

RESEARCH ARTICLE

Projected changes in bird assemblages due to climate change in a Canadian system of protected areas

Marcel A. Gahbauer¹*, Scott R. Parker²*, Joanna X. Wu³, Cavan Harpur², Brooke L. Bateman³, Darroch M. Whitaker⁴, Douglas P. Tate⁵, Lotem Taylor³, Denis Lepage⁶

1 Canadian Wildlife Service, Environment and Climate Change Canada, Ottawa, Ontario, Canada, **2** Parks Canada, Tobermory, Ontario, Canada, **3** National Audubon Society, New York City, New York, United States of America, **4** Parks Canada, Rocky Harbour, Newfoundland and Labrador, Canada, **5** Parks Canada, Nipigon, Ontario, Canada, **6** Birds Canada, Port Rowan, Ontario, Canada

* These authors contributed equally to this work.

* Marcel.Gahbauer@ec.gc.ca (MAG); Scott.Parker@canada.ca (SRP)



OPEN ACCESS

Citation: Gahbauer MA, Parker SR, Wu JX, Harpur C, Bateman BL, Whitaker DM, et al. (2022) Projected changes in bird assemblages due to climate change in a Canadian system of protected areas. *PLoS ONE* 17(1): e0262116. <https://doi.org/10.1371/journal.pone.0262116>

Editor: Angela Marie White, USDA Forest Service, UNITED STATES

Received: August 13, 2021

Accepted: December 17, 2021

Published: January 21, 2022

Copyright: © 2022 Gahbauer et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the manuscript and its [Supporting Information](#) files.

Funding: Parks Canada provided funding to the National Audubon Society to model future bird distributions for each park. No specific funding was provided to any of the authors or organizations for the functional analyses, data verification or preparation of the manuscript. The views and conclusions contained in this document are those of the authors and should not be interpreted as

Abstract

National parks often serve as a cornerstone for a country's species and ecosystem conservation efforts. However, despite the protection these sites afford, climate change is expected to drive a substantial change in their bird assemblages. We used species distribution models to predict the change in environmental suitability (i.e., how well environmental conditions explain the presence of a species) of 49 Canadian national parks during summer and winter for 434 bird species under a 2°C warming scenario, anticipated to occur in Canada around the mid-21st century. We compared these to existing species distributions in the 2010s, and classified suitability projections for each species at each park as potential extirpation, worsening, stable, improving, or potential colonisation. Across all parks, and both seasons, 70% of the projections indicate change, including a 25% turnover in summer assemblages and 30% turnover in winter assemblages. The majority of parks are projected to have increases in species richness and functional traits in winter, compared to a mix of increases and decreases in both in summer. However, some changes are expected to vary by region, such as Arctic region parks being likely to experience the most potential colonisation, while some of the Mixedwood Plains and Atlantic Maritime region parks may experience the greatest turnover and potential extirpation in summer if management actions are not taken to mitigate some of these losses. Although uncertainty exists around the precise rate and impacts of climate change, our results indicate that conservation practices that assume stationarity of environmental conditions will become untenable. We propose general guidance to help managers adapt their conservation actions to consider the potentially substantive changes in bird assemblages that are projected, including managing for persistence and change.

representing the opinions or policies of the Government of Canada.

Competing interests: The authors have declared that no competing interests exist.

Introduction

The on-going and projected impacts of climate change to the survival and distribution of biodiversity is global in scale [1–3] and is even felt within protected areas that have been established to safeguard and conserve species [4–8]. Climate change creates an increasingly complex and uncertain context for protected areas, one which may render unachievable traditional conservation goals, such as maintaining current or historic assemblages of species [9–12]. Indeed, because protected areas are often established in extreme or atypical landscapes (e.g., high latitudes, high elevations, coastal areas, or arid regions) they may be disproportionately affected by climate change [6]. However, the challenges associated with biodiversity conservation would be even greater without protected areas [13–15], and managers of such sites must therefore have access to information on how to adapt effectively in this period of rapid environmental change.

Since 1948, when nation-wide records have been available, Canada has experienced an increase in mean annual temperature and a general increase in total annual precipitation, and these changes are expected to continue or even accelerate because of climate change [16]. These changes have triggered habitat alteration through shifts in factors such as snow and ice cover, wildfire regimes, sea level, hydrology, vegetation composition and structure, and growing season phenology [17–19], all of which influence the distribution and extent of suitable environmental conditions for species. While each species has a preferred range of climatic suitability, responses to changing conditions may vary [20–23]. Some species may be unaffected or find a means to adapt to local conditions, such as by advancing the timing of nesting [24], while others are more sensitive and less adaptable and will need to either shift their range or face extirpation or extinction [25, 26].

There has already been a substantial decline in North American bird populations over the past half-century, with concern that ongoing and future threats will result in further losses [27]. To examine climate-induced changes in bird populations, near-future suitability projections can be used [28], and have already been shown to estimate contemporary species distribution shifts [29]. Projecting potential changes in bird assemblages in an area can reduce future uncertainty and inform more effective conservation actions.

As climatic conditions change and bird assemblages are modified, there will also be shifts in functional traits [30, 31] of the assemblage that reflect the ecological roles of species (e.g., seed dispersal, biological control, pollination), as well as the processes (e.g., nutrient cycling, energy flow, productivity) that characterize and maintain an ecosystem [32–34]. As assemblages change, taxon-free indicators such as functional traits will become increasingly useful in conservation efforts, including monitoring and assessing ecosystem state [12].

Our primary objective was to describe projected changes in environmental suitability for bird assemblages (i.e., species composition) in Canada's national park system, similar to work previously completed for the U.S. National Park Service [35]. Additionally, we updated and used 2019 distribution models and examined the functional traits of the current and future assemblages, to provide some understanding of potential changes to ecosystem function. By classifying parks according to relative trends in species turnover, we also begin to identify possible adaptation options and pathways for consideration by managers. We expect these projections to also help inform the public and partners about the potential impacts of climate change in Canada more broadly, and provide guidance for conservation and stewardship activities [30].

Methods

Study area

We based our study on the 2018 system of 50 Canadian national parks, national marine conservation areas, and national urban park, spanning all provinces and territories (S1 Fig); hereafter “parks”. Although there are differences in designations, they are all administered by Parks Canada to protect nationally significant examples of Canada’s natural and cultural heritage and to represent the country’s terrestrial and marine natural regions [36, 37]. We excluded only Quttinirpaaq from analyses, as it was beyond the northern limits of the developed models, leading to a final set of 49 parks, encompassing 297,844 km² of land and 10,089 km² of marine and fresh waters, with an average park size of 6,284 km² (median = 1,377 km², range 13 km² to 45,554 km²). For the national marine conservation areas, we limited analyses to the islands and coastal components. We classified parks into the ecological regions defined in Marshall et al. 1999 [38].

Data and species distribution modelling

We used previously published species distribution model (SDM) projections for 604 North American bird species [39, 40] to project change in environmental suitability as a value from 0–1, with a score of 1 indicating environmental conditions that best explain the presence of a species. The underlying models incorporated over 58 million bird occurrence records from 70 + data sources, such as eBird, North American Breeding Bird Survey, Global Biodiversity Information Facility, and NatureCounts (see Bateman et al. 2020 [39] for list of data sources). They accounted for 27 bioclimatic variables, vegetation types, terrain ruggedness, and anthropogenic land cover, as well as water presence for relevant birds. Models related occurrence with environmental data and were built using boosted regression trees (BRTs) and maximum entropy (MaxEnt), which are appropriate for exploring non-linear species-habitat relationships [41, 42]. The best performing model (i.e., baseline models for 2010s) was selected for each species and season using median AUC. These baseline models were then used to project future suitability at +2.0°C increase in global mean surface temperature above pre-industrial levels, which is anticipated to occur around mid-century (2041–2070) under the RCP8.5 (Representative Concentration Pathway) scenario [43, 44]. SDMs used an ensemble of 15 general circulation models (GCMs) that capture a range of bioclimatic conditions, and a model consensus approach to assess agreement across GCMs, calculated multiple model thresholds (including mean occurrence, maximized sensitivity + specificity, maximum Kappa, and others), and utilized expert opinion combined with a minimal decrease in model performance to select a final species-specific threshold above which a species is likely to occur (see Bateman et al. 2020 [39] for details). The result was 1x1 km resolution surfaces for each bird species and season with suitability values based on the percent change between the +2.0°C scenario compared to a 2010s baseline suitability. Bateman et al. 2020 [39] classified each 1x1 km cell as: 1) Potential extirpation: species was present in 2010 models but not under the +2.0°C scenario; 2) Worsening: -100% to -25% change in suitability; 3) Stable: -25% to 25% change; 4) Improving: >25% change in suitability; 5) Potential colonisation: species was not present in 2010s models but suitability improves to above the species-specific threshold. For this study, we rasterized park boundaries to match the 1x1 km cell resolution of the models. We summarized suitability change for each species and season across all cells each park comprises. For each species, we assigned summer and winter projections for a park based on which of the five categories above is associated with the largest number of cells within each park. We considered species with extirpation, worsening, stable, and improving projections as present in the 2010s.

We considered species with worsening, stable, improving, and potential colonization projections as present under the +2.0°C scenario. We conducted these analyses in R versions 3.4.4 and 4.0.2 using *raster* and *tidyverse* packages.

Species assemblages

Because climate-based species distribution models project locations of suitable conditions rather than definitive occurrence [45], and our aim is to provide park managers with the most realistic results possible, we systematically reviewed species outputs. We compared the species modelled as currently being present against contemporary lists for each park, based primarily on the NatureCounts database [46], which compiles data from a wide variety of citizen science programs and avian monitoring efforts. For each of summer and winter, species lists from modelled projections were reviewed by Parks Canada staff and other regional experts, and records considered to be from transient, migrant, or accidental species were excluded from the 2010s baseline projection to avoid overprediction. We removed 17% of modelled records from the analyses because their presence was unconfirmed.

To increase model accuracy, we also filtered out future model projections that represented a highly improbable colonisation scenario based on distance or habitat. Examples include projections of isolated records >1000 km beyond projected future range limits, species crossing the continent from the Pacific to eastern Arctic or Atlantic coasts or from the Rocky Mountains to Labrador without intermediate records, prairie species projected to colonise mountain parks, marine species projected to colonise inland waters, and conifer-crop dependent species projected to colonise high Arctic parks where trees may start to establish in the coming decades but would not grow sufficiently by 2041–2070 to support these birds. We removed 3.2% of records for which the projected future trend was considered as being improbable.

With the final set of present (2010s) and future (+2.0°C scenario) species, we calculated metrics comparing the present and potential future species assemblages within each park under a +2.0°C warming scenario. We chose the Sørensen similarity index [47] to quantify species turnover as it is based on presence-absence data, and compared to the Jaccard index, has a slightly higher focus on shared species than outliers [48]. We also measured species richness (SpRich), the raw number of species present at a park [49].

To understand how parks compare to each other, we classified them into relative groups based on the proportion of potential colonisations to potential extirpations, following Hole et al. 2011 [50]. We plotted the proportion of colonisations against the proportion of extirpations, then divided the resulting plot into five sectors based on the median and quartiles: high turnover, high potential extirpation, high potential colonisation, intermediate change, and low change. We calculated Sørensen similarity index using the *vegdist* function in the R (version 3.4.4) package *vegan*.

Species functional indices

Preliminary analysis of functional traits indicated extreme outliers in the Arctic Region parks and Sable Island. We therefore excluded these nine parks from the functional analyses to avoid improperly skewing the overall results.

To quantify changes in functional traits, we created a species-by-trait matrix for the modelled bird species. We classified each species with respect to five functional traits based on Rodewald 2015 [51]: 1) feeding behavior; 2) primary food type; 3) preferred habitat; 4) nesting behavior; and, 5) relative size. These categories describe resource needs (e.g., type and amount) and the behaviors employed to obtain them. We used the *daisy* function of the *Cluster* package version 2.1 in R (version 4.0.4) [52] to convert the species-by-trait matrix into a distance

matrix using Gower distance, which is commonly used to represent functional distances that are characterized by both quantitative and qualitative variables. We used a principal coordinates analysis to create the functional space representing the distance matrix. We used six axes to calculate the functional metrics, as this enabled functional richness to be calculated for all parks, including those with lower species richness [53, 54], it avoided computational problems derived from high-dimensional convex hulls (e.g., 10 dimensions), and it provided an improved fit over lower-dimensional spaces (mean squared deviation summer = 0.021, winter = 0.017, assessed using the `quality_funcnt_space` function; [55]).

Functional richness quantifies the proportion of trait space occupied by a given assemblage, by comparing a convex hull linking the species with the most extreme trait values within an assemblage to the volume occupied by the maximum convex hull that can be created using the global species pool [53]. Functional dispersion represents the functional variability within an assemblage by measuring the mean dispersion of an assemblage's species from its centroid in trait space [54]. For comparison across parks and between current and projected assemblages, we scaled dispersion values to the maximum dispersion value possible, given the global species pool (i.e., an assemblage with only the two most distant species). Occurrence data can be used to describe both the range of functional space an assemblage occupies (functional richness) and diversity within an assemblage (functional dispersion) [54, 56]. Higher levels of either are viewed as an assemblage being more buffered against environmental perturbations (i.e., greater capacity to respond to change) [30, 54, 57]. We calculated functional richness and dispersion using the `dbFD` function in the *FD* package in R (version 4.0.4) [54, 58].

We used the taxon restrictedness function in the *funrar* package (version 1.2.1) in R (version 4.0.4) [59]. Taxon restrictedness is a regional-scale index that represents a species distribution across parks scaled between zero and one. For this study a taxon restrictedness value of zero indicates a species is absent from all parks (i.e., completely restricted) and a value of one indicates a species is present at all parks (i.e., no restriction) [60, 61]. For this analysis we analyzed only species that occurred in both current and future communities in each season (356 species in summer; 215 species in winter).

We assessed functional change between current and projected assemblages for each of the above indices, plus species richness, using model II major axis (MA) regression, with the `lmodel2` function in the *lmodel2* package version 1.7.3 in R (version 4.0.4) [62]. We chose model II MA regression because both the x and y variables are in the same units, subject to error, and we did not assume a causal relationship between them [63, 64]. We assessed the significance of the model parameters and the correlation coefficient using 999 permutations to determine whether the communities differed significantly from the null model of a 1:1 relationship.

Results

The final analyses of 49 parks included 434 species (424 summer and 272 winter). The average number of species analyzed per park for summer was 137.2 ± 6.2 (SE) (range 16–201) and for winter was 70.0 ± 5.6 (range 1–159). A complete list of species and trends can be found in [S1 Table](#). By mid-century, the average projected species turnover per park is 24.9% in summer and 30.3% in winter, as measured by the Sørensen similarity index (Tables 1 and [S2](#)). The greatest projected rates of summer turnover are in two of the high Arctic region parks, Auyuittuq and Aulavik, at 42% and 33%, respectively ([S2 Table](#)), but species turnover rates are also projected to be high among many of the parks along Canada's east coast, including some in both the Atlantic Maritime and Boreal regions ([Fig 1](#)). Conversely, over half of the parks projected to have low turnover are in the Mountain and Mixedwood Plain regions ([Fig 2](#)).

Table 1. Regional and national summaries of potential changes in bird species with +2.0°C warming: 1) # of parks used in regional and national calculations; 2) mean (± SE) change in species richness per park; 3) mean (± SE) number of potential colonisation per park; 4) mean (± SE) number of potential extirpations per park; and, 5) mean (± SE) change in Sorenson similarity turnover index per park.

Region	# of Parks	Species Richness		Potential Colonisation		Potential Extirpation		Turnover	
		Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Arctic	7	19.6 ± 6.5	7.1 ± 5.2	26.7 ± 7.0	7.1 ± 5.2	7.1 ± 1.5	0	0.32 ± 0.04	0.24 ± 0.10
Atlantic Maritime	7	-12.6 ± 5.7	29.3 ± 6.1	21.9 ± 4.0	35.4 ± 5.3	34.4 ± 6.1	6.1 ± 1.5	0.29 ± 0.02	0.32 ± 0.07
Boreal	12	-18.4 ± 9.0	23.1 ± 3.7	24.8 ± 4.3	29.1 ± 3.4	43.3 ± 5.7	6 ± 0.9	0.26 ± 0.02	0.32 ± 0.03
Hudson Plain	1	4	15	29	15	25	0	0.23	0.31
Mixedwood Plain	6	-20.5 ± 3.7	20.8 ± 6.0	12.5 ± 2.2	26.3 ± 5.8	33 ± 3.5	5.5 ± 0.7	0.19 ± 0.02	0.19 ± 0.04
Mountain	7	-3.3 ± 10.6	33.6 ± 6.4	24.7 ± 4.6	38.1 ± 6.0	28 ± 8.1	4.6 ± 1.3	0.19 ± 0.03	0.44 ± 0.09
Pacific Maritime	3	-3 ± 13.4	30.3 ± 1.5	19.3 ± 8.4	34.7 ± 1.5	22.3 ± 6.0	4.3 ± 0.3	0.21 ± 0.05	0.16 ± 0.02
Prairie	1	-24	13	10	13	34	0	0.2	0.16
Taiga	5	16.4 ± 7.4	19.8 ± 4.6	38.6 ± 5.9	19.8 ± 4.6	22.2 ± 3.9	0	0.26 ± 0.02	0.38 ± 0.05
National	49	-5.4 ± 3.7	22.7 ± 2.2	24 ± 2.0	26.6 ± 2.2	29.4 ± 2.6	3.9 ± 0.5	0.25 ± 0.01	0.30 ± 0.03

<https://doi.org/10.1371/journal.pone.0262116.t001>

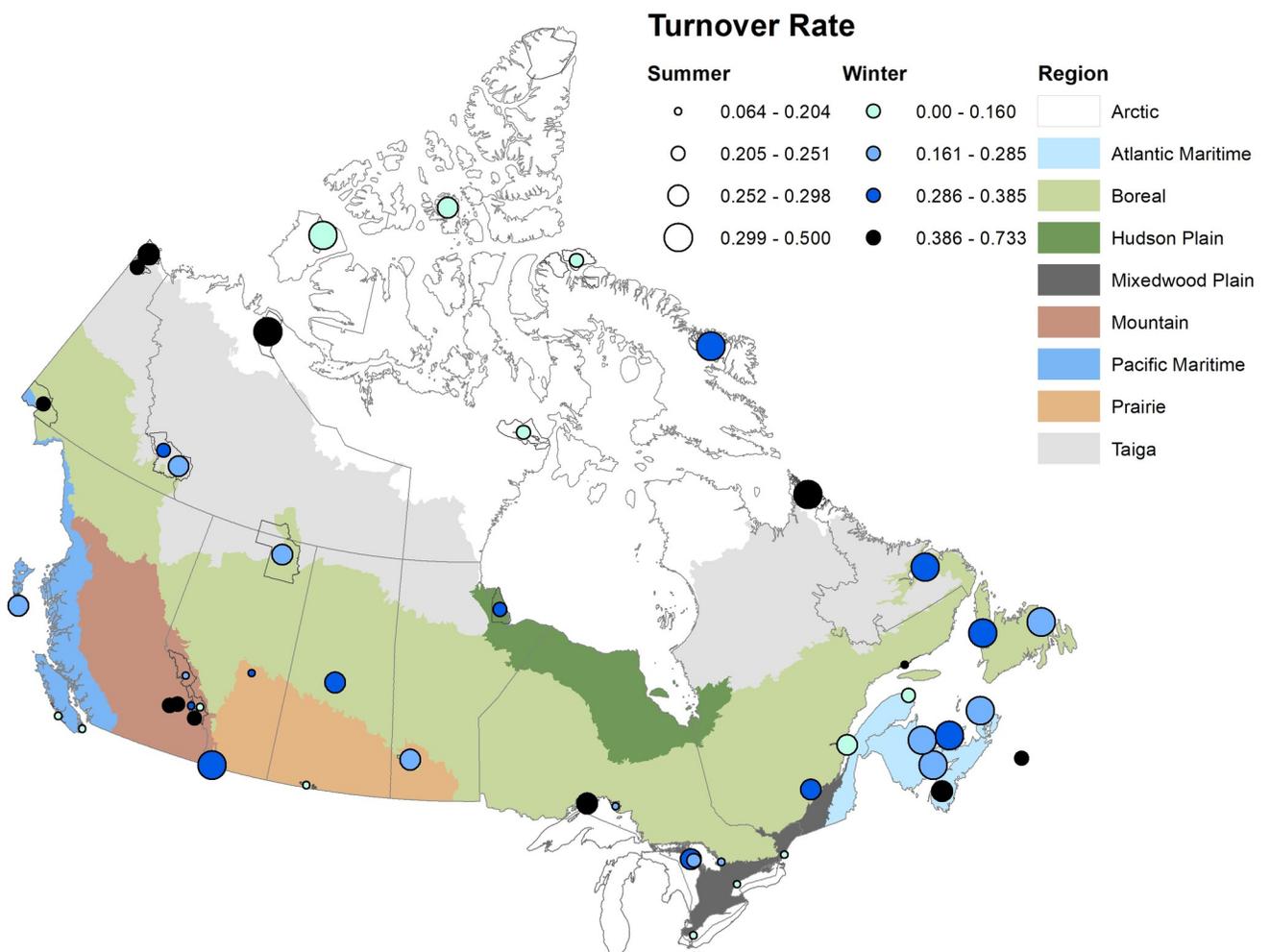


Fig 1. Projected species turnover (Sorenson) for +2.0°C warming scenario across all 49 parks, with 0 being no change and 1 being complete. Values can also be understood in terms of percent turnover (e.g., 0.252 = 25.2%). Circle diameter represents summer rates and color represents winter rates. Breaks in classes are based on quartiles.

<https://doi.org/10.1371/journal.pone.0262116.g001>

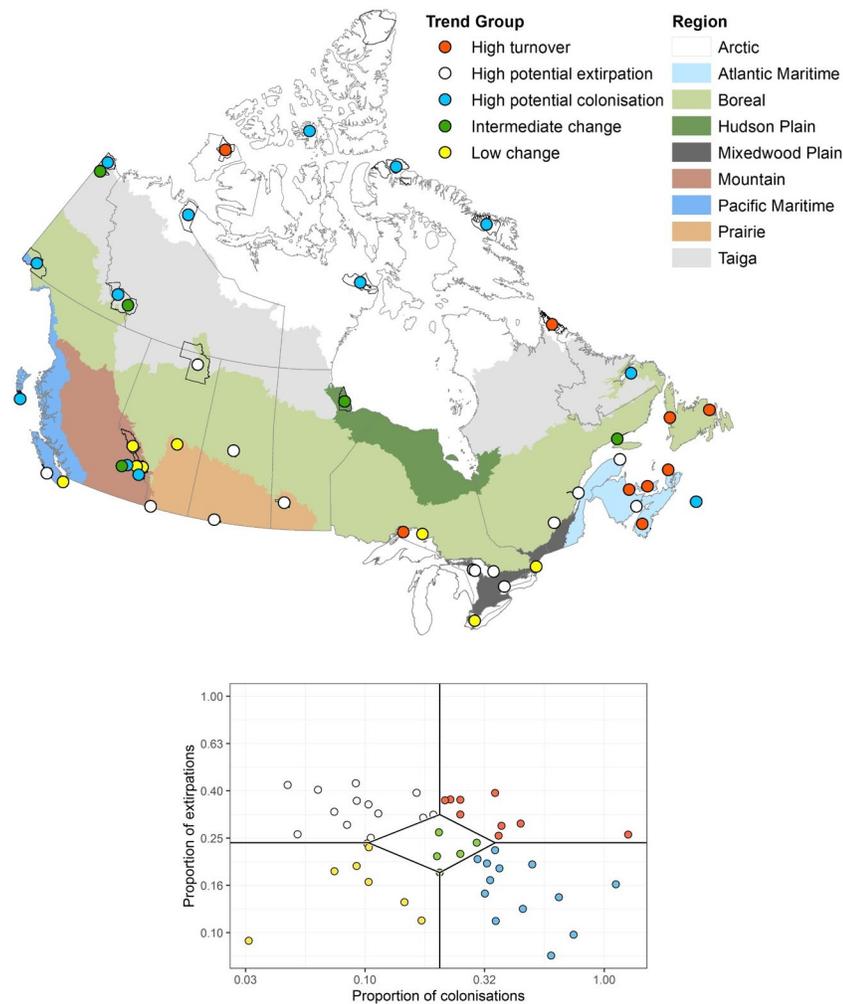


Fig 2. Classification of parks into relative trend groups based on the proportion of potential colonisations to potential extirpations in summer. Each circle represents a park and its modeled projection.

<https://doi.org/10.1371/journal.pone.0262116.g002>

Across all species, parks, and both seasons, 70% of projections of suitability (i.e., how well environmental conditions explain the presence of a species) are expected to change (i.e., improving or worsening suitability, or potential colonisation or extirpation, [S1 Table](#)). For parks where one or more species are projected to experience potential colonisation or potential extirpation (i.e., all 49 parks in summer, 46 parks in winter), potential extirpation exceeds potential colonisation in 55% of parks in summer, whereas in winter potential colonisation exceeds potential extirpation everywhere except Rouge National Urban Park, where the rates are projected to be equal. Overall, the number of potential coloniser species is much higher in winter than in summer ([Table 1](#)).

Figs 3–6 ([S3](#) and [S4](#) Tables) illustrate the changes between current and future species assemblages in terms of species richness, functional richness, functional dispersion, and taxon restrictedness. In each case, Model II MA regression analyses found a significant positive correlation between the current and projected future conditions. However, correlation was stronger in winter for species richness and functional richness, and stronger in summer for functional dispersion ([Table 2](#)).

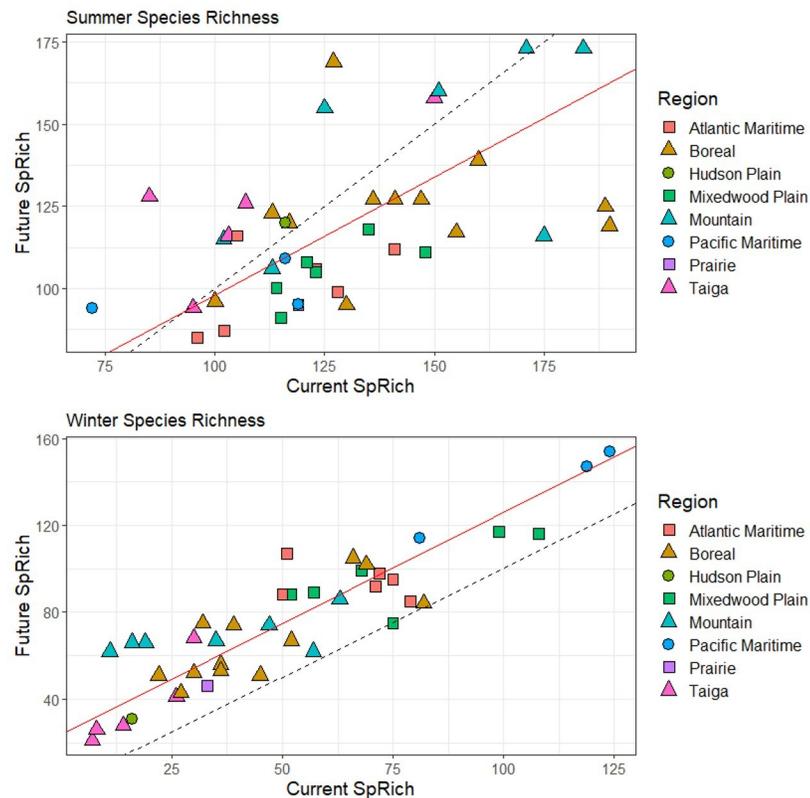


Fig 3. Change between current and future species richness (SpRich) across 41 parks (classified by region) for both summer and winter bird assemblages. The dashed line represents the null model (1:1 relationship); the red line is the model II major axis regression line (summer $y = 26.38 + 0.72x$, $r = 0.53$; winter $y = 23.84 + 1.02x$, $r = 0.89$).

<https://doi.org/10.1371/journal.pone.0262116.g003>

In summer, no significant shifts are projected at a national scale for any of species richness, functional richness, and functional dispersion, indicating no systematic change between current and future assemblages. Rather, the analyses project a mix of increases and decreases among parks. Summer species richness is projected to increase in most Taiga and Mountain parks, and to decline in most Atlantic Maritime and all Mixedwood Plains parks (Fig 3); the pattern is similar for functional richness, other than there are both increases and decreases among the Mountain parks (Fig 4). Projections of functional dispersion are more varied, with no regional patterns apparent (Fig 5). Overall taxon restrictedness is expected to change little in summer, although the distribution of common species will be reduced more than rare species (Fig 6).

Greater differences are projected in winter. Species richness is expected to increase in all regions, most notably in the Mountain and Atlantic Maritime parks (Fig 3). Similarly, functional richness is projected to increase in all regions, though none stand out, and instead it is individual parks with the lowest current functional richness that on average are expected to see the greatest gains (Fig 4). Future functional dispersion is expected to vary much less among parks than it does currently, with most of the largest gains occurring among the Mountain and Boreal parks, and only minor declines in a small number of parks, mostly in the Mixedwood Plain and Atlantic Maritime regions (Fig 5). The model trend crossed the 1:1 line (null model of no change) showing that the parks with the highest current functional dispersion are projected to decrease; however, the low correlation value ($r = 0.33$) indicates there was high

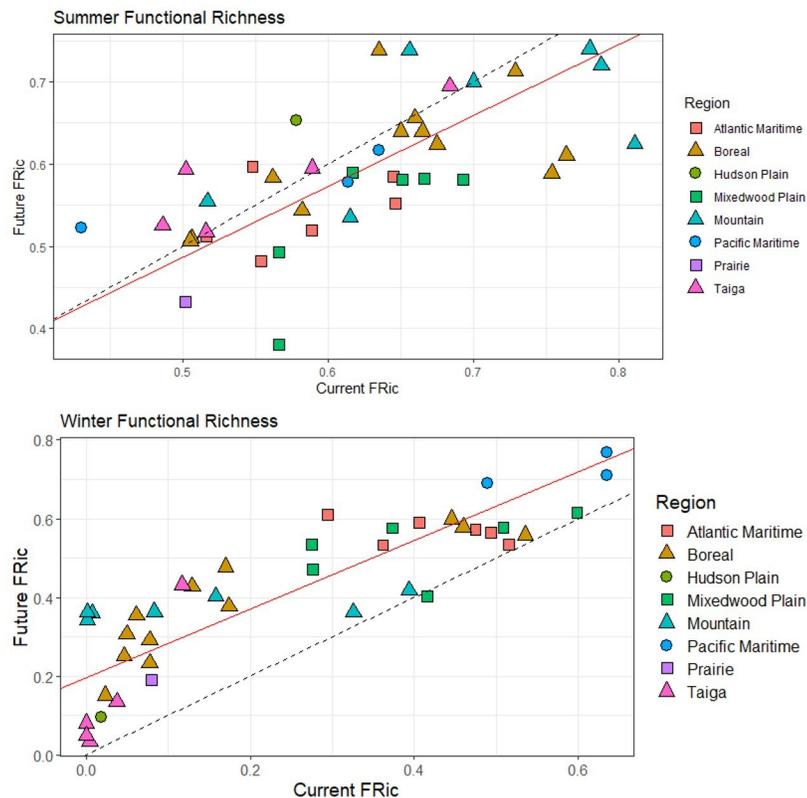


Fig 4. Change between current and future functional species richness (FRic) across 41 parks (classified by region) for both summer and winter bird assemblages. The dashed line represents the null model (1:1 relationship); the red line is the model II major axis regression line (summer $y = 0.06 + 0.86x$, $r = 0.66$; winter $y = 0.20 + 0.87x$, $r = 0.86$). Functional richness represents the volume occupied by a park in multidimensional trait space.

<https://doi.org/10.1371/journal.pone.0262116.g004>

variability around the overall trend. In winter, taxonomic restrictedness models show that most species are projected to expand their distribution with common species expanding most (Fig 6).

Discussion

By mid-century, climate change is expected to have substantial impacts on bird communities in Canada's system of national parks, with a potential turnover (change in species composition) of 24.9% in summer and 30.3% in winter. Environmental suitability is projected to be maintained for only 30% of species occurrences across seasons and parks. However, our results suggest considerable variability in the distributional shift of individual species, and in the resulting changes in community composition at individual parks.

Overall, the number of potential coloniser species is expected to be much higher in winter than in summer, consistent with the finding that wintering bird communities in Europe and North America are more rapidly tracking suitable habitat than summer breeding communities [65]. This is partly attributable to many species that are likely to become year-round residents in regions of Canada in future, especially in southern parks but also to a lesser extent in the north (e.g., Snow Bunting, *Plectrophenax nivalis*, in Auyuittuq). This includes winter colonisation by some species considered to be broadly declining in Canada, such as Cassin's Finch, *Haemorhous cassinii* and Red-headed Woodpecker, *Melanerpes erythrocephalus* [66, 67].

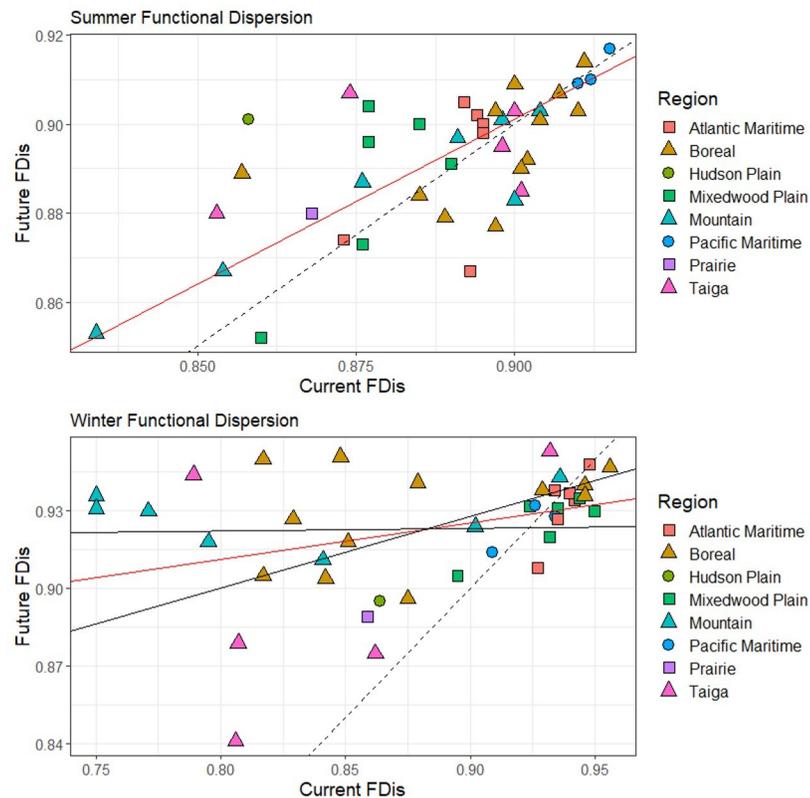


Fig 5. Change between current and future functional dispersion (FDIs) across all 41 parks (classified by region) for both summer and winter bird assemblages. The dashed line represents the null model (1:1 relationship); the red line is the model II major axis regression line (summer $y = 0.23 + 0.74x$, $r = 0.66$; winter $y = 0.80 + 0.14x$, $r = 0.33$). Functional dispersion represents the mean distance of all species to the centroid of the assemblage in multidimensional trait space.

<https://doi.org/10.1371/journal.pone.0262116.g005>

Future changes are difficult to predict with accuracy in complex, interrelated ecological systems, and climate change is likely to catalyze other stressors such as species invasion, habitat loss, water quality degradation [68], changes in species interactions [69], and many other factors that affect bird survival but cannot be readily modeled. However, there is evidence that some appear to already be expanding their range in Canada. For example, as our models projected, Red-bellied Woodpecker, *Melanerpes carolinus* and Northern Cardinal, *Cardinalis cardinalis* are steadily moving north in Ontario and into southern Quebec [70–72], while Black-necked Stilt, *Himantopus mexicanus* and White-faced Ibis, *Plegadis chihi*, are substantially increasing their presence in the Prairie region [72, 73]. Conversely, other species may expand their range more slowly than the shift in climate if they are less successful at gaining a share of already occupied habitats, such as White-eyed Vireo, *Vireo griseus* and Tufted Titmouse, *Baeolophus bicolor*, that have largely stalled their northward movement into Ontario since the early 2000s [72].

An important limitation of our results is that the underlying species distribution models do not definitively outline future ranges; rather, they should be interpreted as projecting a potential distribution based on changes in broad-scale factors such as climate and vegetation. Although climate is a dominant driver of bird distributions in North America [74], models developed using only climate variables can lead to overestimates of species' distributions [75]. We therefore included additional factors such as land cover, habitat availability, and

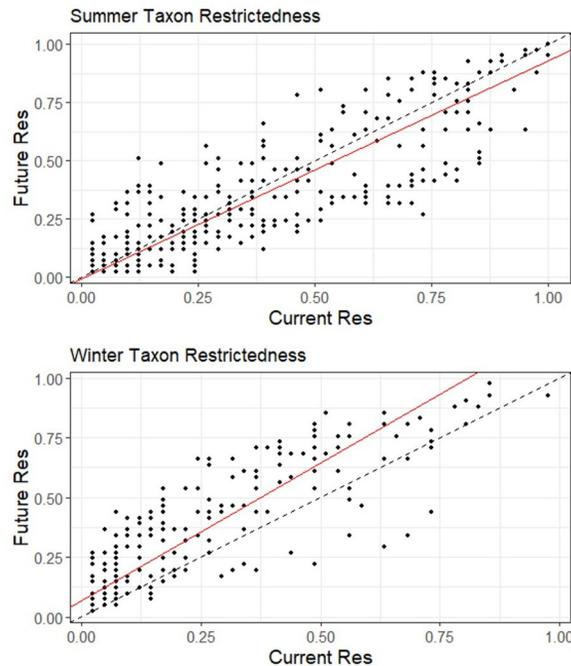


Fig 6. Change between current and future taxon restrictedness (TRes) across all 41 parks (classified by region) for both summer and winter bird assemblages. The dashed line represents the null model (1:1 relationship); the red line is the model II major axis regression line (summer $y = (-0.01) + 0.94x$, $r = 0.86$; winter $y = 0.07 + 1.15x$, $r = 0.85$). Restrictedness represents an index value between 0 and 1, where 0 indicates a species is absent from all parks (i.e., completely restricted) and 1 indicates present at all parks (not restricted).

<https://doi.org/10.1371/journal.pone.0262116.g006>

topography in the models, but recognize that actual changes in species distribution can also be influenced through park-based factors such as habitat quality, food abundance, and interspecific interactions. We attempted to account for this with park-based independent validation of contemporary occurrence data, but future projections could still overestimate range expansion and potential colonisation.

Table 2. Slope and intercept values, including 95% confidence intervals (C.I.), and regression coefficients for the Model II MA Regression models comparing the species richness (SpRich), functional richness (FRic), functional dispersion (FDis), and taxon restrictedness (TRes) between current and projected bird assemblages (null model 1:1).

Index	Season	Slope (C.I.)	Intercept (C.I.)	R
SpRich	Summer	0.72 (0.40–1.18)	26.38 (-33.47–67.74)	0.53*
	Winter	1.02 (0.87–1.20)	23.84 (14.60–31.67)*	0.89*
FRic	Summer	0.86 (0.58–1.24)	0.06 (-0.18–0.22)	0.66*
	Winter	0.87 (0.72–1.06)	0.20 (0.15–0.24)*	0.86*
FDis	Summer	0.74 (0.50–1.07)	0.23 (-0.05–0.45)	0.66*
	Winter	0.14 (0.01–0.28)*	0.80 (0.67–0.91)*	0.33*
Tres	Summer (n = 356)	0.94 (0.88–0.99)*	-0.01 (-0.03–0.11)	0.86*
	Winter (n = 215)	1.15 (1.06–1.25)*	0.07 (0.04–0.089)*	0.85*

Values with “*” indicate statistical significance ($p < 0.05$). Forty-one parks were used for the SpRich, FRic, and FDis analyses, whereas n indicates the number of bird species used in the TRes analysis.

<https://doi.org/10.1371/journal.pone.0262116.t002>

Also of note, several of the parks in our study are close to others, in some cases even sharing a common border (S1 Fig). There is some lack of independence among these parks, and correspondingly a degree of auto-correlation in their model output. However, examination of the models showed that contemporary assemblages and projected changes can differ considerably even in immediately neighbouring parks, based on factors such as topographic diversity and being just within or slightly beyond the limits of shifting species distributions. For example, although most of the Mountain region parks are closely clustered, projected colonisation rates vary substantially. Choosing to include certain parks but exclude others would require development of a prioritisation framework and would obscure some locally specific predictions with valuable management implications. We therefore retained all parks covered by the model, while acknowledging that the inclusion of adjacent parks may give some proportionately greater weight to the Mountain and Taiga regions in particular. Furthermore, any clear effect of park size may be masked by correlations between park size and factors such as latitude, remoteness, and adjacent land use, as parks in more developed southern regions are typically much smaller than those in remote northern locales. Despite these limitations, species distribution modelling does have utility for priority-setting and targeting species and habitat management [76], especially when it can be combined with local knowledge to more comprehensively assess species needs in a given area [77, 78].

Although bird communities in protected areas may be more resistant and resilient to climate change than those in more developed or working landscapes [15, 79, 80], protected areas remain vulnerable and there is already evidence of changes to terrestrial biomes and bird assemblages in some of Canada's national parks [26, 81–84]. As our findings illustrate, substantial further changes are expected, and although they appear to be park- and species-specific, some regional patterns are evident. For example, the relatively low rates of change projected in most of the Mountain region parks are consistent with theories of climate refugia occurring in areas of high topographic diversity that allow for different climates to exist in close proximity, and perhaps persist, through variation in attributes such as solar exposure, snow persistence, air flow, water inputs and canopy cover [85]. Topographic variability thus increases the likelihood that similar climatic conditions to those being lost might continue to occur nearby and be within reach of volant species such as birds [86]. Habitat connectivity is also an important factor [87], and in the case of some parks in the Mountain region (e.g., Banff, Jasper, Yoho, Kootenay) the proximity of adjacent protected areas and associated habitat may help bird assemblages persist regionally.

In the Arctic region a very different pattern is emerging. All of the parks in this region are projected to experience high potential colonisation or high turnover (i.e., both high colonisation and high extinction rates; Fig 2). This is not surprising, as Arctic regions are among those experiencing the most rapid change globally [2]. These parks are very different from those in the Mountain region noted above, as they are lacking in canopy cover and (except for Auyuituq and Torngat Mountains) are largely flat, and therefore have little capacity for topographically supported climate refugia. On the contrary, conditions in the Arctic region parks can promote positive feedback loops with negative climatic consequences, such as decreased ice cover and increased thawing of permafrost and associated carbon emissions [88]. Changes in vegetation, and resulting habitat for bird species, are already being seen in the Arctic region [84, 89–91]. However, our models show a limit to northward range shifts, consistent with other studies [92, 93].

We conducted functional analyses to understand whether changes in bird assemblages are likely to extend beyond just increases or decreases in species richness. As mentioned earlier, because of their disproportionate influence on overall results, we excluded the eight Arctic region parks and Sable Island National Park Reserve from the functional analyses. In summer,

only three parks (i.e., Point Pelee, Mount Revelstoke and Gulf Islands) are projected to experience a decrease in species richness, functional richness, and functional dispersion. Such a decrease in all three attributes suggests that the future assemblage may exhibit less adaptive capacity and resilience to disturbance and environmental conditions [94]. There are 22 parks, mainly across the Boreal, Atlantic Maritime, and Mixedwood Plain regions, that are projected to experience decreases in species richness and functional richness, but increases in functional dispersion. This suggests that while there may be a loss of extreme or specialized species (which can inflate the area that defines functional richness in trait space), that the predominant species in the future assemblage would be more spread out in a reduced overall space, thus may maintain a greater degree of diversity to respond to specific changes [27, 31, 94]. A decrease in functional dispersion, on the other hand, would suggest a shift towards the trait centroid for that park, with an assemblage of species with more similar traits.

In winter, most parks are projected to experience increases in both species richness and functional richness, suggesting that new species colonising the parks will increase trait combinations (bring novel trait combinations). The greatest differences in winter are with respect to functional dispersion, with many parks in the Boreal and Atlantic Maritime regions increasing in species richness, functional richness, and functional dispersion, whereas many parks in the Mixedwood Plain, Pacific Maritime, and Taiga regions are increasing in species richness and functional richness, but decreasing in functional dispersion. The former scenario, where all three attributes are projected to increase, suggests an assemblage that may have more adaptive capacity and resilience to an uncertain future [95]. The latter suggests that while some species are bringing in new trait combinations (inflating the trait space), many of the colonising species may be similar in functional traits (closer to the trait centroid). In general, the analyses suggest varied changes in the functional traits across assemblages, and as with other studies [33, 96], we recommend further examination of how these projected changes in species composition and functional traits may affect ecosystem structure and function.

While uncertainty exists around the precise rate and impacts of climate change, it is clear that conservation practices that assume stationarity, i.e., “the idea that natural systems fluctuate within an unchanging envelope of variability” [97], are no longer valid [98, 99] and that forward-looking, adaptive strategies are needed [10, 100–102]. To protect species and ecosystems, conservation practices have traditionally focused on resisting change or building resilience to support post-disturbance recovery to a historic state (i.e., persistence, [103]). However, as climate change continues to accelerate, this may no longer be tenable [104, 105] and efforts to maintain or restore the “composition and abundance of native species” and “supporting processes” (e.g., as per the definition of ecological integrity in Canada National Parks Act, [36]) may no longer be practical or possible in every park [10, 106]. As species are lost or gained in parks and ecosystems transform into potentially novel states, management will be faced with either accepting the outcome or attempting to direct it in part or in whole [98, 107, 108]. Managing for change would not only be a departure from traditional approaches, but also presents social and ecological challenges regarding difficult and unavoidable decisions about future desired states and conservation goals [32, 101, 109]. Park-level responses may need to consider not only changes to the status of individual species, but also the functional traits associated with them.

To help managers identify priorities, Fig 2 identifies each park's anticipated trend group based on projected changes in species distribution. The parks expected to have low or intermediate change in species composition are most suitable to be managed for persistence. In these, landscape-scale bird conservation can be pursued by emphasizing actions that protect species in situ and help to build or maintain system resilience, including managing disturbances within the historic range of variability, practicing climate-smart restoration, and reducing

exposure to non-climatic stresses (e.g., invasive species, fragmentation, road mortality, pollutants) [107, 110]. However, for parks in the high turnover, high potential colonisation, and high potential extirpation trend groups, managing for change is likely to be more effective with a focus on maintaining ecological structure and function, diversity, and redundancy of functional traits [111, 112]. Of particular concern are parks that also face a high loss in functional richness (e.g., Waterton Lakes, Rouge, Prince Albert, Riding Mountain, Bruce Peninsula, Cape Breton Highlands). This loss could be mitigated by facilitating the ability of species to adapt, such as improving habitat connectivity at a landscape scale, more intensive management actions (e.g., protection of key structures and functions such as nest sites), accepted or directed transformations (e.g., adaptive management, scenario-based planning, recalibration of management goals for novel ecosystems), and providing support for public engagement, social learning and good governance across scales [10, 107, 110, 113]. In practice, managers may simultaneously apply aspects of managing for persistence and change, and consider new approaches to conservation in the face of climate change.

Conclusion

Canada's national parks, national marine conservation areas, and national urban park are vulnerable to the impacts of a rapidly changing climate [114]. By examining species distribution models for 434 bird species, we anticipate that average species turnover at parks is expected to be approximately 25% in summer and 30% in winter by mid-century. In general, we found greater potential colonisation in winter, as warmer conditions permit more species to maintain year-round residency, contrasting with an increase in potential extirpation across parks in summer. Although it is impossible to account for the full array of changes in bird assemblages, as that will be confounded by interactions with other species and habitat factors [7], it is projected that all parks in the system will experience changes in species richness and functional traits by mid-century if climate continues to track RCP8.5.

Our results highlight potentially unavoidable and difficult challenges that require adaptive and strategic responses, where conservation decisions will include managing for persistence and change [98, 107, 113, 115]. By providing projections of future species richness, functional traits, and colonisation and extirpation potential, as well as suggesting management actions, our approach provides information that may help managers prepare for and reduce their park's vulnerabilities.

Regardless of projected changes to a particular park, it is important to recognize that protected areas and protected area networks will remain an important cornerstone and nature-based solution for conservation during this period of unprecedented environmental change [116–118]. As one final reminder, these are projections not predictions and by reducing greenhouse gas emissions and supporting efforts to sequester and store carbon, including in natural systems, we may be able to mitigate or avoid some of the worst impacts to our protected areas [39, 119].

Supporting information

S1 Fig. Park locator map.

(XLSX)

S1 Table. Projected future species trend for all parks, including species removed from analyses.

(XLSX)

S2 Table. Park-specific trend group and turnover projection.

(XLSX)

S3 Table. Current and projected future functional indices and species richness for all parks.

(XLSX)

S4 Table. Species functional traits and calculated taxon restrictedness.

(XLSX)

Acknowledgments

We extend our gratitude to our Parks Canada colleagues and local experts who contributed to refining the park species lists. That exercise highlighted the varied state of inventories and the important role that other government departments, academic researchers, and thousands of dedicated Canadian citizen scientists play in documenting birds in these places. We are also thankful to Gregor Schuurman, U.S. National Park Service, for his early support and ideas. Finally, thank you to the anonymous reviewers who helped to improve this manuscript.

Author Contributions

Conceptualization: Scott R. Parker, Joanna X. Wu, Brooke L. Bateman.

Data curation: Scott R. Parker, Joanna X. Wu.

Formal analysis: Marcel A. Gahbauer, Scott R. Parker, Joanna X. Wu, Cavan Harpur, Lotem Taylor.

Funding acquisition: Scott R. Parker.

Investigation: Marcel A. Gahbauer, Scott R. Parker, Joanna X. Wu, Cavan Harpur, Brooke L. Bateman, Darroch M. Whitaker, Douglas P. Tate, Lotem Taylor, Denis Lepage.

Methodology: Marcel A. Gahbauer, Scott R. Parker, Joanna X. Wu, Cavan Harpur, Brooke L. Bateman.

Project administration: Scott R. Parker, Brooke L. Bateman.

Resources: Joanna X. Wu.

Software: Scott R. Parker, Joanna X. Wu, Cavan Harpur.

Supervision: Scott R. Parker, Brooke L. Bateman.

Visualization: Scott R. Parker, Cavan Harpur.

Writing – original draft: Marcel A. Gahbauer, Scott R. Parker, Joanna X. Wu, Cavan Harpur, Brooke L. Bateman.

Writing – review & editing: Marcel A. Gahbauer, Scott R. Parker, Joanna X. Wu, Cavan Harpur, Brooke L. Bateman, Darroch M. Whitaker, Douglas P. Tate, Lotem Taylor.

References

1. Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, et al. Global Biodiversity: Indicators of Recent Declines. *Science*. 2010; 328(5982):1164–8. <https://doi.org/10.1126/science.1187512> WOS:000278104700046. PMID: 20430971
2. IPCC. Global Warming of 1.5°C. Intergovernmental Panel on Climate Change, 2018.

3. IPBES. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, 2019.
4. Hannah L. Protected Areas and Climate Change. In: Ostfeld RS, Schlesinger WH, editors. Year in Ecology and Conservation Biology 2008. Annals of the New York Academy of Sciences. 1134. Oxford: Blackwell Publishing; 2008. p. 201–12.
5. Monzon J, Moyer-Horner L, Palamar MB. Climate Change and Species Range Dynamics in Protected Areas. *Bioscience*. 2011; 61(10):752–61. <https://doi.org/10.1525/bio.2011.61.10.5> WOS:000299805400005.
6. Gonzalez P, Wang F, Michael N, Vimont DJ, Williams JW. Disproportionate magnitude of climate change in United States national parks. *Environ Res Lett*. 2018; 13(10):104001. <https://doi.org/10.1088/1748-9326/aade09>
7. Holsinger L, Parks SA, Parisien M-A, Miller C, Batllori E, Moritz MA. Climate change likely to reshape vegetation in North America's largest protected areas. *Conservation Science and Practice*. 2019; e50 (0):e50. <https://doi.org/10.1111/csp2.50>
8. Batllori E, Parisien M-A, Parks SA, Moritz MA, Miller C. Potential relocation of climatic environments suggests high rates of climate displacement within the North American protection network. *Glob Change Biol*. 2017. <https://doi.org/10.1111/gcb.13663> PMID: 28211141
9. Hobbs RJ, Cole DN, Yung L, Zavaleta ES, Aplet GH, Chapin FS, et al. Guiding concepts for park and wilderness stewardship in an era of global environmental change. *Frontiers in Ecology and the Environment*. 2010; 8(9):483–90. <https://doi.org/10.1890/090089>
10. Lemieux CJ, Beechey TJ, Gray PA. Prospects for Canada's protected areas in an era of rapid climate change. *Land Use Pol*. 2011; 28:928–41. <https://doi.org/10.1016/j.landusepol.2011.03.008>
11. Lynch AJ, Thompson LM, Beever EA, Cole DN, Engman AC, Hawkins Hoffman C, et al. Managing for RADical ecosystem change: applying the Resist-Accept-Direct (RAD) framework. *Frontiers in Ecology and the Environment*. 2021;n/a(n/a). <https://doi.org/10.1002/fee.2377>.
12. Barnosky AD, Hadly EA, Gonzalez P, Head J, Polly PD, Lawing AM, et al. Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science*. 2017; 355(6325):10. <https://doi.org/10.1126/science.aah4787> WOS:000393636700038. PMID: 28183912
13. Dudley N, Stolton S, Belokurov A, Krueger L, Lopoukhine N, MacKinnon K, et al. Natural Solutions: Protected areas helping people cope with climate change. Gland, Switzerland, Washington DC and New York, USA: IUCN WCPA, TNC, UNDP, WCS, The World Bank and WWF, 2010.
14. Murti R, Buyck C. Safe Havens: Protected Areas for Disaster Risk Reduction and Climate Change Adaptation. Gland, Switzerland: International Union for Conservation of Nature and Natural Resource (IUCN), 2014.
15. Peach MA, Cohen JB, Frair JL, Zuckerberg B, Sullivan P, Porter WF, et al. Value of protected areas to avian persistence across 20 years of climate and land-use change. *Conservation Biology*. 2019; 33 (2):423–33. <https://doi.org/10.1111/cobi.13205> WOS:301131094300019.
16. Bush E, Lemmen DS. Canada's Changing Climate Report. Ottawa, ON: Government of Canada, 2019.
17. Warren FJ, Lemmen DS, editors. Canada in a Changing Climate: Sector Perspectives on Impacts and Adaptation. Ottawa, ON: Government of Canada; 2014.
18. Lemmen DS, Warren FJ, James TS, Mercer Clarke CSL, editors. Canada's Marine Coasts in a Changing Climate. Ottawa, ON: Government of Canada; 2016.
19. Wang JA, Sulla-Menashe D, Woodcock CE, Sonnentag O, Keeling RF, Friedl MA. Extensive land cover change across Arctic-Boreal Northwestern North America from disturbance and climate forcing. *Glob Change Biol*. 2020; 26(2):807–22. <https://doi.org/10.1111/gcb.14804> WOS:000486743500001. PMID: 31437337
20. Tingley MW, Monahan WB, Beissinger SR, Moritz C. Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences of the United States of America*. 2009; 106:19637–43. <https://doi.org/10.1073/pnas.0901562106> WOS:000271907100002. PMID: 19805037
21. Auer SK, King DI. Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. *Glob Ecol Biogeogr*. 2014; 23(8):867–75. <https://doi.org/10.1111/geb.12174> WOS:000339110400004.
22. Cumming SG, Stralberg D, Lefevre KL, Solymos P, Bayne EM, Fang S, et al. Climate and vegetation hierarchically structure patterns of songbird distribution in the Canadian boreal region. *Ecography*. 2014; 37(2):137–51. <https://doi.org/10.1111/j.1600-0587.2013.00299.x> WOS:000329927800006.

23. Clement MJ, Nichols JD, Collazo JA, Terando AJ, Hines JE, Williams SG. Partitioning global change: Assessing the relative importance of changes in climate and land cover for changes in avian distribution. *Ecol Evol*. 2019; 9(4):1985–2003. <https://doi.org/10.1002/ece3.4890> WOS:000461114900035. PMID: 30847087
24. Socolar JB, Epanchin PN, Beissinger SR, Tingley MW. Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts. *Proceedings of the National Academy of Sciences of the United States of America*. 2017; 114(49):12976–81. <https://doi.org/10.1073/pnas.1705897114> WOS:000417339700041. PMID: 29133415
25. Radchuk V, Reed T, Teplitsky C, van de Pol M, Charmantier A, Hassall C, et al. Adaptive responses of animals to climate change are most likely insufficient. *Nat Commun*. 2019; 10(1):3109. <https://doi.org/10.1038/s41467-019-10924-4> PMID: 31337752
26. Whittington J, Shepherd B, Forshner A, St-Amand J, Greenwood JL, Gillies CS, et al. Landbird trends in protected areas using time-to-event occupancy models. *Ecosphere*. 2019; 10(11):e02946. <https://doi.org/10.1002/ecs2.2946>
27. Rosenberg KV, Dokter AM, Blancher PJ, Sauer JR, Smith AC, Smith PA, et al. Decline of the North American avifauna. *Science*. 2019; 366(6461):120–+. <https://doi.org/10.1126/science.aaw1313> WOS:316043137000068.
28. Langham GM, Schuetz JG, Distler T, Soykan CU, Wilsey C. Conservation Status of North American Birds in the Face of Future Climate Change. *Plos One*. 2015; 10(9):16. <https://doi.org/10.1371/journal.pone.0135350> WOS:000360613800029. PMID: 26333202
29. Saunders SP, Michel NL, Bateman BL, Wilsey CB, Dale K, LeBaron GS, et al. Community science validates climate suitability projections from ecological niche modeling. *Ecological Applications*. 2020; 17. <https://doi.org/10.1002/eap.2128> WOS:322230298900001.
30. Schipper AM, Belmaker J, de Miranda MD, Navarro LM, Bohning-Gaese K, Costello MJ, et al. Contrasting changes in the abundance and diversity of North American bird assemblages from 1971 to 2010. *Glob Change Biol*. 2016; 22(12):3948–59. <https://doi.org/10.1111/gcb.13292> WOS:000387813300011. PMID: 27002684
31. Barnagaud JY, Gauzere P, Zuckerberg B, Prince K, Svenning JC. Temporal changes in bird functional diversity across the United States. *Oecologia*. 2017; 185(4):737–48. <https://doi.org/10.1007/s00442-017-3967-4> WOS:000415027100018. PMID: 29058124
32. Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E. The influence of functional diversity and composition on ecosystem processes. *Science*. 1997; 277(5330):1300–2. <https://doi.org/10.1126/science.277.5330.1300> WOS:A1997XT82700053.
33. Luck GW, Carter A, Smallbone L. Changes in Bird Functional Diversity across Multiple Land Uses: Interpretations of Functional Redundancy Depend on Functional Group Identity. *PLoS ONE*. 2013; 8(5):11. <https://doi.org/10.1371/journal.pone.0063671> WOS:236968447900053.
34. Bregman TP, Lees AC, MacGregor HEA, Darski B, de Moura NG, Aleixo A, et al. Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. *Proc R Soc B-Biol Sci*. 2016; 283(1844):10. <https://doi.org/10.1098/rspb.2016.1289> WOS:000390404200006. PMID: 27928045
35. Wu JX, Wilsey CB, Taylor L, Schuurman GW. Projected avifaunal responses to climate change across the U.S. National Park System. *PLOS ONE*. 2018; 13(3):e0190557. <https://doi.org/10.1371/journal.pone.0190557> PMID: 29561837
36. Canada National Parks Act, c. 32, (2000).
37. Canada National Marine Conservation Areas Act, c. 18, (2002).
38. Marshall IB, Schut PH, Ballard M. A National Ecological Framework for Canada: Attribute Data. Ottawa/Hull: Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, 1999.
39. Bateman BL, Wilsey C, Taylor L, Wu J, LeBaron GS, Langham G. North American birds require mitigation and adaptation to reduce vulnerability to climate change. *Conservation Science and Practice*. 2020; 2(8):18. <https://doi.org/10.1111/csp2.242> WOS:000567417300011.
40. Wilsey C, Taylor L, Bateman B, Jensen C, Michel N, Panjabi A, et al. Climate policy action needed to reduce vulnerability of conservation-reliant grassland birds in North America. *Conservation Science and Practice*. 2019; 1(4). <https://doi.org/10.1111/csp2.21>
41. Elith J, Leathwick JR, Hastie T. A working guide to boosted regression trees. *J Anim Ecol*. 2008; 77(4):802–13. <https://doi.org/10.1111/j.1365-2656.2008.01390.x> WOS:000256539800020. PMID: 18397250

42. Radosavljevic A, Anderson RP. Making better Maxent models of species distributions: complexity, overfitting and evaluation. *J Biogeogr.* 2014; 41(4):629–43. <https://doi.org/10.1111/jbi.12227>.
43. IPCC. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland: Intergovernmental Panel on Climate Change (IPCC). 2014.
44. Schwalm CR, Glendon S, Duffy PB. RCP8.5 tracks cumulative CO2 emissions. *Proceedings of the National Academy of Sciences of the United States of America.* 2020; 117(33):19656–7. <https://doi.org/10.1073/pnas.2007117117> WOS:000570306900014. PMID: 32747549
45. Bateman BL, Pidgeon AM, Radeloff VC, VanDerWal J, Thogmartin WE, Vavrus SJ, et al. The pace of past climate change vs. potential bird distributions and land use in the United States. *Glob Change Biol.* 2016; 22(3):1130–44. <https://doi.org/10.1111/gcb.13154> WOS:000370491400015. PMID: 26691721
46. Birds Canada. NatureCounts. Port Rowan, Ontario: 2018.
47. Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlenn D, et al. *vegan: Community Ecology Package.* 2017.
48. Hao MH, Corral-Rivas JJ, Gonzalez-Elizondo MS, Ganeshiah KN, Nava-Miranda MG, Zhang CY, et al. Assessing biological dissimilarities between five forest communities. *For Ecosyst.* 2019; 6:8. <https://doi.org/10.1186/s40663-019-0188-9> WOS:000471020800001.
49. Sanders HL. Marine Benthic Diversity: A Comparative Study. *Am Nat.* 1968; 102(925):243–&. <https://doi.org/10.1086/282541> WOS:A1968C246100005.
50. Hole DG, Huntley B, Arinaitwe J, Butchart SHM, Collingham YC, Fishpool LDC, et al. Toward a Management Framework for Networks of Protected Areas in the Face of Climate Change. *Conservation Biology.* 2011; 25(2):305–15. <https://doi.org/10.1111/j.1523-1739.2010.01633.x> WOS:000288460000014. PMID: 21284728
51. Rodewald P, editor. *The Birds of North America.* Ithaca, NY: Cornell Laboratory of Ornithology; 2015.
52. Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K. *cluster: Cluster Analysis Basics and Extensions.* R package version 2.1.0. 2019.
53. Villéger S, Mason NWH, Mouillot D. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology.* 2008; 89(8):2290–301. <https://doi.org/10.1890/07-1206.1> WOS:000258236400023. PMID: 18724739
54. Laliberté E, Legendre P. A distance-based framework for measuring functional diversity from multiple traits. *Ecology.* 2010; 91(1):299–305. <https://doi.org/10.1890/08-2244.1> WOS:000275458500033. PMID: 20380219
55. Maire E, Grenouillet G, Brosse S, Villeger S. How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. *Glob Ecol Biogeogr.* 2015; 24(6):728–40. <https://doi.org/10.1111/geb.12299> WOS:000354121600012.
56. Mason NWH, Mouillot D, Lee WG, Wilson JB. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos.* 2005; 111(1):112–8. <https://doi.org/10.1111/j.0030-1299.2005.13886.x> WOS:000231864900012.
57. Schleuter D, Daufresne M, Massol F, Argillier C. A user's guide to functional diversity indices. *Ecol Monogr.* 2010; 80(3):469–84. <https://doi.org/10.1890/08-2225.1> WOS:000279801300006.
58. Laliberté E, Legendre P, Shipley B. *FD: measuring functional diversity from multiple traits, and other tools for functional ecology.* R package version 1.0–12. 2014.
59. Grenié M, Denelle P, Tucker CM, Munoz F, Violle C. *funrar: An R package to characterize functional rarity.* R package version 1.2.1. 2017.
60. Grenié M, Denelle P, Tucker CM, Munoz F, Violle C. *funrar: An R package to characterize functional rarity.* *Divers Distrib.* 2017; 23(12):1365–71. <https://doi.org/10.1111/ddi.12629>
61. Violle C, Thuiller W, Mouquet N, Munoz F, Kraft NJB, Cadotte MW, et al. Functional Rarity: The Ecology of Outliers. *Trends Ecol Evol.* 2017; 32(5):356–67. <https://doi.org/10.1016/j.tree.2017.02.002> WOS:000399451900011. PMID: 28389103
62. Legendre P. *'lmodel2': Model II Regression.* R package version 1.7–3. 2018.
63. Sokal R, Rohlf F. *Biometry: the principles and practice of statistics in biological research.* 3rd ed. New York: W. H. Freeman Company; 1995 04/27.
64. Legendre P, Legendre L. *Numerical Ecology.* Amsterdam: Elsevier Science Ltd; 1998.
65. Lehtikoinen A, Lindström Å, Santangeli A, Sirkiä PM, Brotons L, Devictor V, et al. Wintering bird communities are tracking climate change faster than breeding communities. *J Anim Ecol.* 2021;n/a(n/a). <https://doi.org/10.1111/1365-2656.13433> PMID: 33496011

66. Rosenberg KV, Kennedy JA, Dettmers R, Ford RP, Reynolds D, Alexander JD, et al. Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States. Partners in Flight Science Committee, 2016.
67. NABCI. The State of Canada's Birds. Ottawa: North American Bird Conservation Initiative Canada, Environment and Climate Change Canada, Ottawa, 2019.
68. Griffith B, Scott JM, Adamcik R, Ashe D, Czech B, Fischman R, et al. Climate Change Adaptation for the US National Wildlife Refuge System. *Environmental Management*. 2009; 44(6):1043–52. <https://doi.org/10.1007/s00267-009-9323-7> WOS:000272615300004. PMID: 19548023
69. Bateman BL, VanDerWal J, Williams SE, Johnson CN. Biotic interactions influence the projected distribution of a specialist mammal under climate change. *Divers Distrib*. 2012; 18(9):861–72. <https://doi.org/10.1111/j.1472-4642.2012.00922.x> WOS:000307389600002.
70. Cadman MD, Sutherland DA, Beck GG, Lepage D, A.R. C, editors. Atlas of the breeding birds of Ontario, 2001–2005. Toronto, ON: Bird Studies Canada, Environment Canada, Ontario Field Ornithologists, Ontario Ministry of Natural Resources, and Ontario Nature; 2007.
71. Robert M, Hachey M-H, Lepage D, Couturier AR, editors. Second atlas of the breeding birds of southern Quebec. Montreal, QC: Regroupement Québec Oiseaux, Canadian Wildlife Service (Environment and Climate Change Canada), and Bird Studies Canada; 2019.
72. eBird: An online database of bird distribution and abundance [Internet]. Cornell Lab of Ornithology. 2021. Available from: <http://www.ebird.org>.
73. Federation of Alberta Naturalists. The atlas of breeding birds of Alberta: a second look. Edmonton, Alberta: Federation of Alberta Naturalists, 2007.
74. Jimenez-Valverde A, Barve N, Lira-Noriega A, Maher SP, Nakazawa Y, Papes M, et al. Dominant climate influences on North American bird distributions. *Glob Ecol Biogeogr*. 2011; 20(1):114–8. <https://doi.org/10.1111/j.1466-8238.2010.00574.x> WOS:000285109200009.
75. Jimenez-Valverde A, Lobo JM, Hortal J. Not as good as they seem: the importance of concepts in species distribution modelling. *Divers Distrib*. 2008; 14(6):885–90. <https://doi.org/10.1111/j.1472-4642.2008.00496.x> WOS:000260116700001.
76. Willis SG, Foden W, Baker DJ, Belle E, Burgess ND, Carr JA, et al. Integrating climate change vulnerability assessments from species distribution models and trait-based approaches. *Biological Conservation*. 2015; 190:167–78. <https://doi.org/10.1016/j.biocon.2015.05.001> WOS:000358972200019.
77. Austin MP, Van Niel KP. Improving species distribution models for climate change studies: variable selection and scale. *J Biogeogr*. 2011; 38(1):1–8. <https://doi.org/10.1111/j.1365-2699.2010.02416.x> WOS:000285300500001.
78. Reside AE, Critchell K, Crayn DM, Goosem M, Goosem S, Hoskin CJ, et al. Beyond the model: expert knowledge improves predictions of species' fates under climate change. *Ecological Applications*. 2019; 29(1):15. <https://doi.org/10.1002/eap.1824> WOS:000454685500001. PMID: 30390399
79. Ray C, Saracco JF, Holmgren ML, Wilkerson RL, Siegel RB, Jenkins KJ, et al. Recent stability of resident and migratory landbird populations in National Parks of the Pacific Northwest. *Ecosphere*. 2017; 8(7):24. <https://doi.org/10.1002/ecs2.1902> WOS:000407654200012.
80. Lehtikoinen P, Santangeli A, Jaatinen K, Rajasärkkä A, Lehtikoinen A. Protected areas act as a buffer against detrimental effects of climate change—Evidence from large-scale, long-term abundance data. *Glob Change Biol*. 2018. <https://doi.org/10.1111/gcb.14461> PMID: 30393928
81. Lemieux CJ, Scott DJ. Climate change, biodiversity conservation and protected area planning in Canada. *Can Geogr-Geogr Can*. 2005; 49(4):384–97. <https://doi.org/10.1111/j.0008-3658.2005.00103.x>
82. Craik SR, Hanson AR, Titman RD, Mahoney ML, Tremblay E. Potential Impacts of Storm Surges and Sea-level Rise on Nesting Habitat of Red-breasted Mergansers (*Mergus serrator*) on Barrier Islands in New Brunswick, Canada. *Waterbirds*. 2015; 38(1):77–85. <https://doi.org/10.1675/063.038.0110> WOS:000370892800009.
83. Turner DME, Nguyen LP, Nol E. Annual Reproductive Success of American Robins (*Turdus migratorius*) at the Northern Edge of their Range. *Wilson J Ornithol*. 2017; 129(3):509–19. WOS:000410546000007.
84. Whitaker D. Expanded Range Limits of Boreal Birds in the Torngat Mountains of Northern Labrador. *Can Field-Nat*. 2017; 131(1):55–62. <https://doi.org/10.22621/cfn.v131i1.1957>
85. Morelli TL, Daly C, Dobrowski SZ, Dulen DM, Ebersole JL, Jackson ST, et al. Managing Climate Change Refugia for Climate Adaptation. *Plos One*. 2016; 11(8):17. <https://doi.org/10.1371/journal.pone.0159909> WOS:000381380400017. PMID: 27509088
86. Dobrowski SZ, Parks SA. Climate change velocity underestimates climate change exposure in mountainous regions. *Nat Commun*. 2016; 7(1):12349. <https://doi.org/10.1038/ncomms12349> PMID: 27476545

87. Morelli TL, Maher SP, Lim MCW, Kastely C, Eastman LM, Flint LE, et al. Climate change refugia and habitat connectivity promote species persistence. *Climate Change Responses*. 2017; 4(1):8. <https://doi.org/10.1186/s40665-017-0036-5>
88. AMAP. Snow, Water, Ice and Permafrost in the Arctic (SWIPA): Climate Change and the Cryosphere. Oslo, Norway: Arctic Monitoring and Assessment Programme (AMAP), 2011.
89. Fraser RH, Olthof I, Carrière M, A. D, Pouliot D. Detecting long-term changes to vegetation in northern Canada using the Landsat satellite image archive. *Environ Res Lett*. 2011; 6(4). <https://doi.org/10.1088/1748-9326/6/4/044015> PMID: 28781607
90. Ju JC, Masek JG. The vegetation greenness trend in Canada and US Alaska from 1984–2012 Landsat data. *Remote Sens Environ*. 2016; 176:1–16. <https://doi.org/10.1016/j.rse.2016.01.001> WOS:000372383200001.
91. Davis E, Trant A, Hermanutz L, Way RG, Lewkowicz AG, Collier LS, et al. Plant-Environment Interactions in the Low Arctic Torngat Mountains of Labrador. *Ecosystems*. 2020; 21. <https://doi.org/10.1007/s10021-020-00577-6> WOS:000585877200001.
92. Rodenhouse NL, Christenson LM, Parry D, Green LE. Climate change effects on native fauna of north-eastern forests. *Can J For Res*. 2009; 39(2):249–63. <https://doi.org/10.1139/x08-160> WOS:000265054300004.
93. Soykan CU, Sauer J, Schuetz JG, LeBaron GS, Dale K, Langham GM. Population trends for North American winter birds based on hierarchical models. *Ecosphere*. 2016; 7(5):16. <https://doi.org/10.1002/ecs2.1351> WOS:000377215200042.
94. Gallagher RV, Hughes L, Leishman MR. Species loss and gain in communities under future climate change: consequences for functional diversity. *Ecography*. 2013; 36(5):531–40. <https://doi.org/10.1111/j.1600-0587.2012.07514.x> WOS:000318167600002.
95. Carpenter SR, Arrow KJ, Barrett S, Biggs R, Brock WA, Crepin AS, et al. General Resilience to Cope with Extreme Events. *Sustainability*. 2012; 4(12):3248–59. <https://doi.org/10.3390/su4123248> WOS:000324044100004.
96. Cooke RSC, Bates AE, Eigenbrod F. Global trade-offs of functional redundancy and functional dispersion for birds and mammals. *Glob Ecol Biogeogr*. 2019; 28(4):484–95. <https://doi.org/10.1111/geb.12869>.
97. Milly PCD, Betancourt J, Falkenmark M, Hirsch RM, Kundzewicz ZW, Lettenmaier DP, et al. Climate change—Stationarity is dead: Whither water management? *Science*. 2008; 319(5863):573–4. <https://doi.org/10.1126/science.1151915> WOS:000252772000023. PMID: 18239110
98. Schuurman GW, Hawkins-Hoffman C, Cole DN, Lawrence DJ, Morton JM, Magness DR, et al. Resist-accept-direct (RAD)—a framework for the 21st-century natural resource manager. Fort Collins, Colorado: US National Park Service, 2020.
99. West JM, Julius SH, Kareiva P, Enquist C, Lawler JJ, Petersen B, et al. US Natural Resources and Climate Change: Concepts and Approaches for Management Adaptation. *Environmental Management*. 2009; 44(6):1001–21. <https://doi.org/10.1007/s00267-009-9345-1> WOS:196366065300001.
100. Wyborn C, van Kerkhoff L, Dunlop M, Dudley N, Guevara O. Future oriented conservation: knowledge governance, uncertainty and learning. *Biodiversity and Conservation*. 2016; 25(7):1401–8. <https://doi.org/10.1007/s10531-016-1130-x> WOS:000379006400011.
101. van Kerkhoff L, Munera C, Dudley N, Guevara O, Wyborn C, Figueroa C, et al. Towards future-oriented conservation: Managing protected areas in an era of climate change. *Ambio*. 2018. <https://doi.org/10.1007/s13280-018-1121-0> PMID: 30448995
102. Stralberg D, Berteaux D, Drever CR, Drever M, Naujokaitis-Lewis I, Schmiegelow FKA, et al. Conservation planning for boreal birds in a changing climate: a framework for action. *Avian Conservation and Ecology*. 2019; 14(1). <https://doi.org/10.5751/ACE-01363-140113>
103. Hansen LJ, Biringer JL, Hoffman JR, editors. *Buying Time: A User's Manual for Building Resistance and Resilience to Climate Change in Natural Systems*: World Wildlife Fund for Nature (WWF); 2003.
104. Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, et al. Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annual Review of Ecology, Evolution and Systematics*. 2004; 35(1):557–81. <https://doi.org/10.1146/annurev.ecolsys.35.021103.105711>
105. Crepin AS, Biggs R, Polasky S, Troell M, de Zeeuw A. Regime shifts and management. *Ecological Economics*. 2012; 84:15–22. <https://doi.org/10.1016/j.ecolecon.2012.09.003> WOS:000312351500003.
106. Glick P, Stein BA, Edelson NA, editors. *Scanning the Conservation Horizon: A Guide to Climate Change Vulnerability Assessment*. Washington, D.C.: National Wildlife Federation; 2011.
107. Stein BA, Glick P, Edelson N, Staudt A. *Climate-Smart Conservation: Putting Adaptation Principles into Practice*. Washington, D.C.: National Wildlife Federation, 2014.

108. Thompson LM, Lynch AJ, Beever EA, Engman AC, Falke JA, Jackson ST, et al. Responding to Ecosystem Transformation: Resist, Accept, or Direct? *Fisheries*. 2020. <https://doi.org/10.1002/fsh.10506>
109. Abrahms B, DiPietro D, Graffis A, Hollander A. Managing biodiversity under climate change: challenges, frameworks, and tools for adaptation. *Biodiversity and Conservation*. 2017; 26(10):2277–93. <https://doi.org/10.1007/s10531-017-1362-4> WOS:000406637700002.
110. Gross JE, Woodley S, Welling LA, Watson JEM. *Adapting to Climate Change. Guidance for Protected Area Managers and Planners*. Gland, Switzerland: IUCN, 2016.
111. Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, et al. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*. 2003; 1(9):488–94. [https://doi.org/10.1890/1540-9295\(2003\)001\[0488:RDECAR\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001[0488:RDECAR]2.0.CO;2). ISI:000221791600016.
112. Sundstrom SM, Allen CR, Barichiev C. Species, Functional Groups, and Thresholds in Ecological Resilience. *Conservation Biology*. 2012; 26(2):305–14. <https://doi.org/10.1111/j.1523-1739.2011.01822.x> WOS:000301981100014. PMID: 22443132
113. NPS. *Planning for a Changing Climate: Climate-Smart Planning and Management in the National Park Service*. Fort Collins, CO: National Park Service (NPS), Climate Change Response Program, 2021.
114. Scott D, Suffling R. *Climate Change and Canada's National Park System: A screening level assessment*. Adaptation and Impacts Research Group, Environment Canada, and University of Waterloo, 2000.
115. Chapin FSI, Carpenter SR, Kofinas GP, Folke C, Abel N, Clark WC, et al. Ecosystem stewardship: sustainability strategies for a rapidly changing planet. *Trends Ecol Evol*. 2010; 25(4):241–9. <https://doi.org/10.1016/j.tree.2009.10.008> PMID: 19923035
116. CPC. *Canadian Parks and Protected Areas: Helping Canada Weather Climate Change*. Parks Canada Agency on behalf of the Canadian Parks Council, 2013.
117. Johnston A, Ausden M, Dodd AM, Bradbury RB, Chamberlain DE, Jiguet F, et al. Observed and predicted effects of climate change on species abundance in protected areas. *Nat Clim Chang*. 2013; 3(12):1055–61. <https://doi.org/10.1038/nclimate2035> WOS:000330126300019.
118. Thomas CD, Gillingham PK. The performance of protected areas for biodiversity under climate change. *Biol J Linnean Soc*. 2015; 115(3):718–30. <https://doi.org/10.1111/bij.12510> WOS:000356368400019.
119. Gonzalez P. *Climate Change Trends, Impacts, and Vulnerabilities in US National Parks*. In: Beissinger SR, Ackerly DD, Doremus H, Machlis GE, editors. *Science, Conservation, and National Parks*. Chicago, IL: University of Chicago Press; 2017.