

Rapid warming is associated with population decline among terrestrial birds and mammals globally

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Abstract

Animal populations have undergone substantial declines in recent decades. These declines have occurred alongside rapid, human-driven environmental change, including climate warming. An association between population declines and environmental change is well established, yet there has been relatively little analysis of the importance of the rates of climate warming and its interaction with conversion to anthropogenic land use in causing population declines. Here we present a global assessment of the impact of rapid climate warming and anthropogenic land use conversion on 987 populations of 481 species of terrestrial birds and mammals since 1950. We collated spatially referenced population trends of at least 5 years' duration from the Living Planet database and used mixed effects models to assess the association of these trends with observed rates of climate warming, rates of conversion to anthropogenic land use, body mass, and protected area coverage. We found that declines in population abundance for both birds and mammals are greater in areas where mean temperature has increased more rapidly, and that this effect is more pronounced for birds. However, we do not find a strong effect of conversion to anthropogenic land use, body mass, or protected area coverage. Our results identify a link between rapid warming and population declines, thus supporting the notion that rapid climate warming is a global threat to biodiversity.

KEYWORDS

biodiversity, climate change, climate warming, extinction risk, global change, land use change, macroecology, population declines

1 | INTRODUCTION

Global animal abundance has declined by 58% since 1970 (WWF, 2016). Key drivers of population declines include climate change and conversion of natural habitat to anthropogenic land uses, both of which have had major impacts on biological systems (Newbold et al., 2016; Rosenzweig et al., 2008) and are widely thought to be global threats to biodiversity (Millennium Ecosystem Assessment, 2005; Thomas et al., 2004). The response of animal populations to these rapid environmental changes has not been consistent: some

populations have experienced increasing abundance and expanding distributions; conversely, other populations have suffered shrinking abundances and distributions (Frishkoff et al., 2016; La Marca et al., 2005; Thomas, Franco, & Hill, 2006). Declines in animal populations result in an erosion of ecosystem function and loss of ecosystem services (Ehrlich & Daily, 1993; Parmesan & Yohe, 2003; Thomas et al., 2006; Winfree, Fox, Williams, Reilly, & Cariveau, 2015).

It is well established that species have responded to climate warming through altitudinal and latitudinal shifts in distribution

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(Parmesan & Yohe, 2003) and with the advancement of phenological events (Root, Price, Hall, & Schneider, 2003). However, the effect of climate warming on animal abundance trends has been less well explored and multispecies studies have thus far been limited to Europe and North America. Martay et al. (2017) found that climate could explain significant country-level population declines in moths and increases in winged aphids across Great Britain, but found no group-wide trends for butterflies, birds or mammals. By contrast, it has been observed that warm-adapted butterflies and beetles in central Europe and warm-adapted birds across Europe and North America have had higher population growth rates under climate warming than those which are cold-adapted (Bowler et al., 2015; Jiguet et al., 2010; Stephens et al., 2016). These trends may lead to a future divergence of population trends, with warm-adapted species increasing in abundance and cold-adapted species declining (Gregory et al., 2009). To our knowledge there has been no previous global multispecies assessment of the observed impacts of climate warming on population trends. Furthermore, aforementioned studies have aggregated climate to country or range level, and population data are often aggregated to species level, which does not allow for population level variation in responses to climate warming.

Previous studies have shown that phenological and latitudinal shifts are greatest in areas that have experienced most warming (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Rosenzweig et al., 2008). Natural variability ensures that many populations can accommodate and respond to various types of change; however, local extinction occurs if the rate of climate warming exceeds the maximum possible rate of adaptive response (the adaptive capacity). To date, there have been no large-scale analyses exploring the relationship between the rate of climate warming (as opposed to the magnitude of warming) and animal population trends. We hypothesized that locations which have undergone faster climate warming will be locations where the threat to biodiversity is greatest and which have experienced more rapid population declines.

Habitat loss and fragmentation are known to be the primary drivers of biodiversity loss (Millennium Ecosystem Assessment, 2005). Global studies have shown that the conversion of natural habitat to anthropogenic land uses leads to local declines in both species richness and abundance and that these declines are greater where conversion to anthropogenic land use has been greater (Newbold et al., 2015). We therefore hypothesized that in areas where conversion to anthropogenic land use has been most rapid, we will see greater population declines.

Threats to biodiversity rarely act independently and can often have exacerbating interactions. In particular, the interaction between anthropogenic land use conversion and climate warming has been described as a “deadly anthropogenic cocktail” (Travis, 2003) because habitat loss reduces the ability of species to adapt to climate change (for instance by inhibiting range shifts; Brook, Sodhi, & Bradshaw, 2008; Mantyka-Pringle, Martin, & Rhodes, 2012; Oliver & Morecroft, 2014). Little is known about how the interaction between climate warming and anthropogenic land use conversion varies across habitats or species (Brook et al., 2008; Eglington & Pearce-

Higgins, 2012; Oliver & Morecroft, 2014; Root et al., 2003). Thus, this interaction remains a source of uncertainty when projecting future biodiversity trends (Sala, 2000). We therefore also hypothesized that there is an interaction between anthropogenic land use conversion and climate warming, such that the greatest population declines will occur where there has been both rapid conversion to anthropogenic land use and climate warming.

We note that there are many other factors which may impact population trends, not least the positive impact of conservation effort (Young et al., 2014) or the influence of species intrinsic traits (Lee & Jetz, 2010). Conservation efforts are often implemented through the creation and management of protected areas; thus, we hypothesized that population trends outside of protected areas will be more likely to be declining than those within them. Additionally, to account for the effect of species traits we explore the relationship between population growth rates and body mass, which is a correlate of many species traits (Brook et al., 2008; Hilbers et al., 2016). Recent research has shown there is a significant relationship between vertebrate body mass and extinction risk, such that heavier species of birds and mammals are likely to be more at risk of extinction (Ripple et al., 2017). We therefore hypothesized that larger bodied birds and mammals are more likely to have declining populations.

We present a global study in which we spatially and temporally link observed changes in abundance for 987 populations of 481 species of birds and mammals (from 1950 to 2005) to changes in climate and land use. The combined historical, spatial and taxonomic coverage of the study allows the drawing out of generalizable trends on the impacts of recent anthropogenic environmental change on observed animal population trends.

2 | MATERIALS AND METHODS

2.1 | Population time series data

We obtained observed population trends from the Living Planet database (http://www.livingplanetindex.org/data_portal), which contains time series of annual population estimates for over 18,000 vertebrate populations observed during the period 1950–2015. The time series are collated from the scientific literature, online databases and gray literature (Collen et al., 2009; McRae, Deinet, & Freeman, 2017). To be included in the database there must be at least 2 years of population estimates and survey methods must be comparable for each year the population is estimated. Detailed criteria for inclusion in the database are outlined in Loh et al. (2005).

For each time series, the population count data were logged (base 10) so that it was possible to compare changes in population trends irrespective of their size (prior to this, zeros were replaced with 1% of the mean population count of the time series so that it was possible to log these values, following Collen et al., 2009). If the number of population counts within each time series was sufficient ($N > 6$) the time series was fit with a Generalized Additive Model (GAM). GAMs are more flexible than linear models and therefore

more appropriate for fitting to population trends which can often be nonlinear (Collen et al., 2009). However, GAMs could not be fit reliably to time series where $N < 6$ data points, so for these time series we fit a linear regression. The smoothing parameter of each GAM was set to $N/2$, because this was found to be a suitable value for fitting the data well without overfitting to noise (Collen et al., 2009). The fit of each linear regression or GAM to the population trends was assessed using R^2 .

For each time series, we calculated the average logged rate of population change ($\bar{\lambda}_Y$), or average lambda:

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

$$\bar{\lambda}_Y = \frac{1}{Y} \sum_0^Y \lambda_y \quad (2)$$

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.

We then filtered the data to only include populations that met the following five criteria: (a) the location is known (many of the population trends in the Living Planet database are nationally aggregated so cannot be spatially linked to environmental data); (b) environmental data and body mass data were available; (c) time series span 5 or more years (because longer time series will better reflect environmental changes); (d) time series had $R^2 \geq 0.5$ when fit to the GAM or linear model (to ensure interpolated population estimates were reasonable); and (e) the population was recorded as being either inside or outside a protected area (any population recorded as both inside and outside a protected area was omitted).

After the populations were filtered based on these criteria, there were 987 remaining populations at 441 unique study sites (Figure 1). These populations were made up of 416 (42.1%) bird populations (292 species and 148 locations) and 571 (57.9%) mammal

populations (189 species and 303 locations). This remaining subset had a mean time series length of 15.6 (± 9.2) years and population estimates for 55.1% of the years within each time series. Values for missing values were estimated using either log-linear interpolation or imputed from the GAMs.

2.2 | Climate data

Global mean temperature data were gathered from the CRU TS v. 3.23 gridded time series (Harris, Jones, Osborn, & Lister, 2014; Figure 1), which provides monthly observations of land surface mean temperature at a spatial resolution of 0.5° . Monthly mean temperatures for the years 1950–2005 were extracted for the location of each observed population time series. The extracted temperatures were filtered to include only the years over which population estimates were available, and an average value was calculated for each year. A linear regression was then fit to those averages, the slope of which gives the annual rate of climate warming (RCW) over the period of observed population estimates.

2.3 | Land use data

Global land use data were gathered from the HYDE database (Klein Goldewijk, Beusen, Van Drecht, & De Vos, 2011), which provides decadal (1940–2000 and 2005) grid cell coverage of cropland and pasture at a spatial resolution of 0.083° . The percentage cover of cropland and pasture were summed to calculate percentage cover of anthropogenic land use in each cell. For each population time series, land use values were extracted for the years covered by the time series and averaged for a $0.25^\circ \times 0.25^\circ$ grid around the cell containing each population (Figure 2). This was done to encapsulate landscape level change around each population. The decadal values of

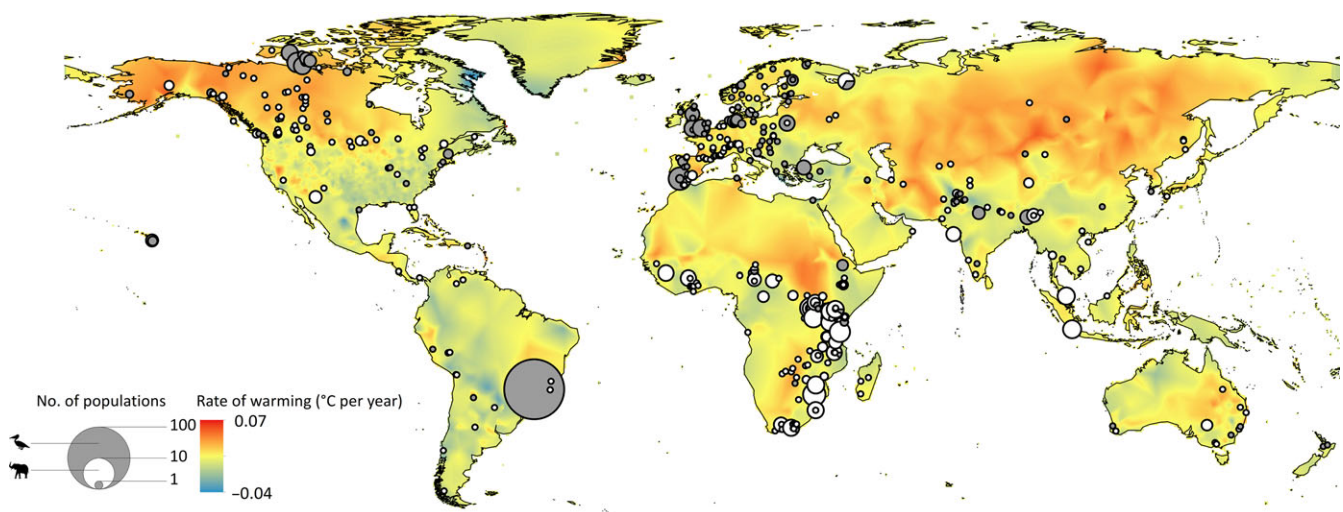


FIGURE 1 The points show the distribution and density of population time series used in the analysis. The black and white points signify bird and mammal populations, respectively, where both taxonomic groups are present the numbers of each are proportionally represented with a pie chart. 77.4% of the locations have one population. The base layer of the map shows the rate of temperature change, in degrees per year, between 1950 and 2005, based on analysis of the CRU TS v. 3.23 gridded time series dataset (Harris et al., 2014)

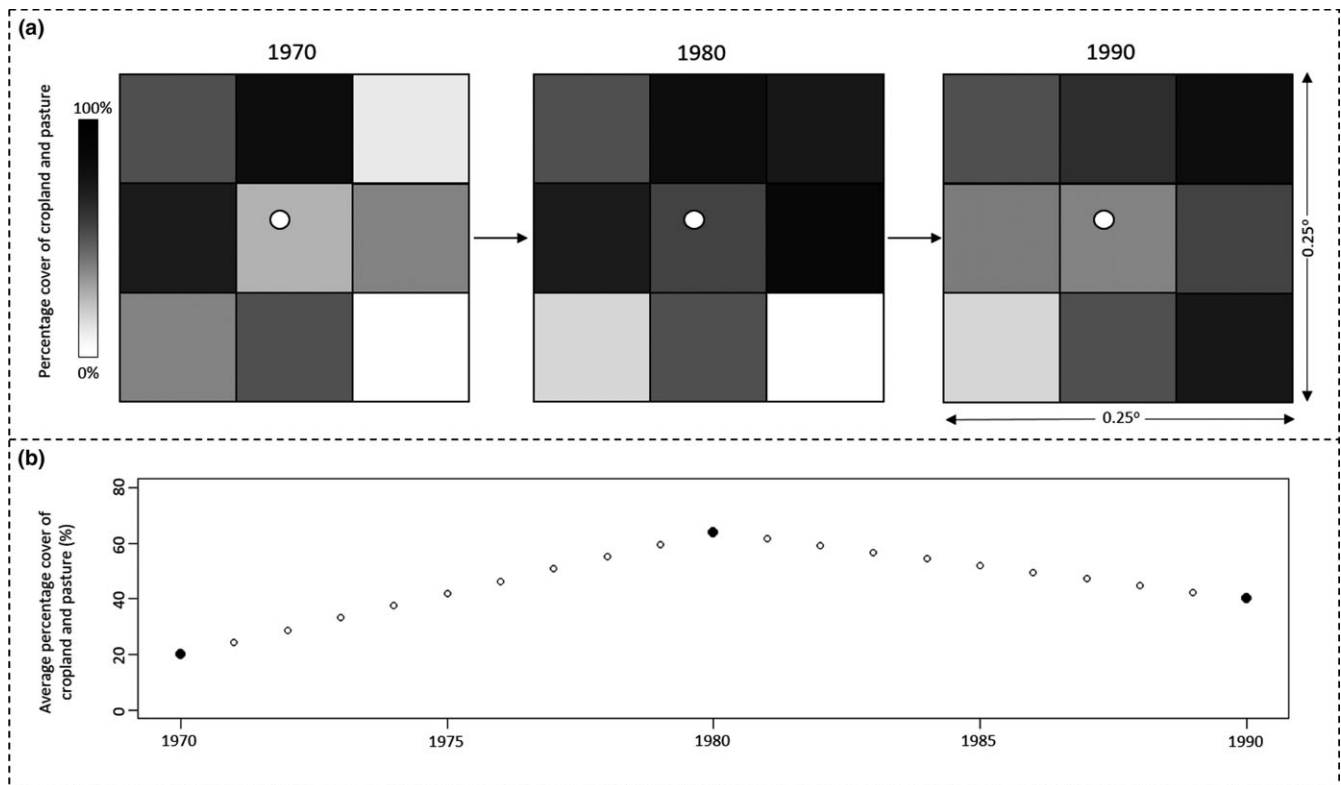


FIGURE 2 Illustration of how the rate of conversion to anthropogenic land use was calculated. (a) Example land use cover data for a population time series (1970–1990), where the white circle depicts the location of the population. Each grid of nine cells represents a decadal section of the HYDE data, which was cropped to the $0.25^\circ \times 0.25^\circ$ grid surrounding each population. (b) The average value of cropland and pasture percentage cover for each decadal grid (black circles) and the linearly interpolated annual values (hollow circles). For each population, we calculated the average annual change in percentage cover of cropland and pasture over the years for which we have population trend data (for this example population the value would be 1%)

anthropogenic land use were linearly interpolated to annual values and from these values the average annual rate of conversion to anthropogenic land use (RCA) was calculated for each population time series, where positive values mean an increase in cropland or pasture cover.

2.4 | Body mass

Adult body mass data for birds and mammals were extracted from the amniote life-history database (Myhrvold, Baldrige, Chan, Freeman, & Ernest, 2015). The body mass values were initially in grams and were logged (base 10) to normalize them. The values were then joined by species name to the corresponding Living Planet population time series. These body mass (BM) data were included as fixed effects in the candidate models.

2.5 | Protected areas

To account for the effect of protected areas on animal population trends we included protected area (PA) coverage as a binary fixed effect in the models. This information is available in the Living Planet Database.

2.6 | Linear mixed effects models

We aimed to test the extent to which bird and mammal population trends could be explained by rates of climate warming and conversion to anthropogenic land use. However, it is likely that there will be important species- and site-specific effects that could mask the impacts of climate warming and conversion to anthropogenic land use. To account for this, we used linear mixed effects models which allow us to understand the magnitude and direction of the effect size of explanatory variables on the response variable. The inclusion of random effects allows for a varying intercept for every grouping factor, here “species” and “site”, thus allowing for responses that are specific for species and site. Nineteen competing linear mixed effects models were constructed for the 987 populations, with the average logged rate of population change ($\bar{\lambda}_Y$) as the response variable and RCW, RCA, an interaction term between RCW and RCA, PA and BM as explanatory variables (Table 1). Species and study site were included as random effects in each of the models (Table 1). To facilitate comparison of effect size and the relative importance of each variable, the continuous fixed effects were scaled and centered by subtracting the mean and dividing by the standard deviation (Bates, Maechler, Bolker, & Walker, 2015).

Where there was no clear best performing model from the selection of competing models, the top models (where the cumulative sum of the AIC weights were ≤ 0.95) were averaged and the coefficients were taken from this averaged model (Burnham & Anderson, 2002; Daskin & Pringle, 2018). The modeling process was carried out separately for birds and mammals because the life-history characteristics of these two taxonomic groups differ enough for us to expect that they will have different responses to environmental change.

All analyses were carried out using the statistical software R (R Core Team, 2015). The `plyr` (Wickham, 2011), `taRifx` (Friedman, 2014), `mgcv` (Wood, 2011), and `zoo` (Zeileis & Grothendieck, 2005) packages were used to format the population trend data. The `GISOperations` (Newbold, 2016), `raster` (Hijmans, 2016), `doParallel` (Microsoft Corporation & Weston 2015), and `reshape2` (Wickham, 2007) packages were used to format and extract the environmental data. The linear mixed effects modeling was undertaken using the `lme4` (Bates et al., 2015) and `MuMIn` (Barton, 2016) packages.

3 | RESULTS

The mixed effects models reveal a strong association between rapidly warming climates and declines in populations for both birds and mammals (Figure 3). This association is more than twice as strong in birds than in mammals.

In our analysis of the impact of RCA and RCW on bird and mammal populations, we find (particularly in mammals) a variety of potential models with no clear “best” model. We therefore took a model averaging approach, combining all models within a 95% confidence set (Burnham & Anderson, 2002; Daskin & Pringle, 2018). We feel that this is a more conservative approach and, given the variability in potential effects within our analysis, more appropriate here. We have also explored using a $\Delta AIC < 6$, which is also recommended in the literature (Burnham & Anderson, 2002), and the difference in our results is negligible (e.g., difference in all coefficients $< 6.5\%$ see Supporting Information Appendix S1).

The top-performing models (based on ≤ 0.95 sum of Akaike weights) can be found in Table 2, with the full table of results in

Supporting Information Table S1 (Supporting Information Appendix S2). All the explanatory variables feature within these top models, suggesting that each of these variables contribute to explaining the variation in observed population trends.

In both the bird and mammal sets of competing models, we found that all the models containing RCW were within the top performing models, comprised of those where the cumulative sum of the Akaike weights was ≤ 0.95 . This suggests that these models are all useful and that RCW is the most important variable for explaining variation in both bird and mammal population trends.

Within the bird results, there are two models where $\Delta AIC < 2$ (highlighted in Table 2). The top performing model, in terms of AIC, is made up of RCW and PA, followed by the model with only RCW. The top performing model explains a large amount of the variation in avian population trends: 8.2% is explained with the fixed effects (marginal R^2) and 78.6% is explained by the fixed and random effects (conditional R^2). This highlights the clear importance of these two variables in explaining bird population trends, which is also reflected in their relatively large effect sizes. We find that populations within protected areas tend to have less negative growth rates than populations outside of protected areas.

Within the mammal results there are six models where $\Delta AIC < 2$, between them containing each of the explanatory variables. This suggests that there are several quite different models that have a similar ability to explain variation in mammal population trends. The results for mammal populations are more complex than for bird populations; however, RCW is clearly an important variable, as evidenced by its presence in each of the six best models, its high relative variable importance (RVI) score of 0.95, and its large effect size. We found that the interaction term (RCW:RCA) was also an important variable in explaining population trends. This means that mammal populations that have experienced both high RCW and RCA tend to have more negative population growth rates. We also find that although the confidence intervals overlap zero larger bodied mammals tend to have less negative population growth rates. The highest ranked model within the mammal data, in terms of AIC, was the model which contained, RCA, RCW, RCW:RCA, and body mass. The fixed effects of this model explain 2.8% (marginal R^2) of

TABLE 1 Parameters used in linear mixed effects models

Parameter	Description	Type of effect
Species name	Species binomial, included to account for species specific responses	Random intercept
Study site	Unique ID based on the coordinates of populations from Living Planet database, included to account for site-specific effects	Random intercept
Rate of climate warming (RCW)	The rate of change in mean temperature per year, over the length of the population time series	Fixed
Rate of conversion to anthropogenic land use (RCA)	The rate of change in percentage cover of cropland and pasture per year, over the length of the time series	Fixed
Body mass (BM)	Logged (base 10) body mass (g) of birds and mammals	Fixed
Inside protected area (PA)	A binary variable recording whether each population is inside or outside a protected area	Fixed

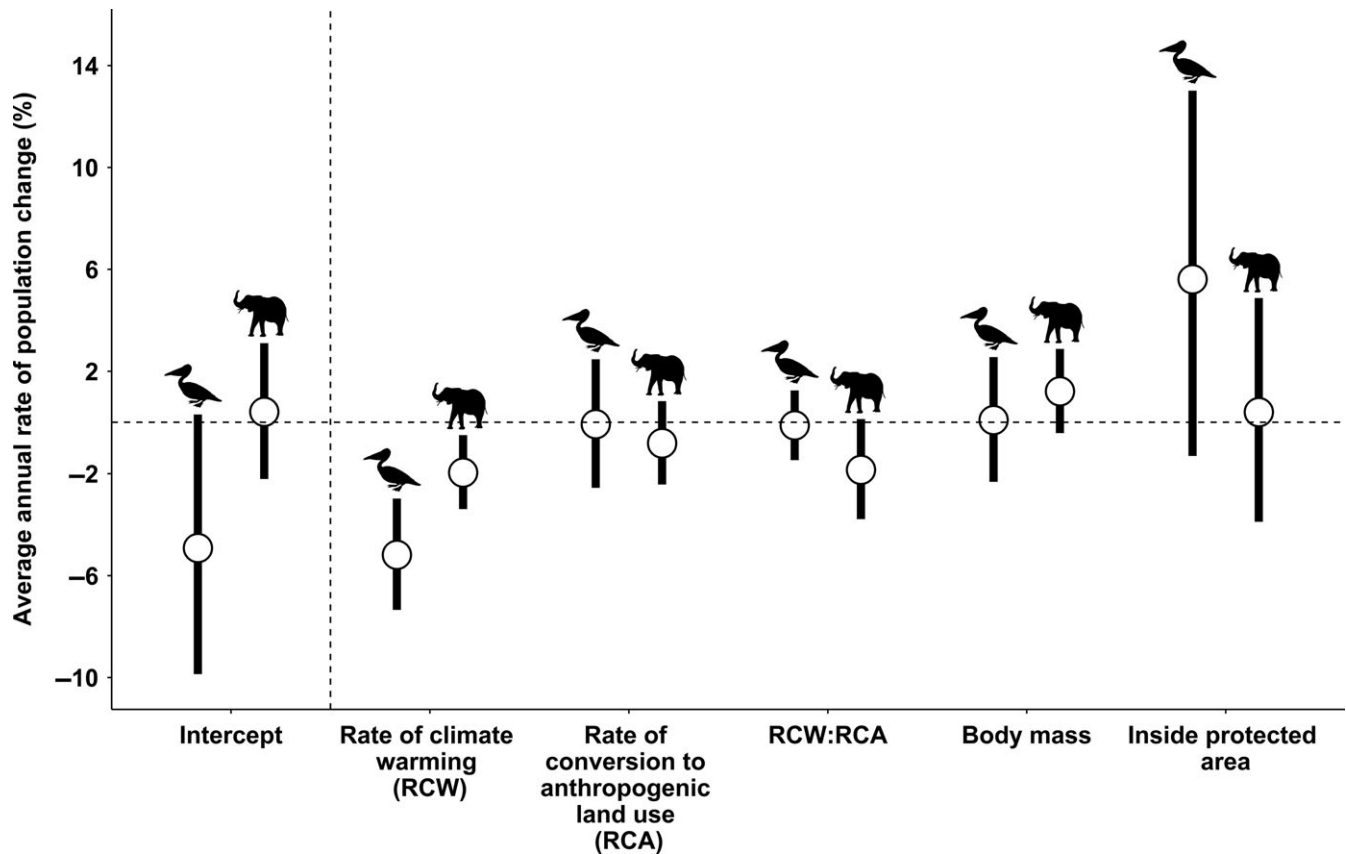


FIGURE 3 The distribution of the coefficients of the average models for bird and mammal populations. Circles show the estimated coefficient values for each variable and solid lines show the 2.5%–97.5% confidence intervals. As the data were scaled and centered prior to modeling the intercept shows the distribution of modeled annual population growth rates outside of protected areas and with mean values for RCA, RCW, and body mass (as the center of these values, when scaled, is now zero). Another consequence of scaling and centering the data is that the coefficients show the change in annual population growth rate given a one standard deviation increase in each explanatory variable. For example, for bird populations, an increase in the rate of mean temperature change of 0.07°C per year would lead to an average annual population decline of 5.09%. Confidence intervals that do not overlap with zero reveal a signal of either a positive or negative effect of a variable. Confidence intervals that overlap with zero show that within the averaged model an increase in a given variable has a mixture of both positive and negative effect sizes on the rate of population change across different populations

the variation in mammal population trends and 44.0% is explained with both the fixed and random effects (conditional R^2).

If we relax the criterion that R^2 for the linear regressions or GAMs must be >0.5 for a population to be included in the study (see Section 2), then the number of populations included in the analysis increases by 87% (total of 883 bird populations and 966 mammal populations) and the results of the mixed effects models remain similar (Supporting Information Appendix S4). This suggests our findings are not only limited to the subset of the populations used in the primary analysis but are also more broadly applicable across observed bird and mammal population trends. We also explored the effect of the heterogeneous distribution of population trends (for details see Supporting Information Appendix S5).

There is less of a clear correlation between population trend and either body mass or RCA. The 95% confidence intervals of the coefficients for these variables overlap zero, meaning that across all the populations the effects of body mass and RCA can be both positive and negative. However, we can use these results to draw out trends

in the data as they reflect the spread of the coefficients. For example, most mammal population trends tend to increase with body mass, whereas the bird population trends are more evenly distributed around zero (Figure 3).

4 | DISCUSSION

Our results reveal a strong association between rapid climate warming and declines of bird and mammal populations globally, showing that population declines have been greatest in areas that have experienced most rapid warming. The averaged model suggests that an increase in the rate of climate warming by one standard deviation (birds = 0.072°C per year, mammals = 0.079°C per year) leads to more severe annual average population declines of 5.1% for birds and 2.0% for mammals (Figure 3). Although these rates are higher than the projected rates of warming under more pessimistic future scenarios (e.g., RCP 8.5, Riahi et al., 2011) we note that these projections are global averages and that within these projections there

TABLE 2 Models included in the average model for explaining the growth rate of bird and mammal populations. The selection of models was based on a ≤ 0.95 cumulative sum of Akaike weights. The models are ranked in order of performance based on AIC, with higher ranking models listed toward the top of each table. Models within $\Delta AIC < 2$ of the highest ranked model are highlighted with bold text. A null model is included for comparison

Model	ΔAIC	Akaike Weight	Marg. R^2	Cond. R^2	Intercept	Rate of climate warming (RCW)	Rate of conversion to anthropogenic land use (RCA)	RCW/RCA	Body mass	Inside protected area
(A) Results from bird population trends										
RCW + PA	0.00	0.27	0.08	0.79	-6.12 (± 2.63)	-5.09 (± 1.17)				5.60 (± 3.50)
RCW	0.42	0.22	0.06	0.79	-3.38 (± 1.88)	-5.29 (± 1.17)				
RCW + BM + PA	2.06	0.10	0.08	0.79	-6.18 (± 2.69)	-5.10 (± 1.16)			0.12 (± 1.24)	5.62 (± 3.51)
RCA + RCW + PA	2.06	0.10	0.08	0.79	-6.13 (± 2.63)	-5.08 (± 1.17)	-0.11 (± 1.28)			5.62 (± 3.50)
RCW + BM	2.48	0.08	0.06	0.79	-3.40 (± 1.94)	-5.30 (± 1.17)			0.04 (± 1.25)	
RCA + RCW	2.48	0.08	0.06	0.79	-3.39 (± 1.88)	-5.29 (± 1.17)	-0.02 (± 1.29)			
RCW*RCA + PA	4.12	0.04	0.08	0.79	-6.12 (± 2.63)	-5.13 (± 1.22)	-0.11 (± 1.28)	-0.11 (± 0.69)		5.60 (± 3.51)
RCA + RCW + BM + PA	4.13	0.04	0.08	0.79	-6.19 (± 2.69)	-5.08 (± 1.17)	-0.12 (± 1.28)		0.13 (± 1.25)	5.64 (± 3.51)
RCA*RCW	4.51	0.03	0.06	0.79	-3.38 (± 1.88)	-5.35 (± 1.22)	-0.02 (± 1.29)	-0.14 (± 0.70)		
Null Model	22.48	<0.01	0.00	0.59	-1.23 (± 1.88)					
				RVI		1.00	0.33	0.09	0.26	0.55
(B) Results from mammal population trends										
RCA*RCW + BM	0.00	0.17	0.03	0.44	0.68 (± 0.94)	-2.20 (± 0.73)	-0.75 (± 0.82)	-1.82 (± 1.02)	1.24 (± 0.82)	
RCA*RCW	0.12	0.16	0.02	0.45	0.38 (± 0.95)	-2.22 (± 0.73)	-0.55 (± 0.81)	-1.88 (± 1.02)		
RCW	1.05	0.10	0.01	0.42	0.38 (± 0.93)	-1.72 (± 0.68)				
RCA + RCW + BM	1.18	0.09	0.02	0.42	0.56 (± 0.93)	-1.71 (± 0.68)	-1.17 (± 0.78)		1.28 (± 0.81)	
RCW + BM	1.41	0.08	0.02	0.42	0.64 (± 0.93)	-1.71 (± 0.68)			1.06 (± 0.80)	
RCA + RCW	1.50	0.08	0.02	0.43	0.26 (± 0.93)	-1.73 (± 0.78)	-0.97 (± 0.68)			
RCA*RCW + PA	1.97	0.06	0.02	0.45	-0.36 (± 1.91)	-2.24 (± 0.73)	-0.58 (± 0.82)	-1.86 (± 1.02)		0.95 (± 2.10)
RCA*RCW + BM + PA	2.06	0.06	0.03	0.44	0.82 (± 2.08)	-2.20 (± 0.73)	-0.74 (± 0.82)	-1.83 (± 1.02)	1.27 (± 0.88)	-0.17 (± 2.25)
RCW + PA	2.93	0.04	0.01	0.42	-0.27 (± 1.88)	-1.74 (± 0.68)				0.40 (± 2.08)
RCA + RCW + BM + PA	3.24	0.03	0.02	0.42	0.62 (± 2.06)	-1.71 (± 0.68)	-1.17 (± 0.79)		1.29 (± 0.87)	-0.07 (± 2.25)
RCA + RCW + PA	3.28	0.03	0.02	0.45	-0.59 (± 1.90)	-1.75 (± 0.68)	-1.01 (± 0.78)			1.09 (± 2.09)
RCW + BM + PA	3.45	0.03	0.02	0.42	0.80 (± 2.07)	-1.70 (± 0.68)			1.09 (± 0.89)	-0.19 (± 2.25)
Null Model	3.69	0.03	0.00	0.39	-0.16 (± 0.92)					
RCA + PA	7.81	<0.01	<0.01	0.41	-0.23 (± 1.90)		-0.98 (± 0.78)			0.69 (± 2.09)
				RVI		0.95	0.72	0.45	0.50	0.27

Notes. The coefficient values have been transformed into percentage population change. According to the top ranked model for birds, an increase in RCW to rates expected under climate scenario RCP 8.5 (5–6°C, 2006–2100) would lead to an annual population decline of 3.85%–4.65% in bird populations and 1.46%–1.76% for mammal populations (for details see Supporting Information Appendix S3). RVI (relative variable importance) is the sum of Akaike weights over all models including the explanatory variable. *p* Values show the results of an ANOVA comparing each model to the null model, and therefore give the probability that for a given model it is purely chance that it explains more of the variation in population trends than the null model. RCW: annual rate of climate warming; RCA: annual rate of conversion to anthropogenic land use; BM: body mass; PA: population inside a protected area.

will be regions, such as the Arctic (AMAP, 2017), which are likely to experience the higher rates of warming found within these models. Under this scenario (RCP 8.5) we would expect to see a 3.85%–4.65% annual population decline in bird populations and 1.46%–1.76% annual population decline in mammal populations (for details see Supporting Information Appendix S3). If the rate of climate warming continues to increase then we can expect greater bird and mammal population declines, these losses will be greatest at locations which experience most rapid climate warming (Supporting Information Figure S3). These findings echo aspects of previous global studies which suggest that future climate change will lead to large range contractions and increased species extinction risk (Jetz, Wilcove, & Dobson, 2007; Thomas et al., 2004). We found the impact of rapid climate warming to be more pronounced for bird populations than mammal populations (Figure 3). This may be because climate change can lead to the desynchronization of bird breeding season and the peak resource availability (Keogan et al., 2018; Stevenson & Bryant, 2000; Visser, Both, & Lambrechts, 2004), whereas the seasonality of breeding in mammals is more flexible (Boutin & Lane, 2014). We note there are geographical differences in the representation of birds and mammals (Figure 1). Within the dataset there are populations of both classes in all continents except Antarctica; however, mammal populations dominate in Africa (59% of populations, 43% of sites) and bird populations in Europe (26% of populations, 45% of sites). This may contribute to the differences we see between the two groups in their response to RCW. It is also important to recognize that there is spatial bias in the dataset, with relatively few sites in tropical forest habitat, particularly in South America and Southeast Asia. The RCW in tropical forests is relatively low (Corlett, 2011); however, species thermal niches tend to be narrower in the tropics meaning that the magnitude of their response to climate warming may be greater (Freeman & Class Freeman, 2014). We do not expect that the addition of sites from these regions would substantially change our conclusions, but further data will be required to test this.

The interaction between RCA and RCW was an important variable in explaining mammal population trends, where it had a similar effect size to RCW (Table 2B). This suggests that mammal populations are likely to have suffered greater declines in areas where there has been both climate warming and rapid conversion to anthropogenic land use. We do not find an effect of the interaction between RCA and RCW for bird populations, this may be because the interaction is complex and context specific (Kampichler, van Turnhout, Devictor, & van der Jeugd, 2012); for example, logging and increased temperatures can lead to a decrease in transpiration and less rainfall (Bagley, Desai, Harding, Snyder, & Foley, 2014), which may be devastating for many populations due to the drying of fuels and increased chance of fire and, or drought (Malhi et al., 2008). However, conversion to agriculture and warmer breeding season temperatures may be beneficial to populations of warm-adapted generalist species (Karp et al., 2018; Pearce-Higgins, Eglington, Martay, & Chamberlain, 2015). Additionally, it may be that historical land use change, which would not be captured by RCA, has altered the

landscape so profoundly that it inhibits future movement of species thus restricting their ability to adapt to climate change (Benning, LaPointe, Atkinson, & Vitousek, 2002).

We did not find RCA to be an important variable when acting in isolation for either birds or mammals. The lack of a clear effect of RCA on bird populations may be because a large proportion (54.8%) are within protected areas and we find that bird populations within protected areas tend to have higher population growth rates than those outside. Within our dataset, 60.3% of bird populations are made up of generalist species (here defined as having suitable habitat in more than one IUCN Level 1 habitat class), which may be more resilient to changing landscapes than specialist species. Additionally, conversion to agriculture does not uniformly disadvantage all bird species; for example, dry-adapted tropical species may have higher abundance in agricultural landscapes (Karp et al., 2018). However, we note that the “winners” of conversion to agriculture tend to be in the minority (McKinney & Lockwood, 1999). As previously mentioned, there are comparatively few population trends from tropical forests. These areas are rich in biodiversity but also heavily threatened by conversion to anthropogenic land use (Wright, 2005). It may be that we would detect a larger effect size for RCA if there were more population trend data from tropical forests.

We do not find PA to be an important predictor for mammal population growth rates; however, we note that 84.6% of the mammal populations are from inside protected areas, making it difficult to capture the effect of protected areas. We also note that other studies have shown the evidence of protected areas successfully conserving species populations is thus far inconclusive (Geldmann et al., 2013). Additionally, the effects of converting to anthropogenic land use are more likely to be detected at fine spatial resolutions (Heikkinen, Luoto, Virkkala, Pearson, & Körber, 2007; Pearson & Dawson, 2003), yet here we used relatively coarse resolution land use data. The coarse resolution of our data may be why we were unable to identify a clear effect of increasing anthropogenic land use on population trends at a global scale, despite it being a well-known driver of biodiversity loss (Millennium Ecosystem Assessment, 2005). The global effect of increased anthropogenic land use on populations has been identified in other global studies, such as the PREDICTS project (Newbold et al., 2015), where finer resolution measures of local land use change were available.

Body mass was not an important predictor of population growth rates for bird populations. This may be because while greater extinction risk is positively linked with increased body mass (Ripple et al., 2017), population declines, particularly of common species may not be captured by extinction risk criteria (Inger et al., 2015). Within mammal populations we found that smaller bodied species were more likely to have declining populations than larger bodied species, although the confidence intervals overlap with zero, so we must be cautious with the interpretation of this result. However, we note that when a less restricted set of population trends are included (see Supporting Information Appendix S4), the confidence intervals around this result are tighter and no longer overlap with zero, although the effect size is not large. This finding goes against our

hypothesis that larger bodied mammals would be more likely to have declining population trends and is contrary to the finding that larger mammals have higher extinction risk (Ripple et al., 2017). This may be because our mammal data are dominated by populations within east African protected areas, where larger mammals may receive greater attention and conservation effort which could mean their populations are buffered (Barnes et al., 2016). We also explored the inclusion of other species traits, but we did not find important effects (for details see Supporting Information Appendix S6).

We find that populations facing greater rates of climate warming are more likely to be declining at a faster rate. However, our analyses do not account for several additional factors, such as species exploitation, pollution, and disease, which may help to further explain the degree of variability in population trends. Nevertheless, we provide evidence that populations facing high rates of climate warming tend to be in decline. Deepening our understanding of the processes that underlie the associations discussed here will be critical for developing improved assessments of species' vulnerability to climate warming (e.g., Pacifici, Foden, & Visconti, 2015).

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