

CONTRIBUTED PAPER

The future of North American grassland birds: Incorporating persistent and emergent threats into full annual cycle conservation priorities

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North American grasslands are one of the most threatened ecosystems in the world, and grassland bird populations have experienced drastic declines over the past half century. Land-use change is widely accepted as the most persistent threat, and climate change is expected to further compromise grassland integrity. The limited consideration of projected future threats is a significant gap in existing conservation priorities for North America's central grasslands. We identified Grassland Climate Strongholds (predicted to have high climate suitability for grassland birds both today and under 21st century climate change scenarios) and Grassland Climate and Land-use Strongholds (predicted to have high climate and land-use suitability for grassland birds today and under 21st century climate change scenarios). Strongholds were mainly distributed across southern Canada, the Dakotas, Montana, Wyoming, Colorado, New Mexico, the Oklahoma Panhandle, Texas, and the Chihuahuan Desert. Strongholds vulnerable to land-use conversion included the Prairie Pothole region and surrounding areas, much of the eastern-central Plains, the Texas Blackland Prairie, the Western Gulf Coastal Plain, and areas west of the Chihuahuan Desert. A maximum of only 9% of strongholds were protected. Strongholds are critical for full annual cycle conservation of declining grassland birds in North America and complement existing grassland priorities.

KEY WORDS

climate suitability, grassland birds, systematic conservation planning, Zonation

1 | INTRODUCTION

Protecting all species from extinction with limited resources is a major challenge (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). This reality has forced the conservation community to prioritize areas for conservation action, and focus on protecting or restoring places that provide the greatest return on investment (Withey et al., 2012). Initial prioritization efforts focused on meeting areal representation targets efficiently, and developed concepts such as complementarity in protected areas networks (Veach, Minin, Pouzols, & Moilanen, 2017). However, current and potential

future threats may be just as important as biodiversity targets in determining where to take immediate conservation action. Real-world conservation decisions balance conservation rewards against a variety of risks including land conversion and climate change (Lawler et al., 2014; Lipsey et al., 2015). Given the myriad challenges associated with establishing representation targets (i.e., inadequate data, conflicting stakeholder interests, economic and political realities), an alternate approach is to set conservation planning priorities that minimize risk by avoiding threats where possible (Schuetz et al., 2015).

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Climate and land-use change are two of the most pervasive global threats to natural ecosystems and wildlife (Jetz, Wilcove, & Dobson, 2007). Recognition of the importance of considering climate change in all aspects of conservation planning has increased in recent years (Stein et al., 2013) and methods have evolved to incorporate both present and predicted future climate suitability for multiple species simultaneously into landscape conservation designs (Carroll, Dunk, & Moilanen, 2010; Schuetz et al., 2015). Rayfield, Moilanen, and Fortin (2009) introduced an approach for incorporating consumer–resource interactions into spatial reserve designs that has been adapted to account for the connectivity between present and future species distributions under a changing climate. Carroll, Dunk, and Moilanen (2010) used this method to incorporate modeled connectivity between present and predicted future distributions into a prioritization scheme. Adaptations of these approaches have been applied to a variety of taxa, such as amphibians and reptiles (Kujala, Moilanen, Araújo, & Cabeza, 2013) and bats (Smith et al., 2016). This analysis is the first application of this spatiotemporal connectivity approach to priority setting for grassland birds.

The central grasslands of North America are one of the most threatened ecosystems in the world (Karl & Hoth, 2005; Samson, Knopf, & Ostlie, 2004). More than 80% of North American grasslands have been converted to agriculture or other land uses (With, King, & Jensen, 2008) and grassland bird populations have been drastically declining over the past 50 years (Knopf, 1994; North American Bird Conservation Initiative [NABCI], 2017). The North American Breeding Bird Survey indicates that 74% of farmland- and grassland-associated species declined from 1966 to 2013, with a few species that breed in the Great Plains of Canada and the United States and winter in the Chihuahuan grasslands of Mexico experiencing population declines of approximately 70–80% (NABCI, 2017; Sauer et al., 2017). These population declines are linked to agricultural conversion, which remains an ongoing threat (Lark, Salmon, & Gibbs, 2015; NABCI, 2017). Incorporation of threats into spatial prioritization is a key component of landscape conservation design (Bartuszevige, Taylor, Daniels, & Carter, 2016), particularly in grassland ecosystems under threat from tilling (Gage, Olimb, & Nelson, 2016).

Existing conservation prioritizations for grasslands are ecologically comprehensive and incorporate current threats, but do not consider projections of future threats. Gauthier, Lafon, Toombs, Hoth, and Wiken (2003) and Karl and Hoth (2005) convened a multi-stakeholder partnership to identify areas of tri-national importance requiring immediate conservation action based on current threatened status and ecological significance. They integrated 120 spatial data layers, conducted a priority-area gap analysis, assessed 20 key grassland bird and mammal species, and ran a workshop with 36 Canadian, U.S., and Mexican experts from a variety

of disciplines to identify Grassland Priority Conservation Areas (GPCAs). These were updated in 2010 (Pool & Panjabi, 2011) and are hereafter referred to as 2010 GPCAs. Comer, Hak, Kindscher, Muldavin, and Singhurst (2018) focused on major grassland ecosystem types, their intactness, and connectivity to identify Grassland Potential Conservation Areas (hereafter referred to as 2018 GPCAs) that were representative of grassland type diversity and had low risk of conflict with present-day competing land uses. Neither of these landscape conservation design efforts accounted for future projections of climate or land-use change; however, the latter acknowledged that addressing predicted future change is recommended by emerging best practices in conservation design (Comer, Hak, Kindscher, Muldavin, & Singhurst, 2018). We build upon these past efforts and fill this major knowledge gap in temperate grassland conservation planning by focusing on the predicted impact of future climate and land-use change on grassland birds and their habitats.

Our main objectives were to (a) to identify Grassland Climate Strongholds (GCSs), defined as areas predicted to have high climate suitability for all priority grassland birds both presently and under 21st century climate change scenarios; (b) identify Grassland Climate and Land-use Strongholds (GCLUSs) defined as areas predicted to have high climate and land-use suitability both presently and under 21st century climate and land-use change scenarios; and (c) to identify Vulnerable Grassland Climate Strongholds (VGCSs), defined as GCSs predicted to have a high risk of conversion to unsuitable land uses (e.g., cropland). To identify these areas we created two landscape rankings based on (a) present and future climate suitability for 39 grassland bird species; and (b) present and future climate and land-use suitability for 39 grassland bird species. Both scenarios accounted for summer and winter distributions, and connectivity between present and future locations of high climate suitability.

2 | METHODS

2.1 | Biodiversity features and environmental data

To address full life cycle conservation for grassland birds, and inform national and international policy, we considered the entire central grasslands of North America extending from Canada to Mexico. The region includes the Great Plains level I ecoregion plus the Chihuahuan Desert, and Western Sierra Madre Piedmont level II ecoregions (Commission for Environmental Cooperation Working Group, 1997), which are of critical importance to many wintering grassland bird species that breed in the Great Plains (Macías-Duarte & Panjabi, 2013).

We built ecological niche models for 39 grassland birds (Table 1) based on bird observation data and climate and

TABLE 1 Species included in the analysis, their normalized State of the Birds Concern Scores, and summer and winter geographic distributions

Common name	Summer norm. concern score	Winter norm. concern score	Summer range	Winter range
Aplomado Falcon	0.63	0.58	United States/Mexico	United States/Mexico
Baird's Sparrow	0.74	0.74	United States/Canada	Mexico
Bobolink	0.58	0.68	United States/Canada	South American Lowlands
Botteri's Sparrow	0.63	0.58	Mexico	Mexico
Burrowing Owl	0.58	0.53	United States/Canada	Mexico
Cassin's Sparrow	0.53	0.53	United States	Mexico
Chestnut-collared Longspur	0.74	0.68	United States/Canada	Mexico
Clay-colored Sparrow	0.42	0.47	United States/Canada	Mexico
Dickcissel	0.47	0.53	United States	South American Lowlands
Eastern Kingbird	0.47	0.53	United States/Canada	South American Lowlands
Eastern Meadowlark	0.53	0.53	United States/Canada	United States/Canada
Ferruginous Hawk	0.47	0.47	United States/Canada	United States/Canada
Grasshopper Sparrow	0.58	0.58	United States/Canada	United States/Mexico
Gray Partridge	NA	NA	United States/Canada	United States/Canada
Greater Prairie-Chicken	0.79	0.79	United States	United States
Henslow's Sparrow	0.63	0.68	United States	United States
Horned Lark	0.42	0.42	United States/Canada	United States
Lark Bunting	0.58	0.58	United States/Canada	Mexico
Le Conte's Sparrow	0.53	0.58	United States/Canada	United States/Canada
Lesser Prairie-Chicken	0.95	0.95	United States	United States
Loggerhead Shrike	0.53	0.53	United States/Canada/Mexico	United States/Mexico
Long-billed Curlew	0.68	0.68	United States/Canada	Mexico
McCown's Longspur	0.74	0.74	United States/Canada	United States/Mexico
Mountain Plover	0.74	0.79	United States	Mexico
Nelson's Sparrow	0.53	0.68	United States/Canada	United States
Northern Bobwhite	0.58	0.53	United States/Mexico	United States/Mexico
Ring-necked Pheasant	NA	NA	United States/Canada	United States/Canada
Savannah Sparrow	0.37	0.37	United States/Canada	United States/Mexico
Scaled Quail	0.58	0.58	United States/Mexico	United States/Mexico
Scissor-tailed Flycatcher	0.47	0.53	US	Pacific Lowlands
Sedge Wren	0.32	0.32	United States/Canada	United States/Mexico
Sharp-tailed Grouse	0.47	0.47	United States/Canada	United States/Canada
Short-eared Owl	0.58	0.58	United States/Canada	United States/Mexico
Sprague's Pipit	0.68	0.68	United States/Canada	Mexico
Swainson's Hawk	0.42	0.58	United States/Canada/Mexico	S. American Lowlands
Upland Sandpiper	0.47	0.47	United States/Canada	Southern Cone
Vesper Sparrow	0.47	0.53	United States/Canada	United States/Mexico
Western Kingbird	0.32	0.42	United States/Canada	Pacific Lowlands
Western Meadowlark	0.42	0.47	United States/Canada	United States/Mexico

Note. NA indicates the species is not native and therefore not included in the state of the birds assessment. We assigned these species a weight of 0.01.

environmental covariates. We included all terrestrial grassland species in our assessment based on NABCI's (2016) State of the Birds report habitat groupings (www.stateofthebirds.org), excluding the Chukar (*Alectoris chukar*), an introduced species with a primarily sagebrush-steppe distribution. After reviewing published range maps to identify species with separate breeding and nonbreeding ranges, we modeled both summer and winter distributions for all species except four whose nonbreeding ranges were in South America, outside the study area (Table 1). For these species we modeled only the breeding season distribution.

Predictions were based on approximately 4.1 million bird observations from >40 datasets spanning grasslands of Mexico, the United States, and Canada. Environmental covariates (Supporting Information Tables S1 and S2) included current and modeled future climate based on a 15-General Circulation Model (GCM) ensemble projection developed by AdaptWest (Wang, Hamann, Spittlehouse, & Carroll, 2016), land-use represented by a static categorical map of current anthropogenic land-use classes (e.g., agriculture and developed) derived from the Commission for Environmental Cooperation's North American Environmental Atlas 2010

land-cover dataset (Canada Centre for Remote Sensing et al., 2013), present and future vegetation extracted from modeled distributions of 46 North American biomes (Rehfeldt, Crookston, Sáenz-Romero, & Campbell, 2012), and terrain ruggedness derived from a digital elevation model to quantify topographic heterogeneity (Riley, Degloria, & Elliot, 1999). We explored models built with both boosted regression trees and Maxent (package dismo) in R (Hijmans, Phillips, Leathwick, & Elith, 2015), evaluated them based on median area under the curve (AUC) across 25 spatially stratified, bootstrapped datasets, and selected the top model for each species. In total, 525 models were evaluated with the goal of producing the best model for each species, in contrast to using a high-throughput one-size-fits-all approach (e.g., Lawler et al., 2009). A detailed description of the modeling process can be found in supporting information and Wilsey et al. (2019).

Land-use and land-cover (LULC) projections were based on downscaled global land-use scenarios (Li et al., 2016). The baseline condition was derived from an improved version of the Finer Resolution Observation and Monitoring-Global Land Cover (FROM-GLC) dataset, which is a 30-m global land-cover dataset for the year 2010 (Gong, Wang, & Yu, 2013). Independent variables included terrain, population, transportation, soils, climate, and protected areas. Scenarios were developed by combining shared socioeconomic pathways with representative concentration pathways (RCPs) to link climate change, greenhouse gas fluxes, and socioeconomic storylines. The macro-scale scenarios spanned the years 1500–2100, had a resolution of 0.5°, and projections for the time period 2010–2100 were downscaled to 1 km using a Cellular Automata (CA) based model. CA-based models capture the complexities of LULC change due to their ability to incorporate spatial and temporal dimensions simultaneously (Li et al., 2016).

All climate and land-use projections were considered at four decadal time steps (2010, 2030, 2060, 2090) each representing 30-year averages, and assumed a climate change scenario of approximately 1.8–3.7°C increase in global mean temperature by the end of century (Intergovernmental Panel on Climate Change, 2013; Moss et al., 2010; van Vuuren

et al., 2011). The 1.8°C temperature increase is equivalent to the Intergovernmental Panel on Climate Change stabilization scenario (RCP 4.5) and the 3.7°C increase is equivalent to the very high emissions scenario (RCP 8.5).

2.2 | Landscape prioritizations

We used Zonation spatial prioritization software (Moilanen et al., 2014) to rank every 1 km² cell in the landscape from 0 to 1 based on current and predicted future species climate suitability, or current and predicted future species climate and land-use suitability. We used the core area zonation (CAZ) ranking method because it prioritizes the highest-quality locations for any species regardless of species richness (Kujala, Moilanen, Araújo, & Cabeza, 2013). The CAZ algorithm searches through all cells in the landscape and calculates a value based on the species that has the highest weighted proportion of its distribution remaining in a given cell, and thus represents the highest biological value to be lost if the cell is removed. The cell which has the lowest value will be removed first, and the process is repeated until all cells are removed. To increase connectivity across high-ranked areas, we included an edge removal parameter that penalized edge length to area ratio by preferentially removing sites at the edges of the remaining analysis area, resulting in more compact shapes (Lehtomäki & Moilanen, 2013). To ensure that low-value areas surrounded by high-value areas were identified and removed without losing high-value cells first, we used the add edge points option ($n = 1000$) to allow the algorithm to identify and remove poor habitat within the interior of the landscape (Moilanen et al., 2014). We ran a total of eight separate zonation analyses (four per scenario) described in Table 2. We generated separate landscape rankings for the summer and winter seasons to avoid potential bias related to the larger number of species breeding than wintering in North America, and combined seasonal rankings into a single landscape ranking by using the maximum rank from either summer or winter for each cell in the landscape. We then re-ranked the combined raster so that cells were evenly distributed from 0 to 1.

Zonation allows the user to customize the analysis using a species weighting scheme. All prioritization schemes

TABLE 2 Individual prioritizations run with zonation for Scenarios 1 and 2

Prioritization scenario	Season	Emissions scenario	Climate years	Land-use/land-cover years
Scenario 1	Summer	RCP 4.5	2010, 2030, 2060, 2090	—
	Winter	RCP 4.5	2010, 2030, 2060, 2090	—
	Summer	RCP 8.5	2010, 2030, 2060, 2090	—
	Winter	RCP 8.5	2010, 2030, 2060, 2090	—
Scenario 2	Summer	RCP 4.5	2010, 2030, 2060, 2090	2010, 2030, 2060, 2090
	Winter	RCP 4.5	2010, 2030, 2060, 2090	2010, 2030, 2060, 2090
	Summer	RCP 8.5	2010, 2030, 2060, 2090	2010, 2030, 2060, 2090
	Winter	RCP 8.5	2010, 2030, 2060, 2090	2010, 2030, 2060, 2090

Note. Summer and winter prioritizations for each representative concentration pathway (RCP) scenario were combined into one landscape ranking using the highest rank across both seasons, and then re-ranked to evenly distribute cells from 0–1.

weighted at-risk species higher than common species, and present conditions higher than future predictions. Species weights were derived from the State of the Birds conservation concern scores for summer and winter (NABCI, 2016). We used min-max normalization to rescale the scores, which originally ranged from 1 to 20. The decision to weight present and near-future predictions higher than late-century predictions reflected the increasing uncertainty of climate change models after approximately 2030 (Knutti & Sedláček, 2013). To weight time steps, we calculated the delta between the upper and lower bounds of one standard deviation from the mean of Coupled Model Intercomparison Project Phase 5 (CMIP5) climate model predictions of global temperature change at each time step (Knutti & Sedláček, 2013) and used the inverse of the delta as the weight (Table S3). Finally, we multiplied the normalized conservation concern scores by the time-step weight to derive the final species weights for the analysis (Table 1).

To address potential dispersal limitations that could constrain a species' ability to shift their distributions with a changing climate, we applied the ecological interactions function in Zonation (Moilanen et al., 2014) to the breeding-season prioritizations. This function down-weights locations further than a species would be expected to disperse from its current distribution over the time period in question (Carroll, Dunk, & Moilanen, 2010; Moilanen et al., 2014; Rayfield, Moilanen, & Fortin, 2009), and thus simulates connectivity across space and time simultaneously. We included ecological interactions between the present and future to prioritize areas in the present that are within dispersal distance to the future (dispersal source to destination), and between the future and present to prioritize areas in the future that are within dispersal distance to the present (stepping stones). Interactions were calculated between each successive time step; 2010–2030, 2030–2060, 2060–2090, and vice versa). In the present to future interactions, the source distribution was modified, and in the future to present interactions the destination distribution was modified. Estimates of mean natal dispersal (BirdLife International, 2017) and generation time (Beauchamp, 2010) were used to generate an estimated dispersal limit for each species in each future time period using the formula: (dispersal distance/generation time) × years in future (Schloss, Nuñez, & Lawler, 2012). We assumed a generation time of 1 year when none was known (e.g., Botteri's Sparrow and Upland Sandpiper).

To identify GCSs and GCLUSs we ran Zonation for two prioritization scenarios: (1) present and future climate suitability for 39 grassland bird species (GCSs); and (2) present and future climate and land-use suitability for 39 grassland bird species (GCLUSs). We accounted for land-use change in Scenario 2 by removing areas predicted to be converted to unsuitable land-cover types in the future. We used the LULC change predictions (Li et al., 2016) to create a condition raster for each time step by reclassifying the nine land-use

classes to either 0 or 1, with 0 representing land-use classes that are incompatible with grassland bird habitat (urban, crop, forest, bare land, snow/ice), and 1 representing compatible land-use classes (shrub, pasture, water, wetland). Although shrub lands provide marginal habitat for many grassland birds, we opted to consider them suitable as they have high potential for restoration. Zonation multiplied the species climate suitability rasters by the condition raster before it began the cell removal process, therefore only cells with a compatible land-use class were retained in the analysis and ranked based on the algorithm described above.

To identify VGCSs, we subtracted the Scenario 2 rank raster from the Scenario 1 rank raster and then reranked the resulting difference raster so that cells were evenly distributed from 0 to 1. High-ranking cells represent locations with suitable climate that are most vulnerable to conversion. We used a range of ranks, from 0.5 to 0.8, to threshold GCSs, GCLUSs, and VGCSs and calculated spatial correspondence between all three and the 2010 and 2018 GPCAs, as well as the mean across all ranks for each GPCA. We also created a consensus prioritization by overlaying the top 20% (a typical lower bound recommended by Lehtomäki & Moilanen, 2013) of the GCSs, GCLUSs, and VGCSs with both sets of GPCAs and calculating the number of prioritizations (1–5) that identified each cell as high priority. We considered the areas identified by all prioritizations to be "Consensus Priorities" and therefore potential candidates for the highest levels of conservation attention.

Finally, we used NatureServe's Current Grassland Range Maps to calculate the proportion of each grassland type in the top 20% of GCSs, GCLUSs, VGCSs, and the highest level of Consensus Priorities, and the proportion of each that is currently under some form of protection. The range maps were developed by extending the LANDFIRE biophysical settings products that correlate field observations with climate, landform, and soil (Rollins, 2009) to Mexico and Canada, and thus provide complete and current distributions of the major grassland types in North America (Comer, Hak, Kindscher, Muldavin, & Singhurst, 2018). We condensed the 12 grassland types to four (desert, shortgrass, mixed-grass, tallgrass) prior to analysis. The Western Great Plains Sand Prairie did not fall neatly into one of these four classes as it shares characteristics with several of them. Consequently, we grouped sand prairie with mixedgrass as the two ranges were highly spatially coincident.

3 | RESULTS

Results were robust to emissions scenario as prioritizations generated with the mid-level emissions scenario (RCP 4.5) were qualitatively similar to the results from the high-emissions scenario (RCP 8.5). Consequently, only the high-emissions scenario results are presented here. GCSs were clustered in the northern and southern Great Plains. In the

north, they were concentrated in Alberta, Saskatchewan, Manitoba, North Dakota, and Montana. In the southern Great Plains and Warm Desert ecoregions, GCSs were concentrated in the Oklahoma Panhandle, New Mexico, Texas, and the Chihuahuan Desert (Figure 1a). GCLUSs were distributed similarly to GCSs in the south, but in the north they were shifted further south and west into Wyoming, Colorado, and South Dakota (Figure 1b). GCSs and GCLUs differ because some species distributions were truncated in Scenario 2 where areas of unsuitable LULC were excluded, causing the complementarity-based rankings to shift. Land-use projections suggested that virtually the entire eastern half of the region may be converted to incompatible land uses by 2100 (Figure 1b). VGCSs included the Prairie Pothole region and surrounding areas, much of the eastern-central Plains, the Texas Blackland Prairie, the Western Gulf Coastal Plain, and the desert grasslands west of the Chihuahuan Desert (Figure 1c).

Spatial correspondence among all prioritizations was highest between GCLUSs and the 2010 GPCAs at all thresholds (0.32–0.75; Table 3). Correspondence was relatively low between VGCSs and 2010 GPCAs as only 9% of GPCA area overlapped the top 20% of VGCSs (Table 3). This suggests that the identification process for the 2010 GPCAs avoided, whether intentionally or not, areas predicted to be highly vulnerable to conversion primarily in the tallgrass and mixedgrass regions. Approximately 30% of all GPCAs had a mean GCS rank below 0.5. Mean GCS, GCLUS, and VGCS ranks for each 2010 and 2018 GPCA and the GPCA

locations can be found in supporting information (Table S4 and Figure S1).

Consensus Priorities among the five prioritizations (top 20% of GCSs, GCLUSs, VGCSs, and both sets of GPCAs) indicated that there were no areas where all five scenarios overlapped (Figure 2). Therefore, the maximum consensus level was four, with an area of approximately 5,318,400 ha. None of the level 4 Consensus Priorities included VGCSs; however, they meet both 2010 and 2018 GPCA criteria, and are predicted to retain suitable climate and land-use conditions to accommodate the full annual cycle for species that breed and winter in the North American grasslands.

Proportions of the four major grassland types coincident with the top 20% of GCSs ranged from 0.2% of tallgrass prairie to 29.9% of desert grassland, GCLUSs ranged from 0.6% of tallgrass prairie to 32.8% of desert grassland, VGCSs ranged from 2.7% of shortgrass prairie to 28.6% of mixedgrass prairie, and level 4 Consensus Priorities ranged from 0% of tallgrass prairie to 2.5% of mixedgrass prairie (Figure 3). Tallgrass prairie had the lowest level of protected GCSs (2.9%) and desert grasslands had the highest, with only 6.7% having some form of protection. Protected GCLUSs ranged from 3.7% in shortgrass prairie to 9.2% in tallgrass prairie, and protected VGCSs ranged from 0.3% in desert grassland to 8.6% in tallgrass prairie. Nearly one quarter (23.2%) of the level 4 Consensus Priorities in mixedgrass prairie were protected (Figure 3).

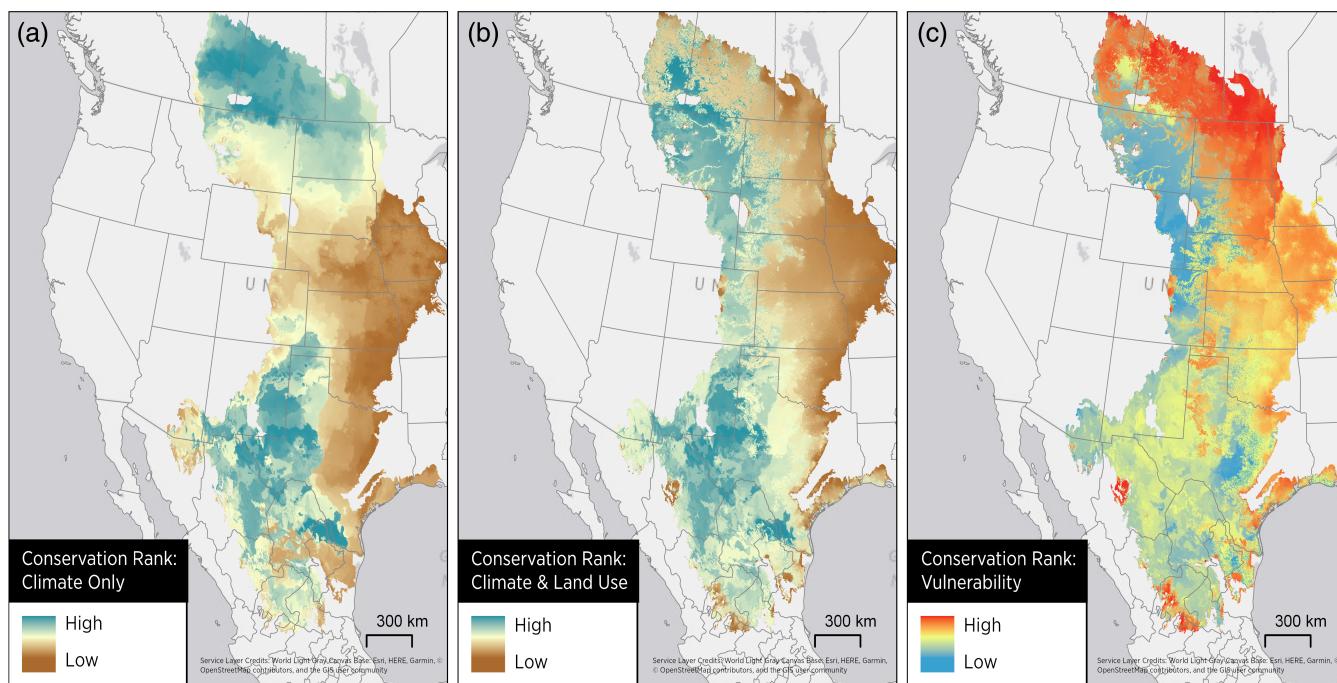


FIGURE 1 Landscape ranks based on: (a) present and future climate suitability for 39 grassland bird species (Scenario 1—Grassland Climate Strongholds; shown in blue-green); and (b) present and future climate and land-use suitability for 39 grassland bird species (Scenario 2—Grassland Climate and Land-use Strongholds; shown in blue-green); and (c) vulnerability, defined as the delta between the present and future climate scenario (Scenario 1, Figure 1a) and the present and future climate and land-use scenario (Scenario 2, Figure 1b); high value = high vulnerability to land-use conversion (shown in red-orange)

TABLE 3 Proportion of total 2010 and 2018 Grassland Priority Conservation Areas (GPCAs) coincident with the top 50% to top 20% of cell ranks in Grassland Climate Strongholds (GCSs) (Scenario 1), Grassland Climate and Land-use Strongholds (GCLUSs) (Scenario 2), and Vulnerable Grassland Climate Strongholds (VGCSs) (Scenario 1 minus Scenario 2)

Threshold (%)	GCSs + 2010 GPCAs	GCLUSs + 2010 GPCAs	VGCSs + 2010 GPCAs	GCSs + 2018 GPCAs	GCLUSs + 2018 GPCAs	VGCSs + 2018 GPCAs
50	0.65	0.75	0.20	0.54	0.52	0.44
40	0.53	0.65	0.16	0.43	0.45	0.33
30	0.42	0.53	0.12	0.34	0.37	0.24
20	0.27	0.32	0.09	0.24	0.26	0.18

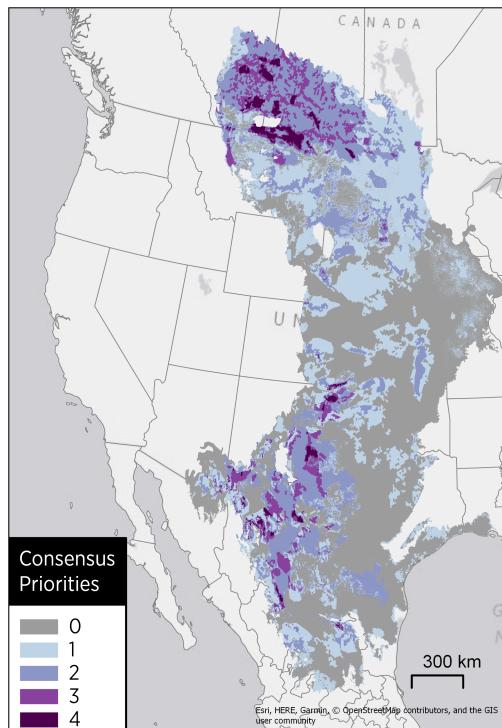


FIGURE 2 Consensus Priorities derived from the top 20% of Grassland Climate Strongholds, Grassland Climate and Land-use Strongholds, and Vulnerable Grassland Climate Strongholds, and the 2010 and 2018 Grassland Priority/Potential Conservation Areas

4 | DISCUSSION

Temperate grassland regions are projected to have some of the highest climate change velocities (a measure of the speed of travel needed to keep pace with climate change) among biomes on Earth (Loarie et al., 2009). Yet, we identified substantial (~20–30%; Figure 3) proportions of shortgrass, mixed-grass, and desert grasslands as GCSs and GCLUSs that are potentially robust to projected future impacts of climate change on the distributions of grassland birds. Grasslands globally are under-protected in spite of their high conservation value (Hoekstra, Boucher, Ricketts, & Roberts, 2005; Samson & Knopf, 1994). A maximum of only 7–9% of the GCSs and GCLUSs in the four major grassland types of central North America are currently designated as protected according to IUCN's World Database on Protected Areas IUCN and UNEP-WCMC (2014). The emerging threat of climate change to grassland birds (Wilsey et al., 2019)

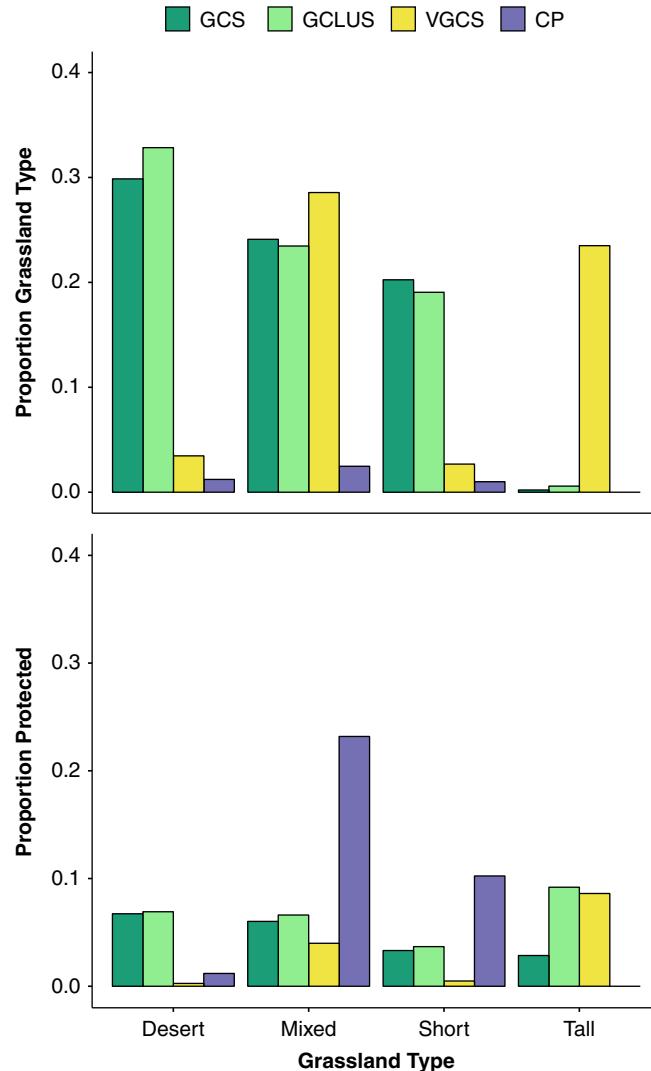


FIGURE 3 Bar graphs depicting the proportion of each grassland type coincident with Grassland Climate Strongholds (GCS), Grassland Climate and Land-use Strongholds (GCLUS), Vulnerable Grassland Climate Strongholds (VGCS), and Consensus Priorities (CP), and proportion of each coincident area currently protected

necessitates that we attempt to account for its impact when identifying conservation priorities in this critically threatened ecosystem upon which their populations depend.

Furthermore, land conversion remains a substantial threat to North American grasslands. We identified VGCSs as GCSs projected to be at high risk of future land conversion. Effective grassland conservation will ultimately require a two-pronged approach; working to limit conversion of the

most vulnerable grasslands, particularly in the tallgrass prairie, while also promoting conservation in GCSs and GCLUSs. The decision whether or not to target vulnerable grasslands for protection or restoration will depend heavily on available resources, as land-use pressure drives up the value of the land. Estimating return on conservation investment by taking conversion risk into consideration (Withey et al., 2012) is one way to inform conservation decision-making. The land-use change projections considered here were downscaled from a global land-use change simulation (Li et al., 2016), which inevitably incorporates error as local-scale drivers of change will differ from those simulated globally. Nonetheless, current rates of land-use change are high in the region. Land conversion rates were locally as high as 10% from 2008 to 2012 in some regions of the United States, with 77% of new cropland converted from grasslands (Lark, Salmon, & Gibbs, 2015). Corn cultivation for ethanol led to 1.5 million ha of converted grasslands within 100 miles of refineries in the Midwestern United States during a similar period (Wright, Larson, Lark, & Gibbs, 2017).

Our results are consistent with the generally observed pattern that the greatest land conversion pressures are occurring in the tallgrass prairies of the eastern Great Plains (Askins et al., 2007; Samson, Knopf, & Ostlie, 2004). The tallgrass prairie is particularly fertile and arable, and conversion to cropland has been most intense in this region (Lark, Salmon, & Gibbs, 2015). Higher precipitation and suitability for irrigated row crops makes this part of the region extremely vulnerable to agricultural development (Lark, Salmon, & Gibbs, 2015). Declines in North American grassland bird populations have been attributed mainly to habitat loss and land-use practices associated with agriculture (Stanton, Morrissey, & Clark, 2018). Our results also indicate that tallgrass prairie has the lowest proportion of area identified as GCSs and GCLUSs (0.2 and 0.6%, respectively; Figure 3), suggesting that remaining fragments of tallgrass prairie may no longer have suitable climate for birds historically dependent on them (Wimberly, Narem, Bauman, Carlson, & Ahlering, 2018). Further, nearly one-quarter of the tallgrass prairie range is vulnerable to conversion or already converted. Indeed, even the largest remaining tallgrass prairie remnant, the Flint Hills of Kansas and Oklahoma (~2 million ha), appears to be unable to support viable bird populations (With, King, & Jensen, 2008). Remnant tallgrass patches are still valuable, however, as they may serve as genetic banks for restoration. Thus, urgent conservation action is required to restore and protect any tallgrass prairie that remains, as these unique ecological systems and the birds that depend on them will likely become extirpated without immediate intervention.

The strongholds identified here complement the previously identified grassland conservation priorities in the region that do not consider future climate or land-use

change. Strongholds capture areas where bird ranges overlap today and in the future, whereas GPCAs consider factors such as grassland vegetation, current threats, and intactness (Comer, Hak, Kindscher, Muldavin, & Singhurst, 2018; Gauthier, Lafon, Toombs, Hoth, & Wiken, 2003; Karl & Hoth, 2005). Our approach focused on complementarity among bird species, while 2018 GPCAs (Comer, Hak, Kindscher, Muldavin, & Singhurst, 2018) emphasized representativeness of grassland vegetation types. A precautionary approach to conservation planning in such a highly threatened ecosystem should account for all of these attributes; therefore, Consensus Priorities may be particularly worthy of attention (Figure 2). The majority of level 4 Consensus Priorities are located in mixedgrass prairie, and over one-quarter of those are already protected. Having been identified by three independent efforts, Consensus Priorities are robust to major differences in prioritization approach, and those remaining unprotected should be given the highest consideration in continental-scale conservation planning. Moreover, the mean stronghold rank assigned to individual GPCAs provides further novel decision support for conservation practitioners who are attempting to consider climate change adaptation in their grassland prioritization goals (Table S4). Although approximately 30% of GPCAs had a mean GCS rank less than 0.5, suggesting that these GPCAs may not remain top priorities for grassland birds under a changing climate, they may retain their value for other taxa. Further research is required to assess the impacts of climate change on nonavian, grassland-dependent species.

Grassland conservation is challenging because 85% of remaining grasslands are on private lands (NABCI U.S. Committee, 2013). Voluntary agri-environment schemes are a primary mechanism for grassland conservation. Through the US Farm Bill, the Conservation Reserve Program (CRP) pays farmers to keep environmentally sensitive lands out of production for 10–15 years and currently protects at least 3.4 million ha of native or planted grasslands across the Great Plains Region (NABCI, 2017). However, most grassland conversion today is occurring on lands being taken out of CRP (Lark, Salmon, & Gibbs, 2015; Morefield, LeDuc, Clark, & Iovanna, 2016). This suggests market incentives have shifted and highlights the precarious nature of conservation gains from voluntary programs (Wright, Larson, Lark, & Gibbs, 2017).

While the CRP focuses on removing land from agricultural production altogether, reducing intensity on agricultural lands benefits birds and other wildlife while maintaining a source of income for farmers. Row crop (e.g., corn, soybean) fields with prairie buffers comprising 10% of the field area had 34–300% higher bird abundance, richness, and diversity than fields without natural buffers (Schulte, MacDonald, Niemi, & Helmers, 2016). Similarly, agricultural fields (including row crops and orchards) with woody hedgerows or riparian buffers had 300–600% higher total bird abundance, 200–300% higher

species richness, and significantly greater species evenness than similar fields without natural margins (Heath, Soykan, Velas, Kelsey, & Kross, 2017). Other intensity-reduction measures that improve agricultural lands for grassland birds include reduction of field sizes (Fahrig et al., 2015), planting and rotating cover crops that provide food to migrating and wintering birds (Wilcoxen, Walk, & Ward, 2018), planting perennial grasses instead of corn for biofuels (Meehan, Hurlbert, & Gratton, 2010), and planting crops such as warm season grasses that are harvested later in the year, enabling grassland birds to fledge young prior to harvest (Hyde & Campbell, 2012).

Reducing agricultural intensity would have the additional benefit of dampening the effect of variability in agricultural production on grassland birds. Agricultural conversion experiences boom and bust cycles, with rates of cropland expansion increasing rapidly during periods of economic growth or biofuels investment, followed by decreases when commodity prices stabilize or drop (Lark, Salmon, & Gibbs, 2015). Moreover, warming and reduced precipitation due to climate change may reduce agricultural productivity, increasing the area needed to grow essential crops and, consequently, leading to further grassland loss (Gornall et al., 2010). Grassland restoration and reduction of agricultural intensity are essential undertakings to ensure sufficient habitat for grassland birds in an uncertain and dynamic future.

Market-based innovations are another important strategy to advance grassland conservation on private lands under threat of conversion. Grazing animals and natural fire regimes have played a key role in grassland ecosystems for millennia (Collins, 2000; Samson, Knopf, & Ostlie, 2004), and grassland bird habitat requirements are strongly linked to the ecological impacts of grazers on the landscape. Vast herds of bison once provided a shifting mosaic of habitat types through their movements, and cattle can be managed in ways that partially mimic the important impacts of their ruminant cousins of the past (Fuhlendorf & Engle, 2001). Conservation nongovernmental organizations have been working with ranchers to promote sustainable ranching practices that provide habitat for birds and other wildlife (Bird Conservancy of the Rockies, 2018; National Audubon Society, 2017; Point Blue, 2018; World Wildlife Fund, 2018). The National Audubon Society's Conservation Ranching Program has gone a step further by developing markets that connect conservation-conscious consumers to ranchers who employ management practices that improve soil health and diversify habitat structure (National Audubon Society, 2017). In addition, market-based incentives that promote sustainable rangeland management, such as prescribed grazing, may also mitigate against climate change by increasing carbon sequestration in soils over time (Chambers, Lal, & Paustian, 2016).

Using projected future ecological change to inform conservation is replete with uncertainty. Here, we have attempted to address some of the uncertainty in the ability of birds to respond to climate change by simulating dispersal limitations between present and future areas of suitable climate and by reducing the contribution of distant future projections to conservation rank. However, we did not address other ecological processes that may be critical in defining a species' biological response to climate change. In particular, while vegetation projections were included in the species climate suitability models, these were not mechanistic and therefore did not reflect the dynamics of range expansion for plants, likely overestimating future range gains and underestimating vulnerability (Stralberg et al., 2015). Current and novel future inter-specific interactions may also influence species' biological responses to climate change (Zarnetske, Skelly, & Urban, 2012).

In this paper, we prioritized areas for grassland bird conservation across the central grasslands of North America. The GCSs, GCLUSs, and Consensus Priorities identified are areas predicted to be critical for many declining grassland birds that rely on North America's grasslands for their full annual cycle, and some are highly vulnerable to land-use conversion. These priorities complement existing GPCAs by addressing the emerging threat of climate change in addition to the ongoing threat of land conversion. This additional information can guide conservation action toward grasslands that are likely to persist over time and provide critical climate and land-use strongholds for grassland birds through the end of the 21st century.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interests.

AUTHOR CONTRIBUTIONS

J.G. and C.W. conceived the study; J.G. conducted the analyses and wrote the manuscript; J.W. contributed to data preparation; N.M., J.W., and C.W. contributed to the species distribution modeling and manuscript writing; and all authors reviewed, edited, and approved the final manuscript.

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REFERENCES

- Askins, R. A., Chávez-Ramírez, F., Dale, B. C., Haas, C. A., Herkert, J. R., Knopf, F. L., & Vickery, P. D. (2007). Conservation of grassland birds in North America: Understanding ecological processes in different regions: "Report of the AOU Committee on conservation". *Ornithological Monographs*, 64, 1–46.
- Bartuszevige, A. M., Taylor, K., Daniels, A., & Carter, M. F. (2016). Landscape design: Integrating ecological, social, and economic considerations into conservation planning: Landscape design. *Wildlife Society Bulletin*, 40, 411–422.
- Beauchamp, G. (2010). Group-foraging is not associated with longevity in North American birds. *Biology Letters*, 6, 42–44.
- Bird Conservancy of the Rockies. (2018). Habitat enhancement. Bird Conservancy.org. Retrieved from <https://birdconservancy.org/what-we-do/stewardship/habitat-enhancement/>
- BirdLife International. (2017). *IUCN Red List for birds*. Retrieved from <http://www.birdlife.org>
- Canada Centre for Remote Sensing, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Comisión Nacional Forestal, Instituto Nacional de Estadística y Geografía, & U.S. Geological Survey. (2013). *2010 Land cover of North America at 250 meters*. Montréal, Québec, Canada: Commission for Environmental Cooperation.
- Carroll, C., Dunk, J. R., & Moilanen, A. (2010). Optimizing resiliency of reserve networks to climate change: Multispecies conservation planning in the Pacific Northwest, USA. *Global Change Biology*, 16, 891–904.
- Chambers, A., Lal, R., & Paustian, K. (2016). Soil carbon sequestration potential of US croplands and grasslands: Implementing the 4 per thousand initiative. *Journal of Soil and Water Conservation*, 71, 68A–74A.
- Collins, S. L. (2000). Disturbance frequency and community stability in native tallgrass prairie. *The American Naturalist*, 155, 311–325.
- Comer, P. J., Hak, J. C., Kindscher, K., Muldavin, E., & Singhurst, J. (2018). Continent-scale landscape conservation design for temperate grasslands of the Great Plains and Chihuahuan Desert. *Natural Areas Journal*, 38, 196–211.
- Commission for Environmental Cooperation Working Group. (1997). *Ecological regions of North America – toward a common perspective*. Montreal, Canada: Commission for Environmental Cooperation, 71 p.
- Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., ... Tischendorf, L. (2015). Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems and Environment*, 200, 219–234.
- Fuhlendorf, S. D., & Engle, D. M. (2001). Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns: We propose a paradigm that enhances heterogeneity instead of homogeneity to promote biological diversity and wildlife habitat on rangelands grazed by livestock. *Bioscience*, 51, 625–632.
- Gage, A. M., Olimb, S. K., & Nelson, J. (2016). Plowprint: Tracking cumulative cropland expansion to target grassland conservation. *Great Plains Research*, 26, 107–116.
- Gauthier, D. A., Lafon, A., Toombs, T., Hoth, J., & Wiken, E. (2003). *Grasslands: Toward a North American conservation strategy*. Montréal, Québec, Canada: Canadian Plains Research Center, University of Regina, Regina, Saskatchewan, and Commission for Environmental Cooperation.
- Gong, P., Wang, J., & Yu, L. (2013). Finer resolution observation and monitoring of global land cover: First mapping results with Landsat TM and ETM + data. *International Journal of Remote Sensing*, 34, 2607–2654.
- Gornall, J., Betts, R., Burke, E., Clark, R., Camp, J., Willett, K., & Wiltshire, A. (2010). Implications of climate change for agricultural productivity in the early twenty-first century. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2973–2989.
- Heath, S. K., Soykan, C. U., Velas, K. L., Kelsey, R., & Kross, S. M. (2017). A bustle in the hedgerow: Woody field margins boost on farm avian diversity and abundance in an intensive agricultural landscape. *Biological Conservation*, 212, 153–161.
- Hijmans, R. J., Phillips, S. J., Leathwick, J. R., & Elith, J. (2015). *Package dismo version 1.0–12*. Retrieved from <http://cran.r-project.org/web/packages/dismo/index.html>
- Hoekstra, J. M., Boucher, T. M., Ricketts, T. H., & Roberts, C. (2005). Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecology Letters*, 8, 23–29.
- Hyde, D., & Campbell, S. (2012). *Agricultural practices that conserve grassland birds*. East Lansing, MI: Michigan State University Extension.
- Intergovernmental Panel on Climate Change (2013). Summary for policymakers. In T. F. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, et al. (Eds.), *Climate Change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 3–29). Cambridge, England and New York, NY: Cambridge University Press.
- IUCN and UNEP-WCMC. (2014). *The World Database on Protected Areas (WDPA)* [On-line], [April 2016], Cambridge, UK: UNEP-WCMC. Retrieved from www.protectedplanet.net
- Jetz, W., Wilcove, D. S., & Dobson, A. P. (2007). Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, 5, 1211–1219.
- Karl, J. W., & Hoth, J. (2005). *North American grassland priority conservation areas* (Technical Report and Documentation).
- Knopf, F. L. (1994). Avian assemblages on altered grasslands. *Studies in Avian Biology*, 15, 247–257.
- Knutti, R., & Sedláček, J. (2013). Robustness and uncertainties in the new CMIP5 climate model projections. *Nature Climate Change*, 3, 369–373.
- Kujala, H., Moilanen, A., Araújo, M. B., & Cabeza, M. (2013). Conservation planning with uncertain climate change projections. *PLoS One*, 8, e53315.
- Lark, T. J., Salmon, J. M., & Gibbs, H. K. (2015). Cropland expansion outpaces agricultural and biofuel policies in the United States. *Environmental Research Letters*, 10, 044003.
- Lawler, J. J., Lewis, D. J., Nelson, E., Plantinga, A. J., Polasky, S., Withey, J. C., ... Radeloff, V. C. (2014). Projected land-use change impacts on ecosystem services in the United States. *Proceedings of the National Academy of Sciences*, 111, 7492–7497.
- Lawler, J. J., Shafer, S. L., White, D., Kareiva, P., Maurer, E. P., Blaustein, A. R., & Bartlein, P. J. (2009). Projected climate-induced faunal change in the Western Hemisphere. *Ecology*, 90, 588–597.
- Lehtomäki, J., & Moilanen, A. (2013). Methods and workflow for spatial conservation prioritization using zonation. *Environmental Modelling & Software*, 47, 128–137.
- Li, X., Yu, L., Sohl, T., Clinton, N., Li, W., Zhu, Z., ... Gong, P. (2016). A Cellular Automata downscaling based 1km global land use datasets (2010–2100). *Scientific Bulletin*, 61, 1651–1661.
- Lipsey, M. K., Doherty, K. E., Naugle, D. E., Fields, S., Evans, J. S., Davis, S. K., & Koper, N. (2015). One step ahead of the plow: Using cropland conversion risk to guide Sprague's Pipit conservation in the northern Great Plains. *Biological Conservation*, 191, 739–749.
- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, 462, 1052–1055.
- Macías-Duarte, A., & Panjabi, A. O. (2013). Home range and habitat use of wintering Vesper Sparrows in grasslands of the Chihuahuan Desert in Mexico. *Wilson Journal of Ornithology*, 125, 755–762.
- Meehan, T. D., Hurlbert, A. H., & Gratton, C. (2010). Bird communities in future bioenergy landscapes of the Upper Midwest. *Proceedings of the National Academy of Sciences*, 107, 18533–18538.
- Moilanen, A., Veach, V., Meller, J., Leppänen, J., Pouzols, F. M., Kujala, H., & Arponen, A. (2014). *Zonation spatial conservation planning framework and software v. 4.0, User manual*. Helsinki, Finland: C-BIG Conservation Biology Informatics Group, Department of Biosciences, University of Helsinki.
- Morefield, P. E., LeDuc, S. D., Clark, C. M., & Iovanna, R. (2016). Grasslands, wetlands, and agriculture: The fate of land expiring from the Conservation Reserve Program in the Midwestern United States. *Environmental Research Letters*, 11, 094005.
- Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., van Vuuren, D. P., ... Wilbanks, T. J. (2010). The next generation of scenarios for climate change research and assessment. *Nature*, 463, 747–756.

- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.
- National Audubon Society. (2017). What in the world is conservation ranching?. *Audubon*. Retrieved from <https://www.audubon.org/news/what-world-conservation-ranching>
- North American Bird Conservation Initiative. (2016). *The state of the birds 2016*. Washington, DC: U.S. Department of Interior.
- North American Bird Conservation Initiative. (2017). *The state of the birds* (p. 2017). Washington, DC: U.S. Department of Interior.
- North American Bird Conservation Initiative, U.S. Committee. (2013). *The state of the birds 2013—Report on private lands*. Washington, DC: U.S. Department of Interior.
- Point Blue. (2018). *Landscape conservation*. Retrieved from <https://www.pointblue.org/our-work/working-landscapes/>
- Pool, D., & Panjabi, A. (2011). *Assessment and revisions of North American grassland priority conservation areas. Background Paper*. Montréal, Québec, Canada: Commission for Environmental Cooperation.
- Rayfield, B., Moilanen, A., & Fortin, M.-J. (2009). Incorporating consumer-resource spatial interactions in reserve design. *Ecological Modelling*, 220, 725–733.
- Rehfeldt, G. E., Crookston, N. L., Sáenz-Romero, C., & Campbell, E. M. (2012). North American vegetation model for land-use planning in a changing climate: A solution to large classification problems. *Ecological Applications*, 22, 119–141.
- Riley, S., Degloria, S., & Elliot, S. D. (1999). A Terrain Ruggedness Index that quantifies topographic heterogeneity. *International Journal of Science*, 5, 23–27.
- Rollins, M. (2009). LANDFIRE: A nationally consistent vegetation, wildland fire, and fuel assessment. *International Journal of Wildland Fire*, 18, 235–249.
- Samson, F., & Knopf, F. (1994). Prairie conservation in North America. *Bioscience*, 44, 418–421.
- Samson, F. B., Knopf, F. L., & Ostlie, W. R. (2004). Great Plains ecosystems: Past, present, and future. *Wildlife Society Bulletin*, 32, 6–15.
- Sauer, J. R., Niven, D. K., Hines, J. E., Ziolkowski, D. J., Pardieck, K. L., Fallon, J. E., & Link, W. A. (2017). *The North American Breeding Bird Survey, Results and Analysis 1966–2015. Version 2.07.2017*. Laurel, MD: USGS Patuxent Wildlife Research Center.
- Schloss, C. A., Nuñez, T. A., & Lawler, J. J. (2012). Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences*, 109, 8606–8611.
- Schuetz, J. G., Langham, G. M., Soykan, C. U., Wilsey, C. B., Auer, T., & Sanchez, C. C. (2015). Making spatial prioritizations robust to climate change uncertainties: A case study with North American birds. *Ecological Applications*, 25(7), 1819–1831.
- Schulte, L. A., MacDonald, A. L., Niemi, J. B., & Helmers, M. J. (2016). Prairie strips as a mechanism to promote land sharing by birds in industrial agricultural landscapes. *Agriculture, Ecosystems and Environment*, 220, 55–63.
- Smith, A., Schoeman, M. C., Keith, M., Erasmus, B. F. N., Monadjem, A., Moilanen, A., & Di Minin, E. (2016). Synergistic effects of climate and land-use change on representation of African bats in priority conservation areas. *Ecological Indicators*, 69, 276–283.
- Stanton, R. L., Morrissey, C. A., & Clark, R. G. (2018). Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. *Agriculture, Ecosystems and Environment*, 254, 244–254.
- Stein, B. A., Staudt, A., Cross, M. S., Dubois, N. S., Enquist, C., Griffis, R., ... Nelson, E. J. (2013). Preparing for and managing change: Climate adaptation for biodiversity and ecosystems. *Frontiers in Ecology and the Environment*, 11, 502–510.
- Stralberg, D., Bayne, E. M., Cumming, S. G., Sólymos, P., Song, S. J., & Schmiegelow, F. K. A. (2015). Conservation of future boreal forest bird communities considering lags in vegetation response to climate change: A modified refugia approach. *Diversity and Distributions*, 21, 1112–1128.
- van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., ... Rose, S. K. (2011). The representative concentration pathways: An overview. *Climatic Change*, 109, 5–31.
- Veach, V., Minin, E. D., Pouzols, F. M., & Moilanen, A. (2017). Species richness as criterion for global conservation area placement leads to large losses in coverage of biodiversity. *Diversity and Distributions*, 23, 715–726.
- Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally down-scaled and spatially customizable climate data for historical and future periods for North America. *PLoS One*, 11, e0156720.
- Wilcoxen, C. A., Walk, J. W., & Ward, M. P. (2018). Use of cover crop fields by migratory and resident birds. *Agriculture, Ecosystems and Environment*, 252, 42–50.
- Wilsey, C., Taylor, L., Bateman, B., Jensen, C., Michel, N., Panjabi, A., & Langham, G. (2019). Climate policy action needed to reduce vulnerability of conservation-reliant grassland birds in North America. *Conserv. Sci. Pract.*, CSP2–18–0014.
- Wimberly, M. C., Narem, D. M., Bauman, P. J., Carlson, B. T., & Ahlering, M. A. (2018). Grassland connectivity in fragmented agricultural landscapes of the north-Central United States. *Biological Conservation*, 217, 121–130.
- With, K. A., King, A. W., & Jensen, W. E. (2008). Remaining large grasslands may not be sufficient to prevent grassland bird declines. *Biological Conservation*, 141, 3152–3167.
- Withey, J. C., Lawler, J. J., Polasky, S., Plantinga, A. J., Nelson, E. J., Kareiva, P., ... Reid, W. (2012). Maximising return on conservation investment in the conterminous USA. *Ecology Letters*, 15, 1249–1256.
- World Wildlife Fund. (2018). *Sustainable ranching initiative*. Retrieved from <https://www.worldwildlife.org/projects/sustainable-ranching-initiative>
- Wright, C. K., Larson, B., Lark, T. J., & Gibbs, H. (2017). Recent grassland losses are concentrated around U.S. ethanol refineries. *Environmental Research Letters*, 12, 044001.
- Zarnetske, P. L., Skelly, D. K., & Urban, M. C. (2012). Biotic multipliers of climate change. *Science*, 336, 1516–1518.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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