Geography, taxonomy, extinction risk, and exposure of fully migratory birds to droughts and cyclones

Running title: Migratory birds - droughts & cyclones exposure

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Abstract

Aim: Anthropogenic climate change is predicted to drive unprecedented increases in the frequency and intensity of extreme climatic events, such as drought and cyclones. The impacts of these events on fully migratory species could be particularly severe and have cascading effects on the functioning of many ecosystems. We explore the relationships between geography, taxonomy, extinction risk, and the exposure of fully migratory birds to drought and cyclones.

Location: Global.

Time period: 1985-2014.

Major taxa studied: 383 fully migratory bird species.

Methods: We assessed exposure of fully migratory birds to cyclones and droughts, quantifying exposure by calculating the percentage of spatial overlap between a species' range and the extent of an extreme event within a given time series. We compared the level of cumulative exposure sustained by species among different taxonomic groups and within their breeding and wintering ranges; we also assessed whether species currently classed as 'threatened' are more cumulatively exposed than 'non-threatened' species.

Results: We identified fully migratory bird species highly exposed to extreme climatic events and global geographic hotspots of species exposure. 4% of species were found to be highly exposed to cyclones and droughts in both their wintering and breeding ranges. Wintering ranges were, on average, more cumulatively exposed to cyclones than breeding ranges; there was no discernible difference in drought exposure between ranges. Species currently classed as threatened were shown to experience higher exposure to droughts than non-threatened ones in both ranges.

Main conclusions: This exposure analysis provides the first step to a full global assessment of fully migratory bird species' vulnerability to extreme climatic events. Many species are at least as exposed to extreme events within their wintering ranges as in their breeding ranges, supporting calls for 'full cycle' assessment of migratory species' vulnerability to climate change. Our identification of hotspots of exposure may help to guide further monitoring, research, and management.

Keywords: climate change, conservation, extinction risk, exposure, extreme climatic events, global assessment, IUCN red list, migratory birds, vulnerability

Introduction

Extreme climatic events are increasing in frequency, intensity, duration, and spatial extent in many parts of the world due to anthropogenic climate change (IPCC, 2021; Murray & Ebi, 2012; Ummenhofer & Meehl, 2017), with their impacts being increasingly felt across ecosystems worldwide. Numerous studies have underscored the dramatic impacts these events can have on wildlife: cyclones have been associated with mass starvation and mortality among North Atlantic seabirds (Clairbaux et al., 2021); heatwaves have triggered mass die-off events in bat populations due to heat stress (WWF, 2020); and droughts have led to local extinction of amphibian communities (Moss et al., 2021; Zylstra et al., 2019). Yet, vulnerability assessments for many taxa currently fail to account for the influence of extreme climatic events on species' extinction risk. This omission could be particularly problematic for fully migratory bird species, for two reasons: (i) these species are likely to be more exposed to extreme climatic events, on average, than their sedentary counterparts. The marathon journeys carried out by long-distance migrants, in particular, can be expected to expose them to a high level of climate variability through space; this increases likelihood of exposure to extreme events as the frequency of these events surges and their distributions become less predictable (IPCC, 2018). (ii) Many migratory species, including birds, already face a heightened risk of extinction (Albers et al., 2023; Wilcove & Wikelski, 2008); intensifying extreme climatic conditions could therefore push populations of these vulnerable species beyond survivable thresholds (Harris et al., 2018; Murali et al., 2023).

Changes in the frequency, distribution, and intensity of extreme climatic events can be expected to have direct and indirect impacts on fully migratory birds. Exposure to extreme events can result in direct mortality, but they can also push individuals beyond their key physiological thresholds (in terms of allostatic stress or resource deficiency), triggering an emergency behavioural response where all energetic resources are devoted to survival (Wingfield et al., 2017). These responses can result in trade-offs, such as delayed arrival to breeding areas or even abandonment of reproduction, depending on when an event hits in a species' yearly cycle (Szostek & Becker, 2015). Carryover effects are thought to compound these deleterious impacts on fitness from one season to the next (O'Connor et al., 2014). By virtue of their life history, migrants have an intrinsic reliance on multiple locations being predictably viable and highly productive within specific temporal windows of opportunity (Mettke-Hofmann, 2017). Some of these sites are essential for breeding and wintering, while others provide a coherent network of stopover sites used by certain species to rest and recover replenish their energy during migration. Given the extreme physiological demands of this annual cycle, exposure to an extreme event at any point is likely to significantly affect survival and reproductive success (Marra et al., 2015).

Unsurprisingly, several studies have documented population-level impacts of extreme climatic events on migratory birds. Direct impacts, such as significantly reduced survival rates for adults and fledglings during periods of extreme weather, have been reported, for example by the lesser kestrel (Falco naumanni) (Marcelino et al., 2020). Extreme events such as storms and cold snaps have moreover caused numerous mass mortality events (Newton, 2007), as illustrated by an event in 1974 that resulted in the death of more than 40% of the breeding population of barn swallows (Hirundo rustica) in northern and central Europe (Møller, 2011). Indirect population-level impacts have also been documented, as seen with delayed onset of breeding in hummingbirds (Graham et al., 2016) and tit species (Glądalski et al., 2014) when exposed to drought events; such delays can coincide with a decline in body condition, as seen in the burrowing owl (Athene cunicularia) and Lapland longspurs (Calcarius lapponicus) (Cruz-Mcdonnell & Wolf, 2016; Krause et al., 2016). In a recent metanalysis (Maxwell et al., 2019), cyclones and droughts were highlighted as the most prevalent types of extreme events affecting birds and drought was highlighted as an ‘under-documented’ phenomenon in need of further study. Yet, surprisingly perhaps, there has never been a systematic global assessment of birds’, and particularly migratory bird species’, exposure to extreme climatic events. Without this information, it is difficult to identify strategically relevant management interventions and coordinate their deployment across regions or nations. Ultimately this knowledge gap impedes our capacity to effectively safeguard these species in a changing climate (IPCC, 2021; Murray & Ebi, 2012; Ummenhofer & Meehl, 2017).

To address this issue, this study assesses the extent to which fully migratory bird species are exposed to extreme climatic events, focusing on both cyclones and droughts. Exposure, when combined with species’ adaptive capacity (the biological traits that shape a species’ ability to adjust to extreme events) and sensitivity (the biological traits that shape a species’ ability to withstand extreme climatic events), makes up vulnerability to environmental pressures (Foden et al., 2019). Exposure alone has been used as a valuable measure of vulnerability for species where comprehensive data are lacking (Foden et al., 2019). Typically, studies assessing the exposure to extreme events of sedentary, spatially scattered species to assume an equal effect across the entirety of a species' geographic distribution (Ameca y Juárez et al., 2013; Duncan et al., 2012; Zhang et al., 2020). However, for fully migratory species with distinct seasonal ranges, another approach is required, and here we assess the seasonal (breeding and wintering) ranges of each species separately. We expect exposure to cyclones to be greater in common overwintering ranges in tropical and subtropical regions such as the North Atlantic and the Western North Pacific (Ramsay, 2017; Fig 1b), where cyclones are frequent. Similarly, droughts are predicted to become more common in the tropics (Naumann et al., 2018), and we expect species ranges in these areas to be most exposed to droughts.

At present, the IUCN Red List of Threatened Species (hereafter 'Red List') does not systematically incorporate extreme climatic events into species assessments (which are updated, on average, every ten years; Cazalis et al., 2022) for determining conservation status. Nevertheless, highly exposed migratory bird species are likely to be experiencing habitat loss and population decline (due to cyclones (Wiley & Wunderle, 1993) and/or persistent droughts (Cruz-Mcdonnell & Wolf, 2016; Maclean et al., 2008)), which are key assessment criteria (IUCN, 2023). Furthermore, intrinsic traits that contribute to a species being listed as threatened (such as a small range, or a high level of habitat specificity) may also increase vulnerability to cyclones and droughts (Ameca y Juárez et al., 2014). Therefore, we expect threatened species to be more exposed to extreme climatic events than non-threatened ones. For similar reasons, we expect some taxonomic groups to be more exposed than others, as particular groups may be limited to certain habitats and regions that are particularly prone to extreme events, and it is more likely that species within a taxonomic group will share these traits than species from different groups. Our study was designed to identify the fully migratory bird species that are under the most pressure from cyclones and droughts, and any possible geographic hotspots of exposure. We examine this both through a spatially explicit analysis, looking at gridded risk globally, and through regional summaries, to highlight particularly exposed regions. This study stands as a proof of concept that can be refined and implemented for other migratory species, with the potential to inform Red List assessments. We hope our method will help to guide monitoring efforts and inform decisions on relevant conservation actions.

Materials and methods

Species data

Species range data were obtained from a global dataset of the world's bird species distribution from BirdLife International (HBW & BirdLife International, 2020) as an ESRI File Geodatabase (v10). We then filtered range polygons to only include 'extant' range polygons for the 'breeding' and 'non-breeding' (i.e., wintering) polygons of fully migratory species. We define fully migratory bird species as those in which the whole population undergoes regular seasonal directional migration between distinct, separate, breeding and wintering ranges. The migration strategy of each species was determined using three databases of avian traits (Bird et al., 2020; Eyres, 2017; Sheard et al., 2020), as well as the descriptions of migratory behaviour from the Cornell Lab of Ornithology's Handbook of the Birds of the World (del Hoyo et al., 2018). Species removed included those where some or all members of the population are noted to be resident, dispersive, or partial-migrants, or where individuals are known to stay within a certain range for longer than one season. In total, 383 species were considered for our analysis (see Supporting Information: Table S1.1).

As many of our analyses required accurate assessment of range size and other area-based metrics, all polygons were reprojected into an equal-area Behrmann projection and then rasterised at a resolution of 9.65 km (0.1° at the projection latitude of true scale at 30° NS). A species was considered present in a cell if the range polygon covered the centre of the cell. For each species, we compiled a list of months of the year when they are typically present in their breeding or wintering range (see Table S2.1) using the Handbook of the Birds of the World (del Hoyo et al., 2018) and eBird (Sullivan et al., 2009). data were deficient for poorly known and rare species, we used inferences from the data of related species to fill the gaps to allow their inclusion in the assessment as per the recommendation of Foden and colleagues (Foden et al., 2019). For each data deficient species, we collated information on all other species in the same genus, or if this was not available (such as for monophyletic species) we used the next viable level of classification. We further filtered to only include related species that migrate during the same quarter of the year from the same continent. This was carried out for 31 species in total (Table S2.1).

For each fully migratory species, we collated several factors that may influence, or be associated with, exposure; namely, IUCN status, taxonomic group and zoogeographic realm.

Taxonomic and IUCN Red List information was obtained from the Handbook of the Birds of the World digital checklist version 5 (HBW & BirdLife International, 2020). Zoogeographic realms were based on those from Holt and colleagues (2013). We used taxon-specific zoogeographic regions based on phylo-distributional data for species of birds only. In addition, we collated information on species' generation length; this was used to standardise exposure metrics across species (see the "*Quantifying Exposure to Cyclones and Drought*" section below). Data on generation length were obtained from a database of avian traits (Bird et al., 2020) for all species except the South Island oystercatcher (Haematopus finschi) for which we used a secondary source (IUCN, 2023). Spatial processing of species ranges and environmental data was conducted using Python version 3.7 within an Anaconda virtual environment (Anaconda, 2016), unless otherwise specified. Subsequent analyses were conducted in R version 4.0.3 (R Core Team, 2020).

Cyclone data

Global cyclone data for the period 1985-2014 were compiled from the IBTrACS database (Knapp et al., 2010), using v03r05 for the events 1970-2010, v03r06 for the events 2011-2012 and v03r07 for the events 2013-2015 (Knapp et al., 2018); data were obtained from the Global Risk Data Platform produced by the UNEP/GRID-Geneva (dataset now deprecated) (UNEP/GRID-Geneva, 2015). This dataset consists of polygons separating the evolution of Saffir-Simpson categories from the speed of sustained winds by date along the track of each individual cyclone event. Polygons were first reprojected to the Behrmann projection, and we then excluded tropical storms and depressions (Saffir-Simpson category 0) and corrected polygon geometry errors by applying and then removing a 10-metre buffer to all polygons. We generated two summary datasets: overall event extent, used to calculate the overlap of individual cyclones with species' ranges, was generated by joining polygons by cyclone event ID; and overall intensity, used to identify the spatial distribution of differing cyclone intensities, was generated by joining polygons by event ID and category.

Drought data

While there are many indices available to measure drought, we selected the Global Precipitation Climatology Centre Drought Index (GPCC-DI) (Ziese et al., 2014) as it has near-global coverage and combines two older, widely used indices: the standardized precipitation-evapotranspiration index (SPEI) (Vicente-Serrano et al., 2010) and the standardized precipitation index (SPI) (McKee et al., 1993) with adaptations from Deutscher Wetterdienst (DWD) (Pietzsch & Bissolli, 2011). The values of these indices correspond to the number of standard deviations that observed anomalies deviate from the long-term mean and allow geographic regions with very different climates to be compared (WMO, 2012). The parameters of the distribution function for SPI-DWD and SPEI in the GPCC-DI dataset were based on the official WMO reference period for climate data, i.e., 1961 to 1990.

We obtained global monthly average GPCC-DI data from The Global Precipitation Climatology Centre (Ziese et al., 2014) at a 1° resolution in a WGS84 projection. The final dataset was compiled from two GPCC-DI datasets; Version 1 (2014 - present) and Version 1.1 retrospective analysis (1952-2013) to cover a desired time frame (1985 – 2014) that captures the variation in species exposure to the recent history of drought events. We used GPCC-DI data with a 12-month accumulation period for our analysis: where 12 consecutive months are compared with the same 12 consecutive months in all previous years of available data. This temporal grain reflects long-term patterns where dryness (indicated by values < 0, Table S1.2) can be associated with a negative impact on the availability of water, food resources, vegetation greenness, and other factors in the migratory birds' habitat that can affect populations (Cady et al., 2019; WMO, 2012; Zhang et al., 2020). We reprojected the GPCC-DI data onto the same 9.65km resolution Behrmann raster grid used for the species ranges. We calculated, for each month during the study period, which grid cells were in drought as a binary variable, using a threshold of ≤ -1.5 (i.e., severe or extreme drought), following McKee's original classification (McKee et al., 1993).

Quantifying Exposure to Cyclones and Drought

Following recommendations from the IUCN-SSC's guidelines for assessing species' vulnerability to climate change (Foden & Young, 2016), we used an exposure analysis to assess the vulnerability of fully migratory birds to cyclones and drought. We quantified exposure by calculating the percentage of spatial overlap between a species' range and the extent of a cyclone or drought event within a given time series (Ameca y Juárez et al., 2013; Duncan et al., 2012; Zhang et al., 2019, 2020). We estimated two metrics of exposure for both cyclones and drought and, in both cases, estimated separate exposure metrics for species' breeding and wintering ranges to climatic events during the period from 1985 to 2014.

1) **Area of exposure**. We calculated the area of overlap of breeding and wintering ranges of each species with all climatic events that occurred during the seasons of occupancy for each range type. For cyclones, we merged cyclone polygons across matching dates and calculated the percentage overlap with species polygon ranges. For droughts, we combined drought raster grids across matching months and calculated the percentage of species raster range cells that experienced drought during the study period. For both events, a range with an area of exposure of 0% did not experience drought or cyclones during the study period. If the entire range has been impacted at least once, then the area of exposure will be 100%. We define any species with an "area of exposure" score of over 25% as a "widely exposed species" (Ameca y Juárez et al., 2013).
2) **Cumulative exposure**. This indicates how much cumulative exposure to cyclones or drought a species' range has experienced. For each climatic event, we estimated the area of exposure of the species for each individual month that a species is present in the breeding and wintering ranges during the study period. We calculated a cumulative exposure score (C) for each climatic event, which was then scaled both by the total number of months (N_m) that the species is exposed in the given range type and the species generation length (T_{gl}) in years, following the method of Zhang and colleagues (2019):

$$\text{Exposure score} = C \times \frac{12}{N_m} \times T_{gl}$$

This metric is expressed per species per season (breeding or wintering) and is effectively unitless, and so only allows relative comparison between species within a single type of climatic event. A higher score indicates the species has been exposed to droughts or cyclones more frequently over a larger proportion of its breeding or wintering range.

For droughts, given a set of N_m months that a species is present in a range type over the study period, C_d is simply the sum across months of the percentage of range (p) which overlaps drought events in each month:

$$C_d = \sum_{N_m}^{i=1} p_i$$

For cyclones, a similar summation (C_c) is made across cyclone events, but the total percentage of the range impacted by an event is scaled by the maximum Saffir-Simpson intensity of the cyclone (w) and the total number of cyclone events impacting the range during the study period (N_c).

$$C_c = \frac{\sum_{N_c}^{i=1} p_i w_i}{\sum_{N_c}^{i=1} w_i} \times N_c$$

To highlight the most exposed species, species were ordered from most to least exposed in breeding and wintering areas using the calculated cumulative exposure scores for that stage in their life cycle. Species were defined as having a high cumulative score if they were among the top 25% of exposed species within either seasonal range, and families and regions containing the highest numbers of most exposed species were documented. These exposure classifications must be interpreted as relative measures and comparison of outputs from studies of other taxonomic groups will not produce meaningful results. However, for a defined taxon and climatic event, this method allows for the selection of species that can be further investigated to determine whether they possess attributes that make them susceptible to environmental changes caused by cyclones and/or drought, and hence likely to be most vulnerable and in need of conservation management (Ameca y Juárez et al., 2013; Foden et al., 2019; Zhang et al., 2019).

Statistical Analyses

All statistical analyses were performed in R version 4.0.3 (R Core Team, 2020). Non-parametric tests were used to test our hypotheses as data (raw and transformed) repeatedly violated the statistical assumptions of parametric tests.

We identified which species had an area of exposure score of more than 25%, species that possessed the 25% highest cumulative exposure scores, areas where these highly exposed species occurred, and investigated whether species were typically exposed in one seasonal range, two seasonal ranges, and to one or both types of extreme event.

To investigate whether there was a difference in the level of cumulative exposure sustained by migratory bird species within their breeding and wintering ranges, we performed paired Wilcoxon Signed-Rank tests on the overall exposure scores for cyclones and drought. Independent two-group Mann-Whitney U tests were used to investigate whether there was a significant difference in the level of cumulative exposure sustained by species currently classed within ‘threatened’ (critically endangered, endangered, vulnerable) or ‘non-threatened’ (near threatened, least concern) categories in the Red List (IUCN, 2023). These tests were run for each extreme event, and breeding and wintering areas separately.

To investigate potential differences in the level of cumulative exposure faced by migratory bird species within different zoogeographic realms, we performed a Kruskal Wallis test with additional post-hoc pairwise independent two-group Mann-Whitney U tests.

Results

Overall, 67 species had a high area of exposure to cyclones in at least one seasonal range, 382 had a high area of exposure to drought, and 67 to both extreme climatic events. 17 species had a high area of exposure to cyclones in both ranges, compared to 378 for drought. In total, 4.4% (*n* = 17) of all species were widely exposed to both phenomena in both ranges. Exposure metrics for all species are provided in the supporting information (Table S4.1)

A hundred and four species had high cumulative exposure to cyclones and 118 species had high cumulative exposure to droughts (Table S1.3) in at least one seasonal range; forty species had high cumulative exposure to both extreme events. Three species - the eastern whip-poor-will (*Antrostomus vociferus*), the grey-faced buzzard (*Butastur indicus*), and the South Island oystercatcher (*Haematopus finschi*) - were found to be highly cumulatively exposed to both extreme climatic events within both ranges. Hotspots of cyclone exposure, defined as regions with the highest median exposure scores, were in Australasia, East Asia, Madagascar, Central America, and the Caribbean (Fig. 1; Supporting Information: S1.1; S1.3; Table S1.4; S1.5). Hotspots of drought exposure, defined as regions with the highest median exposure scores, were in Australasia, Madagascar, the Congo Basin, Sub-Saharan Africa, the Arctic, Eurasia, and East Asia. (Fig. 1; S1.2; S1.4; Table S1.4; S1.6).

Species with the highest cumulative exposure to cyclones within their breeding range were mainly found within eastern North America and East Asia (Fig. 1c). Species classed with the highest level of cumulative exposure in their wintering range were most densely concentrated within Central America, the Caribbean, South-East Asia, and East Asia (Fig. 1d). Hotspots for species with the highest cumulative drought exposure in their breeding range were the Arctic regions and northern East Asia (Fig. 1e). Species with the highest levels of cumulative exposure in their wintering range tended to be found in sub-Saharan Africa, the Congo Basin, southern Asia, and East Asia (Fig. 1f). There was a significant difference in exposure between seasonal ranges for cyclones (paired Wilcoxon Signed-Rank test: $z = -5.62$, $p < 0.001$), and no statistical difference for drought ($z = -1.43$, $p = 0.15$). Wintering ranges were on average more cumulatively exposed to cyclones than breeding ranges (Fig. 2a), with wintering ranges experiencing a median exposure score of 0.45 (IQR = 5.54) versus 0.06 (IQR = 1.80) in breeding ranges. There was no discernible difference between the drought exposure scores (Fig. 2b), though the most extreme cases of exposure were found within the breeding ranges.

Gruiformes ($n = 10$) and Caprimulgiformes ($n = 9$) were found to be the most cumulatively exposed to cyclones in the breeding range, and the Anseriformes ($n = 21$) to be the most exposed within the wintering ranges (see Fig. S1.5). The most cumulatively exposed species within these groups were associated with regions that are frequently hit by cyclones: the North Atlantic and Western North Pacific (see Fig. S1.3). For droughts, we found the Accipitriformes ($n = 8$) and Anseriformes to be the most cumulatively exposed within both ranges (see Fig. S1.6). As with cyclones, the most cumulatively exposed species within these groups associate with specific hotspots of drought; typically wintering in regions such as Central and Northeast Asia, and breeding in sub-Saharan Africa and South-East Asia. A species that typifies this pattern is the endangered steppe eagle (*Aquila nipalensis*), which ranked as the most cumulatively exposed species to drought within its wintering range. Additionally, many species of Gruiformes were ranked amongst the highest species exposed, though with a high level of variation (Table S1.3). Many species within this group, including the Siberian crane (*Leucogeranus leucogeranus*), were found to have very small ranges located in Northeast Asia resulting in extremely high exposure scores.

Threatened species (*n* = 44) were shown to experience higher exposure to drought on average than non-threatened ones (*n* = 339) in both breeding (Fig. 3c) and wintering (Fig. 3d) ranges. The median difference in exposure between threatened and non-threatened species (approximate Hodges-Lehmann estimator) was 43.22 for breeding and 49.03 for non-breading ranges. As the maximum exposure score for drought was 1214.95 in breeding ranges, and 966.28 in wintering ranges, this means exposure scores were approximately 3.56% higher for threatened species in breeding ranges, and 5.07% higher for threatened species in wintering ranges. Results were significantly different for both the breeding (Mann-Whitney U test: $U = 9690$, $p = 0.001$) and the wintering ranges ($U = 9677$, $p < 0.001$). Many of the most extreme instances of exposure recorded were for species that are classed as threatened. There was a significant difference in cumulative exposure to cyclones between threatened and non-threatened species in the wintering range (Mann-Whitney U test: $U = 6012.5$, $p = 0.03$) (Fig. 3b); however, this difference in exposure was small (approximate Hodges-Lehmann estimator: 0.01). As the maximum exposure score for cyclones was 119.97 in wintering ranges, this means exposure scores were <0.01% higher in wintering ranges. There was, however, no significant difference for the breeding range (Mann-Whitney U test: $U = 6501$, $p = 0.15$) (Fig. 3a).

Discussion

This study provides the first global assessment of fully migratory bird species' exposure to two key extreme climatic events, namely droughts and cyclones. Our findings suggest that almost all the species considered have been directly exposed to cyclones (81%), and droughts (100%) at some point in their life cycle in recent history. By examining the exposure of seasonal ranges separately, we have shown that fully migratory birds are more exposed to cyclones within their wintering ranges, while there is little difference between the ranges for droughts. Furthermore, we have identified 182 species that are highly cumulatively exposed to one of these phenomena within at least one seasonal range, and we have described geographic hotspots where species are found to be most exposed to cyclones and droughts. Cyclones and droughts have a widely documented capacity to impact populations through habitat loss, resource shortage, and increased interspecies conflict (Zhang et al., 2019, 2020); being able to accurately and comprehensively identify species threatened by these extreme events is thus key to secure their future. Exposure analyses utilising historic and spatial data, such as those carried out here, could offer a systematic approach to objectively identify assessments where such threats should be listed. Such an approach could further enhance the accuracy, transparency, and efficiency of species threat assessments, facilitating decision making in the face of climate change.

Our work suggests that extreme climatic events, such as cyclones and droughts, could potentially be currently underrepresented as threats to migratory birds in Red List assessments. Only 10 (2.6%) of the fully migratory bird species included in this study are currently listed with cyclones as a threat under the Red List's 'climate change and severe weather' category, and only 18 (4.7%) are listed with droughts (IUCN, 2023). Of the species known to be affected by extreme events in the Red List threat criteria, two species are found to be classed as 'highly cumulatively exposed' to cyclones in this study, and eleven species to droughts. For cyclones, this includes the vulnerable chimney swift (*Chaetura pelagica*) and near-threatened piping plover (*Charadrius melodus*) – and for drought, this includes critically endangered species such as the sociable lapwing (*Vanellus gregarius*) and non-threatened species such as the grasshopper buzzard (*Butastur rufipennis*).

The classification of 182 'highly cumulatively exposed' species (Table S1.3) could represent a substantial increase in the number of species listed under the Red List's threat categories for cyclones and droughts. For this to happen, though, vulnerability to these events needs to be established; this may be done by demonstrating high sensitivity or low adaptive capacity. This can be done using trait-based assessments (Foden et al., 2019). For example, we found Gruiformes and Caprimulgiformes were the taxonomic groups most exposed to cyclones, while Acciptriformes were the most exposed to drought; Anseriformes were among the most exposed groups to both types of extreme events. Insight into the life history of these species can help inform how vulnerable these groups may be. Gruiformes and Anseriformes, for example, are found in places where cyclones may result in extensive flooding and habitat loss, and where drought may result in the loss of key prey or habitat patches. Gruiformes, Acciptriformes, and Anseriformes moreover typically have long lifespans, low reproductive output and therefore a long generation time. For such species, loss of breeding habitat for a single year may not have significant population-level impacts, but large adult mortality events could. Alternatively, vulnerability could be determined by building on recently developed methods that can supplement our work on species' exposure, for example those aiming at calculating intrinsic susceptibility scores (Zhang et al., 2019). Previous research into the effects of climate change on migratory birds has suggested that we are likely to be underestimating the number of threatened species by 18–49% (Zurell et al., 2018). Underestimating the level of threat that extreme climatic events pose to migratory birds could soon put some species at higher risk of extinction by missing current opportunities to support vulnerable populations. Relevant conservation actions, in that respect, may include setting up new, effective, protected areas; habitat restoration; additional shelter provision; food supplementation; translocations to augment species distributions; and the abatement of other concurrent threats (Runge et al., 2015; Hakkinen et al. 2023).

Several species (including the aquatic warbler *Acrocephalus paludicola* and the buff-breasted sandpiper *Calidris subruficollis*) that are not highly exposed to cyclones or drought in our assessment are listed as threatened by extreme events on the Red List (8 species for cyclones, 7 for drought). It is possible that these species have an elevated vulnerability to extreme events due to a heightened sensitivity, resulting in an elevated perceived threat. For example, a species' high specialisation and dependence on specific habitats and food resources susceptible to cyclones and drought may elevate their vulnerability to extreme events. Similarly, some of these species may be more sensitive to extreme climatic events because they are already likely facing other threats that would limit their ability to resist or recover from the impacts caused by events such as drought or cyclones. It is thought that historic exposure to a particular disturbance event can shape the life history of a species such that they are better equipped to cope with repeated exposures (Grant et al., 2017; Wright, 1999). There are limits to this, however, and it is important to note that the climate these species initially adapted to has and is continuing to change; with the potential to exceed their thresholds for coping (Harris et al., 2018). As many species have sustained repeated exposure to extreme events over the 30 years of this study we expect a baseline level of resilience, but as climatic baselines shift it may be tough for the intrinsic traits of many species to adapt quickly enough to avoid declines. Equally, it is important to acknowledge that while some species can exhibit rapid adaptation to changing environmental conditions, others may struggle to cope with high levels of environmental variability and could potentially face local extirpation.

One pattern of specific interest uncovered by this study is the indication that species categorised as 'threatened' on the Red List are more exposed to drought than other species (Fig. 3). There was also a significant difference in exposure to cyclones between threatened and non-threatened species in their wintering ranges (with threatened species being on average less exposed to cyclones than non-threatened species). However, the difference in exposure to cyclones was extremely small. For droughts, the difference in exposure was substantial, and areas with multiple highly exposed and threatened species are present in Central America, Sub-Saharan Africa, Asia, Southern Europe, and Arctic regions; regions that are also known to be under increasing anthropogenic pressures. In these areas, synergistic interactions between multiple pressures (for example, land use change and climate change) could play a growing role in shaping the local distribution and population dynamics of migrating birds, with, for example, anthropogenic degradation of species' habitats likely to compromise their coping strategies (Ameca y Juárez et al., 2012).

For migratory birds, timing is everything. Their whole life cycle is defined by synchronous pulses of resources. Correspondingly, mismatches resulting from small alterations to this pattern can have a devastating impact on the fitness of the individual (Carey, 2009). A species' level of adaptive capacity and sensitivity is also determined by timing; or rather, what part of the life cycle exposure occurs within (Wingfield et al., 2017). If an individual is lucky, it may be able to use facultative dispersal to evade the impacts of an extreme event; but this can be extremely disruptive, and can only be employed as a last resort at more sensitive periods of their cycle such as when breeding or moulting (Wingfield et al., 2017). Furthermore, due to the scale of many drought events and the rapid onset of cyclone events, this strategy may be in vain and has its own associated physiological costs. Many climate change assessments of migratory birds have so far almost exclusively focused on breeding ranges (Foden et al., 2019; Gardali, 2012), yet our results highlight the need to consider all seasonal ranges, thereby supporting calls for 'full cycle' assessment of migratory birds' vulnerability to climate change.

On a global scale, the conservation of migratory species is key to maintaining the functional diversity of ecosystems and avoiding cascades of extinction in the face of growing anthropogenic pressures (Bauer & Hoye, 2014). This study has identified fully migratory bird species with relatively high exposure to two extreme climatic events, and geographic hotspots where these species are concentrated. By analysing the seasonal ranges separately, we have highlighted the importance of full-cycle analyses of migratory birds and isolated life stages that are likely to need further monitoring. When combined with a trait-based assessment, this information will be vital to inform large-scale conservation planning exercises and highlights where more detailed assessments are needed.

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Conflict of Interest Statement

None declared.

Data accessibility statement

All the underlying data will be made available on Dryad following acceptance of the manuscript.

FIGURES

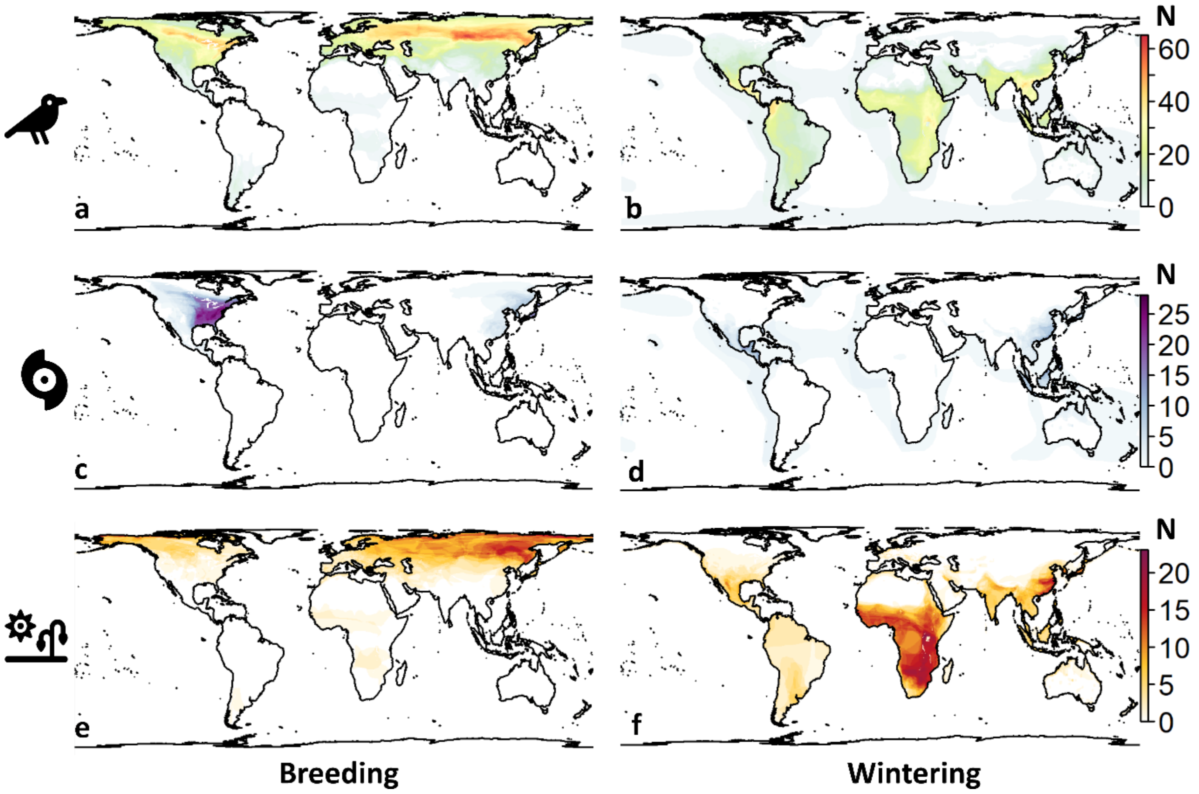

Figure 1. Species richness and exposure to cyclones and droughts of fully migratory bird species in their breeding (left panels) and wintering ranges (right panels). Fully migratory bird species are those species in which the whole population undergoes regular seasonal directional migration between distinct, separate, breeding and wintering ranges. Overall species richness is shown (a, b) and then the richness of species with the highest 25% of cumulative exposure to cyclones (c, d) and drought (e, f). Cumulative exposure scores were calculated from extreme climatic events for the period 1985-2014.

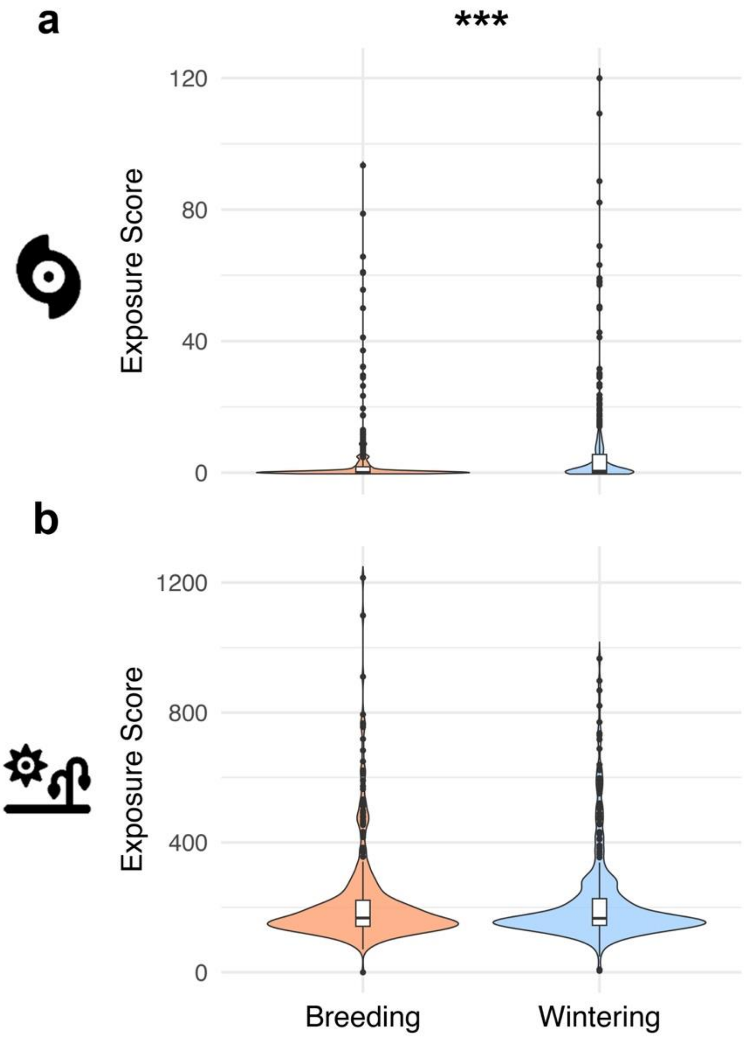

Figure 2. The distribution of fully migratory birds' cumulative exposure scores within breeding and wintering ranges for cyclones (a) and droughts (b) for the period 1985-2014. Boxplots display the median and interquartile range of each group. Note that exposure scores for droughts and cyclones are on different scales and should not be directly compared.

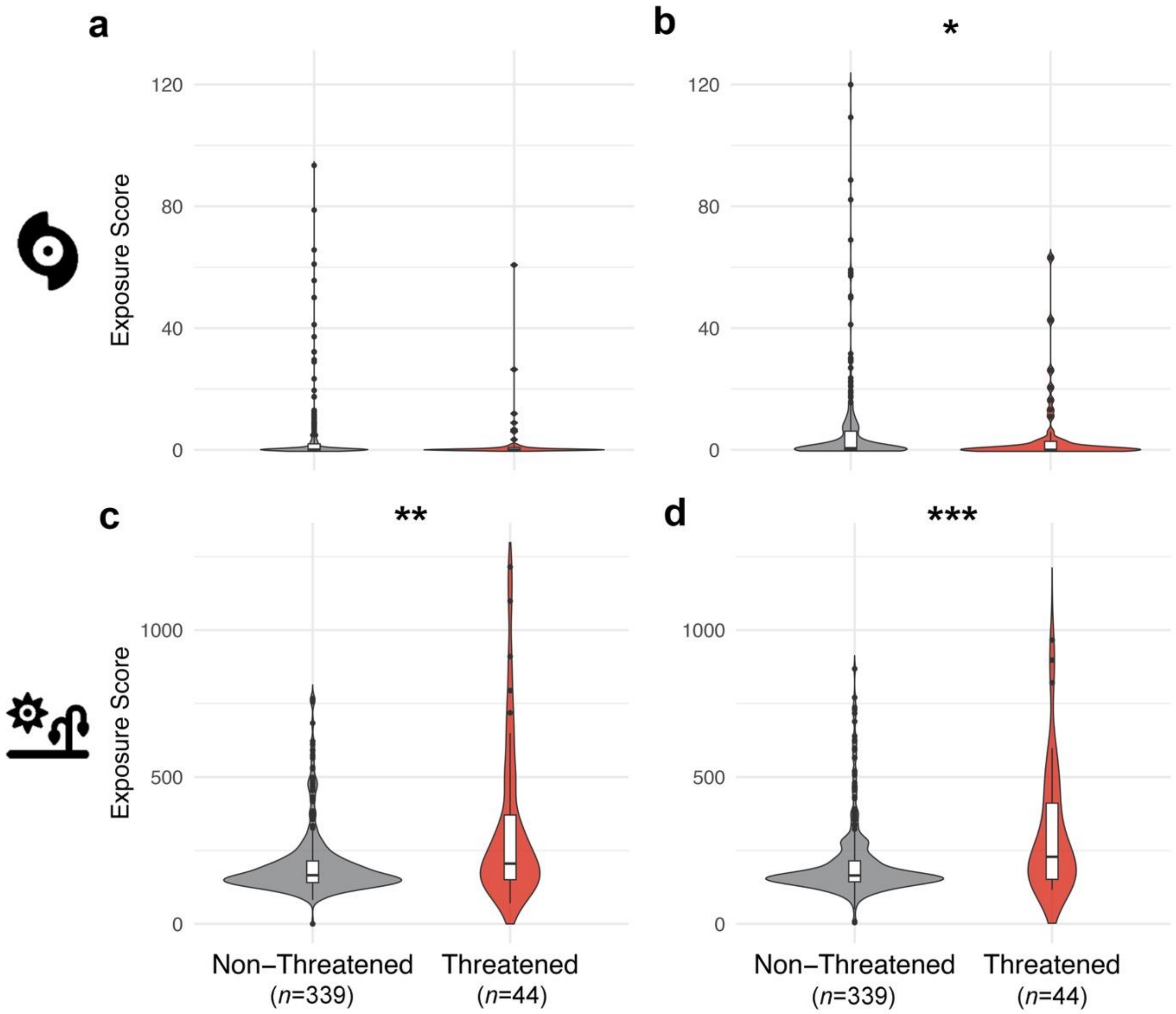

Figure 3. The distribution of cumulative exposure scores to cyclones (a, b) and droughts (c, d) for migratory bird species listed as ‘Threatened’ or ‘Non-Threatened’ in the Red List. The first column (a, c) shows exposure scores during the breeding season. The second column (b, d) shows exposure scores during the wintering season. Boxplots display the median and interquartile range of each group. Note that exposure scores for droughts and cyclones are on different scales and should not be directly compared.