

## RESEARCH ARTICLE

## U.S. National Wildlife Refuge System likely to see regional and seasonal species turnover in bird assemblages under a 2°C warming scenario

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### ABSTRACT

The National Wildlife Refuge System (NWRS) provides one of the United States' greatest protected area networks for wildlife conservation. As climate changes beyond historical ranges of variability, refuge managers are confronted with assessing the utility of refuges, including how to best manage refuges both individually and as a system to help species cope with rapid change. Using published species distribution models, we projected species-specific changes in environmental suitability for 590 native North American bird species under a 2°C future warming scenario (~2050s under RCP8.5) at 525 refuges. For each species, we classified projected changes in suitability (i.e., improving, stable, or worsening suitability) and whether they crossed a model-derived persistence threshold at a refuge (i.e., potential colonization or potential extirpation). Overall, we found that a quarter of species (23% in summer, 26% in winter) could be different (i.e., turnover) across the refuge system despite protections. Summer and winter communities are not equally affected, so managers should consider different strategies for the different seasons. We forecast a slight net species loss in summer, from a mean of  $109.0 \pm 0.8$  to  $102.0 \pm 0.7$  species per refuge. In winter, we forecast a net gain in species, from a mean of  $97.1 \pm 2.2$  to  $118.5 \pm 1.8$  species per refuge. This includes an average of 12 species per refuge that may overwinter rather than migrate south. Refuges at northern latitudes will see relatively more turnover in species, while southern and coastal refuges will see fewer changes. Despite these species changes, dominant habitat association groups (e.g., waterbirds, forest birds) will generally stay the same across most of the NWRS. Some species may be lost from the entire NWRS and can benefit in the near term from targeted management. Regions of high extirpation and colonization (i.e., at northern latitudes) can be prioritized for strategic additions of new refuges.

**Keywords:** birds, climate change, National Wildlife Refuge System, projections, protected areas management, species distribution models

### LAY SUMMARY

Approximately a quarter of bird species observed on National Wildlife Refuges may be different by the 2050s. Refuges may see a slight net loss of species in summer (from 109.0 to 102.0 species per refuge) and a net gain in winter (from 97.1 to 118.5 species per refuge). Some species may be lost from the entire NWRS and can benefit in the near term from targeted management aimed at preventing species loss. The refuge system has capacity to mitigate loss for some of the most climate-vulnerable species in a Resist-Adapt-Direct framework. For example, managers can help the Clay-colored Sparrow by providing more grassland habitat via crop set-aside programs. The Nelson's Sparrow will likely benefit from resisting coastal wetland development. Regions of greater species turnover (i.e., at northern latitudes) might be prioritized for strategic additions of new refuges, ensuring proportions of habitats protected reflect the need.

### El Sistema Nacional de Refugios de Vida Silvestre de EEUU probablemente experimente recambio regional y estacional de especies en los ensambles de aves bajo un escenario de calentamiento de 2°C

### RESUMEN

El Sistema Nacional de Refugios de Vida Silvestre (NWRS por sus siglas en inglés) proporciona una de las redes de áreas protegidas más grandes de Estados Unidos para la conservación de la vida silvestre. A medida que el clima cambia

más allá de los rangos históricos de variabilidad, los gestores de los refugios se enfrentan a la evaluación de la utilidad de los mismos, incluyendo cómo gestionar de la mejor manera los refugios, tanto individualmente como a nivel de sistema para ayudar a las especies a hacer frente a los cambios rápidos. Usando modelos publicados de distribución de especies, proyectamos cambios específicos en la aptitud ambiental de 590 especies de aves nativas de América del Norte bajo un escenario de calentamiento futuro de 2°C (~2050 bajo la trayectoria de concentración representativa 8.5) en 525 refugios. Para cada especie, clasificamos los cambios proyectados en la aptitud (es decir, mejora, estabilidad o empeoramiento de la aptitud) y evaluamos si cruzaron un umbral de persistencia derivado del modelo en un refugio (es decir, colonización potencial o extirpación potencial). En general, encontramos que una cuarta parte de las especies (23% en verano, 26% en invierno) podrían ser diferentes (i.e., recambio) a través de todo el sistema de refugios a pesar de las protecciones. Las comunidades de verano e invierno no se ven afectadas por igual, por lo que los gestores deben considerar diferentes estrategias para las diferentes estaciones. Pronosticamos una ligera pérdida neta de especies en verano, para una media de  $109,0 \pm 0,8$  a  $102,0 \pm 0,7$  especies por refugio. En invierno, pronosticamos una ganancia neta de especies, para una media de  $97,1 \pm 2,2$  a  $118,5 \pm 1,8$  especies por refugio. Esto incluye un promedio de 12 especies por refugio que pueden pasar allí el invierno en lugar de migrar hacia el sur. Los refugios en las latitudes del norte verán relativamente más recambio de especies, mientras que los refugios del sur y costeros verán menos cambios. A pesar de estos cambios de especies, los grupos de asociaciones de hábitat dominantes (e.g., aves acuáticas, aves del bosque) generalmente permanecerán iguales en la mayor parte del NWRS. Algunas especies pueden perderse de todo el NWRS y podrían beneficiarse a corto plazo de un manejo específico. Las regiones de alta extirpación y colonización (i.e., en latitudes del norte) podrían ser priorizadas mediante incorporaciones estratégicas de nuevos refugios.

**Palabras clave:** aves, cambio climático, manejo de áreas protegidas, modelos de distribución de especies, proyecciones, Sistema Nacional de Refugios de Vida Silvestre

## INTRODUCTION

In the face of anthropogenic global change, an urgent question is how climate change affects species in protected areas (Beale et al. 2013). Historically, birds are more abundant and have higher temporal stability inside protected areas compared to outside (Devictor et al. 2007, Wood et al. 2014, Pavón-Jordán et al. 2015, Dettling et al. 2021). Model projections suggest protected areas may maintain higher species richness than unprotected areas (Virkkala et al. 2014) and mitigate some effects of climate change for bird communities (Gaüzère et al. 2016, Wu et al. 2018). However, because some climate-driven community changes may be unavoidable even in protected areas (e.g., Velásquez-Tibatá et al. 2013), protected areas may need to adapt their management strategies to mitigate the effects of global environmental change. Changes in species community composition are likely even in protected areas as species shift their ranges in response to a changing climate (Stralberg et al. 2009, Prince and Zuckerberg 2015), and management strategies need to account for new and dynamic biological communities. Birds are an ideal taxon to study climate change effects, as their range limits are generally associated with climate (Root 1988, Thomas 2010), and globally birds have already responded to contemporary climate change through range shifts (Parmesan 2006, VanDerWal et al. 2013, Stephens et al. 2016).

Stewards of the National Wildlife Refuge System (NWRS), the largest protected areas system in the world, are uniquely positioned with an ecological mandate to maintain biological integrity and diversity (Griffith et al. 2009). The U.S. Fish and Wildlife Service (USFWS), along with other protected areas agencies, are considering how management of the refuge system may

evolve with a changing climate (U.S. Fish and Wildlife Service 2011, Magness et al. 2011). Species distribution modeling and projecting are tools that provide insights for decision-makers (Pidgorna 2007, Beale et al. 2013, Rushing et al. 2020). Whereas climate-based projections are not definitive predictions of future distributions (Engler et al. 2017, Sofaer et al. 2018), they help reduce uncertainties about potential future conditions and bird assemblages in the NWRS. Species forecasts add value to the suite of tools available to conservation planners and managers (Willis et al. 2015, Rushing et al. 2020), especially when used in conjunction with results from existing studies on climate vulnerability, extreme weather events, and changes in spring onset across the refuge (Magness et al. 2011; Martinuzzi et al. 2015, 2016; Waller et al. 2018).

Here, we use species distribution models incorporating climate and land-use variables at a 1-km scale for 590 bird species across North America (Bateman et al. 2020) to understand potential changes in avian communities across 525 refuges, providing both refuge-specific projections and system-wide patterns. As birds are a key management group for the NWRS, understanding how climate change may affect at-risk bird species and communities is imperative. We predict substantial changes in bird communities across the refuge by mid-century, despite their protected status. We expect variable rates of change across NWRS regions due to greater climate velocity at higher latitudes (Loarie et al. 2009, Wu et al. 2018). Results from this assessment can be used in a Resist-Adapt-Direct framework, a management tool that considers forward-looking strategies to respond to climate change within each unit based on local changes (Schuurman et al. 2020, Thompson et al. 2021).

## METHODS

### Study Area

We included all 525 USFWS National Wildlife Refuges (NWRs) that fell within the boundaries of the continental United States (U.S.) and Alaska (see data repository for full table of refuges analyzed), which comprised a total land area of 428,892 km<sup>2</sup>. Mean refuge area was 817 km<sup>2</sup>, ranging from <1 km<sup>2</sup> to 84,470 km<sup>2</sup> (median = 34.7 km<sup>2</sup>). The average elevation of the refuges we analyzed is 379 m, ranging from -70 m to 2,511 m (median = 147 m). Refuges are unevenly distributed across the U.S. (Scott et al. 2004) but represent all major land cover types. Across the continental U.S. and Alaska, the most dominant total land cover types at refuges are shrubland (40.2% total, 23.1% of the total being shrub/scrub and 17.1% being Alaskan dwarf scrub <20 cm), forest (17.4%), and wetlands (14.7%). When compared to land cover across the continental U.S. and Alaska (U.S. Geological Survey 2011), forests are underrepresented by 1.4 times at refuges while shrubland and wetlands are overrepresented by 2.7 and 1.6 times, respectively. Of the 525 refuges, 476 are categorized as National Wildlife Refuges, 40 as Wetland Management Districts or Waterfowl Production Areas, and 9 as Wildlife or Waterfowl Management Areas. The refuges span 24.5–68.6°N and 67.2–167.8°W and represent 11 USFWS geographic regions (Figure 1).

### Changes in Climate and Vegetation

We draw on previously published studies (Rehfeldt et al. 2012, Wang et al. 2016) that projected changes in climate and vegetation from 2010s to a 2°C mean rise in global temperatures scenario, translating to IPCC's (Intergovernmental Panel on Climate Change) high emissions trajectory (Representative Concentration Pathway; RCP8.5) for mid-century (2050s). While there is debate about which RCP most closely represents current global trajectories (Hausfather and Peters 2020), our assessment period is the 2050s, for which RCP8.5 and RCP4.5 are not very divergent (Hausfather and Peters 2020). We have also chosen RCP8.5 because it tracks cumulative CO<sub>2</sub> emissions to 2050, which is the time frame of our study, better than RCP4.5, due to taking into account biotic feedbacks in soil, permafrost, and other dynamics (Schwalm et al. 2020). We assessed changes in mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), mean annual precipitation (MAP), and climate moisture deficit (CMD) using locally downscaled climate data based on an ensemble of 15 general circulation models (GCMs; Wang et al. 2016, Wilsey et al. 2019). We calculated percent change in vegetation class from 2010s to mid-century from North American vegetation projections (an ensemble from 3 GCMs; Rehfeldt et al. 2012) for all grid cells within

each refuge. We overlaid refuge boundaries and calculated the projected changes within each refuge using mean for MWMT, MCMT, MAP; median for CMD; and change in dominant vegetation type.

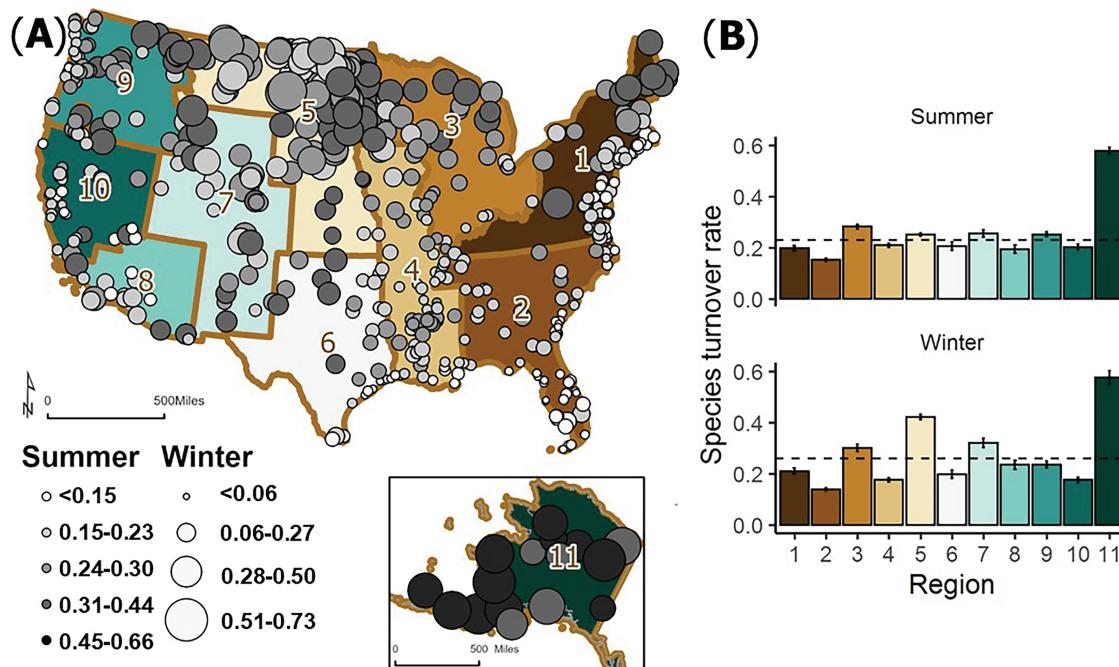
### Species Distribution Modeling

Our analysis uses previously published species distribution models (SDMs) of 604 North American birds at a continental scale across both summer and winter (Wilsey et al. 2019, Bateman et al. 2020). The modeling included 9 climate variables (e.g., Supplementary Material Figures S1 and S2), terrain ruggedness, natural vegetation projections (Supplementary Material Figure S3), and anthropogenic land cover projections. Species were placed into primary habitat affiliation groups (arctic, coastal, boreal forest, western forest, eastern forest, subtropical forest, generalist, grassland, aridland, marsh, waterbirds, and urban/suburban) and modeled with additional ecologically relevant covariates, such as surface water for waterbirds and marsh birds (Pekel et al. 2016), and distance to coast for coastal birds (Wessel and Smith 1996). Models were built with 2 algorithms, boosted regression trees (BRTs) and maximum entropy (Maxent, version 3.3.3k) in the *dismo* package in R (Version 3.6.1). The top-performing model was selected using median AUC (Wilsey et al. 2019, Bateman et al. 2020).

Previous work (Bateman et al. 2020) also classified each 1-km cell across North America as having either an improving, stable, or worsening trend in environmental suitability based on the percent change between the current to 2°C projections. A percent change of ≥25% was classified as improving, 25% to -25% classified as stable, and less than or equal to -25% as worsening. Additionally, grid cells that crossed a species-specific minimum threshold for occurrence (based on model performance and expert opinion; see Bateman et al. 2020) were classified as indicating potential extirpation or potential colonization.

### Species Change Metrics

In this analysis, we overlaid refuge boundaries with percent change surfaces and calculated the most frequent suitability trend (i.e., mode) for each 590 native bird species by 525 NWR combination. For 107 refuges that were 0.01–4.9 km<sup>2</sup> (median 1.4 km<sup>2</sup>) in size or that encompassed marine areas where we did not have projections (e.g., Oregon Islands National Wildlife Refuge), we first buffered the refuge by 2.5 km, an ecologically reasonable area for vagile birds to be using (Paradis et al. 1998, Sutherland et al. 2000), before summarizing suitability trends (see data repository for refuge buffer status). We considered all species in classes except "potential colonization" as present in the 2010s, and all species in classes except "potential extirpation" as present in the future. To account for model overprediction, we



**FIGURE 1.** (A) Projected Sørensen species turnover rates from the present to 2050s for each of the 525 refuges across the eleven Fish and Wildlife Service regions in 49 continental U.S. states. Alaska, the Midwest, and Rocky Mountain regions have the highest species turnover across seasons. Turnover rates are calculated under the assumption that all potential extirpations and colonizations are realized, with 0 being no change and 1 being complete turnover in bird assemblage. Circle colors represent turnover ranges in summer, and sizes represent ranges in winter. Alaska is shown in the inset map. (B) Mean and standard error of the mean of turnover index by FWS region. The dotted lines show the mean turnover index across regions in both summer (mean  $\pm$  SE =  $0.23 \pm 0.004$ ) and winter ( $0.26 \pm 0.006$ ). Analysis of variance indicated significant differences among regions in summer ( $F_{1,523} = 66.23, P < 0.001$ ) and winter ( $F_{1,523} = 27.97, P < 0.001$ ).

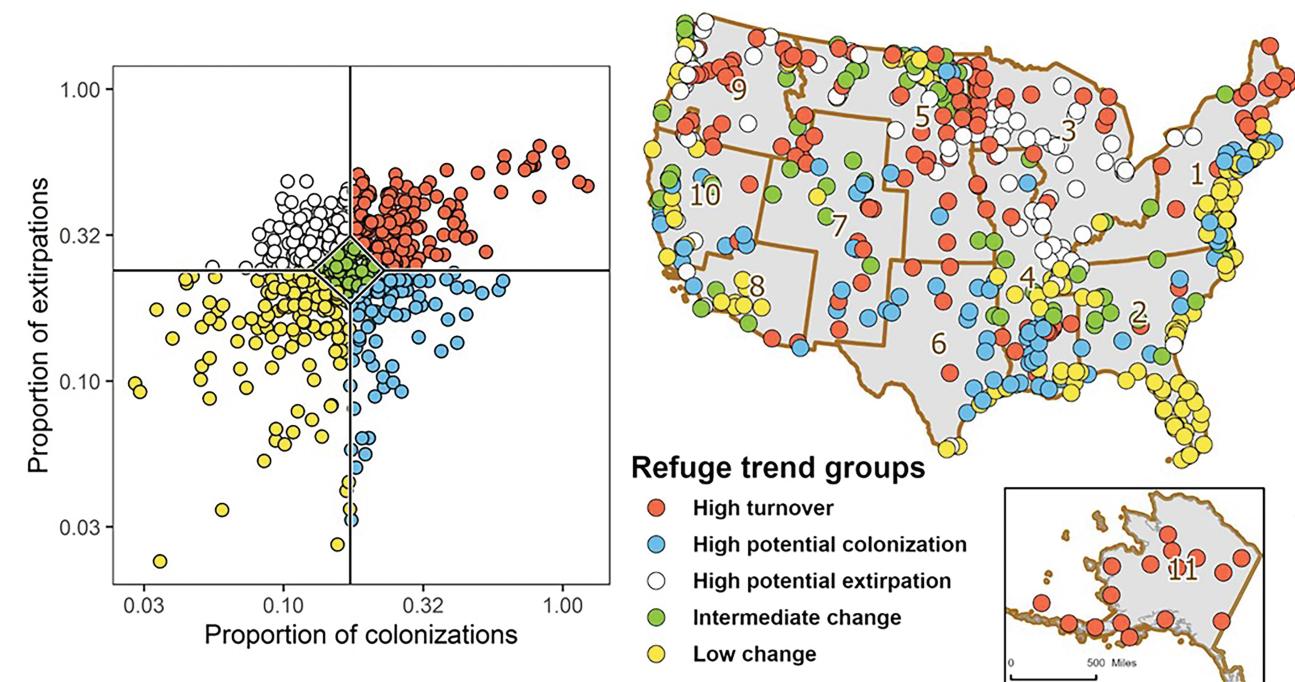
filtered the 2010s species lists at each refuge by our database of 58+ million bird observations (see Bateman et al. [2020] for data sources) currently found in that refuge or the county, parish, or borough that refuge is in (total species \* season \* refuge = 156,183; median = 146 species per refuge per season), so that species not observed in the vicinity of a refuge were excluded from the 2010s list. For each refuge, we tabulated the number of species experiencing substantial changes in climate suitability (i.e., not having a “stable” projection under the 2°C warming scenario) as well as percent of current species projected to colonize or become extirpated at a refuge. Results are reported primarily for the 2°C mean rise in global temperature scenario and compared to additional warming scenarios (~1.5°C, or RCP4.5 by 2050s, and ~3.0°C, or RCP8.5 by 2080s).

We also calculated the rate of projected species loss and turnover between mid-century and the 2010s using the Sørensen turnover index in the *vegan* R package (Version 2.5–6). We chose the Sørensen index because it provides a standardized measure of beta diversity that accounts for both extirpation (i.e., nested species loss) and colonization (i.e., change in species composition), and thus serves as a summary metric evaluating the impact of these two distinct processes on community composition (Baselga 2010). We

summarized potential overwintering additions (i.e., species that currently migrate for winter but may find conditions suitable to stay year-round) by identifying species that are present at a refuge in summer but not winter and matching those with potential colonizers in winter at that same refuge. We also looked for species that may no longer be supported by the NWRS, defined as species projected to be present in 5 or fewer refuges in either season after Pidgorna (2007).

### Vulnerability of Refuge Species to Climate Change

Each species at a refuge in the present or future was assigned a range-wide vulnerability classification derived from range gains and losses from the species distribution models (Wilsey et al. 2019, Bateman et al. 2020). Vulnerability is based on a combination of a species’ sensitivity (determined by projected range loss) and adaptive capacity (defined as ratio of range gain to range loss). With this approach, species that experience greater proportional range loss without making up for it in range gain are considered climate-vulnerable. Species that have more potential for range gain are considered not vulnerable (for details, see Wilsey et al. 2019). Within each refuge, we tabulated species by their vulnerability status and summarized counts across regions. To compare rates of vulnerability across seasons, we used



**FIGURE 2.** Classification of refuges into trend groups based on the proportion of potential colonizations and extirpations shows highest overall turnover in Alaska and northern refuges, and lower turnover at coastal refuges. Each circle represents a refuge in 49 continental U.S. states. The x-axis of the plot represents the proportion of trends at each refuge that are potential colonizations, and the y-axis represents the proportion of potential extirpations; a logarithmic scale is used for both axes. Solid vertical and horizontal lines mark the median proportion of colonizations and extirpations across refuges under the high-emissions trajectory in summer, used to classify refuges into all trend groups except intermediate change. The boundaries of the intermediate change group, represented by the diamond in the center of the plot, are delimited by the upper and lower quartiles of each axis.

the Shapiro-Wilk test to test the assumption of normally distributed data, and then used a 2-sample *t*-test.

### System-Wide Summaries

On a regional scale, we tallied the total area each habitat affiliation group occupies across the NWRs in each region in the present and future to assess potential regional changes in species groups. To assess latitudinal effects across refuges, we used beta regression to analyze rates of colonization, extirpation, and species turnover within each refuge and season as a nonlinear function of latitude with both linear and quadratic forms of latitude. We separated the Alaskan refuges from the latitudinal trend analysis because of the gap in latitude between the contiguous U.S. and Alaska, as well as the smaller number of refuges in Alaska.

Lastly, we classified refuges into management strategy groups based on their proportions of potential colonizations and extirpations forecasted by mid-century (Hole et al. 2011). We used summer rates to match the species' overall geographic distribution to the U.S. jurisdiction of the NWRS. Refuges were grouped into one of 5 classes: high turnover, high potential colonization, high potential extirpation, intermediate change (for refuges within a quartile of the median of both axes), and low change, based on

quartiles along the axes representing colonization and extirpation to inform management of the system as a whole (Wu et al. 2018, Gahbauer et al. 2022; Figure 2). We conducted all analyses in R 4.0.2. We treated individual refuges as sampling units and aggregated outputs to the system-wide level. Mean  $\pm$  standard error (SE) are reported in results.

## RESULTS

### Changes in Climate and Vegetation

Under a 2°C global warming scenario, local mean temperatures are expected to increase by 1.7–5.1°C during the warmest month and by 0.7–13.7°C during the coldest month across refuges (Supplementary Material Figure S1). Changes in mean annual precipitation range from –209 to +537 mm across refuges in the conterminous U.S. and from –48 to +2,148 mm across refuges in Alaska (Supplementary Material Figure S2). Despite some increases in precipitation, available moisture across all refuges is projected to decrease due to increases in evapotranspiration. Vegetation class will generally not change across most of the Eastern U.S. and Great Plains, but change is expected across the Intermountain West, Southwest, and Alaska (Supplementary Material Figure S3).

**TABLE 1.** Mean projected number of species ( $n$ ) (mean  $\pm$  SE) and ratio of potential future (under a 2°C warming scenario, or ~2050s under RCP8.5) to present number of species, by region and season. Regions differ in their current and future average number of species, but 9/11 are expected to see a net loss in summer and 10/11 a net gain of species in winter.

Region (no. of refuges)	Summer			Winter		
	Present	2°C future	Ratio future to present	Present	2°C future	Ratio future to present
1. North Atlantic-Appalachian (71)	116.3 $\pm$ 0.1	114.1 $\pm$ 0.2	0.98:1	108.5 $\pm$ 0.4	131.8 $\pm$ 0.3	1.21:1
2. South Atlantic-Gulf (70)	97.8 $\pm$ 0.1	92.2 $\pm$ 0.1	0.94:1	139.8 $\pm$ 0.5	150.2 $\pm$ 0.4	1.07:1
3. Great Lakes (57)	119.6 $\pm$ 0.3	97.0 $\pm$ 0.2	0.81:1	63.4 $\pm$ 0.4	88.9 $\pm$ 0.4	1.40:1
4. Mississippi Basin (58)	86.6 $\pm$ 0.2	84.9 $\pm$ 0.1	0.98:1	104.0 $\pm$ 0.5	126.5 $\pm$ 0.5	1.22:1
5. Missouri Basin (91)	109.1 $\pm$ 0.2	98.1 $\pm$ 0.2	0.90:1	37.5 $\pm$ 0.2	64.5 $\pm$ 0.2	1.72:1
6. Arkansas-Rio Grande-Texas-Gulf (30)	90.1 $\pm$ 0.5	97.1 $\pm$ 0.4	1.08:1	131.1 $\pm$ 1.6	154.8 $\pm$ 1.2	1.18:1
7. Upper Colorado Basin (27)	111.0 $\pm$ 0.5	110.0 $\pm$ 0.5	0.99:1	75.5 $\pm$ 1.1	101.6 $\pm$ 0.8	1.35:1
8. Lower Colorado Basin (16)	125.4 $\pm$ 0.7	117.1 $\pm$ 0.5	0.93:1	171.4 $\pm$ 1.2	160.1 $\pm$ 0.9	0.93:1
9. Columbia-Pacific Northwest (47)	124.1 $\pm$ 0.3	106.5 $\pm$ 0.3	0.86:1	113.6 $\pm$ 0.6	141.0 $\pm$ 0.6	1.24:1
10. California-Great Basin (42)	121.6 $\pm$ 0.5	114.4 $\pm$ 0.4	0.94:1	140.4 $\pm$ 0.9	145.6 $\pm$ 0.7	1.04:1
11. Alaska (16)	105.6 $\pm$ 1.3	128.3 $\pm$ 1.1	1.22:1	28.8 $\pm$ 1.1	85.5 $\pm$ 2.8	2.97:1

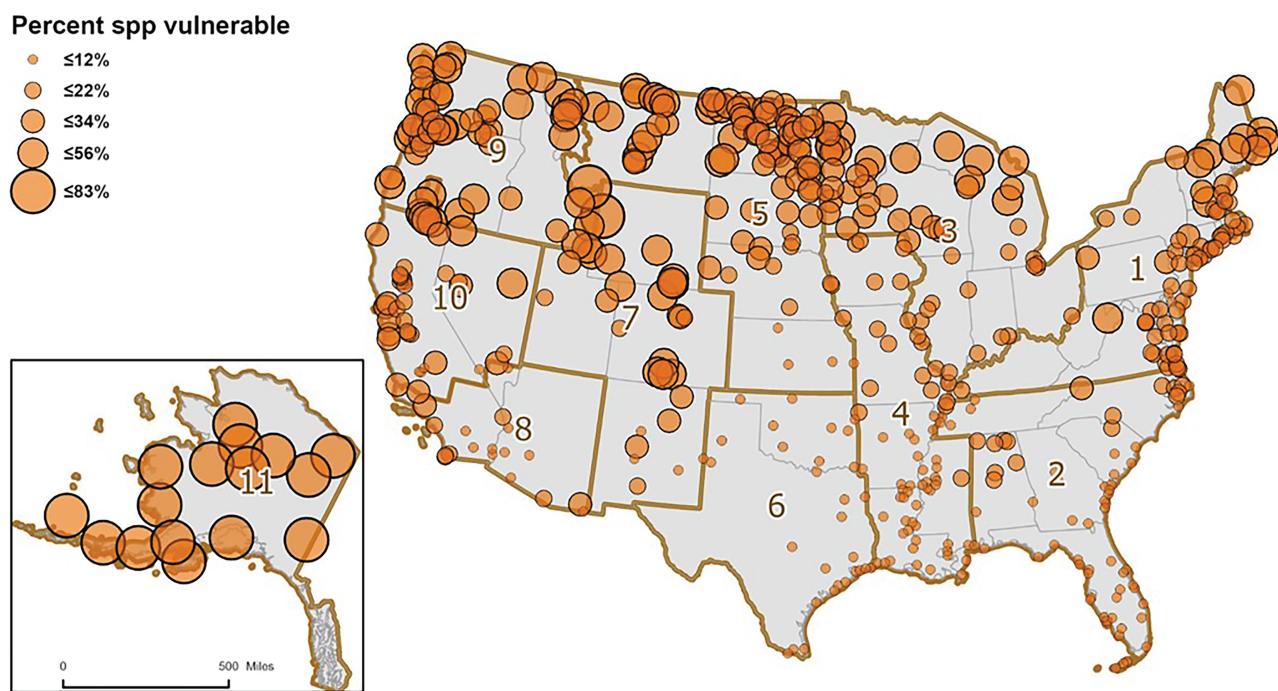
**TABLE 2.** Nineteen species across the taxonomy that may be near-extirpated (i.e., be present at 5 or fewer refuges in 1 or more season) from the National Wildlife Refuge System under a 2°C future. Numbers shown are the number of refuges projected to host the following species presently and under a 2°C future (~2050s under RCP8.5).

Species	Summer		Winter	
	Present	2°C future	Present	2°C future
Emperor Goose ( <i>Anser canagicus</i> )	5	0	–	–
Tundra Swan ( <i>Cygnus columbianus</i> )	5	0	–	–
Rock Ptarmigan ( <i>Lagopus muta</i> )	16	1	16	2
Willow Ptarmigan ( <i>Lagopus lagopus</i> )	16	11	16	3
Dusky Grouse ( <i>Dendragapus obscurus</i> )	18	2	18	2
Snail Kite ( <i>Rostrhamus sociabilis</i> )	10	0	5	17
Rufous Hummingbird ( <i>Selasphorus rufus</i> )	32	2	19	24
Clark's Nutcracker ( <i>Nucifraga columbiana</i> )	37	8	36	3
Yellow-billed Magpie ( <i>Pica nuttalli</i> )	17	3	18	2
Black-throated Blue Warbler ( <i>Setophaga caerulescens</i> )	18	0	–	–
Black-throated Green Warbler ( <i>S. virens</i> )	37	3	5	9
Blackburnian Warbler ( <i>S. fusca</i> )	32	0	–	–
Thick-billed Longspur ( <i>Rhynchophanes mccownii</i> )	19	0	8	13
Baird's Sparrow ( <i>Centronyx bairdii</i> )	53	0	–	–
Clay-colored Sparrow ( <i>Spizella pallida</i> )	100	0	5	25
Nelson's Sparrow ( <i>Ammospiza nelsoni</i> )	51	0	24	24
Black Rosy-Finch ( <i>Leucosticte atrata</i> )	1	0	16	1
Brown-capped Rosy-Finch ( <i>L. australis</i> )	1	0	5	0
Gray-crowned Rosy-Finch ( <i>L. tephrocotis</i> )	13	1	41	4

### Species Change Metrics

Fifty-two percent of all bird species assessed within the NWRS in summer and 48% of birds in winter may experience positive or negative change in environmental suitability under the 2°C warming scenario. More species have positive projections (improving suitability or potential colonization) in winter (33% of species across refuges) than summer (23%), and conversely, more species have negative projections (worsening suitability or potential extirpation) in summer (29%) than in winter (15%). Fewer species face changing suitability under 1.5°C of warming (35% of birds in summer, 30% of birds in winter) while more do under 3°C of warming (64% of birds in summer, 61% of birds in winter).

Large changes in environmental suitability may lead to changes in species composition within refuges. Overall, refuges are projected to see more species in winter, but slightly fewer species in summer. Mean species turnover by mid-century is  $23 \pm 0.4\%$  in summer (range: 3–66%), and  $26 \pm 0.6\%$  in winter (range: 6–72%; [Figure 1](#)), meaning that ~23% and ~26% of the species composition in summer and winter, respectively, may be different from today across the NWRS. On average, refuges currently support  $109.0 \pm 0.8$  species in summer, which is projected to decrease to  $102.0 \pm 0.7$  species under the 2°C scenario. In winter, refuges currently support  $97.1 \pm 2.2$  species, which is projected to increase to  $118.5 \pm 1.8$  species. The ratio of



**FIGURE 3.** Maximum (across seasons) percent of a refuge's current species that are climate vulnerable, meaning they stand to lose more of their range across North America than they are likely to gain back. Refuges towards the northern latitudes of the U.S., coastal regions, and in Alaska, have higher percentages of species that are highly climate vulnerable. In 523 of 525 refuges analyzed, the percent of species vulnerable is higher in summer than in winter.

current to future species richness is 1:0.94 in summer and 1:1.22 in winter and differs by region (Table 1).

Some species that are currently at refuges only in summer may stay to overwinter as winter conditions become suitable. An average of 12 species per refuge (11% of the average number of current summer species) may stay to overwinter across the 525 refuges, ranging from no overwintering additions at 7 refuges to 55 potential overwintering additions at Alaska Maritime National Wildlife Refuge. The birds that may shift from summer only to year-round residents at the largest number of refuges include Wood Duck (*Aix sponsa*; 149 refuges), American Kestrel (*Falco sparverius*; 124 refuges), Mourning Dove (*Zenaida macroura*; 113 refuges), Cedar Waxwing (*Bombycilla cedrorum*; 106 refuges), Black-crowned Night-Heron (*Nycticorax nycticorax*; 104 refuges), and Brewer's Blackbird (*Euphagus cyanocephalus*; 104 refuges). On the other hand, with a mean potential extirpation rate of  $20 \pm 0.5\%$  across seasons (range: 1–64%; Supplementary Material Figure S4), some species may be found in fewer than 5 refuges by the 2050s. High elevation or high latitude species such as Tundra Swan (*Cygnus columbianus*), Emperor Goose (*Anser canagicus*), Clark's Nutcracker (*Nucifraga columbiana*), and the rosy-finches (*Leucosticte sp.*) are particularly prone to climate-related losses (Table 2).

#### Vulnerability of Refuge Species to Climate Change

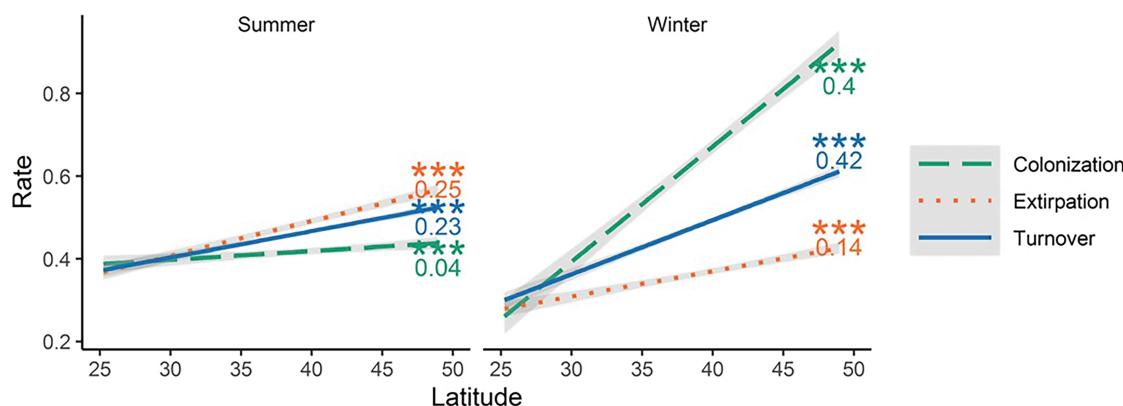
Refuges support many species that have moderate to high range-wide vulnerability to climate change, particularly

among waterbirds and forest birds (Supplementary Material Figure S5). A significantly higher percentage of species at refuges in summer ( $27 \pm 0.7\%$ ) were vulnerable ( $P < 0.001$ ,  $t = 26.25$ ) than in winter ( $7 \pm 0.3\%$ ). All but 2 refuges have a higher percentage of species vulnerable in summer than in winter. A maximum of 83% of a refuge's current number of species are climate-vulnerable (Figure 3; mean  $23 \pm 0.7\%$ ). Despite lower overall vulnerability in winter, western forest species are the most vulnerable group, with 44% of species analyzed in winter being climate-vulnerable (Supplementary Material Figure S5).

#### System-Wide Changes

The primary vegetation association group is projected to stay the same between the 2010s and 2050s in most regions. There is one notable exception: in summer, the dominant group across region 11 (Alaska) refuges is currently waterbirds, but by mid-century boreal forest species are projected to become the most dominant group.

Rates of change, species colonization, extirpation, and turnover in overall assemblage are all projected to be greater at the higher latitudes (Figure 4 and Supplementary Material Figure S4). The quadratic relationship in latitude was not significant (i.e., rates of change were linearly related to latitude), so we present linear results. Alaska is a clear outlier in regional analyses, with high percentages of climate-vulnerable



**FIGURE 4.** Colonization, extirpation, and turnover rates and their relationship to latitude at 509 refuges in the lower 48 U.S. states. Alaskan refuges were not plotted due to the gap in latitude. Asterisks (\*\*\* indicates  $P \leq 0.001$  in the beta regression, and numbers represent pseudo  $R^2$ . Shading indicates the 95% confidence interval of the fit of a linear model, which we show for visualization only.

species (Figure 3) and high rates of species turnover in both seasons (Figure 1). Alaska is projected to see nearly 60% change in its species composition in both seasons (Figure 1B).

There were 103 refuges grouped in the high potential colonization class, 107 refuges in the high potential extirpation class, 117 refuges in the high turnover class, 81 refuges in the intermediate change class, and 117 refuges in the low change class (Figure 2). Many refuges with high potential colonization are in the South or along coasts (Regions 1, 4, 6, 10), while many refuges facing high potential extirpation are scattered across the Midwest and West (Regions 3, 4, 5, 9, 10). All Alaskan refuges (Region 11) fell into the high turnover category, along with some refuges in the Midwest, Northeast, and Northwest (Regions 1, 3, 5, and 9). Refuges with low or intermediate change were dispersed across the coasts, in the Central Plains, and Southeast (Regions 1, 2, 4, 8, 10; Figure 2).

## DISCUSSION

### Substantial Changes for the NWRS Under Climate Change

The NWRS faces substantial changes; on average, approximately a quarter (23% in summer, 26% in winter) of bird species across the entire Natural Wildlife Refuge System may be different by 2050 due to potential range shifts caused by climate change. Because of the rapid nature and magnitude of climate change, it would benefit the NWRS to continue adoption of the Resist-Adapt-Direct (Schuurman et al. 2020, Thompson et al. 2021, Williams 2022) framework in planning, some of which we discuss below. Our projected species turnover rates over the next half century are comparable to turnover rates found in historic climate change studies in the western

United States (median = 35%, Tingley and Beissinger 2013; mean = 4–14%, Karanth et al. 2013). There is a clear seasonal difference in our projected changes; refuges are likely to host many more species in winter in the coming decades and may lose species in summer. Similarly, studies of continent-wide population trends have also noted greater declines in summer than in winter: Breeding Bird Survey data across the U.S. show 57% of species declined from 1966–2015 (Sauer et al. 2017), while Christmas Bird Count data show 68% of species had increasing trends during the same period (Soykan et al. 2016). Whereas these contemporary studies examined changes in abundance rather than suitability, the abundant niche-centroid relationship proposes a positive relationship between these two measures (Osorio-Olvera et al. 2020). As winters become milder, we predict continued increases in winter abundance and an overall northward expansion in range. Birds have been reducing migration distances between their breeding and overwintering ranges (Visser et al. 2009, Pulido and Berthold 2010), and our study projects an average of 12 species per refuge may be from species overwintering rather than migrating south by mid-century. Our results corroborate past findings that broad-scale community-level changes are expected across North America (LaSorte and Frank III 2007, Stralberg et al. 2009, Prince and Zuckerberg 2015). New species will interact, especially in winter, when species are less site-faithful and show greater community changes (Lehikoinen et al. 2021).

Refuges will likely have separate trajectories in summer vs. winter and seasonal communities should be managed accordingly when possible. For example, a coastal stewardship program may be adapted to benefit a newly arrived breeding shorebird, while changes to water management in an impoundment may be necessary if waterfowl overwinter where they used to migrate through (Isola et al. 2000, Michel et al. 2021). Depending on the management goal of individual refuges or regions, refuges can either

prioritize actions that would aid individual species facing the most climate threats (such as those in [Supplementary Material Table S1](#)) or focus on actions that save the most species. The refuge system may serve as a refugia for the 27% of climate-vulnerable species (defined in [Bateman et al. 2020](#)) projected to remain within the NWRS. These species will likely lose more range area than they are able to gain across North America, and when looking across the system, we can identify which refuges may continue to host such at-risk species, such as Rock Ptarmigan (*Lagopus muta*) or Emperor Goose (*Anser canagicus*). Notably, all arctic species analyzed are vulnerable to climate change in summer and will almost certainly face climate-related challenges ([Bateman et al. 2020](#)).

### Regional Patterns

Projections across the NWRS are heterogeneous. Regions anticipating lower change (southeastern and coastal regions; e.g., Regions 1, 2, 4, 6, 8, 10) can continue to maintain habitat conditions to support the current-day bird community ([Magness et al. 2011](#), [Hansen et al. 2014](#), [Fisichelli et al. 2016](#)). Regions anticipating high potential change (e.g., high potential colonization, high potential extirpation, or high turnover) can focus on adapting to accommodate both species gains and losses. Refuges in the Midwest (Regions 3 and 5), mountainous West (Region 7), and especially Alaska (Region 11) may see particularly high rates of bird species turnover (up to 60%) in both seasons ([Figure 1](#)). This pattern warrants concern, as climate change velocity is higher towards the northern latitudes in the northern hemisphere ([Loarie et al. 2009](#), [Dobrowski and Parks 2016](#), [Waller et al. 2018](#)). Coupled with geographic constraints on poleward and upslope range shifts, northern species are particularly prone to negative impacts of climate change and consequently deserve more attention to mitigate potential harm.

Alaskan protected areas, including refuges, will be more important for birds in the coming decades as more species colonize ([Wu et al. 2018](#)). Although the primary vegetation association groups are projected to remain the same across most NWRS regions, the primary group in Alaska is projected to change from waterbirds to boreal forest birds. This could be indicative of a large-scale ecological change as boreal forest species expand northward, potentially into northern Alaska refuges. This fits with studies reporting drying wetlands ([Yoshikawa and Hinzman 2003](#), [Klein et al. 2005](#)) and a decrease in lake size and waterfowl species richness at Yukon Flats NWR ([Roach and Griffith 2015](#)). However, another study found no change in waterfowl response in relation to shrinking lake area between 1985–1989 and 2010–2012, which suggests some resilience at the higher trophic levels compared to invertebrates ([Lewis et al. 2016](#)). Nonetheless, anticipated changes in Alaska bring into consideration management options like

resisting a transition to a grass-dominated system and accelerating the dispersal of trees that match emerging climate conditions ([Magness et al. 2022](#)).

### The Role of Protected Areas and Strategic Additions

Protected areas have an important role to play in supporting species and dynamic ecosystems as global change continues. We found some refuges will continue to support vulnerable species under climate change. However, elsewhere species may be lost in the coming decades, and mitigation actions and/or strategic additions of protected areas may be needed. The NWRS is only one piece of the larger protected area network in North America that is collectively important for wildlife conservation ([Martinuzzi et al. 2015](#)), though of course not all-encompassing in safeguarding species' existence. However, in light of rapidly changing environmental conditions, solely relying on existing protected areas to conserve birds may not be enough, in part due to the fragmented nature of protected landscapes. Government entities should work with landowners, Indigenous communities, and other groups for collaborative conservation ([Monzón et al. 2011](#)).

Our outputs can also help identify preferred locations to expand the refuge system ([Liang et al. 2018](#)). Regional offices might look at which species are in the greatest peril both currently and due to future climate threats and consider strategies to mitigate losses, which may potentially drive choices with regard to land acquisition. Many studies point to the importance of connecting protected areas of various jurisdictions to retain climate conditions and allow movement and gene flow ([Soulé and Terborgh 1999](#), [Hoffmann and Sgrò 2011](#), [Mazaris et al. 2013](#)). In addition, the effectiveness of protected areas is related to adjacent land use activities ([Svancara et al. 2009](#)). Housing development is often high in areas adjacent to National Wildlife Refuges ([Svancara et al. 2009](#), [Hamilton et al. 2016](#)), limiting habitat connectivity around these protected areas and negatively affecting bird diversity within protected areas ([Wood et al. 2014](#)). Forward-looking management should work with private landowners and other entities to prioritize landscape connectivity to allow species to respond to changing conditions.

### Planning for a Future of Change and the Resist-Adapt-Direct Framework

This study provides information that can be useful for planning during a period of rapidly changing environmental conditions in a Resist-Adapt-Direct framework ([Schuurman et al. 2020](#), [Thompson et al. 2021](#)). Region- and refuge-specific results can help the NWRS identify where to preserve current conditions and resist change, promote adaptation ([Willis et al. 2015](#)), or direct change to a new state. Grouping refuges into management classes relative to each other can help managers prioritize different strategies for handling change throughout the system.

Refuges that fall in the low and intermediate change groups, which are mostly in the Southeast and along coasts, can best support landscape-scale bird conservation by *resisting* change and taking actions that support the current bird community (e.g., maintaining current conditions, reducing introduced stressors, and restoring natural habitats). For the 327 refuges that fell into one of the high change groups (high turnover, high potential colonization, or high potential extirpation), which are mostly interior and northern refuges, managers and conservation planners should focus on actions that increase species' ability to *adapt* to environmental changes. These may include working with cooperating agencies and landowners to facilitate movement of various species across boundaries, reducing harmful impacts of the changing disturbance regime (e.g., fire, flooding), and possibly incorporating more intensive management actions on a species-specific basis as needed (e.g., nest site management, translocations). A management strategy applicable to all classes is establishing a range of environmental conditions in protected areas that best retains future habitat for a variety of species—*directing* change—for example; a mosaic of forest, wetland, and other habitats (Sekercioglu 2012). In drought-prone areas, for example, adaptation efforts could include maintaining or improving riparian habitat to provide species with continued access to food and water (Martinuzzi et al. 2016).

These results can also help identify which species of concern may be most threatened by climate change and thus appropriately direct conservation efforts. For example, the Clay-colored Sparrow (*Spizella pallida*) population declined by 57% across North America between 1966 and 2019 (Rosenberg et al. 2019), is a key management species facing extirpation across much of the NWRS and is vulnerable to the effects of climate change (Bateman et al. 2020). Though its biggest threat is the loss of tallgrass prairie on breeding grounds, crop set-aside incentives such as the Conservation Ranching Program and the Posted County Price program have increased Clay-colored Sparrow numbers since 1985 (Grant and Knapton 2020). Another at-risk species is the Nelson's Sparrow (*Ammospiza nelsoni*), which is climate-vulnerable in both seasons, faces worsening suitability across the NWRS, and thus may warrant particular attention. The Nelson's Sparrow is threatened by drainage and development of coastal wetlands in its wintering range (Shriver et al. 2020), which may require a conservation approach of resisting these alterations, directing habitat states back to coastal marsh in the immediate future, and supporting marsh migration as sea level rises. Overlaying climate projections with other metrics can help prioritize species of concern and potential strategies for focusing limited resources (Griffith et al. 2009).

### Caveats

As all projections are uncertain, it is important to ground them in local knowledge for conservation planning (Villero et al. 2017). Whereas the SDMs used in this analysis provide

a forecast of what may happen under climate change, they are not definitive predictions of species ranges, so should not be taken as guaranteed outcomes. Additionally, significant changes in suitability, as measured here, will not always result in a species response. Multiple other factors mediate responses to climate change, including habitat availability, ecological processes that affect demography, biotic interactions that inhibit and facilitate species' colonization or extirpation, and phenotypic plasticity (e.g., behavioral adjustments). Our climate vulnerability assessments incorporated species-specific natal dispersal abilities, though dispersal estimates are not perfect reflections of whether species can track climate conditions (Nadeau and Fuller 2016). Importantly, our SDMs assume no evolutionary adaptation (Willis et al. 2015). Future changes are difficult to predict with accuracy in complex, interrelated ecological systems, and climate change is likely to catalyze other environmental stressors, such as species invasion, habitat loss, water quality degradation (Griffith et al. 2009), and many other factors that affect bird survival but that our models cannot account for. Despite these limitations, predictive modeling does have utility for priority-setting and targeting species and habitat management (Willis et al. 2015). General trends are still indicative of potential changes, and outputs can be used to guide preemptive conservation in the face of climate change.

We remind readers that we focused only on distribution, or presence of species, rather than abundance. Consequently, projected extirpations from refuges are losses of a species rather than declines in the population of a species, though these outcomes may be related (Ralston et al. 2016; Osorio-Olvera et al. 2020; however, see Pironon et al. 2015). Future studies can examine and incorporate bird abundances in predictive modeling (e.g., Cadieux et al. 2020). Our study also treated each NWR as a separate unit of analysis when they varied in size and thus in their environmental variability and ability to enable species persistence. Finally, the NWRS is only one of many protected areas networks worldwide. Our analysis is limited to 525 National Wildlife Refuges in the U.S. and misses projections for other protected areas, such as Canadian National Parks, Indigenous Protected Areas, Provincial Parks, Migratory Bird Sanctuaries, U.S. National Forests, U.S. National Parks, state parks, and more. For a more complete picture of how birds may persist in protected areas, additional analyses including other protected areas should be conducted.

### Conclusions

Our study provides predictions that can help NWRS managers respond to changing environmental conditions through their stewardship practices, land acquisitions, partnership development, and policy changes (Nichols et al. 2011, Magness et al. 2011). Safeguarding the existing

conservation investment represented by the refuge system requires urgent action and a forward-looking approach to natural resource management that explicitly recognizes the prospect of climate-driven ecological change beyond historical ranges of variability. Effective conservation as climate change advances will require landscape-level thinking, including working with other protected areas and landowners to encourage connectivity and allow for species movement to more suitable environmental conditions. Managers, using such thinking, can apply various approaches—resist, adapt, or direct ecological change toward specific new desired conditions (Thompson et al. 2021)—to allow species to persist at current locations or move to more suitable environments. Monitoring to identify changes in bird assemblages in relation to their habitats (e.g., Saunders et al. 2020) will inform the adequacy of treatment and future selection of appropriate management responses.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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**Author contributions:** B.L.B., P.J.H., and C.B.W. conceived the research. J.X.W., L.T., and H.W. performed the analyses. J.X.W., B.L.B., L.T., and P.J.H. wrote or substantially edited the paper. J.X.W., L.T., and B.L.B. developed the methodology. P.J.H., A.J.A., D.G., N.L.M. contributed to data or advised on methodology, analysis, and interpretation.

**Data availability:** Analyses reported in this article can be reproduced using the data provided by Wu et al. (2022). All scripts and links to previously published datasets used in this paper are also provided at <https://github.com/audubongit/ClimateChangeBirdsFWS>. For projections of species-specific trends within each refuge, please see individual refuge briefs at <https://www.audubon.org/news/climate-change-management-briefs-525-national-wildlife-refuges>.

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