Spatially explicit risk mapping reveals direct anthropogenic impacts on migratory birds

Running title: Anthropogenic threats to migratory birds

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ABSTRACT

Aim: Migratory species rely on multiple ranges across the annual cycle, rendering them vulnerable to a wide range of spatially disparate anthropogenic threats. The spatial distribution of these threats will strongly influence the magnitude of their population-scale effects, but this has not been quantitatively assessed for most species.

Location: Europe, Central Asia, Western Asia, Africa.

Time period: Modern.

Major taxa studied: Aves.

Methods: We combined remote-sensed data and expert opinion to map sixteen anthropogenic threats relevant to migratory birds across Europe, Africa and the Middle East – including the first spatially-explicit pan-continental assessment of relative hunting pressure. By combining the resulting composite threat maps with species range polygons and morpho-behavioural traits-based weightings (reflecting relative threat susceptibility), we created species-specific risk maps for 103 Afro-Palaearctic migratory birds breeding in Europe and evaluated how spatial threat vulnerability relates to long-term population trends.

Results: We found that greater vulnerability to direct mortality threats (including hunting pressure, infrastructure and nocturnal lights), especially in the non-breeding season, is associated with declining bird population trends.

Main conclusions: Our results emphasise the importance of spatially explicit approaches to quantifying anthropogenic drivers of population declines. Composite risk maps represent a valuable resource for spatial analyses of anthropogenic threats to migratory birds, allowing for targeted conservation actions.

Keywords: threat mapping, migratory birds, Afro-Palaearctic, breeding, non-breeding, anthropogenic change, hunting

1 INTRODUCTION

Increasingly sophisticated modelling of satellite-derived data has transformed biodiversity monitoring and conservation (Goldewijk et al., 2011; Hansen et al., 2013; Turner, 2014), allowing high-resolution mapping of anthropogenic impacts on the natural world. Studies often focus on evaluating spatial exposure of populations to individual threats (Buchanan et al., 2020; Møller et al., 2014; Tracewski et al., 2016), but effects of these can be difficult to detect when viewed in isolation, especially if different threats are interactive or their effects only manifest cumulatively (Akresh et al., 2019; Howard et al., 2020; Kennedy et al., 2019; Mahon et al., 2019; Raiter et al., 2014). Large-scale mapping of combined stressors offers a powerful approach to gain a more holistic understanding of human impacts on biodiversity, including composite threat assessment for terrestrial and marine ecosystems (Bowler et al., 2020; Halpern et al., 2008; Theobald, 2013; Venter et al., 2016), freshwater threats and water security (Vörösmarty et al., 2010), and conservation prioritisation (Allan et al., 2013; Kennedy et al., 2019). Here we present the first application of this multidimensional spatial approach to threat evaluation in migratory bird species.

Migrants' reliance on resources found in geographically distinct areas throughout the annual cycle may render them particularly vulnerable to human-induced threats (Newton, 2004; Robinson et al., 2009; Wilcove & Wikelski, 2008), necessitating more spatially-nuanced conservation efforts than are needed for non-migratory species (Runge et al., 2014, 2015; Sanderson et al., 2016). Migratory birds breeding in Europe and North America – especially long-distance migrants – are declining at a greater rate than non-migratory species (Laaksonen & Lehikoinen, 2013; Robbins et al., 1989; Sanderson et al., 2006; Vickery et al., 2014), potentially as a result of their cumulative exposure to spatially disparate threats.

A suite of anthropogenic threats are known to impact bird populations, ranging from human settlement and associated infrastructure, overharvesting, land-use change, and anthropogenic climate change (Bairlein, 2016; Kirby et al., 2008; Loss et al., 2015; Maxwell et al., 2016). Accounting for spatial variation in the degree of vulnerability to threats is essential in pinpointing areas for conservation intervention

(Tulloch et al., 2015). Identifying the relative importance of conditions within migrants' spatially disparate seasonal ranges is necessary to understand and counter mechanisms driving negative population trends. Pronounced declines in long-distance migrants suggest a substantial influence of conditions during migration or on the non-breeding grounds, with population trends being sensitive to migratory routes (Hewson et al., 2016; Newton, 2006; Tøttrup et al., 2008), as well as non-breeding climatic conditions (Ockendon et al., 2012) and habitat change (Adams et al., 2014; Cresswell et al., 2007). However, influential anthropogenic threats may occur throughout the annual cycle (Sergio et al., 2019; Thaxter et al., 2010), and seasonal effects can interact with potential carryover effects from conditions experienced earlier in the annual cycle (Buchan et al., 2021; Morrison et al., 2013). This potential for between-season cumulative and/or synergistic effects highlights the need for full-cycle approaches for understanding – and ultimately, targeting – threats to migratory species (Calvert et al., 2009; Marra et al., 2015; Martin et al., 2007; Small-Lorenz et al., 2013; Zurell et al., 2018).

Here, we combine a suite of large-scale data sources to generate novel composite risk maps for anthropogenic threats across the Afro-Palearctic region, including the first spatially explicit map of hunting pressure for migratory birds. We then examine the extent to which spatially explicit indices of threat vulnerability correlate with breeding population trends for 103 Afro-Palaearctic migratory birds. We assess cumulative exposure to risk by grouping threats according to whether they pose direct mortality threats to birds (Loss et al., 2012; 2015) (e.g. overharvesting, collision risks), threats mediated through diffuse impacts of environmental change (habitat degradation, e.g. through loss of foraging resources) or the potential for both (climate change, e.g. extreme events, decline in resource availability). By grouping the threats in this manner, we aim to isolate elements of anthropogenic change that pose immediate survival threats from those that may pose more chronic and indirect threats, and from climate threats which may pose a complex combination of direct and indirect threats and potential benefits. Following Foden et al. (2013), we define vulnerability as the combination of exposure, sensitivity and capacity to respond to environmental change. We use traits-based weightings as measure of species sensitivity, combined with range-level threat exposure, to calculate combined risk vulnerability across species' seasonal ranges, allowing us to partition the effects of different anthropogenic risks on population trends, and evaluate the extent to which these vary between the breeding and non-breeding ranges.

2 METHODS

2.1 Data layers

2.1.1 Overview of risk mapping

We assembled sixteen spatial datasets covering the Afro-Palaearctic region (see *Supplementary Materials: Data Layers*) representing three broad anthropogenic threat types: direct mortality, habitat change and climate change. Each layer measured the current distribution (median measurement 2017, range 2013–2020) of human modification of the natural environment, relative either to an historic baseline period (mean of 1961–1990 for climate variables, 1985 for afforestation), or to an equivalent un-modified landscape (i.e. with no human land-use change or infrastructure development) (Table 1). We combined the constituent layers for each threat type into composite surfaces using either linear summation for threats posing additive risks or fuzzy algebraic summation for potentially correlative threats (Kennedy et al., 2019) – see *2.4 Composite risk-mapping algorithm*. We adapted generic threat maps into species-specific risk surfaces (where risk is the combination of threat with vulnerability) by applying trait-based threat vulnerability weightings (D'Amico et al., 2019; Foden et al., 2013; Mason et al., 2019) (see *2.3 Species' threat-vulnerability weightings*) for each constituent threat layer (Figure 1).

2.1.2 Direct mortality threats

Infrastructure associated with human settlement poses significant collision mortality risks – particularly to nocturnally migrating birds – in the form of roads (Erritzoe et al., 2003; Loss, Will, & Marra, 2014; Santos et al., 2016) and buildings (Loss et al., 2015; Loss et al., 2014). To capture these threats, we used maps of urbanisation (Corbane et al., 2018) and total roads density (Meijer et al., 2018), combining all road types. For species that make nocturnal movements, bird-building collision risks are exacerbated by artificial light at night (Lao et al., 2020; Van Doren et al., 2017); we mapped this using the DMSP-OLS Nighttime Lights Time Series (NOAA, 2013). We used human population density (CIESIN, 2018) as an index to capture other direct anthropogenic mortality risks (Anadón et al., 2010; Kerr & Currie, 1995;

McKee et al., 2004) including disturbance (Gill, 2007; Mallord et al., 2007) and invasive species (Newbold et al., 2015; Spear et al., 2013) – in particular the impacts of domestic and feral cats (*Felis catus*) (Aegerter et al., 2017; Loss et al., 2012, 2013b).

Bird mortality due to powerline collision or electrocution can occur at rates sufficient to have population-level effects (Bernardino et al., 2018; Loss et al., 2012; Schaub et al., 2010), and bring about changes in migratory behaviour (Palacín et al., 2017). To map overhead powerlines we combined World Bank (World Bank, 2017) and OpenStreetMap (Garrett, 2018) datasets. Windfarms also pose direct collision risks to birds (Loss et al., 2013a, 2015; Zimmerling et al., 2013), which we mapped using a OpenStreetMap-derived global windfarm dataset available from Dunnett et al. (2020).

Overharvesting is among the most significant direct threats to birds (Kirby et al., 2008), linked to population declines (Jiguet et al., 2019; Kamp et al., 2015) and even extinction (Hung et al., 2014). While it is well known that high levels of hunting occur in Palaearctic/Eurasian hotspots, e.g. of waterfowl in Gyzylagach Bay in Azerbaijan, and of passerines in Mediterranean island nations (Brochet et al., 2016; Brochet, Jbour, et al., 2019; Schneider-Jacoby & Spangenberg, 2010), and in parts of Africa e.g. of raptors and hornbills in West African markets and forest hunting camps (Buij et al., 2016; Whytock et al., 2016), relative hunting pressure has not previously been systematically mapped for migratory birds. To map hunting threats at a pan-continental scale, we surveyed expert opinion on legal and illegal hunting of migratory birds within each country in the study region. We targeted specific experts for this survey by approaching the BirdLife International partner organisations and their contacts, other local ornithological institutes and conservation NGOs monitoring bird hunting, hunters and hunting federations, and academics researching bird hunting in the relevant areas. We received 137 responses for 98 countries, with high agreement among responses for multi-expert nations (Supplementary materials: Data layers). Hunting pressure varies between species as well as spatially (Brochet, Van Den Bossche, et al., 2019; Schneider-Jacoby & Spangenberg, 2010); we therefore asked respondents to rank country-level and within-country regional variation in the relative levels of hunting of small- and large-bodied birds separately (size relative to a feral pigeon), and modified the resulting spatial hunting indices according to metrics of accessibility (roads and human population density – see Supplementary materials: Data layers) (Milner-Gulland et al., 2003; Venter et al., 2016). Following Benítez-López et al. (2019), we masked areas with >90% urban cover (Corbane et al., 2018) or with the highest levels of protected area status (UNEP-WCMC and IUCN, 2019) from hunting pressure surfaces due to low likelihood of hunting taking place there (Figure 2). We validated the results of the hunting survey by relating country-level responses to the estimated number of birds illegally killed given in Brochet et al. (2016), Brochet, Jbour, et al. (2019), and Brochet, Van Den Bossche, et al. (2019), showing moderate correlation (Spearman's ρ values between 0.43 and 0.64, see Supplementary Table S4) between our estimates and published values for the subset of countries for which quantitative hunting values are available – see Supplementary materials: Data layers.

2.1.3 Habitat change

Conversion of natural habitat to agricultural land has previously been linked to declines in migratory birds (Adams et al., 2014; Cresswell et al., 2007; Vickery et al., 2014; Walther, 2016), as has afforestation for farmland, steppe and wetland specialists (Butler et al., 2010; Goriup & Tucker, 2007; Gunnarsson et al., 2006; Voříšek et al., 2010); we mapped agricultural expansion using cropland and grazing layers for 2017 produced by Klein Goldewijk et al. (2017). As no single land-cover dataset had the temporal spread necessary to measure long-term change in forest cover, we mapped afforestation (forest regeneration, maturation and plantations) as the positive change in forest land cover between an historic baseline map for 1985, created to provide land cover estimates consistent with modern satellite imagery (Meiyappan & Jain, 2012), and a 2017 forest layer created from MODIS land cover data (Friedl & Sulla-Menashe, 2015) (Supplementary Table S1 and accompanying text). We used the urbanisation layer created for the direct mortality threats (see above) to map natural habitat converted to urban land, to which fewer avian species can adapt (Chace & Walsh, 2006).

The use of agrochemicals (particularly pesticides and fertilizers) associated with agricultural intensification may also affect species through toxicity (Calvert et al., 2013; Mineau & Whiteside, 2013), reduction in prey availability (Bright et al., 2008; MacDonald, 2006), and habitat degradation (Vickery et al., 2001). We mapped pesticide and fertilizer use within agricultural lands (see above) using United Nations estimates of mean per-country tonnage per km^2 for the years 2009-2017 (masked to cropland only for pesticides, cropland and grazing land for fertilizers) (FAO, 2019a, 2019b).

2.1.4 Climate change

Climate change, including more frequent extreme climatic events (Ummenhofer & Meehl, 2017), can have a range of negative demographic impacts on birds (Both et al., 2006, 2010; Møller et al., 2008; Szép, 1995; Tøttrup et al., 2012; Van Gils et al., 2016), but the speed and magnitude of climatic change varies considerably in space (IPCC, 2013). We mapped climate change threats using CRU TS Version 4.03 (Harris et al., 2020), generating monthly temperature and precipitation anomalies for each grid cell by subtracting monthly mean values for 1961–1990 (baseline period) from monthly mean values for 2009–2018 (modern period). To quantify changes in within-year climatic variability at the cell level, we also calculated the standard deviation around mean monthly values for the modern and baseline periods, and subtracted the baseline standard deviations from the modern standard deviations to yield monthly series of temperature and precipitation variability anomalies as a metric of changes in climatic volatility (Foden et al., 2013; IPCC, 2013). We converted each monthly series (temperature anomaly, temperature variability anomaly, precipitation anomaly, precipitation variability anomaly) to absolute anomalies (larger values indicating size of anomaly in either direction), and finally averaged these for the temperate breeding season (March–August) and non-breeding season (September–February) (Devictor et al., 2008; Lehikoinen et al., 2021).

2.2 Relating risk vulnerability to population trends

The Pan-European Common Bird Monitoring Scheme (PECBMS) collates national survey data to create population trends and indices for 170 bird species breeding in Europe (EBCC/BirdLife/RSPB/CSO, Brlík et al., 2021; Gregory et al., 2005). We obtained the European Long-term Trends (calculated from a median base year of 1980, https://pecbms.info/trends-and-indicators/species-trends/) for the 124 PECBMS species classified as migrants by BirdLife International (BirdLife International, 2020), together with their seasonal range polygons (BirdLife International & Handbook of the Birds of the World, 2019), which we then filtered to 103 non-pelagic migratory species with extant breeding and non-breeding (wintering) ranges within the Afro-Palaearctic region (Figure 3, see Supplementary Table S6 for species exclusion criteria). We did not include passage areas as these are poorly defined for many species; we included resident ranges in both the breeding and non-breeding ranges. We used the PECBMS Long-term Trends calculated up to 2019 (n=94) – or up to 2016 (n=9) for species excluded from the 2019 PECBMS update – as these are temporally representative of the impacts captured in our risk layers, which are measured relative to a long-term baseline or unmodified landscape (see *2.1 Data layers*).

2.3 Species' threat-vulnerability weightings

We generated species susceptibility weightings for each of the sixteen threat layers (Figure 1) to account for among-species variation in threat relevance. Each layer was min-max bounded so that values fell between 0 (lowest/no threat) to 1 (maximum threat). For each threat, weightings were also min-max bounded, with 0 representing the lowest susceptibility to a given threat, and 1 the highest susceptibility across our species pool. Resulting maps therefore reflect relative risk vulnerability, rather than absolute risk magnitude – where risk vulnerability is the combination of threat exposure with susceptibility (Foden et al. 2013).

2.3.1 Direct mortality

We weighted species sensitivities to collisions with buildings using vulnerability scores previously calculated by Loss et al. (2014) as a function of morphology and behavioural traits, assigning the values of the nearest ecological and morphological equivalents to species not included in their dataset (Supplementary Table S7 and accompanying text). For susceptibility to nocturnal lights, we used these same building collision weightings, but reduced the weighting to zero for species that do not migrate at night (Families: Accipitridae (minus *Circus* sp. (Spaar & Bruderer, 1997)), Ciconidae and Gruidae) (Cramp et al., 1994). Species that regularly persist in urban areas are considered less vulnerable to negative effects of human disturbance (Bonier et al., 2007; Samia et al., 2015), while flocking species are thought more vulnerable to disturbance. To reflect this, we weighted species' sensitivity to roads and human population density using a score derived from the combination of these two traits using information extracted from Cramp et al. (1994) and D'Amico et al. (2019) – see Supplementary materials: Species' threat-vulnerability weightings.

To weight direct risks from powerlines and windfarms, we used a combination of morphological and behavioural traits considered indicative of collision vulnerability (e.g. wingload proxy, vision and flight characteristics), adapted from the powerline collision susceptibility weightings developed by D'Amico et al. (2019) – see Supplementary materials: Species' threat-vulnerability weightings. Taxonomic orders revealed by this method to be most at-risk to windfarm collisions broadly aligned with those found elsewhere (Desholm, 2009; Thaxter et al., 2017). We did not create species-specific weightings for hunting susceptibility as many of the most widely-used methods (e.g. mist netting) are indiscriminate. For each species, we therefore used mass to determine the relevant hunting layer (small- or large-bodied); corvids (Family: Corvidae), raptors (Order: Accipitriformes) and waders (Order: Charadriiformes) were all considered 'large-bodied' species, regardless of mass.

2.3.2 Habitat change

Anthropogenic conversion of habitats only poses a significant risk to species that are unable to exploit the novel habitat. We therefore extracted habitat-use traits for each species from Cramp et al. (1994) and weighted each anthropogenic land-use according to binary indices indicating whether or not they are regularly used by the species (cropland, grassland, forest cover and urban areas). For agrochemicals, only species that use cropland habitats were assumed to be vulnerable to pesticides, whereas vulnerability to fertilizers was also extended to species that use pastoral habitat (Vickery et al., 2001). For species whose use of anthropogenic habitat varies between seasons (Cresswell, 2014; Pérez-Tris &

Tellería, 2002), we created separate season-specific habitat vulnerability maps. Finally, evidence indicates that habitat generalist species are less susceptible to the effects of land-use change (Blackburn & Cresswell, 2015; Hewson & Noble, 2009). We therefore multiplied the overall combined habitat change risk surface for each species by a habitat specialism score (min-max bounded within the subset of our species) extracted from Morelli et al. (2019).

2.3.3 Climate change

Ecological specialism can influence species vulnerability to climate change (Foden et al., 2008; Pearce-Higgins et al., 2015), as can dispersal ability (Foden et al., 2013). We used ordinal dispersal scores for each species created by Foden et al. (2013) to give more dispersal-limited species higher vulnerability weightings to climate change. We extracted the dietary and habitat specialism scores from Morelli et al. (2019) to calculate the final climate risk weighting for each species as the natural log of the product of degree of dietary specialism, degree of habitat specialism and dispersal vulnerability.

2.4 Composite risk-mapping algorithm

Composite risk mapping is complicated by the possibility that risks posed by certain threat layers might be increasive but non-additive, meaning that the presence of multiple spatially contiguous threats may increase the total risk, but to a lesser degree than would be implied by direct summation of threat values (Kennedy et al., 2019). To account for this, we grouped risk layers whose threats were likely to pose non-independent threats (e.g. human population density, roads and urbanisation), and combined them using fuzzy algebraic sums (Theobald 2013, 2016). The fuzzy algebraic sum of a set of values between 0 and 1 is given by 1 minus the product of $(1-x)$, where x is each member of the set, such that the final fuzzy summed value is less than the literal sum of its parts, and tends towards a maximum value of 1 (Bonham-Carter 2014). In cases where threats were independent and thus truly additive (e.g. threat posed by hunting pressure) we used simple summation. As the structure of independent and non-independent threats varied between the three risk types (Supplementary Figure S2), final risk surfaces were given by three different formulae. In all cases, where s is species and i is a cell:

$$Direct\ mortality\ risk_{s,i} = [1 - \prod_{j=1}^{5}\left(1 - M_{i,j}C_{s,j}\right)] + \frac{N_i D_s}{n(j)} + \frac{H_{i,s}}{n(j)}$$

Where j ($1 \leq j \leq 5$) indicates one of five non-independent direct mortality layers: {urbanisation, population density, roads, windfarms, powerlines}. $M_{i,j}$ is therefore the value for threat layer j in cell i. $C_{s,j}$ is the vulnerability weighting (between 0 and 1) for species s with respect to layer j. N is the nocturnal lights layer, and D_s is the nocturnal lights weighting coefficient for species s. $H_{i,s}$ is the hunting risk for species s in cell i, which varies spatially and between species (see *2.3 Species' threat-vulnerability weightings*). $n(j)$ denotes the number of layers within j, in this case five.

$$Habitat\ change\ risk_{s,i} = \left\{1 - [1 - \sum_{h=1}^{5}\left(A_{i,h}E_{i,s,h}\right)][1 - \frac{F_i G_{i,s}}{n(h)}]\right\} \times W_s$$

Where h ($1 \leq h \leq 5$) indicates one of five independent habitat layers: {pesticides, cropland, afforestation, urbanisation, grazing}, with $A_{i,j}$ being the value for layer j in cell i. $E_{i,s,h}$ is a season-specific weighting coefficient for species s in cell i with respect to layer h. F is fertilizer and $G_{i,s}$ the season-specific fertilizer weighting coefficient for species s in cell i. W_s is the habitat specialism weighting for species s. $n(h)$ denotes the number of layers within h, in this case five.

$$Climate\ change\ risk_{s,i} = [2 - \left(1 - P_{s,i}\right)\left(1 - V_{s,i}\right) - \left(1 - T_{s,i}\right)\left(1 - Y_{s,i}\right)]\ Z_s$$

Where $P_{s,i}$ is anomaly in precipitation, $V_{s,i}$ is anomaly in precipitation variability, $T_{s,i}$ is anomaly in temperature and $Y_{s,i}$ is anomaly in temperature variability. Z_s is the climate sensitivity weighting for species s.

We clipped the resulting risk surfaces to the relevant species' breeding and non-breeding distribution polygons (BirdLife International & Handbook of the Birds of the World, 2019), using these to calculate mean season-specific vulnerability for direct mortality risk, habitat change risk and climate change risk for each species.

2.5 Statistical analysis

We calculated zonal statistics to summarise broad geographic patterns and those in relation to elevation. We used linear models with a Gaussian distribution to assess the influence of direct mortality, habitat change and climate change risk vulnerability on species population trends. We weighted population trends by their inverse standard error, thereby giving greater emphasis in the model to more accurate trend estimates. We also included migratory distance and (logged) body size in all models to control for population trend variation driven by threats arising during the active phase of migration (e.g. energetic costs) and life history characteristics outside those captured in our threat maps. Migratory distance was calculated as the great circle distance between the centroids of the breeding and nonbreeding ranges (Vágási et al., 2016). To avoid over-parameterisation, we created a series of models containing up to eight predictors, considering all plausible eight-way combinations of predictor variables, as well as the effects of biologically relevant two-way interactions between variables, ensuring any correlated variables ($\rho > 0.7$) were not present within the same model. We tested for phylogenetic autocorrelation by modelling the residuals of the two final models as a function of taxonomic Order, finding no evidence for any phylogenetic signal (likelihood ratio tests $P > 0.05$ in both cases). Elsewhere, little evidence has been found for a phylogenetic structure to the PECBMS population trends (Morelli et al., 2020).

We followed an information theoretic approach (Burnham & Anderson, 2002), in which for each model, a set of reduced models are ranked using Akaike's Information Criterion adjusted for small sample size (AICc) – considering models within two AICc units competitive. To avoid model-averaging over interaction terms (Cade, 2015), we based inference on models with the fewest parameters within two AICc units of the top model (Burnham & Anderson, 2002). We scaled and centred all continuous variables via z-score transformation prior to analysis.

Statistical and spatial analyses were undertaken using R (R Core Team, 2018), with particular reliance on packages 'MuMIn' (Bartoń, 2019) and 'raster' (Hijmans, 2020).

3 RESULTS

3.1 Spatial threat patterns

At broad spatial scales, Europe consistently emerged as having higher levels of most threat categories than elsewhere within the Afro-Palearctic region (Supplementary Table S8); all threat layers showed considerable local-scale variation (Figure 4). Lower values of habitat change threats were related to elevation (Supplementary Table S9), with the Alps, Carpathians, Cantabrians and Dinarides mountain ranges all having noticeably lower levels of habitat change than surrounding regions (Figure 4, Supplementary Figure S3, (Danielson & Gesch, 2010). The reverse was true for climate change threats, where the smallest anomalies were generally found in lower altitude regions (Figure 4, Supplementary Figure S4, Supplementary Table S9). Hotspots of high composite threat levels also exist in the Nile delta, Western Levant and Indus valley, where concentrated direct mortality risks such as human population density, associated infrastructure and intensive land-use also notably coincide with high species richness of migratory birds (Figure 3, Supplementary Figure S5).

3.2 Population trend analysis

Species-specific estimates of breeding season climate change vulnerability and non-breeding season climate change vulnerability were strongly correlated ($\rho = 0.92$) and therefore not included within the same models. Of the four models within two AICc units (Supplementary Table S10), three were nested subsets of the same model, we therefore base inference on the model with the fewest parameters; the other model was not a subset, and contained a different plausible interaction. This left us with two similarly well-performing minimum adequate models that were indistinguishable by AICc (Supplementary Table S10). In both models, population trends increased with body size, and decreased with migratory distance and vulnerability to non-breeding range direct mortality (Figure 5); coefficient size and direction for these parameters were similar between the models (Table 2). Both competitive models retained an additional (but different) two-way interaction. Model1 retained a negative influence of non-breeding climate change that weakened with increasing migratory distance (Figure 5b). Model2 retained a negative effect of direct mortality risk vulnerability in the breeding range, mediated by the extent of breeding range habitat change (weaker for species whose ranges had lower levels of habitat loss; Figure 5d). We generated bivariate maps to show the relative co-occurrence of each risk type in space (Figure 6). These maps highlight the relatively low vulnerability to climate change for long-distance migrants wintering in parts of central Africa (yellow cells in Figure 6a) relative to those travelling to eastern and southern Africa where composite climate anomalies are greater (purple tones in Figure 6a). They also highlight the high congruence of direct mortality and habitat change threats for species wintering in the Sahel region (purple tones in Figure 6b), with humid zones of central Africa showing higher direct mortality risks but lower habitat change (blue tones in Figure 6b) and the opposite in southern Africa (yellow tones in Figure 6b).

4 DISCUSSION

Our composite threat maps demonstrate the variation in intensity and spatial distribution of threats to migratory birds across species' seasonal ranges. Range-scale species risk vulnerability explained important variation in population trends across species. We found a consistent negative relationship between population trends and range-scale vulnerability to direct mortality risks during the non-breeding season, suggesting that anthropogenic factors influencing survival during winter and during migration (including hunting, nocturnal lights and infrastructure) play an important role in driving declines. We also found some evidence for a negative effect of non-breeding range climate change, mediated by migratory distance, and a negative effect of breeding range direct mortality risk, mediated by extent of habitat change.

Non-breeding season direct mortality

Our results represent the first evidence for overarching population-scale effects of anthropogenic sources of mortality on avian migrants at a continental scale (see also US bird mortality estimates presented in Loss et al. (2012; 2015)). Despite relative threat levels being slightly lower across non-breeding range areas than breeding ranges on average (Figure 4, Supplementary Figure S6), non-breeding season direct mortality risk vulnerability more consistently explained variation in population trends than that for the breeding season (Table 2). As our models accounted for a negative effect of migratory distance on population trends, this result indicates that vulnerability to direct mortality risks may have particularly acute effects on individuals in the non-breeding season (though this may include threats faced during migratory transit within the non-breeding range). This finding could be related to differences in behaviour, movement or local habitat use between seasons – for example, as birds are generally central place foragers in the breeding season (with movements limited by proximity to nest), their vulnerability to direct mortality risks such as infrastructure collision and hunting may be reduced relative to the non-breeding season. Birds are typically more itinerant outside of the breeding season, possibly putting them at greater risk of exposure to direct mortality threats within their surroundings

(Silva et al., 2014; Thaxter et al., 2019); at a population scale, trends of species with low migratory dispersion may be particularly susceptible to any adverse effects of non-breeding season conditions (Gilroy et al., 2016).

Climate change effects mediated by migratory distance

We found a negative effect of climate change risk vulnerability on the non-breeding grounds, but only for short distance migratory birds (Figure 5b). The shorter-distance migrants within our dataset largely remain within Europe year-round; these species therefore generally face greater exposure to climate anomalies than those reaching sub-Saharan Africa in the temperate winter (Figure 6a). Population trends of the longest distance migrants in our dataset were less negatively influenced by non-breeding climate change (although with considerable uncertainty around these slopes). Many long-distance migrants have previously shown to be highly sensitive to non-breeding season climate, particularly rainfall levels within the Sahel (Szép, 1995; Winstanley et al., 1974). There is some evidence for increased rainfall and greening in the Sahel in recent decades (Biasutti, 2019; Maidment et al., 2015; Olsson et al., 2005), as well as in Southern Africa, where climate anomaly levels were high (Figure 6d), potentially improving wintering conditions for migrants to these regions. This result contrasts with that of Howard et al. (2020), who found population trends of short-distance migrants were better explained by breeding season climate than non-breeding season. This divergence may be explained by the use of different methodology to quantify habitat and climate change, and our inclusion of direct mortality threats as a predictor (not accounted for in the models of Howard et al. (2020)), as this variable explains a significant amount of trend variation, and may therefore influence the direction or magnitude of patterns detected for other variables.

Breeding season direct mortality mediated by habitat change

We found a synergistic interaction between vulnerability to direct mortality risks and habitat change risks within the breeding range, with a negative effect of direct mortality vulnerability on population trends exacerbated by greater habitat change vulnerability (Figure 5d). Populations inhabiting low-quality habitats may be more vulnerable to stochastic mortality, while those in high quality sites may be buffered from population-level effects of direct mortality (Morrison et al., 2013), perhaps through compensatory density dependent effects (McGowan et al., 2011; Péron et al., 2012). Species whose breeding ranges have undergone high levels of habitat change may also be more vulnerable to direct mortality, via, for instance, increased foraging distance (Tremblay et al., 2004) leading to greater exposure to sources of direct mortality such as human infrastructure within home ranges.

This between-threat interaction was not detected for the non-breeding range, again potentially indicating seasonal differences in threat relevance, as detected elsewhere (Howard et al., 2020; Vickery et al., 2014). Our findings contrast with recent evidence for the importance of non-breeding season land-cover for population trends (Howard et al., 2020), but again this may be explained by the inclusion of non-breeding direct mortality threats in our analysis. Our risk surfaces suggest that habitat in Africa has generally undergone less drastic habitat degradation than in Europe (Figure 4), perhaps explaining the weaker interaction with direct mortality. Also, avian habitat requirements during the non-breeding season are typically more generalist than in the breeding season (Blackburn & Cresswell, 2015), potentially making migrants less vulnerable to habitat change outside the breeding season.

Hunting patterns

Hunting is a complex and sensitive cultural issue, with a wide variety of drivers (subsistence/bushmeat, sport, tradition/heritage, magic/fetish), each varying and interacting with culture and geography (Buij et al., 2016; Hirschfeld & Heyd, 2005; Milner-Gulland et al., 2003). Our relative bird hunting pressure maps (Figure 2) broadly align with local patterns identified elsewhere (Brochet et al., 2016; Brochet, Jbour, et al., 2019; Brochet, Van Den Bossche, et al., 2019; Schneider-Jacoby & Spangenberg, 2010). In sub-Saharan Africa, demand for bushmeat is increasing (Whytock et al., 2016), as is accessibility through construction of roads (Milner-Gulland et al., 2003). We show Nigeria, Malawi and the Republic of Guinea to be particular hotspots for bird hunting, with survey respondents noting drivers relating to subsistence, fetish (see Buij et al. (2016)), increasing availability of guns, and a particularly significant culture of hunting in the Republic of Guinea. In contrast, our survey revealed low relative levels of bird hunting in Eritrea and Djibouti, and respondents pointed to the demilitarisation of Mozambique as contributing to low hunting pressure there. Hunting of large-bodied species – particularly waterfowl – was generally greater in northern and eastern European countries, and hunting small-bodied species generally more intense in southern Europe (Figure 2), where respondents noted the prevalence of trapping small passerines for the songbird trade, and specifically mentioned the locations of hunting hotpots being driven by the stopover sites of migrating turtle doves (*Streptopelia turtur*); respondents for many European nations also noted poor enforcement of hunting legislation. Ultimately, our findings reinforce that drivers of hunting pressure are complex interactions of geographical, cultural, political, and socioeconomic factors.

Study limitations

The results presented here are only as reliable as the underlying data. Greater knowledge of species' ecology outside breeding ranges could improve the fine-tuning of threat vulnerability (Faaborg et al., 2010), particularly for non-breeding season ecological requirements, as well as better-defined wintering areas and migratory routes / connectivity (Martin et al., 2007). Indeed, other studies have identified high rates of mortality on migration (Klaassen et al., 2014; Sillett & Holmes, 2002), and strong links between migratory route and population trends (Hewson et al., 2016; Lisovski et al., 2020). Explicitly combining the threat layers assembled here with detailed tracking data will shed light on the processes underlying declines of migratory species. The approaches demonstrated here are robust for the species within our dataset, but could be extended to include more detailed species-level assessment of threat-sensitivity, which is likely to be particularly complex among highly specialised taxa (e.g. more pronounced effects of climate change on high-altitude specialists).

We adopted a uniform approach to capturing change across species' breeding and non-breeding ranges, aiding interpretation of the resultant maps, and facilitating wider applicability to other systems. Our approach is unable, however, to account for variation in threat sensitivity within a species' range.

This limitation may be particularly pertinent for climate change risks, where the impacts of local climate anomalies may be highly non-uniform depending on whether they occur in areas at the centre of margin of a species' climatic niche. Future work could address these potential spatial biases in susceptibility through more nuanced methods, such as within-species climate niche modelling (Ruegg et al., 2021).Our threat layers almost certainly under-estimate some risks, particularly in regions outside of Europe where non remote-sensed data is often more coarse. While our hunting layer is the first assessment of pan-continental bird hunting pressure, it relies on expert opinion and may therefore be vulnerable to bias. Limitations in the number of species for which we could obtain population trend and threat-susceptibility data meant we were unable to explore interactive and non-additive effects of threats within each of the three risk groupings.

For certain species included in our analysis, parts of the non-breeding range are occupied by individuals from populations breeding outside of the PECBMBS geographic range – particularly in the earlier years of 35-year trend calculation period, as western European countries' monitoring schemes often started earlier than those of eastern European countries. However, evidence indicates that migratory connectivity is weak in most Euro-African migrants (Finch et al., 2017) – such that sub-populations intermix across the whole non-breeding range after passing through the migratory flyway bottlenecks – limiting the effect any such bias may have on our results. Our trend analyses may also be sensitive to the timescale over which impacts have occurred. Certain threats, particularly energy infrastructure, have accelerated in recent years, the effects of which may be only weakly reflected (if at all) in the c. 35-year PECBMS trends. The inverse may also be the case, if PECBMS trends suffer 'shifting baseline syndrome' (Papworth et al., 2009). The period over which the PECBMS trends are calculated begins in 1980; elsewhere, analysis of species breeding in England has found that the greatest declines in trans-Saharan migrants occurred prior to 1986, particularly in those migrants to arid-savannah regions (Thaxter et al., 2010). In general, species' responses to anthropogenic threats may be non-linear, idiosyncratic, and suffer from time-lag effects (Bonnet-Lebrun et al., 2021; Buchanan et al., 2020; Menéndez et al., 2006), weakening our ability to detect overarching population-scale effects.

Conclusions

We present a macroecological approach to comprehensive risk mapping for migratory species. Spatially explicit risk mapping allowed us to detect novel evidence for population-level effects of direct mortality risks among Afro-Palaearctic migratory birds, and novel patterns of between-risk synergy. Our results point to the potential for cumulative and interactive effects of different direct mortality threats, with both habitat loss and climate change being important in mediating more direct threats such as hunting and infrastructure development. Risks posed by direct mortality threats may be both the easiest to detect and the easiest to mitigate, due to the ‘acute’ nature of immediate mortality threats in contrast to chronic, insidious effects of changes to habitat and climate (Doherty et al., 2021). Successful mitigation of threats to migratory species will rely on comprehensive understanding of potentially complex interactions between threats; our results emphasise the importance of full-season and spatially explicit approaches to quantifying anthropogenic drivers of population declines.

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DATA ACCESSIBILITY

The relative hunting risk layers created in this manuscript are available as geotiffs from Figshare at https://doi.org/10.6084/m9.figshare.19745830 (Buchan et al. 2022a); all other layers are derived from publicly available sources listed in Table 1. The composite risk scores used in the analysis are available from Figshare at https://doi.org/10.6084/m9.figshare.19745983 (Buchan et al. 2022b).

TABLES

Table 1 – Summary of risk layers and respective data sources. Spatial resolutions are of the raw input data for each raster layer, these were transformed and resampled where necessary to ensure a single spatial resolution of 5′ – see Supplementary materials: Data layers.

Threat layer	Risk type	Data source(s)	Reference	Timeframe	Spatial resolution
Roads	Direct mortality	GLOBIO GRIP4	Meijer et al., 2018	2018	5′
Nocturnal lights	Direct mortality	DMSP OLS	NOAA, 2013	2013	0.5′
Human population density	Direct mortality	GPW 4.11	CIESIN, 2018	2015	2.5′
Hunting	Direct mortality	Survey of expert opinion	-	2020	NA
		UNEP Protected Planet*	UNEP-WCMC and IUCN, 2019	2019	NA
		GLOBIO GRIP4*	Meijer et al., 2018	2018	5′
		GPW 4.11*	CIESIN, 2018	2015	2.5′
		EC JRC GHS-BUILT*	Corbane et al., 2018	2014	250 m
Powerlines	Direct mortality	OpenInfra	Garrett, 2018	2018	NA
		World Bank	World Bank, 2017	2017	NA
Windfarms	Direct mortality	Global wind 2020	Dunnett et al., 2020	2020	NA
Urbanisation	Direct mortality and habitat change	EC JRC GHS-BUILT	Corbane et al., 2018	2014	250 m
Cropland	Habitat change	HYDE 3.2.1	Klein Goldewijk et al., 2017	2017	5′
Grazing land	Habitat change	HYDE 3.2.1	Klein Goldewijk et al., 2017	2017	5′
Fertilizer use	Habitat change	UN FAO	FAO, 2019a	2009–2017	NA
		HYDE 3.2.1	Klein Goldewijk et al., 2017	2017	5′
Pesticide use	Habitat change	UN FAO	FAO, 2019b	2009–2017	NA
		HYDE 3.2.1	Klein Goldewijk et al., 2017	2017	5′
Afforestation	Habitat change	ISAM LUCC	Meiyappan & Jain, 2012	1985	30′
		NASA MODIS	Friedl & Sulla-Menashe, 2015	2017	3′

Absolute temperature anomaly	Climate change	CRU TS 4.03	Harris et al., 2020	1961–1990 2009–2018	30’
Absolute temperature variability anomaly	Climate change	CRU TS 4.03			
Absolute precipitation anomaly	Climate change	CRU TS 4.03			
Absolute precipitation variability anomaly	Climate change	CRU TS 4.03			

*for masking out protected areas, accessibility and urban concentrations. See text for full description of creation of hunting layer

Table 2 – Coefficient estimates (β) and associated standard errors (SE), 95% confidence intervals (L95 and U95), t-statistic (t) and p-values (P) for the two best-supported models to explain species population trends. Bold text indicates variables significant/important in the model (alpha level = 0.05/confidence intervals excluding zero). NBR: non-breeding season vulnerability, BR: breeding season vulnerability.

	Coefficient	Figure	β	SE	L95	U95	*t*	*P*
Model1 Adj. R^2: 0.18								
	Intercept	-	0.06	0.08	-0.09	0.20	0.81	0.420
	Migratory distance	**-**	**-0.28**	**0.08**	**-0.44**	**-0.13**	**-3.60**	**< 0.001**
	Body mass	**-**	**0.22**	**0.09**	**0.05**	**0.40**	**2.59**	**0.011**
	Direct mortality NBR	**5a**	**-0.32**	**0.09**	**-0.50**	**-0.14**	**-3.59**	**< 0.001**
	Climate change NBR	-	-0.10	0.08	-0.25	0.06	-1.25	0.213
	Climate change NBR : Migratory distance	**5b**	**0.18**	**0.07**	**0.03**	**0.32**	**2.41**	**0.018**
Model2 Adj. R^2: 0.18								
	Intercept	-	0.10	0.08	-0.07	0.26	1.15	0.255
	Migratory distance	**5c**	**-0.22**	**0.07**	**-0.37**	**-0.07**	**-2.98**	**0.004**
	Body mass	**-**	**0.27**	**0.09**	**0.09**	**0.44**	**3.07**	**0.003**
	Direct mortality NBR	**-**	**-0.27**	**0.13**	**-0.53**	**-0.01**	**-2.08**	**0.040**
	Habitat BR	-	-0.04	0.11	-0.25	0.18	-0.33	0.740
	Direct mortality BR	-	-0.05	0.13	-0.31	0.22	-0.36	0.717
	Direct mortality BR : Habitat BR	**5d**	**-0.24**	**0.09**	**-0.42**	**-0.06**	**-2.60**	**0.011**

FIGURES

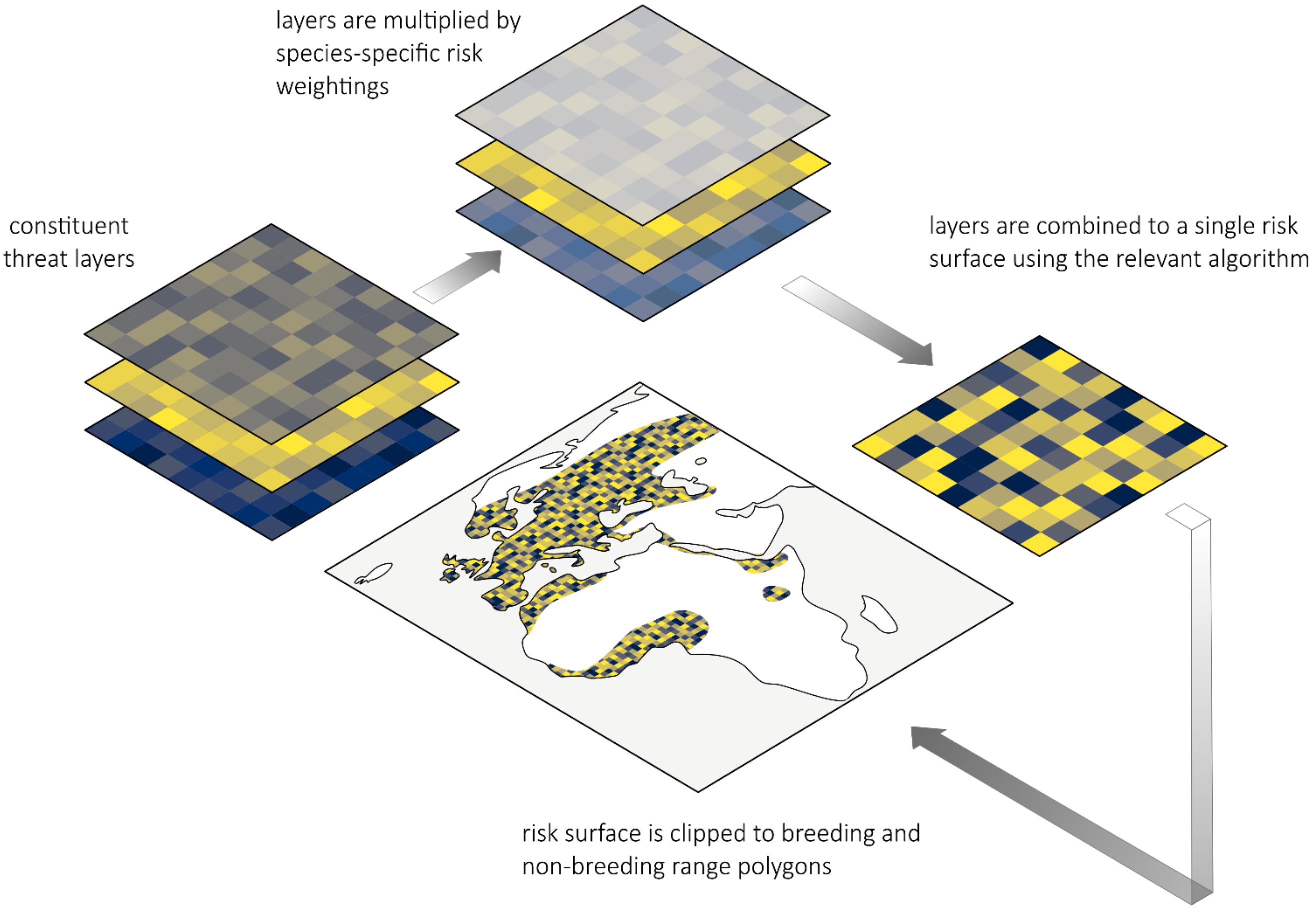

Figure 1 – Schematic illustrating the process of deriving composite risk surfaces from individual constituent threat layers for each of the three risk types (direct mortality, habitat change and climate change; Table 1) for each species' (n=103) breeding and non-breeding ranges.

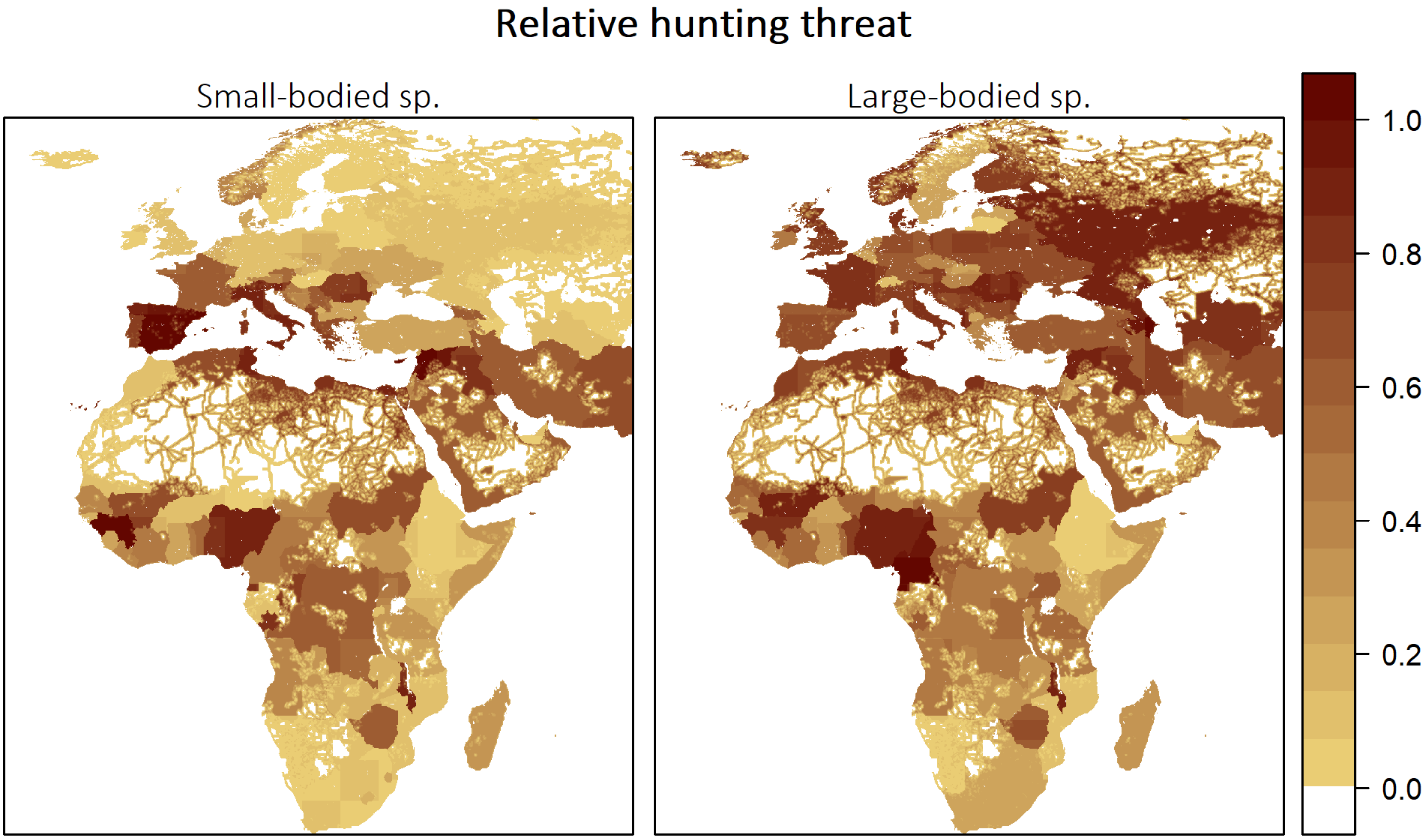

Figure 2 – Relative levels of hunting of small- and large-bodied birds across the study region, where 0 represents no hunting threat and 1 represents the maximum relative threat.

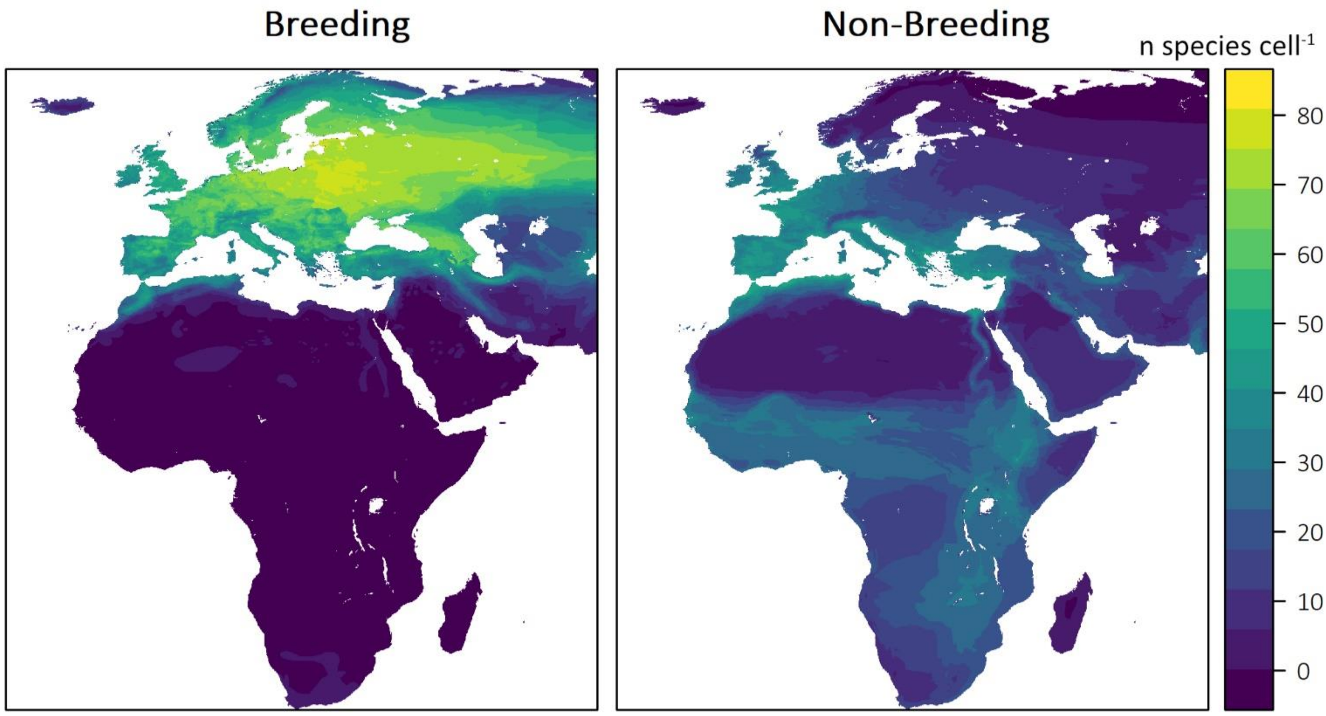

Figure 3 – Species richness of breeding and non-breeding ranges of the 103 species included in the analysis across the Afro-Palaearctic study area.

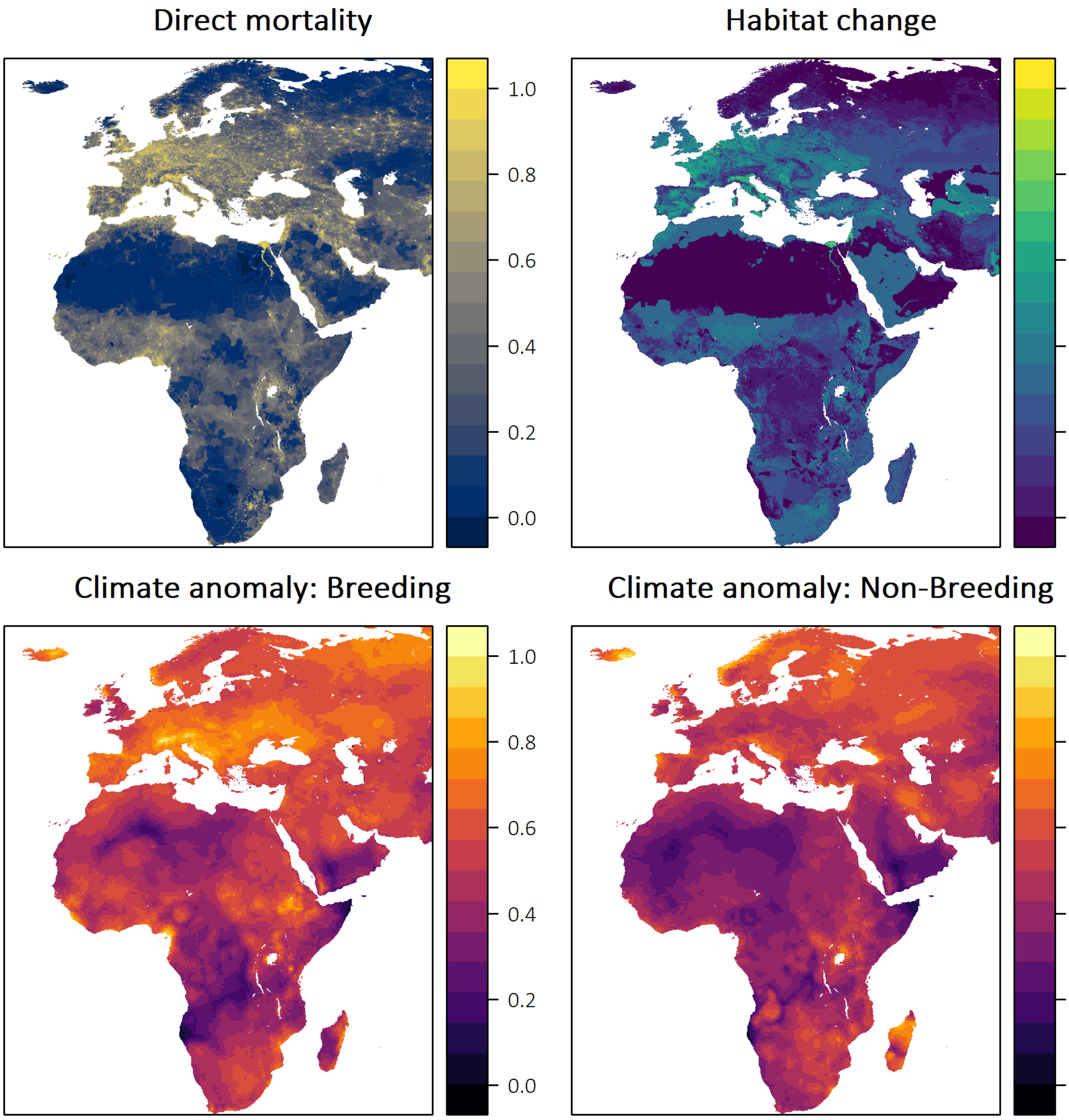

Figure 4 – Composite maps for the three risk layer groups. In all cases, 1 indicates the maximum relative risk level and 0 indicates minimum relative risk level. Climate anomalies vary seasonally, so we created separate risk surfaces for the breeding and non-breeding seasons. Maps represent the unweighted combination of their constituent layers, i.e. with no species-specific information fed into their creation.

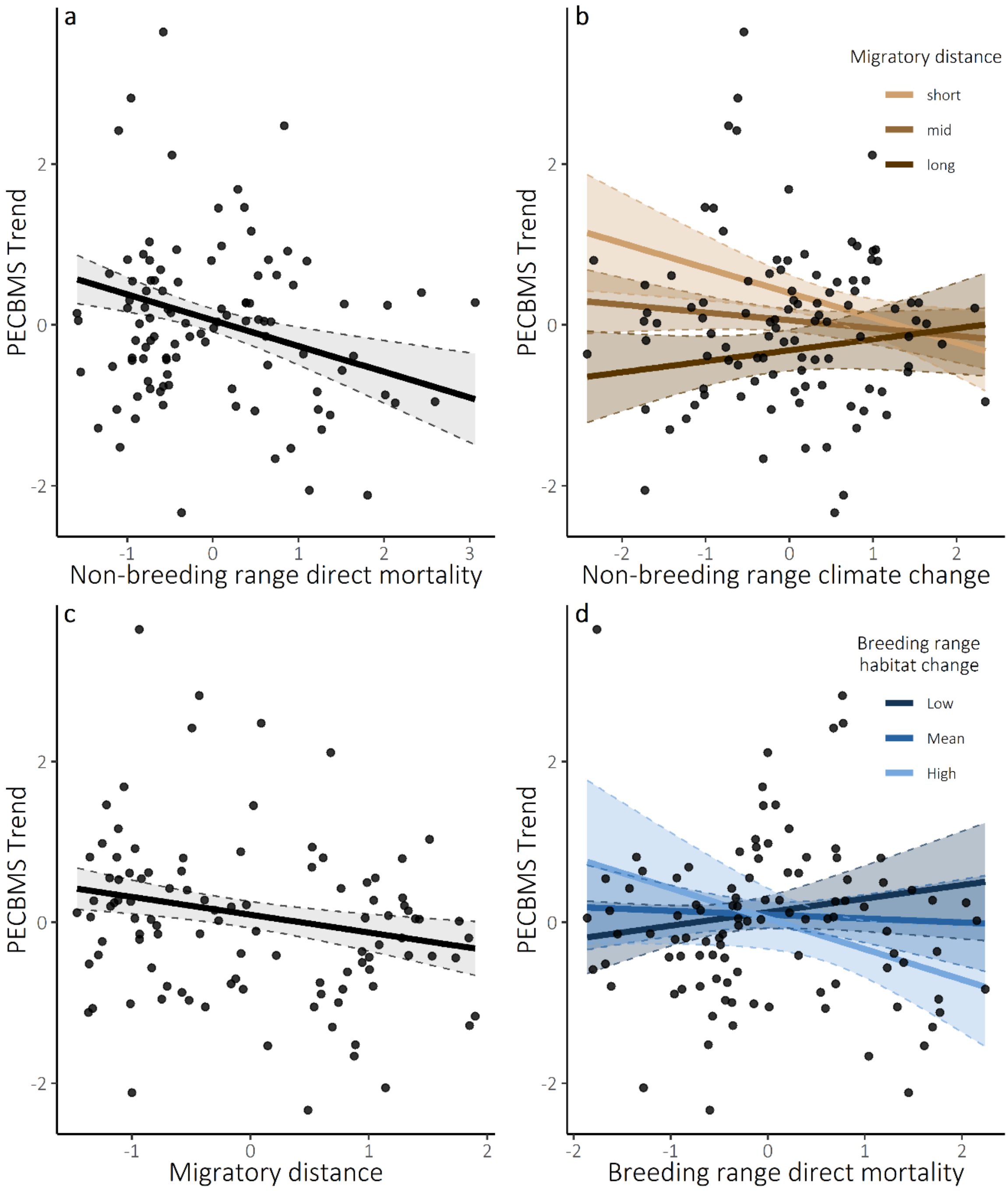

Figure 5 – Effects of spatially quantified threats on species population trends: a) Non-breeding direct mortality risk vulnerability*; b) non-breeding climate change risk* vulnerability, *with model-predicted slopes for short (10th percentile), mean and long (90th percentile) migration distances; c) Migratory distance; d) Breeding range direct mortality risk* vulnerability, *with slopes predicted for low (10th percentile), mean and high (90th percentile) levels of breeding range habitat change. Dashed lines represent associated 95% confidence intervals, and points indicate raw values for each species.*

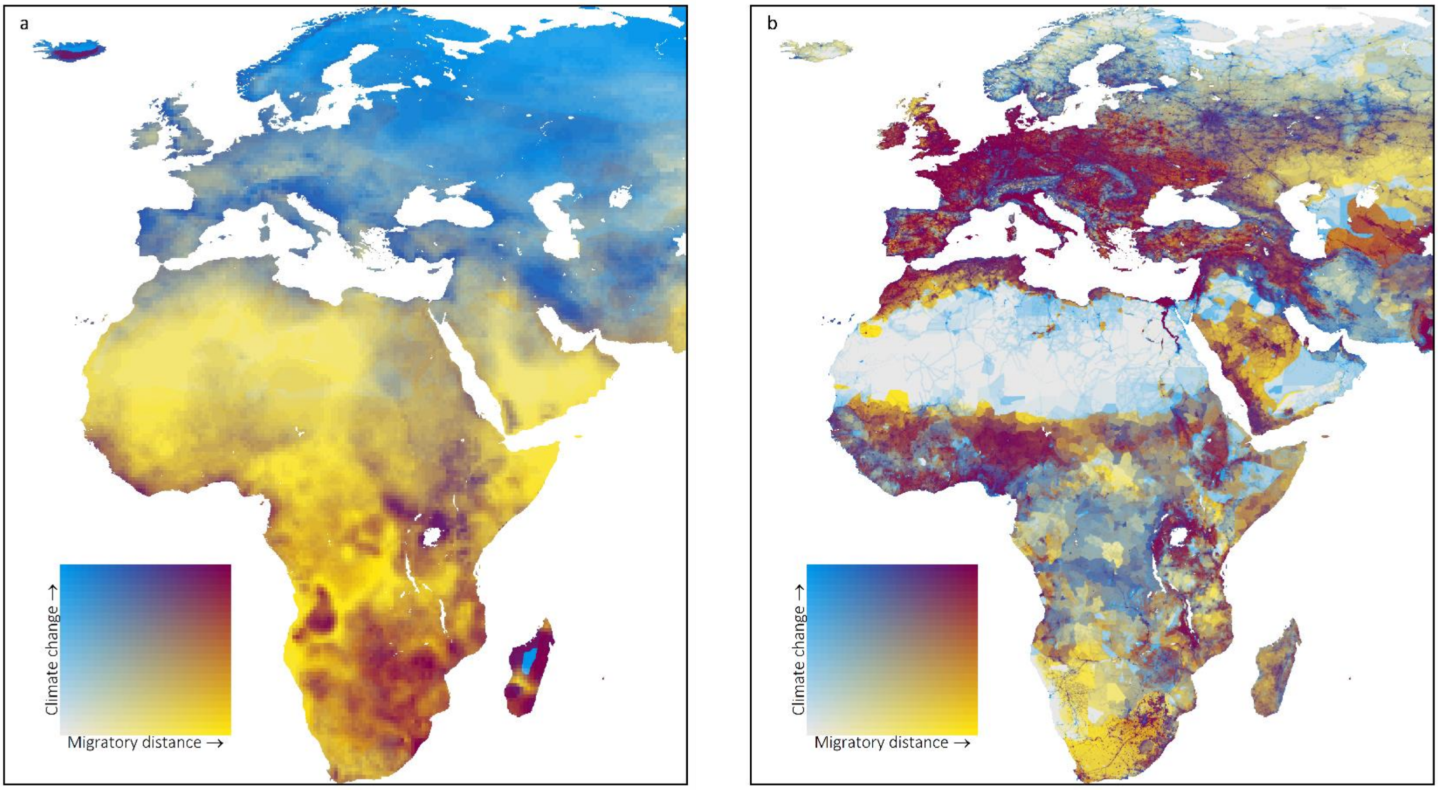

Figure 6 – a) Bivariate map showing the unweighted climate change risk surface for the non-breeding season (grey to blue y-axis) and the mean migratory distance undertaken by PECBMS species occurring in each cell in the non-breeding season (grey to yellow x-axis). Purple and red regions indicate where high levels of non-breeding climate change coincide with longer-distance migratory species; b) Bivariate map showing the unweighted risk surface for habitat change (grey to yellow x-axis) and unweighted risk surface for direct mortality (grey to blue y-axis). Purple and red regions indicate where high levels of both direct mortality risk and habitat change risk coincide.