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## Long-distance migratory birds threatened by multiple independent risks from global change

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### Abstract

Many species migrate long distances annually between their breeding and wintering areas<sup>1</sup>. While global change affects both ranges, impact assessments have generally focused on breeding ranges and ignore how environmental changes influence migrants across geographic regions and the annual cycle<sup>2,3</sup>. Using range maps and species distribution models, we quantified the risk of summer and winter range loss and migration distance increase from future climate and land cover changes on long-distance migratory birds of the Holarctic (n=715). Risk estimates are largely independent of each other and magnitudes vary geographically. If seasonal range losses and increased migration distances are not considered, we strongly underestimate the number of threatened species by 18-49% and the overall magnitude of risk for 17-50% species. Many of the analysed species facing multiple global change risks are not listed by IUCN as threatened or near threatened. Neglecting seasonal migration in impact assessments could thus seriously misguide species' conservation.

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#### Data availability

All data except the GLOBIO land cover data are publicly available; bird range maps at [www.birdlife.org](http://www.birdlife.org), climate data at [www.worldclim.org](http://www.worldclim.org), bird trait data at <https://doi.org/10.6084/m9.figshare.c.3306933>, and bird phylogenetic data at [www.birdtree.org](http://www.birdtree.org). The GLOBIO land cover scenarios were provided by courtesy of Michel Bakkenes and are not publicly available.

#### Author contributions

D.Z. and N.E.Z. conceived the general idea and designed the study with the help of all authors. D.Z. ran the analyses and led the writing. All authors interpreted results and significantly contributed to writing and editing the manuscript.

#### Competing financial interests statement

The authors declare no competing financial interests.

Global warming and land use change are causing substantial species range shifts, contractions and (local) extirpations<sup>4,5</sup>. Migratory species could be particularly vulnerable to these changes because they move between distinct geographic areas and thus are influenced by factors experienced in different parts of the world<sup>1,6</sup>. Through carry-over effects, environmental conditions experienced in one location (breeding grounds, wintering grounds or migratory route) can affect the fitness in subsequent locations and the long-term population dynamics<sup>1,3</sup>. In recent decades, migratory bird populations have declined worldwide<sup>7</sup> and it is often unclear where in the annual cycle these declines occur and how they could be reversed<sup>8</sup>.

An increasing number of studies have analysed climate change effects on migratory birds but most are limited to a few species<sup>9–11</sup>, have focused on phenological shifts<sup>12</sup>, and are biased towards the breeding season<sup>13</sup>. Species distribution models<sup>14</sup> have been widely used to project biodiversity response to environmental change<sup>15,16</sup>. However, only few studies have explicitly forecasted the effects of global change on both the breeding and wintering ranges of migratory birds<sup>17</sup> and the potential changes in migration patterns between seasonal ranges<sup>18,19</sup>, meaning that large-scale impact assessments focussing on the full annual cycle are largely missing<sup>2,20</sup>. Furthermore, most forecasts quantified only potential climate change effects, although land cover has been reported to strongly affect range changes in birds and other taxa<sup>11,21</sup>.

Here, we assess the individual and combined effects of future climate and land cover change on long-distance migratory birds breeding in the Holarctic ( $n=715$ , excluding very rare species). We concentrate on three key aspects of migratory species' biology (breeding, wintering, and migration) and quantify large-scale environmental change impacts in terms of: (i) summer (breeding) range loss, (ii) winter range loss, and (iii) increased migration distance resulting from seasonal range shifting in opposing directions (Fig. 1). First, we assess the magnitude of these risks over different global change scenarios and ask whether land cover change could reinforce or counteract any negative climate change impacts. Second, we investigate whether the three proposed risks are interdependent or threaten species independently. Strong interdependence would be surprising because forecasted changes in climate and land cover are not uniform throughout the year and across the globe<sup>22</sup>. Third, we analyse the relationship between species risks and geographic and ecological traits as well as species' current IUCN red list status. Last, we evaluate how many species are facing multiple risks but are currently not recognized as being of conservation concern.

For each species, we estimated species distribution models from range maps (at 0.5° resolution) and projected potential mid-century (2040-2061) changes in summer and winter range area and range position for scenarios of climate and land cover change. Consensus projections were derived from three statistical distribution models, five general circulation models and one global land use change model, considering three different storylines derived from combinations of two representative concentration pathways and three shared socio-economic pathways. We assumed species to move to newly suitable areas with a maximum dispersal of 1000 km over the considered time period (other dispersal scenarios were tested and showed consistent results).

We found stronger projected changes in species richness during summer compared to winter (Fig. 2), which is consistent with previous analyses (e.g., *Sylvia* warblers<sup>18</sup>). Climate change was the main driver of these changes. Only projected changes in winter richness in the Southern hemisphere could be partly attributed to land cover change (Fig. S1). Earlier projections of global bird diversity indicated much stronger land cover effects, but mainly in the tropics while climate impacts were strongest in high latitudes (> 30° N)<sup>21,23</sup>, which corroborates our results.

Under a low emission scenario, most long-distance migrants were projected to shift their ranges northwards by  $2.21^{\circ} \pm 1.15^{\circ}$  (mean  $\pm$  sd;  $246 \pm 128$  km) in summer and  $1.61^{\circ} \pm 1.50^{\circ}$  ( $179 \pm 167$  km) in winter (Fig. 3), which is comparable to previous studies on European breeding birds<sup>17,18</sup>. As hypothesised, the projected global change risks were largely independent of each other. Indeed, we found only a weak correlation between summer range loss and (latitudinal) migration distance increase ( $R^2=0.09$   $p=0.02$ ) and no correlation between the other measures. We projected strong summer range contractions in 83% of the species while winter range loss was slightly less severe and influenced 65% of the species. This corroborates earlier results on Palearctic birds<sup>17,18,23</sup>. However, our cross-continental analyses including the entire Holarctic indicated pronounced regional differences in projected range changes with equal winter range losses and gains in Nearctic migrants whereas most Palearctic migrants face winter range reductions. Projected migration distance increased by  $3 \pm 7\%$  (mean  $\pm$  sd) for Nearctic and Western Palearctic migrants (up to  $8.96^{\circ}$ , 997 km) and decreased by  $1 \pm 9\%$  for Eastern Palearctic migrants (up to  $4.78^{\circ}$ , 533 km; Figs. 3, S2). The magnitude of the risks was mainly driven by climate change. Land cover change had only a minor effect on range areas and migration distance; for low emission scenarios it slightly reinforced and for high emission scenarios it slightly counteracted negative effects from climate change (regardless of dispersal assumptions; Fig. S3).

Phylogenetic regressions showed that global change risks had a stronger association with species' geographic traits than with ecological traits (Table 1). Species located close to the poles experienced higher range losses than equatorial species, which is in line with the expected increase in climate warming magnitude toward Northern latitudes<sup>22</sup>. Summer range loss was higher for migrants breeding further north, and winter range loss was more pronounced for species overwintering further south (Fig. S4). Furthermore, species with small environmental niches were at higher risk from summer range loss and from migration distance increase while current extinction risk status (IUCN red list) was only weakly associated with projected global change risks (Table 1). The latter indicates that all species, regardless of their IUCN category, are similarly susceptible to future global change threats (Fig. 3, Fig. S5).

To quantify how many species face multiple risks, we classified species as potentially at risk if their projected summer or winter population reduction or migration distance increase was larger than 10%. Population reduction was estimated as the proportional change between the sums of current and future habitat suitability derived from SDMs<sup>24</sup>. For the low emission scenario, we found that 560 out of 715 migrants (78%) face at least one of the three proposed risks, with 61% (341 species) projected to suffer from a single threat and 39% (219

species) from multiple threats, mostly a combination of summer and winter range loss (Fig. 4 a,c). The cumulative number of risks typically increased for species with small environmental niches (Table 1). If focussing on summer ranges only, as is usually done in large-scale impact assessments, 139 species (25%) would be misclassified as unthreatened by global change, and the risk level of 210 species (38%) would be underestimated by the omission of multiple risks. These patterns were similar between species listed as “least concern” by IUCN (Fig. 4a) and those listed as “near threatened” and “threatened” (Fig. 4c). To justify listing a species as “near threatened”, the IUCN defines a 10% threshold for projected population declines in populations of intermediate sizes (<15,000 mature individuals) and a 20-25% threshold for larger populations<sup>24</sup>. We thus evaluated the robustness of our results for a 20% threshold and for low and high emission scenarios (Fig. S6). These supplementary estimates confirm that impact assessments focussing exclusively on summer ranges might underestimate the number of potentially threatened species by 18-49% (ratio of overlooked vs. recognized species) and may further underestimate potential negative impacts from multiple risks for 17-50% of the species (1 - proportion of species facing summer population reduction as single vs. part of multiple risks; Figs. 4, S6).

We found distinct geographic patterns in the distribution of migrants facing multiple risks. Palearctic species face mainly a combination of summer and winter population reduction. Nearctic migrants face combinations of increased migration distances with summer or winter population reductions (Figs. 4b). Many species that could suffer from multiple global change risks are not currently listed by IUCN as threatened or near threatened. As a consequence, over large geographic areas, for example in Western North America and Europe, the threats of long-distance migrants to global change might be underestimated (Figs. 4d, S7). Similar geographic patterns were found for species facing only a single global change threat, with western US and Europe showing a high discrepancy between numbers of long-distance migrants currently listed as (near) threatened by IUCN and migrants at risk from future environmental change (Fig. S7).

Our risk estimate based on migration distance is simple and does not consider any direct global change effects, for example changing wind regimes<sup>25</sup>. Furthermore, we chose to use proportional (rather than absolute) increases in migration distance for classifying species as at risk (using the same thresholds for migration risks as for population reduction: 10% or 20%) for two main reasons. First, we assumed that seasonal ranges and associated migration distances have evolved over long (evolutionary) timescales and, thus, that a proportional change of 10–20% could potentially increase mortality risk during migration. Second, our species-level analysis based on range maps does not account for population- and individual-level flyways and we thus approximated migration distances by latitudinal distance between range centroids. This prohibits the calculation of accurate absolute migration distances. Nevertheless, optimal migration theory predicts that any increase in migration distance will cause the species to expend more energy<sup>26</sup>, and refuelling will necessitate longer overall stopover duration<sup>27</sup>. Such extra time costs may not be easy to accommodate in the annual cycle of many migrants given the complex trade-offs in the timing of migration, breeding and moult and its synchronisation with food resources<sup>1,28</sup>. For example, a prolonged spring migration would require earlier departure at the risk of not finding enough food resources *en route*, or late arrival at the risk of reduced breeding success. In the future, it will be

important to better understand how relative and absolute changes in migration distance may affect population dynamics of migratory birds.

In conclusion, our study provides a comprehensive overview of the complexity of large-scale impacts from climate and land cover change on long-distance migratory birds in the Holarctic. We find that global change can affect summer ranges, winter ranges and migration distances independently<sup>18</sup>. As a direct consequence, impact assessments focussing on summer ranges alone will underestimate the number of potentially threatened species as well as the potential impact from multiple risks. Ignoring seasonal ranges in impact assessments could thus seriously misguide conservation targets<sup>2</sup>, both spatially and at the species level. Instead, the full annual cycle should be considered in future forecasting studies, and where possible complemented with finer-scale and more mechanistic approaches. Our results can only provide initial estimates and rely on a number of assumptions. For example, correlative species distribution models are not able to disentangle realised from fundamental niches, which could bias future projections if the range limiting factors changed<sup>29–30</sup>. Large-scale range maps may not be equally accurate for all species and less precise for winter than for summer ranges. Also, at finer spatial resolution, species habitat relations and land cover and land use change may prove more important than at the coarse scale considered here<sup>11</sup>. Furthermore, our dispersal module ignored the effects of fragmentation and species interactions on population spread<sup>30</sup>. As more data become available on distribution, demography and behaviour throughout the annual cycle, they should be used in mechanistic models that assess potential behavioural adaptations and population-level consequences of environmental change. For example, we can explore when migration is advantageous over residency. Our results indicate that migration distances could become shorter for many species (Fig. S2) potentially making it advantageous to cease migration. Empirical data suggest that some species are evolving partial migration<sup>1</sup>. While GPS telemetry has advanced our understanding of individual and population level migration and wintering behaviour for some species<sup>3,9</sup>, we still know little about how global change affects the annual cycle of migratory species and how this translates to overall species vulnerability. We hope that our global assessment will inspire more detailed work embracing this complexity.

## Methods

### Species data

Summer (breeding) and winter (non-breeding) ranges were derived from a global dataset of the world's bird species distributions<sup>31</sup> (data available online [www.birdlife.org](http://www.birdlife.org)). Polygons were gridded at a 0.5° resolution, which matches the resolution of the land cover change scenarios and those of previous analyses using the same data<sup>32,33</sup>. Grid cells were considered as presences if the polygon covered the centre of the grid cell. We considered only long-distance migrants breeding in Palearctic and Nearctic (with range centroids north of 30° latitude, and east resp. west of -18° longitude, and with minimum distance of 10° latitude between breeding and non-breeding range centres). Overall, we identified 825 extant long-distance migrants breeding in the Holarctic. In subsequent analyses, we only included those 715 species (329 Nearctic breeding migrants, 386 Palearctic breeding migrants) that had at least 40 presences (meaning 40 grid cells at 0.5° resolution) both in their summer

range and winter ranges, for which trait and phylogenetic data were available<sup>34,35</sup>, and for which taxonomic classification was consistent between range, trait and phylogenetic data. Of these 715 species, 17 were pelagic specialists (but with pronounced association to land as ensured by our minimum presence threshold); including or excluding these from subsequent analyses did not qualitatively change the results.

### Climate and land cover data

Current and future climate data were extracted from WorldClim at 10' resolution<sup>36</sup> ([www.worldclim.org](http://www.worldclim.org)) and aggregated to 0.5° resolution. For each season, we selected two climate variables to describe the abiotic environment that reflect known direct and indirect drivers of bird distributions and have been used previously in the study of seasonal niches<sup>37</sup>: mean temperature and total precipitation during summer season (May-July) and during winter season (November-January). Future climate by 2050 (average for 2041-2060) was represented by a set of five general circulation models (GCMs) from the CMIP5 database for two RCPs (representative concentration pathways; RCP4.5 “stabilisation of radiative forcing by 2100”, and RCP8.5 “business as usual”). GCMs included CCSM4, IPSL-CM5A-LR, HadGEM2-ES, MIROC-ESM and MPI-ESM-LR, covering a wide range of CMIP5 model performances and reflecting predictions ranging from pessimistic to optimistic<sup>22</sup>.

Current and future (2050) global land cover scenarios were simulated by the GLOBIO model (v3.5) at 0.5° resolution<sup>38</sup>. We chose three SSPs (shared socio-economic pathways) consistent with the socio-economic assumptions of the RCPs<sup>39</sup>: SSP1 “global sustainable development” (consistent with RCP4.5), SSP 3 “Regional competition” and SSP5 “Economic optimism” (consistent with RCP8.5). These new scenarios can be mapped onto the SRES illustrative scenarios, such that a combination RCP4.5-SSP1 would correspond to a B1 world, RCP8.5-SSP3 to a A2 world, and RCP8.5-SSP5 to a A1F1 world<sup>39</sup>. Land cover classes in GLOBIO follow the classification scheme of the Global Land Cover 2000 Project (GLC 2000). We further aggregated current and future land cover into seven proportional land cover classes: water, woodland, shrubland, grassland, cropland, bare ground, and urban/built. We thus considered two climate and seven land cover variables in subsequent modelling. These variables were only weakly correlated with absolute Pearson correlation coefficients  $|r|$  between 0 and 0.44. These values are well under a threshold of 0.7, a collinearity that is generally regarded as unproblematic<sup>40</sup>. In the species distribution models, we only included species-specific sets of 4-5 variables as explained below.

### Species distribution models

Species distribution models (SDMs) were calibrated separately for the summer and winter range of each species using three statistical algorithms, namely: generalized linear models (GLM), generalized additive models (GAM), and random forests (RF) within the ensemble modelling platform *biomod*<sup>241</sup> in R<sup>42</sup>. We only included the five most important variables (four variables for species with 40-50 presences) in the SDMs. We chose this upper limit of five variables in order to avoid overfitting of the models (according to rules of thumb in SDMs, the maximum amount of predictor variables should be chosen such that at least 10 presences are available per predictor variable<sup>14</sup>). The final predictors were chosen depending on their univariate variable importance, which was determined by AIC from

univariate GLMs including linear and quadratic terms<sup>40</sup>. We randomly sampled background data at 0.5° resolution and outside the known range with a sample size ten times larger than the number of presences, following general recommendations for the selection of pseudo-absences<sup>43</sup>. For Nearctic breeders, background data were sampled from the entire Americas. If Palearctic breeders overwintered in Europe and Africa only (Western Palearctic) or in Australasia only (Eastern Palearctic), then winter background data were only sampled from regions east and west of 65° longitude, respectively. Background data were downweighted in the models such that, for each species, the weighted sum of all background data equals the sum of all presences<sup>43</sup>. We evaluated final model performance using a split-sample approach, where models were calibrated using a random sample of 70% of the initial data and were evaluated against the remaining 30%, using the True Skill Statistic (TSS)<sup>44</sup> and the Area Under the receiver operating characteristic Curve (AUC). This 70:30 split-sample approach was repeated three times, which confirmed very good to excellent model performances (Fig. S8).

### Spatial autocorrelation

Spatial autocorrelation in SDM residuals was assessed using spline correlograms in the R package *ncf*<sup>45</sup>. These indicated significant spatial autocorrelation in model residuals for distances of 1000–2000 km on average (Fig. S9). We thus tested whether spatial autocorrelation could be reduced by gridding the range maps at coarser resolution of 1° as recommended previously<sup>46</sup> and by spatial thinning of the presence records with minimum distances of 250 km and 500 km between presence points (using the package *red*<sup>47</sup>). Our results showed that a coarser resolution did not reduce residual spatial autocorrelation (Fig. S9). Low spatial autocorrelation could only be achieved when spatially thinning the data to minimum distances of 250 and 500 km between presence points. However, spatial thinning would reduce the number of species that could be modelled to 174 and 13, respectively, out of initially 715 species. Our sensitivity analysis nevertheless showed that the estimated global change impacts were robust against the spatial resolution and spatial thinning (Fig. S9). Specifically, the estimated area loss and the estimated migration distance increase were not significantly smaller when applying a coarser resolution or spatial thinning. By contrast, estimated area loss tended to be even larger. Thus, we chose the 0.5° resolution as a more conservative estimate of range and migration distance changes and also to cover as many species as possible.

### Projected species distributions and dispersal buffers

For each species, we predicted current and projected future distributions for all RCPs and SSPs and their logical combinations<sup>39</sup>, and we generated consensus maps using un-weighted ensemble means. Occurrence probabilities were then transformed into binary maps using TSS-maximising values as thresholds. Unlimited dispersal scenarios at a global scale may lead to unrealistic occurrence predictions, for example on continents outside the known historic range or outside the evolved seasonal ranges of species because of analogue environments. Therefore, we tested different buffer distances (500 km, 1000 km, 2000 km, unlimited dispersal) representing dispersal abilities by setting the occurrence probability of a species to zero in cells further away than the buffer distance from any known occurrence<sup>48</sup>. Goodness-of-fit between different observed and predicted current-day range properties



decreased with increasing buffer distances (Fig. S10). For subsequent analyses, we chose the 1000 km buffer distance. This buffer distance is slightly less conservative than used previously for birds<sup>48</sup>. However, it still ensures acceptable goodness-of-fit values (Fig. S10). Furthermore, migratory birds are reported to have considerably larger dispersal distances than resident birds (while still being constraint to some degree), and previous analyses have shown mean natal dispersal distances of 21.13 km per year for migrants corresponding to 1056.5 km over the 50 years of global change as considered here<sup>49</sup>. Also, estimates of species sensitivity to global changes were largely robust against different buffer distances (Fig. S3).

### Species sensitivities to global change

For each species, we estimated three global change risks: (i) percentage decrease in summer and (ii) winter range size, and (iii) percentage increase in migratory distance. To do so, we projected the potential distribution (presence and absence) of each species during summer and winter season under current and future environments, and calculated the respective range sizes (in km<sup>2</sup>, explicitly accounting for cell size differences across latitudes). Migratory distance was calculated as the latitudinal distance between projected summer and winter range centroids under current and future environments. Range centroids were calculated as the centre of gravity of the projected distribution weighted by cell size using the package *SDMTools* 50.

We classified species as “at risk from global change” if their percentage decreases in summer or winter population size, or percentage increases in migration distance exceeded 10%. For this risk classification, we used potential reductions in population size rather than predicted range changes following recommendations by IUCN. Relative changes in population size were derived by summing the predicted habitat suitability values in the predicted current ranges and projected future ranges (weighted by cell size), and subsequently calculating the proportional changes. The relationship between population size and habitat suitability is not always linear<sup>51</sup>, but it is considered as an acceptable assumption if more specific information is missing (cf. section 12.1.9 in red list guidelines<sup>24</sup>). According to IUCN definitions, listing species as near threatened would be justified if the population is projected to decline by 10% within three generations for intermediate or smaller population sizes (<15,000 mature individuals) and otherwise by 20-25%<sup>24</sup>. A 10% risk threshold is thus rather pessimistic and we additionally evaluated the robustness of our results for a higher threshold of 20%.

### Phylogenetic and functional analyses

We used phylogenetic regression in the R package *phylolm*<sup>52</sup> to test whether risk estimates were associated with specific ecological and spatial traits as well as IUCN threat status while controlling for non-independence between species due to phylogenetic relatedness<sup>53</sup>. Trait information were extracted from Wilman et al.<sup>35</sup> and phylogenetic information from Jetz et al.<sup>34</sup> ([www.birdtree.org](http://www.birdtree.org)). Species names were matched by checking their different synonyms. Seventeen species had to be excluded from functional and phylogenetic analyses because their taxonomic classification changed recently. Functional traits included body mass and dominant diet type (invertebrates; vertebrates including fish and carrion; fruits and

nectar; plants and seeds; all species that could not be assigned to one dominant diet category were classified as omnivores). Additionally, we tested for variation in risk estimates related to summer longitude, to summer and winter latitude (calculated from range centroids), to total niche breadth (considering environmental conditions in both summer and winter range; calculated following Laube et al.37), and to the IUCN red list status (coded as an ordinal extinction risk variable; 0 = LC, 1 = NT, 2 = VU, 3 = EN, 4 = CR).

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

## Acknowledgements

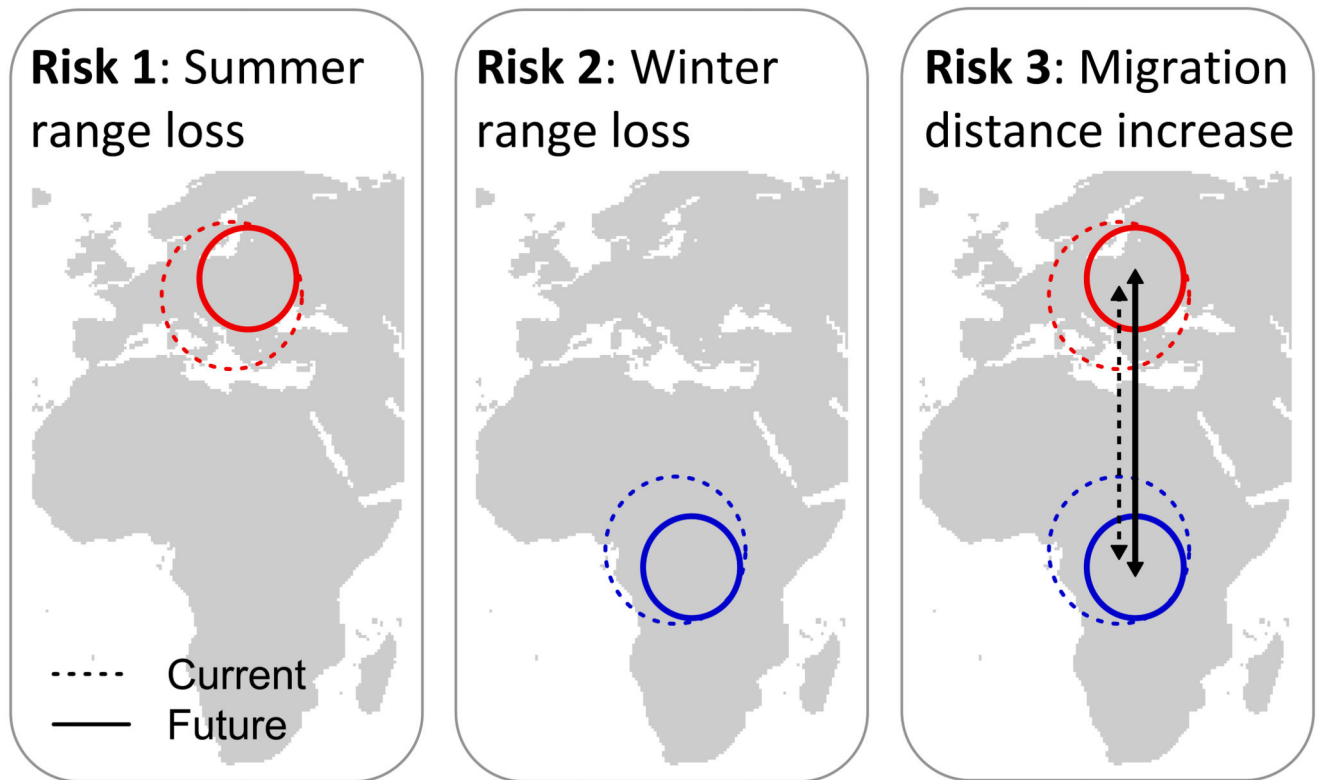
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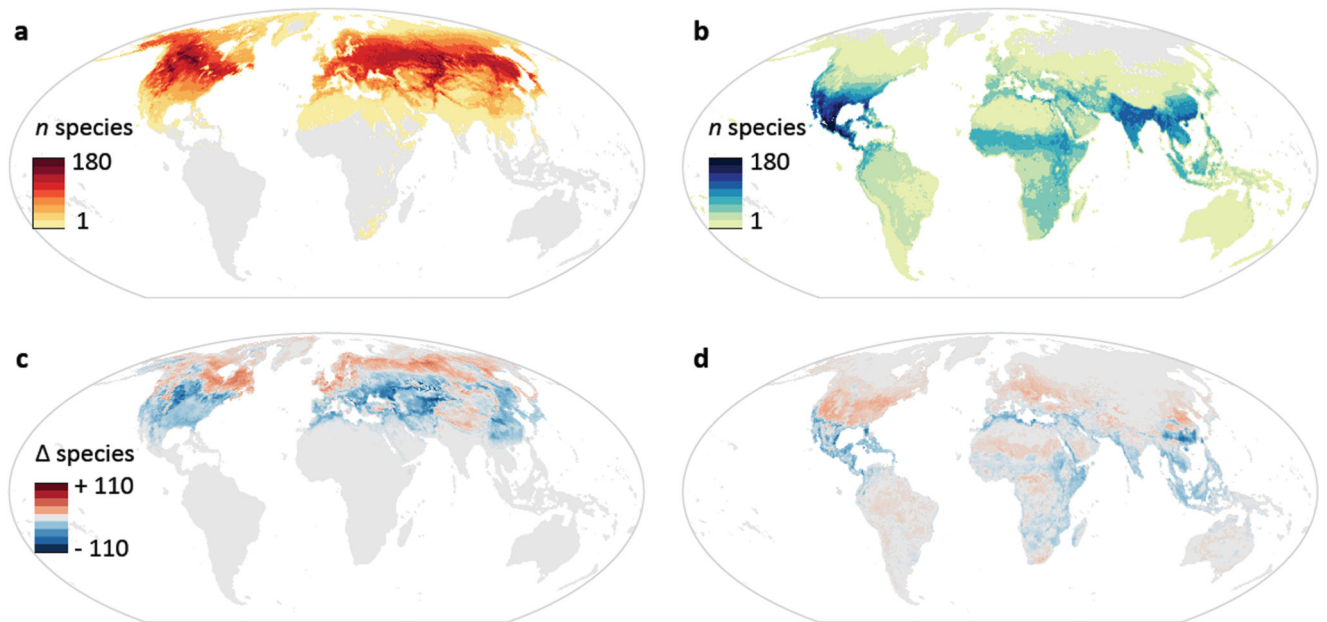
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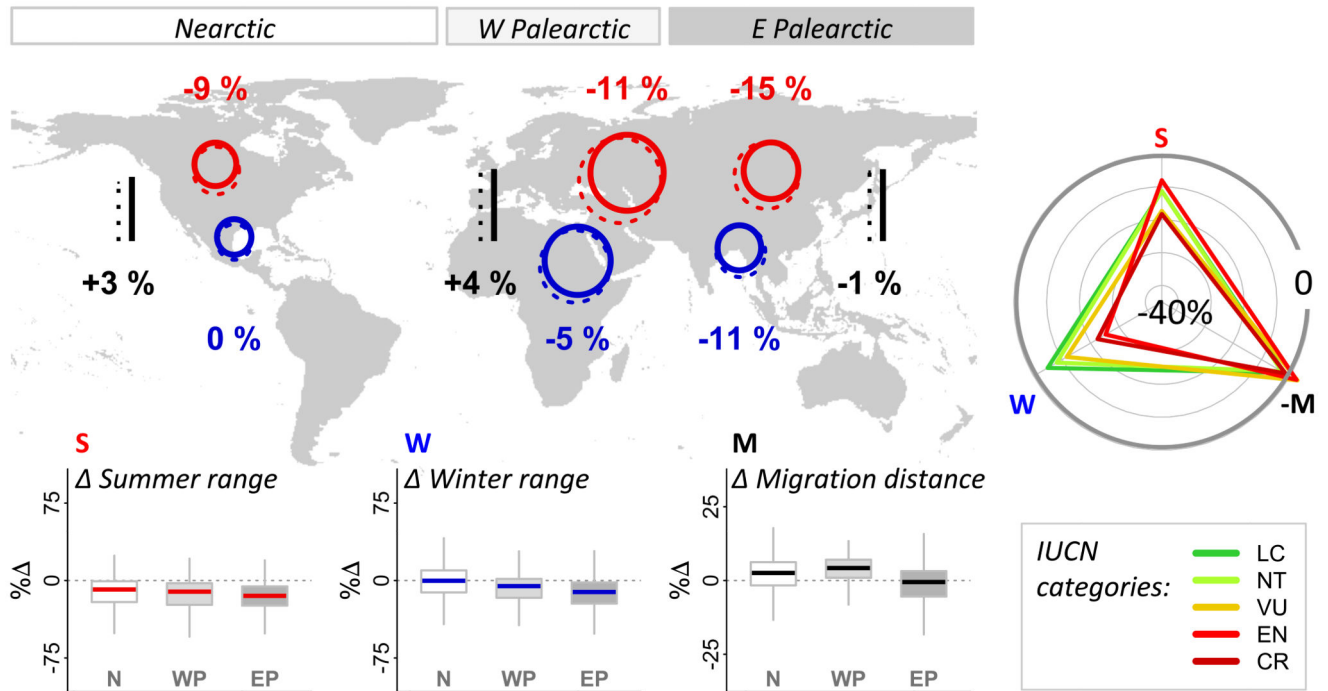
**Figure 1. Three proposed global change risks for migratory birds.**

Global environmental change may negatively impact summer range size and winter range size in long-distance migrants as well as the connectivity between seasonal ranges.

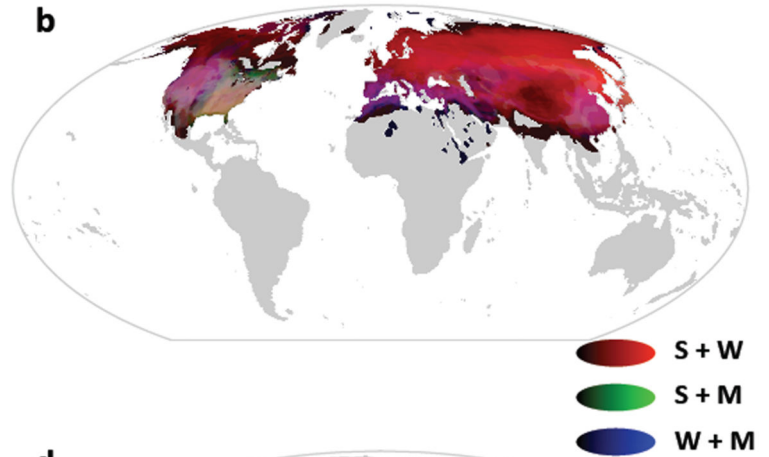
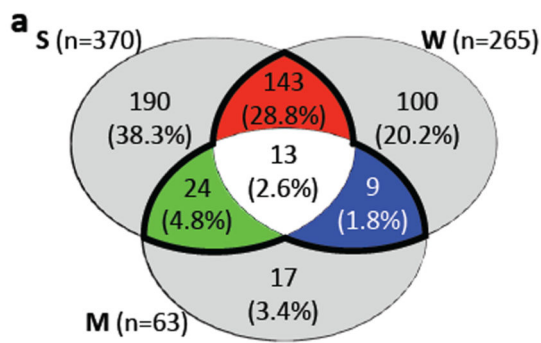
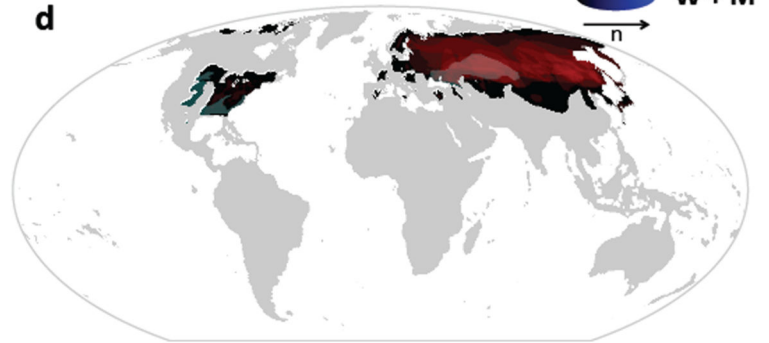
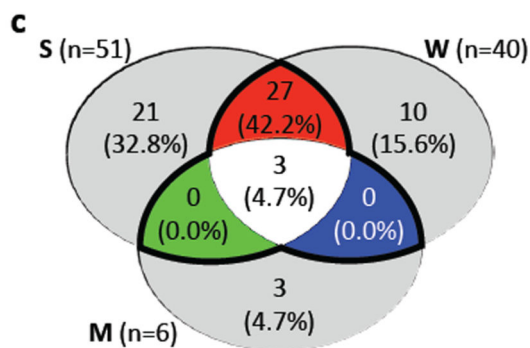


**Figure 2. Seasonal species richness of long-distance migratory birds and projected changes in species richness for 2050.**

**a,b** predicted current-day species richness in summer (**a**) and in winter (**b**). **c,d** projected changes in summer (**c**) and winter (**d**) richness derived from the ensemble means over all climate and distribution models for the scenario RCP4.5-SSP1, with a maximum dispersal distance of 1000 km.



**Figure 3. Projected change in summer and winter range size and in migratory distance.** Circles and lines in the map present the median range positions (red: summer; blue: winter) and median migratory distances (black), under current (dashed) and future conditions (solid). Boxplots depict the median and variance over all species for different regions (top; N Nearctic, WP Western Palearctic, EP Eastern Palearctic); outliers are not shown. The radial plot shows the median changes for different IUCN risk categories (LC least concern, NT near threatened, VU vulnerable, EN endangered, CR critically endangered; changes in migration distance are inverted for simplicity). Projections correspond to ensemble means for RCP4.5-SSP1 and a maximum dispersal distance of 1000 km.

**IUCN: Least concern****IUCN: (Near) Threatened**

**Figure 4. Overlap in global change risks for different IUCN categories.**

**a,c** Venn diagrams illustrate number of species projected to experience single and multiple risks (summer population reduction S, winter population reduction W, migration distance increase M). We classified species as at risk if population reduction or migration distance increase exceeded 10% (a:  $n=415$ ; c:  $n=58$ ). **b,d** RGB maps illustrate the relative number of species facing multiple risks (corresponding to coloured areas of Venn diagrams). Dark to light colours indicate increasing species numbers. Colour bands represent specific risk combinations; mixed colours indicate that species with different risk combinations are present. Projections correspond to ensemble means for the RCP4.5-SSP1 scenario and a maximum dispersal distance of 1000 km.



**Table 1**  
**Phylogenetic generalized linear models testing how projected global change impacts are associated with species' traits and IUCN red list status.**

Trait effects were tested for single risks (summer and winter range loss, migration distance increase under RCP4.5-SSP1 scenario), and for the total number of risks experienced by each species (between 0 and 3; log-transformed prior to modelling). Species were classified as at risk if projected population reduction or migration distance increase exceeded 10%. IUCN status was coded as ordinal variable (0 = LC, 1 = NT, 2 = VU, 3 = EN, 4 = CR). AIC-based stepwise variable selection was used to identify the most parsimonious models. Significance levels are indicated by \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ , †  $p < 0.1$ .

		% summer range loss	% winter range loss	% migration distance increase	Number of risks
Trophic traits	Vertebrates	-	-	-	-
	Invertebrates	-	-0.04±0.02 *	-	-
	Plants/Seeds	0.05±0.02 *	-	-	-
	Fruits/Nectar	0.10±0.05 †	-	-	3.23±1.65 †
	Body mass	-	-	-0.004±0.002 *	-
Niche breadth	Total climate and land cover niche breadth	-0.08±0.01 ***	-	-0.02±0.01 *	-2.40±0.34 ***
Range position	Summer longitude	-	0.11±0.01 ***	-0.02±0.005 ***	-
	Summer latitude	0.21±0.07 **	-0.18±0.07 *	-0.13±0.03 ***	-
	Winter latitude	-	-0.11±0.04 **	-0.08±0.02 ***	-
IUCN red list status	Extinction risk	-	0.02±0.01	-	-
	Pagel's lambda	0.08	0.07	0.0	0.01
	<b>Explained variance</b>	<b>0.08</b>	<b>0.13</b>	<b>0.13</b>	<b>0.07</b>