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Cows and Plows: Science-based Conservation for Grassland Songbirds in Agricultural Landscapes

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COWS AND PLOWS: SCIENCE-BASED CONSERVATION FOR GRASSLAND SONGBIRDS IN AGRICULTURAL LANDSCAPES

By

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Cows and plows: Science-based conservation for grassland songbirds in agricultural landscapes

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Temperate grasslands are among earth’s most imperiled ecosystems. In North America, steep declines of endemic songbird populations indicate that grassland loss and degradation may be approaching critical levels. Grasslands are agricultural landscapes largely (~85%) under private ownership with little formal protection status. Remaining bird populations depend on grazing lands that have not been converted to cropland. We combine regional data from a hotspot for grassland bird diversity (northeast Montana, USA; 26,500-km^2) with continental data spanning the northern Great Plains (1,000,000-km^2) to evaluate how land use and management influence bird distribution and abundance. Regionally, habitat used by seven grassland specialists spanned a gradient of sparse to dense herbaceous cover. Livestock grazing influenced cover and birds but its effect was highly dependent on precipitation and soil productivity. Species distributions were variable across relatively broad spatial scales and only large landscapes ($\geq$ 1,492-km^2) were sufficient to capture maximum diversity and stability in community composition. At this scale, more grassland habitat and a wider range in herbaceous cover values were associated with high bird diversity. Sprague’s Pipit (*Anthus spragueii*), Baird’s Sparrow (*Ammodramus bairdii*), Chestnut-collared (*Calcarius ornatus*) and McCown’s (*Rhynchophanes mccownii*) longspurs were particularly sensitive to habitat amount and had reduced densities in grass-poor landscapes despite local conditions. Continentally, the breeding range of Sprague’s Pipit was restricted to areas with a high proportion of continuous grassland and a relatively cool, moist climate. Most of the pipit population (70%) relied on private lands and a quarter occurred in habitat at risk of future tillage. Spatially hierarchical models placing response to local habitat within its landscape context revealed that broad-scale patterns in land use and grassland productivity constrained the continental distribution of pipits and Chestnut-collared Longspur. Findings suggest that maintenance of large and intact grassland landscapes should be a top conservation priority. Remaining populations rely on private land, emphasizing the importance of voluntary approaches that incentivize good stewardship. Accounting for interactions between climate, soils and livestock within existing grassland landscapes may enable managers to maintain high bird diversity.

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TABLE OF CONTENTS

CHAPTER 2- SIZE MATTERS: USING ECOLOGICAL SCALE TO DETERMINE HABITAT DRIVERS OF GRASSLAND SONGBIRD DIVERSITY…..………………30

CHAPTER 3- ONE STEP AHEAD OF THE PLOW: USING CROPLAND CONVERSION RISK TO GUIDE GRASSLAND SONGBIRD CONSERVATION….59

LIST OF TABLES

LIST OF FIGURES

PREFACE

This dissertation is organized into four primary chapters (1-4), each of which is formatted in general for submission as a peer-reviewed research article. Chapter 5 (“Grassland bird management in agricultural landscapes: A vision for conservation at scale”) provides a synopsis of research implications for grassland bird management, and is intended to serve as a resource for conservation practitioners. At the time of submission, Chapter 3 (“Cows and Plows: Using cropland conversion risk to guide grassland songbird conservation”) is in review with Biological Conservation. Because submitted articles will have more than one author (2-7), I use the plural pronoun “we” throughout.

CHAPTER 1- PRECIPITATION AND SOIL PRODUCTIVITY EXPLAIN EFFECTS OF GRAZING ON GRASSLAND SONGBIRDS

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Abstract

Temperate grasslands are a globally imperiled ecosystem and habitat loss in North America has resulted in steep declines of endemic songbirds. Private rangelands grazed by livestock are the primary land use supporting remaining bird populations. Some conservationists suggest using livestock as “ecosystem engineers” to increase habitat heterogeneity in rangelands because birds respond to a spectrum of sparse to dense vegetation cover. Grazing effects remain poorly understood, however, because local studies do not account for other environmental constraints on herbaceous growth. We surveyed grassland birds in northeast Montana, USA (26,500-km^2) to assess how distribution and abundance were affected by weather, soils, and grazing. We modeled abundance to characterize regional bird response to cover, manipulated grazing experimentally to isolate its effect, and then scaled back up to evaluate interactions between grazing and environmental constraints in the region. Species distributed themselves along a gradient of herbaceous cover with predictable shifts in community composition. We demonstrated experimentally that sites with higher grazing intensities had more Chestnut-collared Longspur (*Calcarius ornatus*) and fewer Baird’s Sparrow (*Ammodramus bairdii*) than lightly grazed sites. Regionally, grazing effects were dependent on precipitation and soil

productivity. Lighter grazing can maintain habitat for species requiring dense cover during drought, and heavier grazing in wet conditions can provide opportunities for species preferring sparse grass. A quarter of our study region is productive grassland where grazing could be managed to benefit specialist species. Shrubland and low productivity grassland were unlikely to provide habitat for the diversity of grassland birds regardless of grazing management. Low productivity grasslands may act as refugia in wet years for species such as McCown's Longspur (*Rhynchophanes mccownii*) that require sparse cover.

Introduction

Temperate grasslands are among earth's most imperiled ecosystems (Hoekstra et al. 2004). In the formerly vast prairies of North America, agricultural conversion spread west following European settlement into the 20th century (Ostlie et al. 1997). Conversion of highly arable tallgrass prairie in the eastern plains is now nearly complete (Samson et al. 2004). Recent demand for ethanol, high commodity prices and advances in agricultural technology have influenced further westward expansion of the corn belt and accelerated losses of mixed-grass prairie (Wright and Wimberly 2013). Seemingly small annual rates of conversion have contributed to cumulative grassland losses that conservation has been unable to mitigate (Doherty et al. 2013). For wildlife species that depend on grasslands, rates of loss have led to an extinction debt that is accumulating rapidly.

One important indicator of habitat loss is the steep and consistent decline of endemic songbird populations (Brennan and Kuvlesky 2005, Sauer et al. 2014). From 1966 to 2011, downward population trends for North American grassland birds were nearly twice that of all avian species combined (57 versus 33%; Sauer et al. 2012) . Two species, Chestnut-collared

Longspur (*Calcarius ornatus*) and Henslow's Sparrow (*Ammodramus henslowii*), are considered globally Near Threatened by the International Union for Conservation of Nature, and a third (Sprague's Pipit [*Anthus spragueii*]) is listed as "Vulnerable" (IUCN 2014). Several others are considered of high concern by individual states and provinces. These populations depend on grasslands to support them and recent declines hint that habitat loss may be approaching a critical level.

Privately owned rangelands have little formal protection status, but support most (85%) remaining grassland habitat (NABCI 2013). Millions of hectares of grassland remain intact within the ranching economy of the western Great Plains. Non-federal rangelands, used for livestock grazing, represent the single largest land-use class in the U.S. (about 167 million ha or 27% of the total land area; NRI 2010). Although quick economic returns from crops and subdivision provide a constant incentive to develop rangeland, the social fabric of rural communities tied to ranching traditions and supported by markets for livestock has shown remarkable resistance to land use change at a continental scale. Even so, these communities are declining as ranches are converted to cropland (GAO 2007) and exurban development (Brunson and Huntsinger 2008).

Birds respond to the structure of grassland vegetation (Fisher and Davis 2010, Keyel et al. 2013), with some species preferring sparse grass and others selecting more dense cover (Knopf 1996). In remaining grassland, structural heterogeneity is therefore important for maintaining species diversity (Bleho 2009, Derner et al. 2009). Many biologists believe that livestock management practices on rangeland have homogenized habitat with negative consequences for diversity (Fuhlendorf and Engle 2001). Several studies report songbird community shifts across a gradient of grazing intensity, with some species increasing under heavier grazing and others decreasing (Bock et al. 1993, Milchunas et al. 1998, Sliwinski 2011). These observations have led to the widespread recommendation to use livestock as “ecosystem engineers” to increase structural heterogeneity in grasslands for the benefit of bird diversity (Fuhlendorf et al. 2006, Derner et al. 2009, Toombs et al. 2010).

Nesting cover is an important habitat feature for ground-nesting songbirds (Davis 2003, Henderson and Davis 2014) and its availability varies with level of grazing (Fondell and Ball 2004, Lusk and Koper 2013). However, reported impacts of grazing on birds are site-specific and generalizations for management have been slow to emerge from the scientific literature. For example, Sprague’s Pipit is a species of conservation concern that is associated with heavy grazing in the mesic portions of its range (Madden et al. 1999) and light grazing in more arid regions (Davis et al. 1999). Because local-scale studies have been unable to account for how grazing interacts with environmental conditions, its role in shaping bird distributions remains poorly understood.

Here we demonstrate that sensitive species’ diverse requirements for cover provide a biological currency through which grazing affects birds. Further, we show that this influence is highly dependent on environmental context. With data from a broad (26,500-km^2) region of northeast Montana, USA, we explore how livestock grazing interacts with the constraints of weather and soil to affect birds using herbaceous cover as the common denominator. First, we use regional data to characterize how the bird community responds to differences in cover. Second, we use controlled, local experiments to isolate the impact of grazing on cover and birds. Lastly, we scale back to the regional level to assess how the environment constrains the effect of grazing. Results provide generalizable insights to optimize the role of grazing in multi-species songbird conservation.

Methods

Study region. The study region includes Phillips and Valley counties in northeast Montana (figure 1). In contrast with continental patterns of grassland ownership, this area contains a high proportion of public land which, along with adjoining tribal and private lands, comprises one of the largest tracts of intact native mixed-grass prairie in the United States (Cooper et al. 2001). More than 70% of the region is rangeland used for livestock grazing (figure A1). Of this, about half is grassland and about a third is shrub-steppe. The remainder includes barren lands, woodland and wetland. Of the grassland, about 30% has low productivity soils with potential for > 1,121-kg/ha normal year biomass production. Productive grasslands with > 1,121-kg/ha normal year production make up about 34% of the rangeland area, or 25% of the total area.

Physiographically, the region is in the Glaciated Missouri Plateau subregion of the Great Plains (Fenneman 1916). Largely glaciated during the Pleistocene (Colton et al. 1961), its landform is characterized by rolling hills with dry drainages. The Milk River bisects the region from the west to its confluence with the Missouri River in the east. Vegetation is dominated by grasses north of the river and sagebrush (*Artemisia* spp.) in the south. Six soil orders are described in the region including Alfisols, Aridisols, Entisols, Inceptisols, Mollisols, and Vertisols (Bingham et al. 1984, Bandy et al. 2004). Climate is cold semi-arid (Peel et al. 2007), characterized by short hot summers and long cold winters (Cooper et al. 2001). Average annual precipitation ranges from 177-492-mm (1981-2014; PRISM 2014), much of which falls as rain in May-July (Cooper et al. 2001, Charboneau 2013). For detailed descriptions of physiography, climate, geology and floristic composition see Charboneau (2013).

Regional sampling. We sampled bird communities and vegetation attributes between 20 May and 11 July 2011-2013. Survey locations were randomly selected across areas classified as grassland by GAP analysis (USGS 2010) and an aggregate of similar natural communities (B. Martin, the Nature Conservancy, unpublished data). Surveys were conducted on publicly managed grazing lands (federal 68%, state 17%), private (10%), and tribal (5%) rangeland.

To maximize variability in landscape and local variables of interest, we stratified locations by categories of distance to livestock watering sources (0-400, 400-800, 800- 1,200 and > 1,200-m) and by proportion of grassland within 1.6-km radii of point counts. We restricted surveys to slopes <5%, without trees and with < 25% shrub cover. Our sampling design prioritized regional variability captured with a wide sampling effort and we did not repeat surveys. We surveyed 818 points, visiting half each year in 2011 and 2012 and adding 16 additional points in 2013 (2%; figure 1).

Grazing experiments. We tested the response of birds to variability in grazing using six pairs of sites where stocking rates were experimentally manipulated in a paired before-after design (figure 1). Experimental grazing was implemented May-October of 2011 and 2012, with each pair consisting of a heavy-use site and a neighboring light-use site. Pasture sizes were typical of those on native vegetation in this region (200-2,500-ha). Typical stocking rates on these pastures were 0.49-0.67 animal-unit-month per ha. In heavy treatments, rates were increased by 15-100% whereas in light treatments they were reduced by 18-100%. Our paired design controlled for variability in pasture size, vegetation and edaphic characteristics.

We designed sampling of experimental sites to isolate the effect of grazing and minimize external variability. To control for vegetation type, we restricted surveys to upland grassland. To cover the expected range of grazing intensity (Adler and Hall 2005), we stratified by distance class from livestock water sources (0-400, 400-800, 800- 1,200 and > 1,200-m), placing survey points randomly within strata. We minimized double-counting of individuals by ensuring at least

200-m between adjacent surveys. At each location, we surveyed birds and vegetation before treatment (2011), after one year of treatment (2012) and after two years of treatment (2013). We surveyed 175 points at least once, repeating 173 (99%) for at least two years and 127 (73%) across all three years.

Survey methods. We conducted 10-minute, 100-m fixed-radius point counts (Hutto et al. 1986) between 0600-1000 MST. We did not sample during precipitation or when maximum wind speeds exceeded 24-km/h. At each survey point, we recorded all birds seen or heard during the count. We collected data on vegetation structural attributes at each location following Hendricks et al. (2007), estimating proportional cover of vegetation classes at two scales: the entire 100-m-radius point count circle and a set of five 1-m-radius "miniplots" distributed within the point count circle. In miniplots, we also estimated maximum vegetation height, average litter depth horizon, and the densities of grasses, forbs, live and dead vegetation.

Measuring livestock use. At experimental sites, we measured local grazing intensity using the height-weight method (Coulloudon et al. 1999). In October-November of 2011 and 2012, after the majority of seasonal grazing was completed, we sampled key forage species every 5-m along a 200-m randomly directed linear transect, centered on point-count locations. When present (83% of sites), we used western wheatgrass (*Pascopyrum smithii*) as the key forage species; we substituted prairie junegrass (*Koeleria macrantha*) when western wheatgrass was absent (17% of sites). We calibrated height-weight relationships based on 15 dry samples of western wheatgrass and 14 dry samples of prairie junegrass, collected concurrently at survey locations.

Incorporating environmental constraints to evaluate grazing. To evaluate the role of livestock grazing at the regional scale, we used density of dung pats as an index of cattle use.

Dung counts have been successfully applied as an index of use for wild and domestic herbivores (Barnes 2001, Hendricks et al. 2005, Bylo et al. 2014). This method was efficient and practical to collect across the wide survey region compared to time-intensive height-weight measurements used to calibrate experimental plots. Observers walked slowly down a 200-m, randomly directed transect, centered on each survey location, counting dung pats within 2-m on either side. We completed dung counts concurrently with vegetation and bird surveys for each point (May-July).

We modeled the effect of environmental constraints using local estimates of precipitation, temperature, soil productivity, shrub cover and exotic grass presence. We derived total precipitation from the preceding two years and mean growing season temperature (April-September) of the current year from 4-km gridded totals (PRISM 2014). Preliminary analysis using linear models indicated that precipitation totals from the preceding two years were most predictive ($R^2 = 0.27$) for vegetation structure of any time period considered between year t and year t-2 ($R^2 = 0.13$-0.26.). We used estimates of normal year rangeland productivity (NYRLP) from NRCS (2014). We recorded estimates of shrub cover (% at 100-m) and presence of exotic grasses (crested wheatgrass [*Agropyron cristatum*] or cheatgrass [*Bromus* spp.]) at each point count location. Precipitation and growing season temperature were moderately correlated ($r = 0.68$) whereas all other environmental predictors showed low correlation ($r < 0.29$).

Statistical analyses. Regionally, we estimated bird response to vegetation using negative binomial generalized linear mixed models (GLMM; Bolker et al. 2009) in R package lme4 (Bates et al. 2013). We used the negative binomial distribution to account for overdispersion present in bird count data (White and Bennetts 1996). Because of significant annual variation in environmental conditions and bird populations, we included survey year as a random effect. For comparison among variables and across species, we used standardized coefficients for vegetation variables, centered on the mean and scaled by standard deviation. To evaluate differences in conditions among sites occupied by different species, we used standard analysis of variance with a post-hoc Tukey test for pairwise comparisons (Tukey 1949). We conducted all analyses in program R (R Development Core Team 2013).

To estimate response of vegetation to experimental grazing intensity we used linear mixed effects models with random effects for survey year, pair and pasture. To control for background variability across sites and isolate the effect of grazing, we included measures from the year prior to treatment as covariates in the model using the form:

$$\text{Vegetation attribute (year } t) = \beta_0 + \beta_1 * \text{Vegetation attribute (year } t_0) + \beta_2 * \text{Grazing Intensity (year } t\text{-}1)$$

where year t is the year of sampling and year t_0 is the year before treatments began (i.e., 2011). We conducted vegetation sampling in the spring before seasonal grazing was complete, so we expected grazing intensity estimates from the previous autumn (year t-1) to be most relevant. To isolate local variability related to changes in grazing and control for pseudo-replication, we included nested random effects for survey year, pair, and site. We combined years following grazing modifications into a single dataset (t = 2012 and t = 2013). For bird abundance response to grazing intensity, we fitted negative binomial GLMM using the same model form.

Regionally, we analyzed the effect of cattle use, measured by dung count, using linear fixed-effect models for vegetation response and negative binomial GLM for bird abundance response in package MASS (Venables and Ripley 2002). We included cattle use, soil productivity, precipitation and their interaction as covariates in regional models of vegetation and bird abundance. Including a random effect for year would have controlled for annual variability, whereas a fixed-effect structure allowed us to model the role of weather explicitly.

Results

Identifying vegetation variables important to birds. We recorded 11 species of grassland songbirds occurring at >10% of survey points (table 1). Most common were Chestnut-collared Longspur (68% of points) and Horned Lark (65%). Least common were Savannah Sparrow (13%) and McCown's Longspur (18%). Proportion shrub, bare ground, litter, depth of litter and total vegetation density were most predictive of abundance across species (table 1). Of variables sensitive to grazing intensity, proportion bare ground, proportion litter and vegetation density had the strongest relationships with abundance (table 1); each a component of herbaceous cover. To isolate response to cover, we calculated a combined cover index using the formula:

$$Cover\ Index = \sqrt{(1 - proportion\ bare) * proportion\ litter * total\ vegetation\ density}$$

We applied a square root transformation to normalize distribution of the index, although a high proportion of zeroes did cause the index to maintain moderate right skewness. Cover index ranged from 0-5.48 with an average of 1.91. Lower values indicated sparser cover and higher values indicated denser cover (figure A2).

Using shrubs to remove non-grassland species from analyses. Shrub cover was the most predictive vegetation variable for bird abundance and it clearly distinguished among species (table 1). We used response to shrubs to identify species that were not grassland specialists. Both Lark Buntings (*Calamospiza melanocorys*), which nest in shrubs, and the parasitic Brown-headed Cowbird (*Molothrus ater*) that targets them, strongly preferred shrubby areas. Neither of these species responded to herbaceous cover (Lark Bunting $\beta = -0.09$, $P = 0.12$; Brown-headed Cowbird $\beta = -0.11$, $P = 0.31$). Western Meadowlark (*Sturnella neglecta*) and Vesper Sparrow (*Pooecetes gramineus*) also preferred shrubby areas but are ground-nesting and selected for denser herbaceous cover (Western Meadowlark $\beta = 0.07$, $P = 0.04$; Vesper Sparrow $\beta = 0.15$, $P = 0.02$).

Response of grassland specialists to herbaceous vegetation. Our interest is in how herbaceous vegetation shapes bird communities and subsequent analyses include only those species that avoided shrubs and varied in their preferences for cover (table 1). These included: Baird's, Savannah and Grasshopper sparrows, Sprague's Pipit, Chestnut-collared and McCown's longspurs and Horned Lark (see table 1 for scientific names). Species distributed themselves along the gradient of herbaceous cover (figure 2; ANOVA, df = 6, $P < 0.001$). McCown's Longspur preferred the sparsest cover whereas Grasshopper Sparrow selected the densest cover (figure 2). As cover increased, modeled relationships suggested predictable shifts in community composition. Comparing the cover preference of each species to average regional conditions allowed us to delineate two distinct groups: sparse- and dense-grass species (figure 2). Sparse-grass species are those that preferred lower than average herbaceous cover, including McCown's Longspur, Horned Lark and Chestnut-collared Longspur (figure 2). Dense-grass species are those that preferred higher than average cover and included Sprague's Pipit, Baird's Sparrow, Grasshopper Sparrow and Savannah Sparrow (figure 2).

Controlled grazing experiments. Experiments created high variability in local grazing intensity. Dry weight removed by livestock in experimental pastures ranged from 0-85% with an average of 16% ($\sigma = 15\%$). Heavy use sites averaged 25% biomass removed (SE = 0.52%) and light use site averaged 9% (SE = 0.95%). Higher grazing intensities reduced litter at the micro-scale while exposing more bare ground and club-moss (table 1). Grazing also reduced density of dead standing grass < 10-cm in height. Grazing did not affect maximum grass height or proportion of shrubs, grass and forbs (table 1).

Experiments showed that manipulating grazing can affect the abundance of species with divergent cover requirements (table 2). Higher experimental intensity increased abundance of Chestnut-collared Longspur and reduced abundance of Baird's Sparrow (figure 3). On average, models suggest that a 10% increase in biomass removed by grazing would result in a 15% increase in the abundance of Chestnut-collared Longspur and a 14% reduction in abundance of Baird's Sparrow. Sprague's Pipit, Horned Lark and Grasshopper Sparrow did not respond to grazing intensity despite being among the most common species surveyed (table 2). Intensity did not measurably affect abundance of McCown's Longspur or Savannah Sparrow but they were seldom observed and we had low power to detect trends.

Regional response to livestock use. Dung count was a useful index of cattle use measured by grazing intensity in experimental sites (by linear model: $\beta = 0.13$, $P < 0.001$, $R^2 = 0.06$). When combined with environmental constraints of weather and soil, models including cattle use accounted for more than a third of variation in herbaceous cover ($R^2 = 0.35$; table 3). Within these models, cattle use was related to abundance of each species (table 3). Without including environmental constraints, however, cattle use was a poor predictor of herbaceous cover (linear model: $\beta = -0.003$, $P = 0.006$, $R^2 = 0.005$).

Regionally, the effect of grazing on herbaceous cover and birds was highly dependent on precipitation. Models suggest that cattle use reduced cover only when precipitation was relatively low (< 500-mm in preceding two years). In this dry scenario, heavier use reduced abundance of dense-grass species (figure 4a) but had little effect on sparse-grass species (figure 4b). In wet conditions (> 800-mm two-year precipitation), variation in use within the observed range had little or no impact on herbaceous cover. In this scenario, heavier livestock use was predicted to increase suitability for sparse-grass species (figure 4d) but have no effect on dense-grass species (figure 4c).

The regional influence of grazing also interacted strongly with soil productivity. Cattle were more likely to use sites atop productive soils (by t-test, $P < 0.001$; 338 patties/ha on low productivity sites versus 588/ha on high). In these areas, high levels of use reduced abundance of dense-grass species (figure 4e) but increased abundance of sparse-grass species (figure 4f). Low productivity grasslands (with < 1121-kg/ha normal year biomass production) represented about 14% of rangelands, or 11% of the study region. These areas were avoided by cattle and had limited potential to provide habitat for dense-grass species at any level of use (figure 4g). Sparse-grass species were predicted to increase with cattle use under any soil conditions. McCown's Longspur and Horned Lark showed a direct preference for poor soils (table 3) and McCown's Longspurs occurred more frequently in low productivity grasslands than expected by area (by χ^2 test, $P = 0.032$).

Discussion

The responses of individual species to grazing were consistent with their distributions along the gradient of herbaceous cover. Our experiment is among the first to demonstrate that changes in grazing can shape bird distribution between breeding seasons with measurable response after a single year. Controlled manipulation of livestock at experimental sites allowed us to isolate the effect of grazing on birds in the context of a complex, working landscape where it is the dominant land use. Our results strengthen suggestions in the literature that vegetation structure, particularly herbaceous cover, is the mechanism through which grazing affects bird distributions (Knopf 1996, Derner et al. 2009).

Climatic variability is a dominant force shaping grassland habitats, with relatively moist, cool areas producing more herbaceous cover. Our results highlight the importance of considering effects of grazing within the constraints of recent weather patterns. Bird response to precipitation was strong and aligned with their respective preferences for level of vegetation cover. As such, dense-grass species were abundant in the observed wet conditions whereas sparse-grass species would be widespread in drought. In this study, grazing reductions had little effect on cover for birds because experiments took place during a historically wet weather pattern. Instead, high grazing intensity was important for creating conditions more suitable for sparse-grass species. In drought we might expect the opposite, with areas of light grazing providing key habitat for dense-grass species. By accounting for the interaction between precipitation and grazing, managers can mitigate natural fluctuations in bird diversity by responding to recent conditions. Lighter grazing can help maintain habitat for dense-grass species during drought and heavier grazing in wet years can provide opportunities for sparse-grass species.

To influence bird abundance and diversity, grazing management should be targeted spatially. Of our study area's 18,500-km^2 of rangeland, only a third is grassland with productive soils where grazing could be managed to benefit grassland specialists. The remaining two thirds is shrubland or low-productivity grassland where shrub-steppe associates and sparse-grass species predominate regardless of grazing intensity. Prairie songbirds avoid woody vegetation (Keyel et al. 2013; Saino et al. 2013), and grassland species avoided shrubs in spite of the suitability of herbaceous cover. Low productivity grasslands probably do act as valuable refugia for sparse-grass species in wet years. For example, McCown's Longspur may have relied on low-productivity areas for sparse cover during the abnormally wet conditions.

Their consistent response to grazing suggests that Chestnut-collared Longspur and Baird’s Sparrow can be managed using livestock. Our experimental findings confirm those from nearby Saskatchewan showing that these two species respond strongly to grazing (Sliwinski 2011, Henderson and Davis 2014). Sprague’s Pipit, Horned Lark and Grasshopper Sparrow were least responsive to experimental grazing and are less likely to be affected by livestock management, especially in wet years. Rarity of McCown’s Longspur and Savannah Sparrow made their response difficult to quantify. Rare species at opposite ends of the cover spectrum should not be discounted in management as these might benefit most from increased heterogeneity. Wet conditions constrained our ability to reduce cover enough to observe a response from McCown’s Longspur, and repeating our experiment during drought would increase certainty in whether grazing shapes their distribution.

Findings suggest a fundamental shift in how conservationists view grazing and its role in shaping bird distributions. To date, science has not produced generalizable guidelines for grazing to benefit birds because local-scale studies have been unable to account for environmental constraints imposed by weather and soils. Instead of a focus on grazing *per se*, we suggest a holistic view in which herbaceous cover is monitored for birds and the role of grazing is situated within the context of environmental constraints. Our work provides initial steps for framing this approach. The first challenge for biologists is to achieve a full understanding of the diverse requirements of different species for cover, and the second is to effectively communicate those requirements to range managers within the appropriate spatial and temporal context. The herbaceous cover index presented here represents an attempt to quantify an important underlying component of habitat quality for grassland birds, but we still lack complete knowledge of requirements for reproduction of each species, and the evolutionary pressures behind habitat selection decisions. A valuable goal for future research would be to identify a simplified cover metric that is both biologically relevant and clearly communicable to range managers.

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Tables

Table 1. Estimated individual, standardized effect of livestock grazing intensity (Util.) on vegetation variables, and individual, standardized effect of vegetation variables on regional bird abundance in northeast Montana, 2011-2013. Shown in descending order of magnitude of bird response measured by average absolute effect on abundance across species (Avg.). Only coefficients with significance at $P < 0.05$ are included.

	Util.	**BAIS**[1]	**BHCO**	**CCLO**	**GRSP**	**HOLA**	**LARB**	**MCLO**	**SAVS**	**SPPI**	**VESP**	**WEME**	***Avg.***
Shrub (100m)		-0.63	0.68	-0.49	-0.31	-0.12	0.57	-0.31	-0.31	-0.63	0.31	0.1	***0.41***
Bare (1m)	***0.59***	-1.16	0.43	-0.53	-0.46	0.09	0.13		-0.4	-0.58	0.19		***0.36***
Grass (100m)		0.36	-0.71	0.41		0.06	-0.33	0.49	0.19	0.33	-0.63	-0.33	***0.35***
Bare (100m)		-0.98	0.39	-0.6	-0.31	0.1			-0.36	-0.57	0.18	0.08	***0.32***
Shrub (1m)		-0.74	0.49	-0.52	-0.27	-0.05	0.25		-0.22	-0.78	0.14		***0.31***
Litter (1m)	***-1.09***	0.11	-0.21	-0.21	0.26	-0.32	-0.57	-0.67			0.33	0.28	***0.27***
Litter (100m)		0.11			0.28	-0.12	-0.58	-0.71			0.4	0.19	***0.22***
Live Density		0.41	-0.33	0.23	0.19	-0.11			0.33	0.34	-0.28	-0.12	***0.21***
Density 10-20cm		0.39	-0.31	0.07	0.2	-0.29		-0.33	0.3	0.25	-0.12		***0.21***
Litter horizon depth		0.34	-0.18	-0.05	0.17	-0.24	-0.3	-0.2	0.36	0.22	-0.2		***0.21***
Veg. density (total)	***-0.80***	0.37	-0.27	0.11	0.18	-0.21	-0.22	-0.25	0.28	0.3		0.07	***0.21***
Grass Density	***-0.81***	0.37	-0.28	0.13	0.19	-0.22	-0.23	-0.23	0.27	0.31			***0.20***
Grass (1m)		0.43	-0.38	0.26	0.09	-0.08	-0.19			0.25	-0.33		***0.18***
Density >20cm		0.18	-0.33		0.19	-0.12	0.13	-0.21	0.29	0.08	-0.26	-0.14	***0.18***
Density <10cm	***-1.05***	0.31		0.13	0.09	-0.14	-0.43	-0.13	0.15	0.31		0.14	***0.17***
Dead Density	***-1.49***	0.24			0.12	-0.24	-0.27	-0.3	0.15	0.18	0.14	0.17	***0.16***
Club-moss cover (1m)	***0.90***		-0.22	0.21	0.11	0.13	0.38	0.28			-0.15	-0.23	***0.16***
Max height		0.12	-0.22		0.21	-0.11	0.19		0.16		-0.27	-0.17	***0.13***
Exotic (100m)			-0.33	-0.08	0.15	-0.13		-0.42		-0.12		0.13	***0.12***
Forb (1m)		0.2		0.12	0.07	0.08	-0.19		0.19	0.28		0.1	***0.11***
Club-moss (100m)				0.1		0.08	0.31	0.23		0.15	0.15		***0.09***
Forb (100m)		0.1		0.05		0.05	-0.17		0.15	0.13			***0.06***
Forb Density			0.17	-0.08							0.13	0.08	***0.04***

[1] BAIS = Baird's Sparrow (*Ammodramus bairdii,* 42% occurrence) ; BHCO = Brown-headed Cowbird (*Molothrus ater*, 10% occurrence); CCLO = Chestnut-collared Longspur (*Calcarius ornatus*, 68% occurrence); GRS*P* = Grasshopper Sparrow (*A. savannarum*, 43% occurrence); HOLA = Horned Lark (*Eremophilia alpestris,* 65% occurrence); LARB = Lark Bunting (*Calamospiza melanocorys,* 29% occurrence); MCLO=McCown's Longspur (*Rhynchophanes mccownii*, 18% occurrence); SAVS = Savannah Sparrow (*Passerculus sandiwchensis,* 13% occurrence); SPPI = Sprague's Pipit (*Anthus spragueii*, 42% occurrence); VESP=Vesper Sparrow (*Pooecetes gramineus,* 21% occurrence); WEME = Western Meadowlark (*Sturnella neglecta,* 48% occurrence)

Table 2. Estimated individual, standardized effect of livestock grazing intensity on bird abundance in experimental pastures, northeast Montana 2011-2013. Grazing intensity measured by proportion dry weight removed by livestock, square root transformed.

	Estimate	**SE**	**t-value**	**p-value**
Baird's Sparrow	-1.26	0.788	-1.596	0.111
Chestnut-collared Longspur	1.18	0.341	3.465	<0.001
Grasshopper Sparrow	-0.37	0.556	-0.662	0.508
Horned Lark	0.11	0.405	0.262	0.794
McCown's Longspur	0.47	1.005	0.470	0.638
Savannah Sparrow	-0.72	1.266	-0.570	0.569
Sprague's Pipit	-0.10	0.557	-0.177	0.860

Table 3. Estimated standardized effect of environmental variables and cattle use models on cover and bird abundance in northeast Montana 2011-2013. Normal year rangeland production (NYRLP) measured in lbs/ac. Asterisks indicate significance at P > 0.05.

	Cover	**MCLO**	**HOLA**	**CCLO**	**SPPI**	**SAVS**	**BAIS**	**GRSP**
(Intercept)	1.63*	-1.08*	0.34*	0.89*	-0.68*	-1.67*	-0.37*	-0.41*
Mean growing season temp. *(Apr-Sep)*	-0.27*	-0.64*	0.06	-0.16*	-0.68*	0.19	-0.69*	0.03
Precipitation *(preceding 2 year total)*	0.92*	0.39*	-0.23*	-0.09*	0.38*	-0.24*	0.45*	0.28*
Log 100m shrub cover	-0.14*	0.06	-0.06*	-0.23*	-0.22*	-0.37*	-0.28*	-0.17*
Log NYRLP	0.23*	-0.19*	-0.17*	0.1*	0.19*	0.07	0.31*	0.24*
Cattle use *(dung count)*	-0.16*	0.18*	0.16*	0.29*	0.16*	-0.16	0.05	-0.09*
NYRLP : Cattle use	-0.09*	0.01	0.04	-0.12*	-0.07	-0.23*	-0.18*	-0.13*
Precipitation : Cattle use	0.07*	0.06	0.05	0.11*	0.06	0.03	0.14*	0.09*
Exotic grass presence	0.09*	-0.12	-0.1*	-0.05*	-0.08	0.04	0.06	0.2*
Model R^2	***0.35***	***0.04***	***0.11***	***0.29***	***0.14***	***0.05***	***0.13***	***0.13***

Figures

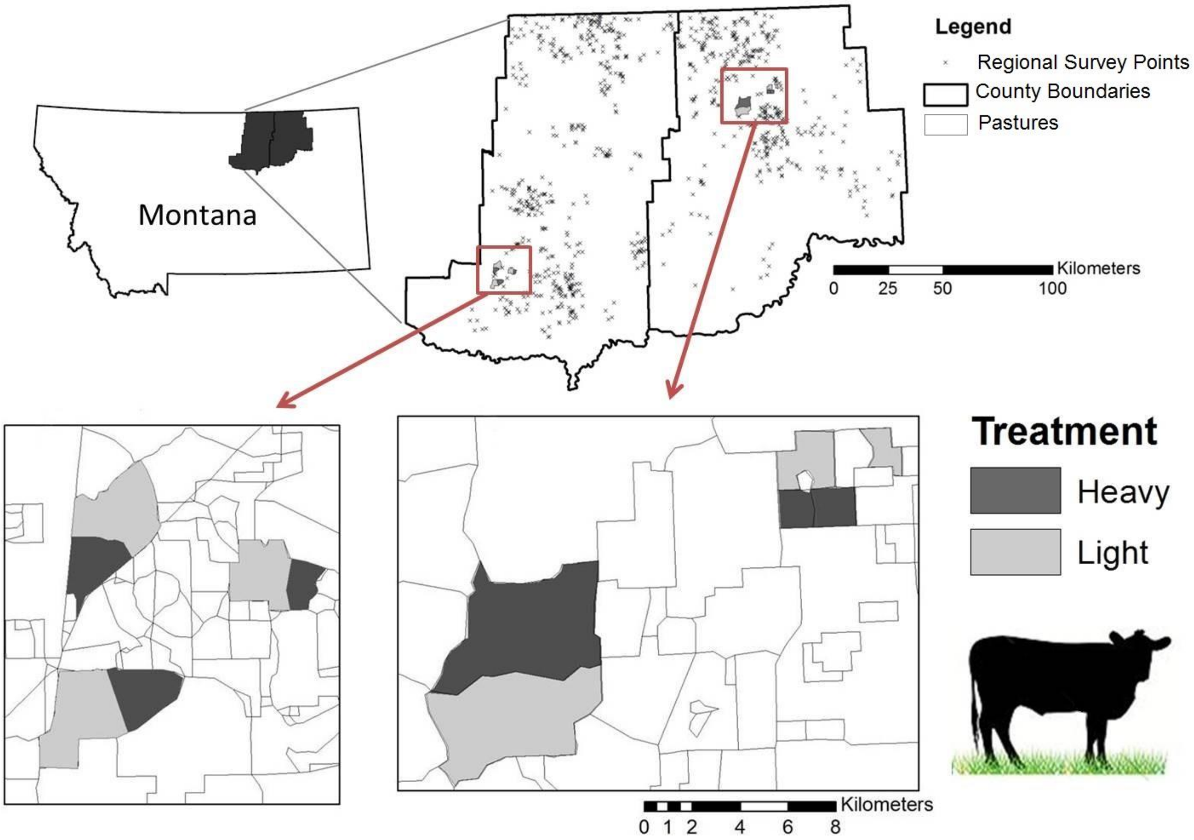

Figure 1. Northeast Montana and location of regional bird sampling points and pastures where grazing was experimentally manipulated, 2011-2013.

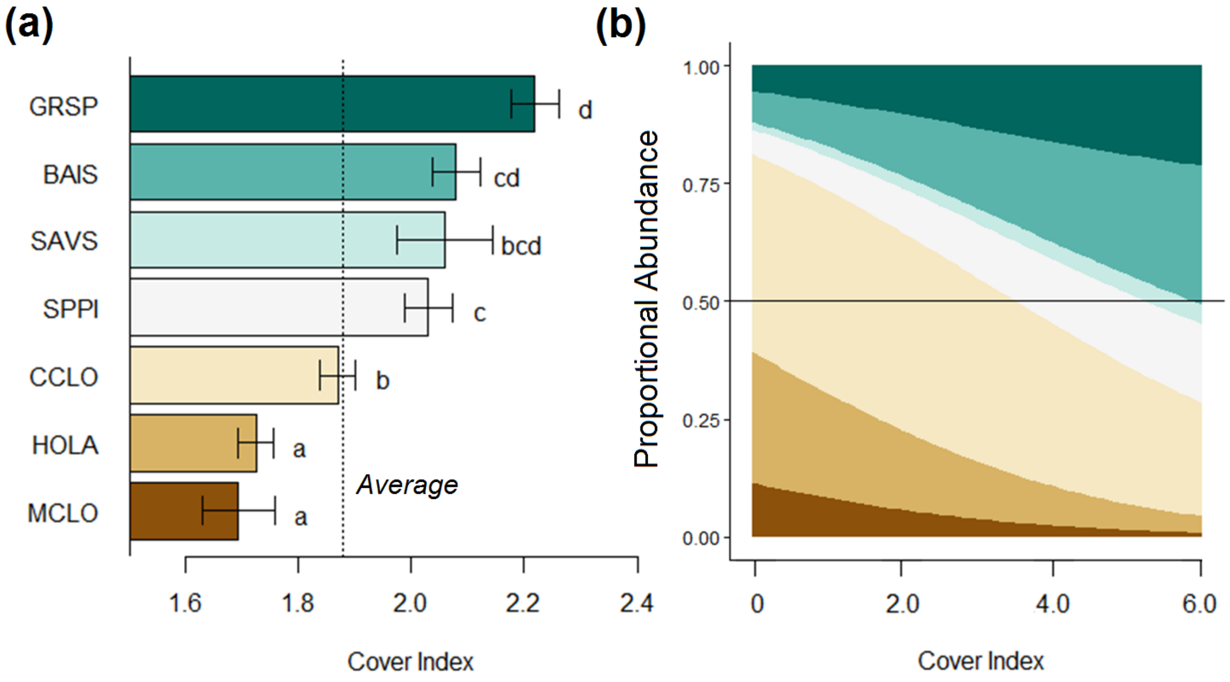

Figure 2. (a) Average cover index at sites where common grassland species occurred in northeast Montana 2011-2013. Cover index calculated as the square root of (1-proportion bare)*proportion litter*total vegetation density. Dashed line indicates regional average. Letters on bars indicate significance at $P < 0.05$ (on one-way ANOVA with post-hoc Tukey test). Error bars indicate ± 1 SE. (b) Predicted shift in species proportional abundance with change in cover using negative binomial mixed models, shown for 2012 with shrubs absent. GRSP = Grasshopper Sparrow, BAIS = Baird’s Sparrow, SAVS = Savannah Sparrow, SPPI = Sprague’s Pipit, CCLO = Chestnut-collared Longspur, HOLA = Horned Lark, MCLO = McCown’s Longspur.

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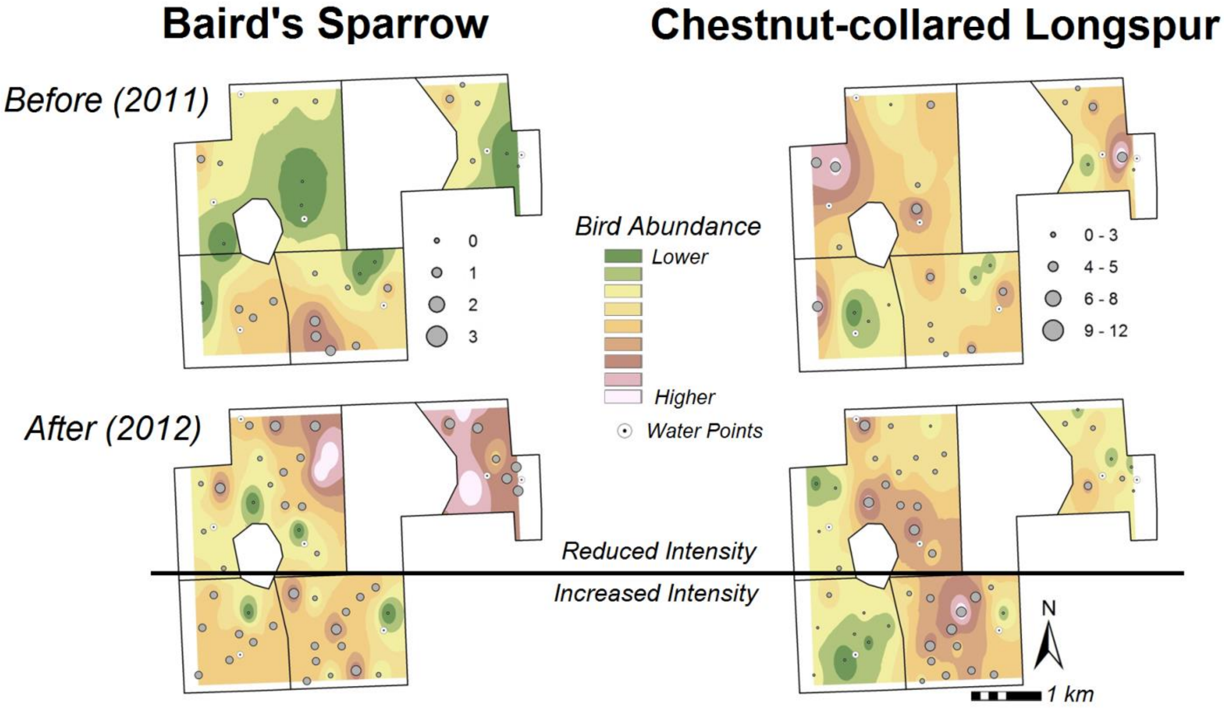

Figure 3. Changes in abundance following implementation of experimental grazing on two pairs of sites in northeast Montana 2011-2012. Size of dots indicates observed abundances of two species. Shading shows relative abundance interpolated by inverse distance weighting. Grazing intensity was reduced between years in northern pastures and increased in southern pastures.

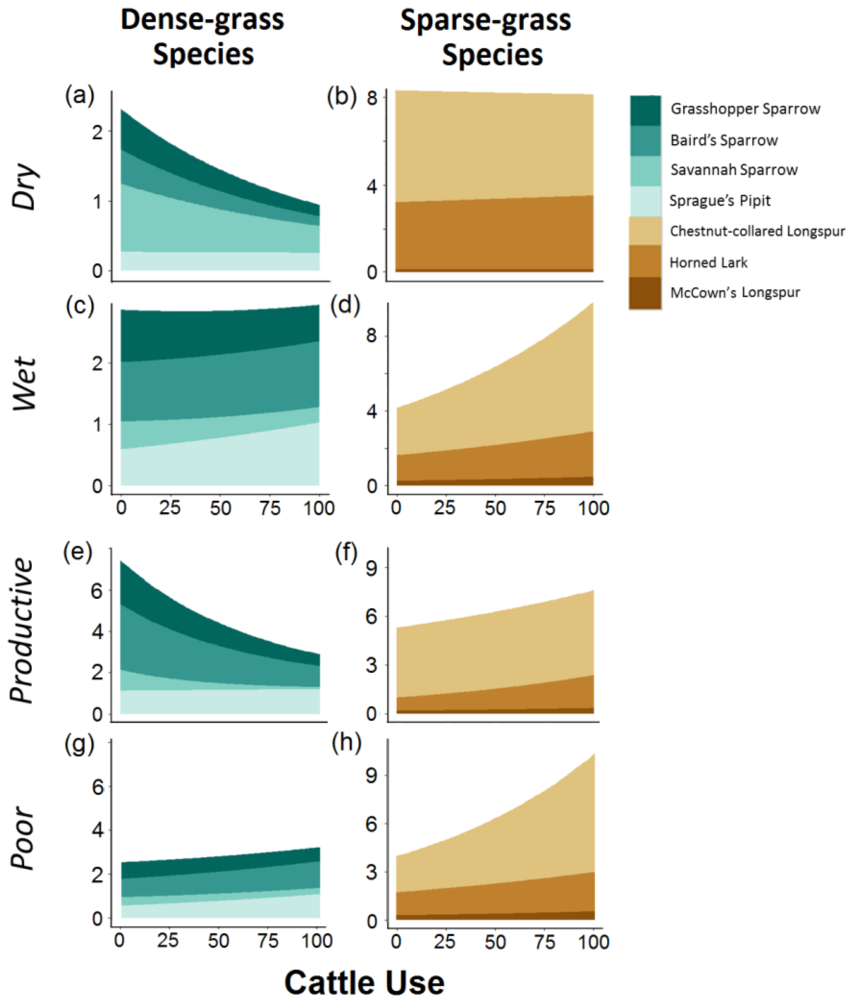

Figure 4. Predicted effect of cattle use on abundance of dense-grass species (a,c,e,g) and sparse-grass species (b,d,f,h) with negative binomial models that control for environmental constraints (table 3). All models fitted with shrubs and exotic vegetation absent and with average growing season temperature of 14.9°C. Moisture measured as total precipitation in the two years preceding bird response (dry = 500-mm, wet = 800-mm). Productivity is measured as normal year rangeland production (productive = 2242-kg/ha, poor = 1121-kg/ha). Effect of moisture (a-d) shown for moderately productive soils (1681-kg/ha) and effect of productivity (e-h) shown under dry conditions (407-mm).

Appendix

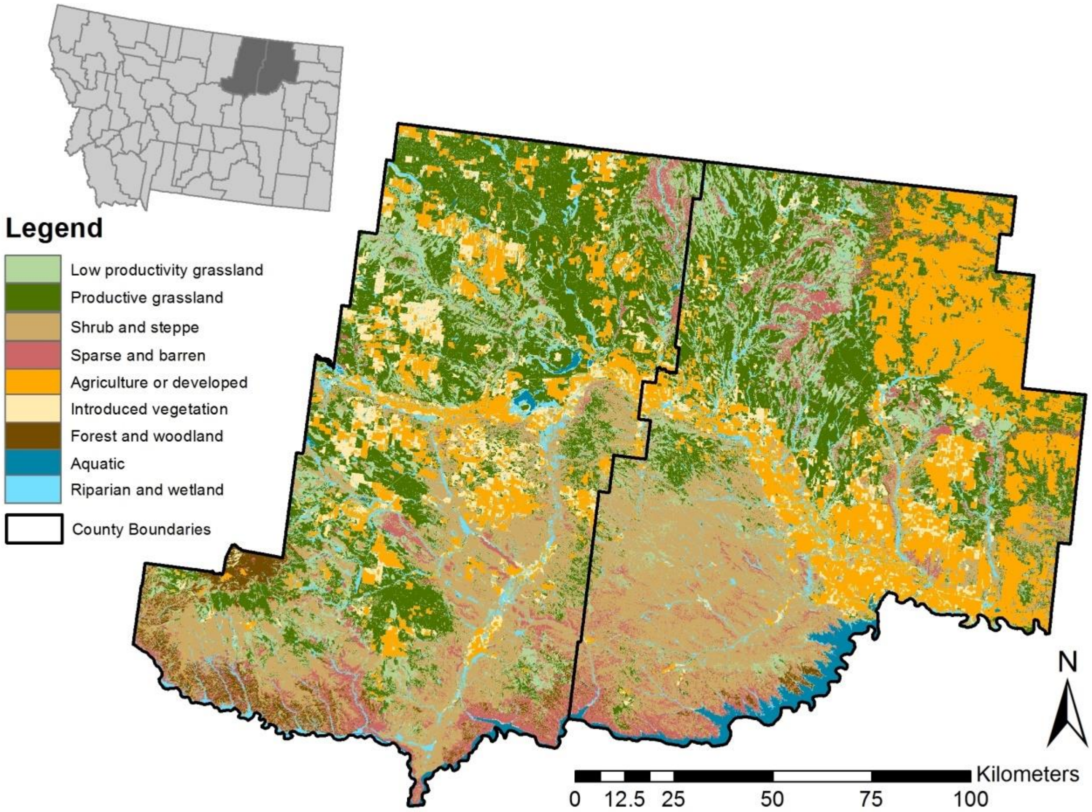

Figure A1. Land cover in Phillips and Valley counties, northeast Montana from USGS GAP analysis (2010). Productive grasslands have > 1,121-kg/ha normal year rangeland production, estimated from NRCS (2014).

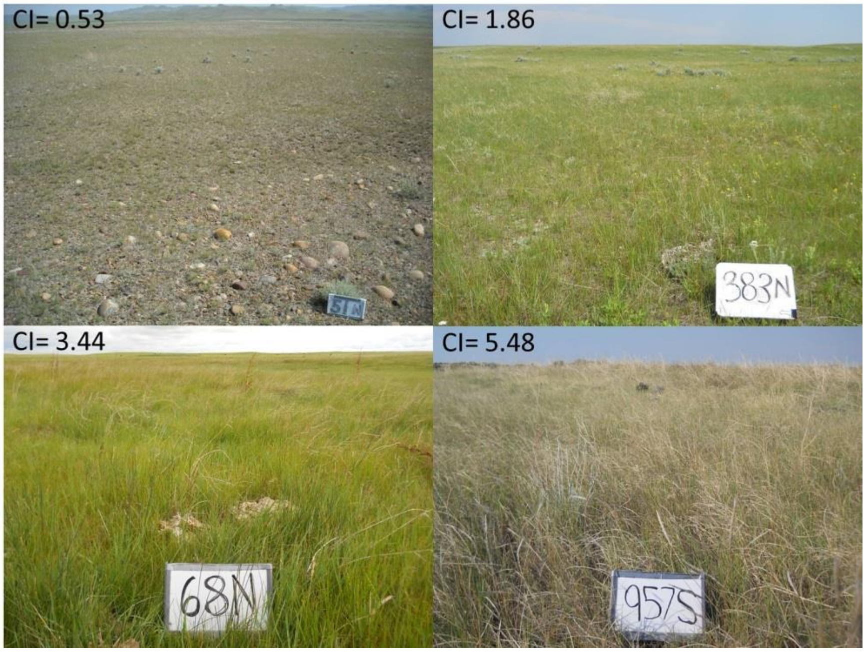

Figure A2. Vegetation at sampling locations in northeast Montana, 2011-2013, illustrating a range of variation in herbaceous cover index (CI).

CHAPTER 2- SIZE MATTERS: USING ECOLOGICAL SCALE TO DETERMINE HABITAT DRIVERS OF GRASSLAND SONGBIRD DIVERSITY

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Abstract

Patterns of animal diversity and their underlying relationships with habitat are fundamental themes in ecology. Theory suggests that diversity is influenced by the amount, productivity and heterogeneity of available habitat but empirical data from arbitrary and inconsistent scales have obfuscated interpretation. From 2011-2013, we surveyed bird communities at 1,293 locations in northeast Montana, USA, a global hotspot for grassland songbird diversity. We applied geostatistical analyses to characterize distribution patterns and evaluate variation in alpha (α) and beta (β) diversity, and used nested linear models to quantify importance of habitat metrics to diversity at four scales (0.7, 2.6, 93 and 1,492-km^2). Differences in observed distribution patterns among species reflected their relative preferences for sparse versus dense grass cover. Of scales evaluated, only the largest (1,492-km^2) exceeded average autocorrelation distances (240-km^2) that characterized patchiness in species distributions. Models at this scale supported the most diverse (α) and stable (β) bird communities and best captured habitat relationships underpinning diversity ($R^2 = 0.51$). Finer scales (0.7 and 93-km^2) had lower diversity and higher rates of species turnover. At the largest scale, habitat amount accounted for most explained variation (51%) followed by productivity (27%) and vegetation heterogeneity (16%). Species

most sensitive to habitat amount also were most imperiled globally, with reductions in their densities producing observed declines in α diversity. Findings show that to benefit bird diversity, maintenance of large and intact grassland landscapes should be a top conservation priority.

Introduction

Theories of diversity. Understanding patterns of animal diversity is a central focus of ecology and conservation (Rosenzweig 1995). Diversity varies across the planet from species-poor deserts to mega-diverse tropical forests, and explanations for these differences have been a priority of ecological research. To date, three dominant hypotheses have been put forward to explain patterns in diversity: the influence of habitat amount, primary productivity, and habitat heterogeneity (figure 1). The tendency for larger areas of habitat to contain more species is perhaps the most universal law in ecology (MacArthur and Wilson 1967, Connor and McCoy 1979, Lawton 1999). Wright (1983) extends this species-area theory to include productivity because more available energy should support more species. Finally, heterogeneous environments provides suitable habitat for a greater variety of species than those that are less complex (Tews et al. 2004, Kallimanis et al. 2008, Allouche et al. 2012).

However, after more than six decades of research, empirical support for these hypotheses is inconsistent and a generalized theory of diversity remains elusive (Rohde 1992, Gaston 2000). Later reviews suggest that Wright’s (1983) species-productivity relationship might be curvilinear, with less diversity than expected in the most productive areas (Rosenzweig 1992, Mittelbach et al. 2001). Further, the hypotheses are not mutually exclusive and often contribute jointly to observed patterns in diversity (Báldi 2008, Allouche et al. 2012), making it difficult to assess the individual importance of each metric especially when they are correlated (Kallimanis et al. 2008, Marshall et al. 2009). Finally, inconsistent treatment of spatial scale profoundly influences the perception of observed patterns in animal diversity and habitat relationships (figure 1; Whittaker et al. 2001, Rahbek 2005).

Diversity and scale. Scale of analysis affects relationships between diversity and habitat amount (Palmer and White 1994), productivity (Waide et al. 1999, Whittaker 2010), and heterogeneity (González-Megías et al. 2007, Stein et al. 2014). Animals select habitats at multiple scales from global migratory routes to seasonal breeding and foraging sites (Johnson 1980, Mayor et al. 2009). Scale of these decisions varies widely according to mobility, behavior and distribution of key habitat components (Mayor et al. 2007). Measures of diversity are therefore highly sensitive to scale and become meaningful only when they align with scales of animal perception or underlying ecological patterns (Gering et al. 2003, Schaefer and Mayor 2007).

Management for diversity. Increasing or maintaining diversity is a common goal for wildlife conservation and management. Often, ecologically relevant scales for diversity are unknown and management is applied on scales of human perception or convenience. But even when appropriate scales are identified, species do not benefit unless resulting science is applied to the landscape through appropriate conservation actions. Habitat amount is undisputedly important and, as such, conservation often prioritizes protection and restoration. Primary productivity is usually beyond the scope of management, although understanding its importance can inform planning because more productive landscapes are often the first to be degraded by land use change (Leu et al. 2008). Enhancing heterogeneity to benefit diversity is a tractable management objective that is increasingly recommended in freshwater (Jähnig and Lorenz

2008), agricultural (Benton et al. 2003), and grassland (Fuhlendorf et al. 2006, Fuhlendorf et al. 2010) systems. However, applications of heterogeneity-based management have met with mixed results (Palmer et al. 2010, McGranahan et al. 2013) and to date the approach has not been widely adopted.

Heterogeneity and grassland birds. In North American grasslands, managing for heterogeneous vegetation structure is thought to be particularly important for conservation of imperiled songbirds because some species prefer sparse grass whereas others prefer dense cover (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006, Toombs et al. 2010). Grasslands are characterized by variability in patterns of climate, fire and ungulate grazing (Samson et al. 2004, Bond and Parr 2010). Although historical evidence is limited, many biologists believe that anthropogenic activities have reduced natural variability in these processes, homogenized grass height and impoverished bird communities (Fuhlendorf and Engle 2001). Several studies report the benefit of heterogeneous patch-burn treatments over homogenous annual burns in a local context (Fuhlendorf et al. 2006, Coppedge et al. 2008, Hovick et al. 2014) and a management approach using fire or livestock grazing to enhance heterogeneity is widely recommended in grassland systems (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006, Derner et al. 2009).

Although a heterogeneity-based approach is conceptually attractive to managers tasked with promoting diversity, two important gaps in knowledge prevent its broad application (figure 1). First, there is little information about the relevant spatial scale(s) for patterns of bird diversity. Second, the importance of heterogeneity compared to habitat amount or productivity is poorly understood. We address these questions by identifying spatial scale(s) appropriate for conservation and by comparing the relative role of habitat amount, productivity and heterogeneity as drivers of bird diversity. We do so within a large (26,600-km^2) region of native mixed-grass prairie in northeast Montana that represents a continental hotspot for grassland bird diversity (Sauer et al. 2014; figure A1).

Methods

Bird surveys. We surveyed birds in grasslands of Phillips and Valley counties, northeast Montana from 20 May to 11 July of 2011-2013 (figure 2). This region contains some of the largest remaining tracts of intact mixed-grass prairie in the country (Cooper et al. 2001), providing habitat for a diversity of grassland birds (figure A1). To target grassland species, surveys were randomly placed across areas classified as grassland by the GAP analysis (USGS 2010) and an aggregate of similar natural communities (B. Martin, unpublished data). Most were on publicly managed grazing lands (federal 68%, state 17%) and the remainder (15%) were on private and tribal rangeland. To maximize variability in landscape and local variables of interest, we stratified random locations by categories of distance to livestock water sources (0-400, 400-800, 800-1200 and >1200-m) and by the proportion of grassland in 8-km^2 around survey locations. To target upland grassland songbirds, we restricted surveys to slopes of <5%, without trees and with low shrub cover (<25%). We collected data during and immediately following two years of record high precipitation (442 and 495 mm for Glasgow, MT in 2010 and 2011, respectively; PRISM 2014).

We conducted 10-minute, 100-meter fixed radius point counts (Hutto et al. 1986), recording species and abundance of all birds observed. We sampled between 0600-1000 MST in dry conditions and when maximum wind speeds did not exceed 24-km/h. We completed 1,293 surveys: 576 in 2011, 562 in 2012, and 155 in 2013. We include in analyses data from all seven native grassland specialists (table 1) that were observed at > 10% of point counts.

Quantifying pattern and scale of bird diversity. We used semi-variograms (variograms) of survey data from 2011-12 to describe patterns of bird distribution across the region. Variograms describe spatial structure of variables by comparing the average square difference (semi-variance) between values at pairs of points separated by a given lag distance to the lag distance itself (Cressie 1993). We used bird abundance to calculate empirical variograms for each species and then fitted a spherical model by weighted least squares (Cressie 1985) to estimate range. Range of a variogram refers to the lag distance at which the variable is no longer spatially correlated, and represents a spatial estimate of the scale of autocorrelation. We fit variograms using the gstat package in program R (Pebesma 2004, R Development Core Team 2013) with an extent of 20-km and a step width of 300-m.

We evaluated how patterns of alpha (α) and beta (β) diversity varied across scales using square landscapes of increasing size. Decomposition of diversity into α and β components provides insight into how patterns in community assemblages change across scale (Whittaker 1960, 1972). Alpha diversity is measured locally, whereas β diversity is the rate of turnover in composition among sampling units (Koleff et al. 2003, Legendre et al. 2013). The relative importance of α and β to regional diversity varies with scale, and the shape of this trade-off provides insight into biologically and environmentally relevant scales for the community (Barton et al. 2013).

We conducted analyses at four landscape scales (A-D; figure 2) relevant to land management in the region (White 1983). Scales included 0.7-km^2 (A; quarter-section), 2.6-km^2 (B; section), 93-km^2 (C; township) and 1,492-km^2 (D; quadrangle). To define landscapes, we overlaid an arbitrary square grid across the region with cell sizes corresponding to each scale. To control for sampling bias from unequal survey allocation among landscapes and scales, we randomly selected three surveys from a given year in each landscape and at each scale of analysis. Landscapes in any year that contained less than three surveys were excluded. Because vegetation and bird distribution vary annually (Jones et al. 2007, Skagen and Yackel Adams 2012), estimates were included for each year that landscapes were adequately sampled. We estimated diversity indices within landscapes at each scale by summing total abundance and richness across the three surveys. For α diversity, we used the Shannon-Wiener diversity index (H'; Shannon 1948), which reflects species richness and proportional abundance (evenness) among species. For β diversity, we estimated Jaccard dissimilarity (Real and Vargas 1996) using package betapart (Baselga et al. 2013).

Quantifying grassland habitat. We calculated the amount of available habitat in each landscape as the proportion grassland classified by the GAP analysis (USGS 2010). To estimate productivity and heterogeneity, we collected data on vegetation attributes (Hendricks et al. 2007) at each survey location. We used five 1-m radius plots distributed within the point-count circle to estimate the proportion bare ground, litter cover and the density of live and dead herbaceous vegetation. We then calculated a combined cover index using the formula: (1-proportion bare)*proportion litter*total vegetation density and applied a square root transformation to normalize its distribution. The cover index ranged from 0-5.48 with an average of 1.91. Low values indicated sparse cover and high values indicated dense cover (figure A2). We estimated productivity using mean cover index which reflects the amount of available biomass and is related to food availability for songbirds (Haddad et al. 2001). Heterogeneity in vegetation structure is thought to be especially important to diversity of grassland birds and we quantified it using standard deviation, range and inter-quartile range of observed cover values.

Linking bird diversity to habitat across scale. To evaluate the role of heterogeneity in shaping patterns of bird diversity, we related habitat data to diversity across the four scales of analysis (A-D; figure 2). To maximize statistical power, we calculated H' and habitat metrics using the maximum number of survey points per landscape at each scale while ensuring a sufficient sample of landscapes for comparison. We randomly selected three surveys from a given year in each landscape at scale A and B, five surveys in each landscape at scale C and 20 surveys in each landscape at scale D. Landscapes that contained fewer surveys per year were excluded. Sample sizes were 55, 105, 79 and 18 landscape-years for scales A-D, respectively.

We related bird diversity to habitat in landscapes of each scale using a nested set of linear models. To assess relative explanatory power, we added habitat amount, productivity and vegetation heterogeneity successively to the model. We measured fit as R^2 between predicted and observed H' and compared models to one another using Akaike's Information Criterion (AIC; Anderson et al. 2000). Because of theoretical support for curvilinear effects of productivity, we also tested the addition of a square term for mean cover index. Correlation between grassland amount and other predictors was low (r = -0.3-0.1) but as expected there was moderate covariance between productivity and heterogeneity in herbaceous cover, especially at broader scales (r = 0.35-0.8). The three metrics of vegetation heterogeneity were highly correlated and were added to models individually. As a post-hoc analysis to assess how individual species' response contributed to observed patterns in diversity, we fitted linear models of log-transformed bird density (individuals/ha) using predictive habitat metrics and scales.

Results

Patterns of bird distribution. We recorded 8,472 individuals of the seven species surveyed (table 1). Abundance of all species was spatially autocorrelated within neighborhoods of ≥ 1.1-km^2. Average area of autocorrelation across species was 240-km^2. Patterns of species distribution emerged as patchy (2 to 7-km^2), variable (1-74-km^2) or dispersed (40-20,100-km^2) based on variogram range estimates (table 1). Distributions aligned with known species' habitat preferences (Chapter 1). The most patchily distributed were larks and longspurs, which prefer sparse grass and were relatively abundant when present at point-counts (table 1). In contrast, the three sparrow species were widely dispersed, prefer dense grass habitat and were comparatively less abundant than larks and longspurs at point-counts where they occurred (table 1). Sprague's Pipit had a habitat preference intermediate to those of other species and its abundance was similar to that of sparrows. Pipits showed variable distribution between years with a dispersed, sparrow-like pattern in 2011 and a patchy, longspur-like pattern in 2012. Autocorrelation estimates for patchily distributed species were similar between years (σ = 1.5 to 3.4-km^2) compared to those for dispersed species (σ = 13 to 14,088-km^2; table 1).

Diversity and scale. Alpha diversity increased with spatial scale (figure 3) indicating that larger extents harbored greater diversity. Alpha diversity was greater at broad (C-D; 93 to 1,492-km^2) versus fine spatial scales (A-B; 0.7 to 2.6-km^2; figure 3). Beta diversity remained high at all but the broadest extent evaluated (figure 2), indicating that species composition was most stable within large landscapes.

Bird diversity and habitat metrics. Models at the scale with the most diverse (α) and stable (β) bird communities (D; 1,492-km^2) also best captured habitat relationships underpinning diversity (table 2). We do not interpret models at smaller scales, A-C (table 2), where bird diversity was lower and species turnover was high. At the largest scale (D), the three habitat metrics together explained half of variation in α diversity (table 2). Habitat amount accounted for most explained variation (51%) followed by productivity (27%) and vegetation heterogeneity (16%). Productivity had a quadratic relationship with diversity (figure 4) indicating that landscapes dominated by dense or sparse grassland cover were less diverse than those that had a mix of both (Figure 5b). For comparison, Sprague's Pipit and three sparrow species were rare or absent when productivity was low at finest scale A (figure 5a). Heterogeneity in cover predicted additional diversity at the broadest scale D ($\Delta R^2 = 0.08$; ΔAIC=1) suggesting that the range of cover available explained unique variation not captured by average productivity (table 2; figure 4).

Habitat amount was the strongest and most consistent predictor of α diversity regardless of scale A-D, accounting for most (51-89%) explained variation (table 2; figure 5c-d). Post-hoc analysis showed that four of seven species including Chestnut-collared and McCown's Longspur, Baird's Sparrow and Sprague's Pipit were sensitive to habitat amount at scale D (figure 5d). Declines in these four species resulted in low α diversity in grass-poor landscapes (figure 4). For instance, a landscape at scale D with 60 versus 20% habitat amount would support more than twice the combined density of sensitive species (1.2 versus 0.5 birds per ha; figure 5d). Horned Lark became rare only at finer scales (A-B) when habitat amount was low. Grasshopper and Savannah Sparrow were not sensitive to habitat amount at any scale evaluated.

Discussion

Explicitly identifying an appropriate scale D (1,492-km^2) for analysis elucidated relationships underpinning diversity and stability of this grassland songbird community. Of four scales evaluated, only the largest (D) exceeded average autocorrelation distance that characterized the patchiness of species distributions (240-km^2). Landscapes at finer scales (A-C) were insufficient to capture patterns of species distribution, resulting in lower α diversity and higher turnover in composition.

Precipitation is a dominant force shaping grasslands and vegetative cover is quick to respond to annual variability (Skagen and Yackel Adams 2012). Differences in observed distribution patterns among species reflected their relative preferences for sparse versus dense cover. Regionally wet conditions that promoted widespread growth of dense cover homogenized distributions of sparrow species as their dense-grass habitat became broadly available. Sparrow distributions showed autocorrelation at spatial scales of 40 to 20,100-km^2, aligning with scales observed for precipitation patterns in other semi-arid regions of the Great Plains (80 to 20,100-km^2; Augustine 2010). Further, average autocorrelation of dense-grass species increased from 87-km^2 in 2011 to 6,858-km^2 in 2012, likely reflecting increased herbaceous growth 1-2 years after the shift to abnormally wet conditions.

In contrast, distributions of larks and longspurs showed spatial variability at scales of 2 to 7-km^2, a pattern that is patchier than expected based on precipitation. These species may have been limited to areas where soil, topography, microclimate or grazing acted locally to produce their sparse-grass habitat. In spite of the rapid shift to wet conditions in 2011, lark and longspur distributions remained patchy (4.4 and 3.1-km^2 for 2011 and 2012, respectively), strengthening inference that precipitation alone did not explain their distribution. These contrasting patterns could reverse themselves during periods of drought, which would likely homogenize the distribution of species preferring sparse grass and restrict those requiring dense cover to locally productive sites.

Influence of habitat amount far outweighed that of vegetation productivity or heterogeneity, explaining 2-3 times more variation in α diversity. This finding is consistent with known patterns of area sensitivity in many grassland birds (Johnson and Igl 2001, Davis et al. 2006, Ribic et al. 2009). Three mechanisms have been proposed to explain area-sensitivity, including unequal area (i.e., passive) sampling bias, habitat diversity and area-per-se (Ribic et al. 2009). Our results support the area hypothesis because we controlled for passive sampling and habitat heterogeneity was not correlated with amount. Cues used by grassland birds during migratory settlement are poorly understood (Ahlering et al. 2009), but evidence suggests that they exhibit behavioral preference for large, relatively flat landscapes with few anthropogenic features and high visual openness (Ribic et al. 2009, Keyel et al. 2011). This preference might result from edge avoidance related to real or perceived risk of predation and parasitism (Winter et al. 2000, Benson et al. 2013, Keyel et al. 2013).

Our post-hoc analysis shows that reduced densities of species dependent upon large and intact grasslands were responsible for observed low diversity (figure 5d). Unsurprisingly, the four songbirds we identified as sensitive are also among those of highest international conservation concern (McCready et al. 2005). Continentally, Chestnut-collared and McCown's longspur, Sprague's Pipit and Baird's Sparrow showed stronger annual population declines from 1966-2013 (-2.93 to -6.18%; Sauer et al. 2014) than Horned Lark, Grasshopper and Savannah sparrow, which were not sensitive to broad-scale habitat amount (-1.3 to -2.8%). Sensitive species were less abundant in grass-poor landscapes even though habitat was locally available. Loss and fragmentation of grassland at broad scales following continental changes in land use have likely contributed to negative population trends for these species.

Availability of extremes in herbaceous cover provided habitat for more species as evidenced by contributions from vegetation productivity and heterogeneity to α diversity. In particular, landscapes at scale D dominated by dense or sparse grass harbored less bird diversity than those with a mix of both (figure 5b). Variability in cover near the mean was not important because the inter-quartile range was not predictive. This suggests that availability of extreme conditions in herbaceous cover, both sparse and dense, supported the most diverse communities. This pattern did not hold across scales and heterogeneity was not predictive at scales A-C.

Conservation of large and intact grassland landscapes rather than a heterogeneity-based approach should be a top priority for maintaining bird diversity. Management actions such as grazing and burning can affect habitat locally but are unlikely to override the dominant influence of existing patterns in habitat amount and productivity. If management tools are applied at inappropriate scale(s) or in an inappropriate landscape context, they could reduce rather than enhance the system' natural variability. For example, implementing fine-scale patch-burn grazing to create high heterogeneity on an especially productive property might reduce the regional availability of dense cover that represents an important resource for some species. In northern mixed-grass prairie, we caution against heterogeneity-based approaches in landscapes smaller than 93-km^2 (C; township). Rather, we recommend conservation and management be implemented at scales >1,492-km^2 to capture the full range of habitat variability that supports diverse and stable communities.

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Tables

Table 1. Species included in analyses, habitat preferences and patterns of abundance and distribution. Distribution patterns from range of autocorrelation in abundance data estimated by spherical variograms with a step width of 300-m and cutoff of 20-km.

Common Name	Scientific name	Mean abundance where present	Grassland Habitat Preference[1]	Distribution Pattern[2]
Chestnut-collared Longspur	*Calcarius ornatus*	3.7	Sparse	Patchy
Horned Lark	*Eremophilia alpestris*	2.1	Sparse	Patchy
McCown's Longspur	*Rhynchophanes mccownii*	2.1	Sparse	Patchy
Sprague's Pipit	*Anthus spragueii*	1.6	Medium	Variable
Grasshopper Sparrow	*Ammodramus savannarum*	1.6	Dense	Dispersed
Savannah Sparrow	*Passerculus sandiwchensis*	1.4	Dense	Dispersed
Baird's Sparrow	*Ammodramus bairdii*	1.8	Dense	Dispersed

[1] *As modified from Chapter 1.*

[2] *Average area of spatial dependence for abundance data from 2011 and 2012: Chestnut-collared Longspur, 4.1 and 2.0-km^2; Horned Lark, 2.0 and 4.9-km^2; McCown's Longspur, 7.1 and 2.3-km^2; Sprague's Pipit, 74 and 1.1-km^2; Grasshopper Sparrow, 40 and 58-km^2; Savannah Sparrow, 177 and 20,100-km^2; Baird's Sparrow, 43 and 415-km^2.*

Table 2. Relative contribution of habitat amount, productivity and heterogeneity in predicting bird diversity (Shannon-Weiner Diversity Index) in northeast Montana, 2011-2013 at four spatial scales. Values show improvement in linear model fit by the addition of each successive variable, estimated as change in R^2 between observed and predicted diversity. Variables were added to the model cumulatively in the order shown with the exception of competing heterogeneity variables which were added individually. Model significance estimated by analysis of variance: asterisk (*) indicates at $P < 0.1$; (**) indicates $P < 0.05$; and (***) indicates $P < 0.01$. Models with the lowest Akaike's Information Criterion for each scale are in bold.

	SCALE	**A**	**B**	**C**	**D**
		0.7-km^2	*2.6-km^2*	*93-km^2*	*1,492-km^2*
Null Model		0	0.01	0.03	0.02
Habitat Amount	*Proportion Grassland*	0.40***	**0.25*** **	**0.14*** **	0.26**
Productivity	*Mean Cover (linear)*	**0.09*** **	0.01	0.01	0
	Mean Cover (quadratic)	0	0	0	0.14*
Heterogeneity	*Standard Deviation*	0	0.01	0.03*	0.05
	Range	0	0.01	0.02	**0.08**
	Inter-quartile Range	0	0.01	0.02	0.01
Maximum R^2		***0.49***	***0.28***	***0.21***	***0.51***

Figures

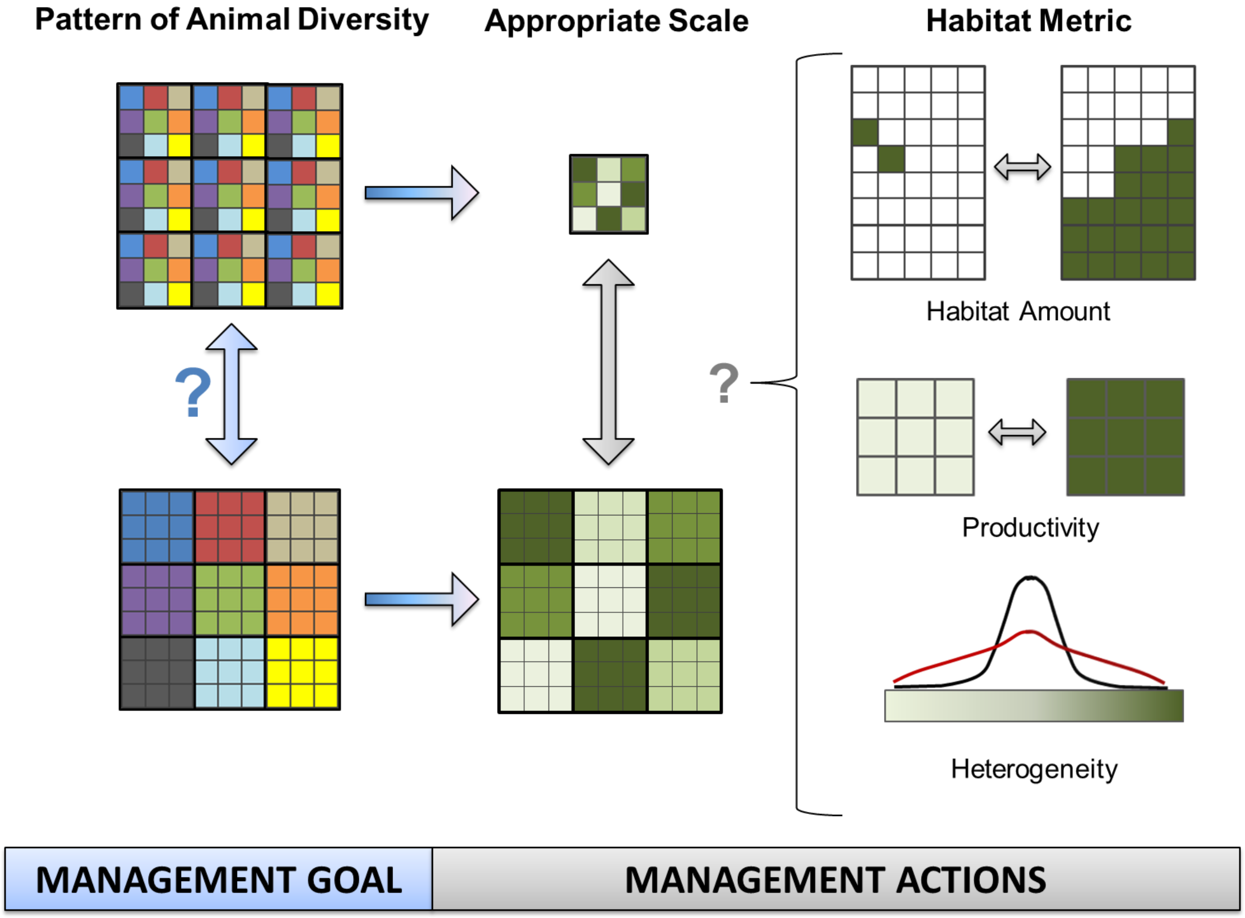

Figure 1. Key concepts in the relationship between animal diversity and habitat. Question marks represent important gaps in knowledge that were a focus for analysis. Colors in pattern of animal diversity represent distributions of various species. Shades of green represent variability in a habitat factor of interest.

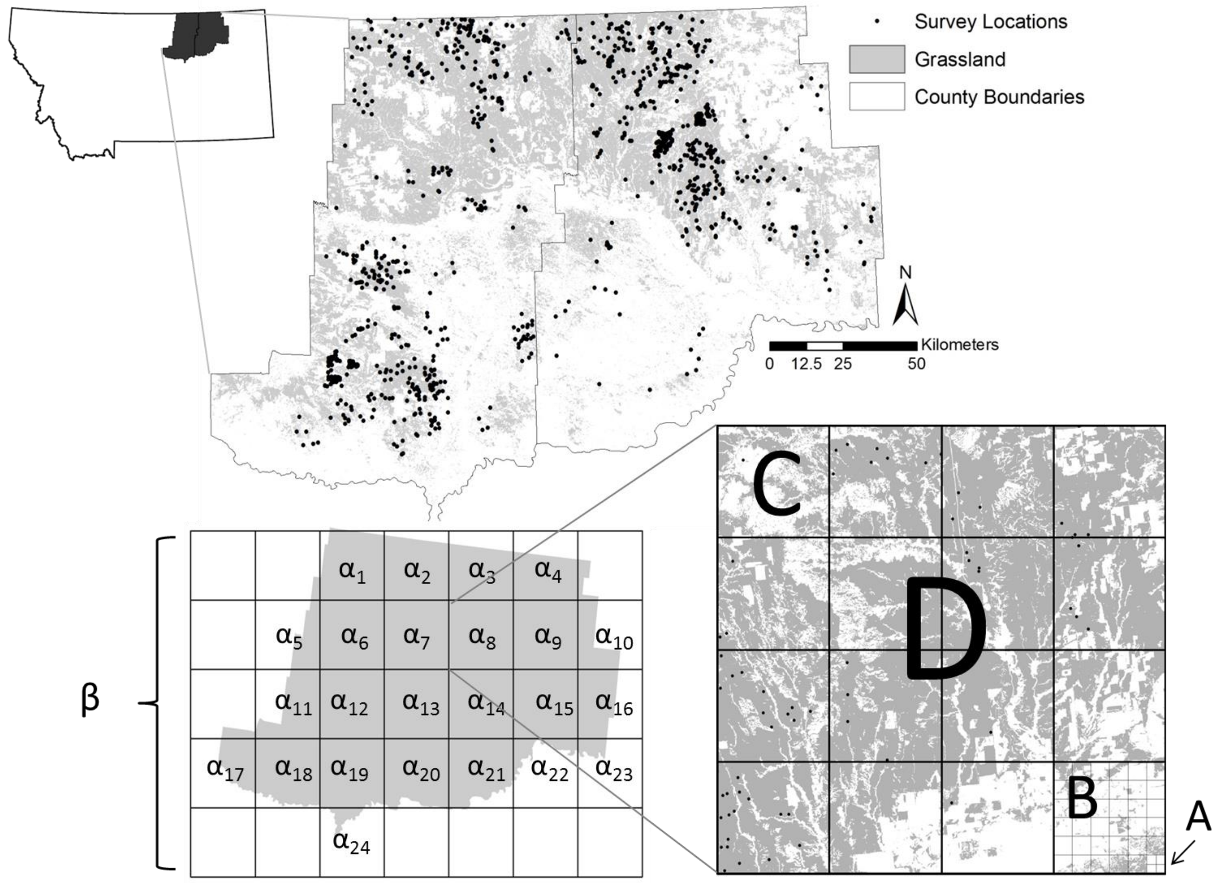

Figure 2. Sampling locations and scales used in northeast Montana, 2011-2013, for analysis of diversity and heterogeneity of grassland songbirds. Scales include 0.7-km^2 (A; quarter-section), 2.6-km^2 (B; section), 93-km^2 (C; township) and 1,492-km^2 (D; quadrangle).

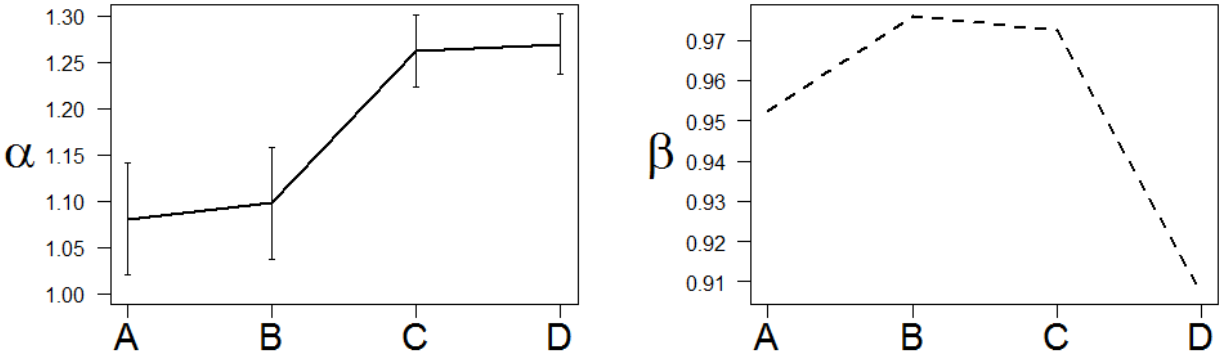

Figure 3. Pattern of α and β diversity within and among landscapes of four spatial extents: (A) 0.7-km^2, (B) 2.6-km^2, (C) 93-km^2 and (D) 1,492-km^2. Values of α show mean Shannon Diversity Index within landscapes of the same size (Shannon 1948). Error bars indicate ± 1 SE of the mean. Values of β show estimated Jaccard dissimilarity across landscapes of the same size (Real and Vargas 1996). Sampling effort was controlled across scales at N = 3 surveys per landscape.

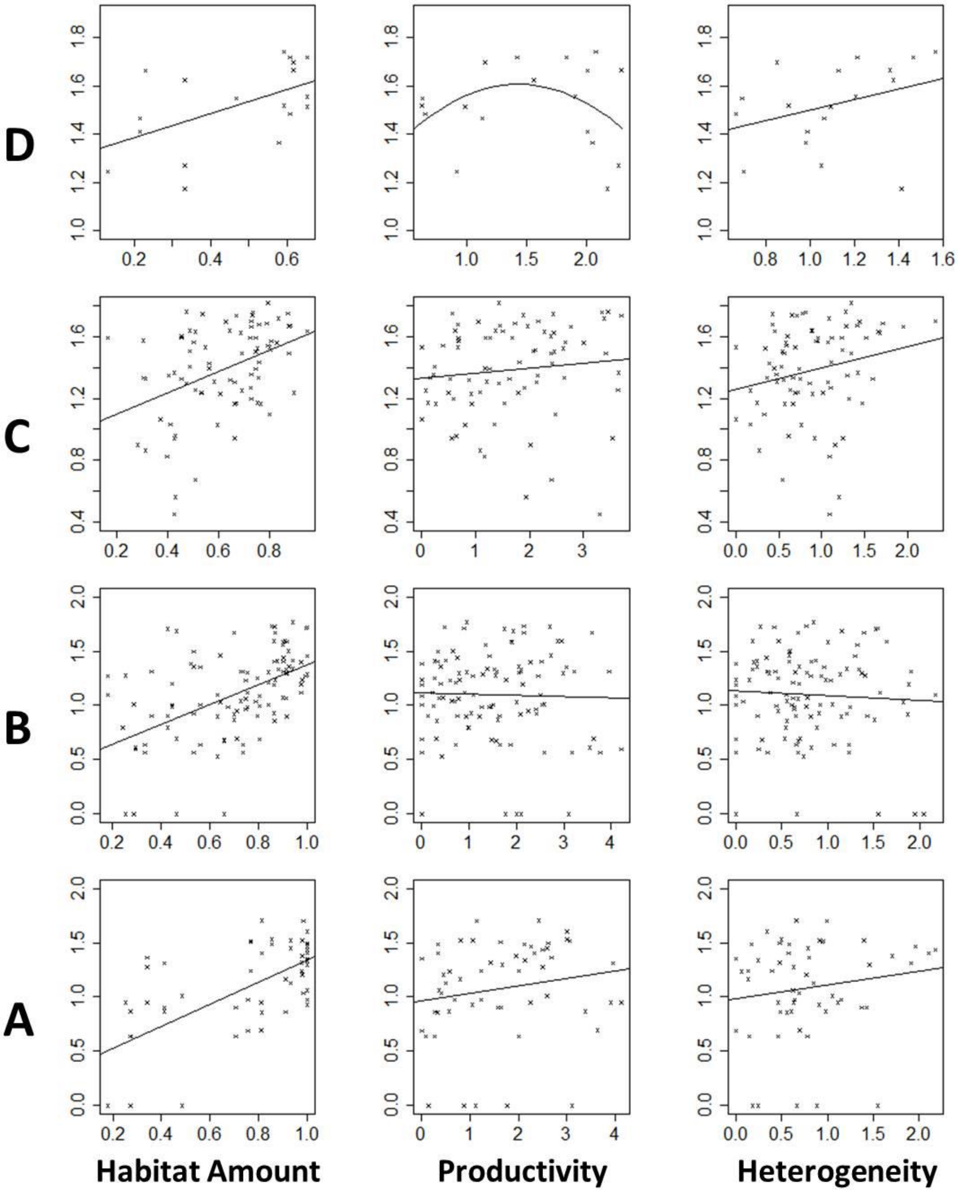

Figure 4. Scatterplots of bird diversity (Shannon index) versus habitat area, productivity and heterogeneity at four spatial scales: (D) 1,492-km^2, (C) 93-km^2, (B) 2.6-km^2, and (A) 0.7-km^2. Habitat amount is the proportion grassland in the landscape. Productivity is mean herbaceous cover index ((1-proportion bare)*proportion litter*total vegetation density, square-root transformed) measured at survey points. Heterogeneity is standard deviation of cover index.

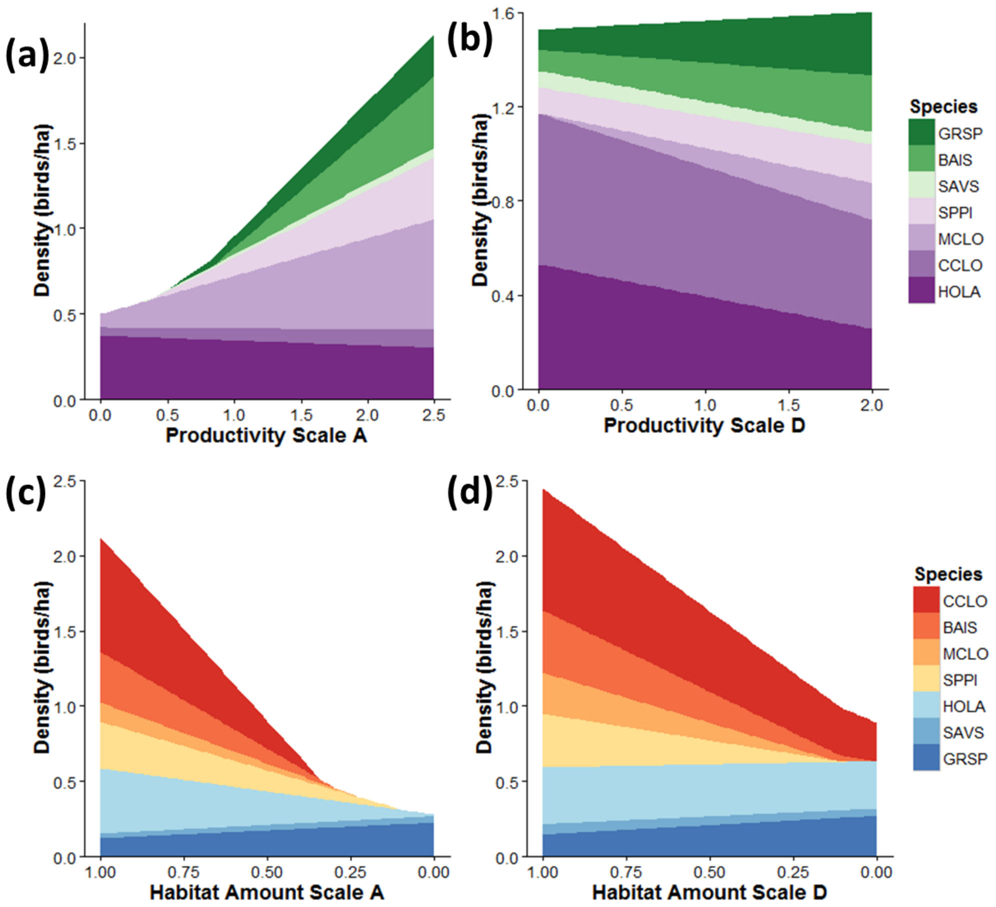

Figure 5. Predicted changes in density of individual bird species in response to vegetation productivity (a-b) and habitat amount (c-d) in landscapes at fine (0.6-km^2; a,c) and broad (1,492-km^2; b,d) scales.

Appendix

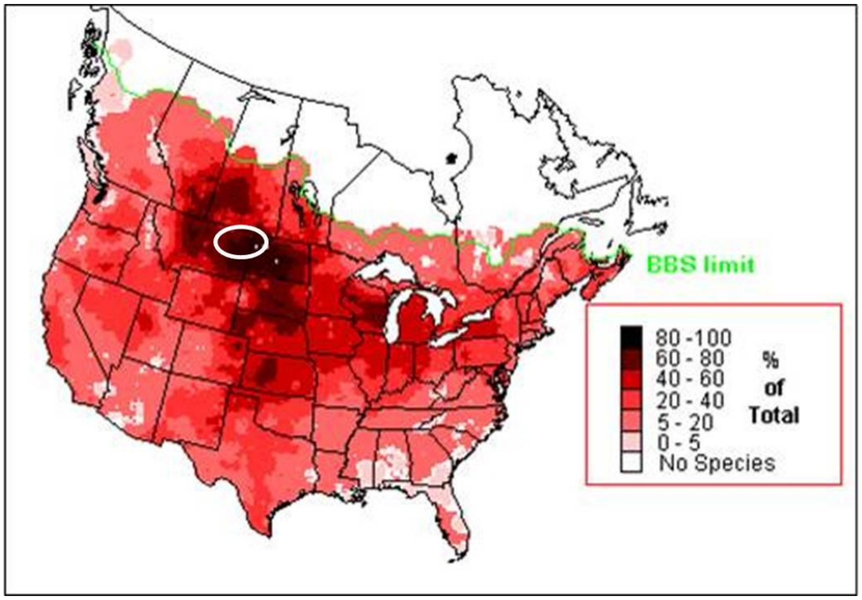

Figure A1. Grassland bird species richness measured by the Breeding Bird Survey (BBS; from Sauer et al. 2014). White oval includes the location of the study region in northeast Montana, 2011-2013.

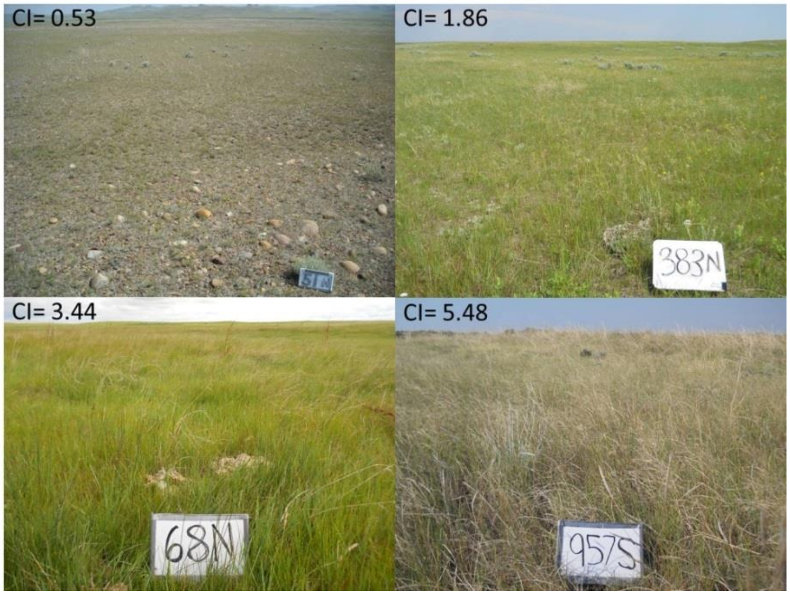

Figure A2. Vegetation at sampling locations in northeast Montana, 2011-2013, illustrating a range of variation in herbaceous cover index (CI).

CHAPTER 3- ONE STEP AHEAD OF THE PLOW: USING CROPLAND CONVERSION RISK TO GUIDE GRASSLAND SONGBIRD CONSERVATION

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Abstract

Rapid expansion of cropland threatens grassland ecosystems across western North America and broad-scale planning is a catalyst motivating partners to accelerate conservation. Sprague's Pipit (*Anthus spragueii*) is an imperiled grassland songbird whose population has been declining rapidly in recent decades. Here, we present a strategic framework for conservation of pipits and their habitat in the northern Great Plains. We modeled pipit distribution across its million-km^2

breeding range in Canada and the U.S. We describe factors shaping distribution, delineate population cores and assess vulnerability to future grassland losses. Pipits selected landscapes with a high proportion of continuous grassland within a relatively cool, moist climate. Sixty-three percent of the global breeding population occurred in Canada and 65% of the U.S. population occurred in Montana. Populations were highly clumped, with 75% of birds within 25% of their range. Approximately 20% of the population occurred on protected lands and over half used lands that were unlikely to be cultivated given current technologies. A quarter of pipits relied on remaining arable grasslands and predicted population impacts varied from 1-25% across habitat loss scenarios. Most of the population (70%) was dependent on private lands, emphasizing the importance of voluntary approaches that incentivize good stewardship. Maps depicting core populations and risks enable partners to accelerate stewardship in landscapes where pipits will benefit most.

Introduction

Grasslands are among the most imperiled ecosystems worldwide (Hoekstra et al. 2004) because their soils provide some of the most productive farmland on earth. As rising global food demand surpasses improvements in yields on existing cropland, additional grassland conversion will be required to feed a projected 11 billion people by 2050 (Foley et al. 2011, Ray et al. 2013). Rising commodity prices exacerbated by demand for biofuels threatens to further expand cropland agriculture (Fargione et al. 2009, Wright and Wimberly 2013). In temperate North America, historic grassland losses total approximately 70%, including complete conversion of the most productive areas where nothing but remnant tracts persist (Samson et al. 2004). In the northern Great Plains where most grasslands remain, accelerated agricultural conversion is happening five times faster than grasslands can be protected (Doherty et al. 2013, Walker et al. 2013).

A steep and consistent decline in songbird populations reflects eroding ecosystem integrity in North American grasslands (Brennan and Kuvlesky 2005, Sauer et al. 2014). Of high concern is Sprague's Pipit (*Anthus spragueii*; herein "pipit"), a grassland obligate species that breeds in the native mixed prairie of Saskatchewan, Alberta, Montana, and the Dakotas (Davis et al. 2014). The pipit has been declining > 3% annually across North America since 1966 (Sauer et al. 2014), is listed as globally Vulnerable by the International Union for Conservation of Nature (IUCN 2014), is federally Threatened in Canada (Environment Canada 2012) and is being considered in 2015 for federal protection under the U.S. Endangered Species Act (ESA; 1973, USFWS 2010). The ESA status assessment focuses attention on pipits and underscores the urgency for conservation of northern grasslands.

Broad-scale planning enables systematic targeting of scarce conservation resources (Bottrill et al. 2008), and sensitive species provide a useful lens for delineating landscapes of high conservation value as well as identifying impacts of human activity (Sanderson et al. 2002). Spatially explicit tools enable practitioners to target implementation where populations will benefit most (Margules and Pressey 2000). We present a three-part analysis that culminates in a framework for strategic conservation of pipits in northern grasslands. First, we depict a range-wide distribution model by integrating survey efforts across a million-km^2 area of Canada and the United States. Using our model, we describe factors shaping pipits' continental distribution and delineate core areas of high bird abundance. Second, we assess vulnerability to future habitat loss using soil capability for agriculture as an index of conversion risk. For the U.S. portion of the range, we employ a quantitative risk model to develop future scenarios of cropland expansion and assess their potential impact on populations. Finally, we explore the relationship between land tenure and population distribution to evaluate the importance of voluntary and incentive-based approaches to conservation of native grassland by private landowners.

Methods

Study area. Our study area includes the intersection of the Breeding Bird Survey range for pipits (Sauer et al. 2014) and the Plains and Prairie Pothole Landscape Conservation Cooperative (PPPLCC; Millard et al. 2012), a consortium of public and private conservation partners (figure A1). The region covers portions of Alberta, Saskatchewan, Montana and the Dakotas. This area is made up of diverse mixedgrass prairie with level to rolling terrain. Ecologically, it encompasses interspersed badlands and sagebrush steppe in the west and pothole wetlands and prairie parklands in the east. The study area includes portions of Great Plains-Palouse Dry Steppe (331), Great Plains Steppe (332) and Prairie Parkland (251) provinces as described in Bailey (1995).

Bird survey data. Range-wide perspectives are required for the conservation of migratory, highly mobile songbirds. Data limitations and inconsistent collection methods have hindered efforts to model bird distributions at broad scales. To describe pipit distribution across its breeding range, we combined data from 76,623 point counts (2007-2012; table A1) into an integrated analysis. Integration allowed us to achieve spatial coverage that made our continental perspective possible. We conducted a sensitivity analysis in the heart of the range (northeast Montana) to assess the influence of point count methods on detectability. Collected in 2012-2013, this dataset contained known distance and time intervals for evaluation (author ML, unpublished data). We truncated data by 1-min time interval (0-1, 0-2, 0-3, etc.) and distance intervals estimated to the nearest 10-m. We then used linear models to estimate the effect of time and distance on observed detection probability and abundance. Detection probability remained relatively insensitive to point count duration (1% increase per minute) and distance (4% per 100m). Distance and duration affected bird abundance more strongly (3 and 8% respectively) so we limited modeling to presence/absence data.

We removed repeated and overlapping records, keeping the most recent records within 200-m of one another based on average point-count radius. Surveys were not targeted for pipits and data were heavily skewed towards absence. Because random forest models are sensitive to zero-inflation (J. Evans, the Nature Conservancy, pers. Comm.), we randomly stratified records to ensure appropriate class balance with 40% occurrence. Because survey locations were highly clumped in some regions, we thinned the dataset to 10,000 records (approximately 30%) using a random sampling algorithm weighted by the inverse proportional kernel density estimate of sampling intensity. Thinning resulted in isolated records being chosen at a higher rate and produced a more even sampling distribution. Some portions of the study region, including the Dakotas and Saskatchewan, had lower data availability and contributed proportionally fewer records even after thinning (figure A1).

Environmental predictors. Climate has a strong relationship with bird distributions in North America and long-term averages reflect envelopes that shape geographic ranges (Thomas 2010, Jiménez-Valverde et al. 2011). Climate variables were highly correlated, so we chose those most relevant to herbaceous vegetation growth and that had correlations ≤ 0.8. We included five variables related to long-term climate patterns for North America averaged across 1961-1990: mean annual precipitation (mm), mean annual temperature (C°/10), total growing season precipitation (mm), summer precipitation balance (Rehfeldt et al. 2006) and average frost free period in days.

Because pipits are sensitive to grassland vegetation structure (Fisher and Davis 2010), we included three shorter-term measures of vegetation growth and moisture, including Gross Primary Productivity (GPP), maximum annual snowfall, and the Palmer Drought Severity Index (PDSI). We averaged short-term measures across 2002-2010, including five years preceding bird surveys because residual vegetation is an important component of grassland bird habitat (Ahlering et al. 2009). Comparable data for 2011-12 were not available at the time of analysis. GPP provides an index of amount of vegetation growth and is derived from Moderate Resolution Imaging Spectrometer satellite imagery at 8-day intervals (Reeves et al. 2006). We represented GPP as the maximum measurement during April-July using values obtained from NASA (2012). Maximum snow depth for winter between October and April were obtained from Snow Data Assimilation System (National Operational Hydrologic Remote Sensing Center 2004). For PDSI we used global 2.5° gridded monthly data for May self-calibrated with the Penman-Monteith potential evapotranspiration formulation, 1900-2010 (Dai and NCAR 2014).

We included attributes for land cover because pipits require relatively large and intact grassland for every aspect of their life history (Davis et al. 2006, Sliwinski and Koper 2012). We used four variables that describe patterns in land-cover: proportion of cropland, forest, and grassland, and a grassland aggregation index. We derived 400-m resolution binary layers of crop, forest and grassland from 30-m land-cover products created by Agriculture Agri-Food Canada (2001) and level II of the United States Geological Survey National Land Cover Dataset (Homer et al. 2007). Land use classes had accuracies of 82% in the U. S. (Wickham et al. 2010) and >85% in Canada (Fisette et al. 2006). We calculated proportional variables using a moving window average of binary raster layers. We chose a window size of 10.4-km^2 because grassland songbirds are known to respond to land use at relatively large scales (e.g. 8-km^2; Bakker et al. 2002), and 10.4-km^2 has been ecologically relevant to prairie birds in past studies (e.g. Reynolds et al. 2006). We used the program FRAGSTATS (McGarigal et al. 2012) to calculate grassland aggregation index using the same window size. This index calculates the proportion of within-class adjacencies among neighboring pixels out of the total number of possible adjacencies, indicating degree of grassland fragmentation within each window. Correlation among land cover variables ranged from -0.19 to 0.81.

Species distribution model. We specified a binominal model with a probabilistic outcome using the nonparametric model Random Forest (Breiman 2001) in program R (R Development Core Team 2013) and the randomForest package (Liaw and Wiener 2002). Random Forest is a bootstrapped Classification and Regression Tree (CART) approach that is based on the principle of weak learning (Hastie et al. 2008), where a set of weak subsample models converge on a stable global model. This method has been shown to provide stable estimates while being robust to many of the issues associated with spatial data (e.g., autocorrelation, nonstationarity). It also fits complex, nonlinear relationships and accounts for high dimensional interactions (Cutler et al. 2007, Evans et al. 2011). We assessed competing models by comparing model importance, which is calculated as smallest out-of-bag (OOB) error, smallest maximum within-class error and fewest parameters (Murphy et al. 2010) in package rfUtilities (Evans and Murphy 2014). Parsimony in Random Forest reduces noise, produces a more interpretable model and results in better model fit (Murphy et al. 2010, Evans et al. 2011). For model validation we calculated OOB error and internal root mean square error (RMSE; Willmott 1981). We calculated model performance using the area under the receiver operating curve (AUC; Metz 1978) in two ways:

first, with data used in model fitting, and second, with data withheld from fitting after thinning (see Section 2.2.1).

Imperfect detections (false absences) in bird survey data can be a significant source of error in models of distribution. Available estimates of detection probability for pipits range between 0.70-0.82 (S. Davis [0.70] and M. Lipsey [0.82], unpublished data). We assessed the effect of false absences on model fit by conducting a sensitivity analysis in the package rfUtilities by randomly changing a proportion ($p=0.28$) of presences to absences and running a series of perturbed models. We observed a small standard deviation ($\delta=0.00098$), across $n=999$ simulations, indicating model stability in spite of potential false absences. This can also be partially attributed to the ability of Random Forests to predict through noise and is an advantage of weak learners (Breiman 2001).

Population core areas. To estimate the regional distribution of populations, we first resampled the model prediction raster from the arbitrary resolution of environmental layers (400 x 400-m or 16-ha) to a unit that approximates territory size for male pipits (160 x 160 m or about 2.6-ha; Fisher and Davis 2011) using bilinear interpolation in ArcGIS (ESRI 2010). We summed the probability of occurrence across all pixels in the study region to generate an index of total population. We then placed each grid cell prediction in context of the study area by dividing the individual probability of occupancy by the total index. Starting with the highest-value pixels, we cumulatively summed the probabilities until a given threshold was met. We set 25, 50 and 75% thresholds to delineate cores as the smallest possible areas containing the largest concentrations of predicted pipits. We estimated proportion of the population within multiple political and ownership boundaries by dividing the sum of occurrence probabilities in each class by our total population index.

Continental cropland risk. To estimate future conversion risk of grassland to cropland, we used existing soil databases to overlay soil capability for agriculture on the pipit distribution. Soil capability classes are ranked 1 to 8, with 1 being the most suitable for crops and 8 the least. We accounted for slight differences in soil classifications between the two countries by combining categories 1-2 (most arable), 3-4 (some limitations) and 5-8 (least arable). Conversion rates tracked soil capability, with the most arable land (classes 1-2) largely already converted (70%). By comparison, only 47 and 5%, respectively, of the moderate (classes 3-4) and least arable soils (5-8) have already been converted. Using the species distribution model probability surface, we calculated the simple proportion of the predicted population on untilled land in each soil class. We also calculated the proportion of land and population that are legally protected from agricultural conversion within each class. We obtained soils data from the Natural Resources Conservation Service web soil survey database (NRCS 2014) in the U.S. and from the Canada Land Inventory in Canada (1998).

U.S. cropland risk scenarios. To identify regions and populations at risk from conversion in the U.S, for which we had more detailed data than we did for Canada, we used a cropland suitability model described in Smith et al. (2015). The model provides a probability surface with values from 0-1, representing the relative suitability of each grid cell for conversion to cropland. We used this surface to develop three potential build-out scenarios, a-c. In each scenario, land above a given probability cut-point was assumed to be converted. Pattern and rate of future grassland loss is difficult to predict; therefore, we use scenarios only as reference points for planning. Scenarios do not reflect variation in rates of conversion, nor do they refer to a given time horizon. They represent the spectrum of plausible absolute losses in grassland area due to cropland expansion based upon observed rates of loss (figure A2; GAO 2007, Doherty et al. 2013).

Scenario (a) represents minimal, or background conversion, scenario (b) represents a constrained growth scenario for cropland, and scenario (c) represents unconstrained cropland growth. We reclassified the probability surface raster to produce predicted conversion layers. Probability cut-points that defined scenarios were selected as (a) 0.98, (b) 0.7 and (c) 0.3 (table 2) after visual inspection of the area accumulation curve derived from the tillage model (figure A2). For each scenario, we removed pixels of predicted new cropland from the original land cover layer of grassland. All federal land and state lands were considered protected from conversion except state school trust lands. Tribal lands included in Bureau of Indian Affairs (BIA) databases were treated as private, thus not protected from conversion. Existing cropland was also excluded. We converted altered grassland layers to proportion and aggregation variables and substituted them into the original model to re-predict Pipit distribution under each scenario.

Ownership. To estimate the composition of land tenure and conservation status of the pipit population in the U.S., we used ownership and protection data compiled for Doherty et al. (2013). In Canada, we built an ownership layer by combining boundaries from provincial, federal, and private conservation areas. To quantify areas protected from cropland in Canada, we obtained parcel boundaries of provincial land that were legally protected from cultivation from the Alberta, Saskatchewan, and Manitoba provincial governments and those of federal lands from Environment Canada. We also obtained information on lands that were privately owned and legally protected from cultivation from private conservation agencies (e.g., Nature Conservancy of Canada, Ducks Unlimited Canada). We considered lands with perpetual conservation easements to be protected from conversion, but lands under volunteer or management agreement to be available for conversion. For each ownership class, we summed the value of the species distribution model probabilities and divided by the total sum to produce a proportional estimate of population density by ownership.

Results

Species distribution model. The most supported and parsimonious model of pipit occurrence included nine predictors: proportion of grassland, grassland aggregation index, PDSI, average maximum snowfall, growing season precipitation, summer precipitation balance, average frost-free period, mean annual precipitation and mean annual temperature (figure 1). RMSE was 0.03 with a 14.4% OOB error rate. The AUC was 0.91 when predicting data not used in model fitting and 0.99 when predicting data that were used (see section 2.2.1). All assessments indicated good model performance with high predictive accuracy (Fawcett 2006).

Landscapes with a high proportion of aggregated grassland and with relatively cool, moist climates were most likely to contain pipits. Effects of environmental and climatic predictors on pipit distribution were nonlinear (figure 1). Strongest predictors were moisture variables (maximum snowfall, PDSI, growing season precipitation and summer precipitation balance) combined with proportion of grassland in 10.4-km^2 around survey points.

Population core areas. Breeding pipits were unevenly distributed across their range and were concentrated in core areas characterized by grassland (figure 2a). The relationship between population density and area was steep, with 25% of the population within 5% of the study area, and 75% of birds within 25% of the study area (figure 2b). Regions of highest pipit density were predicted in southeast Alberta, southwest and south-central Saskatchewan, and northeast

Montana. Our final model also predicted several small core areas in southwest Manitoba and in central portions of the Dakotas. About 62% of the population occurred in Canada, with 38% in the U.S. Alberta and Saskatchewan together contained more than 90% of the Canadian population and about 60% of the global population. Montana contained 65% of the U.S. population, with most of the remainder in the Dakotas (table 1).

Continental cropland risk. Observed frequency of pipits was three times lower in cropland (13%) than across all land use classes combined (40%). Continentally, we estimate that 21% of breeding pipits occupied grasslands that are legally protected from conversion to cropland. Conversely, a quarter of the continental pipit population occupied unprotected grasslands at risk of future conversion (soil capability classes 1-4; figure 3b). Pipits occupied protected grasslands underlain by arable soils (classes 3-4) more than expected (figure 3a; $\chi 2$ test, df = 1, t =4.06, P = 0.044). In contrast, they avoided the most arable, unprotected landscapes (classes 1-2) where widespread conversion has already impacted grasslands ($\chi 2$ test, df = 1, t = 2.95, P = 0.086). Protection from conversion was inversely related to soil capability, with grasslands on more arable soils less protected. Protection status was low with 2% of the most arable soils protected (classes 1-2), 8% of classes 3-4 and 23% of classes 5-8 protected.

U.S. cropland risk scenarios. Within the U.S., predicted population-level impacts of 1-23% varied with grassland loss across three conversion scenarios (figure 4). Our model indicated a 1% population impact with background growth (figure 4; scenario a), a 9% loss with constrained growth (b) and 23% loss with unconstrained growth (c; table 2). Background rate of conversion in scenario (a) predicted few grassland losses with only the easternmost fringe of core areas affected. Under the constrained conversion scenario (b), additional core populations were at risk, particularly in smaller habitat blocks along margins of the pipit range. Scenario (b) also predicted habitat loss in the largest core area in the U.S. in northern Montana (figure 4). Unconstrained cropland expansion in scenario (c) resulted in habitat losses across most of the eastern portion of the range and the western margins along the Rocky Mountain Front. Intact grasslands were predicted to remain in the south and central portions of the U.S. distribution (figure 4).

Ownership analysis. Land tenure was heavily skewed to private ownership amidst a mosaic of federal, tribal, and state/provincial lands. Our model suggests that 70% of the global breeding population was located on lands under private ownership. We also document that both state/provincial and Tribal/First Nation lands contained considerable portions of the population (table 3).

Discussion

A broad-scale perspective can inform systematic approaches to achieving conservation with limited resources. Anchored within core areas of high abundance, our approach links vulnerable populations to landscape conservation at a continental scale. In western North America, core areas are being used to guide investments for high-profile and at-risk species like woodland caribou (Schneider et al. 2010) and Greater Sage-Grouse (Doherty et al. 2010, Copeland et al. 2013, USFWS 2013). Often, core areas for focal species coincide with important habitat for other species of interest, as recently demonstrated for mule deer and Sage-Grouse in Wyoming (Copeland et al. 2014). Indeed, predicted core populations of pipits in northeast Montana and southern Saskatchewan overlapped qualitatively with important migratory corridors for pronghorn (Poor et al. 2012) and sage-grouse (Tack et al. 2011). At state and provincial scales, efficiency of conservation for pipits would be maximized by focusing initial investments in southeast Alberta, southwest and south-central Saskatchewan, and northeast Montana (figure 2).

Our distribution model suggests that broad-scale climate patterns strongly influence pipit habitat selection (see also George et al. 1992, Wiens et al. 2008). Climate variables, especially those related to precipitation, were highly predictive and pipits selected an envelope of moderate moisture at a continental scale in a non-linear fashion. Whether this moisture envelope produces vegetation structure that is relatively sparse or dense depends on geographic context as well as management (Madden et al. 2000, Bakker et al. 2002). This may explain why recent regionally based models (e.g. Niemuth et al. 2008) did not report relationships between climate and pipit abundance. Variability captured in our range-wide approach boosted power to detect climate relationships, and our random forest approach is well suited to characterize non-linear response (figure 1). Studies from the more mesic eastern portion of the range reported that pipits respond positively to fire and grazing (e.g. Madden et al. 1999) whereas those from the semi-arid West suggest a negative response to grazing (e.g. Owens and Myres 1973, Davis et al. 1999). Our continental-scale analysis explains variation in local-scale studies by capturing the range of environmental conditions that shape populations.

Our analysis of soil capability for agriculture demonstrates that continentally, the distribution of pipits has contracted in response to cumulative impacts of tillage in arable grasslands (figure 3). This pattern is supported by spatial variability in trend estimates in the Breeding Bird Survey (figure A3; Sauer et al. 2014). Despite avoidance, low predicted densities across 56.4 million hectares of cultivated land could represent up to 30% of the breeding population. Current evidence suggests that pipits strongly avoid cropland (Owens and Myres 1973, Davis et al. 1999) and future research is needed to evaluate the contribution of individuals occurring in or around cropland to population growth (Pulliam 1988, Donovan and Thompson 2001).

Unconstrained cropland growth predictions suggest that risk to the population is moderate and that patterns are comparable at U.S. (23%) and continental (25%) scales. However, tillage of an additional 12.5 million hectares in the U.S. is unlikely and losses can be mediated through proactive and targeted action. Conservation of this species depends on a shared vision for sustainable ranching as 70% of pipits rely on privately owned grasslands, which are often maintained as rangelands for livestock production. Moreover, another proportion of the population breeds on provincial lands in Saskatchewan that are privately managed. Public lands support less than a third of populations, though scenarios suggests that these are continentally important for insulating against increased cropland expansion.

Our results are specific to effects of cropland conversion on breeding pipits, and similar analyses for winter range would inform a more holistic strategy throughout the life cycle. Also, next-generation analyses should incorporate other potential risks such as climate change (Skagen and Yackel Adams 2012) and energy development. We did not include energy infrastructure data in this analysis and if development was correlated with agricultural tillage, latent effects may have been inappropriately attributed to cropland. Studied effects of energy infrastructure on pipits are negative (Hamilton et al. 2011) or equivocal (Kalyn Bogard and Davis 2014) but other songbirds in shrub-steppe are sensitive to oil and gas development (Gilbert and Chalfoun 2011). An additional 50,000 new oil and gas wells are added annually in central North America (Allred et al. 2015), and if drilling continues as anticipated, regional analysis of potential impacts to pipits is warranted.

Because 70% of all pipits surveyed appear to occur in private lands, the conservation of northern grassland depends upon a systematic approach that invests heavily in private land partnerships. Identification of priority landscapes for pipits is intended to enhance decision-making and catalyze accelerated conservation. Private landowners are willing to implement beneficial practices for wildlife (Henderson et al. 2014) and the capacity to do so is growing as coordinated approaches become available (Neudecker et al. 2011). Voluntary incentives can help offset high economic returns from cropland by compensating producers for the conservation value of native grasslands. Partnerships should work to develop a portfolio of incentives relevant to the diverse needs of landowners. Some examples include conservation easements (Fishburn et al. 2009), rangeland improvements, drought mitigation and marketing of livestock products raised on native grasslands. Accelerated pipit conservation would benefit from additional coordinated funding.

Improvements in agricultural policy that incentivize ranching would also curb tillage expansion. For example, the new ‘Sodsaver’ provision in the 2014 Farm Bill (U.S. Agricultural Act of 2014; H.R. 2642) renders recently converted cropland ineligible for full federal insurance subsidy (Miao et al. 2014). Additional modification of subsidies could further reduce conversion of marginal land because incentives still favor farming over ranching (GAO 2007). Higher returns from cropland also entice policy makers to lease public lands for farming where permitted. For example, prohibiting tillage on state school-trust lands would remove a primary threat to grassland cores in Montana. Other policy incentives that generate and maintain interest in grassland conservation should also be considered. One approach would be to modify the U.S. Conservation Reserve Program allowing more frequent grazing, mirroring the Permanent Cover program in Canada (McMaster and Davis 2001).

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Tables

Table 1. Global and national distribution of Sprague's Pipit across political boundaries. Values derived from the proportion of the summed probability of occurrence layer produced by the Random Forest model in each class. Values shown as percentages.

		Global	**National**
Countries	Canada	61.8	100
	USA	38.2	100
States/Provinces	Alberta	30.9	50.1
	Saskatchewan	28.3	45.8
	Montana	25.2	65.8
	North Dakota	8.9	23.3
	South Dakota	3.3	8.7
	Manitoba	2.6	4.2
	Minnesota	0.6	1.6
	Wyoming	0.3	0.7

Table 2. Cropland build-out scenarios used in this analysis and resulting predicted loss of the U.S population of Sprague's Pipit.

	Scenario	**Risk Cutoff**	**New Crop Ha (10^6)**	**New Crop Ac (10^6)**	**Pop. Loss**
a	Background Loss	0.98	0.48	1.19	< 1%
b	Constrained Growth	0.7	5.94	14.67	9%
c	Unconstrained Growth	0.3	12.52	30.94	23%

Table 3. Global and national distribution of Pipits across land ownership classes. Values derived from the proportion of the summed probability of occurrence layer produced by the Random Forest model in each class. Values shown as percentages.

	United States		**Canada**		**Global Total**
	Global (%)	National (%)	Global (%)	National (%)	Total (%)
Private	25.6	66.9	45.1	72.9	70.7
Tribal/First Nations	5.2	13.6	0.9	1.4	6.1
Federal	4.9	12.8	3.7	6.0	8.6
State/Provincial	2.4	6.4	11.9	19.3	14.3
Other Conservation	0.1	0.3	0.2	0.4	0.3

Figures

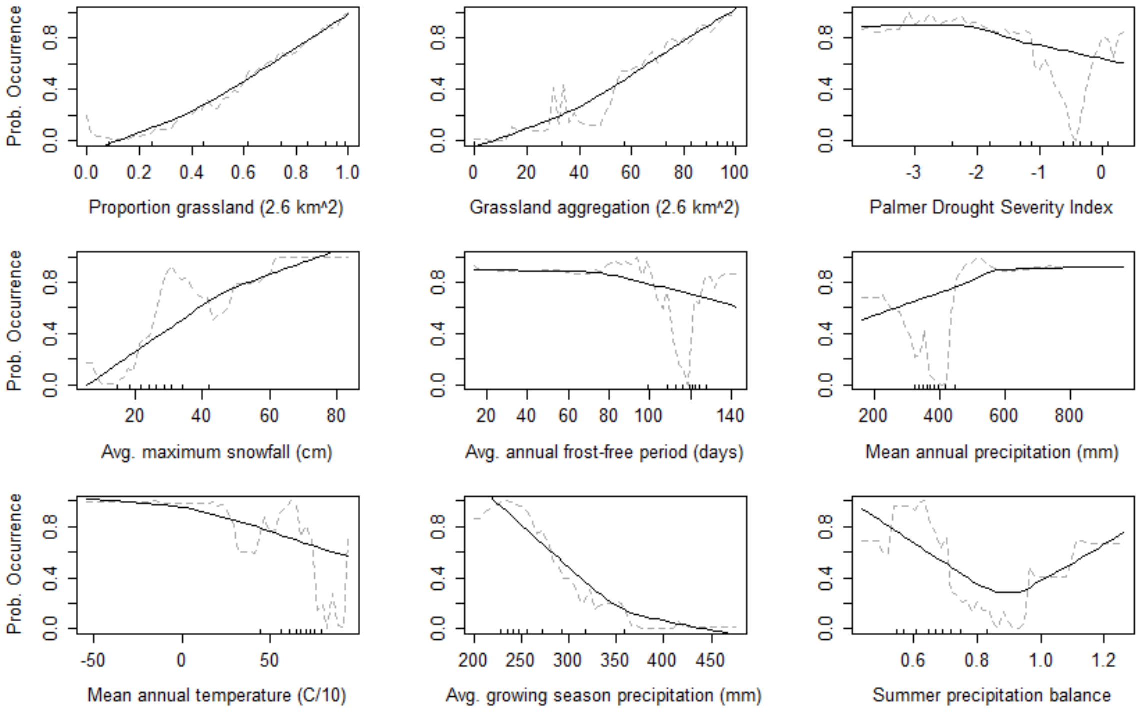

Figure 1. Partial plots for variables included in the Random Forest Model. Gray dotted lines indicate raw data, black lines show data smoothed with a Lowess function. Tick marks above x-axes indicate deciles in the dataset. See Liaw and Wiener (2002) for derivation.

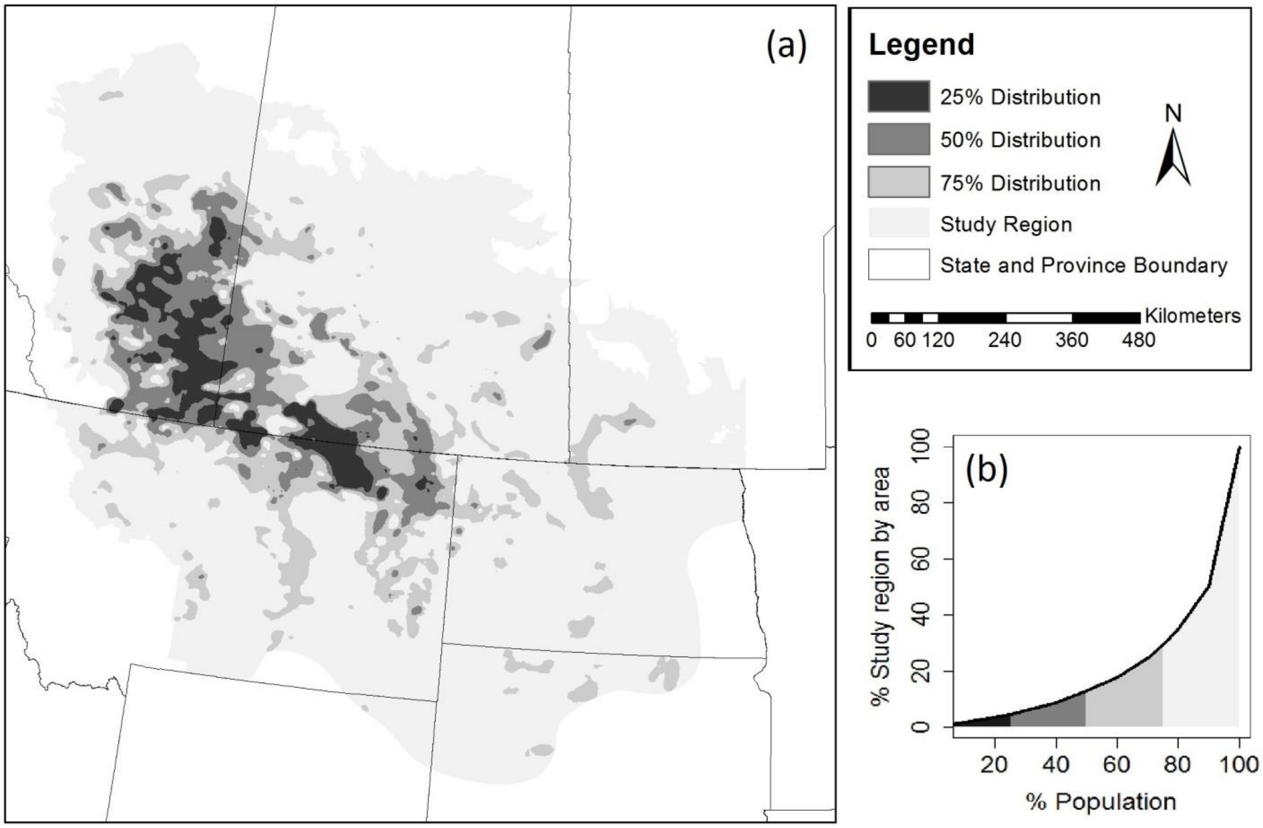

Figure 2. Predicted population density distribution of Sprague’s Pipit across its breeding range (a) and the proportional relationship between area and population density distribution (b). Raw model predictions were smoothed using 16 x 16-km moving window mean.

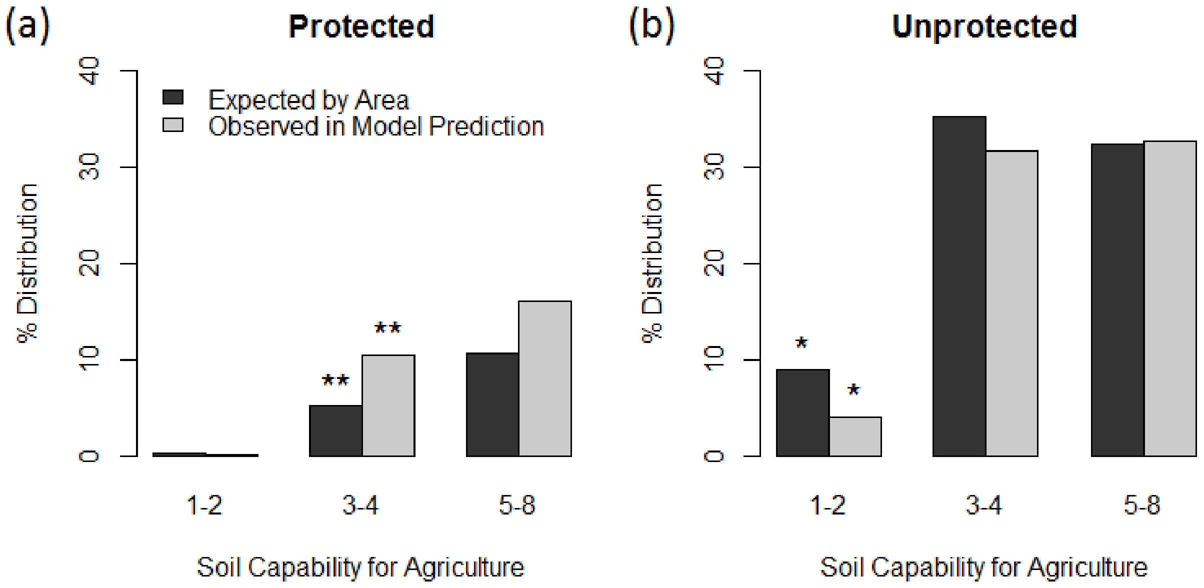

Figure 3. Sprague's Pipit expected and predicted distribution by soil capability class on lands that are protected (a) and unprotected (b) from future tillage. Soils more suitable for cropland have a lower classification (1 is most arable, 8 is least). Asterisks (*) indicate classes where proportion of modeled population deviates from expected based on area (by $\chi 2$ test, * indicates $P < 0.1$, ** indicates $P < 0.05$).

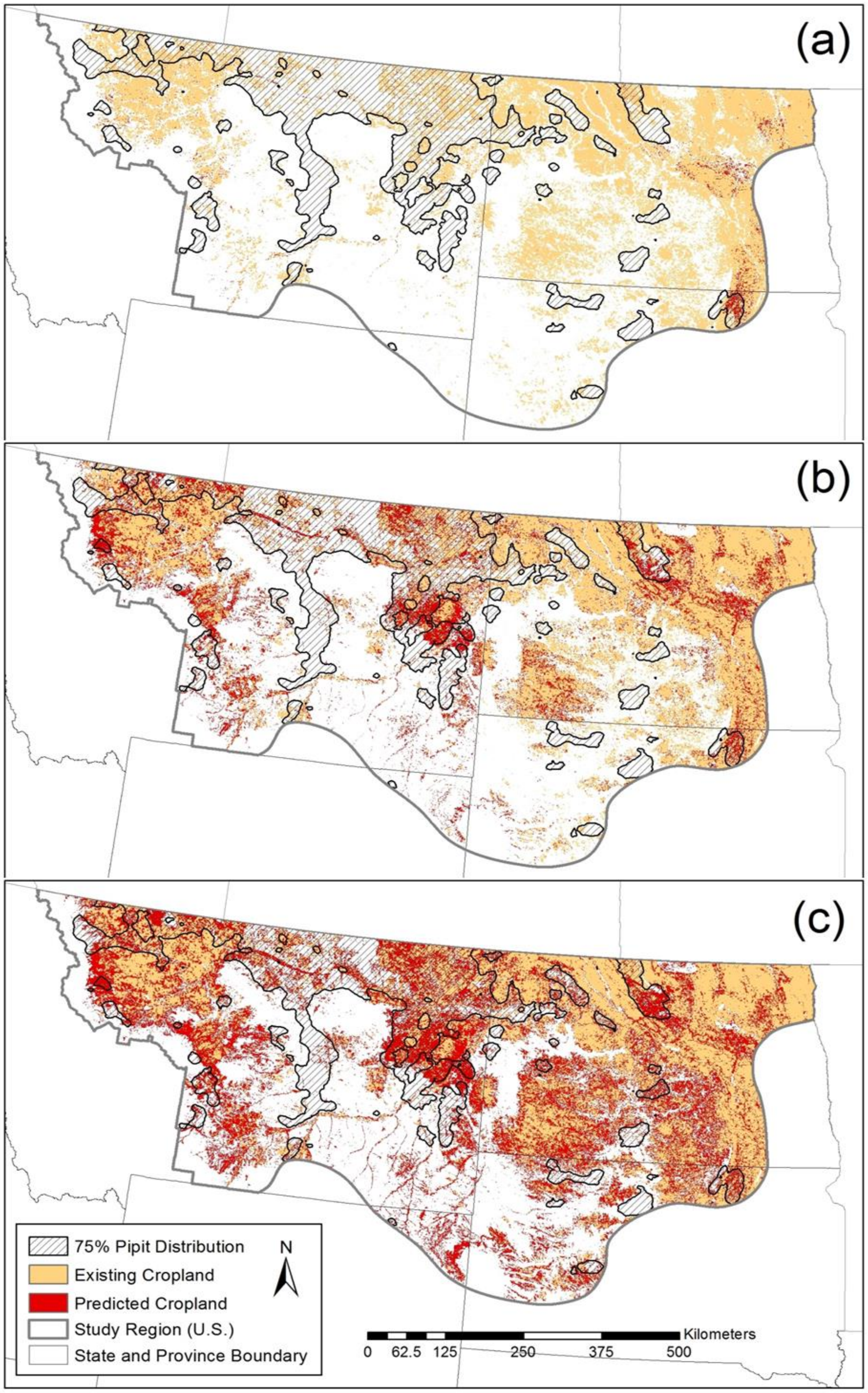

Figure 4. Predicted cropland expansion under three future build-out scenarios: background (a), constrained (b) and unconstrained (c). Hatched area shows core region containing about 75% of the U.S. Sprague's Pipit population.

Appendix

Table A1. Sources and point-count methods for data used in model fitting (AB-FWMIS = Alberta Fisheries and Wildlife Management Information System. BBS = North American Breeding Bird Survey, CWS= Canadian Wildlife Service, EC-CWS = Environment Canada and the Canadian Wildlife Service, MTNHP-UMT = Montana Natural Heritage Program and the University of Montana, RMBO = Rocky Mountain Bird Observatory, UM = University of Manitoba).

Agency or Institution	*Number of Records Used*	*Point-Count Duration*	*Point-Count Distance*	*Reference*
AB-FWMIS	2666	various	various	Unavailable
BBS	2235	3 minutes	400m	Link and Sauer (1998)
CWS	1273	5 minutes	100m	Kalyn Bogard and Davis (2014)
EC-CWS	30	5 minutes	250m	Dale and Wiens (2014)
MTNHP-UMT	2151	10 minutes	100m	Hendricks et al. (2008)
RMBO	1564	5 minutes	Unlimited	Hanni et al. (2009)
UM	81	5 minutes	100m	Ranellucci et al. (2012)

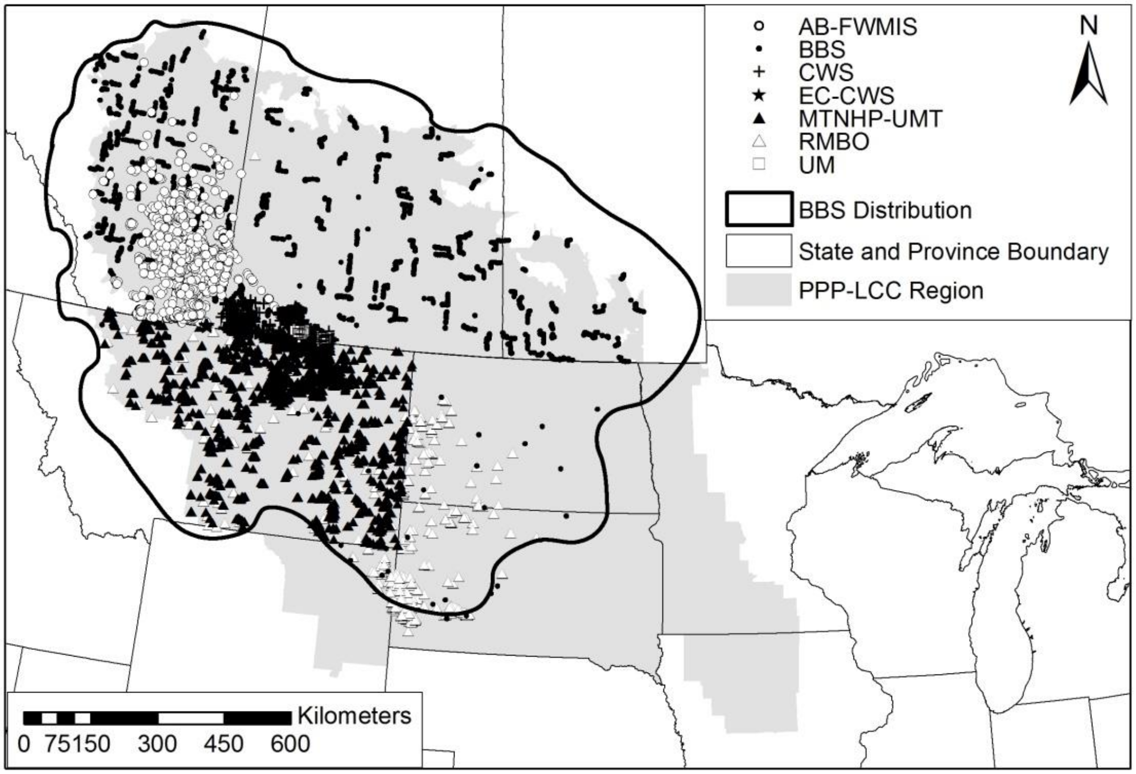

Figure A1. Location and sources of data used in model fitting (AB-FWMIS = Alberta Fisheries and Wildlife Management Information System, BBS = North American Breeding Bird Survey, CWS= Canadian Wildlife Service, EC-CWS = Environment Canada and the Canadian Wildlife Service, MTNHP-UMT = Montana Natural Heritage Program and the University of Montana, RMBO = Rocky Mountain Bird Observatory, UM = University of Manitoba).

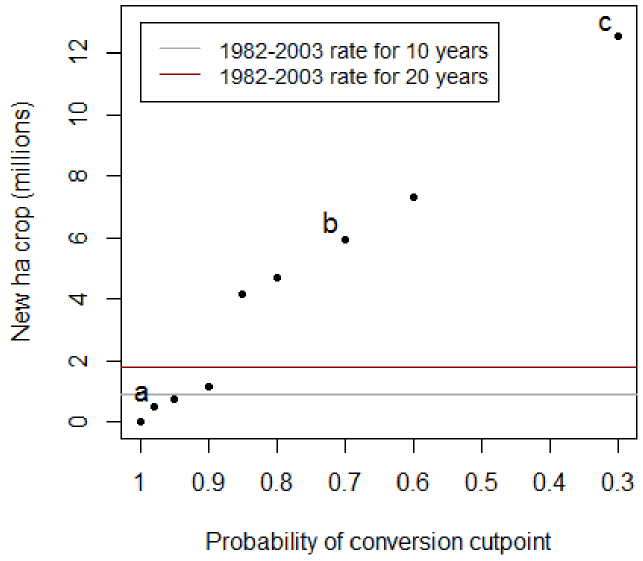

Figure A2. Area accumulation plot for the U.S. portion of the study area, derived from tillage expansion model probabilities (Smith et al. 2015). Background (0.98), constrained (0.7) and unconstrained (0.3) scenario cutpoints indicated by a, b and c respectively. Estimated 1982-2003 annual expansion rate of 0.635% (0.32-0.95%) from GAO (2007).

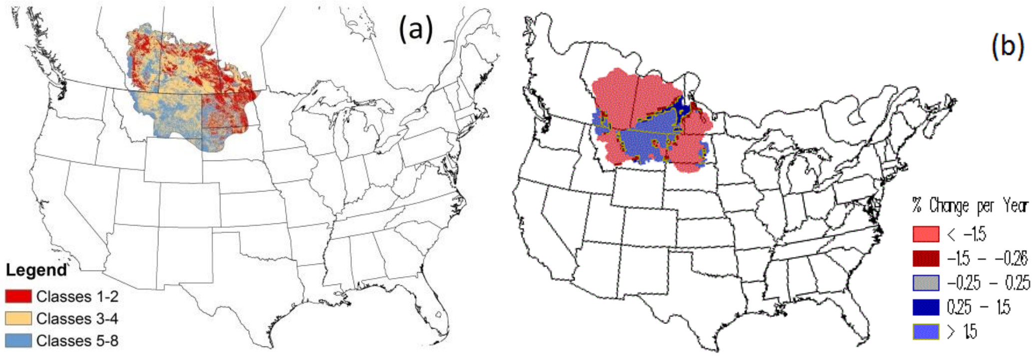

Figure A3. Soil capability class for agriculture (a) and observed population trends for Sprague's Pipit (b; from Sauer et al. 2012) across the study area. Soils classes 1-2 are most arable, 3-4 have some limitations, and classes 5-8 are least arable.

CHAPTER 4- EXTENDING UTILITY OF HIERARCHICAL MODELS TO HABITAT: CAPTURING MULTI-SCALE SELECTION WITHOUT COLLINEARITY OR OVERLAPPING LANDSCAPES

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Abstract

Habitat selection is a central theme in ecology that informs conservation. Because selection is a hierarchical process, characterizing animal response across multiple spatial scales is a priority for research. Problems of cross-scale collinearity and overlapping landscapes, however, have limited the utility of multi-scale models of selection. Our objective is to present a spatially hierarchical modeling approach that addresses these problems by integrating animal response conditionally across scales, and to compare outcomes to traditional modeling approaches. We illustrate our approach with models of the breeding distribution of two North American grassland songbirds of conservation concern, Sprague's Pipit (*Anthus spragueii*) and Chestnut-collared Longspur (*Calcarius ornatus*). Our application successfully captured bird response to local habitat within the broader landscape context, even when selection occurred in opposite directions across scales. Conditional probabilities of bird occurrence were more strongly affected by local habitat when landscape context was favorable than when it was unfavorable. Traditional habitat models extended problems of scale into spatially explicit predictions by over-estimating occurrence where conditions were locally favorable but regionally unsuitable. The inclusion of spatial

scales as levels within hierarchical models promises to greatly advance our understanding of multi-scale species habitat selection.

Introduction

The study of habitat selection is a central focus of ecology that informs wildlife management and conservation (Boyce and McDonald 1999, Manly 2002). Habitat selection is a hierarchical process, with animals making movement decisions that vary from long-range dispersal or migration to micro-scale selection of nesting or foraging sites (Wiens 1973, Johnson 1980, Hutto 1985). Models of selection therefore are highly sensitive to scale, which includes the resolution of sampling (grain) and the size of the study area (extent; Boyce 2006, Mayor et al. 2007, Schaefer and Mayor 2007). Grains that are too large for animal or habitat data will miss patterns at a finer scale, whereas extents that are too small constrain the order of selection captured and restrict inference (Johnson 1980, Boyce 2006).

Biologists often want to identify ecologically important scales of selection and to understand how relationships with habitat change across scale. Understanding scale(s) of selection can be particularly important for conservation management applications. For example, the United States Endangered Species Act (ESA 1973) is the country's strongest conservation law. It mandates that critical habitat for endangered species must be identified and protected but does not specify scale. Ignoring how variables across scales influence habitat suitability could lead to inappropriate or ineffective critical habitat designations. Because of their known importance, multi-scale analyses are commonly included in species-habitat studies (Mayor et al. 2009). However, two major obstacles have plagued attempts to characterize selection across scales: (1) cross-scale collinearity and (2) the problem of overlapping landscapes.

Collinearity. Collinearity among predictors is a common challenge facing habitat models (Dormann et al. 2013), which is compounded in multi-scale studies (Battin and Lawler 2006). Habitat attributes are almost always autocorrelated in space, meaning that local-scale factors show a strong relationship with similar measures at broader scales (figure 1a; Purtauf et al. 2005). Frequently, researchers address collinearity by dropping all but the single "best" variable from a highly correlated cross-scale group. While this does reduce collinearity within predictors, it is not desirable because potentially important information is lost from other scales. Further, ecological variables behave in an unpredictable and often unintuitive way across scales, making selection of a single best scale a nontrivial task that has profound implications for model interpretation (Wheatley 2010).

Another common approach when dealing with cross-scale collinearity is to model animal response separately at several scales and then compare model likelihoods (Lawler and Edwards 2006). But this approach can be misleading because variables modeled at any one scale may still include substantial information from latent cross-scale correlations (Cushman and McGarigal 2002, Battin and Lawler 2006, Mahon et al. 2008). For example, Bakermans and Rodewald (2006) reported that availability of insect prey was not a good predictor of Acadian Flycatcher (*Empidonax virescens*) abundance in riparian forests of central Ohio, in spite of its known importance for territory selection and reproductive success. Broader scales of analysis revealed that the birds were avoiding more urbanized areas that also happened to have higher than average insect abundance (Bakermans and Rodewald 2006). In this case, the broad-scale correlation between insect abundance and land use was likely confounding observed patterns of local selection. Without the broad-scale analysis, the results of this study could have led to conflicting conclusions or inappropriate management.

Overlapping landscapes. Although broad-scale processes like land-use change almost certainly influence distributions of many species, the ability to detect these effects is often limited by sampling constraints. In particular, survey data are usually clustered at a relatively fine scale, leading to an increasingly high degree of overlap in surrounding landscapes as scale of analysis increases (figure 1b). Use of habitat data from overlapping landscapes equates to pseudoreplication in most modeling frameworks and can result in non-independence of residuals (Eigenbrod et al. 2011, Zuckerberg et al. 2012), artificially narrow confidence intervals (Legendre 1993), and diminished statistical power from reduced variability in predictors (Eigenbrod et al. 2011).

Ecologists have used three basic strategies to mitigate the problem of overlap, none of which is entirely satisfactory (Zuckerberg et al. 2012). Some researchers proactively design sampling to minimize clustering and overlap (Eigenbrod et al. 2011), whereas others thin data by removing overlapping sites *a posteriori* (Koper and Schmiegelow 2006). The first approach reduces the efficiency of data collection and the second results in information loss and wasted sampling effort. Most frustrating perhaps is that the elimination of overlap does not necessarily remove autocorrelation in the data, and neither method guarantees statistical independence (Zuckerberg et al. 2012). A third approach controls for autocorrelation directly by modeling it and removing its effect (Dormann et al. 2007, Thogmartin and Knutson 2007). However, because autocorrelation often reflects underlying biological or environmental processes, its removal can actually obscure patterns of interest and should be avoided in mechanistic models of habitat selection (Legendre 1993, Dormann et al. 2007).

Spatially hierarchical models. Hierarchical models represent an elegant solution to the problems of collinearity and overlapping landscapes in studies of multi-scale habitat selection. In a hierarchical model, parameters are related to one another through a joint probability that reflects the dependence among them (Gelman et al. 2004). This framework provides the basis for the rapidly growing field of occupancy modeling, which has already supplied myriad novel and innovative ways to analyze biological data. Occupancy modeling was first developed as a method to integrate imperfect detection in survey data as a nested process within species distribution models (MacKenzie et al. 2006). It differs from standard logistic regression because the probability of occupancy (Ψ) is separated from the probability of detection (P), which is parameterized through repeated sampling in time or space (MacKenzie et al. 2006). Structure of occupancy models is naturally hierarchical, wherein the detection process is constrained by the occupancy state. For example, if a species is absent it cannot be detected no matter how high the probability of detection. Occupancy models have already been extended to address diverse ecological questions including habitat selection (MacKenzie et al. 2002), species abundance and diversity (Royle 2004), spatial replicates (Kery and Royle 2008), multiple observers (MacKenzie et al. 2006), multiple detection methods (Nichols et al. 2008) and multi-scale occupancy (Nichols et al. 2008, Mordecai et al. 2011, Pavlacky et al. 2012).

This paper extends the spatially hierarchical occupancy framework pioneered by Nichols et al. (2008), Pavlacky et al. (2012) and Mordecai et al. (2011) to incorporate a multi-scale habitat selection process. Nichols et al. (2008) were the first to apply an occupancy model hierarchically across two spatial scales, separating species use of sample units from presence at individual survey sites. Pavlacky et al. (2012) use this multi-scale framework to effectively account for non-independence of spatially replicated monitoring data, but do not include habitat covariates. Mordecai et al. (2011) apply a two scale model to analyze distribution of Louisiana waterthrush (*Seiurus motacilla*) in the southeastern U.S. Although these authors do associate habitat with distribution across scales, variables are each measured at only one scale. Here, we extend their approach by scaling habitat variables with occupancy and relating them across multiple nested scales. Our method represents a novel adaptation of the occupancy modeling framework that addresses some of the most common problems facing studies of multi-scale habitat selection.

The hierarchical structure of occupancy modeling allows for conditional integration of multi-scale covariates without collinearity or overlapping landscapes, and clarifies interpretation of species-habitat relationships across scale (figure 1c). Cross-scale collinearity is eliminated because the dependence among scales is modeled explicitly through a joint probability. Because occupancy is also hierarchical in space, habitat covariates at broad scales are related to landscape occupancy at the same scale prior to integration across scales so landscapes have no need to overlap (figure 1c). Here, we apply the spatially hierarchical framework to investigate how variables of known local importance scale up to broader extents and how patterns at broad extents constrain local selection. To illustrate model application, we analyze the breeding distribution of two at-risk grassland songbird species in the northern Great Plains of North America and compare results to those from traditional multi-scale logistic regression.

Methods

Modeling framework. Ours is the first application of spatially hierarchical models to use a consistent set of variables estimating integrated response to habitat across scales. We conducted analyses in Program R (R Development Core Team 2013) and estimated model parameters with Bayesian inference using JAGS (Plummer 2003) and package R2jags (Su and Yajima 2012). We chose a Bayesian approach because it is capable of fitting multi-level hierarchical models, and the existence of prior distributions allows estimation over large regions of zeroes and missing data that are common in broad-scale species distribution models (P. Lukacs, University of Montana, pers. comm.).

Traditional models of habitat selection seldom include the same covariate measured at different scales because collinearity violates model assumptions and confuses interpretation. The separation of scales of analysis into different levels of a hierarchical model allows us to overcome these limitations. Our model is spatially hierarchical where occupancy at finer scales is conditional on occupancy at broader scales. The parameter ψ represents broad-scale occupancy and can be interpreted as the proportion of broad-scale units that are occupied in the study region. The parameters for finer scale occupancy correspond to species occurrence conditional on presence in the scale(s) above. Intermediate-scale occupancy (θ) is conditional on ψ and local occupancy (ϕ) is conditional on θ and ψ. The conditional product $\psi|\theta|\varphi$ corresponds to local-scale occupancy. Within each level, habitat covariates can be included in logistic regression to estimate level-specific probability of occurrence. The model for nested units of three scales i, j and k (figure 1) is specified as:

Broad-scale process model in unit i:

$$Occupancy_i \sim Bernoulli(\psi)$$

$$Logit(\psi) = \beta_0 + \beta_x * covariate_{x\ldots}$$

Intermediate-scale observation model in unit i,j:

$$Occupancy_{ij} \sim Bernoulli(Occupancy_i * \theta)$$

$$Logit(\theta) = \alpha_0 + \alpha_y * covariate_y \ldots$$

Local-scale observation model in unit i,j,k:

$$Occupancy_{ijk} \sim Bernoulli(Occupancy_{ij} * \phi)$$

$$Logit(\phi) = \delta_0 + \delta_z * covariate_z \ldots$$

where covariates are measured at the scale of occupancy in each level.

Case study: grassland songbirds in the northern Great Plains. Scale-dependent habitat selection is well recognized in migratory songbirds (Battin and Lawler 2006; Hutto 1985; Wiens 1973). To test application of our multi-scale modeling approach, we analyzed the breeding distribution of two grassland songbird species of high conservation concern. Sprague's Pipit (*Anthus spragueii;* herein 'pipit') is a northern grassland specialist that breeds in relatively moist, native mixed-grass prairie (Davis et al. 2014). Chestnut-collared Longspur (*Calcarius ornatus;* herein 'longspur') shares a similar breeding distribution but prefers grassland that is drier or more heavily grazed (Hill and Gould 1997). Both species have been declining across North America > 3% annually since 1966 (Sauer et al. 2014) and are federally Threatened in Canada (COSEWIC 2009, Environment Canada 2012). The International Union for Conservation of Nature lists the pipit as globally Vulnerable and the longspur as Near-Threatened (IUCN 2014).

Bird data. We assembled songbird data from 32,204 point counts from 2007-2012 within the boundary of the Plains and Prairie Pothole Landscape Conservation Cooperative, a 1.4 million-km^2 region that includes portions of Alberta, Saskatchewan, Montana, North and South Dakota, Manitoba, Minnesota and Iowa (Millard et al. 2012). Surveys were > 200-m apart and were not repeated.

Scales. We superimposed an arbitrary, hierarchically nested lattice across the study region with cells corresponding to three spatial scales of analysis (figure 1c). We used scales defined by the public land survey system (White 1983) because these form the basis of land ownership patterns and are relevant to managers in the region. The scales included 2.6-km^2 (section), 93-km^2 (township) and 1,492-km^2 (quadrangle; figure 1c). At the finest scale of analysis (2.6-km^2) each unit contained from 0-10 individual survey points. Due to processing limitations, we excluded 1,134 survey points that fell in units containing > 10 points. We selected these for exclusion based on date, keeping the most recent.

Occupancy. Observed patterns of species occupancy were the dependent variable in each level of analysis. We translated occupancy across scales using simple presence/absence: if a species was observed in a given survey, the local, intermediate and broad-scale cell containing the survey point were each considered occupied (figure 1c). Species were absent only if all surveys in the unit were non-detections. Units containing no surveys were treated as missing data. Because the number of surveys per fine-scale unit varied from 0-10, those containing fewer surveys faced a risk of non-detection or false absence from insufficient sampling. We corrected for this by including a fourth parameter to the model (P) to estimate species availability for detection in individual surveys. To control for sampling effort across fine-scale units, we also included the number of surveys (0-10) as a covariate in the section-level observation model. We used uninformative, uniform priors constrained between -10 and 10 for all parameters. We ran 102,000 Markov Chain Monte Carlo (MCMC) iterations with 3 chains and a burn-in of 2000.

The use of a multi-year dataset greatly improved spatial coverage compared to data from any single year. However, the inclusion of multiple breeding seasons violates the assumption of closure and P therefore refers only to availability for detection in a survey given that the cell has been occupied at any time during sampling. This parameter accounts for annual differences in true occupancy and non-detections in an occupied cell within the same year. This is desirable because our intended scope of inference was to evaluate general patterns of occupancy across the breeding distribution within the five year timeframe.

Habitat metrics. We included two habitat metrics as model covariates across scales: proportion grassland and Normalized Differential Vegetation Index (NDVI). Grassland amount is a crucial component of habitat for both study species because it provides resources important throughout their life history (Hill and Gould 1997, Davis et al. 2014). We derived a binary layer of grassland from 30-m land-cover products created by Agriculture Agri-Food Canada (2001) and the United States Geological Survey National Land Cover Dataset program (Wickham et al. 2010). We calculated proportional variables using a moving window mean of the binary layer at each relevant spatial scale.

We included NDVI because grassland birds show strong responses to vegetation biomass that vary among species (Fisher and Davis 2010). NDVI allows remote detection of live green plant canopies, where higher values correspond with greater fractional vegetation cover and leaf area in the sampled pixel (Carlson and Ripley 1997). We used remotely sensed NDVI from Moderate Resolution Imaging Spectroradiometer (MODIS) data sampled at a 250-m resolution for July (LP DAAC 2014), averaged across the five year timeframe (2007-2012). July is approximately the peak of vegetative growth in the region and allows good biomass discrimination (Wang et al. 2005). To control for the variability in NDVI caused by non-grassland vegetation like wetland or woodland, we included an interaction term between grassland amount and NDVI. To facilitate Bayesian parameter estimation and allow direct comparison of coefficients, we standardized all habitat covariates by centering on the mean and scaling by standard deviation.

Comparison with traditional approach. To compare performance of spatially hierarchical models with a traditional multi-scale approach, we fit models for each species and each scale using standard logistic regression (Hosmer and Lemeshow 2000) using the same set of survey data from hierarchical model estimation. We calculated habitat covariates with concentric rectangular buffers around survey locations corresponding to the scales used in hierarchical models (2.6, 93 and 1,492-km^2). We determined the level of cross-scale collinearity among predictors using Pearson correlation coefficients (r). We fitted logistic regression models and then used Akaike's Information Criterion (AIC; Anderson et al. 2000) to identify the most predictive scale individually for each covariate (Boyce 2006). Finally, we fit full models for each species that included the two covariates at their selected scale(s) and their interaction. To allow comparison of coefficients between hierarchical and traditional models, we standardized covariates by centering on the mean and scaling by standard deviation.

We compared strength of model fit to the original dataset by calculating area under the receiver operating curve (AUC; Metz 1978) for each species and method. To assess how well model predictions matched observed patterns of distribution, we compared them to data from the Breeding Bird Survey (BBS; Sauer et al. 2014). We used package OptimalCutpoints (Lopez-Raton et al. 2014) to identify probability surface cut-points for each model that maximized both sensitivity and specificity of predictions, and used these to create maps of predicted occurrence for each species. To validate models, we overlaid them with known BBS distribution and calculated proportion of overlap by area.

Results

Scale. By nesting species responses across scale, spatially hierarchical models identified the importance of broad-scale habitat metrics in shaping distributions (table 1). By contrast, cross-scale collinearity in traditional concentric buffers (figure 1a) was high for both habitat metrics (r=0.79-0.90 and r=0.92-0.97 for proportion grassland and NDVI, respectively), necessitating the choice of a single scale for inclusion in models. In traditional models, highly overlapping buffers (figure 1b) led to overestimated importance of fine scale variables. For both species, proportion of grassland at the finest scale had by far the lowest AIC when compared to intermediate (ΔAIC = 736 and 147 for pipit and longspur, respectively) and broad scales (ΔAIC = 2539 and 1008). Similarly, NDVI measured at a fine scale also had overwhelming support when compared to intermediate (ΔAIC = 83 and 135) and broad scales (ΔAIC = 408 and 538). We therefore used fine-scale metrics for covariates in traditional models.

Occupancy. Estimates of occupancy from spatially hierarchical models (Ψ, θ and ϕ) indicated that species were widely distributed within the study region and that this pattern was relatively consistent across scales (table 2). In general, about half (34-58%) of sample units at any scale were predicted to be occupied by each species. Birds were most patchily distributed below the intermediate scale (93-km^2). Survey-level availability for detection was comparable and high for both species (0.65-0.67), suggesting that distributions were not highly variable below the finest scale (2.6-km^2) and that patterns of occupancy across years were relatively stable.

Sprague's Pipit habitat. Nested habitat metrics across scales allowed us to characterize how species' local response to habitat varied with the broader landscape context (table 1; figure 2). Grassland was the primary factor shaping distribution of pipits across scales, and grass availability at intermediate scales (93-km^2) was particularly important (table 1). Pipits were also positively associated with high NDVI at all scales and there was a positive interaction between grassland and NDVI at broad and intermediate scales (table 1). Pipits' response to local habitat varied depending on landscape context, and the traditional model was unable to capture this difference. For example, the hierarchical model predicted that probability of occurrence for pipits in a high quality local site (100% grass cover) was up to three times greater (0.6 versus 0.2) when the landscape also contained a high proportion of grass (figure 2a,b). The traditional model overestimated importance of local-scale grass cover by as much as 450% (probability of occurrence 0.9 versus 0.2) when landscape context was poor (figure 2).

Chestnut-collared Longspur habitat. Habitat relationships for longspurs were similar to those for pipits, as both showed multi-scale selection for grassland cover. However, longspurs responded most strongly to grass at the broadest scale whereas pipits were more closely associated at the intermediate scale (table 1). Longspurs' relationship with NDVI is another example of the importance of landscape context in habitat selection. Locally, longspurs selected low NDVI and the traditional model suggested a weak negative relationship (table 1; figure 3). However, the hierarchical model revealed that longspurs in fact preferred productive green landscapes at broad scales and only selected for dry patches within these landscapes (table 1; figure 3). For example, a site with a locally low NDVI of 0.3 would have 400% higher probability of occurrence for longspurs if it was within a high-NDVI landscape (0.4 versus 0.1; figure 3a,b). The traditional model was unable to account for broad-scale NDVI and overestimated local suitability in dry landscapes by as much as three times (figure 3).

Spatially explicit example. Models had moderate fit for both species and fit was comparable between the hierarchical and traditional approaches (hierarchical model AUC =0.77 for both species, traditional model AUC of 0.78 and 0.77 for pipit and longspur, respectively). Predicted distributions from hierarchical models more closely matched BBS distributions than those of traditional models for both species. For pipits, the hierarchical prediction had more overlap with BBS (80%) than that of the traditional model (75%). Improvement for longspurs was even more marked (96 versus 84%; figure 4).

Discussion

Spatially hierarchical models offer a deeper, more integrated understanding of multi-scale habitat selection than traditional approaches to modeling occurrence. Nested relationships adjust response to local habitat according to the broader landscape context. For instance, pipits were three times more likely to occupy the same habitat inside (0.59) versus outside a high grassland landscape (0.19; figure 3a,b). The traditional modeling approach could not capture this variability and instead overestimated occupancy in locally favorable habitats. Moreover, effect of habitat at multiple scales became cumulative when the direction of response was consistent. Conditionally integrated responses revealed that changes in local conditions had a stronger influence on occupancy in suitable landscapes, which were already more likely to be occupied. For pipits, local conditions could affect probability of occupancy by as much as 30% in high grassland landscapes versus only 10% in grass-poor landscapes (figure 3). In this case, the spatially hierarchical approach enables targeting that could triple the expected beneficial outcomes of grassland conservation or restoration for songbirds.

Many models of habitat selection include multiple scales, including a recent study by DeCesare et al. (2012) that uses-integrated resource selection functions (SRSF) across scales. These authors show that a single SRSF can be used to simultaneously predict habitat suitability at three scales and demonstrate how inclusion of multiple scales can affect critical habitat designations under ESA. The approach is similar to the one presented here, except that in DeCesare et al. (2012), probability of use at each scale is estimated separately prior to integration. Without the joint probability distribution of a hierarchically-nested structure, collinearity remains a concern in SRSF and variables at each scale must be assumed to be independent. By contrast, our spatially hierarchical approach is capable of capturing complex nested patterns of response, even when variables are highly correlated across scale(s).

Spatially hierarchical models were also uniquely able to capture selection when it occurred in opposite directions across scales (Thogmartin and Knutson 2007, Wheatley 2010). Longspurs occupied grassland landscapes with high NDVI but locally selected drier sites with less cover (table 2). Measured traditionally at a single scale, these responses were contradictory and strength of longspurs' local preference for low NDVI was diluted by landscape associations. Sign changes in response to habitat across scale have been reported for other species but never modeled explicitly. In one example, the influence of moisture in prairie hardwood transition forests on Wood Thrush (*Hylocichla mustelina*) was negative at local and landscape scales but positive at intermediate scales (Thogmartin and Knutson 2007). Authors interpreted findings as selection for dry patches within wet landscapes, but were unable to model this nested response in an integrated fashion.

We identified important spatial scales of selection that are orders of magnitude broader than those previously recognized for grassland songbirds. Few studies measure response to habitat in landscapes > 1000-ha, and even fewer consider much broader scales (e.g. 80,000-ha; Thogmartin et al. 2006). Cross-scale collinearity limited our traditional models to a single scale of analysis for habitat metrics and over-estimated the importance of local variables. Despite the importance of landscape context in hierarchical models, overlapping buffers in the traditional approach biased model selection heavily towards local scales. Inference from hierarchical models could be further strengthened by incorporating biologically relevant scales of analysis (Wheatley and Johnson 2009). We commend recent techniques that use count (Bellier et al. 2012) and movement data (Frair et al. 2005) to characterize the spatial scales of animal perception and movement. Including relevant scales as levels within a hierarchical approach promises great advances in our understanding of species-habitat relationships.

The inherent problem of scale in traditional habitat modeling extends into spatially explicit predictions that guide real-world conservation decision-making. Findings presented here demonstrate that traditional models over-predicted occurrence where conditions were locally favorable but regionally unsuitable. For example, maps of traditional output for longspurs wrongly identified the southwest part of our study region as a priority for conservation (figure 4a,b). Longspurs are in fact so rare in the southwest that BBS excludes it from the species range (figure 4c,d). This xeric region was largely unoccupied by longspurs because locally favorable conditions were not embedded within more productive landscapes as identified by NDVI. Had this map been used to inform conservation, resulting actions that would be better placed in the north and east would be wasted in the southwest.

Although our spatially hierarchical approach offers improved insight into multi-scale species-habitat relationships, its use comes with several caveats. Not least among these is the considerable processing time required for parameter estimation in multi-level models using MCMC. The four-level examples presented here each took > 20 hours to fit on a standard computer, making it impractical to compare a large number of competing models. Further, there is no direct correlate of AIC for Bayesian inference and model selection when using this approach is mathematically and logistically challenging, especially for multi-level models (Chipman et al. 2001, Kery and Schaub 2012). Lastly, while the Bayesian framework easily handles missing data in the response variable it is unable to cope with it in the covariate predictors, making integration of habitat data difficult if comparable measurements do not exist for each animal location.

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Tables

Table 1. Occupancy estimates for two species at three nested spatial scales and availability for detection (P) at survey points within occupied fine-scale units in central North America, 2007-2012. Scales include: broad (Ψ; 1,492-km^2), intermediate (θ; 93-km^2) and fine (ϕ; 2.6-km^2).

	Sprague's Pipit			**Chestnut-collared Longspur**		
	Mean	*95% Lower*	*95% Upper*	Mean	*95% Lower*	*95% Upper*
Ψ	**0.48**	*0.41*	*0.56*	**0.40**	*0.32*	*0.48*
θ	**0.58**	*0.54*	*0.62*	**0.51**	*0.46*	*0.57*
ϕ	**0.40**	*0.37*	*0.43*	**0.34**	*0.31*	*0.37*
P	**0.65**	*0.64*	*0.66*	**0.67**	*0.66*	*0.68*

Table 2. Coefficients of models of two species to habitat covariates in central North America, 2007-2012, using a traditional, single-scale logistic regression (shaded) and for three nested scales in a spatially hierarchical model. Covariates were standardized by centering on the mean and scaling by standard deviation. Scales include: broad (1,492-km^2), intermediate (93-km^2) and fine (2.6-km^2).

		Traditional	**Spatially Hierarchical**		
		Fine	*Broad*	*Intermediate*	*Fine*
Sprague's Pipit	*Intercept*	**-1.63**	-0.07	**0.33**	**-0.40**
	Grassland	**1.37**	0.24	**1.10**	**0.54**
	NDVI	**0.28**	0.13	**0.50**	**0.33**
	*Grass*NDVI*	**0.36**	**0.36**	**0.41**	0.00
Chestnut-collared Longspur	*Intercept*	**-2.01**	**-0.43**	0.06	**-0.66**
	Grassland	**1.16**	**1.15**	**0.73**	**0.14**
	NDVI	**-0.14**	0.05	**0.32**	**-0.22**
	*Grass*NDVI*	**0.14**	**0.79**	0.07	**-0.19**

Figures

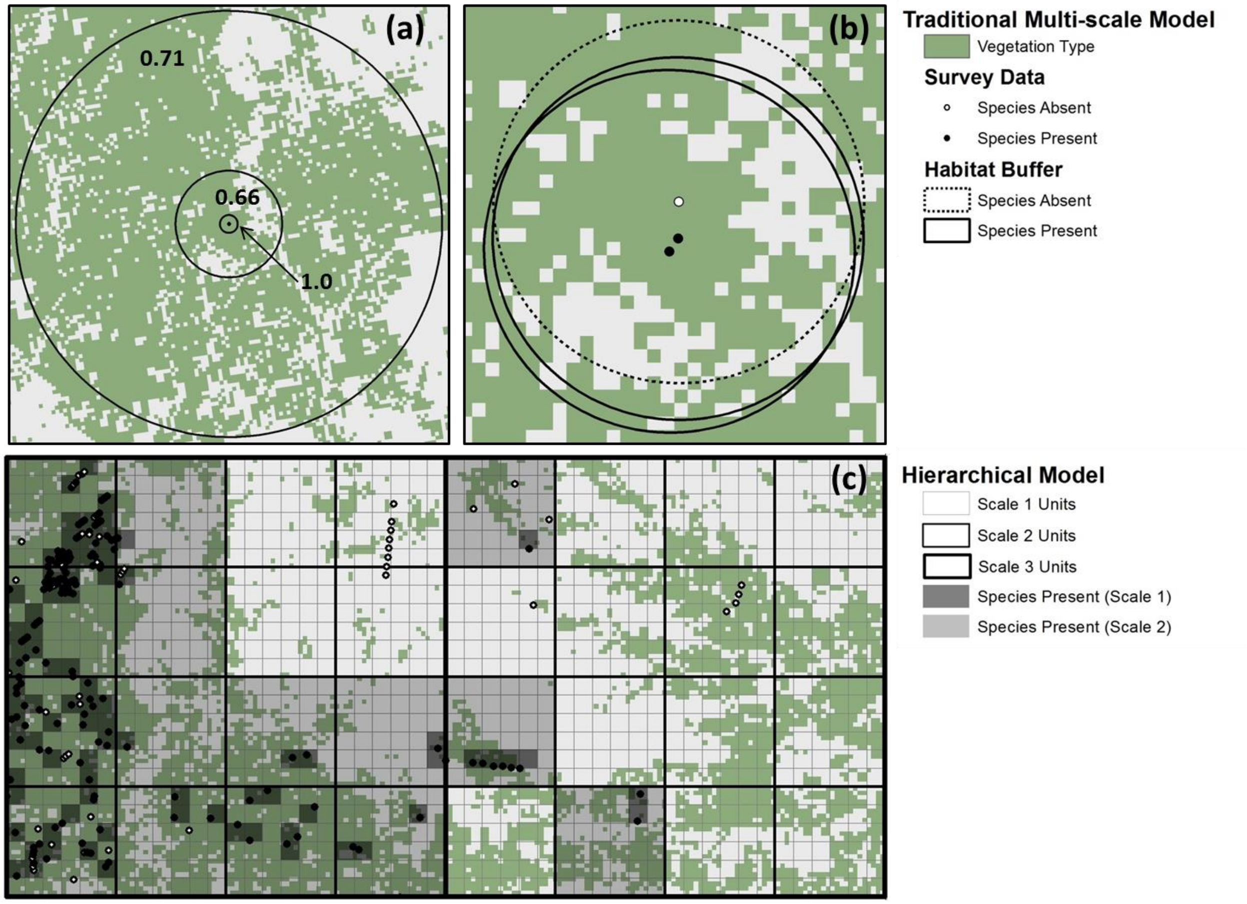

Figure 1. Common problems facing studies of habitat selection at multiple scales compared with our spatially hierarchical approach. (a) Concentric buffers often lead to cross-scale collinearity in habitat covariates. Numbers indicate proportional cover of a vegetation type in each buffer. (b) Overlapping landscapes result from clustering of survey points and artificially decrease variability in the predictor. (c) Two broad-scale units from the spatially hierarchical sampling frame. Shaded units are considered occupied.

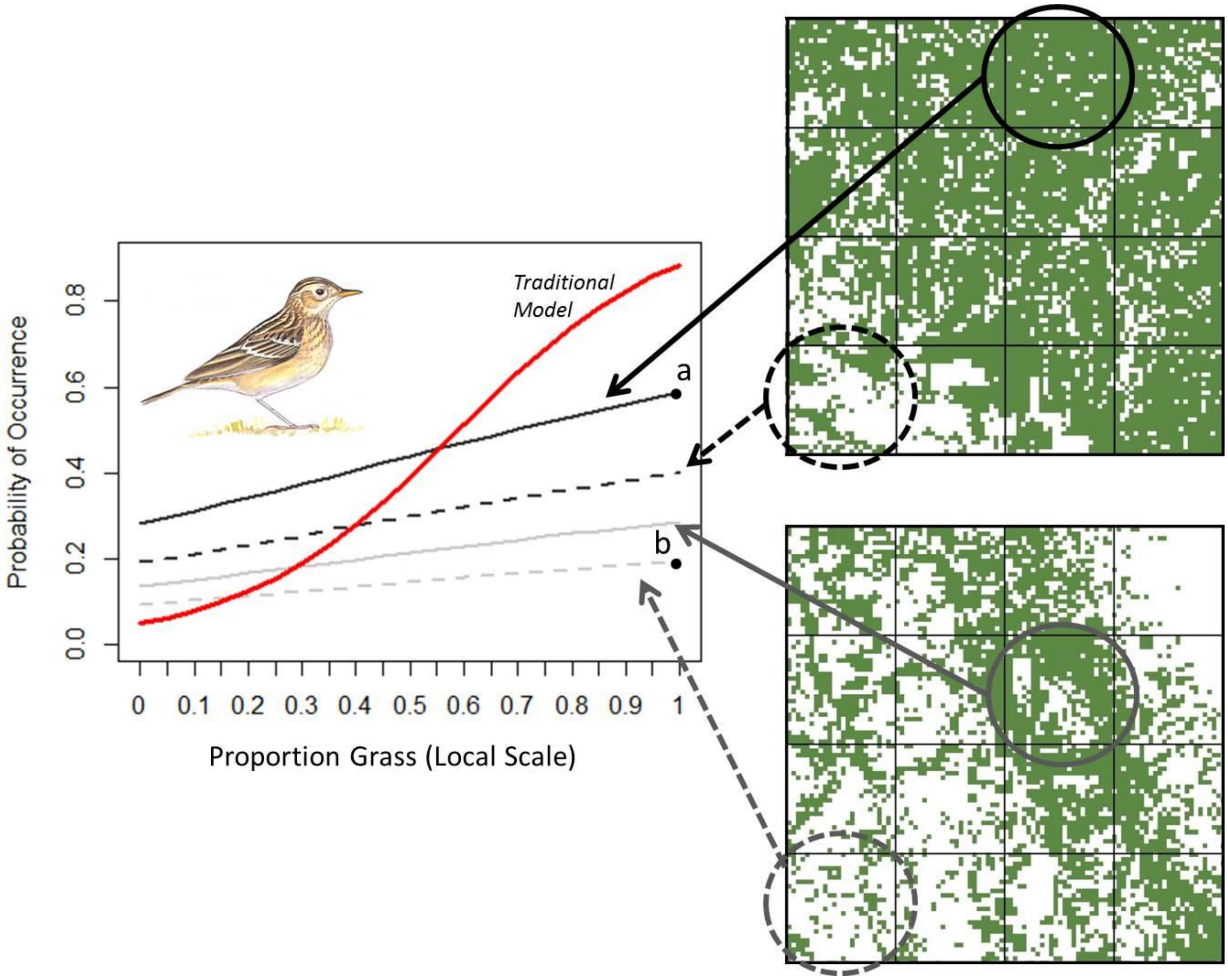

Figure 2. Response of Sprague's Pipit (*Anthus spragueii*) to fine-scale (2.6-km^2) grassland amount depends on landscape context in central North America, 2007-2012. Red line shows prediction from traditional, logistic regression models using fine-scale habitat data. Black lines show predicted response in a broad-scale landscape (1,492-km^2) with high grass cover (100%), grey lines show response in a landscape with low grass cover (10%). Solid lines show response with high grass cover (100%) at the intermediate scale (93-km^2), dashed lines show response with low intermediate-scale grass cover (30%). Estimated with above-average Normalized Differential Vegetation Index (0.75) at all scales. A suitable fine-scale site would be three times more likely to be occupied in the high-grass landscape (a) than the low-grass landscape (b).

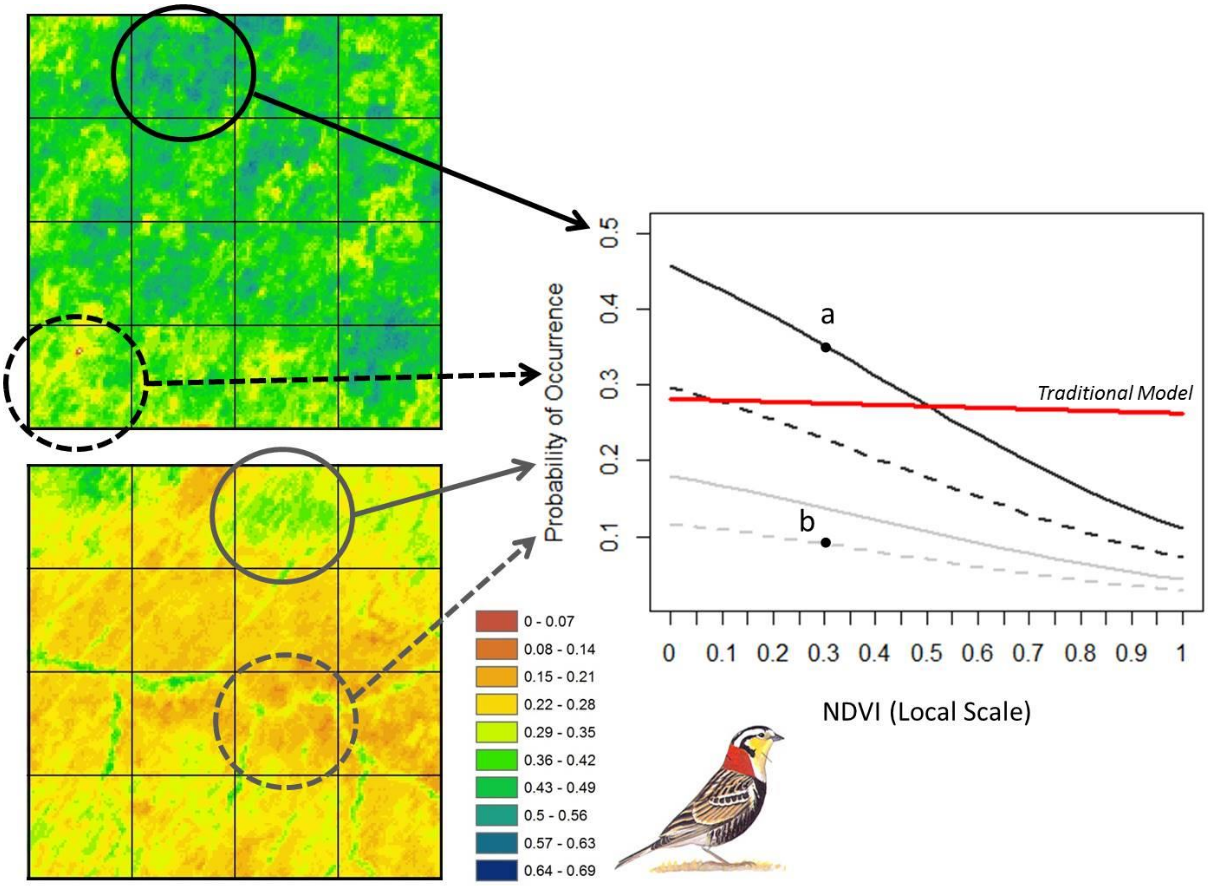

Figure 3. Response of Chestnut-collared Longspur (*Calcarius ornatus*) to fine-scale (2.6-km^2) Normalized Differential Vegetation Index (NDVI) depends on landscape context in central North America, 2007-2012. Red line shows prediction from a traditional logistic regression model using fine-scale data. Black lines show predicted response in a broad-scale landscape (1,492-km^2) with above-average NDVI (0.75), grey lines show response in a landscape with below-average NDVI (0.4). Solid lines show response with above-average NDVI (0.7) at the intermediate scale (93-km^2), dashed lines show response with below-average intermediate-scale NDVI (0.3). Estimated with above-average grassland cover (60%) at all scales. A suitable fine-scale site would be four time more likely to be occupied in the high-NDVI landscape (a) than the low-NDVI landscape (b).

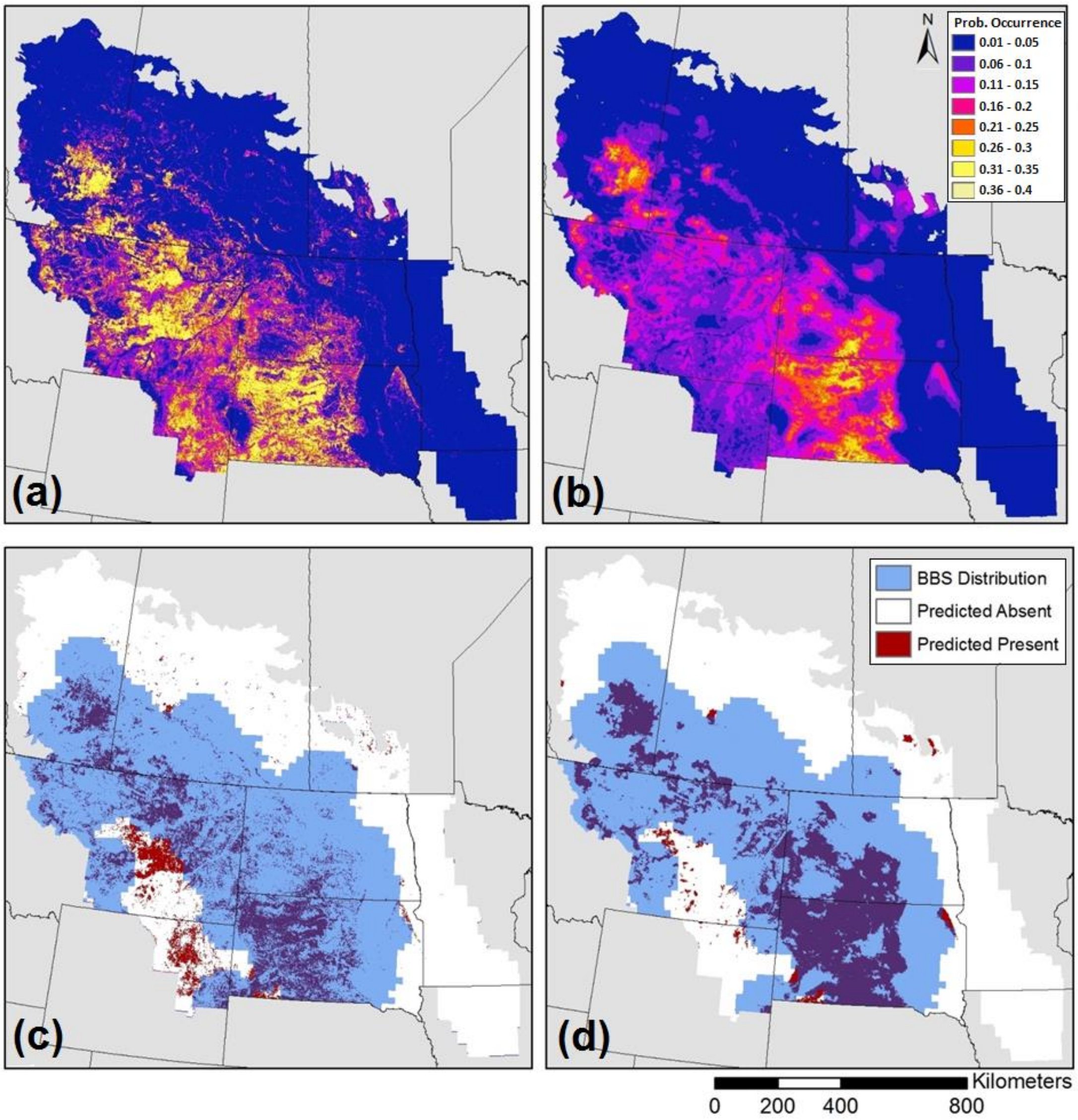

Figure 4. Spatial predictions from traditional logistic regression (a,c) and spatially hierarchical models (b, d) for Chestnut-collared Longspur (*Calcarius ornatus*) distribution in central North America, 2007-2012. Continuous predicted probability surfaces shown in a-b. Optimal cut-points of 0.24 and 0.13 were used for traditional and hierarchical models, respectively, to generate predicted distributions (c-d). Observed distribution from the Breeding Bird Survey (BBS; Sauer et al. 2014) shown in transparent blue on top of predictions in c-d.

GRASSLAND BIRD MANAGEMENT IN AGRICULTURAL LANDSCAPES: A VISION FOR CONSERVATION AT SCALE

Introduction

Grassland conservation is a growing priority for natural resource managers across North America as cultivation continues to expand and habitat for wildlife becomes ever scarcer. Often considered indicators for the ecosystem, many grassland songbird populations have dropped precipitously since surveys began in the 1960’s (Sauer et al. 2014). Although most have stabilized in recent decades, a subgroup of species in the western and northern Great Plains continues steep declines (NABCI 2014). Myriad scientific studies focus on grassland birds and their habitat requirements. Research over recent decades has characterized bird response to local vegetation conditions (Fisher and Davis 2010), grassland area (Ribic et al. 2009b) and non-grassland edges (Sliwinski and Koper 2012). However, though we have learned much about species’ needs in local contexts, a broader vision for management remains poorly defined. By nature, grasslands are large and variable landscapes where wildlife evolved with extreme fluctuations in conditions through time and space. Perhaps for more than any other system, selecting appropriate management scales in grasslands is crucial. In this final chapter, we offer some guidelines for managers based on insights gained from grassland bird research at scale.

Protection and restoration

Think big. Vast spatial scales are an ecological property of grassland landscapes. Despite unpredictable weather and disturbance regimes, grassland species evolved to exploit the sheer scale of the landscape through their capacity to move adaptively. Many of the most notable mammal migrations occur in grasslands (Berger 2004), and grassland birds are among the least philopatric avian groups, shifting distributions annually in response to conditions (Jones et al. 2007). Scale is therefore a central consideration for grassland managers. Chapters 2-4 show that negative implications of habitat loss and fragmentation for birds manifest at much broader extents than formerly recognized. For example, previous evidence suggests that Sprague's Pipit (*Anthus spragueii*), a species of high conservation concern, requires grassland patches of at least 145-ha (Davis 2004) and avoids cropland edges by up to 0.91-km (Sliwinski and Koper 2012). However, hierarchical models presented in chapter 4 successfully embedded local influences within their broader landscape context. Results suggested that a 260-ha patch of grassland (i.e., one square mile) was three times more likely to be occupied by Sprague's Pipit if situated in a landscape with a high versus low proportion of grass at intermediate (93-km^2; township) and broad (1,492-km^2; quadrangle) scales. This finding expands the scope of management for Sprague's Pipit by a factor of more than 1,000 over prior best available knowledge (149,200 vs. 145-ha).

We also show for seven specialist species (chapter 2 table 1) that large, intact grasslands are essential for maintaining high diversity and for supporting at-risk species. Chapter 2 demonstrates that bird distributions were patchy at relatively broad scales (average autocorrelation of 240-km^2), probably reflecting underlying patterns in precipitation and soil productivity. Importantly, declines in species sensitive to broad-scale habitat loss had a strong influence on diversity across the landscape. Sprague's Pipit, Baird's Sparrow (*Ammodramus bairdii*), Chestnut-collared Longspur (*Calcarius ornatus*) and McCown's Longspur (*Rhynchophanes mccownii*) were the most sensitive to grassland loss and are also of highest conservation concern as reflected by their steep population declines. Slowing or reversing declines will require conservation of large extents of existing grasslands in landscapes of 1,492-km^2 (quadrangle, or 368,640-ac). Although achieving 100% grassland cover at this scale is unlikely, a reasonable guideline based on findings from chapter 2 (figure 5d) is to prioritize conservation in quadrangles with maximum remaining grassland cover, or at least 25% (figure 1). For example, models suggest that in northeast Montana, a 40,469-ha (100,000-ac) protected area in a quadrangle with 40% grass would support roughly 3,500 McCown's Longspurs, 4,900 Sprague's Pipits, 6,600 Baird's Sparrows and 19,300 Chestnut-collared Longspurs. In contrast, the same area in a landscape with 15% grass would only be expected to support 400, 800, 2400 and 13,900 birds of each species, respectively.

Think connected. Whenever possible, conservation should also be targeted to areas adjoining existing protected grasslands such as easements, reserves or cores of public land. We show that landscapes containing a high proportion of grassland are most likely to support sensitive species, and the prioritization of continuous parcels within these minimizes the role of fragmentation. Although it is difficult to separate the effects of grassland loss and fragmentation (Fahrig 2003), both probably shape distributions. Grassland amount and aggregation index were selected as important predictors of Sprague's Pipit distribution in chapter 3, indicating that continuous tracts of grassland were more likely than fragmented regions to support birds. Continuous tracts are also important for other species such as migratory pronghorn (Poor et al. 2012), which would not benefit proportionately from conservation of fragmented parcels.

Prioritize protection and target investments. Maps of core population distribution, as presented for breeding Sprague's Pipits in chapter 3, are valuable tools for targeting conservation across the landscape. Funding for conservation is always limited, and the goal of planning should be to achieve maximum biological return for minimum investment (Bottrill et al. 2008). The value of grassland habitat is greatly amplified when it occurs inside species core areas, particularly where risk of land use change is high. The core area and tillage risk analysis outlined in chapter 3 suggests a natural prioritization scheme for grassland conservation. When quantitative model predictions are available, they can be overlaid with risk to directly target protection and restoration. In general and when quantitative models are unavailable, top priority for managers should be protecting existing habitat inside core areas and in quadrangles with the highest grass cover, following the suggested ranking (table 1). Within cores, securing parcels adjacent to existing grassland and those with highest risk of conversion to cropland are the most crucial conservation needs (table 1). In general, protection of existing habitat should be prioritized over restoration, as costs often exceed those of protection and the value of restored habitat is poorly understood (Fletcher and Koford 2002). However, in cases where funding is designated for restoration or at-risk grassland has already been protected, restoration can be considered within the same prioritization framework (table 1).

Focus on private lands to maintain grazing landscapes. Bird populations depend heavily (70%; chapter 3) on private grasslands that remain intact as rangelands for livestock grazing. Such grazing landscapes, maintained by rural communities and supported by ranching traditions, are a cornerstone of grassland conservation. Yet many ecological benefits provided by ranchland go unrecognized and uncompensated. Tradition and a strong land ethic often motivate ranchers to eschew profits and subsidies associated with farming, sometimes incurring considerable financial loss (Gentner and Tanaka 2002, Brunson and Huntsinger 2008). The contribution of these landowners to conservation should be acknowledged and successful efforts to maintain productive rangeland, manage grazing and control invasive plants in native grasslands should be rewarded. Conservation easements and voluntary incentives for good stewardship are the primary tools through which agencies and conservation groups can support grazing landscapes. But non-traditional approaches such as marketing premiums for beef raised on native pasture, or grassbanks that leverage additional conservation (Gripne 2005) also represent valuable efforts to support habitat on private lands.

Grazing management

Because grazing is the dominant land use in remaining grassland bird habitat, it is often a focus for management. Chapter 1 shows that, at least in years of recent high moisture, grazing by itself has little effect on bird abundance. Environmental constraints like precipitation, soil productivity and shrub cover were most influential (chapter 1 table 3) and the impact of grazing was only measurable as it interacted within these. By contrast, the effect of grassland amount was strong and consistent across analyses. Protection and restoration should therefore be prioritized over grazing management as a rule. However, for existing grassland landscapes where protection is secured and grazing is a primary land use, we offer some guidelines for management.

Think big, again. Chapters 1-2 show that thinking big is as critical for grazing management as it is for conservation planning. Suggestions in the scientific literature urge managers to apply variable livestock grazing to create heterogeneous habitat for a diversity of bird species. However, previous research offers few indications of how and where such heterogeneity-based management should be implemented. Limiting analyses to a group of grassland specialists allowed us to identify dense-grass and sparse-grass species and to quantify the relationship of each with herbaceous cover and livestock use (chapter 1 figure 2). Importantly, grazing only influenced cover and birds under certain environmental conditions, with precipitation and soil productivity acting as primary constraints. Spatial analysis in chapter

2 revealed that variability in bird distributions, presumably shaped by underlying patterns in environmental variables, occurred across large extents (mean patch size of 240-km^2). This broad patchiness is reflected in metrics of alpha (α) and beta (β) diversity across scale. When the landscapes considered were large enough to contain substantial environmental variability, maximum bird diversity was captured (high α; chapter 2 figure 3) and neighboring landscapes had similar communities (low β; chapter 2 figure 3). These results indicate that appropriate scales for heterogeneity-based management are much broader than previously assumed.

In particular, we suggest that managers consider landscapes at the scale of at least a quadrangle (1,492-km^2 or 368,640-ac) when implementing heterogeneity-based approaches. Chapter 2 results show that diversity is highest when the range in herbaceous cover (difference between densest and sparsest cover) is maximized in large grassland landscapes (chapter 2 table 2). Specifically, managers should consider balancing the availability of sparse versus dense herbaceous cover at broad scales using targeted grazing management. A reasonable goal would be to increase or maintain areas with extreme values of cover within each landscape, which includes cover that is both very low and very high. Application of a heterogeneity approach to smaller landscapes should be avoided because it is unlikely to affect diversity (chapter 2 table 2) and could result in wasted effort and resources. Worse, if placed in the wrong context, fine-scale management might be counterproductive. For example, introducing patches of heavy grazing on a highly productive ranch with historically low stocking rates would increase local heterogeneity but might also reduce the regional availability of dense cover, negatively impacting diversity. Conversely, implementing grazing reductions on a property that has historically high stocking rates might reduce regional availability of sparse cover. In both cases, consideration of the larger landscape context must guide decision-making.

Target grazing management. Chapter 1 demonstrates that environmental constraints control the influence of grazing. Specifically, shrublands and grasslands with poor soils (< 1,121-kg/ha or 1000-lbs/ac normal year estimated production) are unlikely to support a diverse grassland bird community in spite of grazing management. For example, only about a third of our northeast Montana study area's 18,500-km^2 of rangeland is grassland with productive soils where grazing could be managed to benefit grassland specialists. To create heterogeneous cover for grassland species, management should not be applied to regions with considerable shrub cover (chapter 1 table 1) or on low productivity grasslands. Instead, shrubland should be managed to benefit at-risk shrub-steppe obligates such as Greater Sage-Grouse (*Centrocercus urophasianus*) and Brewer's Sparrow (*Spizella breweri*), whereas low productivity grasslands should be maintained as refugia for species like McCown's Longspur that require sparse cover.

Adapt to recent conditions. To influence grassland birds, grazing management must be targeted in time as well as in space. Precipitation plays a dominant role in shaping habitat and chapter 1 shows that increased grazing intensity can benefit sparse-grass species in wet years whereas reduced intensity can benefit dense-grass species in dry years. Conversely, increases in dry years or reductions in wet years may be detrimental to dense-grass and sparse-grass species, respectively. Because total precipitation in the two years preceding breeding was most predictive of cover ($R^2 = 0.27$), we recommend adjusting management adaptively on an annual basis according to recent conditions. For northeast Montana, we suggest a threshold of < 500-mm (19.7-in) of precipitation in two years to indicate dry conditions and > 800-mm (31.5-in) to indicate wet conditions.

When conditions are average (500-800-mm or 19.7-31.5-in in two years), we suggest an approach using variable stocking rates to balance availability of high versus low cover across productive grasslands. Grazing plans must be tailored to local conditions and ownership patterns, and technical or financial assistance can be offered as necessary to help producers attain cover targets. In dry conditions, maintaining dense cover should be prioritized and grazing reductions implemented where feasible on productive grasslands. Highly productive soils are most likely to retain biomass in dry conditions and represent good targets for reductions. If public or other conservation lands are not sufficient to maintain cover, creative incentives might be required to achieve targets on working ranches. Some ideas include technical assistance for improved grazing systems, concentrating cattle in areas with exotic or planted grasses, allowing "emergency" grazing of non-native Conservation Reserve Program lands (CRP), providing additional pasture in regions without dry conditions, or provisioning hay. In wet conditions, high intensity grazing can be used to create sparse cover where feasible, although we suggest applying it to no more than half of available productive grasslands. Rapid shifts to wet conditions might outpace the ability of cow-calf herds to expand, making it necessary to retain yearlings or source stocker animals from elsewhere to achieve cover goals. In this case, soils with intermediate productivity (e.g. 1,121-1,681-kg/ha or 1000-1500-lbs/ac) are most likely to show cover reductions.

Focus on cover outcomes. Chapter 1 presents evidence that changes in herbaceous cover are the proximal cause of grassland bird response to livestock grazing. As such, birds are only likely to respond to grazing when it impacts cover. Many external factors contribute to observed cover, and these vary greatly depending on local conditions. A given stocking rate might have very different implications for birds when applied on two different ranches, or even on the same ranch in two different years. Instead of prescribing stocking rates or rotations, we suggest a simplified approach to management that is based on herbaceous cover outcomes. Targeting available cover in spring would free biologists from detailed range management planning which can be time-consuming and may be outside their expertise. Further, communicating requirements to ranchers or range managers would engage them as valuable partners who can apply existing skills and local knowledge to benefit wildlife.

Management outside the lines: a shifting paradigm

The vision presented here suggests a shifting paradigm for grassland management. Our research demonstrates that scales of conservation planning and scope of management must expand by orders of magnitude. The shift has significant implications for managers of refuges, reserves and other conservation lands because even relatively large protected tracts cannot ensure biological outcomes. It is not enough for managers to uphold high standards within their own boundaries if they simply throw up their hands just across the fence. To be successful, management actions should always be placed and prioritized within the broader landscape context. Managers of public land and private conservation areas including reserves, refuges, etc., should not consider their jurisdictions to be islands of habitat, but instead as forming a basis for leveraging conservation in surrounding grassland landscapes. For example, the Nature Conservancy's 60,000-ac Matador Ranch is using a grassbank model to influence more than 250,000-ac of surrounding private ranchland in Phillips County, MT. Such broad-scale impact undoubtedly benefits birds beyond any management that could be applied within ranch boundaries. The Matador's model and other creative collaborations between private landowners, agencies and non-governmental organizations will be critical for achieving the scale required to conserve grassland birds in the northern Great Plains. We urge more managers to think outside the lines.

Needs for future research

Research presented here provides a starting point for a new paradigm in grassland bird conservation but is by no means a comprehensive guide. Much remains poorly understood and there is a great need for continued research. In particular, we addressed only one of several threats to Sprague's Pipit by mapping potential tillage risk in chapter 3. Effects of energy development and climate change on birds have been poorly studied and might have serious implications for populations. Further, analyses presented here focus only on breeding songbirds and relatively little is known about threats to the wintering grounds (Pool et al. 2014). Understanding population dynamics throughout a full life cycle of declining species would provide valuable guidance for conservation.

The value for songbirds of restored native grassland habitat represents another priority for research. Previous work has shown some benefit of CRP lands for selected species (Johnson 2000, Niemuth et al. 2007, Ribic et al. 2009a), but there is little information about effective restoration of cropland or non-native vegetation to native grassland habitat.

Finally, designing an effective approach to grazing management will require thorough knowledge of cover requirements for birds' successful reproduction. Chapter 1 results demonstrate that abundance is associated with cover, but it remains unclear whether associations hold for nest density and/or success at the scale of a management unit (e.g. pasture). Development of clear guidelines for range managers should be a research priority. In particular, we highlight two primary needs. First is identification of a cover metric that is relevant to birds and easily communicable to range managers. Second is understanding how that metric relates to nest density and success at a scale relevant to management. Quantifying average conditions in a management unit would be preferable to conditions at nests because birds exhibit non-random nest placement (Davis 2005) and average conditions have direct implications for abundance and nest density that are not captured by nest-site measures.

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Table

Table 1. Suggested prioritization of conservation investments for grassland specialist songbirds in the northern Great Plains.

Range-wide	*Target*	1. Near center or within species cores
		2. Where grassland cover is highest in surrounding quadrangle (figure 1)
Local	*Protect*	1. Grassland that has highest predicted suitability for target species (if model is available)
		2. Native grassland at high risk of conversion and adjoining other grassland
		3. Native grassland adjoining other grassland
		4. Native grassland at high risk of conversion
		5. Any native grassland that is unprotected
	Restore	6. Cropland that has highest predicted suitability for target species (if model is available)
		7. Parcels in high-grass townships (93-km^2) adjoining other grassland
		8. Any parcels in high-grass townships (93-km^2)
		9. Any parcels adjoining other grassland

Figure

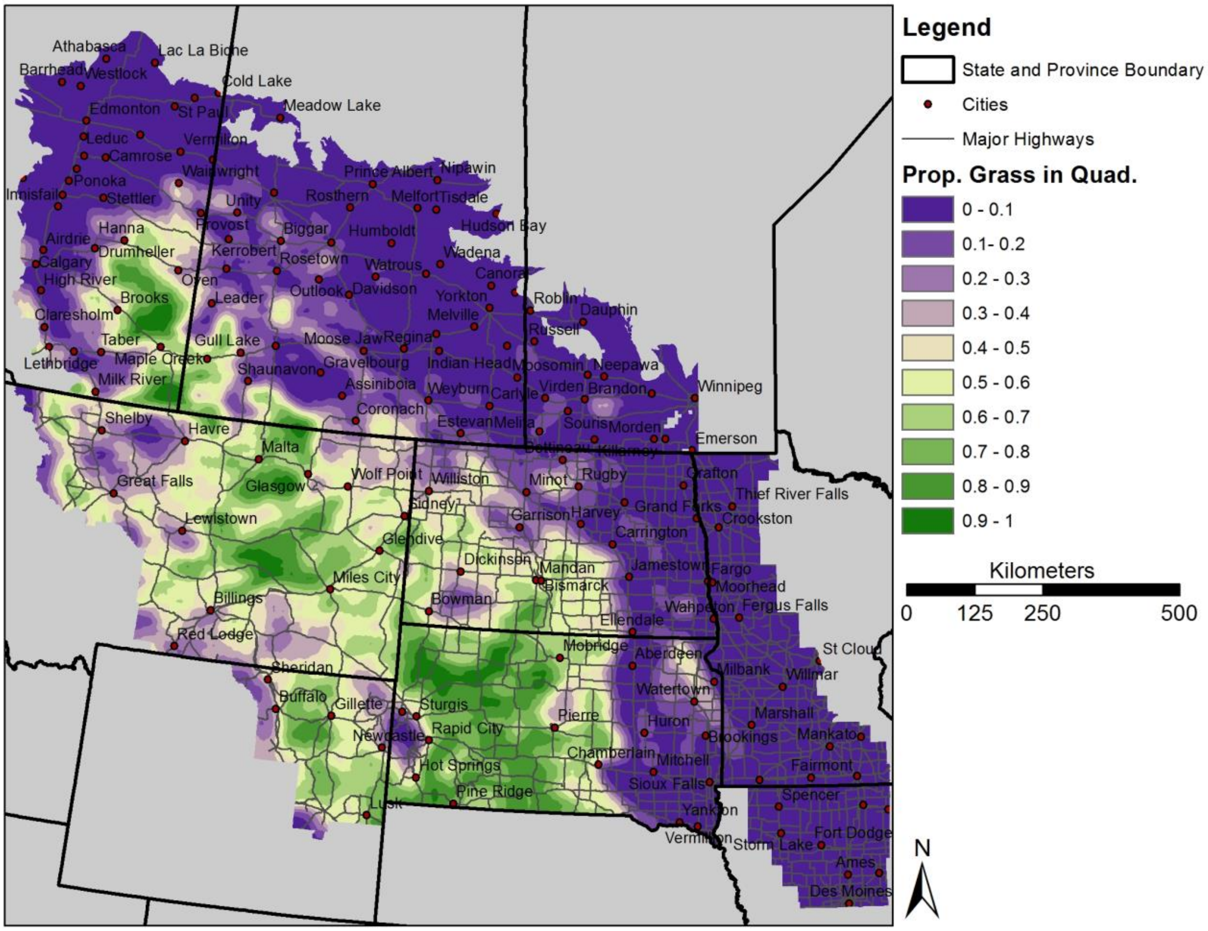

Figure 1. Proportion of grassland in surrounding quadrangle (1,492-km^2 or 368,640-ac) in the northern Great Plains. Grassland cover circa 2010-2011 from Homer (2015) in the United States and Agriculture and Agri-Food Canada (2015) in Canada.