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Migration in the Anthropocene: how collective navigation, environmental system, and taxonomy shape the vulnerability of migratory species

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Abstract

Recent increases in human disturbance pose significant threats to migratory species using collective movement strategies. Key threats to migrants may differ depending on behavioural traits (e.g. collective navigation), taxonomy, and the environmental system (i.e. freshwater, marine, or terrestrial) associated with migration. We quantitatively assess how collective navigation, taxonomic membership, and environmental system impact species' vulnerability by 1) evaluating population change in migratory and non-migratory bird, mammal, and fish species using the Living Planet Database (LPD), 2) analysing the role of collective navigation and environmental system on migrant extinction risk using International Union for Conservation of Nature (IUCN) classifications, and 3) compiling literature on geographic range change of migratory species. Likelihood of population decrease differed by taxonomic group: migratory birds were more likely to experience annual declines than non-migrants, while mammals displayed the opposite pattern. Within migratory species in IUCN, we observed that collective navigation and environmental system were important predictors of extinction risk for fishes and birds, but not for mammals, which had overall higher extinction risk than other taxa. We found high phylogenetic relatedness among collectively navigating species, which could have obscured its importance in determining extinction risk. Overall, outputs from these analyses can help guide strategic interventions to conserve the most vulnerable migrations.

Keywords: migration, birds, mammals, fishes, Living Planet Database, collective navigation

Introduction

Migration is one of life's most complex and ecologically consequential behaviours. In recent years, while technological advances have enabled scientists to describe for the first time the complex social mechanisms (e.g. collective navigation) that facilitate many migrations [1,2], scientists have also suggested that many such migrations may be in peril [3,4]. However, more spatially and taxonomically ambitious analyses are needed to help identify what specific factors may control the extinction risk and population status of collectively navigating and other migratory species.

Loss of migration is non-trivial: migratory species have been shown to provide unique functions to ecosystems, such as vectoring nutrients and seeds long distances, maintaining grassland ecosystems through cyclical grazing, and providing pulses of prey to resident predators (reviewed in [5]). Economies that are reliant on tourism or harvesting migratory species (e.g. wildebeest migrations in the Serengeti) could suffer from their decline [6,7]. Collective navigation (i.e. group-level pooling of information) aids migratory species' ability to travel long distances, and conserving this behaviour requires maintaining a minimum population size [8], which helps drive important ecological processes [5].

Several studies have reported declines of migratory species, although this research has primarily focused on specific taxonomic groups [4], or is qualitative [9]. Sanderson et al. [10], for example, found European long-distance migratory birds to have declined relative to resident European birds. Similarly, Harris et al. [11] reported that of the twenty-four large-bodied migratory ungulates they reviewed, six migrations have been lost. However, studies on extinction risk found that migration was not an important predictor of extinction risk [12]. One study on birds even suggested that migration decreased risk of extinction [13].

In light of these contradicting predictions, exploring how collective navigation, environmental system (i.e. the freshwater, marine, or terrestrial system associated with the migratory population), and taxonomy shape vulnerability to population decline and extinction risk could help focus efforts to preserve migrations. Species that travel long distances and rely on multiple habitat types are likely to be disproportionately impacted by human actions [10,14]. Road building, agricultural development, and dam construction create barriers for long-distance migratory species [15,16], and such impacts can be further compounded by habitat loss, overharvest, and climate change [3,17]. Threats may be even more serious for collectively navigating species. If these populations fall below a threshold size, Allee effect-caused collapses might occur that are difficult or impossible to reverse [8].

The environmental system through which a species migrates can also alter which threats they face; for example, landscape fragmentation and urban development are terrestrial disturbances that will likely have a greater impact on species that migrate on land than on marine or freshwater migrants. Similarly, the comparative lack of human infrastructure and associated fragmentation in marine systems could potentially leave migrating marine species at less risk of extinction [18]. The discrete and comparatively easy-to-modify nature of many freshwater ecosystems (e.g. dams in rivers) may increase risk of extinction for species migrating through these systems [19].

However, some characteristics of migratory species could increase their ability to circumvent potential threats. For example, the synthesized integration of environmental cues can help collective migrants traverse fragmented and complex landscapes [20]. Furthermore, migratory species with large geographic ranges and flexible movement patterns may reduce risk by moving to a new habitat when part of their range is fragmented or degraded [21].

In this study, we follow previous definitions of migration, defining it as cyclical and directed round-trip movement of animals between discrete areas [4]. We restrict this definition to include only movements greater than 100 km in one direction [22]. We leverage the power of two large datasets (International Union for Conservation of Nature Red List; IUCN and Living Planet Database; LPD) to examine the status of migrations from three perspectives: 1) by comparing population change over time; 2) by analysing the role of collective navigation and environmental system (freshwater, marine, terrestrial, and their combination) on migrant extinction risk; and 3) by examining contemporary shifts in the geographic range of migratory species. The results from these multiple perspectives contribute to our general understanding of how well migrations will fare in the Anthropocene and better position us to strategically respond to these risks.

Methods

Population change over time

Data selection and coding

To evaluate the relative vulnerability of migratory birds, mammals, and fishes, we created indices using population change data from the Living Planet Database (LPD) [23]. Reptiles, amphibians, and invertebrates were excluded from the analyses because of a lack of information in the LPD. The LPD is one of the largest repositories of time-series data relevant to recent population change (see [24] for further details).

For this analysis, we included data on all LPD populations of birds, mammals, and fishes (Actinopterygii only, as adequate trend data were available) with sufficient information to determine migratory status. Each population record was coded by its ecological affiliation to three different environmental systems: freshwater, marine, and terrestrial. Environmental systems were assigned based on a number of considerations, including where the population spends the majority of its time, which environmental system(s) help sustain the population, and where the population is most threatened (electronic supplementary material, table S1). Seven candidate biogeographic realms were assigned to terrestrial and freshwater populations and five realms were assigned to marine populations (electronic supplementary material, table S1).

We used the Global Register of Migratory Species (GROMS) for migratory coding [22]. As above, GROMS also defines migration as predictable and cyclical movements of more than 100 km. For details on migratory coding, see electronic supplementary material, tables S2 and S6.

After removing replicates (populations monitored in the same location and at the same time), the final data set created for analysis included 11,717 populations of 2,978 species (electronic supplementary material, table S3).

Data analysis and statistical methods

To estimate patterns of abundance change, we followed the Living Planet Index (LPI) method and calculated the geometric mean of trends for each species whereby each population time-series with six or more data points was modelled using a Generalised Additive Modelling (GAM) framework [24]. Population time-series with fewer than six data points or those that resulted in a poor GAM fit were modelled using the chain method [25]. In cases with more than one population time-series per species, the modelled annual trends for each population were averaged within each realm, class, and realm/class combination to provide a single set of annual trends for each species. These were then averaged across species and converted to index values with a baseline year of 1970. For each index, we generated 95% confidence intervals using a bootstrap resampling technique for 10,000 iterations [24]. These confidence intervals demonstrate the uncertainty in the index values inherited from the baseline in 1970 and propagated through the time-series. An R package, *rlpi*, for calculating these index values is available at https://github.com/Zoological-Society-of-London/rlpi.

Using these population trends, we explored a range of models to examine the relationship between migratory behaviour and population trends. For total change in abundance across all years we constructed linear mixed effects models in R using the lme4 package [26,27]. For likelihood of annual increases, beta-binomial models were used to model the ratio of increasing and decreasing years for each population using the glmmadmb package in R [28]. In these comparisons, we also excluded populations with no available GROMS status. Across all models, species and realm were included as random effects. Models were compared using the Akaike Information Criterion (AIC).

To examine how these differences in migration vulnerability varied by taxonomic grouping all analyses were repeated for birds, mammals, and fishes (for taxonomic breakdown see electronic supplementary material, table S3).

We then further analysed differences for taxonomic groups in select regions for which there were sufficient data for robust comparison between taxa and systems. Although system was not an important factor for birds and mammals overall, regional differences between systems were explored. Many regions did not have sufficient data to run these finer-scale analyses or to compare to other systems or taxa (see electronic supplementary material tables S4 and S5 for breakdown by realm). To illustrate the nature of these regional level differences, we focused on the Palearctic and northern temperate Pacific realms because these regions had sufficient data for taxonomic and system comparisons.

Species extinction risk

Data selection and coding

Our second analysis investigated patterns of migrant extinction risk using data from the IUCN Red List [29]. The IUCN database collects information from global assessments based on standardized protocols, which are linked to population size and structure, population trends, and geographic range. We extracted data on the threat status and environmental system (terrestrial, marine, freshwater, or their combination) for all bird, mammal, and fish species listed in both GROMS and IUCN (n = 3,447) [29]. The migratory status of each species was coded using GROMS. IUCN species were classified as terrestrial, freshwater, marine, or a combination of the three environmental systems based on IUCN's classification scheme (electronic supplementary material, table S6). IUCN threat status was converted to a 1 to 6 ordinal numerical index (following [30]).

We used the resultant database to test the effects of environmental system (referred to as "system") and tendency to collectively navigate on migratory species extinction risk. Due to considerable gaps in information on whether species directly exhibit collective movement or collective navigation, we coded each species based on proxy measures. Based on findings from the literature exploring the emergent dynamics of collective navigation [8,31], we coded migratory species as putative "collective navigators" if they were determined to travel in social groups (e.g. pods, herds, flocks, etc., as distinguished from loose aggregations of non-interacting individuals). Principle databases used for these determinations were FishBase and IUCN Red List (fishes); Avibase, NatureServe, USFWS Migratory Bird Data Center, and BirdLife International (birds); and IUCN and NOAA Fisheries Office of Protected Resources (mammals); which were supplemented with literature searches. Mammals were coded at the species level.

Birds and fishes were coded at higher taxonomic levels, to overcome strong geographic biases in data resolution, lack of data accessibility, and extreme intraspecific variation in migratory behaviour [32]. Birds were coded at the family level. Fishes were initially coded at the order level for those with strong phylogenetic association of schooling, and groups with mixed schooling behaviour were more thoroughly examined and coded at the family or genus level (electronic supplementary material, table S6).

Data analysis

We used cumulative link models (clms) to test the effect of system and its interaction with collective movement on IUCN risk category (EW, EX, CR, EN, VU, NT, LC) for birds, mammals, and fishes. Within each taxonomic class, species were typically found in only a subset of the systems available. For birds, very low sample sizes in freshwater, freshwater/marine, and marine systems required that we pool those groups into terrestrial/freshwater, terrestrial/freshwater/marine, and terrestrial/marine respectively. For fishes, only the systems freshwater, freshwater/marine, and marine were applicable, and low sample sizes required we pool the highest threat categories (CR, EX, and EN) into one highest risk category. For mammals, species that were classified as inhabiting any system that included freshwater (freshwater, freshwater/marine, freshwater/terrestrial, and freshwater/marine/terrestrial) were grouped as freshwater to retain an adequate sample size for analyses. When comparing across taxonomic groups, we did not have the proportional odds to compare all threat categories, so the categories were grouped into Lower Risk (LC, NT, VU) and Threatened (EN, CR, EW, EX).

We modelled extinction risk with clms using a flexible threshold and logit link function [33] using the ordinal package in R [34]. We then compared all model subsets using AIC to select the best model of extinction risk. Analysis of deviance tables (ANODE) were then used to evaluate the importance of parameters in the best model [34]. Finally, we conducted Tukey-adjusted pairwise comparisons of the nominal effects of the best model to identify significantly different groupings using the lsmeans package [35].

Geographic range shifts

Data collection and coding

To examine changes in the spatial distribution of migratory species, we conducted a literature search investigating geographic range shifts of any type for migratory species of birds, mammals, fishes, and insects. Insects were included in these analyses (and not above) because data were sufficient in the literature to include them in this compilation. All searches were conducted in Web of Science using the search terms “migra*” and “range”, six terms for taxonomic groupings (mammal*, marine mammal*, bird*, fish*, insect*), and four terms denoting geographic change (i.e. shift*, contract*, expand*, change*). We also searched within the citations of the relevant papers for additional papers. This resulted in a total of 5163 papers, of which 66 had quantitatively investigated geographic range shifts in migratory species and produced results concluding some change or no change had occurred (not predictive). All species treated in this literature search were confirmed to match our definition of migration. For each paper, we recorded the study species, taxonomic class, and the system and realm as defined by IUCN and matched to the LPD. We then categorized the type of geographic range change for each species as one of four possible categories: contraction, shift, no change, or expansion. The data were split taxonomically and by type of geographic range change. See electronic supplementary material, table S7 for coding and literature.

Results

Population change over time

Global patterns

When data derived from the LPD from all species, systems, and realms were examined together there was no significant difference between migratory and non-migratory species ($p = 0.138$) (Fig. 1A).

Effect of migration on likelihood of annual increase differed by taxonomic group, with migratory birds significantly more likely to have faced declines than non-migratory birds ($p < 0.001$; Table 1) and migratory mammals significantly less likely to experience annual declines than non-migratory mammals ($p = 0.032$; Table 1). From AIC, the best model for predicting the likelihood of annual increase for birds and mammals was determined to be the simplest model, with Migratory as the only explanatory variable (no interaction between migration and system). However, the best model for fishes was determined to be Migratory*System, which includes the interaction between migration status and system (freshwater and marine). There was no significant difference found between migratory and non-migratory fishes in either system (Table 1).

Regional patterns

Data from the LPD were sufficiently robust in nine cases to permit further subdivision and analyses of pattern at finer regional levels. Of the nine regional trends, six show migratory populations tending to perform worse than non-migratory populations (Fig. 2 and electronic supplementary material, figures S1-S4).

In the Palearctic and Pacific regions, migratory populations performed worse than non-migratory populations for each group (Fig. 2), with the exception of Pacific marine birds, for which migratory and non-migratory species appear to have been on similar trajectories (electronic supplementary material, fig. S2). Terrestrial and freshwater Palearctic migratory birds are both faring worse than non-migrants (Fig. 2A and 2B), which matches the taxonomic level results. The trend for terrestrial Palearctic mammal change over time is different from the overall results for mammals; here, Palearctic terrestrial migrants are doing worse than non-migrants (Fig. 2C). Similarly, migratory Pacific marine fishes appear to be doing worse than non-migrants (Fig. 2D), whereas there was no significance in the taxonomic analysis. For Living Planet Indices used to create the figures see electronic supplementary material, table S8.

Species extinction risk

Within all migratory species, analysis of IUCN data indicates that extinction risk differed significantly among taxonomic groups. Migratory mammals were more likely to be placed in a higher extinction risk category than either migratory fishes or birds (Table 2). Analyses within taxonomic groups yielded additional insights: for birds and fishes, the best model included model terms System, Collective behaviour, and their interaction. However, no model outperformed the null for mammals (electronic supplementary material, table S9). Extinction risk was higher for non-collective migratory birds in some systems, but not all (Table 2). Migratory birds in terrestrial/marine systems (seabirds) had a higher risk of extinction than avian migrants in other systems; non-collective migratory seabirds were at greater risk of extinction than collective migratory seabirds.

For fishes, the best model included the full model that included the interaction of system and collective behaviour. The interaction was significant ($p<0.001$; Table 2); for collective migrants, marine fishes were placed in lower risk categories than their freshwater counterparts. Non-collective freshwater and anadromous migrants were substantially more at risk of extinction than any marine migrants (Table 2).

Geographic range shift

The literature review of geographic range change of migratory species produced different patterns of change for birds (n = 451), mammals (n = 30), fishes (n = 138), and insects (n = 107) (Fig. 3). Eighty percent of the bird records indicated shifts in geographic range, with the remaining records indicating contractions or expansions. Fish literature produced the second-largest source of records on geographic range change of all the taxonomic groups with the majority (73%) of these records experiencing range contractions. Although there were relatively few records of mammal geographic range change, 47% of mammal records indicated range contractions. There was extremely low taxonomic diversity in data available on insect geographic range, with all records identified coming from Lepidoptera. Seventy percent of these records showed range expansions.

Discussion

Our global analysis of population change across all taxa did not reveal discernible differences between migratory and non-migratory species; however, analyses of spatially and taxonomically disaggregated data revealed that migration vulnerability and extinction risk are highly context-dependent.

Overall taxonomic vulnerability

Across all taxonomic groups, migration did not consistent predict vulnerability to population decline. This suggests characteristics of taxonomic groups, such as evolutionary history, determine how migration interacts with other variables (i.e. environmental system and collective navigation).

Birds

In agreement with previous studies that used different data sources and analytical approaches [10,36], we observed elevated vulnerability for migratory birds relative to non-migratory birds (Table 1). One possible explanation for the elevated vulnerability of migratory birds is that they are subject to “multiple jeopardy” because they require many different sites throughout their annual cycles: stopover sites, overwintering habitat, and breeding grounds [14]. Recent field studies have found disproportionate rates of bird mortality during migratory periods (e.g. raptor mortality was six times higher during migration than stationary periods; [37]), and habitat loss in breeding or overwintering grounds are a significant threat to migratory birds [38]. While migratory birds are disproportionately vulnerable to population decline compared to non-migratory birds, overall extinction risk for birds in IUCN is lower than mammal extinction risk (Table 2). This indicates that while migratory bird populations are more likely to decrease than non-migratory birds, many migratory bird populations are still relatively robust and there is high potential for conservation.

Mammals

Contrary to the well-documented losses of high profile mammal migrations [11,39], our population analysis suggests that migratory mammals were more likely to increase annually than non-migrants. The vagility of migratory mammals could aid their ability to escape anthropogenic threats in areas where non-migrants would have more difficulty moving territories. Additionally, migratory mammals appear to receive disproportionate conservation attention due to their visibility (e.g. ungulate herds and great whales) and influence on tourist-based economies (e.g. safaris and whale-watching), which have helped motivate the direct investment of conservation funds and attention to such species (e.g. rinderpest eradication; [40]).

Despite the increases of migratory mammals relative to non-migrants, IUCN lists migratory mammals in higher threat categories than birds or fishes (Table 2). This discrepancy likely derives from different time periods and variables considered (e.g. IUCN considers variables such as population size and connectivity that the LPD does not). This is likely true for birds and fishes as well.

It is also important to note that increasing the abundance of migratory mammals is a necessary but not sufficient condition for the persistence of the migrations themselves. South African wildlife, for example, is often managed in carefully controlled fenced plots. This has facilitated population increases for a number of species in recent years, but this management strategy effectively eradicates migration potential [41,42].

Fishes

There was no significant difference in the likelihood of annual population increase between migratory and non-migratory fishes. In our environmental system-level analyses of IUCN data, however, migratory freshwater fishes were at more risk of extinction than migratory marine fishes (Table 2). Marine fishes face immense threats from overharvest; but, as with other taxa, the mobility of marine migrants could allow migrants to more successfully avoid anthropogenic threats, whereas migratory freshwater fishes are less able to escape habitat modification, pollution, and water extractions [16,43].

Regional vulnerability

Data limitations made regional analyses challenging, but in the northern temperate Palearctic and Pacific realms, migrants were more vulnerable to extinction than non-migrants across all environmental systems (Fig. 2). Terrestrial and freshwater migratory birds were again more vulnerable than non-migrants (Fig. 2A and 2B); although, the heightened vulnerability of terrestrial mammal and marine fish migrants relative to non-migrants differs from the overall results for mammals and fishes (Fig. 2C and 2D). This suggests declines in migratory populations can be obscured in the aggregated data and emphasizes the need to examine migrants in their local context.

Collective navigation

As previously discussed, collective navigation could be either an aid or a liability for migratory species. While the best model for bird and fish extinction risk included collective navigation, extinction risk did not differ significantly between collective and non-collective species for most groups. However, the lower risk of collectively-moving migratory seabirds relative to non-collectively moving migratory seabirds suggests there might be some benefit to seabirds moving in flocks, in that they are more able to avoid threats than their non-flocking counterparts (e.g. [44]). It is interesting to note that migratory seabirds have the highest risk of extinction as compared to the migratory birds in other environmental systems (Table 2). The reliance of seabirds on both terrestrial spaces for breeding and marine spaces for feeding could elevate their extinction risk [45], while collective navigation could aid their immense movements and unique use of different resources and habitats. Although collective navigation seems to aid migratory seabirds, the overall population declines in migratory birds are concerning, given the observed relationship between collective navigation and population abundance [8]. With continued decline, collectively moving migrants could face the threat of population collapse.

We did not find evidence in migratory mammals for an effect of collective movement. However, the small sample size of migratory mammals in several environmental systems may have played a role in our inability to detect differences between collective and non-collective migrants. It is interesting to note, however, that the most threatened migratory mammal (i.e. Critically Endangered and Extinct in the Wild) species were collective migrants. While largely a benefit, the reliance of collectively navigating species on inter-individual cues can also result in cascading consequences when one individual makes a mistake (e.g. failed wildebeest river crossings). Increasing anthropogenic change could result in greater potential for mistakes and greater cost to collective migrants.

Although fishes similarly showed no significant interactions between extinction risk and collective movement, non-collectively moving freshwater and diadromous fishes were more likely to be placed in higher threat categories than the rest of the migratory fishes, once again at least partially suggesting some benefit to moving collectively.

Finally, while coding for collective movement we found that species which tend to move in social groups were typically phylogenetically related (electronic supplementary material Table S6). The interrelatedness of collectively moving species could be a confounding factor in this analysis, potentially obscuring the importance of collective navigation.

Geographic range

Restricting movement, particularly access to key resources, also endangers migrations [11]. As with previous results, the literature review on migratory species geographic range suggests that the type of range change differs between taxonomic groups. Insects (i.e. butterflies) mostly exhibited expansions in range (Fig. 3), which have largely been attributed to increasing temperatures in temperate areas such as Europe, where many such studies are concentrated [46]. The majority of studies on bird ranges only documented overall shifts, likely because many bird studies were not able to track bird populations across their entire range, thus limiting their ability to conclude whether an absence in one area represented a contraction or simply a change in geographic location. Shifts in migratory birds could be due to a variety of factors, including habitat loss and climate change [47]. The contractions in migratory mammals seem to support the notion that while migratory mammals are faring better than non-migrants in respect to population change, threats to the functional integrity of mammal migrants may still exist. Both freshwater and marine fishes exhibited contractions, with the contractions in freshwater fishes largely due to damming of rivers [48] and marine fish contractions likely caused by intense fishing pressure extirpating even highly mobile species from parts of their range [49].

It is interesting to note that aerially mobile migratory groups (i.e. insects and birds), experienced many expansions and shifts while the groups restricted to land and water movement (i.e. mammals and fishes) appeared to experience more contractions in range. The energetic cost of moving on land and the potential for barriers in aquatic and terrestrial systems might decrease the ability of mammals and fish to respond to anthropogenic changes relative to aerially mobile species [15]. We posit that these patterns support the idea that locomotion on land or in water might expose migratory species to increased threat from anthropogenic habitat fragmentation (e.g. roads, dams, deforestation), but other correlates need to be considered to make such links definitive.

Caveats

We draw attention to four key limitations inherent to these analyses. First, we highlight the recent nature of the abundance comparisons (population trends were examined relative to a baseline of 1970), which would not detect population declines for species that were negatively impacted prior to 1970 (e.g. marine mammals). Second, the Living Planet Index relies on aggregated publicly available data and is therefore prone to biases associated with over-representation of certain taxa and regions [50], specifically toward temperate regions (electronic supplementary material, tables S4 and S5). We analysed the LPD data in both aggregate and within disaggregated regions, but were unable to use the diversity-weighted approach normally employed to account for such biases [50] due to availability of data and species numbers. While we fully agree there are biases and pitfalls to this approach, previous analyses of these biases indicate that even an unweighted index is likely indicative of overall patterns [24]. While the LPD does contain trends on commercially important species, the impact of these is reduced through the inclusion of harvest or catch data only if they include a measure of effort. Third, our study purposefully does not thoroughly examine correlates for extinction risk, as many studies have already usefully done [13,30]. We focused on patterns and trends in migratory species, necessitating further study to conclusively identify mechanisms behind observed patterns of vulnerability and extinction risk for migrants. Fourth, GROMS does not comprehensively cover all migratory species. GROMS includes a total of 4,472 records, of which approximately 3,400 migratory species are also in IUCN.

Conclusions

In the instances where migration is indeed under threat, we risk losing important ecological functions and charismatic biological phenomena. From these analyses, it is clear that migration vulnerability is dependent on complex interactions between behavioural traits, taxonomy, and the environmental system through which the species navigates. Species with a high potential for collective navigation might be able to more efficiently avoid threats in certain environmental systems (i.e. marine birds, freshwater and diadromous fishes), but collective navigation could amplify the vulnerability of declining species, such as migratory terrestrial mammals in the Palearctic. Migratory bird populations are disproportionately vulnerable compared to non-migrants, whereas migratory mammals are vulnerable than non-migrants. However, the overall pattern of high extinction risk in mammals, coupled with the high proportion of range contractions experienced by migratory mammals, is concerning. Spatial distribution of migratory mammals, rather than population declines, might be more relevant to preserving their migrations. While there is certainly cause for concern, some of our results suggest possibilities for recovery, namely: recent increases in certain migratory mammals, potential benefits of collective navigation, and remaining high abundances of birds despite declines.

Of note, if we aim to recover the functional significance of migration, we cannot simply focus on increasing the population sizes of migratory species, but need to ensure that these important increases are matched with recovered ecological potential for these larger groups to meaningful execute migration. In our increasingly fragmented world, the latter goal perhaps is more challenging than the former. The broader patterns reported here suggest both an opportunity and a roadmap for mounting strategic interventions to protect this ecologically, socially, and economically important part of the behavioural portfolio of life.

Additional Information

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Data Accessibility

All IUCN, geographic range data and LPD model outputs and synthesized information used in this project are included as supplementary material. LPD raw data can be found at http://www.livingplanetindex.org/.

Author Contributions

MHM, DJM, GCT, ED, KS, HSY, MK, AB, AMK, DO, LFH designed the concept of the study. MHM, GCT, EMD, KS, MK, AB, AMK, DO, LFH found, synthesized, and interpreted data. RF and SD provided, analysed, and helped interpret all LPD data. GCT analysed IUCN data. EMD and KS analysed geographic range data. MHM wrote the manuscript with input from DJM, and all authors contributed to revisions.

Competing Interests

We have no competing interests.

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Tables

Table 1.

Taxonomic Group	Environmental System	Odds Ratio	Standard Error	Z score	P-value
Birds	All	1.317	0.11 (1.12 – 1.55)	-4.10	< 0.001
Mammals	All	0.668	0.10 (0.496 – 0.901)	2.15	0.032
Fishes	Freshwater	1.173	0.15 (0.91 – 1.51)	-1.37	0.171
	Marine	0.756	0.15 (0.51 – 1.13)	1.256	0.210

Table 2.

Analysis of Deviance for best model					Pairwise comparisons of groups		
Taxa	**Predictor**	**Df**	**Chisq**	**P**	**Collective Migrant**	**Environmental System**	**Group**
 Birds					No	Terrestrial	**a**
					No	Terrestrial/Freshwater	**abc**
	System	3	448.48	< 0.001	Yes	Terrestrial/Freshwater	**ab**
	Collective	1	343.47	< 0.001	Yes	Terrestrial	**ab**
	System:Collective	3	98.91	< 0.001	Yes	Terrestrial/Freshwater/Marine	**b**
					No	Terrestrial/Freshwater/Marine	**abcd**
					Yes	Terrestrial/Marine	**c**
					No	Terrestrial/Marine	**d**
 Fishes					No	Marine	**a**
	System	2	79.402	< 0.001	Yes	Marine	**ab**
	Collective	1	69.103	< 0.001	Yes	Freshwater/Marine	**abc**
	System:Collective	2	10.114	< 0.01	Yes	Freshwater	**bc**
					No	Freshwater	**c**
					No	Freshwater/Marine	**c**
 Mammals		N/A				All levels equivalent	
Overall extinction risk					Birds		**a**
	Class	2	1023.6	<0.001	Fishes		**a**
					Mammals		**b**

Figure and table captions

Fig. 1. Abundance indices measured over time relative to 1970 baseline values for non-migratory (nm; orange) and migratory (mig; green) species derived from the Living Planet Database. The data in this figure represent a compilation of population time series from monitored sites around the world. Data are (A) aggregated across all birds, mammals, and fishes, and subdivided by taxon (B-D). Number of species included in analyses are provided on each figure.

Fig. 2. Regional abundance indices measured relative to 1970 for data rich northern temperate terrestrial and aquatic species in either the Palearctic or Pacific realm. Data is derived for non-migratory (nm; orange) and migratory (mig; green) species from the Living Planet Database. The data in this figure represent a compilation of population time series from monitored sites around the world. Graphs depict change in abundance indices for A) Palearctic terrestrial birds, B) Palearctic freshwater birds, C) Palearctic terrestrial mammals, and D) Pacific marine fishes. Number of species included in analyses are provided on each figure.

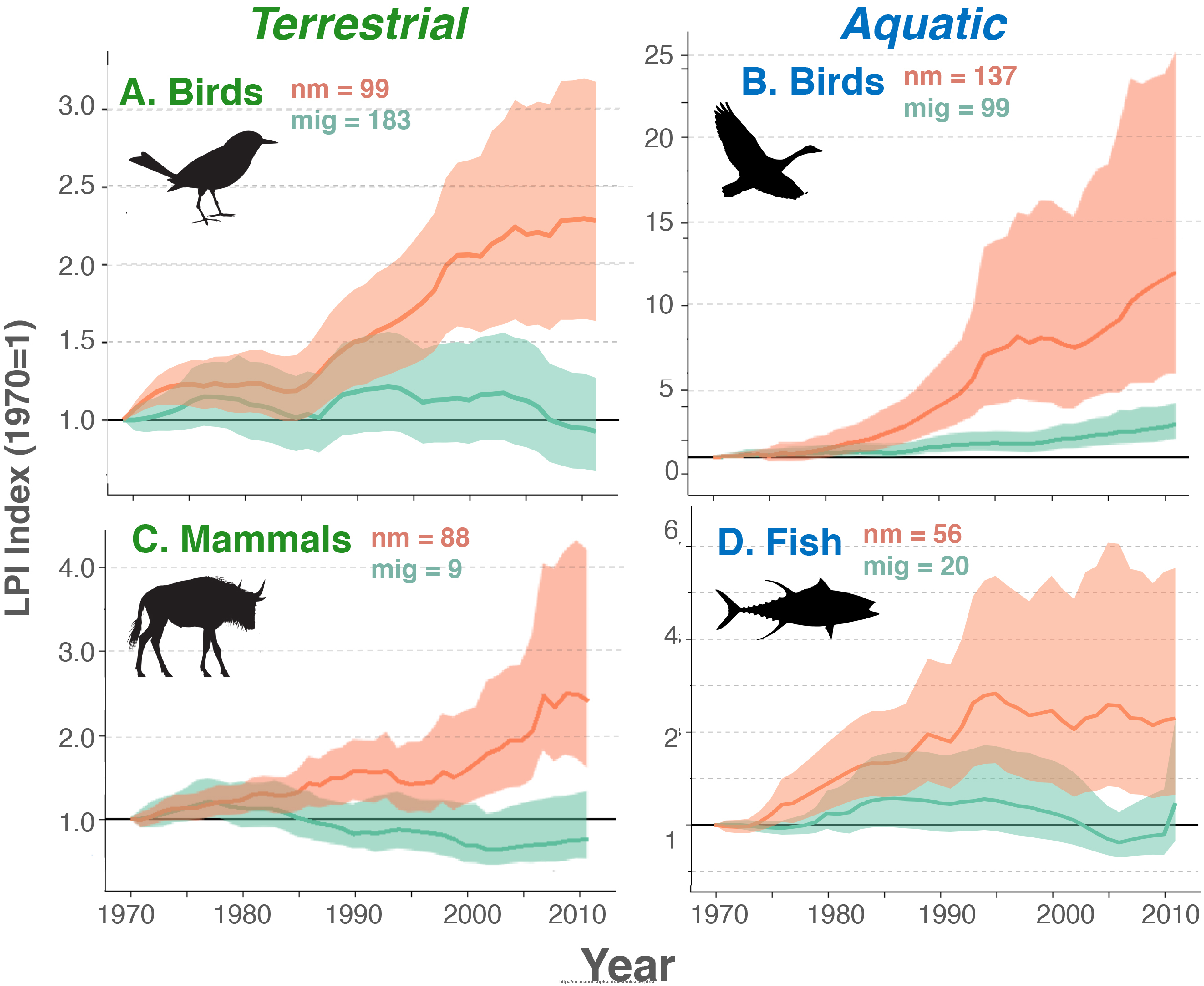
Fig. 3. Proportion of types of migratory range changes reported for migratory insects (i.e. butterflies), birds, mammals, and fishes. Range changes can be contractions, shifts (i.e. change in geographic location), expansions, or no change. Width of x-axis represents relative sample size of taxonomic groups. The number of records of change for each taxonomic group is reported.

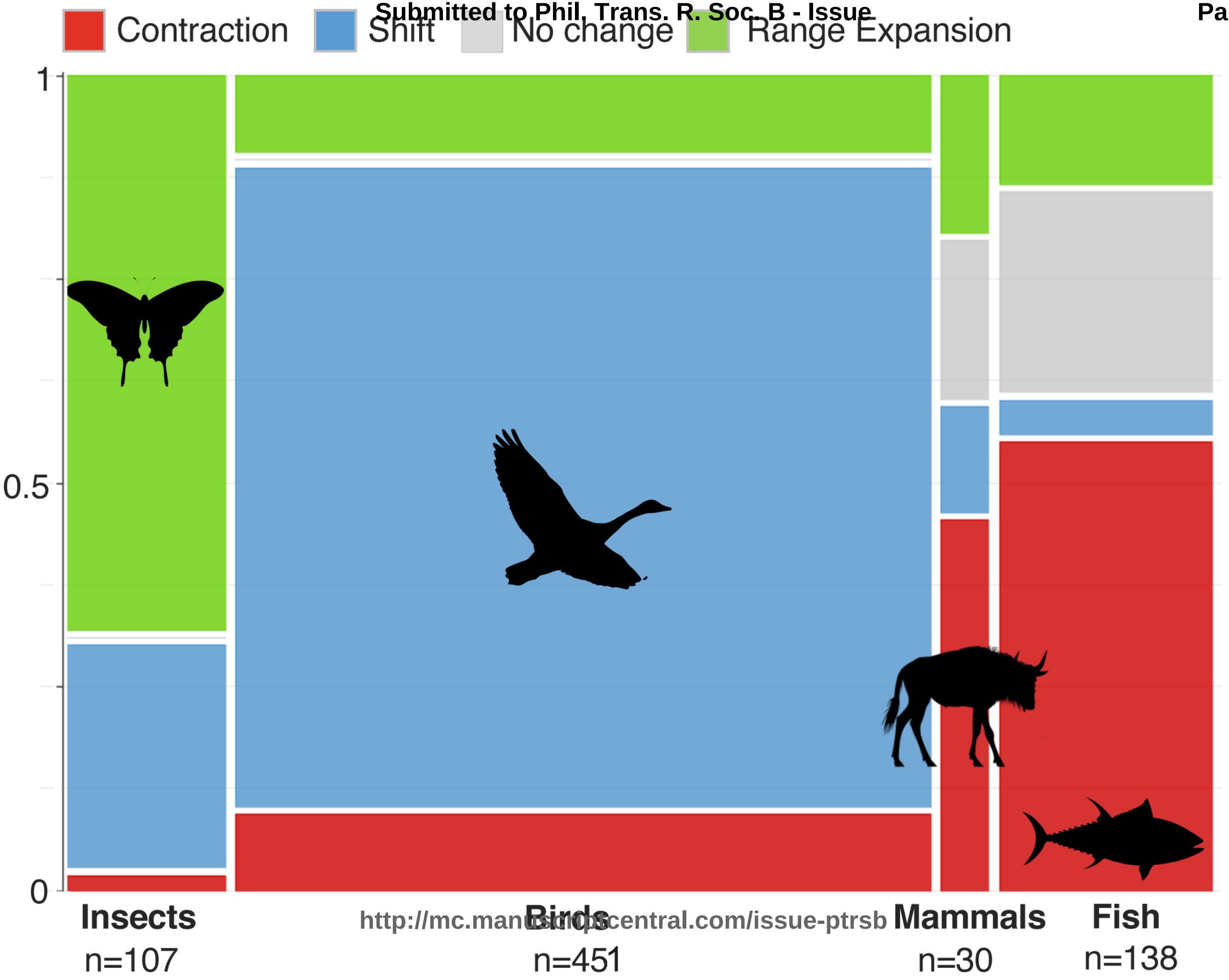
Table 1. Model results from Living Planet Database likelihood of annual increase analysis for birds, mammals, and fishes. Odds ratio, standard error with confidence intervals, Z score and P-value are reported for each taxonomic group, with fishes split into freshwater and marine systems.

Table 2. Analysis of Deviance (ANODE) table and Tukey-adjusted pairwise comparisons of model coefficients for all IUCN extinction risk analyses. ANODE results shown at left correspond to the best model of extinction risk for each analysis. Pairwise comparisons for group differences in each best model are shown on the right. Species were coded as collective migrants

based upon database or literature indicating they travel in social groups. Environmental system (freshwater, marine, terrestrial, or their combination) was coded from IUCN classifications. The mammal model showed no difference from the null and thus comparisons were not possible. Group levels denote significant differences from pairwise comparisons within each dataset for birds, fishes, mammals, and all taxa. Lower lettering (i.e. “a”) indicates a lower risk of extinction than higher lettering “b-d”. Least-square means and asymptotes of their 95% confidence limits were used to differentiate groups, but their numeric values are arbitrary; these are listed in Table S9.


A. All taxa
nm = 2091
mig = 1138
1.2
1.0
0.8
B. Birds
nm = 716
mig = 938
1.4
1.2
1.0
0.8
C. Mammals
nm = 465
mig = 74
9
5
1
D. Fish
nm = 871
mig = 255
2.4
1.8
1.0
LPI Index (1970=1)
1970
1980
1990
2000
2010
Year


Terrestrial
Aquatic
A. Birds
nm = 99
mig = 183
B. Birds
nm = 137
mig = 99
C. Mammals
nm = 88
mig = 9
D. Fish
nm = 56
mig = 20
LPI Index (1970=1)
Year
3.0
2.5
2.0
1.5
1.0
25
20
15
10
5
0
4.0
3.0
2.0
1.0
6
4
2
1
1970
1980
1990
2000
2010
1970
1980
1990
2000
2010


🟥 Contraction
🟦 Shift
⬜ No change
🟩 Range Expansion
1
0.5
0
Insects
n=107
Birds
n=451
Mammals
n=30
Fish
n=138