



North American birds require mitigation and adaptation to reduce vulnerability to climate change

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Abstract

In an emerging climate crisis, effective conservation requires both adaptation and mitigation to improve the resilience of species. The currently pledged emissions reductions outlined in the Paris Agreement framework would still lead to a +3.2°C increase in global mean temperature by the end of this century. In this context, we assess the vulnerability of 604 North American bird species and identify the species and locations most at risk under climate change. We do this based on species distribution models for both the breeding and nonbreeding seasons, projected under two global warming scenarios (an optimistic mitigation scenario 1.5°C and an unmitigated 3.0°C scenario). We evaluate vulnerability under each season and scenario by assessing sensitivity and adaptive capacity based on modeled range loss and range gain, respectively, and based on species specific dispersal abilities. Our study, the first of its magnitude, finds that over two-thirds of North American birds are moderately or highly vulnerable to climate change under a 3.0°C scenario. Of these climate-vulnerable species, 76% would have reduced vulnerability and 38% of those would be considered nonvulnerable if warming were stabilized at 1.5°C. Thus, the current pledge in greenhouse gas reductions set by the Paris Agreement is inadequate to reduce vulnerability to North American birds. Additionally, if climate change proceeds on its current trajectory, arctic birds, waterbirds, and boreal and western forest birds will be highly vulnerable to climate change, groups that are currently not considered of high conservation concern. There is an urgent need for both (a) policies to mitigate emissions and (b) prioritization to identify where to focus adaptation actions to protect birds in a changing climate.

KEY WORDS

biodiversity, birds, climate change policy, climate change vulnerability, global change, IPCC, Paris agreement, range shift, species distribution model

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1 | INTRODUCTION

Climate change exacerbates the global biodiversity crisis (Thomas et al., 2004), with 24–50% of bird species vulnerable to climate change alone and 11–15% both vulnerable to climate change and already threatened with extinction per the IUCN Red List (Foden et al., 2013). Birds are already responding to contemporary climate change with range shifts (Hitch & Leberg, 2007; La Sorte & Thompson, 2007; Prince & Zuckerberg, 2015; Root et al., 2003; Warren et al., 2013; Wiens, 1989). Moreover, on our current emissions trajectory, contemporary climate change is anticipated to be 20 times faster in the next century than at any period over the last 2 million years (Mann et al., 2008), and even common and widespread species are anticipated to experience significant range contractions (Warren et al., 2013). This rapid pace of climate change will push birds to either adapt to novel environmental conditions or seek new suitable locations at a greater velocity (Bateman, Pidgeon, Radeloff, Flather, et al., 2016; Bateman, Pidgeon, Radeloff, VanDerWal, et al., 2016), leading to more range shifts (Williams & Blois, 2018) and drastically reshuffling the avian communities of North America (Prince & Zuckerberg, 2015; Stralberg et al., 2009).

Effective conservation requires an understanding of species' vulnerability to climate change. Vulnerability is based on species' specific *exposure*, *sensitivity*, and *adaptive capacity* (Foden & Young, 2016; Moritz & Agudo, 2013; Williams, Shoo, Isaac, Hoffmann, & Langham, 2008; Wilsey et al., 2019); that is, the local pressures to be experienced from a changing climate, the characteristics that result in sensitivity to change, and how well a species may be able to cope with change, respectively. We must utilize our understanding of vulnerability to inform climate change *mitigation* and *adaptation* to reduce vulnerability and improve species' ability to cope with climate change (IPCC, 2007; Morecroft, Crick, Duffield, & Macgregor, 2012; Williams et al., 2008). Identifying appropriate strategies for *mitigation*, interventions to reduce the magnitude of climate change as much as possible through the reduction in the sources of greenhouse gases (GHG) or the enhancement of GHG sinks, and *adaptation*, interventions to help species or natural systems cope with, or adjust to, the consequences of inevitable climate change, are thus imperative (IPCC, 2013, 2018).

To understand how mitigation could potentially alter species vulnerability to climate change, we apply species distribution models (SDMs) to assess the vulnerability of birds in North America in the context of accepted future climate trajectories. The Intergovernmental Panel on Climate Change (IPCC) recommends a limit in global mean temperature to less than 2.0°C above pre-industrial levels

and preferably to 1.5°C if possible (IPCC, 2013, 2018; Meinshausen et al., 2009; United Nations, 2015). Currently, we are on track to surpass this limit: ~1.0°C (0.8–1.2°C) of warming has already occurred (IPCC, 2018), and 3.0°C is expected by 2100 under a conservative business-as-usual trajectory (Climate Transparency, 2018). In order to provide relevant information for national policies that would address the threat of climate change, we focus here on three scenarios that reflect current and potential climate change emissions reduction targets: 1.5°C, 2.0°C, and 3.0°C increases in global mean temperature (IPCC, 2018).

Successful adaptation strategies will depend on prioritizing where to focus conservation efforts. To do this, we need to determine which bird species and locations are most at risk under possible climate change scenarios. High-resolution, continental-scale SDMs are able to provide information at the spatial scale relevant to on-the-ground actions. SDMs can give us a snapshot of potential futures to help identify which scenarios will be problematic and which regions and species might be at risk. Birds serve as a helpful study group to forecast potential realities in a changing climate using SDMs (Langham, Schuetz, Distler, Soykan, & Wilsey, 2015). First, they are a ubiquitous taxon, and the millions of geo-located observations covering much of North America are now available in global databases. Second, birds serve as a conservative baseline for other taxa facing climate change. Given their higher dispersal rates and migration capacity, it is likely that birds will fare better than less vagile species (Bateman, Murphy, Reside, Mokany, & VanDerWal, 2013; Lawler et al., 2009). Paired with the continental-scale availability of high-resolution environmental data, remote sensing products, and future projections of climate and vegetation change, and with a well-developed field of SDM research (Araújo et al., 2019), these data sets allow us to provide future projections that are relevant for landscape-scale conservation prioritization and planning (Araújo et al., 2019; Grand, Wilsey, Wu, & Michel, 2019; Wu, Wilsey, Taylor, & Schuurman, 2018) and determine how or where local adaptation planning efforts should be focused.

In this work, we compile more than 140 million observations to develop SDMs and assess climate change vulnerability for 604 North American bird species at a continental scale in both breeding and non-breeding seasons and under multiple global climate change scenarios. We aim to identify how different warming targets translate to potential changes in bird communities across North America in order to aid in both mitigation policy and adaptation planning and prioritization to ameliorate the impacts of global climate change on birds.

2 | METHODS

We assess species' vulnerability to climate change as a function of a species' climate change exposure, sensitivity, and adaptive capacity (Foden & Young, 2016) for 604 species across Canada, the United States, and Mexico using a combination of species distribution models (SDMs) and trait-based information (Willis et al., 2015). We utilize the methods from Wilsey et al. (2019) in our modeling effort, which includes data extraction and filtering, model building and evaluation, threshold selection, and model projection under climate change (Wilsey et al., 2019).

2.1 | Response variable: Bird data

2.1.1 | Occurrence data

We compiled 141,126,651 bird occurrence records from 70+ datasets across Canada, the United States, and Mexico for 604 species in the breeding and non-breeding seasons. These data included a combination of both structured and unstructured avian surveys, so we took action to reduce sampling biases that are inherent in non-systematically designed surveys (described below). Our final data set included 58,458,971 unique occurrence records for our 604 species, which ranged from 45 to 403,517 occurrence records (across all species) per Bird Conservation Region (BCRs; NABCI, <http://nabci-us.org/resources/bird-conservation-regions-map/>), and from 0.01 to 5.09 occurrences/km² based on area per BCR. See the Supporting Information for more information on our data sources (Bird Data Sources S1), the number of bird occurrence records per BCR (Number of Bird Records by BCR S2), a list of the 604 species included in this analysis (Bird Species Table S3), and full details on how we processed the occurrence data (Methods S4).

We included bird species with breeding or nonbreeding ranges primarily within the United States and Canada (Langham et al., 2015), and species that had sufficient data availability to build a well-performing model. To distinguish breeding and nonbreeding occurrence records, we first assigned each species a resident status based on published range maps (Rodewald, 2015), life history (Rodewald, 2015), and expert opinion. Species were classified as breeding-only (nonbreeding range outside of North America), two-season (separate breeding and nonbreeding ranges within North America), or permanent resident (non-migratory). We consulted with experts to define default breeding (June to July) and nonbreeding (January to February) seasonal date ranges that worked well for most species, and custom seasonal date

ranges for species with different migration timing (breeding season of June only for plovers, sandpipers, and hummingbirds; wintering season of December only for hummingbirds and swallows, December to January for grassland birds). We assigned each species to a habitat affinity group based on NABCI's 2009 State of the Birds report (www.stateofthebirds.org), which classifies species based on their main geographic or habitat association. These included arctic, aridlands, boreal forests, coastal, eastern forests, generalists, grasslands, marshlands, subtropical forests, urban/suburban, waterbirds, and western forests (range in the number of species per group = 9–89). For species encompassing more than one group, we selected the group that best matched their habitat needs during each season, or where the majority of their range and/or abundance was situated geographically (e.g., Pileated Woodpecker occurs in both eastern and western forests, but was placed in eastern forests). In a few instances, we grouped species in different habitats for breeding and non-breeding seasons based on their ecology (e.g., Whimbrel was placed in the arctic group in summer as an inland nester and the coastal group in winter). See Bird Species Table S3 for all information on migratory status type, seasonal date ranges, and habitat affiliation assigned.

2.2 | Trait-based data

For our species trait-based data, we used mean natal dispersal (BirdLife International, 2017) and generation time (Beauchamp, 2010) in both resident and breeding season models to generate a dispersal limit for each species and future time period. These dispersal limits were used to constrain each species' ability to shift their ranges within their biological limits. Including inherent dispersal limitations in species distribution models is one way to address trait-based assessment of a species capacity to adapt to change (Willis et al., 2015). See Bird Species Table S3 for dispersal limits for each species.

2.3 | Predictor variables: Climate and environmental data

2.3.1 | Climate data

We used current and modeled future climate developed by AdaptWest as covariates in the SDMs (Wang, Hamann, Spittlehouse, & Carroll, 2016). Each gridded climate data layer consisted of 23 million cells covering North America at a 1-km resolution. For the present, we used statistically downscaled climate normals for the

time period of 1981–2010 derived from the Climatic Research Unit Time series 3.22 data set (Wang et al., 2016). For future projections, we used Coupled Model Intercomparison Project phase 5 (CMIP5) projections from three individual general circulation models (GCMs) and in addition an ensemble of 15 GCMs (composed of an average of ACCESS1-0, CCSM4, CESM1-CAM5, CNRM-CM5, CSIRO-Mk3-6-0, CanESM2, GFDL-CM3, GISS-E2R, HadGEM2-ES, INM-CM4, IPSL-CM5A-MR, MIROC-ESM, MIROC5, MPI-ESM-LR, MRI-CGCM3; AdaptWest Project, 2015). The three individual GCMs capture a range of intermediate (CCSM4), warm-wet (GFDL-CM3), and cold-dry (INM-CM4) future conditions for the continent (Wang et al., 2016). We included two greenhouse gas representation concentration pathways (RCPs; RCP4.5 and RCP8.5) for two future time periods (2041–2070, hereafter 2050s, and 2071–2100, hereafter 2080s). To provide climate scenarios relevant to policy, we associated a 1.5°C global mean temperature rise with RCP4.5 for the 2050s, 2.0°C with the RCP8.5 for the 2050s, and 3.0°C with the RCP8.5 2080s. Multiyear climate averages have been shown to be a sufficient temporal scale to capture species ranges and projections for species distribution models (Bateman, Pidgeon, Radeloff, VanDerWal, et al., 2016).

According to Wilsey et al. (2019), we reduced a set of 27 bioclimatic variables using hierarchical agglomerative clustering of 100,000 random points across the study area to address collinearity (Crowther et al., 2015). The final set of climate covariates consisted of four variables used in both breeding and nonbreeding season models (climatic moisture deficit, number of frost-free days, mean annual precipitation, and precipitation as snow), three breeding season-specific variables (mean temperature of the warmest month, chilling degree days [degree-days below 0°C], and summer heat moisture index), and two nonbreeding season-specific variables (mean temperature of the coldest month, and growing degree days [degree-days above 5°C]). For more details on climate data and selection, see Wilsey et al. (2019)).

2.4 | Environmental data

We included key environmental predictor variables to capture habitat-specific information based on ecological knowledge of North American bird species. For all habitat groups, we included vegetation type (Rehfeldt, Crookston, Sáenz-Romero, & Campbell, 2012), terrain ruggedness (methods following Riley, Degloria, & Elliot, 1999), and anthropogenic land cover (Canada Centre for Remote Sensing [CCRS]; CCRS et al., 2013). For specific habitat groups, we used ecologically relevant

variables such as the presence of surface water in each grid cell for waterbirds and marshbirds (Pekel, Cottam, Gorelick, & Belward, 2016), wetland type (Lehner & Döll, 2004) for waterbirds and marshbirds, distance to wetlands for waterbirds, distance to coast (excluding inland water bodies) for coastal birds, distance to shore (including inland water bodies; Wessel & Smith, 1996) for marshbirds and waterbirds, and a human influence index (Wildlife Conservation Society-WCS; Center For International Earth Science Information Network-CIESIN-Columbia University, 2005) for urban/suburban birds.

Most habitat variables were only available for the present, except vegetation type. Future vegetation projections represented a consensus across three GCMs (CGCM3, HadCM3, GFDL CM2.1) and two Special Report on Emissions Scenarios (SRES) emissions scenarios (A2 and B1 or B2) from CMIP3, as outlined in Rehfeldt et al. (2012). CMIP3 and CMIP5 projections are more similar than distinct (Knutti & Sedláček, 2013) and for these purposes represent the best available vegetation projections on the continental scale (Wilsey et al., 2019). We used the mid-century vegetation projections to align with the 1.5°C and 2.0°C, and late-century projections for the 3.0°C global mean temperature scenarios. For all other habitat variables, current conditions were included in future projections as the best available information.

2.5 | Species distribution modeling

2.5.1 | Model building

We approached our modeling effort by integrating the latest modeling approaches with knowledge of the natural history of each species, with the goal of producing the best model for each species instead of a one size fits all approach (Lawler, White, Neilson, & Blaustein, 2006). We modeled each species within a habitat group context, using the aforementioned ecologically relevant variables for each group. We built both breeding season and nonbreeding season models for two-season and resident species to capture the seasonal differences in bird species ranges. We also included a multistep expert review process where we had an expert visually assess the mapped bird occurrence data, modeled current range, and projected future range for each species and season (Reside et al., 2019). We built models with two algorithms, boosted regression trees (BRTs) and maximum entropy (Maxent, version 3.3.3 k), implemented in the dismo package in R. Both approaches are well regarded in the literature for accuracy and their ability to model nonlinear species-habitat relationships (Elith &

Leathwick, 2014; Elith, Leathwick, & Hastie, 2008; Radosavljevic & Anderson, 2014).

2.5.2 | Model parameters and performance

To address bias and avoid model over-fitting (Boria, Olson, Goodman, & Anderson, 2014; Veloz, 2009), we applied both a geographic filtering approach and a target-group background approach (Phillips et al., 2009), weighting our background sampling by the number of occurrence points within each grid cell. We included all available bird occurrence data across North America for our 604 species in order to sample occurrences from the full range of environmental conditions possible for each species. To ensure that the geographic extent of our data was appropriate, we defined the extent from which we sampled both the occurrence and background points using a movement-hypothesis approach. This approach accounts for regions that a species could have experienced historically through movement (Peterson et al., 2011) and are potentially suitable and accessible, but do not include areas beyond this (Araújo et al., 2019), by incorporating these areas in background sampling. This approach helps provide a realistic background sample for a species and improves model performance and generalizability (Boria et al., 2014). For detailed methods on background point sampling and subsampling of data for model performance and selection, please see Methods S4.

We first built BRTs to evaluate an appropriate filtering resolution (i.e., 1, 10, or 50 km). Model performance was evaluated using area under the receiver operating characteristic curve (AUC) across 25 bootstrapped training and tests split of the spatially stratified training datasets. We compared filtering scenarios using median AUC and the top-performing filtering approach to build Maxent models. We built Maxent models that varied the regularization parameter from 0.5 to 4.0 and compared model performance with median AUC as above. As our goal was projection under future climate change scenarios, we aimed to maximize generalizability and reduce overfitting (Veloz, 2009) by selecting the top-performing model based on median AUC across all BRT and Maxent model runs. We then used the top model for model prediction and results of variable importance in the model building process.

2.6 | Thresholding projection surfaces

We evaluated multiple thresholding approaches to define a value that converts the continuous suitability surface output by the models into a binary range map where

values above this threshold are considered part of each species' range for each season, a common practice when applying SDMs to conservation applications (Jiménez-Valverde & Lobo, 2007; Pearson, 2007). After expert review, a final threshold was selected that aligned with expert opinion and minimized a decrease in model performance. We calculated multiple thresholds using the SDMTools package in R (VanDerWal, Falconi, Januchowski, Shoo, & Storlie, 2014); these included mean occurrence prediction (mo ; mean suitability prediction for the occurrence records), maximum sensitivity specificity (tss ; maximized sensitivity + specificity), 10% omission (om_{10} ; excludes 10% of occurrence records), sensitivity specificity (eq ; sensitivity is equal to specificity), maximum Kappa (mk ; maximum Kappa statistic), minimum occurrence prediction, (min_pred ; minimum suitability prediction across all occurrence records), and a derived custom threshold to fall between the minimum occurrence prediction and 10% omission thresholds ($(om_{10} + min_pred)/3$). For each threshold applied, we calculated the true positive (commission error) and true negative (omission error) rate for how each model classified presence and background points. To ensure models approximated ecological reality, we first compared each species and season model to range maps (Rodewald, 2015), then outputs were evaluated externally by at least two experts per species. Expert reviewers had access to a map of occurrence and background points, projected current range maps with continuous suitability outputs and all possible thresholds mapped, as well as modeled future range maps based on the selected threshold from the first pass comparison. They also reviewed all data associated with each species occurrence data and data cleaning (see Methods S4) and background data including number of background points, and the BCRs sampled from (i.e., the area of sampling based on the movement-hypothesis). Where species models deviated from known ecology (e.g., errors in occurrence record locations, over- and under-predictions), efforts were taken to re-model. Steps included for re-modeling included dropping erroneous occurrence records based on BCRs, adding or dropping BCRs from the species background, or changing the selected threshold. After review, a final threshold was selected that aligned with expert opinion and minimized a decrease in model performance (based on true positive and true negative rates). See S3 Bird Species Table for BCRs that were dropped or added for each species and for final choice of threshold.

2.7 | Model projection

We generated high-resolution (1 km) predictive occurrence maps for each season and scenario (1.5, 2.0, and

3.0°C). For each scenario, we projected onto an ensemble as well as three individual GCMs that represent a range of future climate conditions (as detailed above). To avoid extrapolating to novel conditions outside of the range of the occurrence and background training data, we included a clamping procedure where we limited extrapolation by only projecting onto vegetation, land-use classes, and climate conditions that were included in the model training datasets for each species. We also use “clamping,” which restricts model extrapolation beyond the range of values in the training data (e.g., values outside of the training range are treated as if they are at the limit of the training range and held constant), to limit extrapolation to novel climates (Elith et al., 2010).

For the trait-based component of sensitivity, in both resident and breeding season models, we estimated dispersal limitations based on mean natal dispersal (BirdLife International, 2017; Santini et al., 2019) and generation time for each species at each future time period according to Wilsey et al. (2019). This trait informs each species' intrinsic climate change-adaptation capacity, where dispersal rate may limit the ability of the species to reach climate-suitable areas in the future (Willis et al., 2015). We clipped projected future distributions by the maximum dispersal distance at each time period to reflect these biological limits (Willis et al., 2015). We did not include dispersal limitations for non-breeding season models, as there is limited information available on nonbreeding movement and site fidelity for the majority of bird species.

To address model commission error and limit biological extrapolation, we applied an expert opinion-based approach that identified BCRs with over-prediction (Reside et al., 2019). We masked, or manually excluded, current and future projections from BCRs with commission error from both current and future projections if it was identified that the BCRs were geographically distinct and/or biological limitations makes it unlikely for the species to disperse there.

2.8 | Vulnerability assessment

We assessed vulnerability of North American birds to climate change under temperature targets associated with multiple climate change scenarios based on a combination of each species' *exposure*, *sensitivity*, and *adaptive capacity* (Foden & Young, 2016; Moritz & Agudo, 2013; Williams et al., 2008; Wilsey et al., 2019). Here, we define *exposure* as the climate change scenario considered, *sensitivity* as the negative impact of climate change on a species through range loss, and *adaptive capacity* as the ability of a species to respond to climate change through range gain relative to range loss based on each species trait-based

dispersal ability. Our possible exposure scenarios reflect relevant climate change mitigation policy target scenarios, with a 1.5°C global mean temperature rise as potential climate stabilization scenario, 2.0°C as in intermediate scenario based on IPCC recommendations, and a 3.0°C scenario as a high-emissions estimate. For each scenario, we compared current and future range maps to classify areas projected to be lost, gained, or maintained for each species and season. Areas that are currently suitable but become unsuitable (i.e., drop below the threshold) are considered loss, areas that are currently unsuitable but become newly suitable (i.e., pass above the threshold) are considered gain, and areas that are suitable in both periods (i.e., remain above the threshold) are considered stable.

We classified the vulnerability of each species for each season and scenario as neutral, low, moderate, or high based on projected range loss and potential range gain (Langham et al., 2015; Thomas et al., 2010; Wilsey et al., 2019) *per* Wilsey et al. (2019); see Methods S4 for more details. We classified climate sensitivity by binning the proportion of range loss into four equal intervals (0–25%, 25–50%, 50–75%, 75–100%) and assigning a value of 0–3 from low to high across bins. We classified adaptive capacity by binning the ratio of range gain to range loss into four classes (>2:1, 1–2:1, 0.5–1:1, and 0–0.5:1) and assigning a value of 0–3 from low to high across the bins. We then summed the climate sensitivity and adaptive capacity scores to get the final vulnerability score for each species and season, classifying them as neutral (sensitivity + adaptive capacity = 0), low vulnerability (sensitivity + adaptive capacity = 1 or 2), moderate vulnerability (sensitivity + adaptive capacity = 3 or 4), and high vulnerability (sensitivity + adaptive capacity = 5 or 6). With this approach, species that experience greater range loss without being able to make up for it in range gain have higher vulnerability. Here, we consider species in the moderate and high vulnerability classes to be vulnerable to climate change. To calculate confidence in our vulnerability scores, we assessed the number of times the vulnerability score agreed across the ensemble model and the three individuals GCMs for each of the future scenarios for a maximum score of four.

We also assess the number of species that we classify as climate vulnerable compared to the species currently listed on the Partners in Flight (PIF) Watch lists (Rosenberg et al., 2016), a list of species considered of highest conservation concern across North America. PIF Watch list data were available for 495 of our 604 species.

2.9 | Spatial assessment

To transfer the species distribution projections into tools to inform and prioritize climate change adaptation, we

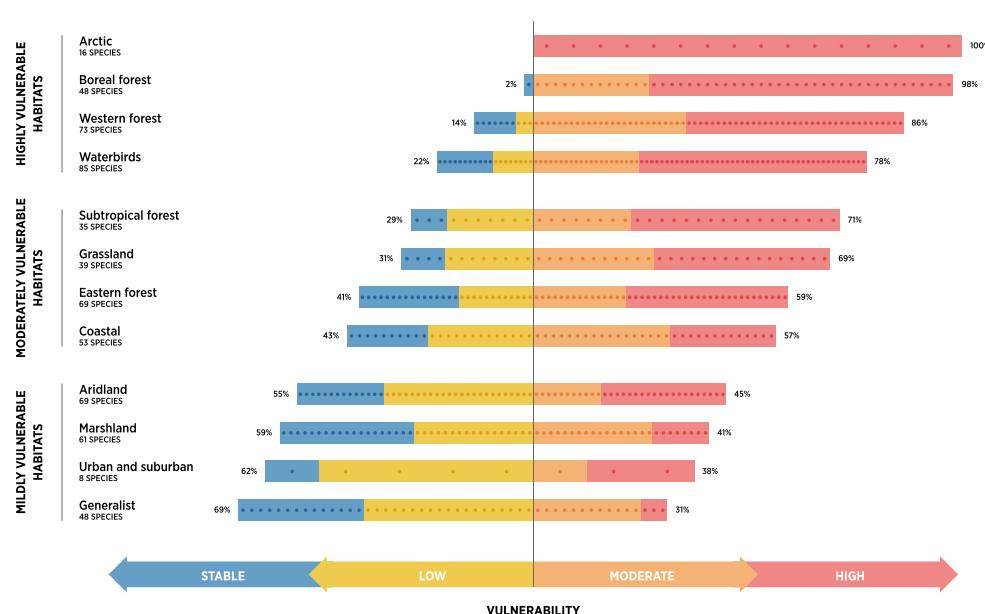
mapped potential changes in bird community composition across North America (Hole et al., 2009; Wu et al., 2018). We mapped areas of aggregated species loss, gain, and net change in community composition for each of the habitat-associated species groups and for all species. Climate change adaptation strategies can be tailored for areas with high projected loss (local extirpation), gain (colonization), or net change (Hole et al., 2011). We also mapped the number of vulnerable species across North American in each season and scenario to identify areas of high conservation value with climate change.

3 | RESULTS

3.1 | Vulnerability scores

Nearly two-thirds, 64% (389/604), of species were climate vulnerable in at least one season and scenario (Species Vulnerability Data S5). Some habitat groups were highly vulnerable across the majority of species (Figure 1), including 100% of arctic birds (16/16), followed by 98% of boreal forest birds (47/48), 86% of western forest birds (63/73), and 78% of waterbirds (66/85). Habitat groups with intermediate vulnerability included subtropical forests (71%, 25/35), grasslands (69%, 27/39), eastern forests (59%, 41/69), and coasts (57%, 30/53). Habitat groups with lower vulnerability included aridlands (45%, 31/69), marshlands (41%, 25/61), urban/suburban (38%, 3/8), and generalists (31%, 15/48), although even in these groups more than a quarter of the species were considered climate vulnerable.

FIGURE 1 Percentage of species vulnerable by bird habitat groupings across all scenarios and seasons. Purple and green indicate percentage of species vulnerable (high and moderate) on a positive axis, and blue and yellow indicate non-vulnerable (low and neutral) on a negative axis



Vulnerability declined in scenarios with reduced warming (Figure 2, Figure S1.1). Nearly two-thirds (63%, 383/604) of all species across either seasons were classified as vulnerable within the 3.0°C scenario, compared to 54% ($N = 327$) at 2.0°C, and 47% ($N = 286$) at 1.5°C global mean temperature rise (Figure S1.1). Only 2% of species (6/389) were vulnerable at 1.5°C and 2.0°C but not at 3.0°C. In fact, across seasons for species considered vulnerable (high and moderate vulnerability) at 3.0°C, 76% (290 unique species of 383, 356 combinations of breeding and nonbreeding) drop at least one climate vulnerability category lower, and 38% (146 unique species of 383, 159 combinations of breeding and nonbreeding) are no longer vulnerable under 1.5°C. One species, the Golden-cheeked Warbler (*Setophaga chrysoparia*), could drop vulnerability by up to three categories, from high vulnerability at 3.0°C, to neutral vulnerability at 1.5°C in the breeding season. See Species Vulnerability Data S5 for sensitivity, adaptive capacity, and final vulnerability scores as well as the proportion of range loss and gain for each species, season, and scenario.

Vulnerability was considerably higher in the breeding season compared to the nonbreeding season. In the breeding season, 58% (345/597) of species are vulnerable at the 3.0°C scenario, compared to 30% (165/546) in the non-breeding season. However, stabilizing global warming at 1.5°C global mean temperature rise would bring this down to 43% (254/597) of breeding species and 19% (104/546) of nonbreeding species. The most vulnerable groups in the breeding season at 3.0°C were arctic (100%) boreal forests (98%), western forests (78%), and waterbirds (78%) (Table S4.1). In these four groups, at

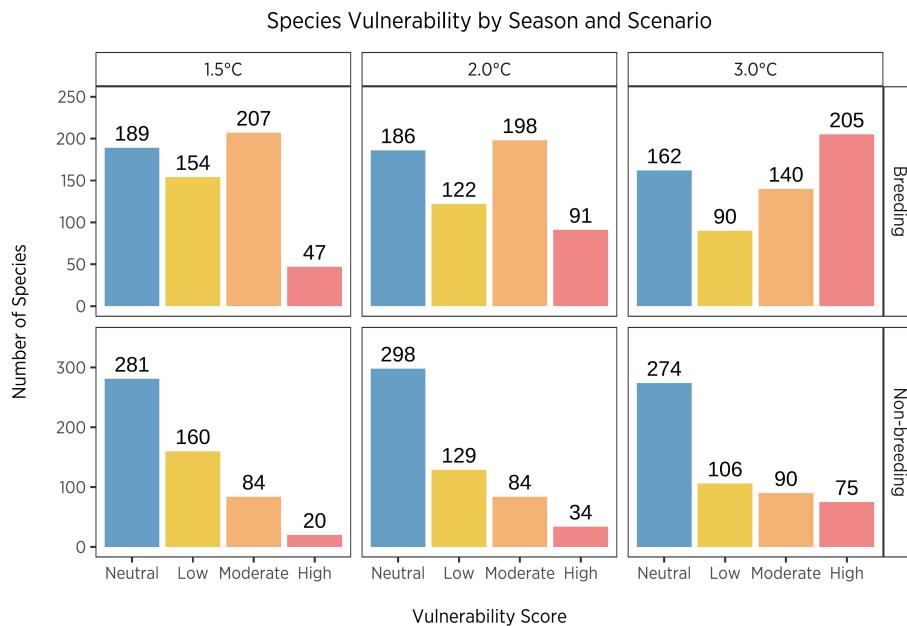


FIGURE 2 Vulnerability classification in the breeding and non-breeding seasons under 1.5°C, 2.0°C and 3.0°C global warming scenarios. Vulnerable species are within the moderate or high vulnerability classes, and non-vulnerable species are within the neutral or low vulnerability classes

least 62% of species were still vulnerable at 1.5°C in the breeding season. Vulnerability in the nonbreeding season was considerably lower across all groups compared to their respective group vulnerability in the breeding season. Yet despite the lower average vulnerability in the nonbreeding season, nearly half or more of the species in some groups are still vulnerable to climate change; that is, subtropical forests (59%), boreal forests (58%), western forests (51%), and arctic (47%) species (Table S4.1). For results on changes in vulnerability by group and season, see Results SI.

3.2 | Spatial patterns of change

The net change in species (number of species gained minus lost) varied across seasons and scenarios (See Methods SI and Figures S4.2 and S4.3). We predict a net decline in species richness across most of North America in both scenarios for the breeding season, except in the tundra and taiga ecoregions, the Southern Great Plains in Texas and New Mexico, and parts of the Rocky and Sierra Madre mountains. Net losses were more widespread in the United States and the boreal region of Canada under the 3.0°C scenario but were still prevalent at 1.5°C (Figure S4.2). In contrast, the nonbreeding season exhibited net gain overall. For this season, limited net loss was projected in North America in either warming scenario, with net loss restricted to Mexico, Florida, California, South Texas, and Sonoran Arizona (Figure 3). Net gains in the nonbreeding season were projected to be greatest under 3.0°C in western Alaska, Newfoundland, Nova Scotia, the Great Lakes, and central Texas. Net change across bird

habitat groups varied geographically and seasonally (Results SI, Figures S4.4–S4.15).

Richness of vulnerable species was consistently higher under a 3.0°C scenario relative to a 1.5°C scenario in both seasons (Figure 4). In the breeding season, as many as 98 vulnerable species co-occurred in any given location, with the most concentrated number of vulnerable species projected to be in the arctic, tundra and taiga, the Northwestern forested mountains, the marine West Coast forests, and, to a lesser extent, central Mexico and the Northeast US and Canadian northern Boreal forests. In the non-breeding season, vulnerable species richness was lower, with a maximum of 35 co-occurring vulnerable species (Figure 4), primarily in taiga, Northwestern forested mountains, central Mexico, and to a lesser extent southern Florida.

4 | CONSERVATION STATUS

The present conservation status of climate vulnerable species varied widely, from high conservation concern (e.g., threatened or endangered species, species on the PIF Watch List) to those not of conservation concern. Fifty of our climate vulnerable species across seasons were also listed on the PIF Watch List (Figure 5; PIF Watch List data available for 589/604 species, 15 introduced species not included). Thus, the adaptive capacity of these species is further diminished by their current conservation threats beyond climate change. These include species from the grasslands ($N = 7$ species); aridlands ($N = 7$); coastal ($N = 8$); subtropical ($N = 3$), western ($N = 7$), eastern ($N = 5$), and boreal forests

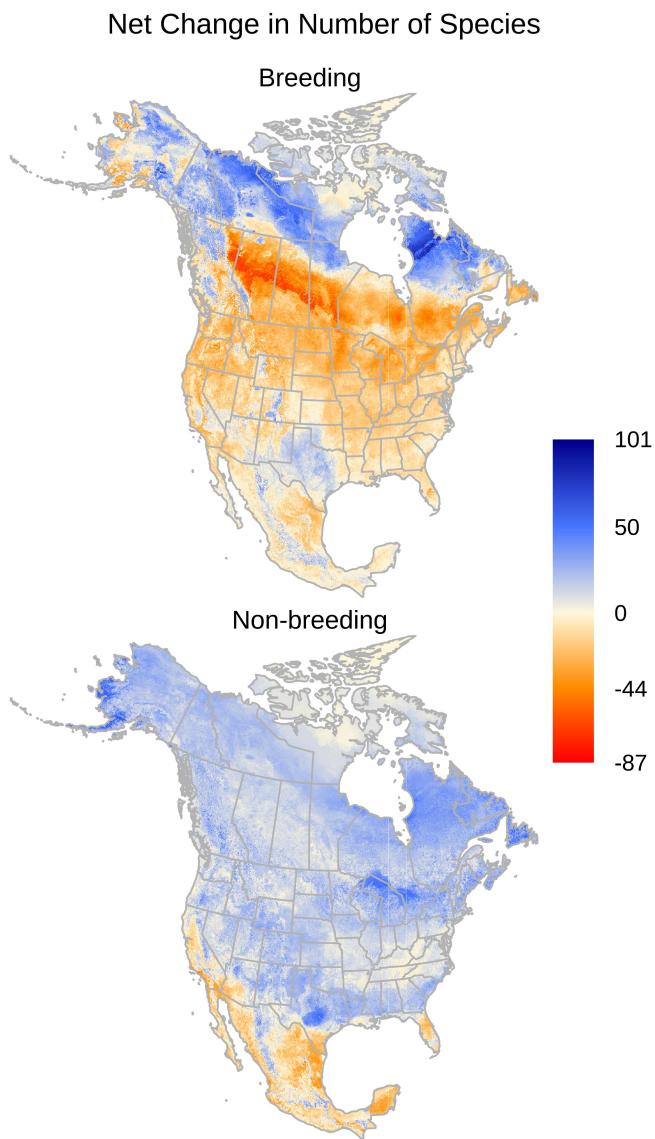


FIGURE 3 Net gain or loss in number of species at the local community level (i.e., per grid cell) across North America for the breeding and non-breeding seasons. The scale ranges from net loss (red) to a net gain (blue) of species under 1.5°C warming (left) and 3.0°C warming (right). Net change in the breeding season ranged from -87 to 101, and from -62 to 97 in the non-breeding under 3.0°C . Under 1.5°C net change in the breeding seasons ranged from -62 to 82, and from -63 to 58 in the non-breeding

($N = 1$); marshlands ($N = 5$); waterbirds ($N = 5$); and arctic ($N = 2$) groups. Furthermore, the bulk (325) of our climate vulnerable species are not currently on the Watch List (Figure 5), suggesting a key emerging conservation need as climate change advances.

5 | MODEL ACCURACY

Overall, models performed well across all species when predicting to spatially independent bootstrapped datasets

(AUC of 0.92 [Interquartile Range (IQR): 0.87–0.96]). Between seasons, breeding models performed slightly better, with a median testing AUC of 0.93 (IQR: 0.88–0.97) compared to 0.91 (IQR: 0.85–0.95) for nonbreeding models. All models across seasons performed better than random with all AUC values above 0.5, and a minimum AUC of 0.62. Although the overall median AUC of BRT models (median AUC = 0.95 breeding; median AUC = 0.92 nonbreeding) was slightly higher than Maxent models (median AUC = 0.93 breeding; median AUC = 0.91 nonbreeding) when comparing the final models chosen across species, Maxent outperformed BRT 83% of the time in the breeding season (Maxent, $N = 496$ species; BRT, $N = 101$ species), and 88% of the time in the non-breeding season (Maxent, $N = 483$ species; BRT, $N = 63$ species) when comparing individual species models (median AUC = $\Delta 0.02$; IQR $\Delta 0.01$ –0.06). A filtering resolution of 1 km ($N = 386$ species in breeding season, $N = 352$ species in nonbreeding season) outperformed other spatial scales (10 km, breeding $N = 146$ species, nonbreeding $N = 148$ species; 25 km, breeding $N = 2$ species, nonbreeding $N = 5$ species; 50 km, breeding $N = 63$ species, nonbreeding $N = 41$ species). For results on thresholds and variable importance, please see Results S4. For final model building and performance results (number of presences and background points, model algorithm, filter resolution, regularization multiplier, choice of threshold, threshold value, true positive rate, true negative rate, and training and testing AUC), see S6 Species Model Evaluation, and S7 All Model Results for results on all species models for model selection.

6 | DISCUSSION

Our results provide strong evidence that mitigation—reducing the amount of climate change—would benefit birds across the North American continent. In addition, these findings provide guidance on adaptation or where to focus efforts to help birds adapt to environmental changes and continue to persist into the future. Despite certain limitations (further discussed in Caveats), our findings that nearly two-thirds of North American bird species assessed here are vulnerable to climate change confirm that climate change is an important, pervasive threat to birds. Projected climate change, though its impacts are not fully predictable, will almost certainly cause disruptions in existing bird communities across North America. Local communities could see changes of more than 100 species under 3.0°C of warming in both the breeding season (dominated by range loss and local extirpation) and the nonbreeding season (dominated by

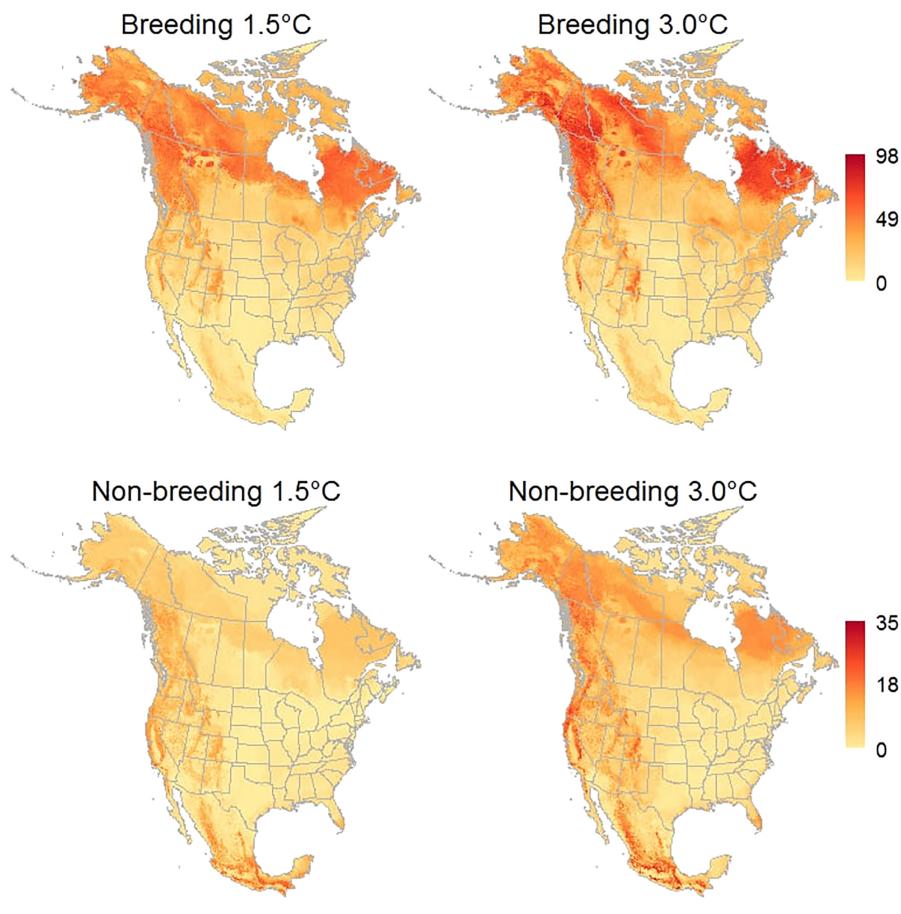


FIGURE 4 Richness in vulnerable bird species (i.e., per grid cell) across North America for the breeding and non-breeding seasons. The scale ranges from 0 (orange) to the high count (red) of the number of vulnerable species per grid cell under 1.5°C warming (left) and 3.0°C warming (right)

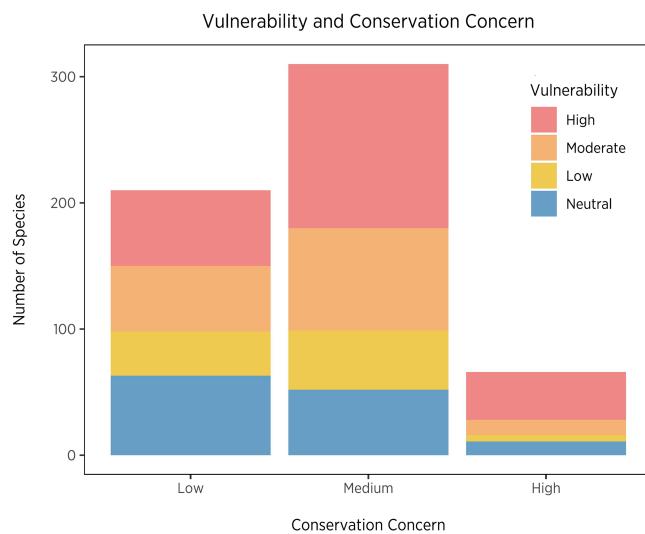


FIGURE 5 Species vulnerability in the breeding season classified as being present on the PIF Watch list for the 3.0°C scenario across both seasons

range gain and local colonization). Changes at this scale could manifest in novel community assemblages, revealing new species interactions (Stralberg et al., 2009) that could lead to population declines and local extinctions if

species are not able to adapt quickly enough to new patterns in co-occurrence (Hughes, 2000).

6.1 | Reduced vulnerability under mitigation

Our results indicate that nearly two-thirds of North American bird species assessed here are vulnerable to climate change, confirming that climate change is an ongoing threat to birds in North America. Reductions in emissions that limit warming to 1.5°C would result in 76% of our vulnerable species dropping at least one category in vulnerability. Of those, 38% would no longer even be vulnerable. Thus, our results provide compelling evidence that climate change mitigation that stabilizes warming to less than 3.0°C, and preferably 1.5°C, would be beneficial to birds. These results align with the recommendations of the IPCC, which has identified a target of 2.0°C global temperature increase—preferably 1.5°C—to avoid severe and irreversible effects of climate change (IPCC, 2018). The current pledged reductions in greenhouse gas emissions set in the Paris agreement at present will lead to at least 3.2°C global increase in mean temperature (Climate Transparency, 2018). In fact, on our

current trajectory, potential warming will likely exceed this ($4.5 + ^\circ\text{C}$) by the end of century (Collins et al., 2013; Gidden et al., 2019; New, Liverman, Schroder, & Anderson, 2011) and result in inevitable warming of 1.5°C globally by 2030–2052. Therefore, we need aggressive climate change mitigation and adequate policies at a national, continental, and global scale.

Our study is the first of its magnitude to assess vulnerability to climate change under multiple warming scenarios for such a large number of species in two seasons. Others have found that 53% of North American birds are vulnerable to climate change (Langham et al., 2015). Meta-analysis studies also concur with our findings that mitigated climate change scenarios reduce extinction risk (Foden et al., 2013; Thomas et al., 2004; Urban, 2015).

6.2 | Prioritization of places and species for climate change adaptation

Projected climate change is set to disrupt bird communities across North America. Changes of more than 100 species within a local community are possible under the 3.0°C scenario in both breeding (dominated by range loss and local extirpation) and nonbreeding seasons (dominated by range gain and local colonization). Winter colonizations and summer extirpations have already been found to occur in North America (LaSorte & Frank III, 2007; McClure, Rolek, McDonald, & Hill, 2012; Prince & Zuckerberg, 2015), and we predict they will become more commonplace with climate change.

Despite data limitations inherent in an analysis of this extent, our study identified important places and groups to prioritize conservation efforts to help species and systems adapt to unprecedented environmental change. Vulnerability classifications help inform community and species-based climate change adaptation prioritization strategies, as the most vulnerable species merit the most attention in a triage framework for climate change adaptation (Lawler, 2009). Of the 389 climate species classified as vulnerable, 50 are also on the PIF Watch List (Rosenberg et al., 2016) and as such are high priority for conservation attention in a changing climate. However, we also identified 325 climate-vulnerable species not included in the PIF Watch List, a pattern replicated with the IUCN Red List, which only lists 6–9% of the 24–50% of bird species vulnerable to climate change globally (Foden et al., 2013). These climate vulnerable species that are not currently on watch lists should be the focus of monitoring to determine if the effects of climate change lead to a change in conservation status (Lawler, 2009).

We identified arctic birds, waterbirds, and boreal and western forest birds as the most vulnerable habitat

groups, with 78–100% of species vulnerable at 3.0°C warming. These findings are similar to a previous trait-based assessment on climate vulnerability of birds of the United States, which also grouped species by habitat (North American Bird Conservation Initiative et al., 2010; hereafter, NABCI). NABCI et al. (2010) found that approximately 72% of arctic and alpine species are vulnerable to climate change whereas we found 100% of arctic species to be vulnerable; they included, however, some alpine species that were classified as boreal forest species here. Like NABCI et al. (2010), we found a relatively low proportion of aridlands species to be climate vulnerable, but our analysis also extended to Mexico, which allows for some range expansion northward for species that occur there. Although we predict the Sonoran Desert may experience net species losses in both seasons, the Mojave Desert may see little to no net loss (Figure 3). However, our estimates may be considered conservative as the avian community in the Mojave Desert has already been experiencing declines due to a century of climate change (Iknayan & Beissinger, 2018). Both our study and NABCI et al. (2010) found grassland and various forest species to be intermediate in climate vulnerability, though we generally found more forest species to be vulnerable. An assessment of California's birds vulnerable to climate change also identified wetland associated birds such as waterbirds as being highly vulnerable (Gardali, Seavy, DiGaudio, & Comrack, 2012) Interestingly, many of these climate-vulnerable habitat groups are not generally classified as being of high conservation concern (Rosenberg et al., 2016), with some (i.e., waterbirds) currently doing well due to habitat conservation efforts (Rosenberg et al., 2019). These groups merit attention, particularly in higher latitudes where the magnitude of climate change is projected to be greater than global averages [twice as fast relative to the rest of the world, with the arctic three times as fast (Bush & Lemmen, 2019)]. A global trait-based analysis of birds similarly found that the arctic regions contain the most species vulnerable to climate change (Foden et al., 2013).

Maps of vulnerable species richness and projected changes in bird community composition can aid in spatial prioritizations for conservation (Grand et al., 2019) and inform place-based adaptation strategies (Hole et al., 2011; Wu et al., 2018). Northern latitudes, including the arctic and boreal regions, emerged with the greatest magnitude of projected change. These areas are also considered some of the most important places for breeding birds, deemed the “nurseries of North American birds” where nearly half of all North American species breed (Blancher & Wells, 2005). This includes 30% of North America's landbirds, 30% of shorebirds, and up to 38% of waterbirds. The alpine and tundra ecoregions may

be replaced by Alaskan subarctic conifer forests, and the boreal may be replaced by temperate deciduous forests and Great Plains grasslands (Rehfeldt et al., 2012; Stralberg et al., 2015). The mountainous west, the northeast United States, Florida and central Mexico also had high projected vulnerable species richness along with large projected changes in community composition. Habitats may be lost and not immediately replaced due to lags in vegetation response (Cadieux et al., 2019; Stralberg et al., 2015). Thus, climate change adaptation efforts for birds may be most effective in these regions by providing stepping stones to facilitate species emigration, and/or reducing habitat transitions to encourage species retention (Hole et al., 2011). Other regions of note include California and the Arizona Sonoran desert, which comprise some of the few areas predicted to have a net loss of species (Figure 3) in winter. A disproportionate number of wetland species have been designated as climate-vulnerable in California (Gardali et al., 2012), and California has several species restricted to wetland habitats, which may partially explain this pattern of net loss in winter.

Conversely, areas projected to see net species gains should also be prioritized as potential areas to protect (Wu et al., 2018). Actions that may be applicable in these areas, depending on desired outcomes, may include using conservation easements or agri-environment options in the surrounding landscape to facilitate species colonization into newly suitable areas, increasing the amount of potential habitat and resources to accommodate additional species, and/or balancing existing disturbance regimes with new disturbance regimes in the direction of change to suit colonists (Hole et al., 2011). The suite of possible actions is complex and best guided by monitoring and a grounded knowledge of local ecology.

Our vulnerability assessment based on bird range shifts in North America is likely a conservative estimate for several reasons. First, the climate projections are limited to the scenarios provided in the fifth IPCC assessment, and end of century projections may indeed be much warmer (up to 5°C) than 3.0°C globally (Collins et al., 2013; Gidden et al., 2019; New et al., 2011). Here, we chose to include representative global temperature scenarios for each time period and RCP scenario based on the IPCC assessment value, and those that were directly relevant to policy and pledges within the Paris Agreement. Our global scenarios are based on mean projected change and represent a simplified potential future within the likely range: 1.5°C corresponds to RCP4.5 for 2046–2065 (likely range 0.9°C–2.0°C), 2.0°C corresponds to RCP8.5 for 2046–2065 (likely range 1.4°C–2.6°C), and 3.0°C corresponds to RCP8.5 for 2081–2,100 (likely range 2.6°C–4.8°C) (IPCC, 2013). While these values represent

the projected change in mean global temperatures, locally the temperature rises will likely be much higher. In the United States by the end of century, mean temperatures could increase by 1.3°C–3.7°C under the RCP4.5 scenario or as much as 3.0°C–6.7°C under the higher RCP8.5 scenario (Reidmiller et al., 2018; Vose, Easterling, Kunkel, LeGrande, & Wehner, 2017). These global warming scenarios also reflect varying precipitation conditions, for example, an increase in heavy precipitation is noted in some regions for all scenarios, but these are more extreme under the RCP8.5 scenario (Reidmiller et al., 2018). From a conservation management or priority-setting perspective, it is thus important to consider the range of values of temperature and precipitation locally for each of our global scenarios.

It is important to note that although our study takes into account future changes in climate and vegetation, we do not assess changes in anthropogenic land use, sea-level rise, extreme events or other global and climate change-related threats to birds. Therefore, some areas identified as suitable based on climate and vegetation may be at risk from other threats not assessed here which could render them unsuitable. In addition, projected species responses will not always be realized for a variety of reasons, including intrinsic factors such as phenotypic plasticity (i.e., the ability to adjust to novel conditions and stay in place; (Socolar, Epanchin, Beissinger, & Tingley, 2017), colonization abilities (e.g., birds track climate but at a slower rate than climate is changing; (Santangeli & Lehikoinen, 2016), evolutionary potential (i.e., genetic diversity), and extrinsic factors, such as unpredicted habitat loss, species competition, and pollution (Beever et al., 2015). Although we did take into account trait-based species dispersal data, we did not account for the potential capacities of species to adapt to changes through behavioral or physical changes. We also did not project onto novel conditions outside the range of environmental conditions in our training data, as to avoid statistical and projection error (Fitzpatrick & Hargrove, 2009). However, we do acknowledge in doing so we may be omitting areas of potential gain as species may adapt to novel conditions or currently unavailable portions of a species fundamental niche (i.e., conditions in which a species can persist, but are not currently available at a given time or place) may arise on the landscape (Veloz et al., 2012). We also did not assess altered species interactions or how community-level changes could determine species realized future ranges. Additionally, while we used a threshold-based approach to identify potential range loss or gain, areas of range stability are in fact changing as well, with some areas improving or worsening with climate change. Areas that are worsening could indeed be of low suitability, enough to reflect low

abundance and population instability (VanDerWal, Shoo, Johnson, & Williams, 2009).

6.3 | Caveats

One challenge with a large-scale continental assessment like this one, especially as compared to regional or habitat-specific assessments (e.g., Wilsey et al., 2019), is that certain parts of the study area are not as well sampled as others, such as Mexico and the Arctic. For these regions, we sought out additional datasets to help address this bias, and were able to obtain sufficient data for the species we modeled. However, researchers interested in these outputs should take care in interpreting modeled results for less sampled species and in less sampled locations within North America. In addition, the use of citizen and community science datasets in the assessment, and the discrepancies of such data collection methods, may violate some assumptions of SDMs (Yackulic et al., 2013). We acknowledge that our bird occurrence data came from various sources, and as such were not sampled in a standardized capacity, with survey location bias and variation in individual detection probabilities and identification skills. We balanced the need to retain as much data as possible to capture species' full ranges across North America but also account for this bias with extensive use of spatially structured data partitioning, bias correction through the use of a target group background, data filtering, and expert review. Models built with small sample sizes have been useful in identifying suitable areas for species (Pearson, Raxworthy, Nakamura, & Peterson, 2007; van Proosdij, Sosef, Wieringa, & Raes, 2015) and are greatly improved when undertaking both spatial filtering and manipulating background sampling to address bias (Boria et al., 2014; Kramer-Schadt et al., 2013). It has been shown that careful partitioning and analysis of avian data can yield important full life-cycle bird distribution models (Hochachka et al., 2012). Therefore, the thoroughness of the process taken here should yield reliable, useful model outputs for most species.

We balanced meeting current standards for SDM-based biodiversity assessments (Araújo et al., 2019) with the effort of modeling 604 species across the continent in two seasons by applying best practices to inform model decisions such as selecting species specific thresholds, cleaning species occurrence data and dealing with outliers, and addressing overprediction in models post hoc. Here, the involvement of avian experts allowed us to make decisions based on species-specific knowledge, an exercise of care rarely taken with large studies across hundreds of species. We included an assessment by bird

experts of each species' range maps individually in both the breeding and nonbreeding season, to establish ecological reality of the model outputs. It has been shown that including experts improves the ecological realism of SDM outputs (Reside et al., 2019). Expert review allowed us to select reasonable thresholds to assess habitat loss and identify regions most at risk to climate change across species, as opposed to a gradient-scale approach that would assess only changes in relative suitability at each location.

Despite our best efforts to develop accurate and precise models, we acknowledge that all SDMs are predictive and include inherent uncertainties and errors and therefore do not represent actual species' ranges. Similarly, there is a degree of uncertainty with future climate change projections, which has implications for range projections. There is also uncertainty on how well species track their climate niche through climate change (e.g., Socolar et al., 2017; found birds adapt by shifting phenology rather than distributions), although recent on-the-ground validation of climate change models by community scientists suggest birds track climate conditions (Saunders et al., 2020). Choice of environmental data may also introduce errors and uncertainty, such as the modeled future projections for vegetation data. The vegetation projections used here are not mechanistic and are themselves based on climate models, likely leading to overestimates of range gains and underestimates of vulnerability (Stralberg et al., 2015). Additionally, while vegetation provides ecologically important information for bird species, continental-scale projections of other habitat conditions (e.g., surface water, shoreline changes) are not readily available. Despite these limitations, we chose to include these variables as the best available data biologically relevant to this type of modeling. Lastly, uncertainties and errors also arise from the choice of SDM and model selection. Given the caveats outlined here, it is imperative that results presented here be combined with other approaches to form a more complete picture of species response to climate change (Foden et al., 2013).

7 | CONCLUSIONS

These findings provide a call to action for aggressive climate mitigation policies for birds in North America and priorities for landscape-scale adaptation efforts. Mitigation and adaptation strategies are needed, both to reduce the impacts of climate change as much as possible and to address the impacts that are inevitable (Wilbanks, Leiby, Perlack, Ensminger, & Wright, 2007). The dire consequences of a 3.0°C warming scenario, and the reduction in species vulnerability if we stabilize global warming at

1.5°C, indicate that we must reduce emissions as much as possible to maintain bird communities. Stabilizing climate at 1.5°C is feasible (Goodwin, Brown, Haigh, Nicholls, & Matter, 2018; Meinshausen et al., 2009), but few deliberate actions have been taken to get us there. The current pledge in greenhouse gas reductions set by the Paris Agreement framework is estimated to equate to a 3.2°C global increase in mean temperature (Climate Transparency, 2018), which is not sufficient to reduce vulnerability to birds. Birds are early responders to climate change and can be important indicators of large-scale ongoing and future ecological change (Rosenberg et al., 2019). Here, we also provide clear priorities as to where we could focus adaptation conservation efforts, and for which species we need to alleviate climate change stressors. We identified arctic birds, waterbirds, and boreal and western forest birds as being highly vulnerable to climate change. Interestingly, those habitat groups most threatened by climate change are not high conservation concern presently. Furthermore, we identified areas of the boreal (Stralberg et al., 2015), arctic (Foden et al., 2013), California, and the Great Plains and Sierra Madre regions of Mexico (Pacifici et al., 2015) to be particularly important to prioritize future conservation efforts as avian communities face unprecedented environmental change. Future efforts should build on these findings to assess “strongholds” (Grand et al., 2019), areas that have both high climate suitability and low exposure to climate change-related threats like land-use change or sea level rise, that may serve as refugia for these groups or specified regions. Areas identified as high climate suitability but at higher exposure to threats could be used to target conservation efforts such as reforestation, wetland restoration, constructions that mitigate threats (e.g., living shorelines), or acquisition for protected area status (Hole et al., 2011). In a future where even birds, a highly mobile taxa, may not keep pace with climate change (Devictor et al., 2012; Radchuk et al., 2019), human intervention is needed. Unless we take both aggressive policy mitigation and adaptation actions to alleviate the effects of climate change, birds and the places they need are under threat.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

Chad Wilsey, Lotem Taylor, Brooke L. Bateman, and Geoffrey S. LeBaron conceived the study; Lotem Taylor and Joanna Wu contributed to data preparation; Brooke L. Bateman, Lotem Taylor, Joanna Wu, and Chad Wilsey contributed to the species distribution modeling and manuscript writing; Geoffrey S. LeBaron made revisions and reviewed model outputs and species lists; and all authors reviewed, edited, and approved the final manuscript.

DATA AVAILABILITY

All species model outputs for two future climate change scenarios (RCP4.5 and RCP8.5) for the 2020s (not presented here), 2050s (i.e., 1.5°C and 2.0°C scenarios), and 2080s (3.0°C scenario) are available for download at <https://adaptwest.databasin.org/pages/audubon-survival-by-degrees>.

ETHICS STATEMENT

To the extent possible, this research was completed in compliance with the Guidelines to the Use of Wild Birds in Research; however, the authors were not directly involved in the collection of the datasets used.

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SUPPORTING INFORMATION

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

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