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RESEARCH ARTICLE

Long-term climatic means affect the magnitude of short-term variability in population growth rates

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Abstract

Aim: Temporal variability in population growth rates is a fundamental property of natural populations with implications for almost any facet in ecology and evolution. Using the framework of nonlinear averaging, we test the hypothesis that the magnitude of short-term variability in population growth rates is influenced by the long-term means of climatic conditions.

Location: The contiguous United States.

Time period: 1970–2019.

Major taxa studied: Birds.

Methods: Our study encompassed 3941 populations of resident birds in 1335 localities across the contiguous United States. For each population, we quantified the standard deviation of annual growth rates over the relevant period and the corresponding long-term mean values of annual temperature and precipitation. We further considered the effects of covariates known to influence temporal variability in population growth, namely the standard deviations of climatic variables, the lifespan and the preferred habitat (forest vs. non-forest) of each species. The effects of climate and species traits on the variability in population growth rates were analysed using linear mixed-effects models.

Results: The magnitude of variability in population growth rate decreased with increasing the long-term mean of annual precipitation and had a U-shaped dependence on mean annual temperature. Variability in climatic conditions increased population growth variability, but this effect was weaker than the effect of the corresponding long-term means. A long lifespan reduced the impact of climatic variability on the variability in population growth rates.

Main conclusions: Our finding that the magnitude of variability in population growth rates is influenced by the long-term characteristics of climatic conditions and species traits extends our perspective on the relationship between climate and population dynamics and should be taken into account in future assessments of spatial and temporal population responses to climate change.

KEYWORDS
BBS, climate change, climate means, growth rate, Jensen's inequality, population dynamics, population fluctuations, temporal variability, thermal performance

1 | INTRODUCTION

Population growth rate (defined as $r = \log\left(\frac{N_{t+1}}{N_t}\right)$, where N is population size) is a fundamental quantity in ecology and evolutionary biology, linking processes operating at the individual, population and community levels (Sibly & Hone, 2002). One of the most important determinants of population growth rate is climate, due to its direct and indirect effects on the physiology and demography of individual organisms (Bozinovic et al., 2011, Jenouvrier, 2013, Colinet et al., 2015, Vasseur et al., 2014). Both climatic variables (Rowell, 2005; Rummukainen, 2012) and population growth rates (Andrewartha & Birch, 1954; Boyce et al., 2006; Hilde et al., 2020; Kalyuzhny et al., 2014; Lundberg et al., 2000) show considerable variation in time at almost any scale of observation, but for simplicity, both are often summarized in terms of means and the degree of variability. Hence, understanding the effects of the mean and variability of climate on the mean and variability of population growth is a fundamental question, which is particularly important for predicting the ecological consequences of global climate change (Drake, 2005; Estay et al., 2011; García-Carreras & Reuman, 2013; Lawson et al., 2015; Le Coeur et al., 2021; Vasseur et al., 2014).

Analysing population responses to temporally variable climate is not trivial due to the nonlinear nature of demographic responses to variation in climatic variables (Barraquand & Yoccoz, 2013; Lawson et al., 2015; Louthan & Morris, 2021; Pickett et al., 2015). Making general predictions on such responses must therefore involve some form of nonlinear averaging (Bernhardt et al., 2018). Previous analyses of population responses to temporally variable climate often focused on the effect of the degree of climatic variability on mean population growth rates, using the mathematical framework of Jensen's inequality (Ruel & Ayres, 1999). According to this inequality, which can be considered as a specific application of nonlinear averaging, short-term variability in climatic conditions (e.g. year-to-year variation in precipitation) may increase, decrease or have no effect on the long-term mean of population growth rate, depending on the functional form relating population growth rate (r) to the relevant climatic factors (the 'population growth response' sensu Lawson et al., 2015, Figure 1). Multiple studies support the value of Jensen's inequality as a conceptual framework for studying the effects of short-term climatic variability on the long-term mean of population growth rate (Bernhardt et al., 2018; Cabrerizo et al., 2021; Drake, 2005; Estay et al., 2011; Pickett et al., 2015).

A few works have also considered the effect of climatic variability on population variability and on the mean growth rate (García-Carreras & Reuman, 2013; Le Coeur et al., 2021). However, among the four basic relationships between (1) the mean and (2) variability of (A) climate and (B) growth rate, we are unaware of works that studied the effects of long-term means of climatic conditions on the magnitude of short-term variability in population growth rates (Figure 1). Such a perspective is important because short-term variability in population growth rates is important for many other properties of populations and communities,

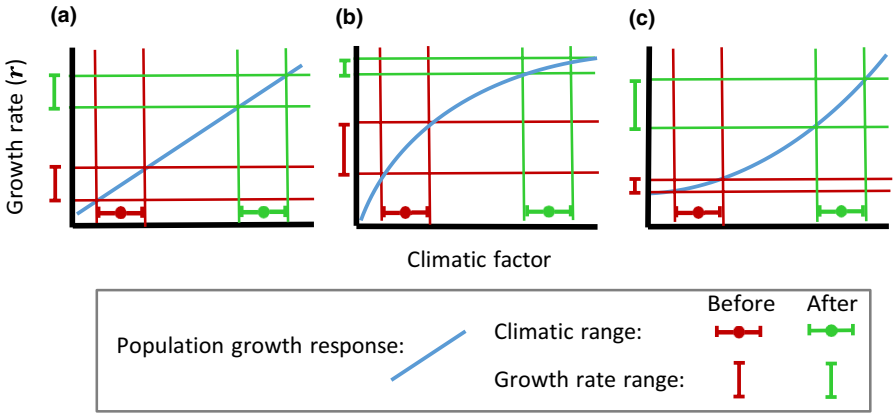

FIGURE 1 Illustration of the consequences of non-linear population responses to climate change. The blue curves represent linear (a), concave (b) and convex (c) population growth responses (which describe the effect of a certain climatic factor on the population growth rate). The horizontal solid lines indicate the temporal range of climatic conditions before (brown) and after (in green) a climatic change (for simplicity, we depict the magnitude of variability by the range of possible values rather than the variance). The vertical solid lines indicate the range of population growth rates that correspond to each climatic range. The dots on the horizontal lines indicate mean values of the climatic factor. Increasing the climatic mean has no effect, a negative effect and a positive effect on the range of the population growth rates for linear (a), concave (b) and convex (c) population growth responses, respectively (see Appendix S1 in Supporting Information for mathematical details). Note that these curves illustrate the effect of climate on growth rates prior to the effect of negative density dependence. See Appendix S2 for a discussion of non-linear population growth responses when density dependence is operating and for a visualization of population dynamics under a density-dependent model based on the three scenarios a–c (Figure S6).

including the risk of extinction (Higgins et al., 2000; Lande, 1993; Legendre et al., 2008; Melbourne & Hastings, 2008), the likelihood of species coexistence (Adler et al., 2006; Chesson et al., 2004), the stability of ecological communities (Dallas & Kramer, 2022; Gonzalez & Loreau, 2009; Houlahan et al., 2007) and the number of species in a community (Danino et al., 2016; Fung et al., 2020; Kalyuzhny et al., 2015). It is therefore important to evaluate whether short-term population growth variability is influenced by long-term climate conditions in a predictable manner.

In this study, we examine this question using data from the North American Breeding Bird Survey (BBS, Sauer et al., 2013). The BBS is one of the largest and most comprehensive data sources available on annual changes in the size of natural populations collected using a standardized protocol, and has already proved a valuable source of information for testing ecological theories (Bertuzzo et al., 2011; Chocron et al., 2015; Keitt & Stanley, 1998; McGill, 2003). Examining 3941 bird populations, we study how the standard deviation of the annual population growth rates (measuring the magnitude of short-term variability in growth rates) depends on the corresponding mean values of annual temperature and annual precipitation (measures of the long-term means of climatic conditions). We also consider the effects of important covariates known to affect growth rate variability, including mean population size, the standard deviation of climatic conditions (measuring their temporal variability) and species traits.

Our main prediction, based on nonlinear averaging (see Appendix S1 for details), was that the long-term means of both temperature and precipitation should influence the magnitude of short-term variability in population growth rates (Figure 1). Making more specific predictions on the form of the dependence is complex, because climate affects bird populations directly through their physiology, but also indirectly through its influence on other species that the birds interact with (resources, competitors and enemies). Nevertheless, assuming that annual precipitation affects population growth mainly through its effect on resource availability (Jenouvrier, 2013) and that increasing resource availability has a positive, concave-down effect on population growth rate (Sibly & Hone, 2002), we expect that increasing mean annual precipitation should decrease the magnitude of variability in population growth rate (as in Figure 1b). Temperature is generally found to have a unimodal effect on many aspects of physiology (Angilletta, 2009; Kingsolver, 2009), likely affecting in this manner both the focal bird species and other species it biotically interacts with. However, since the relative importance of direct and indirect effects is unknown, and neither is the distance from the optimal temperature, we tested both a unimodal and a linear effect of temperature.

2 | METHODS

2.1 | Bird population data

The North American Breeding Bird Survey (BBS) is an annual survey of breeding birds that began in 1966 (Pardieck et al., 2020; Sauer et al., 2013). A standard survey is conducted every year during the breeding season in June, documenting the population size of more than 700 species in over 5000 routes (secondary roads) across North America. Each route is 40 km long, and every 800 m the observer stops for a 3-min count of breeding birds seen or heard within a 400-m radius (Sauer et al., 2013).

We limited the analysis to permanent resident species (species that do not migrate) in order to reduce the complexity caused by differences in climatic conditions between breeding and wintering sites (Pasinelli et al., 2011; Saether et al., 2006). We classified species as permanent residents based on Sauer et al. (2013). We also classified species as forest versus non-forest species and determined the maximum lifespan of each species (using data from Barnagaud et al., 2017) since previous studies indicate that forest habitats (Jarzyna et al., 2016; LeBrun et al., 2016) and a long lifespan (Dalgleish et al., 2010; Le Coeur et al., 2021; Morris et al., 2008, but see Saether et al., 2005) may buffer the effects of climatic variability on population growth rates. Only routes approved as 'certified' by the BBS and located within the contiguous USA were included in the analysis. The first 4 years of the survey were not included due to insufficient and less reliable data. Hence, the years included in the data were 1970–2019. We also removed every observer's first year of observation on each route to minimize measurement errors due to first year observer effects (Kendall et al., 1996; Sauer et al., 1994).

The basic unit of analysis was an abundance time series of a particular species in a particular route. For each time series, we determined the annual growth rates for all pairs of successive years as $\mathrm{Log}_2 \frac{N_{t+1}}{N_t}$. The standard deviation of these annual growth rates was used as a measure for the magnitude of short-term variability in population growth rate (hereafter SD_r) and the mean value of $\mathrm{Log}_2 N_t$ was used as a measure of the long-term mean of population size over the relevant period (hereafter $MEAN_{POPULATION}$). In order to avoid zero values when performing the log transformation while keeping all years of observations in the time series (to avoid biases related with omitting only certain years), time series including values of zero abundance were omitted from the analysis. Furthermore, in order to obtain reliable estimates of the standard deviation of annual growth rates, only time series with at least 20 pairs of successive observations were selected for the analysis. Finally, in order to obtain a reasonable sample size for individual species, only species that were present in at least 30 routes after applying the above filters were selected for the analysis. The resulting data set included 3941 time series, representing 18 species in 1335 routes across the contiguous United States (see Figure 2 a,b for the spatial distributions of these variables for single populations per route across the US, Figure S1 for the distribution of the number of populations per route and Figure S2 for distribution maps of individual species).

2.2 | Climate data

Previous studies have confirmed that both temperature and precipitation are important in determining population growth rates and abundance of birds (Illán et al., 2014; Jenouvrier, 2013;

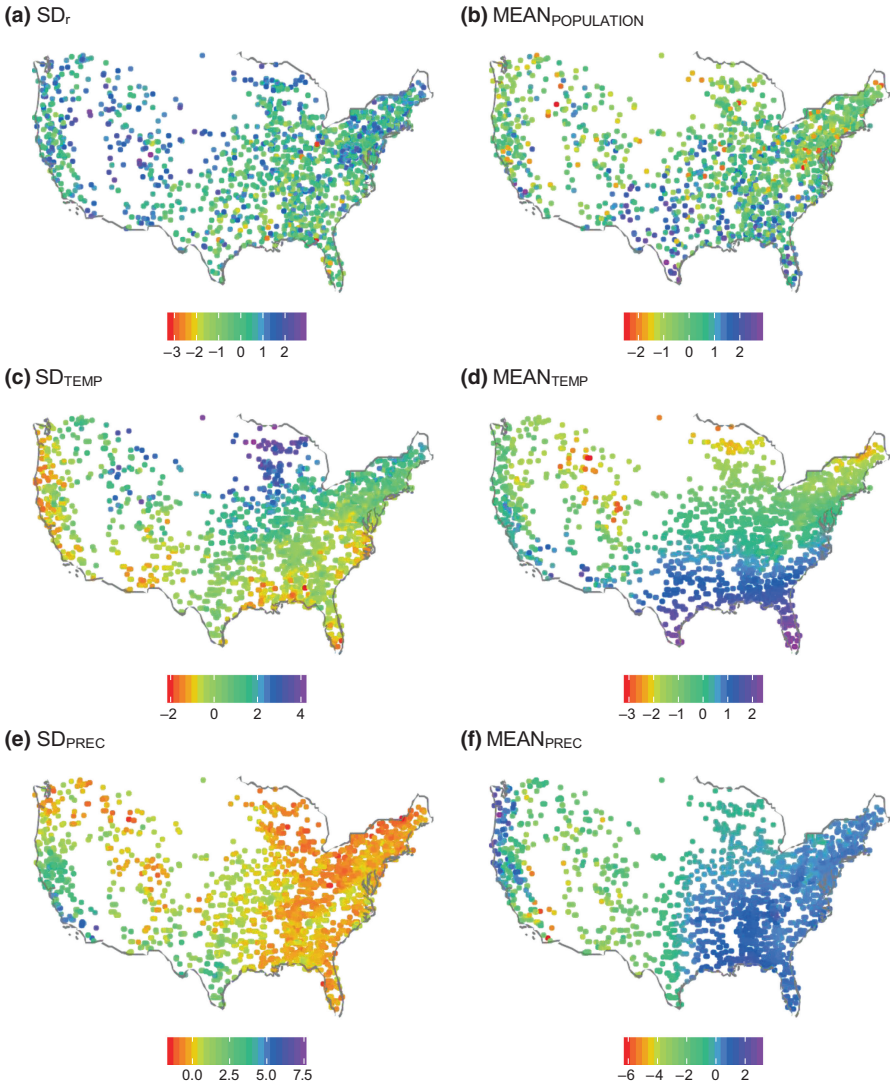

FIGURE 2 Spatial distributions of the main variables in our analysis. The points represent the locations of the analysed BBS routes, coloured by the values of the standardized variables. (a) The temporal variability in growth rates (the dependent variable in our analysis); (b) shows the mean log population size. In panels (a, b), whenever more than one population was analysed in a route, a single one was randomly selected to be presented in both panels. (c) and (d) present the standard deviation and mean annual temperature, respectively. (e) and (f) present the standard deviation and mean annual precipitation, respectively.

Pearce-Higgins, Eglington, et al., 2015). We compiled monthly temperature and precipitation data for the period 1970–2019 from the PRISM Climate Group data set (PRISM Climate Group, 2021). The climate data were at a 4-km resolution across the contiguous United States. Since BBS observers report bird counts for a distance of up to 400 m from the route, we averaged the climate records of all PRISM cells that intersected with a buffer of 400 m around the route for each climatic variable in each year. Based on these data, we determined for each year in each route the mean annual temperature (°C) and the total amount of precipitation (mm). These were averaged across years to obtain the mean annual temperature and annual precipitation for each time series (hereafter $MEAN_{TEMP}$ and $MEAN_{PREC}$, respectively). Precipitation data were log_2-transformed before calculating the mean values in order to improve the normality of their distribution. While more complex indices of climatic means could be quantified (e.g. monthly means, season-specific means, means based on maximum or minimum values, etc., Bowler et al., 2017; Chocron et al., 2015; Pearce-Higgins, Ockendon, et al., 2015), we preferred to focus on simple and commonly used indices. See Figure 2c–f for the spatial distributions of these variables across the United States.

2.3 | Statistical analysis

The main model we used was a linear mixed model to test the effects of the long-term means of temperature ($MEAN_{TEMP}$) and precipitation ($MEAN_{PREC}$) on the magnitude of annual variability in population growth rates (SD_r), while accounting for the effect of other variables. For the effect of $MEAN_{TEMP}$, we compared models with a quadratic term ($MEAN_{TEMP}^2$) and models that have only a linear term. The response variable (SD_r) was log-transformed to stabilize its variance and improve the linearity of the models. Mean population size ($MEAN_{POPULATION}$) was included as a covariate, because the magnitude of variability in population growth rates is inherently related to population size (Box 1, Lande et al., 2003; Saether et al., 2011).

We further wanted to take into account the potential effects of short-term climatic variability and its interaction with the long-term climatic means and species properties in determining the magnitude of variability in population growth rates. We introduced short-term climatic variability as a covariate because it is correlated with mean climate, and it has an influence on population variability (Appendix S1). To this end, we determined, for each population, the standard deviations

BOX 1 The relationship between short-term variability in population growth rates and population size

The variance in population growth rate cannot be considered independently of population size, as it is expected to decrease with increasing population size. The reason is that increasing population size decreases the impact of demographic stochasticity. This has been studied in detail by considering the reproductive factor λ ($\lambda = e^r$) In principle, $Var(\lambda)$ can be expressed as the sum of two components (Lande et al., 2003): the variance due to environmental fluctuations (environmental stochasticity, σ_e^2) and the variance due to random demographic events (demographic stochasticity, $\frac{\sigma_d^2}{N}$):

$$\text{var}(\lambda) = \sigma_e^2 + \frac{\sigma_d^2}{N} \quad (2)$$

The second component (demographic stochasticity) decreases strongly with increasing population size because the independent, individual-level stochasticity averages out as the number of individuals in the population increases (Lande et al., 2003). As a result, an increase in population size is expected to reduce the magnitude of variability in population growth rates (see Saether et al., 2008, 2011 for empirical evidence).

of the yearly changes in mean annual temperature (SD_{TEMP}) and log annual precipitation (SD_{PREC}) during the relevant period. We also determined for each species its preferred habitat (forest vs. non-forest) and maximum lifespan (using Barnagaud et al., 2017 for both), following previous evidence that these variables may mediate the effects of climatic variability on population growth rates (Jarzyna et al., 2016; Le Coeur et al., 2021). We included the habitat preference of the species (HABITAT, as a dummy variable with forest = 1 and non-forest = 0), the species maximum lifespan (LIFESPAN) and the interactions between the standard deviation of each climatic factor and each species property ($SD_{TEMP} \times$ HABITAT, $SD_{TEMP} \times$ LIFESPAN, $SD_{PREC} \times$ HABITAT and $SD_{PREC} \times$ LIFESPAN). The interactions between the means and standard deviations of each climatic factor ($MEAN_{TEMP} \times SD_{TEMP}$ and $MEAN_{PREC} \times SD_{PREC}$) were also included in the models following previous evidence that such interactions might be common and might influence the population growth rates (Bozinovic et al., 2011; Lawson et al., 2015; Vasseur et al., 2014). All variables were standardized to reduce multicollinearity and facilitate comparison. Non-standardized models gave qualitatively similar results.

To account for the non-independence of species within a single route and of time-series of the same species across routes, we incorporated species identity and BBS route as random effects. Furthermore, to account for broad geographic trends, potentially generating spatial autocorrelation, we added Bird Conservation Region (BCR) as another random effect. All random effects were incorporated through the intercept. As an alternative approach to model spatial structure, we incorporated exponential spatial autocorrelation instead of BBS route and BCR, while keeping the effect of species identity. This model proved much worse than the main model we used (ΔAIC ≈170) while giving qualitatively similar estimates, hence it is reported only in the Appendix (Table S1).

We assessed the influence of variables by examining their effect size and its significance in the main model. Furthermore, we compared the main model to several alternative, simpler models using AIC values with the aim of testing several hypotheses and evaluating the goodness of fit of the best model and the robustness of the conclusions. Specifically, we expected that removing mean climatic variables and their interactions with their standard deviations (model A); only the interactions between the means and standard deviations of climatic variables (model D); the interactions between the standard deviations and species traits (model E) and the standard deviations and all their interactions (model C) would all substantially worsen the model (i.e. by more than 2 units of AIC). We also considered whether removing $MEAN_{TEMP}^2$, leaving only a linear effect of $MEAN_{TEMP}$, worsens the model (model B).

Collinearity was quantified based on the variance inflation ratios (VIF values). Standard diagnostic tools were used to evaluate the stability of the variance and the normality of the residuals in all models (Zuur et al., 2010). To assess the spatial autocorrelation of the residuals of the main model, we examined the spatial correlogram of the main model using the NCF package (Bjornstad, 2022). Statistical analyses were done using R and most mixed models were fitted using the package LME4 (Bates et al., 2015), while the model with exponential autocorrelation was fitted with package NLME (Pinheiro, Bates, & R Core Team, 2023). The marginal effects of predictors were plotted using the package Sjplot (Lüdecke, 2023).

3 | RESULTS

Diagnostic analyses for the main model confirmed that the residuals were approximately normally distributed and the variances were fairly constant (Figure S3), with acceptable levels of collinearity and correlation between predictor variables (Tables S2 and S3). Furthermore, the spatial autocorrelation of the residuals was negligible (Figure S4).

Our basic prediction that the long-term means of climatic conditions should influence the magnitude of short-term variability in population growth rates was fully supported by the results: the long-term means of both temperature ($MEAN_{TEMP}$) and precipitation ($MEAN_{PREC}$) had highly significant effects on the magnitude of variability in population growth rates and substantially improved the model (Figures 3 and 4, ΔAIC = 59.4 for model A, Table S3). As we hypothesized, an increase in mean annual precipitation decreased the magnitude of variability in population growth rates (Figures 3–5b). Increasing the long-term mean of annual temperature had a U-shaped effect on SD_r (Figure 5a), with a highly significant positive

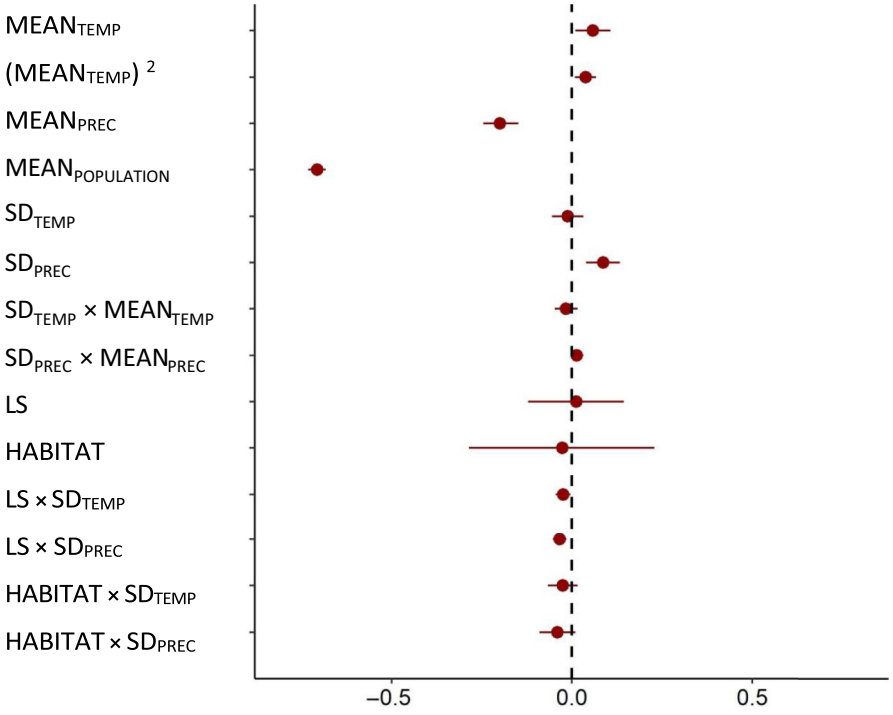

FIGURE 3 Standardized coefficients (±CI) of the main model. The response variable is the log-transformed magnitude of temporal variation in annual growth rates of bird populations in North America (SD_r). The model includes the effects of mean annual temperature ($MEAN_{TEMP}$), mean annual precipitation ($MEAN_{PREC}$), mean population size ($MEAN_{POPULATION}$), the magnitude of annual variability in temperature (SD_{TEMP}) and precipitation (SD_{PREC}), the species lifespan (LS), whether the species prefers forest or non-forest habitats (HABITAT, coded as 1 or 0, respectively), and relevant interaction terms.

	Model					
Predictor	**Full**	**A**	**B**	**C**	**D**	**E**
$MEAN_{POPULATION}$	−0.71	−0.71	−0.71	−0.71	−0.69	−0.71
$MEAN_{TEMP}$	0.058		0.049	0.084	0.061	0.06
$MEAN_{PREC}$	−0.19		−0.19	−0.19	−0.17	−0.19
SD_{TEMP}	−0.012	0.02	−0.019		0.002	−0.019
SD_{PREC}	0.087	0.12	0.066		0.033	0.068
SD_{TEMP} X $MEAN_{TEMP}$	−0.016		−0.037			−0.009
SD_{PREC} X $MEAN_{PREC}$	0.014		0.012			0.014
LS	0.012	0.016	0.018	−0.019	0.012	−0.023
HABITAT	−0.026	−0.062	−0.016	−0.053	−0.033	−0.054
LS X SD_{TEMP}	−0.024	−0.015	−0.025		−0.025	
LS X SD_{PREC}	−0.034	−0.026	−0.036		−0.044	
HABITAT X SD_{TEMP}	−0.025	−0.025	−0.023		−0.036	
HABITAT X SD_{PREC}	−0.04	−0.056	−0.046		−0.028	
$MEAN_{TEMP}^2$	0.038			0.047	0.045	0.046
ΔAIC	0	+ 59.4	+ 4.8	+15.1	−0.5	+ 11.8
Marginal R^2	0.561	0.499	0.561	0.531	0.555	0.543
Conditional R^2	0.71	0.724	0.711	0.712	0.7101	0.711

FIGURE 4 Effect sizes and their statistical significance in the main model and alternative, simpler models that omit selected variables (A–E), as well as their R^2 and AIC difference compared to the main model. Negative effects are coloured in orange if they are significant ($p < 0.05$) and in red if they are highly significant ($p < 0.01$). Positive effects are coloured in pale green if they are significant ($p < 0.05$) and in green if they are highly significant ($p < 0.01$). Greyed variables are not included in the model. The models include the effects of mean annual temperature ($MEAN_{TEMP}$), mean annual precipitation ($MEAN_{PREC}$), mean population size ($MEAN_{POPULATION}$), the magnitude of annual variability in temperature (SD_{TEMP}) and precipitation (SD_{PREC}), the species lifespan (LS), whether the species prefers forest or non-forest habitats (HABITAT, coded as 1 or 0, respectively), and relevant interaction terms.

quadratic term whose removal substantially worsened the model (Figures 3 and 4, ΔAIC = 4.8 for model B, Table S3). However, an accurate estimation of the functional form of the relationship between mean temperature and SD_r in the data is difficult because of the substantial SE for the linear and quadratic terms. Moreover, the overall effect of annual temperature is not very strong, as can be seen from Figure 5 and from the moderate effect of dropping the quadratic term in model B (Figure 4). Furthermore, the long-term mean of population size ($MEAN_{POPULATION}$) had a highly significant and strong negative effect on the magnitude of variability in population growth rates (Figures 3 and 4, Table S3). All these effects were highly consistent over all models.

Further insights were gained into the nature of the relationship between climate and population growth rates. First, the standard

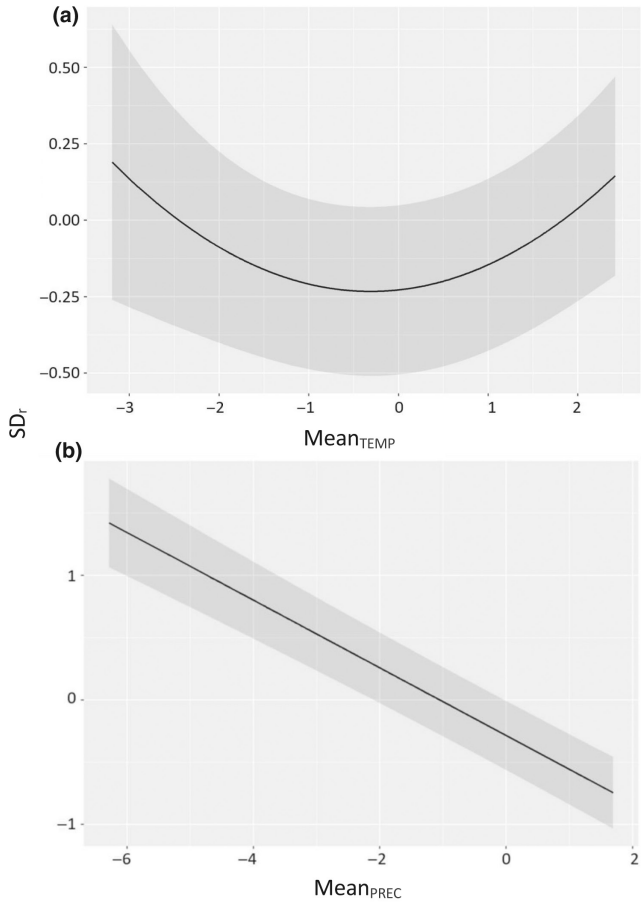

FIGURE 5 Marginal effects of (a) mean annual temperature ($MEAN_{TEMP}$) and (b) mean annual precipitation ($MEAN_{PREC}$) on the log-transformed standard deviation of annual growth rates of bird populations in North America (SD_r) as estimated by the main model. All variables are standardized. Note the difference in the scale of the *Y*-axis.

deviation of precipitation, but not temperature, significantly increased SD_r, and removing the climatic standard deviations substantially worsened the model (Figures 3 and 4, ΔAIC = 15.1 for model C). However, in contrast to our hypothesis, we did not find evidence that long-term climatic means interact with the standard deviations in determining the magnitude of variability in population growth rates (Figures 3 and 4, ΔAIC = −0.5 for model D). Finally, both measures of climatic variability (SD_{TEMP} and SD_{PREC}) interact with lifespan in determining the magnitude of variability in population growth rates (Figures 3 and 4, ΔAIC = 11.8 for model E), but a similar effect was not observed for habitat preference (Figures 3 and 4).

The main conclusions were further supported by a much simpler model with only the key predictors (Table S4).

4 | DISCUSSION

While multiple previous studies have focused on the effects of climate on the long-term means of population growth rates, as far as we are aware, our study is the first demonstration that the long-term means of climatic conditions affect the magnitude of short-term variability in population growth rates. This finding is consistent with theoretical expectations based on nonlinear averaging (Figure 1, Appendices S1 and S2) and extends our perspective about the relationship between climate and population dynamics. Importantly, although the original motivation of our study was to better understand the potential consequences of global climate change, our results also (and even more directly) apply to geographical gradients of climatic conditions, thereby pointing to the possible existence of a previously unrecognized macroecological pattern of climate–population dynamics relationship.

Our results indicate that increasing the long-term mean of annual precipitation decreases the magnitude of short-term variability in population growth rates in the study populations (Figures 3–5). Although such a negative effect may result from either a positive concave or a negative convex population growth response, we believe that the former option is more reasonable, because the main effect of precipitation on bird populations is through its positive effect on food availability (Jenouvrier, 2013) and population responses to increasing food availability are usually positive and concave (Lawson et al., 2015; Sibly & Hone, 2002, though see Altwegg & Anderson, 2009). We also found a U-shaped effect of the long-term mean of annual temperature on the magnitude of short-term population growth variability. Such U-shaped dependence is expected if temperature has a unimodal, concave effect on performance, as is commonly accepted (Angilletta, 2009; Kingsolver, 2009), and this performance translates to population growth. If that is the case, then an increase from low to intermediate temperatures has a positive, decelerating effect on growth, leading to a decrease in population growth variability (as in Figure 1b), but a further increase in temperature has a negative accelerating effect on growth, leading to an increase in population growth variability (a reflection of Figure 1b).

Short-term population growth variability also increased with the variability in climate, in line with the findings of previous works (García-Carreras & Reuman, 2013; Le Coeur et al., 2021) and theoretical considerations (Appendix S1). The effect of variability in precipitation on the magnitude of variability in population growth rates was highly significant (Figure 4, Table S3), but weaker than that of the long-term mean of precipitation. The effect of variability in annual temperature was not significant (Figure 4, Table S3), suggesting that, for most populations included in our study, fluctuations in mean annual temperature are not important in generating fluctuations in population size. Thus, our overall results lead to the unexpected conclusion that climatic variability is less important than climatic means in determining variability in population growth rates of the study populations.

Still, the influence of climate variability is complicated by important interactions with lifespan, as both measures of climatic variability (SD_{TEMP}, SD_{PREC}) showed significant negative interactions with species lifespan. These interactions are consistent with multiple works showing that a long lifespan may function as a buffering mechanism that averages the effects of environmental stochasticity

on population growth rates, thereby reducing the magnitude of short-term fluctuations in population size (Dalgleish et al., 2010; Le Coeur et al., 2021; Morris et al., 2008). The corresponding interactions with habitat preference were statistically insignificant (Figure 4, Table S3).

As we expected, larger populations had a lower magnitude of fluctuations. We anticipated this result because the effect of demographic stochasticity tends to average out at larger population sizes (as noted in Box 1), and population sizes in our study were rather low (mean ± SD = 23.6 ± 17.8, median = 18.3, Figure S5), making them susceptible to such effects. This negative effect of population size on population variability is also consistent with results of previous large-scale studies (Saether et al., 2008, 2011). An alternative explanation for this negative effect is that observation errors, for which the BBS is notoriously famous (Dennis et al., 2006; Kalyuzhny et al., 2014), also tend to average out for larger populations. Another possibility is that sites having better environmental conditions have both larger populations and lower fluctuations (Appendix S2). However, while the existence of the effect of population size was predicted based on theoretical considerations, we did not expect that it would be much more important than all climatic effects.

Global change models predict, and empirical measurements confirm, that anthropogenic climate change is causing a decrease in precipitation and an increase in temperature, as well as an increase in climatic variability, in many parts of the world (Easterling et al., 2000; Rowell, 2005; Rummukainen, 2012; Salinger, 2005). According to our results, both changes in mean climate, as well as increases in climatic variability, are expected to affect population growth rate variability among North American birds. Interestingly, an examination of the standardized coefficients of the variables and of the consequences of removing either the means or standard deviations from the full model (Figure 4, models A, C) indicates that the long-term means of climatic conditions are more important than short-term climatic variability in determining the magnitude of variability in population growth rates (Figures 3 and 4, Table S3). This difference is particularly pronounced in the case of precipitation: For all models, mean precipitation was the most important climatic factor affecting the magnitude of population fluctuations and its effect was much larger than that of the variability in either precipitation or temperature. While a decrease in mean precipitation is expected to increase population variability, the effect of increasing temperature would probably be to increase variability at the southern part of species' ranges (where temperature is already high) and to decrease variability at the northern, colder part, due to the U-shaped dependence. These conclusions, along with the result that short-lived species are more vulnerable to climate fluctuations, can help focus attention on populations and localities that would be more severely impacted by climate change.

It is important to acknowledge, however, that our analysis and interpretation apply to relatively (locally) common resident birds at intermediate spatial scales. Furthermore, the effects of most climatic variables included in our models were relatively small, suggesting that climate change may not have a drastic impact on the magnitude of fluctuations in the study populations. However, our analysis focused on climatic means and standard deviations, while extreme weather events could have a stronger effect. Extrapolating this conclusion to scenarios of rapid future climate change, beyond the conditions that we modelled, should be done with caution. Future studies should evaluate the degree to which our findings can be generalized to other groups of organisms, to other characteristics of climatic conditions and to the community level. The framework applied in this study (Figure 1) provides an effective approach for future studies of this sort.

The theoretical foundation for our work is that population growth responds to climate in a (likely) non-linear manner (the 'population growth response'), creating a dependence of the magnitude of year-to-year fluctuations on the environmental means due to non-linear averaging. The mathematical details are laid out in Appendices S1 and S2, but here we would like to emphasize three key aspects. First, the variance (magnitude) of year-to-year fluctuations in the abundance of a given population in a given habitat depends on how rapidly the growth rate of that population changes when climate changes. Mathematically, to a first order, this variance depends on the squared first derivative of the population growth response at the mean environmental condition in the population's habitat (Equation S7). Second, comparing two populations subject to two different climates (or before and after climate change) and assuming that the population growth response is monotonic (as in Figure 1), the second derivative determines whether a change in the mean would increase or decrease the variance (as can be deduced from the first argument). Finally, while the concept of population growth response does not consider density dependence, we show in Appendix S2 that very similar results are expected if population growth is density-regulated and populations are bounded, and we derive the mean and variance of population size and population fluctuations in this case.

One other point regarding the population growth response is worth noting. While our work, as well as several previous works (e.g. Drake, 2005; Lawson et al., 2015) consider the effect of climate on the *intrinsic* growth rate (r), it is also possible to describe how climate affects the multiplicative growth factor ($\lambda = \frac{N_{t+1}}{N_t}$, note that $r = \log(\lambda)$). Similar considerations as in Figure 1 and Appendices S1 and S2 can be applied in this case, and regardless of the specific description, mean climate is expected to influence the variability of population growth, except in some borderline cases (e.g. Figure 1a).

Our analysis of ~4000 time series of bird populations in North America demonstrates that the long-term means of both temperature and precipitation affect the magnitude of variability in population growth rates. At a broader perspective, a synthesis paper focusing on ecological processes published 20 years ago argued that 'No ecological study, to date, has attempted to separate the effect of changing the mean from that of altering the variance of a predictor variable, either on the mean or on the variance of a response variable' (Benedetti-Cecchi, 2003). Since then, there has been much progress on testing the effects of climatic means and

variances on population means, but much less progress in testing the effects of climatic means and variances on population variances (Bozinovic et al., 2011; Drake, 2005; García-Carreras & Reuman, 2013; Lawson et al., 2015; Morris et al., 2008; Pickett et al., 2015; Vasseur et al., 2014). We believe that this question should receive more attention in future studies of climate change and population ecology in general.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The data used in this work are publicly available and referenced to. BBS data are available at https://doi.org/10.5066/P9J6QUF6. Bird body mass and habitat data are available at https://doi.org/10.1007/s00442-017-3967-4 (Supplementary Material 3 therein). Migratory status is based on https://doi.org/10.3996/nafa.79.0001 (Appendix B therein). Climate data are available at: http://prism.oregonstate.edu. Full code and processed data available at https://zenodo.org/doi/10.5281/zenodo.10456668.

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BIOSKETCH

Liraz Bistritz performed the study as an MSc student at the Hebrew University of Jerusalem, under the supervision of Michael Kalyuzhny and Ronen Kadmon. She is interested in understanding the potential consequences of global climate change on population dynamics.

Ronen Kadmon is an ecologist at the Hebrew University of Jerusalem. His main interest is in the mechanisms affecting the dynamics and structure of ecological communities.

Curtis H. Flather was a research ecologist with the US Forest Service, Rocky Mountain Research Station. His research focused on understanding the response of biodiversity to changing climate, natural disturbance and land management activities.

Michael Kalyuzhny is an ecologist at the Hebrew University of Jerusalem, interested in the interplay between spatial and temporal variability and species diversity.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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