Results

Environmental Responses

Of the 10 environmental variables measured on 21 paired areas, three differed between treated and untreated areas: live shrub foliar cover, grass foliar cover, and total basal cover. As predicted, live shrub cover was lower on treatment areas ($F = 47.58$; $df = 1$; $p < 0.001$; Fig. 3). Grass cover was higher on treated than untreated areas ($F = 12.94$; $df = 1$; $p = 0.001$), due primarily to differences in perennial species found in grassland reference states ($F = 7.45$; $df = 1$; $p = 0.009$). Total basal cover was also higher on treatment areas ($F = 6.37$; $df = 1$; $p = 0.02$). Most of these differences in shrub and grass

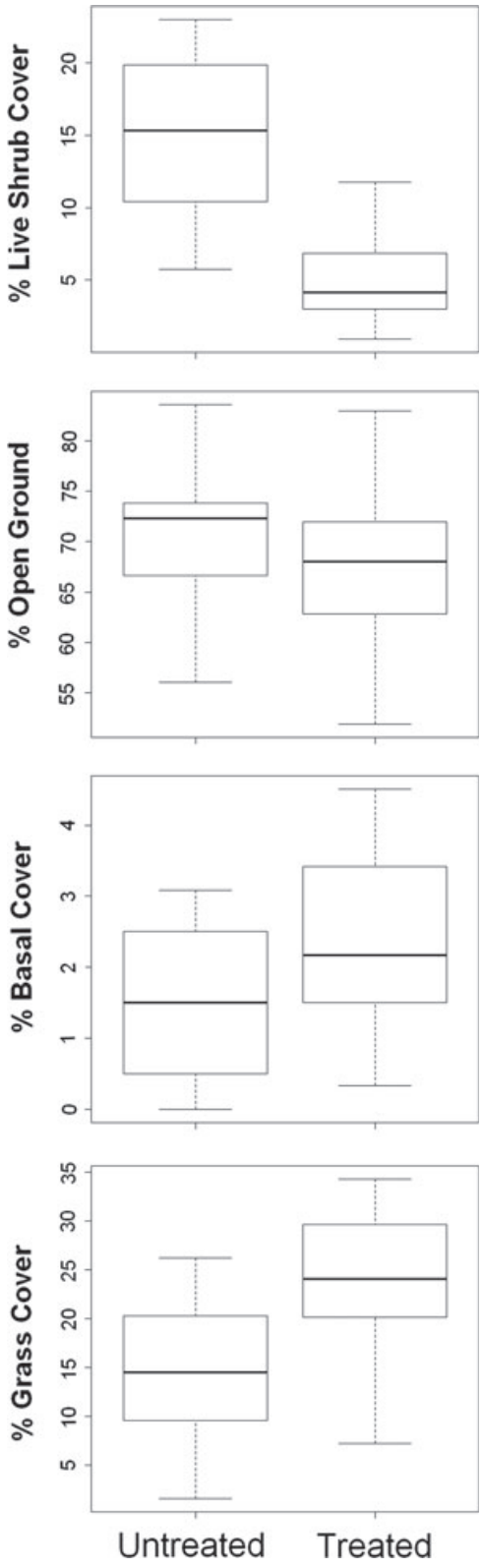

Figure 3. Box plots of four environmental variables sampled on 21 paired treated and untreated areas. The horizontal line within box is the median, box indicates 25th and 75th percentile. Whiskers represent the range of values.

cover held for both young and old treatment areas. On old treatment areas, however, total basal cover did not differ from untreated areas. Higher grass cover on old treatment areas ($F = 5.22$; $df = 1$; $p = 0.035$) was driven by a greater cover of disturbance-associated grasses compared with untreated areas ($F = 5.46$; $df = 1$; $p = 0.032$). In contrast, young treatment areas had higher total basal cover ($F = 4.83$; $df = 1$; $p = 0.04$) and grass cover ($F = 8.19$; $df = 1$; $p = 0.01$) than untreated areas due to increases in species associated with grassland reference states ($F = 6.86$; $df = 1$; $p = 0.1$). Shrub cover in all treated areas ($n = 28$; median = 3.917; range = 0.92–15.25) was higher than that in reference grasslands ($n = 5$; median = 2; range = 0.08–2.83; $W = 18$, $p = 0.009$). Percent grass cover, total basal cover, and open ground did not differ between treated and reference grassland areas, but grass cover of grasslands was less variable (range = 22.17–27.25) than in treatment areas (range = 5.58–52.91).

Bird Species Responses

BISA identified only one species, the shrubland specialist *Polioptila melanura* (black-tailed gnatcatcher), that was reliably associated with untreated areas (indicator value = 30%; Table S1). In 2010, three species of grassland specialists and facultative species (Cassin's sparrow, eastern meadowlark, and scaled quail) and two shrubland specialists (loggerhead shrike and the western kingbird; *Tyrannus verticalis*) exhibited higher indicator values in treated areas than would be expected by chance. In 2011, the traditional ISA found the shrubland specialist *Amphispiza bilineata* (black-throated sparrow) was associated with untreated areas (49%; Table S2). No species were indicators of treated areas in 2011. Two grassland specialists, eastern meadowlarks (86%) and horned larks (93%), were associated with reference grassland areas.

We modeled individual bird species–environment relationships using the three variables that differed between treated and untreated areas (live shrub, grass, and total basal cover) and open ground (due to its recognized importance in habitat selection by grassland birds; Fisher & Davis 2010). The best habitat model generally featured a single environmental variable (Fig. 4). Grass cover predicted the occurrence of the grassland specialist Cassin's sparrow in 2010. Horned lark occurrence had a negative relationship with shrub cover and loggerhead shrike occurrence had a unimodal relationship with basal cover (Fig. 4). Eastern meadowlark and scaled quail occurrences had negative relationships with shrub cover for at least 1 year.

Bird Community Responses

For both 2010 and 2011, richness, average abundance, and Fisher's alpha diversity did not differ between treated and untreated areas (Table S3). The magnitude of treated–untreated differences of richness, abundance, and diversity did not vary with treatment age or survey year (Table S4). Richness, abundance, and diversity were all higher in 2010 than in 2011, which paralleled patterns for average annual precipitation (2010 = 245 cm, 2011 = 165 cm).

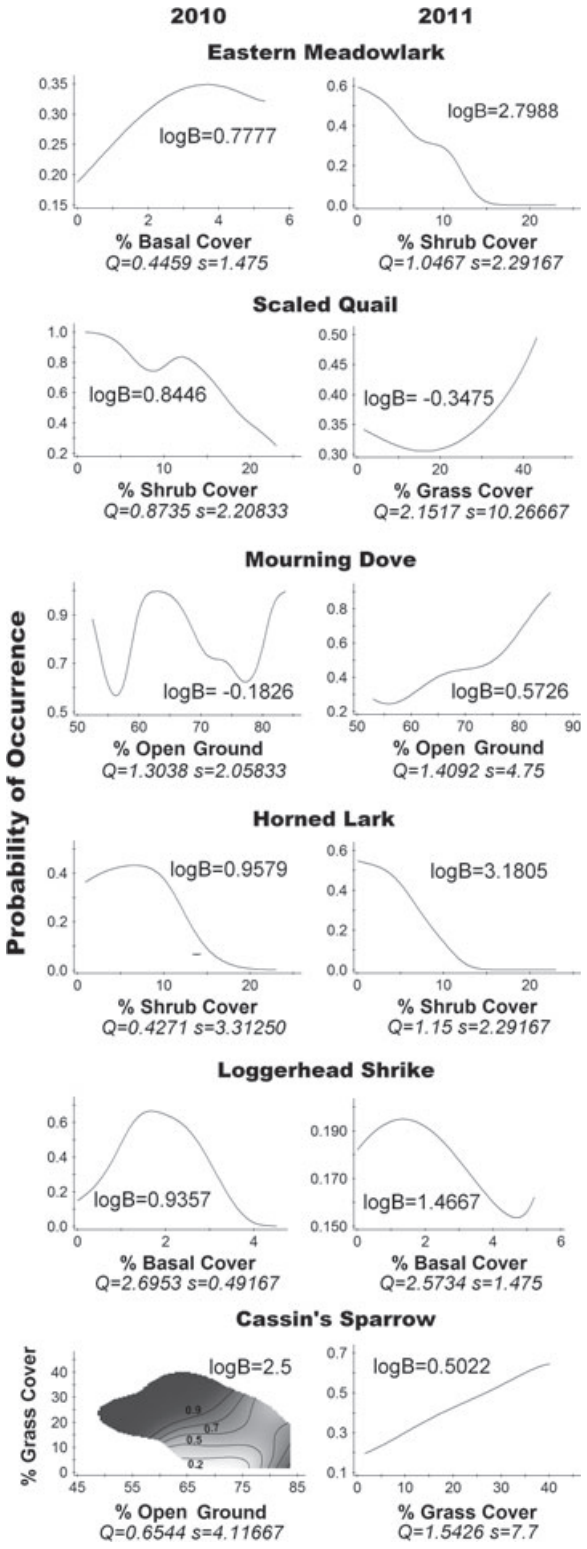

Figure 4. Estimated probability of occurrence for bird species as a function of four environmental variables determined by nonparametric multiplicative regression for 16 paired areas in 2010 and 21 paired areas in 2011. Below each predictor is the sensitivity (Q) and tolerance (s) calculated from the model. The Cassin's sparrow model for 2010 had two variables that best explained probability of occurrence.

PERMANOVA revealed significant differences in community composition between treated and untreated areas for the 16 pairs sampled in 2010 ($F = 12.08$; $p < 0.001$, NMS plot in Fig. S1a) and the 21 pairs sampled in 2011 ($F = 3.8497$; $p = 0.002$, NMS plot in Fig. S1b). We also found an effect of treatment age on bird community composition in young versus old treatment areas for 2011 ($F = 4.5037$; $p = 0.002$), but not for 2010 ($F = 1.7971$; $p = 0.119$). MRPP conducted on all 54 areas (reference grasslands, untreated shrub-dominated, and treated areas) indicated that bird communities on grasslands were distinct from those of both untreated ($A = 0.0184$, $p < 0.001$) and treated areas ($A = 0.1045$, $p < 0.001$, NMS plot in Fig. S2).

Discussion

Our results indicate that shrub removal did not completely restore the attributes of historical (reference) grasslands. Shrub removal can be interpreted to have created a novel ecosystem (sensu Hobbs et al. 2009) across a broad spatial extent. The treated areas are distinct in plant composition, habitat structure, and bird communities from both reference grasslands and shrub-dominated states. Recognizing treated areas as novel ecosystem types (or hybrid systems sensu Hobbs et al. 2009) conveys that shrub removal appears not lead to recovery (within the maximum 30 year time frame of our assessment) of the full complement of habitat conditions present in reference grasslands.

Nonetheless, several regionally declining grassland specialist bird species (Sauer et al. 2012) had higher abundances in treated compared with untreated areas, contributing to strong differences in community composition in both sampling years. Models indicate grassland specialist and facultative species, including scaled quail, eastern meadowlark and horned lark respond positively to decreasing shrub cover. These results support our prediction that grassland specialists tolerant of moderate shrub cover (i.e. Cassin's sparrow and eastern meadowlark) should respond positively to treatments. Smythe and Haukos (2010) observed a similar response of Cassin's sparrows in herbicide-treated sand shinnery oak (*Quercus havardii*) communities of Southeastern New Mexico. Also consistent with our results, Block and Morrison (2010) found that horned larks were absent in areas of moderate shrub cover and instead occurred primarily in pure grasslands where they avoided even short-stature woody cover.

Not all bird species responded positively to habitat conditions created by treatments. The association of a shrubland specialist (black-tailed gnatcatcher) with untreated areas suggests that habitat quality for these birds may be reduced by shrub removal. For some shrubland specialist species such as loggerhead shrikes and mourning doves, we did not find clear evidence of treatment effects; instead their abundance may be governed by landscape-scale patterns (Gutzwiller & Barrow 2002; St-Louis et al. 2010). Another shrubland specialist, the black-throated sparrow, used both treated and untreated areas, perhaps reflecting the use of different habitat types for foraging or nesting, or responses to habitat elements that were unchanged by the manipulations (Table S1; Paritte 2010). To favor declining species, it may be valuable to expand representation of habitat conditions produced by shrub-removal treatments. Nonetheless, preservation of shrub-dominated areas is also warranted due to the positive effects of shrubs on black-tailed gnatcatchers found here and on bird diversity found in other studies (Naranjo & Raitt 1993; Whitford 1997).

While current agency restoration objectives are centered on increasing grass cover within areas dominated by shrubs, it can be valuable to manage for habitat heterogeneity at broader spatial scales (Fuhlendorf et al. 2006). Because grassland loss in the Chihuahuan Desert can be difficult or impossible to reverse (Bestelmeyer et al. 2009); however, diligent efforts must be made to preserve existing grassland states if they are to be represented at all. The current distribution of habitat types likely overrepresents shrub-dominated habitat, so shrub removal treatments may help to sustain regional bird diversity by favoring some grassland specialist species. Our interpretation of shrub-removal efforts for the Chihuahuan Desert contrasts with that of Kutt and Martin (2010) for north-eastern Australian woodlands. These authors concluded that the majority of bird species predicted to decline with increasing vegetation density were open habitat-specialists that were increasing in abundance at a national scale. In our case, however, bird species associated with open grassland habitats are declining regionally (Sauer et al. 2012). Thus, interpretations about the effects of woody plant removal on bird diversity depend strongly on regional species pools and land change history.

Our results support the utility of woody plant removal as a tool to restore, at least in part, the local abundance of grassland specialist bird species in semiarid grasslands of the Southwestern United States. Furthermore, our approach illustrates how quantitative evaluations of restoration interventions can inform cost-benefit analysis for subsequent decisions (Miller & Hobbs 2007). Restoration can then be considered with regard to specific effects on both habitat attributes and ecosystem services, instead of relying on incomplete historical records and vague notions of similarity to reference conditions.

Implications for Practice

- The efficacy of woody plant removal efforts to increase biodiversity is poorly documented and controversial, so there is a clear need for regional tests of biodiversity responses.
- Shrub removal by herbicides in the Chihuahuan Desert favored the abundance of some grassland specialist bird species that are in regional decline. Shrub removal also reduced the abundance of a shrub specialist species.
- Shrub removal produced a novel ecosystem type that differed from reference grasslands and did not support other grassland specialist bird species. Thus, shrub removal should not be viewed as means to mitigate the loss of additional grasslands.
- Selective shrub removal combined with management to preserve unencroached grasslands may be an effective means to sustain biodiversity in semiarid grasslands.

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Supporting Information

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

Figure S1. Nonmetric multidimensional scaling of breeding bird communities sampled in 2010 in 16 treated–untreated pairs (a) and in 2011 in the 21 pairs (b). Old treatments (1982–1989) are symbolized with filled triangles and connected with lines to paired untreated areas (open circles). Young treatments (1995–2004) are symbolized with filled squares and connected to the paired untreated area (X).

Figure S2. Nonmetric multidimensional scaling of breeding bird communities sampled in 2011 including paired treatments (old treatment are filled triangles and young treatments are filled squares) and unpaired treatments (filled circles), untreated shrub-dominated areas (open circles paired with young and X's paired with old treatments), and reference grassland areas (filled diamonds).

Table S1. Blocked indicator species analysis for 30 species. *Denotes no data, bold numbers denote significance ($p = 0.05$). Functional groups are Sh, shrubland specialist; G, grassland specialist; GF, grassland facultative.

Table S2. Indicator species analysis between untreated shrub-dominated, treated formerly shrub-dominated, and reference grassland areas for data collected in 2011.

Table S3. Community structure metrics between treated (TRT) and untreated areas (UNT).

Table S4. Student's t test results for magnitude differences in community structure metrics (2010 and 2011) and four environmental variables (2011 only) for old and young treatments (Δ = treated − untreated).

Appendix S1. HyperNiche™ analysis details.