

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

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Many species migrate long distances annually between their breeding and wintering areas¹. Although global change affects both ranges, impact assessments have generally focused on breeding ranges and ignored how environmental changes influence migrants across geographical regions and the annual cycle^{2,3}. 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 that face multiple global change risks are not listed by International Union for Conservation of Nature as threatened or near threatened. To neglect seasonal migration in impact assessments could thus seriously misguide species' conservation.

Global warming and land use change are causing substantial species range shifts, contractions and (local) extirpations^{4,5}. Migratory species could be particularly vulnerable to these changes because they move between distinct geographical areas and thus are influenced by factors experienced in different parts of the world^{4,6}. Through carry-over effects, the 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^{4,3}. In recent decades, migratory bird populations have declined worldwide⁷ and it is often unclear where in the annual cycle these declines occur and how they could be reversed⁸.

An increasing number of studies have analysed climate change effects on migratory birds but most are limited to a few species^{9–11}, have focused on phenological shifts¹² and are biased towards the breeding season¹³. Species distribution models¹⁴ are widely used to project biodiversity responses to environmental changes^{15,16}. However, only a few studies explicitly forecast the effects of global change on both the breeding and wintering ranges of migratory birds¹⁷ and the potential changes in migration patterns between seasonal ranges^{18,19}, which means that large-scale impact assessments that focus on the full annual cycle are largely missing^{2,20}. Furthermore, most forecasts quantify only potential climate change

effects, although land cover has been reported to strongly affect range changes in birds and other taxa^{11,21}.

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: (1) summer (breeding) range loss, (2) winter range loss and (3) increased migration distance that result from the 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 globe²². Third, we analyse the relationship between species risks and geographical and ecological traits as well as species' current International Union for Conservation of Nature (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 (2041–2060) changes in the summer and winter range areas and range positions for scenarios of climate and land cover change. Consensus projections were derived from three statistical distribution models, five general circulation models (GCMs) and one global land use change model, and three different storylines derived from combinations of two representative concentration pathways (RCPs) and three shared socio-economic pathways (SSPs) were considered. We assumed species to move to newly suitable areas with a maximum dispersal of 1,000 km over the considered time period (other dispersal scenarios were tested and showed consistent results).

We found stronger projected changes in species richness during the summer compared to the winter (Fig. 2), which is consistent with previous analyses (for example, *Sylvia* warblers¹⁸). 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 (Supplementary Fig. 1). Earlier projections of global bird diversity indicated much stronger land cover effects, but mainly in the tropics, whereas climate

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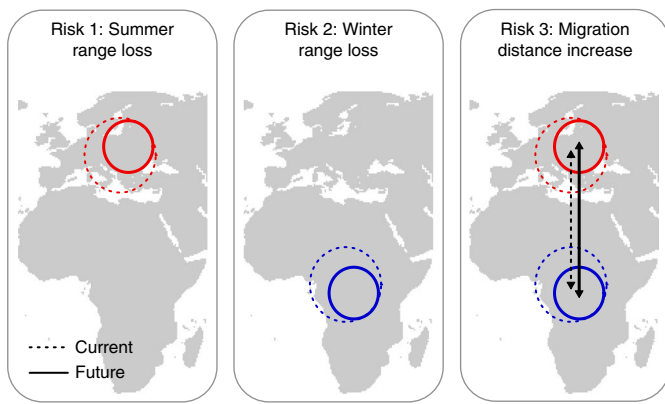


Fig. 1 | Three proposed global change risks for migratory birds. Global environmental change may negatively impact the summer range size and winter range size in long-distance migrants as well as the connectivity between seasonal ranges.

impacts were strongest in high latitudes ($>30^{\circ}\text{N}$)^{21,23}, 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 s.d., $246 \pm 128\text{km}$) in the summer and $1.61^{\circ} \pm 1.50^{\circ}$ ($179 \pm 167\text{km}$) in the winter (Fig. 3), which is comparable to the results of previous studies on European breeding birds^{17,18}. As hypothesized, the projected global change risks were largely independent of each other. Indeed, we found only a weak correlation between the 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, whereas the winter range loss was slightly less severe and influenced 65% of the species. This corroborates previous results on Palaearctic birds^{17,18,23}. However, our cross-continental analyses, which included the entire Holarctic, indicated pronounced regional differences in the projected range changes with equal winter range losses and gains in Nearctic migrants, whereas most Palaearctic migrants face winter range reductions. The projected migration distance increased by $3 \pm 7\%$ (mean \pm s.d.) for Nearctic and Western Palaearctic migrants (up to 8.96° , 997km) and decreased by $1 \pm 9\%$ for Eastern Palaearctic migrants (up to 4.78° , 533km) (Fig. 3 and Supplementary Fig. 2). 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 the negative effects of climate change, regardless of dispersal assumptions (Supplementary Fig. 3).

Phylogenetic regressions showed that global change risks had a stronger association with species' geographical 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 latitudes²². Summer range loss was higher for migrants that breed further north, and winter range loss was more pronounced for species that overwinter further south (Supplementary Fig. 4). Furthermore, species with small environmental niches were at a higher risk from summer range loss and from migration distance increase, whereas the current extinction risk status (IUCN red list) was only weakly associated with projected global change risks (Table 1). The latter indicates that all the species, regardless of their IUCN category, are similarly susceptible to future global change threats (Fig. 3 and Supplementary Fig. 5).

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 the current and future habitat suitability derived from species distribution models (SDMs)²⁴. 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. 4a,c). The cumulative number of risks typically increased for species with small environmental niches (Table 1). If we focus 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 populations²⁴. We thus evaluated the robustness of our results for a 20% threshold and for low and high emission scenarios (Supplementary Fig. 6). These supplementary estimates confirm that impact assessments that focus exclusively on summer ranges might underestimate the number of potentially threatened species by 18–49% (ratio of overlooked versus recognized species) and may further underestimate the potential negative impacts from multiple risks for 17–50% of the species (1 – the proportion of species that face summer population reduction as single versus part of multiple risks) (Fig. 4 and Supplementary Fig. 6).

We found distinct geographical patterns in the distribution of migrants that face multiple risks. Palaearctic 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 (Fig. 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 geographical areas, for example in western North America and Europe, the threats of long-distance migrants to global change might be underestimated (Fig. 4d and Supplementary Fig. 7). Similar geographical patterns were found for species that face only a single global change threat, with western United States 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 (Supplementary Fig. 7).

Our risk estimate based on migration distance is simple and does not consider any direct global change effects, such as changing wind regimes²⁵. Furthermore, we chose to use proportional (rather than absolute) increases in migration distance to classify 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 the associated migration distances have evolved over long (evolutionary) timescales and, thus, that a proportional change of 10–20% could potentially increase the 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 energy²⁶, and refuelling will necessitate longer overall stopover durations²⁷. 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

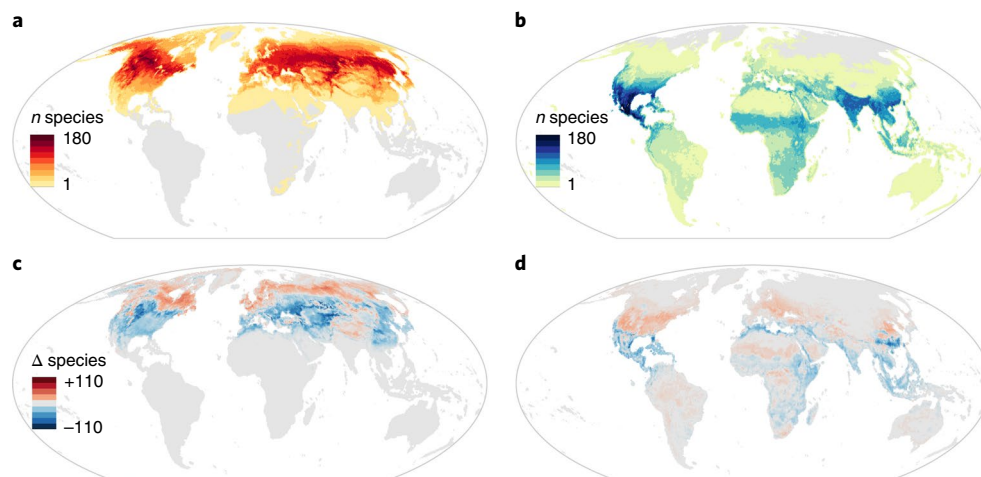


Fig. 2 | Seasonal species richness of long-distance migratory birds and projected changes in species richness for 2050. a, b, Predicted present-day species richness in the summer (**a**) and winter (**b**). **c, d**, Projected changes in the summer (**c**) and winter (**d**) richness derived from the ensemble means over all climate and distribution models for the scenario RCP4.5-SSP1, with a maximum dispersal distance of 1,000 km.

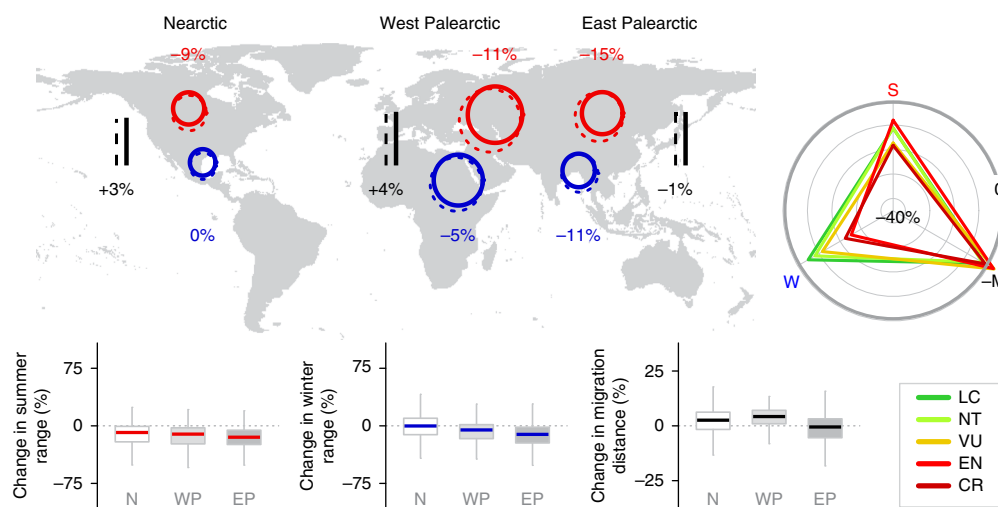


Fig. 3 | Projected changes in the summer and winter range sizes and in migratory distances. The circles and lines in the map present the median range positions (red, summer; blue, winter) and median migratory distances (black) under the current (dashed line) and future conditions (continuous line). Box plots depict the median and variance over all species for different regions (outliers are not shown). The radial plot shows the median changes for different IUCN risk categories (changes in migration distance are inverted for simplicity). Projections correspond to the ensemble means for RCP4.5-SSP1 and a maximum dispersal distance of 1,000 km. S, summer; W, winter; M, migratory distance; N, Nearctic; WP, Western Palearctic; EP, Eastern Palearctic; LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered.

and moult and their synchronization with food resources^{1,28}. For example, a prolonged spring migration would require an earlier departure at the risk of not finding enough food resources en route or a late arrival at the risk of reduced breeding success. For the future, it is important to better understand how relative and absolute changes in migration distance may affect the 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 found that global change can affect summer ranges, winter ranges and migration distances independently¹⁸. As a direct consequence, impact assessments that focus 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 targets², both spatially and at the species level. Instead, the full annual cycle should be considered in future forecasting studies and, where possible, be 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 realized from fundamental niches, which could bias future projections if the range limiting factors changed^{29,30}. Large-scale range maps may not be equally accurate for all species and less precise for winter than for summer ranges. Also, at a finer spatial resolution, species habitat relations and land cover and land use change may prove more important than at the coarse scale considered here¹¹. Furthermore, our dispersal module ignored the effects of fragmentation and species interactions on population spread³⁰. As more data become available on

Table 1 | Phylogenetic generalized linear models that show projected global change impacts associated with species' traits and IUCN red list status

		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	-	-
	Page's lambda	0.08	0.07	0.0	0.01
Explained variance		0.08	0.13	0.13	0.07

Trait effects were tested for single risks (summer and winter range loss and migration distance increase under the 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 the projected population reduction or migration distance increase exceeded 10%. IUCN status was coded as the 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: **** $P < 0.001$, *** $P < 0.01$, ** $P < 0.05$, * $P < 0.1$.

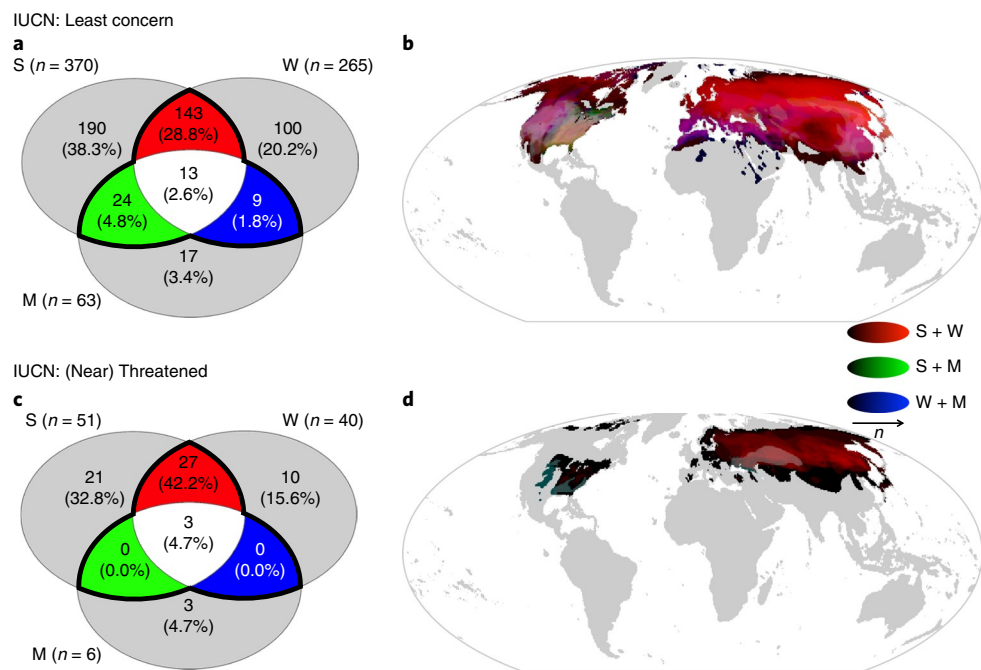


Fig. 4 | Overlap in global change risks for different IUCN categories. a, c, Venn diagrams illustrate the number of species projected to experience single and multiple risks (S, summer population reduction; W, winter population reduction; M, migration distance increase). We classified species as at risk if population reduction or migration distance increase exceeded 10% (**a**, $n = 415$; **c**, $n = 58$). **b, d,** The RGB maps (which correspond to the coloured areas of the Venn diagrams) illustrate the relative number of species that face multiple risks. Lighter colours indicate an increase in species numbers. The 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 1,000 km.

distribution, demography and behaviour throughout the annual cycle, they should be used in mechanistic models that assess the potential behavioural adaptations and population-level consequences of environmental changes. For example, we can explore when migration is advantageous over residency. Our results indicate that migration distances could become shorter for many

species (Supplementary Fig. 2), which potentially makes it advantageous to cease migration. Empirical data suggest that some species are evolving partial migration¹. Although global positioning system telemetry has advanced our understanding of individual and population level migration and wintering behaviour for some species^{3,9}, we still know little about how global change affects the annual cycle

of migratory species and how this translates into overall species vulnerability. We hope that our global assessment will inspire more detailed work to embrace this complexity.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at <https://doi.org/10.1038/s41558-018-0312-9>

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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 interests

The authors declare no competing interests.

Additional information

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Methods

Species data. Summer (breeding) and winter (non-breeding) ranges were derived from a global data set of the world's bird species distributions³¹ (data available at www.birdlife.org). Polygons were gridded at 0.5° resolution, which matches the resolution of the land cover change scenarios and those of previous analyses using the same data^{32,33}. Grid cells were considered as presences if the polygon covered the centre of the grid cell. We considered only long-distance migrants that breed in the Palaearctic and Nearctic (with range centroids north of 30° latitude and extending east and west of 18° W, respectively, and with minimum distance of 10° latitude between the breeding and non-breeding range centres). Overall, we identified 825 extant long-distance migrants that breed in the Holarctic. In subsequent analyses, we only included those 715 species (329 Nearctic breeding migrants and 386 Palaearctic breeding migrants) that had at least 40 presences (which means 40 grid cells at 0.5° resolution) in both their summer ranges and winter ranges for which trait and phylogenetic data were available^{34,35} and for which the 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 the subsequent analyses did not qualitatively change the results.

Climate and land cover data. Current and future climate data were extracted from WorldClim at 10' resolution³⁶ (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^{37,38}: mean temperature and total precipitation during the summer season (May–July) and during the winter season (November–January). Future climate by 2050 (average for 2041–2060) was represented by a set of five GCMs from the CMIP5 database for RCP4.5 (stabilization of radiative forcing by 2100) and RCP8.5 (business as usual). The GCMs included CCSM4, IPSL-CM5A-LR, HadGEM2-ES, MIROC-ESM and MPI-ESM-LR, which cover a wide range of CMIP5 model performances and reflect predictions that range from pessimistic to optimistic²².

Current and future (2050) global land cover scenarios were simulated by the GLOBIO model (v3.5) at 0.5° resolution³⁹. We chose three shared SSPs consistent with the socio-economic assumptions of the RCPs⁴⁰: SSP1 'global sustainable development' (consistent with RCP4.5), SSP3 'Regional competition' and SSP5 'Economic optimism' (consistent with RCP8.5). These new scenarios can be mapped onto the illustrative scenarios of the Special Report on Emissions Scenarios, such that a combination RCP4.5-SSP1 would correspond to a B1 world, RCP8.5-SSP3 to an A2 world and RCP8.5-SSP5 to an A1FI world⁴⁰. Land cover classes in GLOBIO follow the classification scheme of the Global Land Cover 2000 Project. 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 below a threshold of 0.7, a collinearity that is generally regarded as unproblematic⁴¹. In the species distribution models, we only included species-specific sets of four to five variables as explained below.

SDMs. SDMs were calibrated separately for the summer and winter ranges of each species using three statistical algorithms, namely generalized linear models, generalized additive models and random forests within the ensemble modelling platform BIOMOD2 (ref. ⁴²) in R (ref. ⁴³). 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 to avoid overfitting of the models (according to the rules of thumb in SDMs, the maximum number of predictor variables should be chosen such that at least ten presences are available per predictor variable⁴⁴). The final predictors were chosen depending on their univariate variable importance, which was determined by Akaike information criterion (AIC) from univariate generalized linear models, which included linear and quadratic terms⁴¹. 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-absences⁴⁴. For Nearctic breeders, the background data were sampled from the entire Americas. If Palaearctic breeders overwintered in Europe and Africa only (Western Palaearctic) or in Australasia only (Eastern Palaearctic), then the 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 the background data equals the sum of all the presences⁴⁴. We evaluated the final model performance with a split-sample approach, in which models were calibrated using a random sample of 70% of the initial data and were evaluated against the remaining 30%, using the true skill statistic⁴⁵ and the area Under the receiver operating characteristic curve. This 70:30 split-sample approach was repeated three times, which confirmed very good to excellent model performances (Supplementary Fig. 8).

Spatial autocorrelation. The spatial autocorrelation in SDM residuals was assessed using spline correlograms in the R package NCF⁴⁶. These indicated significant

spatial autocorrelation in model residuals for distances of 1,000–2,000 km on average (Supplementary Fig. 9). We thus tested whether spatial autocorrelation could be reduced by gridding the range maps at a coarser resolution of 1°, as recommended previously⁴⁷, and by spatial thinning of the presence records with minimum distances of 250 km and 500 km between presence points (using the package RED⁴⁸). Our results showed that a coarser resolution did not reduce the residual spatial autocorrelation (Supplementary Fig. 9). Low spatial autocorrelation could only be achieved when spatially thinning the data to minimum distances of 250 and 500 km between the presence points. However, spatial thinning would reduce the number of species that could be modelled to 174 and 13, respectively, out of the initial 715 species. Our sensitivity analysis nevertheless showed that the estimated global change impacts were robust against the spatial resolution and spatial thinning (Supplementary Fig. 9). Specifically, the estimated area loss and the estimated migration distance increase were not significantly smaller when a coarser resolution or spatial thinning was applied. By contrast, the 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 the current and projected future distributions for all RCPs and SSPs and their logical combinations⁴⁰, and we generated consensus maps using unweighted ensemble means. Occurrence probabilities were then transformed into binary maps using true skill statistic-maximizing 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, 1,000 km, 2,000 km and unlimited dispersal) to represent the dispersal abilities by setting the occurrence probability of a species to zero in cells further away than the buffer distance from any known occurrence⁴⁹. Goodness-of-fit between different observed and predicted present-day range properties decreased with increasing buffer distances (Supplementary Fig. 10). For subsequent analyses, we chose the 1000 km buffer distance. This buffer distance is slightly less conservative than used previously for birds⁴⁹. However, it still ensures acceptable goodness-of-fit values (Supplementary Fig. 10). Furthermore, migratory birds are reported to have considerably larger dispersal distances than resident birds (although still constrained 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 here⁵⁰. Also, estimates of species sensitivity to global changes were largely robust against different buffer distances (Supplementary Fig. 3).

Species sensitivities to global change. For each species, we estimated three global change risks: (1) percentage decrease in summer and (2) winter range size, and (3) 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 km², 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*⁵¹.

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 linear⁵², but it is considered as an acceptable assumption if more specific information is missing (cf. section 12.1.9 in red list guidelines²⁴). 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%²⁴. 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*⁵³ 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 relatedness⁵⁴. Trait information were extracted from Wilman et al.³⁵ and phylogenetic information from Jetz et al.³⁴ (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).

Data availability

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

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