Rapid shifts in Arctic tundra species' distributions and inter-specific range overlap under future climate change

Floris Beest, Larissa Beumer, Asbjørn Andersen, Sophia Hansson, Niels Schmidt

Received: 9 January 2021 | Revised: 18 May 2021 | Accepted: 26 May 2021

DOI: 10.1111/ddi.13362

RESEARCH ARTICLE

Diversity and Distributions WILEY

Rapid shifts in Arctic tundra species' distributions and inter-specific range overlap under future climate change

Floris M. van Beest[1,2] | Larissa T. Beumer[1,2] | Asbjørn S. Andersen[1] | Sophia V. Hansson[3] | Niels M. Schmidt[1,2]

[1]Department of Bioscience, Aarhus University, Roskilde, Denmark

[2]Arctic Research Centre, Aarhus University, Aarhus C, Denmark

[3]Laboratoire Ecologie Fonctionnelle et Environnement (UMR-5245), CNRS, Université de Toulouse, Castanet Tolosan, France

Correspondence
Floris M. van Beest, Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark.
Email: flbe@bios.au.dk

Editor: Zhixin Zhang

Abstract

Aim: The Arctic is one of the planet's most rapidly warming regions, with trends expected to intensify in the future. Projections of shifts in species distributional ranges under future climate change are thus far lacking for most vertebrate species using the Arctic tundra. Our aim was to assess possible climate-induced changes in distributional ranges and inter-specific overlap of an Arctic species assemblage within the world's largest land-based protected area.

Location: During 1979–2013 location data of eight Arctic birds and mammals, Arctic fox (*Vulpes lagopus*), Arctic hare (*Lepus arcticus*), Arctic wolf (*Canis lupus arctos*), muskox (*Ovibos moschatus*), polar bear (*Ursus maritimus*), rock ptarmigan (*Lagopus muta*), snow bunting (*Plectrophenax nivalis*) and snowy owl (*Bubo scandiacus*) were collected in the Northeast Greenland National Park.

Methods: The maximum entropy (MaxEnt) algorithm and Schoener's D niche overlap index were used to assess shifts and changes in overlap of species-specific distributions under recent (1979–2013) and future (2061–2080; representative concentration pathways [RCPs] 2.6, 4.5 and 8.5) bioclimatic conditions.

Results: Species distributions were projected to shift northward and upwards across all scenarios, and at higher rates than previously reported. Future distributions were also forecasted to become spatially less clustered and to expand in size for all species. Species-specific shifts in distribution ranges altered inter-specific overlap, most notably by an increase in overlap under scenario RCP 8.5.

Main conclusions: The rapid shifts in distribution ranges detected here underline that climate change impacts are most pronounced in areas with higher levels of warming, leading to accelerated shifts in species' ranges towards the poles. However, the concomitant range expansions we found may suggest that future climatic conditions in north-east Greenland may not have such a detrimental impact on the distribution of cold-adapted species as generally expected, at least in the near future.

KEYWORDS
Arctic vertebrates, climate change, Eltonian Noise Hypothesis, inter-specific range overlap, MaxEnt, species distribution models

1 | INTRODUCTION

Climate is a major determinant of species distribution ranges (Louthan et al., 2015). Future changes in climate are expected to shift distribution ranges poleward (higher latitude) and/or upward (higher elevation) (Lenoir et al., 2008; Parmesan & Yohe, 2003). Yet, due to regional variation in the magnitude and direction of climatic changes, impacts will vary between ecosystems (IPCC, 2013). Moreover, differences in physiological traits (e.g. thermal tolerance) between species can lead to divergent responses to global warming (Bennett et al., 2019). In agreement, species distributions have been shown to shift, contract or expand (Chen et al., 2011; Scheffers et al., 2016), which can lead to a restructuring of biotic communities over large areas (Lavergne et al., 2010).

The impacts of climate change are believed to be particularly pronounced for cold-adapted species residing in the Arctic, an area disproportionally affected by climate change relative to most other regions in the world (Gilg et al., 2012; Post et al., 2009). While the ecology and evolution of some resident Arctic species are already being affected by a warming climate (Gilg et al., 2012; Taylor et al., 2020), most of the evidence is based on marine (Clairbaux et al., 2019; Kovacs et al., 2011; Neukermans et al., 2018) and invertebrate (Høye et al., 2020; Nielsen & Wall, 2013) species. Projections of distributional range changes by an assemblage of vertebrate species found on the Arctic tundra and possible implications for inter-specific overlap are currently lacking. Such knowledge is crucial given that the Arctic tundra has low species richness with relatively few species interactions, where even small changes in inter-specific range overlap can have important implications for terrestrial food-web dynamics (Schmidt et al., 2017). Estimating climate-induced shifts in distributions of Arctic species is therefore urgently needed to facilitate assessments of potential implications for ecosystem functioning (Pecl et al., 2017) and to inform possible conservation strategies (Elsen et al., 2020).

Here, we estimated changes in distribution ranges as well as inter-specific overlap over time and space for eight Arctic vertebrate species from different trophic levels (Figure 1) that are resident to the world's largest land-based protected area (Northeast Greenland National Park). Specifically, we contrasted species-specific distribution ranges and overlap based on recent climatic conditions (1979–2013) with projected estimates under future climatic conditions (2061–2080) using multiple global circulation models (GCMs) and scenarios of representative concentration pathways (RCPs 2.6, 4.5 and 8.5) that were part of the collection of model runs used in the IPCC's 5th Assessment Report (IPCC, 2013). As such, our study is focussed on investigating potential impacts of changes in large-scale, abiotic conditions on species distributions as put forward under the Eltonian noise hypothesis (ENH: Soberón & Nakamura, 2009). Following the general notion that climate change impacts are more pronounced in areas with higher levels of warming, such as the Arctic (Chen et al., 2011; IPCC, 2013), we expected species distribution ranges to expand northwards in latitude and up the elevation gradient over time (P_1). We also expected the speed of northward and upward shift to depend on the severity of climate change (i.e. RCP scenarios) (P_2). Moreover, we expected species-specific responses to climate change to alter inter-specific range overlaps in space and time (P_3).

2 | METHODS

2.1 | Study area and location data

Data for this study were collected in the Northeast Greenland National Park (Figure 1). The size of the park is 972,000 km^2 including the interior ice sheet (ca 70% of the area). Apart from a few permanent, small meteorological and military outposts, the national park has no permanent human residents. Only researchers and few tourists visit the park during summer months, and anthropogenic disturbance is thus considered low. Large areas of the ice-free part of the national park are patrolled by the Sirius Dog Sled Patrol, a special unit within the Danish defence. The patrol consists of 6 dog sled teams, each conducting one reconnaissance trip in spring and one in autumn of each year. The exact routes are classified, but trips cover the same geographical areas, each covering over a thousand kilometres across several months. During reconnaissance trips, vertebrate wildlife encounters are registered, specifying date, species, location and group size.

Here, we used species observation data collected during 1979–2013. Observations collected during 2001–2013 were available in a digital format while observations from 1979 to 2000 were available on paper only. We first digitized these observations, considering only records with known species identity, date and location. The locations of most observations were provided in lat/long, but in some cases, only local place names were given, which were subsequently converted into lat/long using GIS (https://data.geus.dk/geusmapmore/stednavnedb/listall.jsp). We could not quantitatively assess the accuracy of the location data, but we assume location error of most observations to be <20 km, which is smaller than the resolution of the bioclimatic variables used in the analyses (see next section). We disregarded information of group size, as this was inconsistently registered for most species.

For our analyses, we focussed on location data of eight vertebrate species that were easily identified by Sirius Dog Sled Patrol personnel due to their size, conservation status or charismatic nature: Arctic fox (*Vulpes lagopus*, Linnaeus, 1758), Arctic hare (*Lepus*

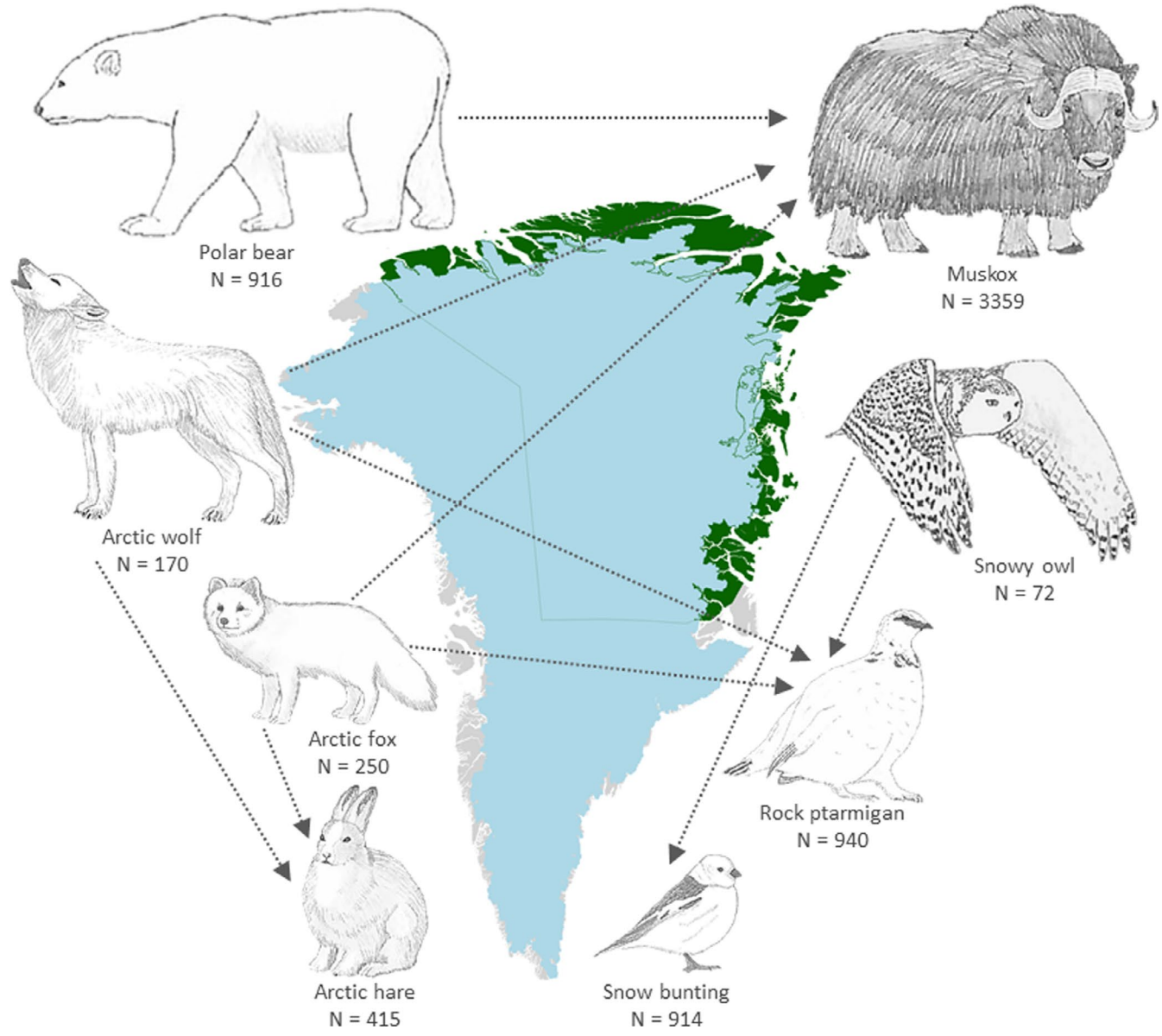

FIGURE 1 Map of Greenland with the Northeast Greenland National Park outlined in green and the Greenland ice sheet in blue. Also shown are the study species: Arctic fox (*Vulpes lagopus*), Arctic hare (*Lepus arcticus*), Arctic wolf (*Canis lupus arctos*), muskox (*Ovibos moschatus*), polar bear (*Ursus maritimus*), rock ptarmigan (*Lagopus muta*), snow bunting (*Plectrophenax nivalis*) and snowy owl (*Bubo scandiacus*) and their respective sample sizes (N is the number of observations over the period 1979–2013) as used in the species distribution models. Arrows indicate the most common, but not exclusive, interactions between carnivorous and herbivorous species. Note that arrows and artwork are for descriptive purposes only and are thus not to scale

arcticus, Ross, 1819), Arctic wolf (*Canis lupus arctos*, Pocoock, 1935), muskox (*Ovibos moschatus*, Zimmermann, 1780), polar bear (*Ursus maritimus*, Phipps, 1774), rock ptarmigan (*Lagopus muta*, Montin, 1776), snow bunting (*Plectrophenax nivalis*, Linnaeus, 1758) and snowy owl (*Bubo scandiacus*, Linnaeus, 1758). Smaller species, such as lemming, were not considered for the analyses as they were less likely to be observed and recorded, even though they may be important to tundra ecosystem functioning (Schmidt et al., 2012). The location data reflect species presences only, as there was no data recorded for true absences of species over time and space. We therefore also considered observations of animal tracks (<1% of location data) in the analyses. Part of the muskox location data collected by the Sirius Dog Sled Patrol has been used previously to assess biotic and abiotic effects on temporal population trends (Forchhammer & Boertmann, 1993).

2.2 | Species distribution modelling

Species distribution ranges were estimated using the maximum entropy machine learning algorithm (MaxEnt; Phillips et al., 2006). MaxEnt relates location data with environmental or climatic background data to produce spatially explicit predictions of species' occurrence probability (Elith & Leathwick, 2009). Although a wide range

of species distribution modelling (SDM) techniques exists, which can be combined into a single ensemble modelling framework (Forester et al., 2013; Naimi & Araújo, 2016), we opted for MaxEnt as the preferred modelling approach as it is particularly suited for presence-only data with relatively small sample sizes (Elith et al., 2006; Phillips et al., 2017; Wisz et al., 2008), which was the case in our study (Figure 1, Figure S1.1 in Appendix S1). We fitted separate models for each species using the procedure outlined below. For more details, we refer to the Overview, Data, Model, Assessment and Prediction (ODMAP) protocol (sensu Zurell et al., 2020) on model development, testing and evaluation in Appendix S1.

Presence data in the MaxEnt models were species' locations collected in the study area during 1979–2013 (Figure S1.2 in Appendix S1). Background points (10,000) were randomly sampled for each species from within the vegetated areas in the Northeast Greenland National Park (Figure S1.3 in Appendix S1), effectively removing all areas with land ice. Moreover, we constructed spatial sampling bias files for each species separately by computing Gaussian kernel density rasters of all sampling locations (Brown et al., 2017). Sampling bias files (Figure S1.4 in Appendix S1) were subsequently included in the species-specific MaxEnt models to up-weight presence-only data points with fewer neighbours in the geographic landscape and to restrict background points to geographic areas where species occurrences were found (Merow et al., 2013; Phillips et al., 2009).

Environmental data considered were bioclimatic variables ($n = 19$) freely available through the CHELSA database (https://chelsa-climate.org/) at a 1 km resolution (Karger et al., 2017). The bioclimatic raster data were downloaded for the periods 1979–2013 (current period) and 2061–2080 (future period). For the latter, we considered data produced by three global circulation models (GCMs) using three scenarios of representative concentration pathways (RCPs). Specifically, the three selected GCMs are part of the CMIP5 collection of model runs used in IPCC's 5th Assessment Report (IPCC, 2013) and were CM5A-LR (Persechino et al., 2013), ESM-MR (Giorgetta et al., 2013) and MIROC5 (Watanabe et al., 2010). Each GCM provides data for scenarios of RCP 2.6, 4.5 and 8.5 (see Appendix S1 for a description of each RCP scenario). All bioclimatic raster data were upscaled to 20 km resolution to minimize possible effects of location inaccuracy and clipped to the vegetated areas in Northeast Greenland National Park (Figure S1.3 in Appendix S1).

Because multicollinearity among bioclimatic predictors was high (variance inflation factor>100 for some variables), and we had no a priori knowledge of which predictor variables were most influential in explaining species-specific probability of occurrence, we employed a completely data-driven variable selection approach through the "SDMtune" package in R (Vignali et al., 2020). This approach selects the variable that best fits the data (using Akaike information criterion value corrected for small sample sizes: AICc) among those that are highly correlated. Starting from a trained model with all variables included, the function checks if the variable ranked as the most important (i.e. highest per cent contribution) is correlated with any of the other variables, here using a threshold of Spearman's rho ≥0.7. If this was the case, a leave-one-out jackknife test was performed, starting with the full model, and among all correlated variables, the one variable that decreased model fit on the training data set the most was discarded. A new model was then trained without this variable, which was again checked for highly correlated variables. The process was repeated until the pairwise correlations among all retained variables had Spearman's rho <0.7. Through this iterative procedure, 8 of the initial 19 predictor variables were (in different combinations) retained in the final species-specific models (Figure S1.5 in Appendix S1): BIO2: Mean diurnal range (mean of monthly (max temp−min temp)°C*10), BIO7: Temperature annual range (°C*10), BIO8: Mean temperature (°C*10) of wettest quarter, BIO10: Mean temperature (°C*10) of warmest quarter, BIO14: Precipitation (mm) of driest month, BIO15: Precipitation seasonality (Coefficient of Variation), BIO17: Precipitation (mm) of driest quarter and BIO18: Precipitation (mm) of warmest quarter.

To protect against overfitting and to reduce model complexity, MaxEnt uses regularization multipliers (RM) (Phillips et al., 2006). RMs give a penalty for each term included in the model and for higher weights given to a term. Here, we tested different settings of RM using the range of 0.5–5.0 in increments of 0.5 for each feature class through the "ENMeval" package in R (Muscarella et al., 2014). Moreover, we restricted all features to "linear" and "quadratic" functions to avoid overly complex response curves that would be hard to explain ecologically. For each species, the optimal model was selected based on goodness of fit by identifying the candidate model with the lowest AICc. Predictive performance of each species-specific optimal model was evaluated by calculating the area under the curve (AUC) of the receiver operating characteristic (ROC) value. AUC values typically range from 0.5 for a model that shows no better than random discriminatory ability, to a theoretical value of 1 for perfect discriminatory ability (Elith et al., 2006). Autocorrelation of location data was considered low (Figure S1.6 in Appendix S1).

Species-specific distribution maps were created by stacking the bioclimatic raster layers into a multi-layered raster and predicting, from the optimal MaxEnt models, the probability of occurrence in each grid cell under both current and future bioclimatic conditions. To ensure that model predictions did not include areas with novel bioclimatic conditions in the future (i.e. conditions for which the model has no training data, thus making predictions unreliable), a multivariate environmental similarity surfaces (MESS) analysis was performed. Following Elith et al. (2010), we used presence locations with associated bioclimatic values under current conditions (1979–2013) as input points and then estimated (dis)similarities in bioclimatic conditions across the study area extent (i.e. vegetated part of the Northeast Greenland National Park) by comparing to the data on future bioclimatic conditions. The MESS analysis was done for each species separately, and we used future conditions from the most stringent RCP 8.5 scenario throughout. Based on the MESS output, we only retained those areas where bioclimatic conditions were similar over time (Figure S1.7 in Appendix S1). Importantly, areas with dissimilar bioclimatic conditions were also removed for model predictions under current climatic conditions to ensure comparability of changes in predicted area sizes over time (see Section 2.3).

2.3 | Shifts in distribution ranges and inter-specific overlap

In order to investigate how changes in bioclimatic conditions might shift distributional ranges, we contrasted the predicted probability of occurrence, as derived from the complimentary log–log (cloglog) output produced by the optimal MaxEnt model, between the current and future periods. To do so, we considered three complementary SDM thresholds (Liu et al., 2013) including Kappa (the value of the probability of occurrence at which Kappa is highest), MSSS (the value of the probability of occurrence at which the sum of the sensitivity (true positive rate) and specificity (true negative rate) is maximized) and P10 (the value of the probability of occurrence for the lowest 10% of occurrence records). In general, the Kappa threshold was most restrictive as it identified areas with relatively high probability of occurrence (i.e. core distribution area). The MSSS threshold identified areas above a moderate probability of occurrence, while the P10 threshold included most areas above a relatively low probability of occurrence across species distributions (Table S1.1 in Appendix S1).

Directional shifts under recent and future climatic conditions (considering the three RCP scenarios) were then assessed quantitatively by calculating the difference in latitude (using the geometric mean, with 1° corresponding to 111.6 km) and elevation (mean m.a.s.l.) between periods (a difference of five decades) and for each SDM threshold. Elevation was extracted from a digital elevation model (20 km resolution) developed by the Shuttle Radar Topography Mission, which is freely available through the WorldClim2 database (http://www.worldclim.com/). Moreover, we computed the absolute change in total area size (km^2) of species ranges and the level of clustering (unitless) (Clark & Evans, 1954). For the latter, we followed Beumer et al., (2019) by calculating the nearest neighbour index (NNI) as a measure of clustering or dispersion. NNI <1 indicates a clustered pattern, and NNI >1 suggests dispersion of probability of occurrence.

For each range shift metric, we used a paired sample *t* test to detect significant ($p < .05$) differences in mean species distributions between the current and future period (normality of data confirmed with Shapiro–Wilk test: $p > .05$) with a separate test for each RCP and SDM threshold considered. Finally, we calculated the proportion of inter-specific overlap, and the changes therein between recent and future species distributions, based on Schoener's *D* niche overlap index (Schoener, 1968), again separating each RCP and SDM threshold considered.

3 | RESULTS

3.1 | Predictive performance and variable importance

Predictive performance of the species-specific MaxEnt models was considered high with a mean AUC >0.75 for all optimal models (Table S2.1 in Appendix S2). The importance of bioclimatic variables in the models and their influence on the probability of occurrence differed between species (see Figure S2.1 for variable importance and Figure S2.2 for response curves). The most consistent and important predictor influencing the probability of occurrence across all species was mean temperature (°C) of the warmest quarter (summer) with the probability of occurrence typically increasing with increasing temperature.

3.2 | Current and future species distribution maps

Spatial mapping of the MaxEnt models' output highlighted that probabilities of species occurrences during 1979–2013 (Figure 2) were highest in the mid-eastern section of the Northeast Greenland National Park (especially for rock ptarmigan) and lowest in the northern parts of the study area. The distribution range of snowy owls during this period was most uniform with a consistent probability of occurrence across the entire area (Figure 2).

Projections of the MaxEnt model results based on bioclimatic conditions for the period 2061–2080 are provided for each species, GCM and RCP combination in Figures 2.3–2.10 in Appendix S2. These forecast maps suggest that the probability of species occurrences will increase and expand geographically and particularly with severity of RCP scenario, a pattern that applied to all species. The maps also suggest that some GCMs produced more spatially restrictive distribution ranges under the same RCP scenario than did others. To accommodate this variance in further analyses, we calculated the mean and standard deviation of the probability of species occurrence for each RCP by aggregating data from the GCM- and species-specific MaxEnt models (Figures S2.11–S2.12 in Appendix S2).

3.3 | Shifts in species distributions

Contrasting species distribution maps for 1979–2013 and for 2061–2080 (using three RCP scenarios), distributions were projected to change markedly (Figure 3). For some species (Arctic fox, Arctic wolf and polar bear), the change in probability of occurrence over time was mostly positive, which became more pronounced with the severity of RCP scenarios considered. In contrast, the change in probability of occurrence over time and space was mainly negative for rock ptarmigans (most pronounced under scenario RCP 2.6 and less so under scenario RCP 8.5). For snowy owls and snow bunting, probability of occurrences remained rather constant over time and space, especially when contrasting current distributions with future distributions under scenarios RCP 2.6 and 4.5 but only a slight positive change in the probability of occurrence under scenario RCP 8.5. For muskoxen and Arctic hares, the change in probability of occurrence over time was positive in some parts of their distribution range and negative in others, a pattern that also became more pronounced with the severity of the RCP scenarios considered (Figure 3).

Quantitative analyses of the above spatiotemporal changes in probability of occurrence revealed significant northward shifts in species distributions over time, a pattern that was evident for all RCP

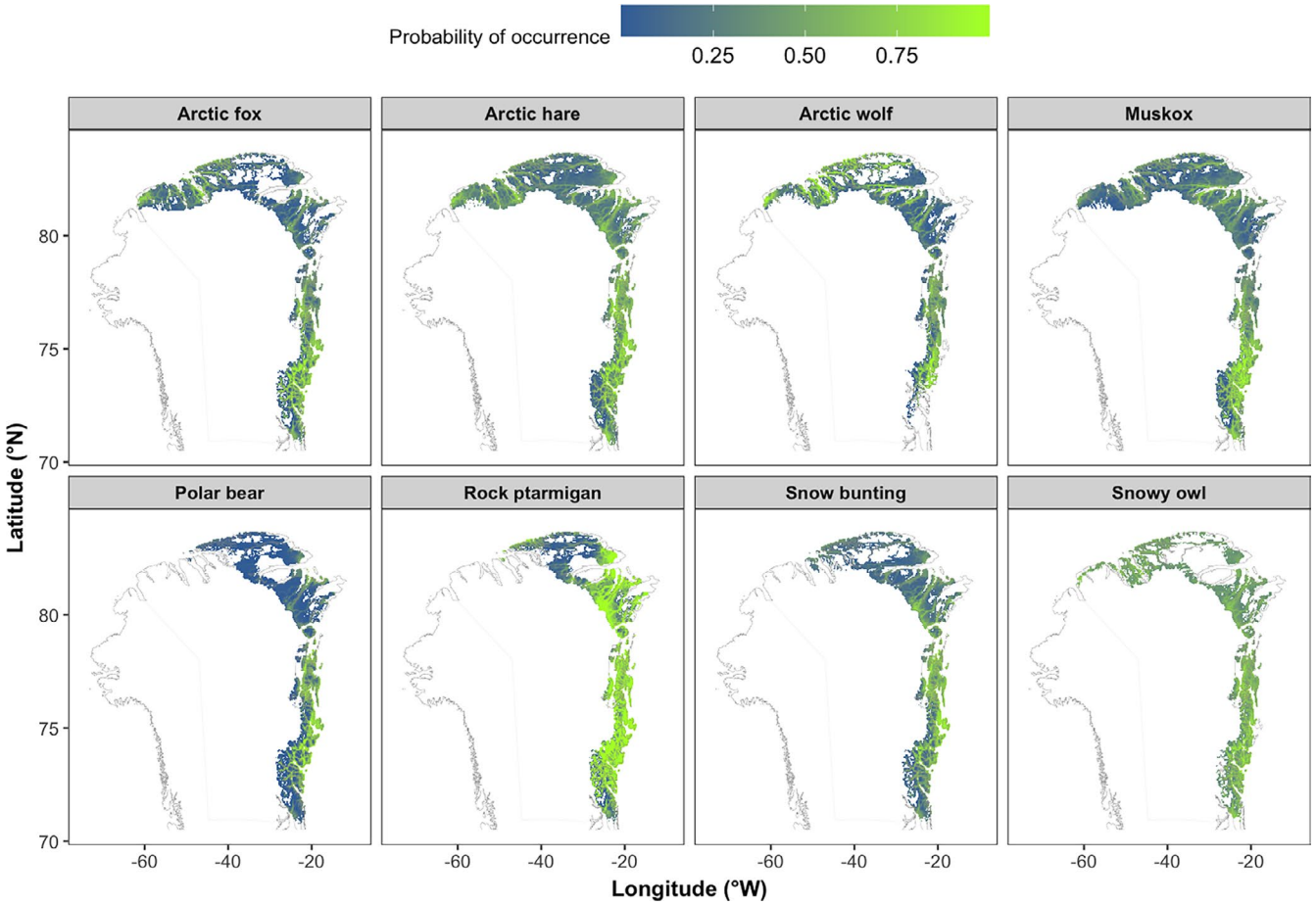

FIGURE 2 Maps of species-specific probability of occurrence for the period 1979–2013 based on the optimal MaxEnt models using location data collected in the Northeast Greenland National Park during the same period. Predicted values are the cloglog output of the species-specific MaxEnt model with values ranging from 0 to 1 depicted by a blue to green scale. Note that values are only provided for vegetated areas in the park, excluding land ice and areas with novel bioclimatic conditions as identified through species-specific multivariate environmental similarity surfaces analyses using data from 1979–2013 and 2061–2080

scenarios and thresholds considered (Figure 4a, Table S2.2). While some species were projected to shift their distribution range faster and further north than others, we quantified an average rate in latitudinal range shifts of 65.8 km/decade ($t = 5.43$, $df = 7$, $p = .001$) when contrasting current (1979–2013) with future (2061–2080) core ranges (Kappa threshold) under scenario RCP 8.5. In comparison, the average rate was 37.4 and 24.3 km/decade under scenarios RCP 4.5 ($t = 3.68$, $df = 7$, $p = .008$) and RCP 2.6 ($t = 3.04$, $df = 7$, $p = .019$), respectively. Rates in latitudinal shifts were lowest for the P10 threshold (i.e. including most of the species ranges) yet remained statistically significant with average rates of 17.7, 16.1 and 14.4 km/decade under scenarios RCP 8.5 ($t = 3.53$, $df = 7$, $p = .010$), RCP 4.5 ($t = 3.82$, $df = 7$, $p = .007$) and RCP 2.6 ($t = 3.50$, $df = 7$, $p = .010$), respectively (Table S2.2b in Appendix S2). Similarly, projected distribution ranges also shifted up the elevational gradient over time for all RCPs and thresholds considered (Figure 4b). The elevational change over time was greatest when considering the core range (Kappa threshold) under scenario RCP 8.5 with an average rate of 34.3 m/decade ($t = 11.95$, $df = 7$, $p < .001$) across all species. The elevational shifts were projected to be less strong and rapid when considering the remaining thresholds and RCP scenarios (Table S2.2b in Appendix S2). The total area size of projected core ranges more than doubled over time for nearly all species and RCP scenarios (Figure 4c, Table S2.2c in Appendix S2), with an average increase of 18,700 km^2/decade across species under RCP 8.5 ($t = 7.47$, $df = 7$, $p < .001$). While we found a general tendency for predicted distribution ranges to become less clustered (i.e. more dispersed) compared with the current situation (Figure 4d), a statistical difference was only found for the MSSS threshold under the scenario RCP 8.5 and for the P10 threshold across RCP scenarios (Table S2.2d in Appendix S2). As such, predicted core ranges were found to largely maintain their current degree of clustering (Figure 4d, Table S2.2d in Appendix S2).

3.4 | Changes in inter-specific range overlap

The projected shifts in species-specific distributions over time led to distinct changes in inter-specific range overlap, though patterns varied between the RCP scenarios and thresholds considered (Figure 5).

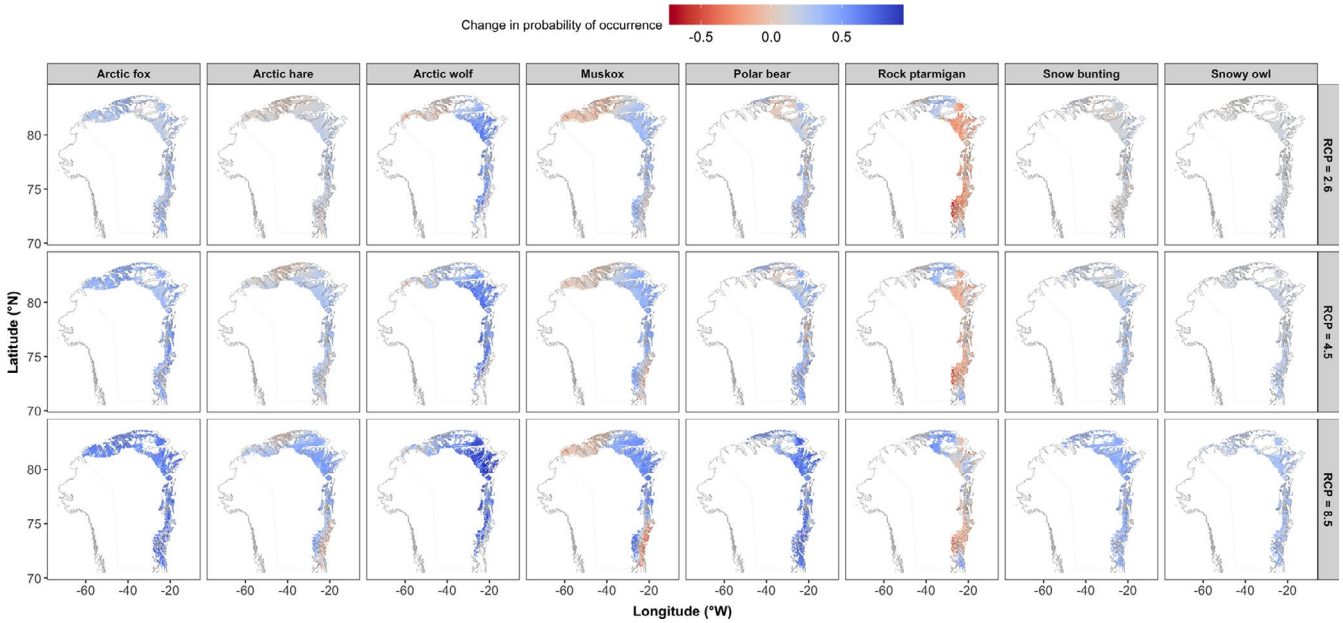

FIGURE 3 Maps of the spatiotemporal change in probability of occurrence for the eight studied vertebrate species in the Northeast Greenland National Park between periods 1979–2013 and 2061–2080 using three RCP scenarios and the mean of three GCMs (see Figures 2.3–2.10 in Appendix S2 for individual GCMs). Areas where probability of occurrences decreased over time (values < 0) are depicted in red, areas with no change (values = 0) are indicated in grey, while areas where probability of occurrences increased over time (values > 0) are depicted in blue

In general, proportional range overlap between most species' combinations increased with severity of the climate change scenarios. However, the increase was most pronounced for the threshold P10. Proportional range overlap for the thresholds Kappa and MSSS was projected to decrease or remain stable between most species' combinations under scenario RCP 2.6 and 4.5 and increase under RCP 8.5 only (Figure 5).

4 | DISCUSSION

This study provides a comprehensive overview of how projected climate change scenarios for north-east Greenland may shift species' distributions and subsequently inter-specific overlap of eight Arctic vertebrate species within the world's largest land-based national park. Following our expectation (P_1), we found strong indications for northwards range shifts by all species when contrasting probability of occurrences between recent (1979–2013) and future (2061–2080) bioclimatic conditions. Similarly, projected distribution ranges were found to move up the elevational gradient (also supporting P_1). Both of these directional shifts were apparent across SDM thresholds considered, and clearly accelerated with the severity of the RCP scenarios (supporting P_2). In fact, the range shifts across RCP scenarios found here were all greater than reported in a previous meta-analysis (16.9 km/decade over the latitudinal gradient) that was based on a wider array of taxa and ecosystems from across the globe (Chen et al., 2011). As such, our Arctic case study underlines the notion that climate change impacts are most pronounced in areas with higher levels of warming, leading to accelerated shifts in species' ranges towards the poles (Chen et al., 2011; IPCC, 2013). Importantly, we also found a clear expansion of species' distribution ranges under future conditions, with core ranges more than doubling in size for nearly all species and RCP scenarios. Together with a general tendency for less clustered distribution ranges under the RCP scenarios considered, we conclude that future climatic conditions in vast areas in north Greenland may not have such a destressing impact on the distribution of cold-adapted species than perhaps previously suspected, at least not within this century.

Species-specific responses to changing climatic conditions are often detected and likely driven by differences in physiological traits (e.g. thermal tolerance), which can culminate into a restructuring of biotic communities over large areas (Lavergne et al., 2010). In agreement, the importance of bioclimatic variables included in our MaxEnt models and their influence on the probability of occurrence differed between species, driving species-specific changes between current and projected distributions. The projected climate-induced shifts in species distributions resulted in altered inter-specific overlap over time and space (as expected under P_3); yet, the direction and strength of changes in overlap varied between the SDM thresholds and RCP scenarios considered and were largely independent of species-pair combinations. For example, we found a decline in overlap of core distribution ranges between all species combinations under the so-called "peak" scenario that would keep global temperature rise below 2°C by 2100 (RCP

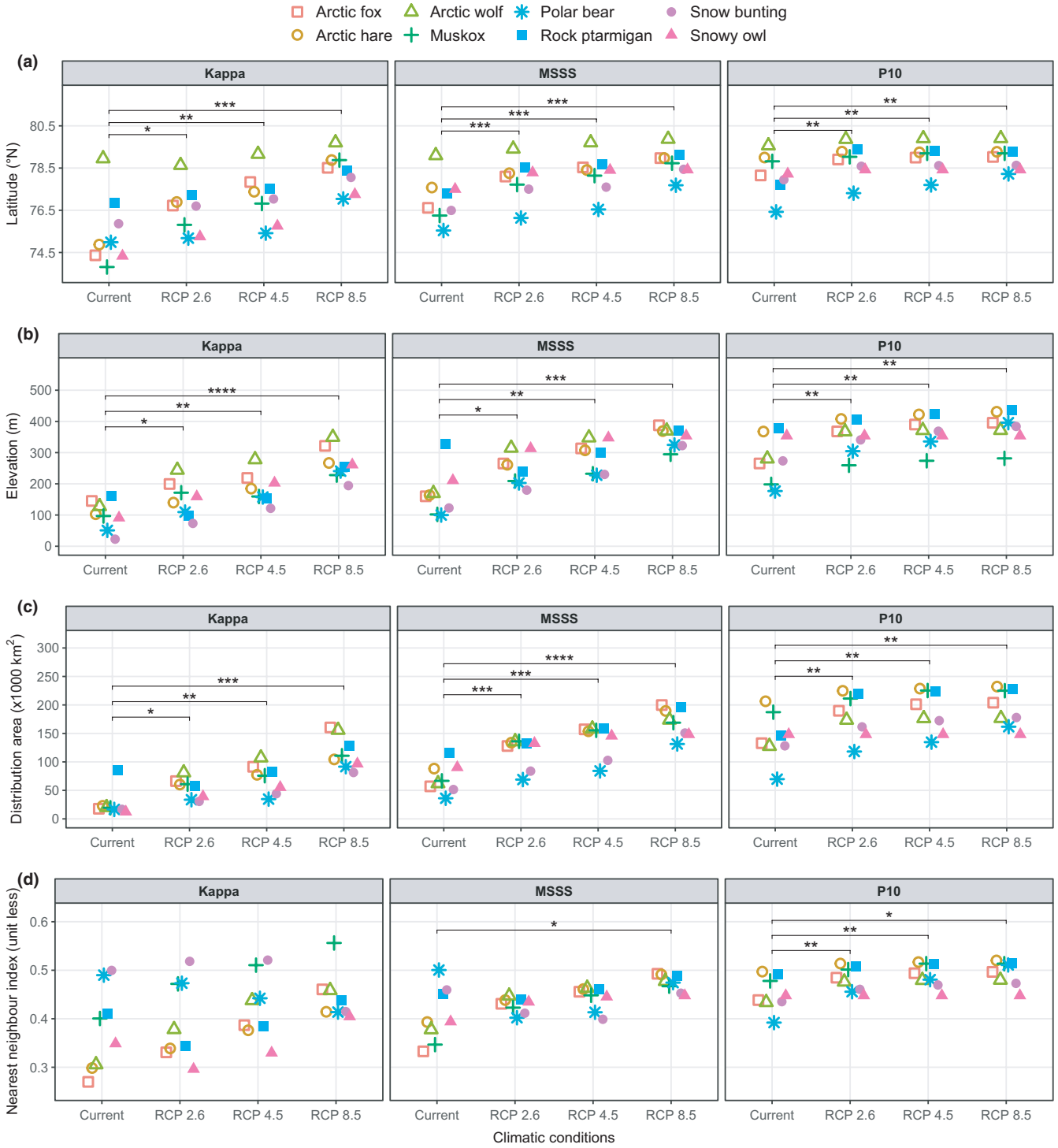

FIGURE 4 Species-specific shifts in distribution ranges across the (a) latitudinal and (b) elevational gradient as well as (c) changes in total area size and (d) clustering of distribution ranges within the Northeast Greenland National Park between the periods 1979–2013 (current) and 2061–2080 (depicted by RCPs 2.6, 4.5 and 8.5). Species are indicated with different colours and symbols as explained in the legend on top. Results are provided for three SDM thresholds: Kappa, MSSS and P10. Significant differences between current and future values, as determined by paired sample *t* tests, are indicated with brackets and stars where * indicates $p < .05$, ** indicates $p < .01$ and *** indicates $p < .001$ (see Table S2.2 in Appendix S2 for full test outputs). Nearest neighbour index values closer to 1 indicate reduced clustering and more evenly dispersion of occurrence. Values were derived based on the species-specific optimal maximum entropy (the complimentary log–log output) models as identified by the Akaike information criterion value corrected for small sample sizes

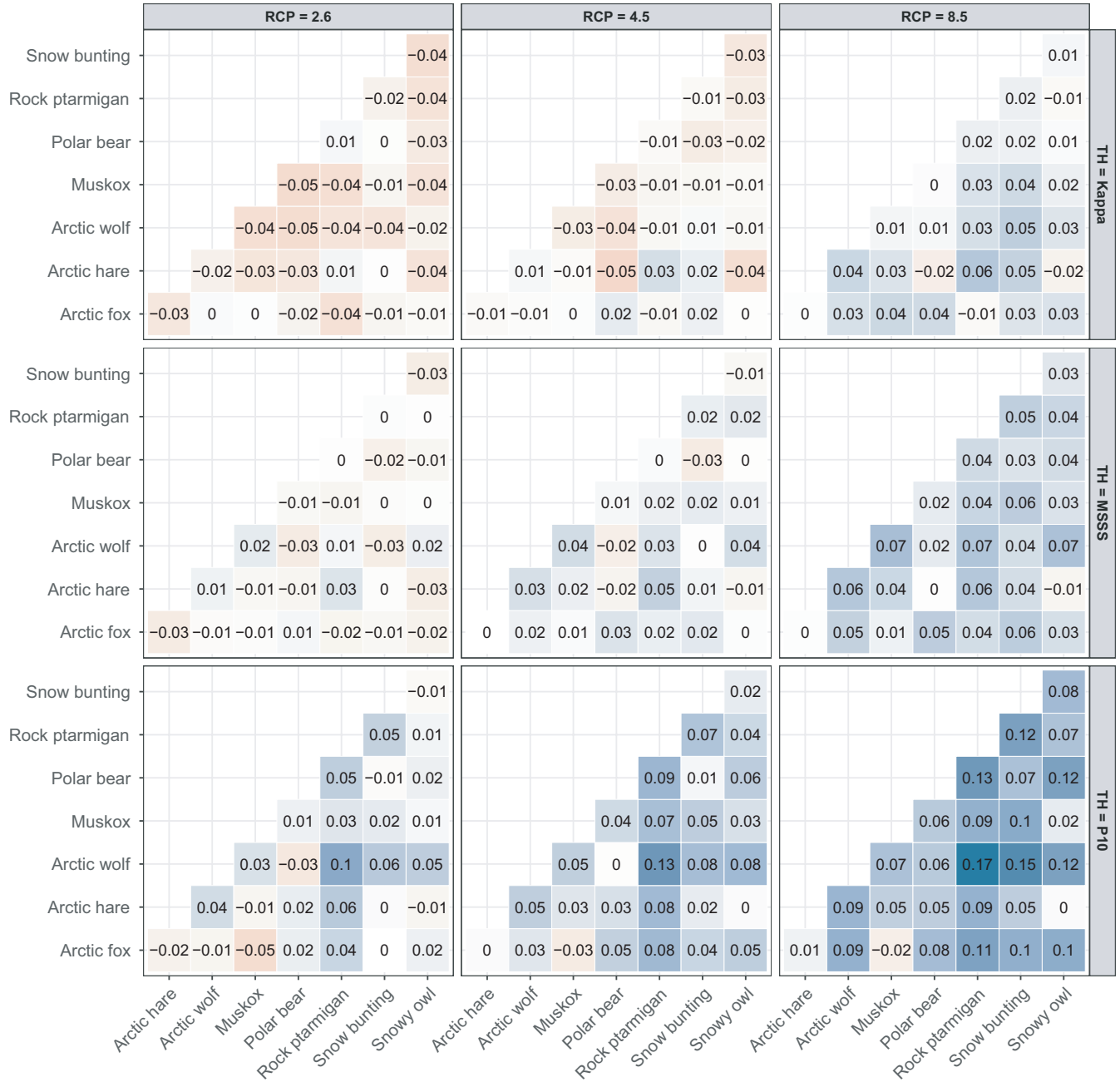

FIGURE 5 Proportional change in inter-specific overlap of distributional ranges as determined by the difference in Schoener's *D* niche overlap index between the periods 1979–2013 (current) and 2061–2080 (depicted by RCPs 2.6, 4.5 and 8.5) for the eight studied Arctic species found in the Northeast Greenland National Park. Results are provided for three SDM thresholds (TH): Kappa, MSSS and P10. Negative values (in salmon colour) indicate a decrease in range overlap between species over time, and zero values (in white) indicate no change, while positive values (in blue) indicate an increase in range overlap between species over time

2.6). In contrast, we found an increase in overlap between all species combinations under the most severe scenario that would limit global temperature rise to 4°C in year 2100 (RCP 8.5). Overall, our findings do not lend much support to the notion that that future climate change in this region will lead to a complete rearrangement of trophic interactions and food-web dynamics, as hypothesized elsewhere (Legagneux et al., 2014), though further studies are required to fully address this issue.

Efforts to predict shifts in species distribution ranges and overlap are critical to inform management and conservation initiatives (Elsen et al., 2020), but estimating climate change effects with SDMs alone remains challenging (White et al., 2018). Our correlative analyses focus purely on estimating possible shifts in distribution ranges based on gradual changes in climatic conditions and ignore possible biotic interactions. Indeed, our approach follows the Eltonian noise hypothesis (ENH), which proposes that although biotic interactions

may be a major driver of species abundance and distribution at relatively small spatial resolutions, their effects are averaged out in large-scale SDMs with coarse resolutions (Soberón & Nakamura, 2009). However, several studies have now uncovered direct effects of biotic factors/interactions on species distributions using large-scale SDMs (de Araújo et al., 2014; Jenkins et al., 2020). Importantly, these studies aimed to quantify current species distributions and did not use forecasting under changing environmental conditions. Although we adopted a purely bioclimatic approach here, we do not dispute the importance of biotic and other factors (e.g. vegetation and ice-melt dynamics) in determining species distributions in the Arctic. We do stress, however, that incorporating interactions between climatic and biotic factors is particularly complex when the aim is to project distribution patterns into the future. For example, including vegetation layers into our SDMs would likely increase confidence in model output for herbivorous species under current conditions. Yet, forecasting changes in high-Arctic vegetation communities under climate change is still in its infancy and currently possible at relatively small spatial scales only (Stewart et al., 2018). Doing so at the landscape scale, as would be required in our forecasting analyses, remains a complicated task (Franklin et al., 2020). This is due to the multitude of biotic and abiotic interactions that vary over space, as well as time lag effects involved between loss of snow/ice cover and the build-up of soil depth and quality that is needed for vegetation growth (Jobbágy & Jackson, 2000). Using bioclimatic variables as surrogates for actual limiting resources, such as forage availability and quality, is often the only reliable alternative to assess possible changes in species ranges under future global warming. We thus interpret our results under the assumption that biotic factors can correlate closely with abiotic variables and that our SDMs capture an important part of the biotic processes involved in species distributions.

Systematically collecting long-term location data of wildlife across large areas in the high-Arctic is extremely challenging and expensive, and thus rare. The here analysed data set is likely the most extensive that is currently available for within Greenland, possibly even within the Arctic region. Nonetheless, some challenges in the data set required consideration so as to reduce prediction uncertainty, which is often neglected in large-scale SDM studies investigating climate change impacts (Beale & Lennon, 2012). First, location accuracy of the presence data was unknown, yet likely poor in comparison with, for example GPS tracking or camera trap data. We attempted to minimize this uncertainty related to location error by using coarse grid cells of bioclimatic raster data (20 km^2). Next, an important assumption of SDM studies is that sampling of location data is adequate and representative, which we could not quantify here given the rather opportunistic nature of how species observations were collected using unknown routes of the Sirius Dog Sled Patrol. To account for this issue as much as possible, we incorporated spatial sampling bias files in the species-specific MaxEnt models, which is an established method to restrict background points to geographic areas where species occurrences were found, leading to more realistic predictions (Phillips et al., 2009). We also tailored the entire analytical procedure to increase reliability of model output as much as possible by, for example incorporating a wide range of emission scenarios, excluding areas with novel bioclimatic conditions in the future and limiting overparameterization through extensive MaxEnt model pruning (Santini et al., 2021). We also explicitly quantified a known source of uncertainty in climate change studies, namely the GCMs considered in forecasting (Thuiller et al., 2019). Finally, it is important to reiterate that our study system is a remote and protected area, currently unaffected by human disturbance. Anthropogenic influences on contemporary species distributions can therefore be considered low, which eliminates an otherwise known bias in forecasting climate change impacts on species ranges (Faurby & Araújo, 2018). However, as the Arctic climate warms and the ice continues to melt, human activity in the region (e.g. oil and mineral extraction) is steadily growing and will likely play an increasingly important role in shaping future distribution ranges of wildlife species resident to the Arctic (Johnson et al., 2005). Despite these caveats, and based on a purely bioclimatic assessment of species-specific shifts in distribution and overlap under future climate change scenarios, our results clearly show that ongoing climate warming is likely to have a strong impact in the Arctic, with rapid and directional shifts in species' distribution ranges towards higher latitudes and elevations. To what extent associated changes in inter-specific overlap of distribution ranges under future conditions will impact local food-web dynamics and ultimately ecosystem functioning remains to be studied in more detail. Our results therefore emphasize that understanding climate change effects on terrestrial food-web dynamics in the Arctic should remain a research priority.

ACKNOWLEDGEMENTS

We thank all sled patrol teams whose dedicated efforts over the years have made this study possible. We also thank the Joint Arctic Command for making the data available to us. We also acknowledge the Editor and an anonymous reviewer for their constructive comments on a previous draft, which greatly improved the paper.

DATA AVAILABILITY STATEMENT

Data and code used in this study are available through Dryad: Data for: Rapid shifts in Arctic tundra species' distributions and inter-specific range overlap under future climate change https://doi.org/10.5061/dryad.2bvq83bq9.

ORCID

Floris M. van Beest https://orcid.org/0000-0002-5701-4927
Larissa T. Beumer https://orcid.org/0000-0002-5255-1889
Sophia V. Hansson https://orcid.org/0000-0001-5874-0720
Niels M. Schmidt https://orcid.org/0000-0002-4166-6218

REFERENCES

Beale, C. M., & Lennon, J. J. (2012). Incorporating uncertainty in predictive species distribution modelling. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1586), 247–258. https://doi.org/10.1098/rstb.2011.0178

Bennett, S., Duarte, C. M., Marbà, N., & Wernberg, T. (2019). Integrating within-species variation in thermal physiology into climate change ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1778), 20180550. https://doi.org/10.1098/rstb.2018.0550

Beumer, L. T., van Beest, F. M., Stelvig, M., & Schmidt, N. M. (2019). Spatiotemporal dynamics in habitat suitability of a large Arctic herbivore: Environmental heterogeneity is key to a sedentary lifestyle. *Global Ecology and Conservation*, *18*, e00647. https://doi.org/10.1016/J.GECCO.2019.E00647

Brown, J. L., Bennett, J. R., & French, C. M. (2017). SDMtoolbox 2.0: The next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ*, *2017*(12), e4095. https://doi.org/10.7717/peerj.4095

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Clairbaux, M., Fort, J., Mathewson, P., Porter, W., Strøm, H., & Grémillet, D. (2019). Climate change could overturn bird migration: Transarctic flights and high-latitude residency in a sea ice free Arctic. *Scientific Reports*, *9*(1), 1–13. https://doi.org/10.1038/s41598-019-54228-5

Clark, P. J., & Evans, F. C. (1954). Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology*, *35*(4), 445–453. https://doi.org/10.2307/1931034

de Araújo, C. B., Marcondes-Machado, L. O., & Costa, G. C. (2014). The importance of biotic interactions in species distribution models: A test of the Eltonian noise hypothesis using parrots. *Journal of Biogeography*, *41*(3), 513–523. https://doi.org/10.1111/jbi.12234

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A. Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. M. Overton, J., Townsend Peterson, A., … E. Zimmermann, N. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29*(2), 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, *1*(4), 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x

Elith, J., & Leathwick, J. R. (2009). Species Distribution Models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Elsen, P. R., Monahan, W. B., Dougherty, E. R., & Merenlender, A. M. (2020). Keeping pace with climate change in global terrestrial protected areas. *Science Advances*, *6*(25), eaay0814. https://doi.org/10.1126/sciadv.aay0814

Faurby, S., & Araújo, M. B. (2018). Anthropogenic range contractions bias species climate change forecasts. *Nature Climate Change*, *8*(3), 252–256. https://doi.org/10.1038/s41558-018-0089-x

Forchhammer, M., & Boertmann, D. (1993). The muskoxen *Ovibos moschatus* in north and northeast Greenland: Population trends and the influence of abiotic parameters on population dynamics. *Ecography*, *16*(4), 299–308. https://doi.org/10.1111/j.1600-0587.1993.tb00219.x

Forester, B. R., DeChaine, E. G., & Bunn, A. G. (2013). Integrating ensemble species distribution modelling and statistical phylogeography to inform projections of climate change impacts on species distributions. *Diversity and Distributions*, *19*(12), 1480–1495. https://doi.org/10.1111/ddi.12098

Franklin, O., Harrison, S. P., Dewar, R., Farrior, C. E., Brännström, Å., Dieckmann, U., Pietsch, S., Falster, D., Cramer, W., Loreau, M., Wang, H., Mäkelä, A., Rebel, K. T., Meron, E., Schymanski, S. J., Rovenskaya, E., Stocker, B. D., Zaehle, S., Manzoni, S., … Prentice, I. C. (2020). Organizing principles for vegetation dynamics. *Nature Plants*, *6*(5), 444–453. https://doi.org/10.1038/s41477-020-0655-x

Gilg, O., Kovacs, K. M., Aars, J., Fort, J., Gauthier, G., Grémillet, D., Ims, R. A., Meltofte, H., Moreau, J., Post, E., Schmidt, N. M., Yannic, G., & Bollache, L. (2012). Climate change and the ecology and evolution of Arctic vertebrates. *Annals of the New York Academy of Sciences*, *1249*(1), 166–190. https://doi.org/10.1111/j.1749-6632.2011.06412.x

Giorgetta, M. A., Jungclaus, J., Reick, C. H., Legutke, S., Bader, J., Böttinger, M., Brovkin, V., Crueger, T., Esch, M., Fieg, K., Glushak, K., Gayler, V., Haak, H., Hollweg, H.-D., Ilyina, T., Kinne, S., Kornblueh, L., Matei, D., Mauritsen, T., … Stevens, B. (2013). Climate and carbon cycle changes from 1850 to 2100 in MPI-ESM simulations for the Coupled Model Intercomparison Project phase 5. *Journal of Advances in Modeling Earth Systems*, *5*(3), 572–597. https://doi.org/10.1002/jame.20038

Høye, T. T., Kresse, J.-C., Koltz, A. M., & Bowden, J. J. (2020). Earlier springs enable high-Arctic wolf spiders to produce a second clutch. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1929), 20200982. https://doi.org/10.1098/rspb.2020.0982

IPCC (2013). Climate change 2013 - The Physical Science Basis Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley (Eds.), *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.

Jenkins, D. A., Lecomte, N., Andrews, G., Yannic, G., & Schaefer, J. A. (2020). Biotic interactions govern the distribution of coexisting ungulates in the Arctic Archipelago – A case for conservation planning. *Global Ecology and Conservation*, *24*, e01239. https://doi.org/10.1016/j.gecco.2020.e01239

Jobbágy, E. G., & Jackson, R. B. (2000). The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications*, *10*(2), 423–436. https://doi.org/10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2

Johnson, C., Boyce, M., Case, R., Cluff, H., Gau, R., Gunn, A., & Mulders, R. (2005). Cumulative Effects of Human Developments on Arctic Wildlife. *Wildlife Monographs*, *160*(1), 1–36. https://doi.org/10.2193/0084-0173(2005)160[1:CEOHDO]2.0.CO;2

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*(1), 1–20. https://doi.org/10.1038/sdata.2017.122

Kovacs, K. M., Lydersen, C., Overland, J. E., & Moore, S. E. (2011). Impacts of changing sea-ice conditions on Arctic marine mammals. *Marine Biodiversity*, *41*(1), 181–194. https://doi.org/10.1007/s12526-010-0061-0

Lavergne, S., Mouquet, N., Thuiller, W., & Ronce, O. (2010). Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, and Systematics*, *41*(1), 321–350. https://doi.org/10.1146/annurev-ecolsys-102209-144628

Legagneux, P., Gauthier, G., Lecomte, N., Schmidt, N. M., Reid, D., Cadieux, M.-C., Berteaux, D., Bêty, J., Krebs, C. J., Ims, R. A., Yoccoz, N. G., Morrison, R. I. G., Leroux, S. J., Loreau, M., & Gravel, D. (2014). Arctic ecosystem structure and functioning shaped by climate and herbivore body size. *Nature Climate Change*, *4*(5), 379–383. https://doi.org/10.1038/nclimate2168

Lenoir, J., Gégout, J. C., Marquet, P. A., De Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, *320*(5884), 1768–1771. https://doi.org/10.1126/science.1156831

Liu, C., White, M., & Newell, G. (2013). Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*, *40*(4), 778–789. https://doi.org/10.1111/jbi.12058

Louthan, A. M., Doak, D. F., & Angert, A. L. (2015). Where and when do species interactions set range limits? *Trends in Ecology and Evolution*, *30*(12), 780–792. https://doi.org/10.1016/j.tree.2015.09.011

Merow, C., Smith, M. J., & Silander, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. *Ecography*, *36*(10), 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x

Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M., & Anderson, R. P. (2014). ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution*, *5*(11), 1198–1205. https://doi.org/10.1111/2041-210x.12261

Naimi, B., & Araújo, M. B. (2016). sdm: A reproducible and extensible R platform for species distribution modelling. *Ecography*, *39*(4), 368–375. https://doi.org/10.1111/ecog.01881

Neukermans, G., Oziel, L., & Babin, M. (2018). Increased intrusion of warming Atlantic water leads to rapid expansion of temperate phytoplankton in the Arctic. *Global Change Biology*, *24*(6), 2545–2553. https://doi.org/10.1111/gcb.14075

Nielsen, U. N., & Wall, D. H. (2013). The future of soil invertebrate communities in polar regions: Different climate change responses in the Arctic and Antarctic? *Ecology Letters*, *16*(3), 409–419. https://doi.org/10.1111/ele.12058

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42. https://doi.org/10.1038/nature01286

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), eaai9214. https://doi.org/10.1126/science.aai9214

Persechino, A., Mignot, J., Swingedouw, D., Labetoulle, S., & Guilyardi, E. (2013). Decadal predictability of the Atlantic meridional overturning circulation and climate in the IPSL-CM5A-LR model. *Climate Dynamics*, *40*(9–10), 2359–2380. https://doi.org/10.1007/s00382-012-1466-1

Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., & Blair, M. E. (2017). Opening the black box: An open-source release of Maxent. *Ecography*, *40*(7), 887–893. https://doi.org/10.1111/ecog.03049

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3), 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecological Applications*, *19*(1), 181–197. https://doi.org/10.1890/07-2153.1

Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., Fox, A. D., Gilg, O., Hik, D. S., Hoye, T. T., Ims, R. A., Jeppesen, E., Klein, D. R., Madsen, J., McGuire, A. D., Rysgaard, S., Schindler, D. E., Stirling, I., Tamstorf, M. P., … Aastrup, P. (2009). Ecological dynamics across the arctic associated with recent climate change. *Science*, *325*(5946), 1355–1358. https://doi.org/10.1126/science.1173113

Santini, L., Benítez-López, A., Čengić, M., Maiorano, L., & Huijbregts, M. A. J. (2021). Assessing the reliability of species distribution projections in climate change research. *Diversity and Distributions*, *27*(6), 1035–1050. https://doi.org/10.1101/2020.06.10.143917

Scheffers, B. R., De Meester, L., Bridge, T. C. L., Hoffmann, A. A., Pandolfi, J. M., Corlett, R. T., Butchart, S. H. M., Pearce-Kelly, P., Kovacs, K. M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W. B., Martin, T. G., Mora, C., Bickford, D., & Watson, J. E. M. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, *354*(6313), aaf7671. https://doi.org/10.1126/science.aaf7671

Schmidt, N. M., Hardwick, B., Gilg, O., Høye, T. T., Krogh, P. H., Meltofte, H., Michelsen, A., Mosbacher, J. B., Raundrup, K., Reneerkens, J., Stewart, L., Wirta, H., & Roslin, T. (2017). Interaction webs in arctic ecosystems: Determinants of arctic change? *Ambio*, *46*(Suppl 1), 12–25. https://doi.org/10.1007/s13280-016-0862-x

Schmidt, N. M., Ims, R. A., Høye, T. T., Gilg, O., Hansen, L. H., Hansen, J., Lund, M., Fuglei, E., Forchhammer, M. C., & Sittler, B. (2012). Response of an arctic predator guild to collapsing lemming cycles. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1746), 4417–4422. https://doi.org/10.1098/rspb.2012.1490

Schoener, T. W. (1968). The anolis lizards of Bimini: Resource partitioning in a complex fauna. *Ecology*, *49*(4), 704–726. https://doi.org/10.2307/1935534

Soberón, J., & Nakamura, M. (2009). Niches and distributional areas: Concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(Suppl. 2), 19644–19650. https://doi.org/10.1073/pnas.0901637106

Stewart, L. L., Simonsen, C. E., Svenning, J.-C.-C., Schmidt, N. M., & Pellissier, L. (2018). Forecasted homogenization of high Arctic vegetation communities under climate change. *Journal of Biogeography*, *45*(11), 2576–2587. https://doi.org/10.1111/jbi.13434

Taylor, J. J., Lawler, J. P., Aronsson, M., Barry, T., Bjorkman, A. D., Christensen, T., Coulson, S. J., Cuyler, C., Ehrich, D., Falk, K., Franke, A., Fuglei, E., Gillespie, M. A., Heiðmarsson, S., Høye, T., Jenkins, L. K., Ravolainen, V., Smith, P. A., Wasowicz, P., & Schmidt, N. M. (2020). Arctic terrestrial biodiversity status and trends: A synopsis of science supporting the CBMP State of Arctic Terrestrial Biodiversity Report. *Ambio*, *49*(3), 833–847. https://doi.org/10.1007/s13280-019-01303-w

Thuiller, W., Guéguen, M., Renaud, J., Karger, D. N., & Zimmermann, N. E. (2019). Uncertainty in ensembles of global biodiversity scenarios. *Nature Communications*, *10*(1), 1–9. https://doi.org/10.1038/s41467-019-09519-w

Vignali, S., Barras, A. G., Arlettaz, R., & Braunisch, V. (2020). *SDMtune*: An R package to tune and evaluate species distribution models. *Ecology and Evolution*, *10*, 11488–11506. https://doi.org/10.1002/ece3.6786

Watanabe, M., Suzuki, T., O'ishi, R., Komuro, Y., Watanabe, S., Emori, S., Takemura, T., Chikira, M., Ogura, T., Sekiguchi, M., Takata, K., Yamazaki, D., Yokohata, T., Nozawa, T., Hasumi, H., Tatebe, H., & Kimoto, M. (2010). Improved climate simulation by MIROC5: Mean states, variability, and climate sensitivity. *Journal of Climate*, *23*(23), 6312–6335. https://doi.org/10.1175/2010JCLI3679.1

White, K. S., Gregovich, D. P., & Levi, T. (2018). Projecting the future of an alpine ungulate under climate change scenarios. *Global Change Biology*, *24*(3), 1136–1149. https://doi.org/10.1111/gcb.13919

Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., Guisan, A., Elith, J., Dudík, M., Ferrier, S., Huettmann, F., Leathwick, J. R., Lehmann, A., Lohmann, L., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. M. C., … Zimmermann, N. E. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, *14*(5), 763–773. https://doi.org/10.1111/j.1472-4642.2008.00482.x

Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J. J., Leitão, P. J., Park, D. S., Peterson, A. T., Rapacciuolo, G., Schmatz, D. R., Schröder, B., Serra-Diaz, J. M., Thuiller, W., … Merow, C. (2020). A standard protocol for reporting species distribution models. *Ecography*, *43*(9), 1261–1277. https://doi.org/10.1111/ecog.04960

BIOSKETCH

The authors are Arctic ecologists and ecogeochemists whose work focusses on the impacts of climate and environmental change on the distribution and abundance of species and transfer of nutrients through local food chains.

Authors contributions: FMvB & NMS conceived the idea. ASA collated and digitized data. FMvB designed the methodology with inputs from all coauthors. FMvB performed the analyses with contributions from LTB. SVH created the artwork. FMvB led the writing of the manuscript. All authors contributed critically to the drafts.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: van Beest FM, Beumer LT, Andersen AS, Hansson SV, Schmidt NM. Rapid shifts in Arctic tundra species' distributions and inter-specific range overlap under future climate change. *Divers Distrib*. 2021;27:1706–1718. https://doi.org/10.1111/ddi.13362