

DISSERTATION

IMPACTS OF CLIMATE CHANGE TO BREEDING AND MIGRATING WATERBIRDS IN THE PRAIRIE POTHOLE
REGION

Submitted by

Valerie Steen

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Fall 2016

Doctoral Committee:

Advisor: Barry Noon

Co-Advisor: Susan Skagen

Curt Flather

Jorge Ramirez

Copyright by Valerie Anna Steen 2016

All Rights Reserved

ABSTRACT

IMPACTS OF CLIMATE CHANGE TO BREEDING AND MIGRATING WATERBIRDS IN THE PRAIRIE POTHOLE REGION

The Prairie Pothole Region (PPR) of the north-central U.S. and south-central Canada contains millions of small prairie wetlands that provide critical habitat to many migrating and breeding waterbirds. Due to their small size and the relatively dry climate of the region, these wetlands are considered at high risk for negative climate change effects as temperatures increase. Using a bioclimatic species distribution modeling (SDM) approach, I explored the potential effects of climate change on 31 breeding waterbird species. The approach involved using a random forest modeling algorithm and downscaled climate data from outputs of two future General Circulation Models (GCMs). By the 2040's, species were projected, on average, to lose 46% of their current habitat in the U.S. portion of the PPR. Species specific projected impacts ranged widely, with three species (Wilson's Snipe, Sora, and Franklin's Gull) projected to lose close to 100% of their U.S. Prairie Pothole habitats and two species (Killdeer and Upland Sandpiper) projected to gain habitat. Bioclimatic SDM approaches, however, have been shown to produce varying projections of species climate change impacts depending on methodological decisions including: choice of GCM, choice of climate covariates, level of collinearity among climate variables, and thresholding procedure used to convert probability values to binary occurrence values. I explored these and found that median projected range loss, across species, was 35%. However, projections for individual species varied widely, typically spanning from 100% range loss to range increases. The largest source of uncertainty was choice of GCM, followed by choice of climate covariate, then thresholding procedure. Level of collinearity contributed relatively little uncertainty. To understand potential impacts of climate change to migrating shorebirds, I explored climate change sensitivity using

historic records from a dry year and a wet year. Using historic data to explore climate sensitivity of migrating shorebirds in the PPR avoids many of the uncertainties of the bioclimatic SDM approach, and can yield insights helpful to guide adaptation planning for climate change. Using binomial generalized linear models, I found shorebirds shifted at the regional scale and selected landscapes with different characteristics in a dry year versus a wet year. This result indicates shorebirds are able to find habitat in the PPR under varying climate conditions, and supports a model of resilience for migrating shorebirds under climate change if wetlands in these varying landscapes are protected from drainage.

ACKNOWLEDGEMENTS

I would like to thank my advisor, Barry Noon, for agreeing to take me into his lab and for providing warm support, astute input to my chapters, and an environment to advance intellectually. I would also like to thank my co-advisor, Susan Skagen, for encouraging me to pursue a PhD in the first place, and for providing research feedback and much indispensable support along the way. Curt Flather, as a committee member, provided very helpful suggestions for improving my chapters.

This dissertation would not have been possible without funding from the Plains and Prairie Potholes Landscape Conservation Cooperative (PPPLCC), the North Central Climate Science Center (NCCSC), and the National Climate Change and Wildlife Science Center (NCCWSC). Furthermore, the PPPLCC and NCCSC provided opportunities for exchanging information and ideas that substantially benefitted the scope and depth of this work.

I appreciated the work of dedicated field assistants that navigated the flooded Prairie Pothole landscape in the spring of 2011: Brian Johnson, Brady Yeo Neiles, and Paul Bjornen. In the office, Katherine Mitsch, Nicole Luchetta, and Tessa Behnke looked up thousands of individual wetlands in ArcMap and made it possible for me to include historic shorebird surveys in chapter 3.

I really valued the opportunities and support offered by my graduate program, the Graduate Degree Program in Ecology, and by my department, the Department of Fish, Wildlife, and Conservation Biology. Thanks to many dedicated faculty for the great and inspired courses and many graduate students for making the intellectual environment shared and fun. The camaraderie and humble brain power of the Noon lab helped me through many trials and tribulations. Thanks especially to Jason Tack, Rekha Warriar, and Pranav Chanchani. Thanks as well to the Cooper Ornithological Society for the

opportunity to be student representative and to all the dedicated ornithologists that make attending society meetings such a rewarding experience. Thanks to my dance family, Sumatra Belly Dance, for giving me a life beyond academia. And, last but not least, thanks to the Steen family for their support.

TABLE OF CONTENTS

ABSTRACT..... ii

ACKNOWLEDGEMENTS..... iv

CHAPTER 1: VULNERABILITY OF BREEDING WATERBIRDS TO CLIMATE CHANGE IN THE PRAIRIE POTHOLE REGION, U.S.A. 1

 INTRODUCTION..... 1

 METHODS..... 2

 RESULTS 11

 DISCUSSION..... 14

 CONCLUSIONS..... 17

LITERATURE CITED 37

CHAPTER 2: PROJECTING AVIAN VULNERABILITY TO CLIMATE CHANGE: EXPLORING UNCERTAINTY FROM MODELING DECISIONS..... 48

 INTRODUCTION..... 48

 METHODS..... 52

 RESULTS 61

 DISCUSSION..... 63

LITERATURE CITED 80

CHAPTER 3: PREPARING FOR AN UNCERTAIN FUTURE: ASSESSING RESPONSES OF MIGRATING SHOREBIRDS TO HISTORIC CLIMATIC FLUCTUATIONS IN THE PRAIRIE POTHOLE REGION 91

 INTRODUCTION..... 91

 METHODS..... 94

 RESULTS 99

 DISCUSSION..... 101

LITERATURE CITED 111

CHAPTER 1: VULNERABILITY OF BREEDING WATERBIRDS TO CLIMATE CHANGE IN THE PRAIRIE POTHOLE REGION, U.S.A.

INTRODUCTION

The Prairie Pothole Region of north-central North America (central Iowa, U.S.A. to central Alberta, Canada; 900,000 km²) contains one of the largest wetland areas (40,000 km²) in the world (Keddy 2000). Historically, most conservation activities have focused on sustaining extensive, high quality duck habitat because of the associated recreational value of duck-hunting across the U.S. (Gleason et al. 2011). Increasingly, emphasis is being placed on the diversity of ecosystem services offered by prairie pothole wetlands, including carbon sequestration, flood control, groundwater recharge, water quality improvement, and biodiversity (Gleason et al. 2011). This includes increasing attention to all 115 species of breeding or migrating waterbirds that depend on the region (Beyersbergen et al. 2004).

Successful management of species requires knowledge of habitat preferences. Strategic management of species also requires identifying those species most vulnerable to future threats. Land conversion continues to be a direct threat to waterbird habitat, but climate change will likely exacerbate loss and interact with changes in land cover. Climate models for the Prairie Pothole Region project increasing temperatures and slight or no increases in precipitation, indicating drier conditions affecting hydroperiods, and the extent and quality of wetland habitat (Solomon et al. 2007, Johnson et al. 2010).

Prairie pothole wetlands are susceptible to climatic variation through impacts on wetland hydroperiod, vegetative condition, and water depth in combination with static factors such as basin size (Johnson et al. 2010). Well-documented causal relations between past variability in wetland condition and extent and waterbird numbers provide insights to future change in waterbird populations under climate change. In dry years, with fewer wet basins, breeding populations of waterbirds are significantly reduced (Johnson and Grier 1988, Niemuth and Solberg 2003). Building on these causal relations,

Sorenson et al. (1998) projected population changes for waterfowl under future warming scenarios. Their projections indicated that by 2060 duck populations would be half of their current level. Johnson et al. (2010) used mechanistic models relating climate to marsh vegetation dynamics, and projected that the Prairie Potholes in North and South Dakota will be too dry to produce suitable wetland vegetative conditions for breeding ducks in the future.

To address how climate change may impact waterbirds in the Prairie Pothole Region, we created empirically-based species distribution models for a focal group of breeding wetland-associated birds. We related bird occurrence (presence/absence) to climate and land cover predictors. As a species' occurrence varies from year to year in response to dynamic wetland conditions, we used multiple years of bird survey data across 41 years, a period that included years of drought and years of heavy precipitation. Although we did not explicitly model wetland condition, we used Random Forests, an ensemble decision tree approach which can capture the interactions between climate variability and the state of wetland basins that drive wetland condition (Breiman 2001). We projected future waterbird occurrence using species distribution models and future climate projections. To assess how climate change may reduce or expand current suitable habitat, for each species we compared the projections of future distribution to their predicted current distribution, and produced a quantitative estimate of how much habitat would be lost or gained under various climate change scenarios. Additionally, we compared our future projections of waterbird species response to a historic dry period.

METHODS

Study Area

The study area (320,000 km²) was the 45% of the Prairie Pothole Region within four U.S. states (North Dakota, South Dakota, Minnesota, and Iowa; Figure 1.1). The study was restricted to the four states because of available and consistent land cover and downscaled climate data. We excluded Iowa

from training the model because too few wetlands remain there to usefully inform the species distribution model, although we did include it in model predictions.

Water-filled glacial depressions termed *potholes* are characteristic of this region and can reach densities greater than 40 per km² (Kantrud et al. 1989). Since European settlement, these wetlands have been extensively converted to cropland, with wetland losses greatest in the eastern portion of the Prairie Pothole Region: Minnesota (85%), Iowa (95%) and North (49%) and South Dakota (35%) (Dahl 1990, Johnson et al. 2008). Losses of surrounding upland prairie habitats follow a similar geographic gradient (greatest in the eastern portion of the Prairie Pothole Region) but have been even more severe than wetland losses (Beyersbergen et al. 2004).

Species Occurrence

We obtained species occurrence (presence/absence) data from the North American Breeding Bird Survey (BBS; Sauer 2007) for waterbirds species with a prevalence of ≥ 0.05 . The BBS consists of >3000 routes on secondary roads throughout the continental U.S. and southern Canada. Routes are surveyed once annually during June between 04.45 AM and 10.00 AM. Route locations generally remain the same year after year, although not all routes are surveyed each year and there is variation in the year when a route is initiated. BBS routes are 39.4-km long with 50 stops spaced 0.8 km apart. Three-minute point-count surveys are conducted at each stop. BBS survey data are available for each species and summarized at route totals or 10-stop route segments (<https://www.pwrc.usgs.gov/bbs/>).

In our study area, BBS surveys took place from late May to early July. This interval extensively overlapped the breeding season (nest-building through brood rearing) for the majority of wetland-dependent species we evaluated. Ten species usually nest during this period and three species occupy brood-rearing habitats. The remainder of the species are engaged in behaviors ranging from incubation to brood-rearing. In addition, seven waterfowl species may be molting body or primary feathers near the end of the survey period.

Even though the breeding cycles of wetland-dependent birds in the Prairie Potholes are not completely synchronous, we believe the BBS survey methods accurately document the presence of all regularly occurring species. Our confidence is based on the overlap between the geographic extent of our survey data, the distribution of our focal species during the breeding season, and the timing of the surveys. The result, we believe, is that the likelihood of correctly documenting the presence of a species was comparable across species, routes, and survey years.

We used data (1971-2011) from high-quality surveys (reported by the BBS as “run type 1”) for 77 routes: these were conducted within the correct survey window and not during poor weather. Due to the potential for extensive variation along a route in habitat types, we chose one 10-stop section to model habitat associations rather than use data from the entire route. To accommodate different timing of peak detectability by species, we chose either the first or third section for a species depending which section had higher detections for that species. Routes were consistently surveyed from stop one, starting around 04.45 AM, to stop 50, ending around 09.00 AM. For all but two species, the first or third section had their highest or second highest number of detections. ‘Presence’ was defined as ≥ 1 detection at a minimum of one stop along the route segment. We identified focal species based on their prevalence (section-level occurrence rate) with species detected at fewer than 5% of route sections not included.

Land Cover Data

We extracted land cover variables (Table 1.1) for North and South Dakota from a GIS raster layer created by the U.S. Fish and Wildlife Service (USFWS; USFWS, Region 6 Habitat and Population Evaluation Team, unpublished data); for Minnesota and Iowa from a GIS raster layer created by the USFWS (USFWS, Region 3 Habitat and Population Evaluation Team, unpublished data); and for uplands in the southern portion of the Iowa Prairie Pothole Region from the 1992 National Land Cover Dataset

(NLCD). The USFWS data layers were based on Landsat Thematic Mapper Satellite imagery of scenes from 2000-2003, and the NLCD on scenes from the early to mid-1990s. All raster layers were at a 30-m resolution.

Wetland basins in the land cover layers were areas of contiguous wetland extent. The basins were derived from a GIS wetland polygons layer (USFWS National Wetlands Inventory, NWI) where multiple contiguous polygons of differing wetland regimes were dissolved to a single polygon. The USFWS Habitat and Population Evaluation Team followed the procedures of Cowardin et al. (Cowardin et al. 1995) and Johnson and Higgins (1997) to describe each wetland basin by its most permanent water regime: temporary, seasonal, semipermanent, lake, and river. Generally, temporary wetlands are flooded in spring for a few weeks after snow-melt, seasonal wetlands hold water until summer, and semipermanent wetlands hold water through the growing season; lake and rivers are permanently flooded wetlands (Stewart and Kantrud 1971a). NWI data are based on aerial photographs taken in the late 1970's and early 1980's. Where water pixels extended beyond NWI polygons, they were labeled as water (wetland regimes, see Cowardin et al. (1979)). We characterized wetlands into nine classes: temporary, seasonal, semipermanent, lake, river, forested, shrub, total, and total palustrine (Table 1.1). Total wetland was the combined composition of temporary, seasonal, semipermanent, lake, river, forested, and shrub; total palustrine wetland was temporary, seasonal, and semipermanent.

We described upland habitat using four land cover classes: cropland, grassland, tree, and developed (Table 1.1). Cropland included areas planted with crops or fallowed. Grassland included native prairie, planted grasses (i.e. previously cropped but now planted with grasses and forbs such as Conservation Reserve Program land), and hayland. Developed land cover included primarily residential areas. Tree habitat included small sections or rows of trees and occasionally areas of forest. Accuracy of the upland land cover data for North and South Dakota, assessed in 2007, was > 90% (M. Estey, personal communication).

To describe habitat associations for our focal waterbird species, we explored composition-based single scale models. In both single-scale and multi-scale models, composition-based predictors, expressed as the amount of a land cover type within a given area, perform better than their distance-based counterparts, expressed as the distance from a sampling location to a land cover type (Martin and Fahrig 2012). We used ArcMap 10.0 to calculate land cover composition for the four upland and nine wetland classes at six spatial scales for the BBS route segments. The scales ranged from 335 ha to 32,200 ha and were based on buffering the segments with radii: 0.2-km, 0.4-km, 1-km, 2-km, 4-km, and 8-km. BBS surveyors record all birds detected within 0.4-km of the survey point. Thus, assuming no decline in detection probability with increasing distance and no landscape effect, we expected 0.4-km to be the appropriate scale to relate land cover to bird occurrence. However, some waterbird species may decline quickly in detection probability with increasing distance from the survey point—therefore, we also explored a 0.2-km scale. Because other species may respond to land cover heterogeneity at broader extents, we also explored a range (1-km to 8-km) of landscape scales. Land cover data were assumed static across current and future years.

Climate Covariates

We used PRISM (PRISM, Parameter-elevation Regressions on Independent Slopes Model) data for historical climate records. These data are available at a 4-km grid scale as monthly temperature and precipitation and were rescaled to an 8-km grid to match the scale of the projected climate data (Coulson and Joyce 2010).

Using monthly values of precipitation and temperature, we derived 18 climate variables (Table 1.1). We calculated mean temperatures for grid points by averaging the minimum and maximum monthly temperatures over different time periods. We delineated seasons as summer (June-August), fall (September-November), winter (December-February), and spring (March-May). We defined year as ending in May to correspond to the June bird surveys. We included seasonal and annual variables

because both seasonal and annual climate explain annual variation in the number of prairie pothole wetlands holding water (Larson 1995). For semipermanent wetlands and (especially) lakes, wet wetland count is related to long-term climate (at least 3 years) (Winter and Rosenberry 1998). We included 5-year and 10-year precipitation and mean temperature variables as proxies for long-term climate effects. We also included the variances in 5-year and 10-year precipitation and temperature data, because large values of these variables may indicate that wetlands are cycling through wet and dry phases, driving dynamic vegetative conditions (Johnson et al. 2010). Climate data from 1971-2011 were used to construct the baseline species distribution models. The species distribution models predicted to climate data from 1981-2000 and 2040-2049 to create current and future projections, respectively, of species occurrence.

Future Climate Data

We used statistically downscaled and high resolution climate projections. Statistically downscaled data refine projections from global circulation models (GCMs) using an empirical relationship to local physiography (e.g. topography and water bodies). These projections assume relations will hold into the future and are less computationally intensive than high resolution models. High resolution models nest a dynamical Regional Climate Model within the GCM, re-running the GCM based on mesoscale (a few to a few hundred kilometers) physical relationships with topographical features and surface characteristics (Giorgi and Mearns 1991). The high resolution projections circumvent the problem associated with lack of “stationarity” when the relationships between GCM output and the fine-scale climate change over time.

The statistically downscaled projections were based on data obtained from output of GCM CGCM3.1MR (Canadian Centre for Climate Modeling and Analysis Third Generation Coupled Global Climate Model Version 3.1, Medium Resolution) (Coulson et al. 2009) and downscaled to an 8-km grid. The high resolution models used the Community Climate System Model (CCSM) to set the boundary

condition and a mesoscale model, Weather Research and Forecasting model (WRF) to refine the data to a 36-km regional scale (J. Stamm, personal communication) (Skamarock et al. 2008). Given that we expected high spatial correlation for monthly temperature and precipitation, we interpolated the 36-km data to the 8-km grid (National Center Atmospheric Research Staff 2014). Both climate models were run with a mid-high IPCC emissions scenario, A2 (Nakicenovic and Intergovernmental Panel on Climate Change. Working Group III. 2000). The high resolution projections were available for 2000-2049, and the statistically downscaled projections were available for 2000-2100. We term the statistically downscaled data “CGCM” after the GCM these data are based on, and we term the dynamically downscaled data “WRFc” after the mesoscale model these data are based on.

Species Distribution Models

We estimated a species distribution model (SDM) for each waterbird species, relating BBS occurrence records (1971-2011) to climate, and wetland and upland land cover (hereafter grouped as “land cover”) predictor variables. We used climate for the same year as the occurrence record from the climate grid point nearest the BBS route segment and land cover surrounding the route segment. We defined occurrence as one or more detection per 10-stop segment by year. The spatial scale used in the final models for land cover calculations was chosen separately for each species based on model performance. We ran six models for each species based on the six different spatial scales of land cover and chose the model with the highest classification accuracy. We used a non-parametric machine learning approach, Random Forests, to create the SDMs (Breiman 2001). We chose Random Forests because of its high predictive power, ability to model unspecified variable interactions and correlated variables, its ranking of variable importance, and its demonstrated use for bioclimatic species distribution models (Lawler et al. 2006, Prasad et al. 2006). Random Forests uses an ensemble of classification (categorical response variable) or regression (continuous response variable) trees, each built with a subset of the data, to model the pattern between predictor variables and the response

variable. We used permutation procedures to assess variable importance, a method based on reduction in predictive accuracy to internally withheld data when values of a given predictor variable are randomly shuffled. We report the top ten variables for each model. Although the choice of the number of variables to report is arbitrary, we expect the top ten will provide an adequate basis for comparing models.

We used the RandomForests package in R to create our models (R Development Core Team 2012). We specified 3000 trees which is a sufficiently large number of trees to capture any patterns in the data. Each tree was constructed with a bootstrapped subsample with replacement of the data records (BBS routes). Because the ratio of presence to absence was often skewed, particularly for either very abundant or rare species, we balanced the data by setting Random Forests to randomly use, for each tree, 25 records where the species was present and another 25 where the species was absent (Chen et al. 2004). A subsample of five predictor variables was evaluated at each binary split in the tree algorithm.

We partitioned the BBS data in a number of ways to strengthen model evaluation and inference. First, we only excluded consecutive years of surveys to reduce the influence of temporal autocorrelation and maximize information content: the “main training set”. The excluded data were used to validate the models created with these data: the “main test set”. Second, we separated out six years of data covering a drought period from 1987 through 1992 (Winter and Rosenberry 1998). We created species distribution models with the drought data to look at variable importance in dry years compared to variable importance for the whole study period (main training set). To assess model transferability, we predicted to the drought data subset using species distribution models created with the remaining wetter years (Schröder and Richter 2000, Guisan and Thuiller 2005).

Model Evaluation

To evaluate each model's ability to forecast to the same range of predictor variables, we predicted to the main test set. To evaluate each model's transferability – that is, to project to a new location or time period where predictor variables may be outside the range of the variables used to build the model – we projected to the drought period with models trained with data from the wet years. The transferability assessment should more realistically evaluate how the models extrapolate to a dry future (Schröder and Richter 2000).

To assess a model's performance, we report patterns of correct classification in a confusion matrix and the area under the receiver operating characteristic curve (AUC) (Hastie et al. 2009). From the confusion matrix, we report the counts of true positives, false positives, true negatives, false negatives and overall classification accuracy based on a 0.5 probability of occurrence threshold for concluding presence. Because we set sample sizes of presence and absence points to be equally subsampled in the Random Forests model, we selected a threshold of 0.5 (see Liu et al. 2005). Overall classification accuracy was calculated by dividing the number of correctly predicted presences and absences by total predictions. AUC is a threshold free assessment of model performance. AUC values range from zero to one and give the probability that a known presence observation has a higher predicted value of presence than an absence observation for a randomly selected pair of presence-absence observations (Hastie et al. 2009). Models with AUC values of at least 0.7 are considered acceptable, between 0.8 and 0.9 good, and greater than 0.9 outstanding (Hosmer and Lemeshow 2000).

Projected Distributional Changes

We created current predictions and future projections of probability of occurrence to each grid cell, for each focal species, by applying the SDMs to the baseline land cover and climate data (the 20-year period for baseline climate data being 1981-2000) and to baseline land cover and future climate data (the 10-year period 2040-2049). Ten to twenty-year time periods were chosen to mitigate the influence of short-term variations in climate.

We created current and future predictive distribution maps for each species in ArcMap 10 based on an assignment of grid point locations as suitable or unsuitable. A grid point was determined suitable if the estimated probability of occurrence (over the time period for the baseline or future data) was greater than 0.5. Three breakpoints within suitable (0.625, 0.75, 0.875) and unsuitable (0.125, 0.25, 0.375) locations showed the degree to which a location was predicted suitable or unsuitable.

We indexed changes between predicted baselines and projected future distributions using change in a species' spatial distribution. To assess change in distribution, we calculated the percent loss (or gain) in the number of grid cells classified as suitable.

RESULTS

Baseline mean temperature (years 1981-2000) was 5.9°C and mean yearly precipitation was 548 mm. By 2040-2049, CGCM projected a 2.9°C increase in mean temperature and a 22 mm (3.9%) increase in annual precipitation while WRFc projected a 3.8°C temperature increase and a 17 mm (3.1%) increase in annual precipitation. Projections of future precipitation fall within the range of historic levels of precipitation, whereas future temperatures projected by both climate models exceed historic temperatures (Figure 1.2). The climate models differed slightly in the spatial distribution of the precipitation increases, with CGCM projecting greater increase in Iowa and WRFc projecting greater increase in North Dakota than other areas (Figure 1.3).

The number of data occurrence records in the main training set was 975. The number of years of survey data included in the main training set, for a given route, ranged from one to 21, with a mean of 13. The number of survey routes included for a given year ranged from 15 to 35. Thirty-one waterbird species had prevalence ≥ 0.05 and were included in the focal group (Table 1.2). The number of records in the main test set was 817. The number of data records in the dry years set was 139. We adjusted the prevalence cutoff to 0.07 (≥ 10 detections), at which 22 species qualified.

Model Evaluation

Most models based on known distributional patterns were acceptable to excellent, indicated by AUC values (Table 1.2). Exceptions were SDMs for the Great Blue Heron and Killdeer. When predicting to dry years only, AUC values indicated the following additional models predicted poorly: Canada Goose, American Wigeon, Mallard, and Green-winged Teal. Overall accuracy of dry year predictions suggested that projected distributional changes for some species should be interpreted with caution, including Blue-winged Teal, Sora, and Common Yellowthroat. For the main datasets, model performance was not related to a species' prevalence according to Spearman's rank correlation (-0.09, p-value 0.62).

Vulnerability

Average projected decline in occurrence rate (spatial distribution) across 31 species under two future climate scenarios was 45%. WRFc models projected slightly more severe distributional changes (-48%) than CGCM (-43%; Table 1.3). Species expected to experience small to no declines in distribution included Blue-winged Teal, Killdeer, and Upland Sandpiper. Species projected to experience severe declines were Franklin's Gull, Sora, and Wilson's Snipe (Table 1.3). In general, species maps depicted declines within the baseline range, rather than distributional shifts to new areas (Supplementary figures S1.2-S1.12).

For most species, future projections of change were consistent with responses of species to historic dry periods (Figure 1.4). Consistent projections were those that exhibited little to no change between the historic dry period and the future, or those that declined more in the future than in the historic dry period. If a species' habitat was not impacted by dry conditions, the species would be expected to experience little to no impact under future dry conditions. Other species may be impacted by drying conditions, thus responding during the historic dry period, and even more if additional drying occurs in the future. However, inconsistent with expectations, models projected reduced distribution of Blue-winged Teal, Northern Pintail, and Pied-billed Grebe in the dry period relative to future projections. Additionally, several species that remained relatively stable in the historic dry period were projected to decrease in distribution under future scenarios, including Canada Goose, Sedge Wren, Marsh Wren, Common Yellowthroat, and Song Sparrow.

Variable Importance

In general, species distributions were strongly influenced by the distribution of wetland basins and land cover classes and moderately influenced by climate, as evidenced by their influence in the SDMs. Land cover variables, wetland and upland, collectively occurred as 67% of the top ten variables in the SDMs but comprised only 42% of the available predictor variables (Table 1.4); wetland and upland variables were 1.5 and 1.8 times more likely to appear in lists of top ten predictors than in the list of available predictors, respectively. Species associations with all wetland types, except rivers, were generally positive. All associations with cropland were negative except for the Song Sparrow, whereas associations with grassland were primarily positive except for Wood Duck (Table 1.4). Climate predictor variables were generally underrepresented in the variables of top importance. Collectively, temperature and precipitation comprised 32% of the top ten variables across the 31 species, although they were 58% of the available predictor variables. Temperature and precipitation variables were similarly influential and were 0.5 and 0.6 times more likely to appear in lists of top ten predictors than in the list of available

predictors, respectively. In general, probability of species occurrence was negatively associated with temperature; relationships with temperature variability were often positive (Table 1.4). Associations with precipitation were often negative, except for Great Blue Heron, Sedge Wren, Song Sparrow, and Wood Duck. Variability in precipitation occurred in the top ten variables for only one species' model (Sedge Wren) and was negatively correlated with probability of occurrence.

Land cover variables were highly influential in observed patterns of species distribution. The importance of these variables is visually apparent when spatial distribution of grasslands and wetlands (Supplementary figure S1.1) and observed climate gradients (Figure 1.3) were compared to baseline distributions (Supplementary figures S1.2-S1.12). Many breeding waterbirds have a high probability of occurrence in the western portion of the study area where grasslands and wetlands co-occur.

Temperature and precipitation predictor variables were more often in the top ten variables for the species with the greatest expected declines (Figure 1.5). Conversely, wetland and upland land cover variables were more often in the top ten variables for the species with smallest expected declines.

Variable Importance: main models versus dry-years models

For dry-years models, climate predictor variables represented 45% of the top ten variables across the 22 species versus 31% for the same 22 species in the main models (Tables 1.4 and 1.5). Of land cover predictors, 65% included wetland variables in the top ten variables in the dry years and a similar 67% in the main models. However, representation of different wetland types varied with more seasonal wetlands (positive relationships only) appearing in the non-drought years (30% versus 17%) and more lakes included in the dry years (32% versus 20%).

DISCUSSION

Our projections of large range reductions for waterbirds breeding in the Prairie Pothole Region are not surprising. Globally, freshwater habitats are expected to be particularly vulnerable to climate change (Kundzewicz et al. 2007). If, as the future climate projections we used indicate, temperatures

rise by ~3.0°C and precipitation rises only by 3% by mid-century in the Prairie Pothole Region, many fewer pothole wetlands will exist on the landscape due to an increased deficit in precipitation relative to evapotranspiration. Similarly, other studies of the Prairie Pothole Region have projected a drier future and concomitant reductions in waterbird habitat (Poiani and Johnson 1991, Sorenson et al. 1998, Johnson et al. 2010).

Past studies in the Prairie Pothole Region that extrapolated from relations between climatic factors and wetlands inferred generalized habitat losses for waterfowl (Sorenson et al. 1998, Johnson et al. 2010). Our species-specific approach indicated large variability in the vulnerabilities of waterbird species to climate change. This is expected as patterns of waterbird habitat selection vary among species for wetland attributes such as size, permanence, and vegetative cover (Weller and Spatcher 1965, Kantrud et al. 1989). Hydrological studies indicate that temperature and precipitation regimes affect not only the number of wetlands and wetland size, but marsh vegetation dynamics and the vegetative coverage patterns at the landscape scale (Johnson et al. 2010). While reducing the overall number of wetlands, a drier climate will likely lead to more extensive coverage of wetlands by dense vegetation rather than wetland conditions characterized by a mixture of open water and vegetation (Johnson et al. 2010). Species are expected to respond differentially to these changes in wetland characteristics. Furthermore, individualistic species' responses appear the norm (Peterson 2003, Matthews et al. 2011, Tingley et al. 2012).

Our projections of future change were not always consistent with documented waterbird responses to a historic dry period which represented one possible expression of a drier climate. The dry historic period, a consequence of reduced precipitation, is not a direct analog of future drying which is expected to be driven by increases in evapotranspiration (Figure 1.2) (Cook et al. 2014). Thus, it is unclear to what extent the historic pattern of drought can be used as a benchmark for future climate change. Therefore, the inconsistencies between the dry historic waterbird response relative to projected

future responses may indicate our models are under- or over- estimating waterbird response to climate change for some species. It is also possible that changes in temperature versus precipitation may result in divergent, and unprecedented, future wetland habitat conditions. In that case, divergent waterbird responses, relative to the past responses, would not be surprising.

The historic range of temperature variability did not overlap future projections and so, our SDMs were projecting beyond known climatic boundary conditions. Model extrapolation to novel conditions is common when projecting species response to future climate (Elith and Leathwick 2009). Our single values for yearly averages (Figure 1.2), indicated almost no overlap in temperature range between historic and projected time intervals. However, because of spatial variation in temperature regimes (i.e., warmer in the south, as shown in Figure 1.3), there were likely many individual grid cells in which future temperatures overlapped the historic range even if the study area yearly means do not. SDMs based on the Random Forest algorithm are constrained when extrapolating beyond the observed values of the predictor variables. For example, when projected temperatures are outside of the range of the training set the algorithm holds the prediction constant at the last known value of temperature (Elith and Graham 2009). Therefore, if future wetland habitat conditions selected by the species become less common with increased temperatures, our estimates of habitat losses for many species may be underestimates.

Ranking predictor variables by their importance provides additional insights into how the 31 waterbird species may respond to changing environmental factors. We included predictors related to suitable waterbird habitat quality, including the amount and type of wetland basins, and temporally scaled temperature and precipitation covariates. Species projected to be most sensitive to anticipated climate change (changes in temperature and precipitation, Table 1.4) consistently reflected the ecology of the species. For example, the two diving ducks, Ruddy Duck and Redhead, primarily selected large wetlands, such as semipermanent basins, and were less susceptible to total drying (Kantrud and Stewart

1977, Johnson et al. 2010). As a consequence of their habitat associations, no climate covariates ranked in the top ten for these two waterbird species. In contrast, waterbirds that rely on shallow water habitat, such as Sora or Sedge Wren, or dynamic habitat such as Black Tern or Mallard, showed a much greater projected change in distribution to future climatic conditions (Weller and Spatcher 1965, Johnson et al. 2010).

The variable importance ranks also suggested that waterbirds may shift their habitat preferences with increased drying. More climate covariates and more permanent wetland regimes appeared in the top variables for dry years. In the Prairie Pothole Region, wetland function can rapidly change with significant changes in the climate. In dry years, for example, semipermanent wetlands may function more like seasonal wetlands, and seasonal wetlands more like temporary wetlands. This differential sensitivity to climate change explains why seasonal wetlands were less important and lakes more important in dry years.

Because bioclimatic SDMs are generally exploratory with many collinear climate predictors, there is concern that these models over-fit the data and thus misrepresent species distributions (Beaumont et al. 2005). However, the inclusion of many collinear climate predictors is often warranted when causal links between specific climate predictors and species' distributions are not established, leading to better model fit and projections (Braunisch et al. 2013). We found that when we reduced our 18 climate and 13 land cover variables to 14 uncorrelated climate and 10 uncorrelated land cover variables model projections were similar: 45% average range reduction for the full model and 48% for the reduced model (results not shown).

CONCLUSIONS

Our results indicated, on average, large decreases in suitable habitat by the 2040s for 31 waterbird species breeding in the Prairie Pothole Region of the U.S.A. Importantly, our results were consistent between two contrasting future climate scenarios. However, there was substantial variability

in species specific responses to projected climate change. Therefore, strategic efforts to mitigate climate change effects should preferentially direct management actions to those species expected to be most vulnerable. In continuing research, we are exploring in greater detail various sources of uncertainty in our projections including additional model algorithms, alternative covariates, and other sources of species distribution data (Beale and Lennon 2012).

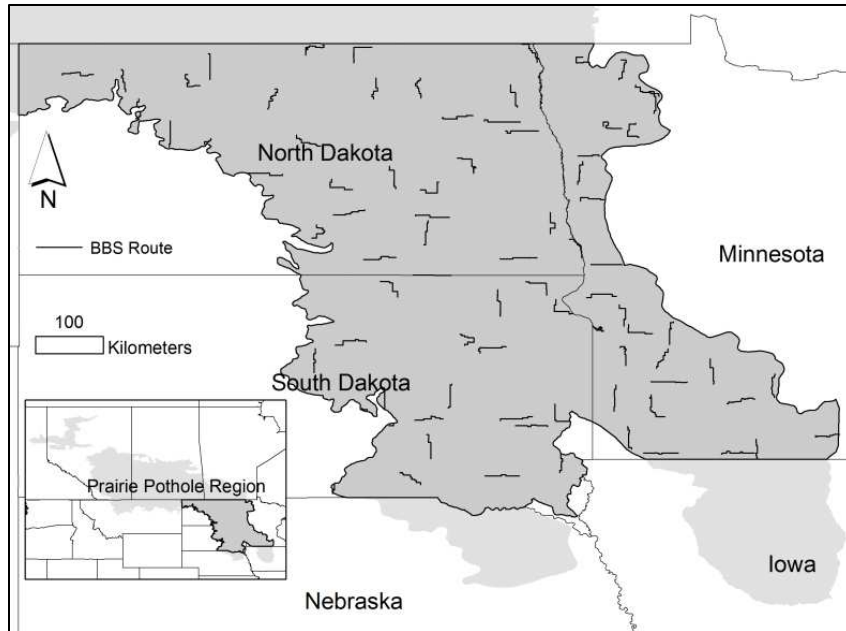


Figure 1.1. Bird occurrence data were obtained from 77 Breeding Bird Survey (BBS) routes throughout the Prairie Pothole Region (PPR) of North Dakota, South Dakota, and Minnesota. Climate-based projections were also made to the PPR of Iowa.

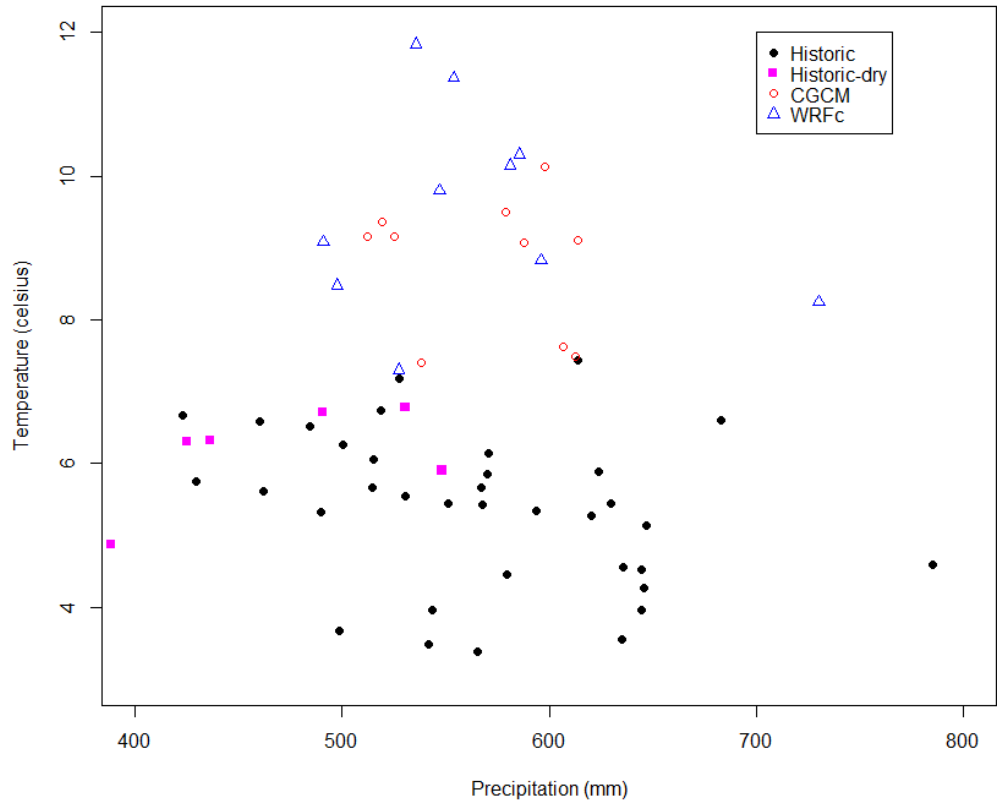


Figure 1.2. Total precipitation versus average temperature by “bird year” (June of year x-1 to May of year x) for the study area (see Figure 1) for the time periods used to train species distribution models and project future distributions. Historic points showed the years and locations from 1971-2011 used to train the species distribution models with six years withheld. The six years were a dry period from 1987-1992 shown as ‘historic-dry’. CGCM and WRFc show two sets of climate projections for the ten year period 2040-49.

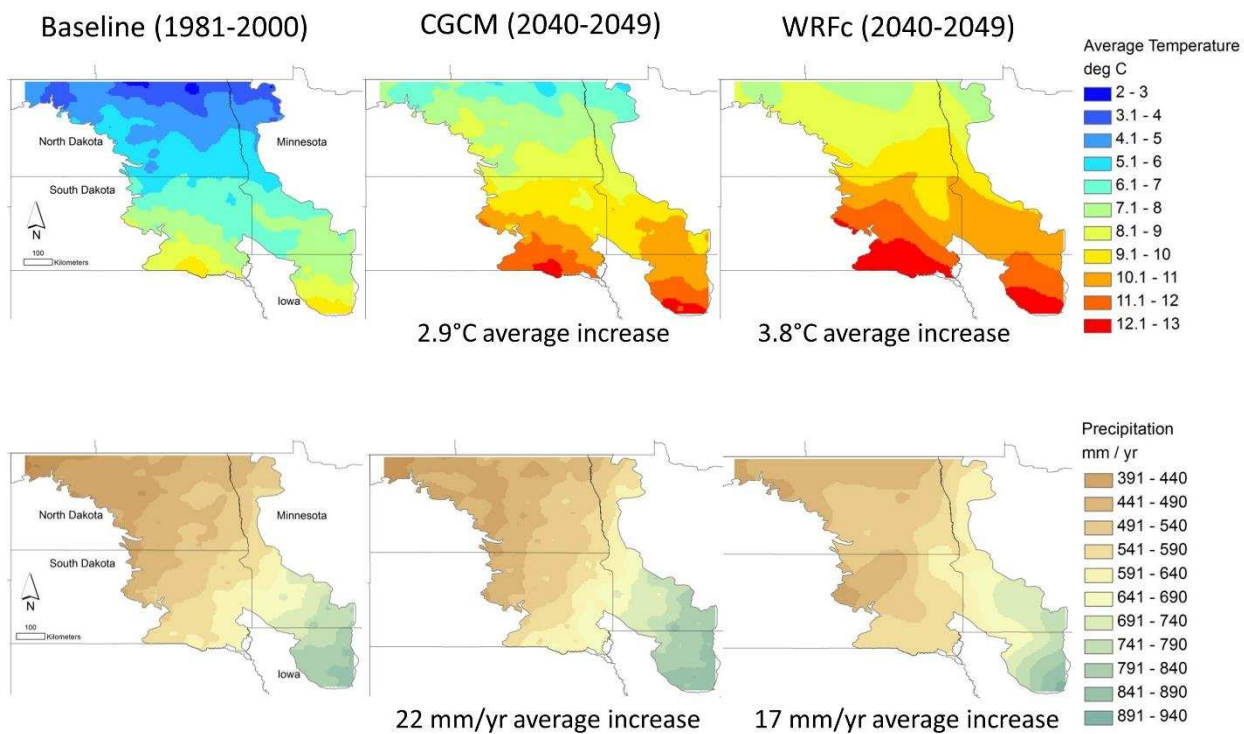


Figure 1.3. Temperature and precipitation for baseline and two future climate projections for the prairie potholes of North Dakota, South Dakota, Minnesota, and Iowa.

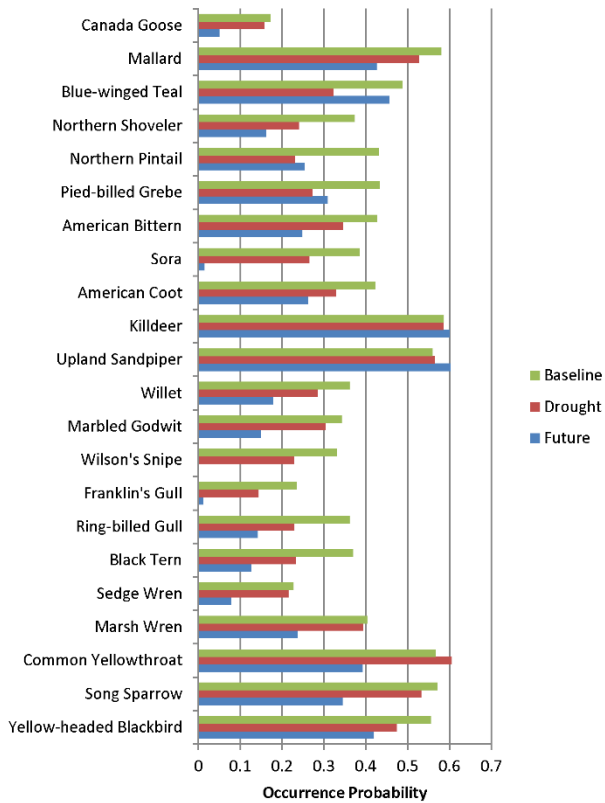


Figure 1.4. Mean rates of predicted species occurrence at 4,957 8-km grid points. Baseline rate was based on 1981-2000 climate records. Dry years showed predicted occurrence rates for the drought period, 1987-1992. Future rates were based on the average projections of two future climate datasets (CGCM-A2 and WRFc) for 2040-2049.

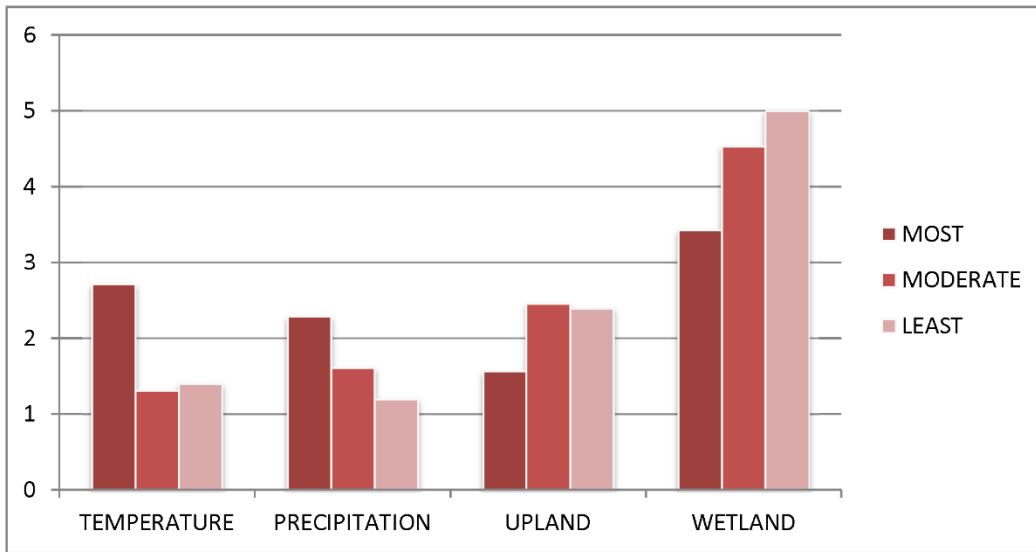


Figure 1.5. The frequency (y-axis) of variable type (x-axis) in top ten variables for waterbird species distribution models, grouped by species sensitivity to climate change. The most sensitive species were projected to lose $\geq 66\%$ of their current habitat; moderately sensitive species 33-65%; and least sensitive $< 33\%$.

Table 1.1 Thirty-one climate and land cover variables used in species distribution models. Temperature calculations were based on averages, while precipitation calculations were based on totals. Land cover variables were based on composition (proportion of total) of that cover type in the landscape. Wetland land cover was apportioned by wetland regime. Total palustrine wetland summed temporary, seasonal, and semipermanent wetlands. Total wetland summed all wetland regimes. Cropland described land planted with crops or fallowed. Grassland included native prairie, conservation reserve program (CRP) land, and hayland.

| <i>Climate</i> | | <i>Land Cover</i> | |
|-----------------------------|-------------------|------------------------|-------------------|
| Temperature | Precipitation | Wetland | Upland |
| Spring (spr) | Spring | Temporary (temp) | Cropland (crop) |
| Winter (wint) | Winter | Seasonal (seas) | Grassland (grass) |
| Fall | Fall | Semipermanent (semi) | Developed (devel) |
| Summer (sum) | Summer | Lake | Tree |
| Yearly (1yr) | Yearly | River | |
| 5-year (5yr) | 5-year | Shrub | |
| 10-year (10yr) | 10-year | Forested (forest) | |
| 5-year std. dev. (5yr_sd) | 5-year std. dev. | Total palustrine (pal) | |
| 10-year std. dev. (10yr_sd) | 10-year std. dev. | Total | |

Table 1.2. Model evaluation showing species prevalence (proportion of data points with species present) for each dataset, and predictive accuracy using the classification matrix and area under the curve (AUC) values. The positive and negative rates show the models ability to correctly predict presence and absence data points in the withheld data based on a 0.5 threshold for classification. Overall accuracy was the proportion of true positive and true negative predictions. AUC critical value = 0.70. Dry year predictions were based on models trained without the dry years.

| Common Name | Scientific Name | Prevalence | | | To withheld data | | | | | | To withheld dry years | |
|-----------------|---------------------------|-----------------------|-----------------------|------------------------|-------------------|--------------------|-------------------|--------------------|----------------------|------|-----------------------|------|
| | | Training data (n=974) | Withheld data (n=817) | Dry years data (n=139) | True positive (n) | False positive (n) | True negative (n) | False negative (n) | Overall accuracy (%) | AUC | Overall accuracy (%) | AUC |
| Canada Goose | <i>Branta canadensis</i> | 0.18 | 0.18 | 0.09 | 92 | 211 | 457 | 60 | 67 | 0.71 | 76 | 0.61 |
| Wood Duck | <i>Aix sponsa</i> | 0.06 | 0.07 | 0.04 | 24 | 187 | 576 | 30 | 73 | 0.70 | 84 | 0.81 |
| Gadwall | <i>Anas strepera</i> | 0.11 | 0.12 | 0.00 | 82 | 183 | 534 | 18 | 75 | 0.89 | 74 | 0.87 |
| American Wigeon | <i>Anas americana</i> | 0.05 | 0.07 | 0.04 | 36 | 129 | 632 | 20 | 82 | 0.84 | 71 | 0.66 |
| Mallard | <i>Anas platyrhynchos</i> | 0.60 | 0.59 | 0.55 | 343 | 101 | 231 | 142 | 70 | 0.77 | 57 | 0.65 |

| | | | | | | | | | | | | |
|-------------------------|------------------------------|------|------|------|-----|-----|-----|-----|----|------|----|------|
| Blue-winged Teal | <i>Anas discors</i> | 0.36 | 0.38 | 0.24 | 259 | 139 | 368 | 51 | 77 | 0.86 | 63 | 0.74 |
| Northern Shoveler | <i>Anas clypeata</i> | 0.17 | 0.18 | 0.09 | 117 | 189 | 481 | 30 | 73 | 0.84 | 68 | 0.81 |
| Northern Pintail | <i>Anas acuta</i> | 0.21 | 0.24 | 0.10 | 153 | 161 | 463 | 40 | 75 | 0.85 | 69 | 0.85 |
| Green-winged Teal | <i>Anas crecca</i> | 0.05 | 0.05 | 0.03 | 29 | 180 | 592 | 19 | 77 | 0.85 | 72 | 0.58 |
| Redhead | <i>Aythya americana</i> | 0.15 | 0.12 | 0.03 | 87 | 126 | 593 | 11 | 83 | 0.91 | 81 | 0.95 |
| Ruddy Duck | <i>Oxyura jamaicensis</i> | 0.13 | 0.11 | 0.06 | 83 | 115 | 612 | 7 | 85 | 0.94 | 83 | 0.92 |
| Pied-billed Grebe | <i>Podilymbus podiceps</i> | 0.22 | 0.24 | 0.11 | 166 | 150 | 474 | 27 | 78 | 0.90 | 73 | 0.81 |
| Double-crest. Cormorant | <i>Phalacrocorax auritus</i> | 0.09 | 0.09 | 0.05 | 64 | 201 | 542 | 10 | 74 | 0.84 | 68 | 0.75 |
| American Bittern | <i>Botaurus lentiginosus</i> | 0.24 | 0.27 | 0.17 | 190 | 173 | 421 | 33 | 75 | 0.84 | 64 | 0.76 |
| Great Blue Heron | <i>Ardea herodias</i> | 0.07 | 0.06 | 0.04 | 29 | 180 | 592 | 19 | 76 | 0.69 | 88 | 0.67 |
| Sora | <i>Porzana carolina</i> | 0.28 | 0.27 | 0.16 | 178 | 154 | 443 | 42 | 76 | 0.86 | 63 | 0.71 |
| American Coot | <i>Fulica americana</i> | 0.28 | 0.29 | 0.15 | 201 | 117 | 467 | 32 | 82 | 0.90 | 72 | 0.86 |
| Killdeer | <i>Charadrius vociferus</i> | 0.88 | 0.92 | 0.86 | 507 | 27 | 41 | 242 | 67 | 0.69 | 69 | 0.59 |
| Upland Sandpiper | <i>Bartramia longicauda</i> | 0.49 | 0.48 | 0.53 | 308 | 128 | 300 | 81 | 74 | 0.82 | 81 | 0.84 |
| Willet | <i>Tringa semipalmata</i> | 0.16 | 0.15 | 0.13 | 111 | 163 | 532 | 11 | 79 | 0.91 | 70 | 0.90 |

| | | | | | | | | | | | | |
|-------------------------|----------------------------------|------|------|------|-----|-----|-----|-----|----|------|----|------|
| Marbled Godwit | <i>Limosa fedoa</i> | 0.19 | 0.18 | 0.24 | 121 | 166 | 505 | 28 | 76 | 0.88 | 75 | 0.90 |
| Wilson's Snipe | <i>Gallinago delicata</i> | 0.19 | 0.20 | 0.14 | 140 | 163 | 494 | 23 | 77 | 0.90 | 72 | 0.80 |
| Wilson's Phalarope | <i>Phalaropus tricolor</i> | 0.10 | 0.12 | 0.04 | 79 | 165 | 550 | 23 | 77 | 0.86 | 66 | 0.84 |
| Franklin's Gull | <i>Leucophaeus pipixcan</i> | 0.10 | 0.11 | 0.09 | 64 | 189 | 538 | 26 | 74 | 0.81 | 73 | 0.86 |
| Ring-billed Gull | <i>Larus delawarensis</i> | 0.12 | 0.16 | 0.12 | 103 | 179 | 510 | 25 | 75 | 0.84 | 66 | 0.78 |
| Black Tern | <i>Chlidonias niger</i> | 0.17 | 0.17 | 0.07 | 112 | 172 | 505 | 28 | 76 | 0.85 | 72 | 0.89 |
| Sedge Wren | <i>Cistothorus platensis</i> | 0.27 | 0.26 | 0.17 | 142 | 168 | 434 | 73 | 71 | 0.76 | 81 | 0.71 |
| Marsh Wren | <i>Cistothorus palustris</i> | 0.23 | 0.24 | 0.17 | 166 | 130 | 493 | 28 | 81 | 0.89 | 73 | 0.78 |
| Common Yellowthroat | <i>Geothlypis trichas</i> | 0.83 | 0.84 | 0.81 | 444 | 41 | 91 | 241 | 65 | 0.74 | 60 | 0.76 |
| Song Sparrow | <i>Melospiza melodia</i> | 0.66 | 0.66 | 0.57 | 425 | 105 | 172 | 115 | 73 | 0.78 | 74 | 0.85 |
| Yellow-headed Blackbird | Xanthocephalus xanthocephalus | 0.54 | 0.56 | 0.56 | 348 | 86 | 321 | 62 | 82 | 0.88 | 64 | 0.76 |

Table 1.3. Values report projected changes in occurrence in the 2040's, relative to 1981-2000 (baseline).

Species distribution models projected species occurrence to 4,957 8-km grid points using climate data for the baseline period and two climate projections (CGCM and WRFc). Negative values indicated the proportion of occupied grid cells for each species, projected to be unoccupied in the future. Positive values indicated the proportion by which occupied cells were projected to increase.

| <i>Species</i> | <i>Change in occurrence (%)</i> | | |
|--------------------------|---------------------------------|------|---------|
| | CGCM | WRFc | Average |
| Canada Goose | -76 | -66 | -71 |
| Wood Duck | -70 | -37 | -54 |
| Gadwall | 49 | -87 | -19 |
| American Wigeon | -58 | -71 | -65 |
| Mallard | -30 | -23 | -27 |
| Blue-winged Teal | -9 | -4 | -7 |
| Northern Shoveler | -51 | -62 | -57 |
| Northern Pintail | -45 | -37 | -41 |
| Green-winged Teal | -46 | -18 | -32 |
| Redhead | -42 | -35 | -39 |
| Ruddy Duck | -30 | -31 | -31 |
| Pied-billed Grebe | -40 | -18 | -29 |
| Double-crested Cormorant | -11 | -20 | -16 |
| American Bittern | -42 | -42 | -42 |
| Great-blue Heron | -72 | -82 | -77 |
| Sora | -94 | -98 | -96 |

| | | | |
|-------------------------|-----|------|------|
| American Coot | -38 | -38 | -38 |
| Killdeer | 5 | 0 | 3 |
| Upland Sandpiper | 8 | 7 | 8 |
| Willet | -43 | -58 | -51 |
| Marbled Godwit | -53 | -61 | -57 |
| Wilson's Snipe | -99 | -100 | -100 |
| Wilson's Phalarope | -42 | -60 | -51 |
| Franklin's Gull | -93 | -98 | -96 |
| Ring-billed Gull | -39 | -83 | -61 |
| Black Tern | -67 | -64 | -66 |
| Sedge Wren | -71 | -60 | -66 |
| Marsh Wren | -40 | -42 | -41 |
| Common Yellowthroat | -26 | -35 | -31 |
| Song Sparrow | -38 | -41 | -40 |
| Yellow-headed Blackbird | -24 | -25 | -25 |

Table 1.4. Variable importance for Random Forest species distribution models. Top ten variables are shown in descending order of rank. Variable categories were denoted by W (wetland), U (upland), P (precipitation), and T (temperature). Signs indicated the relationship between the predictor and the species response: + (positive), - (negative), m (unimodal), and ~ (equivocal).

| Rank | Canada Goose | Wood Duck | Gadwall | American Wigeon | Mallard | Blue-winged Teal | Northern Shoveler | Northern Pintail | Green-winged Teal |
|------|--------------|--------------|--------------|-----------------|--------------|------------------|-------------------|------------------|-------------------|
| 1 | W-lake(+) | W-temp(-) | T-5yr_sd(-) | W-lake(+) | W-pal(+) | W-total(+) | W-pal(+) | U-tree(-) | U-tree(-) |
| 2 | P-wint(+) | P-wint(+) | P-10yr_sd(-) | U-tree(-) | W-semi(+) | W-pal(+) | W-total(+) | W-pal(+) | P-wint(+) |
| 3 | W-river(-) | U-grass(-) | U-tree(-) | W-semi(+) | W-river(-) | W-seas(+) | W-semi(+) | P-10yr(-) | W-lake(+) |
| 4 | T-sum(-) | U-crop(-) | T-spr(-) | W-temp(-) | W-total(+) | W-semi(+) | W-temp(+) | W-seas(+) | W-seas(+) |
| 5 | T-spr(-) | U-tree(+) | U-grass(+) | P-5yr(-) | T-10yr_sd(+) | U-grass(+) | W-seas(+) | W-semi(+) | U-crop(-) |
| 6 | T-10yr_sd(+) | U-devel(-) | P-10yr(m) | P-spr(-) | W-temp(+) | W-temp(+) | U-tree(-) | P-5yr(-) | P-fall(~) |
| 7 | T-10yr(m) | W-semi(+) | U-crop(-) | W-pal(+) | U-tree(-) | U-tree(-) | U-crop(-) | U-grass(+) | W-shrub(-) |
| 8 | T-5yr(m) | T-10yr_sd(+) | T-10yr_sd(+) | W-total(+) | T-spr(-) | W-river(-) | U-grass(+) | W-river(-) | W-temp(+) |
| 9 | T-1yr(-) | T-sum(~) | W-total(+) | P-10yr(-) | U-grass(+) | U-crop(-) | T-spr(-) | T-spr(-) | P-5yr(-) |
| 10 | W-total(+) | W-total(+) | W-river(-) | P-1yr(-) | T-5yr_sd(+) | P-10yr(-) | P-10yr(-) | W-total(+) | T-5yr(-) |

| Rank | Redhead | Ruddy Duck | Pied-billed Grebe | Double-crested Cormorant | American Bittern | Great-blue Heron | Sora | American Coot | Killdeer |
|------|------------|------------|-------------------|--------------------------|------------------|------------------|------------|---------------|------------|
| 1 | W-semi(+) | W-semi(+) | W-semi(+) | W-semi(+) | U-crop(-) | T-spring(-) | P-10yr(-) | W-semi(+) | W-semi(+) |
| 2 | W-total(+) | W-total(+) | W-total(+) | U-tree(~) | W-total(+) | P-10yr(+) | T-sum(-) | W-total(+) | W-pal(+) |
| 3 | W-lake(+) | W-lake(+) | W-pal(+) | W-temp(-) | U-grass(+) | U-tree(+) | T-5yr(-) | W-pal(+) | W-river(-) |
| 4 | U-tree(-) | W-pal(+) | W-seas(+) | T-10yr_sd(+) | W-semi(+) | P-5yr(+) | W-seas(+) | W-seas(+) | U-tree(-) |
| 5 | W-temp(-) | U-tree(-) | U-crop(-) | W-lake(+) | W-pal(+) | P-spr(+) | T-1yr(-) | W-river(-) | W-total(+) |
| 6 | W-pal(+) | W-seas(+) | W-lake(+) | T-5yr(~) | W-seas(+) | P-1yr(+) | W-river(-) | P-10yr(-) | W-seas(+) |
| 7 | W-river(-) | W-river(-) | T-10yr_sd(+) | P-5yr(+) | P-10yr(-) | T-10yr(-) | W-total(+) | W-lake(+) | U-devel(-) |
| 8 | W-seas(+) | W-temp(-) | U-grass(+) | P-spr(-) | T-5yr(-) | W-shrub(+) | W-pal(+) | U-crop(-) | P-wint(~) |
| 9 | U-crop(-) | U-crop(-) | T-sum(-) | P-fall(~) | T-sum(-) | P-sum(+) | P-5yr(-) | U-grass(+) | W-temp(+) |
| 10 | U-grass(+) | U-grass(+) | U-tree(-) | T-5yr_sd(-) | T-1yr(-) | T-1yr(-) | U-grass(+) | T-5yr(-) | U-grass(+) |

| Rank | Upland Sandpiper | Willet | Marbled Godwit | Wilson's Snipe | Wilson's Phalarope | Franklin's Gull | Ring-billed Gull | Black Tern | Sedge Wren |
|------|------------------|------------|----------------|----------------|--------------------|-----------------|------------------|------------|--------------|
| 1 | W-seas(+) | U-tree(-) | U-tree(-) | T-5yr(-) | U-tree(-) | U-tree(+) | W-semi(+) | W-seas(+) | P-10yr_sd(-) |
| 2 | U-grass(+) | P-10yr(-) | U-crop(-) | T-10yr(-) | U-grass(+) | W-pal(+) | W-lake(+) | W-pal(+) | U-tree(+) |
| 3 | U-tree(-) | P-5yr(-) | W-lake(+) | W-total(+) | U-crop(-) | T-10yr(-) | W-pal(+) | W-total(+) | U-crop(-) |
| 4 | P-10yr(-) | U-grass(+) | W-total(+) | U-crop(-) | P-10yr(-) | W-total(+) | W-total(+) | W-semi(+) | P-10yr(+) |
| 5 | W-pal(+) | W-pal(+) | P-10yr(-) | W-pal(+) | P-5yr(-) | W-seas(m) | U-tree(-) | W-temp(+) | T-sum(-) |
| 6 | U-devel(-) | W-semi(+) | U-grass(+) | W-lake(+) | W-lake(m) | U-grass(~) | U-grass(+) | U-crop(-) | P-5yr(+) |
| 7 | W-river(-) | W-total(+) | T-10yr(-) | T-sum(-) | W-semi(+) | W-temp(+) | P-5yr(-) | P-10yr(-) | T-10yr_sd(+) |
| 8 | U-crop(-) | U-crop(-) | P-5yr(-) | U-tree(~) | W-seas(+) | W-lake(+) | W-seas(+) | T-5yr(-) | W-pal(+) |
| 9 | W-semi(+) | T-10yr(-) | W-semi(+) | W-river(-) | P-spr(~) | U-crop(-) | W-river(-) | P-wint(+) | U-grass(+) |
| 10 | P-5yr(-) | W-river(-) | W-river(-) | W-seas(~) | W-total(+) | P-sum(~) | T-5yr(-) | P-5yr(m) | P-1yr(+) |

| Rank | Marsh Wren | Common Yellow- throat | Song Sparrow | Yellow- headed Blackbird |
|------|------------|-----------------------------|-----------------|--------------------------------|
| 1 | W-semi(+) | W-total(+) | U-grass(-) | W-semi(+) |
| 2 | W-total(+) | W-temp(+) | U-crop(+) | W-pal(+) |
| 3 | W-pal(+) | W-seas(+) | U-tree(+) | W-total(+) |
| 4 | U-crop(-) | W-pal(+) | P-10yr(+) | W-seas(+) |
| 5 | W-seas(+) | U-tree(+) | W-semi(-) | U-grass(+) |
| 6 | U-grass(+) | W-semi(+) | P-sum(+) | P-10yr(-) |
| 7 | W-lake(+) | U-devel(-) | T-10yr_sd(+) | U-crop(-) |
| 8 | T-sum(-) | W-lake(+) | T-sum(-) | T-sum(-) |
| 9 | W-river(-) | T-5yr(-) | T-10yr(-) | U-tree(-) |
| 10 | T-10yr(-) | P-5yr_sd(-) | P-5yr(+) | P-5yr(-) |

Table 1.5. Variable importance from 22 Random Forest species distribution models for the particularly dry period, 1987-1992. Top ten variables shown in descending order of rank. Variable categories were denoted by W (wetland), U (upland), P (precipitation), and T (temperature). Signs indicated the relationship between the predictor and the species response: + (positive), - (negative), m (unimodal), and ~ (equivocal).

| Rank | Canada Goose | Mallard | Blue-winged Teal | Northern Shoveler | Northern Pintail | Pied-billed Grebe | American Bittern | Sora | American Coot |
|------|--------------|------------|------------------|-------------------|------------------|-------------------|------------------|--------------|---------------|
| 1 | P-5yr_sd(+) | W-semi(+) | W-total(+) | W-semi(+) | U-tree(-) | W-lake(+) | U-grass(+) | T-10yr_sd(+) | W-semi(+) |
| 2 | T-sum(+) | W-total(+) | W-semi(+) | T-1yr(m) | W-semi(+) | U-crop(-) | W-semi(+) | T-sum(-) | W-lake(+) |
| 3 | T-spr(-) | W-pal(+) | U-crop(-) | T-wint(m) | T-spr(-) | U-grass(+) | W-total(+) | W-river(-) | W-total(+) |
| 4 | T-10yr(-) | W-river(-) | W-lake(+) | W-total(+) | P-10yr(-) | W-semi(+) | U-crop(-) | W-total(+) | W-pal(+) |
| 5 | P-10yr_sd(-) | U-crop(-) | P-fall(+) | W-lake(+) | T-1yr(-) | W-seas(m) | W-lake(+) | P-5yr_sd(-) | U-crop(-) |
| 6 | T-1yr(-) | P-10yr(-) | W-pal(+) | P-10yr_sd(-) | P-fall(+) | W-total(+) | W-pal(+) | W-pal(+) | T-5yr_sd(+) |
| 7 | T-wint(-) | W-temp(+) | U-grass(+) | T-5yr(-) | W-total(+) | T-wint(+) | T-sum(-) | W-seas(+) | T-10yr_sd(+) |
| 8 | T-5yr(-) | T-wint(+) | T-wint(+) | U-crop(-) | T-5yr(-) | P-5yr_sd(-) | U-devel(-) | U-tree(-) | P-spr(-) |
| 9 | W-seas(-) | T-spr(~) | P-sum(+) | T-10yr(-) | T-wint(-) | W-pal(+) | P-fall(+) | W-temp(+) | W-temp(+) |
| 10 | P-10yr(-) | W-shrub(-) | T-sum(-) | W-seas(-) | W-pal(+) | U-devel(-) | W-seas(+) | W-lake(+) | W-seas(m) |

| Rank | Killdeer | Upland Sandpiper | Willet | Marbled Godwit | Wilson's Snipe | Franklin's Gull | Ring-billed Gull | Black Tern | Sedge Wren |
|------|--------------|------------------|--------------|----------------|----------------|-----------------|------------------|-------------|--------------|
| 1 | P-10yr_sd(-) | U-grass(+) | P-10yr(-) | W-lake(+) | W-lake(+) | W-total(+) | W-lake(+) | U-crop(-) | T-sum(-) |
| 2 | T-5yr_sd(-) | U-tree(-) | P-5yr(-) | U-tree(-) | W-total(+) | W-lake(+) | U-crop(-) | W-pal(+) | W-total(+) |
| 3 | U-grass(+) | W-seas(+) | W-total(+) | W-total(+) | T-10yr(-) | T-10yr(-) | P-fall(+) | W-lake(-) | T-1yr(-) |
| 4 | U-devel(+) | U-crop(-) | U-tree(-) | P-10yr(-) | T-5yr(-) | P-fall(~) | P-10yr(-) | W-temp(+) | T-10yr_sd(-) |
| 5 | T-fall(-) | P-10yr(-) | W-semi(+) | U-crop(-) | P-5yr_sd(-) | P-5yr_sd(+) | P-spr(-) | W-semi(+) | W-lake(+) |
| 6 | W-semi(+) | W-total(+) | W-pal(+) | W-river(-) | W-temp(+) | T-10yr_sd(-) | U-grass(+) | T-5yr_sd(+) | T-10yr(-) |
| 7 | T-sum(+) | W-pal(+) | W-seas(+) | T-10yr(-) | T-1yr(-) | T-spr(-) | P-5yr(-) | W-total(+) | U-crop(-) |
| 8 | U-tree(-) | W-semi(+) | P-10yr_sd(-) | P-5yr(-) | U-tree(-) | T-5yr(-) | T-fall(-) | T-spr(-) | P-10yr(+) |
| 9 | T-5yr(-) | W-temp(+) | T-sum(m) | T-5yr(-) | W-seas(-) | T-1yr(-) | P-10yr(-) | T-fall(m) | P-5yr(+) |
| 10 | P-1yr(-) | T-wint(+) | U-crop(-) | W-pal(+) | T-spr(-) | U-devel(-) | P-10yr_sd(-) | T-5yr(-) | W-forest(+) |

| Rank | Marsh Wren | Common Yellow- throat | Song Sparrow | Yellow- headed Blackbird |
|------|---------------|-----------------------------|-----------------|--------------------------------|
| 1 | W-semi(+) | W-semi(+) | U-grass(-) | W-semi(+) |
| 2 | W-total(+) | U-crop(-) | U-tree(+) | P-10yr(-) |
| 3 | W-lake(+) | W-temp(+) | W-semi(-) | W-pal(+) |
| 4 | U-grass(+) | W-pal(+) | U-crop(+) | W-total(+) |
| 5 | W-pal(+) | W-total(+) | P-sum(+) | P-5yr(-) |
| 6 | U-crop(-) | U-tree(+) | P-10yr(+) | W-seas(+) |
| 7 | T-10yr(+) | P-5yr_sd(-) | P-1yr(+) | U-crop(-) |
| 8 | T-fall(+) | W-lake(+) | U-devel(+) | U-grass(+) |
| 9 | T-5yr(+) | T-5yr(-) | T-10yr(-) | P-10yr_sd(-) |
| 10 | W-seas(-) | W-seas(+) | T-5yr(-) | U-tree(-) |

LITERATURE CITED

- Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* **43**:1223-1232.
- Araujo, M. B., R. G. Pearson, W. Thuiller, and M. Erhard. 2005a. Validation of species-climate impact models under climate change. *Global Change Biology* **11**:1504-1513.
- Araujo, M. B., R. J. Whittaker, R. J. Ladle, and M. Erhard. 2005b. Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography* **14**:529-538.
- Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* **157**:101-118.
- Austin, M. P. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling* **200**:1-19.
- Ballard, T., R. Seager, J. E. Smerdon, B. I. Cook, A. J. Ray, B. Rajagopalan, Y. Kushnir, J. Nakamura, and N. Henderson. 2014. Hydroclimate Variability and Change in the Prairie Pothole Region, the "Duck Factory" of North America. *Earth Interactions* **18**.
- Barbet-Massin, M., B. A. Walther, W. Thuiller, C. Rahbek, and F. Jiguet. 2009. Potential impacts of climate change on the winter distribution of Afro-Palaeartic migrant passerines. *Biology Letters* **5**:248-251.
- Bates, D., M. Machler, B. M. Bolker, and S. C. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* **67**:1-48.
- Beaumont, L. J., L. Hughes, and M. Poulsen. 2005. Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecological Modelling* **186**:250-269.

- Beerli, O. and R. L. Phillips. 2007. Tracking palustrine water seasonal and annual variability in agricultural wetland landscapes using Landsat from 1997 to 2005. *Global Change Biology* **13**:897-912.
- Beyersbergen, G. W., N. D. Niemuth, and M. R. Norton. 2004. Northern Prairie and Parkland waterbird conservation plan. A plan associated with the Waterbird Conservation for the Americas initiative. Prairie Pothole Joint Venture, Denver, CO, USA.
- Booth, T. H., H. A. Nix, J. R. Busby, and M. F. Hutchinson. 2014. BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MAXENT studies. *Diversity and Distributions* **20**:1-9.
- Braunisch, V., J. Coppes, R. Arlettaz, R. Suchant, H. Schmid, and K. Bollmann. 2013. Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change. *Ecography* **36**:971-983.
- Brekke, L., B. Thrasher, E. Maurer, and T. Pruitt. 2013. Downscaled CMIP3 and CMIP5 climate and hydrology projections: Release of downscaled CMIP5 climate projections, comparison with preceding information, and summary of user needs. US Dept. of the Interior, Bureau of Reclamation, Technical Services Center, Denver.
- Buisson, L., W. Thuiller, N. Casajus, S. Lek, and G. Grenouillet. 2010. Uncertainty in ensemble forecasting of species distribution. *Global Change Biology* **16**:1145-1157.
- Cramer, J. S. 1999. Predictive performance of the binary logit model in unbalanced samples. *Journal of the Royal Statistical Society Series D-the Statistician* **48**:85-94.
- Dahl, T. E. 1990. Wetlands losses in the United States 1780's to 1980's. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C.
- Dillane, D. M. 2006. Deletion diagnostics for the linear mixed model. Trinity College.
- Dormann, C. F. 2007. Promising the future? Global change projections of species distributions. *Basic and Applied Ecology* **8**:387-397.

- Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carre, J. R. G. Marquez, B. Gruber, B. Laffourcade, P. J. Leitaó, T. Munkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schroder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**:27-46.
- Elith, J., M. Kearney, and S. Phillips. 2010. The art of modelling range-shifting species. *Methods in Ecology and Evolution* **1**:330-342.
- Elith, J. and J. R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology Evolution and Systematics* **40**:677-697.
- Euliss, N. H., D. A. Wrubleski, and D. M. Mushet. 1999. Wetlands of the Prairie Pothole Region: invertebrate species composition, ecology, and management.
- Fielding, A. H. and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**:38-49.
- Fischelli, N., G. Schuurman, A. Symstad, A. Ray, B. Miller, M. Cross, and E. Rowland. 2016. Resource management and operations in southwest South Dakota: Climate change scenario planning workshop summary January 20-21, 2016, Rapid City, SD. Natural Resource Report. National Park Service, Fort Collins, CO.
- Fletcher, J., Robert J and R. R. Koford. 2004. Consequences of rainfall variation for breeding wetland blackbirds. *Canadian Journal of Zoology* **82**:1316-1325.
- Fordham, D. A., H. R. Akcakaya, M. B. Araujo, D. A. Keith, and B. W. Brook. 2013. Tools for integrating range change, extinction risk and climate change information into conservation management. *Ecography* **36**:956-964.
- Freeman, E. A. and G. G. Moisen. 2008. A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecological Modelling* **217**:48-58.

- Garcia, R. A., N. D. Burgess, M. Cabeza, C. Rahbek, and M. B. Araujo. 2012. Exploring consensus in 21st century projections of climatically suitable areas for African vertebrates. *Global Change Biology* **18**:1253-1269.
- Gaston, K. J. 2003. *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford.
- Green, R. E., Y. C. Collingham, S. G. Willis, R. D. Gregory, K. W. Smith, and B. Huntley. 2008. Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. *Biology Letters* **4**:599-602.
- Gregory, R. D., S. G. Willis, F. Jiguet, P. Vorisek, A. Klvanova, A. van Strien, B. Huntley, Y. C. Collingham, D. Couvet, and R. E. Green. 2009. An Indicator of the Impact of Climatic Change on European Bird Populations. *Plos One* **4**.
- Hawkins, E. and R. Sutton. 2009. The potential to narrow uncertainty in regional climate predictions. *Bulletin of the American Meteorological Society* **90**:1095.
- Heikkinen, R. K., M. Luoto, M. B. Araujo, R. Virkkala, W. Thuiller, and M. T. Sykes. 2006a. Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography* **30**:751-777.
- Heikkinen, R. K., M. Luoto, and R. Virkkala. 2006b. Does seasonal fine-tuning of climatic variables improve the performance of bioclimatic envelope models for migratory birds? *Diversity and Distributions* **12**:502-510.
- Heikkinen, R. K., M. Marmion, and M. Luoto. 2012. Does the interpolation accuracy of species distribution models come at the expense of transferability? *Ecography* **35**:276-288.
- Jimenez-Valverde, A., N. Barve, A. Lira-Noriega, S. P. Maher, Y. Nakazawa, M. Papes, J. Soberon, J. Sukumaran, and A. T. Peterson. 2011. Dominant climate influences on North American bird distributions. *Global Ecology and Biogeography* **20**:114-118.

- Jimenez-Valverde, A. and J. M. Lobo. 2007. Threshold criteria for conversion of probability of species presence to either-or presence-absence. *Acta Oecologica-International Journal of Ecology* **31**:361-369.
- Johnson, D. H. and J. W. Grier. 1988. Determinants of Breeding Distributions of Ducks. *Wildlife Monographs*:1-37.
- Johnson, R. R., F. T. Oslund, and D. R. Hertel. 2008. The past, present, and future of prairie potholes in the United States. *Journal of Soil and Water Conservation* **63**:84a-87a.
- Johnson, W. C., S. E. Boettcher, K. A. Poiani, and G. Guntenspergen. 2004. Influence of weather extremes on the water levels of glaciated prairie wetlands. *Wetlands* **24**:385-398.
- Johnson, W. C., B. Werner, G. R. Guntenspergen, R. A. Voldseth, B. Millett, D. E. Naugle, M. Tulbure, R. W. H. Carroll, J. Tracy, and C. Olawsky. 2010. Prairie Wetland Complexes as Landscape Functional Units in a Changing Climate. *Bioscience* **60**:128-140.
- Kantrud, H. A., G. L. Krapu, and G. A. Swanson. 1989. Prairie basin wetlands of the Dakotas : a community profile. U.S. Dept. of the Interior, Fish and Wildlife Service, Research and Development, Washington, DC.
- Kantrud, H. A. and R. E. Stewart. 1984. Ecological Distribution and Crude Density of Breeding Birds on Prairie Wetlands. *Journal of Wildlife Management* **48**:426-437.
- Knutti, R., R. Furrer, C. Tebaldi, J. Cermak, and G. A. Meehl. 2010. Challenges in Combining Projections from Multiple Climate Models. *Journal of Climate* **23**:2739-2758.
- Knutti, R. and J. Sedlacek. 2013. Robustness and uncertainties in the new CMIP5 climate model projections. *Nature Clim. Change* **3**:369-373.
- Konar, M., M. J. Todd, R. Muneeppeerakul, A. Rinaldo, and I. Rodriguez-Iturbe. 2013. Hydrology as a driver of biodiversity: Controls on carrying capacity, niche formation, and dispersal. *Advances in Water Resources* **51**:317-325.

- Kuhn, M. and K. Johnson. 2013. Applied predictive modeling. Springer, New York.
- Kutner, M. H., C. Nachtsheim, and J. Neter. 2004. Applied linear regression models. 4th edition. McGraw-Hill/Irwin, Boston ; New York.
- Larson, D. L. 1995. Effects of Climate on Numbers of Northern Prairie Wetlands. *Climatic Change* **30**:169-180.
- Lawler, J. J., S. L. Shafer, D. White, P. Kareiva, E. P. Maurer, A. R. Blaustein, and P. J. Bartlein. 2009. Projected climate-induced faunal change in the Western Hemisphere. *Ecology* **90**:588-597.
- Lawler, J. J., D. White, R. P. Neilson, and A. R. Blaustein. 2006. Predicting climate-induced range shifts: model differences and model reliability. *Global Change Biology* **12**:1568-1584.
- Leppi, J. C., D. J. Rinella, R. R. Wilson, and W. M. Loya. 2014. Linking climate change projections for an Alaskan watershed to future coho salmon production. *Global Change Biology* **20**:1808-1820.
- Liang, X. 1994. A two-layer variable infiltration capacity land surface representation for general circulation models.
- Linz, G. M., D. C. Blixt, D. L. Bergman, and W. J. Bleier. 1996. Responses of Red-winged Blackbirds, Yellow-headed Blackbirds and Marsh Wrens to glyphosate-induced alterations in cattail density. *Journal of Field Ornithology* **67**:167-176.
- Liu, C. R., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**:385-393.
- Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* **38**:921-931.
- Marmion, M., M. Parviainen, M. Luoto, R. K. Heikkinen, and W. Thuiller. 2009. Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions* **15**:59-69.

- Maurer, E. P., L. Brekke, T. Pruitt, and P. B. Duffy. 2007. Fine-resolution climate projections enhance regional climate change impact studies. *Eos, Transactions American Geophysical Union* **88**:504-504.
- McEvoy, D. J., J. L. Huntington, M. T. Hobbins, A. Wood, C. Morton, J. Verdin, M. Anderson, and C. Hain. 2016. The Evaporative Demand Drought Index: Part II—CONUS-wide Assessment Against Common Drought Indicators. *Journal of Hydrometeorology*.
- Millett, B., W. C. Johnson, and G. Guntenspergen. 2009. Climate trends of the North American prairie pothole region 1906-2000. *Climatic Change* **93**:243-267.
- Murkin, H. R., E. J. Murkin, and J. P. Ball. 1997. Avian habitat selection and prairie wetland dynamics: a 10-year experiment. *Ecological Applications* **7**:1144-1159.
- Nenzen, H. K. and M. B. Araujo. 2011. Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling* **222**:3346-3354.
- Niemuth, N. D. and J. W. Solberg. 2003. Response of waterbirds to number of wetlands in the Prairie Pothole Region of North Dakota, USA. *Waterbirds* **26**:233-238.
- Niemuth, N. D., B. Wangler, and R. E. Reynolds. 2010. Spatial and Temporal Variation in Wet Area of Wetlands in the Prairie Pothole Region of North Dakota and South Dakota. *Wetlands* **30**:1053-1064.
- Pearson, R. G. and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* **12**:361-371.
- Peterson, A. T. and Y. Nakazawa. 2008. Environmental data sets matter in ecological niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*. *Global Ecology and Biogeography* **17**:135-144.
- Peterson, G. D., G. S. Cumming, and S. R. Carpenter. 2003. Scenario planning: a tool for conservation in an uncertain world. *Conservation Biology* **17**:358-366.

- Pliscoff, P., F. Luebert, H. H. Hilger, and A. Guisan. 2014. Effects of alternative sets of climatic predictors on species distribution models and associated estimates of extinction risk: A test with plants in an arid environment. *Ecological Modelling* **288**:166-177.
- R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computer, Vienna, Austria.
- Rapacciuolo, G., D. B. Roy, S. Gillings, R. Fox, K. Walker, and A. Purvis. 2012. Climatic Associations of British Species Distributions Show Good Transferability in Time but Low Predictive Accuracy for Range Change. *Plos One* **7**.
- Reside, A. E., J. J. VanDerWal, A. S. Kutt, and G. C. Perkins. 2010. Weather, Not Climate, Defines Distributions of Vagile Bird Species. *Plos One* **5**.
- Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2011. The North American Breeding Bird Survey, Results and Analysis 1966-2010. USGS Patuxent Wildlife Research Center, Laurel, MD.
- Schlaepfer, D. R., W. K. Lauenroth, and J. B. Bradford. 2012. Effects of ecohydrological variables on current and future ranges, local suitability patterns, and model accuracy in big sagebrush. *Ecography* **35**:374-384.
- Shjeflo, J. B. 1968. Evapotranspiration and the water budget of prairie potholes in North Dakota. U.S. Govt. Print. Off., Washington, D.C.
- Smith, A. B., M. J. Santos, M. S. Koo, K. M. C. Rowe, K. C. Rowe, J. L. Patton, J. D. Perrine, S. R. Beissinger, and C. Moritz. 2013. Evaluation of species distribution models by resampling of sites surveyed a century ago by Joseph Grinnell. *Ecography* **36**:1017-1031.
- Smith, R. I. 1970. Response of Pintail Breeding Populations to Drought. *Journal of Wildlife Management* **34**:943-946.

- Snover, A. K., N. J. Mantua, J. S. Littell, M. A. Alexander, M. M. McClure, and J. Nye. 2013. Choosing and Using Climate-Change Scenarios for Ecological-Impact Assessments and Conservation Decisions. *Conservation Biology* **27**:1147-1157.
- Sofaer, H. R., S. K. Skagen, J. J. Barsugli, B. S. Rashford, G. C. Reese, J. A. Hoeting, A. W. Wood, and B. R. Noon. 2016. Projected wetland densities under climate change: habitat loss but little geographic shift in conservation strategy. *Ecological Applications*.
- Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. Averyt, M. Tignor, and H. L. Miller. 2007. IPCC, 2007: Climate change 2007: The physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. SD Solomon (Ed.).
- Steen, V., S. K. Skagen, and B. R. Noon. 2014. Vulnerability of Breeding Waterbirds to Climate Change in the Prairie Pothole Region, USA. *Plos One* **9**.
- Steen, V. A. and A. N. Powell. 2012. Wetland Selection by Breeding and Foraging Black Terns in the Prairie Pothole Region of the United States. *Condor* **114**:155-165.
- Steen, V. A., S. K. Skagen, and C. P. Melcher. 2016. Implications of Climate Change for Wetland-Dependent Birds in the Prairie Pothole Region. *Wetlands*:1-15.
- Stewart, R. E. and H. A. Kantrud. 1973. Ecological Distribution of Breeding Waterfowl Populations in North-Dakota. *Journal of Wildlife Management* **37**:39-50.
- Stralberg, D., S. M. Matsuoka, A. Hamann, E. M. Bayne, P. Solymos, F. K. A. Schmiegelow, X. Wang, S. G. Cumming, and S. J. Song. 2015. Projecting boreal bird responses to climate change: the signal exceeds the noise. *Ecological Applications* **25**:52-69.
- Synes, N. W. and P. E. Osborne. 2011. Choice of predictor variables as a source of uncertainty in continental-scale species distribution modelling under climate change. *Global Ecology and Biogeography* **20**:904-914.

- Thorne, J. H., C. Seo, A. Basabose, M. Gray, N. M. Belfiore, and R. J. Hijmans. 2013. Alternative biological assumptions strongly influence models of climate change effects on mountain gorillas. *Ecosphere* **4**.
- Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology* **10**:2020-2027.
- Thuiller, W., B. Lafourcade, R. Engler, and M. B. Araujo. 2009. BIOMOD - a platform for ensemble forecasting of species distributions. *Ecography* **32**:369-373.
- Thuiller, W., S. Lavorel, M. B. Araujo, M. T. Sykes, and I. C. Prentice. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America* **102**:8245-8250.
- Trenberth, K. 2010. More knowledge, less certainty. *Nature reports climate change*:20-21.
- van der Valk, A. G. 2005. Water-level fluctuations in North American prairie wetlands. *Hydrobiologia* **539**:171-188.
- van der Valk, A. G. and C. B. Davis. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology*:322-335.
- Warton, D. I. and F. K. C. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* **92**:3-10.
- Weller, M. W. and C. S. Spatcher. 1965. Role of habitat in the distribution and abundance of marsh birds. Ames, Iowa.
- Wenger, S. J., N. A. Som, D. C. Dauwalter, D. J. Isaak, H. M. Neville, C. H. Luce, J. B. Dunham, M. K. Young, K. D. Fausch, and B. E. Rieman. 2013. Probabilistic accounting of uncertainty in forecasts of species distributions under climate change. *Global Change Biology* **19**:3343-3354.
- Winter, T. C. and D. O. Rosenberry. 1998. Hydrology of prairie pothole wetlands during drought and deluge: a 17-year study of the Cottonwood Lake wetland complex in North Dakota in the

- perspective of longer term measured and proxy hydrological records. *Climatic Change* **40**:189-209.
- Wood, A. W., L. R. Leung, V. Sridhar, and D. P. Lettenmaier. 2004. Hydrologic implications of dynamical and statistical approaches to downscaling climate model outputs. *Climatic Change* **62**:189-216.
- Woodhouse, C. A. and J. T. Overpeck. 1998. 2000 years of drought variability in the central United States. *Bulletin of the American Meteorological Society* **79**:2693-2714.
- Zhang, B., F. W. Schwartz, and G. Liu. 2009. Systematics in the size structure of prairie pothole lakes through drought and deluge. *Water Resources Research* **45**.
- Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**:3-14.

CHAPTER 2: PROJECTING AVIAN VULNERABILITY TO CLIMATE CHANGE: EXPLORING UNCERTAINTY FROM MODELING DECISIONS

INTRODUCTION

Bioclimatic species distribution models (SDMs) are useful tools for assessing the potential impacts of future climate change on biological diversity (Thuiller et al. 2005, Barbet-Massin et al. 2009, Lawler et al. 2009). These models relate species location data to climate covariates to derive probabilities of occurrence over a range of climatic conditions. When applied to future climate data, projected species distributions may shift spatially, and ranges may contract or expand. Recognizing the limitation of SDMs because of failure to adequately address interspecific interactions, phenotypic plasticity, or evolutionary change is important (Pearson and Dawson 2003). However, unavoidable decisions made during model development including the choice of model algorithm and covariates produce substantial uncertainty and may even exceed the uncertainty in future climate change itself (Thuiller 2004, Buisson et al. 2010, Synes and Osborne 2011, Garcia et al. 2012). These choices, integral to conventional climate change impacts assessments, are a key area for improvement in projecting future distributions of species.

One source of model variability that has been underexplored is that associated with selection of climate covariates (Gaston 2003, Synes and Osborne 2011, Pliscoff et al. 2014). Although guidelines exist, in practice, data and knowledge limitations may overshadow the selection process (Gaston 2003, Austin 2007, Dormann 2007). To structure our thinking and study, we define three types of climate covariates: temporal, bioclimatic, and hydrological. These can also be considered working hypotheses of how climate explains organismal distribution. Temporal covariates represent monthly, seasonal, and annual variation in temperature and precipitation such as spring average temperature or yearly total precipitation and may be thought of as a general hypothesis that climate drives organismal distribution

via multiple temporal scales and the variability therein. Bioclimatic covariates represent extremes and variability in temperature and precipitation and may include, for example, precipitation of the driest quarter or the range in annual temperature. These covariates were originally developed to describe process-based climatic relationships with plant growth (Booth et al. 2014), but have since been widely applied to model the distribution of animal species as well (e.g. Lawler et al. 2006, Green et al. 2008, Gregory et al. 2009, Elith et al. 2010, Jimenez-Valverde et al. 2011). Hydrological covariates describe water availability, integrating the effects of precipitation and temperature. Because precipitation is not a reliable representation of water availability and many ecological processes are water limited, hydrological variables may more directly relate to ecological response (McEvoy et al. 2016). Drought or moisture indices, for example, have been explored by some researchers (Austin 2007, Schlaepfer et al. 2012, Konar et al. 2013).

The potential for the covariance relationships among climate covariates to change further complicates the selection of which climate covariates to include in SDMs. A common practice in predictive species distribution modeling is to first filter candidate covariates to minimize collinearity to mitigate against overfitting (Beaumont et al. 2005) and thus potentially improve projections to future times or novel locations (Beaumont et al. 2005, Heikkinen et al. 2012, Dormann et al. 2013). However, because statistically high performing variables may belie true causal relationships between climate and distribution, statistical criteria will not reliably lead to selecting the better covariate (Austin 2002, Heikkinen et al. 2006a). Because climate variables may not change in a parallel fashion, the current covariance structure among climate covariates may not be representative of the future structure making collinearity a potential asset for mitigating error in climate change projections, in contrast to conventional wisdom (Braunisch et al. 2013).

An additional source of methodological uncertainty - threshold choice - is invoked when creating maps of species distributions. To estimate range change, extinction risk, or assess areas of high conservation value, continuous probability values traditionally are thresholded to create binary predictions of presence and absence. However, the choice of thresholding procedure can also produce substantial uncertainty in projections of climate change impacts (Nenzen and Araujo 2011). While guidance exists for thresholding predictions under a static climate (Fielding and Bell 1997, Liu et al. 2005, Jimenez-Valverde and Lobo 2007, Freeman and Moisen 2008), we are not aware of any such assessment for a changing climate.

Future climate change uncertainty is inherent uncertainty in climate change impacts research. GCM projections provide a range of plausible futures with variability in GCM projections having two underlying sources beyond natural interannual variability: the level of greenhouse gas emissions and the GCMs themselves. The Intergovernmental Panel on Climate Change (IPCC) produces several scenarios describing different emissions pathways and does not take a position on which one is the most likely (Solomon et al. 2007). GCM uncertainty results from different GCMs representing physical processes differently. The state of the science of climate modeling is such that this range of uncertainty is unlikely to narrow significantly in the near future (Hawkins and Sutton 2009, Trenberth 2010, Knutti and Sedlacek 2013) with natural variability and GCM uncertainty dominating scenario uncertainty until around mid-21st century (Hawkins and Sutton 2009). Thus, currently it is recommended that ecologists address plausible future climatic outcomes by selecting a range of GCMs and for projections extending beyond mid-century include different emissions scenarios as well (Knutti et al. 2010).

An additional challenge for species distribution modeling is selecting models that can be generalized across space and time. Because the future is unknowable, most studies assess model performance by partitioning one dataset into training and testing data to “cross-validate”. Cross-validation is not as rigorous as validation based on truly independent data, thus, the ability of SDMs to

reliably extrapolate outside the spatial extent or temporal time frame of the training data is only weakly evaluated (Elith and Leathwick 2009). Furthermore, high model performance in cross-validation tests may result from a model that closely fits noise in the data (Heikkinen et al. 2012). Importantly, some recent studies tested the generalizability of differing model algorithms using spatially or temporally independent test datasets (Araujo et al. 2005a, Heikkinen et al. 2012, Rapacciuolo et al. 2012, Smith et al. 2013). However, the generalizability of other methodological decisions remains underexplored.

To evaluate the uncertainty in projections of climate-driven distributional changes, we developed SDMs for wetland-dependent birds breeding in a climatically variable landscape - the Prairie Potholes of the northern Great Plains of North America. Prairie Pothole habitats are highly dynamic, reflecting recent climatic conditions by varying in number, size, and vegetative cover on an annual basis (Larson 1995, Johnson et al. 2010, Niemuth et al. 2010) with distribution of migratory birds reflective of current year's wetland conditions (Smith 1970, Johnson and Grier 1988, Niemuth and Solberg 2003, Fletcher and Koford 2004). Our bird occurrence dataset represents a long times series and includes extensive climatic variation from flood to drought conditions. This allowed us to predict to pronounced drought periods in the historic dataset based on models trained to more normal climatic conditions—that is, to evaluate model performance when projecting to a climatically non-stationary period.

In our research, we address the following questions:

- (1) What is the amount of uncertainty in projections of range change attributable to a) climate covariate hypothesis; b) degree of collinearity; c) threshold; and d) GCM?
- (2) How is the amount of projected range change effected by choices of a) climate covariate hypothesis; b) degree of collinearity; c) threshold; and d) GCM?
- (3) Which choices provide the best ability to extrapolate to a drought period? Are the same choices recommended based on cross-validation?

METHODS

Study system

The Prairie Pothole Region (PPR), located in the northern Great Plains of the U.S. and Canada, is a mosaic of grassland, cropland, and pothole wetlands. Prairie potholes are glacial depressions that hold water on a permanent, semi-permanent, or seasonal basis and, in some areas, reach densities greater than 40 km⁻² (Kantrud et al. 1989). Most pothole wetlands are small and shallow, however, they range widely in size (Zhang et al. 2009). Because the underlying glacial till is typically of low permeability and surface connectivity is limited, the principal source of water for wetlands is precipitation (Shjeflo 1968, Winter and Rosenberry 1998).

In a typical year, the PPR receives snowfall during winter months and increasing amounts of precipitation in spring and summer followed by drier fall conditions (Woodhouse and Overpeck 1998). Total annual precipitation does not always exceed evaporative loss, and the resulting water balance produces a dynamic wetland landscape where shallow wetlands usually dry up during summer months. In addition, the region is characterized by high climatic variability across years, and periods of drought or excessive precipitation may extend over multi-year periods. Historic multi-year droughts include the 10-year “dust bowl” drought in the 1930s and a 5-year drought from 1988-1992. During these pronounced drought periods, even many of the larger wetlands became dry (Shjeflo 1968, Winter and Rosenberry 1998, Johnson et al. 2004). Multi-year wet periods, or deluges, also occur and produce contrasting conditions with most landscape depressions holding surface water (Beeri and Phillips 2007, Niemuth et al. 2010). The juxtaposition of wet and dry periods promote dramatic annual changes in marsh vegetative cover and high productivity (Euliss et al. 1999, van der Valk 2005, Johnson et al. 2010). Under sustained wet or dry conditions, marshes with high water levels have little emergent vegetation and those with low water levels support dense vegetative cover (van der Valk and Davis 1978, Johnson et al. 2004).

The spatially extensive and highly productive wetlands of the PPR provide core breeding habitat to 46 migratory waterbird species (Steen et al. 2016). Annual waterbird counts are strongly positively correlated with that year's wetland counts, demonstrating an immediate response to recent climatic conditions (Stewart and Kantrud 1973, Niemuth and Solberg 2003). The amount and type of vegetative cover and wetland size are additional climate-mediated conditions that influence the distribution of waterbird species in the PPR (Weller and Spatcher 1965, Kantrud and Stewart 1984, Linz et al. 1996, Murkin et al. 1997, Johnson et al. 2010, Steen and Powell 2012).

Our study area within the PPR was approximately 290,000 km² in size and included portions of three U.S. states: North Dakota, South Dakota, and Minnesota (Supplementary figure S2.1). During our study period, mean annual temperature ranged from 3°C to 9°C from north to south and mean annual precipitation ranged from 300mm to 800mm west to east (Millett et al. 2009). Since European settlement, wetlands in the PPR have been extensively converted to cropland with wetland losses greatest in the eastern portion of our study area (Dahl 1990, Johnson et al. 2008). Losses of surrounding grassland habitats have a similar geographic pattern (greatest in the eastern portion of the PPR) but have been even more extensive than wetland losses (Beyersbergen et al. 2004).

Bird data

We obtained species occurrence (presence/absence) data from the North American Breeding Bird Survey (BBS; Sauer et al. 2011) for our focal species. BBS routes are located on secondary roads throughout the U.S. and southern Canada. Surveys are conducted once annually during June between the hours of 0445 and 1000. Route locations generally remain the same from year to year, although routes vary in year of initiation and not all routes are surveyed each year. BBS routes consist of 50 survey stops spaced 0.8 km apart for a total length of 39.4 km. At each survey, stop observers record all birds seen or heard within 400 m for three minutes. BBS survey data are available for each species and summarized as route totals or 10-stop totals (1/5 section of a route; <https://www.pwrc.usgs.gov/bbs/>).

We used results from high-quality surveys (reported by the BBS as “run type 1”) for the years 1971-2010 derived from 72 routes within our study area. Hydrological data were not comprehensive for 2000-2010 in Minnesota, thus 19 (of 24) Minnesota routes included surveys only through 1999. Due to variation in land cover along the 39.4-km BBS routes in our study area, we used avian count data from a single section (set of 10 consecutive point-count surveys) from each BBS route in each year. Because each BBS route was consistently surveyed in one direction, from the first stop, starting around 0445, to stop 50, ending around 0900, we assumed that bird activity level and thus, detection probability, would be higher for the first ten-stop section. From previous work, we used consistently either the first or third section for a species depending on which section had higher detections for that species across all surveys (Steen et al. 2014). We identified our set of focal species based on their prevalence (section-level occurrence rate)—that is, species detected at fewer than 5% of route sections were not included in our subsequent analyses.

Land Cover Data

We extracted land cover variables to associate with BBS routes from GIS raster layers created by the U.S. Fish and Wildlife Service (USFWS; USFWS Regions 6 and 3 Habitat and Population Evaluation Teams, unpublished data). The USFWS data layers were at a 30-m resolution and a combined product based on classified Landsat Thematic Mapper Satellite imagery from 2000-2003 and USFWS National Wetlands Inventory (NWI) wetland polygons based on aerial imagery from the late 1970’s and early 1980’s. Classification accuracy of the upland land cover data for North and South Dakota, assessed in 2007, was > 90% (M. Estey, personal communication). We characterized wetlands into six classes: temporary, seasonal, semi-permanent, lake, river, and water. Temporary, seasonal, and semi-permanent wetlands are palustrine wetland classes describing the typical period they hold water, e.g. from a few weeks for a temporary wetland to multiple years for a semi-permanent wetland. Water is a label applied to locations where water pixels in the newer imagery extended beyond NWI wetlands. We

described upland habitat using four land cover classes: cropland, grassland, tree, and developed. Cropland included areas planted with crops or fallowed. Grassland included native prairie, planted grasslands, and hayland. Developed land cover included towns and residential areas. Tree habitat included small sections or rows of trees and, occasionally, areas of forest.

To describe habitat associations for the focal waterbird species, we estimated the proportion of the land cover types in the surrounding landscape within a 0.4-km buffer centered on each BBS route segment. We used ArcMap 10.0 to calculate land cover composition for the six wetland types and four upland land cover classes. We chose a buffer of 0.4-km because it matched the maximum bird survey distance from the BBS survey route and because land cover covariates based on different buffer sizes were highly correlated. Land cover was assumed static across the survey interval (1971-2010) and for future projections.

Observed and projected climate data

Both simulated past climate ("hindcast") and projections of future climate (temperature, precipitation) were obtained from the "Downscaled CMIP3 and CMIP5 Climate and Hydrology Projections" archive (Brekke et al. 2013). This dataset provides Coupled Model Intercomparison Project Phase 5 (CMIP5) General Circulation Model (GCMs) data downscaled to $1/8^\circ$ spatial resolution using the BCSD (Bias-Corrected Spatially Disaggregated) approach (Wood et al. 2004, Maurer et al. 2007). In our study area, $1/8^\circ$ represents an east to west spacing of approximately 10 km and north to south spacing of approximately 14 km. This downscaled temperature and precipitation data also had been processed through the Variable Infiltration Capacity (VIC) macroscale hydrologic model (version 4.1.2h, Liang 1994), to obtain projections of hydrological variables.

We used the output from 10 randomly selected CMIP5 GCMs (represented as circled numbers in Supplementary figure S2.2). These GCMs well-represent the range of plausible futures in the GCMs, from less warming ($\sim 1.5^\circ\text{C}$) to greater warming (over $+4^\circ\text{C}$) and from a decrease of $\sim 7\%$ in annual

precipitation to an increase of ~20%. Whereas only one GCM projected a notable decrease in precipitation, the risk of less precipitation coupled with the higher temperature increase in that GCM (+ ~4 °C; #27) is an important risk to consider for the Prairie Pothole Region and an important risk to include in the analysis. We chose only GCMs run with the RCP 8.5 greenhouse gas emissions pathway for our mid-century projections (Snover et al. 2013).

Climate variable sets

We developed candidate covariate sets for each of the three climate hypotheses based on previous bird and Prairie Pothole studies (Table 2.2). The candidate covariates in our temporal hypothesis included seasonal, yearly, and multi-year summaries as well as temporal variation (standard deviation) because research in the prairie potholes has shown the influence of shorter and longer term climate as well as the variability in driving wetland habitats (Larson 1995, Johnson et al. 2010). For the bioclimatic hypothesis, we defined candidate bioclimatic covariates compiled from Synes and Osborne (2011) which used a “generic selection based on previous bird studies” and from Jimenez-Valverde et al. (2011) that describe potential distributional constraints experienced by North American birds. The candidate covariates in our hydrological hypothesis included those that predict yearly density of wetlands holding water in the PPR (Sofaer et al. 2016) as well as additional hydrological covariates representing seasonal wetness patterns expected to change in the future (Ballard et al. 2014) and late spring and early summer wetness patterns that may affect settling patterns of migratory birds (Heikkinen et al. 2006b). The hydrological hypothesis included covariates from the VIC hydrological model and derivations of temperature and precipitation.

Candidate covariates for each of the three hypotheses were reduced in number based on their degree of collinearity as assessed by variance inflation factors (VIFs). The first cutoff VIF was set at the commonly recommended value of 10 and the second was set at two, using a more stringent recommendation for ecological studies (Kutner et al. 2004, Zuur et al. 2010). Starting with 16 candidate

covariates for the temporal hypothesis, covariates were reduced to 14 and finally 11 (Table 2.2). For the bioclimatic hypothesis, reductions were from 12 to 9 to 6 and for the hydrological hypothesis, 15 to 13 to 10.

Species distribution models

For each species' SDM, we used the species' yearly occurrence – defined as ≥ 1 detection per 10-stop segment – as the response variable and climate and land cover covariates as predictor variables. To exclude the effects of temporal autocorrelation in occurrence patterns, we excluded consecutive years of survey data. Climate covariates assigned to a given BBS route were based on the nearest gridded climate data point and were temporally matched to the year of the BBS survey. Temporal climate matching is appropriate in our dynamic study system and may be appropriate for vagile species such as birds in general, although is not commonplace (Reside et al. 2010). Wetland and upland land cover (hereafter grouped as “land cover”) covariates characterized the composition of the landscape surrounding each route (see land cover data). Focal species were removed when no model algorithm achieved a minimum AUC < 0.65 for that species.

We fit our occurrence data using the ensemble modeling platform BIOMOD implemented in the R package Biomod2 (Version 3.3-7; Thuiller et al. 2009). In this package, we employed seven modeling algorithms to fit covariates to species occurrence data. These included generalized linear models (GLM) with polynomial terms and without model selection, generalized boosted models (GBM), random forests (RF; with 2500 trees), multivariate adaptive regression splines (MARS), artificial neural networks (ANN), classification tree analysis (CTA), and flexible discriminant analysis (FDA). For additional information on settings of models, see the default settings for Biomod2. Because consensus probabilities are generally expected to perform better than probabilities based on a single modeling technique, we used the consensus of the probability of occurrence as our prediction (Araujo et al. 2005b, Marmion et al. 2009, Garcia et al. 2012). Consensus was estimated from the weighted mean probability of occurrence across

those modeling algorithms that achieved a predictive performance of $AUC \geq 0.65$. The weights were based on the AUC values for each model. Twenty-nine waterbird species, including nine waterfowl, five songbird, five shorebird, three gull and tern, two rail, two heron, two grebe, and one cormorant species met the criteria for inclusion (Table 2.1).

Threshold

We evaluated 12 of 14 probability of occurrence thresholds (Table 2.3) assessed by Nenzen and Araujo (2011). We did not include precision-recall minimized (PRmin) and maximize sum of sensitivity and specificity (SeSpmax) because we found they were highly similar to predicted prevalence equals observed prevalence ($PredPrev=ObsPrev$) and the true skill statistic (TSS), respectively.

Calculating projected climate change impacts for each species

To assess species-specific climate change impacts, we calculated the range change index (RCI; Thuiller et al. 2005, Buisson et al. 2010, Synes and Osborne 2011, Fordham et al. 2013). Based on specified suitable/unsuitable threshold and predicted probability of occurrence maps for current and future distributions, RCI is the number of pixels gained minus the number of pixels lost divided by the number of pixels currently occupied. It compares the size of the projected and current distributions for species with unlimited dispersal capabilities as expected for vagile bird species, although does not assess spatial shifts. Models for predicting RCI were trained with the full training dataset (Table 2.1). Biomod was executed over three repetitions with an 82:18 random data split to match the data split created in the wet/normal versus dry dataset division.

Attributing uncertainty in range change projections

Using a factorial design to evaluate key sources of uncertainty in SDM development, we evaluated all possible combinations of uncertainty including: 10 GCMs, three covariate hypotheses, three cut-offs for collinearity, and 12 threshold criteria (Figure 2.1). The result was 1,080 sets of range change projections per species. To summarize the variation in projections attributable to each source,

we applied a GLM with normal error distribution to log-transformed RCI output for each species to evaluate the relative contribution to estimated range change arising from GCM selection, covariate hypothesis, degree of collinearity, and threshold criteria. We alternately withheld each source to assess the proportional reduction in model deviance attributable to inclusion of that factor as a model covariate (Buisson et al. 2010). For example, the proportion of deviance explained by GCM, for a given species, was calculated as the difference between the deviance remaining in the model without GCM and the deviance remaining in the model with all factors. This difference was then divided by the null (intercept only) model deviance. We then summarized the distribution of deviance reduction values across species for each uncertainty source.

Effects of modeling decisions on amount of projected range change

We assessed the effects of decisions regarding the covariate hypotheses tested, degree of covariate collinearity, and thresholding procedures on estimates of range change using generalized linear mixed models (GLMMs; Figure 2.1). In these models, we treated species as a random effect and assumed RCI to be a log normally distributed response variable. GLMMs were created using the R package lme4 (R Development Core Team 2012, Bates et al. 2015). We set reference levels to those that predicted the smallest RCI. To qualify the degree of change to RCI estimates produced by the alternate decisions compared to choosing the reference level, we describe “none”, “low”, “moderate”, “high”, or “very high” reflecting coefficient estimates of 0, <0 to -0.2, <-0.2 to -0.4, <-0.4 to -0.6, and <-0.6 to -0.8, respectively.

Effects of modeling decisions on model performance when extrapolating

To create independent test data, we partitioned drought years from the years representing wet and normal conditions. We defined seven drought years: 1988-1992 and 2004-2005. The years 1988-1992 cover a drought considered second in severity only to the dust-bowl drought of the 1930's and resulted in a greatly reduced number of wetlands including the loss of some lakes (Winter and

Rosenberry 1998, Niemuth et al. 2010). During the 2004-2005 drought years, lakes remained largely unaffected but the number of temporary and seasonal wetlands were reduced to below half their maximum number, and sizes of semipermanent wetlands were reduced by ~50% (Niemuth et al. 2010). Extrapolation model performance was assessed using models trained with data from the 82% of the data that represented wet/normal years and projected to the 18% of the data that represented drought years. Cross-validation model performance was assessed using 10 randomized splits of the wet/normal years' data using the same proportions as for extrapolation (82:18).

We assessed model performance using four metrics: 1) Cohen's kappa statistic (kappa) is widely used and corrects overall prediction success by expected correct predictions occurring by chance (Manel et al. 2001); 2) True Skill Statistics (TSS), proposed as an alternative to Cohen's kappa, maximizes the sum of sensitivity and specificity and is unaffected by prevalence (Allouche et al. 2006); 3) Area under the receiver operating characteristic curve (AUC) is based on a plot of sensitivity versus 1-specificity across all thresholds (Fielding and Bell 1997); and 4) prevalence match, defined as 1 minus the difference between predicted and actual prevalence. For modeling purposes, all metrics were logit transformed, and a normal error distribution was assumed (Warton and Hui 2011).

We modelled the effects of climate covariate hypothesis, degree of collinearity, and thresholding procedure on model performance for each performance metric. We used GLMMs with species as a random effect (using lme4). For climate covariate hypothesis and thresholding procedure we selected reference levels for the GLMMs based on those that were intermediate in effect, thus allowing other levels to have a positive or negative effect on model performance relative to the intermediate effect of the reference. Using model coefficients, we qualified the relative impact to model

performance in extrapolation owing to alternate decisions relative to choosing the reference level. We describe “positive”, “intermediate”, or “negative” performance impacts corresponding to coefficient estimates that are positive, zero, or negative, respectively.

To evaluate the ability of choices based on higher performance in cross-validation tests to improve performance for extrapolation as well, we assessed the correlation between cross-validation and extrapolation results for each performance metric. For each of the four performance metrics, we used GLMMs to predict the extrapolation performance value using a fixed effect of cross-validation performance value and a random effect of species. We then assessed the correlation between the prediction and the actual extrapolation performance value using Spearman’s rank-based correlation (ρ).

We assessed influential species as diagnosed by the relative variance change measure in the R package HLMdiag by alternately removing each species and observing whether interpretation of model results changed (Dillane 2006). Influential species in one or more GLMM included Great-blue Heron (*Ardea herodias*), Green-winged Teal (*Anas crecca*), American Wigeon (*Anas americana*), Franklin’s Gull (*Leucophaeus pipixcan*), Sedge Wren (*Cistothorus platensis*), Common Yellowthroat (*Geothlypis trichas*), Killdeer (*Charadrius vociferus*), Eared Grebe (*Podiceps nigricollis*), and Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*). However, because their removal did not impact the interpretation of the results, we retained them.

RESULTS

Attributing uncertainty in range change projections

Range change estimates were highly variable. Although median projected range change was negative for all but one species, the majority of range change projections varied widely and included both negative and positive projections—that is, inferences to the direction and amount of range change depended critically on model-building decisions (Figure 2.2). GCM selection contributed the most

uncertainty followed by the covariate hypothesis evaluated and thresholding technique (Figure 2.3).

Degree of collinearity retained in the covariate set was a minor source of uncertainty.

Effects of modeling decisions on amount of projected range change

According to the GLMMs of RCI, the GCM that predicted the least range change (median RCI = -0.16) also projected the least warming and the greatest increase in precipitation (# 34 Supplemental figure S2.2 and Supplemental figure S2.5). The GCM that projected the greatest range change (median RCI = -0.55) had near-zero change in precipitation accompanied by the largest increase in temperature (# 1). Using bioclimatic and temporal climate covariates resulted in moderately more projected range loss compared to hydrological covariates (Table 2.4). Bioclimatic covariates projected an average of 94% more median range loss than hydrological covariates and temporal covariates projected 98% more range loss (Supplemental figure S2.6). The difference in range loss projected by bioclimatic and temporal covariates was not statistically significant (Supplemental figure S2.3). The impact of varying collinearity was low with the highest degree of collinearity projecting 9% more median range loss relative to the lowest (Table 2.4 and Supplemental figure S2.7). The impact of using the fixed (0.5) threshold was very high compared to those that produced the least change (observed prevalence and averaged predicted probability) and resulted in projections of 94% more median range loss (Table 2.4 and Supplemental figure S2.8). Numerous other thresholds resulted in moderate or low impacts to the amount of projected range loss (Table 2.4).

Effects of modeling decisions on model performance when extrapolating

The model's ability to extrapolate to drought conditions was variously improved or diminished by different modeling decisions (Table 2.4). The temporal covariate hypothesis generally had a positive impact on extrapolation ability, while the bioclimatic hypothesis generally had a negative impact compared to the hydrological hypothesis which was intermediate. Higher collinearity benefited

extrapolations. For locational accuracy and prevalence accuracy, five thresholding procedures improved and three diminished projections compared to the reference levels of Fmeasure and SeSpeql, respectively.

All correlation coefficients assessing correlation between predictions of extrapolation performance based on cross-validation performance and actual extrapolation performance were positive indicating cross-validation performance measures provide value for making modeling decisions for extrapolating under climate change. Although all positive, they varied in strength, with $\rho = 0.93$ for AUC, $\rho = 0.91$ for TSS, $\rho = 0.86$ for kappa, and $\rho = 0.72$ for prevalence match. The climate covariate hypothesis used to define the covariate set and the level of collinearity led to varying performance, with some differences between cross-validation and extrapolation (Supplemental figure S2.4). Impact of thresholding decision was the same when evaluated by TSS in cross-validation and extrapolation, whereas with prevalence match the optimal threshold was not consistently the same in cross-validation and for extrapolation (Supplemental figure S2.4). When evaluated by kappa, threshold decisions were not impactful for extrapolation (except the fixed threshold which resulted in reduced performance, Supplemental figure S2.4).

DISCUSSION

Attributing uncertainty in range change projections

Whereas most other studies found various methodological uncertainties to be larger than the uncertainty in climate change itself, our study lends evidence that the plausible range of future climate itself is the largest unknown (but see also Wenger et al. 2013, Stralberg et al. 2015). We chose a random 10 GCMs for our study area that encompassed a range of expected climate system response to rising greenhouse gas emissions by mid-century and found this uncertainty source in projections of range change for 29 bird species exceeded that of climate covariate hypothesis, degree of collinearity, or

thresholding procedure. Whereas some studies have suggested that a subset of GCMs can be selected that represent an area or physical process, there is little agreement on metrics to separate “good” or “bad” models (Knutti et al. 2010), thus a better approach is to represent the range of variation in GCMs (e.g., Leppi et al. 2014, Fisichelli et al. 2016, Sofaer et al. 2016). Studies interested in late century conditions should also consider multiple emissions scenarios which underlie much of the variation among outcomes (Snober et al. 2013), whereas for mid-century projections such as ours, most of the variation can be represented by GCM variation.

We also observed substantial variation in projected future distributions depending on which covariate hypothesis was being tested. The underlying climate data were the same for all climate datasets, eliminating this factor as a source of variation among projections and pointing towards the importance of how the relationship between climate and species distribution is hypothesized and the resulting derivations of climate and climatic variation that are represented. Other studies corroborate this finding for spatial projections and extinction risk estimates for plants in western South America (Plischoff et al. 2014) and for spatial projections and range change estimates for the great bustard (*Otis tarda*) in Europe (Synes and Osborne 2011) indicating this issue applies broadly.

We filtered our covariate sets using three different degrees of collinearity based on variance inflation factor thresholds and found relatively little variation in range change projections. While posited as a serious concern with conflicting recommendations for best practices when projecting species distributions (Beaumont et al. 2005, Braunisch et al. 2013, Dormann et al. 2013), we found the impact of this decision to be relatively small. This may, in part, reflect our approach which started with a relatively large number of covariates ($\bar{x} = 14$) and ended in a moderate number ($\bar{x} = 9$), thus potentially maintaining a lot of redundancy in covariate information. Beaumont et al. (2005) also cited the redundancy of covariates as an explanation for their similar finding of little difference in relative distributional change.

We found that thresholding probabilities of occurrence into presence-absence – an important step for quantifying species’ range loss or gain - can generate almost as much uncertainty, on average, as hypothesizing a relationship with climate. Serious concerns about threshold choice have been raised for predictions to current conditions (Liu et al. 2005, Jimenez-Valverde and Lobo 2007, Freeman and Moisen 2008), so it is not surprising that threshold choice contributes substantial uncertainty for future projections as Nenzen and Araujo (2011) also found.

Effects of modeling decisions on amount of projected range change

Our work highlights the need to account for uncertainty in future climate as our inclusion of a reasonable range of GCMs from those that predicted wetter futures to drier futures appeared to explain the high uncertainty in species range change attributable to future climate. As expected, while increasing precipitation coupled with modest temperature increases in our wetland-based study system resulted in little projected range loss for wetland-dependent birds, large increases in only temperature produced high projected range loss.

Because the temporal and bioclimatic hypotheses were likely more similar based on how they were computed – based on simple summaries and derivations, versus an additional hydrological model – perhaps it is not surprising that they produced similar levels of range change. Why they predicted, on average, twice the range loss of the hydrological covariates is less clear. One possibility is that increases in temperature are tempered when precipitation also increases – which it typically did in our study – in the water balance formulas of the hydrological model. This possibility should be explored in future research, given the evidence we found for large differences in projected climate change impacts when using hydrological covariates.

While including more covariates generally produces more restricted predictions of ranges, the impacts of collinearity in projections of range change – where the measure is a difference in proportions of future and current ranges – has rarely been addressed. In our analysis, higher collinearity led to

increases in projected range loss as may be consistent with the expectation that higher collinearity leads to overfit models that are not generalizable to new times or places. This is consistent with Thorne et al. (2013) who found much more optimistic estimates of climate change impacts going from a 13 covariate set to a model with one covariate. However, Beaumont et al. (2005) did not find a tendency for more severe range losses with increasing covariates.

The fixed threshold of 0.5 produced the most alarming projections of range loss and nearly twice that of the thresholds that produced the most moderate projections of range loss, namely, observed prevalence and average predicted probability. While the fixed 0.5 threshold is known to overestimate occurrences of common species and underestimate occurrences of rare species, we did not examine the relationship between species prevalence and projected range loss under this threshold to assess how this bias might influence our climate change projections (Jimenez-Valverde and Lobo 2007, Freeman and Moisen 2008). In differentiating among thresholds, previous studies compared threshold predictive performance for static conditions, however for climate change impacts assessments comparing the magnitudes of projected range change under different thresholding schemes is also critical and should be examined further (but see also Nenzen and Araujo 2011).

Effects of modeling decisions on model performance when extrapolating

Bioclimatic covariates have a stronger theoretical link to niche modelling, are widely used for modelling climate change impacts, and are assumed to have numerous advantages; however, they produced diminished model performance in extrapolation relative to temporal covariates. The simpler summaries of temporal variation in temperature and precipitation could, in some situations, have the advantage of representing more variability in climate if more months are represented in the ultimate set. This apparent advantage of the temporal covariate set, could then come down to which bioclimatic variables versus which temporal variables defined each set. In our case, the bioclimatic set had fewer covariates, and this may have ultimately produced our result. However, Peterson and Nakazawa (2008)

also found that bioclimatic variable sets underperformed relative to other climatic variable sets. They suggested that the indirect methods used to estimate the bioclimatic covariates relative to more direct use of means and summaries of other climate covariates may put bioclimatic variables at a disadvantage. Of additional concern is that some bioclimatic covariates that represent extreme conditions such as, for example, “wettest quarter” may project in misrepresentative ways if the seasonality of future climate changes. Different timing of the covariate in the future would change the relevance of the covariate for many migratory species that cannot readily adjust to shifting phenology.

Hydrological variables have the advantage of representing the interaction of temperature and precipitation, including the balance between precipitation inputs and temperature driven evaporative water loss. However, their extrapolative performance – although better than bioclimatic covariates – underperformed relative to temporal covariates. The noise introduced by the additional model required to derive these covariates could conceivably diminish the theorized benefit to these covariates and this tradeoff should be explored further.

Our results for extrapolation generally corroborated previous work assessing performance of thresholds under a static climate. For locational accuracy, like Liu et al. (2005) we found that sensitivity-specificity based approaches (ROC, SeSpeqI, TSS) as well as average probability and observed prevalence offered improved performance while the fixed threshold produced the poorest performance. The very poor performance of the fixed threshold, is likely due to the bias in probability estimates when prevalence data deviate from 0.5, as ours do (Cramer 1999, Jimenez-Valverde and Lobo 2007, Kuhn and Johnson 2013). For prevalence accuracy, like Freeman and Moisen (2008), we found kappa and predicted prevalence equals observed prevalence improved this metric, although our results additionally recommend Fmeasure, mid-point probability, and overall prediction success. Because recommended thresholding procedures varied depending on whether locational accuracy or prevalence accuracy was

desired, we recommend basing threshold choice on whether study objectives align more with projecting specific locations accurately or projecting prevalence accurately.

Positive correlation values between model performance in cross-validation and extrapolation for all performance metrics (AUC, kappa, prevalence match, and TSS) indicates that cross-validation performance can be used to select best choices for bioclimatic species distribution modeling. However, the smaller value for prevalence match indicates lower reliability of this metric, or, alternatively, the challenge of extrapolating prevalence. Conversely, the relatively high correlation values for AUC and TSS indicate these metrics may be among the better for making modeling decisions.

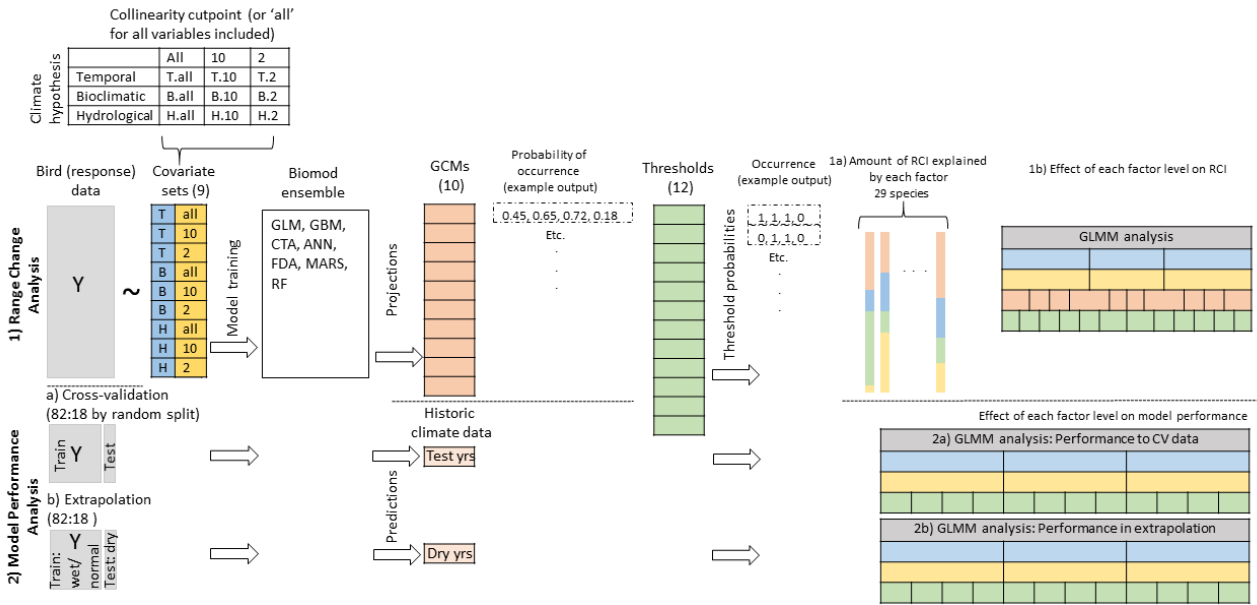


Figure 2.1. Schematic representation of workflow starting with creating nine species distribution models (SDMs) by training with each of nine covariate sets using the Biomod ensemble and following two objectives: (1) the range change analysis involved projections of each SDM to 10 GCMs to obtain future probabilities of occurrence, then thresholding each projection 12 different ways to obtain occurrence (0/1) values, then calculating range change (range change index; RCI) based on the difference between future versus hindcast occurrence (not shown); (2) the model performance analysis involved predictions of each SDM to subsets of historical climate data based on (a) cross-validation data splits or (b) extrapolation data split to obtain historic probabilities of occurrence, then thresholding each prediction 12 different ways to obtain occurrence values, and then assessing model performance based on predicted versus actual occurrence. Inference was based on four summary analyses. For objective (1), with 1,080 (9 x 10 x 12) projections per species we (1a) modeled deviance in RCI explained by each uncertainty source, and, (1b) modeled the factor level contributions to RCI for the 31 (9+10+12) factors. For the 108 (9 x 12) historical predictions per species we modeled the factor level relationship across the 21 (9+12) factors with model performance in cross-validation (2a) and extrapolation (2b).

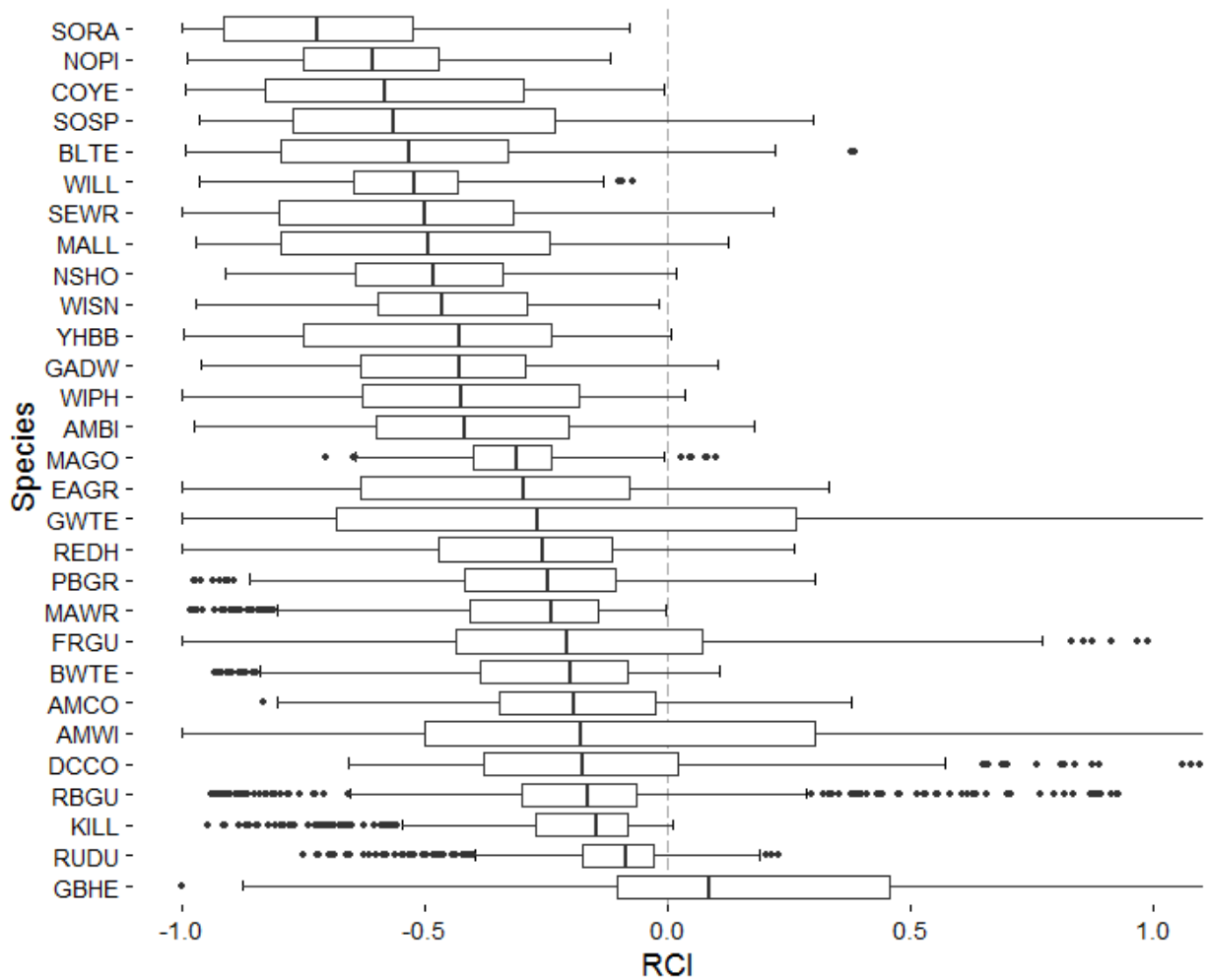


Figure 2.2. Variation in projected range change (range change index; RCI) to mid-century for 29 species based on 1,080 individual projections. Boxplots show the median, and first and third quartiles, with whiskers showing the 1.5 inter-quartile range. The overall median RCI value was -0.35, with average distance between the 25% and 75% quartiles of 0.41, and average distance of 1.14 describing 95% of distributions. Variation stems from multiple sources of uncertainty: climate covariate hypothesis, degree of collinearity, thresholding procedure, and GCM. See Table 2.1 for species abbreviations.

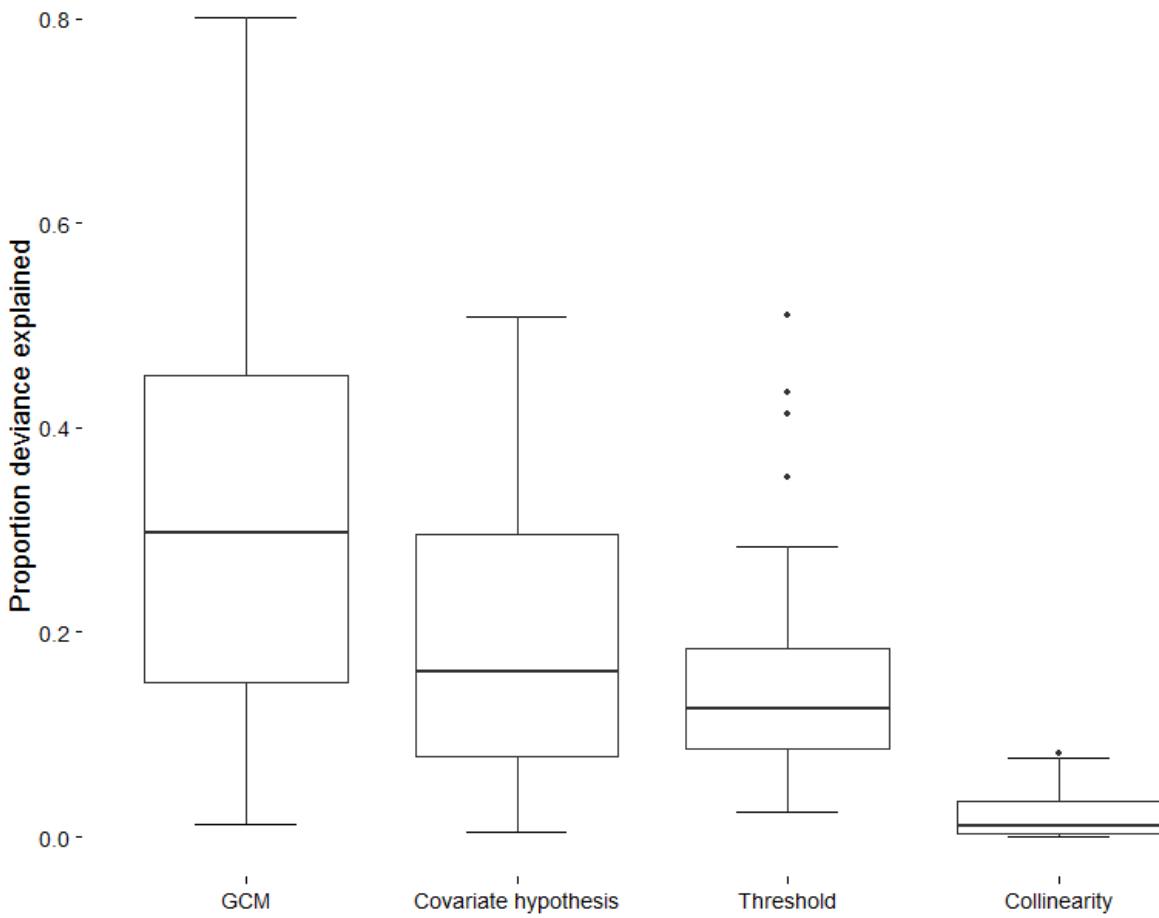


Figure 2.3. Proportion of deviance in range change index (RCI) explained by uncertainty sources: GCM, covariate hypothesis, threshold, and collinearity. Boxplots show the median, and first and third quartiles, with whiskers showing the 1.5 inter-quartile range.

Table 2.1. Species, species alpha code, and prevalence (proportion of data points with species present) for each dataset.

| Common Name | Scientific Name | Alpha Code | Prevalence | | |
|-----------------------------|----------------------------------|------------|-----------------------------------|----------------------------------|----------------------|
| | | | Training (all years; n=854) | Wet & Normal years (n=702) | Dry years (n=152) |
| Gadwall | <i>Anas strepera</i> | GADW | 0.28 | 0.28 | 0.26 |
| American Wigeon | <i>Anas americana</i> | AMWI | 0.06 | 0.06 | 0.04 |
| Mallard | <i>Anas platyrhynchos</i> | MALL | 0.6 | 0.6 | 0.58 |
| Blue-winged Teal | <i>Anas discors</i> | BWTE | 0.39 | 0.42 | 0.3 |
| Northern Shoveler | <i>Anas clypeata</i> | NSHO | 0.18 | 0.19 | 0.14 |
| Northern Pintail | <i>Anas acuta</i> | NOPI | 0.24 | 0.26 | 0.16 |
| Green-winged Teal | <i>Anas crecca</i> | GWTE | 0.06 | 0.06 | 0.05 |
| Redhead | <i>Aythya americana</i> | REDH | 0.13 | 0.14 | 0.11 |
| Ruddy Duck | <i>Oxyura jamaicensis</i> | RUDU | 0.13 | 0.14 | 0.11 |
| Eared Grebe | <i>Podiceps nigricollis</i> | EAGR | 0.04 | 0.04 | 0.05 |
| Pied-billed Grebe | <i>Podilymbus podiceps</i> | PBGR | 0.23 | 0.26 | 0.11 |
| Double-crested Cormorant | <i>Phalacrocorax auritus</i> | DCCO | 0.10 | 0.09 | 0.11 |
| American Bittern | <i>Botaurus lentiginosus</i> | AMBI | 0.23 | 0.25 | 0.15 |
| Great Blue Heron | <i>Ardea herodias</i> | GBHE | 0.06 | 0.06 | 0.05 |
| Sora | <i>Porzana carolina</i> | SORA | 0.27 | 0.30 | 0.15 |
| American Coot | <i>Fulica americana</i> | AMCO | 0.29 | 0.32 | 0.12 |

| | | | | | |
|----------------------------|----------------------------------|------|------|------|------|
| Killdeer | <i>Charadrius vociferus</i> | KILL | 0.83 | 0.84 | 0.78 |
| Willet | <i>Tringa semipalmata</i> | WILL | 0.17 | 0.17 | 0.16 |
| Marbled Godwit | <i>Limosa fedoa</i> | MAGO | 0.20 | 0.20 | 0.23 |
| Wilson's Snipe | <i>Gallinago delicata</i> | WISN | 0.19 | 0.19 | 0.16 |
| Wilson's Phalarope | <i>Phalaropus tricolor</i> | WIPH | 0.11 | 0.12 | 0.11 |
| Franklin's Gull | <i>Leucophaeus pipixcan</i> | FRGU | 0.12 | 0.12 | 0.08 |
| Ring-billed Gull | <i>Larus delawarensis</i> | RBGU | 0.14 | 0.14 | 0.14 |
| Black Tern | <i>Chlidonias niger</i> | BLTE | 0.19 | 0.21 | 0.12 |
| Sedge Wren | <i>Cistothorus platensis</i> | SEWR | 0.24 | 0.25 | 0.22 |
| Marsh Wren | <i>Cistothorus palustris</i> | MAWR | 0.23 | 0.24 | 0.23 |
| Common Yellowthroat | <i>Geothlypis trichas</i> | COYE | 0.83 | 0.83 | 0.81 |
| Song Sparrow | <i>Melospiza melodia</i> | SOSP | 0.66 | 0.66 | 0.63 |
| Yellow-headed Blackbird | Xanthocephalus xanthocephalus | YHBL | 0.56 | 0.56 | 0.55 |

Table 2.2. Nine sets of climate covariates were used in species distribution models. Sets varied by three hypotheses (temporal, bioclimatic, and hydrological) and each hypothesis originally included all candidate covariates prior to variable reduction to reduce collinearity. Variables were eliminated based on their variance inflation factor (VIF) values relative to two thresholds: 10 and 2. Rows in the table are ordered according to type of variable (precipitation, mixed precip./temp., and temperature) and within these types are ordered from finest temporal scale to broadest (e.g. from month to 10-yr). Year was a biological year defined to match the annual cycle of migratory birds—that is, the 12 month period leading up to and including May - the typical month of breeding initiation for our group of species.

| Covariate | Temporal | | | Bioclimatic | | | Hydrological | | |
|------------------------------------|----------|--------|-------|-------------|--------|-------|--------------|--------|-------|
| | All | VIF=10 | VIF=2 | All | VIF=10 | VIF=2 | All | VIF=10 | VIF=2 |
| Precip., driest month | | | | X | X | X | | | |
| Precip., wettest month | | | | X | X | X | | | |
| Precip., spring | X | X | X | | | | | | |
| Precip., winter | X | X | X | | | | | | |
| Precip., fall | X | X | X | | | | | | |
| Precip., summer | X | X | X | | | | | | |
| Precip., summer + September | | | | X | X | X | | | |
| Precip., current year | | | | X | | | | | |
| Precip., 5 year (inc. current yr) | X | | | | | | | | |
| Precip., 10 year (inc. current yr) | X | X | | | | | | | |
| Precip. std. dev., 5 year | X | X | X | | | | | | |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Precip., std. dev., 10 year | X | X | X | | | | | | |
| Soil moisture content, May | | | | | | | X | | |
| Soil moisture content, October | | | | | | | X | X | X |
| Runoff, April | | | | | | | X | X | X |
| Runoff, May | | | | | | | X | X | X |
| Soil moisture content, May - June | | | | | | | X | X | X |
| Precip. – PET, spring | | | | | | | X | X | |
| Precip. – PET, winter | | | | | | | X | X | X |
| Precip. – PET, fall | | | | | | | X | X | X |
| Precip.- PET, summer | | | | | | | X | X | X |
| Precip.- PET, annual | | | | | | | X | | |
| PET, annual | | | | | | | X | X | |
| Moisture Index | | | | X | X | | | | |
| Precip.- PET, 5-yr with 1-yr lag | | | | | | | X | X | |
| Growing degree days | | | | X | X | X | | | |
| Temp. range, first month with mean above freezing | | | | | | | X | X | X |
| Temp., max of max summer monthlies | | | | | | | X | X | X |
| Temp., coldest month | | | | X | X | X | | | |

| | | | | | | | | | |
|--|---|---|---|---|---|---|---|---|---|
| Temp., warmest month | | | | X | X | X | | | |
| Temp., mean of max spring monthlies | | | | | | | X | X | X |
| Temp., mean, coldest quarter | | | | X | X | | | | |
| Temp., mean, warmest quarter | | | | X | X | | | | |
| Temp., spring | X | X | X | | | | | | |
| Temp., winter | X | X | | | | | | | |
| Temp., fall | X | X | X | | | | | | |
| Temp., summer | X | X | X | | | | | | |
| Temp., annual | | | | X | | | | | |
| Temp., 5 year | X | | | | | | | | |
| Temp., 10 year | X | X | | | | | | | |
| Temp., std. dev., 5 year | X | X | X | | | | | | |
| Temp., std. dev., 10 year | X | X | X | | | | | | |

Table 2.3. Description of thresholding techniques (these taken from Nenzen and Araujo 2011).

| Technique | Description |
|----------------------------|--|
| AveProb | Mean of probabilities for just the presence data points |
| Fixed (0.5) | Traditional method of using 0.5 probability across models |
| Fmeasure | Maximize $F=2*\text{true positives}/(\text{presences} + \text{true positive} + \text{false positive})$ |
| Kappa | Maximize Cohen's kappa statistic |
| MidptProb | Median of probabilities between presences and absences in the dataset |
| ObsPrev | Observed prevalence (proportion of presences) |
| OPS | Overall prediction success; sum of true positives and true negatives divided by the number of observations |
| PredPrevObs | Predicted prevalence matches observed prevalence |
| PRplotbased | Precision-recall plot; minimize distance to upper left corner of precision-recall plot |
| ROC | Minimize distance to the upper left corner of the receiver operator curve |
| SeSpeql | Minimize difference between sensitivity and specificity |
| TSS (True Skill Statistic) | Maximize sensitivity + specificity -1 |

Table 2.4. Effects on projections of range loss (using Range Change Index, RCI) and model performance in extrapolation tests. Interpretations presented in this table are based on model coefficients and confidence intervals (Supplementary figures. S2.3 and S2.4). For the RCI model, reference levels always predicted the least loss, and we compared how much more loss was predicted by the alternative decisions. We label additional loss as: “none”, “low”, “moderate”, “high”, and “very high” which correspond to coefficient estimates of 0, <0 to -0.2, <-0.2 to -0.4, <-0.4 to -0.6, and <-0.6 to -0.8, respectively. For the model performance results, reference levels were those intermediate in performance. “Positive”, “intermediate”, and “negative” correspond to coefficient estimates that are positive, zero (confidence intervals overlapped zero), or negative, respectively. “Tendency” means that most, but not all, performance metrics indicate this result. For thresholding decisions, model performance is divided into locational accuracy and prevalence accuracy because results generally differed by these two sets of metrics. Locational accuracy is represented only by TSS because kappa generally did not differentiate among thresholding procedures in extrapolation and AUC is not based on unique thresholds. Prevalence accuracy is represented by the prevalence match metric.

| Decision | Group/level | Effects on increased range loss | Effects on model performance in extrapolation | |
|------------------------------|--------------|--|---|---------------------|
| Climate covariate hypothesis | Temporal | Moderate | Positive (tendency) | |
| | Bioclimatic | Moderate | Negative (tendency) | |
| | Hydrological | None (<i>reference</i>) | Intermediate (tendency; <i>reference</i>) | |
| Collinearity | NA | Low impact of <i>increasing</i> collinearity | Benefit to moderate (ten VIF) or higher collinearity (tendency) | |
| Threshold procedure | | | Locational accuracy | Prevalence accuracy |

| | | | | |
|--|-------------|-------------------------|------------------------------------|------------------------------------|
| | AvgProb | None | Positive | Negative |
| | Fixed (0.5) | Very High | Negative | Intermediate |
| | Fmeasure | Moderate | Intermediate <i>(reference)</i> | Positive |
| | Kappa | Moderate | Intermediate | Positive |
| | MidptProb | Moderate | Negative | Positive |
| | ObsPrev | None <i>(reference)</i> | Positive | Negative |
| | OPS | Moderate | Intermediate | Positive |
| | PredPrevObs | Moderate | Negative | Positive |
| | PRplotbased | Low | Intermediate | Intermediate |
| | ROC | Low | Positive | Intermediate |
| | SeSpeql | Low | Positive | Intermediate <i>(reference)</i> |
| | TSS | Low | Positive | Negative |

LITERATURE CITED

- Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* **43**:1223-1232.
- Araujo, M. B., R. G. Pearson, W. Thuiller, and M. Erhard. 2005a. Validation of species-climate impact models under climate change. *Global Change Biology* **11**:1504-1513.
- Araujo, M. B., R. J. Whittaker, R. J. Ladle, and M. Erhard. 2005b. Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography* **14**:529-538.
- Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* **157**:101-118.
- Austin, M. P. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling* **200**:1-19.
- Ballard, T., R. Seager, J. E. Smerdon, B. I. Cook, A. J. Ray, B. Rajagopalan, Y. Kushnir, J. Nakamura, and N. Henderson. 2014. Hydroclimate Variability and Change in the Prairie Pothole Region, the "Duck Factory" of North America. *Earth Interactions* **18**.
- Barbet-Massin, M., B. A. Walther, W. Thuiller, C. Rahbek, and F. Jiguet. 2009. Potential impacts of climate change on the winter distribution of Afro-Palaeartic migrant passerines. *Biology Letters* **5**:248-251.
- Bates, D., M. Machler, B. M. Bolker, and S. C. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* **67**:1-48.
- Beaumont, L. J., L. Hughes, and M. Poulsen. 2005. Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecological Modelling* **186**:250-269.

- Beerli, O. and R. L. Phillips. 2007. Tracking palustrine water seasonal and annual variability in agricultural wetland landscapes using Landsat from 1997 to 2005. *Global Change Biology* **13**:897-912.
- Beyersbergen, G. W., N. D. Niemuth, and M. R. Norton. 2004. Northern Prairie and Parkland waterbird conservation plan. A plan associated with the Waterbird Conservation for the Americas initiative. Prairie Pothole Joint Venture, Denver, CO, USA.
- Booth, T. H., H. A. Nix, J. R. Busby, and M. F. Hutchinson. 2014. BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MAXENT studies. *Diversity and Distributions* **20**:1-9.
- Braunisch, V., J. Coppes, R. Arlettaz, R. Suchant, H. Schmid, and K. Bollmann. 2013. Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change. *Ecography* **36**:971-983.
- Brekke, L., B. Thrasher, E. Maurer, and T. Pruitt. 2013. Downscaled CMIP3 and CMIP5 climate and hydrology projections: Release of downscaled CMIP5 climate projections, comparison with preceding information, and summary of user needs. US Dept. of the Interior, Bureau of Reclamation, Technical Services Center, Denver.
- Buisson, L., W. Thuiller, N. Casajus, S. Lek, and G. Grenouillet. 2010. Uncertainty in ensemble forecasting of species distribution. *Global Change Biology* **16**:1145-1157.
- Cramer, J. S. 1999. Predictive performance of the binary logit model in unbalanced samples. *Journal of the Royal Statistical Society Series D-the Statistician* **48**:85-94.
- Dahl, T. E. 1990. Wetlands losses in the United States 1780's to 1980's. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C.
- Dillane, D. M. 2006. Deletion diagnostics for the linear mixed model. Trinity College.
- Dormann, C. F. 2007. Promising the future? Global change projections of species distributions. *Basic and Applied Ecology* **8**:387-397.

- Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carre, J. R. G. Marquez, B. Gruber, B. Laffourcade, P. J. Leitaó, T. Munkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schroder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**:27-46.
- Elith, J., M. Kearney, and S. Phillips. 2010. The art of modelling range-shifting species. *Methods in Ecology and Evolution* **1**:330-342.
- Elith, J. and J. R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology Evolution and Systematics* **40**:677-697.
- Euliss, N. H., D. A. Wrubleski, and D. M. Mushet. 1999. Wetlands of the Prairie Pothole Region: invertebrate species composition, ecology, and management.
- Fielding, A. H. and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**:38-49.
- Fisichelli, N., G. Schuurman, A. Symstad, A. Ray, B. Miller, M. Cross, and E. Rowland. 2016. Resource management and operations in southwest South Dakota: Climate change scenario planning workshop summary January 20-21, 2016, Rapid City, SD. Natural Resource Report. National Park Service, Fort Collins, CO.
- Fletcher, J., Robert J and R. R. Koford. 2004. Consequences of rainfall variation for breeding wetland blackbirds. *Canadian Journal of Zoology* **82**:1316-1325.
- Fordham, D. A., H. R. Akcakaya, M. B. Araujo, D. A. Keith, and B. W. Brook. 2013. Tools for integrating range change, extinction risk and climate change information into conservation management. *Ecography* **36**:956-964.
- Freeman, E. A. and G. G. Moisen. 2008. A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecological Modelling* **217**:48-58.

- Garcia, R. A., N. D. Burgess, M. Cabeza, C. Rahbek, and M. B. Araujo. 2012. Exploring consensus in 21st century projections of climatically suitable areas for African vertebrates. *Global Change Biology* **18**:1253-1269.
- Gaston, K. J. 2003. *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford.
- Green, R. E., Y. C. Collingham, S. G. Willis, R. D. Gregory, K. W. Smith, and B. Huntley. 2008. Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. *Biology Letters* **4**:599-602.
- Gregory, R. D., S. G. Willis, F. Jiguet, P. Vorisek, A. Klvanova, A. van Strien, B. Huntley, Y. C. Collingham, D. Couvet, and R. E. Green. 2009. An Indicator of the Impact of Climatic Change on European Bird Populations. *Plos One* **4**.
- Hawkins, E. and R. Sutton. 2009. The potential to narrow uncertainty in regional climate predictions. *Bulletin of the American Meteorological Society* **90**:1095.
- Heikkinen, R. K., M. Luoto, M. B. Araujo, R. Virkkala, W. Thuiller, and M. T. Sykes. 2006a. Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography* **30**:751-777.
- Heikkinen, R. K., M. Luoto, and R. Virkkala. 2006b. Does seasonal fine-tuning of climatic variables improve the performance of bioclimatic envelope models for migratory birds? *Diversity and Distributions* **12**:502-510.
- Heikkinen, R. K., M. Marmion, and M. Luoto. 2012. Does the interpolation accuracy of species distribution models come at the expense of transferability? *Ecography* **35**:276-288.
- Jimenez-Valverde, A., N. Barve, A. Lira-Noriega, S. P. Maher, Y. Nakazawa, M. Papes, J. Soberon, J. Sukumaran, and A. T. Peterson. 2011. Dominant climate influences on North American bird distributions. *Global Ecology and Biogeography* **20**:114-118.

- Jimenez-Valverde, A. and J. M. Lobo. 2007. Threshold criteria for conversion of probability of species presence to either-or presence-absence. *Acta Oecologica-International Journal of Ecology* **31**:361-369.
- Johnson, D. H. and J. W. Grier. 1988. Determinants of Breeding Distributions of Ducks. *Wildlife Monographs*:1-37.
- Johnson, R. R., F. T. Oslund, and D. R. Hertel. 2008. The past, present, and future of prairie potholes in the United States. *Journal of Soil and Water Conservation* **63**:84a-87a.
- Johnson, W. C., S. E. Boettcher, K. A. Poiani, and G. Guntenspergen. 2004. Influence of weather extremes on the water levels of glaciated prairie wetlands. *Wetlands* **24**:385-398.
- Johnson, W. C., B. Werner, G. R. Guntenspergen, R. A. Voldseth, B. Millett, D. E. Naugle, M. Tulbure, R. W. H. Carroll, J. Tracy, and C. Olawsky. 2010. Prairie Wetland Complexes as Landscape Functional Units in a Changing Climate. *Bioscience* **60**:128-140.
- Kantrud, H. A., G. L. Krapu, and G. A. Swanson. 1989. Prairie basin wetlands of the Dakotas : a community profile. U.S. Dept. of the Interior, Fish and Wildlife Service, Research and Development, Washington, DC.
- Kantrud, H. A. and R. E. Stewart. 1984. Ecological Distribution and Crude Density of Breeding Birds on Prairie Wetlands. *Journal of Wildlife Management* **48**:426-437.
- Knutti, R., R. Furrer, C. Tebaldi, J. Cermak, and G. A. Meehl. 2010. Challenges in Combining Projections from Multiple Climate Models. *Journal of Climate* **23**:2739-2758.
- Knutti, R. and J. Sedlacek. 2013. Robustness and uncertainties in the new CMIP5 climate model projections. *Nature Clim. Change* **3**:369-373.
- Konar, M., M. J. Todd, R. Muneeppeerakul, A. Rinaldo, and I. Rodriguez-Iturbe. 2013. Hydrology as a driver of biodiversity: Controls on carrying capacity, niche formation, and dispersal. *Advances in Water Resources* **51**:317-325.

- Kuhn, M. and K. Johnson. 2013. Applied predictive modeling. Springer, New York.
- Kutner, M. H., C. Nachtsheim, and J. Neter. 2004. Applied linear regression models. 4th edition. McGraw-Hill/Irwin, Boston ; New York.
- Larson, D. L. 1995. Effects of Climate on Numbers of Northern Prairie Wetlands. *Climatic Change* **30**:169-180.
- Lawler, J. J., S. L. Shafer, D. White, P. Kareiva, E. P. Maurer, A. R. Blaustein, and P. J. Bartlein. 2009. Projected climate-induced faunal change in the Western Hemisphere. *Ecology* **90**:588-597.
- Lawler, J. J., D. White, R. P. Neilson, and A. R. Blaustein. 2006. Predicting climate-induced range shifts: model differences and model reliability. *Global Change Biology* **12**:1568-1584.
- Leppi, J. C., D. J. Rinella, R. R. Wilson, and W. M. Loya. 2014. Linking climate change projections for an Alaskan watershed to future coho salmon production. *Global Change Biology* **20**:1808-1820.
- Liang, X. 1994. A two-layer variable infiltration capacity land surface representation for general circulation models.
- Linz, G. M., D. C. Blixt, D. L. Bergman, and W. J. Bleier. 1996. Responses of Red-winged Blackbirds, Yellow-headed Blackbirds and Marsh Wrens to glyphosate-induced alterations in cattail density. *Journal of Field Ornithology* **67**:167-176.
- Liu, C. R., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**:385-393.
- Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* **38**:921-931.
- Marmion, M., M. Parviainen, M. Luoto, R. K. Heikkinen, and W. Thuiller. 2009. Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions* **15**:59-69.

- Maurer, E. P., L. Brekke, T. Pruitt, and P. B. Duffy. 2007. Fine-resolution climate projections enhance regional climate change impact studies. *Eos, Transactions American Geophysical Union* **88**:504-504.
- McEvoy, D. J., J. L. Huntington, M. T. Hobbins, A. Wood, C. Morton, J. Verdin, M. Anderson, and C. Hain. 2016. The Evaporative Demand Drought Index: Part II—CONUS-wide Assessment Against Common Drought Indicators. *Journal of Hydrometeorology*.
- Millett, B., W. C. Johnson, and G. Guntenspergen. 2009. Climate trends of the North American prairie pothole region 1906-2000. *Climatic Change* **93**:243-267.
- Murkin, H. R., E. J. Murkin, and J. P. Ball. 1997. Avian habitat selection and prairie wetland dynamics: a 10-year experiment. *Ecological Applications* **7**:1144-1159.
- Nenzen, H. K. and M. B. Araujo. 2011. Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling* **222**:3346-3354.
- Niemuth, N. D. and J. W. Solberg. 2003. Response of waterbirds to number of wetlands in the Prairie Pothole Region of North Dakota, USA. *Waterbirds* **26**:233-238.
- Niemuth, N. D., B. Wangler, and R. E. Reynolds. 2010. Spatial and Temporal Variation in Wet Area of Wetlands in the Prairie Pothole Region of North Dakota and South Dakota. *Wetlands* **30**:1053-1064.
- Pearson, R. G. and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* **12**:361-371.
- Peterson, A. T. and Y. Nakazawa. 2008. Environmental data sets matter in ecological niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*. *Global Ecology and Biogeography* **17**:135-144.

- Pliscoff, P., F. Luebert, H. H. Hilger, and A. Guisan. 2014. Effects of alternative sets of climatic predictors on species distribution models and associated estimates of extinction risk: A test with plants in an arid environment. *Ecological Modelling* **288**:166-177.
- R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rapacciuolo, G., D. B. Roy, S. Gillings, R. Fox, K. Walker, and A. Purvis. 2012. Climatic Associations of British Species Distributions Show Good Transferability in Time but Low Predictive Accuracy for Range Change. *Plos One* **7**.
- Reside, A. E., J. J. VanDerWal, A. S. Kutt, and G. C. Perkins. 2010. Weather, Not Climate, Defines Distributions of Vagile Bird Species. *Plos One* **5**.
- Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2011. The North American Breeding Bird Survey, Results and Analysis 1966-2010. USGS Patuxent Wildlife Research Center, Laurel, MD.
- Schlaepfer, D. R., W. K. Lauenroth, and J. B. Bradford. 2012. Effects of ecohydrological variables on current and future ranges, local suitability patterns, and model accuracy in big sagebrush. *Ecography* **35**:374-384.
- Shjeflo, J. B. 1968. Evapotranspiration and the water budget of prairie potholes in North Dakota. U.S. Govt. Print. Off., Washington, D.C.
- Smith, A. B., M. J. Santos, M. S. Koo, K. M. C. Rowe, K. C. Rowe, J. L. Patton, J. D. Perrine, S. R. Beissinger, and C. Moritz. 2013. Evaluation of species distribution models by resampling of sites surveyed a century ago by Joseph Grinnell. *Ecography* **36**:1017-1031.
- Smith, R. I. 1970. Response of Pintail Breeding Populations to Drought. *Journal of Wildlife Management* **34**:943-946.

- Snover, A. K., N. J. Mantua, J. S. Littell, M. A. Alexander, M. M. McClure, and J. Nye. 2013. Choosing and Using Climate-Change Scenarios for Ecological-Impact Assessments and Conservation Decisions. *Conservation Biology* **27**:1147-1157.
- Sofaer, H. R., S. K. Skagen, J. J. Barsugli, B. S. Rashford, G. C. Reese, J. A. Hoeting, A. W. Wood, and B. R. Noon. 2016. Projected wetland densities under climate change: habitat loss but little geographic shift in conservation strategy. *Ecological Applications* **26**:1677-1692.
- Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. Averyt, M. Tignor, and H. L. Miller. 2007. IPCC, 2007: Climate change 2007: The physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. SD Solomon (Ed.).
- Steen, V., S. K. Skagen, and B. R. Noon. 2014. Vulnerability of Breeding Waterbirds to Climate Change in the Prairie Pothole Region, USA. *Plos One* **9**.
- Steen, V. A. and A. N. Powell. 2012. Wetland Selection by Breeding and Foraging Black Terns in the Prairie Pothole Region of the United States. *Condor* **114**:155-165.
- Steen, V. A., S. K. Skagen, and C. P. Melcher. 2016. Implications of Climate Change for Wetland-Dependent Birds in the Prairie Pothole Region. *Wetlands*:1-15.
- Stewart, R. E. and H. A. Kantrud. 1973. Ecological Distribution of Breeding Waterfowl Populations in North-Dakota. *Journal of Wildlife Management* **37**:39-50.
- Stralberg, D., S. M. Matsuoka, A. Hamann, E. M. Bayne, P. Solymos, F. K. A. Schmiegelow, X. Wang, S. G. Cumming, and S. J. Song. 2015. Projecting boreal bird responses to climate change: the signal exceeds the noise. *Ecological Applications* **25**:52-69.
- Synes, N. W. and P. E. Osborne. 2011. Choice of predictor variables as a source of uncertainty in continental-scale species distribution modelling under climate change. *Global Ecology and Biogeography* **20**:904-914.

- Thorne, J. H., C. Seo, A. Basabose, M. Gray, N. M. Belfiore, and R. J. Hijmans. 2013. Alternative biological assumptions strongly influence models of climate change effects on mountain gorillas. *Ecosphere* **4**.
- Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology* **10**:2020-2027.
- Thuiller, W., B. Lafourcade, R. Engler, and M. B. Araujo. 2009. BIOMOD - a platform for ensemble forecasting of species distributions. *Ecography* **32**:369-373.
- Thuiller, W., S. Lavorel, M. B. Araujo, M. T. Sykes, and I. C. Prentice. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America* **102**:8245-8250.
- Trenberth, K. 2010. More knowledge, less certainty. *Nature reports climate change*:20-21.
- van der Valk, A. G. 2005. Water-level fluctuations in North American prairie wetlands. *Hydrobiologia* **539**:171-188.
- van der Valk, A. G. and C. B. Davis. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology* **59**:322-335.
- Warton, D. I. and F. K. C. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* **92**:3-10.
- Weller, M. W. and C. S. Spatcher. 1965. Role of habitat in the distribution and abundance of marsh birds. Ames, Iowa.
- Wenger, S. J., N. A. Som, D. C. Dauwalter, D. J. Isaak, H. M. Neville, C. H. Luce, J. B. Dunham, M. K. Young, K. D. Fausch, and B. E. Rieman. 2013. Probabilistic accounting of uncertainty in forecasts of species distributions under climate change. *Global Change Biology* **19**:3343-3354.
- Winter, T. C. and D. O. Rosenberry. 1998. Hydrology of prairie pothole wetlands during drought and deluge: a 17-year study of the Cottonwood Lake wetland complex in North Dakota in the

- perspective of longer term measured and proxy hydrological records. *Climatic Change* **40**:189-209.
- Wood, A. W., L. R. Leung, V. Sridhar, and D. P. Lettenmaier. 2004. Hydrologic implications of dynamical and statistical approaches to downscaling climate model outputs. *Climatic Change* **62**:189-216.
- Woodhouse, C. A. and J. T. Overpeck. 1998. 2000 years of drought variability in the central United States. *Bulletin of the American Meteorological Society* **79**:2693-2714.
- Zhang, B., F. W. Schwartz, and G. Liu. 2009. Systematics in the size structure of prairie pothole lakes through drought and deluge. *Water Resources Research* **45**.
- Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**:3-14.

CHAPTER 3: PREPARING FOR AN UNCERTAIN FUTURE: ASSESSING RESPONSES OF MIGRATING SHOREBIRDS TO HISTORIC CLIMATIC FLUCTUATIONS IN THE PRAIRIE POTTHOLE REGION

INTRODUCTION

The migratory period of a migratory bird's life-cycle may be the most critical to its survival (Faaborg et al. 2010, Marra et al. 2015). In contrast to relatively predictable conditions on breeding and wintering ground habitats, stopover habitats may expose birds to unknown or unavoidable threats such as predation or starvation (Newton 2006, Faaborg et al. 2010). Furthermore, energetic requirements are high during migration and hampered resource availability at stopover sites has been linked to reduced reproduction, migration speeds, body condition, and, in some cases, to population declines (Newton 2006). Climate change is advancing phenology, impacting the hydrological cycle, and potentially increasing the strength of tropical storms, thus posing novel challenges during migration (Parmesan and Yohe 2003, Webster et al. 2005, Held and Soden 2006). Although the importance and challenges of migration are well documented, climate change vulnerability assessments, key for directing resources for climate change adaptation, do not adequately address the migration period for most migratory species (Small-Lorenz et al. 2013).

Shorebirds that breed at high latitudes may be especially impacted by climate change because they require disparate wintering, migratory, and breeding habitats (Brown et al. 2001, Sutherland et al. 2012). Long-distance migrants, including many high-latitude breeding shorebirds species, may have a hard time adjusting to advancing phenology on their migratory stopover habitats and breeding grounds because signals to depart their wintering grounds are largely under endogenous control (Hagan et al. 1991, Both and Visser 2001, Lehikoinen et al. 2004). They may undertake long flights, across hazards such as oceans where they can become exposed to severe storms. As many shorebird species rely on narrow coastal areas for at least part of their life-cycle, sea-level rise will impact and reduce these areas

(Norris et al. 2004). Additionally, algal blooms are promoted by warming, can impact oceanic and freshwater wetlands habitats throughout the world, and produce toxins which can poison shorebirds (Landsberg 2002).

Many shorebirds species that utilize seasonal freshwater wetlands in the semi-arid Great Plains landscape of interior North America for migratory stopover habitat are in decline (Morrison et al. 2006, Thomas et al. 2006). Anthropogenic disturbance including conversion of native habitats to cropland and concurrent wetland drainage have already reduced the availability of shorebird habitat (Johnson et al. 2008). Changes in seasonal precipitation patterns and earlier spring warm-up from climate change will impose additional challenges by altering the distribution and availability of wetland habitats. Of particular importance to shorebirds is the Prairie Pothole Region (PPR) of the northern Great Plains in the U.S. and Canada. This region of North America has high densities of wetlands and hosts millions of migratory shorebirds thus making this area of critical importance for shorebird conservation (Skagen et al. 2008).

The PPR is at the center of three air masses, thus creating “one of the most extreme and dynamic climates on Earth” with high temporal and spatial variability in temperature and precipitation (Millett et al. 2009). The small and shallow wetlands that typify the region respond rapidly to annual variation in weather, and many are dry or reduced in dry years and overflowing in wet years. Breeding wetland dependent birds respond in kind with densities and distribution tightly correlated from year to year with wetland availability and condition (Smith 1970, Stewart and Kantrud 1973, Niemuth and Solberg 2003). This unique system offers a real time window into the sensitivity of species to climate change and their adaptive capacity.

Similar to most regions across the world, the range of variability in climate change projections for the PPR is large (Hawkins and Sutton 2011). Projections range from forecasts of moderate increases in temperature accompanied by large increases in precipitation to large increases in temperature with

no increases in precipitation (Sofaer et al. 2016). As a result, projections range from anticipated increases to decreases in wetland availability (Sofaer et al. 2016). This uncertainty challenges mitigation and conservation planning efforts. Species distribution models (SDMs), parameterized by bioclimatic covariates are commonly used to assess future impacts of climate change (Pearson and Dawson 2003). However, these vulnerability assessments may be highly uncertain due to both uncertainties about future climate conditions as well as inherent methodological uncertainties associated with the SDMs themselves (Thuiller 2004, Heikkinen et al. 2006). Fortunately, where historic records of climate variability exist, such as in the PPR, investigating past species responses to climate variability can provide insights into species' sensitivities and adaptive capacities as a first step towards planning for an uncertain future.

To explore shorebird sensitivity and adaptive capacity to climate change, we combined historic distribution data with multi-scale habitat selection models and compared shorebird wetland selection between a historic dry and wet year. We define a species' sensitivity to climate change as shifts in habitat selection behavior at the wetland scale in response to changes in the availability of different wetland types and environmental cues that stimulate selection. We define adaptive capacity as a species' ability to express changes in its habitat selection behaviors at landscape and regional scales. For example, species with the ability and proclivity to extend their migration movements, may respond to broad-scale climate change by large geographic shifts as well as selecting different wetland types. Adaptive capacity and sensitivity are components of species climate change vulnerability (Glick et al. 2011). Our use of sensitivity and adaptive capacity concepts are consistent with Foden et al. (2013) who defined sensitivity as the "lack of potential for a species to persist in situ" and adaptive capacity as "a species' ability to avoid the negative impacts of climate change through dispersal and/or micro-

evolutionary change". Thus, sensitivity refers to the potential for shorebirds to find suitable stopover wetlands consistently in the same location and adaptive capacity as their ability to disperse and find suitable wetlands elsewhere.

METHODS

Study Area

Our study area was the PPR in Minnesota, North Dakota, and South Dakota, an area of 302,250 km² (Figure 3.1). This area covers a strong east-west gradient in average annual precipitation ranging between 400 mm to 800 mm and a difference of 7 degrees Celsius in mean annual temperature from north to south (Steen et al. 2014). The pace and extent of land cover conversion to cropland follows a spatial gradient from east to west with loss of virtually all prairie and wetlands in Minnesota to retention of extensive prairie and wetland habitats in the western borders of the PPR in North and South Dakota. The PPR has ecophysiological subregions that vary in key land features from flat topography, high cropland coverage and few remaining wetlands (glacial Lake Agassiz Plain), to low rolling topography with more temporary and seasonal wetlands varying to high cropland coverage (Drift Prairie), to higher elevation, hilly topography, more semipermanent and seasonal wetlands and lower cropland coverage (Prairie and Missouri Coteaus; Kantrud 1989; Figure 3.1).

Bird and habitat surveys

In 2002 and 2011, we conducted surveys at wetlands within randomly chosen townships in the PPR (Figure 3.1). Townships are 36 square mile land units devised by the U.S. Public Land Survey System. We selected 96 townships using a stratified random sample based on median proportions of wetland (> 8% = "high"; < 8% = "low") and cropland (> 60% = "high"; < 60% = "low") land cover classes within the study area. This resulted in four strata: 1) high wetland, high cropland; 2) high wetland, low cropland; 3) low wetland, high cropland; and 4) low wetland, low cropland. Surveyors drove multiple roads within townships, stopping at and surveying wetlands within the randomly selected townships. To mitigate

against distance-based declines in detection, only wetlands or portions of wetlands within 200 meters of the road were surveyed and wetlands that extended beyond 200 meters were not surveyed beyond that distance. We scanned all potential shorebird habitat (shallow water, mudflats, and shoreline areas) with a spotting scope, or if the habitat was close, with binoculars. We visually estimated the number of each species of shorebird at each survey wetland. We recorded the percentage of the wetland within 200 meters in 2011. In 2002, this percentage was estimated via GIS digitized land cover (see next section). We also recorded the percent of the wetland that was visible to the surveyor and not obstructed by trees or land form. In 2002 surveyors drove an average of 10.6 roads per township and in 2011 drove an average of 8.9. The 2002 dataset included 1,230 wetland surveys across 79 townships and the 2011 dataset included 4,522 wetland surveys across 96 townships.

To characterize local habitat conditions at wetland sites, we estimated current wet surface area of each wetland using either an ocular estimate of wetland acres or by describing the percentage of the wetland holding water. Our estimates were compared to a National Wetlands Inventory (NWI) map of the wetland before deriving the final value along with the NWI wetland area information (see *GIS Landcover* below). In addition, we recorded: 1) the surrounding landscape cover type based on assessing the primary cover type in a 500-m radius of the wetland: tilled cropland, pasture, grassland, other cropland, hayland, trees/forest, and farm (barns, outbuildings, etc.); and 2) the primary cover class surrounding the periphery of the wetland out to 30 m according to the same classes (from a GIS landcover layer in 2002 and from ocular estimates in 2011). Wetlands with a linear form such as a ditch, river, or creek were not included in our analysis due to the low proportion of these wetlands in the dataset and low shorebird use of these wetlands.

Study years and climatic conditions

Based on the Palmer Drought Severity Index (PDSI) for May, 2011 was a very wet year in the PPR (Figure 3.2). In contrast, 2002 was a moderately dry year and surveys of wetland basins indicate less

than 20% of temporary wetlands and less than 40% of seasonal wetlands contained water (Niemuth et al. 2010).

GIS Landcover

To describe features of surveyed wetlands and surrounding landscape, we extracted data from spatial layers in ArcMap 10.2 (ESRI, Redlands, California). We used the NWI layer to extract the periphery length of the mapped wetland. We calculated the periphery of each wetland within the survey distance (200 m) of roads by buffering the road and clipping to create a new wetland layer within that distance. We used the NWI layer to extract information on wetland regime: temporary, seasonal, semipermanent, or lake. Temporary, seasonal, and semipermanent relate to the typical duration the wetlands hold water with temporary wetlands holding water for 1-2 months following spring thaw, seasonal wetlands for 2-3 months, and semipermanent wetlands only drying out during prolonged dry periods (Stewart and Kantrud 1971).

To estimate upland land-cover and wetland basin coverage at the landscape scale, we used raster data created by U.S. Fish and Wildlife Service (USFWS) Habitat and Population Evaluation Teams. The USFWS used 30-m resolution Landsat Thematic Mapper Satellite imagery of scenes from 2000-2003. For Minnesota and North and South Dakota, they classified uplands into: cropland, grassland, planted grass, hayland, developed, and tree. Accuracy of the upland land cover data for North and South Dakota, assessed in 2007, was > 90% (M. Estey, personal communication). Grassland, planted grass, and hayland are often considered functionally similar classes for wildlife in the region because they represent non-tilled vegetative land-cover and are negatively correlated with cropland at the landscape scale. Developed and tree land cover classes are rare in the PPR landscape. Therefore, we described upland habitats by the proportion of cropland in the landscape; because of the negative correlation between cropland and grassland, landscapes with high cropland have low grassland, and vice versa. The USFWS wetland basin coverage represented wetlands classified from contiguous NWI wetlands based on the

most permanent wetland regime of the constituent wetlands following procedures outlined in previous papers (Cowardin et al. 1995, Johnson and Higgins 1997). Wetland basins were classified as: temporary, seasonal, semipermanent, lake, river, and forested wetland. We described wetland landscape coverage according to the proportion of temporary, seasonal, and semipermanent wetlands. Rivers and lakes were relatively uncommon. Forested wetlands, which are seldom used by our focal species, were uncommon and occurred only in Minnesota. Thus, we did not include river, lake, or forested wetland coverage in our analysis.

Covariates

We selected our covariates a priori based on previous work in the Great Plains which found: migratory shorebirds selected landscapes with temporary and/or semipermanent wetlands (Albanese 2013, Niemuth 2006), cropped landscapes regardless of dry or wet conditions (Skagen et al. 2005), and shallower wetlands or wetlands with shallow water areas (Davis and Smith 1998, Webb et al. 2010). To describe wetland-scale selection we included wetland depth and surrounding upland covariates. Wetland depth was devised as a continuous numerical value reflecting the permanency of that class (temporary = 1, seasonal = 2, semipermanent = 3, and lake = 4), because wetland type is correlated with water depth. We also included the quadratic form of this covariate to reflect selection for intermediate depths. We included a factor indicating whether the periphery of the wetland was primarily cropland and a factor indicating whether this was the case in the surrounding (500-m) landscape. To describe landscape-scale selection, we included the proportion of a township composed of temporary wetlands, seasonal wetlands, semipermanent wetlands, and cropland. To describe selection at the regional scale we used geographic covariates: degrees latitude and longitude in linear and quadratic forms. Because migratory shorebird occurrence is highly temporally dynamic we included date-of-survey covariates in linear and quadratic forms.

Models

Our data were geographically and statistically structured—wetlands nested within townships. Wetlands within the same township were expected to experience more similar environmental conditions than wetlands from different townships. Therefore, we used hierarchical regression models (Gelman and Hill 2007) which allowed us to explore both township and wetland specific covariates and to model variation among townships. We refer to wetlands as a local scale of measurement and townships as a landscape scale.

To describe multi-scale habitat selection, we assessed occurrence (presence/absence) of shorebirds at wetland sites using hierarchical binomial random effects models as implemented in the R package lme4 (Bates et al. 2015). We selected from en route only shorebird migrants four focal species or species groups based on their being relatively common on surveys: Yellowlegs (Lesser Yellowlegs and Great Yellowlegs), Least Sandpiper, Baird's/White-rumped Sandpiper (Baird's Sandpiper in 2011 and White-rumped Sandpiper in 2002), and Pectoral Sandpiper. We grouped Baird's and White-rumped Sandpipers because they are similar species based on body size, habitat use, and foraging water depths, and because Baird's was common only in 2011 and White-rumped was common only in 2002 (Skagen et al. 1999). For each species, we described a null model that included, along with the intercept, an offset (covariate with coefficient fixed at 1) of the length of shoreline (periphery) that was surveyed, the Julian date of the survey and its quadratic form, and a random intercept effect of the survey township. Candidate covariates included the multi-scaled covariates (described in the section above): wetland depth (local), wetland in cropland (local), proportion cropland (landscape), proportion temporary wetland (landscape), proportion seasonal wetland (landscape), proportion semipermanent wetland (landscape), latitude (regional), and longitude (regional). For each species and year, we first considered alternative models based on all additive combinations of candidate covariates and the null model set. Covariates contained in the most parsimonious model (based on minimum AICc) for each year were

used to build a “years-combined” model for each species. AICc calculation for all model subsets was performed using the R package MuMin (Bartoń 2013). The “years-combined” model was estimated from data collected in both years. This model included candidate covariates that were in ≥ 1 of the individual year models and year interaction terms for each candidate covariate. We report the most parsimonious “years-combined” model for each species. We also evaluated the most parsimonious “years-combined” models using a measure of pseudo R-squared. This measure was calculated as the difference between variance of the residuals of the null model (no predictors and random intercepts) and the most parsimonious model divided by the variance of the residuals of the null model. To assess the relative values of the variances among townships and within townships we report the intraclass correlation coefficient. This correlation was calculated as the variance among the random intercepts for township (among township variance), divided by the sum of the among township variance and within township variance.

To model predicted shorebird distributions, we considered the geographic and landscape candidate covariates only in models by year for each species. Using calculations of AICc based model weights for each model subset, we derive a final probability of occurrence value summing over the weighted prediction for each model. All statistical analyses were performed in R 3.2.4 (R Development Core Team 2012).

RESULTS

In 2002, Yellowlegs were detected on 107 surveys (84% were Lesser Yellowlegs and 16% were Greater Yellowlegs), Least Sandpiper on 51, White-rumped Sandpiper on 44, and Pectoral Sandpiper on 38. In 2011, Yellowlegs were detected on 78 surveys (97% were Lesser Yellowlegs and 3% were Greater Yellowlegs), Least Sandpiper on 29, Baird’s Sandpiper on 23, and Pectoral Sandpiper on 16.

Spatial Components of Variance in Occurrence Patterns

Intraclass correlation coefficients for three species in 2002 were higher than in 2011 (Table 3.1). Thus, relatively greater variance was explained by township than covariates in the models in 2002 versus 2011.

Hierarchical Models Including Covariates

For all species, the most parsimonious models explaining species occurrence patterns included geographic location and covariates from both landscape and wetland scales (Figure 3.3). Pseudo r^2 for the Yellowlegs model was 0.248, 0.285 for the Least Sandpiper, 0.330 for the Baird's/White-rumped Sandpiper, and 0.282 for the Pectoral Sandpiper. Thus, for these species > 65% of the variation in spatial occurrence patterns remained unexplained by the included covariates.

In general, decisions made at the local scale were consistent between years whereas landscape-scale and regional decisions showed differences between years. Most species were distributed more southerly in the wet year (2011), and more westerly in both years. In the dry year, Least and Pectoral Sandpipers selected townships with more semipermanent wetlands but avoided them in the wet years. Baird's/White-rumped Sandpipers selected townships with more seasonal wetlands in the dry year but avoided them in the wet year. Yellowlegs avoided townships with more temporary wetlands in the dry year but selected them in the wet year. Pectoral Sandpipers and Baird's/White-rumped Sandpipers selected townships with more cropland in both years. The extent of cropland cover at 500-m was not included in any final models, but the condition of a wetland being adjacent to cropland was important with all species showing some preference for wetlands in croplands in both years. However, in 2011, this preference was stronger. This pattern was most pronounced in 2011 when temporary wetlands were more available. Most species selected for shallower wetlands in both years. However, because in 2002 most temporary wetlands were dry, use of seasonal wetlands greatly increased, whereas in 2011 use of temporary wetlands increased (Supplementary. figure 3.1).

The predicted probability of occurrence maps (Figure 3.4) illustrate the dynamic shifts in spatial distribution across wet and dry years. In general, both our survey data and predicted occurrences show more southerly distributions in a wet year (2011) and more central and northerly distributions in a dry year (2002). In addition, species' distributions are more concentrated in wet versus dry years.

DISCUSSION

Shorebird migration patterns through the climatically dynamic Great Plains are known to be highly variable with opportunistic use of different wetlands from year-to-year (Skagen and Knopf 1993, 1994, Skagen et al. 2005, Albanese et al. 2012). However, to the best of our knowledge, our multi-scaled assessment of changes in habitat use patterns and spatial distribution is the first empirical documentation of these dynamic patterns across a large region. The degree of spatial variation in distribution during migration has implications for the ability of migrating shorebirds to respond adaptively to climate change and mitigate climate change impacts, while the degree of variation in selection of wetland characteristics has implications for the sensitivity of shorebirds to climate change impacts to wetlands. We contrasted shorebird distributions and habitat selection in a dry and wet year and found significant spatial shifts within the region and differential selection for landscape composition indicating high adaptive capacity. However, at the scale of individual wetlands, we found selection to be consistent across years indicating high sensitivity to wetland characteristics.

That covariates in three models explained relatively less variation compared to the random effect of township itself in 2002 versus 2011 indicates that, generally, migrating shorebirds found more widely available habitat regardless of township in 2011, the wet year. In 2002, because some townships, especially those with low densities of more permanent wetland types (seasonal and semipermanent wetlands) had low wetland abundance, landscape-scale variation in wetland abundance was a stronger driving factor of shorebird occurrence.

At the regional scale, we found that shorebirds in a wet year had a more southerly distribution than in a dry year, presumably in response to more widespread availability of wetland habitats. We hypothesize that in a system with dispersed and unpredictable suitable stopover habitat, migrating birds will stop at first available suitable habitat, triggered by energetic requirements, and overfly subsequently encountered suitable habitat (Gudmundsson et al. 1991, Iverson et al. 1996, Buler et al. 2007). Although the birds in our study would have flown over states further south by the time they reached the PPR, the PPR may be more critical because of the relatively higher densities of wetlands than those areas.

All of our focal species (or species groups) showed differing selection patterns for landscape cover type between years and these selection patterns varied among species. However, species consistently selected for landscapes with an abundance of wetlands as expressed by the significant interaction between climatic conditions and wetland type in a given year. For example, Yellowlegs selected for landscapes with high amounts of temporary wetlands in the wet year but avoided these same areas in the dry year when temporary wetlands held little water. In dry years few temporary wetlands hold water but in wet years these same wetlands are a source of shallow water suitable for foraging. In addition, the abundance and spatial extent of these and associated flooded shallow water areas can form an important landscape level cue to habitat availability. Least and Pectoral Sandpipers selected landscapes with higher numbers of semipermanent wetlands only in the dry year. Semipermanent wetlands hold water through short-term droughts and may represent an important landscape-level selection cue when surrounding landscapes are dry. Similarly, Baird's/White-rumped Sandpipers selected for landscapes with high amounts of seasonal wetlands only in the dry year. This suggests that along with landscapes with high proportions of semipermanent wetlands, landscapes with high proportions of seasonal wetlands may be important in dry years for certain shorebird species.

Selected landscapes and associated landscape-scale covariates varied between dry and wet years, but at the wetland scale habitat selection between years was relatively invariant. Buler et al. (2007) suggested that migrants may use landscape variability as a cue to underlying habitat quality. In the dynamic wetland landscape of the PPR, wetland abundance at the landscape scale may serve as a cue to suitable wetlands. In both years, our top models for Yellowlegs, Least Sandpiper, and Pectoral Sandpiper indicated selection for shallower wetlands (i.e., temporary wetlands in 2011 and seasonal wetlands in 2002; Supplementary figure 3.1). In both years, all species showed at least moderate selection for wetlands surrounded by cropland. That this selection pattern was stronger in the wet year could be a result of the relatively higher proportion of cropland in landscapes selected in the wetter year. In the PPR, landscapes with a high proportion of temporary wetlands typically have more cropland, and those with a high proportion of semipermanent wetland typically have more grassland. Selection for agricultural wetlands by migrating and wintering shorebirds is widely observed in spite of lower food availability than wetlands in grassland because these wetlands may provide more open habitats that are attractive to shorebirds (Elphick and Oring 1998, Euliss et al. 1999, Skagen et al. 2005, Stutzman 2012).

Of major conservation concern is the fact that shorebirds in the PPR use unprotected, widely dispersed, and threatened wetlands that occur primarily on private agricultural lands (Skagen et al. 2008). Furthermore, land-use planning to allow for an adaptive response by migratory shorebirds requires planning in the context of a highly uncertain future and over broad spatial extents. Seasonal evaluations based on the average climate projection across 37 climate models suggest conditions in the PPR in spring will be wetter while summer and fall will be dryer. Given these projections, shorebird habitat will be available in landscapes with more temporary wetlands during spring migration and in landscapes with more seasonal and semipermanent wetlands during fall migration (Ballard et al. 2014). However, GCM projections vary in their forecasts with some models projecting wetter conditions and some projecting drier conditions (Sofaer et al. 2016). Although shorebirds demonstrated high sensitivity

to climate change because of their consistent requirements for shallow water wetlands, often found adjacent to agricultural areas, their high adaptive capacity demonstrated by their ability to find these wetlands in different landscapes and in different parts of the region suggests migrating shorebirds may have resilience to some degree of climate change. Thus, resilience planning (Lawler et al. 2004) as a strategy to mitigate climate change in this system suggest preserving agricultural wetlands widely distributed across the PPR region and diverse and high density wetland landscapes.

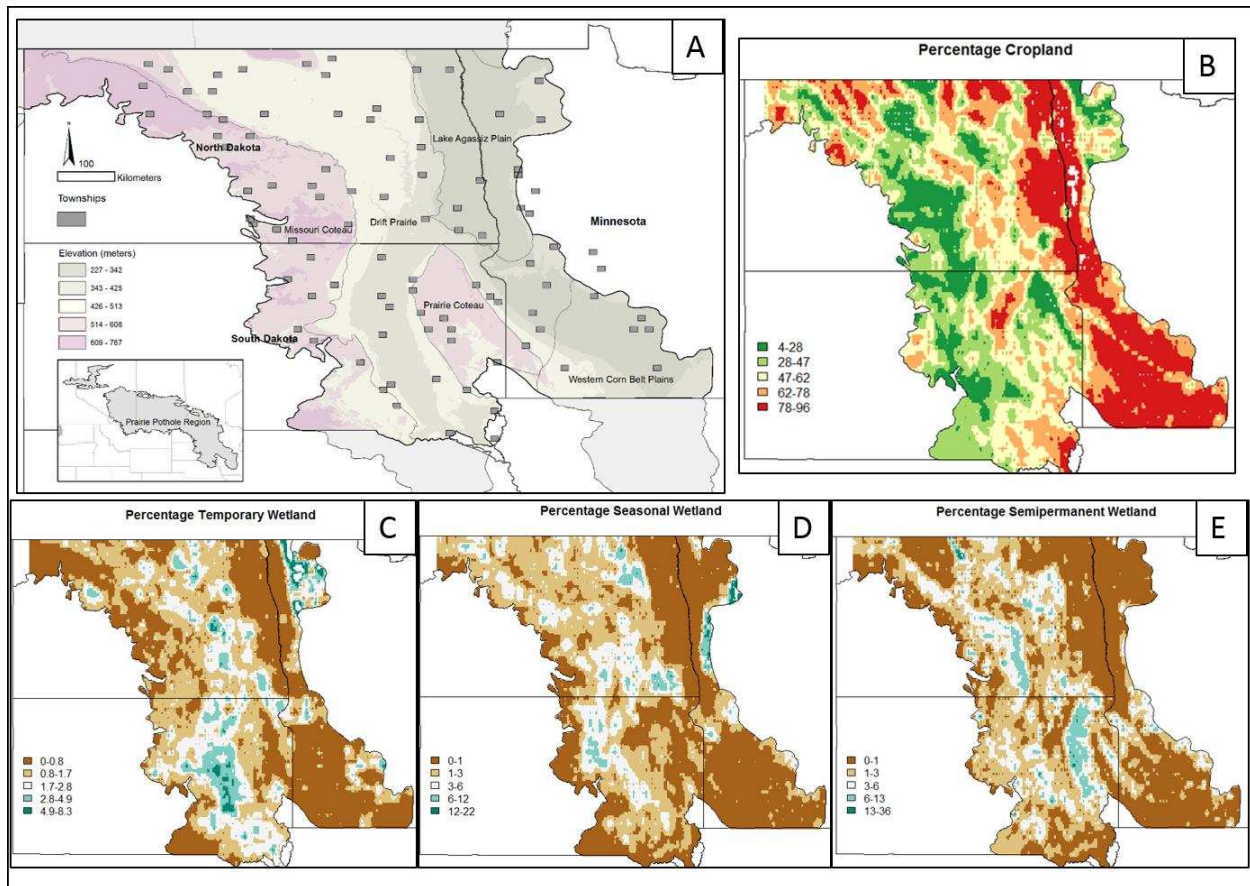


Figure 3.1. The Prairie Pothole Region (PPR) study area includes the PPR in Minnesota, North Dakota, and South Dakota. (A) The 96 selected townships within which a subset of wetlands were surveyed in 2002 (79 townships) and 2011 (96 townships). Subregions are delineated on the basis of cropland and amount of different wetland types. (B) The percentage of landscape that is cropland showing a majority of the landscape in cropland in the eastern portion of the study area and the decline in croplands and an increase in grassland moving west. (C) The percentage of landscape in temporary wetland is highest in the drift prairie as well as northern Minnesota. However, in northern Minnesota temporary wetland is represented by, typically, saturated wetland. (D) Seasonal wetlands are most common in the Missouri Coteau and northern Drift Prairie and central-west Minnesota. (E) Semipermanent wetlands are most common in both the Prairie and Missouri Coteau.

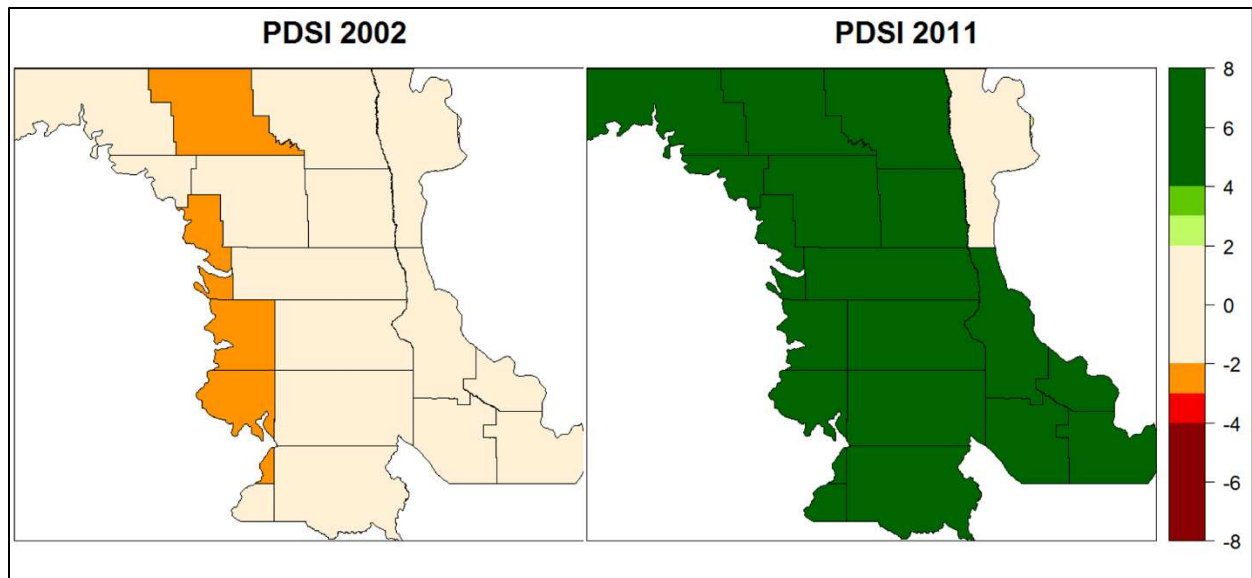


Figure 3.2. Palmer drought severity index (PDSI) showing data for May of both study years from the National Climate Data Center. Values between 2 and -2 are considered mid-range. Values between -2 and -3 indicate moderate drought and values exceeding +4 are considered extremely moist.

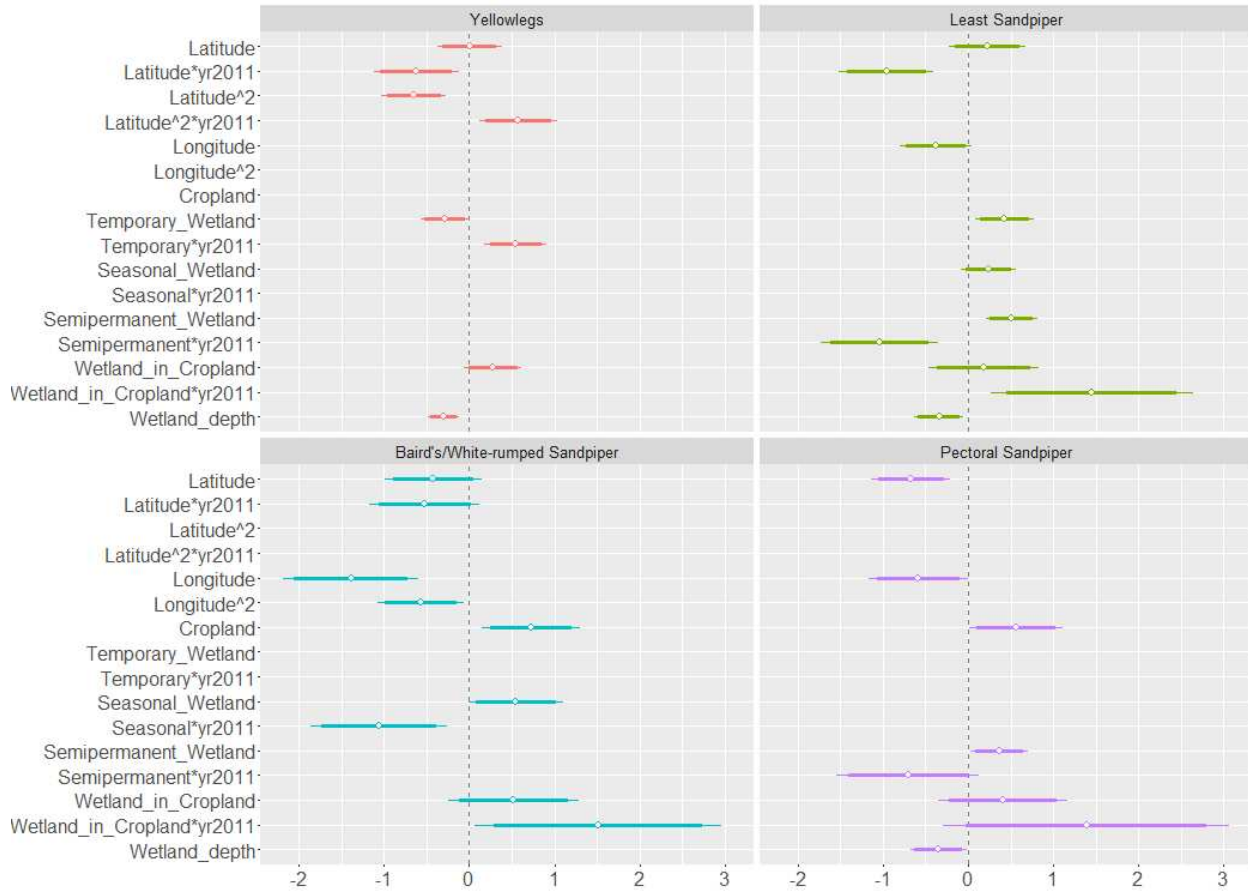
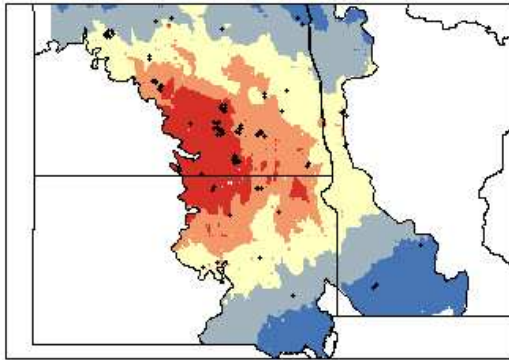
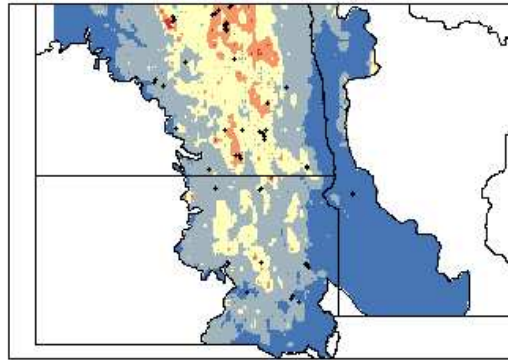


Figure 3.3. Multi-scale habitat selection model results for four shorebird species (or species pair for Baird's and White-rumped Sandpipers, and Greater Yellowlegs and Lesser Yellowlegs) based on binomial models of occurrence in 2002 and 2011. Regional-scale selection is represented by latitude and longitude. Landscape-scale selection is represented by cropland, temporary, seasonal, and semipermanent proportional cover values in the township. Local-scale selection is represented by water depth of the wetland and whether the wetland is in cropland. Coefficient means and 95% confidence intervals for covariates included in the most parsimonious models (lowest AICc) are shown.

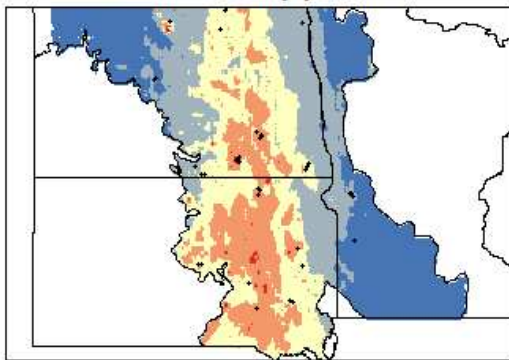
Yellowlegs 2002



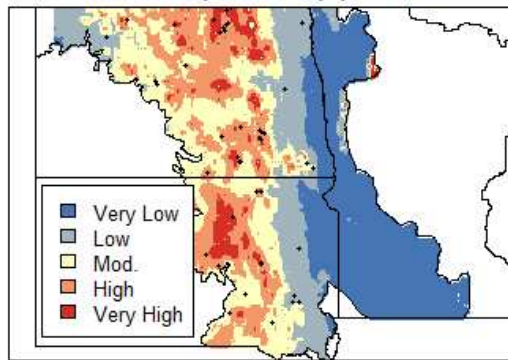
Least Sandpiper 2002



Pectoral Sandpiper 2002



White-rumped Sandpiper 2002



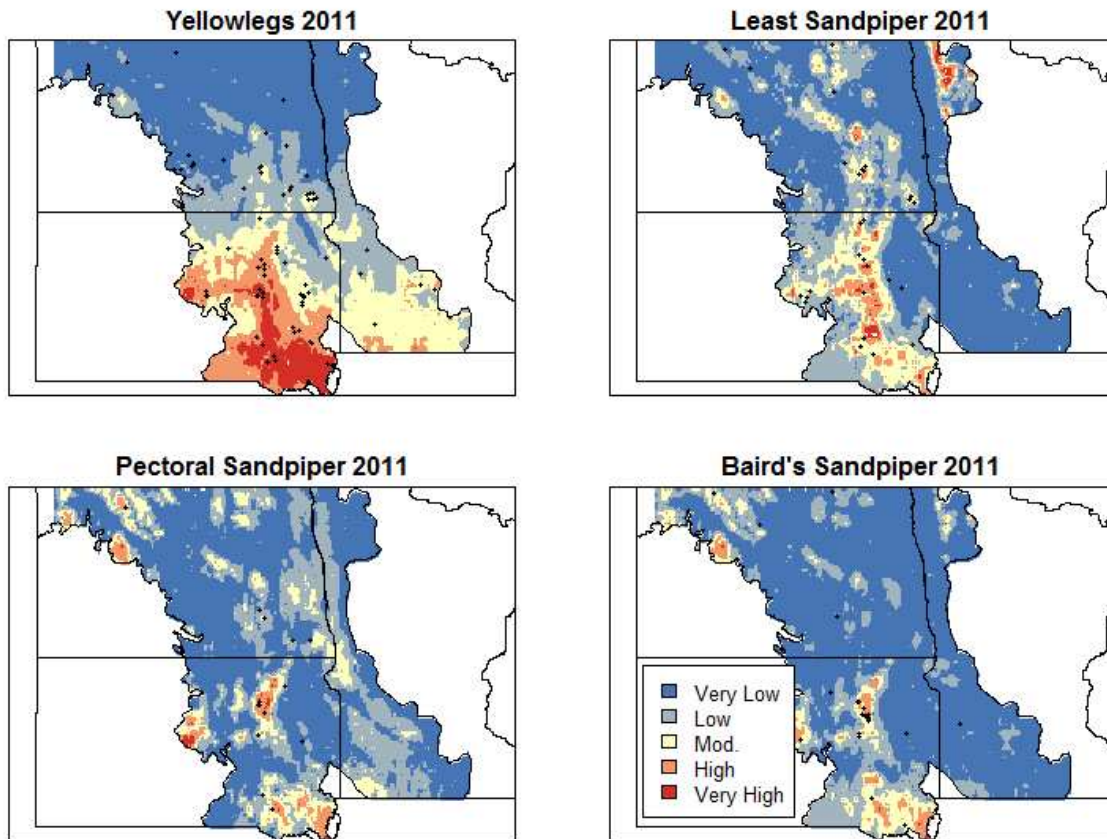


Figure 3.4. Predictive model maps showing relative probability of shorebird occurrence in 2002 and 2011. Predictive models are based on regional and landscape-scale land-cover covariates. Probabilities are based on sums across AICc weighted model predictions.

Table 3.1. Intraclass correlation coefficients based on most parsimonious models for each year and species. Values near 0 indicate little variance among townships and near 1 indicate little variance within townships.

| | 2002 (dry) | 2011 (wet) |
|--|------------|------------|
| Yellowlegs | 0.123 | 0.098 |
| Least Sandpiper | 0.167 | 0.000 |
| Pectoral Sandpiper | 0.443 | 0.000 |
| White-rumped Sandpiper (2002); Baird's Sandpiper (2011) | 0.181 | 0.391 |

LITERATURE CITED

- Albanese, G., C. A. Davis, and B. W. Compton. 2012. Spatiotemporal scaling of North American continental interior wetlands: implications for shorebird conservation. *Landscape Ecology* **27**:1465-1479.
- Ballard, T., R. Seager, J. E. Smerdon, B. I. Cook, A. J. Ray, B. Rajagopalan, Y. Kushnir, J. Nakamura, and N. Henderson. 2014. Hydroclimate Variability and Change in the Prairie Pothole Region, the "Duck Factory" of North America. *Earth Interactions* **18**.
- Bartoń, K. 2013. (Bartoń): multi-model inference, (R Development Core Team) package version 1.9.13.
- Bates, D., M. Machler, B. M. Bolker, and S. C. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* **67**:1-48.
- Both, C. and M. E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**:296-298.
- Brown, S., C. Hickey, B. Harrington, and R. Gill. 2001. The U.S. Shorebird Conservation Plan. Manomet Center for Conservation Sciences, Manomet, MA.
- Buler, J. J., F. R. Moore, and S. Woltmann. 2007. A multi-scale examination of stopover habitat use by birds. *Ecology* **88**:1789-1802.
- Cowardin, L. M., T. L. Shaffer, P. M. Arnold, and United States. National Biological Service. 1995. Evaluations of duck habitat and estimation of duck population sizes with a remote-sensing-based system. U.S. Dept. of the Interior, National Biological Service, Washington, D.C.
- Davis, C. A. and L. M. Smith. 1998. Ecology and management of migrant shorebirds in the Playa Lakes Region of Texas. *Wildlife Monographs*:5-45.
- Elphick, C. S. and L. W. Oring. 1998. Winter management of Californian rice fields for waterbirds. *Journal of Applied Ecology* **35**:95-108.

- Euliss, N. H., D. A. Wrubleski, and D. M. Mushet. 1999. Wetlands of the Prairie Pothole Region: invertebrate species composition, ecology, and management.
- Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, D. J. Levey, P. P. Marra, C. L. Merkord, E. Nol, S. I. Rothstein, T. W. Sherry, T. S. Sillett, F. R. Thompson, and N. Warnock. 2010. Recent advances in understanding migration systems of New World land birds. *Ecological Monographs* **80**:3-48.
- Foden, W. B., S. H. M. Butchart, S. N. Stuart, J. C. Vie, H. R. Akcakaya, A. Angulo, L. M. DeVantier, A. Gutsche, E. Turak, L. Cao, S. D. Donner, V. Katariya, R. Bernard, R. A. Holland, A. F. Hughes, S. E. O'Hanlon, S. T. Garnett, C. H. Sekercioglu, and G. M. Mace. 2013. Identifying the World's Most Climate Change Vulnerable Species: A Systematic Trait-Based Assessment of all Birds, Amphibians and Corals. *Plos One* **8**.
- Gelman, A. and J. Hill. 2007. Data analysis using regression and hierarchical/multilevel models. Cambridge University Press: Cambridge, UK.
- Glick, P., B. A. Stein, and N. A. Edelson. 2011. Scanning the Conservation Horizon: A Guide to Climate Change Vulnerability Assessment. National Wildlife Federation, Washington, D.C.
- Gudmundsson, G. A., A. Lindstrom, and T. Alerstam. 1991. Optimal Fat Loads and Long-Distance Flights by Migrating Knots *Calidris-Canutus*, Sanderlings *C-Alba* and Turnstones *Arenaria-Interpres*. *Ibis* **133**:140-152.
- Hagan, J. M., T. L. Lloyddevans, and J. L. Atwood. 1991. The Relationship between Latitude and the Timing of Spring Migration of North-American Landbirds. *Ornis Scandinavica* **22**:129-136.
- Hawkins, E. and R. Sutton. 2011. The potential to narrow uncertainty in projections of regional precipitation change. *Climate Dynamics* **37**:407-418.

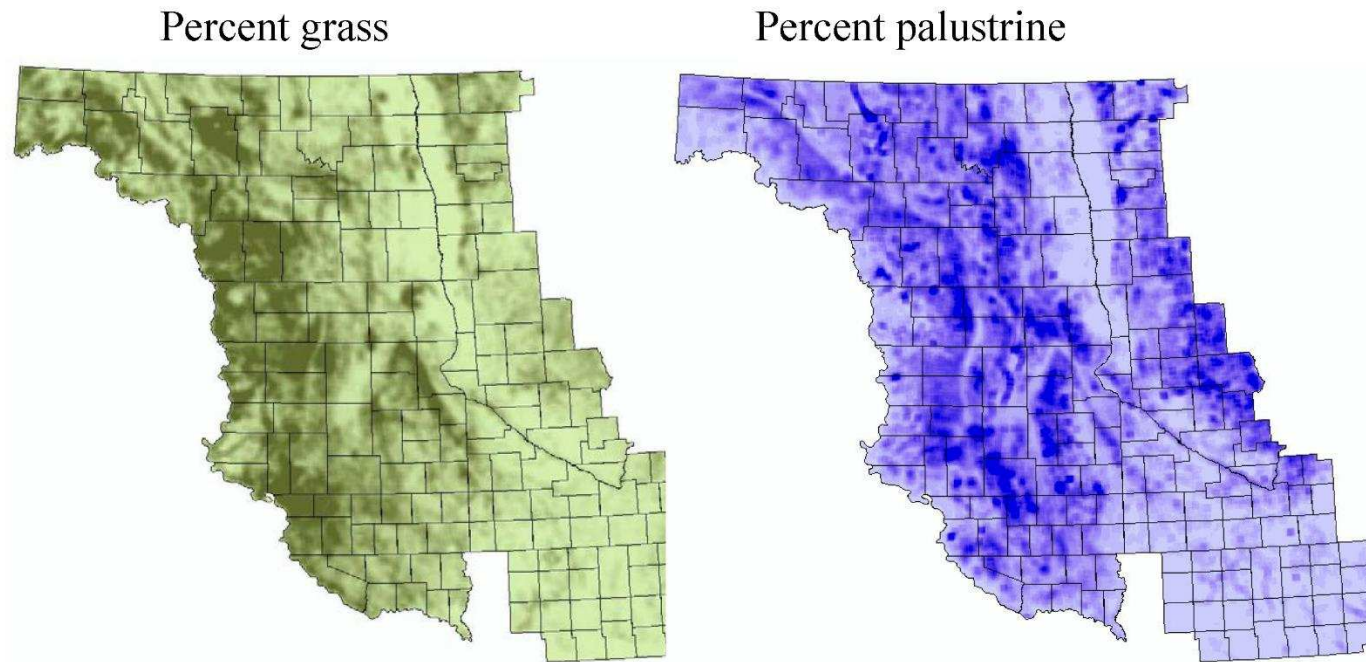
- Heikkinen, R. K., M. Luoto, M. B. Araujo, R. Virkkala, W. Thuiller, and M. T. Sykes. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography* **30**:751-777.
- Held, I. M. and B. J. Soden. 2006. Robust responses of the hydrological cycle to global warming. *Journal of Climate* **19**:5686-5699.
- Kantrud, H. A., G. L. Krapu, and G. A. Swanson. 1989. Prairie basin wetlands of the Dakotas : a community profile. U.S. Dept. of the Interior, Fish and Wildlife Service, Research and Development, Washington, DC.
- Iverson, G. C., S. E. Warnock, R. W. Butler, M. A. Bishop, and N. Warnock. 1996. Spring migration of Western Sandpipers along the Pacific Coast of North America: A telemetry study. *Condor* **98**:10-21.
- Johnson, R. and K. Higgins. 1997. Wetland resources of eastern South Dakota. South Dakota State University, Brookings, SD, USA.
- Johnson, R. R., F. T. Oslund, and D. R. Hertel. 2008. The past, present, and future of prairie potholes in the United States. *Journal of Soil and Water Conservation* **63**:84a-87a.
- Landsberg, J. H. 2002. The effects of harmful algal blooms on aquatic organisms. *Reviews in Fisheries Science* **10**:113-390.
- Lawler, J. J. 2009. Climate Change Adaptation Strategies for Resource Management and Conservation Planning. *Year in Ecology and Conservation Biology 2009* 1162:79-98.
- Lehikoinen, E., T. H. Sparks, and M. Zalakevicius. 2004. Arrival and departure dates. *Birds and Climate Change* **35**:1-31.
- Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra. 2015. A call for full annual cycle research in animal ecology. *Biology Letters* **11**.

- Millett, B., W. C. Johnson, and G. Guntenspergen. 2009. Climate trends of the North American prairie pothole region 1906-2000. *Climatic Change* **93**:243-267.
- Morrison, R. I. G., B. J. McCaffery, R. E. Gill, S. K. Skagen, S. L. Jones, G. W. Page, C. L. Gratto-Trevor, and B. A. Andres. 2006. Population estimates of North American shorebirds. *Wader Study Group Bulletin* **111**:67-85.
- Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology* **147**:146-166.
- Niemuth, N. D. and J. W. Solberg. 2003. Response of waterbirds to number of wetlands in the Prairie Pothole Region of North Dakota, USA. *Waterbirds* **26**:233-238.
- Niemuth, N. D., B. Wangler, and R. E. Reynolds. 2010. Spatial and Temporal Variation in Wet Area of Wetlands in the Prairie Pothole Region of North Dakota and South Dakota. *Wetlands* **30**:1053-1064.
- Norris, K., P. W. Atkinson, and J. A. Gill. 2004. Climate change and coastal waterbird populations - past declines and future impacts. *Ibis* **146**:82-89.
- Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**:37-42.
- Pearson, R. G. and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* **12**:361-371.
- R Development Core Team. 2012. *R: A language and environment for statistical computing*. R Foundation for Statistical Computer, Vienna, Austria.
- Skagen, S. K., S. Brown, and R. Johnson. 2005. Implications of different shorebird migration strategies for habitat conservation. Pages 680–683 in *Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference*, vol. 2 (C. J.

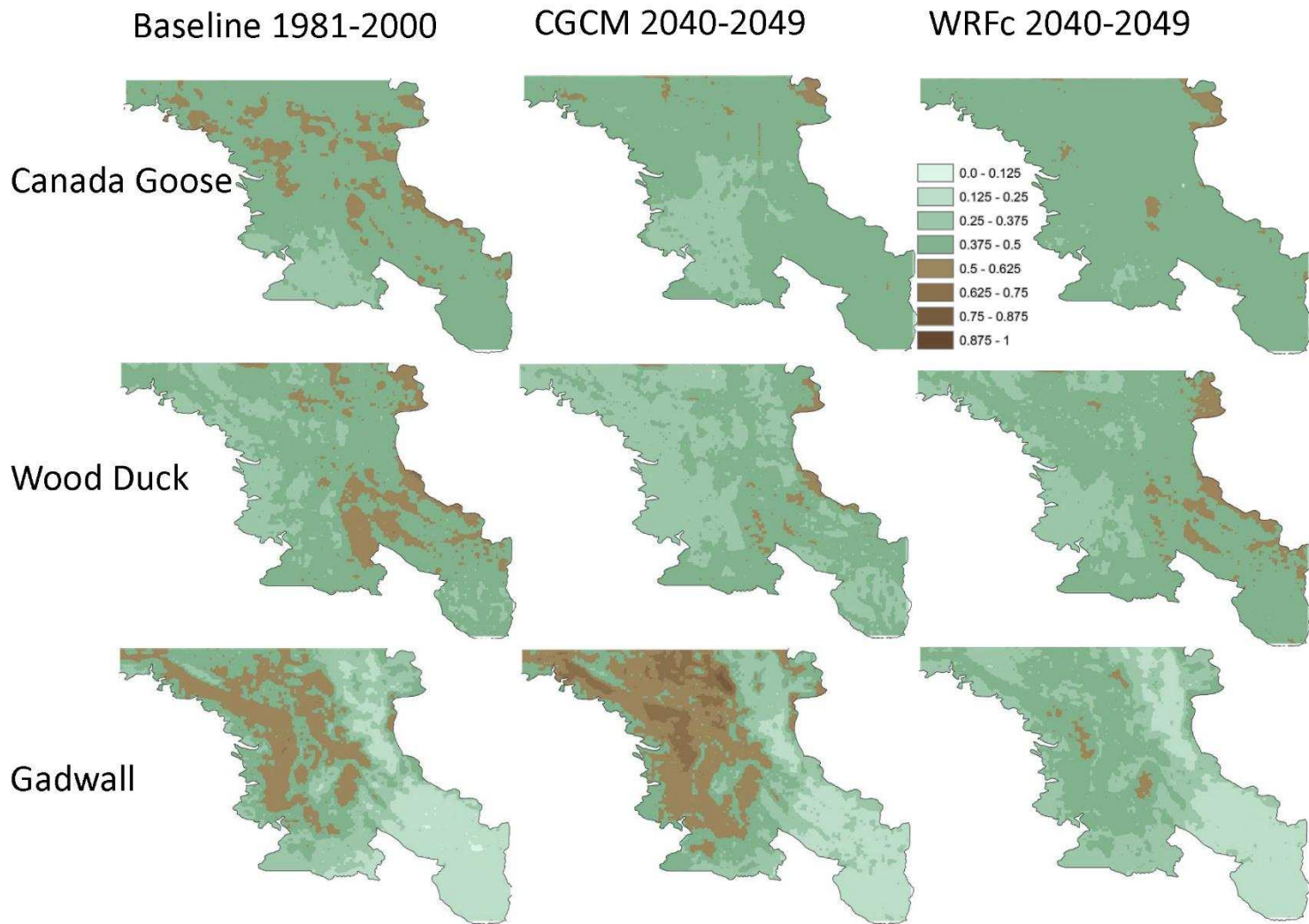
- Ralph and T. D. Rich, Eds.). U.S. Department of Agriculture, Forest Service, General Technical Report PSW-GTR-191.
- Skagen, S. K., U.S. Geological Survey and U.S. Prairie Pothole Joint Venture. 1999. Biogeographical profiles of shorebird migration in midcontinental North America. U.S. Dept. of the Interior, U.S. Geological Survey ; Springfield National Technical Information Service distributor, Fort Collins, CO.
- Skagen, S. K., D. A. Granfors, and C. P. Melcher. 2008. On determining the significance of ephemeral continental wetlands to north American migratory shorebirds. *Auk* **125**:20-29.
- Skagen, S. K. and F. L. Knopf. 1993. Toward Conservation of Midcontinental Shorebird Migrations. *Conservation Biology* **7**:533-541.
- Skagen, S. K. and F. L. Knopf. 1994. Migrating Shorebirds and Habitat Dynamics at a Prairie Wetland Complex. *Wilson Bulletin* **106**:91-105.
- Small-Lorenz, S. L., L. A. Culp, T. B. Ryder, T. C. Will, and P. P. Marra. 2013. A blind spot in climate change vulnerability assessments. *Nature Clim. Change* **3**:91-93.
- Smith, R. I. 1970. Response of Pintail Breeding Populations to Drought. *Journal of Wildlife Management* **34**:943-946.
- Sofaer, H. R., S. K. Skagen, J. J. Barsugli, B. S. Rashford, G. C. Reese, J. A. Hoeting, A. W. Wood, and B. R. Noon. 2016. Projected wetland densities under climate change: habitat loss but little geographic shift in conservation strategy. *Ecological Applications*.
- Steen, V., S. K. Skagen, and B. R. Noon. 2014. Vulnerability of Breeding Waterbirds to Climate Change in the Prairie Pothole Region, USA. *Plos One* **9**.
- Stewart, R. E. and H. A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Bureau of Sport Fisheries and Wildlife; for sale by the Supt. of Docs., Washington,.

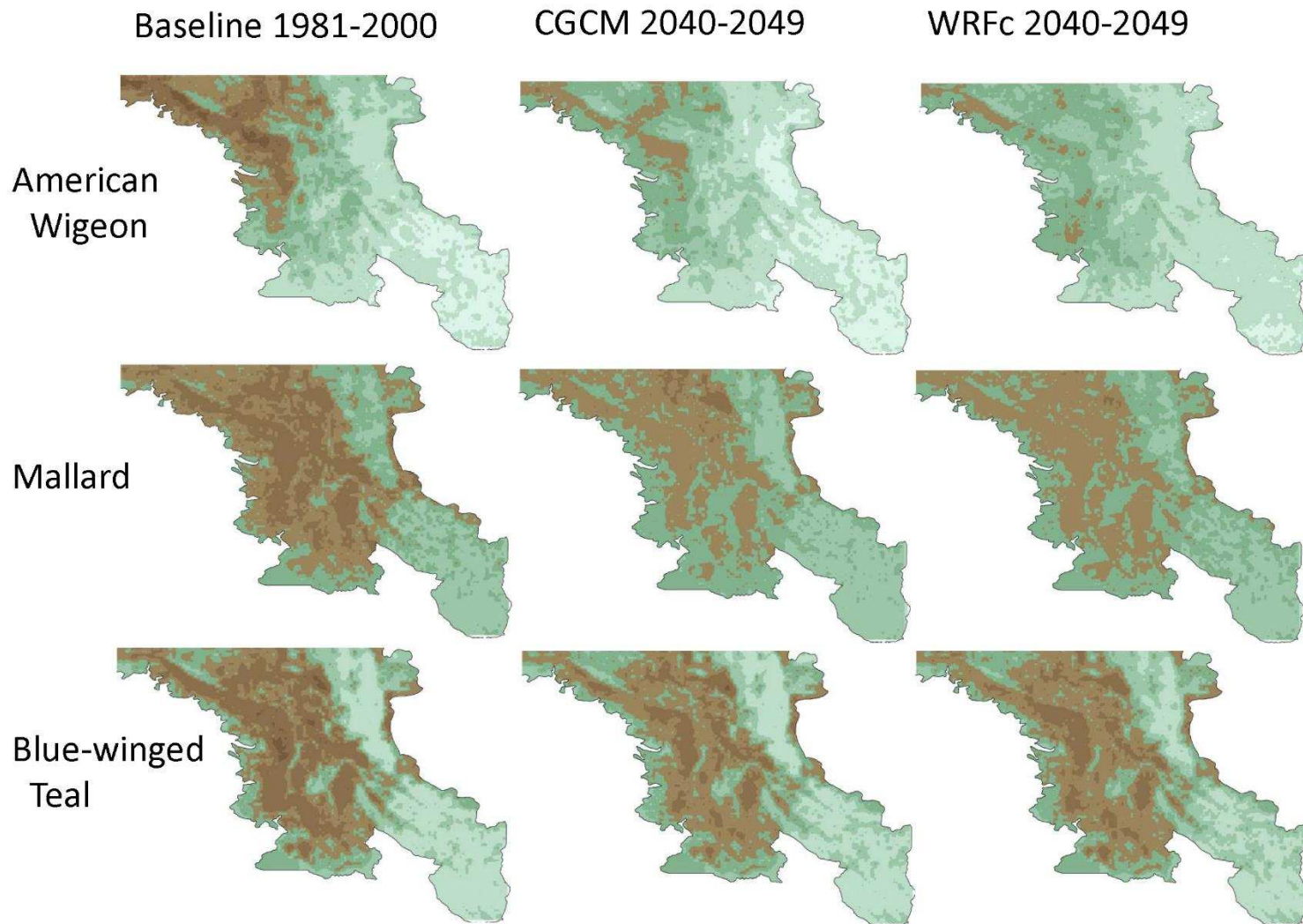
- Stewart, R. E. and H. A. Kantrud. 1973. Ecological Distribution of Breeding Waterfowl Populations in North-Dakota. *Journal of Wildlife Management* **37**:39-50.
- Stutzman, R. 2012. Stopover Decisions of Migratory Shorebirds: An assessment of Habitat Use, Food Availability, Behavior and Phenology. University of Nebraska-Lincoln, Lincoln.
- Sutherland, W. J., J. A. Alves, T. Amano, C. H. Chang, N. C. Davidson, C. M. Finlayson, J. A. Gill, R. E. Gill, P. M. Gonzalez, T. G. Gunnarsson, D. Kleijn, C. J. Spray, T. Szekely, and D. B. A. Thompson. 2012. A horizon scanning assessment of current and potential future threats to migratory shorebirds. *Ibis* **154**:663-679.
- Thomas, G. H., R. B. Lanctot, and T. Szekely. 2006. Can intrinsic factors explain population declines in North American breeding shorebirds? A comparative analysis. *Animal Conservation* **9**:252-258.
- Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology* **10**:2020-2027.
- Webb, E. B., L. M. Smith, M. P. Vrtiska, and T. G. Lagrange. 2010. Effects of Local and Landscape Variables on Wetland Bird Habitat Use During Migration Through the Rainwater Basin. *Journal of Wildlife Management* **74**:109-119.
- Webster, P. J., G. J. Holland, J. A. Curry, and H. R. Chang. 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* **309**:1844-1846.

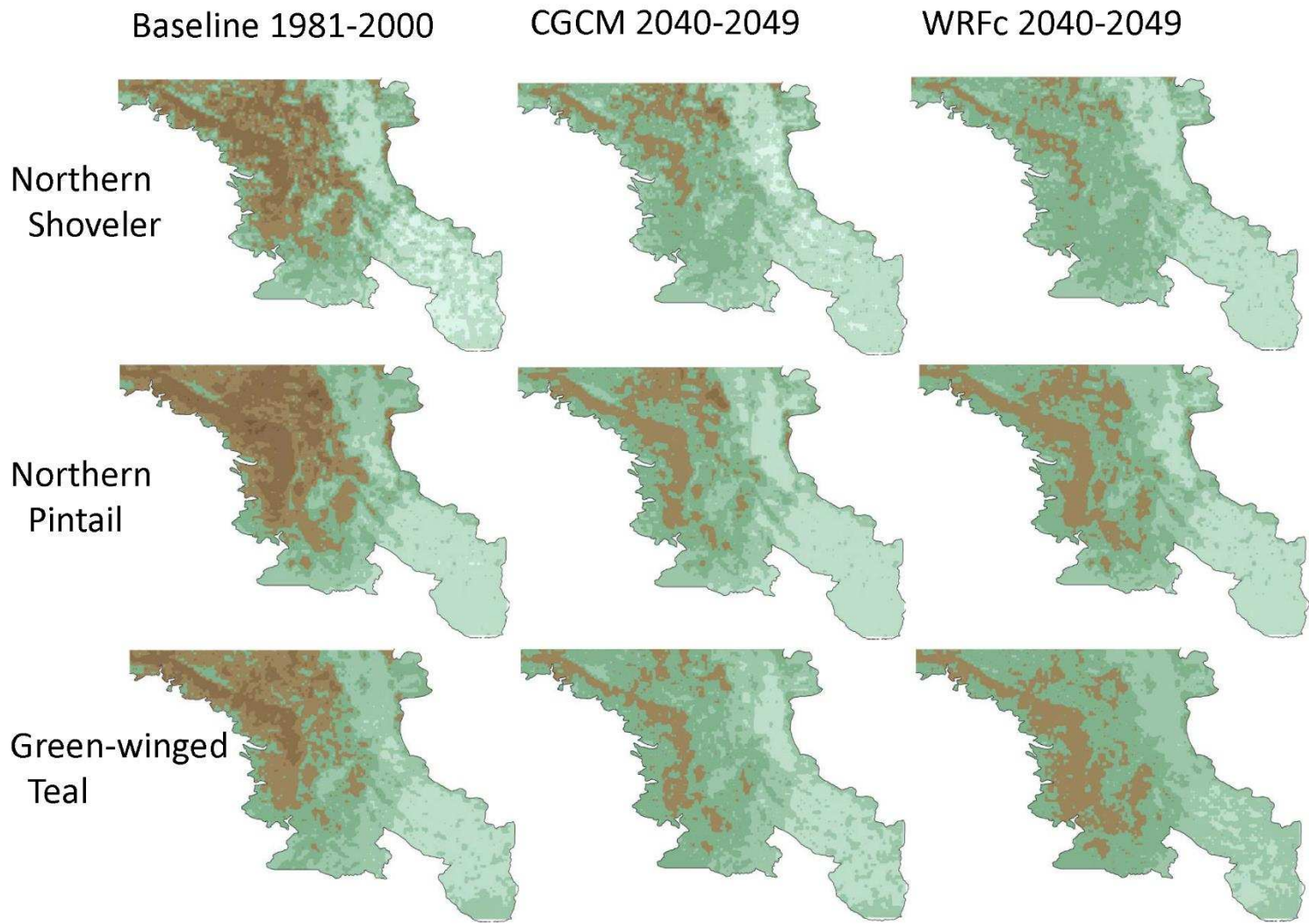
APPENDIX



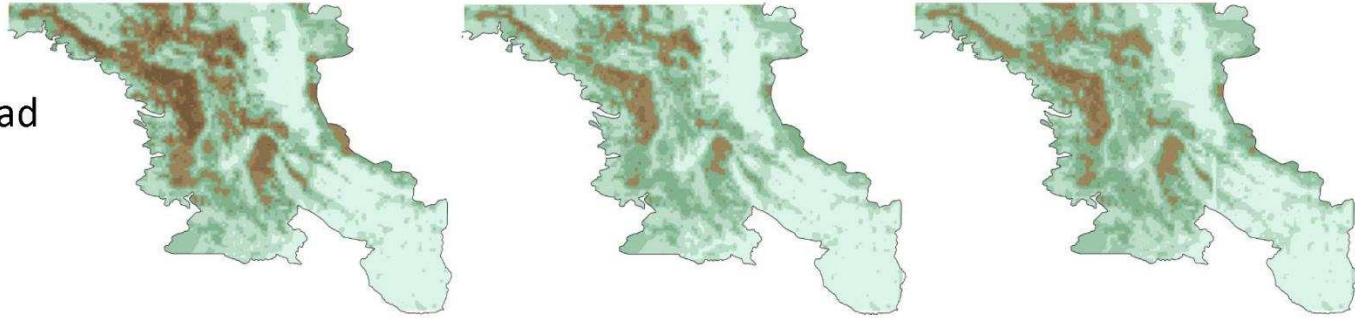
Supplementary figure S1.1. Distribution of grassland and palustrine wetlands on the U.S. Prairie Pothole Region landscape. Darker shades represent greater coverage of grassland (versus cropland) and greater areal coverage of wetlands (log transformed).



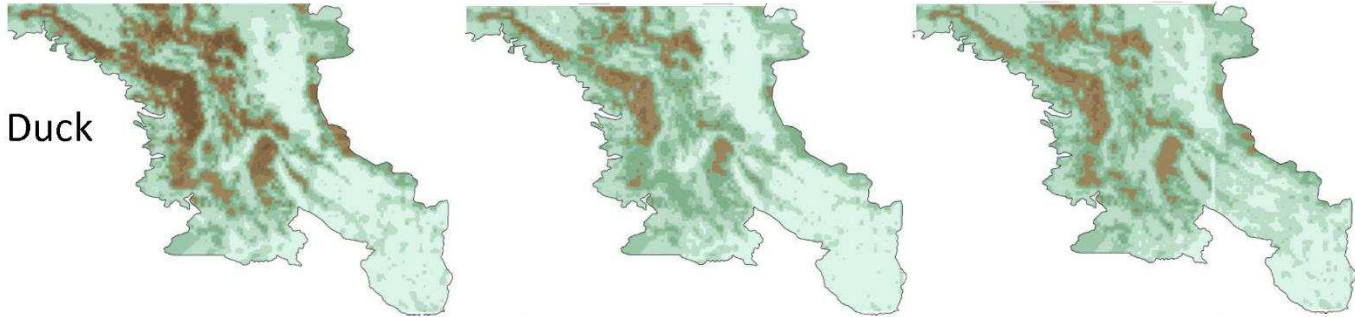




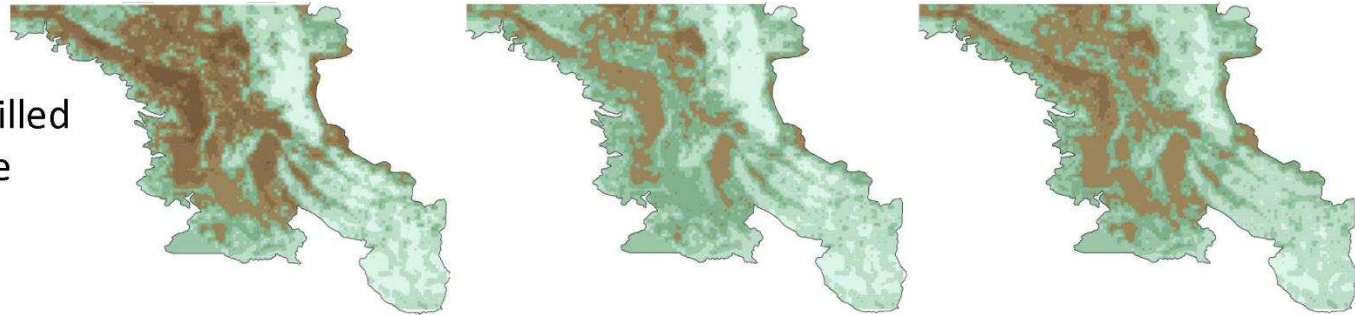
Redhead

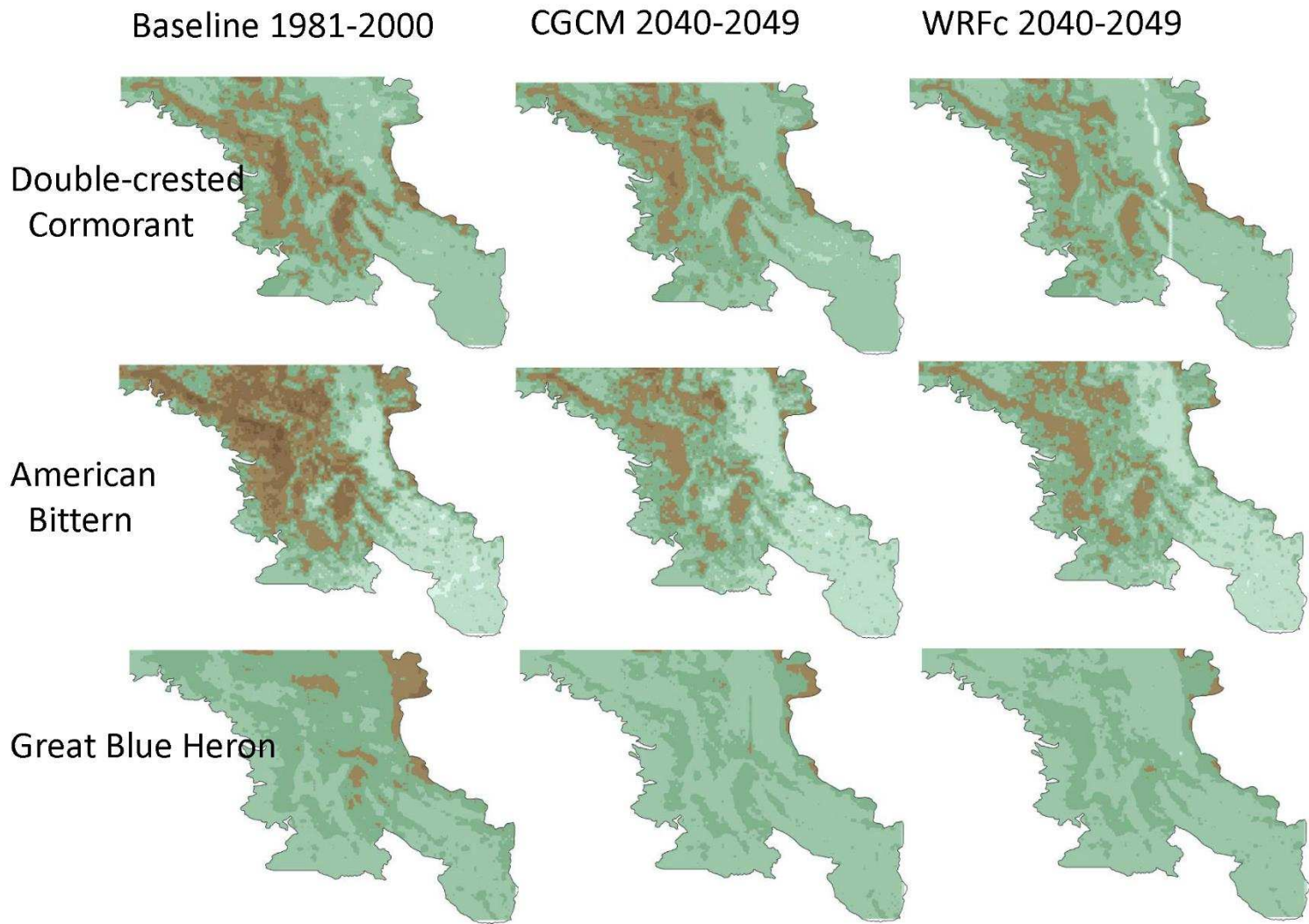


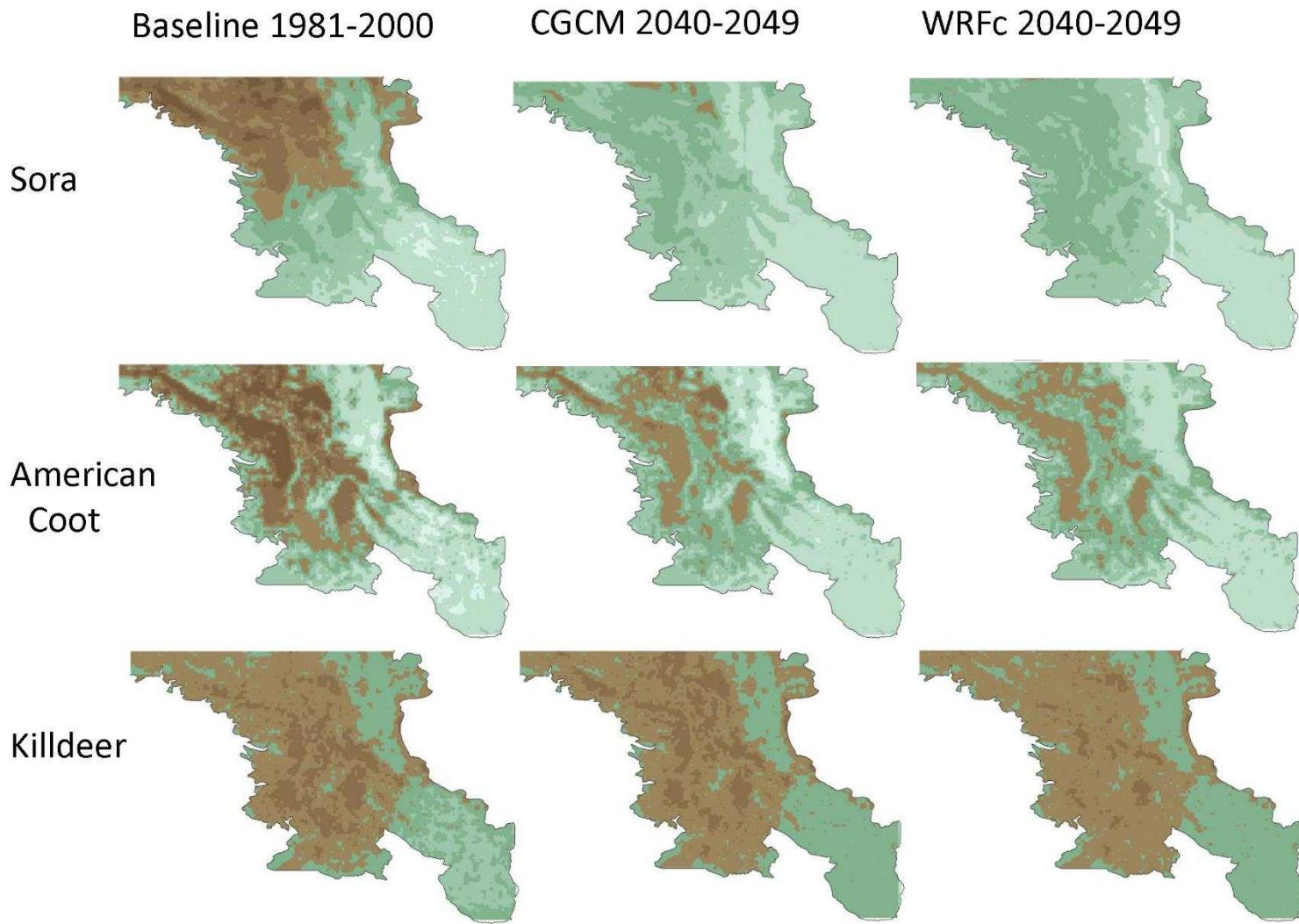
Ruddy Duck

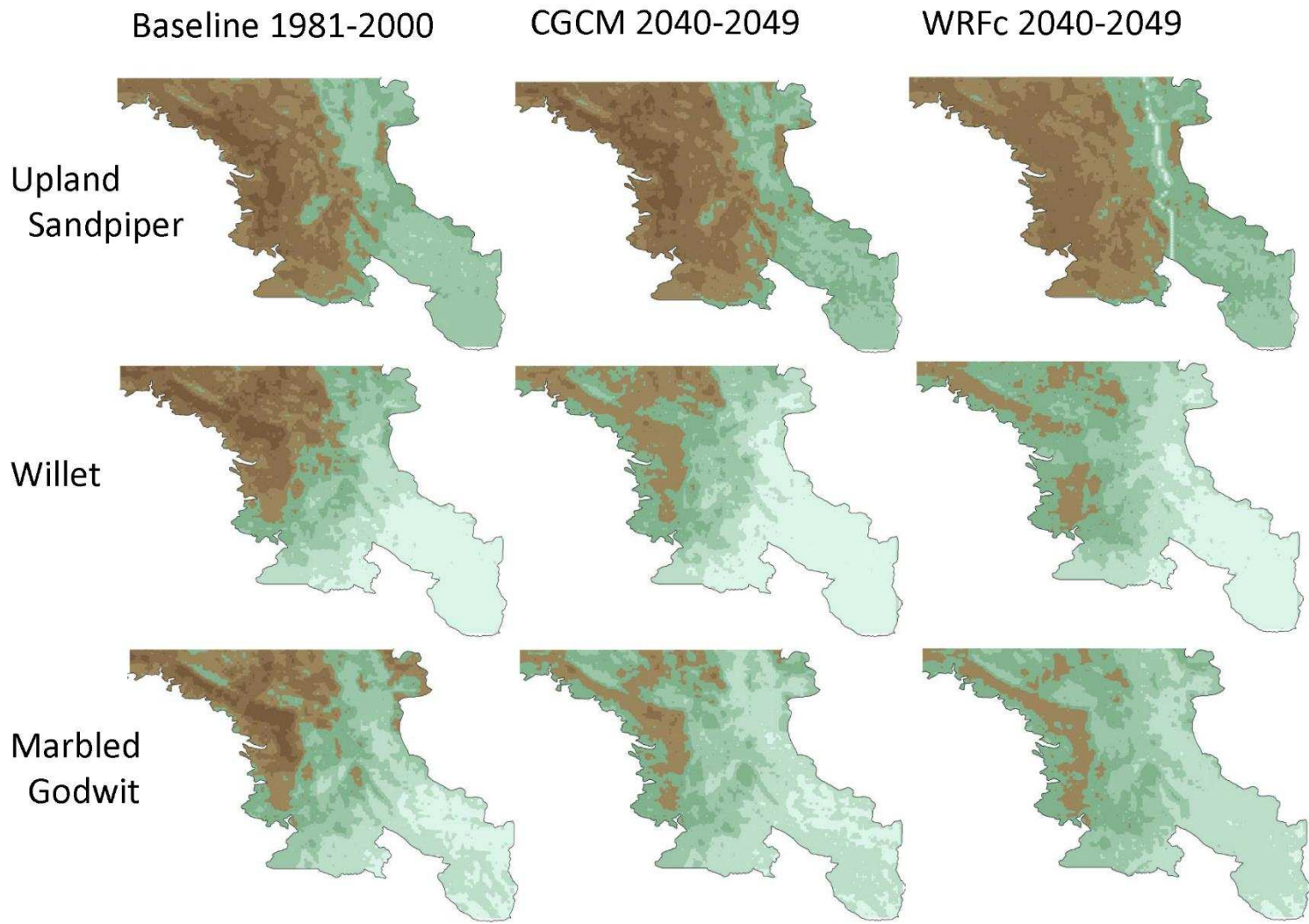


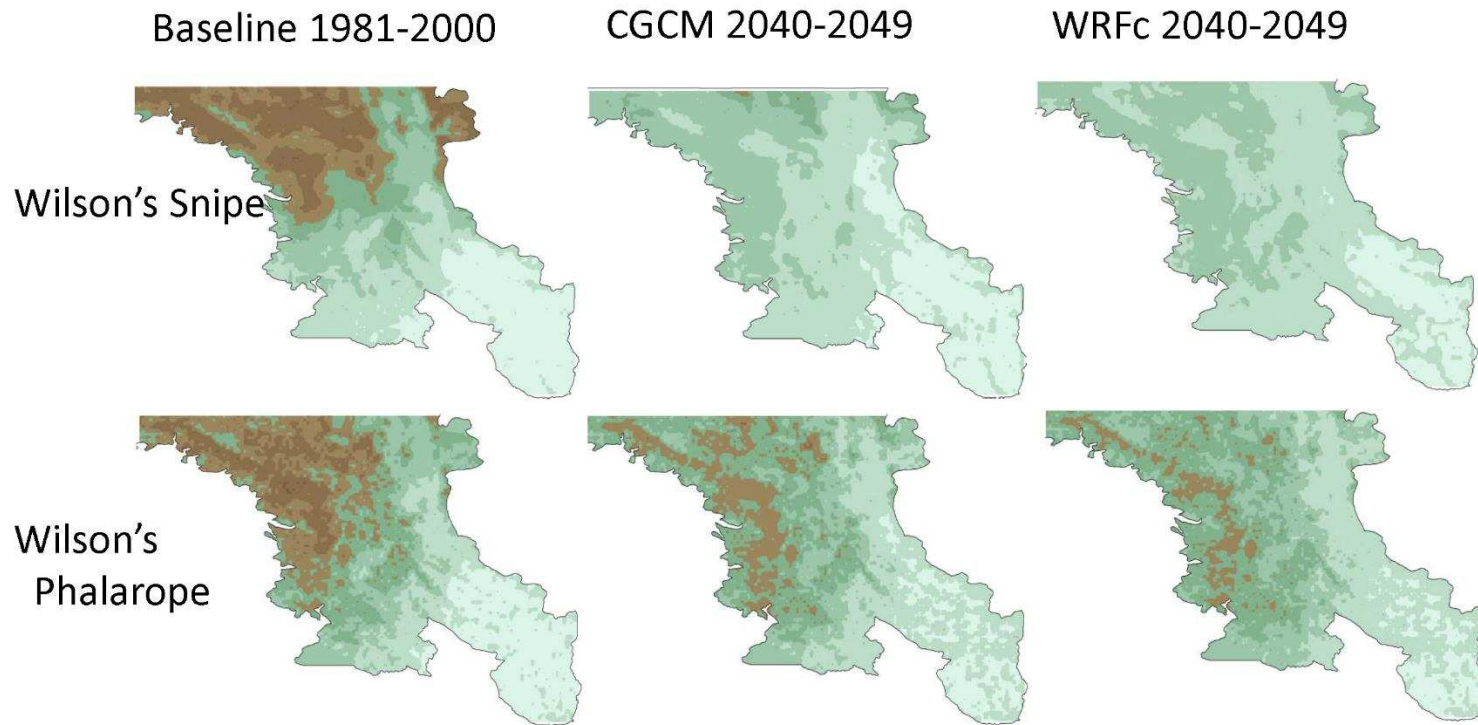
Pied-billed
Grebe

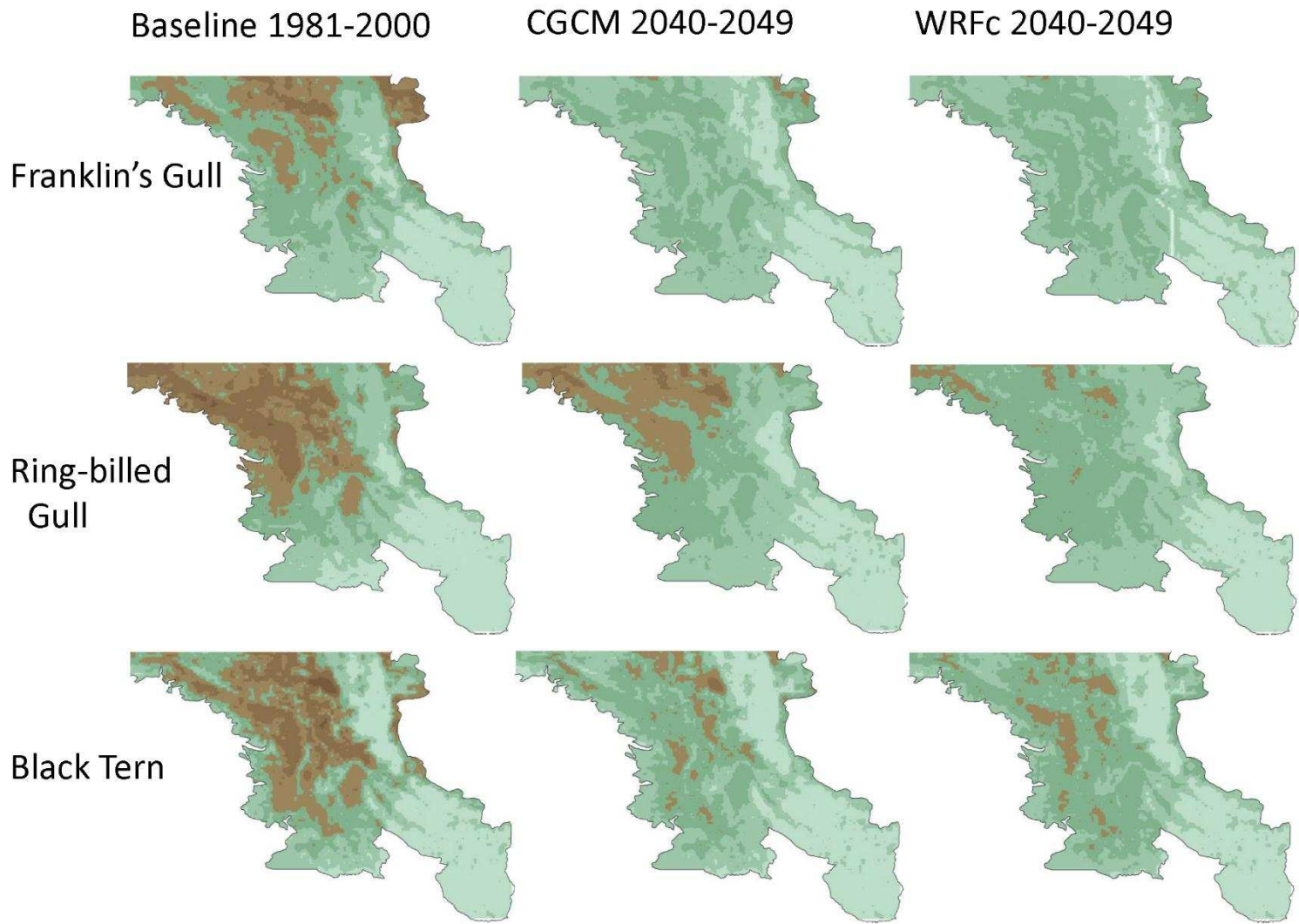


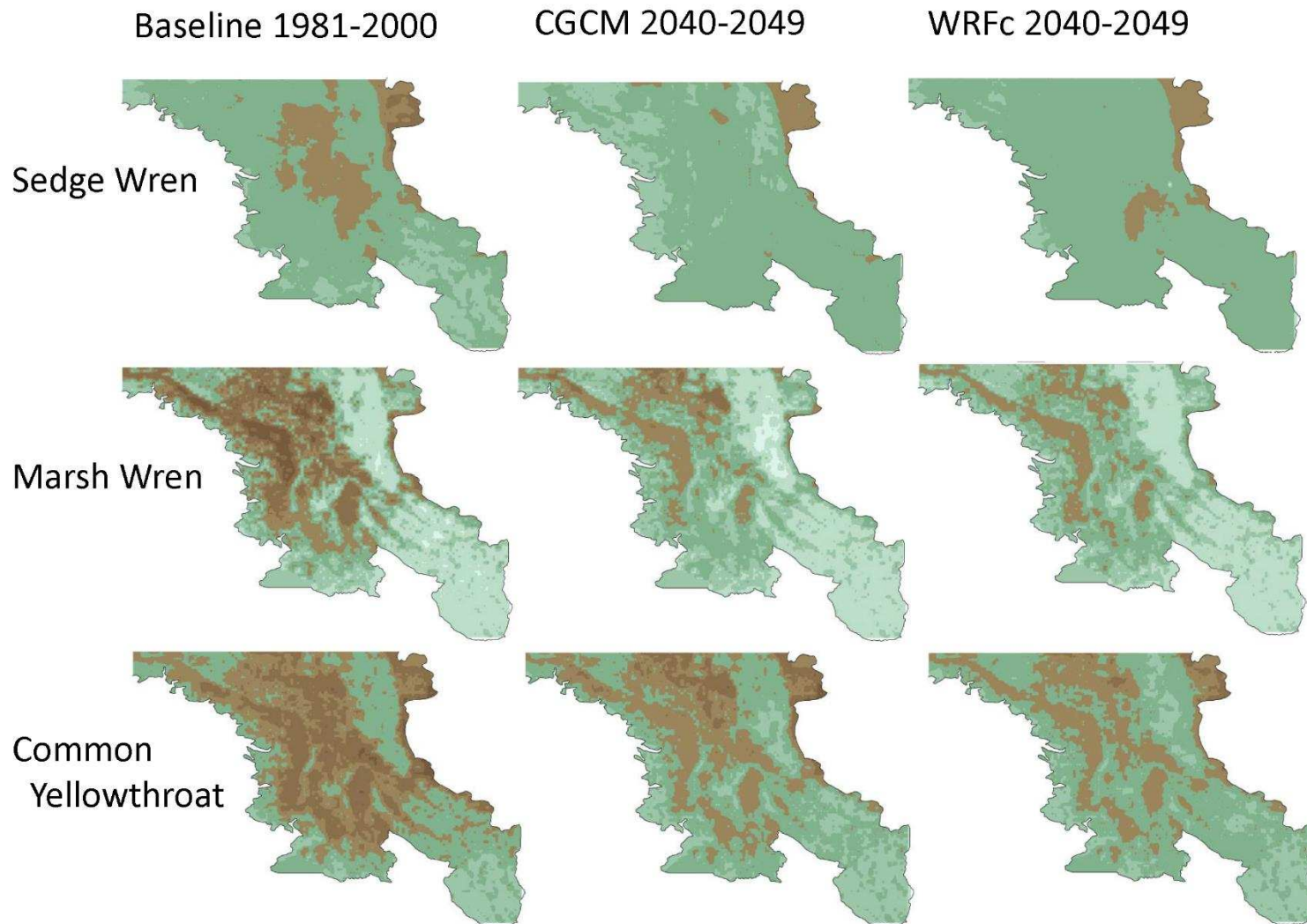


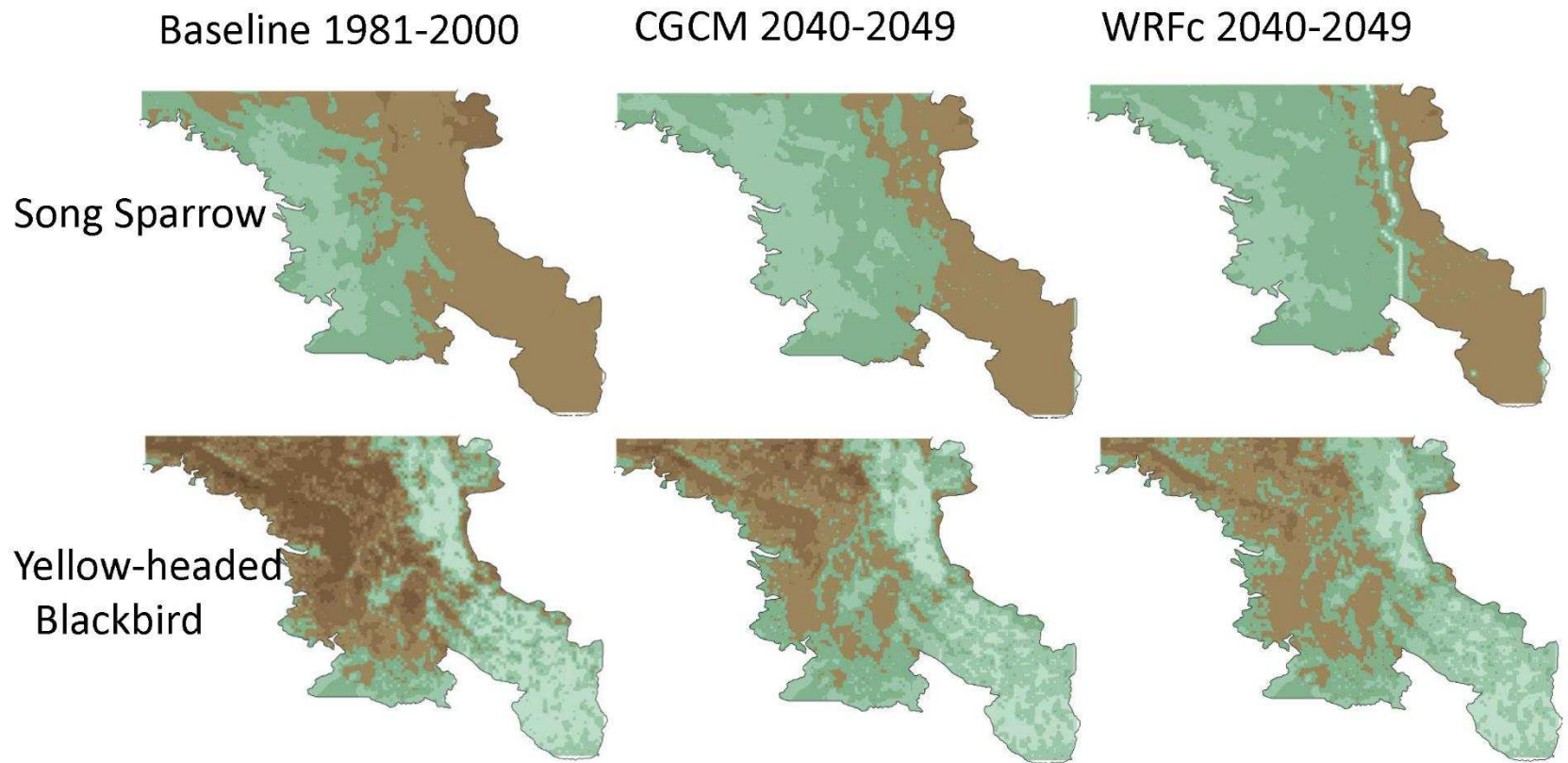






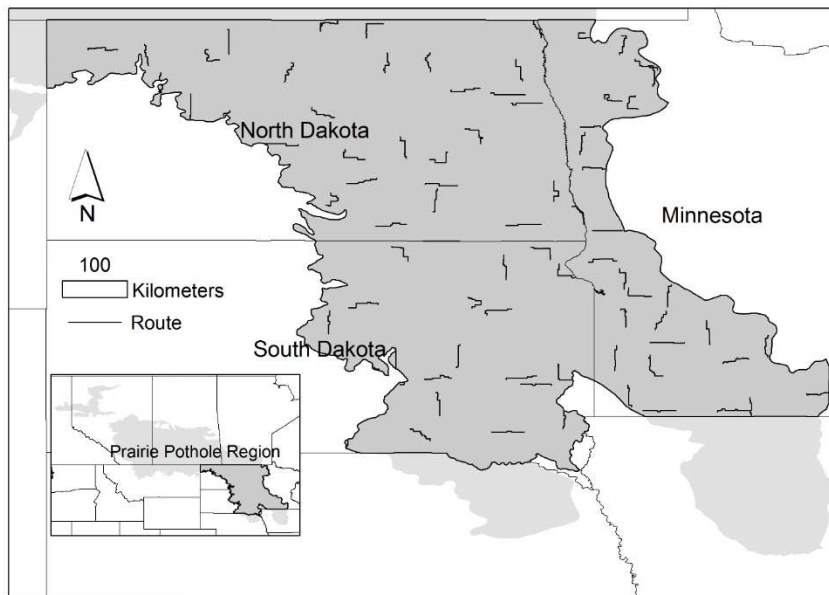




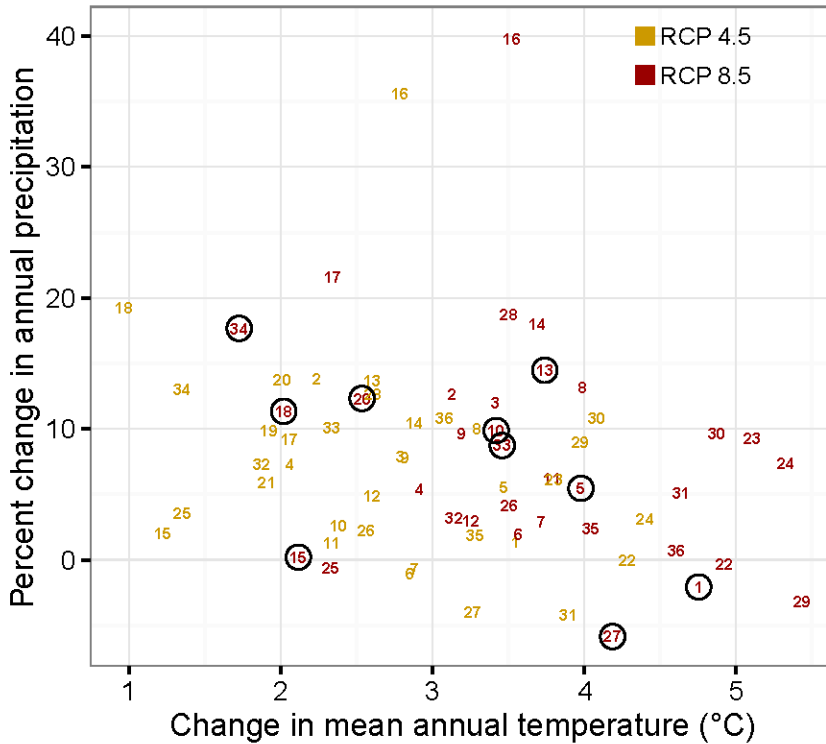


Supplementary figures S1.2-S1.12. Maps of species distributions for baseline and two future climate projections. Brown indicates areas where the species is predicted to occur and green represents areas where the species is not predicted to occur.

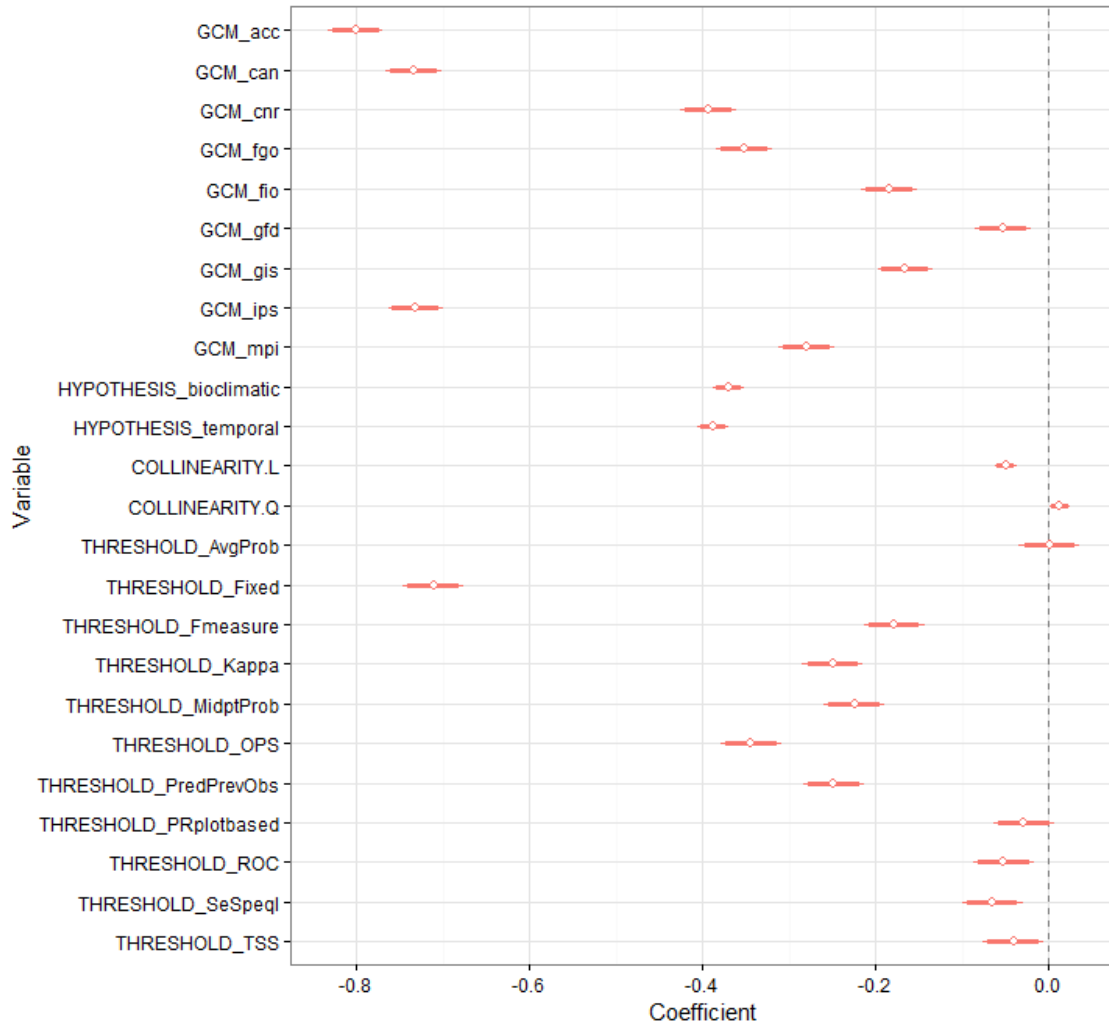
Supplemental Figures:



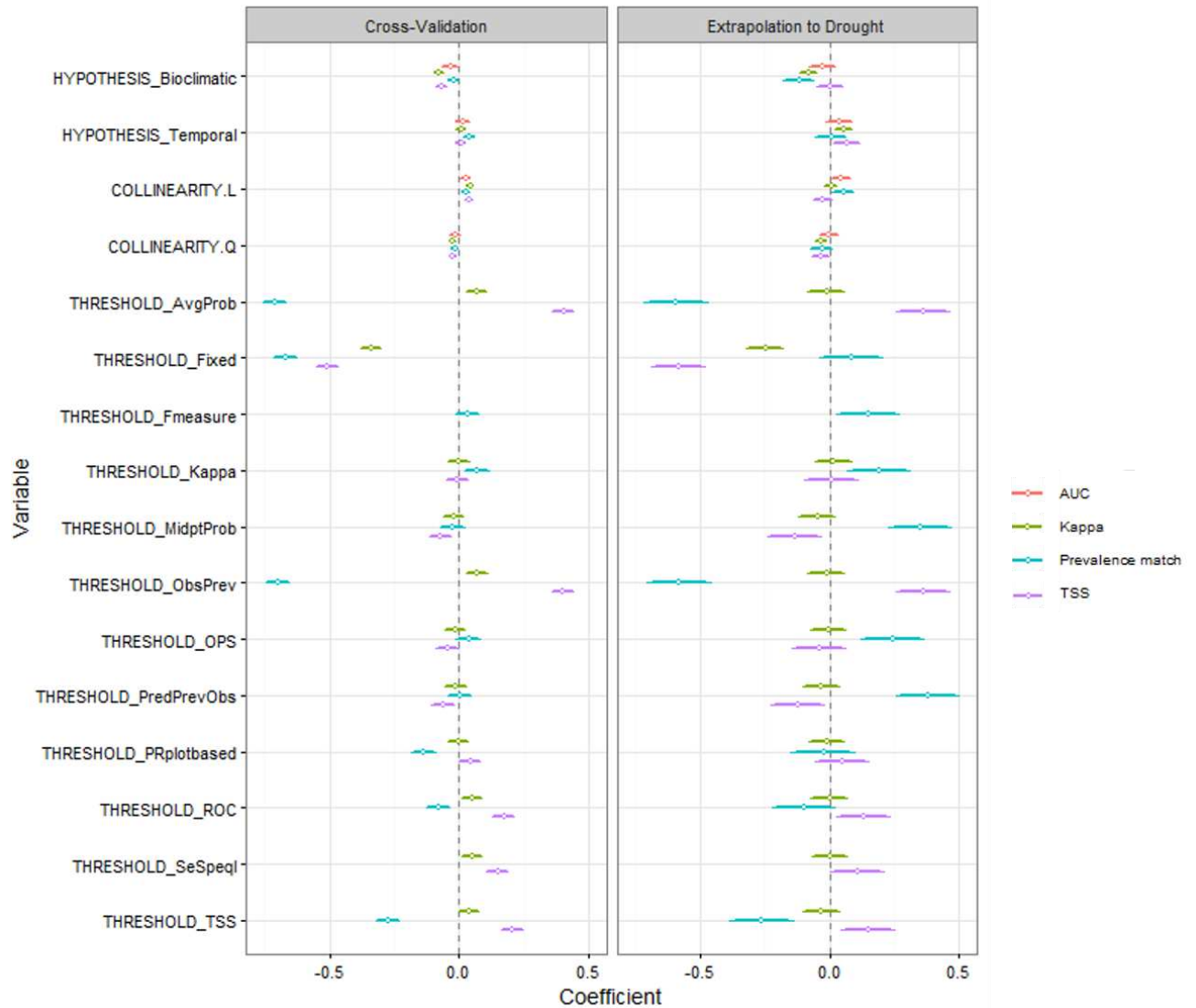
Supplementary figure S2.1: Study area in the U.S. Prairie Pothole Region with 72 Breeding Bird Survey routes for bird occurrence data.



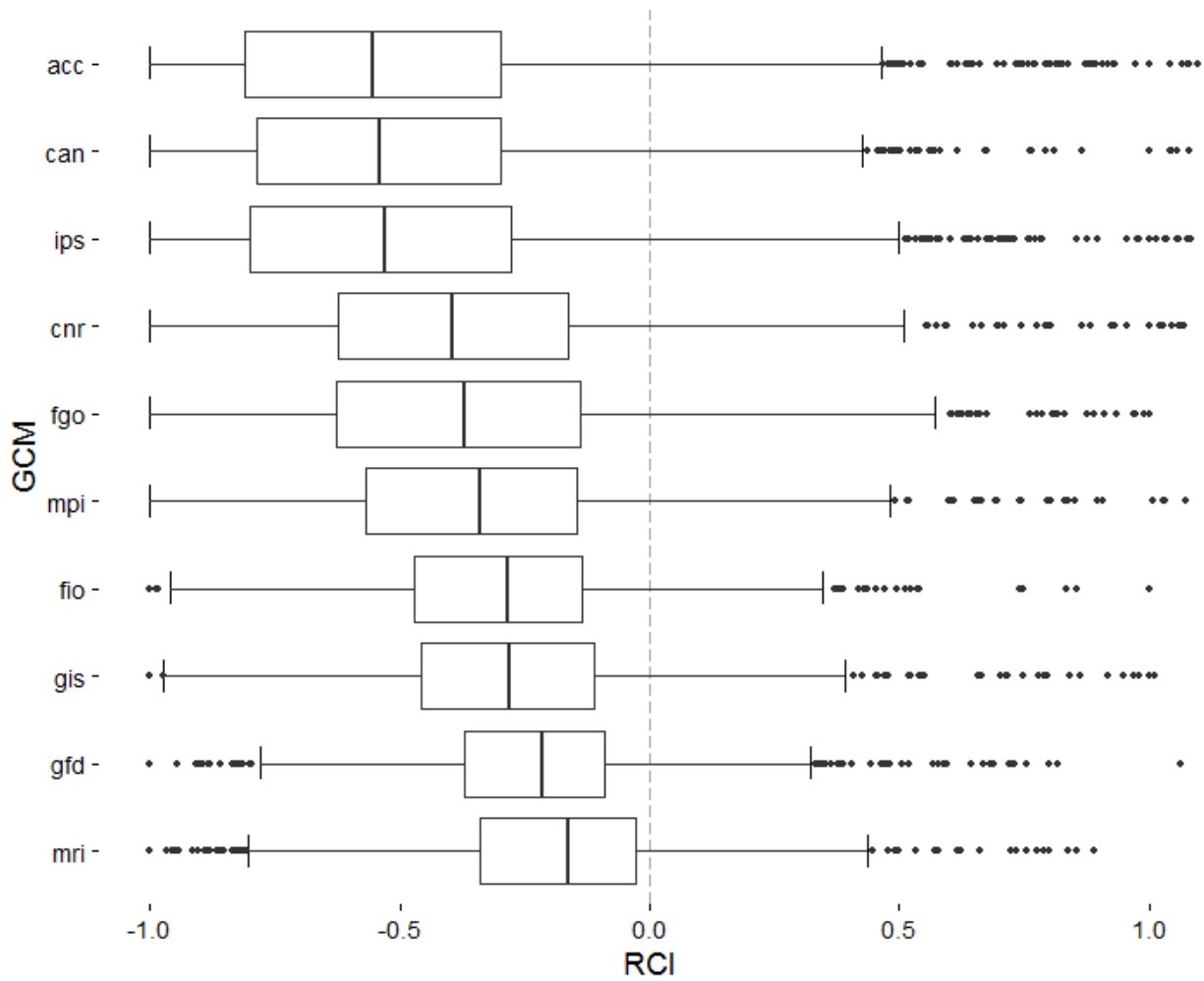
Supplementary figure S2.2: Change in temperature and precipitation projected by 2041-2070 relative to 1971-2000 for bias-corrected GCMs under RCP 4.5 and RCP 8.5 in the U.S. Prairie Potholes in North Dakota, South Dakota, and Minnesota. The ten GCMs used in this study are circled. Each GCM is identified by a number: 1 = ACCESS2.3-0; 2 = ACCESS2.3-3; 3 = BCC-CSM1-1-M; 4 = BCC-CSM1-1, 5 = CanESM2, 6 = CCSM4, 7 = CESM1-BGC, 8 = CESM1-CAM5, 9 = CMCC-CM, 10 = CNRM-CM5, 11 = CSIRO-Mk3-6-0, 12 = EC-EARTH, 13 = FGOALS-g2, 14 = FGOALS-S2.4, 15 = FIO-ESM, 16 = GFDL-CM3, 17 = GFDL-ESM2G, 18 = GFDL-ESM2M, 19 = GISS-E2-H-CC, 20 = GISS-E2-R, 21 = GISS-E2-R-CC, 22 = HadGEM2-AO, 23 = HadGEM2-CC, 24 = HadGEM2-ES, 25 = INMCM4, 26 = IPSL-CM5A-LR, 27 = IPSL-CM5A-MR, 28 = IPSL-CM5B-LR, 29 = MIROC-ESM, 30 = MIROC-ESM-CHEM, 31 = MIROC5, 32 = MPI-ESM-LR, 33 = MPI-ESM-MR, 34 = MRI-CGCM3, 35 = NorESM1-M, 36 = NorESM1-ME. Data provided by M. Talbert.



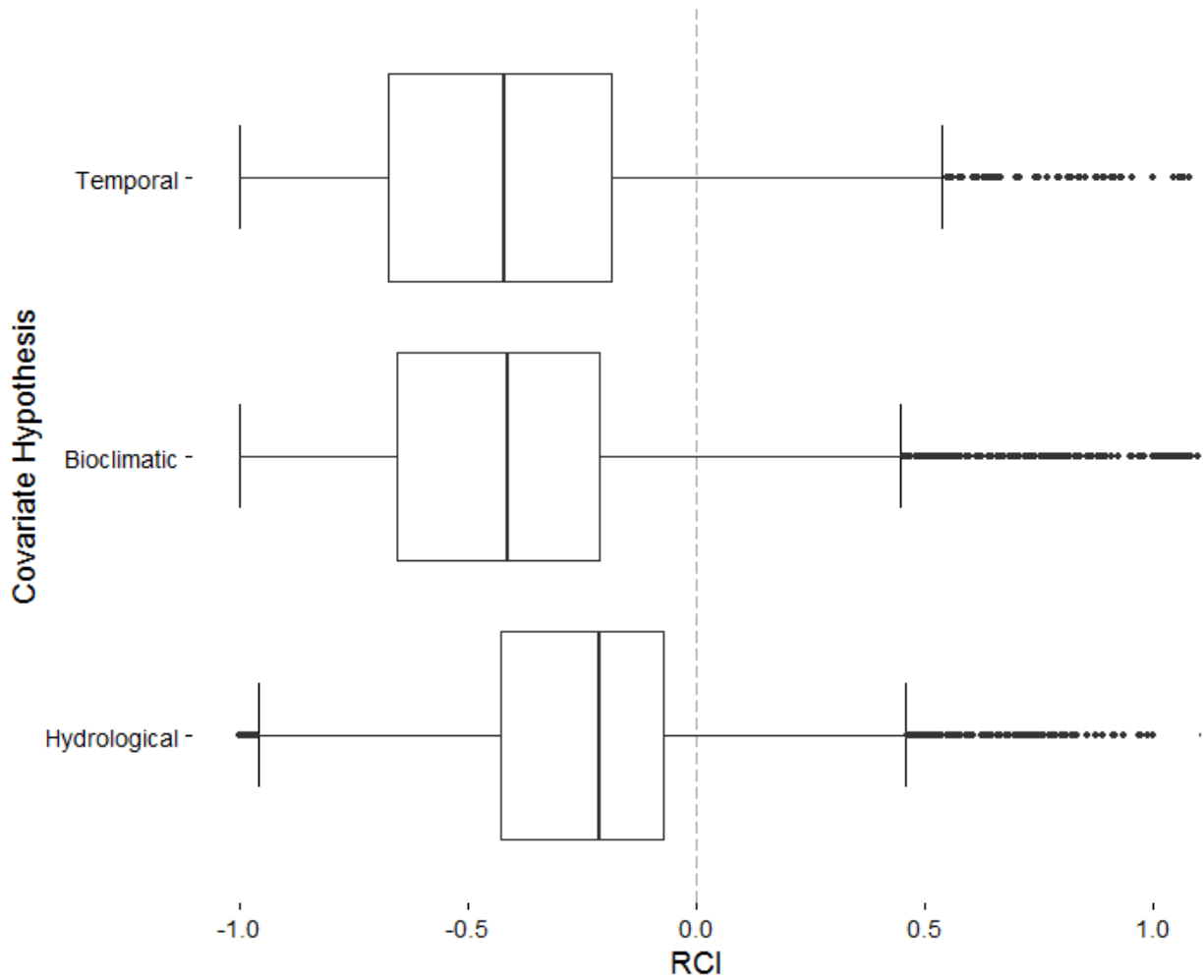
Supplementary figure S2.3. Estimates of relationships between factor levels and range change index (RCI). Reference levels (thus, not shown in the plot) were chosen for each factor based on the level with the smallest negative relationship with RCI: ObsPrev (threshold), hydrological (hypothesis), and mri (GCM). The “Q” and “L” suffixes on collinearity denote quadratic and linear effects of higher collinearity. Thick portions of bars represent 90% confidence intervals with thin portions extending to 95% confidence intervals.



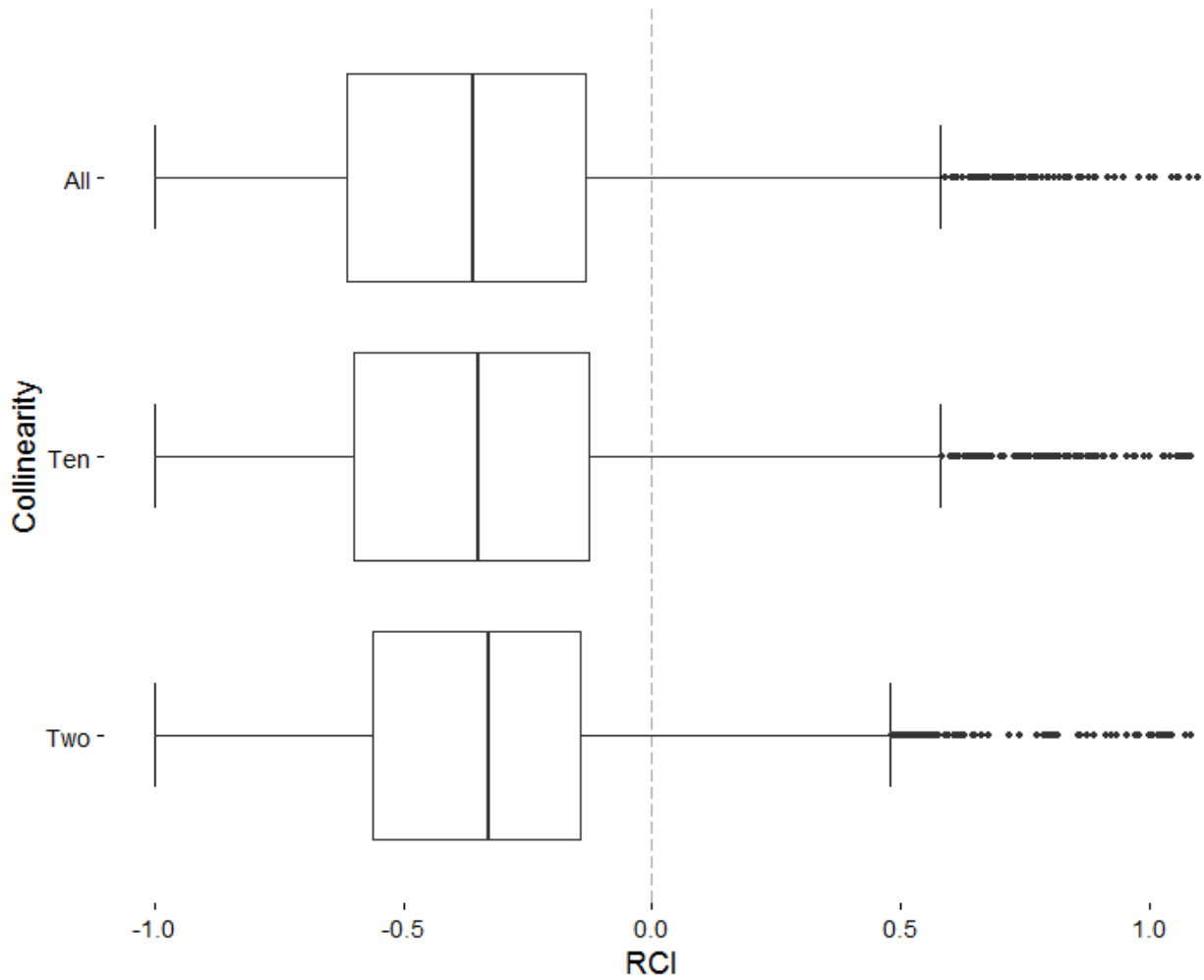
Supplementary figure S2.4. Estimates of relationships between factor levels and model performance for four model performance metrics: AUC, True Skill Statistic (TSS), kappa, and prevalence match. Cross Validation results reflect predictions to randomly subsetted data. Extrapolation results reflect predictions from models trained with normal and wet years data and evaluated on drought years. Not shown because they were used as reference levels in the model are: hydrological, Fmeasure (kappa and TSS models) and SeSpeql (prevalence match model). The “Q” and “L” suffixes on collinearity denote quadratic and linear effects of higher collinearity. Thick portions of bars represent 90% confidence intervals with thin portions extending to 95% confidence intervals.



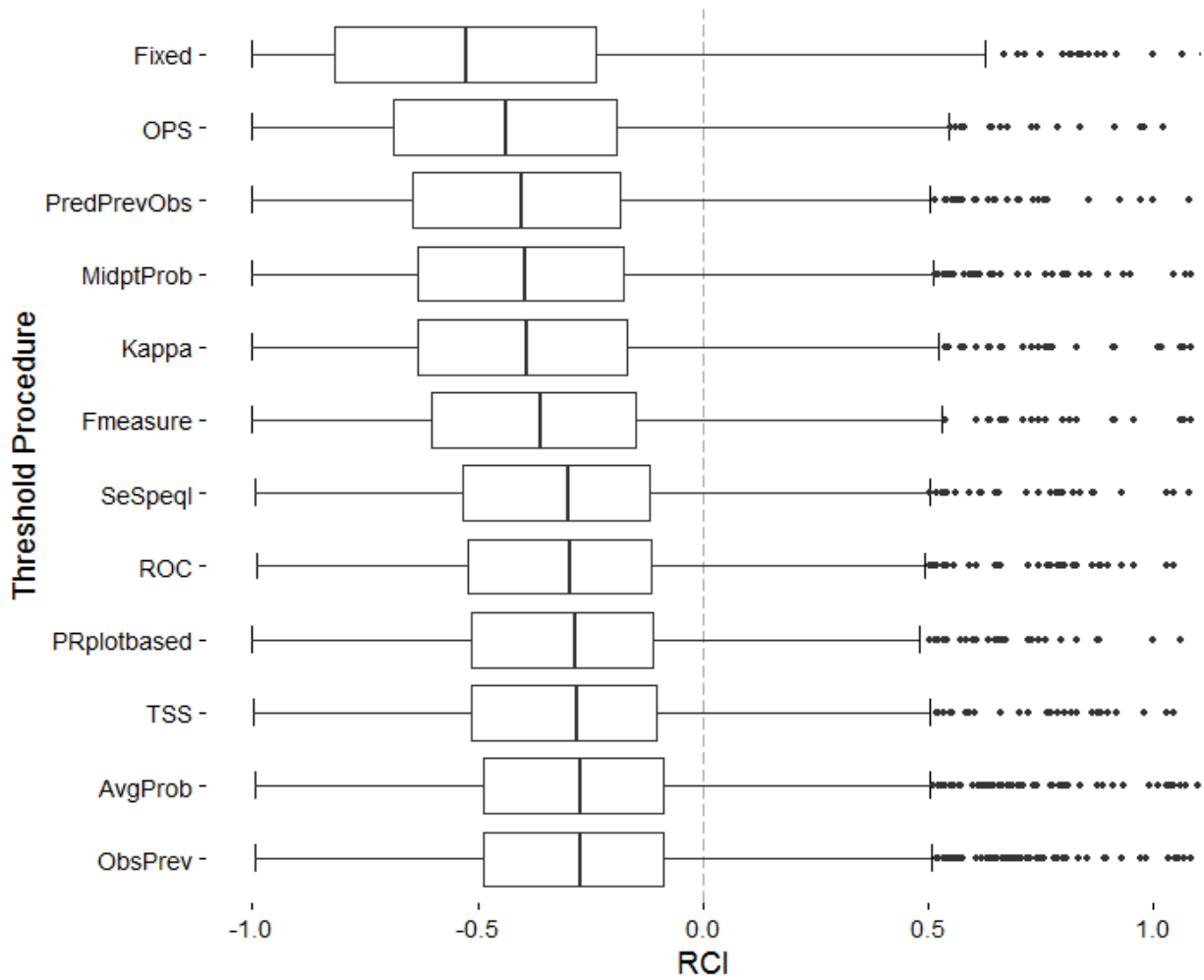
Supplementary figure S2.5. Variation in Range Change Index (RCI) by GCM. Boxplots show the median, and first and third quartiles, with whiskers showing the 1.5 inter-quartile range.



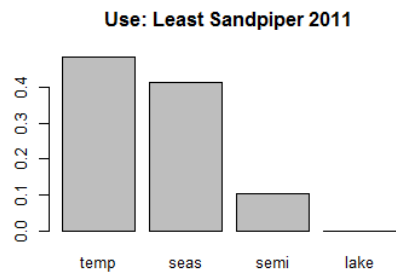
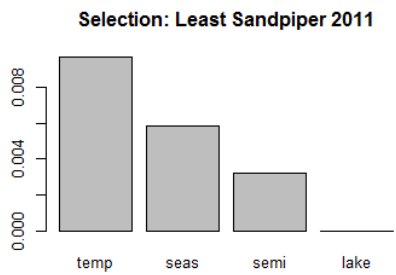
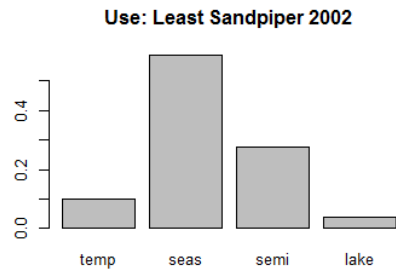
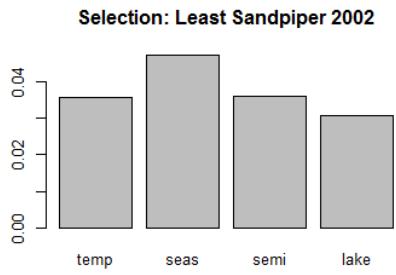
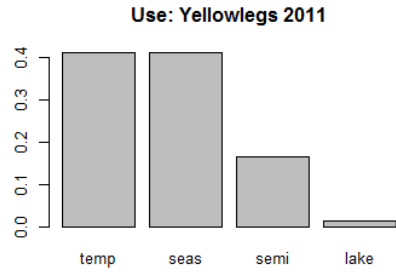
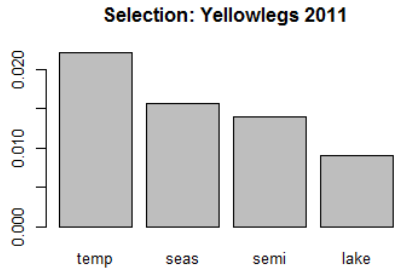
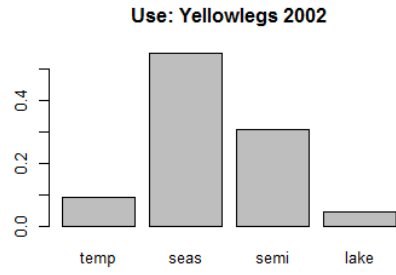
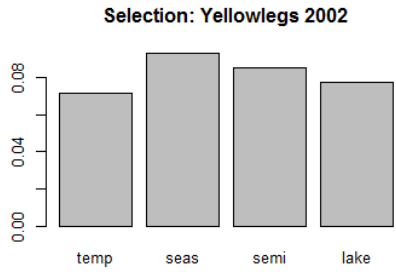
Supplementary figure S2.6. Variation in RCI by covariate hypothesis. Boxplots show the median, and first and third quartiles, with whiskers showing the 1.5 inter-quartile range.

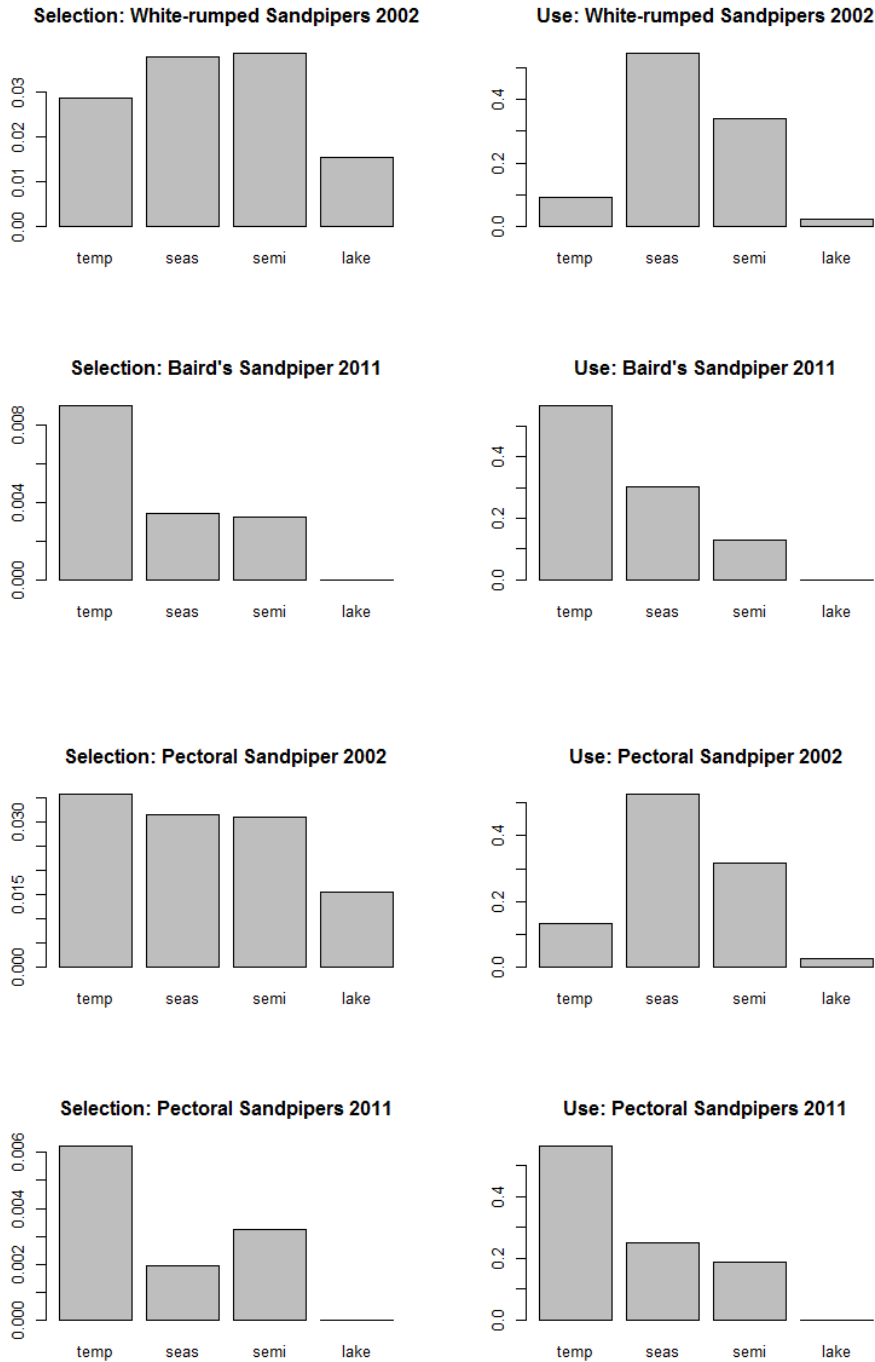


Supplementary figure S2.7. Variation in Range Change Index (RCI) by degree of covariate collinearity: all covariates, covariate sets reduced to a moderate variance inflation factor (VIF) of ten, and covariate sets reduced to a more stringent VIF of two. Boxplots show the median, and first and third quartiles, with whiskers showing the 1.5 inter-quartile range.



Supplementary figure S2.8. Variation in Range Change Index (RCI) by thresholding procedure. Boxplots show the median, and first and third quartiles, with whiskers showing the 1.5 inter-quartile range.





Supplementary figure S3.1. Graphs show, by year, local-scale selection and use of wetlands by type (temporary, seasonal, semipermanent and lake). Selection shows use of that wetland type given its availability. Use shows the proportional use of each wetland type relative to other wetland types.