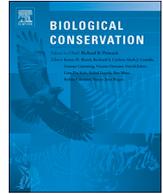




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Woody plant encroachment restructures bird communities in semiarid grasslands

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ABSTRACT

The abundance and distribution of woody plants have increased in grassland ecosystems worldwide. Robust generalizations about the consequences of this transformative process on animal communities have been elusive, especially in semiarid regions where populations of many species have declined. We evaluated how distributions and species richness of breeding birds responded to woody plant encroachment by using spatial variation in woody cover as a proxy for the temporal process by which grasslands transform into shrub savannas. Specifically, we surveyed breeding birds and vegetation on 140 10-ha plots in semiarid grasslands that spanned the gradient of cover by *Prosopis* (mesquite), a genus of shrubs that has proliferated in semiarid grasslands worldwide. We used a multispecies occupancy model to characterize distributions of breeding bird species along the encroachment gradient. Distributions of 29 of 35 species changed markedly in response to encroachment, with distributions of most obligate grassland species contracting and most facultative grassland species expanding. Species richness increased sharply as cover of woody plants increased and peaked at ~22% cover; this increase was driven by recruitment of generalist and shrub-associated species, many of which are common at regional scales. Lastly, we identified thresholds of woody cover where distributions contracted or expanded markedly, which provide targets for conservation and restoration efforts. Our results highlight the importance of understanding species-specific responses to woody plant encroachment as the basis for explaining community-level patterns because increases in diversity at local scales might ultimately reduce diversity at broader scales as grassland specialists are displaced.

1. Introduction

Grasslands are among the most endangered ecosystems on Earth, primarily because of transformational changes in land use (Henwood, 2010; Hoekstra et al., 2005). In North America, for example, <3% of the 60 million ha of tallgrass prairie that was present prior to European settlement remains extant (Henwood, 2010; Sampson and Knopf, 1994). Concerns about the decline and fragmentation of grasslands have fostered preservation efforts, but even those grassland remnants that are formally protected are threatened by changes in vegetation structure and composition that compromise their ecological function (D'Antonio and Vitousek, 1992; Fulbright et al., 2017; Sampson and Knopf, 1994). One of the most pronounced and systemic threats to grass-dominated biomes worldwide is encroachment by woody plants, which have increased in abundance and distribution markedly during the past century (Sala and Maestre, 2014). These increases are thought to be driven by numerous co-occurring and interacting factors, including changes in land use, climate, fire frequency and intensity,

concentrations of atmospheric CO₂, and nitrogen deposition (Archer et al., 2017). Proliferation of woody plants can alter grassland plant communities and ecosystem processes. For example, woody plant encroachment generally accelerates rates of wind and water erosion (Breshears et al., 2009; Wainwright et al., 2000), decreases density, cover, and biomass of herbaceous vegetation (Van Auken, 2009), decreases species richness of plants (Ratajczak et al., 2012), and alters rates of carbon sequestration (Eldridge et al., 2011; Pacala et al., 2001). Although the process of woody plant encroachment (hereafter “WPE”) has occurred across latitudes and precipitation regimes, it has been especially prevalent in semiarid regions, which cover >40% of the terrestrial surface of the Earth and constitute a large proportion of the global grassland biome (Van Auken, 2009; Stanton et al., 2018).

A principal consequence of WPE in grassland ecosystems is a marked increase in the vertical and horizontal structure of vegetation (Archer et al., 2017). Because vegetation structure is a key determinant of animal diversity and community structure (Tews et al., 2004), increases in woody vegetation can have pronounced effects on grassland

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faunas (Archer et al., 2017; Steidl et al., 2013). Robust, broad-scale generalizations concerning the effects of WPE on community-level responses of vertebrates have been elusive, however, in part because studies have varied in the spatial scales considered and because few have evaluated responses across entire encroachment gradients (Archer et al., 2017; Stanton et al., 2018). Although responses of vertebrates to WPE vary, responses within taxa are more consistent, with generally negative effects on species richness or total abundance of mammals and herpetofauna and neutral or positive effects on birds (Stanton et al., 2018). In semiarid regions, responses of vertebrates to WPE tend to be more consistently negative than in mesic regions (Stanton et al., 2018). Consequently, effects of WPE on birds in understudied semiarid grasslands may differ directionally and be less consistent than in more-mesic grasslands and savannas. For example, species richness of birds has been reported to increase (Lloyd et al., 1998; Pidgeon and Mathews, 2001; Rosenstock and Riper, 2001), peak at intermediate levels (Sirami et al., 2009), or remain unchanged (Kaphengst and Ward, 2008) in response to increases in dominance of woody plants in semiarid grasslands and savannas.

Although community-level responses of birds to WPE have been variable, effects of woody plants on grassland specialists have been more consistent, with the occurrence (Cunningham and Johnson, 2006; Grant et al., 2004; Patten and Shochat, 2006) or abundance (Murray et al., 2008; Renfrew et al., 2005; Thompson et al., 2014; Winter et al., 2006) of many species decreasing as dominance of woody plants increases. Most studies have focused on North American prairies, however, which differ from semiarid grasslands in ways that might influence responses of grassland birds. Semiarid grasslands, for example, are not as amenable to agriculture as their prairie counterparts and consequently have not been eliminated or fragmented to the same extent (Gori and Enquist, 2003; Henwood, 2010). Additionally, because precipitation limits woody cover (Sankaran et al., 2005), the distribution of woody plants can differ markedly between these grassland types. In prairie grasslands, woody plants are often distributed in high densities in discrete patches (e.g., woodlots) or as linear strips (e.g., windbreaks), where the transition to open grassland is sharp; in semiarid grasslands, woody plants are often well-distributed throughout encroached areas, but rarely reach densities that eliminate the herbaceous layer (Archer et al., 2017).

Improving our understanding of the effects of WPE on semiarid grassland birds is increasingly important given forecasts of increased aridity for many grassland ecosystems with climate change (Dai, 2011; Seager et al., 2007), the vulnerability of grassland birds to increasing temperatures and aridity (Gorzo et al., 2016; Nixon et al., 2016), and because many populations of semiarid grassland birds have already declined precipitously (Brennan and Kuvlesky, 2005; Sauer et al., 2017b). In North America, for example, the two groups of birds that have declined most are those obligate to grasslands and aridlands, both of which declined by >37% between 1968 and 2011 (Sauer et al., 2017b; Sauer and Link, 2011).

To understand how WPE in semiarid grasslands can affect bird communities, we used spatial variation in woody cover as a proxy for the temporal process through which grasslands transform into shrub savannas (Sirami and Monadjem, 2012). Specifically, we evaluated variation in species richness and distributions of breeding birds across a gradient of woody cover in semiarid grasslands of southeastern Arizona, USA. These grasslands provide a useful model for studying this general process because the primary encroaching woody species, *Prosopis velutina* (velvet mesquite), represents a genus that has proliferated aggressively into semiarid grasslands and savannas worldwide, including Africa, Asia, Australia, and South America (Archer et al., 2017; Sharma and Dakshini, 1991).

Our primary objectives were to explore the effects of WPE on breeding semiarid grassland birds at both the community and species levels and to identify the thresholds of woody cover that precipitate marked changes in the occurrence of grassland birds. These thresholds

are not well established, which can hinder conservation and restoration efforts (Archer et al., 2017). We anticipated that changes in vegetation structure associated with WPE would increase habitat features for shrub-associated birds and decrease habitat features for grassland specialists. Therefore, we hypothesized that local composition of the breeding bird community would vary with the amount of woody cover, reflecting species-specific responses to WPE. We expected distributions of grassland specialists to contract in response to WPE, with obligate grassland species responding more strongly than facultative grassland species (as defined in Vickery et al., 1999). Although we expected species richness of breeding birds to increase initially during the early stages of WPE as generalist and shrub-associated species joined the bird community, we anticipated that these gains would be accompanied by losses of grassland specialists, many of which are species of high conservation concern (Brennan and Kuvlesky, 2005; Sauer and Link, 2011).

2. Materials and methods

2.1. Study area

We surveyed birds and vegetation in upland grasslands of southeastern Arizona, USA at three sites that encompassed the gradient of vegetation structure and management strategies in semiarid grasslands: Appleton-Whittell Research Ranch, Fort Huachuca Military Reservation, and Las Cienegas National Conservation Area (Fig. 1). Semiarid grasslands in this region have been relatively free of the changes in land use that have fragmented and reduced the extent of many grasslands, but over 70% has been encroached by woody plants (Gori and Enquist, 2003). These grasslands occur between 1350 and 1550 m elevation and annual precipitation averages 350 to 450 mm, most of which falls during a monsoon season between July and September that is preceded by 2–3 months that are hot and dry (Bock and Bock, 2000; McClaran, 1995). Although the spatial and temporal distribution of precipitation can vary markedly throughout this region, summer rainfall across the area was near historic averages during the study. Livestock have been excluded from Fort Huachuca Military Reservation since 1950 and Appleton-Whittell Research Ranch since 1968. Grasslands at Las Cienegas National Conservation Area are grazed by cattle, therefore we excluded areas that were scheduled to be grazed during the study.

2.2. Sampling design

To ensure that we surveyed areas that spanned the full gradient of woody cover present in this region, we first classified upland grasslands into areas with low, medium, and high woody cover using aerial imagery (2010 1-m NAIP). We then established 140 10-ha circular plots (180-m radius) at random and in proportion to coverage of each cover class. We excluded areas with obvious anthropogenic features (e.g., roads or buildings), areas scheduled to be grazed during the survey period, and areas that had been burned or otherwise treated to remove woody vegetation during the previous three years. Plots centers were located at least 360 m apart (mean distance between nearest neighbors = 551 m). We surveyed 50 plots in 2013, 50 in 2014, and 40 in 2015. Twenty plots were located at Appleton-Whittell, 45 at Fort Huachuca, and 75 at Las Cienegas (Fig. 1).

2.3. Surveys

We surveyed breeding birds with point-based methods (Buckland et al., 2001). Because peaks of breeding activity vary widely among species in the grasslands we studied (Corman and Wise-Gervais, 2005), a single observer surveyed each plot four times per year between late-May and late-August. The observer recorded all birds seen or heard from the center of each plot during 10-min surveys and classified each bird to species and by sex and age class whenever possible. All surveys

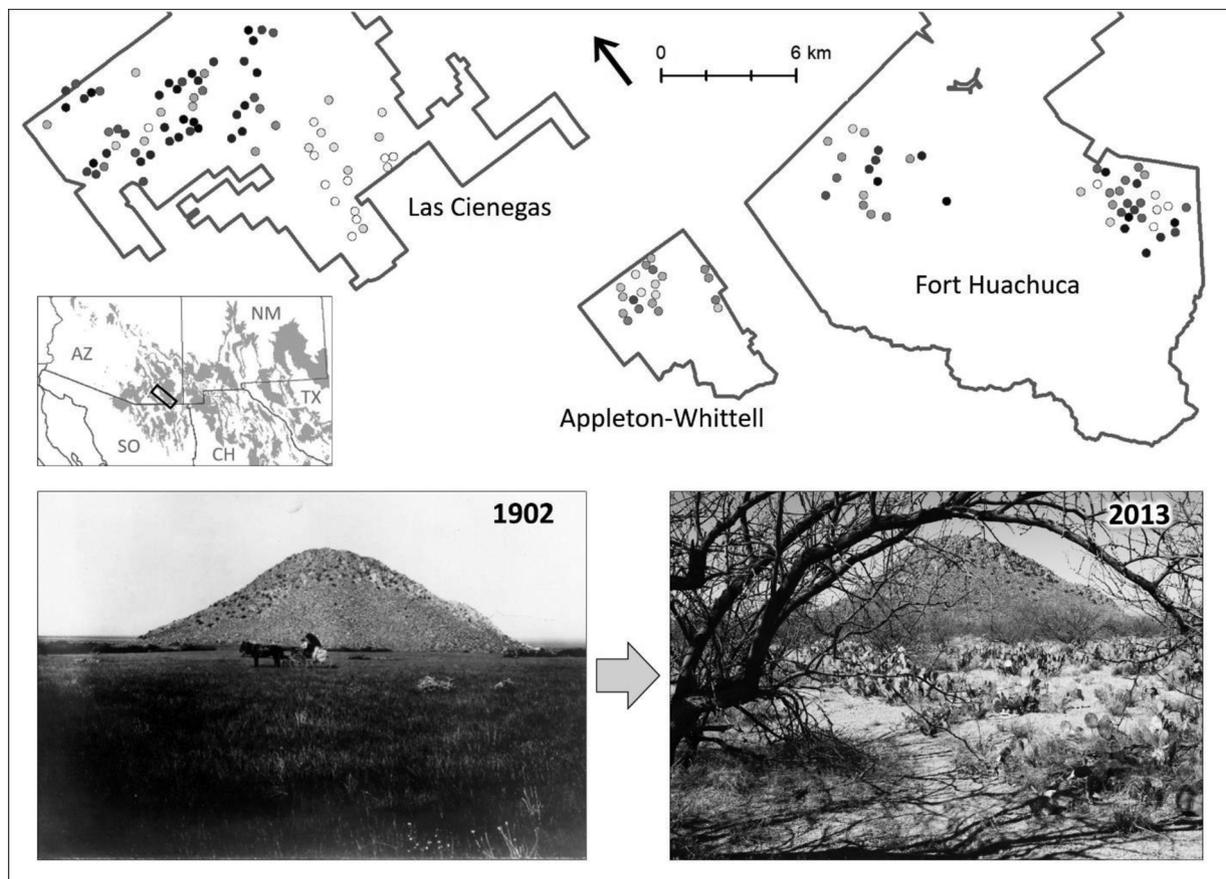


Fig. 1. Location of 140 10-ha plots established at three sites in southeastern Arizona, USA representative of semiarid grasslands in North America, which are indicated by the shaded region on the overview map. Intensity of shading on plot symbols (circles) indicates the amount of woody cover (range = 0–37%), which has increased through time as woody plants encroach grasslands (bottom photographs, which depict a semi-arid grassland ~15 km east of our study area). Photographs were provided by the Santa Rita Experimental Range Digital Database (McClaran et al., 2002).

were initiated within three hours of sunrise, and between visits we rotated the sequence in which we surveyed plots.

Although our primary objective was to evaluate responses of birds to WPE, bird populations and communities also reflected variation in other vegetation features. Therefore, we characterized species composition and structure of the entire plant community on each plot by surveying 12 10-m diameter subplots, three along each cardinal axis and located 25 m, 75 m, and 125 m from plot-center. Two observers surveyed vegetation on all plots, each surveying half of the subplots. On each subplot, we visually estimated canopy cover and species composition (as percentage of total cover) of woody plants, succulents, grasses, and forbs (herbaceous dicots), and surface cover of litter and bare ground by combining estimates from four quadrants. For woody plants, we considered only individuals ≥ 0.5 m tall because we could not reliably detect shorter individuals in tall grasses; these shrubs contributed little to total woody cover. Additionally, we measured grass height at eight points spaced systematically along the perimeter of each subplot. Although we also estimated height of woody plants, height and woody cover were correlated ($r = 0.42$, $P < 0.0001$), so we excluded height from analyses to reduce the potential for confounding. For analysis, we averaged estimates of vegetation cover, composition, and grass height from all subplots on each plot. We surveyed vegetation in September when birds had finished breeding, biomass of grasses had peaked, and identification of grasses was aided by the presence of inflorescences.

2.4. Data analyses

We evaluated how distributions and species richness of breeding

birds varied with WPE by using a Bayesian formulation of a hierarchical, multispecies occupancy model (Dorazio et al., 2006; Dorazio and Royle, 2005) extended to incorporate the influence of environmental and survey covariates on probabilities of occupancy and detection (Russell et al., 2009). This model enabled us to evaluate the aggregate response of the bird community to WPE by estimating simultaneously the species-specific probabilities of occupancy and detection for each of the 35 species of breeding birds we detected during surveys (Table 1).

In the model for occupancy, we included five plot-level covariates: linear and quadratic terms for woody cover to evaluate the influence of WPE and three components from a principal components analysis to account for the influence of other environmental features that were likely to influence distributions of breeding birds. These three principal components captured 65% of the original variation in nine non-focal environmental features: cover of bare ground, litter, succulents, forbs, and grasses; grass height and diversity (Shannon's index); relative cover of nonnative grasses; and topographical variation, which we quantified as the standard deviation of elevations within a plot as calculated by GIS (based on 1/3 arc-second National Elevation Dataset). In our model of the observation process, we included four survey-level covariates that we expected to influence detections of birds during surveys: Julian day (as both linear and quadratic terms), minutes-past-sunrise, and cover of woody plants.

We standardized all covariates to Z-scores (mean = 0, SD = 1) to improve numerical convergence and we specified diffuse prior distributions for all parameters. Specifically, we specified a normal distribution (mean = 0, SD = 1000) for means and uniform distributions (min = 1, max = 100) for variances of hyperparameters of the species-

Table 1

Breeding birds classified as obligate and facultative grassland species (Vickery et al. 1999), their four-letter species code, common and Latin names, number of individuals detected, and number of plots where detected ($n = 140$ surveyed) in semiarid grasslands of southeastern Arizona, USA, 2013–2015.

Classification	Code	Common name	Latin name	No. indiv.	No. plots
Obligate	BOSP	Botteri's sparrow	<i>Peucaea botterii</i>	1580	139
	CASP	Cassin's sparrow	<i>Peucaea cassinii</i>	128	56
	EAME	eastern meadowlark	<i>Sturnella magna</i>	350	109
	GRSP	grasshopper sparrow	<i>Ammodramus savannarum</i>	515	61
	HOLA	horned lark	<i>Eremophila alpestris</i>	94	19
	MONQ	Montezuma quail	<i>Cyrtonyx montezumae</i>	21	18
Facultative	AMKE	American kestrel	<i>Falco sparverius</i>	20	16
	ATFL	ash-throated flycatcher	<i>Myiarchus cinerascens</i>	182	70
	BHCO	brown-headed cowbird	<i>Molothrus ater</i>	122	45
	CAKI	Cassin's kingbird	<i>Tyrannus vociferans</i>	53	34
	CANT	canyon towhee	<i>Melospiza fusca</i>	84	42
	LOSH	loggerhead shrike	<i>Lanius ludovicianus</i>	77	49
	MODO	mourning dove	<i>Zenaidura macroura</i>	368	110
	RCSP	rufous-crowned sparrow	<i>Aimophila ruficeps</i>	100	38
	SCQU	scaled quail	<i>Callipepla squamata</i>	29	17
	WEKI	western kingbird	<i>Tyrannus verticalis</i>	103	49
	Other spp.	BEWR	Bewick's wren	<i>Thryomanes bewickii</i>	24
BLGR		blue grosbeak	<i>Passerina caerulea</i>	276	95
BTSP		black-throated sparrow	<i>Amphispiza bilineata</i>	503	102
BUOR		Bullock's oriole	<i>Icterus bullockii</i>	64	30
CACW		cactus wren	<i>Campylorhynchus brunneicapillus</i>	31	21
CBTH		curve-billed thrasher	<i>Toxostoma curvirostre</i>	24	17
GIWO		Gila woodpecker	<i>Melanerpes uropygialis</i>	13	10
GRRO		greater roadrunner	<i>Geococcyx californianus</i>	12	12
HOFI		house finch	<i>Haemorrhous mexicanus</i>	56	26
LASP		lark sparrow	<i>Chondestes grammacus</i>	227	53
LBWO		ladder-backed woodpecker	<i>Picoides scalaris</i>	87	53
LUWA		Lucy's warbler	<i>Oreothlypis luciae</i>	154	46
NOFL		northern flicker	<i>Colaptes auratus</i>	16	12
NOMO		northern mockingbird	<i>Mimus polyglottos</i>	197	66
PYRR		pyrrhuloxia	<i>Cardinalis sinuatus</i>	24	16
SCOR		Scott's oriole	<i>Icterus parisorum</i>	30	19
VEFL		vermillion flycatcher	<i>Pyrocephalus rubinus</i>	55	25
VERD		verdin	<i>Auriparus flaviceps</i>	13	9
WWDO		white-winged dove	<i>Zenaidura asiatica</i>	16	14

specific regression parameters (Kery and Royle, 2015); we specified a uniform distribution (0, 1) for the community occupancy parameter. We fitted the model using Markov-chain Monte-Carlo simulation implemented in JAGS (Plummer, 2003) with the R package jagsUI (Kellner, 2016). We sampled the posterior distribution with three independent Markov chains, each set to 100,000 samples with a burn-in of 25,000 samples and thinned chains by 10. We assessed convergence by visual inspection of chains and Brooks-Gelman-Rubin statistics (assuming convergence when $\hat{R} < 1.05$; Gelman et al., 2004). We considered species distributions to be influenced by WPE if the 90% credible interval excluded zero for either linear or quadratic woody cover terms. We used this conservative criterion to increase the likelihood of capturing ecologically meaningful responses by uncommon species that were detected infrequently. Lastly, we used simple linear regression to describe how non-focal environmental features varied with woody cover.

3. Results

3.1. Vegetation

The plots we surveyed spanned the full encroachment gradient, as woody cover ranged from 0 to 37%, which is near the maximum expected for semiarid uplands with similar precipitation regimes in this region (Archer et al., 2017; Table 2, Fig. 1). Velvet mesquite was the dominant woody species, comprising approximately 87% of all woody cover and 99% of cover for plants > 2 m tall. For the vegetation features we measured (Table 2), only cover of perennial grasses and bare ground varied systematically with cover of woody plants. Specifically, for every

Table 2

Mean, standard deviation, minimum and maximum values for vegetation features across plots ($n = 140$) in semiarid grasslands of southeastern Arizona, USA, 2013–2015

Measure	Category	Mean	SD	Min	Max
Cover (%)	woody plants	9.7	8.9	0.0	36.5
	bare ground	21.2	12.9	3.3	65.0
	litter	5.1	4.5	0.3	29.8
	succulents	0.4	1.2	0.0	9.3
	forbs	8.9	8.1	0.3	52.7
	grasses	67.8	16.5	25.0	93.4
Height	woody plants (m)	3.4	0.9	0.5	7.2
	grasses (cm)	57.6	11.3	30.7	86.7
Diversity (H')	grasses	1.3	0.5	0.1	2.3
Composition (%)	nonnative grasses	49.8	30.5	0.0	98.7

1% increase in cover of woody plants, cover of perennial grasses decreased by 0.7% (SE = 0.17, $t_{138} = -4.20$, $P = 0.0001$) and cover of bare ground increased by 0.4% (SE = 0.12, $t_{138} = 3.71$, $P = 0.0002$).

3.2. Breeding birds

We detected 5,648 individuals of 35 species of breeding birds during 560 surveys (Table 1). As woody cover increased, occupancy for the entire breeding bird community (i.e., the aggregate response of all of breeding species) increased (Fig. 2; estimates for all model terms in Appendix A Table S1). Consequently, species richness of breeding birds increased sharply as cover of woody plants increased, peaking at approximately 22% cover (Fig. 3). Cover of woody plants influenced the

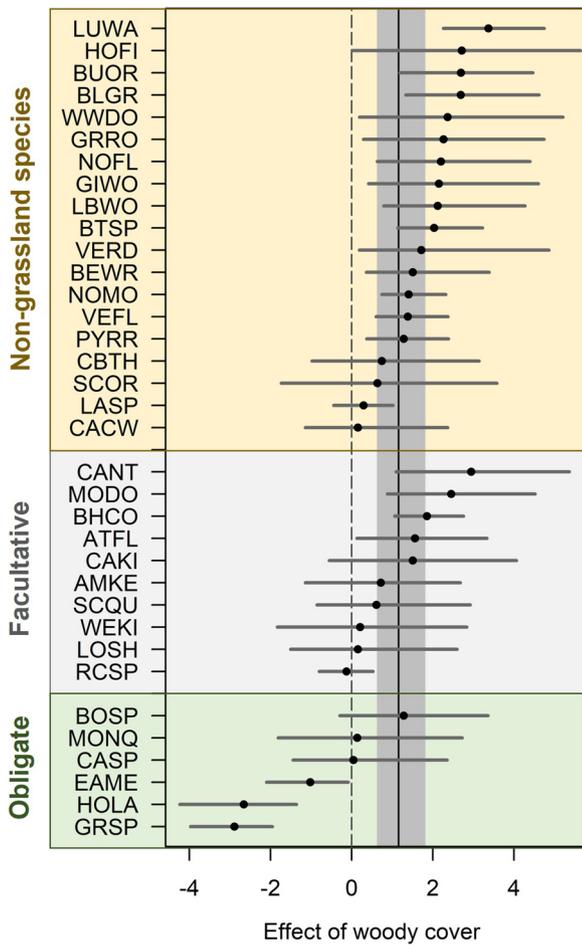


Fig. 2. Linear effect of woody cover on probability of occupancy (Z-score on the logit scale) for 35 breeding species (species abbreviations in Table 1) in semiarid grasslands of southeastern Arizona, USA, 2013–2015 ($n = 140$). Solid vertical line indicates the posterior mean and dark gray shading the 90% CRI for the aggregate response of all breeding species (i.e., estimate of the hyperparameter for mean community occupancy); black points represent the mean for each species and horizontal lines its 90% CRI. Species are grouped as obligate grassland species (bottom), facultative grassland species (middle), and species not associated strongly with grasslands (top). There was evidence of curvature in the responses to woody cover (quadratic term) for all species except AMKE, BOSP, LOSH, MONQ, RCSP, and SCQU.

distributions of 29 of the 35 (83%) breeding species we observed, including 4 of 6 (67%) obligate grassland species, 6 of 10 (60%) facultative grassland species, and all 19 (54%) species not associated strongly with grasslands (Fig. 4). These distributional shifts in response to WPE restructured the breeding bird community.

Breeding birds varied markedly in their responses to WPE. As cover of woody plants increased, occupancy decreased for 5 of 29 (14%) species, two during early stages of WPE and three during later stages (Fig. 4). In contrast, occupancy increased for 24 of 29 (69%) species during early stages of WPE (Fig. 4). As cover continued to increase in later stages of WPE, occupancy continued to increase or plateaued for 15 (63%) of these species and decreased for nine (38%) species. For the nine species that occurred most frequently at intermediate levels of woody cover, occupancy peaked between 10–20% cover for four species and between 20–30% for five species (Fig. 4). Species obligate to grasslands responded to WPE differently than facultative species, with distributions of most obligate species contracting and distributions of most facultative species expanding with increasing woody cover (Fig. 4). The patterns we observed reflect population trends for these species across North America, with the grassland obligates declining

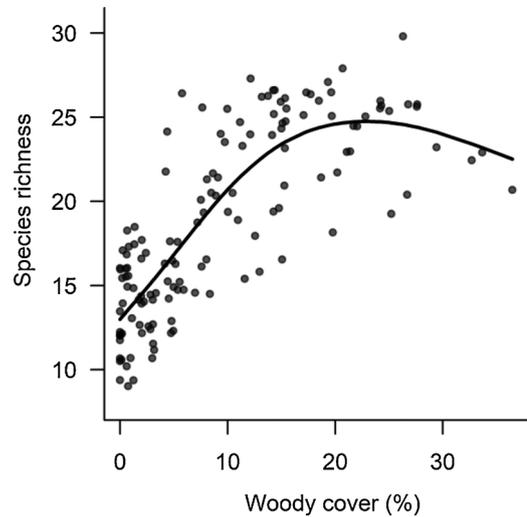


Fig. 3. Effect of woody cover on species richness of breeding birds in semiarid grasslands of southeastern Arizona, USA, 2013–2015. Points represent estimates of species richness on 140 10-ha plots.

more steeply range-wide than both the facultative species and species not associated strongly with grasslands (Table 3). Responses were not consistent for all members of these groups, however, and occasionally varied among closely related species. For example, responses to WPE varied markedly among the three most common grassland obligates in the family Passerellidae (New World sparrows). Specifically, grasshopper sparrows (scientific names in Table 1) were absent from grasslands where woody cover exceeded ~10%, Cassin’s sparrows were likely to occupy grasslands where woody cover was <20% but less likely where woody cover was >20%, and Botteri’s sparrows were largely unaffected by the amount of woody cover (Figs. 2 & 4).

4. Discussion

Proliferation of woody plants into biomes once dominated by grasses has transformed the structure and composition of many of these threatened plant communities (Van Auken, 2009). These changes have altered the quantity and quality of habitat for animals, although the linkages between increases in woody vegetation and effects on animal communities are not well understood despite their importance to many imperiled populations (Archer et al., 2017). Recent meta-analyses suggest that, compared to other vertebrates, the structure of bird communities may be especially resilient to encroachment by woody plants (WPE; Stanton et al., 2018). In contrast, we found that WPE by *Prosopis*, a genus of woody plants that has proliferated in grassland and savanna ecosystems worldwide (Archer et al., 2017; Sharma and Dakshini, 1991), affected the distributions of most breeding birds in semiarid grasslands of southeastern Arizona. Changes in distributions functioned to restructure the breeding bird community, with species being added or lost as species-specific thresholds of woody cover were surpassed.

4.1. Species-specific responses

Species-specific responses to WPE govern changes in composition of animal communities as woody plants proliferate in grasslands and increase in dominance through time. In early stages of encroachment, woody plants increase the vertical structure of vegetation substantially, which increases the diversity of resources and niche spaces available for animals, consistent with the habitat heterogeneity hypothesis (MacArthur and MacArthur, 1961; Tews et al., 2004). Species capable of exploiting these new niches join the community of grassland specialists that are present prior to and during early stages of

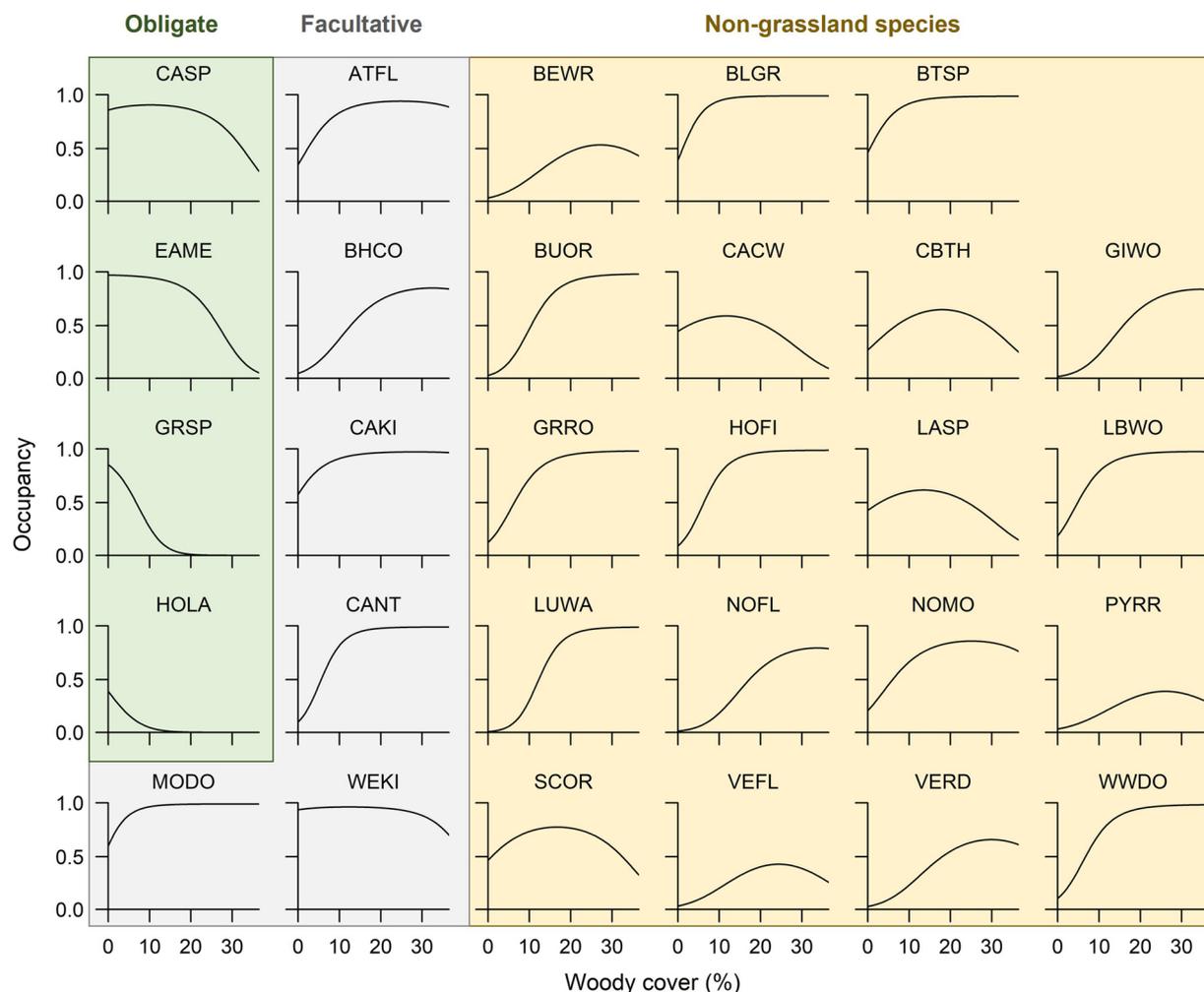


Fig. 4. Effect of woody cover on occupancy of 29 species of breeding birds (species abbreviations in Table 1) in semiarid grasslands of southeastern Arizona, USA, 2013–2015 ($n = 140$). Species are grouped as obligate grassland species (left), facultative grassland species (middle), and species not associated strongly with grasslands (right). Steepness of slopes indicate the narrowness of the threshold of woody cover at which species entered or exited the bird community. An additional six breeding species were not affected markedly by woody cover.

Table 3

Linear effect of woody cover on probability of occupancy (Z-score on the logit scale) from this study and survey-wide population trends (percent change annually) for two periods from the Breeding Bird Survey (Sauer et al., 2017a) for obligate grassland, facultative grassland, and other species (not classified as grassland specialists by Vickery et al., 1999) in semiarid grasslands of southeastern Arizona, USA, 2013–2015. Species comprising each group are provided in Table 1. Trend data were not available for two of the grassland obligate species we studied.

Metric	Species group		
	Obligate	Facultative	Other
Effect of woody cover (this study)	-0.9	1.2	1.8
Annual trends (Breeding Bird Survey)			
1966-2015	-2.3	-0.6	-0.5
2005-2015	-1.9	0.1	-0.1

encroachment, increasing species richness (Sirami et al., 2009). In the grasslands we studied, several species classified as facultative grassland species were absent from grasslands without woody plants but joined the bird community during early stages of WPE. Examples include species that require shrubs for nesting (e.g., canyon towhee) or perches for foraging (e.g., ash-throated flycatcher). As woody plants continue to proliferate, shrub-associated bird species colonize encroached

grasslands and become more common, but the thresholds of woody cover at which these species join the bird community vary. For example, occupancy exceeded 0.8 for several shrub-nesting species (e.g., black-throated sparrow, blue grosbeak) before woody cover reached 10%, whereas for other species (e.g., Bullock’s oriole, Lucy’s warbler), occupancy did not reach 0.8 until woody cover neared 20%.

As grasslands transition to shrub savannas, species associated most strongly with grasslands are likely to disappear from the community as the quantity and quality of their habitat is reduced (Block and Morrison, 2010; Coffman et al., 2014; Coppedge, 2004; Skowno and Bond, 2003). These decreases can occur gradually as encroachment intensifies, as demonstrated by eastern meadowlarks, or quickly, as demonstrated by grasshopper sparrows and horned larks, the two species most sensitive to WPE in the grasslands we studied. These two species were eliminated when woody cover exceeded about 10%. As encroachment continues, some shrub-associated species that join the bird community during early stages of WPE become less common. Curve-billed thrashers and Scott’s orioles, for example, occurred less commonly in encroached grasslands when woody cover exceeded 20%. In later stages of encroachment, cover of woody plants can approach maximum values dictated by local climatic and topographic constraints (Sankaran et al., 2005), creating habitat for species associated with woodlands, such as Bewick’s wrens. During these latter stages of encroachment, maturing woody plants develop habitat elements that

some species require for nesting. For example, the three woodpecker species that bred in encroached grasslands occurred more frequently as woody cover increased and trees became large enough to support nesting cavities. These cavities provided breeding opportunities for secondary cavity nesters such as ash-throated flycatchers and Lucy's warblers, which also became increasingly likely to occur as woody cover increased.

4.2. Community-level responses

Effects of WPE on community-level metrics such as species richness are governed by the aggregate responses of individual species (Zipkin et al., 2009). Accordingly, the stage of WPE at which richness of an animal community is maximized will depend on thresholds at which members of the regional species pool are added to or lost from the community; that is, where gains of new species outweigh losses of existing species (Archer et al., 2017). In grass-dominated ecosystems with large numbers of grassland specialists, richness will likely be maximized early in the encroachment process when habitat is created for species that require a woody-plant component, but before grassland specialists are displaced (Fig. 5). If the regional pool of species that use woody plants is similar numerically to the pool of grassland specialists, richness will likely be maximized at intermediate stages of encroachment (Fig. 5), a pattern documented for arthropods (Blaum et al., 2009) and mammalian carnivores (Blaum et al., 2007) in semiarid savannas and for birds in mesic savannas (Sirami and Monadjem, 2012). If the regional pool of species that rely on woody plants is larger than the pool of grassland specialists, however, richness may continue to increase throughout the encroachment process (Fig. 5). This pattern may hold for semiarid systems in which grasslands exist within a mosaic of plant communities dominated by woody plants. In the southwestern United States, for example, semiarid grasslands occur at intermediate elevations where they are bordered by desert shrublands at lower elevations and woodlands at higher elevations, as well as being interspersed with riparian channels or swales that historically supported woody plants (Van Auken, 2000). This assemblage of plant communities supports a large regional pool of bird species that can colonize grasslands encroached by woody plants, resulting in a net increase in species richness despite elimination of grassland specialists. In our study, species richness doubled when woody cover increased from 0 to about 22%, then decreased slightly as woody cover approached maximum values for encroached grasslands in this region.

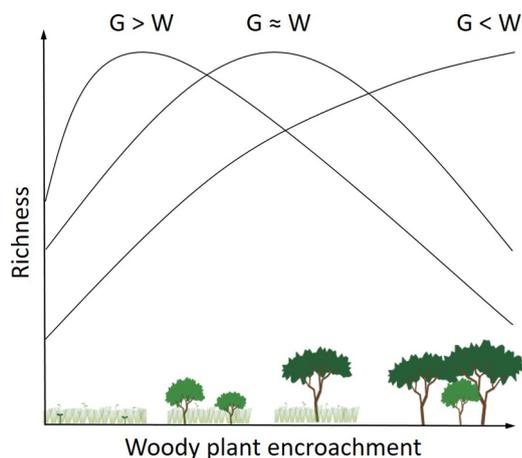


Fig. 5. The stage of woody plant encroachment in grassland ecosystems when species richness of animals is maximized likely depends on the number of grassland-specialist species (G) relative to the number of species dependent on woody plants (W) in the regional species pool available to colonize encroached grasslands.

4.3. Conservation implications

Our results highlight the importance of understanding species-level responses to WPE as the basis for explaining community-level patterns because increases in (alpha) diversity at local scales might ultimately reduce (gamma) diversity at broader scales as grassland specialists are displaced. In our study, for example, species richness of breeding birds increased as woody plants encroached grasslands, but these increases were driven by expansions in the distributions of generalist and shrub-associated species, many of which are widespread and common at regional scales (Corman and Wise-Gervais, 2005). Importantly, all species whose distributions contracted markedly in response to encroachment were obligate grassland specialists whose abundances decreased by -0.8 to -3.3% annually across North America over the past 50 years (Sauer et al., 2017a; Sauer and Link, 2011).

We also found that responses to encroachment differed between obligate and facultative grassland species, with positive or neutral effects on distributions of most facultative species and negative effects on most obligate grassland species. Although abundances of some facultative species that occur in the region we studied have declined in North America, when considered collectively, populations of these facultative species increased marginally (an average of 0.1% annually) from 2005 to 2015 whereas the obligate species we studied declined by an average of -1.9% annually (Table 3; Sauer et al., 2017a). These differences in responses between groups highlight the importance of prioritizing grassland obligates when developing conservation strategies to curtail the effects of WPE. Because of their usefulness as indicators of grassland condition (Browder et al., 2002), management actions that benefit grassland obligate birds are likely to have positive and cascading effects on other grassland-specialist taxa and ecosystem function.

As anthropogenically driven processes continue to degrade and fragment grasslands and woody plants continue to compromise remaining grasslands remnants, developing strategies to reduce the effects of WPE on grassland endemics is increasingly important to maintain populations of these declining species (Correll et al., 2019). Mechanical clearing, herbicide application, and prescribed burning are viable management options for reversing or controlling rates of WPE, but these approaches are expensive and require a commitment to repeated treatments through time (Thompson et al., 2016). Integrated brush management systems provide an ecological framework for combining local information on vegetation, climate, soils, and topography that can help to determine the most effective type, sequence, and timing for treatments (Archer et al., 2017). Identifying thresholds where WPE begins to influence distributions and demography of individual grassland species in other grassland systems should be a priority because these thresholds provide specific targets for conservation and restoration efforts that will maximize benefits for species of conservation concern.

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Declaration of Competing Interest

Both authors have no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2019.108276>.

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