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Projected wetland densities under climate change: habitat loss but little geographic shift in conservation strategy

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Abstract. Climate change poses major challenges for conservation and management because it alters the area, quality, and spatial distribution of habitat for natural populations. To assess species' vulnerability to climate change and target ongoing conservation investments, researchers and managers often consider the effects of projected changes in climate and land use on future habitat availability and quality and the uncertainty associated with these projections. Here, we draw on tools from hydrology and climate science to project the impact of climate change on the density of wetlands in the Prairie Pothole Region of the USA, a critical area for breeding waterfowl and other wetland-dependent species. We evaluate the potential for a trade-off in the value of conservation investments under current and future climatic conditions and consider the joint effects of climate and land use. We use an integrated set of hydrological and climatological projections that provide physically based measures of water balance under historical and projected future climatic conditions. In addition, we use historical projections derived from ten general circulation models (GCMs) as a baseline from which to assess climate change impacts, rather than historical climate data. This method isolates the impact of greenhouse gas emissions and ensures that modeling errors are incorporated into the baseline rather than attributed to climate change. Our work shows that, on average, densities of wetlands (here defined as wetland basins holding water) are projected to decline across the U.S. Prairie Pothole Region, but that GCMs differ in both the magnitude and the direction of projected impacts. However, we found little evidence for a shift in the locations expected to provide the highest wetland densities under current vs. projected climatic conditions. This result was robust to the inclusion of projected changes in land use under climate change. We suggest that targeting conservation towards wetland complexes containing both small and relatively large wetland basins, which is an ongoing conservation strategy, may also act to hedge against uncertainty in the effects of climate change.

Key words: climate change impacts; conservation planning; hydrological projection; Prairie Pothole Region; vulnerability assessment; waterfowl.

Introduction

Before conservation actions are initiated, a formal process of spatial prioritization is often required (Moilanen et al. 2009). That is, researchers and managers need a logical, defensible procedure to identify those locations that are priorities for acquisition, restoration, and management. Climate change poses a major challenge for decision-makers because priority investments and land-use designations under current climatic conditions may be less valuable in the future due to species declines or distributional shifts (Peters and Darling 1985, Araújo et al. 2011). Changes in a species' distribution and abundance can occur in response to the direct effects of climate, as when physiological tolerances are exceeded (Kearney and Porter 2009), or to the effects of climate on the distribution of suitable habitat and biotic communities. While latitudinal and elevational shifts in species distributions are most prominent (Parmesan 2006), changes in distributional patterns vary among species and are often complex (Tingley et al. 2012, Staudinger et al. 2013), making distribution modeling an important tool for long-term conservation planning (Pearson and Dawson 2003). Nevertheless, there are relatively few examples where projected distributional changes have been incorporated into decision-making and management (Guisan et al. 2013). Research that evaluates the potential for trade-offs between resource

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allocation under current vs. future climatic conditions, that explores uncertainties and identifies locations likely to provide robust investments, and that considers the joint impacts of climate change and land-use patterns can provide a basis for the development of efficient and effective strategies for long-term management and conservation.

North America's Prairie Pothole Region (PPR) has continental-level significance for biodiversity and exemplifies the potential for climate change to shift the optimal spatial allocation of conservation investments (Ando and Mallory 2012). The PPR contains millions of small, glacially derived wetland basins that are highly sensitive to drought, with their abundance falling in dry years and their annual distribution closely tracking spatial variation in precipitation (Larson 1995, Sorenson et al. 1998, Niemuth et al. 2010). Collectively, these wetlands are critical for North American waterfowl production (U.S. Fish and Wildlife Service 2015), provide habitat for other wetland-dependent species (Balas et al. 2012, Steen et al. 2014), and generate ecosystem services including groundwater recharge and carbon sequestration (Gleason et al. 2011). Avian populations track the distribution and abundance of wetlands over space and time, reflecting both habitat selection and population dynamics (Derksen and Eldridge 1980, Johnson and Grier 1988, Niemuth and Solberg 2003). In addition, the productivity of Prairie Pothole wetlands increases in response to fluctuating water levels, which promote plant regeneration and support the insect communities at the center of the avian food web (Murkin 1989). Despite the dynamic nature of the Prairie Pothole ecosystem, practical considerations have meant that many conservation investments are static in space. Specifically, land and easement purchases are a major management tool, with approximately US$19 million per year spent on these long-term investments (Doherty et al. 2013).

A trade-off between current and future conservation investments may arise because general circulation models (or global climate models; GCMs) on average project a warmer climate in the PPR, along with a relatively small average increase in precipitation (Ballard et al. 2014). The net effect is projected to be a drier climate, particularly during summer, as the increase in precipitation is not expected to offset projected higher rates of evapotranspiration associated with higher temperatures (Cook et al. 2014). These changes could strengthen the existing moisture gradient, in which the western PPR is approximately three times drier than the eastern part of the region (Millett et al. 2009). Indeed, hydrological models have projected that the western and central PPR, where conservation investments are currently concentrated, may become too dry to continue to provide productive habitat for breeding waterfowl (Johnson et al. 2005, 2010, Rashford et al. 2016). Yet conservation in the eastern PPR is challenging because of higher land values and the need for significant restoration, as the region is dominated by agriculture and small wetlands have largely been drained. Previous research suggests that weather and land use interact to affect wetland abundance and condition (van der Kamp et al. 1999, Voldseth et al. 2007, Forcey et al. 2011, Anteau 2012, Withey and Van Kooten 2013), and the productivity of upland nesting waterfowl is often lower in landscapes dominated by row crops (Reynolds et al. 2001, Stephens et al. 2005, but see Walker et al. 2013*b*). Therefore, citing conditions that have been wetter than normal over the last decade and the uncertainties surrounding climate change, other studies have suggested that investment should remain concentrated in the western and central PPR where currently suitable habitat remains unprotected and the costs of conservation actions are lower (Loesch et al. 2012, Niemuth et al. 2014). This controversy remains unresolved, and a diversified strategy has been proposed (Ando and Mallory 2012).

We used hydrology projections forced by downscaled Coupled Model Intercomparison Project Phase 5 (CMIP5) GCM climate projections as a basis for modeling the effects of climate change on the distribution and abundance of wetlands in the PPR. We statistically modeled the relationship between variation in weather and wetland counts based on more than 40 years of aerial wetland surveys and incorporated several analytical strategies that are underused in ecology. First, we included physically based measures of hydrological balance, which considers both precipitation and evaporation, as covariates in our wetland model to capture the interactions between changes in temperature, precipitation, wind, and other variables. Second, as the baseline for our climate impacts analysis, we used hydrological and climate projections based on the historical climate simulation for each GCM, hereafter referred to as the hindcast. Comparisons between predictions based on GCM hindcasts and future projections (forecasts) isolate the impacts of climate change by incorporating the effects of model misspecification and bias into the baseline. In contrast, ecological studies may compare historical climate data with GCM forecasts, or may apply a change in climate, generally in mean temperature and/or precipitation, as a basis for future projections (i.e., the delta method). The former can conflate modeling error with the impacts of climate change, while the latter may not take into account all the dimensions of change in a GCM, including spatial variation and change in other variables. Our strategy of comparing projections based on GCM hindcasts and forecasts allowed us to use an internally consistent set of hydrologic and climatic variables as a basis for our projections.

We analyzed how the relative climatic suitability of different regions of the PPR may be affected by climate change, and how it may interact with land use. We compared projections from the wetland model based on three land-use scenarios: (1) existing land use and land cover, (2) a uniform proportion of land planted with row crops and a uniform number of wetland basins across the landscape, and (3) projected changes in row crops based on a model that projected the effects of climate change on land-use patterns. The second comparison isolated the effect of climate from that of land cover to evaluate their relative contributions to patterns of wetland densities. The third comparison incorporated the potentially countervailing processes by which climate affects wetland habitats, because wetter climates should fill wetland basins but also may favor agricultural production (Rashford et al. 2016). Given the importance of prairie wetlands to biodiversity and the magnitude of resources invested in their conservation, many studies have investigated the effects of weather and land use on wetland characteristics (e.g., Poiani and Johnson 1991, Larson 1995, Johnson et al. 2005, Liu and Schwartz 2011, 2012, Ouyang et al. 2014). However, there is a need to evaluate the variability among climate projections and their implications for projected wetland densities in the PPR, as well as to understand the potential interactions between climate and land-use change. Our work therefore represents an integrative approach for projecting shifts in wetland distribution and abundance and for identifying potential trade-offs between priority areas for conservation investment under current versus future climatic conditions.

Methods

Data sources and covariates

We analyzed the distribution and abundance of wetlands based on annual counts conducted each May during the U.S. Fish and Wildlife Service Waterfowl Breeding Populations and Habitat Survey (Smith 1995; *data available online*).[8] The U.S. portion of the aerial survey includes multiple flight transects over North Dakota, South Dakota, and Montana, which are divided into segments approximately 27 km long. Wetlands expected to persist longer than 3 weeks post-survey are counted on one side of the plane out to a distance of 200 m. We analyzed segment-level wetland count data from the U.S. portion of the survey, excluding central Montana (stratum 42) and an additional flight transect in Montana with incomplete land-cover data (Appendix S1: Fig. S1). Our dependent variable was log-transformed pond density, which was calculated as one plus the count of observed ponds on a given segment divided by the area of a 200-m buffer around each segment. The log transformation addressed the lack of normality in the distribution of observed pond densities. We analyzed 44 yr of data, from 1967 to 2010. We modeled the variation in wetland densities as a function of land cover and historic climatic and hydrological conditions, and then compared predicted wetland densities under GCM projections of historical and future conditions to assess the impacts of climate change.

Spatial variation in the distribution and abundance of wetlands in the PPR largely reflects the distribution of wetland basins and patterns of human land-use, whereas annual and decadal variation in wetland counts largely reflects variation in weather because a wetland basin may or may not contain water in a given year (van der Valk 2005, Loesch et al. 2012). Throughout this manuscript, we use the term wetland basin to describe depressions in the landscape that may be wet or dry, depending on the prevailing hydrological conditions. We use the term wetlands to refer to wetland basins containing water during the aerial surveys, thus wetland density quantifies only basins containing water, not dry basins. To capture spatial variation affecting wetland densities, we summarized the number and types of wetland basins, the proportion of upland areas planted with row crops (i.e., not counting pasture and hay), and mean topographical ruggedness (based on differences in elevation between each cell and its neighbors; Hijmans 2015) within a 200-m buffer of each survey segment from the National Wetlands Inventory (*data available online*), the National Land Cover Database (Fry et al. 2011), and the National Elevation Dataset (Gesch 2007), respectively.[9] Wetland types were classified as temporary, seasonal, or semipermanent wetlands, or lakes (Cowardin et al. 1979). Partially drained wetlands were excluded as these are often subsequently fully drained (Oslund et al. 2010). The land-use and wetland basin covariates were assumed to be static among years because available data do not capture land conversion and wetland drainage over the time scale of our study. Most land conversion to row crops occurred before 1970 (Waisanen and Bliss 2002), after which conversion rates were relatively low for several decades (Drummond et al. 2012). However, conversion rates have increased since about 2006 to an average of 1–1.5% per year (Rashford et al. 2011, Doherty et al. 2013, Wright and Wimberly 2013). Because land-use and wetland basin covariates were static rather than reflecting these temporal dynamics, we expect our wetland model to be conservative in estimating the magnitude of their effects. We also included a binary covariate for whether the midpoint of each segment was within the PPR, as our study area included portions of western North Dakota and South Dakota outside this physiographic region.

To characterize variation in weather, we derived climate covariates from gridded monthly historical temperature and precipitation data (Maurer et al. 2002) and hydrological covariates from gridded output from the variable infiltration capacity (VIC) macroscale hydrologic model version 4.1.2 h (Liang et al. 1994). VIC was originally developed to improve the realism of the land surface within climate models, but is now more commonly used as an independent hydrology model in analyses at watershed to global scales. In the context of climate change analyses, VIC is often forced by daily precipitation, temperature minima and maxima, and

[8] https://migbirdapps.fws.gov/mbdc/databases/mas/maydb.asp

[9] http://www.fws.gov/wetlands

wind speed, and assumes static and seasonal parameters to describe soil and vegetation characteristics. VIC simulates major storage and flux terms of the water and energy cycle, including snow water equivalent, sublimation and evapotranspiration, surface runoff and baseflow, infiltration of water into soil, and soil moisture.

Climate covariates for each survey segment were estimated on an annual basis to capture the hydrological processes driving wetland filling and drying. To estimate the runoff from spring snowmelt that fills wetlands, we included April and May surface runoff from the hydrological VIC model (monthly sum in mm). The amount of soil moisture in the fall can persist through the winter as the land surface freezes, and then can continue to regulate runoff versus infiltration processes in the subsequent spring. To capture this dynamic, we included total soil moisture during the previous October (first of the month) as a predictor. Runoff is also affected by the speed of snowmelt, which was captured via the difference between minimum and maximum temperatures in the first month of the calendar year in which mean temperature was above 0°C; a large range suggests sunnier weather and higher maximum temperatures, implying more rapid snowmelt. We also used the mean of monthly maximum temperatures in March, April, and May as a measure of spring warmth.

The balance between precipitation and evapotranspiration is the major regional driver of wetland levels (Poiani and Johnson 1993, Rosenberry et al. 2004). In dry regions, actual evapotranspiration is largely a reflection of precipitation (P) or irrigation, while potential evapotranspiration (PET) reflects atmospheric demand. Thus, P minus PET, hereafter P-PET, is a measure of the overall surplus or deficit in the water balance, and a standardized version of P-PET is used as a drought index (Vicente-Serrano et al. 2010, Cook et al. 2014). We used P-PET as a predictor in our models and use the terms P-PET and "water balance" interchangeably for convenience. Potential evapotranspiration (PET) was estimated with the Penman-Monteith formula, which is favored because it does not overestimate drought (Allen et al. 1998, Sheffield et al. 2012). We used a parameterization of PET that represents evaporation from open water (i.e., with resistances set to zero). For each year's wetland survey, we summed the net of precipitation and potential evapotranspiration from June in the previous year through May of the surveyed year, and we used the sum of P-PET from June to May over the previous 5 yr (i.e., not including the past year) to capture effects of longer term climate variability on wetland and water table levels (Larson 1995). Finally, we selected the highest monthly maximum temperature among the months of June, July, August, and September, as evaporation during summer affects water levels in deeper wetlands the following spring.

We used climate and hydrology projections from 10 randomly chosen GCMs to evaluate the effects of climate change on wetland distribution and abundance. We randomly selected models because model quality depends on the metric used, and the culling or weighting of models does not have a large effect on the distribution of outcomes as long as a sufficient number of models is considered (Brekke et al. 2008, Pierce et al. 2009, Harding et al. 2012); this has been demonstrated for ensembles of 10 models (Santer et al. 2009). Along with the projected values of temperature and precipitation (gridded at 1/8° spatial resolution), the associated VIC model output is available from an online archive (Bureau of Reclamation 2014).[10] We used datasets downscaled via the BCSD (bias-corrected spatially disaggregated) approach (Wood et al. 2004, Maurer et al. 2007), a common method of statistical downscaling. Importantly, the bias-correction applied to these GCM hindcast and forecast projections was done relative to the Maurer et al. (2002) historical climatology dataset that we used for estimation of the wetland model.

We quantified how climate change may alter annual wetland distribution and abundance between two 30-yr time periods, 1971–2000 (the hindcast) and 2041–2070 (the forecast). For climate projections to mid-century, there is more variation in climate among GCMs than among representative concentration pathways (RCPs) of greenhouse gas emissions (Appendix S1: Fig. S2; Snover et al. 2013); we therefore considered 10 GCMs forced by the RCP 8.5 (see Appendix S1 for details of selected GCMs). RCP 8.5 represents a high level of emissions that leads to roughly an effective quadrupling of CO_2 by 2100. The 10 GCMs used in our study encompassed most of the range of variation of CMIP5 climate models under RCP 8.5 and showed substantial overlap with projections based on RCP 4.5 (Appendix S1: Fig. S2).

To assess the impacts of climate change, we projected wetland densities based on GCM hindcast and forecast climate conditions, and used the ratio of wetland densities under forecast and hindcast conditions as our measure of climate impact. Projected impacts were similar when using differences (subtraction) and ratios (division) of projected wetland densities between the two periods (see Appendix S1). The major advantage of using GCM-based hindcasts (rather than historical observations) as the reference climate condition is that the effects of climate forcing are isolated from any model misspecification, bias, or imprecision in the GCM, the hydrological model, or wetland model, that could otherwise be incorporated into differences attributed to climate change. This approach is common in the hydrological literature (e.g. Harding et al. 2012) but is not prominent in ecological studies.

Land-use and land-cover scenarios

To assess how the effects of climate on future PPR wetland densities will be sensitive to land use and land cover, we developed three scenarios that differed in the

[10] http://gdo-dcp.ucllnl.org/downscaled_cmip_projections/dcpInterface.html

spatial patterns of land use and wetland basin abundance used to generate predictions from our statistical model. Our baseline scenario assumed that land-use and wetland basin distributional patterns would not change in the future (historical crops). This comparison captured the joint effects of climate and existing land cover on wetland densities. To complement this scenario, we developed two other scenarios: one that more clearly separated the impacts of climate change from existing patterns of row crop and wetland basin distributions, and one that considered the potential indirect effects of climate change that may occur via changing patterns of land use.

Our second land-use scenario sought to isolate changes in climate suitability for high wetland densities, irrespective of land use. Therefore, the wetland basin counts and the proportion of upland areas used for row crops were specified as uniform (at their mean values) across the landscape (uniform crops). The mean terrain ruggedness index and whether a segment was within the PPR were kept at existing values for each location because these cannot be influenced by restoration. This second comparison was not intended to capture realistic relationships between the proportion of the landscape used for row crops and the number of wetland basins but rather was designed to isolate the effects of climate change from those of agricultural patterns and wetland basin distributions.

Climate change is likely to affect spatial patterns of agricultural production, and these changes are likely to affect wetland density and condition via interactions with the direct effects of climate on wetland hydrology (Rashford et al. 2016). Our third scenario (projected crops) was designed to evaluate how the potential effects of climate change on the proportion of the landscape in row crops could in turn affect wetland densities during spring counts. We forecasted land use under each climate scenario (i.e., each GCM) using a statistical land-use change model recently developed for the region (see Rashford and Reese 2015). The land-use change model estimates the annual probability that land converts between row crops and grassland as a function of economic (e.g., commodity prices), landscape (e.g., soil quality), and climate covariates (e.g., average temperature and precipitation). The model was estimated using plot-level observations (30-m resolution) of land use for the PPR and Northern Great Plains from the Cropland Data Layer (Boryan et al. 2011), which is similar to the National Land Cover Database but has data at annual intervals for recent years. Similar to the procedures in Lawler et al. (2014), we projected crop portions by (1) calculating the expected land-use conversion probabilities for each focal time period by exponentiating the annual conversion probabilities; this process generates a matrix of Markov conversion probabilities indicating the probability that a given plot of row crops or grass in the current period will convert to the alternative state in the future period conditional on climate covariates; and (2) calculating the forecasted proportion of row crops by summing the conversion probabilities that end in row crops (i.e., crop-to-crop and grass-to-crop) across all land-use plots within each buffer. These projections implicitly assume that all non-climate covariates in the land-use model remain static.

As in our wetland model, the impact of climate change on land conversion was assessed by projecting the land-use model under GCM hindcast and forecast climatic conditions. For each GCM, we projected future row crop proportions under 40 yr of average hindcast conditions (i.e., assuming historical climate prevails into the future), and under 20 yr of average hindcast conditions, followed by 20 yr of average forecast conditions. We used 20 yr of forecast conditions to avoid assuming that climate changes projected for mid-century would have occurred immediately. The 20–20 assumption approximates a linear transition from the historic to future climate and is not limiting since the probabilities will converge given sufficient years under a given climate regime. Projected climate change impacts differed in direction and spatial pattern among GCMs (Appendix S1: Fig. S3). Projected changes in the proportion of the landscape planted in row crops were generally small (mean change = 0.01), but included increases of over 0.25 of the landscape and declines of over 0.3 of the landscape (Appendix S1: Fig. S3). Conversion probabilities responded to precipitation as expected, with an increase in precipitation associated with higher probabilities that grass converts to crops and lower probabilities that crops convert to grass.

To develop projections of wetland densities under the projected crops scenario, we used the wetland model to predict to climatic conditions and proportions of the landscape planted in row crops based on each GCM's hindcast and compared those projections to those based on that GCM's forecast. Our land use and wetland projections were therefore internally consistent. Although conversion to row crops and wetland drainage are broadly associated, we did not alter the number of wetland basins from the historically observed distribution because the relationships between land use, seasonal rainfall, geography, and surface hydrology are complex and defy simple predictions (Dumanski et al. 2015, McCauley et al. 2015, Roy 2015). For example, partially drained wetlands often contain water during the survey period in May, and conversion to row crops may be most likely in locations that were formerly part of the Conservation Reserve Program, where drainage ditches may already be in place (M. Anteau, *personal communication*).

Statistical analyses

We compared three statistical methods to analyze the relationship between log-transformed wetland densities and climate and land cover covariates: a linear regression model, a Bayesian geostatistical model fit in R-INLA (Rue et al. 2009, Lindgren et al. 2011; see Appendix S1), and the random forest machine-learning method. Random forest uses an ensemble of regression trees in which a random subset of the predictor variables are available for selection at each node of each tree; this process reduces the correlation between trees and thereby reduces the variance in averaged predictions (Hastie et al. 2009). We compared the predictive ability of the three modeling methods using both a spatial estimation/validation data split, in which all years for 121 randomly chosen segments (of 421 total) constituted the validation dataset, and a temporal estimation/validation split, in which all locations from five randomly chosen years constituted the validation dataset. Because the effects of hydrological balance on wetland counts depend on the number of wetland basins to fill, the linear model and the geostatistical model included interactions between the number of wetlands of each type and each of the two measures of overall water balance: P-PET in the past year, and P-PET over the previous 5 yr; interactions are implicitly included in tree-based methods such as random forest. Predictions from the three types of models were highly correlated (random forest vs. geostatistical model: $r = 0.89$ for spatial split, $r = 0.93$ for temporal split; random forest vs. linear model: $r = 0.91$ for spatial and temporal splits; geostatistical vs. linear model: $r = 0.92$ for spatial and temporal splits). All models over-predicted at low wetland densities and under-predicted at high densities, reducing the variability in predictions (observed log-transformed pond densities from 1971 to 2000 had a standard deviation of 2.1, version 1.8 for predictions based on gridded climate data from the same years). There were therefore fewer extreme values in our predictions compared with observed data (Appendix S1: Fig. S4A). Nevertheless, models explained a substantial portion of the variation in wetland densities in space and time (e.g., random forest pseudo-R^2 = 0.66 and pseudo-R^2 = 0.65; linear model R^2 = 0.51 and R^2 = 0.50, based on spatial and temporal splits, respectively). The random forest models, which were ensembles of 3000 trees, had the lowest mean squared prediction error for both the spatial and the temporal validation datasets (Appendix S1: Table S1). Therefore, we used random forest to fit models with all locations and years of historical data available for inclusion in each tree and used the ensemble to make inferences regarding the impacts of climate change.

For each of our three land-use scenarios, the random forest ensemble was used to generate predicted wetland densities for each year for each GCM under hindcast (1971–2000) and forecast (2041–2070) climatic conditions. Predictions for each year were exponentiated (to address the log-transformation), and averaged at each location for each GCM for each time period. The ratio of the mean wetland predictions under future (forecast) versus retrospective (hindcast) climatic conditions was used as a measure of projected climate impact for each GCM. We calculated the mean and standard deviation of this projected climate impact across all GCMs. Data processing (Wickham 2007, Bivand et al. 2014, Bivand and Rundel 2014, Pierce 2014, Wickham and Francois 2014, Hijmans 2015), statistical analyses (Liaw and Wiener 2002, Rue et al. 2009, Lindgren et al. 2011), and plotting (Wickham 2009) were done in R (R Core Team 2014).

Results

Annual variation in weather was a major driver of observed historical variation in wetland densities. In our random forest ensemble, the two most important predictors of wetland density were P-PET over the previous year and the mean of maximum monthly temperatures during spring (Fig. 1). Wetlands were most numerous in years with more positive water balance and with cooler spring temperatures (Appendix S1: Fig. S5A,B). The

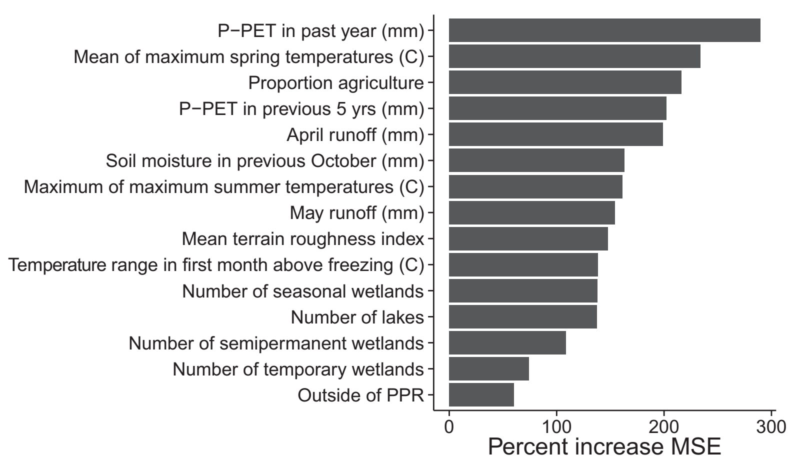

Fig. 1. Overall water balance (precipitation minus potential evapotranspiration; P-PET) and maximum spring temperatures were the most important climate predictors of wetland densities, while the proportion of upland areas used for agriculture was the most important land-use and land-cover covariate. Variable importance in the random forest ensemble was calculated by randomly permuting the values of each predictor variable and calculating the increase in mean square error (MSE) of log-transformed pond densities.

proportion of each survey segment's upland area planted in row crops was the most important land use predictor of wetland densities (Fig. 1), with fewer wetlands in areas with more agriculture (Appendix S1: Fig. S5C).

For the two most important climate covariates, we compared estimates from the historical period, GCM hindcasts, and GCM forecasts to assess the degree of extrapolation in climatic conditions. We found good correspondence in the central tendency of historical and hindcast estimates, but hindcast climates were somewhat less variable (Appendix S1: Fig. S6). Predicted wetland densities based on GCM hindcasts were less variable than historical observations of wetland densities, but the central tendency was well approximated (Appendix S1: Fig. S4; log-transformed observed 1971–2000 pond densities, SD = 2.1; predictions based on 1971–2000 hindcasts, SD = 1.7). This comparison was informative because it illustrated that the decline in variability in predictions to GCMs was an artifact of both the wetland and climate models, whereas a comparison between historical observations and GCM forecasts might have concluded that wetland densities would be less variable in the future. The magnitude of the error in predictions to GCM hindcasts, relative to historical estimates, was highest in parts of South Dakota both within and outside of the PPR (Appendix S1: Fig. S7). GCM forecasts occupied a climate space in which P-PET generally differed from hindcast data at the extremes of the water balance, and in which maximum spring temperatures were warmer on average than those in the historical and GCM hindcast datasets (Appendix S1: Fig. S6B).

As expected, historical observations from wetland surveys in May showed wetland basins reached their highest densities in the Missouri Coteau, near the western border of the PPR in North Dakota and parts of South Dakota (Fig. 2). The Missouri Coteau is a glacial moraine where wetland basins are at a high density and substantial grassland cover remains (Appendix S1: Fig. S1). Similarly, the Prairie Coteau, near the eastern boundary of North and South Dakota, is another glacial moraine with intact wetlands and grasslands. These areas are a high priority for current conservation investments (Loesch et al. 2012). The mean (Fig. 2a) and standard deviation (Fig. 2b) of historical observations of wetland densities provide a basis for comparing the projected effects of climate change.

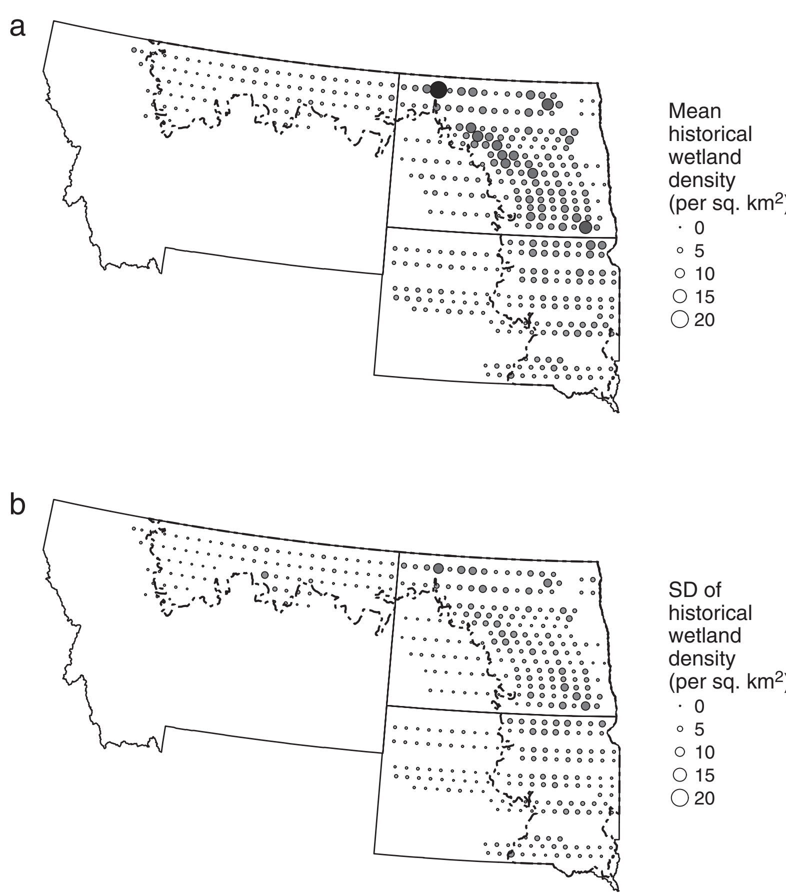

Fig. 2. Historical observations from annual May surveys of wetlands show substantial variation in mean wetland densities (a) over space and (b) over time, here represented by the standard deviation at each location. The PPR boundary is shown with a dashed line.

Results from our scenario based on existing land use and land cover (historical crops) showed considerable variation in the projected impacts of climate change among GCMs. There was a lack of agreement across the GCMs over whether climate change would have a positive or negative impact on wetland abundance (Fig. 3). This reflected variation among GCMs in the magnitude and direction of projected change in P-PET (Appendix S1: Fig. S8) and in the magnitude of the increase in spring temperatures; all GCMs agreed that spring temperatures would increase (Appendix S1: Fig. S9). Projected wetland densities based on GCM hindcasts and forecasts showed a spatial pattern similar to that of observed wetland densities, but wetland densities were projected to be lower in the forecast (Fig. 4). The mean projected impact across GCMs was negative overall, with the steepest average projected declines in the Missouri Coteau (Fig. 4, bottom left panel), where wetland densities are highest (Fig. 2). The greatest disagreement in projected impact among GCMs was farther east and south (Appendix S1: Fig. S10).

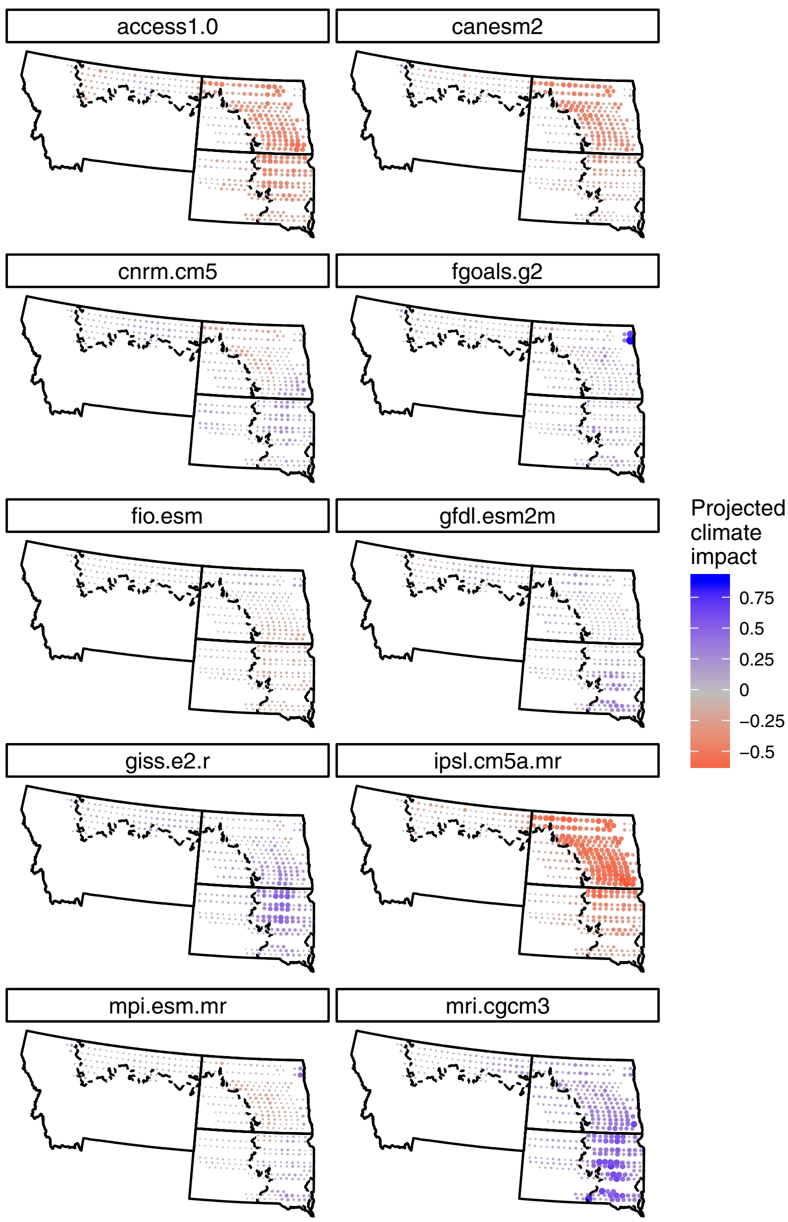

Fig. 3. Projected climate impact for each of 10 GCMs, calculated as the mean of predictions based on the GCM forecast (2041–2070) climatic conditions divided by the mean of predictions based on the GCM hindcast (1971–2000) climatic conditions. We subtracted 1 for ease of interpretation; for example, −0.2 corresponds to 20% lower projected wetland densities in the forecast period.

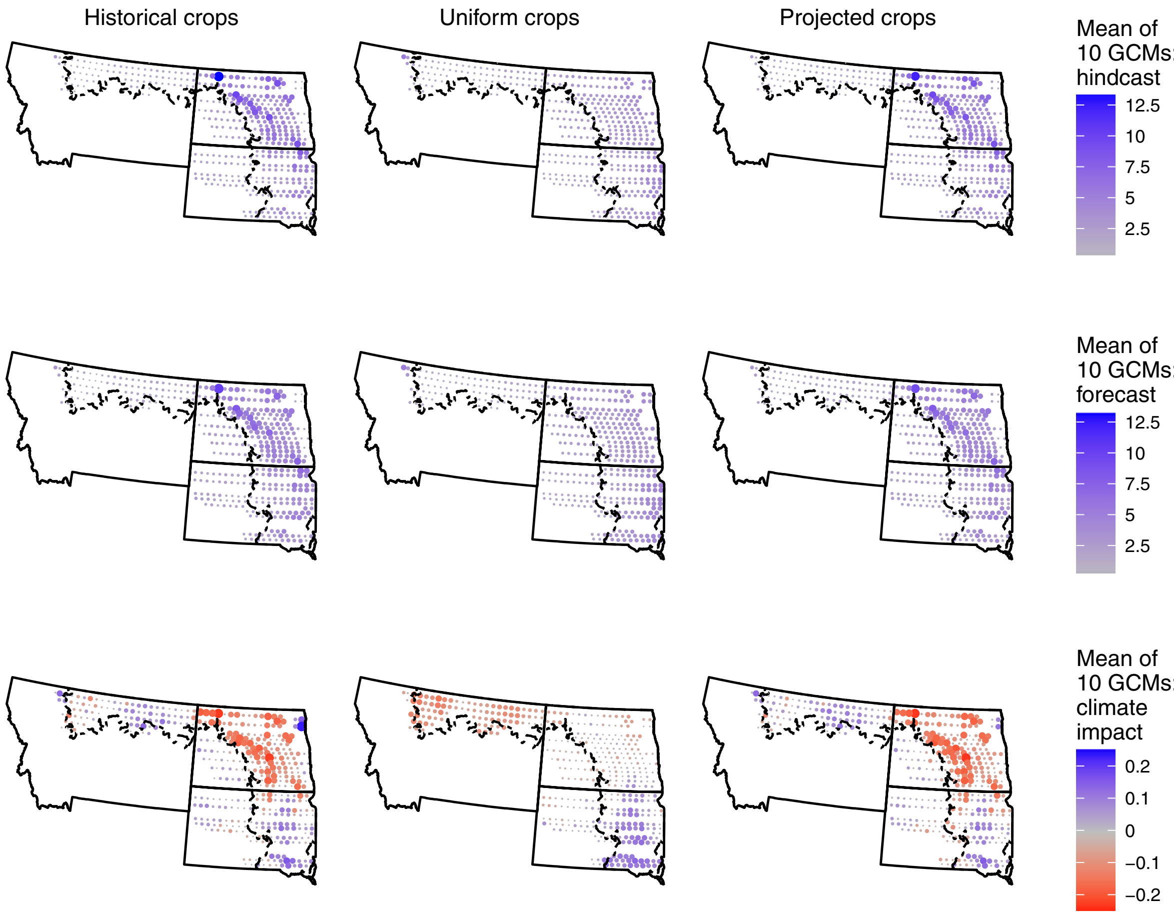

FIG. 4. Comparison of projected wetland densities and climate change impacts across three land-use and land-cover scenarios. Top and central panels show projected wetland densities under hindcast and forecast projected climatic conditions, respectively. Bottom panels show projected climate impact, calculated as in Fig. 3. All are mean values over 10 GCMs; see Appendix S1: Fig. S10 for standard deviations across this GCM ensemble.

Despite our projections that the Missouri Coteau will experience, on average, the greatest declines in wetland densities, we project that this area will continue to support the highest densities of wetlands in midcentury (Fig. 5a). The Prairie Coteau will also continue to support high wetland densities. The standard deviation of these projections is high (Fig. 5b) because predictions to each GCM differ in wetland densities; however, across GCMs the highest densities are consistently predicted in the Missouri and Prairie Coteau regions (Appendix S1: Fig. S11). This is not surprising given the negative effect of agricultural land use (Appendix S1: Fig. S5) and the positive effect of the number of wetland basins on wetland model predictions. Under relatively hot and dry conditions projected by several GCMs (e.g., access1.0, canesm2, and especially ipipsl.cm5a.mr), wetland densities will be much lower in the future. Our major results were robust to the metric by which we measured the impact of climate change: when we calculated climate impact as the difference between predictions to future and past conditions (i.e., subtracting the predictions, rather than dividing them; Appendix S1: Fig. S12), we again found that the decline in wetland densities will, on average, be highest in the Missouri Coteau and that this region will continue to host the most wetlands in midcentury.

Results from our scenario based on uniform land-use and land cover differed substantially from our results based on historical land-use and land cover. This scenario (uniform crops) had no spatial variation in the proportion of upland areas planted with row crops or in numbers of wetland basins across the landscape and therefore isolated the effects of changing climatic suitability. As expected, the lack of spatial variation in key landcover covariates reduced projected spatial variation in wetland densities (Fig. 4). The wetter eastern portion of the region was most climatically suitable for wetlands during both projected hindcast and forecast periods, but this pattern was relatively subtle compared with the magnitude of spatial patterns in the scenario based on historical land-use and land cover (Fig. 4). Similarly, the projected effects of climate change on changes in wetland densities were

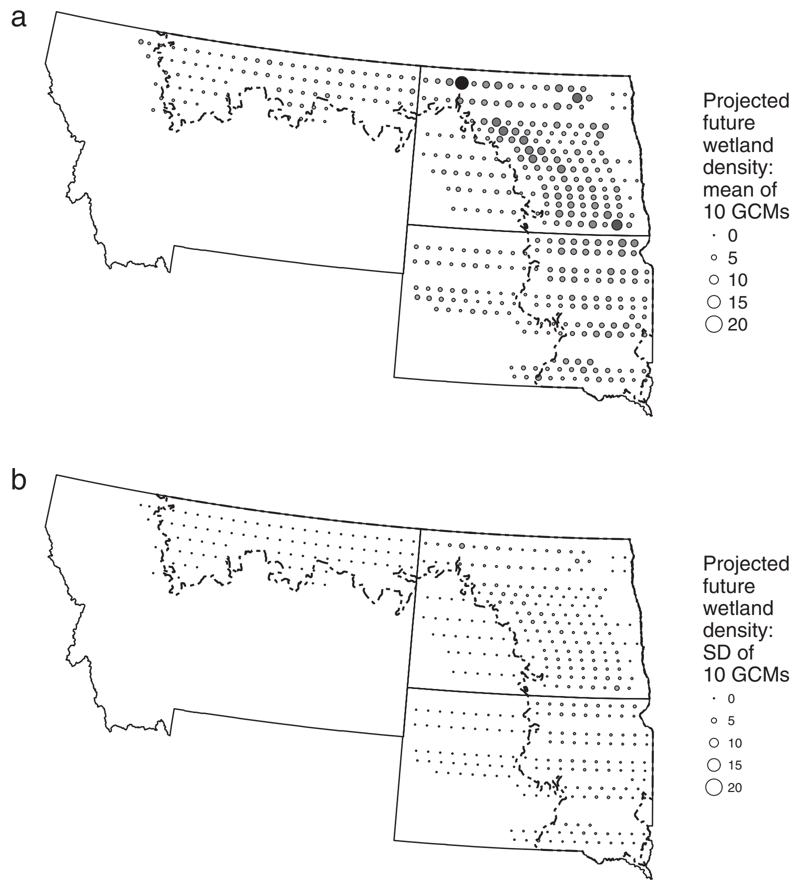

Fig. 5. Projections of wetland densities in midcentury (2041–2070): (a) mean and (b) standard deviation across 10 GCMs. Projected future wetland densities for each GCM were calculated as the historical average (Fig. 2) multiplied by the projected impact of climate change (Fig. 4 bottom left).

smaller in magnitude than projected effects under existing land-use patterns, particularly in North Dakota (Fig. 4). This finding emphasizes the importance of interactions between climate, agricultural land-use, and numbers of wetland basins. On average, predictions to each GCM suggested a further decline in climatic suitability in the westernmost portion of the PPR in Montana (Fig. 4). However, our findings did not suggest that climatic conditions would shift eastwards overall; we projected that the greatest average increase in climatic suitability would occur in southeastern South Dakota (Fig. 4). Therefore, while the climatic gradient from drier conditions in the west to wetter conditions in the east creates a gradient in climatic suitability for wetlands, most GCMs do not project a simple pattern of drying that would steepen the existing gradient (Appendix S1: Fig. S8).

Results from the scenario based on projected land-use under climate change (projected crops) were similar to those based on historical land-use patterns. Under both hindcast and forecast projected climates, wetland densities were expected to be highest in the Coteau regions (Fig. 4). Similarly, the projected climate change impact based on the ensemble mean of 10 GCMs closely mirrored the projected impact under historical land-use (Fig. 4). This is likely because the major spatial gradients of agricultural production were projected to remain consistent (i.e., more agriculture in the eastern Dakotas compared to the western Dakotas). In addition, the sharpest projected declines in row crops occurred in western Montana (Appendix S1: Fig. S3), which has few wetland basins. Divergence in projected impact was most prominent along the PPR boundary in the Dakotas and in the Glacial Lake Agassiz basin (Appendix S1: Fig. S13). We did see some evidence that changes in climate and those in land use may have opposing effects on wetland densities. For example, a GCM from NASA's Goddard Institute for Space Studies (giss.e2.r in our figures) projected a wetter climate overall (i.e., positive change in P-PET; Appendix S1: Fig. S8), was associated with some of the largest projected increases in row crops in the Missouri Coteau (Appendix S1: Fig. S3), and led to more positive projections of climate impact under the historical crop scenario (Fig. 3) than under the scenario that included agricultural projections (Appendix S1: Fig. S13).

Nevertheless, in most cases the similarity between the historical crops and projected crops scenario was striking, likely because these scenarios had a shared distribution of wetland basins across the landscape, as well as broadly similar geographic patterns in proportions of row crops.

Discussion

Climate change will likely exacerbate the conservation challenges associated with maintaining target population sizes of wetland-dependent species (Doherty et al. 2013). Many conservation efforts in the U.S. Prairie Pothole Region are currently targeted towards wetlands and grasslands in the Missouri and Prairie Coteau regions, reflecting the importance of those regions for waterfowl productivity (Loesch et al. 2012). Our results affirm the potential for negative impacts of climate change on wetlands in the PPR, particularly because the greatest average decline in wetland densities was projected along the Missouri Coteau (Fig. 4) where wetland densities have historically been highest (Fig. 2). We found little evidence, however, for a trade-off between the values of conservation investments under historical vs. future climatic conditions, suggesting that current spatial prioritization strategies would continue to provide the best return on investment under average projected climate conditions during midcentury. Specifically, the Missouri and Prairie Coteau regions will continue to host the highest average densities in the future despite projected declines in those regions (Fig. 5). These patterns are maintained when including the potential for climate change to also impact the proportion of the landscape planted in row crops (Fig. 4). However, confidence in these patterns based on the GCM ensemble's average projections is tempered by the considerable variation in both projected future climate (Appendix S1: Figs. S6 and S7) and future wetland densities (Fig. 3; Appendix S1: Fig. S8). Not all GCMs projected drier conditions and fewer wetlands, but collectively our results point towards a shift in the future risk profile such that the probability of drought is higher within North Dakota and Montana.

Synthesis of projected future conditions

Several studies have projected that climate change will decrease wetland abundance, area, and connectivity in the Prairie Pothole Region (e.g., Larson 1995, Sorenson et al. 1998, McIntyre et al. 2014, Ouyang et al. 2014). Our work integrates the most recent climate and hydrological models to corroborate the negative projected effects on wetland densities and highlights the strong and interactive effects of climate and land use and land cover. Because indices of avian population sizes track indices of wetland abundance or density (e.g., Krapu et al. 1983, 1997, Austin 2002, Niemuth and Solberg 2003), climate change is expected to have negative overall effects on population sizes of waterfowl and other wetland-dependent species. Nevertheless, assessing the impacts of projected hydroclimatic changes on wildlife population dynamics remains a major challenge, not only because habitat requirements vary among species (Skagen and Knopf 1994, Murkin et al. 1997, Naugle et al. 1999), but also because of the multifaceted nature of the effects of climate change on wetland systems.

Studies of different measures of wetland abundance and condition are providing an increasingly nuanced view of the projected effects of climate change. For example, our results complement rather than contradict work by Johnson et al. (2005, 2010), whose mechanistic model of wetland function suggested that climatic conditions were historically most suitable in the central PPR but would shift eastward with warmer temperatures. Those studies focused on wetland hydroperiods and cycles of vegetative structure within wetlands that affect productivity. Consistently wet conditions more typical of the eastern PPR lead to fewer fluctuations in water levels and hence less cycling in vegetation structure and lower productivity (Johnson et al. 2010, Werner et al. 2013). Our model shows that the wetter conditions in the eastern PPR should fill wetland basins and would promote high wetland densities if more wetland basins were available. The uniform crops land-use and land-cover scenario, which is most comparable to the assumptions in Johnson et al. (2005, 2010), showed that the eastern portion of our study area had the most suitable climatic conditions for high wetland densities for both GCM hindcast and GCM forecast conditions (Fig. 4). However, under both the historical crops and projected crops scenarios, wetland densities were highest in the Coteau regions under hindcast as well as forecast climatic conditions (Fig. 4), reflecting fewer row crops and more wetland basins in those areas. The similarity between the historical crops and projected crops scenarios is consistent with Rashford et al. (2016), who found that the effects of climate change on prairie wetland function were generally similar given current vs. projected land-use. Given these results and those of previous studies, it appears most probable that wetland densities may remain highest in the central PPR (Fig. 5) but that increased evapotranspiration due to hotter summer temperatures will shorten hydroperiods and could decrease wetland productivity in this region (Johnson et al. 2010, Ballard et al. 2014).

Management challenges in an uncertain future

Management under climate change has become synonymous with management under uncertainty. The greatest long-term source of uncertainty specific to climate change is associated with human behavior, i.e., predicting future emissions trajectories, but this is less important for projections to mid-century (Appendix S1: Fig. S2). Additional uncertainties are introduced by the climate models, both in the physical processes determining climate sensitivity to increasing greenhouse gases, as well as the specific decisions made when applying the models (e.g., setting initial conditions; Snover et al. 2013, Harris et al. 2014). Although much of the uncertainty associated with climate change is irreducible, the same is true for uncertainty surrounding the sociopolitical and economic drivers of management considerations, such as the future risk of land conversion to agriculture. Other sources of uncertainty are encountered in many contexts, including measurement and classification errors in historical wetland and land-use data and the effect of choices regarding statistical modeling methods and covariate selection.

A general feature of climate models is that patterns and trends in precipitation are more uncertain than those for changes in temperature. Continental scale projections show a predominately north to south gradient in projected changes in both temperature and precipitation, supporting our finding that there may be little longitudinal shift in climatic suitability for wetlands. In the PPR, all models project increasing temperatures and most models project some increase in annual precipitation, but models diverge in the projected magnitude of each of these trends (Appendix S1: Fig. S2). As a consequence, GCMs show considerable variability in projections of future water balance (Appendix S1: Fig. S8), leading to qualitative variation in the projected change in average wetland densities across the landscape (Fig. 3). Understanding spatial variation in projected climate change can inform the spatial prioritization of conservation investments. However, the PPR is temporally dynamic, and decadal variation in precipitation has been a major, if not the dominant, component of historical variation in pothole water balance (Euliss et al. 2004, van der Valk 2005). The pattern of boom and bust years and decades for waterfowl and other wildlife populations in the PPR is likely to continue, but low-frequency (i.e., decadal) natural variability is entangled with anthropogenically forced precipitation trends in future climate projections (Deser et al. 2014). What is most certain is that temperatures will increase; this suggests that although we continue to expect variation in precipitation between years, increased evapotranspiration will make both wet and dry years effectively drier from a wetland standpoint.

Management effectiveness under climate change calls for strategies that are relatively robust to the major sources of uncertainty. A leading approach for addressing uncertainty in ecology is adaptive management, which aims to reduce uncertainty by learning from a system's response to ecological variation and human manipulations. A rigorous program to monitor wildlife populations in relation to wetland densities, condition, and land-use practices would provide important new information for quantifying the ecological impacts of variation in weather (Niemuth et al. 2014). However, climate change impacts are best assessed on multi-decadal scales, leading to a temporal mismatch that makes it difficult to use adaptive management to reduce the uncertainties associated with climate change. Regardless, spatially extensive data are needed on the relationship between upland conversion to row crops and drainage of small wetlands, and on how these human impacts interact with weather to affect spring water levels, hydroperiods, and function of different sized wetlands.

A goal of robust management planning is to develop strategies that hedge against damaging future scenarios. One strategy for bet hedging is to develop a diversified portfolio that favors increased investments in the eastern PPR as climate impacts become increasingly likely (Ando and Mallory 2012). The Prairie Coteau in northeastern South Dakota may be one location where existing habitat can be conserved while building a buffer against the effects of climate change because average projections suggest an increase in climatic suitability (Fig. 4, climate impact under uniform scenario). In contrast, directing conservation resources to other eastern areas has been controversial because these parcels have higher acquisition and restoration costs (Loesch et al. 2012). Another conservation strategy is to direct resources to wetland complexes that include larger and deeper wetlands. Small wetlands provide high biodiversity benefits and have been disproportionately drained (Van Meter and Basu 2015), whereas larger wetlands can serve as a buffer against declining hydroperiods under climate change. However, many larger wetlands have become less temporally dynamic due to consolidation drainage, potentially altering biotic communities and impacting productivity (McCauley et al. 2015). Targeting conservation action towards wetland complexes that contain a diversity of wetland types and sizes has been recommended to support the habitat requirements of a diversity of avian species under variable weather conditions and is a hallmark of the current conservation strategy (Skagen and Knopf 1994, Haig et al. 1998, Naugle et al. 2001, Skagen 2006, Doherty et al. 2013, Walker et al. 2013*a*); it also may prove to be a judicious method to hedge against climate change.

Assessing climate impacts

Integrating projections from GCMs into decision-making is a major challenge because methodological decisions in studies assessing vulnerability to climate change contribute to the uncertainty in projected impacts. Our work highlights two approaches that remain underused in ecological studies of climate impacts. First, we used hydrological projections, including an index of water balance, to provide realistic links between weather and wetland densities. Water balance may often underlie organisms' distributional shifts and declines, but drought indices are rarely included as covariates in species distribution models (Barbet-Massin and Jetz 2014). This suggests an opportunity to improve ecological inference by more closely integrating climatic, hydrologic, and ecological projections.

The second strategy we used was to compare predicted wetland densities under GCM hindcast and forecast conditions to quantify the projected impacts of climate change. This method isolates the effects of climate change because changes in greenhouse gas concentrations drive the differences between GCM hindcasts and forecasts, in contrast to direct comparisons between GCM projections and historic climate observations. Our covariates based on GCMs were less variable than those based on historic data (Appendix S1: Fig. S6), which in turn yielded a lower variance in projected wetland densities (Appendix S1: Fig. S4). Using predictions to hindcasts as our baseline made it clear that these differences should not be attributed to climate change. We emphasize that impact assessments using this methodology should visually compare the distributions of historically observed data with the distributions of covariates (Appendix S1: Fig. S6) and predicted responses (Appendix S1: Fig. S4) based on GCM hindcasts, as projections based on hindcasts may not always be realistic. Compared with the more common delta method, our methodology allowed us to take advantage of the full dimensionality captured by GCMs while maintaining the correlation structure between variables (e.g., the relationship between temperature and precipitation). Our approach may therefore be useful for many climate change impact assessments, and the application of these methods to develop projected changes in land use, as well as projected changes in wetland densities, demonstrates their relevance across disciplines and modeling frameworks.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1890/15-0750.1/suppinfo

Data accessibility:

Data associated with this work are available at https://www.sciencebase.gov/catalog/item/56b3e649e4b0cc79997fb5ec