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Setting priorities for climate change adaptation of Critical Sites in the Africa-Eurasian waterbird flyways

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Abstract

Despite their importance for biodiversity and ecosystem services, wetlands are among the most threatened ecosystems globally. The conservation of many migratory waterbirds depends on the conservation of a network of key sites along their flyways. However, the suitability of these sites is changing under climate change, and it is important that management of individual sites in the network adapts to these changes. Using bioclimatic models that also account for changes in inundation, we found that projected climate change will reduce habitat suitability for waterbirds at 57.5% of existing Critical Sites within Africa-Eurasia, varying from 20.1% in Eastern Europe to 87.0% in Africa. African and Middle East sites are particularly threatened, comprising 71 of the 100 most vulnerable sites. By highlighting priority sites for conservation and classifying Critical Sites into Climate Change Adaptation Strategy (CCAS) classes, our results can be used to support the climate change adaptation of both individual sites and the entire site network.

KEYWORDS
adaptation, climate change, conservation, policy instruments, Ramsar, site management, species distribution models, waterbirds

1 | INTRODUCTION

Wetlands are characterized by high species diversity and deliver substantial ecosystem services for human well-being (Gardner et al., 2015; Millennium Ecosystem Assessment, 2005; Ramsar Convention on Wetlands, 2018), such as drinking water supply, fishing and crop irrigation. Despite their importance, wetlands are among the most threatened ecosystems on earth and have experienced severe rates of loss and degradation in recent decades (Dudgeon et al., 2006; Gardner et al., 2015; Millennium Ecosystem Assessment, 2005; Ramsar Convention on Wetlands, 2018; Secretariat of the CBD, 2010). The impact of climate change on wetlands (Erwin, 2009) and the increasing risk of human conflicts over freshwater (Gleik, 2018) are likely to further increase the pressure on wetlands in the future, with uncertain implications for the biodiversity and ecosystem services that they support.

Waterbirds represent an important component of wetland biodiversity, and are the focus of strong monitoring networks and policy instruments. Waterbirds provide provisioning (e.g. meat, eggs, down), supporting (e.g. dispersal of plants and animals, nutrient cycling), regulating (e.g. pest control) and cultural (sport hunting, birdwatching, spiritual) ecosystem services (Green & Elmberg, 2014). Over 70 million waterbirds migrate every year between Europe, the Middle East and Africa (Wetlands International, 2018). They are especially vulnerable because increasing temperatures and changing water regimes can adversely affect their habitats anywhere within their range (Maclean et al., 2007). Migrating waterbirds depend on a network of wetlands within and between their breeding and non-breeding areas which should be safeguarded nationally through a combination of protected areas and Other Effective area-based Conservation Measures (OECMs; Jonas et al., 2018) and as a transcontinental network through international policy instruments. The Ramsar Convention on Wetlands of International Importance was originally established for the conservation and wise use of wetlands as stepping stones for waterbird migrations (Ramsar Convention Secretariat, 2016). A more comprehensive flyway network focus is provided by the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA), established under the auspices of the Convention on Migratory Species, which aims to maintain a coherent and climate-resilient flyway network of key sites and habitats (AEWA, 2008). Critical Sites represent an inventory of known sites of international importance for waterbirds (for details, see Methods). Only 55.9% of Critical Sites are completely or partially covered by formal protected areas, with strong geographical variation: 85.1% of sites located in the European Union are covered by protected areas vs. 33.0% outside of the EU (Figures S8 and S10). Although Critical Sites have been identified based on their current importance for waterbird populations, it is recognized that climate change may impact the future effectiveness of site networks (Hole et al., 2009; Johnston et al., 2013). The projected impacts of climate change on species populations and distributions are wide ranging (Maclean et al., 2007; Pearce-Higgins & Green, 2014), including distributional shifts and ultimately threatening species with local

extinctions (Urban, 2015) resulting in range fragmentation, and even global extinction. Therefore, the importance of individual sites for the conservation of a particular population is likely to change in the future. However, existing sites may become more important for other species. Depending on how the suitability of a site is likely to change for a suite of species in the future, different site-level climate change adaptation strategies can be appropriate to guide actions enabling adaptation to the impacts of climate change at the level of the site network (Hole et al., 2011; Johnston et al., 2013). We assessed the impact of climate change on the network of 2601 Critical Sites in the light of projected changes in their climatic and hydrological suitability for waterbird populations. Site-specific management actions (such as habitat restoration, disturbance-regime management and site expansion, see table 1 in Hole et al., 2011) can enable a site network to accommodate climate change impacts by facilitating the re-distribution of populations among sites (Franklin et al., 2014; subsequently, we use the term 'adaptation' in this technical sense as the active management of sites to increase the ability of the network to conserve species under climate change).

Several approaches have been developed recently for assessing the vulnerability of species to climate change (Foden et al., 2019; Pacifici et al., 2015; Willis et al., 2015), among which Species Distribution Models (SDMs) (Guisan et al., 2013, 2017; Pearson & Dawson, 2003; Rodríguez et al., 2007) are prominent. To compile a climate change vulnerability assessment, we developed SDMs and projected current and future distributions for 247 waterbird species in the African-Eurasian flyway (see Table S5 and Methods). We developed a priority index (*PI*) to highlight those sites that are currently very important for waterbirds (because they harbour a high number of threatened species or a high proportion of the entire population of particular species; see Methods) and are either (a) very vulnerable to climate change or (b) their importance for waterbird conservation may further increase in the future because of increasing habitat suitability for one or more species. While some sites have particular priority for climate change adaptation actions, management of all sites in the network should be adapted to the redistribution of waterbird populations across the flyway that is taking place under climate change. In addition, many waterbird species are highly dispersed either during the breeding or the non-breeding season, when the site-based conservation should be complemented by climate change adaptation measures in the wider landscape (Franks et al., 2018; Hole et al., 2011). However, in this paper, we focus only on the adaptation to climate change of existing sites in the Critical Site network. For each site, we identified particular Climate Change Adaptation Strategy (CCAS) classes based on the species turnover characteristics of the site (i.e. the relationship between the numbers of species of conservation concern that are expected to persist at the site, colonize it or disappear from it owing to loss of suitable climate). Each CCAS class is associated with a set of management aims and relevant management actions (see table 1 in Hole et al., 2011) that can support conservation planning and integration of flyway-scale climate change adaptation into local site management. Combining each site's strategy class with estimates of its current importance (Figures 1
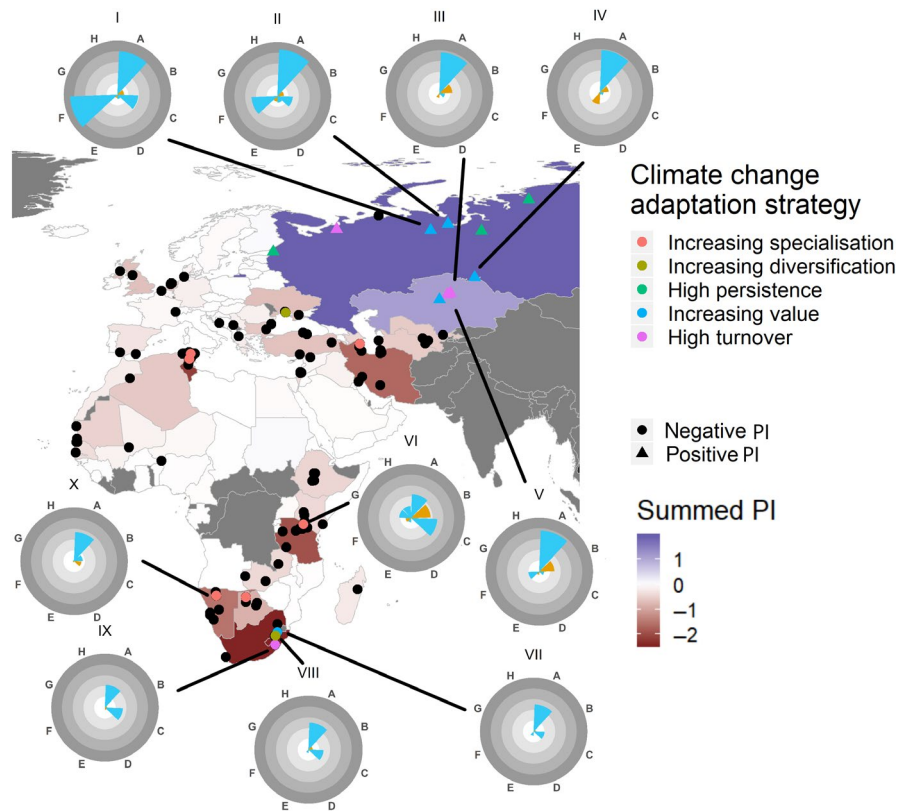
FIGURE 1 Climate vulnerability of the study region. Colour shading for countries shows the summed priority index values (ranging from −2.42 to 1.90) for all Critical Sites in each country (red shades showing negative values and blue shades showing positive values; grey shades indicate countries outside of the study region or that do not contain Critical Sites). The dots represent the 100 Critical Sites with highest priority for climate change adaptation (negative PI; black dots), the 10 sites with highest priority for climate change adaptation (coloured dots) and the 10 sites with most positive future value (positive PI; coloured triangles). Red symbols show sites with increasing specialization (high emigration, low colonization), olive with increasing diversification (intermediate emigration and intermediate colonization), green with high persistence (low emigration and low colonization), blue with increasing future value (low emigration and high colonization) and purple with high turnover (high emigration and high colonization). The radar charts show projected changes in climate variables by 2050 (blue colour: increases; orange colour: decreases) at the five sites with highest predicted future value (I: Dvuob'ye; II: Lover Ob'; III: Kurumbel'skaya steppe; IV: Kurumbel'skaya steppe; V: Korgalzhyn State Nature Reserve) and the five most vulnerable sites (VI: Lake Natron and Engaruka basin; VII: Grassland Biosphere Reserve (proposed); VIII: Bedford/Chatsworth; IX: Franklin vlei; X: Etosha National Park) with A = Annual mean temperature change (white area: 0–1°C, darkest grey area: +4–5°C); B = Mean diurnal temperature range (white area: 0–0.25°C, darkest grey area: +1–1.25°C); C = Annual precipitation (white area: 0–50mm, darkest grey area: 200–250mm); D = Precipitation of driest month (white area: 0–10mm, darkest grey area: 40–50mm); E = Precipitation seasonality (white area: 0–10, darkest grey area: 40-50mm); F = Area seasonally inundated (white area: 0–0.625km², darkest grey area: 2.5–3.125km²); G = Area permanently inundated (white area: 0–0.625km², darkest grey area: 2.5– 3.125km²); H = Standard deviation of spatially varying inundation durations (see Table S2 for more details)

and 2) provides useful information for conservation practitioners to inform site management.

2 | METHODS

2.1 | Species and background data for modelling

2.1.1 | Critical Sites

In the AEWA study region, a network of 3087 Critical Sites for waterbirds were previously identified under the Wings over Wetlands project (https://www.unep-aewa.org/en/project/wings -over-wetlands-wow-unep-gef-african-eurasian-flyways-project) using Important Bird and Biodiversity Area data from BirdLife International and International Waterbird Census data from Wetlands International available up to 2007 (http://critical-sites. wetlands.org/en/about). Critical Sites were identified using two criteria: (1) The site is known or thought regularly or predictably to hold significant numbers of a population of a globally threatened waterbird species; (2) The site is known or thought regularly or predictably to hold >1% of a flyway or other distinct population of a waterbird species. 1% thresholds to identify Critical Sites are based on the 4th edition of the Waterbird Population Estimates (1990–2005). These criteria mirror the definition of IBA Criterion A1 and A4 (http://dataz one.birdlife.org/site/ibacritglob).
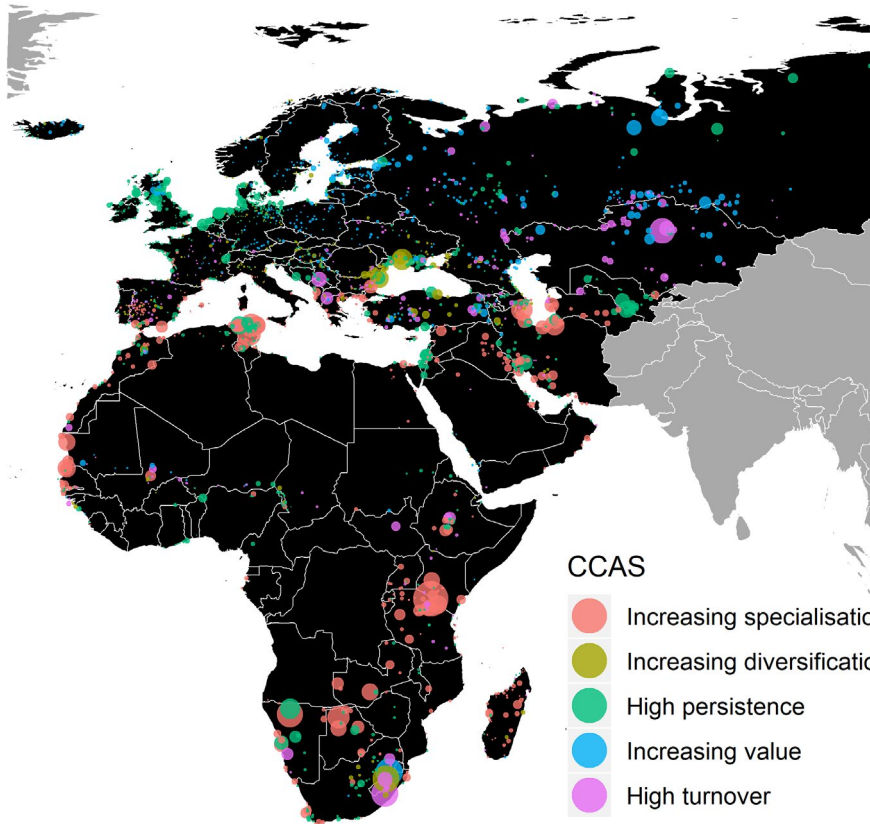
FIGURE 2 Climate Change Adaptation Strategy (CCAS) categories for existing Critical Sites for waterbirds (red: 'increasing specialization'; olive: 'increasing diversification'; green: 'high persistence'; blue: 'increasing value'; purple: 'high turnover'; see Fig. S11 for details). Larger circles represent higher site importance, calculated by summing for each site the product for each species of (1) its IUCN Red List category (Least Concern = 1; Near Threatened = 2; Vulnerable = 3; Endangered = 4; Critically Endangered = 5), (2) the proportion of its flyway population supported by the site, (3) the proportional change in its modelled range size and (4) the proportional change in its habitat suitability at the site (see text and Figures S2–S7 for details)

In the analysis, we used 2,601 Critical Sites. In all, 42 sites are no longer listing qualifying species, 54 sites were excluded because they were not covered by the environmental predictors (Table S2) and 390 sites were removed because (a) the site fulfils a site selection criterion for seabirds, for species associated with coastal mudflats or restricted range species with very few observations (see Table S5), (b) the model was judged too poor to be included (see Table S5) or (c) the site was not predicted as suitable by the models (and hence no PI-value or CCAS class can be defined).

2.1.2 | Species data and observation bias

We used presence-only data, together with background information (sometimes referred to as Pseudo-Absences), for fitting Species Distribution Models. Various data sources were used to collect species occurrence information for modelling species' distributions. Occurrence data, ranging from 1990 to 2016, originated from systematic monitoring schemes such as the International Waterbird Census (IWC, which includes data from 112 national schemes such as the Coordinated Waterbird Counts in South Africa; Wetlands International, 2017), the Russian breeding bird atlas (Kalyakin and Voltzit, 2020), the atlas of the birds of Moscow city (Kalyakin et al., 2014) and the atlas of breeding waders in the Russian Arctic (Lappo et al., 2012) as well as from observational databases: BirdTrack (*British Trust for Ornithology: BirdTrack data extract from 03/26/2018. https://www.bto.org/our-science/projects/birdtrack*), eBird (*eBird Basic Dataset. Version: EBD_relMay-2018. Cornell Lab of Ornithology,*

Ithaca, New York. May 2018.), Observation International (*Observation International: Data extract from 06/30/2017. https://observation.org/*) and the Global Biodiversity Information Facility (*GBIF.org (31 August 2017) GBIF Occurrence Download https://doi.org/10.15468/dl.rtkm8s*), which also included data from the South African Breeding Bird Atlas. The inclusion of casual presence-only data may add noise because they are geographically biased towards densely populated, touristic and easily accessible areas, and contributors may be more likely to report unusual observations like irregular vagrants which may add 'false presences'. Therefore, waterbird experts carefully evaluated the casual observations to verify observations that occurred outside of the flyway boundaries (http://critical-sites.wetlands.org/en/species) and excluded observations of vagrant or likely misidentified birds (we kept 66% of 1,603,532 records after aggregating data to a 10 × 10 km grid frame and removing duplicated observations, and removed another 28,592 unreliable records).

We calculated breeding and wintering ranges by splitting the data into four annual cycle categories (breeding, passage, wintering and resident). We used alpha-hulls (Pateiro-López & Rodriguez-Casal, 2011) around the wintering and the breeding areas of the range maps (BirdLife International & Handbook of the Birds of the World, 2017) and added occurrences from the European breeding bird atlas (Hagemeijer & Blair, 1997) to calculate breeding ranges. If an observation was recorded within the geographical breeding range of a species and within the breeding period (according to del Hoyo et al. (2018) for African and Cramp and Simmons (2006) for Western Palaearctic breeding birds), the observation was defined as breeding. Observations in the wintering range and in the wintering

period (according to del Hoyo et al., 2018 and Cramp & Simmons, 2006) were classified as wintering stage. All the remaining observations (outside the breeding period and inside the breeding range as well as outside the breeding range and outside the wintering period) were classified as passage.

A shortcoming in our occurrence data was a strong observation bias. Western-, Central- and Northern Europe and South Africa were intensively sampled, while Eastern Europe, Siberia and much of Africa, especially West-Africa, were under-sampled (Figure S15). However, we preferred to use observational data rather than range maps which represent distributional limits rather than occupancy patterns, leading to false positives (commission errors) and reducing our ability to relate fine-grain occurrences to detailed climatic and particularly hydrological variables at the site level.

2.1.3 | Addressing the sampling bias problem

The strong sampling bias of the occurrence data (Figure S15) led to equally biased current predictions, with over-predictions in Europe and South Africa due to increased sampling effort, and under-predictions in the rest of the range. We tested a series of different approaches to overcome this issue on a subset of African resident waterbirds, where issues of bias were most extreme. First, we restricted species data to the International Waterbird Census (IWC) because it follows a systematic sampling procedure (Wetlands International, 2010) and provides count and absence information. However, the IWC counts are implemented only in January. In addition, the quality of abundance information from these data was geographically heterogeneous and also the sampling methodology varied regionally. Moreover, only a small number of sites are monitored for the IWC in most of Africa and Eastern-Europe. Therefore, this dataset did not cover the full distribution of species as shown in range maps (BirdLife International & Handbook of the Birds of the World, 2017). This was particularly apparent for rare species and species which do not entirely depend on wetlands. By the nature of their selection criteria, IWC sites are biased towards wetlands and thus under-represent dryland habitats. This led to over-predictions in dryland areas (because absence information was missing here), and under-estimated the importance of predictor variables describing inundation which characterize wetland habitats. Therefore, we added casual observations from various sources, such as BirdTrack, eBird, observation.org and GBIF as well as from different atlases, for example, the Russian breeding bird atlas, which reduced the problem.

We tested a series of different approaches to overcome the strong sampling bias of the occurrence data. After removing duplicate observations per species and grid cell, we tested three different approaches: (a) to weight each observation individually in the models based on a sampling bias value of the underlying grid cell (Figure S15); (b) to split the data into two sets: one including casual observations (presence only), such as from GBIF, and background data, and another one including presence–absence data from IWC sites; we

evaluated the predictions from models of the two subsets with the opposite subset and built an ensemble weighted by AUC scores. (c) A resampling strategy using the following steps: (1) The sampling bias grid (Figure S15) was binarized using an appropriate threshold that leads to a small number of distinct, homogeneous polygons (1050 occupied cells), rather than a smaller value that leads to more fragmented coverage (Figure S16). Within the oversampled areas, occurrence information was resampled for each species by (2) removing stepwise and randomly species observations with a lower or equal minimum distance of 50 km to their nearest neighbouring observation. This process of thinning-out was repeated until the minimum distance to the nearest neighbour was more than 50 km for all observations, or the number of observations within the oversampled area equalled the number of observations in the under-sampled area. (3) After the thinning-out process, half of the observations in the under-sampled area and the same number of observations in the over-sampled area were randomly selected and used for model calibration (see an example in Figure S17). The remaining hold-out data were used for model evaluation. (4) The whole process of thinning-out and resampling was repeated 10 times. Steps 2–4 were repeated for observations classified as breeding, passage, wintering and resident.

We assessed the different methods by their ability to predict the mapped range of the species, with a special focus on under-sampled regions. The resampling strategy (c) was the only method which clearly corrected for the biased predictions, with less over-prediction to over-sampled areas and less under-predictions to under-sampled areas; hence, we deemed the resampling strategy as most appropriate. The evaluation was based on visual comparisons of species-by-species predictions with range maps (BirdLife International & Handbook of the Birds of the World, 2017) by waterbird experts. We used expert evaluation rather than statistical indices (both can be found in Table S5) as the latter can only show how well models fit the test data and will, therefore, lead to selection of the models that best reproduce the known distribution from a spatially biased dataset. Additionally, the statistical indices from a to c are not comparable with each other because they use different datasets, and independent, unbiased data were unavailable for testing these various approaches to bias correction.

2.1.4 | Selection of the background data

We tested a set of approaches for selecting real absence data, pseudo-absences, background data and combinations between these approaches for modelling (for details, see Supplementary Material). As a result of these tests and in the absence of reliable and sufficient absence information, we used two sets of 10,000 geographical randomly selected background points (sometimes also called pseudo-absences), one to fit and one to evaluate the models. The background was selected from the entire study area, and thus accessible to species as recommended (Barve et al., 2011). Because most modelling methods require both presence and absence

information to fit the models, background data are commonly used in the absence of real absences, with randomly selected background points being the standard approach (Barbet-Massin et al., 2012; Guisan et al., 2017).

2.2 | Environmental data and hydrologic models

Five bioclimatic predictors characterizing the climatic niche of waterbirds and five predictors characterizing waterbird habitat were used to determine current and future (2050) water bird distributions (for details, see Table S2). The habitat layers contained a terrain roughness index, urban area and three layers from a hydrological inundation model: permanently inundated areas, seasonally inundated areas and the standard deviation of spatially varying inundation lengths. Incorporating inundation as a predictor to model the distribution of waterbirds is important to capture the downstream impact of climate change on the availability of wetlands in river catchments. We assessed both the ecological relevance (as described in Table S2) and the collinearity among various climatic predictors before starting the modelling. We preferred selecting ecologically meaningful predictors with low collinearity and high relevance for a broad suite of species over an automated variable selection because automated solutions to predictor selection and contribution cannot replace a sound pre-selection of eco-physiological predictors (Araújo & Guisan, 2006; Austin, 2002). The selection of predictors based on sound ecological knowledge was shown to optimize model transferability compared to many automated procedures (Petitpierre et al., 2017). Moreover, the limitations of scores and metrics to select predictor variables and assess their importance are well-known (Fourcade et al., 2018). The overall correlation between the predictors used was low with a maximum Pearson correlation coefficient of $r = 0.638$ between annual mean temperature and precipitation seasonality, and some negligible multicollinearity with a maximum variation inflation factor of 2.29. The environmental predictors were transformed to the World Eckert IV projection (EPSG 540102) and aggregated to a grid frame of 10 × 10 km resolution. We have selected only non-climatic predictors that are important ecologically for waterbirds but unlikely to change as the result of climate change. Anthropogenic land cover (e.g. farmland and forest) was omitted due to the uncertainty of their future extent as a result of climate change or human activities.

2.2.1 | Inundation and discharge modelling

Maps of inundation duration under current and future climate conditions were generated specifically for this project with a statistical inundation model relating local streamflow and inundation extent (Anand, 2018). First, baseline (1993–2007) monthly inundation extents, including waterbodies and flooded vegetation, were mapped by downscaling coarse-resolution remote sensing imagery to a 500 m grid cell resolution following the methodology of the

GIEMS-D15 dataset (Fluet-Chouinard et al., 2015). Furthermore, baseline (1971–2000) monthly discharge estimates were provided by the global integrated water balance model WaterGAP (version 2.2) (Döll et al., 2003; Müller Schmied et al., 2014). The WaterGAP data were spatially downscaled from their original 0.5 degree grid cell resolution to the 500 m resolution of the HydroSHEDS river network (Lehner et al., 2008) using geo-statistical techniques (Lehner & Grill, 2013). A validation of the downscaled discharge estimates against observations at 3003 global gauging stations (provided by the Global Runoff Data Centre, https://www.bafg.de/GRDC), representing river sizes from 0.004 to 180,000 $m^3 s^{-1}$, confirmed good overall correlations for long-term average discharges ($R^2 = 0.99$ with 0.2% positive bias and a symmetric mean absolute percentage error (sMAPE) of 35%, improving to 13% for rivers ≥100 $m^3 s^{-1}$). Finally, the monthly GIEMS-D15 inundation extent layers were correlated with the monthly WaterGAP river discharge estimates to identify local streamflow thresholds at which inundation occurs. These discharge–inundation relationships were derived for sub-catchment units which were delineated based on topography and hydrological connectivity as provided by the HydroSHEDS database. A performance evaluation showed that the discharge-based inundation model was able to correctly simulate the inundation duration of the remote-sensing-based GIEMS-D15 dataset within a range of plus/minus one month for 92% of all 500 m grid cells.

To simulate changes in future discharges and their associated changes in inundation extent, the most recent version 3 of the WaterGAP model (Eisner, 2016; Flörke et al., 2018) (at 5 arc-minute resolution) was used to calculate percent changes in discharge between the baseline time period (1971–2000) and the future period (2036–2065) representing the year 2050. The future changes in discharge were downscaled and converted into changes in inundation extent based on the relationships developed on baseline conditions as described above. Future discharge and inundation extents were generated under two future scenarios for 2050 (HadGEM2-ES and IPSL-CM5A-LR using the Representative Concentration Pathway RCP 6.0).

To create the required predictor variables for the waterbird distribution model, the mapped inundation durations (months year^{-1}) for both baseline and future conditions were aggregated at the 10 × 10 km resolution into three indices: extent of permanently inundated areas (inundation duration ≥11 months year^{-1}), extent of seasonally inundated areas (inundation duration 2–10 months year^{-1}) and the standard deviation of the spatially varying inundation durations within each 10 km grid cell. For more details on the rationale and calculation of these indices, see Table S2. An overview of the resulting changes in inundation duration between the baseline and 2050 conditions within the region of the Africa-Eurasian flyway is provided in Figure S32.

2.3 | Species distribution modelling approach

We used an ensemble-modelling approach for modelling waterbird distributions using the Biomod R-package (Thuiller et al., 2009,

2017). We ran four modelling techniques (GLM, Maxent, GBM and RF) in the ensemble for the breeding, passage, wintering and resident stages for each species. Two background sets of 10,000 background points were sampled over the entire study area, of which one was used for model calibration and one for model evaluation (more information on why we chose background data for modelling is given in the Supplementary Material). Similarly, we used two sets of occurrence data, one for model calibration and a hold-out set for model evaluation. For selecting the hold-out observation data, we used the rules of the resampling process as described above except for species with a low number of observations (<100) to avoid losing too many data for model calibration. Instead, for these species, we used a 10x repeated random 5-fold split-sampling procedure, where 75% of the data was used for calibration and 25% for evaluation.

For calibrating the models, the background data were weighted equally to the number of presences for each species, which is the recommended practice for species distribution modelling (Barbet-Massin et al., 2012). We used Somers' D, a rescaled version of the Area under the Curve (Somers' D = 2*AUC-1), to evaluate each model and to average four modelling techniques to an ensemble, weighted by the mean Somers' D. The models were projected to the current extent of species' flyways with an added buffer of 300 km for current climate models (i.e. the current habitat suitability map) and the same two future scenarios for the year 2050 as for the inundation layers (HadGEM2-ES and IPSL-CM5A-LR using the Representative Concentration Pathway RCP 6.0). We limited the extent of the projected area to a 300 km buffer around its current known population boundaries to reduce the risk of over-predictions in areas far away from a species' current range. For birds in general, annual shifts in geographical distribution of less than 10 km have been reported (Auer & King, 2014; EPA, 2016; Gillings et al., 2015; Virkkala & Lehikoinen, 2014; Zuckerberg et al., 2009). These studies provide estimates of average range shift 0.48–1.84 km/year (i.e. 14–55 km in 30 years, with maximum values ranging between 171 and 464 km over a similar period). However, waterbirds by their nature tend to have high dispersal capability, often at continental scales as an adaptation to the ephemeral nature of many wetlands (Roshier et al., 2001). Therefore, we took the maximum value from the maximum estimate from Europe (Gillings et al., 2015) and conclude that 300 km is an adequate buffer to limit dispersal.

The projected habitat suitability maps were binarized to calculate range size and to identify Critical Sites predicted to be suitable using thresholds from the True Skills Statistics (TSS: maximizing sensitivity and specificity of the models) which is an appropriate thresholding approach (Liu et al., 2013).

2.4 | Priority index PI

We combined the projected climate change impacts from our models and current site importance to calculate a priority index (PI)

to highlight those sites that are particularly important for climate change adaptation in the flyway context. The inclusion of current site importance ensures that the analysis focuses on sites that are already of high conservation importance, and index values are not unduly influenced by the potential over-prediction of some species that are limited by non-climatic factors not included in the models (see Supplementary Material). Current site importance was calculated as the proportion of the flyway population at a site weighted by the IUCN Red List category of extinction risk of each species, summed across all species for which the site fulfils the site selection criteria mentioned above in one or more seasons (hereafter 'qualifying species'). To calculate the site PI, the site importance was weighted by the projected change in suitability of the site for the population and the exposure of the whole population to climate change in the relevant season, summed across all qualifying species. Thus, PI relates to the current importance and the projected future exposure to climate change for each of the 2,601 Critical Sites; it can be used to highlight priority sites for local site management. The index was scaled between –1 and 1, for each of the 2,601 existing Critical Sites (see above) by multiplying each value by 1 divided by the maximum absolute value of PI:

$$\text{Site importance} = \sum_i \frac{p_i}{P_i} \times T_i$$

$$\text{Exposure} = \sum_i \frac{p_i}{P_i} \times T_i \times \Delta s_i$$

$$\text{Responsibility} = \sum_i \frac{p_i}{P_i} \times T_i \times V_i$$

$$PI = \sum_i \frac{p_i}{P_i} \times T_i \times V_i \times \Delta s_i$$

where:

i: population of a qualifying species at the site for a specific season (breeding, passage, wintering or resident).

p_i/P_i: The proportion of the entire population (P) that is comprised by the current population (p) at a site.

T_i: Global IUCN Red List category of extinction risk for the species i (Least Concern: 1; Near Threatened: 2; Vulnerable: 3; Endangered: 4; Critically Endangered: 5).

V_i: projected current range loss of population i to climate change (where zero is 100% overlap and one is no overlap): Range loss was calculated by subtracting the proportional overlap between the species' projected current and future distribution from one and ranges from zero (100% overlap, i.e. all current range will remain in the future) to one (no overlap, i.e. all current range will be lost in the future).

Δs_i: projected change in habitat suitability (i.e. the output from the Species Distribution Models) for population i at the site.

The PI is calculated from existing Critical Sites for qualifying species of a specific season (breeding, passage, wintering and resident)

but does not identify new sites where occupancy is predicted by the models to avoid the influence of false positives. The *PI* therefore identifies any existing important Critical Sites that are projected to change their suitability due to changes in climatic or hydrological condition.

Sites that hold a high proportion of one or more populations in a season receive a higher site importance index than sites that support smaller proportions and for fewer species (Harebottle & Underhill, 2016; Nilsson & Nilsson, 1976). The global Red List category of the species represents a positive weighting factor when calculating the *PI*. The exposure index weights the site importance according to the projected change in suitability. As the consequence, it highlights the sites that are projected to suffer large negative or positive changes in suitability for their qualifying species. The responsibility index of the site is higher if most of the populations it hosts are projected to suffer from large range losses in that season. Sites with strongly negative *PI* values are higher priority for climate change adaptation measures because they (a) support a higher proportion of the entire population of (b) a more threatened species with populations that (c) are predicted to suffer higher range losses in the relevant seasons and that (d) are projected to experience large reductions in site suitability.

The *PI* separates sites projected to have increased suitability for their current species in future (*PI* > 0) from those projected to have reduced suitability, that is, sites that are exposed to climate change (*PI* < 0). Sites with high positive values share the same characteristics in respect of attributes (a–c) of a negative *PI*, that is, they are highly important for an already threatened species that is projected to suffer high range loss, but the climatic suitability of the site is projected to improve. Hence, these are also priorities for adaptation management in the light of the overall range contraction of an already high conservation priority species. Site priority is therefore highest with a positive or negative value of 1 and lowest with a value of 0. Alternate approaches to calculating this index had little impact on our conclusions (Supplementary Materials).

SDMs were computed and projected at the species level. However, in the context of the AEWA and the Ramsar Convention, sites are designated for populations. Therefore, we extracted spatial information from the SDMs for each population (i.e. projected current range loss and projected change in habitat suitability) using the delineations of the flyway populations published on the Critical Site Network Tool 2.0.

2.5 | Climate change adaptation strategy (CCAS)

For each site, we identified particular CCASs by plotting the proportion of projected emigrant species (those for which the site is projected to become unsuitable in the future) against the proportion of projected colonist species (those for which the site is projected to become suitable) for each Critical Site in the network. We divided the area of the resulting graph into five sectors using the median, lower quartile and upper quartile of values (Figure

S11) and classified each site into one of five CCAS categories following Hole et al., 2011 (see also Table S3): high persistence (low colonization, low emigration), where the site should be managed to maintain viable populations of the persistent populations, increasing specialization (low colonization, high emigration) where the site should be managed to retain populations of projected emigrants, high turnover (high colonization, high emigration) where it is important to facilitate the transformation of habitats to become suitable for the immigrants as well as managing habitats to retain populations of emigrants, increasing value (high colonization, low emigration), where sites should be managed to maintain populations of persistent species and facilitate the transformation of habitat for immigrants, and increasing diversification (intermediate colonization, intermediate diversification) where the management should focus on maintaining populations of persistent species and reprioritize management objectives if emigration or immigration commences.

3 | RESULTS

In total, 57.5% of all 2601 analysed sites are projected to be negatively affected by climate change but there is strong geographical variation. Sites with the greatest overall deterioration in suitability are located across Sub-Saharan Africa (where 84.9% of 372 sites deteriorate in suitability), North Africa (89.9% of 148 sites) and the Middle East (80.8% of 266 sites), whereas sites with the greatest improvement in suitability are located across Eastern Europe (80.0% of 421 sites improve) and Kazakhstan (84.5% of 58 sites) (Figures 1 and 2 and Figures S6 and S7).

Of the 100 Critical Sites projected to be most vulnerable to climate change, that is, sites with negative *PI*, 55 are in Africa, particularly Tunisia (9), Tanzania (7), Namibia (6) and South Africa (6), with additional concentrations of vulnerable sites around the Mediterranean and Middle East (including 8 sites in Iran) (Table S1 and Figure 1). Those sites with the highest positive values of *PI*, that is, where climate change is projected to result in large increases in overall site suitability, are located in the Russian Federation and Kazakhstan, highlighting the potentially increasing value of these countries for waterbirds in the future (Table S1, Figure 1 and Figures S5–S7).

Our models predict that by 2050 the average latitude of suitable breeding and wintering sites of Palaearctic migrants shift on average 137 ($\pm$10.3) km and 178 ($\pm$13.3) km northwards, respectively (Figure S14). For the same time horizon, the mean distance between breeding and wintering sites projected to be suitable for Palaearctic migrants that breed below 45°N declines by up to 460 km (Figure 3).

4 | DISCUSSION

Our study found that most priority sites for migrating waterbirds that are vulnerable to climate change are located in Africa and the Middle
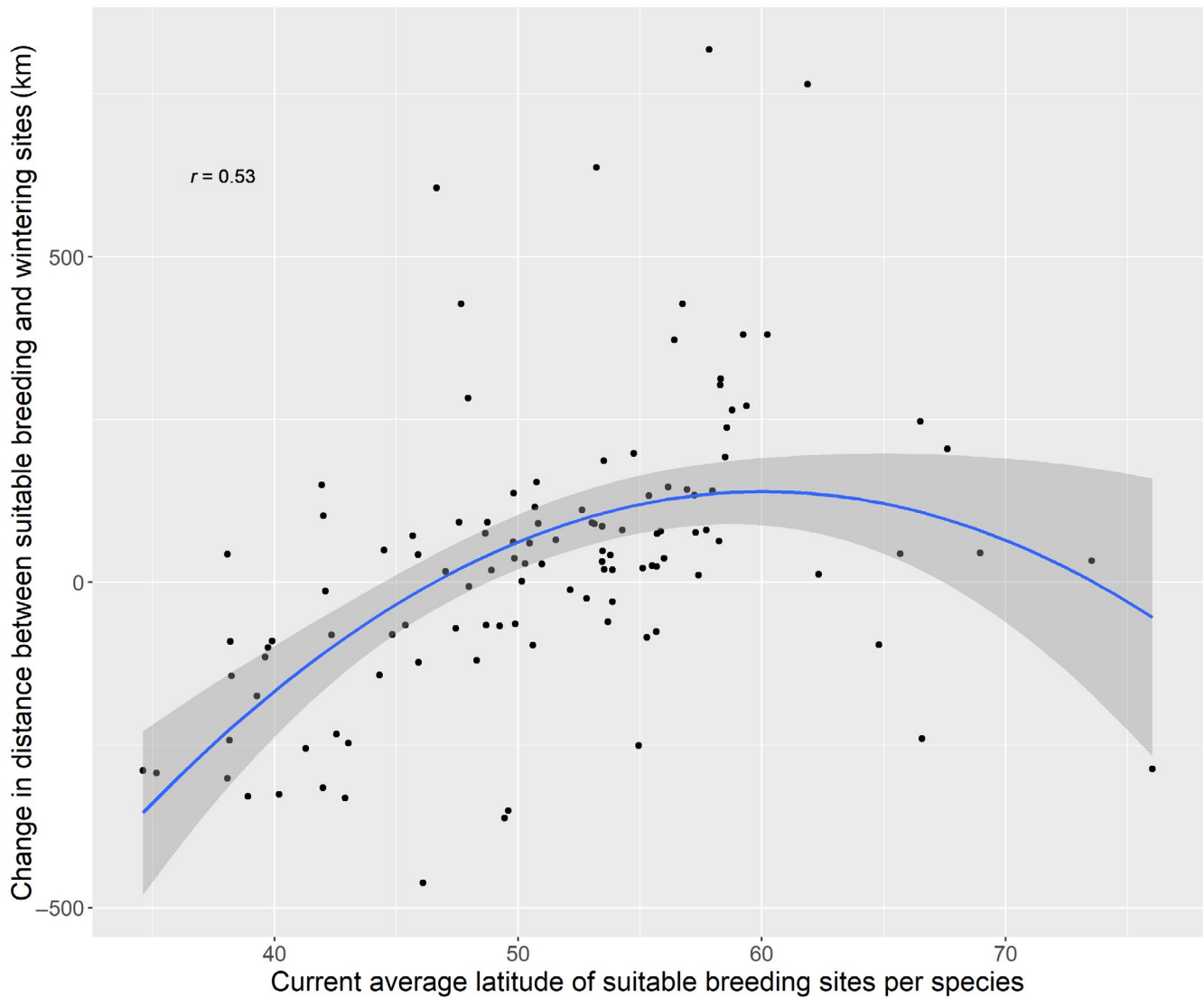
FIGURE 3 The relationship between mean latitude of breeding sites and mean change in Euclidean distance between breeding and wintering sites per species ($n = 114$). Palaearctic migrating waterbirds breeding at low latitudes (35–45°) are projected to experience reduced migration distances by 2050, whereas species breeding at intermediate latitudes (35–60°) are projected to migrate longer distances between their breeding and wintering sites. The ANOVA table of the linear model is shown in Table S4

East and are not legally protected (Figure S8), despite national commitments to conserve wetlands and waterbirds under both AEWA and the Ramsar Convention (Figure S9). These sites are also located in countries with suboptimal conditions for effective conservation, that is, with a low gross domestic product (and thus little financial capacity for protection) and/or with less effective governance, one of the most important factors for effective conservation (Amano et al., 2018) (Figure S9). This mismatch between impacts of climate change on Critical Sites and the capacity to conserve them contrasts with member states of the European Union (including the UK to the time of the analyses) where Critical Sites are well covered by Special Protection Areas under the EU Birds Directive (Figure S10). Coverage of critical sites and other Key Biodiversity Areas by protected and conserved areas is likely to continue to be used as an indicator of progress in achieving Convention on Biological Diversity

(CBD) targets. Hence, our results can be used to target expansion of protected areas and recognition of OECMs to help achieve these targets.

Sites with projected increases in overall site suitability are located in the Russian Federation and Kazakhstan (Table S1, Figure 1 and Figures S5–S7). These sites will require strict protection alongside proactive conservation measures to ensure that they can accommodate the populations losing suitable climatic conditions along the trailing edge of the range.

Eastern Europe and West Siberia host the highest number of sites with increasing value for waterbirds (Figure 2). These sites should be of high priority for future conservation, both to maintain existing populations and to provide areas for colonization of species, with management balancing the needs of both groups. Expanding the network of protected sites would enhance

its robustness in this increasingly important subregion. There is a strong impetus for such an expansion, because the post-2020 Global Biodiversity Framework currently being negotiated under the CBD contains a target to conserve 30% of terrestrial, freshwater and marine environments, particularly areas of importance for biodiversity, through protected areas and OECMs, by 2030. This represents a substantial expansion from 17% terrestrial coverage currently.

Large parts of Africa are characterized by sites with increasing specialization, where the focus should be on restoration and habitat management by maximizing suitable conditions for relevant species. Ideally, this would improve site resistance while also supporting climate change mitigation and nature-based solutions to climate-change, although potential conflicts with competing objectives may occur and will require careful consideration (Morecroft et al., 2019). Measures to fill gaps in the network, enhance connectivity and facilitate the colonization of new sites should also be prioritized for populations projected to lose the largest extent of suitable conditions under climate change. Central Europe includes many sites with high persistence, where site conservation and management for those persisting species should continue to be prioritized (Figure 2).

The high concentration of Critical Sites exposed to climate change in Africa and the Middle East (Figures 1 and 2; Figures S5 and S7 and Table S1) and the increasing specialization of these sites emphasize the need to focus conservation efforts in these regions on maintaining important wetland areas for persisting species which are unable to retreat to other sites, and to facilitate the dispersal of threatened populations to other, more resilient sites for emigrating species.

Critical Sites in Africa are projected generally to become less suitable for waterbirds. Consequently, Palaearctic waterbirds in the Africa-Eurasia region may increasingly shift their non-breeding range north-eastwards to winter in Europe instead of in Africa (Figure S14; Maclean et al., 2007; Pavón-Jordán et al., 2015). Therefore, migration distances may decrease for most (Visser et al., 2009) but not all (Zurell et al., 2018) species (Figure 3), suggesting that such species may substantially alter their migratory strategies and use of the site network under climate change. Maintaining a coherent and resilient flyway network for waterbirds will allow species to colonize other wetlands in the site network as they become suitable in the future. Changes in distributions may drive inter-species competition, although this is difficult to study (Maclean et al., 2007; Pearce-Higgins & Green, 2014).

African resident species associated with seasonal wetlands are less migratory and more limited by their habitat becoming periodically unsuitable because of droughts (Maclean et al., 2007). Maintaining high habitat quality across the whole African site network is thus essential for these species, making it necessary to manage the entire network holistically, with the management of each site considering impacts across the whole network (Nagy et al., 2021). CCASs should therefore be applied across the whole network of sites to allow coherent management responses (Franklin et al., 2014) for waterbirds, which will require better international

coordination and more transboundary collaboration in shared catchments.

Moreover, and especially in Africa, gaps in the network of Critical Sites must be filled and sites effectively conserved, either by establishing and effectively managing protected areas (Figure S8) or by OECMs.

Although we identified CCAS categories for each site to support planning, the exact management interventions that are appropriate at a particular site will depend on the particular species for which the site is currently and/or potentially suitable in future, their habitat requirements and the management actions needed to deliver these. Appropriate actions will also depend on the hydrological regime, surrounding land use, human population density and distribution, engagement of the local community and authorities, and the financial resources and capacity available. Investing in conservation planning and adaptive management to create a climate-resilient network of wetlands not only facilitates waterbird conservation but will also benefit other species and communities depending on healthy wetlands (Millennium Ecosystem Assessment, 2005; Ramsar Convention on Wetlands, 2018). Priority areas for climate change adaptation for waterbirds closely overlap with priority areas for climate change adaptation for humans, and a better integration between conservation and disaster risk reduction and livelihood-focused efforts is needed. Effective protection of wetlands can therefore result in a win–win situation by securing critical ecosystem services, conserving waterbirds and honour international agreements.

4.1 | Strengths and limitations

Here, we integrated the effects of long-distance hydrological changes with climatic predictors in species distribution models, predicting not only changes in the breeding distribution of waterbirds, but also changes in their wintering and passage distributions, and applied the results to the management framework of Hole et al., 2011 for an entire group of species (waterbirds) at flyway scale. To our knowledge, this is the first study that (a) uses such a comprehensive set of waterbird distribution data, (b) integrates changes in inundation into the assessment of climate change, (c) identifies adaptation strategies and (d) ranks critical sites to identify those with highest priority for adaptation actions. The novelty of this work is to combine these aspects, apply them at flyway scale and interpret the results for conservation efforts under an international flyway conservation treaty, the AEWA.

Despite these novel aspects, our climate change impact projections also share limitations with previous assessments: (i) the gathered species data used were biased towards Central- and Western Europe and South Africa, while species data from Russia and large parts of Africa are under-represented (Figure S15). However, we made concerted efforts to gather species occurrence

data from relevant monitoring and atlas projects and citizen science platforms (see Methods). We believe that our collection of observations is the most comprehensive available for waterbirds in the African-Eurasian flyway, and consider that the combined dataset provides a more robust basis for our models than using only range maps (Zurell et al., 2018). We carefully evaluated for each population how well the modelled seasonal distribution reflected the relevant part of the range as mapped by BirdLife International and Handbook of the Birds of the World (BirdLife International & Handbook of the Birds of the World, 2017), with the distribution of each population defined by the population boundaries published on the Critical Site Network Tool 2.0. We removed those models for which the projected suitability clearly under- or overestimated these areas (where the overlap between the modelled range and the mapped range was less than 50%). This expert evaluation was necessary as we modelled the distribution of each species rather than each biogeographical population separately to avoid truncating the environmental space used by species, and also because the ranges of different populations of the same species often overlap in the breeding or in the non-breeding season. Therefore, we extracted range size and site suitability for the *PI* for each population from the species-level models. Hence, model evaluation scores apply to models at the species level. Despite using only 50% of the data for calibration and the remainder for evaluation (except for rare species; see Methods), the model evaluation scores were very high (mean AUC: 0.975 ± 0 [range: 0.939–1] and TSS of 0.856 ± 0.055 [range: 0.718–1]). The sampling bias was less problematic for naturally rare waterbirds with restricted ranges because they only occasionally occur in both over- and under-represented areas. However, given the underlying imbalanced species data, it was not possible to entirely control for sampling bias (see Supplementary Materials).

(ii) We used occurrence instead of abundance data for modelling. Especially for migrating and wintering stages, sites must support large populations because some waterbirds are highly aggregated at stop-over sites and modelling abundances could better reflect these patterns. However, only a small subset of the data we analysed (IWC data) contains abundance estimates, and these are not comparable between countries. Modelling abundances would therefore entail a substantial reduction in observation data (by 61.8% for 75% of the species and by 73.7% for 50% of the species). Moreover, current abundance is factored into the estimates of *PI* and although not modelled explicitly, does contribute to the estimation of site importance.

(iii) We considered only the effect of abiotic processes and did not consider biotic processes that could alter the projections (e.g. competition, food supply), although modelled relationships with climate are at least as likely to reflect biotic as abiotic processes (Ockendon et al., 2014) (iii) we did not consider the indirect impacts caused by human responses to climate change, such as altered land use, although this is also likely to drive a component of the modelled species responses to climate; (iv) we assumed similar responses in space and time, and ignored potential evolutionary processes that could increase bird adaptations to climate change, and (v) there is some mismatch between the period of survey data (1990–2016) and the climate data (1950–2000) (Hijmans et al., 2005) available at the time of the study, although this does account for a likely lag that occurs between climate change and impacts on species occurrences, and given the generally strong predictive model performance it does not appear to have been a major limitation. Moreover, a test on using predictors from different climatic baselines showed only marginal effects on the *PI* (Figure S23 in Supplementary Materials). (vi) Our study focuses on 2.601 existing Critical Sites and did not consider the potential for new sites to be added to the network. This limitation is shared by many other previous studies (e.g. Johnston et al., 2013). However, identifying new priority sites for conservation solely based on the result of modelling is inadvisable because of the high uncertainties inevitably involved in such studies (see Pearce-Higgins & Green, 2014). Our study aimed to inform flyway-scale conservation of the existing site network given the expected redistribution of species across it. Reviewing the network and identifying new sites based on the latest data are ongoing as part of the wider efforts to identify and conserve Key Biodiversity Areas, but is outside the scope of our paper. Regardless, resolving these issues in future studies would further improve the projections at the species level, but would be unlikely to affect the overall pattern of responses across species presented here.

5 | CONCLUSIONS

By considering the combined effects of long-distance hydrological changes and more localized responses to bioclimatic variables, we modelled the impacts of climate change on the year-round distribution of both migratory and resident waterbirds across the African-Eurasian flyway. This enabled us to provide a comprehensive assessment of the sites and species that are most significantly impacted by climate change. Importantly, we highlight projected negative impacts across 57.5% of sites, with the majority of these located in Africa and the Middle East, primarily associated with impacts of warming. In contrast, sites in Eastern Europe, Central Asia and West Siberia are projected to increase in importance. We use these results to recommend appropriate climate change adaptation responses across the flyway. We emphasize the importance of adequate resources, governance mechanisms and institutional capacity in the most affected regions, and the critical role that international policy instruments, such as the Ramsar Convention and AEWA, can play in supporting climate change adaptation. Given the role of waterbirds as indicators of wetland quality and extent and their consumptive and recreational use by humans, these results also highlight potential wider climate-driven pressures on the delivery of ecosystem services from wetlands across the flyway that warrant further investigation, particularly if potential conflicts between climate change adaptation for people and nature are to be avoided (Morecroft et al., 2019).

CONFLICT OF INTEREST

Authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

Conceptualization: SN and MvL. Data acquisition (Russian breeding atlas): MK and OV. Methodology: FB, SN, LH, BL, MA, MF and EFC. Investigation: FB and SN. Visualization: FB. Funding acquisition: SN and MvL. Project administration: SN and MvL. Supervision: SN, AG, JPH, SB and LH. Writing – original draft: FB. Writing – review and editing: FB, SB, AG, VJ, JPH, SN, BL, MA, MF and EFC.

DATA AVAILABILITY STATEMENT

The species data that support the findings of this study are available from Wetlands International (http://iwc.wetlands.org), GBIF.org, British Trust for Ornithology (https://www.bto.org/our-science/projects/birdtrack), Cornell Lab of Ornithology (eBird.org), the atlas of the birds of Moscow city, the atlas of breeding waders in the Russiana Arctic and the Russian breeding bird atlas (in prep.). Details can be found in the reference list.

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