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Life-history predicts global population responses to the weather in the terrestrial mammals

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Abstract

With the looming threat of abrupt ecological disruption due to a changing climate, predicting which species are most vulnerable to environmental change is critical. The life-history of a species is a promising candidate for explaining differences in climate-change responses, but we now need data linking population change, weather and life-history to explore these predictions. Here, we use long-term abundance records from 157 species of terrestrial mammals to investigate the link between weather and annual population growth rates. Overall, we found no consistent effect of temperature or precipitation anomalies on annual population growth rates, but there was variability in weather responses for populations within a species. Crucially, however, long-lived mammals with smaller litter sizes had responses with a reduced absolute magnitude compared to their shorter-living counterparts with larger litters. These results highlight the role of species-level life-history in driving responses to the environment.

Introduction

Climate change is one of the greatest challenges we face in the twenty first century[1]. Although habitat loss and direct exploitation are currently the greatest drivers of extinction in the natural world[1,2], changes to the climate are predicted to cause widespread declines to global biodiversity in the coming decades[3–5]. For mammals and birds, temperature increases are already associated with declining population trends[6] and many endangered species have already been negatively impacted by climate change in at least part of their range[7]. Perhaps more worryingly, abrupt ecological disruption due to runaway climate change has been predicted to have large negative impacts on biodiversity, with tropical ecosystems being affected as early as 2030[8]. Furthermore, these future impacts will likely be exacerbated by synergism between the climate and other drivers of extinction such as habitat loss[9,10]. Research highlighting the species and ecosystems that are most vulnerable to climate change impacts will therefore provide crucial knowledge to prevent future losses to global biodiversity.

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Not all species are equally vulnerable to climate change. Species vary in their climatic niches and in their behavioural, physiological, and demographic responses to environmental change and we therefore expect there to be both climate 'winners' and 'losers'[11–13]. At a macro-scale, species occupancy data highlight that geographic range shifts are the key response associated with climate change across taxa, resulting in changes to community composition, but not necessarily population decline[14,15]. Recent broad assessments of biodiversity change metrics from species assemblage and abundance records mirror this paradigm with both occupancy and abundance trend patterns suggesting a balanced frequency of winners and losers[15,16]. In the Marine realm, species richness increases were associated with warming temperatures, consistent with the expectation that warming marine ecosystems will receive an influx of species tracking suitable temperatures[12]. However, there was no consistent temperature-related biodiversity change effect on land[12]. Changes in species richness and other biodiversity metrics however do not necessarily equate to population declines. For birds and mammals average abundance trends were negatively associated with rates of climate warming[6]. Studies unpicking how changes in weather patterns cause population change are therefore vital[17], and a growing body of literature is exploring the relationship between the climate and the demographic processes driving population decline[18–22]. Applying these concepts at a comparative scale and assessing finer-scale population changes with respect to changes in the weather, and their relationship to species traits, will aid in illuminating consistent or disparate climate change responses across the tree of life[21,23].

Variation in the demographic responses of organisms climate change suggests that life-history is a promising target for explaining responses to environmental change. The timing of demographic events relating to the key demographic rates of survival and recruitment are evolved responses to the environment, and characteristics relating to both 'slow' and 'fast' life-histories are therefore adaptive in different environmental contexts[24]. Indeed, Pacifici et al.[7] concluded that intrinsic traits, including habitat specialisation and aspects of life-history, were associated with negative climate-mediated population effects reported in mammals and birds. Life-history differences between three amphibian species in Western Europe drove differences in survival and reproduction in response to the North Atlantic Oscillation[25]. Generally, we expect that organisms with slower life-histories are better-adapted to cope with fluctuations in the environment. Longer-lived organisms have a reduced relative effect of variability in vital rates, variability which is expected during environmental change, on population growth rates[26] and long-lived plants have weaker absolute demographic responses to weather[23]. Furthermore, the recently developed concept of demographic resilience uses demographic rates characterising the life cycle of an organism to quantify their resilience to perturbations[27]. Comparative approaches linking life-history traits to climate change responses may therefore provide a crucial predictive link to improve our understanding of climate vulnerability.

In this study, we investigated annual population responses to temperature and precipitation in populations of terrestrial mammals across the world's ecosystems. Importantly, we tested whether life-history predicts population responses to the weather, and therefore its utility in assessing vulnerability

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to climate change. We addressed these questions using 486 long-term (≥10 years) abundance records from 157 species of terrestrial mammal obtained from the Living Planet Database[4], by implementing a two-step meta-regression framework. First, for each abundance record, we assessed how observed annual population growth rates were influenced by weather anomalies (annual deviation from long-term average weather patterns) using autoregressive additive models that accounted for temporal autocorrelation in abundance records and overall abundance trends. Then, we used a phylogenetically controlled Bayesian meta-regression with weather effect coefficients as the response variable to address three key questions: 1) Are there consistent temperature and precipitation effects on abundance change across the terrestrial mammals? 2) How are these patterns influenced by covariance both within and between species, and are there vulnerable biomes? 3) Can species-level life-history traits predict the magnitude of population responses to the weather? The terrestrial mammals are an ideal study system to explore the predictors of population responses to climate change because they are a well-studied group with a combination of intensive abundance monitoring across the globe[4], detailed life-history information for hundreds of species[28,29] and a highly-resolved phylogeny to facilitate phylogenetic comparative analyses[30]. Furthermore, there is growing evidence from the mammals of the mechanistic links between the climate, demography, and population dynamics[17,20–22].

In light of previous findings from studies exploring biodiversity change metrics and life-history theory in the context of environmental change, we make the following predictions related to our three key questions. First, reflecting the complexity of overall biodiversity change and the paradigm of climate winners and losers[12,15,16], we predict that across the mammals there will be no consistent responses to temperature and precipitation. Second, recent evidence has highlighted phylogenetic covariance between demographic traits[31], which may also scale to population responses. However, spatial variation between study sites, heterogeneity across a species range and the complex interaction of demographic traits to drive population dynamics may reduce phylogenetic covariance. Finally, we predict that organisms with slow life-histories will be more resilient to weather effects, reflecting an evolutionary adaptation to buffer against fluctuating environments[26]. We therefore expect responses to weather to have a higher magnitude in short-living organisms with larger reproductive output compared to their longer-lived counterparts.

Results

We assessed population responses to weather in 486 long-term abundance time-series records of 157 species of terrestrial mammals from across the world's ecosystems (Fig. S1). The time-series records ranged in duration from 10 years to 35 years, with mean and median record lengths across records of 15.7 and 14 years, respectively (Fig. S1). The records were distributed across 13 terrestrial biomes, including both tropical and temperate regions, but were generally biased towards north western Europe and North America. We had records from 12 of 27 mammalian orders recognised by the IUCN Red List for threatened species[32], but most densely in the Artiodactyla (n = 172), Carnivora (n = 127) and

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Rodentia (n = 82) (Fig. S1). The number of records for each species ranged from 1-17, with a mean of 3.1 and median of 2 records per species.

No consistent population response to weather

Overall, we found no consistent effect of either temperature or precipitation anomalies on annual population growth rates in the terrestrial mammals (Fig.1). The raw weather effects on population growth rates, ω, varied across species and records but were centred close to 0, with a mean temperature coefficient of -0.08 ($\pm$0.73 SD; Fig. 1a) and mean precipitation coefficient of 0.02 ($\pm$0.36 SD; Fig. 1b). Furthermore, 95% of records had temperature and precipitation coefficients between -1.87-1.38 and -0.59-0.83, respectively. Nevertheless, approximately 10% (n = 51) of temperature effects and 3% of precipitation were greater than 1 or less than -1, indicating that small clusters of populations experienced more extreme annual responses to the weather (Fig.1). Our Bayesian meta-regression, controlling for both within species variance, phylogenetic covariance and differences in sample size (number of years) between records, mirrored the lack of consistent weather effects on population growth. The posterior mean global intercept, $\bar{\alpha}$, for temperature effects was 0.07 [-0.17-0.33] (95% credible intervals) and for precipitation effects was -0.06 [-0.28-0.14] (Fig.1a and Fig.1b). There was, however, a small positive effect of the number of years of population data for a record and the response to temperature, with a linear slope, β_N of 0.09 [0.0-0.18]. Together with the results of the global intercept $\bar{\alpha}$, this suggests that shorter records were associated with more negative temperature effects. Overall, these results highlight the paradigm of the existence of both winners and losers in weather responses, but no clear effect across the Mammalia.

Spatial effects and variation between species

We tested whether there were differences in weather responses among ecological biomes because biome effects may be indicative of more extreme responses to weather in some habitats. Using leave-one-out cross-validation, we compared the predictive performance of the model including the effect of biome relative to the base model, and we found no evidence for an influence of biome on either temperature (Δelpd = -0.67 relative to base model) or precipitation (Δelpd = -0.73) effects (see Fig. S15-16 for more information). Furthermore, we explored the role of spatial autocorrelation at driving differences in weather coefficients across records using Morans I tests and spatially explicit meta-regressions but did not find evidence for spatial autocorrelation in weather effects (Figs. S18-S20). We also incorporated both phylogenetic covariance (σ^2_{PHYLO}) and species-level variance ($\sigma_{SPECIES}$) to capture both among- and within-species variation. Interestingly, we found far greater levels of within-species variation in temperature responses compared to among-species variance (Fig. 1c). The posterior mean for species-level variance in temperature effects was 0.2 [0.01-0.4] which was 20 times greater than the posterior estimate of 0.01 [0.0-0.03] for phylogenetic covariance (Fig. 1c). Similarly, for precipitation the

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posterior mean for species-level variance was five times greater than for phylogenetic covariance, with a value 0.05 [0.0-0.15] compared to 0.01 [0.0-0.02] (Fig. 1c). These patterns are reflected in the temperature and precipitation coefficients, for which large variation can be seen among records of the same species. For example, *Myodes glareolus* (bank vole) in the Rodentia had 9 population records, and a range of temperature/precipitation effects of -1.64-3.59 and -1.27-1.44 respectively, compared to -3.32-5.67 and -1.27-1.44 across Rodentia as a whole (Fig.1). This result highlights the potential importance of within-species variability in population responses to environmental change.

Life-history predicts population responses to weather

Across the terrestrial mammals, we found that both maximum longevity and mean litter size at the species-level predicted the magnitude of population responses to weather. We tested a set of Gamma models incorporating univariate, multivariate and 2-way interactions between maximum longevity, litter size, and adult body mass and their influence on the absolute magnitude of temperature/precipitation effects using model selection and leave-one-out cross-validation (Table S1 & S2). As with our Gaussian models of overall weather effects, we found that the sample size of a record had strong negative impact on the absolute temperature and precipitation responses, with posterior estimates on the linear predictor scale of β_N = -0.26 [-0.35- -0.16] and β_N = -0.35 [-0.46- -0.24], respectively (Fig. S17). Namely, shorter records were associated with temperature and precipitation responses of a larger magnitude. We found no association between adult body mass and either temperature ($\beta_{BODYMASS}$ = -0.01 [-0.19-0.16]) or precipitation responses ($\beta_{BODYMASS}$ = 0.03 [-0.20-0.25]). Furthermore, we found no strong evidence for any two-way interactions between life-history variables (Table S1 & S2). For both temperature and precipitation effects, the most competitive model was the univariate model including mean litter size (Δelpd = 3.03 and Δelpd = 3.00, compared to the base model for temperature and precipitation, respectively; Table S1 & S2). However, univariate models including maximum longevity alone also had a higher predictive performance than the base model (Δelpd = 0.94 and Δelpd = 1.67 for temperature and precipitation, respectively). In both cases the second-best predictive model was the one that included univariate effects for longevity, bodymass and litter size (Δelpd = 2.88 and Δelpd = 2.94; Table S1 & S2). Therefore, we selected the models including all univariate life-history effects.

For both temperature and precipitation, our results highlight that shorter-living mammals with greater litter sizes experienced weather effects of a significantly greater magnitude than longer-living, slowly reproducing mammals (Fig. 2). The magnitude of weather responses was negatively associated with longevity, with posterior means on the linear predictor scale of $\beta_{LONGEVITY}$ = -0.19 [-0.44-0.07] and $\beta_{LONGEVITY}$ = -0.24 [-0.57-0.07] for temperature and precipitation, respectively (Fig. 2a & 2c). Thus, a maximum longevity change from 10 months (*Akodon azarae*) to 80 years (*Loxodonta africana*) was associated with a 2.3-fold and 2.9-fold decrease in the predicted magnitude of responses to

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temperature and precipitation. So, for every additional 5 years of life, there was a 14% decrease in the magnitude of responses to temperature and 18% decrease in the magnitude of responses to precipitation. An organism's longevity is strongly correlated to their body mass, but the effect of longevity held irrespective of whether adult body mass was also included in the model. In contrast, but also following key predictions from life-history theory, the magnitude of weather responses had a strong positive association with litter size, with posterior means of β_{LITTER} = 0.33 [0.13-0.52] and β_{LITTER} = 0.30 [0.06-0.54] for temperature and precipitation, respectively (Fig. 2b & 2d). In other words, mammals bearing more offspring in a single litter had greater responses to temperature and precipitation. A change in litter size from 1 (monotocous species, various) to 17 (*Thylamys elegans*) was associated with a 4.17-fold and 3.71-fold increase in the predicted magnitude of temperature and precipitation responses. For every additional offspring invested into at the litter stage, there is a 24% increase in the magnitude of temperature responses and 22% increase in the magnitude of precipitation responses.

Discussion

Our results provide an important empirical link between a species' life-history and its population responses to environmental change. While we found no consistent patterns of responses to temperature and precipitation anomalies across the mammals, life-history traits relating to the pace of life were associated responses to weather. Namely, shorter-living species with increased litters sizes, or species characterised with 'fast' life-history traits, responded with a greater magnitude compared to those with 'slow' life-history traits. While it has long been theorised that an organism's life-history traits evolve in response to, and as an adaptation to, environmental conditions[24], rarely has this theory been tested at a global scale. We find strong support for the hypothesis that longevity, and 'slow' life-history characteristics more generally, buffer organisms against variability in the environment[26] and add to a small number of studies linking population demography and the climate[21,23]. Critically, our results highlight the potential utility of life-history traits for predicting species vulnerability to climate change. Based on our findings, abrupt ecological disruption from climate change will disproportionately impact shorter-lived species with higher reproductive output.

Demography has a vital role to play in predicting population declines in the Anthropocene and in highlighting targets for conservation management[28,33]. Our study emphasises this role, demonstrating the predictive power of demographic life-history traits when investigating responses to environmental change. However, there are limitations and barriers to the utility of demography in conservation. Only 1.3% of tetrapods globally have sufficient demographic information with which to estimate population dynamics[28]. Here, we used summary traits that are available for many species (maximum longevity and mean litter size), but in particular maximum recorded longevity, while sufficient as a broad indicator, is strongly influenced by sampling variance and a flawed measure of longevity differences between taxa[34]. Ideally, lifetables with mortality and reproduction trajectories across the lifecycle can be combined data on external drivers to investigate detailed patterns in population dynamics[35,36]. The

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recent development of the demographic resilience framework, which uses demographic data across the lifecycle to simulate how a population may respond to perturbations[27], has excellent potential in extending these findings to explore demographic relationships with climate responses in detail. Unfortunately, however, detailed (st)age-specific demographic information is not currently available for a majority of species, but growing in availability rapidly[37]. Therefore, there is a need to continue to increase the collection of demographic data (and other traits) for many more species than are currently available[28], so that we may predict population changes with respect to environmental change. Achieving this target may revolutionise the way we quantify species vulnerability to climate change[12,15,16,21], helping to prevent extinctions before they occur.

In line with recent global assessments of biodiversity in the face of climatic change[21], we did not find an overall consistent effect of weather anomalies on population growth rates. This may in part reflect the fact that abundance changes are a higher-order process determined by complex interactions between demographic processes that counteract each other[16,21]. However, our results contrast with findings of linear associations between mammal abundance and temperature change[6]. These differences may reflect our approach to investigate annual changes, rather than long-term trends. Significant population trends from long time-series are detectable from smaller component time-series even when sampling is incomplete[38], and thus responses detected in trends may reflect broader changes in response to the climate that are not detected in models of annual change. Furthermore, we estimated linear, annual effects of weather on population growth rates, where population responses may actually be more complex non-linear patterns or lagged effects. However, the detection of climate effects on average trends may also be confounded by effects of other (sometimes more dominant) drivers (e.g. habitat loss)[2]. Nevertheless, our findings can be explained in light of recent studies from the Living Planet Database that have found that the large majority of records do not exhibit population declines[16].

Interestingly, we did not find evidence for phylogenetic covariance in weather responses between species. Recent evidence from birds indicated strong phylogenetic covariance in vital rates, particularly in adult survival, and the incorporation of phylogenetic information greatly improved predictive performance when imputing vital rates[31]. Therefore, as with overall patterns, our findings may reflect the trade-offs between vital rates, which cancel one another out when scaling up to population-level processes such as population growth rates in response to the weather[21]. Furthermore, for long-term time-series, there may also be temporal trade-offs in vital rates, where for example investing heavily into survival in one year (in response to climate) may impact subsequent reproduction for several years, decreasing the magnitude of population growth rates. The extent of phylogenetic covariance in vital rate responses and trade-offs remains unknown, understanding how the climate impacts demographic rates across species may provide a useful tool for imputing population responses to the climate across the tree of life[31].

We highlight the importance of variation in population responses to climate within a species range. Sampling heterogeneity has recently been shown to have broad implications for metrics of

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population dynamics, where demographic rates are poorly correlated among sampling sites for the same species[39,40]. Therefore, inferences obtained from monitoring single populations or studies may not accurately portray species-level variability. This has broad implications for macroecology, particularly for population viability assessments (PVA) and species-distribution modelling. First, as well as suffering from data quality issues in their parameterisation[41], our findings suggest that PVAs based on data from a single population may not accurately reflect population viability across a species' geographic range. Therefore, incorporating detailed demographic data, and investigating differences in population responses across a range, could greatly improve our perspective on population viability[36]. Second, presence-only models of species distributions that do not account for the fact that responses to the environment within a species range do not accurately represent species distributions[42]. Moving towards trait-based monitoring and explicitly including demographic processes with mechanistic links to appropriate drivers into species distribution models could greatly improve predictions of climate change impacts on the biosphere[8].

Ultimately, improving our predictions of how humans are influencing the natural world is paramount to prevent rapid declines to global biodiversity[43]. This however requires a large shift towards both broad and detailed monitoring of global biodiversity. We show that linking species traits such as life-history to changes in the environment may equip us with tools to predict and prevent future losses.

Methods

To assess the effects of weather on population growth rates we collated information on global weather and the abundance, life-history and phylogeny of the terrestrial mammals. All analyses were carried out using R version 4.0.4[44]. For all data on the terrestrial mammals, taxonomies were resolved using the *taxize* package version 0.9.98[45] and matched using the Global Biodiversity Information Facility database (https://www.gbif.org/). All code used in the current study and full descriptions of the analyses are archived in the Zenodo repository (doi:10.5281/zenodo.4707232), which was created from the following GitHub repository https://github.com/jjackson-eco/mammal_weather_lifehistory.

Time-series abundance data

Annual time-series abundance data from across the terrestrial mammals were obtained from the Living Planet Database found at https://livingplanetindex.org/data_portal. This database was developed by the World Wildlife Fund and the Zoological Society of London as a tool to monitor global biodiversity, and contains over 20,000 population records for over 4000 species of vertebrate[4]. The records measure annual abundance in a variety of ways (e.g. full population counts, density, indices), and contain information on the location, realm, biome and taxonomy of the species in the record. First, we included only data for the terrestrial mammals that had species-level life-history information and coordinate locations, which referred to either specific or more general locations for each population (accounted for using weather data from a buffered radius around each location). We natural-log-transformed the raw

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abundance data to ensure that weather coefficients were comparable across records and abundance measure types. Because our analyses were focussed on estimating weather effects on annual population growth rates using regression models with several variables, we included only long-term records with 10 or more consecutive years of abundance data, and only for years in which there was also weather data (1979-2013). In one record (for *Bettongia penicillata*), there were two blocks with ≥10 years of data, which were analysed separately. We also removed records with a high proportion (>32%) and consecutive occurrences of 0 in the raw abundance time-series. Our final dataset contained 486 records from 157 terrestrial mammal species, which was used in all subsequent analyses (Fig. S1).

Global weather data

We used version 1.2.1 of the CHELSA monthly gridded temperature and precipitation timeseries dataset, which is at a spatial resolution of 30 arc seconds (~ 1km^2) for all months between 1979-2013 across the globe's land surface. The CHELSA datasets can be obtained from Karger et al.[46]. Raster files of the raw monthly mean temperature and total precipitation data were processed using the *raster*, *rgeos*, and *sf* packages[47–49]. Using the Living Planet Database record coordinate locations as a centroid, we averaged the monthly weather data for a buffered radius of 5km around each record location to account for the lack of specificity in record locations using the *exactextractr* package[50]. Averaged weather variables and weather effects for alternate buffer radii (50m and 50km) were highly correlated (Fig. S2; Fig. S7). Generally, we expect that organisms will respond to deviations in the weather compared to the average values, as opposed to raw weather variables. Furthermore, across the globes surface the variance in weather variables changes substantially, which may influence population responses. Thus, we explored population responses for the key weather variable of standardised annual anomalies, and then validated our approach using annual weather variance. For the anomalies, we decomposed z-transformed averaged monthly weather data for each location for the full timeseries (1979-2013) using a Seasonal-Trend Decomposition by Loess (STL). We used a seasonal window of 7 and trend window of 1000 for the decomposition and extracted the anomaly component, which describes the remainder when accounting for the trend and seasonal components of the timeseries. We then used annual mean temperature and precipitation anomalies as the key weather variables in subsequent analyses. These weather anomalies are the average deviation of the temperature and precipitation from expected values in a given year. We also investigated population responses to weather using annual weather variance, which was calculated as the annual variance of monthly mean temperature and total precipitation values.

Species-level life-history and phylogeny

We used three key traits that broadly characterise species-level life-history that are available for a large number of species: maximum longevity, litter size and adult body mass. We collected these traits from the compendium developed by Conde et al.[28], combining information from three primary database sources: The Amniote Life-History Database[29], PanTHERIA[51] and AnAge[52] databases. Adult body

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mass data was obtained exclusively from the Amniote Life-History Database[29]. Where multiple records were available for a single species, we took the largest maximum longevity value and the mean litter size/adult body mass. We removed erroneous raw litter size data for *Hydrochoerus hydrochaeris* and *Marmota broweri*. For analysis, we z-transformed the natural-logarithm of raw life-history trait data, and verified that the life-history variables were represented across the range of weather anomaly variables in the raw data (Fig. S3). The mammal phylogeny was obtained from Upham et al.[30], which uses a 'backbone-and-patch' Bayesian approach for a newly assembled 31-gene supermatrix and is part of the Vertlife project (https://vertlife.org/). We used the maximum clade credibility tree in analysis, which was processed using the *ape* package[53]. *Loxodonta cyclotis* (African forest elephant) was considered as *Loxodonta Africana* (African elephant) for analysis so that the abundance record and phylogenetic data matched.

Weather effects on annual population growth rates

To assess comparative population responses to weather in the terrestrial mammals we used a two-step meta-regression approach. First, for each record we estimated the effect of annual weather anomalies (and weather variance) on population growth rates. We calculated the realised, proportional population growth rate in year t as

$$\lambda_t = \frac{X_{t+1}}{X_t}, \qquad (1)$$

where X is the natural logarithm of abundance in year t. Then, with λ_t as the response variable, we estimated the effect of temperature and precipitation anomalies on population growth using generalised additive mixed models (GAMMs) fit using the *gamm* function of the *mgcv* package[54]. Changes in abundance are influenced by several drivers of population dynamics including habitat loss[2] and population processes such as density dependence[55], which may confound any influence of the weather on abundance. Therefore, because we aimed to assess the isolated impact of weather anomalies, accounting for these trends in abundance and temporal autocorrelation was crucial. We initially explored the extent of autocorrelation in abundance patterns using timeseries analysis and found evidence for lag 1 autocorrelation in abundance, but not for greater lags (Fig. S4-5). Furthermore, we tested the potential impact of density dependence on estimating environmental effects using an autoregressive timeseries simulation and found that environmental effects were robust to density dependence even for short timeseries (Fig. S6). Thus, for each record, we model population growth rate in each year as

$$\lambda_t = \beta^0 + \omega W_t + f(y_t), \qquad (2)$$

where β^0 is the intercept and ωW_t is a linear parametric term with coefficient ω for the weather W (temperature or precipitation anomaly) in year t. Here, positive coefficients indicate that positive weather anomalies i.e. hotter/wetter years, were associated with population increases, and *vice versa*. Identical additive regression models were run using weather variances as the weather variable W. The

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term $f(y_t)$ captures the effect of year y_t as a non-linear trend, where the function f is a thin plate regression spline with a basis dimension of five[56]. The function f was also fitted with an order 1 autoregressive (AR(1)) correlation structure, as specified in the *nlme* package[57]. Thus, the term $f(y_t)$ incorporates both the non-linear trend in abundance and temporal autocorrelation. Finally, we validated our additive model approach by testing other models to calculate weather effects, including linear regressions both including and excluding temporal trends or density dependence, and a temporally autocorrelated model fit using the *glmmTMB* package[58] (Fig. S8-S9). Weather coefficients ω generated using linear year effects were positively correlated to those from additive models (Fig. S10).

Bayesian meta-regression

Second, with the weather effects ω from each record as the response variable, we explored comparative patterns in population responses to weather using a Bayesian meta-regression framework implemented in the *brms* package[59]. Separate models were fit for temperature and precipitation. Bayesian meta-regression was used to address three key questions: 1) Were there consistent population responses to weather across the terrestrial mammals? 2) How did population responses vary within and between species and were there spatial patterns across biomes? 3) Does life-history predict the magnitude of population responses? To address questions 1 and 2, we used Gaussian models controlling for both phylogenetic and species-level covariance. The full model for record i and species j is given by equation 3

$$
\begin{aligned}
&\underline{\text{Linear model}} \\
&\omega \sim \text{MVNormal}(\mu, \mathbf{S}) \\
&\mu_i = \alpha_{SPECIES[j]} + \beta_{BIOME[i]} + \beta_N N_i \\
&\underline{\text{Varying effects}} \\
&\mathbf{S} = \sigma^2_{PHYLO}\mathbf{V} \\
&\alpha_j \sim \text{Normal}(\bar{\alpha}, \sigma_{SPECIES}) \\
&\underline{\text{Priors}} \\
&\bar{\alpha} \sim \text{Normal}(0, 0.3) \\
&\beta_{BIOME} \sim \text{Normal}(0, 0.15) \\
&\beta_N \sim \text{Normal}(0, 0.5) \\
&\sigma^2_{PHYLO} \sim \text{Exponential}(8) \\
&\sigma_{SPECIES} \sim \text{Exponential}(8)
\end{aligned}
$$

where the weather effect ω (z-transformed for analyses), is given by a multivariate normal distribution with mean μ and phylogenetic covariance matrix $\boldsymbol{S}$. The global intercept is given by $\bar{\alpha}$, which estimates overall patterns in weather effects across records, addressing question 1. We incorporated phylogenetic covariance using a Brownian motion model, with the correlation matrix given by $\boldsymbol{V}$ (calculated from the maximum clade-credibility tree) and variance factor σ^2_{PHYLO}, from which between-species variance was estimated. We incorporated an intercept-only varying effect for species with the term $\alpha_{SPECIES[j]}$, from which within-species variance was estimated with $\sigma_{SPECIES}$. The term β_{BIOME} gives the spatial

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effect of biome on weather responses. Thus, estimating within ($\sigma_{SPECIES}$) species variance, between (σ^2_{PHYLO}) species variance and the spatial effect of biome (β_{BIOME}), we explored question 2. All meta-regression models also included the linear effect of record length N (scaled number of years in the record) on weather effects, which was estimated using β_N. For all meta-regression models, we used regularising priors obtained from prior predictive simulations of the slope, intercept and exponential variance terms[60,61], to reflect the constraints in the raw data across species (see S1 and Fig. S11-14 for details). Gaussian meta-regression models were also fit for weather effects calculated using the annual weather variance, and the results obtained were largely identical to those obtained for weather anomalies (Fig. S21).

For question 3, although on average we expect that species life-history influences the magnitude of responses to the environment, we have little evidence to suggest that life-history *per se* influences the directionality of responses[26]. Thus, to address this question we explored how maximum longevity, litter size and adult body mass influenced the absolute magnitude of weather responses, $|\omega|$, using Gamma regression models with a log link. The full model for record i and species j is given by equation 4

$$
\begin{aligned}
&\underline{\text{Linear model}} \\
|\omega| &\sim \text{Gamma}(\eta, \mu) \\
\log \mu_i &= \alpha_{SPECIES[j]} + \gamma_{PHYLO[j]} + LH + \beta_N N_i \\
&\underline{\text{Varying effects}} \\
\alpha_j &\sim \text{Normal}(\bar{\alpha}, \sigma_{SPECIES}) \\
\gamma_j &\sim \text{MVNormal}(0, \mathbf{S}) \\
\mathbf{S} &= \sigma^2_{PHYLO}\mathbf{V} \\
&\underline{\text{Priors}} \\
\bar{\alpha} &\sim \text{Normal}(0, 0.3) \\
\beta_{LH} &\sim \text{Normal}(0, 0.2) \\
\beta_N &\sim \text{Normal}(0, 0.3) \\
\sigma^2_{PHYLO} &\sim \text{Exponential}(11) \\
\sigma_{SPECIES} &\sim \text{Exponential}(2) \\
\eta &\sim \text{Gamma}(2, 0.6)
\end{aligned}
$$

where η is a shape parameter that was fit with a Gamma prior, and LH refers to a set of linear life-history terms ($\beta_1 x_1 + \cdots \beta_k x_k$) that were explored using model selection. Specifically, for the three life-history traits, we explored a set of models incorporating univariate, multivariate and 2-way interaction terms, as well as a base model excluding all life-history effects. For the full set of ten candidate models please refer to the supplementary information (table S1 & S2). All life-history effects were fit with the same Normal prior, with mean 0 and standard deviation 0.3 (S1; Fig. S13). We assessed the predictive performance of candidate models using leave-one-out cross-validation implemented in the *loo* package[62]. Models were compared using the Bayesian LOO estimate of out-of-sample predictive performance, or the expected log pointwise predictive density (elpd)[62]. All final meta-regression models

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were run over 3 Markov chains, with 4000 total iterations and 2000 warmup iterations per chain. Model convergence was assessed by inspecting Markov chains, and the degree of mixing between chains using $\hat{R}$.

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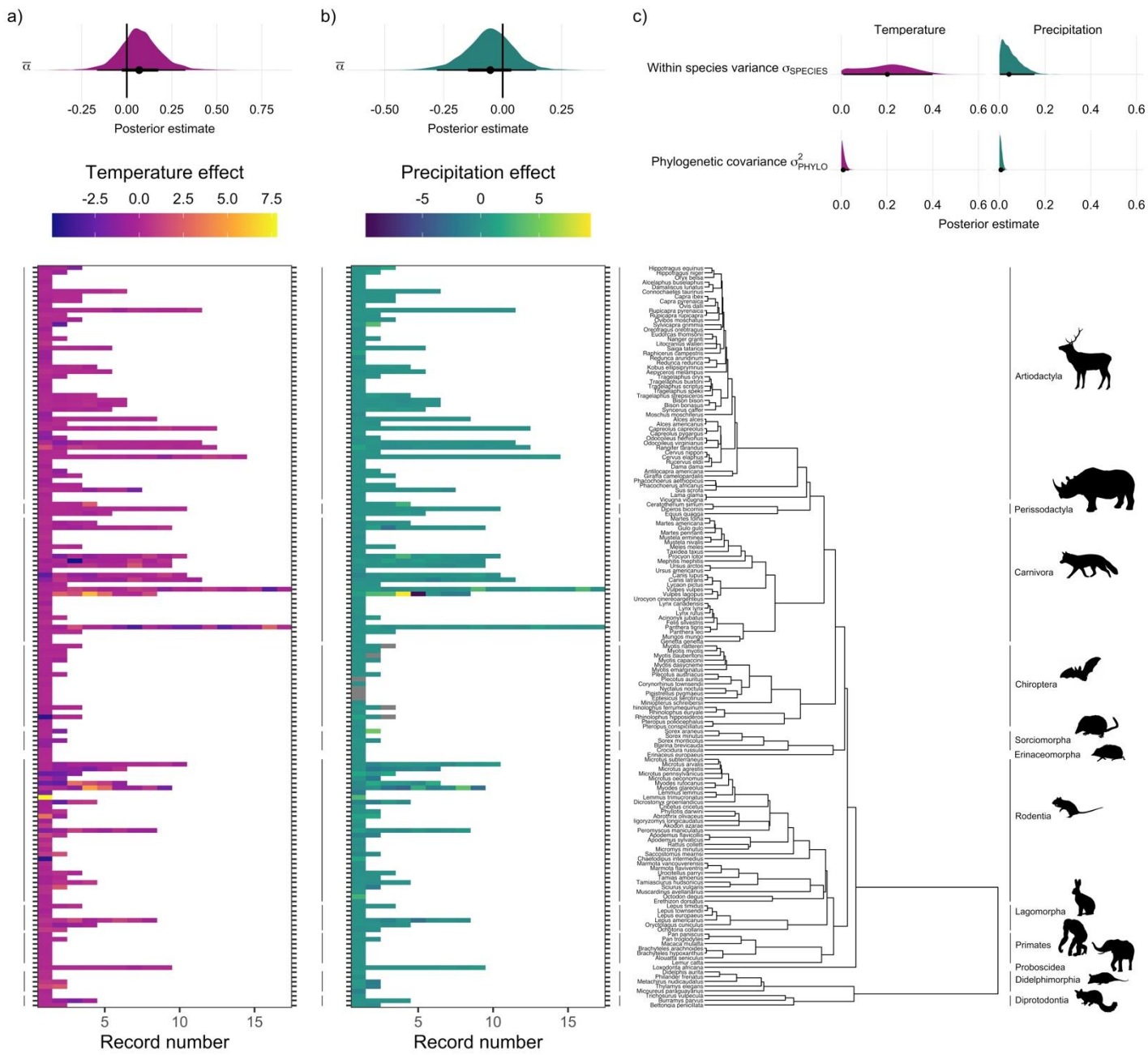
a)
b)
c)
Temperature
Precipitation
Within species variance $\sigma_{SPECIES}$
Phylogenetic covariance σ^2_{PHYLO}
Posterior estimate
Temperature effect
Precipitation effect
Record number
Artiodactyla
Perissodactyla
Carnivora
Chiroptera
Sorciomorpha
Erinaceomorpha
Rodentia
Lagomorpha
Primates
Proboscidea
Didelphimorphia
Diprotodontia

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Figure 1. **Global population responses to weather in the terrestrial mammals.** Heatmaps for population responses to temperature (a) and precipitation (b) for 157 species of terrestrial mammal. Each row of the heatmap is a species, and coloured rectangles are the population records. The colour denotes the coefficient of temperature/precipitation effects derived from autoregressive additive models. Here, positive numbers indicate that positive temperature/precipitation anomalies (hotter/wetter than average in a given year) were associated with increases in population size, and *vice versa*. The distribution half-eye plots in (a) and (b) (top) are summaries of the posterior distribution for the global intercept ($\bar{\alpha}$) of temperature and precipitation responses across records, fit with a Gaussian Bayesian meta-regression. The points give the approximate posterior mean and the error bar is calculated using a cumulative distribution function. Bayesian models were fit incorporating phylogenetic covariance using the maximum clade credibility tree from Upham et al.[59], which is plotted on the right with annotations indicating the mammal order[60]. The distribution half-eye plots in (c) are the posterior distribution summaries for phylogenetic covariance and within-species variance from the Gaussian Bayesian meta-regression.

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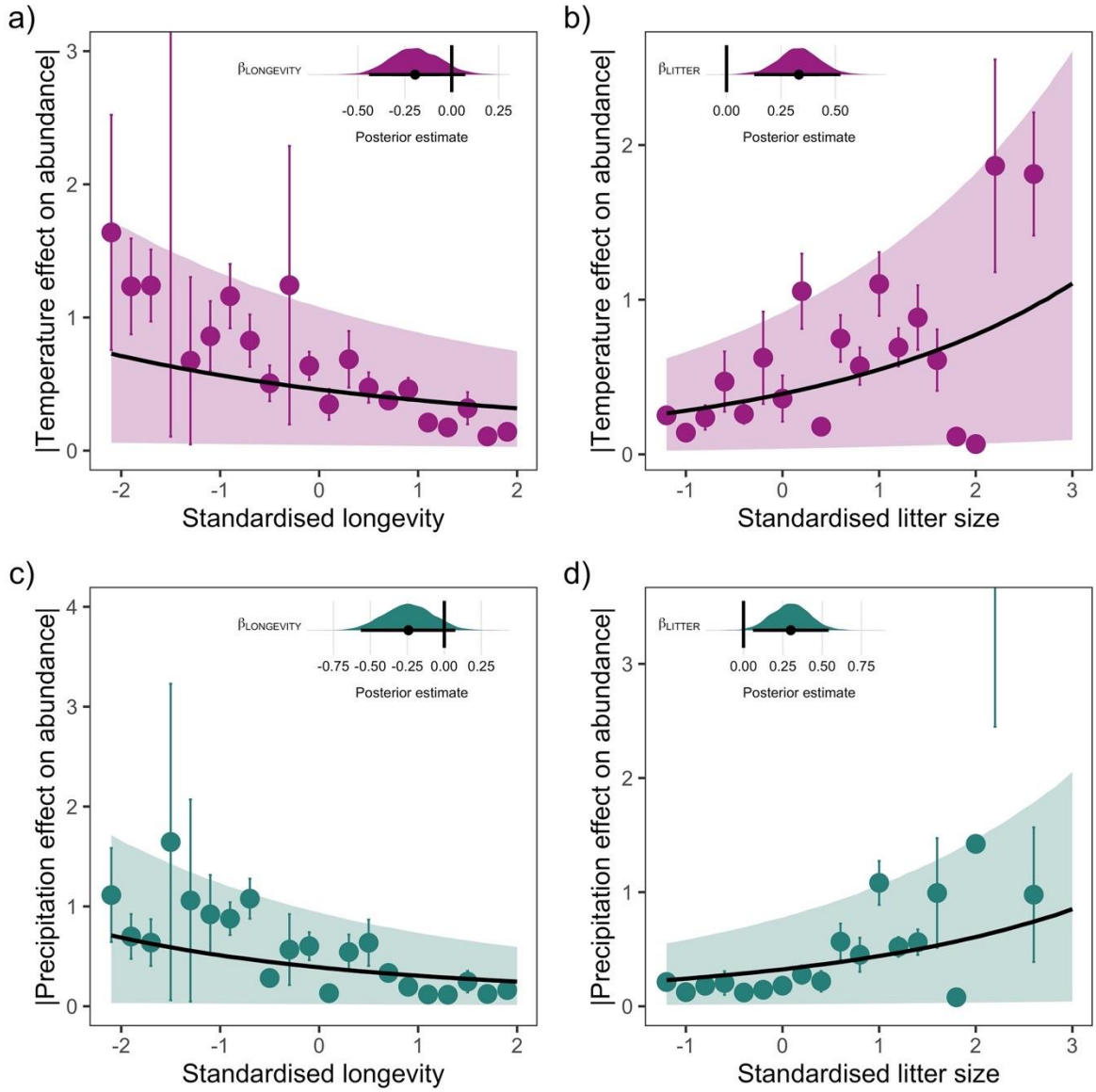

Figure 2. **Life-history predicts population responses to weather in the terrestrial mammals**. Each panel presents the mean absolute effect of temperature (a & b) and precipitation on population growth rates, $|\omega|$, for standardised maximum longevity (a & c) and standardised mean litter size (b &d). Standardisation was performed using a z-transformation of natural-log of the raw life-history trait. The values on each x-axis are split into equal bins of 0.2 from the minimum to the maximum life-history value. Points are coefficient means, with standard error bars. The black lines are the mean posterior predictions from the best predictive model, where predictions were calculated averaging over all other covariates and varying effects in the model. The shaded intervals are the 80% prediction intervals calculated in the *rethinking* package[60]. Panel insets give posterior distribution summaries for the slope terms presented in each panel. Two points are omitted from the plotting panel due to large mean coefficient values and high standard errors, which are visible on the plot.