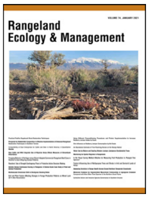
Rangeland Ecology & Management 78 (2021) 15–25

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: www.elsevier.com/locate/rama



Integrating Wildlife Count Models With State-and-Transition Models to Enhance Rangeland Management for Multiple Objectives[☆,☆☆]

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ARTICLE INFO

Article history:
Received 23 February 2020
Revised 4 April 2021
Accepted 19 April 2021

Key Words:
Alternative state
Count model
Ecosystem service
Sagebrush
Songbirds
State-and-transition model

ABSTRACT

State-and-transition models (STMs) are tools used in rangeland management to describe linear and nonlinear vegetation dynamics as conceptual models. STMs can be improved by including additional ecosystem services, such as wildlife habitat, so that managers can predict how local populations might respond to state changes and to illustrate the tradeoffs in managing for different ecosystem services. Our objective was to incorporate songbird density into an STM developed for sagebrush rangelands in northwest Colorado to guide local management of sagebrush birds. The STM included two shrub-dominated community phases, a native grassland state, and a shrubland and grassland phase within an exotic-dominated state. We surveyed plots for songbirds, collected a suite of vegetation indicators at each plot, and quantified songbird habitat relationships with count-based regression models. We then used the estimated models to predict songbird density based on average vegetation conditions per state or community phase. Moderate or increasing shrub cover were important predictors for shrubland-associated species, and responses to understory components varied by species. In the STM, we predicted higher densities of shrubland-associated bird species in the shrub-dominated phases and higher densities of grassland-associated bird species in the state and phase lacking shrub cover. No single state or phase captured the highest density for all songbirds, illustrating the value of alternative states. Our results also demonstrate the utility of displaying traditional wildlife count models against the range of vegetation conditions associated with each state or phase to understand how wildlife density can vary within states and phases. Our approach can assist land managers to gauge the potential impacts of land-use decisions and natural vegetation variability on wildlife, especially for species of conservation concern.

Introduction

The sagebrush biome of western North America once encompassed > 60 million ha but now occupies approximately half of its former distribution (Knick et al. 2003; Miller et al. 2011). The invasion of exotic grasses, such as cheatgrass *(Bromus tectorum)*, and changing fire regimes have contributed to the loss of diverse sagebrush rangelands, in addition to increasing energy development, conifer expansion, and climate change (Miller et al. 2011). Given the fragmentation and deterioration of sagebrush rangelands, populations of many avian species in this ecosystem have declined (Knick and Rotenberry 2002). Some species rely entirely on sagebrush ecosystems for activities such as nesting and foraging (e.g., sagebrush sparrow *[Artemisiospiza nevadensis]*, Brewer's sparrow *[Spizella breweri]*, and sage thrasher *[Oreoscoptes montanus]*), whereas others rely on shrub cover in general (e.g., green-tailed towhee *[Pipilo chlorurus]*; Braun et al. 1976). Several songbird species that rely on sagebrush during the breeding season have declined in all or part of their range (Knick and Rotenberry 2002).

[☆] This study was supported by a USDA NRCS Conservation Innovation Grant 69-3A75-12-213 and Colorado Agricultural Experiment Station project COL00698A. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

[☆☆] doi: 10.1016/j.rama.2021.04.005

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https://doi.org/10.1016/j.rama.2021.04.005

State-and-transition models (STMs) are among the tools currently used for rangeland management as a way to organize and communicate information about rangeland dynamics (Bestelmeyer et al. 2017). STMs are conceptual models that describe ecosystem change, allowing both alternative stable states and linear successional dynamics (Westoby et al. 1989). STMs are typically composed of a reference state (based on historical or "healthy" ecosystem conditions) and often several alternative states (US Department of Agriculture Natural Resources Conservation Service [USDA NRCS] 1997; Bestelmeyer et al. 2017). A state is a persistent vegetation community that is determined by both soil properties and vegetation structure (Stringham et al. 2003). Transitions are the trajectories or drivers of change between states (Bestelmeyer et al. 2017). Within a state, plant composition can shift among phases and along reversible pathways in response to weather or disturbance events, reflecting the natural dynamics of different plant communities; these community phases are transient plant communities (Stringham et al. 2003).

States were historically described in terms of productivity for livestock forage, but describing a state in terms of multiple properties like plant species richness, composition, structure, and ecological function could allow a broader inclusion of the services a state provides, such as wildlife habitat (Twidwell et al. 2013; Bestelmeyer et al. 2017). Land managers could then use STMs to predict how wildlife habitat, and thus local populations, may change in response to changing vegetation conditions (Holmes and Miller 2010). Incorporating habitat relationships for multiple species of concern within an STM would also illustrate the different habitats provided by alternative states and phases, which are likely necessary to support wildlife diversity (Fuhlendorf et al. 2012, 2017). Recent studies have examined avian occurrence within ecological sites and STMs (Doherty et al. 2011) or evaluated the potential for ecological sites and STMs to incorporate measures that assess wildlife habitat (Williams et al. 2011). For instance, grasshopper sparrow *(Ammodramus savannarum)* abundance was greatest in a native perennial grassland community phase, and a shift to a sagebrush or annual grassland community phase reduced sparrow abundance (Holmes and Miller 2010).

We sought to improve upon previous efforts by integrating habitat relationships for multiple songbird species of conservation concern within an STM as an additional ecosystem service. The STM we used was generalized across multiple ecological sites (Tipton 2015) to make it more likely to be used by landowners and managers (Bestelmeyer et al. 2016). An STM usually corresponds to one ecological site, which has distinctive soil, climatic, and topographical properties that determine a site's characteristic plant community (Bestelmeyer et al. 2003). However, landowners may prefer to manage by vegetation types or ecosystems rather than at finer scales of ecological sites and soil map units (Knapp and Fernandez-Gimenez 2009). We also used an STM developed in collaboration with multiple stakeholders (e.g., ranchers, state wildlife biologists, range ecologists; Bruegger et al. 2016) so that the results would be more relevant to local land managers (Knapp et al. 2011; Kachergis et al. 2013).

Our first objective was to incorporate habitat relationships for several songbird species into an STM to predict how songbird density might respond to state or community phase changes and illustrate the tradeoff in managing for alternative states. Our second objective was to display the habitat relationships against the range of vegetation conditions associated with each state or phase to illustrate how this range affects songbird densities. We collected vegetation and songbird count data in three study areas dominated by sagebrush in northwest Colorado and used the vegetation data from STM development to model songbird counts. We then used the models to predict songbird density for states and community phases in an STM developed for one of the study areas and displayed the models for a shrubland and grassland-associated songbird against the variability in vegetation conditions for each state and phase.

Methods

Study Area

We collected vegetation and songbird data at three sagebrush-dominated study areas in northwest Colorado from 2013 to 2015 (Fig. 1). The western Moffat County study area (≈13 420 ha in size) was characterized by low sagebrush *(Artemisia arbuscula)* and Wyoming big sagebrush *(A. tridentata wyomingensis)* communities on sandier soils and salt shrub (*Atriplex* spp.) communities on clayey soils; however, soils were highly intermingled relative to the other study areas (USDA NRCS 2013). Wyoming big sagebrush communities and loamy or sandy soils dominated the eastern Moffat County study area (≈38 200 ha in size; USDA NRCS 2013). The study area in Routt County (≈1 700 ha in size) was dominated by mountain big sagebrush *(A. t. vaseyana)* on loamy soils and low sagebrush on clayey soils (USDA NRCS 2013). A bunchgrass (e.g., Sandberg bluegrass [*Poa secunda*]) or western wheatgrass *(Pascopyrum smithii)* dominated the understory in each study area. Annual precipitation during the study varied from ≈10 to 20 cm for western Moffat, 20 to 30 cm for eastern Moffat, and 30 to 50 cm for Routt (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu 2015). Three wildfires occurred before the study in eastern Moffat County: a 2010 wildfire (3 185 ha), a 2008 wildfire (10 243 ha), and a smaller 2008 fire (1 505 ha; Tipton 2015). Past mechanical treatments to reduce shrub density in eastern Moffat included mow, brush beat, and drag treatments, each < 200 ha in size and 13–19 years old as of 2015 (Tipton 2015).

In each study area, STM development was collaborative in that local stakeholders critiqued drafts of STMs and provided input after data collection and analyses (Tipton 2015; Bruegger et al. 2016). We used a stratified random sampling design across all three study areas and focused the sampling effort in each study area based on local stakeholder questions and interest and availability of existing ecological site descriptions. Although we used songbird and vegetation data collected at all three study areas to model habitat relationships, we only include STM development details for eastern Moffat because we only predicted songbird densities within the STM developed for the eastern Moffat study area.

In the eastern Moffat study area, stakeholders were most interested in sandy and loamy ecological sites as they were the predominant sites in the study area. Stakeholders also wanted to know about the effects of mechanical shrub treatments and wildfire on birds and plants. Therefore, we randomly allocated sampling plots within past treatments (i.e., burned and mechanically treated areas) and areas with no known treatments on Sandyland (R034AY330CO) and Rolling Loam (R034AY298CO) ecological sites (USDA NRCS 2013). Although an STM typically corresponds to one ecological site (Bestelmeyer et al. 2003), Tipton (2015) developed one STM across the two ecological sites. Because she found little difference in plant response to disturbance based on ecological site, and landowners also observed little difference in plant response to management actions across ecological sites, one generalized STM was sufficient. The STM (Fig. 2A) included a shrub-dominated state with two community phases (diverse shrubland and needle-and-thread *[Hesperostipa comata]* shrubland), a native grassland (predominantly western wheatgrass and Sandberg bluegrass) state with < 5% shrub cover, and a grass-dominated and shrub-dominated phase within a crested wheatgrass *(Agropyron cristatum)*–dominated state. In this STM, plant communities were most strongly associated with fire and seeding

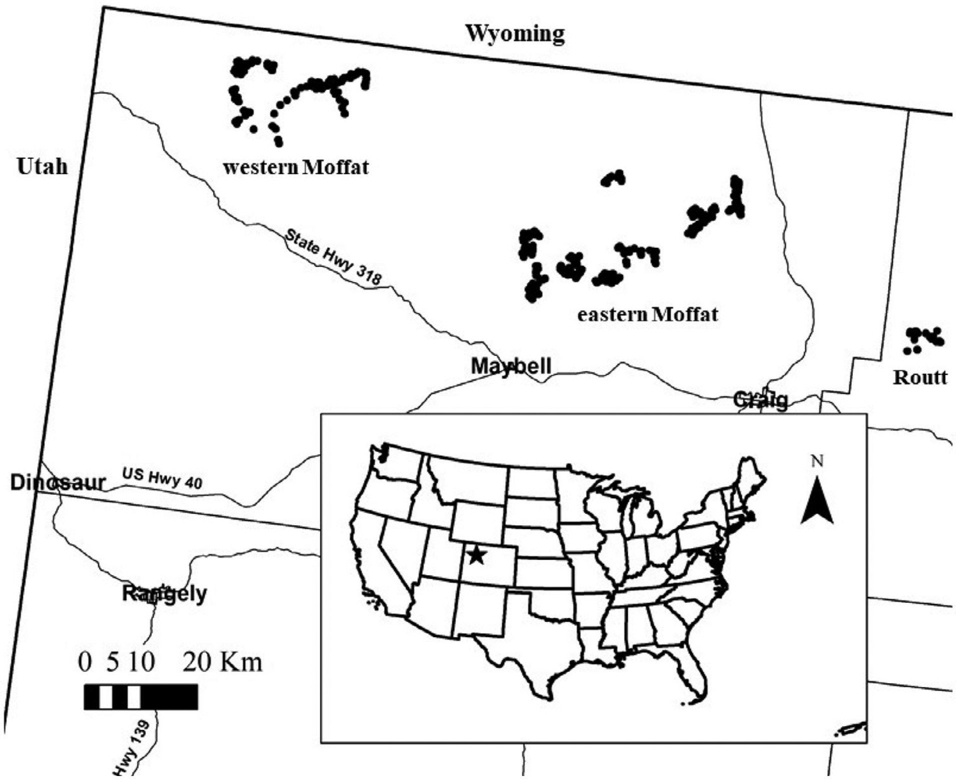

Figure 1. Locations of songbird, vegetation, and soil surveys, 2013–2015, in northwest Colorado with three study areas labeled (western Moffat, eastern Moffat, and Routt). We collected vegetation, soil, and songbird data in all three areas to quantify songbird habitat relationships but predicted songbird densities in just the state-and-transition model developed for eastern Moffat (Tipton 2015).

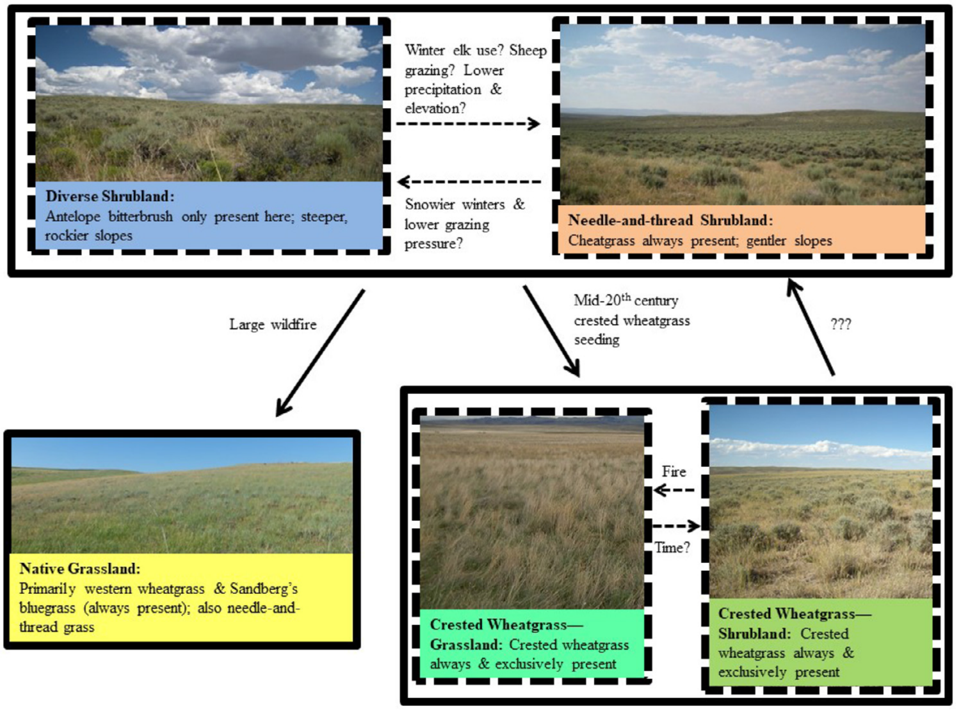

Figure 2. A, State-and-transition model developed for eastern Moffat County on Sandyland and Rolling Loam ecological sites in northwest Colorado, 2013–2015 (based on Tipton 2015) with states and transitions represented by *solid borders* and *arrows* and community phases and pathways represented by *dashed borders* and *arrows*. Photo credits: Jennifer Timmer, CSU. B, Average and minimum-maximum values for vegetation attributes in each state and community phase. Production estimates include grasses and forbs. See Tipton (2015) for full description of possible transition drivers and determination of states and phases.

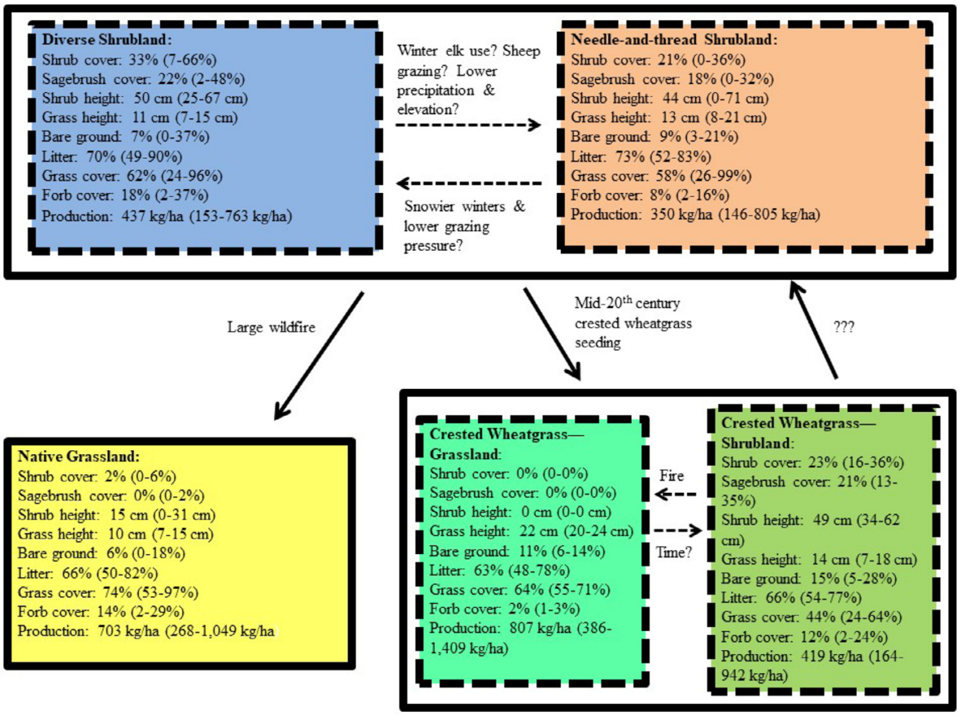

Figure 2. Continued

history. Tipton (2015) classified plant communities associated with crested wheatgrass (average 41% cover) as one state, but due to functional and structural differences, we divided this state into two community phases: shrubland and grassland dominated (Bestelmeyer et al. 2003). Both phases resulted from past crested wheatgrass seeding (Tipton 2015), and the grassland-dominated phase had experienced a wildfire in 2010.

Field Surveys

We surveyed 144 plots for songbirds across the study areas (73 in eastern Moffat, 52 in western Moffat, and 19 in Routt; see Fig. 1) mid-May to late June 2013–2015. To estimate songbird abundance, we conducted standard point count surveys at the center of each plot following a distance sampling protocol (Buckland et al. 2001). The protocol included focusing on detections at and surrounding the point and measuring radial distance with rangefinders to the point where each bird was first detected (Buckland et al. 2001). We identified birds both aurally and visually within a 6-min interval at each point and recorded detected individuals only once. We conducted surveys during the breeding season from sunrise to approximately 4 h after sunrise, depending on weather. We did not conduct surveys during inclement weather, such as rain or windy conditions when activity of the birds or detectability of the birds was hindered. We also conducted surveys beginning at lower-elevation plots earlier in the breeding season and moved up in elevation as the season progressed to capture the phenology of the birds' breeding activity (Hanni et al. 2013). We surveyed each plot for songbirds once a field season.

We measured a suite of ecological site metrics (e.g., vegetation and soils attributes; Herrick et al. 2005) at all survey plots late June through mid-August 2013–2015. We collected the vegetation measurements during this period rather than concurrently with bird count surveys because STMs typically describe the vegetation at peak biomass, and our intent was to link states and phases to avian habitat relationships. Thus, the vegetation metrics described what the birds' habitat would look like in mid to late summer when they are nesting or raising young as opposed to attracting mates (Billerman et al. 2020). For predictors in the songbird count models, we primarily used foliar cover by species, litter, rock, dung, and bare ground as measured with the line-point intercept (LPI) method (Bonham 1989; Herrick et al. 2005) on five parallel 50-m transects at 1-m intervals. We summed foliar cover by species to determine cover by functional group (e.g., shrub cover). For further details on the ecological site metrics, see Tipton (2015). We collected several additional metrics to further characterize songbird habitat. We assessed visual obstruction (VO) with a modified Robel pole (Robel et al. 1970). We recorded VO at five evenly spaced points along two transects per plot, with VO viewed from each ordinal direction per point. We also measured grass height of the nearest plant to each VO reading and averaged the 10 heights per plot. We measured height of the tallest shrub (excluding inflorescences) intercepting the transect when taking LPI measurements.

Data Analyses

Songbird Detection Probabilities

We restricted analyses to the more commonly detected songbirds in the study areas, both shrubland-associated (Brewer's sparrow, green-tailed towhee, sage thrasher, and sagebrush sparrow) and grassland-associated (horned lark *[Eremophila alpestris]*, vesper sparrow *[Pooecetes gramineus]*, and western meadowlark *[Sturnella neglecta]*) species (Wiens and Rotenberry 1981). To estimate songbird density and examine potential variables affecting detectability, we used program Distance 6.0 (Thomas et al. 2010). We excluded outlier detections on the basis of visual inspection of detection histograms and binned distances accordingly (Buckland et al. 2001). Detectability variables included start time; Julian date; observer; how the bird was detected (i.e., calling, singing, or visual); temperature; cloud cover; and wind speed (Hanni et al. 2013). We selected the best detection model for each species using Akaike's information criterion (AIC; Burnham and Anderson 2002) and used the best model to predict density estimates for each plot. We also compared density estimates for the most common songbirds across plots surveyed in multiple years to determine if we could pool data from multiple field seasons (eq. 3.102 in Buckland et al. 2001). Most of the plots (105 out of 144) were surveyed only once during the three field seasons. We did not compare vegetation metrics across years because all plots with vegetation data were surveyed only once over the three field seasons.

Songbird Count Model Development and Evaluation

We evaluated count-based regression models (i.e., generalized linear models) for songbird counts (i.e., response variables) with the vegetation metrics (i.e., predictor variables) collected at each plot. We first identified the appropriate distribution, Poisson or negative binomial, for each species using an intercept-only model and Vuong's test (Hilbe 2011). For each songbird model, we excluded songbird counts beyond the truncation distance, as determined by detection histograms, and included an offset term, which accounted for plot-specific variability in detection and survey effort (eq. 2.2 in Buckland et al. 2009). This allowed us to model observed songbird counts while incorporating differences in detectability across plots as determined from distance sampling. We then used the data in an exploratory approach to determine the appropriate model structure for each species and predictor variable. We examined scatterplots of raw counts and predictor variables to check for nonlinear relationships, outliers, and predictor variables with limited distributions in the study areas. If plots showed evidence of nonlinearity, we evaluated a linear and a quadratic regression model with Bayesian information criterion (BIC) to determine which model structure to retain (i.e., retained the model form with the lowest BIC score). We used BIC for evaluation of the models because BIC penalizes model complexity more heavily than AIC (Burnham and Anderson 2002), and given many predictor variables, we wanted to prevent models from becoming overly complex (Johnson and Omland 2004). We used Pearson's correlation coefficient to test individually if any of the predictor variables were correlated (i.e., $r \geq |0.7|$; Zar 2010).

For each species, we determined the best shrub structure variable (i.e., sagebrush cover, shrub cover, or VO) to include in all candidate models by evaluating univariable models with BIC. We then evaluated all model combinations of predictor variables to determine the best models explaining songbird counts and retained only the highest-ranking model for each species. For all species, we included the best shrub structure variable in each model and also evaluated a shrub structure-only model. Most species included in the analysis are shrub-obligate species, and models without a shrub structure variable would not be as useful for management of sagebrush rangelands. We tested all possible combinations of uncorrelated variables, provided the model included the best shrub structure variable. We only excluded variables from a species' candidate model set if they were correlated with the best shrub structure variable for that species. We examined variance inflation factors (VIF) for each species' top model that contained multiple variables (Menard 1995) and excluded models with mean VIF scores > 2 (Chatterjee et al. 2000) to further reduce multicollinearity. We also excluded models when coefficients of predictor variables were unstable (i.e., reversed their relationship to the response variable across models; Arnold 2010).

To assess the amount of variation explained by our fitted models over an intercept-only model, we calculated a McFadden's pseudo-R^2 value (Zar 2010). We also used a chi-square likelihood ratio test with the lrtest function in package "lmtest" (Hothorn et al. 2019) to determine goodness-of-fit for the top model over an intercept-only (null) model. We evaluated predictive ability for each model by measuring the root mean squared error using five-fold cross validation (Hastie et al. 2009) with the cvFit function in package "cvTools" (Alfons 2015). We performed all analyses in Program R 3.3.2 (R Core Team 2015).

Songbird Density by State or Community Phase

To incorporate songbird density into the STM, we used our best count model for each species to predict the number of individual songbirds per hectare for each state or community phase. For each state or phase, we calculated average vegetation conditions for predictor variables (e.g., shrub cover and bare ground) and average offset terms for songbird detectability. We then used the average vegetation conditions and offset terms per state and phase to predict songbird density per state and phase using each species' best count model. We calculated variability around each predicted density estimate using 95% confidence intervals for the vegetation variables associated with each state or phase because we wanted density estimates to reflect the variability in vegetation conditions. We used a T distribution rather than a normal distribution to calculate the confidence intervals because the population standard deviations were unknown and vegetation sample sizes used to build the STM were small ($n < 33$ plots for each state and phase). Finally, we displayed the variation in predicted songbird density as a function of vegetation variables in the top model for a shrubland and grassland-associated species. We used violin plots to show the distribution of a given vegetation variable within each of the states and community phases from the STM where each violin is plotted at mean predicted density for the songbirds for each state or phase.

Results

Songbird Detection Probabilities

We detected a total of 367 Brewer's sparrows on 109 plots, 97 green-tailed towhees on 45 plots, 129 sagebrush sparrows on 49 plots, 103 sage thrashers on 56 plots, 353 horned larks on 93 plots, 166 vesper sparrows on 64 plots, and 230 western meadowlarks on 77 plots. On the basis of 39 plots surveyed in consecutive field seasons, we did not find a difference among years in density estimates for the most common songbirds and, therefore, pooled data across years. We grouped songbird counts into six or seven bins of distance from the point count and truncated distances > 200–250 m.

Songbird Count Model Development and Evaluation

Detectability offset values, represented as constants in each species' model, were 0.25 for Brewer's sparrows, 1.29 for green-tailed towhees, 1.27 for sagebrush sparrows, 1.42 for sage thrashers, 0.66 for horned larks, 0.71 for vesper sparrows, and 1.79 for western meadowlarks. We detected one horned lark and no sagebrush sparrows or sage thrashers in the Routt study area; therefore, we restricted model development for these species to data collected only in the eastern and western Moffat study areas.

Of the 11 predictor variables considered (Table 1), sagebrush cover, total shrub cover, and VO were correlated, so we retained only the best variable for each species. Shrub height and VO, as well as grass and herbaceous cover, were positively correlated, and bare ground was negatively correlated with litter, grass cover, and herbaceous cover. For species' models that were restricted to the eastern and western Moffat study areas, shrub height was also correlated with sagebrush and shrub cover, and litter and grass were correlated. Therefore, we did not include these variables in the same model. For species' models that were restricted to the eastern and western Moffat study areas (i.e., horned lark, sage thrasher,

Table 1
Definitions of vegetation predictors used in count-based regression models for sagebrush-associated songbirds in northwest Colorado, 2013–2015.

Predictor[1]	Predictor description
sb	Absolute sagebrush foliar cover as measured via line-point intercept (LPI)[2]
shrub	Absolute shrub foliar cover as measured via line-point intercept
VO	Visual obstruction as measured via a modified Robel pole[3]
shrubHT	Height (cm) recorded for the tallest part of a shrub (excluding inflorescence) intercepting the transect line via line-point intercept
grassHT	height (cm) of nearest grajss measured while recording VO
grass	Absolute grass foliar cover as measured via line-point intercept
bg	Absolute bare ground cover as measured via line-point intercept
litter	Absolute litter and woody litter cover as measured via line-point intercept
herb	Total herbaceous foliar cover as measured via line-point intercept
exotic	Absolute exotic plant foliar cover as measured via line-point intercept
forb	Absolute forb foliar cover as measured via line-point intercept

[1] All predictors were collected in 50 × 50 m or 20 × 50 m plots.
[2] Bonham 1989. Absolute cover was obtained based on the proportion of any LPI hits out of the total hits, and total cover was obtained on the basis of the proportion of top hits out of the total hits (Tipton 2015).
[3] Robel et al. 1970. See text for further description.

and sagebrush sparrow), we included forb and exotic cover as they had an even distribution across these two areas; the variables had limited distribution across all three study areas, so they were excluded from the other species' models.

We determined the negative binomial distribution was the best model structure for all songbird species. Abundances of all shrubland-associated songbirds were better explained by variation in total shrub cover rather than just sagebrush cover (Table 2). For both Brewer's sparrow and sage thrasher, the best model was based on shrub attributes with no additional improvement in the model from herbaceous or ground layer attributes (Table 3). For green-tailed towhees, abundance was inversely associated with the amount of bare ground (see Table 3). For sagebrush sparrows, abundance was inversely associated with total cover of grasses and exotic plant cover (see Table 3).

For the grassland-associated birds, the best models were based on shrub cover and bare ground, with density consistently declining with increasing shrub cover across all three species (horned lark, vesper sparrow, western meadowlark; see Tables 2 and 3). Horned larks increased with decreasing litter cover (see Table 3), which was inversely correlated with bare ground exposure; thus, horned lark abundance increased with more bare ground (see Table 3). In contrast, vesper sparrows and western meadowlarks declined with increasing bare ground exposure (see Table 3).

All species' top models explained more variation than a null model with the exception of sage thrasher. Green-tailed towhee, sagebrush and vesper sparrow, horned lark, and western meadowlark models explained the most variation and had good to excellent fit (see Table 2; McFadden 1979). All top models had low root mean squared errors from fivefold cross validation (see Table 2).

Songbird Density by State or Community Phase

In general, we predicted higher densities for shrubland-associated songbirds in the shrub-dominated community phases and higher densities for grassland-associated songbirds in the native grassland state and crested wheatgrass–grassland phase (Table 4). For example, we predicted approximately 3.3 Brewer's sparrows/ha in the diverse shrubland phase compared with 0.8 Brewer's sparrows/ha in the crested wheatgrass–grassland phase; for western meadowlarks, we predicted approximately 4.4 birds/ha in the native grassland state compared with 1.1 birds/ha in the crested wheatgrass–shrubland phase (see Table 4). Predicted songbird densities reflected relationships between songbird species and ground and shrub cover variables associated with the states and phases. Shrubland-associated species that preferred more shrub cover and taller shrubs (i.e., Brewer's sparrow and green-tailed towhee) had higher predicted densities in the diverse

Table 2
Count-based regression models for sagebrush-associated songbirds in northwest Colorado, 2013–2015. We report log-likelihood (LL), number of parameters (K), Bayesian information criterion (BIC), difference in BIC compared with lowest BIC of the model set (ΔBIC), BIC weight (*w*), pseudo-R^2 value, root mean squared error (error) from 5-fold cross validation, and *P* value from likelihood ratio test for models with ΔBIC < 2 and intercept-only models.

	Model[1]	*LL*	*K*	BIC	Delta	*w*	R^2	Error	*P* value
Brewer's sparrow:	Shrub + shrubHT	277.19	4	574.26	0.00	0.45	0.06	2.78	< 0.001
	Shrub + shrubHT + herb + herb^2	272.42	5	574.65	0.39	0.37	0.08	2.78	< 0.001
	Shrub + grassHT + shrubHT + herb + herb^2	270.63	7	576.06	1.80	0.18	0.09	2.77	< 0.001
	Intercept only	295.93	2	601.80	27.54	0.00	0.00	2.85	NA[2]
Sage thrasher:	Shrub + shrub^2	137.11	4	293.53	0.00	0.38	0.04	1.66	0.01
	Intercept only	142.26	2	294.18	0.65	0.28	0.00	1.47	NA[2]
	Shrub + shrub^2 + L	135.28	5	294.71	1.18	0.21	0.05	1.64	0.003
Sagebrush sparrow:	Shrub + shrub^2 + grass + exotic	139.52	6	308.01	0.00	0.36	0.21	2.89	< 0.001
	Shrub + shrub^2 + grass	142.17	5	308.48	0.47	0.29	0.20	2.93	< 0.001
	Shrub + shrub^2 + bg + exotic	140.18	6	309.34	1.33	0.19	0.21	2.95	< 0.001
	Shrub + shrub^2 + L + exotic	140.32	6	309.62	1.61	0.16	0.21	3.05	< 0.001
	Intercept only	176.701	2	363.06	55.05	0.00	0.00	1.88	NA[2]
Green-tailed towhee:	Shrub + shrubHT + bg	131.83	5	288.51	0.00	0.57	0.19	2.29	< 0.001
	Intercept only	162.159	2	331.05	42.54	0.00	0.00	1.66	NA[2]
Horned lark:	Shrub + L	239.95	4	499.22	0.00	0.55	0.12	3.22	< 0.001
	Shrub	242.89	3	500.26	1.04	0.33	0.10	3.21	< 0.001
	Intercept only	271.24	2	552.14	52.92	0.00	0.00	3.36	NA[2]
Vesper sparrow:	Shrub + bg	179.76	4	379.39	0.00	0.57	0.15	2.07	< 0.001
	Shrub + grassHT + bg	177.56	5	379.98	0.58	0.43	0.16	2.11	< 0.001
	Intercept only	212.45	2	434.84	55.45	0.00	0.00	1.98	NA[2]
Western meadowlark:	Shrub + bg	223.22	4	466.33	0.00	0.88	0.15	2.38	< 0.001
	Intercept only	261.09	2	532.12	65.79	0.00	0.00	2.39	NA[2]

[1] Predictor variables described in Table 1.
[2] Did not run the likelihood ratio test to compare a null (intercept only) model against a null model.

Table 3
Beta coefficient estimates (β), standard errors (SE), and 95% confidence intervals for model parameters in the highest-ranked count-based regression model for sagebrush-associated songbirds in northwest Colorado, 2013–2015.

	Variable[1]	β	SE	95% Lower	95% Upper
Brewer's sparrow:	Intercept	−0.39	0.18	−0.77	−0.02
	Shrub	0.01	0.01	0.002	0.03
	ShrubHT	0.02	0.01	0.01	0.03
	Dispersion	3.45	1.06	1.37	5.53
Green-tailed towhee:	Intercept	−2.57	0.51	−3.67	−1.58
	Shrub	0.01	0.01	−0.01	0.04
	ShrubHT	0.03	0.01	0.01	0.05
	bg	−0.07	0.02	−0.10	−0.04
	Dispersion	1.08	0.39	0.32	1.83
Sage thrasher:	Intercept	−3.16	0.49	−4.23	−2.26
	Shrub	0.11	0.04	0.04	0.20
	Shrub^2	−0.002	< 0.001	−0.004	−0.001
	Dispersion	1.98	1.12	−0.21	4.16
Sagebrush sparrow:	Intercept	−2.03	0.87	−3.85	−0.37
	Shrub	0.26	0.08	0.11	0.43
	Shrub^2	−0.01	0.002	−0.01	−0.003
	Grass	−0.03	0.01	−0.05	−0.01
	Exotic	−0.03	0.01	−0.06	−0.005
	Dispersion	1.40	0.48	0.46	2.33
Horned lark:	Intercept	1.78	0.25	1.28	2.28
	Shrub	−0.06	0.01	−0.07	−0.04
	Litter	−0.01	0.004	−0.02	−0.002
	Dispersion	4.69	1.91	0.94	8.44
Vesper sparrow:	Intercept	1.02	0.20	0.62	1.43
	Shrub	−0.04	0.01	−0.05	−0.03
	bg	−0.07	0.01	−0.09	−0.05
	Dispersion	1.87	0.76	0.38	3.37
Western meadowlark:	Intercept	0.65	0.23	0.19	1.14
	Shrub	−0.04	0.01	−0.06	−0.03
	Bg	−0.08	0.01	−0.10	−0.06
	Dispersion	1.08	0.26	0.57	1.59

[1] Predictor variables described in Table 1.

shrubland community phase (see Table 4) because it was associated with greater shrub cover and taller shrubs on average (see Fig. 2B). Horned lark predicted density was higher for the crested wheatgrass–grassland phase than the native grassland state (see Table 4), likely reflecting the bird's positive relationship with bare ground; average bare ground was greatest for the crested wheatgrass–grassland phase (see Fig. 2B). Western meadowlark abundance increased with less shrub cover and bare ground (see Table 3), so predicted densities were highest for the native grassland state (see Table 4), which had less bare ground on average than the crested wheatgrass–grassland phase (see Fig. 2B).

Discussion

We modeled songbird counts as a function of local vegetation attributes and incorporated these models in an STM developed for the sagebrush steppe in eastern Moffat County, Colorado. Our approach demonstrates how traditional wildlife habitat relationships can be included in an STM as an additional ecosystem service to describe the value of alternative states and how the range of vegetation conditions associated with a state or community phase influences songbird density.

Incorporating Songbird Count Models into STMs to Understand Change

Managers can use our quantitative approach to understand how vegetation or state change may affect songbird populations. A transition from the diverse shrubland community phase in a shrub-dominated state to a native grassland state, likely the result of a large fire (see Fig. 2A), is predicted to reduce Brewer's sparrow density from 3.3 birds/ha to 1.2 birds/ha (see Table 4). In contrast, density of a grassland-associated species, the vesper sparrow, is predicted to increase in response to this transition from 0.96 birds/ha to 3.2 birds/ha (see Table 4). In the STM, changes between a shrub-dominated state or community phase and a grassland-dominated state or phase resulted in significant differences for most predicted songbird densities (see Table 4). This is likely due to structural differences between a shrub-dominated and a grass-dominated landscape for shrubland- and grassland-associated species (Knick and Rotenberry 1995). Changes in songbird densities between similar-structured community phases, however, were less noticeable, likely because there was considerable overlap in ranges for vegetation indicators associated with the phases, such as shrub cover and shrub height (see Fig. 2B). For example, confidence intervals for predicted Brewer's sparrow densities overlapped for the diverse shrubland, needle-and-thread shrubland, and crested wheatgrass–shrubland phase (see Table 4). Brewer's sparrows are typically the most common songbird found in sagebrush rangelands (Rotenberry et al. 2020), so managing for any of the shrub-dominated community phases would likely benefit this species. In other regions, however, structural and/or functional differences between community phases in sagebrush rangelands may result in larger differences in associated wildlife densities (Holmes and Miller 2010).

Managing for Alternative States and Different Ecosystem Services

Not surprisingly, we predicted greater densities of shrubland-associated songbirds and lower densities of grassland-associated songbirds in the shrub-dominated community phases (see Table 4). Within shrubland-associated songbirds, we also observed differences in peak predicted densities among the three shrub-dominated phases. These differences reflect nuanced shrub and ground cover preferences for each species and different life history traits. For example, green-tailed towhee densities peaked with greater shrub cover, taller shrubs, and less bare ground (see Table 3). Green-tailed towhees are often found in higher-elevation, montane shrub communities where greater shrub and ground cover provide ample foraging opportunities for seeds and insects

Table 4
Predicted densities of sagebrush-associated songbirds for states and community phases in a state-and-transition model developed in northwest Colorado, 2013–2015 (Tipton 2015). 95% confidence intervals for each density estimate are in parenthesis and are based on variability in the vegetation attributes for each state or phase.

	Diverse shrubland phase	Needle-and-thread shrubland phase	Crested wheatgrass shrub-dominated phase	Crested wheatgrass grass-dominated phase	Native grassland state
Brewer's sparrows/ha	3.31 (2.85-3.80)	2.88 (2.26-3.65)	2.78 (2.06-3.75)	0.84 (0.83-0.85)	1.15 (1.03-1.29)
Green-tailed towhees/ha	1.10 (1.08-1.11)	0.53 (0.46-0.61)	0.56 (0.42-0.75)	0.10 (0.05-0.19)	0.21 (0.21-0.22)
Sage thrashers/ha	0.93 (0.86-0.92)	0.66 (0.51-0.76)	0.85 (0.59-0.95)	0.13 (0.11-0.14)	0.16 (0.15-0.18)
Sagebrush sparrows/ha	0.20 (0.06-0.56)	0.52 (0.26-0.72)	0.49 (0.10-0.94)	0.01 (< 0.01-0.02)	0.05 (0.04-0.05)
Horned larks/ha	0.93 (0.69-1.30)	1.63 (1.16-2.30)	1.91 (1.12-3.25)	6.24 (4.26-9.13)	5.48 (4.94-6.07)
Vesper sparrows/ha	0.96 (0.65-1.45)	1.16 (0.76-1.77)	0.81 (0.28-2.32)	2.40 (1.19-4.85)	3.20 (2.53-4.04)
Western meadowlarks/ha	1.49 (0.96-2.39)	1.52 (0.93-2.46)	1.11 (0.32-3.75)	3.27 (1.42-7.59)	4.43 (3.63-5.84)

and a diversity of taller shrubs for nesting (Aldridge et al. 2011; Dobbs et al. 2020). Thus, green-tailed towhee predicted densities were highest for the diverse shrubland community phase, which contained the greatest shrub cover, the tallest shrubs, and less bare ground on average than the other shrubland phases (see Fig. 2B).

Within grassland-associated songbirds, differences in peak predicted densities among the grassland phase and state also reflected different life history traits. Horned larks typically forage on the ground and place their nests in the open on bare ground (Beason 1995). Thus, horned lark predicted density was greatest for the crested wheatgrass–grassland phase, which was associated with more bare ground on average (see Fig. 2B). In contrast, vesper sparrows usually conceal their nests with grasses and forbs or other vegetation (Jones and Cornely 2020). Vesper sparrow abundance increased with less bare ground, so predicted vesper sparrow density was highest in the native grassland state, which had less bare ground on average than the crested wheatgrass-grassland phase.

These results reflect the value of alternative states within sagebrush ecosystems to support a diverse avian community. Although it is a shrub-dominated system, disturbances, management actions, and abiotic factors promote structural diversity within the sagebrush landscape. This structural diversity is represented by shrub- and grass-dominated states and community phases and supports both shrubland- and grassland-associated species (Rotenberry and Wiens 1980; Wiens and Rotenberry 1981). We likely would not have observed as many grassland species, such as horned larks, if fires had not created grassland patches in the study area. Even shrubland-associated songbirds have different habitat needs within sagebrush rangelands, from green-tailed towhees that prefer more sagebrush and herbaceous cover (i.e., the diverse shrubland phase) to sagebrush sparrows that prefer less shrub and ground cover (i.e., the needle-and-thread shrubland phase; Timmer et al. 2019). Indeed, no single state or phase in the STM captured the highest density for all species. By incorporating habitat relationships for shrubland and grassland-associated species in an STM, we can see the value of different states and phases for supporting bird diversity (Fuhlendorf et al. 2012). Our approach also allows managers to evaluate the tradeoff in ecosystem services from a state or community phase change. Shrubland-associated songbird densities may decline in response to a fire that transitions a native shrubland state to a native grassland state, but grassland bird densities and forage production for livestock would likely increase (see Fig. 2B).

Although our approach illustrates the value of alternative states and community phases in the sagebrush steppe, our models for songbird abundance did not incorporate landscape-level effects of the size or juxtaposition of different vegetation patches on songbird abundance. Such spatially explicit information may be especially important in predicting habitat quality or abundance for species, such as greater sage-grouse *(Centrocercus urophasianus)*, that use multiple patch types across different seasons (Connelly et al. 2011). However, the bird species that we modeled all have relatively small breeding season home ranges that typically encompass a single vegetation patch type (at least at the scale at which we measured different states and phases) and then migrate out of the region during the nonbreeding season (Billerman et al. 2020). Our approach of predicting how abundance varies across states and community phases within an STM is especially suited for these types of wildlife species. We also acknowledge that our study area consisted of large expanses of the diverse shrubland and needle-and-thread shrubland phases, interspersed with smaller patches of the native grassland and crested wheatgrass states (Tipton 2015). As a result, we cannot assess the degree to which our model predictions would apply to landscapes with extensive grasslands interspersed with smaller shrubland patches.

Managing for Variability in Vegetation Conditions Within States and Community Phases

One limitation of predicting songbird densities into states and community phases based on average vegetation conditions is that it obscures the influence of variability in vegetation conditions within a state or phase. Simply identifying the diverse shrubland community phase as the optimal phase for green-tailed towhees masks the influence of bare ground on their abundance because bare ground exposure varies from 0% to 37% within the diverse shrubland phase. Our count model predicts that towhee density can vary from ≈0.2 birds/ha at 37% bare ground to ≈1.1 birds/ha at 0% bare ground (see Fig. 3A). Similarly, vesper sparrow density was greatest in the native grassland state (see Table 4), and managing for average bare ground exposure in this state (6%) is predicted to result in ≈1.6 vesper sparrows/ha. However, vesper sparrow density varies from ≈3.2 vesper sparrows/ha at 0% bare ground exposure to < 1 vesper sparrow/ha at 18% bare ground exposure (see Fig. 3B).

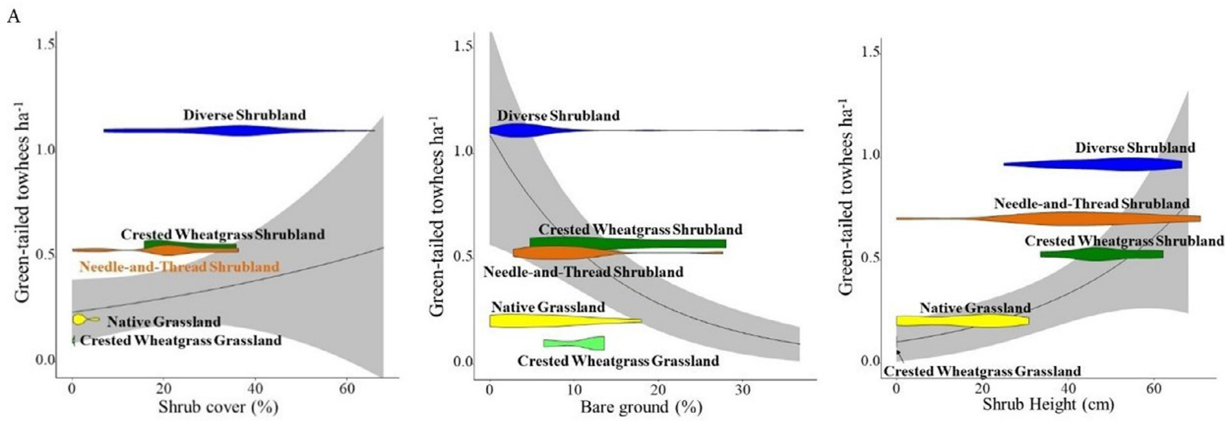

Figure 3. Variation in predicted density of green-tailed towhees (**A**) and vesper sparrows (**B**) displayed as a function of vegetation indicators with 95% confidence intervals shown in gray. In each panel, variation in the height of the colored violin plots indicates the distribution of the given vegetation attribute (x-axis) within each of the states and community phases from a state-and-transition model developed for the sagebrush steppe in northwest Colorado, 2013–2015. Each violin is plotted at mean predicted density (y-axis) for each species for each state or phase.

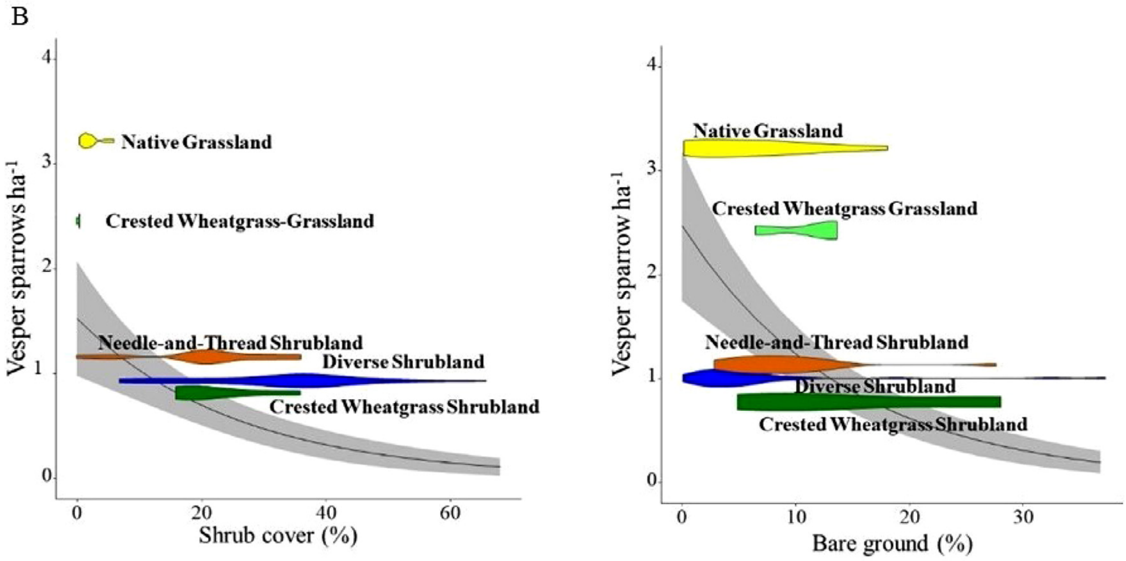

Figure 3. Continued

For both of these species, it is easy to visualize the benefit of managing for less bare ground, which is often a land management objective (Morgan 2005). However, this approach could be especially useful for visualizing how species with different habitat needs, such as a shrubland- and grassland-associated songbird, respond to variation in vegetation conditions from management actions, like shrub removal. There could be a threshold of treatment that minimizes negative impacts to both species or maximizes benefit to the species of greatest conservation concern. Understanding the effect of vegetation variability on wildlife populations within a state or phase could therefore increase management options and promote progress toward wildlife population goals (Hiers et al. 2016).

Conclusion

By incorporating songbird count models into an STM developed for the sagebrush steppe in northwestern Colorado, we can predict songbird response to vegetation change among states and community phases in a way that can be clearly communicated to land and wildlife managers. Managers can also see how alternative states and community phases within an STM benefit songbird species of concern within and across habitat associations. Further, understanding how songbird density varies with the natural range of vegetation conditions rather than just average conditions provides greater flexibility when managing multiple species of concern with different habitat needs (Hiers et al. 2016). Because rangeland systems are complex and dynamic, we argue that STMs should communicate ecosystem change both among and within states and phases, as well as how these changes impact ecosystem services in order to be useful tools for rangeland managers.

Management Implications

If managers or landowners within the sagebrush steppe of northwestern Colorado manipulate understory or ground vegetation, then our approach provides them with a tool to gauge how songbird densities may change in response. For example, if a manager promotes vegetation characteristics associated with the diverse shrubland state, such as greater shrub and herbaceous cover and taller shrubs, then green-tailed towhees would likely benefit. Our approach also allows managers to evaluate the tradeoffs in managing for one songbird species or one state or phase over another. We predicted the highest green-tailed towhee density for the diverse shrubland community phase and the highest sagebrush sparrow density for the needle-and-thread shrubland phase. If managers treated one of these shrubland phases as the management standard or reference condition and promoted it on the landscape above other states and phases (USDA NRCS 1997), this could have negative consequences for other songbirds (Derner et al. 2009; Fuhlendorf et al. 2012).

A manager may also want to understand the range of songbird densities within a state or phase based on the natural variability of understory and ground conditions. For example, shrub height within the diverse shrubland phase varied from 25 cm to 67 cm (see Fig. 2B). Therefore, a manager could expect green-tailed towhee density to vary across this phase on the basis of minimum (≈0.2 birds/ha) and maximum (≈0.7 birds/ha) shrub height and also predict the effect of managing for average shrub height conditions (≈0.4 birds/ha; see Fig. 3A). Finally, managers can estimate how other ecosystem services might respond to a landscape disturbance, such as fire. In our study area, a fire transitioning the needle-and-thread shrubland community phase to a native grassland state is predicted to reduce Brewer's sparrow density by ≈2 birds/ha (see Table 4) but increase forage for domestic or wild ungulates by roughly 350 kg/ha (see Fig. 2B). These tradeoffs can be empirically evaluated by using traditional wildlife count models to predict wildlife densities across ecological states and phases in an STM (Ritten et al. 2018).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We acknowledge participating landowners who generously allowed us to sample on their land. Participating landowners and additional stakeholders in Moffat and Routt counties also provided their time and input for sampling locations and study questions. We also acknowledge field technicians, J. W. Schas, J. A. F. Wendt, and J. L. McCartey, for assistance collecting and compiling data. We thank the editors and two anonymous reviewers for improving this manuscript.

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