# Populations of cooperatively breeding birds are buffered against annual variation in precipitation and temperature

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**Abstract**

Cooperative breeding is a reproductive system wherein other than parents care for offspring. It has been suggested to provide advantages in harsh and unpredictable climates. Support for this idea stems from detailed population studies, or phyla-wide comparative studies, but both approaches are insufficient to assess the demographic benefits of cooperative breeding. Here, we use abundance time-series from 1843 populations of 505 bird species coupled with local climate to show that population growth rates of family-living and cooperatively breeding species are less sensitive to annual variation in temperature and precipitation. Moreover, larger species are demographically more buffered than smaller ones, while climatic sensitivity displays latitudinal gradients. Our study demonstrates that cooperative breeding is a reproductive strategy increasing the demographic resilience of populations in the face of climatic variability. Ultimately, these findings reveal the demographic mechanism enabling cooperative breeders to successfully inhabit a wide range of environments, including harsh and unpredictable ones.

## Introduction

Cooperative breeding is a reproductive system wherein members of a social group act as alloparents by providing care to offspring of conspecifics (Ben Mocha et al., 2023; Cockburn, 1998). It evolved across taxa and is relatively common in birds (Cockburn, 2006) and mammals (Ben Mocha et al., 2025; Jennions & Macdonald, 1994). These species live in groups often (though not always) composed of extended families whereby offspring remain with their parents beyond independence and help raise younger siblings (Griesser et al., 2017). Phylogenetic comparative analyses have attempted to find associations between the occurrence of cooperative breeding across species and the ecological, climatic, and life-history features they experience and/or exhibit (Cockburn, 2020). They have found that cooperative breeding is associated with a slower life-history pace (i.e., small clutch sizes, high adult survival), which likely contributes to family formation (Arnold & Owens, 1998; Griesser et al., 2017). Importantly, global analyses have found that cooperative breeders are more likely to be found in locations with more predators (Bliard, Dufour, et al., 2024), and in variable and harsh environments (Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017). These geographical patterns have been suggested to stem from benefits to individuals' physiological state (Kikusui et al., 2006) and vital rates in the face of changing environmental conditions (Komdeur & Ma, 2021), in which their abilities to sustain breeding even in bouts of harsh conditions effectively shield them from unfavourable conditions (Warrington et al., 2024). The combination of slower life history (Covas & Griesser, 2007), higher survival (Zhu et al., 2023), and more stable reproductive output (Bourne et al., 2020; Groenewoud & Clutton-Brock, 2021) hints at demographic benefits that allow cooperative breeders to inhabit varied and unpredictable environments (Gonzalez et al., 2013; Johnson et al., 2023) and persist even under harsh conditions (Cornwallis et al., 2017; Martin et al., 2020). However, this potential demographic advantage, whereby cooperative breeders' population growth rate would be less sensitive to climatic variation, has yet to be properly tested in a cross-comparative framework.

Two major shortcomings have limited our understanding of the demographic benefits gained by cooperative breeders. First, only a few detailed population studies have attempted

to assess the effect of local climatic conditions and sociality on long-term population dynamics. For instance, group size has been found to mitigate risks of local extinction under varying climatic scenarios in meerkats *Suricata suricatta* (Paniw et al., 2019), and the presence of helpers has been linked to population persistence in Seychelles warblers *Acrocephalus sechellensis* (Borger et al., 2023; Busana et al., 2022). While this “single species - local climate” approach is critical and highlights the importance of long-term individual-based monitoring, it is ultimately limited in yielding a broader understanding of the demographic benefits gained by cooperative breeders across species. Second, large scale comparative analyses have been performed at the species level, using global climatic metrics and the entire geographic distributions of species (Cornwallis et al., 2017; Gonzalez et al., 2013; Griesser et al., 2017; Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017). This “many species - global climate” approach has advanced our understanding of the eco-climatic drivers of cooperative breeding. However, it is ultimately too coarse given the reliance on climatic data averaged throughout whole species geographical distributions, which is unlikely to be representative of the climatic conditions actually experienced by any given population.

Cross-species evidence of an association between sociality and population dynamics remains scant, limiting our understanding of the potential social buffering of populations against climatic variation. For instance, cooperatively breeding birds were not found to have more stable demographic histories across evolutionary timescales (Bliard et al., 2026). A study on 152 species spread across the animal kingdom used matrix population models from the COMADRE database (Salguero-Gómez et al., 2016) to explore the associations between the degree of social organisation and a range of demographic properties (Salguero-Gómez, 2024). Interestingly, this study did not find clear differences in asymptotic population growth rates depending on sociality, but populations of social species were found to be more resistant to disturbances (Salguero-Gómez, 2024). However, this study was based on diverse taxa, whereby sociality classifications might not be directly comparable. Additionally, it did not link the demographic properties of populations to the local climatic conditions they have

experienced. Therefore our understanding of the sensitivity of population growth rates to climatic variation depending on their sociality remains incomplete.

Here, we use a global dataset of abundance time series from the Living Planet Index database (Collen et al., 2009; Loh et al., 2005), comprising thousands of populations from hundreds of bird species to determine whether cooperative breeders are less sensitive to annual climatic variation. By linking the dynamics of these populations to the local climatic conditions they have experienced (Jackson et al., 2022), we can overcome the shortcomings that have riddled cooperative breeding research to date. We estimate the sensitivity of the growth rates of bird populations in the face of environmental variation (magnitude of λ change for a given change in a climatic variable) and explore its relation to key life-history and behavioral traits. This approach enables us to consider a broad geographic and phylogenetic scale and investigate in much greater detail the purported social buffering benefits, or lack thereof, for the population dynamics of family living and cooperative breeding bird species. We predict that the population growth rate of family living and cooperative breeding species should be less sensitive to climatic variation.

## Methods

### Demographic time series data

The demographic data was obtained from the Living Planet database (LPD) (Collen et al., 2009; Loh et al., 2005), which at the time of analysis contained more than 40000 abundance time series since 1950 from populations of over 5000 vertebrate species. We retrieved the 2024 LPD from https://livingplanetindex.org/data_portal on April 24th 2026. We only kept populations of bird species, restricting our data to records with at least 10 consecutive years of abundance data. Additionally, we excluded records with occurrences of 0 in the abundance time series, as such occurrences can prove problematic to estimate population growth rates (Jackson et al., 2022). The final dataset consisted of 2382 blocks of at least 10 consecutive years from 2322 unique populations (several populations had more than one block of >10 consecutive years, in which case they were analyzed separately), for a total of 598 bird

species (Figure S1). Note that population monitoring was not necessarily performed on a population's breeding grounds.

**Climate data**

We used changes in yearly mean temperature and yearly total precipitation as the main climatic variables in our analyses of population sensitivity to climatic variation. We obtained global climate data from the Copernicus Climate Data Store. Specifically, we downloaded global datasets of mean temperature and total precipitation from the "ERA5 monthly averaged data on single levels from 1940 to present" (Hersbach et al., 2023), gridded at a 0.25 degree resolution (~27km at the equator). We extracted the relevant local climatic data at the monitoring location for each Living Planet Index population of our dataset in each year using the *raster* R package (Hijmans et al., 2025), averaging mean temperature across all months and summing precipitation to yearly totals.

**Sociality and life-history data**

Data on the offspring care system of bird species follow Griesser et al. (2017) and were updated to include 505 species out of the 598 species with LPI data. The offspring care system was characterized in three incremental levels of sociality: non-family living, family living, and cooperative breeding (Bliard, Dufour, et al., 2024; Drobniak et al., 2015; Griesser et al., 2017). Non-family living is characterized by species with offspring dispersing away from their parents within 50 days of nutritional independence. Family living is an evolutionary stepping stone between non-family living and cooperative breeding (Griesser et al., 2017), and is defined by offspring staying at least 50 days beyond nutritional independence but not providing alloparental care. This threshold reflects association of offspring with the parents beyond the onset of less favourable autumn conditions. Cooperative breeding is defined by offspring staying with their parents and providing alloparental care.

We obtained data on body mass, migratory strategies, and hand-wing index (a proxy for dispersal capabilities; Claramunt, 2021; Weeks et al., 2022) for all species from the AVONET database (Tobias et al., 2022).

**Phylogenetic data**

The most up-to-date bird phylogeny was obtained from McTavish et al. (2025), as a synthesis tree aligned with the Clements taxonomy (Clements et al., 2023). This consensus tree is updated yearly, and combines phylogenetic information from more than three hundred published studies. For our comparative analysis, we accounted for shared ancestry among species by using a phylogenetic variance-covariance matrix derived from v.1.6 of McTavish's (2025) maximum clade credibility tree.

**Estimating population sensitivity to climatic variation**

We followed the methodology developed by Jackson et al. (2022), matching annual demographic responses of populations with the annual local climate they have experienced. For each population time series, we used each yearly change in abundance to calculate the yearly population growth rate λ (i.e., the log of the ratio between abundance in year *t+1* and abundance in year *t*). The advantage of estimating population growth rates is that they are comparable across population time series, even though different abundance measures were used (e.g., density, full population count, population index). We then used the time series of log λ obtained for each population to estimate the effect of climatic variation on population growth rate. Climatic variation is here defined as the year-to-year change in climatic variables (i.e., the difference between year *t+1* and year *t*). We used a generalized additive model for each population time series, using the yearly growth rate log λ as the response variable, and the yearly change in either total precipitation or mean temperature as a linear term, with the estimated slope representing the population's sensitivity to climatic variation. Following the workflow of Jackson et al. (2022), we added a smoothing function on year, to capture non-linear temporal effects. This was done in the form of a thin plate spline (Wood, 2003), with a basis size of five. We also included an autoregressive term of order 1, to account for potential temporal autocorrelation in the population growth rate. Altogether, this ensures that we estimate the sensitivity of the growth rate of each population to climatic variation, while accounting for potential long-term non-linear trends and temporal autocorrelation (Jackson et al., 2022).

**Meta-regression to estimate the effect of sociality on growth rate sensitivity to climatic variation**

In the previous step, we estimated the sensitivity of the population growth rate to changes in temperature and precipitation for each population (Figure S2, Figure S3). These sensitivity estimates are all expressed on a comparable scale (change in log λ for a 100mm change in total yearly precipitation, or 1 degree Celsius change in mean yearly temperature). Following the approach used in Jackson et al. (2022), we used a Bayesian phylogenetic meta-regression approach to estimate the effect of sociality and other life-history traits on the absolute values of the sensitivity estimates. We used the absolute sensitivities because we are interested in the overall sensitivity of populations to variation in climatic variables, and not necessarily in the directionality of the responses. The final dataset for the meta-regression, keeping only populations for which we had information on their offspring care system, included a total of 1843 populations from 505 bird species.

We used a Gamma regression with a log-link (Compagnoni et al., 2021; Ickin et al., 2025; Jackson et al., 2022), wherein the absolute sensitivities to either temperature changes or precipitation changes were used as a response variable. We included the offspring care system as a covariate. Given the incremental nature of this variable, we parametrized this ordinal predictor using a monotonic effect (Bürkner & Charpentier, 2020), which ensures a monotonic increase or decrease across categories, while the magnitude of change between adjacent categories is allowed to vary. Log body mass was also included as it is a key life-history trait characterizing a species pace-of-life and likely to influence both the offspring care system of species (Griesser et al., 2017) and the sensitivity of populations to climatic variation (Buckley & Kingsolver, 2012; Compagnoni et al., 2021; Paniw et al., 2018). The absolute latitude was included to account for potential latitudinal differences in both offspring care systems and climatic sensitivities. We included both hand wing-index and migratory strategies (categorised as “sedentary”, “partial migratory”, and “migratory”) to account for species differences in dispersal abilities, and the fact that populations of migratory species are not only experiencing the climatic conditions of the location where abundance was monitored. Finally,

we included the length of the monitoring period, as more extreme sensitivity estimates were found for populations with shorter monitoring periods (Figure S4). We controlled for the phylogenetic relationship between species by including the phylogenetic variance-covariance matrix as a random effect, thus allowing us to estimate the among-species variance in climatic sensitivity. Finally, given that the data include multiple populations per species, we also included a species random effect to account for within-species variance in climatic sensitivity.

**Model implementation**

All analyses were conducted in R version 4.5.2 (R Core Team, 2025). We used the *brms* R package (Bürkner, 2017, 2018) to implement the models in Stan (Carpenter et al., 2017; Gabry & Češnovar, 2020) using Hamiltonian Monte Carlo simulations. All the models described above ran on 3 chains sampling for 1000 iterations after an initial burn-in period of 1000 iterations, therefore resulting in a total of 3000 posterior samples for all model parameters. Convergence was ensured visually as well as using the Gelman-Rubin diagnostic (Gelman & Rubin, 1992).

## Results

Overall, using a phylogenetically controlled two-step meta-regression, our models found clear evidence that the population growth rate of family-living and cooperative breeding species is less sensitive to annual variation in both temperature (median monotonic effect size on the log scale, representing the average change from one category to the next = -0.12 [89% Credible Intervals: -0.25, -0.01], Figure 1) and precipitation (-0.13 [-0.26, -0.00], Figure 2), and these results were overall robust to methodological choices (Figure S5, Figure S6). Modelling monotonic effects allows us to estimate effects that vary in their magnitude between adjacent categories (Bürkner & Charpentier, 2020). Interestingly, the reduction in sensitivity to temperature tends to be more pronounced between family-living and cooperative breeding species (proportion of the total effect = 0.59 [0.13, 0.95], Figure 1) than between non-family living and family living species (0.41 [0.05, 0.87], Figure 1).

The magnitude of within-species variance in temperature sensitivity (0.17 [0.04, 0.28]) and precipitation sensitivity (0.34 [0.24, 0.44]) was greater than among-species phylogenetic variance (temperature: 0.03 [0.02, 0.04]; precipitation: 0.04 [0.03, 0.06]), highlighting the importance of including multiple populations per species in the analyses.

We also found that populations of larger-bodied species were less sensitive to variation in temperature (median effect size = -0.14 [-0.22, -0.05], Figure 1) and precipitation (-0.10 [-0.21, -0.00], Figure 2). Populations of migratory species were also less sensitive to climatic variation, while populations of species with higher hand-wing index (indicative of higher dispersal abilities) were more sensitive to climatic variation.

Finally, we found diverging results for the association of absolute latitude with populations' sensitivity to temperature and precipitation, with absolute latitude being negatively associated with temperature sensitivity (-0.34 [-0.40, -0.29], Figure 1) but positively associated with precipitation sensitivity (0.08 [0.02, 0.14], Figure 2).

## Discussion

Altogether, our results help unravel the demographic advantages gained by family-living and cooperative breeding in the face of climatic variation, thus ultimately providing a clearer picture of the evolutionary benefits and geographical incidence of these social systems. Using thousands of populations and the local climate they have experienced over at least a decade, our analyses revealed that the annual growth rate of populations of family living and cooperative breeding birds was less sensitive to annual variation in both temperature and precipitation, buffering their population dynamics. Crucially, our study offers a mechanistic understanding of the demographic benefits enabling cooperative breeders to inhabit and persist in a wide variety of environments, including habitats characterised by harsh and variable conditions (Jetz & Rubenstein, 2011).

Similarly to findings across mammalian populations (Jackson et al., 2022), we found a clear association between life history and the climatic sensitivity, with the population growth rate of larger bird species being overall less sensitive to annual variation in temperature and

precipitation. This highlights that life history plays an important role in mediating population dynamics and climatic sensitivity across the tree of life (Bliard, Paniw, et al., 2024; Compagnoni et al., 2021; Morris et al., 2008; Paniw et al., 2018; Touzot & Paniw, 2024), with slower life histories often being buffered against environmental variability. In addition, our results highlight a role of other life-history traits on climatic sensitivity. Migratory species tend to be less sensitive to local climatic conditions, suggesting that migrating could be an advantageous strategy to deal with environmental variation. However, this finding is likely to stem in part from methodological limitations, as we used the climate experienced by populations at the monitoring location, while species with migratory strategies will experience these local conditions only during a part of their annual cycle. Similarly, the effect of hand-wing index on climatic sensitivity could potentially be due to species with high dispersal abilities being able to move based on large-scale spatial variation in climatic conditions (Bowler & Benton, 2005; Dieckmann et al., 1999; Jocque et al., 2010; Sheard et al., 2020), thus moving in and out of the monitored population. This would lead to large fluctuations in the population growth rate at a given monitoring site, which would make dispersive species appear less buffered than they might be in reality.

Interestingly, our results show clear, opposite effects of latitude on population sensitivity to annual variation in temperature and precipitation, the effect being negative for temperature and positive for precipitation (Figure 1, Figure 2). Latitudinal gradients in demographic sensitivity to climatic variation are not well studied (Louthan et al., 2021), but high latitude populations should be expected to be less sensitive to temperature variability, in line with our findings. Indeed, following the demographic buffering hypothesis (Hilde et al., 2020), high latitude populations, which are exposed to large seasonal temperature variations, are expected to have evolved mechanisms minimising variation in their vital rates, thus limiting the influence of temperature variability on population growth rate (Louthan et al., 2021). However, contrasting results have been found across plant species, with high latitude species being more sensitive to climatic drivers (Morris et al., 2020). Conversely, we found the opposite effect for precipitation, with low latitude species being less sensitive. This could

potentially reflect that annual variation in total precipitation in low latitude areas might be less relevant for populations given that these regions are characterised by abundant and regular precipitation (Hersbach et al., 2023; Jiang et al., 2017). In high latitude regions, annual variation in precipitation could be critical for populations (Malinowska et al., 2026), potentially determining food abundance (Maresh Nelson et al., 2024) and phenology (Deng et al., 2025; Irons et al., 2017).

Despite the benefits of using thousands of abundance time series and linking them to local climatic conditions, it is important to note that limitations pertaining to the use of LPI data exist, such as geographical biases, coarseness of the time series, and inherent intractability of underlying vital rate trajectories from population-level data. First, as in most comparative analyses, geographical biases exist in both the LPI data (Jackson et al., 2022) and in our knowledge of cooperative breeding (Cockburn, 2020), due to many species lacking both demographic monitoring and life-history data in tropical areas with dense vegetation. Second, LPI data consists only of yearly abundance data that we linked to annual local climatic conditions, thus potentially missing finer-scale demographic patterns (Ozgul et al., 2023), ignoring phenological mismatches (Miller-Rushing et al., 2010; Visser & Gienapp, 2019) or short, episodic, and potentially extreme climatic events (Descamps et al., 2015; Hansen et al., 2019; Regan & Sheldon, 2023) that can all strongly influence the demography of populations. Third, abundance data aggregates several demographic processes (i.e., birth, death, immigration, emigration) that cannot be disentangled easily without more detailed data. The collection of individual-based data, or trajectories in both survival and reproductive success (Levin et al., 2022; Ronget et al., 2026), would allow a more detailed understanding of the dynamics of populations, and potentially inform on the specific social shielding mechanisms leading cooperative breeders to be less sensitive to climatic variation (Warrington et al., 2024).

To conclude, by linking thousands of population time series from hundreds of bird species with local climatic conditions, we provide the clearest comparative evidence to date that populations of family living and cooperative breeding species are buffered against

environmental variability, whereby social shielding leads populations to have a more stable demography, thus enabling cooperative breeders to inhabit a wide range of environments.

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**Author contributions:** LB designed the study, performed the analyses and wrote the first draft of the manuscript. MG collected the data on offspring care systems. All authors significantly contributed to the writing and editing of the manuscript.

**Data and code accessibility statement:** The climatic data is publicly available from the Copernicus Climate Data Store https://doi.org/10.24381/cds.f17050d7. The Living Planet Index database is publicly available and can be retrieved from https://livingplanetindex.org/data_portal. Functional traits data were obtained from Avonet https://doi.org/10.1111/ele.13898. The phylogenetic tree was obtained from https://github.com/McTavishLab/AvesData. All code to retrieve relevant data from the LPI database and to perform analyses are publicly available on the following GitHub repository https://github.com/lbiard/coop_breed_climate_variation, and will be archived on Zenodo upon acceptance of the manuscript.

## Figures

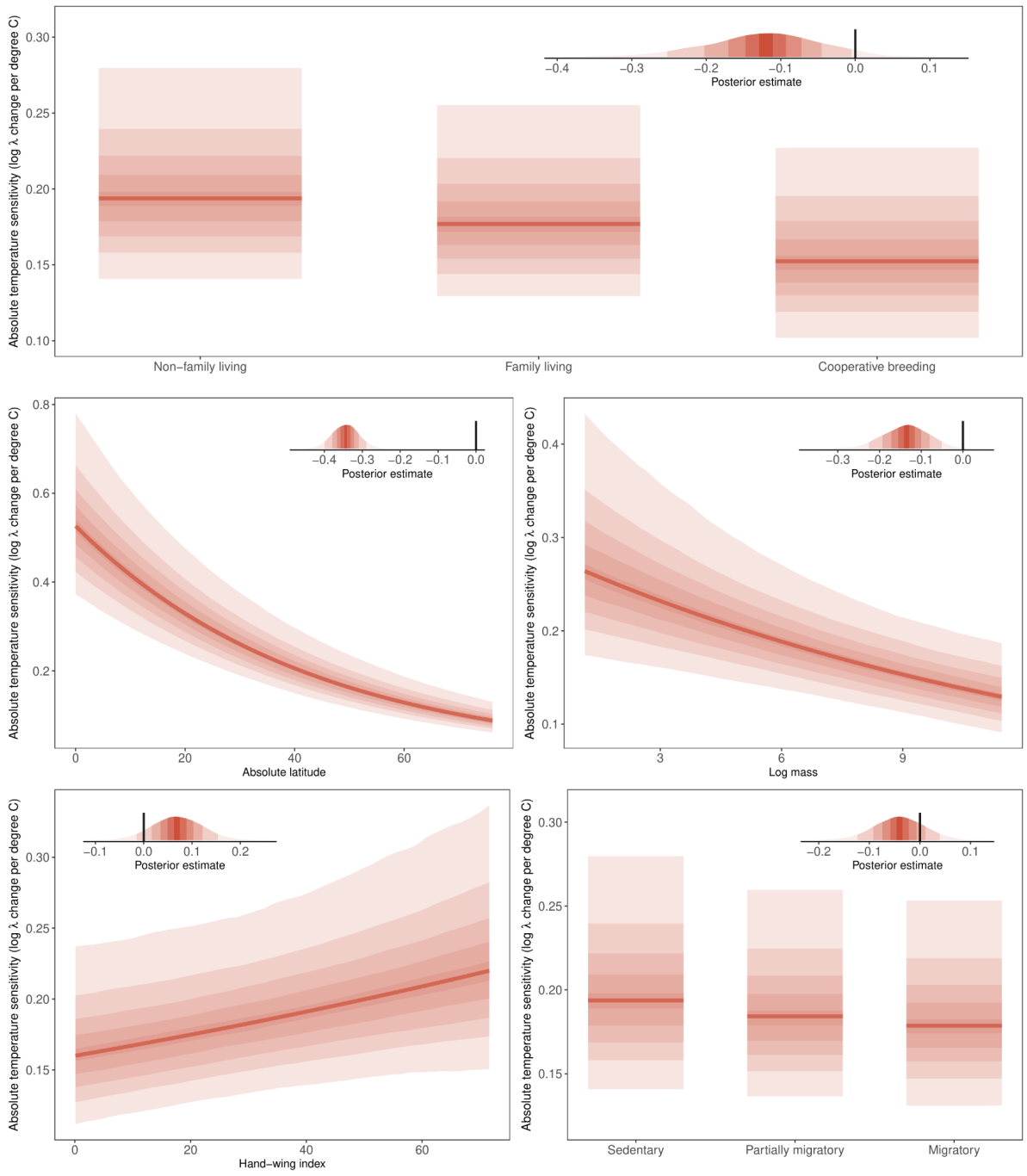



Figure 1: Associations between the sensitivity of populations' growth rates to variation in temperature and relevant covariates, respectively offspring care systems (top panel), absolute latitude (middle left panel), log body mass (middle right panel), hand-wing index (bottom left panel), and migratory strategy (bottom right panel). Posterior median effect sizes from the phylogenetic meta-regression are represented by the darker lines, alongside their 10% to 90%

credible intervals represented by the shaded bands. Panel insets display the posterior distribution for the effect estimated from the meta-regression.

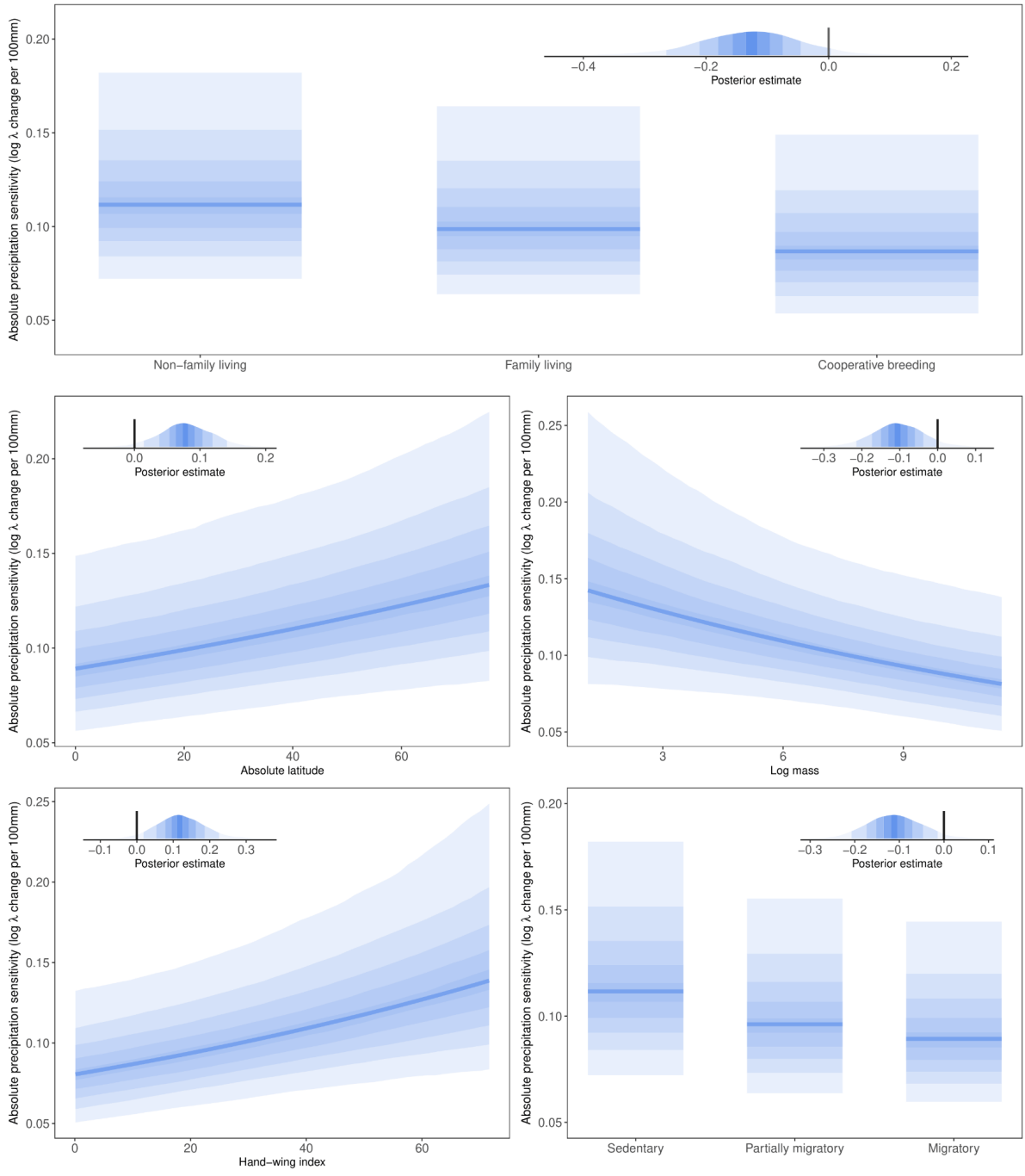



Figure 2: Associations between the sensitivity of populations' growth rates to variation in precipitation and relevant covariates, respectively offspring care systems (top panel), absolute latitude (middle left panel), log body mass (middle right panel), hand-wing index (bottom left panel), and migratory strategy (bottom right panel). Posterior median effect sizes from the

phylogenetic meta-regression are represented by the darker lines, alongside their 10% to 90% credible intervals represented by the shaded bands. Panel insets display the posterior distribution for the effect estimated from the meta-regression.

**Supplementary materials**

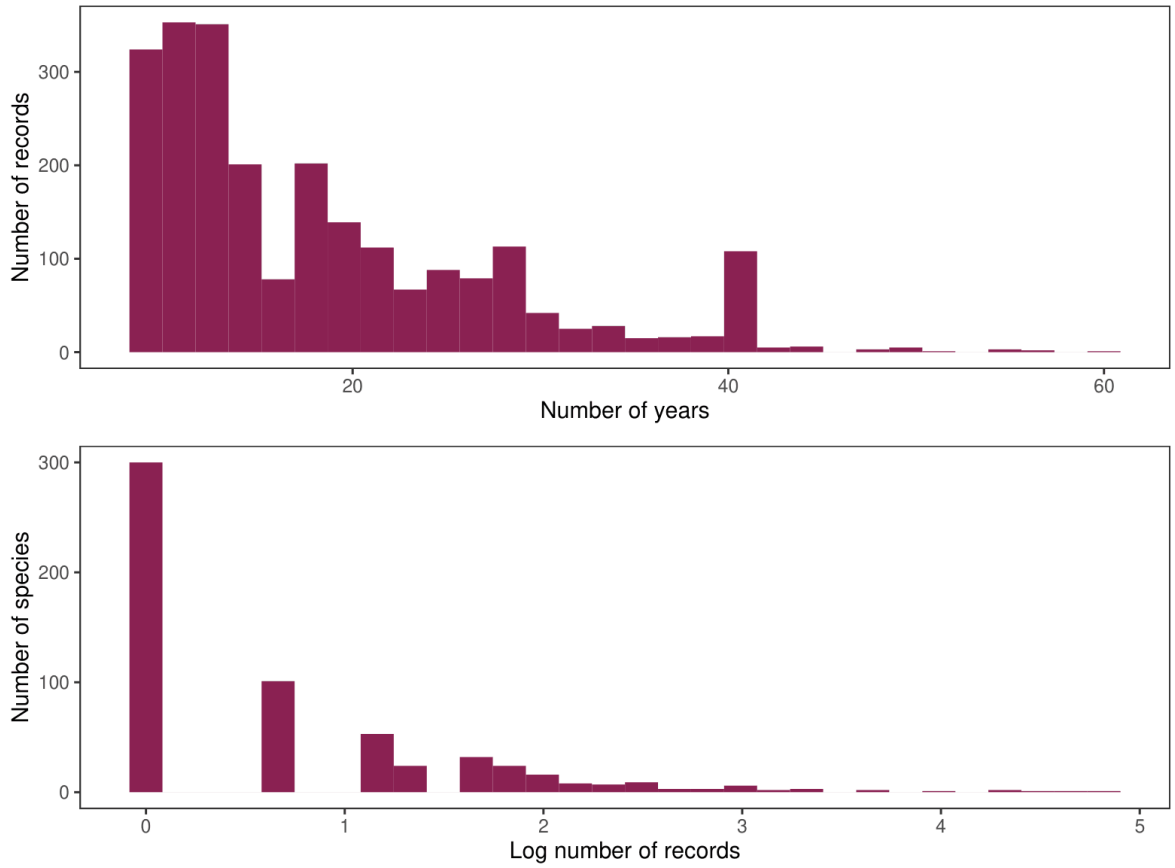



Figure S1: Histogram of the number of records (i.e., population monitored) with >10 consecutive years depending on the length of the record (top panel). Histogram of the number of bird species depending on the number of records with >10 consecutive years (bottom panel).

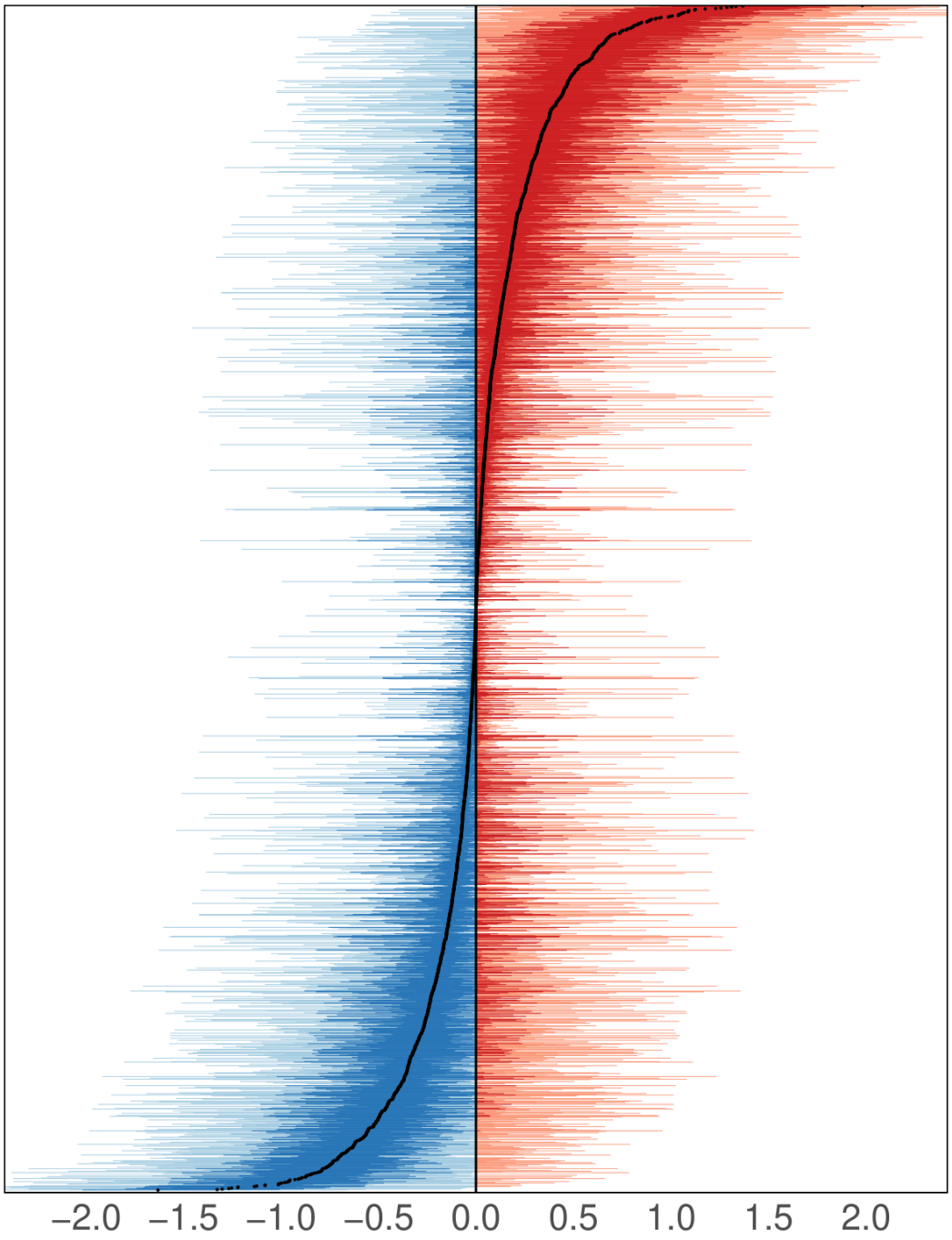



Figure S2: Forest plot of the estimated effect size of changes in temperature on the log population growth rate for 2382 populations of 598 bird species. Each horizontal bar represents the effect size for a population, displaying the 50% and 89% credible intervals, while the black dots represent the median effect sizes.

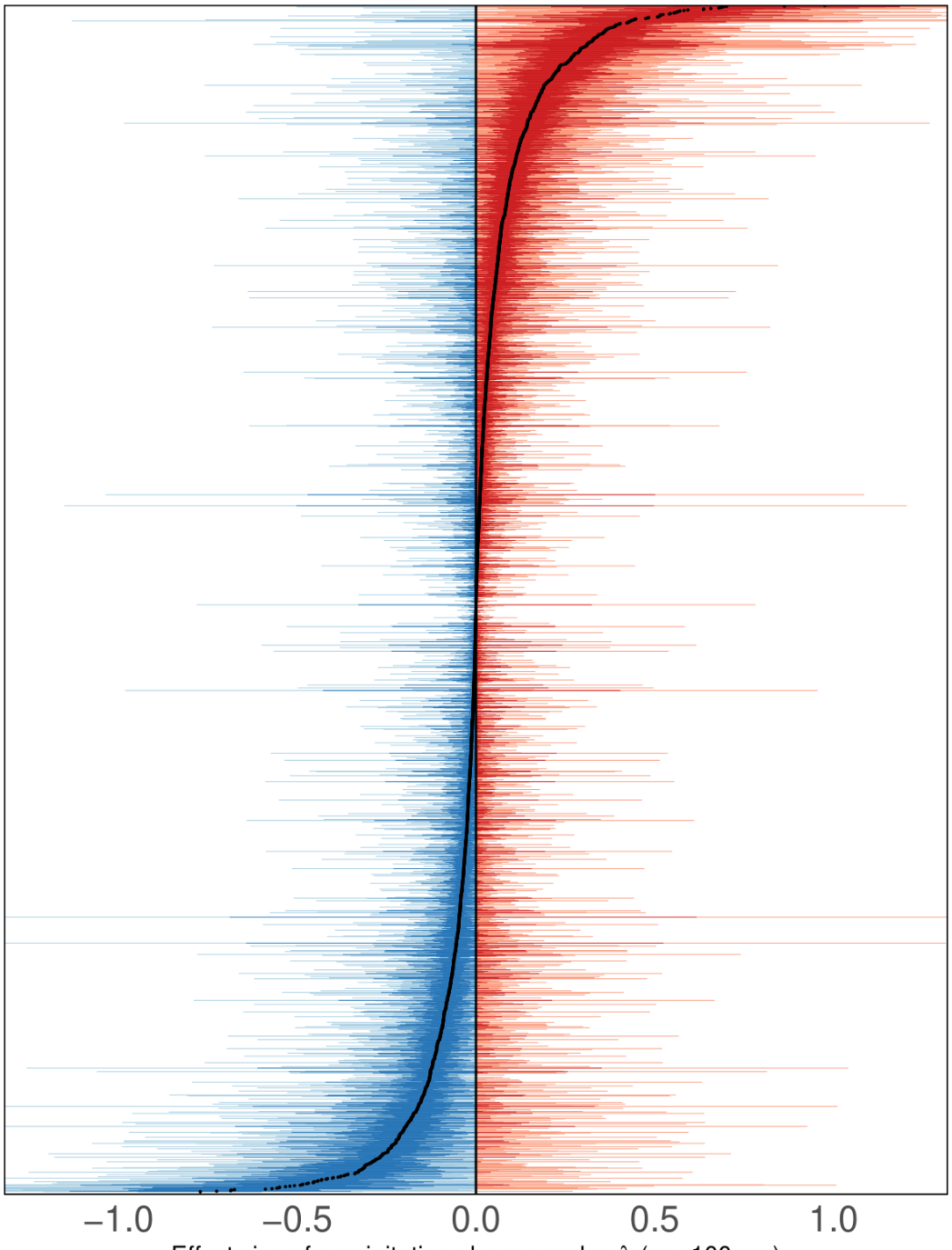
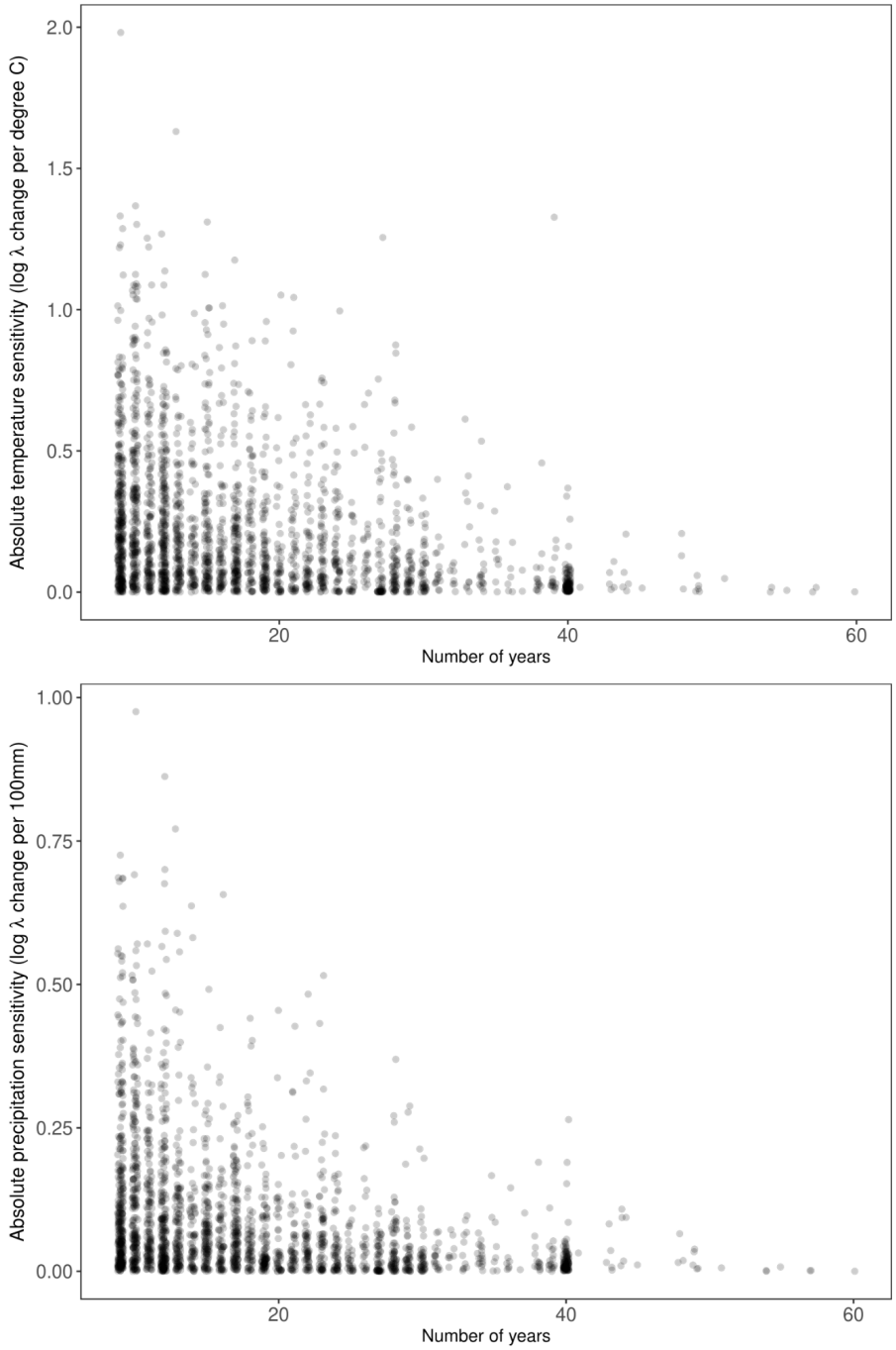



Figure S3: Forest plot of the estimated effect size of changes in precipitation on the log population growth rate for 2382 populations of 598 bird species. Each horizontal bar represents the effect size for a population, displaying the 50% and 89% credible intervals, while the black dots represent the median effect sizes.

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427 Figure S4: Association between the length of population time series and the absolute effect
428 size estimated for temperature sensitivity (top panel) and precipitation sensitivity (bottom
429 panel). This highlights that shorter time series are more likely to yield larger effect sizes.

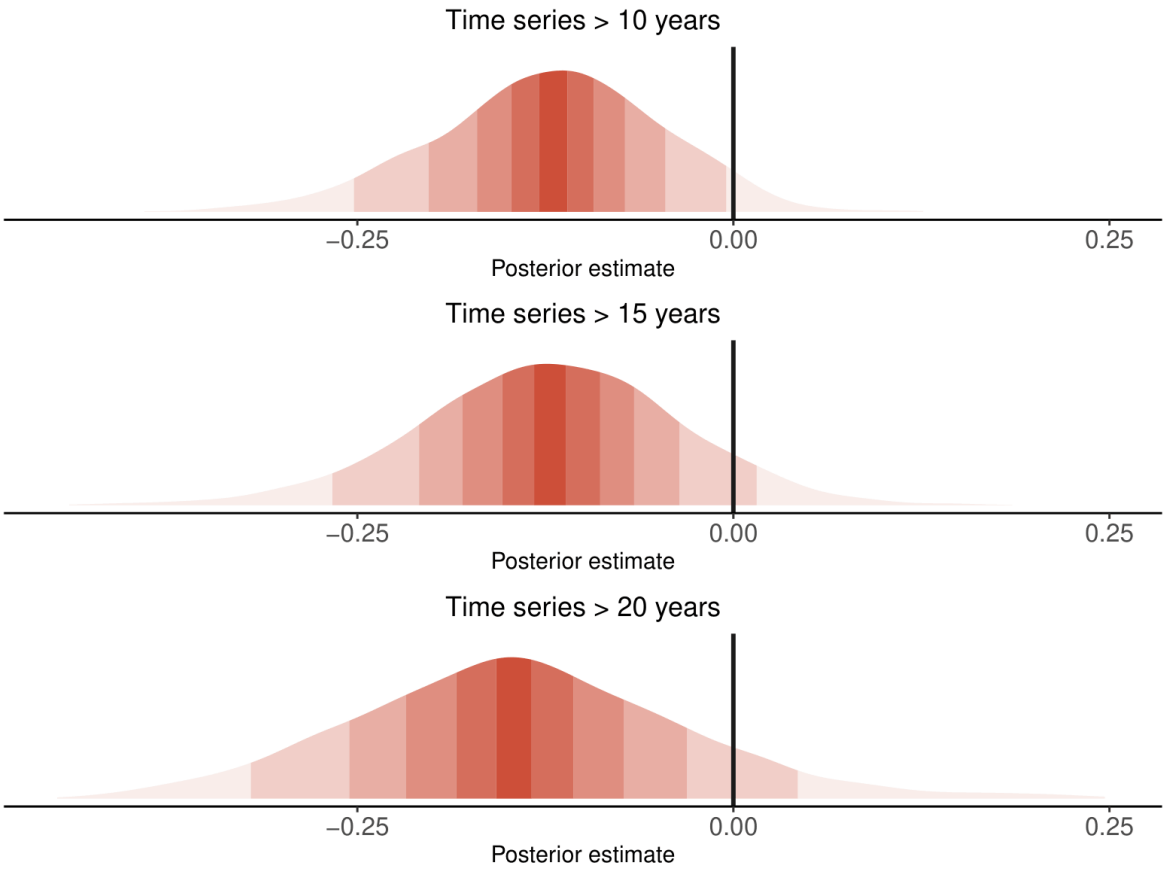


Figure S5: Posterior distribution for the effect of offspring care systems on the sensitivity of populations' growth rates to variation in temperature depending on the threshold used for the length of time series. Top panel: keeping all time series of at least 10 consecutive years (1843 populations from 505 species). Middle panel: keeping all time series of at least 15 consecutive years (1071 populations from 408 species). Bottom panel: keeping all time series of at least 20 consecutive years (656 populations from 336 species).

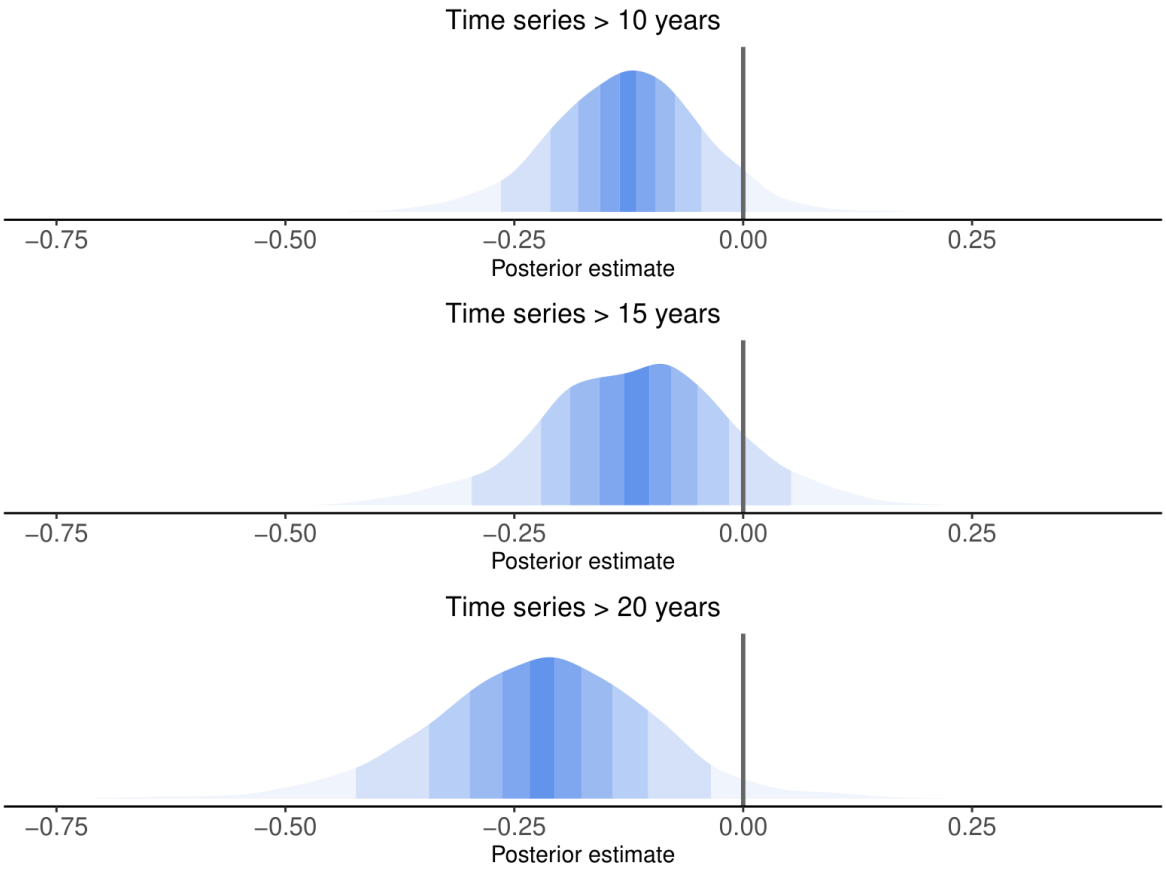


Figure S6: Posterior distribution for the effect of offspring care systems on the sensitivity of populations' growth rates to variation in precipitation depending on the threshold used for the length of time series. Top panel: keeping all time series of at least 10 consecutive years (1843 populations from 505 species). Middle panel: keeping all time series of at least 15 consecutive years (1071 populations from 408 species). Bottom panel: keeping all time series of at least 20 consecutive years (656 populations from 336 species).

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