Landscape Ecol
https://doi.org/10.1007/s10980-020-01050-4

RESEARCH ARTICLE

Implications of future climate- and land-change scenarios on grassland bird abundance and biodiversity in the Upper Missouri River Basin

A. P. Baltensperger · M. D. Dixon · D. L. Swanson

Received: 19 December 2019 / Accepted: 1 June 2020

Abstract

Context Over the past decades, numerous threats from climate- and land-use change to ecosystems have been identified. Grassland ecosystems are among the most endangered in the world and ongoing grassland declines in the Great Plains have been a major concern for avian biodiversity conservation.

Objectives Threat mitigation may include biofuel cultivation, CO_2 emissions reductions, and land conservation strategies. However, spatially explicit and species-specific population responses to future scenarios remain unknown. We show how future land-use and climate scenarios may affect abundance and biodiversity patterns for grassland birds in the Upper Missouri River Basin.

Methods We used georeferenced abundance records, 20 environmental predictors, and gradient boosting machines to create spatial abundance models for 24 grassland bird species. Models were scored to current conditions and seven future landcover/climate-change scenarios to spatially predict changes in bird abundance for 2050.

Results Model accuracy varied by species ($0.2\% \leq \text{NRMSE} \leq 39.3\%$) but spatial predictions were highly accurate ($.03 \leq \text{MAE} \leq 7.67$). Mean abundances declined for eight species in at least one scenario, whereas abundances increased for 16 species. Multi-species change analyses identified areas of decreasing abundance, particularly in the southeast, whereas increasing were predicted at higher elevations to the west. Important predictors included temperature, forest distance, and elevation.

Conclusions Predicted abundances varied by species and geography. Abundances and distributions expanded for most species, but multi-species declines also occurred in many low-elevation areas. These models may improve understanding of species-specific responses to environmental change by identifying emerging areas of avian conservation concern.

Keywords Biofuels · Ecological niche model · Gradient boosting machines · Great plains · Land-use/land-change

Introduction

North American temperate grasslands are among the most threatened and heavily degraded biomes in the world (Hoekstra et al. 2004). Grasslands provide numerous ecosystem services, including serving as

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10980-020-01050-4) contains supplementary material, which is available to authorized users.

A. P. Baltensperger (✉) · M. D. Dixon · D. L. Swanson
Department of Biology, University of South Dakota,
Vermillion, SD 57069, USA
e-mail: abaltens@alaska.edu

important wildlife habitat (White et al. 2000), sequestering carbon (Silver et al. 2010), providing grazing lands for livestock production, and providing clean drinking water for an estimated 44 million people (Havstad et al. 2007; WWF 2018). In North America, over 60–80% of native mixed grass prairie and 20–85% of shortgrass prairie have been lost (Samson and Knopf 1994). The conversion of native grassland habitats into agricultural lands (both cultivated croplands and rangelands) is the largest contributor to land-use change in North America (Gage et al. 2016; Stanton et al. 2018; Correll et al. 2019). Incursions by oil and gas infrastructure are degrading the continuity of grasslands and leases now occur on 21% of all North American grasslands (Copeland et al. 2011; Bernath-Plaisted and Koper 2016). Encroachment by woody shrubs (Maestre et al. 2016; Greer et al. 2016) and exotic species (Saalfeld et al. 2016) has also resulted in reductions in grassland habitat, and that which remains is becoming increasingly fragmented and degraded (Hamer et al. 2006).

Biomass biofuel cultivation is one means of harnessing the carbon sequestration capabilities of grasslands. Cultivation of bioenergy crops, including switchgrass (*Panicum virgatum*) and canola (*Brassica napus*), aims to remove carbon from the atmosphere using a BECCS (Bioenergy with Carbon Capture and Storage) pathway (van Vuuren et al. 2013). Crops sequestering atmospheric carbon in tissues are then harvested and combusted in power-plants equipped with carbon capture technology (Stoy et al. 2018; Dolan et al. 2019). The theoretical end result is a net reduction in atmospheric carbon. But the cultivation of land for biomass biofuels requires land and water that could also be used to produce food or provide habitat for native grassland fauna. Some bioenergy crops, such as switchgrass, may offer benefits for certain grassland birds (Murray et al. 2003; Robertson et al. 2012; Blank et al. 2014), but if native grasslands are brought under cultivation to meet increased bioenergy demand, biofuel cultivation may also accelerate biodiversity losses and compromise ecosystem services even as it counteracts carbon emissions (Beringer et al. 2011; Hof et al. 2018).

Climate change is also threatening many species by shifting climatic envelopes, altering environmental pressures on species and pushing migratory and breeding phenologies earlier (Swanson and Palmer 2009; Brookshire and Weaver 2015; Boelman et al. 2017). Grassland specialist birds, which rely exclusively on native prairie ecosystems or predictable seasonality of resources, and species with already small ranges are most vulnerable to the synergistic effects of environmental change (Staudt et al. 2013; Correll et al. 2019). These species may be poorly equipped to cope with novel climatic conditions that strain physiological limits and rearrange ecological communities (Williams and Jackson 2007; Hof et al. 2018; Correll et al. 2019). Further research to predict spatially explicit, species-specific population responses to landscape change, including incorporating satellite-derived Ecosystem Functional Attributes (ESA) to improve model predictions, is still needed to improve models and direct conservation actions (Arenas-Castro et al. 2019).

Avian abundance has declined by ~ 30% (3 billion breeding birds) in North America over the past half-century, with grassland birds suffering the greatest population declines (Peterjohn and Sauer 1999; Schipper et al. 2016; Rosenberg et al. 2019). These declines have been attributed partially to habitat losses on the breeding grounds caused by a combination of land-use and climate change (Wright and Wimberly 2013; Gage et al. 2016; Rosenberg et al. 2019). Fragmented and degraded habitats reduce species diversity, abundance, and nesting success among grassland birds (Bakker and Higgins 2009; Greer et al. 2016). About 53% of original grasslands remain in the Great Plains, with 87% of these occupying soils that are marginal for cultivation (WWF 2018). However, as the global demands for food and energy grow, cultivation of native grasslands will result in additional habitat loss and further declines for many grassland birds unless significant conservation actions are taken (Lipsey et al. 2015; Wright and Wimberly 2013).

Here we aimed to predict spatially explicit population responses of grassland birds to a range of potential future land-use and climate scenarios. Applications of machine learning to develop ecological niche models that predict species distributions (presence/absence) under current and future scenarios are widespread (Elith et al. 2006; Evans et al. 2011; Baltensperger and Huettmann 2015a, b). More recently, boosting algorithms have been used to make spatially explicit predictions of abundance from surveyed populations (Howard et al. 2015; Lipsey et al. 2015; Fox et al. 2017). Using an ecological niche modeling framework, we used a gradient boosting machine algorithm to estimate current population distributions for 24 species of grassland birds in the Upper Missouri River Basin (UMRB; 516,832 km^2; Fig. 1) and to project population changes using seven climate/land-use change scenarios for 2050.

We included bird species if they were grassland obligates or facultative users of grasslands for foraging or nesting. The 24 species selected for modeling included waterfowl (n = 4), upland game birds (n = 3), raptors (n = 2), shorebirds (n = 3) and passerines (n = 12), so study species comprise a broad taxonomic sample. Of these, seven (greater sage-grouse, greater prairie-chicken, Sprague's pipit, chestnut-collared longspur, McCown's longspur, Baird's sparrow, bobolink; see Table 1 for scientific names) are listed as "species of continental concern" for ongoing population declines and threats to future persistence (Rosenberg et al. 2016). An additional two (lark bunting and grasshopper sparrow) are also listed as common birds that have shown steep population declines (Rosenberg et al. 2016). We hope that by identifying geographic areas of population change common to many species, private land owners and wildlife managers may more proactively focus conservation efforts in the northern Great Plains.

Methods

Training data

We accessed field data from the Bird Conservancy of the Rockies for a spatially balanced survey of

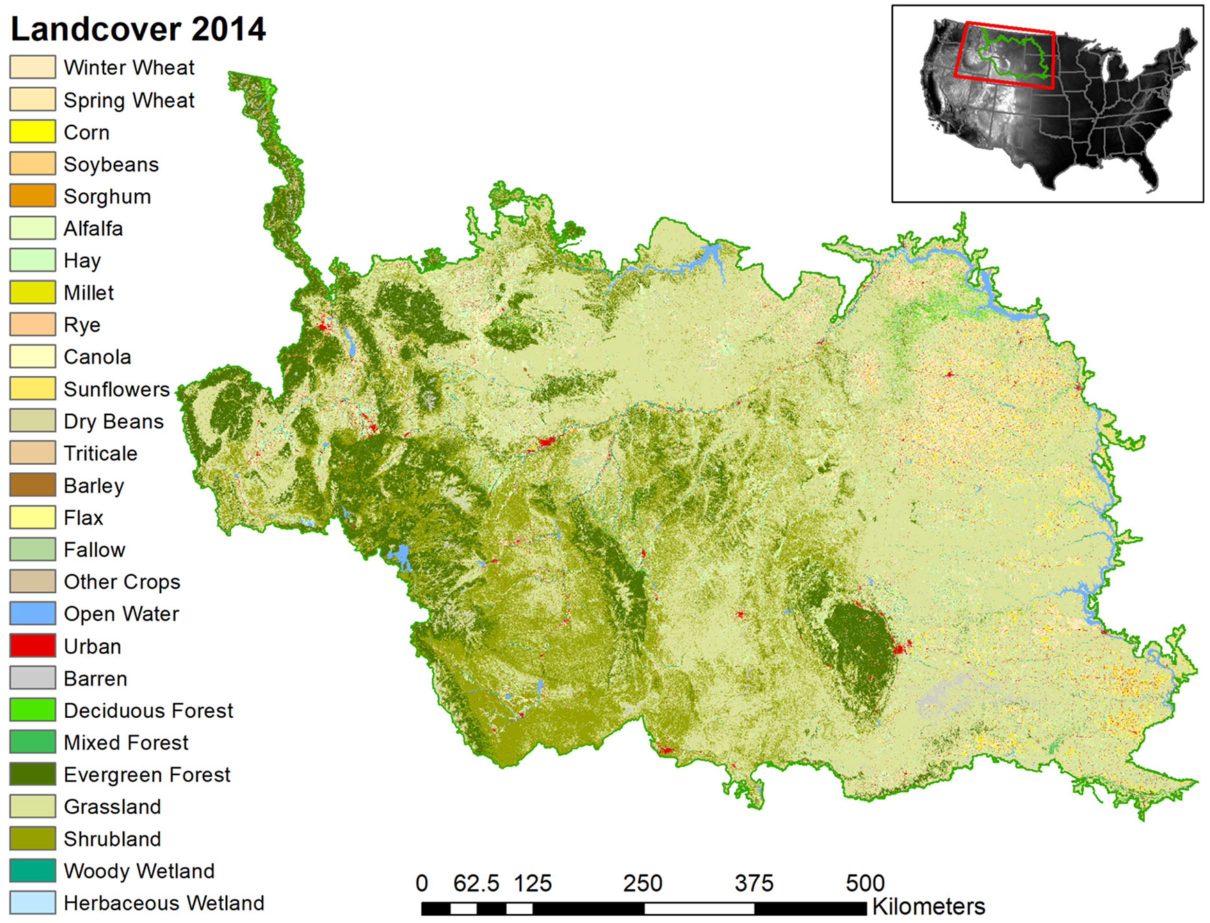


Fig. 1 Map of the Upper Missouri River Basin study area, depicting baseline landcover conditions (Sohl et al. 2019) as of 2014 and broader position of the UMRB within a digital elevation map of the continental U.S

Table 1 Common names, scientific names, and American Ornithological Union (AOU) codes for 24 species for which population distribution models were developed

Common name	Scientific name	AOU Code	Non-zero Training Points (*n*)	Mean observed abundance	Mean predicted abundance	Model NRMSE	Spatial MAE
Baird's sparrow	*Ammodramus bairdii*	BASP	67	0.70 ± 3.10	0.58 ± 1.50	3.9	0.59
Bobolink	*Dolichonyx oryzivorus*	BOBO	94	2.80 ± 8.30	2.80 ± 5.20	0.8	1.05
Blue-winged teal	*Anas discors*	BWTE	163	0.60 ± 2.20	0.80 ± 1.20	11.6	0.32
Chestnut-collared longspur	*Calcarius ornatus*	CCLO	125	3.60 ± 13.70	3.30 ± 7.60	2.9	1.70
Dickcissel	*Spiza americana*	DICK	62	0.90 ± 6.10	1.20 ± 3.30	6.9	0.37
Ferruginous hawk	*Buteo regalis*	FEHA	30	0.10 ± 0.50	0.10 ± 0.20	5.0	0.03
Gadwall	*Mareca strepera*	GADW	86	0.60 ± 2.40	0.70 ± 1.30	4.1	0.24
Grasshopper sparrow	*Ammodramus savannarum*	GRSP	479	11.70 ± 16.60	10.90 ± 12.50	0.2	3.29
Greater prairie-chicken	*Tympanuchus cupido*	GPCH	22	0.30 ± 2.80	0.50 ± 2.20	39.3	0.18
Greater sage-grouse	*Centrocercus urophasianus*	GSGR	26	0.20 ± 1.80	0.20 ± 0.70	9.2	0.07
Lark bunting	*Calamospiza melanocorys*	LABU	334	14.90 ± 30.70	18.10 ± 24.10	1.5	3.19
Lark sparrow	*Chondestes grammacus*	LASP	516	6.40 ± 8.50	6.10 ± 5.20	1.2	2.13
Long-billed curlew	*Numenius americanus*	LBCU	77	0.60 ± 3.00	0.80 ± 1.60	4.6	0.32
Marbled godwit	*Limosa fedoa*	MAGO	72	0.40 ± 1.80	0.50 ± 1.00	7.5	0.57
Mallard	*Anas platyrhynchos*	MALL	303	1.80 ± 3.10	2.20 ± 1.80	0.9	0.16
McCown's longspur	*Rhynchophanes mccownii*	MCLO	20	0.20 ± 2.70	0.20 ± 1.00	14.9	0.08
Northern pintail	*Anas acuta*	NOPI	77	0.30 ± 1.20	0.40 ± 0.70	4.0	0.18
Savannah sparrow	*Passerculus sandwichensis*	SASP	164	2.30 ± 8.00	3.89 ± 6.80	3.0	1.45
Sprague's pipit	*Anthus spragueii*	SPPI	46	0.30 ± 1.80	0.30 ± 0.80	11.9	0.07
Sharp-tailed grouse	*Tympanuchus phasianellus*	STGR	151	0.90 ± 3.50	0.90 ± 1.50	2.1	0.32
Swainson's hawk	*Buteo swainsoni*	SWHA	92	0.30 ± 0.90	0.40 ± 0.50	3.1	0.12
Upland sandpiper	*Bartramia longicauda*	UPSA	356	3.40 ± 5.80	3.90 ± 4.40	1.4	0.92
Vesper sparrow	*Pooecetes gramineus*	VESP	520	9.00 ± 12.30	10.00 ± 8.40	1.2	3.03
Western meadowlark	*Sturnella neglecta*	WEME	687	45.60 ± 40.70	44.00 ± 28.50	0.6	7.67

Training sample sizes (number of points where species were detected), mean observed and predicted mean abundances (individuals/km^2) with standard deviations across all 786 training locations. Mean-normalized root mean square errors (NRMSE), and mean absolute error (MAE) of predicted versus observed abundances are also included landbirds conducted across Montana (MT), Wyoming (WY), Colorado (CO), North Dakota (ND), and South Dakota (SD) between 2007 and 2018 (Hanni et al. 2018). Field technicians conducted point counts of birds for 6 min at each of 16 points spaced 250 m apart and arranged in a 1 km × 1 km sampling grid (Hanni et al. 2018). We limited records to the UMRB as defined by Sohl et al. (2019; Fig. 1), resulting in a dataset totaling 170,610 observations for 24 species at 4578 points among sampling grids (Table 1).

We assumed each point in a grid was independent, with a maximum detection radius of 125 m, so total area sampled in each full grid (16 points) was ~ 1 km^2. We collapsed raw species counts into mean relative abundances (hereafter 'abundance') using a cross-tabulation query to sum species detections across all points in a grid for the years sampled. Using the 'mean center' tool in ArcGIS 10.5 (ESRI, Inc., Redlands, CA, USA) we determined the geographic center of each sampling grid and assigned corresponding mean abundances to these 786 points. Sampling grids where a species was never detected during the 12-year study were assigned a value of 0.0, to train absences in models.

We did not correct abundance estimates for detectability because we used georeferenced, spatially explicit point-level count data to calculate average numbers of detected birds in each sampling grid, rather than calculating densities by habitat. Because calculation of the detection function is based on many points within a habitat type, we decided not to correct point-level count data. Our results, therefore, underestimate actual bird densities, as birds farther from points were less likely to be detected. Because surveys were conducted in open grassland habitats, primarily mixed- and shortgrass prairies, we assumed within-species detectability was similar among points, so errors in abundance estimates should be systematic across the UMRB.

Model development

All abundances and associated geographic coordinates were attributed in R 3.6.1, with 20 climatic, topographic, and anthropogenic raster predictors hypothesized to influence population distributions of grassland birds in the region (Online Material 1). Climatic predictors were downloaded from WorldClim 1.4 (worldclim.org/data/cmip5.html) and we used the BCC-CSM1-1 global climate model (GCM) projections, downscaled to 30 s resolution and averaged over 2010–2018.

To predict species abundances across the UMRB, we used a gradient boosting machine algorithm with inverse distance weighting (IDW; *spm* package in R 3.6.1; R Core Team 2019; Li et al. 2019). The *gbmidwcv* function allowed for tenfold cross-validation of tree predictions and selection of the most accurate models using the lowest root-mean square error (RMSE). This algorithm was more accurate than others we tried, including randomForest in R (stat.berkeley.edu/~breiman/RandomForests), TreeNet (Minitab, LLC, State College, PA) and gradient boosting machines without inverse-distance weighting. To compare among species, we calculated the normalized RMSE (NRMSE) by dividing RMSE by the observed mean abundance for each species (Willmott et al. 1985). Predictive spatial accuracy was assessed using mean absolute error (MAE) of predicted versus observed abundances, standardized by standard deviation.

Gradient boosting machines are a type of machine learning algorithm that uses binary recursive decision trees in sequence to parse data into terminal nodes that minimize within-group variances. Machine learning methods are non-parametric and are adept at incorporating multi-variate interactions among collinear predictors to analyze large or inconsistent datasets. As such, they are effective tools to describe and predict the complexity of ecological systems (Craig and Huettmann 2009; Oppel et al. 2009; Wiersma et al. 2011).

In addition to using environmental predictors to develop models, *gbmidwcv* also incorporates IDW to tune predictions to appropriate numeric ranges. This becomes especially important when correlative patterns between environmental predictors and training points become less informative as the non-zero training sample gets smaller. We varied the number of trees grown (2000–10,000), learning rate (0.0001–0.01), minimum number of observations per node (3–10), and the inverse distance power (1–3) in order to identify the hyper-parameters that produced the most accurate models. To avoid biases associated with high-level categorical predictors (> 20 categories) in decision tree models, and to ensure the most accurate predictions, we treated landcover (29 categories; see Sohl et al. 2019; Fig. 1) and geology (63 categories; see mrdata.usgs.gov/geology/kb.html) as continuous predictors. Slightly penalizing their contribution maximized predictive accuracy and ensured models were not dominated by any single predictor, as often occurs with high-level categorical predictors (Steinberg 2006; Hofner et al. 2011). Default settings were used for all other model parameters.

Prediction scenarios

Models were scored to a set of regularly spaced grids of points (1 km resolution), attributed with the same environmental predictors (Online Material 1), to make current predictions. We also scored models to a set of seven future landcover/climate scenarios consisting of combinations of WorldClim 1.4 climate predictions and FORE-SCE land-use/land-change scenarios for the UMRB (Sohl et al. 2007, 2019). Projections were based on the 5th IPCC (2018; International Panel on Climate Change) report using the BCC-CSM1-1 GCM averaged over 2041–2060. We selected this model for its availability for the time periods and representative concentration pathways (RCP) of interest. Scored models were smoothed using IDW to generate continuous rasters of predicted species abundances, given future landcover and climate conditions.

Scenarios included RCP4.5, 6.0, and 8.5 climate projections (IPCC 2018; Online Resource 2) in conjunction with five FORE-SCE landcover scenarios (Sohl et al. 2019). Of 33 available FORE-SCE land-use/landcover-change scenarios (sciencebase.gov/catalog/item/5c61bf67e4b0fe48cb32fd30), we used five to model 7 future scenarios (model names in parentheses) for each species. Scenarios were selected to represent a range of responses including low, medium, and high carbon emissions, agricultural change, biomass biofuel expansion, and prioritization of environmental conservation. A business-as-usual scenario (bau), based on extrapolation of recent (2001–2014) landcover trends as derived from remote-sensing data, was paired with corresponding RCP8.5 climate predictions (bau_rcp8.5). The gcam4.5 landcover scenario, which is consistent with GCAM 4.5 land-use model runs of natural/non-anthropogenic vegetation, was paired with RCP4.5 climate responses (gcam4.5_rcp4.5). The sresb2 land-use scenario, wherein environmental conservation is highly valued and the agricultural footprint is small, was paired with RCP6.0 (sresb2_rcp6.0). We used Billion Ton Update scenarios (USDOE 2016) with farmgate prices of $40/dry ton of biofuel crop biomass (btu40) and $80/dry ton (btu80) that were each paired with RCP4.5 (btu40_rcp4.5; btu80_rcp4.5) and RCP8.5 climate scenarios (btu40_rcp8.5; btu80_rcp8.5).

Analyses

We calculated means of predicted abundances for each species across the UMRB for each scenario. Current predictions were subtracted from future predictions using the *Diff* tool in ArcGIS to quantify pixel-by-pixel changes in abundance predicted for 2050 under different scenarios. We then reclassified continuous change rasters into binary change rasters to quantify increasing and decreasing trends separately. For each species/scenario combination, we tallied the total areas of both the decreasing and increasing abundance classes and calculated predicted changes in area as of 2050. Spatially summing change rasters across species and scenarios allowed for the identification of regional hotspots, where abundance increases or decreases were predicted for multiple species. We also calculated the mean number of species predicted to increase or decrease across 7 scenarios for the UMRB. To better understanding model responses to individual predictors, we made partial dependence plots for predictors in each model. In order to better visualize class responses, we treated landcover and geology as categorical predictors for this analysis.

Results

Model performance

Models accurately predicted observed mean abundances for most species ($0.2 \leq \text{NRMSE} \leq 39.3$; Table 1). The best models were for grasshopper sparrow (NRMSE = 0.2), western meadowlark (NRMSE = 0.6), and bobolink (NRMSE = 0.8). Models for several species with small training samples, including greater prairie-chicken (NRMSE = 39.3), McCown's longspur (NRMSE = 14.9), and Sprague's pipit (NRMSE = 11.9) were among the least accurate (Table 1). However, spatial predictions were highly accurate ($0.03 \leq \text{MAE} \leq 7.67$) for all species, especially after accounting for the range of variation in observed abundances (Table 1).

Relative predictor importance

The relative importance of predictors varied widely among species, but among the most influential (> 10%) were: forest distance (15 species), winter temperature (10 species), elevation (10 species), and summer temperature (6 species; Online Resource 1). Landcover was generally less influential than climate in most models, influencing 7 models (i.e., dickcissel, savannah sparrow, grasshopper sparrow, mallard, upland sandpiper, vesper sparrow, and Swainson's hawk). For these species, some patterns among landcover classes were consistent. Winter and spring wheat were associated with higher abundances for all of these species, except grasshopper sparrow. Canola (biofuel) was positively correlated with abundance in all but the dickcissel and vesper sparrow models, and open water was directly related to higher predicted abundances in all but the savannah sparrow and Swainson's hawk models. Grassland was positively correlated with grasshopper sparrow, upland sandpiper, and vesper sparrow abundance in the models (Online Resource 3).

Predicted population distribution change

Future abundance projections for 24 species in the UMRB using seven scenarios resulted in a total of 168 future models, for which change statistics were calculated as compared to current models (Figs. 2, 3). Responses were highly variable by species, scenario, and local geography, and mean statistics for the UMRB tended to obscure nuanced local responses (e.g., Fig. 4, Online Resource 4, www.osf.io/8bgvt/files). For seven species (i.e., Baird's sparrow, bobolink, greater sage-grouse, lark sparrow, long-billed curlew, savannah sparrow, and vesper sparrow) models consistently predicted either increases or decreases in mean abundance across the UMRB in 2050, depending on the scenario (Fig. 2). Lark bunting was predicted to decline across all scenarios, whereas abundances of the remaining 16 species were predicted to increase across the UMRB under all scenarios (Fig. 2).

While most scenarios resulted in similar responses by species, the sresb2_rcp6.0 scenario was a notable exception (Fig. 2). For bobolink, chestnut-collared longspur, and gadwall, the sresb2_rcp6.0 scenario resulted in the largest increases in population abundance (versus current predictions) as compared to other scenarios. In contrast, this scenario accounted for the smallest predicted increases for dickcissel, greater prairie-chicken, grasshopper sparrow, marbled godwit, upland sandpiper, and western meadowlark.

The btu40_rcp8.5 scenario produced the largest increases in population abundances for many of these same species (dickcissel, marbled godwit, mallard, Swainson's hawk, upland sandpiper, and western meadowlark). However, this scenario also resulted in the largest predicted declines of blue-winged teal, savannah sparrow, and greater sage-grouse across the UMRB. Errors bars indicated that lark bunting, western meadowlark, and grasshopper sparrow responses were highly variable under all scenarios, exemplified by opposing responses that depended on geography (Figs. 2, 4, Online Resource 4).

Most species models (n = 17) predicted areas of increasing abundance that exceeded areas of decreasing abundance across the UMRB under all scenarios (e.g. dickcissel, sharp-tailed grouse, and upland sandpiper). Seven species showed total areas of decrease that exceeded areas of increase across some or all scenarios (chestnut-collared longspur, greater sage-grouse, long-billed curlew, savannah sparrow, vesper sparrow, lark bunting and McCown's longspur; Fig. 3). Both lark bunting and McCown's longspur (whose mean abundances were not predicted to decrease overall) had a total area of decline that exceeded the area of gain under all scenarios, indicating that abundance increases were concentrated in just a few hotspots while small declines were predicted across the remainder of the UMRB (Fig. 3). Most species predicted to decline in abundance (except Baird's sparrow, bobolink, and lark sparrow) also had areas of decline that exceeded areas of gain for one or more scenarios: greater sage-grouse (6 scenarios), savannah sparrow (4 scenarios), vesper sparrow (4 scenarios), long-billed curlew (2 scenarios), and chestnut-collared longspur (1 scenario; Fig. 3).

Ten species were predicted to decline in either abundance or in occupied area, under at least one scenario, including 8 passerines, 1 upland game bird (greater sage-grouse), and 1 shorebird (long-billed curlew). In contrast, 14 species were exclusively predicted to increase in both abundance and occupied

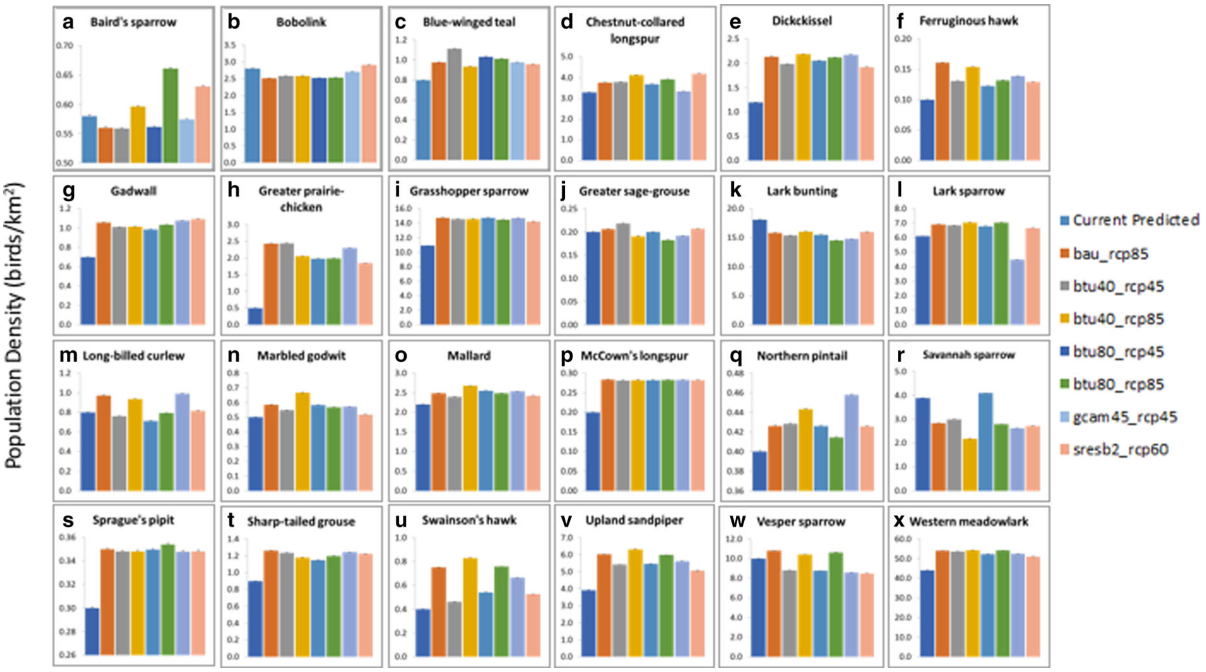


Fig. 2 Predicted abundances and standard errors using current conditions and seven future scenarios for 24 grassland bird species in the Upper Missouri River Basin for 2050

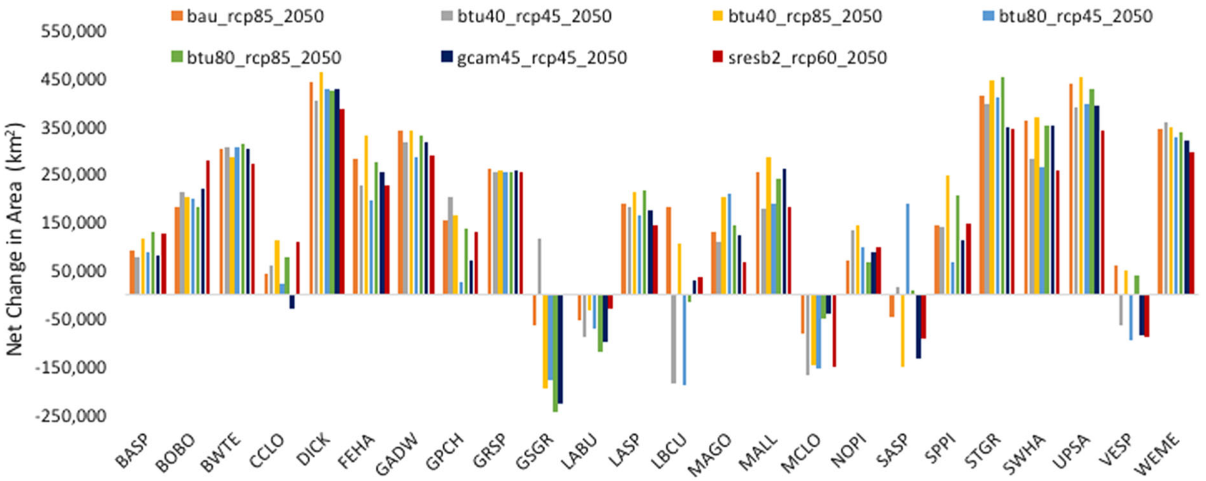


Fig. 3 Predicted net change in area where population density is increasing minus where it is decreasing for each of 24 bird species in the Upper Missouri River Basin given seven future land use change and climate scenarios for 2050

area, including all 4 waterfowl species, both raptors, 2 of 3 upland gamebirds, and 2 of 3 shorebirds. But, just 4 of 12 passerines were predicted to increase across all scenarios using both area and abundance metrics, indicating differential responses to landscape change by taxonomic order (Fig. 4; see Online Resource 4 for detailed descriptions of passerine model predictions).

Predicted areas of cross-species change

Focusing specifically on areas of predicted abundance decline across species, we identified some areas where all species were predicted to decline, primarily in the eastern third of the UMRB (Fig. 5). Locations of multi-species declines were largely consistent across future scenarios, varying only in number of species and relative extent. Models of multi-species abundance increases occurred from the Black Hills through central MT to the northern edge of the UMRB (Fig. 6).

In general, scenarios that included the RCP8.5 climate data tended to have smaller mean total areas of decline per species than the RCP4.5 or 6.0 scenarios (Fig. 5). The btu80_rcp4.5 scenario predicted the most intense areas of decline and the largest mean affected land area (187,209 km^2). The sresb2_rcp6.0 scenario resulted in a smaller mean area of decline (183,056 km^2), and also had smaller numbers of declining species. The scenario with the smallest mean predicted area of decline was btu40_rcp8.5 (162,981 km^2). Other scenarios predicted modest mean areas of decline (gcam4.5_rcp4.5 = 185,167 km^2, btu40_rcp4.5 = 178,362 km^2, btu80_rcp8.5 = 171,208 km^2, bau_rcp8.5 = 165,899 km^2). The overall mean area of predicted abundance declines across all scenarios was 185,490 km^2.

Mirroring predicted abundance declines, models that included the RCP8.5 scenario showed the largest total area of abundance gains (Fig. 6). The btu40_rcp8.5 scenario predicted the largest mean increases in area across species (353,806 km^2), followed by bau_rcp8.5 (329,355 km^2), and btu80_rcp8.5 (324,046 km^2). The smallest predicted areas of total increase were for btu80_rcp4.5 (308,045 km^2), gcam4.5_rcp4.5 (310,087 km^2), sresb2_rcp6.0 (312,199 km^2), and btu40_rcp4.0 (316,892 km^2). The mean predicted area of abundance increases for the ensemble mean across all models was 352,827 km^2.

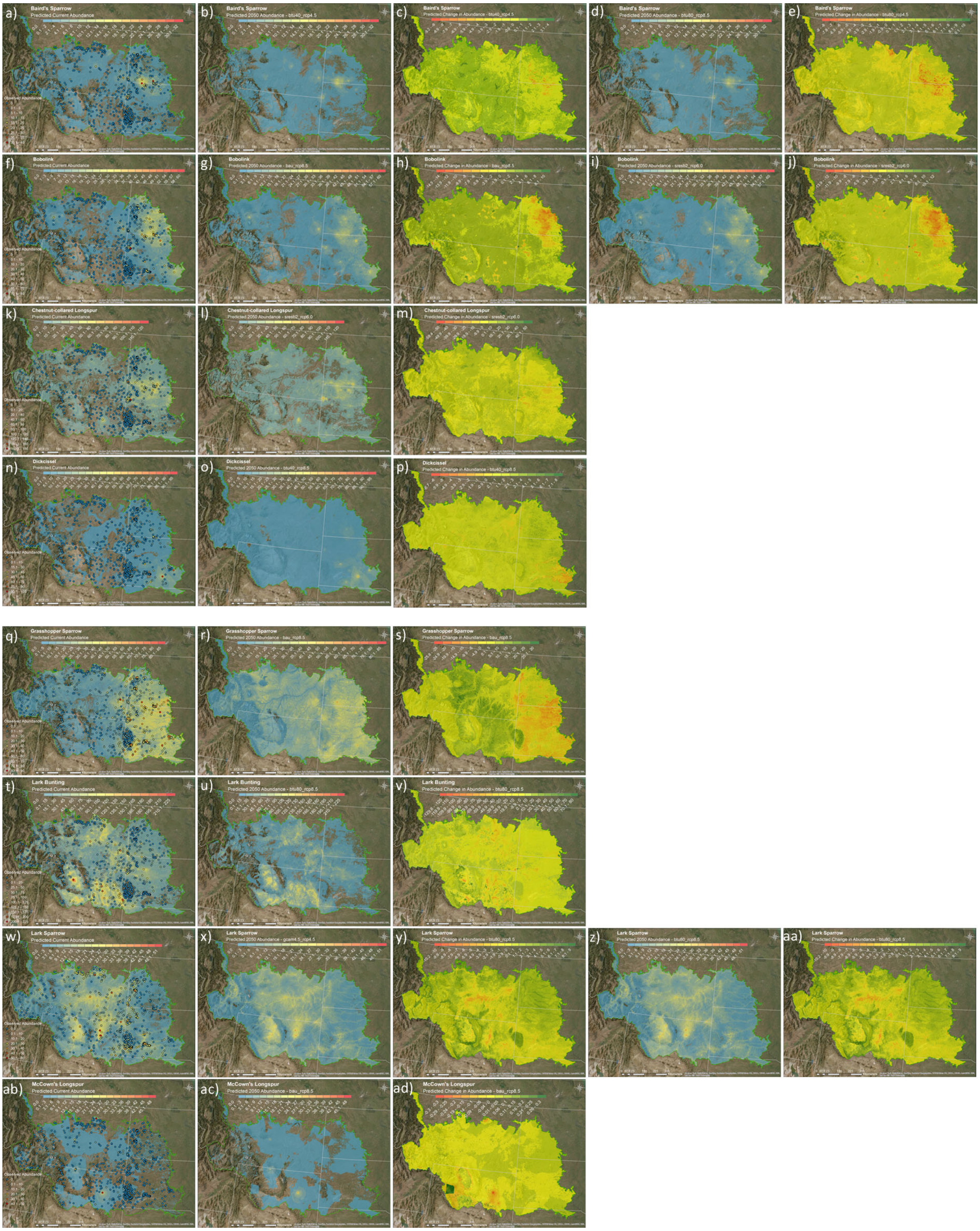
Discussion

We predicted distributions for 24 species of grassland birds across the UMRB, and projected changes in abundance by 2050 for seven climate and landcover-change scenarios (Table 1). Responses were species-specific and varied extensively across the UMRB. Sixteen species were predicted to undergo increases in mean abundance for all future scenarios, whereas eight species were projected to experience abundance declines in at least one scenario (Fig. 2). Models predicted seven species to have total areas of decline that exceeded areas of gain for at least one scenario, whereas the total area of increasing abundance was greater than areas of decreasing abundance for the remaining 17 species across all scenarios (Fig. 3). Results were geographically variable and all species were predicted to experience both increases and declines in abundance in different portions of the study area (Fig. 4). Across the majority of species, spatial analyses highlighted three main areas predicted to experience abundance declines: western Dakotas, lower Yellowstone River Valley, MT, and along the eastern front of the Rocky Mountains in the northwestern UMRB (Fig. 5). The main area of increasing abundances common to many species extended from the Black Hills to central MT (Fig. 6).

Variability in results within and across species was consistent with findings from other similar analyses, but our predictions are somewhat more optimistic than recent, continental declines in grassland bird abundance might indicate (Peterjohn and Sauer 1999; Sohl 2014; Rosenberg et al. 2019). Maps of species richness and population change developed from Breeding Bird Survey (BBS; 1966–1996) data indicated that the highest avian species richness occurred across the non-mountainous portions of the UMRB (Peterjohn and Sauer 1999). Our models predicted this same region to undergo the largest abundance declines, whereas patches of increasing populations were most common to the Rocky Mountains and central MT and WY. Cumulative population trends and projections using BBS data also showed temporally and geographically heterogeneous, species-specific responses (Peterjohn and Sauer 1999; Sohl 2014; Sauer et al. 2017a).

Avian population changes

Our population change predictions for 2014–2050 indicated more positive trends than those reported by Peterjohn and Sauer (1999), who found just 6 of 25 grassland bird species had increased from 1966 to 1996 across the continental U.S. Increases in abundance during this time were most significant for wetland birds, woodland birds, raptors, and permanent residents, which may be related to increased wetland protections (Peterjohn and Sauer 1999; Sohl 2014; Sauer et al. 2017a, b). Between 1993 and 2015, grassland bird populations had more positive trajectories than during preceding decades, with 10 species showing increasing trends (Sauer et al. 2017a, b). Our results, which projected 35 years into the future, predicted 16 species to experience increasing abundances across the UMRB through 2050.


a)
Baird's Sparrow
Predicted Current Abundance
Observed Abundance
b)
Baird's Sparrow
Predicted 2050 Abundance - btu40_rcp4.5
c)
Baird's Sparrow
Predicted Change in Abundance - btu40_rcp4.5
d)
Baird's Sparrow
Predicted 2050 Abundance - btu80_rcp8.5
e)
Baird's Sparrow
Predicted Change in Abundance - btu80_rcp4.5
f)
Bobolink
Predicted Current Abundance
Observed Abundance
g)
Bobolink
Predicted 2050 Abundance - bau_rcp8.5
h)
Bobolink
Predicted Change in Abundance - bau_rcp8.5
i)
Bobolink
Predicted 2050 Abundance - sresb2_rcp6.0
j)
Bobolink
Predicted Change in Abundance - sresb2_rcp6.0
k)
Chestnut-collared Longspur
Predicted Current Abundance
Observed Abundance
l)
Chestnut-collared Longspur
Predicted 2050 Abundance - sresb2_rcp6.0
m)
Chestnut-collared Longspur
Predicted Change in Abundance - sresb2_rcp6.0
n)
Dickcissel
Predicted Current Abundance
Observed Abundance
o)
Dickcissel
Predicted 2050 Abundance - btu40_rcp8.5
p)
Dickcissel
Predicted Change in Abundance - btu40_rcp8.5
q)
Grasshopper Sparrow
Predicted Current Abundance
Observed Abundance
r)
Grasshopper Sparrow
Predicted 2050 Abundance - bau_rcp8.5
s)
Grasshopper Sparrow
Predicted Change in Abundance - bau_rcp8.5
t)
Lark Bunting
Predicted Current Abundance
Observed Abundance
u)
Lark Bunting
Predicted 2050 Abundance - btu80_rcp8.5
v)
Lark Bunting
Predicted Change in Abundance - btu80_rcp8.5
w)
Lark Sparrow
Predicted Current Abundance
Observed Abundance
x)
Lark Sparrow
Predicted 2050 Abundance - gcam4.5_rcp4.5
y)
Lark Sparrow
Predicted Change in Abundance - btu80_rcp8.5
z)
Lark Sparrow
Predicted 2050 Abundance - btu80_rcp8.5
aa)
Lark Sparrow
Predicted Change in Abundance - btu80_rcp8.5
ab)
McCown's Longspur
Predicted Current Abundance
Observed Abundance
ac)
McCown's Longspur
Predicted 2050 Abundance - bau_rcp8.5
ad)
McCown's Longspur
Predicted Change in Abundance - bau_rcp8.5

◀**Fig. 4** Predicted current population distribution (Column 1), predicted 2050 population distribution under scenario exhibiting the largest change in mean population (Column 2), and the predicted change in per-pixel population abundance under that scenario (Column 3). For Baird's sparrow, bobolink, lark sparrow, Savannah sparrow and vesper sparrow, future population distribution (Column 4) and change maps (Column 5) are included for scenarios which resulted in mean population trends that contrasted with those of the other 6 scenarios

Based on the high relative importance of climatic predictors and low importance of landcover in most models, and the scale at which changes were predicted to occur, we ascribe predicted changes primarily to orographic climate effects (i.e., warmer climates at higher elevations in the future). Landcover was less influential than climatic predictors in our study in part because it was penalized for having a high number of classes, so further investigation may be necessary. Our results are, however, consistent with findings that indicate more influence by climate than landcover at broad scales (Pearson et al. 2004; Barbet-Massin et al. 2012; Sohl 2014). Species distribution models typically perform best when both climate and land-use/landcover-change are included (Sohl 2014), although this is likely scale dependent (Pearson et al. 2004; Arenas-Castro et al. 2018). Effects of landcover and forest distance in models were more evident locally, especially in the agriculturally dominated, eastern third of the UMRB. Our methods focused primarily on making accurate predictions, which were subsequently used to explore correlative patterns of predictor contribution to models. We hope our results may inspire further research to determine the effects of scale, different GCMs, and to quantify effect sizes of system drivers.

Patterns of predicted increasing abundance across much of the central UMRB may have two explanations. First, large-scale losses to native grassland habitats have largely already occurred, so additional landcover changes predicted for 2050 may have only limited effects on populations. Second, broad, geographic shifts in climate envelopes likely outweigh the effects of small-scale landcover changes on bird abundances (Barbet-Massin et al. 2012; Sohl et al. 2014). The warmer/wetter conditions expected by

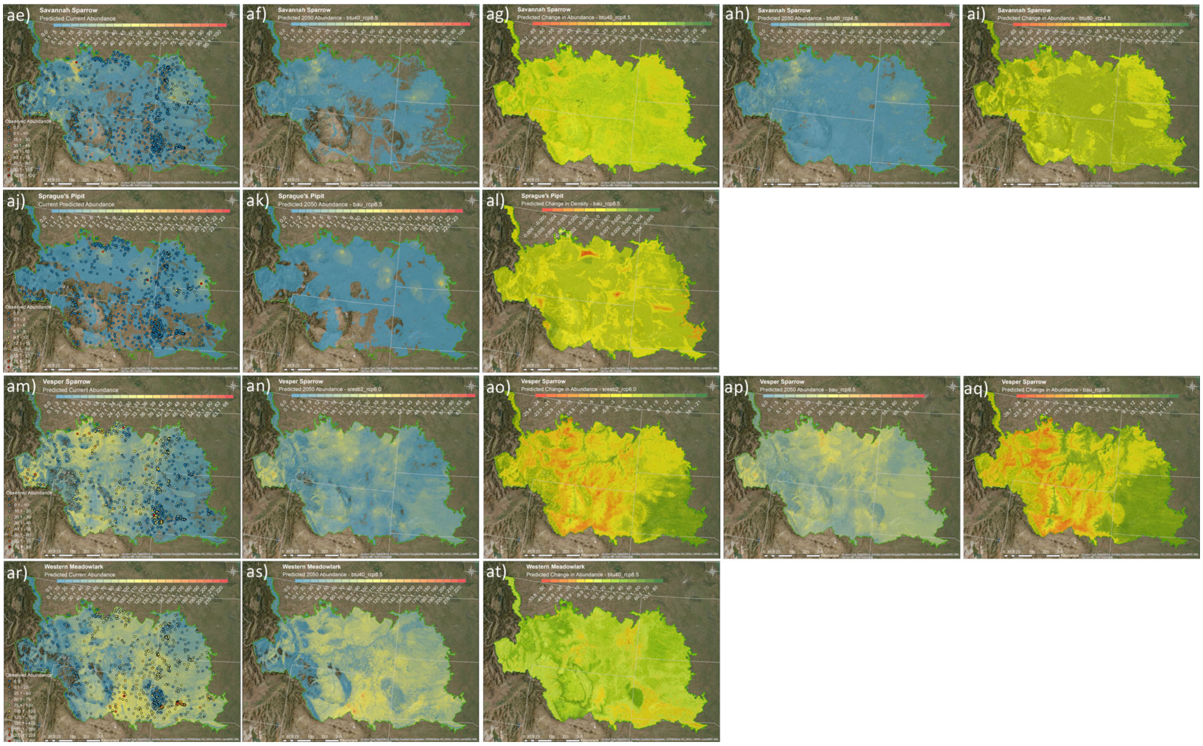


Fig. 4 continued

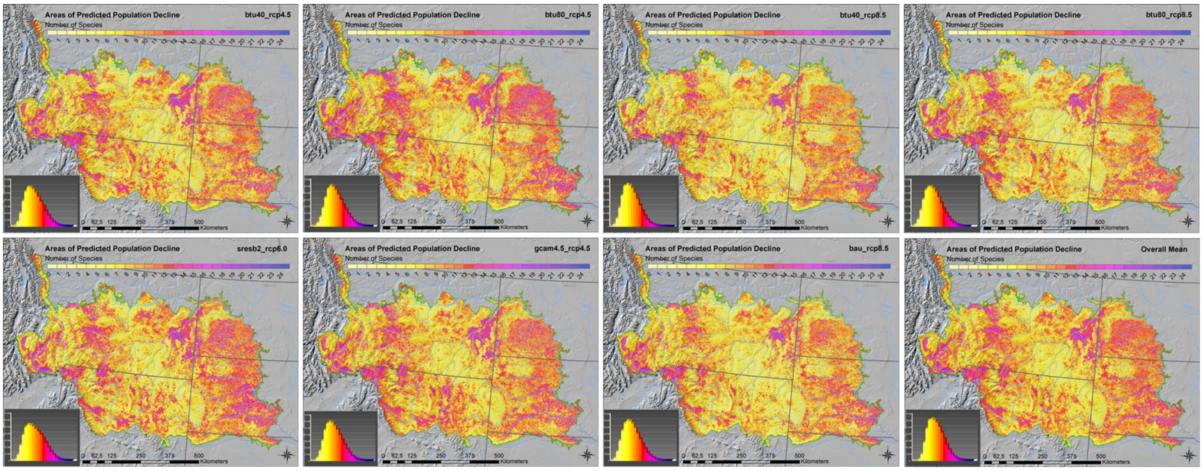


Fig. 5 Species richness maps depicting the number of species predicted to decline in population for each pixel in the Upper Missouri River Basin between 2014 and 2050 under each of seven scenarios **a** btu40_rcp4.5, **b** btu40_rcp8.5, **c** btu80_rcp4.5, **d** btu80_rcp8.5, **e** sresb2_rcp6.0, **f** gcam4.5_rcp4.5, **g** bau_rcp8.5, and **h** grand mean of all scenarios. Insets show the frequency distribution of predicted species declines depicted in the maps

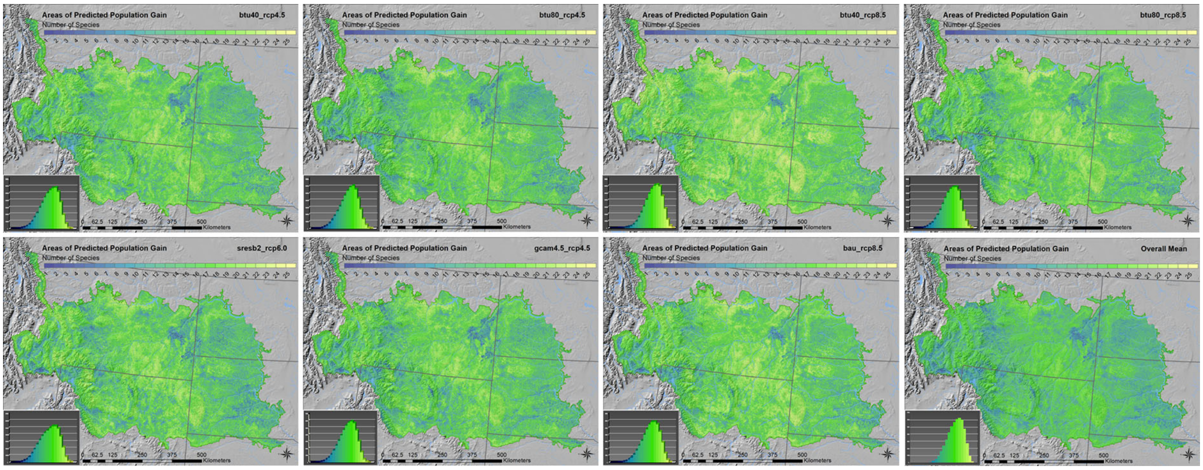


Fig. 6 Species richness maps depicting the number of species predicted to increase in population for each pixel in the Upper Missouri River Basin between 2014 and 2050 under each of seven scenarios **a** btu40_rcp4.5, **b** btu40_rcp8.5, **c** btu80_rcp4.5, **d** btu80_rcp8.5, **e** sresb2_rcp6.0, **f** gcam4.5_rcp4.5, **g** bau_rcp8.5, and **h** grand mean of all scenarios. Insets show the frequency distribution of predicted species declines depicted in the maps

2050 may actually assist over-winter survival and fecundity of resident species, while exacerbating cumulative stress for winter migrants.

Areas of declining abundance common across many species were especially pronounced in areas of western SD, where a warming, arid climate resulted in predicted declines from areas documented as avian biodiversity hotspots by Sauer and Peterjohn (1999). Increased aridity in this region is already causing reduced clutch sizes and fecundity in some species, which have led to observed population declines (Kunkel et al. 2013; Wilson et al. 2018). In contrast, the northern Great Plains is projected to experience increased mean annual precipitation resulting in wetter, more productive environments, likely benefiting waterfowl and raptors in the future (Jonas et al. 2018; Sauer et al. 2017). Multi-species abundance increases predicted from the Black Hills through central MT are likely due to elevational differences. Because this region is $\sim$ 900 to 2100 m higher than the Missouri River Valley and includes several large protected grassland areas, it may provide thermal refuge for species as the broader region warms.

Among land-use scenarios, high-intensity ($80/ton) conversion of agricultural lands to support bioenergy crops (excluding corn ethanol) combined with modest climate change (RCP4.5) resulted in moderate species losses across both grass- and croplands (van Vuuren et al. 2011). Large increases in temperatures under RCP8.5 may benefit many species by releasing them from cold-weather constraints. But combined with intense biomass biofuel cultivation, (e.g., btu80_rcp8.5), declines in grassland birds were larger. At $40/ton, predicted population declines were smaller than without the incentive, so low levels of biomass biofuel cultivation may be compatible with population stability. The effects of biofuel cultivation may be either tempered or exacerbated by climate change depending on local geography, species biology, and other environmental conditions, but the effects of high prices and demand for biomass biofuels could come at larger costs to grassland birds than under land-change scenarios without a biofuel component (Hof et al. 2018).

Implications of climate change on grassland birds

Climatic predictors were among the most important in our models, and even small changes in magnitude resulted in broad, landscape-level effects across the region. But climate effects vary both geographically and locally, and trends in temperature, precipitation, elevation, and land-use interact in complex ways that may counteract one another and lead to unexpected patterns in local bird abundance. Climate projections for the region indicate that temperatures in the southern UMRB are predicted to warm by as much 2–4 °C by 2050, especially in winter, and precipitation is predicted to decrease, resulting in a more arid climate in this largely agricultural region (worldclim.org). Our models indicate that larger climatic changes could avail new habitat at higher elevations, allowing birds to increase more under RCP8.5 by expanding into new areas than under milder scenarios.

Warmer temperatures are already causing northward and upward elevational shifts in observed distributions of numerous species worldwide (Parmesan and Yohe et al. 2003; Baltensperger and Huettmann 2015b). For most birds, winter temperatures and capacity to maintain internal body temperatures influence species distributions and cold-range limits (Swanson and Garland 2009; Stager et al. 2016; Buckley et al. 2018). Because of the large elevational gradient in the UMRB, mountainous areas in the west are projected to provide climatic niche conditions analogous to those currently at lower elevations in the east (Williams and Jackson 2007). As species follow suitable climatic niche space, a longitudinal, elevational gradient may account for predicted increases in mean population abundance and mean occupied area observed for many species across the UMRB.

Warmer winter temperatures may relieve some thermal stress for non-migratory species near their northern or elevational limits, leading to increased abundance. Because increasing winter temperatures impacted projected abundances for many species, this may allow some residents, constrained by cold temperatures near their northern limits, to expand. Other species, already at their southern limits, may be forced to move northward, westward, or upward to track geographic shifts in cooler ecological niche space. Migratory species should be less sensitive to changes in winter temperatures, but resultant phenological shifts in limiting resources may indirectly affect these populations as well (Travers et al. 2015; Boelman et al. 2017).

Implications of landcover change on grassland birds

Future land-use/landcover-change scenarios (FORE-SCE; Sohl et al. 2019) predicted total grassland area to decline under all scenarios except for sresb2_rcp6.0. If landcover contributed more to our models, one would expect this scenario to show the largest abundance increases, yet we predicted the opposite. Any benefits from increased grassland area were outweighed in the models by more powerful, large-scale effects of climate, so further investigation into the scale-dependent influence of landcover in spatial abundance models is warranted (Pearson et al. 2004). Because the sresb2_rcp6.0 scenario also included the smallest 2050 temperature increases, this scenario provided the smallest broad-scale, climatic benefits to bird populations. FORE-SCE scenarios also indicated that winter wheat may become increasingly common, especially in the more arid southern regions (Sohl et al. 2019).

Such land-use changes could be detrimental to grassland bird populations if productive habitats (e.g., native grasslands and hay fields) are converted into less-hospitable types (e.g., wheat). Furthermore, a recent trend towards harvesting hayfields in June, instead of August, is converting relatively productive agricultural habitats into population sinks and resulting in higher brood losses (Bollinger et al. 1990; Rodenhouse et al. 1993). Some species are resilient in the face of agricultural changes, but resilience may only occur within the constraints of new, often inescapable, climatic regimes in the region.

Constraints on realized population growth

These models predict increases in abundance across the UMRB for many grassland bird populations as they follow the expansion of suitable climatic zones into new areas. However, the existence of analogous climatic niche space within the UMRB does not necessarily mean that birds will be able to disperse to or thrive in these new areas (Nixon et al. 2016). While much of the UMRB predicted to undergo abundance increases is already dominated by grasslands, other areas are currently, and may remain, forested by 2050. Warmer, wetter conditions would be unlikely to result in the expansion of grassland areas, whereas a warmer, drier climate could result in such a transition, but would require disturbance to allow such a state change to occur. High-intensity fires capable of burning to mineral soil are capable of producing grassland patches in forests (Baker 2015). While fire is not currently a major force in the UMRB, it could become more important for opening new grassland habitat at higher elevations as climate change increases the likelihood and intensity of fires in existing forests (Baker 2015). Major pest outbreaks capable of decimating mature, cone-bearing stands may also contribute to forest-to-grassland transitions (McFarlane et al. 2012; Mullen et al. 2018). Additional research is necessary to determine whether landcover changes will keep pace with climate changes that are directing species distributions and abundances.

Conclusion

Projected changes in grassland bird abundances were highly variable across species and local geographies. While all species were projected to experience both increased and decreased abundances in different areas of the UMRB, waterfowl, shorebirds, upland gamebirds, and raptors were generally predicted to increase over the coming decades. These species appear poised to benefit from increasing temperature and precipitation that may reduce cold stress and avail new habitats at higher elevations, especially under RCP8.5 scenarios. Scenarios that included high-intensity bioenergy cultivation were more likely to result in smaller population gains, but low-levels of biofuel cultivation may be sustainable for some species. In contrast, abundances for several passerines and greater sage-grouse were predicted to decrease because of warming climatic conditions, possibly due to increased thermal stress in summer. Projected decreases were especially pronounced in agricultural areas of ND, SD and MT, where changing crop composition under biofuel scenarios may exacerbate climate stress. Abundance increases were predicted in WY and MT where natural grassland habitats are more likely to persist, and conservation of existing grasslands is paramount. Land managers and avian conservationists should carefully monitor grassland bird populations in areas of projected decline, while also planning dispersal corridors that link existing and emerging grassland habitats under a warmer, drier future. Successful species persistence will ultimately depend on the extent of climate change, the connectivity of suitable dispersal habitat, and the adaptive capacity of individual species.

Acknowledgements We thank T. Sohl for providing the FORE-SCE landcover scenarios and for providing feedback regarding model construction and analysis. J. Timmer supplied the BCR data that served to train avian abundance models. K. Bakker provided background and species context based on prior experience sampling grassland birds in SD. This work was funded by NSF OIA-1632810.

References

Arenas-Castro S, Gonçalves J, Alves P, Alcaraz-Segura D, Honrado JP (2018) Assessing the multi-scale predictive ability of ecosystem functional attributes for species distribution modelling. PLoS ONE 13(6):e0199292

Baker WL (2015) Are high-severity fires burning at much higher rates recently than historically in dry-forest landscapes of the Western USA? PLoS ONE 10(9):e0136147

Bakker KK, Higgins KF (2009) Planted grasslands and native sod prairie: equivalent habitat for grassland birds? West N Am Nat 69:235–242

Baltensperger AP, Huettmann F (2015a) Predictive spatial niche and biodiversity hotspot models for small mammal communities in Alaska: applying machine-learning to conservation planning. Landsc Ecol 30:681–697

Baltensperger AP, Huettmann F (2015b) Predicted shifts in small mammal distributions and biodiversity in the altered future environment of Alaska: an open access data and machine learning perspective. PLoS ONE 10(7):1–21

Barbet-Massin M, Thuiller W, Jiguet F (2012) The fate of European breeding birds under climate, land-use and dispersal scenarios. Glob Change Biol 18(3):881–890

Beringer T, Lucht W, Schaphoff S (2011) Energy production potential of global biomass plantations under environmental and agricultural constraints. Bioenergy 3:299–312

Bernath-Plaisted J, Koper N (2016) Physical footprint of oil and gas infrastructure, not anthropogenic noise, reduces nesting success of some grassland songbirds. Biol Conserv 204:434–441

Blank PJ, Sample DW, Williams CL, Turner MG (2014) Bird communities and biomass yields in potential bioenergy grasslands. PloS One 9(10):e109989. https://doi.org/10.1371/journal.pone.0109989

Boelman NT, Krause JS, Sweet SK, Chmura H, Perez JH, Gough L, Wingfield JC (2017) Extreme spring conditions in the Arctic delay spring phenology of long-distance migratory songbirds. Behav Ecol 185:69–80

Bollinger EK, Bollinger PB, Gavin TA (1990) Effects of hay-cropping on eastern populations of bobolink. Wildl Soc Bull 18:142–150

Brookshire ENJ, Weaver T (2015) Long-term decline in grassland productivity driven by increasing dryness. Nat Commun 6:1–7

Buckley LB, Khaliq I, Swanson DL, Hof C (2018) Does metabolism constrain bird and mammal ranges and predict shifts in response to climate change? Ecol Evol. https://doi.org/10.1002/ece3.4537

Copeland HE, Pocewicz A, Kiesecker JM (2011) Geography of energy development in Western North America: potential impacts on terrestrial ecosystems. In: Naugle DE (ed) Energy development and wildlife conservation in Western North America. Island Press, Washington, pp 7–22

Correll MD, Strasser EH, Green AW, Panjabi AO (2019) Quantifying specialist avifaunal decline in grassland birds of the Northern Great Plains. Ecosphere 10(1):e02523

Craig E, Huettmann F (2009) Using “blackbox” algorithms such as TreeNet and Random Forests for data-mining and for finding meaningful patterns, relationships, and outliers in complex ecological data: an overview, example using golden eagle satellite data and an outlook for a promising future. In: Wang HF (ed) Intelligent data analysis: developing new methodologies through pattern discovery and recovery. Idea Group Inc., Hershey, pp 65–84

Dolan KA, Stoy PC, Poulter B (2019) Land management and climate change determine second-generation bioenergy potential of the U.S. Northern Great Plains. GCB Bioenergy. https://doi.org/10.1111/gcbb.12686

Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberon J, Williams S, Wisz MS, Zimmermann NE (2006) Novel methods improve prediction of species’ distributions from occurrence data. Ecography 29(2):129–151

Evans JS, Murphy MA, Holden ZA, Cushman SA (2011) Modeling species distribution and change using Random Forest. In: Drew CA, Wiersma YF, Huettmann F (eds) Predictive species and habitat modeling in Landscape Ecology. Springer, Berlin, pp 139–160

Fox CH, Huettmann F, Harvey GKA et al (2017) Predictions from machine learning ensembles: marine bird distribution and abundance on Canada’s Pacific coast. Mar Ecol Prog Ser 566:199–216

Gage AM, Olimb SK, Nelson J (2016) Plowprint: tracking cumulative cropland expansion to target grassland conservation. Great Plains Res 26:107–116

Greer MJ, Bakker KK, Dieter CD (2016) Grassland bird response to recent loss and degradation of native prairie in Central and Western South Dakota. Wilson J Ornithol 128(2):278–289

Hamer TL, Flather CH, Noon BR (2006) Factors associated with grassland bird species richness: the relative roles of grassland area, landscape structure, and prey. Landsc Ecol 21:569–583

Hanni DJ, White CM, Van Lanen NJ, Birek JJ, Berven JM, McLaren MF (2018) Integrated monitoring in bird conservation regions (IMBCR): field protocol for spatially-balanced sampling of land bird populations. Bird Conservancy of the Rockies, Brighton

Havstad KM, Peters DPC, Skaggs R, Brown J, Bestelmeyer B, Fredrickson E, Herrick J, Wright J (2007) Ecological services to and from rangelands of the United States. Ecol Econ 64(2):261–268

Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2004) Confronting a biome crisis: global disparities of habitat loss and protection. Ecol Lett 8:23–29

Hof C, Voskamp A, Biber MF, Böhning-Gaese K, Engelhardt EK (2018) Bioenergy cropland expansion may offset positive effects of climate change mitigation for global vertebrate diversity. Proc Natl Acad Sci USA 115(52):13294–13299

Hofner B, Hothorn T, Kneib T, Schmid M (2011) A framework for unbiased model selection based on boosting. J Comput Graph Stat 20(4):956–971

Howard C, Stephens PA, Pearce-Higgins JW, Gregory RD, Willis SG (2015) The drivers of avian abundance: patterns in the relative importance of climate and land use. Glob Ecol Biogeogr 24(11):1249–1260

IPCC (2018) Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty In: Masson-Delmotte V, Zhai P, Pörtner H-O, Roberts D, Skea J, Shukla PR, Pirani A, Moufouma-Okia W, Péan C, Pidcock R, Connors S, Matthews JBR, Chen Y, Zhou X, Gomis MI, Lonnoy E, Maycock T, Tignor M, Waterfield T (eds) In Press.

Jonas JL, Buhl DA, Symstad AJ (2015) Impacts of weather on long-term patterns of plant richness and diversity vary with location and management. Ecology 96(9):2417–2432

Kunkel KE, Karl TR, Easterling DR et al (2013) Probable maximum precipitation and climate change. Geophys Res Lett 40(7):1402–1408

Lipsey MK, Doherty KE, Naugle DE, Fields S, Evans JS, Davis SK, Koper N (2015) One step ahead of the plow: using cropland conversion risk to guide Sprague′s Pipit conservation in the northern Great Plains. Biol Conserv 191:739–749

Maestre FT, Eldridge DJ, Soliveres S (2016) A multifaceted view on the impacts of shrub encroachment. Appl Veg Sci 19:369–370

McFarlane BL, Parkins JR, Watson DOT (2012) Risk, knowledge, and trust in managing forest insect disturbance. Can J For Res 42(4):710–719

Mullen K, Yuan F, Mitchell M (2018) The mountain pine beetle epidemic in the Black Hills, South Dakota: the consequences of long term fire policy, climate change. J Geogr Geol 10:69–82

Murray L, Best L (2003) Short-term bird response to harvesting switchgrass for biomass in Iowa. J Wildl Manage 67:611

Nixon AE, Fisher RJ, Stralberg D, Bayne EM, Farr DR (2016) Projected responses of North American grassland songbirds to climate change and habitat availability at their northern range limits in Alberta, Canada. Avian Conserv Ecol. https://doi.org/10.1111/ddi.13057

Oppel S, Strobl C, Huettmann F (2009) Alternative methods to quantify variable importance in ecology. University of Munich, Munich, pp 1–6

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 42(2):37–42

Pearson RG, Dawson TP, Liu C (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. Ecography 27(3):285–298

Peterjohn BG, Sauer JR (1999) Population status of North American grassland birds from the North American breeding bird survey 1966–1996. Stud Avian Biol 19:27–44

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing,Vienna, Austria. https://www.R-project.org/

Robertson BA, Rice RA, Sillett TS, Ribic CA, Babcock BA, Landis DA, Herkert JR, Fletcher RJ, Fontaine JJ, Doran PJ, Schemske DW (2012) Are agrofuels a conservation threat or opportunity for grassland birds in the United States? Condor 114(4):679–688

Rodenhouse NL, Best LB, Oconnor RJ, Bollinger EK (1993) Effects of temperate agriculture on neotropric migrant landbirds. In: Finch DM, Stangel PW (eds) Status and management of neotropical migratory birds. USDA Forest Service, Fort Collins, pp 280–295

Rosenberg KV, Dokter AM, Blancher PJ, Sauer JR, Smith AC, Smith PA, Stanton JC, Panjabi A, Helft L, Parr M, Marra PP (2019) Decline of the North American avifauna. Science 366:120–124

Rosenberg KV, Kennedy JA, Dettmers R, Ford R, Reynolds D, Alexander J, Beardmore C, Blancher PJ, Bogart R, Butcher G, Camfield A, Couturier A, Demarest DW, Easton WE, Giocomoco JJ, Keller RH, Mini AE, Panjabi AO, Pashley DN, Rich TD, Ruth JM, Stabins H, Stanton J, Will T (2016) Partners in flight landbird conservation plan: 2016 revision for Canada and Continental United States. Partners in Flight Science Committee, pp. 119

Saalfeld DT, Saalfeld ST, Conway WC, Hartke KM (2016) Wintering grassland bird responses to vegetation structure, exotic invasive plant composition, and disturbance regime in coastal prairies of Texas. Wilson J Ornithol 128(2):290–305

Samson F, Knopf F (1994) Prairie conservation in North America. Other Publ Wildl Manag 41:418–421

Sauer JR, Niven D, Hines JE, Ziolkowski DJ Jr, Pardieck K, Link W (2017a) The North American Breeding Bird Survey, results and analysis. Version 2.07.2017. USGS Patuxent Wildlife Research Center, Laurel, MD

Sauer JR, Pardieck KL, Ziolkowski DJ Jr, Smith AC, Hudson M, Rodriguez V, Berlanga H, Niven D, Link W (2017b) The first 50 years of the North American Breeding Bird Survey. Condor 119(3):576–593

Schipper AM, Belmaker J, de Miranda MD, Navarro LM, Bohning-Gaese K, Costello MJ, Dornelas M, Foppen R, Hortal J, Huijbregts MAJ, Martin-Lopez B, Pettorelli N, Queiroz C, Rossberg AG, Santini L, Schiffers K, Steinmann ZJN, Visconti P, Rondinini C, Pereira HM (2016) Contrasting changes in the abundance and diversity of North American bird assemblages from 1971 to 2010. Glob Change Biol 22(12):3948–3959

Silver WL, Ryals R, Eviner V (2010) Soil carbon pools in California's annual grassland ecosystems. Rangeland Ecol Manage 63(1):128–136

Sohl TL (2014) The relative impacts of climate and land-use change on conterminous Unites States bird species from 2001 to 2075. PLoS ONE 9:1–18

Sohl TL, Dornbierer J, Wika S (2019) 33 high-resolution scenarios of land use and vegetation change in the Prairie Potholes. In: Survey USG. (ed). Sioux Falls, SD

Sohl TL, Sayler KL, Drummond MA, Loveland TR (2007) The FORE-SCE model: a practical approach for projecting land cover change using scenario-based modeling. J Land Use Sci 2(2):103–126

Stager M, Pollock HS, Benham PM, Sly ND, Brawn JD, Cheviron ZA (2016) Disentangling environmental drivers of metabolic flexibility in birds: the importance of temperature extremes versus temperature variability. Ecography 39(8):787–795

Stanton RL, Morrissey CA, Clark RG (2018) Analysis of trends and agricultural drivers of farmland bird declines in North America: a review. Agr Ecosyst Environ 254:244–254

Staudt A, Leidner AK, Howard J, Brauman KA, Dukes JS, Hansen LJ, Paukert C, Sabo J, Solórzano LA (2013) The added complications of climatechange: understanding and managing biodiversity and ecosystems. Front Ecol Environ 11:494–501

Steinberg D (2006) Modeling tricks with TreeNet: Treating Categorical Variables as Continuous. Dan Steinberg's Blog, Accessed 2016, 17 edn. Salford Systems, Inc., San Diego, CA; https://www.salford-systems.com/blog/dan-steinberg/modeling-tricks-with-treenet-treating-categorical-variables-as-continuous

Stoy PC, Ahmed S, Jarchow M, Rashford B, Swanson D, Albeke S, Bromley G, Brookshire E, Dixon MD, Haggerty J, Miller P, Peyton B, Royem A, Spangler L, Straub C, Poulter B (2018) Opportunities and trade-offs among BECCS and the food, water, energy, biodiversity, and social systems nexus at regional scales. Bioscience 68:100–111

Swanson DL, Garland T (2009) The evolution of high summit metabolism and cold tolerance in birds and its impacts on preset-day distributions. Evolution 63(1):184–194

Travers SE, Marquardt B, Zerr NJ, Finch JB, Boche MJ, Wilk R, Burdick SC (2015) Climate change and shifting arrival date of migratory birds over a century in the Northern Great Plains. Wilson J Ornithol 127(1):43–51

U.S. Department of Energy (2016) 2016 Billion-Ton Report: advancing domestic resources for a thriving bioeconomy. In: Langholtz MH, Stokes BJ, Eaton LM (eds) ORNL/TM-2016/160. Oak Ridge National Laboratory, Oak Ridge, TN, p 448

van Vuuren DP, Edmonds J, Kainuma M, Riahi K, Thomson A, Hibbard K, Hurtt GC, Kram T, Krey V, Lamarque J-F, Masui T, Meinshausen M, Nakicenovic N, Smith SJ, Rose SK (2011) The representative concentration pathways: an overview. Clim Change 109(1):5

van Vuuren DP, Deetman S, van Vliet J, van den Berg M, van Ruijven BJ, Koelbl B (2013) The role of negative CO2 emissions for reaching 2°C—insightsfrom integrated assessment modelling. Clim Change 118(1):15–27

White RP, Murray S, Rohweder M (2000) Pilot analysis of global ecosystems: grassland ecosystems. World Resources Institute, Washington, DC

Wiersma YF, Huettmann F, Drew CA (2011) Landscape modeling of species and their habitats: history, uncertainty, and complexity. In: Drew CA, Wiersma YF, Huettmann F (eds) Predictive species and habitat modeling in landscape ecology. Springer, New York, pp 1–8

Williams JW, Jackson ST (2007) Novel climates, no-analog communities, and ecological surprises. Front Ecol Environ 5(9):475–482

Willmott CJ, Ackleson SG, Davis RE, Feddema JJ, Klink KM, Legates DR, O'Donnell J, Rowe CM (1985) Statistics for the evaluation and comparisonof models. J Geophys Res 90:8995–9005

Wilson S, Smith AC, Naujokaitis-Lewis I (2018) Opposing responses to drought shape spatial population dynamics of declining grassland birds. Divers Distrib 24:1687–1698

Wright CK, Wimberly MC (2013) Recent land use change in the Western Corn Belt threatens grasslands and wetlands. Proc Natl Acad Sci 110:4134–4139

WWF (2018) The plowprint report. World Wide Fund for Nature, Bozeman, pp 1–7