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Environmental Variability Shapes Life History of the World's Birds

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ABSTRACT

Theory suggests life history plays a key role in the ability of organisms to persist under fluctuating environmental conditions. However, the notion that environmental variability has shaped the distribution of life history traits across large spatial and taxonomic scales has gone largely untested using empirical data. Synthesising a collection of data resources on global climate, species traits, and species ranges, we quantified the role that environmental variability over time has played in shaping pace of life across the world's non-migratory, non-marine bird species ($N = 7477$). In support of existing theory, we found that species that experience high inter-annual temperature variability tended to have a slower pace of life, while the opposite was true for high intra-annual temperature variability. The effect of precipitation variability was less pronounced and more uncertain. These observed patterns were apparent despite the vastly different ecologies of our study species and evidence of strong phylogenetic constraint. Additionally, we highlight the importance of contextualising rates of environmental change in terms of the historical variability of environmental systems and species' pace of life. Species experiencing higher rates of relative environmental change, in terms of standard deviations per generation, may be most susceptible to climate change.

1 | Introduction

Fluctuating environmental conditions pose a challenge for organisms, which must cope with perennial variation to persist (Levins 1968). As such, environmental variability has played a pivotal role in shaping ecological systems. It has been proposed that variability impacts species plasticity, acclimation capacity (Dobzhansky 1950; Shah et al. 2017), and range limits (Chan et al. 2016; Pintor, Schwarzkopf, and Krockenberger 2015), and ultimately dictates the conditions under which species are likely to persist (Capdevila et al. 2022; Janzen 1967). Environmental conditions can vary across a range of time scales, for instance, within a given year (i.e., intra-annual variation) as well as across years (i.e., inter-annual variation).

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Over time, natural selection is expected to act in such a way that maximises long-term growth rates (Cole 1954) and minimises the risk of extinction (Mountford 1973) for a given species. Long-standing theoretical assertions postulate that life history strategies play a key role in this optimisation and that these strategies should vary according to the degree and characteristics of environmental variability experienced by a species (Stearns 1976). Life history traits are often collapsed into a continuum referred to as 'pace of life' (Ricklefs and Wikelski 2002), with slow life histories characterised by traits such as high survival, late age of maturity, and low rates of reproduction and fast life histories the converse (Healy et al. 2019). For iteroparous species with generation lengths of at least 1 year (most vertebrate species (Wingfield 2008)), life history theory suggests that species (or populations) with a slower pace of life should be buffered from inter-annual environmental variation. In this scenario reproductive effort can be distributed across longer periods of time, integrating environmental conditions experienced over an individual's lifespan (Murphy 1968; Schaffer 1974). Simulation-based work has come to similar conclusions, that slower pace of life is a type of bet-hedging strategy to overcome short-term environmental variability (Le Coeur et al. 2022; Metcalf and Koons 2007; Morris et al. 2008; Paniw, Ozgul, and Salguero-Gómez 2018; Schmid et al. 2022); this idea is supported by evidence linking dampened population-level fluctuations with slower pace of life (Capdevila et al. 2022; Jackson, Le Coeur, and Jones 2022). However, the notion that these processes have shaped the distribution of life history traits across large spatial and taxonomic scales has gone largely untested using empirical data, having been explored in only taxonomically limited contexts (Nevoux et al. 2010).

In contrast to proposed associations between slower life histories and higher *inter*-annual variation, empirical evidence supports the opposite pattern when considering *intra*-annual variation. High intra-annual environmental variation (generally associated with greater seasonality) is associated with increased clutch sizes (Jetz, Sekercioglu, and Böhning-Gaese 2008) and lower rates of adult survival (Ricklefs 1997) in birds as well as faster metabolic rates (Yanco, Pierce, and Wunder 2022). This pattern has been attributed to the bottleneck of resources that may occur in environments with high variability (e.g., fewer food resources in winter months at high latitudes). Given a low probability of surviving to the next breeding season due to scarce resources in the non-breeding season, individuals should invest resources in raising more young (Martin 2004; McNamara et al. 2008).

These two dimensions of environmental variability, inter- and intra-annual variation, however, have typically been considered in isolation regarding their impact on life history traits. Many environments exhibit similar variation on both inter- and intra-annual scales, while others exhibit very different variation across these scales. Understanding the associations between environmental variability and life history is also critical if we are to predict how species will respond to future changes in the environment given recent and potential future changes in both inter- (Diffenbaugh et al. 2017; Hansen et al. 2014; van der Wiel and Bintanja 2021) and intra-annual environmental variability (Donat et al. 2016; Feng, Porporato, and Rodriguez-Iturbe 2013). Climate change is likely to impact species in different ways depending on their life history characteristics and the historical conditions (i.e., variability) under which they have evolved. Other factors, such as a species' dietary niche, may also mediate how organisms experience environmental variability. For example, there is an expectation that species that rely on widely available and reliable resources will exhibit faster life histories (Sibly and Brown 2007).

In this study, we test long-standing theoretical assertions linking environmental variability and life history traits by synthesising a collection of data resources on global climate, species traits, and species ranges. We quantified inter- and intra-annual variability in both temperature and precipitation and examined its effects on generation length, a representative metric of pace of life, across the world's non-migratory (i.e., resident) bird species ($N = 7477$). Birds are an ideal taxonomic group for this purpose given their large geographic distribution, diversity of life histories, past avian-focused research in this area, and robust data resources. We asked two questions: (1) To what degree are both inter- and intra-annual environmental variability associated with pace of life as predicted by ecological theory?; (2) How can we put the rate of environmental change experienced by species into the appropriate context by taking into account both environmental variability and species' pace of life? Using a flexible hierarchical Bayesian approach, we decouple the role of these two dimensions of environmental variability while considering shared evolution histories of these birds and relevant ecological traits, such as body mass and dietary niche. Our framework allowed us to quantify and propagate uncertainty in our data throughout the analyses, accommodating the complexities of these global data resources. We furthermore derive rates of relative environmental change for these species, in terms of standard deviations per generation, which provides the long-term, evolutionary context for assessing which species and communities might be most resilient to environmental change.

2 | Materials and Methods

2.1 | Characterising Environmental Variability

We obtained global monthly temperature (2 m height) and precipitation data spanning 1950–2022 from the ERA5 climate reanalysis, provided on a $0.25° \times 0.25°$ grid (Bell et al. 2021; Hersbach et al. 2020). We considered these metrics as indicators of general environmental variability, given the important role they play in structuring ecological communities (Jiang et al. 2017; Letten et al. 2013; Moore et al. 2018). We applied a square-root transformation for precipitation due to the right skew nature of the data. To derive inter-annual variability, we first averaged temperature and precipitation across all months, for each cell north of 60° S latitude, in each year. While deriving season-specific metrics would be valuable, accurate estimates of breeding period dates were not available for all species. For each cell, we detrended yearly averages using a linear regression to prevent bias that directional change might introduce. For temperature, we calculated the standard deviation of the detrended time series, resulting in a single estimate of inter-annual temperature variation (τ_{inter_T}) for each cell. Since variation in precipitation should be larger in areas with greater mean precipitation, we used the coefficient of variation (standard deviation/mean) of the detrended time series rather than the standard deviation (τ_{inter_P}). Temperature is 'interval-scale' data, where 0 does not represent some absolute value, while precipitation is considered 'ratio-scale', where 0 represents an absence of precipitation, which is why we use different variability metrics for temperature and precipitation.

To derive metrics for intra-annual variability, for each cell in each year, we calculated the standard deviation for temperature and the coefficient of variation for precipitation across all months, following the method used to derive 'seasonality' in WorldClim (Fick and Hijmans 2017). We then averaged these year-specific standard deviations across all years of our time series, resulting in a single estimate of intra-annual temperature variation (τ_{intra_T}) and a single estimate of intra-annual precipitation variation (τ_{intra_P}) for each cell. While data used to characterise variability are relatively contemporary in nature and processes prior to this study period have undoubtedly shaped our study species, there exists a tradeoff between the length, the accuracy, and the resolution of the climate record. The 73-year time series that we made use of provided us with a relatively long-term (multi-generational), accurate, and high-resolution perspective of environmental variability and how conditions have shifted in response to environmental change over this period.

2.2 | Bird Trait Data, Range Data, and Associated Environmental Variability

We focused our analyses on all non-migratory bird species found in non-marine environments to understand global-scale patterns of pace of life. We excluded marine birds based on taxonomic order (i.e., excluding Sphenisciformes, Procellariiformes, Pelecaniformes, Suliformes, Phaethontiformes, and Charadriiformes), as marine habitat use is highly conserved across species. While some non-marine species exist in these orders, these are very few in number.

Migratory species were excluded as seasonal migration may, in and of itself, be a bet hedging strategy (Somveille, Rodrigues, and Manica 2015), in addition to the fact that conditions experienced in multiple locations (i.e., breeding compared to non-breeding grounds) may influence life history processes (Cooper et al. 2024). Marine species (i.e., seabirds) were excluded as there exists fundamental differences between marine and non-marine environments that may confound reliable inference (Carr et al. 2003). Moreover, conditions in both marine and terrestrial environments are likely to have important implications for seabird life history. These species nest on land and foraging patterns are influenced by conditions in the terrestrial environment, however they rely on food resources located in the marine environment (Schreiber 2002). As such, the relevant environmental processes for life history likely differ between non-marine and marine birds, presenting challenges for inference when both groups are included in the same analysis.

We obtained generation length data, defined as the average age of parents in any population, for all relevant species, from Bird et al. (2020). Generation length is highly correlated with other life history metrics and is a key indicator of a species' position along the slow-fast pace of life continuum (Gaillard et al. 2005; Healy et al. 2019). We obtained species range data from BirdLife International (2022), data on body mass and dietary niche from AVONET (Tobias et al. 2022), and phylogenetic information from BirdTree (Jetz et al. 2012). Dietary niche was a trait with 10 categories (predator aquatic, frugivore, granivore, herbivore aquatic, herbivore terrestrial, invertivore, nectarivore, omnivore, scavenger, and vertivore). Dietary niche data were missing for 5 species of tropical owls in the genus *Otus*—we classified these species as 'vertivore'.

We manually reconciled all taxonomic discrepancies across datasets to the BirdLife taxonomy Version 2022.2 (BirdLife International and Handbook of the Birds of the World 2022). While all datasets used the BirdLife taxonomy, different taxonomy versions were used in each dataset. Name mismatches were reconciled using the taxonomic status change descriptions across different BirdLife versions. Once complete, all data sources were linked to the version of the BirdLife taxonomy used by BirdTree using the taxonomy crosswalk provided by AVONET, resulting in complete data for all but 5 species in the final dataset which were excluded (*Lophura hatinhensis*, *Hypositta perdita*, *Phyllastrephus leucolepis*, *Anthus longicaudatus*, *Polioptila clementsi*). When generation length or trait data from Bird et al. (2020) and AVONET for multiple species corresponded to one species in the BirdTree taxonomy, we took the average of any continuous variable (e.g., body mass) across species and assigned that to the single BirdTree species. All categorical variables (e.g., trophic niche) were consistent across multiple species that were assigned to one BirdTree species. If multiple range maps corresponded to one species in the taxonomy, we joined the ranges. If one range map corresponded to more than one species in the taxonomy, we duplicated the range.

For each species, we extracted range-wide mean and standard deviations for inter- and intra-annual temperature and precipitation (τ_{inter_T}, τ_{inter_P}, τ_{intra_T}, τ_{intra_P}), after excluding any extreme outliers in that range, defined as values that fell outside of 3 median absolute deviations from the median (Leys et al. 2013). We used the calculated standard deviations to account for the spatial variation in environmental variability across species' ranges (Figure S1). In this way, each species had one mean value and one standard deviation for each of these metrics. In total our dataset represented 7477 species from 29 orders and 198 families. We processed data in R 4.3.2 (R Core Team 2023) using the 'tidyverse' 2.0.0 family of packages (Wickham et al. 2019), as well as the 'sf' 1.0–15 (Pebesma 2018) and 'terra' 1.7–55 packages (Hijmans et al. 2021) for spatial data processing.

2.3 | Pace of Life as a Function of Environmental Variability

Using a hierarchical Bayesian approach, we modelled generation length for each species as a function of environmental variability. We simultaneously assessed the impact of both inter- and intra-annual variation in temperature and precipitation in our model. Because body mass is known to be strongly associated with generation length and we sought to estimate the effect of environmental variability in the absence of this metric, it was also included as a predictor variable in the model. Separate intercepts were estimated for each trophic niche category, to account for and estimate the effect that this might have on pace of life.

We used an observation model to account for uncertainty in generation length, our response variable. To calculate the magnitude of uncertainty to be used in our model, we used a simulation approach based on the methods used by Bird et al. (2020) to derive estimates of generation length. Bird et al. (2020) calculated generation length using observed and predicted (i.e., imputed) values for age at first breeding, maximum longevity, and annual adult survival (Equation 1 from Bird et al. 2020). We used this approach to generate an initial set of generation lengths for each species. If the life history parameters are considered to be measured without error, these represent the 'true' generation lengths. However, each of these life history parameters has some associated uncertainty, given by the associated R^2 values provided by Bird et al. (2020). This is a measure of how well predictions matched the observed data. For each of 100 different replicates, we drew random values for each of these life history parameters, using the provided values in Bird et al. (2020) as the mean, and the associated R^2 values for each parameter to calculate the variance for the gaussian noise added to each variable. From $R^2 = 1 - \frac{\text{residual variance}}{\text{total variance}}$, we have $\text{residual variance} = \left(1 - R^2\right) \times \text{total variance}$, with the residual variance representing the associated error and the total variance representing the total variance of the life history variable. We calculated generation length using the approach following Bird et al. (2020) for each species in each replicate and then compared the calculated generation lengths using the 'true' parameters to generation lengths calculated using the parameters sampled with some uncertainty. The median R^2 values across the 100 simulations was 0.87. Using the above formulation to calculate the residual variance, our uncertainty (standard deviation) for our response variable (represented as τ) was calculated to be 0.14 log generation lengths.

We modelled our observed log generation length (y) for each species (i) as normally distributed, with some known uncertainty τ,

$$y_i \sim N\left(z_i, \tau\right), \tag{1}$$

where z is the latent true state for each species i. To account for spatial variability in environmental variables over each species range, we included a Berkson error component for our covariates. Berkson error models can be used to accommodate scenarios where the observed variation is smaller than the true variance (Buonaccorsi 2010; Foster, Shimadzu, and Darnell 2012) – in our case where we have a single value for each environmental variable, for each species, yet this variable varies across each species' range. We modelled w, the latent value for a given environmental variable, as normally distributed, with mean x, the mean value calculated across that species range, and standard deviation τ_x, the calculated standard deviation in that environmental variable across that species range,

$$w_i \sim N\left(x_i, \tau_{x_i}\right). \tag{2}$$

This introduces uncertainty into the model, according to the spatial variation that exists for each species. We use the variable M below to refer to a 7477 (i.e., number of species) by 5 design matrix containing log body mass, as well as the latent w values for each environmental variable (τ_{inter_T}, τ_{inter_P}, τ_{intra_T}, and τ_{intra_P}) for each species. Variable z was modelled as normally distributed.

$$z_i \sim N\left(\kappa + \gamma_j + \alpha_i + M_i\beta, \sigma\right), \tag{3}$$

where κ represents the grand intercept, γ represents an intercept for each niche category (j), α represents the phylogenetic intercept, β is a vector of length 5 representing the effect of the predictor variables on generation length, and σ is the residual error. Parameter estimates for a given element of β can be interpreted as 'the effect of a specific covariate, while accounting for the effect of all other covariates, diet, and phylogenetic effects'. Variance inflation factors for predictors were all under 3, suggesting that multicollinearity was not an issue for inference (Zuur, Ieno, and Elphick 2010). In other words, any relationship between the predictor variables, such as relationships between body size and environmental variables, did not have a substantial impact on parameters estimated in the model.

Parameter γ was modelled as normally distributed, with mean 0 and standard deviation σ_γ,

$$\gamma_j \sim N\left(0, \sigma_\gamma\right). \tag{4}$$

Parameter α was included to account for the phylogenetic non-independence among species, that is, the degree to which shared ancestry might account for similarities in generation length across species. The BirdTree phylogeny was rescaled using the Pagel's (1999) lambda transformation using the 'geiger' 2.0.11 (Pennell et al. 2014) and 'phytools' 2.1–1 packages (Revell 2012), before deriving a correlation matrix based on the branch lengths of the scaled tree. Transformations such as these provide flexibility in modelling phylogenetic relationships beyond assuming a Brownian motion model of evolution (Harmon 2019). Parameter α was modelled as a zero-centred multivariate normal,

$$\alpha_i \sim MVN\left(0, P\sigma_{phylo}\right), \tag{5}$$

where P is a correlation matrix derived from the scaled phylogenetic correlation matrix and σ_{phylo} is a parameter that scales the magnitude of the phylogenetic intercepts.

A Bayesian approach afforded us the flexible framework to fit this model and provided a means to accurately assess the uncertainty in our parameter estimates. We fit this model with R package 'cmdstanr' 0.6.1 (Gabry, Češnovar, and Johnson 2023) to interface with Stan 2.33.1 (Carpenter et al. 2017) in R 4.3.2 (R Core Team 2023). We used R package 'MCMCvis' 0.16.3 (Youngflesh 2018) to summarise, visualise and manipulate all Bayesian model output. We ran four chains for 4000 iterations, with a warm-up of 2000 iterations for each model. All parameters had R-hat values ≤ 1.01 and number of effective samples > 400. No divergent transitions were present (Carpenter et al. 2017). Weakly informative priors were provided for all parameters.

Graphical posterior predictive checks indicated that the data simulated from the posterior predictive distribution were similar to the observed data (Figure S2).

For all model results, we present the posterior mean estimates in addition to the 89% credible intervals (McElreath 2018). This choice of interval is arbitrary but quantifies uncertainty while avoiding any suggestion that Bayesian intervals are analogous to tests of significance or that this represents some threshold for an effect. Instead, we seek to quantify the effect size. To present the degree of evidence for the parameter estimates, we report the probability that a given parameter is positive as $p > 0$. This was calculated as the proportion of the posterior that was > 0. $p > 0$ values close to 1 or 0 represent strong support for a given parameter estimate, while $p > 0$ values close to 0.5 denote a positive value being as likely as a negative value.

2.4 | Rates of Relative Environmental Change

For each bird species, we calculated a metric of relative environmental change over our study period, scaled by both the inter-annual environmental variation and the generation length of the species. This metric is similar to the *haldane* used in evolutionary biology, which characterises rates of phenotypic change in terms of standard deviations per generation (Hendry and Kinnison 1999). We took the median estimated change in temperature and precipitation as a function of time (i.e., step one in the detrending procedure; θ) over the range of each species and scaled these by τ_{inter_T} and $\tau_{inter_P} \times \mu_P$, where μ_P is the mean precipitation for that cell (used to convert τ_{inter_P}, which represents the coefficient of variation, to the standard deviation), for temperature and precipitation, respectively, as well as generation length.

We use inter-, rather than intra-annual, variability as this reflects variation over time for any given portion of a species full annual cycle. For instance, for a species that breeds in a temperate environment, τ_{inter_T} is an indicator of how much temperature varies from one breeding season to the next. This is important given that species may have different physiological requirements across different portions of the full annual cycle. Our metrics of relative change are defined as,

$$\begin{gathered}\frac{\theta_{Ti}}{\tau_{\mathrm{inter}_{Ti}}} \times G_i = \delta_{Ti} \\ \frac{\theta_{Pi}}{\tau_{\mathrm{inter}_{Pi}} \times \mu_P} \times G_i = \delta_{Pi}\end{gathered}, \quad (6)$$

where i represents species, and G represents generation length. Parameter δ represents the rate of temperature and precipitation change in terms of standard deviations per generation for a given species. The scaling of θ (typically presented in terms of units per decade) allows us to interpret the rate of environmental change in the context of both baseline environmental conditions and species pace of life. Positive values indicate a species has experienced an increase in temperature or precipitation over time, while negative values indicate a species has experienced a decrease in temperature or precipitation over time.

3 | Results

3.1 | Environmental Variability, Species Traits, and Pace of Life

Inter- and intra-annual variability in both temperature and precipitation differed across the globe (Figure 1). As expected, in many areas (particularly when considering temperature in high latitude regions) variation was larger within than among years (median τ_{inter_T} and τ_{intra_T} equal to 0.38 and 1.19, respectively; median τ_{inter_P} and τ_{intra_P} equal to 0.15 and 0.52, respectively). Generation length varied across species, with a median of 3.0 years (inter-quartile range = 2.5–3.8 years; Figure 2). Double-barred finch (*Taeniopygia bichenovii*) had the shortest generation length at 1.4 years, while sulphur-crested cockatoo (*Cacatua galerita*) had the longest generation length at 27.2 years.

There was a positive estimated relationship between inter-annual variation in temperature and generation length. For each 1 standard deviation (across species) increase in inter-annual temperature variation (τ_{inter_T}), generation length increased by 0.52% (89% CI (0.011, 0.94), $P(>0) = 0.98$) – this corresponds to a 3.88% difference in generation length across the range of inter-annual temperature variability experienced by these species (Equation 3). The same relationship was seen for inter-annual precipitation, though the estimated effect of precipitation was somewhat uncertain. For each 1 standard deviation increase in inter-annual precipitation (τ_{inter_P}), generation length increased by 0.32% (89% CI [−0.038, 0.68], $p[>0] = 0.92$) – this corresponds to a 6.44% difference across the span of inter-annual precipitation (Figure 3). The effect of variability on generation length is multiplicative as the response variable is logged (i.e., percent change per SD is reflected by $\left(e^{\beta \times sd(\tau_{inter})} - 1\right) \times 100$).

We found the opposite pattern for intra-annual variation in temperature. For each 1 standard deviation (across species) increase in intra-annual temperature (τ_{intra_T}), generation length decreased by 2.21% (89% CI [−2.69, −1.73], $p[>0] = 0$) – this corresponds to a 16.38% difference across the span of intra-annual temperature experienced by species. Essentially no effect of intra-annual variation in precipitation was found. For each 1 standard deviation increase in intra-annual precipitation (τ_{intra_P}), generation length decreased by 0.04% (89% CI [−0.44, 0.37], $p[>0] = 0.56$) (Figure 3).

Body mass was strongly associated with generation length. For each 1 standard deviation increase in log(body mass), generation length increased by 40.8% (89% CI [39.6, 42.1], $p[>0] = 1$). Trophic niche was also associated with generation length (Figure 4). The largest difference in generation length between any two trophic niche categories was 18.56% (89% CI [10.85, 26.34], $p[>0] = 1$), between Herbivore Aquatic and Aquatic Predator (Figure S3; Equation 4). Strong phylogenetic signal appeared to be present for generation length across species (Pagel's

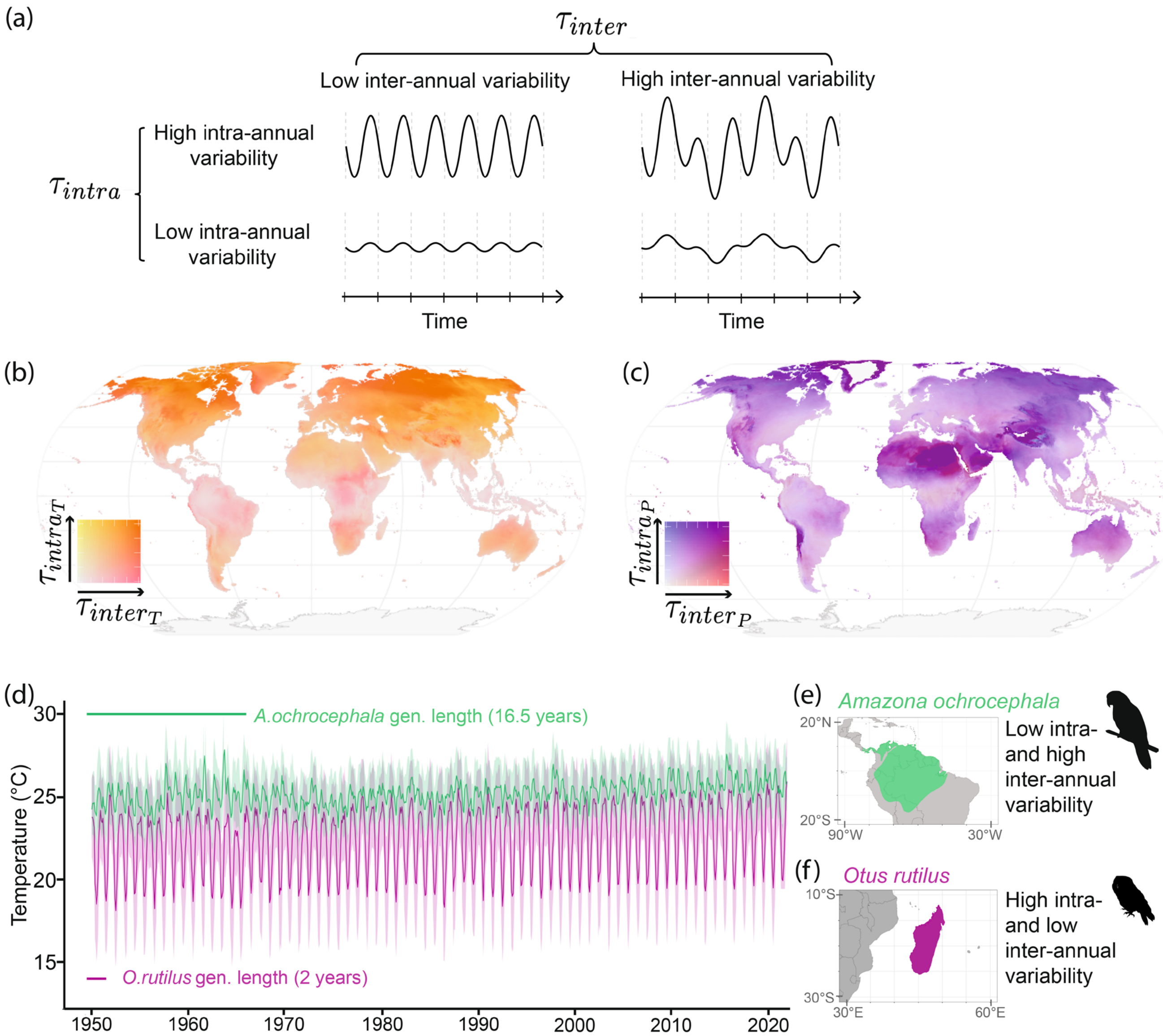

FIGURE 1 | Long-term data provide an opportunity to characterise global patterns of temporal environmental variation. (a) For a given area, environmental variation over time can be decomposed into inter-annual (across years, τ_{inter}) and intra-annual (within years, τ_{intra}) components for both (b) temperature and (c) precipitation. (b) Red hues represent high inter-annual and low intra-annual variation, yellow hues represent low inter-annual and high intra-annual variation, and orange hues represent both high inter-annual and high intra-annual variation. (c) Pink hues represent high inter-annual and low intra-annual variation, blue hues represent low inter-annual and high intra-annual variation, and purple hues represent both high inter-annual and high intra-annual variation. (d) Variation in temperature over time for two focal species: Yellow-crowned amazon (*Amazona ochrocephala*) exhibiting a slow pace of life (i.e., long generation length), low intra-annual and high inter-annual variation; Madagascar scops owl (*Otus rutilus*) exhibiting a fast pace of life, high intra-annual and low inter-annual variation. The magnitude of inter-annual variation is generally smaller than intra-annual variation across the globe. (e) Distribution of *A. ochrocephala*. (f) Distribution of *O. rutilus*.

Lambda = 0.96, where 0 represents no phylogenetic signal and 1 is maximal signal).

3.2 | Rates of Environmental Change Relative to Inter-Annual Variability and Generation Length

Across species, temperatures increased at a rate of 0.14 temperature standard deviations per generation (median δ_T, inter-quartile range = 0.10–0.21) from 1950 to 2022 (Equation 6). Approximately 76% of species experienced rates of temperature change $> 0.1\left|\delta_T\right|$, while 12% of species experienced rates of change $> 0.3\left|\delta_T\right|$ (Figure 5a). Thresholds of 0.1 and 0.3 are derived from maximal rates of estimated evolutionary change from Bürger and Lynch (1995) and Gingerich (2009). Precipitation was found to be increasing at a rate of 0.04 precipitation standard deviations per generation (median δ_P, inter-quartile range = 0.01–0.08) over this period. Approximately 17% of species experienced rates of precipitation change $> 0.1\left|\delta_P\right|$, while 1% of species experienced rates of change $> 0.3\left|\delta_P\right|$ (Figure 5b). Parameters δ_T and δ_P were positively correlated ($\rho = 0.47$). Change experienced per generation (δ) was positively correlated with generation length (G;

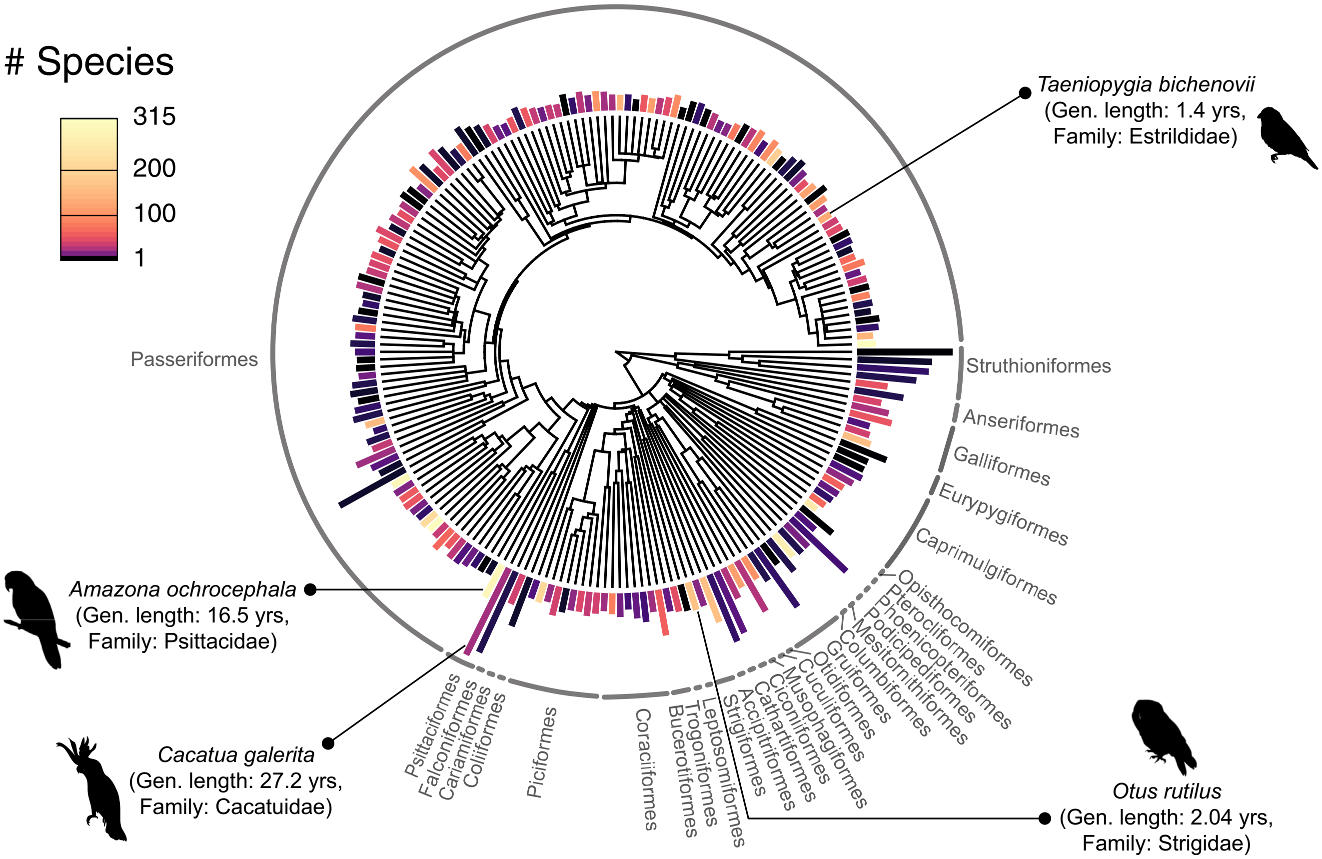

FIGURE 2 | Pace of life varies across the avian tree of life. The phylogeny shows 198 families of non-migratory birds corresponding to 29 orders, representing 7477 species. Mean generation length per family is given by the height of the bars while the number of species in each family is indicated by the colour ramp. Pointers show the two focal species from Figure 1 (*Amazona ochrocephala* and *Otus rutilus*) representing contrasting patterns of environmental variation and pace of life, as well as the species with the longest (sulphur-crested cockatoo *Cacatua galerita*) and shortest generation lengths (double-barred finch *Taeniopygia bichenovii*) on record.

$\rho_T = 0.69$, $\rho_P = 0.47$) and with relative rates of environmental change ($\frac{\theta}{\tau}$; $\rho_T = 0.64$, $\rho_P = 0.82$).

4 | Discussion

Integrating a collection of global data resources, we demonstrate a link between both inter- and intra-annual environmental variation and the life history of 7477 species of birds from around the world, representing nearly the entirety of the world's non-marine, non-migratory bird species. In support of long-standing theory, higher inter-annual variability in temperature was associated with a slower pace of life. Higher intra-annual (generally associated with seasonal) temperature variability, however, was associated with a faster pace of life. Associations between precipitation variability and pace of life were more uncertain. While data complexities present a significant challenge for global analyses such as this, we accommodated this structure, including uncertainty in both response and predictor variables using a flexible hierarchical Bayesian framework. Adapting an approach from evolutionary biology, we derived rates of environmental change relative to both the environmental variability experienced by species as well as their pace of life. Results demonstrate the rapid nature of these changes from an evolutionary perspective and illustrate how species are differentially experiencing environmental change due to differences in life history and environmental variability.

4.1 | Bet Hedging in the Face of Inter-Annual Variation

Our global analysis provides empirical support for the theoretical assertion that a slower pace of life can act as a mechanism to buffer organisms from inter-annual variability (Capdevila et al. 2022; Jackson, Le Coeur, and Jones 2022) – an idea for which there stands a substantial body of theory dating back to the 1960s (Le Coeur et al. 2022; Metcalf and Koons 2007; Murphy 1968; Stearns 1976). A slower pace of life, characterised by longer generation lengths, will result in reproductive effort spread across more years (Stearns 1976). For 'slow' species, 1 year with poor environmental conditions for reproduction will tend to have a relatively small impact on an individual's lifetime reproductive output as well as the total number of individuals in the population (Morris et al. 2008). This is due to the tendency for adult survival to vary less from year to year in response to fluctuating environmental conditions and for

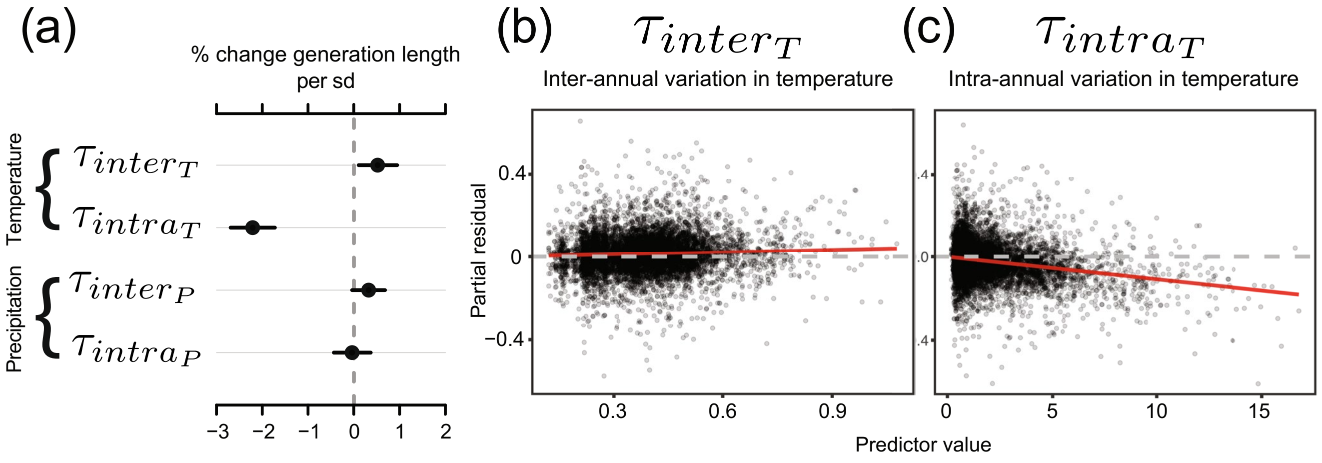

FIGURE 3 | Both inter- and intra-annual temperature variability are associated with pace of life across the world's birds. (a) Parameter estimates can be interpreted as the percent change in generation length per one standard deviation change in the associated predictor (τ_{inter_T}, τ_{intra_T}, τ_{inter_P}, and τ_{intra_P}). Points represent posterior medians while lines represent 89% credible intervals. (b) Partial residual plots for τ_{inter_T} and (c) τ_{intra_T}, showing their relationship with generation length given other variables included in the model (Equation 3). The red lines represent the effect size of that element of environmental variation while each point represents one species. One outlier not visible for the purposes of visualisation.

population growth rates to be relatively insensitive to changes in reproductive output (i.e., fecundity) for species with a slow pace of life (Gaillard and Yoccoz 2003; Sæther and Bakke 2000). For species that exhibit a slow pace of life, individuals may skip breeding entirely in years with poor environmental conditions (Martin and Mouton 2020; Talis et al. 2022). Slow pace of life can be thought of as a 'risk averse' or 'bet hedging' strategy, similar to buffering strategies seen in other ecological contexts (Zohner et al. 2017). Species with alternating boom-bust dynamics that are likely to result from fast pace of life in highly variable environments (Jackson, Le Coeur, and Jones 2022; Rademaker, Van Leeuwen, and Smallegange 2024) would, on average, be expected to exhibit a higher overall probability of local extinction over the long-term (Murphy 1968). Over time, this is likely the mechanism by which slow pace of life has come to be associated with higher inter-annual variability (Figure 3).

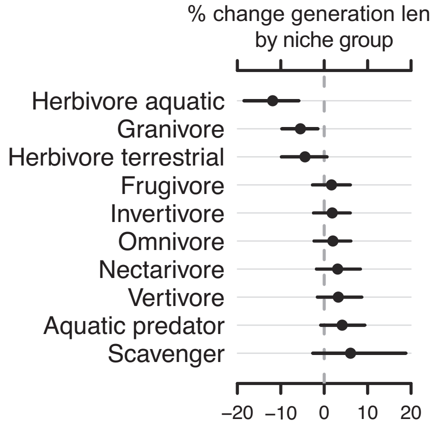

FIGURE 4 | Pace of life varies by niche group. Parameter estimates can be interpreted as the percent change in generation length relative to the cross-niche group mean, given membership in a particular niche group, as provided in AVONET. Points represent posterior medians while lines represent 89% credible intervals.

4.2 | Faster Pace of Life With Higher Intra-Annual Variation

In contrast to inter-annual variation, higher intra-annual variation in temperature was associated with a faster pace of life. Intra-annual variation is indicative of the differences that a species experiences over the full annual cycle (Marra et al. 2015), over which species may have different energetic requirements and exhibit different behaviours. Our findings are in agreement with previous studies showing that higher seasonality is associated with traits typically linked to a faster pace of life (Jetz, Sekercioglu, and Böhning-Gaese 2008; Yanco, Pierce, and Wunder 2022). Past work has placed a particular focus on observed differences in bird clutch sizes between the Nearctic (characterised by high intra-annual environmental variability and large clutch sizes) and Neotropics (characterised by low intra-annual environmental variability and small clutch sizes) (Lack 1947; Martin 1995; Skutch 1949). Observed patterns have been proposed to result from lower adult survival in the more seasonally variable Nearctic, where inhospitable conditions during the non-breeding season, including cold temperatures and limited food resources, may create a demographic bottleneck (Martin 2004; Martin et al. 2000; Ricklefs 1997). This pattern holds in our results. It should also be noted, however, that despite our interpretation of intra-annual variation in environmental conditions as tightly linked with seasonality, variation within a given year that might not necessarily be considered seasonality (i.e., what might be thought of as stochastic, unpredictable variation within a year) will also contribute to these measures.

4.3 | An Integrated Approach to Understanding Life History

Because of the contrasting effects of inter- and intra-annual variability (Figure 3) and variation in each of these metrics across the globe (Figure 1), it is critical to assess their effects on life history simultaneously, a key contribution of our study

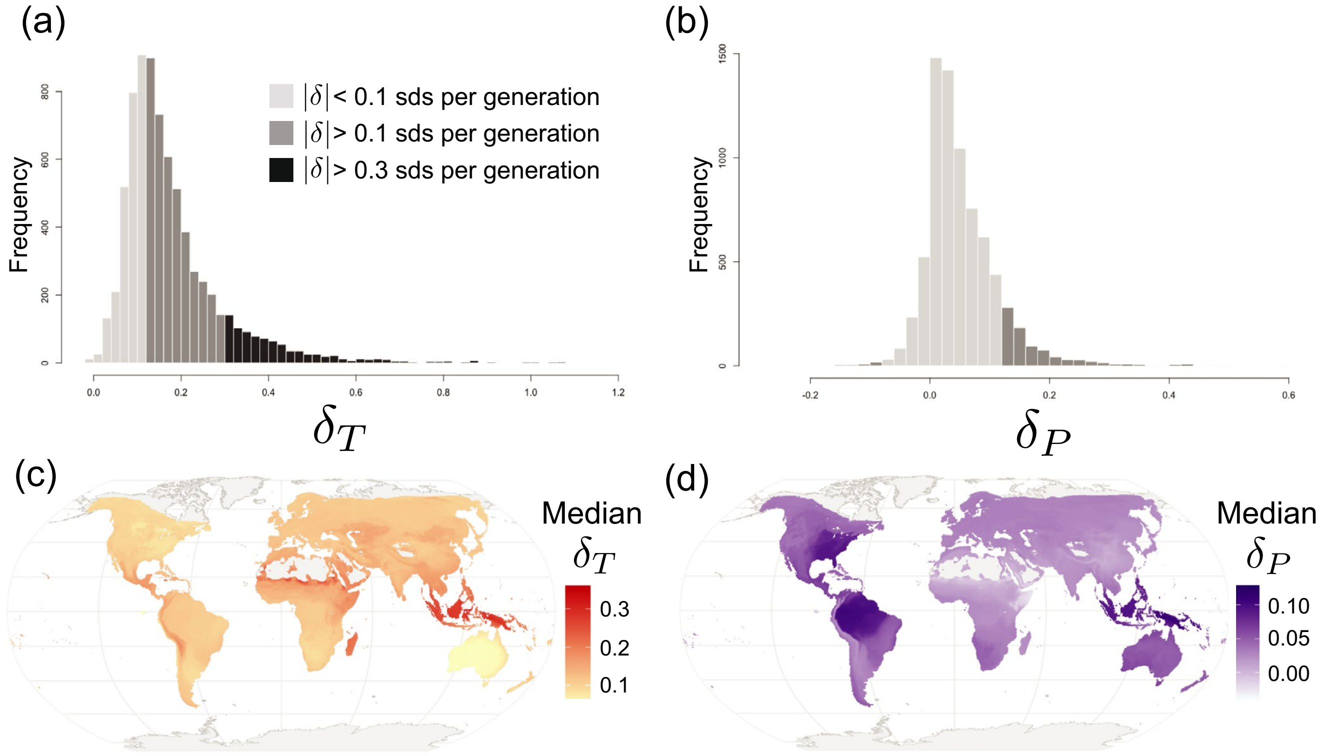

FIGURE 5 | Environmental change over the last 73 years is relatively rapid considering the variability of these systems and species generation lengths. Histograms show the rates of (a) temperature change (δ_T; Equation 6) and (b) precipitation change (δ_P; Equation 6) experienced by the world's non-migratory bird species. Dark grey and black bars represent those species where the rate of experienced change (either positive or negative) is > 0.1 and 0.3 standard deviations per generation, respectively. (c) Median δ_T and (d) δ_P across all species in each cell across the world. Cells with fewer than 10 species are shown in grey.

(Figure S4). The effect of intra-annual variation in temperature on pace of life was larger than that of inter-annual variation in temperature. Some support exists for the effect of inter-annual precipitation, though some uncertainty exists. That variability in temperature showed a more pronounced effect than variability in precipitation highlights the complex effects of precipitation that might vary across ecological systems (Liu et al. 2020) (Figure 3). Ultimately, these metrics are proxies for conditions that are likely to impact demographic rates, such as resource availability. Other elements of environmental variation, such as temporal autocorrelation in conditions (i.e., the propensity for a consecutive string of favourable years), may play a role in shaping life history as well (Bitter et al. 2021; Marshall and Burgess 2015; Metcalf and Koons 2007). However, in our dataset, measures of temporal autocorrelation were positively correlated with our measures of variability, preventing us from parsing the effect of one from the other.

While the effect size of environmental variability on pace of life is relatively small, these observed patterns were apparent despite the vastly different ecologies of our study species, which spanned 29 taxonomic orders. Given the pronounced phylogenetic signal present for generation length, it is likely that there are some limitations (McKitrick 1993) on the degree to which generation length can change over evolutionary time scales (i.e., there exists some phylogenetic constraint). A number of other factors, including predation (Taylor and Gabriel 1992) and competition (Wright et al. 2019) might also play a role in shaping pace of life. However, a recent synthesis suggests that evidence for the role of predation and competition is limited (at least on relatively short time scales) (Grainger and Levine 2022). Other mechanisms besides pace of life may also help organisms cope with variable conditions, including the use of cooperative breeding strategies (Rubenstein and Lovette 2007), developmental and behavioural plasticity (Bauer, McNamara, and Barta 2020), metapopulation dynamics (Hanski 1998), and seasonal migration (Somveille, Rodrigues, and Manica 2015). These mechanisms may explain why, despite the general trends we observe here, we see a range of pace of life strategies in many environments. It should also be noted that intra-annual variability varies across a latitudinal gradient. A number of ecological variables have been found to vary across latitude, including species richness (Hillebrand 2004), body size both within (Youngflesh et al. 2022) and among species (Meiri, Yom-Tov, and Geffen 2007), and range size (Stevens 1989), with varying explanations as to their cause, including temperature, productivity, and competition. The degree to which these processes, that might covary with environmental variability or mediate its impact, deserves more attention in future work.

We found that pace of life was associated with both body size, which is known to have a strong association with life history, as well as dietary niche. Life history, especially reproduction, has long been thought to depend on food availability (Lack 1947), though this has been the subject of some dispute in the literature (Jetz, Sekercioglu, and Böhning-Gaese 2008; Owens and Bennett 1995). Prior work in mammals has suggested that more offspring (a trait associated with a faster pace of life) are generally produced by species with more reliable food resources (Sibly and Brown 2007). Our results support this notion, with those species that rely on vegetation and seeds (likely a more consistent resource from year to year) to generally have a faster pace of life, and species that consume other terrestrial animals to exhibit a slower pace of life (Sibly et al. 2012; Figure 4). In this way, dietary niche represents an additional dimension of how organisms experience environmental variability.

4.4 | Putting Rates of Environmental Change Into the Appropriate Contexts

In assessing how species are experiencing ongoing environmental change, it is critical that we consider both the historical conditions experienced by those species as well as their pace of life, which necessarily impact how they experience their environment. Species that experience a wider range of environmental conditions (i.e., variation around some mean) are more likely to be tolerant of a wider range of conditions. This idea has been formalised in the context of thermal tolerances, in the form of the climate variability hypothesis (Gaston 2003; Janzen 1967; Stevens 1989), where broader thermal tolerances are expected in more variable climates. This principle can be extended to consider any dimension of environmental variability. Simply put, if a species cannot cope with existing environmental variability, it will cease to persist in that environment. In the context of global change, organisms in more variable environments would be expected to experience a lower effective degree of change compared to organisms in a more constant environment, given the same degree of change (i.e., directional change in that mean) over time (Deutsch et al. 2008; Jenouvrier et al. 2022).

Pace of life must also be considered, however, when putting rates of environmental change into context. While organisms with a slower pace of life (i.e., longer generation lengths) are expected to be more robust to environmental variability (Le Coeur et al. 2022; Metcalf and Koons 2007; Stearns 1976), these species will tend to adapt to directional change in those conditions at a slower rate (Lande 1982; Schmid et al. 2022). Fewer generations over a given period means fewer opportunities for selection to operate and thus slower evolutionary adaptation. As such, species experiencing higher rates of environmental change per generation may likely be those that suffer the greatest consequences.

In scaling rates of environmental change by both the variability of a given system and a species' pace of life, we can build a more accurate picture of how species are experiencing this change. We found relatively rapid rates of change for temperature and precipitation from 1950 to 2022 for a large fraction of the bird species considered (Figure 5). More than 75% of species experienced rates of temperature change >0.1 standard deviations per generation (δ; Equation 6), while more than 10% experienced rates >0.3 standard deviations per generation. For context, 0.1 standard deviations per generation was previously estimated to be the maximum rate of sustained evolutionary change for a phenotypic trait (Bürger and Lynch 1995), though rates of up to 0.3 standard deviations have been observed (Gingerich 2009). While species' capacities to adjust to environmental change might not map to rates of phenotypic change 1:1, these hypothesised limits provide a useful benchmark for interpreting how rapidly the environment is changing. Species are also adapting to climate change in ways other than phenotypic change, including shifts in species' ranges (Chen et al. 2011; Rushing et al. 2020) and phenology (Parmesan and Yohe 2003), however, research suggests these responses are also not keeping pace with climate change and exhibit considerable complexities (Liang et al. 2018; Youngflesh et al. 2021, 2022, 2023). We suggest that while rates of environmental change are typically reported in units such as degrees per decade, the magnitude of these changes should be put into the appropriate context if we hope to determine which species or systems are likely to be most susceptible to climate change.

5 | Conclusions

Despite the many factors and constraints on species' life history, our results illustrate how environmental variability has played a key role in shaping pace of life across the world's non-marine, non-migratory birds. Importantly, environmental variability is multi-dimensional. The scale at which this variability occurs influences how species experience and interact with their environment. While we focus on variation across and within years, variability across other time scales, particularly for species with generation lengths of <1 year (e.g., many invertebrates), also likely play a relevant role. Ultimately, these findings contribute to our understanding of the macroecological and eco-evolutionary processes that shape these communities and support long-standing theoretical predictions for the relationship between environmental variation and life history.

These theoretical and empirical efforts represent a critical component in elucidating the impacts of global change, particularly given potential future increases in environmental variation (Donat et al. 2016; Hansen et al. 2014), and the projected increased frequency of extreme events (Diffenbaugh et al. 2017). These changes may themselves be driving shifts in species life histories over time (Ozgul et al. 2023), and rates of environmental change must be interpreted in light of both the degree of historical variability and species pace of life. Such an integrated perspective is needed if we are to effectively target conservation efforts to species and systems of greatest concern.

Author Contributions

C.Y., K.K., A.U., P.J.W., and L.K. conceived of the study, C.Y., K.K., A.U., P.J.W., J.W.D., L.K., and P.L.Z. designed the study. C.Y., K.K., A.U., P.J.W., J.W.D., and L.K. synthesised the data and performed analyses, C.Y. led the organisation of the manuscript, and all authors contributed to writing and/or editing.

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Data Availability Statement

Data necessary to fit the models presented here in addition to derived metrics of environmental variability are archived with the Environmental Data Initiative (DOI: https://doi.org/10.6073/pasta/31b676ea512fe95e8702d209c75dd5fb). All code to reproduce analyses are freely available on GitHub (https://github.com/IBEEM-MSU/ibeem_variability) and are archived with the Environmental Data Initiative (DOI: https://doi.org/10.6073/pasta/31b676ea512fe95e8702d209c75dd5fb). Raw climate data are available from the National Center for Atmospheric Research (1950–1978 DOI: https://doi.org/10.5065/JAXB-X906, 1979–2022 DOI: https://doi.org/10.5065/P8GT-0R61), bird range maps are available from (BirdLife International, 2022), bird generation length data are available from Bird et al. (2020) (DOI: https://doi.org/10.1111/cobi.13486), bird trait data are available from Tobias et al. (2022) (DOI: https://doi.org/10.1111/ele.13898), and bird phylogeny data are available from Jetz et al. (2012) (DOI: https://doi.org/10.1038/nature11631).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.