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The future distribution of wetland birds breeding in Europe validated against observed changes in distribution

Alaaeldin Soultan[1], Diego Pavón-Jordán[2], Ute Bradter[2], Brett K. Sandercock[2], Wesley M. Hochachka[3], Alison Johnston[3,4], Jon Brommer[5], Elie Gaget[5,6], Verena Keller[7,8], Peter Knaus[8], Karen Aghababyan[9], Qenan Maxhuni[10], Alexandre Vintchevski[11], Károly Nagy[12], Liutauras Raudonikis[13], Dawn Balmer[14], David Noble[14], Domingos Leitão[15], Ingar Jostein Øien[16], Paul Shimmings[17], Elchin Sultanov[18], Brian Caffrey[19], Kerem Boyla[20], Dimitrije Radišić[21], Åke Lindström[22], Metodija Velevski[23], Clara Pladevall[24], Lluís Brotons[25,26,27], Šťastný Karel[28], Draženko Z. Rajković[29], Tomasz Chodkiewicz[30,31], Tomasz Wilk[32], Szép Tibor[33], Chris van Turnhout[34,35], Ruud Foppen[34,35], Ian Burfield[36], Thomas Vikstrøm[37, 38], Vlatka Dumbović Mazal[39], Mark Eaton[40,41], Petr Vorisek[42], Aleksi Lehikoinen[43], Sergi Herrando[7,25,44], Tatiana Kuzmenko[45], Hans-Günther Bauer[46], Mikhail V. Kalyakin[47], Olga V. Voltzit[47], Jovica Sjeničić[48], and Tomas Pärt[1]

[1]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

[2]Department of Terrestrial Ecology, Norwegian Institute for Nature Research (NINA), P.O. Box 5685 Torgarden, N-7485 Trondheim, Norway

[3]Cornell Lab of Ornithology, Cornell University, Ithaca, NY, 14850, U.S.A.

[4]Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, CB2 3QZ, U.K.

[5]Department of Biology, University of Turku, Turku, 20500, Finland

[6]International Institute for Applied Systems Analysis (IIASA), Laxenburg, Austria

[7]European Bird Census Council, Nijmegen, The Netherlands

[8]Swiss Ornithological Institute, Sempach, Switzerland

[9]BirdLinks Armenia NGO, 87b Dimitrov, apt 14, Yerevan 0020 Armenia

[10]Kosovo Institute for Nature Protection, Str. L. Haradinaj, ex-Rilindja, 10000 Prishtine, Kosovo

[11]CEO, APB-BirdLife Belarus, Belarus

[12]MME BirdLife Hungary, H-4402 Nyiregyháza PO.Box 16, Hungary

[13]BirdLife Lithuania, Naugarduko g. 47-3, LT-03208 Vilnius, Lietuva

[14]British Trust for Ornithology,The Nunnery, Thetford, Norfolk, IP24 2LD, UK

[15]SPEA – Portuguese Society for the Study of Birds, Lisboa, Portugal

[16]NOF-BirdLife Norway, Sandgata 30 B, NO-7012 Trondheim, Norway

[17]Norsk Ornitologisk Forening / BirdLife Norway, Sandgata 16 B, NO 7012 Trondheim, Norway

[18]Azerbaijan Ornithological Society, Baku, Azerbaijan Republic

[19]BirdWatch Ireland, Ireland

[20]eBird National Editor, Turkey

[21]Department of Biology and Ecology, Faculty of Sciences, University of Novi Sad, Serbia

[22]Department of Biology, Biodiversity unit, Lund University, S-223 62 Lund, Sweden

[23]Macedonian Ecological Society, North Macedonia

[24]Andorra Research and Innovation, Principality of Andorra

[25]Forest Science Centre of Catalonia (CTFC), 25280 Solsona, Spain

[26]CREAF, 08193 Cerdanyola del Vallès, Spain

[27]CSIC, 08193, Cerdanyola del Vallès, Spain

[28] Faculty of Environmental Sciences, Czech University of Life Sciences, Prague, Czech Republic

[29]Center for Biodiversity Research, 21000 Novi Sad, Serbia

[30]Museum & Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warszawa, Poland

[31]Polish Society for the Protection of Birds (OTOP), Odrowaza 24, 05-270 Marki, Poland

[32]Polish Society for the Protection of Birds (OTOP), Kraków, Poland

[33]Institute of Environmental Sciences, University of Nyíregyháza, Nyíregyháza, Hungary

[34]Sovon Dutch Centre for Field Ornithology, Nijmegen, The Netherlands

[35]Department of Animal Ecology & Ecophysiology, Institute for Water and Wetland Research, Radboud University, Nijmegen, The Netherlands

[36]BirdLife International, Cambridge, UK

[37]Dansk Ornitologisk Forening, Denmark

[38]BirdLife, Denmark

[39]Institute for Environment and Nature, Zagreb

[40]Centre for Conservation Science, The Royal Society for the Protection of Birds, UK

[41]European Bird Census Council, UK

[42]Czech Society for Ornithology, Czech Republic

[43]The Helsinki Lab of Ornithology, Finnish Museum of Natural History, P.O. Box 17, Helsinki, Finland

[44]Catalan Ornithological Institute, Natural History Museum of Barcelona. Pl. Leonardo da Vinci 4-5. 08019 Barcelona, Catalonia, Spain

[45]Ukrainian Society for the Protection of Birds, Ukraine

[46]Max Planck Institute of Animal Behavior, 78315 Radolfzell, Germany

[47]Zoological museum of the Lomonosov Moscow State University, Bolshaya Nikitskaya Str., 2, Moscow, 125009, Russia

[48]Ekološka istraživanja i zaštita životne sredine, Bosna i Hercegovina

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Abstract

Wetland bird species have been declining in population size worldwide as climate warming and land-use change affect their suitable habitats. We used species distribution models (SDMs) to predict changes in range dynamics for 64 non-passerine wetland birds breeding in Europe, including range size, position of centroid, and margins. We fitted the SDMs with data collected for the first European Breeding Bird Atlas (EBBA1) and climate and land-use data to predict distributional changes over a century (the 1970s–2070s). The predicted annual changes were then compared to observed annual changes in range size and range centroid over a time period of 30 years using data from the second European Breeding Bird Atlas (EBBA2). Our models successfully predicted ca. 75% of the 64 bird species to contract their breeding range in the future, while the remaining species (mostly southerly breeding species) were predicted to expand their breeding ranges northward. The northern margins of southerly species and southern margins of northerly species, both, predicted to shift northward. Predicted changes in range size and shifts in range centroids were broadly positively associated with the observed changes, although some species deviated markedly from the predictions. The predicted average shift in core distributions was ca. 5 km/year towards the north (5% Northeast, 45% North, and 40% Northwest), compared to a slower observed average shift of ca. 3.9 km/year. Predicted changes in range centroids were generally larger than observed changes, which suggests that bird distribution changes may lag behind environmental changes leading to "climate debt". We suggest that predictions of SDMs should be viewed as qualitative rather than quantitative outcomes, indicating that care should be taken concerning single species. Still, our results highlight the urgent need for management actions such as wetland creation and restoration to improve wetland birds' resilience to the expected environmental changes in the future.

Introduction

Considerable effort has been invested in conserving biodiversity over recent decades. Yet, biodiversity losses continue at an unprecedented rate, as reflected by ongoing declines in population size and range contractions for many species worldwide (Tittensor *et al* 2014, Pievani 2014). The observed changes in the distribution of many species during recent decades have been primarily attributed to the ongoing rapid climate change, and to large-scale habitat loss (Reif and Flousek 2012, Gillings *et al* 2015, Brommer *et al* 2012, Pavón-Jordán *et al* 2019, Hovick *et al* 2016). Historical data clearly show that species may respond to climate and habitat changes by adjusting their spatial distributions (Brommer *et al* 2012, Pavón-Jordán *et al* 2019, Parmesan *et al* 1999, Thomas and Lennon 1999, Littlefield *et al* 2017). Therefore, it is recommended to consider climate as well as land-use variables to better describe drivers of species distribution changes (Newbold 2018).

Bird species that are ecologically dependent on wetlands are commonly used as indicators of wetland ecosystem health (Williamson *et al* 2013) and provide valuable ecosystem services such as food supply, pest control, seed dispersal, and cultural services such as recreation and hunting (Hamilton *et al* 1994, Lehikoinen *et al* 2017, Teo 2001, Green and Elmberg 2014). Still, many species of wetland birds have been declining worldwide and a subset has been classified as threatened species during the 20th century (Wang *et al* 2018, BirdLife International 2021).

The expected changes in environmental conditions due to increases in global temperatures and changes in the land-use patterns that are likely to affect species distributions in the 21st century (IPCC 2014). Determining the expected change in range dynamics such as the direction and the magnitude of change in range margins and centroid allows for evaluating current networks and boundaries of protected areas with the possibility of moving from static to dynamic designs where the boundaries of protected areas change over time (Rayfield *et al* 2008, Cashion *et al* 2020). The range centroid is the center of gravity of a distribution polygon and represents the core distribution of a species, where the abiotic conditions are assumed to be optimal for the species' biological and ecological functions (Sales *et al* 2020). Range dynamics may differ between the centroid and the margins but relatively few studies have considered the multiple changes in range characteristics (i.e. changes in range size, centroid, and margins). Huntley *et al* (2007) used a climatic-surface model on European birds to predict overall changes in range characteristics considering climate scenarios only and did not incorporate land-use scenarios. However, studies have shown that incorporating land-use information with climate information can significantly improve the predictive ability of species distribution models (Sohl 2014, Lee and Jetz 2011).

Despite the surge in use of species distribution models (SDMs) to predict future distributions during the last two decades (Newbold 2018, Soultan *et al* 2019), few studies have been able to use independent data to evaluate the predictive accuracy and temporal transferability of SDMs (Areias Guerreiro *et al* 2016, Barbet-Massin *et al* 2018). Nevertheless, the few studies available have reported interesting differences between the observed and predicted changes in species ranges, which provide new insights that will help to improve SDM methods (Brun *et al* 2016, Virkkala and Lehikoinen 2014).

Here, we investigate the potential impacts of projected climate and land-use changes on the breeding distributions of 64 non-passerine wetland bird species in Europe, based on distribution data collected for the first European Breeding Bird Atlas (Hagemeijer and Blair 1997). We advance upon previous analyses for wetland birds in Europe (Huntley *et al* 2007, 2008) by (i) incorporating land-use change scenarios together with climate change scenarios, (ii) using ensemble SDMs, and (iii) comparing predicted changes from the SDMs to the

146 actual observed changes from the second European Breeding Bird Atlas (EBBA2, Keller *et al* 2020).

Methods

Species occurrences for 64 non-passerine wetland bird species that breed in Europe were obtained from the first Atlas of European Breeding Birds (Hagemeijer and Blair 1997), hereafter "EBBA1", which was compiled and published by the European Bird Census Council (EBCC). Appendix S1: Species data and study area.

Four climatic variables from the CHELSA database, known to have high ecological relevance for bird distribution, were considered in the SDMs (Karger *et al* 2017, Karger and Zimmermann 2018): 1) mean seasonal temperature during April–July (Araújo *et al* 2009), 2) total seasonal precipitation during April–July (Barbet-Massin *et al* 2012), 3) seasonal growing degree-days >5°C (GDD) (Barbet-Massin *et al* 2012, Newbold 2018), and 4) the seasonal water balance (Skov and Svenning 2004, Newbold 2018). Appendix S2: Environmental variables.

Four land-use variables were considered in the SDMs: 1) "wetland habitat" (Lehner and Döll 2004), 2) "pasture" henceforth referred to as the "agricultural land", 3) "forest land", and 4) "urban land" as defined by Hurtt *et al* (2019, 2020). Land-use variables were compiled for 1984 which was the mid-year of the 24-year period for EBBA1 (1972 to 1995, Appendix S2: Environmental variables).

For future projections, we obtained climatic variables for the future period 2061–2080 (henceforth referred to as the "2070") based on five Global Climate Models (GCMs), bcc-csm1-1, CCSM4, GISS-E2-R, HadGEM2-AO, and MRI-CGCM3, under four representative concentration pathways (RCP2.6, RCP4.5, RCP6, and RCP8.5) from CHELSA (Karger *et al* 2017, Karger and Zimmermann 2018). The land-use scenarios for the future period 2070 were obtained from land-use harmonization (Hurtt *et al* 2020). The four RCPs represent different socioeconomic models, ranging from low (RCP2.6) to high (RCP8.5) scenarios of greenhouse gas emissions (Polaina *et al* 2021). Appendix S3: Future environmental variables.

We modeled the breeding ranges of wetland birds by fitting ensemble SDMs using four commonly used presence-absence SDM algorithms (GLM, GAM, GBM, and RF) with default settings available within the "biomod2" R package (Thuiller *et al* 2016, R Core Team 2016). SDM predictive performance was evaluated using the area under the curve (AUC; a threshold-independent metric) (Fielding and Bell 1997) and the True Skill Statistic (TSS; a threshold-dependent metric) (Allouche *et al* 2006). Appendix S4: Model performance.

The modeled breeding ranges during the reference period 1972–1995 for EBBA1 were projected into the future (2070) under four RCPs and five GCMs. To minimize the prediction uncertainty due to the large variability among the GCMs, we used the median of five GCMs (Goberville *et al* 2015, Cianfrani *et al* 2018, Soultan *et al* 2019). Extrapolation Detection tool (ExDet) (Mesgaran *et al* 2014) was used to assess the presence of non-analog environmental conditions and to determine the degree of extrapolation (Appendix S5: non-analog environments and extrapolation). Last, the reference and future distribution ranges were classified into suitable and unsuitable ranges using a threshold that maximizes both model sensitivity and specificity (Liu *et al* 2013).

Three metrics were used to quantify the impact of environmental changes on the dynamics of breeding ranges for wetland birds: (1) percent change in the area of the breeding range, (2) directionality and displacement shifts for the range centroid, and (3) latitudinal shifts of the northern and southern margins of the range (km/year). Changes in breeding range size were measured by calculating the range expansion (number of gained pixels; G) and range contraction (number of lost pixels; L), and relating them to the size of the reference range

194 (total number of pixels; N) using "*BIOMOD_RangeSize*" function in the "biomod2" R package (Thuiller *et al* 2016). Directionality and displacement shifts of the geographic range centroid were quantified by delineating Standard Deviational Ellipse (SDE) (Furfey 1927, Johnson and Wilson 2009) over the reference and future ranges of a given species. As such, the centroid of SDE was used to represent species ranges' centroid. We quantified the directionality and displacement shifts in the range centroid by calculating the direction as a bearing relative to true north (0°) and the linear distances respectively, between the centroids of the reference and future ranges. SDE was calculated using "*calc_sde*" function implemented in "*aspace*" R package (Bui *et al* 2012), while both bearing and linear distance were calculated using "*bearing*" and "*distGeo*" functions, respectively, implemented in "geosphere" R package (Hijmans 2019). It is expected that in case of expanding range size, the ranges of southerly species breeding in southern Europe might move northward, whereas the range of northerly species breeding in northern Europe might expand southward Similarly, in the case of contracting range size, the ranges of southerly species would retract southward, whereas the ranges of northerly species would retract northward (Kujala *et al* 2013, Thomas and Lennon 1999). Therefore, based on the centroids of breeding ranges (i.e. the centroid of SDE), we classified our species into either northerly or southerly species if the breeding range's centroid was above or below the mean latitude of the study area of 5500000 meters, (Thomas and Lennon 1999, Zuckerberg *et al* 2009).

For the latitudinal shifts of southerly species, we measured the linear distance between the northern margin at the reference period and the predicted future periods for a given species (Carroll *et al* 2015, Ordonez and Williams 2013). The northern margin was defined as the mean value of the upper 90% latitudes (90^{th} percentile) of the pixels that were predicted suitable. For northerly species, we measured the linear distance between the southern margin at the reference period and the predicted future periods for a given species (Carroll *et al* 2015, Ordonez and Williams 2013). The southern margin was defined as the mean value of the lower 10% latitudes (10th percentile) of the pixels that were predicted suitable.

Shifts in the latitudinal range margins are sensitive to original range size because small ranges can have larger potential shift (Williams and Blois 2018), and to natural barriers within the species' biogeographic regions such as Arctic ocean for northerly species. Therefore, to test whether a relationship exists between the predicted shifts in a range's latitudinal margins and the predicted changes in range size, we applied the approach developed by Thomas & Lennon (1999). We statistically estimated shifts in the southern margins of the northerly species and northern margins of the southerly species as the intercept of a regression line depicting the linear relationship between shifts in species range latitudinal margins and the changes in range size (Thomas and Lennon 1999, Taheri *et al* 2016). The change in range size was calculated as *log10* of the proportion of the number of occupied pixels in the future over the number of occupied pixels in the reference range (Brommer *et al* 2012, Williams and Blois 2018). The regression intercept value, the parameter of interest, gives the average shift in range margins independent from changes in range size, where a positive intercept indicates a northward shift in range margins (Zuckerberg *et al* 2009, Kujala *et al* 2013).

Comparing predicted changes in species range with observed changes

The second Atlas of European Breeding Birds (EBBA2) was recently published by European Bird Census Council (Keller *et al* 2020). EBBA2 is based on nationally collected data on breeding birds' distributions in Europe between 2013 and 2017 at a spatial resolution of 50 × 50 km grid cell and using the same methodological standards as for EBBA1. Comparisons of bird distributions collected during two time periods that were three decades apart (EBBA1: 1984, EBBA2: 2015) gave us a unique opportunity to evaluate and test predictions of SDMs.

Our study objective was to compare the predicted changes in range size and range centroid from EBBA1 data with the observed changes (log10-transformed) calculated from EBBA2 data, assuming a constant rate of changes (linear) over the time.

We measured the displacement shifts of the range centroid by delineating SDE over EBBA1 and EBBA2 data of a given species. We measured the displacement shifts in the range centroid by calculating the linear distances between the centroids of the observed SDE of EBBA1 and SDE of EBBA2 data. The shifts in range centroids and changes in range sizes were calculated over different time scales, ~30 years for the observed and ~85 years for the predicted. Estimated shifts in range centroids were scaled to average annual shifts by dividing the observed and the predicted shifts in range centroids by the number of years, i.e. 30 and 85 respectively. We ran a linear regression to quantify the relation between the observed and predicted average annual shifts in range centroids. In the same way, we compared the predicted changes in range size with the observed changes. The observed changes in range size were calculated using "*BIOMOD_RangeSize*" function in the"biomod2" R package (Thuiller *et al* 2016).

Results

We used occurrence data for 64 non-passerine wetland birds breeding in Europe with taxa representing 14 families (table S1). The most species-rich families included Anatidae (24 species) and Scolopacidae (nine species). All ensemble SDMs showed good predictive performance (TSS mean = 0.72, SD = 0.11, and AUC mean = 0.92, SD = 0.04; table S1).

Changes in breeding range size

Our ensemble models predicted significant changes in the breeding ranges for most wetland birds under the projected future environmental conditions in Europe. Almost 75% of the species were predicted to contract their ranges, whereas ca. 20% of the species were predicted to expand their ranges (figure 1, figure S2, and table S2). The extent of the change in species range varied among species and according to the four different RCPs. For instance, ca. 25% and ca. 20% of the species were predicted to expand their breeding ranges by 2070 according to RCP 2.6 and 8.5, respectively. Four species with south-central distributions, Little Egret (*Egretta garzetta*), Great White Egret (*Ardea alba*), Red-crested Pochard (*Netta rufina*), and Kentish Plover (*Charadrius alexandrinus*), were predicted to markedly expand their breeding ranges in the future (table S2). Other species such as Common Moorhen (*Gallinula chloropus*) and Little Grebe (*Tachybaptus ruficollis*) were predicted to maintain their reference breeding range in the future.

Range contractions were predicted for several northerly species, whereas almost all species that were predicted to expand their breeding range were southerly species (Table S2). The pattern of change in range size was fairly consistent among the RCPs, with only a few species showing an inconsistent pattern of change such as Black-crowned Night Heron (*Nycticorax nycticorax*) and Red-throated Diver (*Gavia stellata*) (table S2).

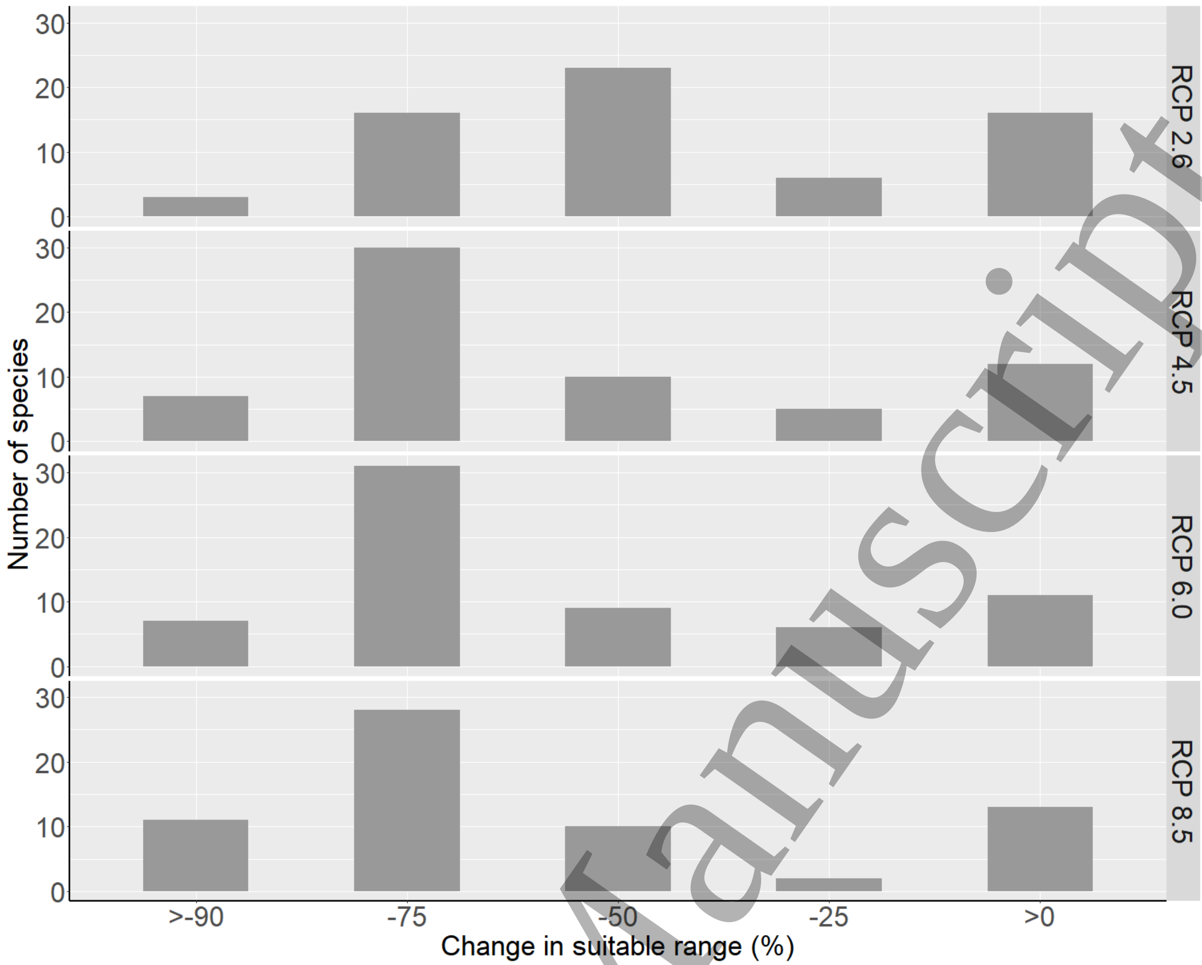

Figure 1 The predicted change in the size of the breeding ranges under four different RCPs (2.6, 4.5, 6.0, and 8.5) in the future period (2070) compared to 1985. Alternative scenarios represent optimistic (RCP2.6) to pessimistic scenarios for emissions (RCP8.5).

Shifts in centroids of breeding ranges

All species were predicted to shift their breeding range centroids, irrespective of the RCPs. A majority of species were predicted to shift their breeding range centroids in a northerly direction (ca. 5% NE, 45% N, and 40% NW) (figure 2 and table S3). The mean displacement shift in range centroid was predicted to be ca. 5 km/year across 64 wetland birds. Appendix S6: Shifts in breeding ranges centroids.

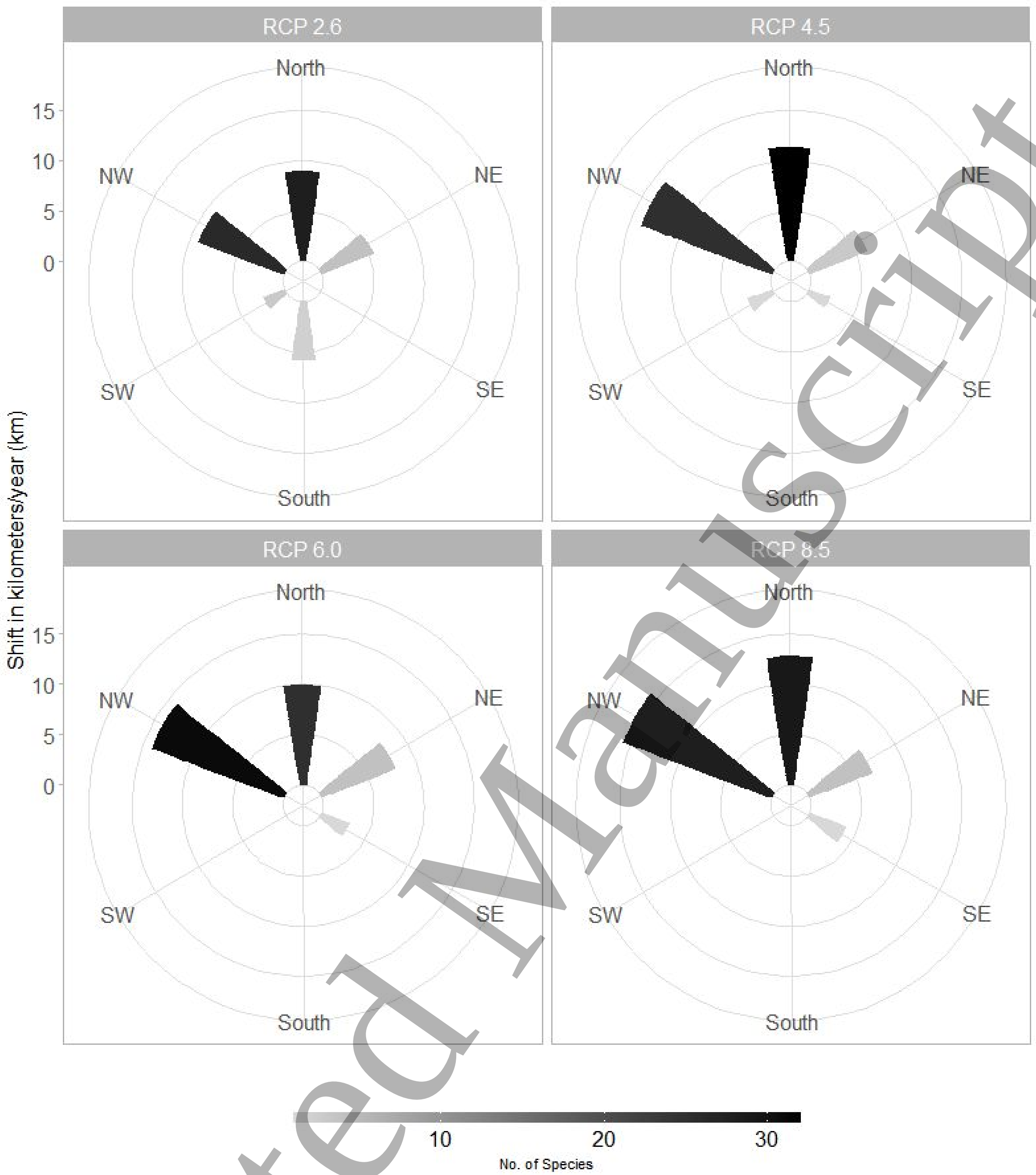

Figure 2 The predicted change in the directions of the centroid of the ranges of breeding birds. The scale bar represents the number of species, and the y-axis is the estimated displacement of the range centroids per year.

Shifts in range margins

Both northern and southern range margins were predicted to shift northward. However, the magnitude of margin shifts was dependent on the species. For northerly species, shifts in their southern margins varied among the RCPs, with a mean displacement shift of ca. 2 km/year (figure 3 and table S4). For southerly species, the shifts in their northern margins varied from ca. 0 to 25 km/year depending on the RCPs with a mean shift of ca. 6 km/year (figure 3 and table 1).

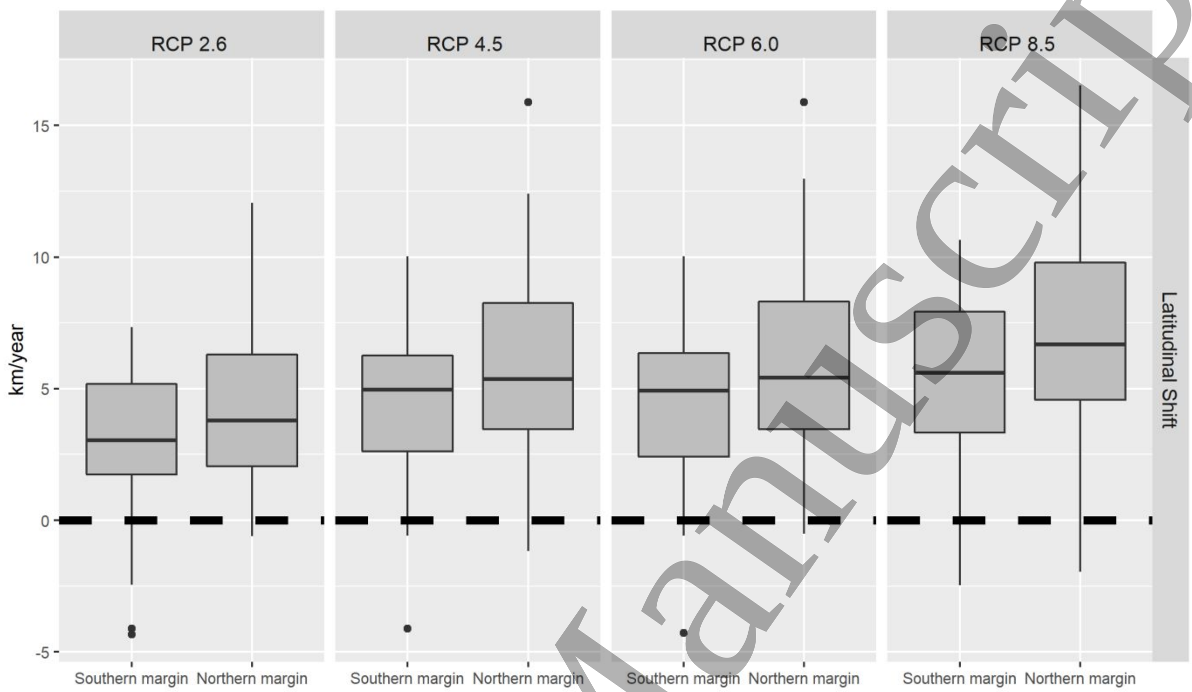

Figure 3 Predicted shifts in the southern and northern margins of breeding ranges of 64 species of wetland birds. Positive values above the dashed line indicate shifts toward the north. The values on the y-axis represent the annual displacement in range margins in km per year.

Changes in range size were positively correlated with the predicted annual shifts in northern margins of southerly species, which suggest an increase in the number of suitable sites at northern boundaries (table 1). Changes in range size were negatively correlated with the predicted annual shifts in southern margins of northerly species, suggesting a decrease in the number of suitable sites at southern margins.

Table 1 *The predicted annual (km/year) latitudinal shifts of southern and northern range margins for 41 northerly and 23 southerly wetland bird species, respectively, as a function of the predicted change in range sizes. The significant positive estimate of latitudinal shift indicates a shift northward, while the negative estimate indicates a shift southward.*

RCP	Parameter	Estimate	t	P	Estimate	t	P
2.6	Latitudinal Shift	4.97	7.37	0.001	2.04	2.18	0.03
	Range change	350.77	1.61	0.12	- 431.03	-1.58	0.12
4.5	Latitudinal Shift	6.68	9.61	0.001	2.26	2.36	0.020
	Range change	90.93	0.45	0.65	-569.81	-2.01	0.006
6.0	Latitudinal Shift	6.56	9.37	0.001	1.36	1.32	0.19
	Range change	83.18	0.42	0.67	-708.81	3.56	0.001
8.5	Latitudinal Shift	8.51	12.97	0.001	0.39	0.36	0.72
	Range change	311.11	1.75	0.09	-881.64	-5.01	0.001
		Northern margin			Southern margin		

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322

323 **Comparing the predicted change in species range with the observed change**

324 There was a significant positive association between the observed and the predicted annual
325 changes in breeding range size and also the annual shifts in centroids (figure 4). The
326 predicted contractions of breeding range sizes were in general larger than what was observed
327 in EBBA2 (intercept= -0.29± 0.15). However, some species were predicted to contract their
328 breeding ranges while they showed no change or a small increase in range such as the Tufted
329 Duck (*Aythya fuligula*), Pochard and Whooper Swan (*Cygnus cygnus*) (figure 4(a) and table
330 S2). The predicted shifts in range centroids were on average greater (ca. 5 km/year) than the
331 observed ones (ca. 3.9 km/year) (intercept= 3.06± 0.31; figure 4(b) and table S3). The
332 differences in predicted *vs* observed shifts were largest for species with small observed shifts
333 in distribution (figure 4(b) and table S3).

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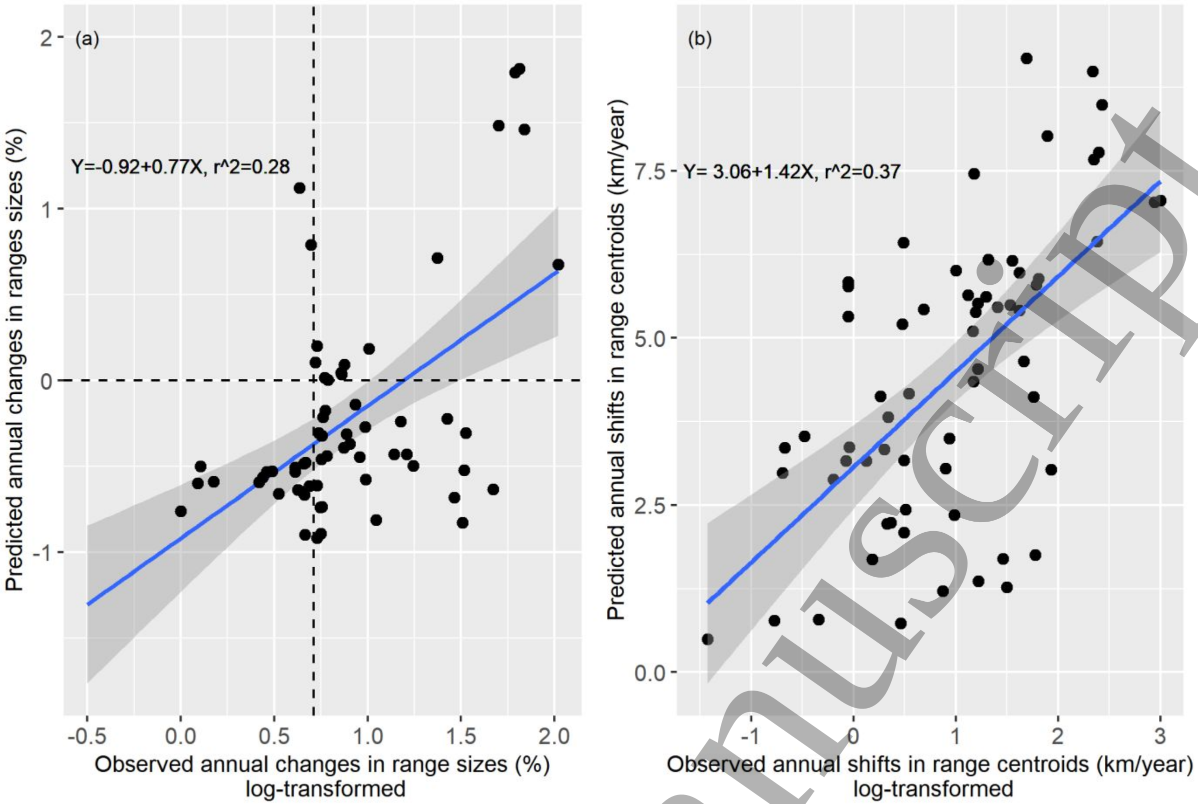

Figure 4 The relationship between the predicted and the observed (log10-transformed) shifts in ranges sizes (a) and the predicted and observed (log10-transformed) changes in ranges centroids (b) of breeding wetland bird species in Europe. The solid blue line and shaded area represent the fitted value and the standard error of the fitted regression model.

Discussion

The ensemble SDMs based on the expected changes in climate and land-use in the coming decades predicted significant contractions in the breeding ranges of many wetland birds, while only a few species were predicted to expand their breeding ranges. In general, most species distributions, as estimated by range centroids and range margins, were predicted to move northwards. The predicted shifts in range centroids were positively associated with the observed shifts in centroids over the 30 years (the 1980s–2010s) from EBBA2 data. Similarly, the predicted and observed changes in breeding distribution range size were positively related although some species displayed marked differences between predicted and observed changes.

Our SDMs predicted: (i) considerable reductions in the size of the breeding ranges size (>50%) for many European wetland birds in the coming decades (figure 1 and table S2), (ii) an average northward shift in breeding range centroids of ca. 5 km/year (figure 2 and table S3), and (iii) corresponding shifts in range margins with average displacement shifts of 2 and 6 km/year for southern range margins of northerly species and northern range margins for southerly species, respectively (table 1). Our results are in line with other studies that have reported shifts of breeding distributions and range size (Huntley *et al* 2007, 2008, Barbet-Massin *et al* 2012, Williams and Blois 2018) and their range margins (Huang *et al* 2017, Hitch and Leberg 2007, Thomas and Lennon 1999, Kujala *et al* 2013, Brommer 2004, Ordonez and Williams 2013, Tayleur *et al* 2015). In reality, observed changes in range size and shifts of range centroids appear generally smaller than those that predicted (Huang *et al* 2017, Hitch and Leberg 2007, Thomas and Lennon 1999, Brommer 2004) because species ranges and abundances are responding to climate with a time lag ('climate debt' sensu (Devictor *et al* 2008, 2012)).

In our study, species with wide southerly breeding distribution such as Red-crested Pochard, Great White Egret, and Little Egret were among those that were predicted to expand their breeding ranges in the future (table S2). The pattern of expansion for these species was also supported by the observed expansion reported by EBBA2 (Keller *et al* 2020). Species with broad distributions often encompass several sub-populations each with distinctive ecological characteristics and dynamics (Stockwell and Peterson 2002). Furthermore, such species are characterized by a wider environmental domain than they currently occupy, so they might benefit from new environmental conditions and, therefore, be able to expand their ranges (Koschová *et al* 2014, Stockwell and Peterson 2002). A second explanation for expansion of the southerly species could be that their ranges are not constrained by the continental border in the north (Koschová *et al* 2014).

About 75% of the modeled bird species were predicted to contract their breeding ranges in Europe in the future. For some species, such as Long-tailed Duck (*Clangula hyemalis*) and Common Snipe (*Gallinago gallinago*), our SDMs predicted major contractions by 2070s. The magnitude of the predicted contractions (>50%) were consistent with results for many other birds at local (Andriamasimanana and Cameron 2013), regional (Virkkala *et al* 2008, Harrison *et al* 2003), and continental-scale (Langham *et al* 2015, Barbet-Massin *et al* 2012). The contractions were partly inconsistent with the observed changes from EBBA2 (Keller *et al* 2020) as many species including Long-tailed Duck and Common Snipe were observed to largely have almost the same range size in 2015 as thirty years earlier (table S2).

Some species also show a marked opposite pattern between predicted and observed range changes such as Common Merganser (*Mergus merganser*) and Smew (*Mergellus albellus*) (figure 4(a)). Large discrepancies may have been a result of some biotic factors not considered in our model. For instance, over the last decades, some species have strongly benefitted from the increased protection and conservation, intensified farming, and milder winters (Keller *et al* 2020, Pavón-Jordán *et al* 2020, Gaget *et al* 2021). We focused on conditions during the breeding season but milder winters have benefitted the population sizes of several short-distance migrants that are wintering in central-north Europe (Musilová *et al* 2018, 2015). Positive effects of wetland protection and mild winters could be possible explanations for predicted decreases but observed increases in range sizes for Grey Heron (*Ardea cinerea*), Common Goldeneye (*Bucephala clangula*), Smew, and Great Cormorant (*Phalacrocorax carbo)* (table S2). Similarly, the divergence between the predicted expansion and the observed contraction in the breeding range of Kentish Plover (table S2) could be attributed to the development in coastal breeding habitats (Montalvo and Figuerola 2006), and changed grazing pressure at coastal grasslands and increased predator populations (Keller *et al* 2020). Further, we assumed a constant linear rate of changes in breeding ranges over time due to the lack of data that can inform a better realistic assumption. For some species, the environmental predictors might not be able to capture the main niche dimensions of species. Examples are many fish-eating species such as Goosander, Smew and Great Cormorant that probably increased in numbers as a result of changed fish communities (Frederiksen *et al* 2018, Østnes and Kroglund 2015), and large grazing birds such as Whooper Swan and Common Crane (*Grus grus*) that have increased due to changes in agricultural practices (Montràs-Janer *et al* 2020).

Why are most species predicted to contract their breeding range? First, the majority of the species that were predicted to contract their ranges are breeding in northern Europe, and thus constrained by the northern continental border (Koschová *et al* 2014, Gregory *et al* 2009). Second, the rate of climate change at northern latitudes could be faster as compared to that of the southern latitudes (Jetz *et al* 2007, Koschová *et al* 2014).

The northward shift of the southern margins was mainly driven by losing suitable sites at lower latitudes (significant negative range shift in table 1), while the northward shift of the northern margins was driven by gaining suitable sites at higher latitudes (significant positive range shift in table 1). A similar pattern has been found in several observational studies and has mainly been attributed to the latitudinal temperature changes (Huang et al 2017, Hitch and Leberg 2007, Thomas and Lennon 1999, Kujala et al 2013, Brommer 2004, Ordonez and Williams 2013).

The predicted average displacement shift of breeding range centroids (5 km/year) is consistent with the average shift predicted in previous SDMs' studies (Russell *et al* 2015, Huntley *et al* 2007). Although most other SDMs' studies predicting a shift in range centroids suggest a shift towards the north, observational data from atlas inventories at country scale suggest these shifts to be smaller than predicted (ca. 1 km/year) (Brommer *et al* 2012, Gillings *et al* 2015, Hickling *et al* 2006, Virkkala and Lehikoinen 2014). The predicted predominant northward (NW, N, and NE) shift for the centroid of the breeding range for most wetland species (Figure 2) have been documented in multiple studies in North America and Europe possibly due to the general south-north latitudinal temperature gradient (Williams and Blois 2018, Huang *et al* 2017, Gillings *et al* 2015, Hickling *et al* 2006). The NW shift of many wetland bird species could reflect a corresponding changed patterns of precipitation (Gillings *et al* 2015). A previous study observed that changes in precipitation patterns resulted in many species undergoing westward shifts (VanDerWal *et al* 2013).

Our models probably overestimate the short-term impacts of environmental change because some of the inherent uncertainties associated with SDMs. A primary source of uncertainty in our study is the unaccounted factors such biotic interactions microclimatic conditions and species adaptability (Polaina *et al* 2021). A further source of uncertainty is the nature of EBBA2 data, which represent the transient distributions for many species including occurrences collected from old steady-state and newly colonized sites.

Our study calls for urgent intervention to preserve, manage, and restore the wetlands across Europe, which requires applying conservation measures at continental and national scales. We recommend to continue applying effective conservation measures such as wetland restoration and creation (Kačergytė *et al* 2021). Where the economic cost for restoring the natural wetlands is high, wetland creation is a potential alternative (Sebastián-González and Green 2016, Lehikoinen *et al* 2017). Additionally, previous studies showed that under effective governance including controlling bird hunting and restoring their potential habitats, wetlands can be refugia for wetland birds (Kirby *et al* 2008, Amano *et al* 2018). We recommend also applying spatial conservation planning, as it may inform the conservationists and decision-makers where to prioritize the conservation efforts.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/10.15468/adtfvf

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