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Population trends are more strongly linked to environmental change and species traits in birds than mammals

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Changes in land use and climate directly impact species populations. Species with divergent characteristics may respond differently to these changes. Therefore, understanding species' responses to environmental changes is fundamental for alleviating biodiversity loss. However, the relationships between land use changes, climate changes, species' intrinsic traits and population changes at different spatial scales have not been tested. In this study, we analysed the effects of land use and climate changes from different time periods and species traits on the population change rates of 2195 bird and mammal populations in 577 species recorded in the Living Planet Database at global, tropical and temperate scales. We hypothesized that both bird and mammal populations will decline owing to climate and land use changes, especially phylogenetically young and small-bodied species. We found that bird population trends were more closely related to environmental changes and phylogenetic age than those of mammals at global and temperate scales. Mammal population trends were not significantly correlated with land use or climate changes but were with longevity at global and temperate scales. Given the divergent responses of bird and mammal populations to these explanatory variables, different conservation strategies should be considered for these taxa and for different regions.

1. Introduction

Globally, wildlife populations have declined by 69% on average from 1970 to 2018 [1], highlighting the seriousness and urgency of actions to reduce these losses and enable population recovery. Declining vertebrate populations signal the ongoing sixth mass extinction [2,3]. The reduction in species abundances will inevitably undermine ecosystem function and ecosystem service provision [4–7]. To date, however, few studies have simultaneously assessed the impacts of land use changes, climate changes and species' intrinsic traits on wildlife population changes. Therefore, the exploration of relationships between these different factors and wildlife population changes could aid the understanding of wildlife population dynamics and offer important insights for global biodiversity conservation [8,9].

Anthropogenic land use changes cause habitat loss and fragmentation, which are the main drivers of population declines and biodiversity losses [8,10–13]. Habitat loss directly reduces population sizes, thus increasing extirpation risk, and can reduce standing genetic variation, limiting species' ability to adapt to environmental change. Habitat fragmentation decreases species' capacity to alter their ranges in response to environmental changes [14]. Population declines and species extirpations can continue even after habitat loss has stabilized, resulting in an extinction debt. When patch size is too small to support the minimum viable population size, the population is too low or other key demographically related thresholds are surpassed, individuals might survive, but populations are no longer functionally viable. As a result, local extirpation will eventually occur when existing individuals die [15]. A global study on forest ecosystems found that temporal lags in population and community changes after forest loss can continue for up to half a century [16].

In addition to changes in land use, climate change is also a significant driver of species distributions and biodiversity patterns [17–23]. Climate changes can impact species in many different ways, both directly and indirectly, through changing food supplies and phenological mismatches. Species must adapt to local changes to maintain stable populations in specific locations, or they risk population decline or extinction [24–27]. These changes in climate can alter the sizes of populations [21,28] and the behaviour and morphology of organisms [29,30]. Climate changes will be harmful to species if the temperature, precipitation or other climate variables exceed the range of tolerance, or the breeding season does not match the peak value of resource availability [18,31,32]. A previous study found that climate warming is associated with population declines in terrestrial birds and mammals globally [21]. Conversely, climate changes can increase primary productivity in some conditions and may increase some species abundances [33,34]. Furthermore, as some regions become less suitable for some species, other species may expand ranges or populations to fill vacant niches or utilize unexploited food (or other) resources [25–27]. Species' responses to climate changes also often have a time lag, which means that species may need decades or even centuries to adapt to the recent climate changes [35,36]. For example, changes in French breeding bird communities lag behind climate warming, resulting in a climate-driven extinction debt [37,38].

The responses of species to these global change factors are also strongly influenced by species' intrinsic traits [23,28,39,40]. For example, many studies have shown significant correlations between body mass and species extinction risk, with larger species facing higher extinction risks, leading to a greater likelihood of population declines [41–43]. However, other studies have found that smaller mammals have a higher likelihood of population decline than larger ones [21]. Long-lived species are more resistant to the effects of environmental changes than short-lived species [44,45]. Long-lived species typically exhibit lower reproductive rates and longer life cycles [46]. This life history strategy can provide a certain degree of buffering in unstable environments and thus maintain population stability over time [44,45]. In addition, individuals of long-lived species usually have higher survival rates, which could also contribute to the stability of their populations [44,45]. Studies also have found that reproductive rates (litter or clutch size and total annual litter or clutch size) can impact a species' ability to adapt to climate changes. Higher reproductive rates provide the capacity for the selection of beneficial phenotypes, enabling species to remain viable in the face of changing climates [9].

In addition to these important functional traits, phylogenetic factors (phylogenetic age, evolutionary distinctiveness and diversification rate) reflect the evolutionary history of species and represent important facets of biodiversity and priorities for conservation [47–50]. For example, a study of forest mammals in Borneo, Southeast Asia, found that species with longer phylogenetic ages have higher specificity and narrower geographical distributions and niches, resulting in poorer abilities to cope with deforestation [51]. Evolutionary distinctiveness is correlated with ecological distinctiveness and geographical remoteness in global primates, so populations with high evolutionary distinctiveness will face a higher threat of extinction [52]. Among mammals, families on branches with higher net diversification rates tend to have higher climate ecological niche differentiation. This means that populations with higher net diversification rates may exhibit greater adaptability to changes in climate and land use [53]. Nowadays, the global vertebrate phylogenetic tree has sufficient coverage to assess inter-relationships between phylogenetic factors and population trends. Therefore, understanding the relative influences of phylogenetic factors could facilitate targeted efforts to better conserve species diversity in the case of environmental changes [54].

This study therefore aims to explore the roles of recent and historical anthropogenic land use and climate changes, as well as the roles of species functional traits and phylogenetic factors, in affecting bird and mammal population sizes. We predict that both bird and mammal populations will decline owing to climate and land use changes, but that birds will decline more than mammals because the stronger dispersal abilities of many species make them more easily able to leave the original changed habitat. We also expect that populations of species with smaller body mass, longer phylogenetic ages, higher evolutionary distinctiveness and lower diversification rates, and populations that have experienced more anthropogenic land use and climate change, will show higher rates of population decline. Because of the frequently lagged responses of vertebrate populations to external impacts, we expect rates of population decline will be influenced by both recent and historical changes in land use and climate. Lastly, tropical regions have higher biodiversity and a greater number of specialist species compared with temperate regions. Therefore, we predict that although populations in both tropical and temperate regions will decline following environmental changes, the decline will be more severe in tropical regions.

2. Material and methods

(a) Population data of birds and mammals

Population data for birds and mammals were obtained from the Living Planet Database (http://www.livingplanetindex.org/data_portal). This is a public database containing over 19 000 populations' abundance time series between 1950 and 2018. These data were collected through multiple methods, including scientific literature, online databases and grey literature. Besides abundance, taxa, region and habitat type are also included in the database. This database includes 11 126 bird populations across 152 families and 5113 mammal populations across 93 families. Excluding international waters and the Antarctic, the database comprises 1733 bird populations and 1314 mammal populations from tropical regions, and 8344 bird populations and 3794 mammal populations from temperate regions. Habitat types include tropical and subtropical moist broadleaf forests, deserts and xeric shrublands, boreal forests/taiga and others. We used 23.5° north and south latitudes to delineate tropical and temperate zones [55]. Cold zones are defined as areas above 66.5° north and south latitude.

The average logged rate of population changes ($\overline{\lambda_Y}$) was calculated following Spooner *et al.* [56]. Before calculating the $\overline{\lambda_Y}$, it was necessary to interpolate the population time series data with missing values. For each population, the zeros were replaced by 1% of full series' mean value (to avoid error when converting the value to logarithms). Then, all the population estimates were converted to $\log_{10}$. For the time series with more than six observed estimates ($n > 6$), a generalized additive model (GAM) was fitted. The smoothing parameter was set as half of the number of observed estimates ($N/2$), which proved effective for fitting time series, without overfitting to noise [56]. For populations with under six counts. a linear regression was used. The missing values were filled with predicted values of the GAM or linear regression. Then $\overline{\lambda_Y}$ was calculated as follows:

$$\lambda_y = \log_{10}\left(\frac{n_y}{n_{y-1}}\right), \tag{2.1}$$

$$\bar{\lambda}_Y = \left(\frac{1}{Y}\right)\sum_{0}^{n}\lambda_y, \tag{2.2}$$

where n is the population estimate of a given year (y), and Y is the total number of years from the first to last population estimates.

The data were filtered by three criteria: (i) $R^2 \geq 0.5$ when fitted to the GAM or linear model (to ensure the interpolated population estimates were reasonable); (ii) the population time series spanned 5 or more years (to reflect long-term effects of environment); and (iii) environmental, phylogenetic and trait data were available. After filtering, 2195 populations remained, including 1200 bird populations (979 in temperate zones, 106 in tropical zones and 115 in cold zones) and 995 mammal populations (554 temperate, 399 tropical and 42 cold; figure 1). These populations included 577 different species, i.e. 321 bird species and 256 mammal species. In terms of phylogenetic coverage, our dataset included 56.8% of the global avian orders, 29.6% of the families and 7.9% of the genera. For mammals, our data included 77.8% of the global orders, 38.5% of the families and 13.4% of the genera. Data from cold zones were only included in the analyses at the global scale and were not used in the analyses of temperate and tropical regions. The population abundance time series had an average length of 11.76 years, with a standard deviation of 9.03 years. The sample distribution showed more samples in certain habitat types, such as grasslands, forests, wetlands and shrublands, while other habitats like deserts, rocky areas, introduced vegetation and caves had relatively fewer samples (electronic supplementary material, figure S1).

(b) Environmental data

Climate data were gathered from CRU TS v. 4.04 [57], which provides monthly land surface temperature and precipitation data at a spatial resolution of 0.5° from 1901 to 2019. We extracted the monthly data at the location of each population time series and converted it into annual data. In order to assess the impact of historical and recent climate changes on each population, the climate data were divided into two periods. The first period was from 1901 to 1950, called 'historical' hereafter. The second period spanned the same period as the population time series (between 1950 and 2018), called 'recent. Both historical and recent climate time series were fitted with linear regressions. The slopes were extracted to represent the rates of change in mean annual temperature and mean annual precipitation for the specific periods.

Land use data were gathered from HYDE v. 3.2 [58], which provides grid cell coverage of cropland and pasture at a spatial resolution of 0.083°. We extracted the coverage data for 1900, 1950 and 2000, and divided them into two periods (1900–1950 and 1950–2000) to assess the impacts of historical and recent anthropogenic land use changes on recent population trends. The differences between the beginning year and the end year of each time period were calculated, to represent the anthropogenic land use changes in the specific periods 1900–1950 and 1950–2000.

(c) Phylogenetic data

The bird phylogenetic tree was downloaded from the global bird tree (https://birdtree.org), using the choice of 'Hackett all specifications: a set of 10 000 trees with 9993 OTUs each' [59]. The mammal phylogenetic tree was downloaded from VertLife (http://vertlife.org), using the choice of 'Mammals birth-death node-dated completed trees (all 5911 species, set of 10 000 trees)' [54]. Five thousand random phylogenetic trees were sampled for birds and mammals, and the maximum clade credibility tree was filtered by BEAST v. 1.10.4 [60]. The final phylogenetic tree was created in FigTree v. 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/). Three phylogenetic factors were extracted for further analyses: phylogenetic age, evolutionary distinctiveness and diversification rate. The phylogenetic age is the overall evolution time of a species, represented by the length of edge branch [61]. Evolutionary distinctiveness (which can relate closely to phylogenetic endemism) describes the isolation level of species on the phylogenetic tree. It was calculated with the fair proportion method [62]. The diversification rate was the reciprocal of the evolutionary distinctiveness calculated by the equal splits method [59].

(d) Trait data

Bird and mammal trait data were extracted from a database of comprehensive amniote life history data [63]. Body mass, a fundamental trait, is highly correlated with various demographic and ecophysiological traits [64]. The body mass values were converted to $\log_{10}$ to have a normally distributed residual. Longevity, litter or clutch size and annual litter or clutch size were also included in analyses to determine the effects of life history traits on population trends. Litter or clutch size indicates the number of offspring per reproductive event, while annual litter or clutch size represents the total number of reproductive events within a year.

(e) Spatial error autoregressive models

Spatial error autoregressive (SAR) models were used to analyse the impacts of environmental changes, phylogenetic factors and functional traits on population trends. The response variable was the average logged rate of population changes ($\overline{\lambda_Y}$). The explanatory variables included the rate of historical temperature change (from 1901 to 1950), the rate of historical precipitation change (from 1901 to 1950), the rate of recent temperature change (between 1950 and 2018), the rate of recent precipitation change between 1950 and 2018, land use changes between 1900 and 1950, land use changes between 1950 and 2000, phylogenetic age, evolutionary distinctiveness, evolutionary rate, body mass, longevity, litter or clutch size and annual litter or clutch size.

Before analyses, all the explanatory variables were standardized (mean value = 0, standard deviation = 1). The variance inflation factor (VIF) was used to test for collinearity. Variables with VIF values >5 were excluded when constructing multivariate models. The Akaike information criterion (AIC) values were used to assess the performance of each combination of variables. The support for each explanatory variable was assessed by aggregating its AIC weights across all models, with the combination of variables having the highest AIC weights being selected as the best-fitting model. In addition, owing to the collinearity between phylogenetic age and evolutionary uniqueness, we partitioned them into two groups for the multivariate SAR model analyses (electronic supplementary material, figure S2). Because the results of the two groups were similar, we only reported the results of the group with phylogenetic age in the main text (tables 1 and 2; electronic supplementary material, tables S1 and S2). To control for the impact of phylogenetic autocorrelation, we employed phylogenetic generalized linear mixed models (PGLMMs) for validation. The results from multivariate PGLMMs were similar to those from multivariate SAR models (electronic supplementary material, tables S3 and S4). In addition to the global analyses, we also analysed the temperate and tropical populations separately.

All analyses were carried out using R v. 4.3.0 [65]. The average logged rate of population changes ($\overline{\lambda_Y}$) was calculated with the help of R package mgcv [66] and stats [65]. Climate and land use data were extracted by R package ncdf4 [67] and raster [68]. R package ape [69] and picante [70] were used to extract phylogenetic age, evolutionary distinctiveness and diversification rate. R package spdep [71] was used to fit multiple SAR models.

3. Results

(a) Anthropogenic land use changes and population trends

Globally, bird population trends were significantly negatively correlated with land use changes from 1950 to 2000, whereas mammal population trends were not significantly related to land use changes (table 1; figure 2). In temperate regions, bird population trends were significantly negatively correlated with land use changes from 1950 to 2000, while mammal population trends were not significantly related to anthropogenic land use changes (table 1; figure 2). In tropical regions, neither bird nor mammal population trends were significantly related to land use changes (table 1; figure 2).

(b) Climate changes and population trends

Globally, bird population trends were significantly positively correlated with temperature changes from 1901 to 1950, and significantly negatively correlated with precipitation changes from 1950 to 2018. Mammal population trends were not significantly related to climate changes (table 1; figure 2). In temperate regions, bird population trends were significantly positively correlated with temperature changes from 1901 to 1950, and significantly negatively correlated with precipitation changes from 1950 to 2018 (table 1; figure 2). In tropical regions, neither bird nor mammal population trends were significantly related to climate changes (table 1; figure 2).

Table 1. Results of multivariate spatial error autoregressive (SAR) models for birds. The model sets included all possible combinations of explanatory variables, except for evolutionary distinctiveness (evolutionary distinctiveness and phylogenetic age are collinear variables). Standardized coefficients ($\mathrm{Coef}_{\mathrm{SAR}}$) of the variables in the model with the highest Akaike weight (w), and the Akaike weight (w) for each variable based on the full model sets are listed. The MAT/MAP change from 1901-1950 represents the rate of historical temperature/precipitation change, while the MAP change from 1950-2018 represents the rate of recent temperature/precipitation change. Values of w and r^2 of the best model are shown in bold. $^{*}p < 0.05$, $^{**}p < 0.01$.

	global		temperate		tropical	
	$\mathrm{Coef}_{\mathrm{SAR}}$	w	$\mathrm{Coef}_{\mathrm{SAR}}$	w	$\mathrm{Coef}_{\mathrm{SAR}}$	w
land use change 1900–1950		0.44	−0.05	0.52		0.41
land use change 1950–2000	−0.07*	0.67	−0.11**	0.95		0.40
MAT change 1901–1950	0.16**	0.98	0.13*	0.86	0.37	0.66
MAP change 1901–1950		0.32		0.27	−0.19	0.48
MAP change 1950–2018	−0.13**	1.00	−0.14**	1.00		0.32
phylogenetic age	0.07*	0.85	0.07**	0.95		0.33
diversification rate	0.05	0.53		0.50		0.45
longevity		0.46	0.05	0.49		0.30
r^2	**0.29**		**0.25**		**0.59**	
w	**0.02**		**0.02**		**0.01**	

Table 2. Results of multivariate spatial error autoregressive (SAR) models of mammals. The model sets included all possible combinations of explanatory variables, except for evolutionary distinctiveness (evolutionary distinctiveness and phylogenetic age are collinear variables). Standardized coefficients ($\mathrm{Coef}_{\mathrm{SAR}}$) of the variables in the model with the highest Akaike weight (w), and the Akaike weight (w) for each variable based on the full model sets are listed. The MAT change from 1950-2018 represents the rate of recent temperature change. Values of w and r^2 of the best model are shown in in bold. $^{*}p < 0.05$, $^{**}p < 0.01$.

	global		temperate		tropical	
	$\mathrm{Coef}_{\mathrm{SAR}}$	w	$\mathrm{Coef}_{\mathrm{SAR}}$	w	$\mathrm{Coef}_{\mathrm{SAR}}$	w
land use change 1900–1950		0.33		0.31	0.09	0.67
MAT change 1950–2018		0.27	−0.05	0.56		0.35
diversification rate		0.29		0.39	−0.11	0.44
longevity	0.10**	0.71	0.18*	0.71		0.33
litter or clutch size		0.60	−0.09	0.74	−0.18*	0.73
no. litters or clutches per year		0.32	0.11*	0.70		0.34
r^2	**0.10**		**0.08**		**0.13**	
w	**0.01**		**0.01**		**0.01**	

(c) Species' characteristics and population trends

Globally, bird population trends were significantly positively correlated with phylogenetic age, whereas mammal population trends were significantly positively correlated with longevity (table 1; figure 2). In temperate regions, bird population trends were significantly positively correlated with phylogenetic age, while mammal population trends were significantly positively correlated with longevity and number of litters or clutches per year (table 1; figure 2). In tropical regions, bird population trends were not significantly related to species traits, whereas mammal population trends were significantly negatively correlated with litter or clutch size (table 1; figure 2).

4. Discussion

(a) Anthropogenic land use changes and population trends

Habitat loss and fragmentation are two of the main drivers of biodiversity loss, and landscapes with higher disturbance generally have higher rates of population loss [10–13]. As expected, we found that land use changes from 1950 to 2000 were a significant anthropogenic factor for bird population declines in global and temperate regions. This is consistent with a previous study, which showed that habitat-constrained species, such as grassland birds, waterbirds and shorebirds, have experienced sharp decreases in numbers owing to land use changes from 1930 to 2019 [72]. Unexpectedly, land use change was not a significant factor in population declines in the tropical region. This may simply reflect the smaller number of studies from the

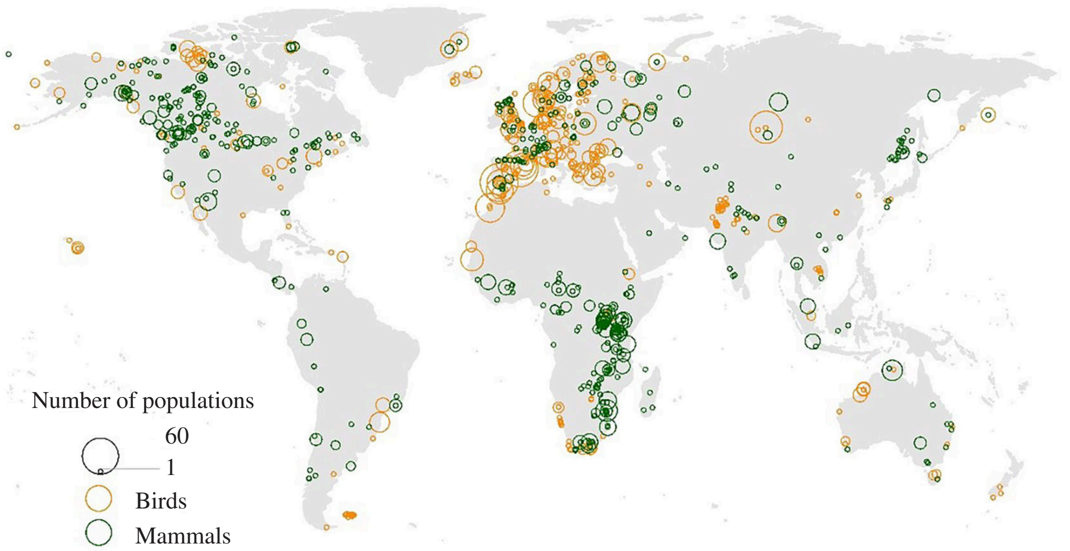

Figure 1. Distribution of the population time series used in this study. The orange and green circles represent bird and mammal populations, respectively. The size of circles indicates the number of populations at each site.

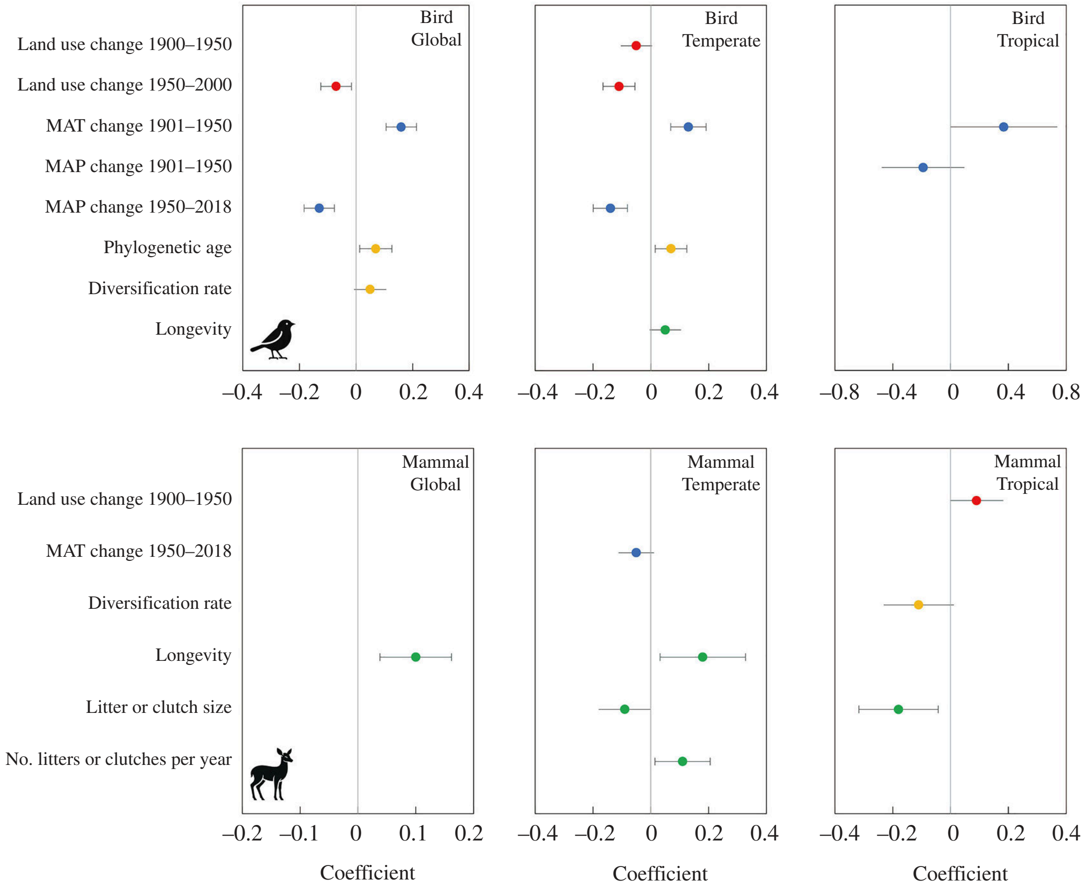

Figure 2. The coefficient distributions from spatial error autoregressive (SAR) models, showing the associations between various variables and the population trends of birds and mammals at the global scale and in tropical and temperate regions. The circles show the standardized coefficient values for each variable. Red circles represent land use changes, blue represent climate changes, yellow represent phylogenetic factors, and green represent functional traits. The solid lines at both sides of the circles indicate the 95% confidence interval of the normalization coefficient. If the 95% confidence interval does not overlap with the grey zero line, then the variable has a significant association with population abundance dynamics (p-value < 0.05).

tropics in our dataset (106 bird populations in the tropics compared with 979 in the temperate region). Also, most tropical data are for easily monitored generalists, which are expected to be less sensitive to land use change, while much of the temperate data is for threatened species.

Also unexpected was that land use change was not a significant factor in population changes for mammals at any scale. This non-significant relationship may be related to the geographical distribution and representativeness of the samples. About 71% of the mammal population data come from protected areas. Our results may primarily reflect the ecological conditions within these areas. It is also possible that land use change is not the main factor affecting mammal populations. Other human activities, such as hunting, logging and grazing, which were not included in the analysis, also impact mammal population numbers [73]. Future research should consider expanding the sample range, including more regions significantly affected by land use change and other human activities. This will allow a more comprehensive assessment of the impact of land use change and other human activities on mammal populations.

(b) Climate changes and population trends

Organisms respond to climate changes by adjusting their physiological and behavioural traits or altering their geographical ranges [74]. Responses to climate changes often exhibit time lags. This is evident in the changing distribution and climate niches of breeding birds in Europe and North America [75,76]. Unexpectedly, we found positive associations between temperature change from 1901 to 1950 and bird population trends at global scale and in temperate regions. This result is contrary to our initial hypothesis and opposite to the result of another study that also used population data from the Living Planet Database. That study found that rapid climate warming is a significant factor contributing to the declines in bird and mammal populations [21]. Our study included data from many more bird populations (1200 compared with 416), more species (321 compared with 292) and a longer study period (1950–2018 compared with 1950–2005). So our result should be more robust, but the reason for the change in sign of the impact is not obvious.

In contrast to the unexpected impact of temperature change, the negative effect of precipitation changes from 1950 to 2018 on bird populations at the global scale and in temperate regions was expected. In addition, climate change was not a significant factor for mammal population changes at any scale. This may be because bird populations are more affected by climate change compared with mammal populations [21]. Climate change can cause a mismatch between breeding seasons and resource availability peaks for birds, whereas mammals have more flexible breeding seasons [21,32,77].

(c) Species' characteristics and population trends

The positive associations between bird population trends and phylogenetic age at global scale and in temperate regions found in this study suggest that more ancient species would increase their abundance or population size. More ancient and phylogenetically distinctive species occupied marginal ecological niches earlier, giving them more time to evolve specialized forms or behaviours [78,79]. This has resulted in less competitive pressure in ecosystems, enabling them to maintain higher population abundances [78,79]. In addition, studies have found that species that are more ancient have been less threatened or endangered [80]. However, there is no significant relationship between mammal population trends and phylogenetic age at any scale. This may be because the phylogenetic age distribution of mammalian populations is right-skewed, with most species being relatively young (electronic supplementary material, figure S3). This may make it statistically difficult to reveal a significant relationship between phylogenetic age and population trends [80].

The global and temperate analysis of mammals showed that long-lived species have experienced population increases. Long-lived species are not only more resilient to environmental changes compared with short-lived species but also have higher individual survival rates, which contributes to maintaining and promoting population growth [44,45]. Additionally, we found that in temperate regions, the number of litters or clutches per year in mammals is significantly positively correlated with population trends. However, a previous study has found that species with fast life history strategies, owing to their rapid growth and reproduction rates, are better adapted to land use changes, resulting in positive population trends [9]. The different results may be due to two reasons. First, those authors used data from a shorter time scale (1992–2019). Second, the final dataset they used included only 1072 populations (including 273 bird species, 137 mammal species and 51 reptile species) [9]. Furthermore, we found that in tropical regions, smaller litter or clutch sizes are favourable for mammal population growth. The reason may be that the tropical mammal population data we used are mainly concentrated in East African protected areas, where conservation measures provide a buffer for mammal populations with smaller litter or clutch sizes in the face of environmental changes [21]. However, we did not find significant associations between bird population trends and longevity, litter or clutch size and litters or clutches per year at all scales. This may be because birds typically face higher environmental variability (such as seasonal migration and habitat changes), resulting in high variations in birds' life history traits. Consequently, the relationships between life history traits and bird population dynamics may be more complex [81,82].

(d) Limitations

Our study offers insights into the complex relationships between land use changes, climate changes, species characteristics and population trends of birds and mammals across different geographical regions using the Living Planet Database. However, we acknowledge several limitations that could influence the interpretation and broad applicability of our findings. First, the availability and quality of data vary significantly across regions, with data on bird populations in tropical regions being underrepresented in global databases. Owing to copyright issues or data sharing being restricted by other agreements or contracts, 18% of the data in the Living Planet Index is marked as confidential. This results in a smaller publicly available dataset and affects the transparency and reproducibility of the corresponding results [83]. Using multiple databases for mutual supplementation may effectively reduce the bias caused by regional data quality differences [8]. Second, using only land use change data derived from cropland and pasture in the HYDE v. 3.2 database does not account for the possible impact of other changes in land use on populations [58]. Other factors not included in our study, such as hunting and trapping, are major causes of declines in many bird and mammal populations. Since a significant portion of the variation in mammal and bird populations is unexplained by our current models, further research into these external factors is necessary to develop better conservation strategies. Finally, owing to the difficulty in obtaining long-term monitoring data on population abundance, most studies use interpolation analysis with data continuously monitored for over 5 years [8,9,21]. However, this approach may not accurately assess the dynamics of long-lived populations. Therefore, future studies on population abundance should include longer monitoring periods where data availability allows and consider incorporating remote sensing technology or genetic-based methods to obtain more comprehensive information on population dynamics.

5. Conclusions

This study emphasizes the important impacts of environmental changes and species characteristics on bird and mammal populations. At the global scale, historical temperature changes and recent precipitation changes are the variables most associated with bird population trends. Notably, there are differences between temperate regions and tropical regions, with more significant variables in temperate regions. In contrast, mammal populations are less affected by these external variables than birds. Mammal population trends are more closely associated with life history traits. Future conservation strategies should account for regional and taxonomic differences to better understand where vulnerabilities are and to better target conservation efforts.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. We have uploaded all the data used in this paper as electronic supplementary material [84].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. X.M.: data curation, formal analysis, methodology, writing—original draft, writing—review and editing; R.D.: data curation, formal analysis, methodology, visualization, writing—original draft, writing—review and editing; A.H.: writing—review and editing; R.T.C.: writing—review and editing; J.-C.S.: writing—review and editing; G.F.: conceptualization, funding acquisition, project administration, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed herein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Almond R, Grooten M, Juffe Bignoli D, Petersen T. 2022 *Living Planet report 2022 - building a nature-positive society*. Gland, Switzerland: WWF.
2. Ceballos G, Ehrlich PR, Dirzo R. 2017 Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl Acad. Sci. USA* **114**, E6089–E6096. (doi:10.1073/pnas.1704949114)
3. Ceballos G, García A, Ehrlich PR. 2010 The sixth extinction crisis: loss of animal populations and species. *J. Cosmol.* **8**, 31.
4. Newbold T, Scharlemann JP, Butchart SH, Şekercioğlu CH, Alkemade R, Booth H, Purves DW. 2013 Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proc. R. Soc. B* **280**, 20122131. (doi:10.1098/rspb.2012.2131)
5. Newbold T, Scharlemann JPW, Butchart SHM, Şekercioğlu ÇH, Joppa L, Alkemade R, Purves DW. 2014 Functional traits, land-use change and the structure of present and future bird communities in tropical forests. *Glob. Ecol. Biogeogr*. **23**, 1073–1084. (doi:10.1111/geb.12186)
6. Winfree R, Fox JW, Williams NM, Reilly JR, Cariveau DP. 2015 Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol. Lett*. **18**, 626–635. (doi:10.1111/ele.12424)
7. Manning P, Cutler GC. 2018 Ecosystem functioning is more strongly impaired by reducing dung beetle abundance than by reducing species richness. *Agric. Ecosyst. Environ*. **264**, 9–14. (doi:10.1016/j.agee.2018.05.002)
8. Williams JJ, Freeman R, Spooner F, Newbold T. 2022 Vertebrate population trends are influenced by interactions between land use, climatic position, habitat loss and climate change. *Glob. Chang. Biol*. **28**, 797–815. (doi:10.1111/gcb.15978)
9. Albaladejo-Robles G, Böhm M, Newbold T. 2023 Species life-history strategies affect population responses to temperature and land-cover changes. *Glob. Chang. Biol*. **29**, 97–109. (doi:10.1111/gcb.16454)
10. Millenium Ecosystems Assessment. 2005 *Ecosystems and human well-being: synthesis*. Washington, DC: Island Press.
11. Newbold T *et al*. 2015 Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45–50. (doi:10.1038/nature14324)
12. Powers RP, Jetz W. 2019 Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nat. Clim. Chang*. **9**, 323–329. (doi:10.1038/s41558-019-0406-z)
13. Jaureguiberry P *et al*. 2022 The direct drivers of recent global anthropogenic biodiversity loss. *Sci. Adv*. **8**, eabm9982. (doi:10.1126/sciadv.abm9982)
14. Northrup JM, Rivers JW, Yang Z, Betts MG. 2019 Synergistic effects of climate and land-use change influence broad-scale avian population declines. *Glob. Chang. Biol*. **25**, 1561–1575. (doi:10.1111/gcb.14571)
15. Newbold T *et al*. 2018 Widespread winners and narrow-ranged losers: land use homogenizes biodiversity in local assemblages worldwide. *PLoS Biol*. **16**, e2006841. (doi:10.1371/journal.pbio.2006841)

16. Daskalova GN, Myers-Smith IH, Bjorkman AD, Blowes SA, Supp SR, Magurran AE, Dornelas M. 2020 Landscape-scale forest loss as a catalyst of population and biodiversity change. *Science* **368**, 1341–1347. (doi:10.1126/science.aba1289)
17. Gregory RD *et al*. 2009 An indicator of the impact of climatic change on European bird populations. *PLoS One* **4**, e4678. (doi:10.1371/journal.pone.0004678)
18. Somero GN. 2010 The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine "winners" and "losers." *J. Exp. Biol*. **213**, 912–920. (doi:10.1242/jeb.037473)
19. Pearce-Higgins JW, Eglington SM, Martay B, Chamberlain DE. 2015 Drivers of climate change impacts on bird communities. *J. Anim. Ecol*. **84**, 943–954. (doi:10.1111/1365-2656.12364)
20. Pacifici M, Visconti P, Butchart SHM, Watson JEM, Cassola FM, Rondinini C. 2017 Species' traits influenced their response to recent climate change. *Nat. Clim. Chang*. **7**, 205–208. (doi:10.1038/nclimate3223)
21. Spooner FEB, Pearson RG, Freeman R. 2018 Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Glob. Chang. Biol*. **24**, 4521–4531. (doi:10.1111/gcb.14361)
22. Herrando S *et al*. 2019 Contrasting impacts of precipitation on Mediterranean birds and butterflies. *Scient. Rep*. **9**, 5680. (doi:10.1038/s41598-019-42171-4)
23. Carrera L, Pavia M, Varela S. 2022 Birds adapted to cold conditions show greater changes in range size related to past climatic oscillations than temperate birds. *Scient. Rep*. **12**, 10813. (doi:10.1038/s41598-022-14972-7)
24. Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011 Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026. (doi:10.1126/science.1206432)
25. Tellería JL, Fernandez-Lopez J, Fandos G. 2016 Effect of climate change on Mediterranean winter ranges of two migratory passerines. *PLoS One* **11**, e0146958. (doi:10.1371/journal.pone.0146958)
26. Pakanen VM, Ahonen E, Hohtola E, Rytkönen S. 2018 Northward expanding resident species benefit from warming winters through increased foraging rates and predator vigilance. *Oecologia* **188**, 991–999. (doi:10.1007/s00442-018-4271-7)
27. Gallant D, Lecomte N, Berteaux D. 2020 Disentangling the relative influences of global drivers of change in biodiversity: a study of the twentieth-century red fox expansion into the Canadian Arctic. *J. Anim. Ecol.* **89**, 565–576. (doi:10.1111/1365-2656.13090)
28. Stephens PA *et al*. 2016 Consistent response of bird populations to climate change on two continents. *Science* **352**, 84–87. (doi:10.1126/science.aac4858)
29. Sinervo B *et al*. 2010 Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**, 894–899. (doi:10.1126/science.1184695)
30. De-Lima AKS, de Oliveira CH, Pic-Taylor A, Klaczko J. 2022 Effects of incubation temperature on development, morphology, and thermal physiology of the emerging Neotropical lizard model organism *Tropidurus torquatus*. *Scient. Rep*. **12**, 17153. (doi:10.1038/s41598-022-21450-7)
31. Bradshaw WE, Holzapfel CM. 2010 Light, time, and the physiology of biotic response to rapid climate change in animals. *Annu. Rev. Physiol*. **72**, 147–166. (doi:10.1146/annurev-physiol-021909-135837)
32. Keogan K *et al*. 2018 Global phenological insensitivity to shifting ocean temperatures among seabirds. *Nat. Clim. Chang*. **8**, 313–318. (doi:10.1038/s41558-018-0115-z)
33. Allen AP, Brown JH, Gillooly JF. 2002 Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* **297**, 1545–1548. (doi:10.1126/science.1072380)
34. Meehan TD, Jetz W, Brown JH. 2004 Energetic determinants of abundance in winter landbird communities. *Ecol. Lett*. **7**, 532–537. (doi:10.1111/j.1461-0248.2004.00611.x)
35. Menéndez R, Megías AG, Hill JK, Braschler B, Willis SG, Collingham Y, Fox R, Roy DB, Thomas CD. 2006 Species richness changes lag behind climate change. *Proc. R. Soc. B* **273**, 1465–1470. (doi:10.1098/rspb.2006.3484)
36. Jackson ST, Sax DF. 2010 Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.* **25**, 153–160. (doi:10.1016/j.tree.2009.10.001)
37. Dullinger S *et al*. 2012 Extinction debt of high-mountain plants under twenty-first-century climate change. *Nat. Clim. Chang*. **2**, 619–622. (doi:10.1038/nclimate1514)
38. Gaget E, Devictor V, Frochot B, Desbrosses R, Eybert MC, Faivre B. 2021 Disentangling the latitudinal and altitudinal shifts in community composition induced by climate change: the case of riparian birds. *J. Biogeogr*. **48**, 526–536. (doi:10.1111/jbi.14016)
39. Morris WF *et al*. 2008 Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* **89**, 19–25. (doi:10.1890/07-0774.1)
40. Li ZY, Zhang H, Xu YJ, Wang SP. 2021 Composition of 'fast–slow' traits drives avian community stability over North America. *Funct. Ecol*. **35**, 2831–2840. (doi:10.1111/1365-2435.13909)
41. Ripple WJ, Wolf C, Newsome TM, Hoffmann M, Wirsing AJ, McCauley DJ. 2017 Extinction risk is most acute for the world's largest and smallest vertebrates. *Proc. Natl Acad. Sci. USA* **114**, 10678–10683. (doi:10.1073/pnas.1702078114)
42. Hilbers JP, Schipper AM, Hendriks AJ, Verones F, Pereira HM, Huijbregts MAJ. 2016 An allometric approach to quantify the extinction vulnerability of birds and mammals. *Ecology* **97**, 615–626. (doi:10.1890/14-2019.1)
43. Brook BW, Sodhi NS, Bradshaw CJA. 2008 Synergies among extinction drivers under global change. *Trends Ecol. Evol.* **23**, 453–460. (doi:10.1016/j.tree.2008.03.011)
44. Wright J, Bolstad GH, Araya-Ajoy YG, Dingemanse NJ. 2019 Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes. *Biol. Rev.* **94**, 230–247. (doi:10.1111/brv.12451)
45. Vinton AC, Gascoigne SJL, Sepil I, Salguero-Gómez R. 2022 Plasticity's role in adaptive evolution depends on environmental change components. *Trends Ecol. Evol.* **37**, 1067–1078. (doi:10.1016/j.tree.2022.08.008)
46. Capdevila P, Stott I, Cant J, Beger M, Rowlands G, Grace M, Salguero-Gómez R. 2022 Life history mediates the trade-offs among different components of demographic resilience. *Ecol. Lett*. **25**, 1566–1579. (doi:10.1111/ele.14004)
47. Collen B, Turvey ST, Waterman C, Meredith HMR, Kuhn TS, Baillie JEM, Isaac NJB. 2011 Investing in evolutionary history: implementing a phylogenetic approach for mammal conservation. *Phil. Trans. R. Soc. B* **366**, 2611–2622. (doi:10.1098/rstb.2011.0109)
48. Stein RW, Mull CG, Kuhn TS, Aschliman NC, Davidson LNK, Joy JB, Smith GJ, Dulvy NK, Mooers AO. 2018 Global priorities for conserving the evolutionary history of sharks, rays and chimaeras. *Nat. Ecol. Evol*. **2**, 288–298. (doi:10.1038/s41559-017-0448-4)
49. Colston TJ, Kulkarni P, Jetz W, Pyron RA. 2020 Phylogenetic and spatial distribution of evolutionary diversification, isolation, and threat in turtles and crocodilians (non-avian archosauromorphs). *BMC Evol. Biol*. **20**, 81. (doi:10.1186/s12862-020-01642-3)
50. Greenberg DA, Pyron RA, Johnson LGW, Upham NS, Jetz W, Mooers AØ. 2021 Evolutionary legacies in contemporary tetrapod imperilment. *Ecol. Lett*. **24**, 2464–2476. (doi:10.1111/ele.13868)
51. Meijaard E, Sheil D, Marshall AJ, Nasi R. 2008 Phylogenetic age is positively correlated with sensitivity to timber harvest in Bornean mammals. *Biotropica* **40**, 76–85. (doi:10.1111/j.1744-7429.2007.00340.x)

52. Redding DW, DeWolff CV, Mooers AØ. 2010 Evolutionary distinctiveness, threat status, and ecological oddity in primates. *Conserv. Biol*. **24**, 1052–1058. (doi:10.1111/j.1523-1739.2010.01532.x)
53. Castro-Insua A, Gómez-Rodríguez C, Wiens JJ, Baselga A. 2018 Climatic niche divergence drives patterns of diversification and richness among mammal families. *Scient. Rep*. **8**, 8781. (doi:10.1038/s41598-018-27068-y)
54. Upham NS, Esselstyn JA, Jetz W. 2019 Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biol*. **17**, e3000494. (doi:10.1371/journal.pbio.3000494)
55. Antão LH, Bates AE, Blowes SA, Waldock C, Supp SR, Magurran AE, Dornelas M, Schipper AM. 2020 Temperature-related biodiversity change across temperate marine and terrestrial systems. *Nat. Ecol. Evol*. **4**, 927–933. (doi:10.1038/s41559-020-1185-7)
56. Collen B, Loh J, Whitmee S, McRae L, Amin R, Baillie JEM. 2009 Monitoring change in vertebrate abundance: the Living Planet Index. *Conserv. Biol*. **23**, 317–327. (doi:10.1111/j.1523-1739.2008.01117.x)
57. Harris I, Osborn TJ, Jones P, Lister D. 2020 Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scient. Data* **7**, 109. (doi:10.1038/s41597-020-0453-3)
58. Klein Goldewijk K, Beusen A, Doelman J, Stehfest E. 2017 Anthropogenic land use estimates for the Holocene – HYDE 3.2. *Earth Syst. Scient. Data* **9**, 927–953. (doi:10.5194/essd-9-927-2017)
59. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012 The global diversity of birds in space and time. *Nature* **491**, 444–448. (doi:10.1038/nature11631)
60. Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A, Drummond AJ. 2014 BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Comput. Biol*. **10**, e1003537. (doi:10.1371/journal.pcbi.1003537)
61. Pittis AA, Gabaldón T. 2016 Late acquisition of mitochondria by a host with chimaeric prokaryotic ancestry. *Nature* **531**, 101–104. (doi:10.1038/nature16941)
62. Isaac NJB, Turvey ST, Collen B, Waterman C, Baillie JEM. 2007 Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS One* **2**, e296. (doi:10.1371/journal.pone.0000296)
63. Myhrvold NP, Baldridge E, Chan B, Sivam D, Freeman DL, Ernest SKM. 2015 An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology* **96**, 3109. (doi:10.1890/15-0846R.1)
64. Kuparinen A, Yeung E, Hutchings JA. 2023 Correlation between body size and longevity: new analysis and data covering six taxonomic classes of vertebrates. *Acta Oecol*. **119**, 103917. (doi:10.1016/j.actao.2023.103917)
65. R CoreTeam. 2021 R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org/.
66. Wood SN. 2011 Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. B Stat. Methodol.* **73**, 3–36. (doi:10.1111/j.1467-9868.2010.00749.x)
67. Pierce D. 2019 *ncdf4: interface to unidata netcdf (version 4 or earlier) format data files*. *R package version 1.17*. See https://CRAN. R-project. org/package= ncdf4.
68. Hijmans R *et al*. 2015 *Package 'raster.' R package*. See https://CRAN.R-project.org/package=raster.
69. Paradis E, Schliep K. 2019 Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526–528. (doi:10.1093/bioinformatics/bty633)
70. Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. 2010 Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464. (doi:10.1093/bioinformatics/btq166)
71. Bivand R *et al*. 2005 *Package 'spdep.' Comprehensive R Archive Network, version*. See https://CRAN.R-project.org/package=spdep.
72. Saunders SP *et al*. 2022 Unraveling a century of global change impacts on winter bird distributions in the eastern United States. *Glob. Chang. Biol*. **28**, 2221–2235. (doi:10.1111/gcb.16063)
73. Harfoot MBJ *et al*. 2021 Using the IUCN Red List to map threats to terrestrial vertebrates at global scale. *Nat. Ecol. Evol*. **5**, 1510–1519. (doi:10.1038/s41559-021-01542-9)
74. Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. 2012 Impacts of climate change on the future of biodiversity. *Ecol. Lett*. **15**, 365–377. (doi:10.1111/j.1461-0248.2011.01736.x)
75. Howard C *et al*. 2023 Local colonisations and extinctions of European birds are poorly explained by changes in climate suitability. *Nat. Commun*. **14**, 4304. (doi:10.1038/s41467-023-39093-1)
76. Huang Q *et al*. 2023 Modeled distribution shifts of North American birds over four decades based on suitable climate alone do not predict observed shifts. *Sci. Total Environ*. **857**, 159603. (doi:10.1016/j.scitotenv.2022.159603)
77. Boutin S, Lane JE. 2014 Climate change and mammals: evolutionary versus plastic responses. *Evol. Appl*. **7**, 29–41. (doi:10.1111/eva.12121)
78. Nosil P. 2002 Transition rates between specialization and generalization in phytophagous insects. *Evolution* **56**, 1701–1706. (doi:10.1111/j.0014-3820.2002.tb01482.x)
79. Nosil P, Mooers AØ. 2005 Testing hypotheses about ecological specialization using phylogenetic trees. *Evolution* **59**, 2256–2263. (doi:10.1111/j.0014-3820.2005.tb00933.x)
80. Verde Arregoitia LD, Blomberg SP, Fisher DO. 2013 Phylogenetic correlates of extinction risk in mammals: species in older lineages are not at greater risk. *Proc. R. Soc. B* **280**, 20131092. (doi:10.1098/rspb.2013.1092)
81. Sæther BE, Bakke Ø. 2000 Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**, 642–653. (doi:10.1890/0012-9658(2000)081[0642:ALHVAC]2.0.CO;2)
82. Stahl JT, Oli MK. 2006 Relative importance of avian life-history variables to population growth rate. *Ecol. Modell*. **198**, 23–39. (doi:10.1016/j.ecolmodel.2006.04.001)
83. Ledger SEH *et al*. 2023 Past, present, and future of the Living Planet Index. *npj Biodivers*. **2**, 12. (doi:10.1038/s44185-023-00017-3)
84. Ma X, Dong R, Hughes A, Corlett RT, Svenning JC, Feng G. 2024 Supplementary material from: Population trends are more strongly linked to environmental change and species traits in birds than mammals. Figshare. (doi:10.6084/m9.figshare.c.7461930)