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Darwin's finches and climate change: insights from a resilient system

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Abstract

Climate change is known to influence biodiversity worldwide, with changes in organismal traits observed in many populations and species. Such effects are not universal, however, with some traits showing remarkable stability through time. Time-series analyses that link environmental variables to trait values can generate useful insights into trait evolution and its ecological bases. We use 24 years of data for beak and body traits in two species of Darwin's finches in the Galápagos Islands, alongside data on temperature and precipitation, to answer three questions: (Q1) is climate change present in our study sites? (Q2) do time-series of beak and body traits show detectable trends that suggest climate change effects? and (Q3) to what extent does weather influence annual variation in beak and body traits? We found that temperature and precipitation have been increasing over the past two decades—although this trend is minor in comparison to year-to-year variation. We next found that time-series of beak and body traits showed no detectable signs of climate change impact, instead they behave either as random walks or stable trajectories. Finally, for both species, analyses for short-term responses show that precipitation has a lagged, negative correlation with beak and body traits (effect size: maximum −0.632, minimum −0.131). Increased precipitation followed smaller traits in subsequent years. Associations of finch traits with temperature were more variable. We discuss reasons why Darwin's finches react to short-term weather changes but not to long-term climatic trends, and how these results relate to other findings in other tropical systems.

Keywords: rapid-evolution; resilience; evolutionary patterns; thermoregulation; climate-warming

Introduction

Climate change can influence biodiversity in many ways, often with far-reaching ecological and evolutionary consequences (Cotto et al., 2017; Karell et al., 2011; Scheffers et al., 2016; van Asch et al., 2013). Most obviously, climate change can influence the evolution of traits related to physiology, behaviour, and morphology that have further effects on the phenology (Franks et al., 2007; van Asch et al., 2013), abundance (Bowler et al., 2017), distribution (Johnston et al., 2013), and life-history of species (Gardner et al., 2011;

Pearson et al. 2014). Some specific examples include the advancement of breeding and migration timing in response to temporal changes in resource availability (e.g., Charmantier & Gienapp, 2014; Crozier et al., 2011; Gienapp et al., 2008; Goodman et al., 2012), changes in the strength of sexual selection between divergent species due to increases in temperature and consequent changes of these species ranges (Qvarnström et al., 2016), altered frequencies of colour morphs responding to habitat changes produced by milder winters (Karell et al., 2011), and changes in body size due to shifting food resources or temperature susceptibility (Blois et al., 2008; Millien et al., 2006; Jirinec et al., 2021; Oke et al., 2020).

Despite these and many other examples of climate-related trait changes, effects are not evident in all instances. Indeed, the meta-analysis by Sanderson et al. (2022) found that the average effect of climate change on organismal traits was not particularly striking—mainly because effects ranged from very large to non-existent. How then might we explain the many instances of minimal change? First, climate change is highly heterogenous at many scales across the globe, and some populations might thus experience little climate change (Foden et al., 2019), or any climate change trend might be trivial in relation to shorter-scale weather variations such as those seen on daily, seasonal, or annual scales. Second, some populations might lack the genetic or plastic potential to respond to climate change (Merilä & Hendry, 2014), and the impact can vary based on the trait under consideration. In birds, e.g., phenological traits seem to be more responsive to climate change, while morphological traits show limited or no change (Radchuk et al., 2019). In these instances, climate change could be strong and thus favour trait change; yet resulting trait changes might be minimal. Third, some organisms might be adapted to specific resources or environments that are relatively insensitive to climate change. In such cases, climate change might be strong, but traits might not change because they are more attuned to environmental features not showing a climate change signal (e.g., thermally buffered microhabitats; Scheffers et al., 2014).

Moreover, the relative influence of different climatic variables on populations is not uniform. Across many systems, precipitation variability often has stronger and more immediate ecological and evolutionary consequences than temperature variability, because rainfall directly governs resource availability, vegetation dynamics, and breeding opportunities (Grant & Grant, 2006; Holmgren et al., 2006; Siepielski et al., 2017). In contrast, temperature effects may act more subtly or indirect, e.g., through thermoregulation, metabolic costs, or parasite dynamics, and thus may produce weaker or less consistent signatures in phenotypes (Huey & Tewksbury, 2009; Khaliq et al., 2014; Scharsack et al., 2016).

A starting point to distinguish among the above scenarios is to analyse time-series of rates and patterns of environment change in relation to rates and patterns of trait change, especially where the genetic and functional bases of the studied traits are well known. First, time-series analyses of climate variables can be used to ask whether a signal of climate change is detectable beyond shorter-scale (e.g., annual) changes in weather (Mudelsee, 2010). Second, time-series analysis can be used to assess trait changes and their potential causes—as has long been the case in paleontology (e.g., Geerts et al., 2015; Hopkins & Lidgard, 2012; Hunt, 2007, 2015). For instance, trait changes in time-series can be used to infer: (1) directional change, whereby trait values show a generally decreasing or

increasing trend over time (Figure 1A), (2) stasis, whereby trait values fluctuate around a population mean with no net change across time (Figure 1B), or (3) random walks, whereby trait values show unpredictable increases or decreases from one year to the next (Figure 1C) (Hunt, 2007; Tëmkin & Elredge, 2015). Time-series analysis can also reveal combinations of these categories, such as a directional trend with reversion to the population mean (Hunt et al., 2015; Lambert et al., 2020). Finally, lagged time-series of phenotypic traits can be compared to time-series of environmental data to identify short-term and long-term associations between environmental and trait variables (Hannisdal et al., 2017; Hunt et al., 2015).

In largely studied systems such as birds, contemporary time-series analyses of climate change impacts on species traits have revealed phenological shifts, such as earlier breeding seasons, and range shifts, including poleward expansions across various bird taxa (Halupka et al., 2023; Parmesan & Yohe, 2003; Visser et al., 1998). Most of these examples come from systems where climate change is noticeable, whereas information from systems that have evolved under naturally high climatic variability remains scarce. In this study, we use time-series analysis to examine trends and potential environment–trait correlations in two species of Darwin's finches in the Galápagos Islands, where climate is highly variable.

Darwin's finches and climate change in Galápagos

The climate of the Galápagos Islands is tied to its location in the Eastern Tropical Pacific about 1,000 km west of the coast of South America. Three primary oceanic currents converge on Galápagos and interact with prevailing winds coming from the southeast (Trueman & d'Ozouville, 2010) to generate two seasons. The warm/wet season prevails from December through May and is characterized in most years by occasional to high precipitation and high temperatures. The dry/cold season prevails from June through November and is characterized by low precipitation and cooler temperatures (Trueman & d'Ozouville, 2010). Importantly, wide variation in temperature and precipitation occurs within and between years and seasons owing to changing ocean conditions that include El Niño and La Niña events. El Niño events occur mostly every 2–7 years and, in Galápagos, are characterized by a rainy season with abnormally high levels of precipitation. La Niña events tend to occur right after El Niño events and, in Galápagos, are characterized by extended periods of drought (Liu et al., 2013; Trueman & d'Ozouville, 2010). Amidst these patterns of seasonal and inter-annual variation, some signs of climate change have been detected. For instance, average annual temperatures on the islands were reported to increase by 0.6 C° from 1980 to 2017 (Paltán et al., 2021), whereas the first two decades of the present century have been in average 40% drier compared to the precipitation on the 1981–1990 decade (Escobar-Camacho et al., 2021). Further, El Niño events over the past two decades appear to have increased in frequency and intensity (Rustic et al., 2015).

For Darwin's finches, precipitation changes may represent the more biologically consequential aspect of climate change. Food availability, shaped by high or low levels of precipitation, influences finch mortality and acts as a strong selective agent on beak size and shape (Beausoleil et al., 2019; Grant & Grant, 1993; 1996; 2002; 2006; 2007). These selection
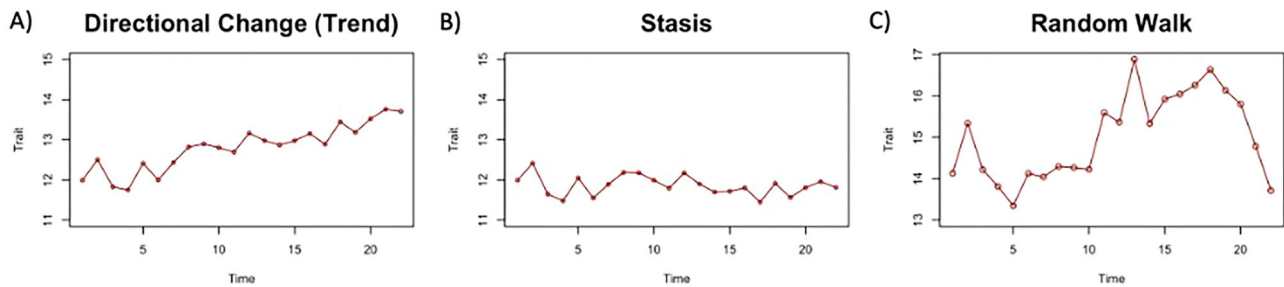
Figure 1. Illustrative example simulations of time-series types for finch beak length. A) Directional change (trend). B) Stasis. C) Random walk. Simulations were generated from original annual mean values of finches beak length between 1999 and 2022 at AB (Academy Bay) in Santa Cruz Island, using an Autoregressive (AR) model of order 1. We used 0.2 standard deviations for modelling the stasis process, and 0.09 slope for modelling the directional change.

events also influence body traits (Grant & Grant, 1993) since they are highly correlated to beak size (Schluter, 1984). In contrast, the impact of temperature increases, and its ecological consequences remain less known, except in contexts such as parasite load in finch nestlings (Dudaniec et al., 2007) or beak thermoregulation (Tattersall et al., 2018), and although other traits have not been directly studied in the context of climate change in Galapagos, studies with other passerines have found declining body mass and size as result of temperature increases (Gardner et al., 2019; Salewski et al., 2010). Therefore, while both climate dimensions warrant study, precipitation changes provide the most direct and consistent ecological linkage to bird trait evolution.

Interpretation of our results will be aided by an uncommonly strong understanding of the genetic and functional basis of several finch traits. First, inter-annual trait changes in beak traits are expected to reflect evolutionary responses (as opposed to plasticity) given the extremely high heritability of beak size (0.87–1.03 h²) and shape (0.75–0.92 h²) (Boag, 1983; Grant & Grant, 1993, 1997). Further, several large-effect genes influencing beak traits are known (Abzhanov et al., 2004; Chaves et al., 2016; Lamichhaney et al., 2016)—and have been documented to experience allele frequency changes that correspond to trait selection (Lamichhaney et al., 2016). Second, beak sizes and shapes are known to be closely tied to local food resources. For instance, the distribution of beak sizes and shapes in finch communities is linked to the types of food resources—especially seed sizes and hardnesses—that are present locally (Abbott et al., 1977; De León et al., 2014; Lack, 1947; Schluter, 1984). Furthermore, temporal changes in plant communities during El Niño and La Niña events lead to rapid evolutionary changes in beak traits (Grant & Grant, 2002, 2006).

With the above motivation and context, we compile 24 years of data on beak and body traits in the small ground finch (*Geospiza fuliginosa*) and the medium ground finch (*G. fortis)* at two sites on Santa Cruz Island, Galápagos, and similarly compile comparable time series for temperature and precipitation. We then use time-series analysis to answer three questions: (Q1) to what extent is weather changing through time (i.e., "climate change") in our study sites, as has been found in other places in Galápagos (Paltán et al., 2021; Escobar-Camacho et al., 2021)? (Q2) to what extent do time-series of beak and body traits show detectable trends consistent with responses to climate change? And finally, (Q3) how does weather (year-to-year changes) influence beak and body traits in our study system, as has been previously reported for other populations or time periods in Galápagos (e.g., Beausoleil et al., 2019; Grant & Grant, 2006, 2007)?

Materials and methods

Study sites and data collection

Our study focused on two lowland sites on Santa Cruz Island: Academy Bay (AB; 0° 44' 21.3" S, 90° 18 '06.3" W) and El Garrapatero (EG; 0° 41' 15.7" S, 90° 13' 18.3" W). Academy Bay lies along the southeastern shore of Santa Cruz, next to the town of Puerto Ayora. El Garrapatero lies along the eastern shore of the island, approximately 10 km northeast of Puerto Ayora. El Garrapatero is relatively far from any human settlement, although a road passes through the site giving tourists access to a beach. The road was paved in 2008. Both sites lie in the lowlands of Santa Cruz and thus are characterized by arid weather and arid-zone vegetation.

Precipitation and temperature data were obtained for the 24 years (1999–2022) of our study. Daily rainfall and temperature data for Santa Cruz were recorded by a gauge maintained at the Charles Darwin Research Station (Charles Darwin Foundation, 2024). These data should be broadly representative of both sites given their similar biotic and abiotic conditions: AB (500 m from the gauge) and EG (10 km from the gauge). However, our personal experience suggests that EG experiences less rainfall than AB, which is supported by a previous study (Carrion et al., 2022) showing lower vegetation cover (Enhanced Vegetation Index) at EG compared to AB.

Morphological data was collected for the medium ground finch (*G. fortis*) and the small ground finch (*G. fuliginosa*) from 1999 to 2022 at the two study sites during the breading season of Darwin's finches (January–May) (Table S1): AB between 1999 and 2022, and EG between 2003 and 2022. Data were not available from 2021 due to the COVID-19 pandemic. Briefly, birds were captured with mist nets and banded with colour and metal leg bands that had unique numbers and combinations to ensure that each bird was included in our dataset only once for a given year. At the time of capture, each bird was classified—when possible—as juvenile, male, or female based on their plumage, beak colour, and the presence of a brood patch (Grant, 1999). Mature males can be easily identified based on their black plumage; however, it can be

difficult to distinguish juveniles from mature females that do not have a brood patch (Grant, 1999).

Each bird was measured following the methods of Boag & Grant (1984—see also Grant, 1999). Specifically, we measured beak length (anterior edge of nares to anterior tip of upper mandible), beak depth (at the nares), beak width (at the base of the lower mandible), body mass (weight), wing chord (length of longest relaxed right primary feather), and tarsus length (between the nuchal notch at the upper end of the right tarsometatarsus and the lowest undivided scute). Beak and tarsus measurements were made to the nearest 0.01 mm using digital calipers. Wing chord was measured to the nearest 0.01 cm using a wing-and-tail ruler. Mass was measured to the nearest 0.01 g using a portable digital scale. In most cases, beak length, depth, and width were each measured three times for each bird, and the median value was then used for subsequent analysis. More information on these sites and their finch communities, as well as our field procedures, can be found in Carrión et al. (2022) and Beausoleil et al. (2023).

Before performing statistical analysis, we removed outliers from the raw data that represent potential hybrids using the interquartile range rule and the *boxplot.stats()* command in R (R Core Team, 2021). After removing outliers, annual mean values were calculated for each morphological (beak length, beak depth, beak width, body mass, tarsus length, and wing chord) and environmental variable (precipitation and temperature) for further analyses. The objective of using annual mean values of temperature and precipitation for analysis rather than seasonal is to obtain a broad sense of climate change in our study site despite the known high interannual and seasonal variation. Furthermore, mean annual values for finch traits were used since we are interested in population level trends across time rather that individual level responses. Yet, acknowledging that differences between seasons can produce different outcomes, analysis using data for only warm or cold seasons were additionally performed and added in supplementary materials.

Each time-series of morphological traits or environmental variable was then checked for autocorrelation and partial-autocorrelation; i.e., whether a variable was correlated with lagged values (between 1 and 5 years) of itself. We performed this analysis using the *acf()* and *pacf()* functions in R (Venables & Ripley, 2002). If autocorrelation was present in a time-series, it was corrected by subtracting (from each of its values) the previous value (for autocorrelation at lag −1), the two previous values (for autocorrelation at lag −2), and so on. This correction was done using the *diff()* function of the timeSeries package in R (Hyndman & Killick, 2023). Overall correlation between temperature and precipitation is rather low ($r = 0.16$, $df = 22$, $p = 0.457$), with similar results when we consider each season individually (warm season: $r = 0.09$, $df = 22$, $p = 0.67$, cold season: $r = 0.35$, $df = 22$, $p = 0.059$). These results allow separate analyses of environmental variables.

Is climate change present in our study sites in Galápagos (Q1)? and, do time-series of beak and body traits show detectable trends consistent with climate change (Q2)?

To identify whether each time-series has a pattern consistent with a random walk, stasis, or a directional trend, we classified each environmental (*Q1)* and finch trait (*Q2)* time-series

following a two-step procedure as in Lambert et al. (2020). First, we classified the series as random walks or stasis (mean-reverting) by estimating their persistence r (relation of current value to past values within a time-series that indicate whether a trait tends to stay stable or drift over time). For this, we fit a Bayesian hierarchical model of first-order auto-regressive process (AR1), where the model predicts current values based on its immediately preceding value (1 year before):

$$z(t) = \rho \cdot z(t-1) + \epsilon(t)$$

where:
$z(t)$ the trait/environmental value at time t,
ρ persistence parameter,
$\epsilon(t) \sim N(0, \sigma^2)$ normally distributed error with variance σ^2.

To account for relationships among traits and to give equal weight to the random walk and stasis hypothesis, we allowed r to vary for all the traits simultaneously using a weak informative prior, yet the individual parameters were drawn from a common normal distribution of the form:

$$\rho(z) \sim N(\bar{\rho}, \tau)$$

where z is the trait or environmental value, $\bar{\rho}$ is the population mean of r, and τ is the s.d. of the population-level distribution.

If the 95th percentile of the posterior distribution of ρ was <1, we classified it as stasis, and if not, as random walk.

After the above process, we estimated the level of bias (trend) in each time-series, δ. If a time-series was previously identified as random walk, we used a model of the form:

$$\Delta \bar{z}(t) = \delta + \epsilon(t)$$

where $\Delta \bar{z}(t) = \bar{z}(t) - \bar{z}(t-1)$, and $\epsilon(t)$ is a normally distributed error term that represents random fluctuations or noise in the data.

If a time-series showed stasis (mean reversion), we used a model of the form:

$$\bar{z}(t) = \delta t + \epsilon(t)$$

For each trait, if the 5th and 95th percentiles of the posterior distribution of δ did not overlap zero, we classified it as directional trend. For each model, we ran four Markov chain Monte Carlo chains with 5,000 iterations to reduce divergent transitions that might be caused by the small sample size and discarded the first half of samples as warm up. We used the R-hat diagnostic metric to assess whether the chains converged to stable posterior distributions. All models presented R-hat < 1.1, which indicates convergence and reliable estimates. The models were run using Stan package in R (Stan Development Team, 2023).

Is weather (year-to-year changes) affecting beak and body traits in Darwin´s finches? (Q3)

We tested for correlations between each morphological trait time-series and each environmental time-series at different lags using cross-correlation analysis with the *ccf()* function in R (Venables & Ripley, 2002). As Darwin's finches have shown evolutionary responses between 1 and up to 3 years after an environmental event (e.g., drought or heavy rain; Boag & Grant, 1981; Gibbs & Grant, 1987; Grant & Grant, 1993), we tested correlations between traits and values of temperature and precipitation lagged between 1 and 5 years. Note also that the rule of thumb for cross-correlation analysis is that the
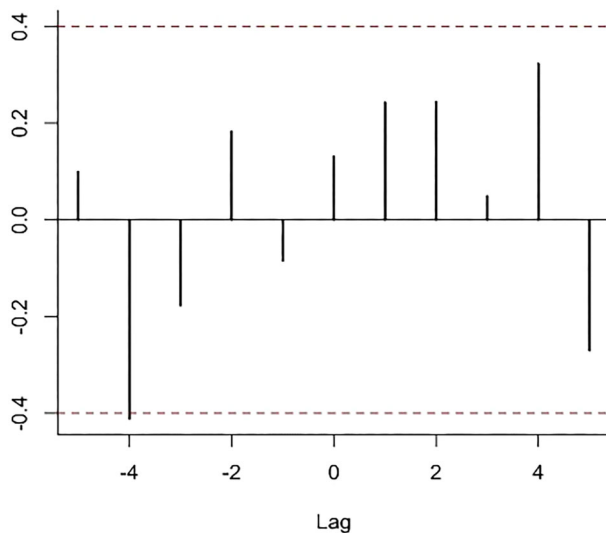
Figure 2. Example of a correlogram between beak length and precipitation time-series. Dotted lines indicate the significance threshold. We are here interested in negative lags because they refer to situations where weather influences finch traits in future years—as opposed to the illogical situation where finch traits would influence weather in future years.

number of lags tested should be no more than $T/4$, where T is the length of the time-series (Hamilton, 1994; Box et al., 2015). The cross-correlation function (CCF) at lag k for two time series $\{Xt\}$ and $\{Yt\}$ is defined as

$$\text{CCF}\ (k)\ =\ \frac{\text{Cov}\left((X_t - \text{mean}\ (X_t)),\ (Y_{t-k} - \text{mean}\ (Y_{t-k})\right)}{\sqrt{\text{Var}\,(X) \cdot\ \text{Var}\,(Y)}}$$

where $\text{Cov}(X_t, Y_{t-k})$ is the covariance between X_t and Y_{t-k} (observations of X at time t and Y at time $t-k$), and $\text{Var}(X)$ and $\text{Var}(Y)$ are the variances of X and Y, respectively.

Positive correlation (CCF) values indicate a positive relationship between the two series at a specific lag, whereas negative values indicate a negative relationship. Similarly, larger positive or negative values indicate a stronger relationship between the two series. Values that cross the dotted line in the resulting correlograms (Figure 2) indicate a significant (z-test) correlation between a time-series and another time-series at lag k. As we were interested in the influence of values of precipitation and temperature on the lagged values of beak and body traits of finches, and not the opposite, only correlations from zero to the left on a correlogram were considered. Finally, the largest CCF coefficient per correlation was noted and reported in the results section. As an illustrative example (Figure 2), beak length correlates negatively with precipitation 4 years prior: in other words, when it rains a lot in 1 year, beak length tends to be shorter 4 years later.

Results

Is climate change present in our study sites in Galápagos (Q1)?

Analysis of trends and classification of time-series revealed similar overall patterns for temperature and precipitation. Precipitation showed positive directional change (trend $d = 0.015$ cm^3, with 95% credible interval ranging between 0.005 and 0.21 cm^3) with increasing fluctuation around the mean ($r = 0.12$ cm^3, with 95% credible interval ranging between -0.21 and 0.45 cm^3) (Figure 3A). This increasing trend is more pronounced during the warm season and almost absent during the cold season, which indicates that present overall trends are mainly driven by changes during the warm season (Figure S1). Temperature also showed positive directional change (trend $d = 0.006$ °C, with 95% credible interval ranging between 0.005 and 0.19 °C) with increasing fluctuations around the mean ($r = 0.11$ °C, with 95% credible interval ranging between -0.24 and 0.50 °C) (Figure 3B). This increasing trend is present in both seasons, although is more pronounced during the warm season (Figure S1). In summary, over the last 24 years, the lowlands of Santa Cruz Island have seen an annual increase of about 0.015 cm^3 in rainfall and 0.006 °C in temperature. Also, note that these are linear trends, whereas non-linear relationships could well be present (Figure 3).

Do time-series of beak and body traits show detectable trends consistent with climate change (Q2)?

Classification analyses for *G. fortis* showed that time-series for beak length, beak depth, and beak width were mostly consistent with random walks, whereas time-series for tarsus length, wing chord, and mass were more consistent with stasis (Figure 4A, Table S4). Analyses for *G. fuliginosa* showed similar patterns: time-series for beak traits were more consistent with random walks, whereas time-series for body traits were more consistent with stasis (Figure 4B, Table S4). None of the time-series for beak and body traits in either species suggested a directional change or trend (Figure 4, Table S4).

Is weather (year-to-year changes) affecting beak and body traits in Darwin's finches (Q3)?

For *G. fortis*, cross-correlation coefficients between precipitation and beak and body traits consistently showed negative relationships at both sites and both seasons (Figure 5A, Table S2). That is, as precipitation increased, trait sizes decreased. These associations were stronger (higher CCF values) during the warm season compared to the cold season. The strongest correlation coefficient for precipitation was with beak width at EG (CCF $= -0.632$, $n = 20$), whereas the weakest was with tarsus length at AB (CCF $= -0.131$, $n = 24$). Cross-correlation coefficients between temperature and beak and body traits showed a variety of positive and negative relationships that also changed across seasons (Figure 5B, Table S2). Overall, as temperatures increased, some traits decreased in magnitude (beak depth, beak width, wing chord, and mass), whereas other traits increased in magnitude (beak length, tarsus length). The strongest correlation coefficient for temperature was with wing chord at AB (CCF $= -0.513$, $n = 24$), whereas the weakest was with beak width at EG (CCF $= -0.121$, $n = 20$).

For *G. fuliginosa*, cross-correlation coefficients between precipitation and beak and body traits also showed negative relationships at both sites and both seasons (Figure 5C, Table S3): again, increasing precipitation led to decreasing trait sizes, being correlations stronger during the warm season. The strongest correlation coefficient for precipitation was
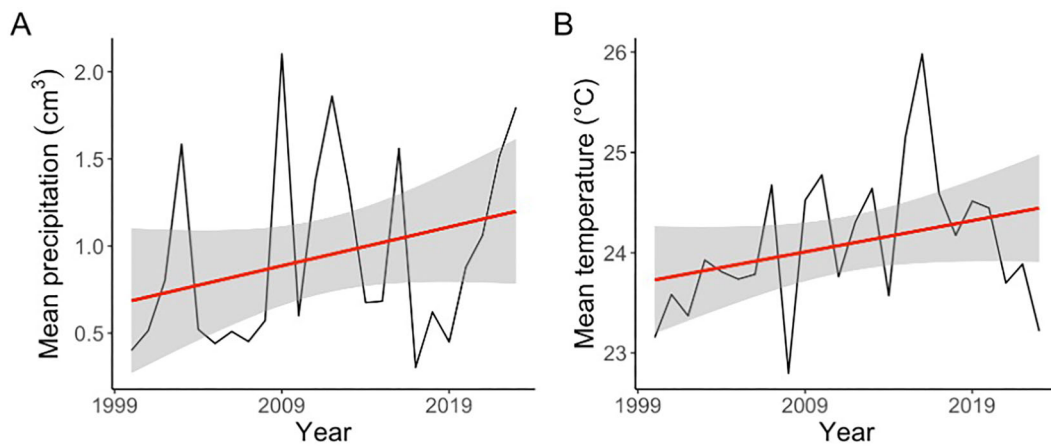
Figure 3. Time-series of A) mean annual precipitation and B) mean temperature in Santa Cruz Island between 1999–2022. Trend lines indicate the estimated linear regression, bars indicate the confidence intervals on that estimate.
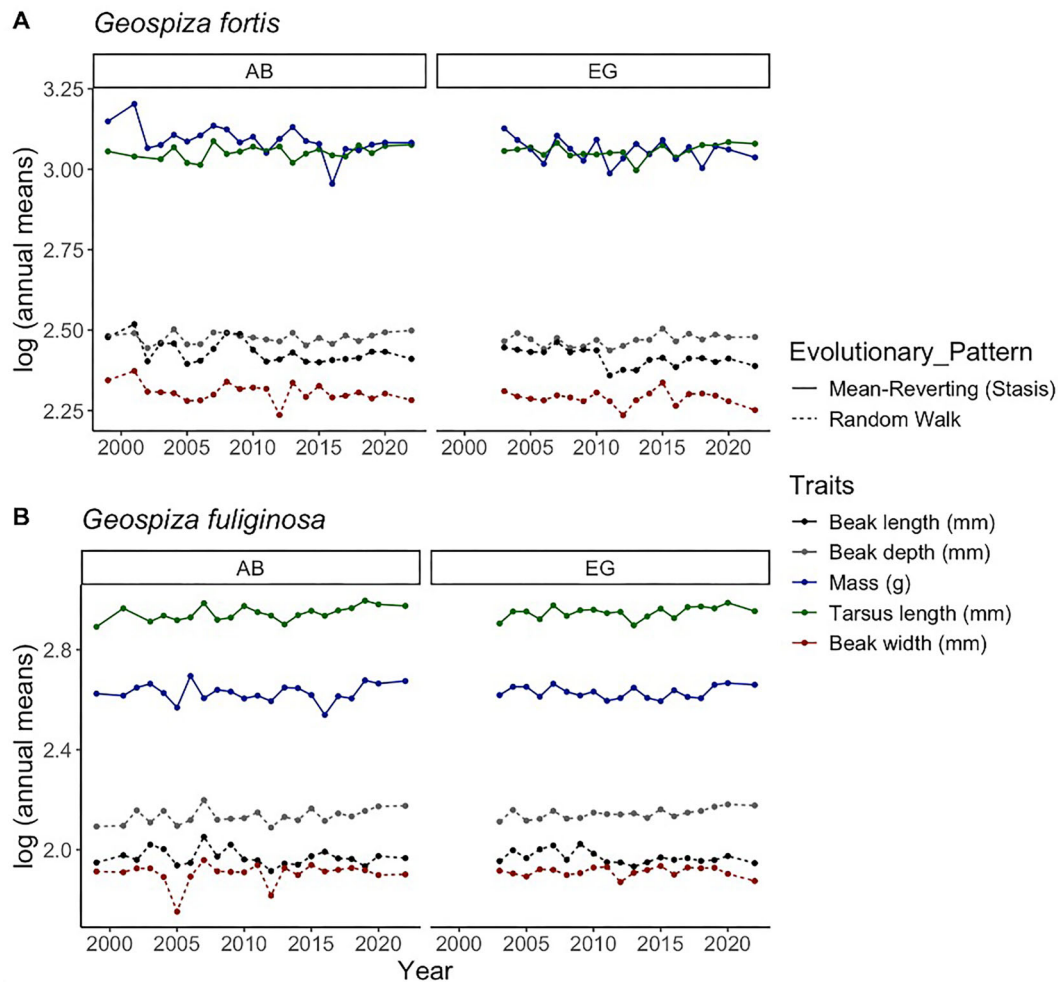
Figure 4. Time-series of beak and body traits for *G. fortis* (A), and *G. fuliginosa* (B) between 1999 and 2022 at two sites (AB and EG) in Santa Cruz Island, Galápagos. Wing chord not displayed as its scale is drastically different.

with beak depth at AB (CCF $= -0.451$, $n = 20$), whereas the weakest was with mass at AB (CCF $= -0.217$, $n = 20$). Cross-correlation coefficients between temperature and beak and body traits for *G. fuliginosa* showed a mix of positive and negative relationships that varied across seasons (Figure 5D,

Table S3)—as was also the case for *G. fortis* (see below). As temperatures increased, beak depth, wing chord, and mass decreased at both sites, whereas other traits increased in magnitude (beak length, beak width, and tarsus length). The strongest correlation coefficient was for beak depth at EG
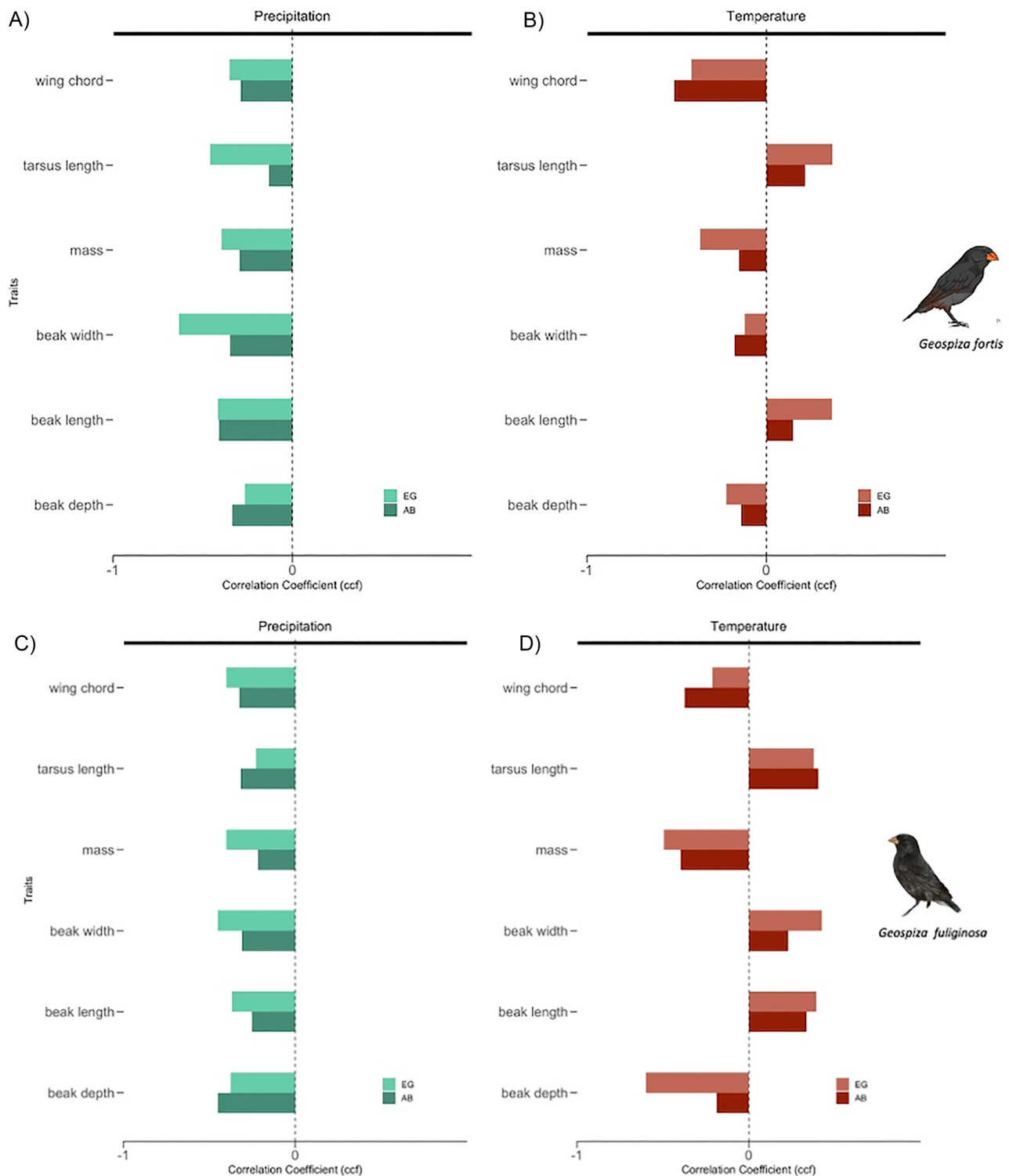
Figure 5. Cross-correlation coefficients (CCFs) between lagged (from 1 to 5 years) time-series of precipitation (left-hand plots) and temperature (right-hand plots) for beak and body traits of *G. fortis* (A and B) and *G. fuliginosa* (C and D) at two sites AB and EG (different shading) on Santa Cruz Island, Galápagos. Bars correspond to the most extreme CCF coefficient per correlation.

(CCF = −0.599, n = 20), whereas the weakest was for beak depth at EG (CCF = −0.187, n = 20).

Discussion

The goal of our study was to test for potential associations of climate change with phenotypic evolution in two species of Darwin's finches in the Galápagos islands, a climatically highly variable place. Studies on many other species have shown diverse impacts of climate change; yet such impacts might be minimal or hard to detect under certain conditions. We might expect minimal impact of climate change in areas where it is not very pronounced, where populations lack the

ability to respond to climate change, or where the resources and conditions the species rely on are not strongly affected by climate change. Time-series analyses of traits with known genetic and functional properties allow some insight into these possibilities. We performed such analyses based on 24 years of data for beak and body traits in the two species, alongside data on precipitation and temperature for the study sites. Bayesian time-series analyses detected precipitation and temperature increases over the 24 years, although the trend was mild and weak relative to year-to-year fluctuations. Second, beak and body traits did not show detectable directional trends, with beak traits mainly showing random walk patterns, and body traits showing stasis. Finally, cross-correlation analysis revealed negative short-term correlations between precipitation and beak and body traits for both species, alongside more variable correlations between temperature and those traits. We now discuss each of these three main results in more detail.

Is climate change present in our study sites in Galápagos (Q1)?

Our analyses suggest that average temperature and precipitation have increased at our study sites over the past two decades (Figure 3 and S1), which agrees with global trends and trends in the equatorial Pacific region (IPCC, 2018). Specifically for Galápagos, Paltán et al. (2021) estimated that the lowlands have seen an increase of 0.6 °C over the past 35 years—much higher than our estimate of 0.01 °C over the past 24 years. Outcomes for precipitation are less consistent. Paltán et al. (2021) concluded that average precipitation decreased over the last 35 years. Escobar-Camacho et al. (2021), on the other hand, did not find any trends for precipitation in the Galápagos lowlands during the 2002–2017 period. These variable outcomes might be related to El Niño events, where unusually large amounts of rain can affect time-series analyses, or can be related to the different number of locations (rain gauges) used to analyse climatic trends. Nevertheless, Paltán et al. (2021) showed that precipitation follows an increasing trend when El Niño years (1982–1983 and 1997–1998) are excluded from the calculation. In our analysis, the period used did not include extreme El Niño years in Galápagos, and the most obvious effect was an increase in rainfall over the last few years from 2019 to 2022 (Figure 3 and S1).

Regardless of any long-term trend in temperature or precipitation, it is critical to emphasize the comparatively large inter-annual variation. For instance, we estimate that average temperature increased by 0.01 °C over 24 years, yet average temperature differed between adjacent years by up to 1.7 °C (e.g., 22.8 °C in 2008 versus 24.5 °C in 2009, Figure 3B). Similarly, average precipitation was estimated to have increased by 0.015 cm^3 over 24 years, yet average precipitation differed between adjacent years by up to 1.53 cm^3 (e.g., 0.57 cm^3 in 2008 vs. 2.10 cm^3 in 2009, Figure 3A). Furthermore, temperature and precipitation can vary within a year—most obviously corresponding to the previously-mentioned "wet/warm" vs. "dry/cold" seasons. Although precipitation and temperature trend directions did not change between seasons in our study site (Figure S1), we found that during the "wet/warm" season trends were more pronounced, which is likely due to higher temperature and precipitation in the lowlands during this period. For instance, at our study site, temperature varied in 2014 from 27 °C during the wet season to 23 °C in the dry

season, whereas precipitation went from 1.17 to 0.33 cm^3 (Figure S1).

In conclusion, patterns in temperature and precipitation in Galápagos are complex, with trends that are highly influenced by inter-annual variation, seasonality and drastic climatic events such as El Niño. These dynamics are comparable to other tropical lowland regions, where climate change signals are often obscured by high natural variability (Malhi et al., 2008; Seddon et al., 2016). This context is important because many tropical systems—including bird populations—may respond less predictably to climate trends than temperate systems (Jirinec et al., 2021; Monge et al., 2023).

Do time-series of beak and body traits show detectable trends consistent with climate change (Q2)?

Time-series of beak and body traits of finches did not show any detectable evolutionary trends over the 24-year period of our study (Figure 4). For beak traits, time-series in both species could not be distinguished from a random walk pattern, meaning that they appear to have changed rather erratically and unpredictably, whereas for body traits patterns showed stasis (Figure 5). These results suggest high inter-annual variability without directional trends which matches patterns documented in other tropical birds. For instance, long-term studies in South and Central America have reported species-specific and weak morphological changes across decades (Monge et al., 2023; Wilcox et al., 2024), in contrast to many temperate-zone birds that had shown gradual decreases in body size or increases in appendage length linked to sustained warming (Gardner et al., 2011; Ryding et al., 2021; Teplitsky & Millien, 2014; Van Buskirk et al., 2010).

In the tropics, subtle climate trends relative to strong seasonal and inter-annual variation may dampen consistent selection pressures. Additionally, resource dynamics and interspecific competition—major drivers of beak morphology in Darwin's finches (Lack, 1947; Schluter & Grant, 1984)—are themselves strongly influenced by irregular climate events (e.g., El Niño) rather than gradual change.

Body traits also lacked directional trends in Darwin's finches despite global meta-analyses showing size reductions in birds and mammals under warming conditions (Scheffers et al., 2016; Sheridan & Bickford, 2011; Yom-Tov & Geffen, 2011). Tropical bird exceptions are not uncommon (Jirinec et al., 2021; Radchuk et al., 2019; Wilcox et al., 2024), likely because thermoregulatory selection (Bergmann's and Allen's rules) is weaker in regions where temperatures are already high and behavioral adaptations are available (Tattersall et al., 2018; Friedman et al., 2019). In our data, beak traits exhibited greater year-to-year variability than body traits, consistent with their more immediate ecological role in food acquisition, while body traits may be constrained by locomotor or structural demands less sensitive to short-term environmental variation. Finally, a 24-year dataset might be still insufficient to identify long-term trends in Darwin's finches thus monitoring of finch populations should continue.

Is weather (year-to-year changes) affecting the beak and body traits in Darwin's finches (Q3)?

Both finch species showed significant negative lagged correlations between precipitation and multiple morphological traits, meaning that wetter years tended to precede smaller beaks and

smaller bodies, and this correlation remains even across seasons. This is consistent with prior research on Darwin's finches (Beausoleil et al., 2019; Boag & Grant, 1981; Grant & Grant, 1993) and aligns with resource-mediated selection processes documented in other tropical birds. In Amazonian floodplain systems, e.g., high-rainfall years can increase the abundance of soft seeds and fruits, favouring smaller or thinner beaks (Haugaasen & Peres, 2007). Conversely, drought years often select for larger, stronger beaks capable of cracking hard seeds that dominate in drier conditions (Boag & Grant, 1981, 1984; Price et al., 1984).

Demographic feedbacks may also contribute. Higher recruitment in wet years can intensify intraspecific competition the following year (Beausoleil et al., 2019), favouring individuals more efficient at exploiting abundant small seeds (often those with smaller beaks). These processes could indirectly influence body size if smaller individuals are competitively favoured under these conditions. In Darwin's finches, beak and body size are highly correlated (Grant, 1981) thus increases in body size can also be an indirect response to changes in beak morphology.

Temperature effects were weaker and inconsistent across traits, offering little support for Bergmann's or Allen's rules. This mirrors findings from other tropical avian studies (Jirinec et al., 2021; Monge et al., 2023), where thermoregulation plays a minor role compared to resource-driven selection.

Overall, our findings underscore that in tropical systems—particularly those with high climate variability—precipitation-driven changes in food availability may be the dominant climatic driver of morphological variation. This stands in contrast to temperate systems, where temperature often exerts the strongest influence. For Darwin's finches, as for other tropical birds, trait trajectories appear shaped less by slow, directional climate change and more by fluctuating, resource-mediated selection pressures that can reverse across years.

Conclusion

Taken together, our results highlight the importance of distinguishing between gradual climate change and high-frequency weather variability when evaluating morphological responses in tropical birds. At our site, weak long-term climate trends combined with strong inter-annual fluctuations mean that selection pressures are rarely unidirectional or sustained. Instead, precipitation-driven resource dynamics appear to dominate, producing lagged trait shifts that differ from the temperature-driven, directional patterns common in temperate-zone species. This suggests that forecasting morphological change in tropical systems will require models that integrate the stochastic nature of rainfall and its ecological consequences, rather than assuming unique responses to rising temperatures.

Finally, and specific to our study system, although Darwin's finches do not show long-term responses to climate change, this does not mean that they are "safe" moving forward. First, finch communities are currently impacted by other forms of environmental change such as invasive predators (Gotanda, 2020; Kleindorfer et al., 2009), invasive parasites (Fessl & Tebbich, 2002; Knutie et al., 2024; Koop et al., 2016; O'Connor et al., 2010), and habitat modification (Cimadom et al., 2014; Harvey et al., 2021), which can be exacerbated by

climate change. Second, climate change might ultimately exceed the buffering capacity of the system that we have detected here. When this happens, a tipping point might be passed that can lead to dramatic changes (Dakos et al., 2019). Third, it is possible that some species in areas we did not study might currently be experiencing strong climate change impacts. Our focus was on abundant and widely distributed species that exist across very large habitat gradients, whereas specialists on rare habitats might be more sensitive.

Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data availability

The data underlying this article is available in OSF at https://doi.org/10.17605/OSF.IO/T76YE.

Author contributions

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Conflict of interest

None declared.

References

Abbott, I., Abbott, L. K., & Grant, P. R. (1977). Comparative ecology of Galápagos ground finches (Geospiza Gould): evaluation of the importance of floristic diversity and interspecific competition. *Ecological Monographs*, 47(2), 151–184. https://doi.org/10.2307/1942615

Abzhanov, A., Protas, M., Grant, B. R., & Tabin, C. J. (2004). Bmp4 and morphological variation of beaks in Darwin's finches. *Science*, 305(5689), 1462–1465. https://doi.org/10.1126/science.1098095

Beausoleil, M. O., Carrión, P. L., Podos, J., & Hendry, A. P. (2023). The fitness landscape of a community of Darwin's finches. *Evolution; International Journal of Organic Evolution*, 77(12), 2533–2546. https://doi.org/10.1093/evolut/qpad160

Beausoleil, M. O., Frishkoff, L. O., M'Gonigle, L. K., & Barrett, R. D. (2019). Temporally varying disruptive selection in the medium ground finch (*Geospiza fortis*). *Proceedings of the Royal Society B: Biological Sciences*, 286(1916), 20192290. https://doi.org/10.1098/rspb.2019.2290

Blois, J. L., Feranec, R. S., & Hadly, E. A. (2008). Environmental influences on spatial and temporal patterns of body-size variation in California ground squirrels (*Spermophilus beecheyi*). *Journal of Biogeography*, 35(4), 602–613. https://doi.org/10.1111/j.1365-2699.2007.01836.x

Boag, P. T. (1983). The heritability of external morphology in Darwin's ground finches (*Geospiza*) on Isla Daphne Major, Galápagos. *Evolution; International Journal of Organic Evolution*, 877–894

Boag, P. T., & Grant, P. R. (1981). Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. *Science*, 214(4516), 82–85. https://doi.org/10.1126/science.214.4516.82

Boag, P. T., & Grant, P. R. (1984). The classical case of character release: Darwin's finches (*Geospiza*) on Isla Daphne Major, Galápagos. *Biological Journal of the Linnean Society*, 22(3), 243–287. https://doi.org/10.1111/j.1095-8312.1984.tb01679.x

Bowler, D. E., Hof, C., Haase, P., & Böhning-Gaese, K. (2017). Cross-realm assessment of climate change impacts on species' abundance trends. *Nature Ecology & Evolution*, 1(3), 0067. https://doi.org/10.1038/s41559-016-0067

Box, G. E., Jenkins, G. M., Reinsel, G. C., & Ljung, G. M. (2015). *Time series analysis: forecasting and control*. John Wiley & Sons.

Carrión, P. L., Raeymaekers, J. A., De León, L. F., & Hendry, A. P. (2022). The terroir of the finch: How spatial and temporal variation shapes phenotypic traits in Darwin's finches. *Ecology and Evolution*, 12(10), e9399.

Charmantier, A., & Gienapp, P. (2014). Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evolutionary Applications*, 7(1), 15–28. https://doi.org/10.1111/eva.12126

Chaves, J. A., Cooper, E. A., Hendry, A. P., & Uy, J. A. C. (2016). Genomic variation at the tips of the adaptive radiation of Darwin's finches. *Molecular Ecology*, 25(21), 5282–5295. https://doi.org/10.1111/mec.13743

Cimadom, A., Ulloa, A., Meidl, P., & Tebbich, S. (2014). Invasive parasites, habitat change, and heavy rainfall reduce breeding success in Darwin's finches. *PLoS One*, 9(9), e107518. https://doi.org/10.1371/journal.pone.0107518

Cotto, O., Wessely, J., Georges, D., & Guillaume, F. (2017). A dynamic eco-evolutionary model predicts slow response of alpine plants to climate warming. *Nature Communications*, 8(1), 15399. https://doi.org/10.1038/ncomms15399

Crozier, L. G., Scheuerell, M. D., & Zabel, R. W. (2011). Using time series analysis to characterize evolutionary and plastic responses to environmental change: a case study of a shift toward earlier migration date in sockeye salmon. *The American Naturalist*, 178(6), 755–773. https://doi.org/10.1086/662669

Dakos, V., Matthews, B., Hendry, A. P., & De Meester, L. (2019). Ecosystem tipping points in an evolving world. *Nature Ecology & Evolution*, 3(3), 355–362. https://doi.org/10.1038/s41559-019-0797-2

De León, L. F., Podos, J., Gardezi, T., & Hendry, A. P. (2014). Darwin's finches and their diet niches: the sympatric coexistence of imperfect generalists. *Journal of Evolutionary Biology*, 27(6), 1093–1104.

Dudaniec, R. Y., Fessl, B., & Kleindorfer, S. (2007). Interannual and interspecific variation in intensity of the parasitic fly, *Philornis downsi*, in Darwin's finches. *Biological Conservation*, 139(3-4), 325–332. https://doi.org/10.1016/j.biocon.2007.07.006

Escobar-Camacho, D., Rosero, P., Castrejón, M., & Cuesta, F. (2021). Oceanic islands and climate: using a multi-criteria model of drivers of change to select key conservation areas in Galápagos. *Regional Environmental Change*, 21(2), 47. https://doi.org/10.1007/s10113-021-01768-0

Fessl, B., & Tebbich, S. (2002). *Philornis downsi*—a recently discovered parasite on the Galápagos archipelago—a threat for Darwin's finches? *Ibis*, 144(3), 445–451. https://doi.org/10.1046/j.1474-919X.2002.00076.x

Foden, W. B., Young, B. E., Akçakaya, H. R., & Huntley, B. (2019). Climate change vulnerability assessment of species. *Wiley Interdisciplinary Reviews: Climate Change*, 10(1), e551.

Foundation, C. D. (2024). CDF Meteorological Database—Base de datos meteorológico de la FCD. *Online data portal—portal de datos*

en línea. http://www.darwinfoundation.org/datazone/climate. Date accessed June 2024.

Franks, S. J., Sim, S., & Weis, A. E. (2007). Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences*, *104*(4), 1278–1282. https://doi.org/10.1073/pnas.0608379104

Friedman, N. R., Miller, E. T., Ball, J. R., & Economo, E. P. (2019). Evolution of a multifunctional trait: shared effects of foraging ecology and thermoregulation on beak morphology, with consequences for song evolution. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1917), 20192474. https://doi.org/10.1098/rspb.2019.2474

Gardner, J. L., Amano, T., Peters, A., & Symonds, M. R. (2019). Australian songbird body size tracks climate variation: 82 species over 50 years. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1916), 20192258. https://doi.org/10.1098/rspb.2019.2258

Gardner, J. L., Peters, A., Kearney, M. R., & Heinsohn, R. (2011). Declining body size: a third universal response to warming? *Trends in Ecology & Evolution*, *26*(6), 285–291. https://doi.org/10.1016/j.tree.2011.03.005

Geerts, A. N., Vanoverbeke, J., Vanschoenwinkel, B., & De Meester, L. (2015). Rapid evolution of thermal tolerance in the water flea Daphnia. *Nature Climate Change*, *5*(7), 665–668. https://doi.org/10.1038/nclimate2628

Gibbs, H. L., & Grant, P. R. (1987). Adult survivorship in Darwin's ground finch (*Geospiza*) populations in a variable environment. *The Journal of Animal Ecology*, *56*, 797–813. https://doi.org/10.2307/4949

Gienapp, P., Teplitsky, C., Alho, J. S., & Merilä, J. (2008). Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology*, *17*(1), 167–178. https://doi.org/10.1111/j.1365-294X.2007.03413.x

Goodman, R. E., Lebuhn, G., Seavy, N. E., & Bluso-Demers, J. D. (2012). Avian body size changes and climate change: Warming or increasing variability? *Global Change Biology*, *18*(1), 63–73. https://doi.org/10.1111/j.1365-2486.2011.02538.x

Gotanda, K. M. (2020). Human influences on antipredator behaviour in Darwin's finches. *Journal of Animal Ecology*, *89*(2), 614–622. https://doi.org/10.1111/1365-2656.13127

Grant, B. R., & Grant, P. R. (1993). Evolution of Darwin's finches caused by a rare climatic event. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *251*(1331), 111–117.

Grant, B. R., & Grant, P. R. (1996). High survival of Darwin's finch hybrids: Effects of beak morphology and diets. *Ecology*, *77*(2), 500–509. https://doi.org/10.2307/2265625

Grant, P. R. (1981). The feeding of Darwin's finches on *Tribulus cistoides* (L.) seeds. *Animal Behaviour*, *29*(3), 785–793. https://doi.org/10.1016/S0003-3472(81)80012-7

Grant, P. R. (1999). *Ecology and evolution of Darwin's finches*. Princeton, NJ: Princeton University Press.

Grant, P. R., & Grant, B. R. (1997). Genetics and the origin of bird species. *Proceedings of the National Academy of Sciences*, *94*(15), 7768–7775. https://doi.org/10.1073/pnas.94.15.7768

Grant, P. R., & Grant, B. R. (2002). Unpredictable evolution in a 30-year study of Darwin's finches. *Science*, *296*(5568), 707–711. https://doi.org/10.1126/science.1070315

Grant, P. R., & Grant, B. R. (2006). Evolution of character displacement in Darwin's finches. *Science*, *313*(5784), 224–226. https://doi.org/10.1126/science.1128374

Grant, P. R., & Grant, B. R. (2007). *How and why species multiply: the radiation of Darwin's finches*. Princeton University Press. https://doi.org/10.1515/9781400837946

Halupka, L., Arlt, D., Tolvanen, J., & Halupka, K. (2023). The effect of climate change on avian offspring production: A global meta-analysis. *Proceedings of the National Academy of Sciences*, *120*(19), e2208389120. https://doi.org/10.1073/pnas.2208389120

Hamilton, J. D. (1994). *Time series analysis*. Princeton University Press. https://doi.org/10.1515/9780691218632

Hannisdal, B., Haaga, K. A., Reitan, T., & Liow, L. H. (2017). Common species link global ecosystems to climate change: dynamical evidence in the planktonic fossil record. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1858), 20170722. https://doi.org/10.1098/rspb.2017.0722

Harvey, J. A., Chernicky, K., Simons, S. R., & Knutie, S. A. (2021). Urban living influences the nesting success of Darwin's finches in the Galápagos Islands. *Ecology and Evolution*, *11*(10), 5038–5048. https://doi.org/10.1002/ece3.7360

Haugaasen, T., & Peres, C. A. (2007). Vertebrate responses to fruit production in Amazonian flooded and unflooded forests. *Biodiversity and Conservation*, *16*(14), 4165–4190. https://doi.org/10.1007/s10531-007-9217-z

Holmgren, M., Stapp, P., Dickman, C. R., & Squeo, F. A. (2006). Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment*, *4*(2), 87–95. https://doi.org/10.1890/1540-9295(2006)004%5b0087:ECESAA%5d2.0.CO;2

Hopkins, M. J., & Lidgard, S. (2012). Evolutionary mode routinely varies among morphological traits within fossil species lineages. *Proceedings of the National Academy of Sciences*, *109*(50), 20520–20525. https://doi.org/10.1073/pnas.1209901109

Huey, R. B., & Tewksbury, J. J. (2009). Can behavior douse the fire of climate warming?. *Proceedings of the National Academy of Sciences*, *106*(10), 3647–3648. https://doi.org/10.1073/pnas.0900934106

Hunt, G. (2007). The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. *Proceedings of the National Academy of Sciences*, *104*(47), 18404–18408. https://doi.org/10.1073/pnas.0704088104

Hunt, G., Hopkins, M. J., & Lidgard, S. (2015). Simple versus complex models of trait evolution and stasis as a response to environmental change. *Proceedings of the National Academy of Sciences*, *112*(16), 4885–4890. https://doi.org/10.1073/pnas.1403662111

Hyndman, R., & Killick, R. (2023). CRAN Task View: Time Series Analysis. *Version 2023-03-06*. https://CRAN.R-project.org/view=TimeSeries. Date accessed June 25, 2023.

IPCC (2018). *Global warming of 1.5°C: an IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty*. Geneva: Intergovernmental Panel on Climate Change.

Jirinec, V., Burner, R. C., Amaral, B. R., & Stouffer, P. C. (2021). Morphological consequences of climate change for resident birds in intact Amazonian rainforest. *Science Advances*, *7*(46), eabk1743. https://doi.org/10.1126/sciadv.abk1743

Johnston, A., Ausden, M., Dodd, A. M., & Pearce-Higgins, J. W. (2013). Observed and predicted effects of climate change on species abundance in protected areas. *Nature Climate Change*, *3*(12), 1055–1061. https://doi.org/10.1038/nclimate2035

Karell, P., Ahola, K., Karstinen, T., & Brommer, J. E. (2011). Climate change drives microevolution in a wild bird. *Nature Communications*, *2*(1), 208. https://doi.org/10.1038/ncomms1213

Khaliq, I., Hof, C., Prinzinger, R., & Pfenninger, M. (2014). Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1789), 20141097. https://doi.org/10.1098/rspb.2014.1097

Kleindorfer, S., Sulloway, F. J., & O'Connor, J. (2009). Mixed species nesting associations in Darwin's tree finches: Nesting pattern predicts predation outcome. *Biological Journal of the Linnean Society*, *98*(2), 313–324. https://doi.org/10.1111/j.1095-8312.2009.01264.x

Knutie, S. A., Webster, C. N., Vaziri, G. J., & Wegrzyn, J. L. (2024). Urban living can rescue Darwin's finches from the lethal effects of invasive vampire flies. *Global Change Biology*, *30*(1), e17145. https://doi.org/10.1111/gcb.17145

Koop, J. A., Kim, P. S., Knutie, S. A., & Clayton, D. H. (2016). An introduced parasitic fly may lead to local extinction of Darwin's finch populations. *Journal of Applied Ecology*, *53*(2), 511–518. https://doi.org/10.1111/1365-2664.12575

Lack, D. L. (1947). *Darwin's finches*. Cambridge [Eng.].

Lambert, B., Kontonatsios, G., Mauch, M., & Leroi, A. M. (2020). The pace of modern culture. *Nature Human Behaviour*, *4*(4), 352–360. https://doi.org/10.1038/s41562-019-0802-4

Lamichhaney, S., Han, F., Berglund, J., & Andersson, L. (2016). A beak size locus in Darwin's finches facilitated character displacement during a drought. *Science*, *352*(6284), 470–474. https://doi.org/10.1126/science.aad8786

Liu, Y., Xie, L., Morrison, J. M., & Kamykowski, D. (2013). Dynamic downscaling of the impact of climate change on the ocean circulation in the Galápagos Archipelago. *Advances in Meteorology*, *2013*(1), 837432.

Malhi, Y., Roberts, J. T., Betts, R. A., & Nobre, C. A. (2008). Climate change, deforestation, and the fate of the Amazon. *Science*, *319*(5860), 169–172. https://doi.org/10.1126/science.1146961

Merilä, J., & Hendry, A. P. (2014). Climate change, adaptation, and phenotypic plasticity: The problem and the evidence. *Evolutionary Applications*, *7*(1), 1–14. https://doi.org/10.1111/eva.12137

Millien, V., Lyons, K., S., O., & Yom-Tov, Y. (2006). Ecotypic variation in the context of global climate change: revisiting the rules. *Ecology Letters*, *9*(7), 853–869. https://doi.org/10.1111/j.1461-0248.2006.00928.x

Monge, O., Maggini, I., Schulze, C. H., & Fusani, L. (2023). Physiologically vulnerable or resilient? Tropical birds, global warming, and redistributions. *Ecology and Evolution*, *13*(4), e9985. https://doi.org/10.1002/ece3.9985

Mudelsee, M. (2010). *Climate time series analysis. Atmospheric and Oceanographic Sciences Library*. (Vol. 397). Springer.

O'Connor, J. A., Sulloway, F. J., Robertson, J., & Kleindorfer, S. (2010). *Philornis downsi* parasitism is the primary cause of nestling mortality in the critically endangered Darwin's medium tree finch (*Camarhynchus pauper*). *Biodiversity and Conservation*, *19*, 853–866.

Oke, K. B., Cunningham, C. J., Westley, P. A. H., & Palkovacs, E. P. (2020). Recent declines in salmon body size impact ecosystems and fisheries. *Nature Communications*, *11*(1), 4155. https://doi.org/10.1038/s41467-020-17726-z

Paltán, H. A., Benitez, F. L., Rosero, P., & Mena, C. F. (2021). Climate and sea surface trends in the Galápagos Islands. *Scientific Reports*, *11*(1), 14465. https://doi.org/10.1038/s41598-021-93870-w

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42. https://doi.org/10.1038/nature01286

Pearson, R. G., Stanton, J. C., Shoemaker, K. T., … Akçakaya, H. R. (2014). Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*, *4*, 217–221. https://doi.org/10.1038/nclimate2113

Price, T. D., Grant, P. R., Gibbs, H. L., & Boag, P. T. (1984). Recurrent patterns of natural selection in a population of Darwin's finches. *Nature*, *309*(5971), 787–789. https://doi.org/10.1038/309787a0

Qvarnström, A., Ålund, M., McFarlane, S. E., & Sirkiä, P. M. (2016). Climate adaptation and speciation: particular focus on reproductive barriers in *Ficedula flycatchers*. *Evolutionary Applications*, *9*(1), 119–134. https://doi.org/10.1111/eva.12276

R Core Team (2021). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Radchuk, V., Reed, T., Teplitsky, C., & Kramer-Schadt, S. (2019). Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications*, *10*(1), 3109. https://doi.org/10.1038/s41467-019-10924-4

Rustic, G. T., Koutavas, A., Marchitto, T. M., & Linsley, B. K. (2015). Dynamical excitation of the tropical Pacific Ocean and ENSO variability by Little Ice Age cooling. *Science*, *350*(6267), 1537–1541. https://doi.org/10.1126/science.aac9937

Ryding, S., Klaassen, M., Tattersall, G. J., & Symonds, M. R. (2021). Shape-shifting: changing animal morphologies as a response to climatic warming. *Trends in Ecology & Evolution*, *36*(11), 1036–1048. https://doi.org/10.1016/j.tree.2021.07.006

Salewski, V., Hochachka, W. M., & Fiedler, W. (2010). Global warming and Bergmann's rule: do central European passerines adjust their body size to rising temperatures?. *Oecologia*, *162*(1), 247–260. https://doi.org/10.1007/s00442-009-1446-2

Sanderson, S., Beausoleil, M. O., O'Dea, R. E., & Hendry, A. P. (2022). The pace of modern life, revisited. *Molecular Ecology*, *31*(4), 1028–1043. https://doi.org/10.1111/mec.16299

Scharsack, J. P., Franke, F., Erin, N. I., & Kalbe, M. (2016). Effects of environmental variation on host–parasite interaction in three-spined sticklebacks (Gasterosteus aculeatus). *Zoology*, *119*(4), 375–383. https://doi.org/10.1016/j.zool.2016.05.008

Scheffers, B. R., De Meester, L., Bridge, T. C., & Watson, J. E. (2016). The broad footprint of climate change from genes to biomes to people. *Science*, *354*(6313), aaf7671. https://doi.org/10.1126/science.aaf7671

Scheffers, B. R., Edwards, D. P., Diesmos, A., & Evans, T. A. (2014). Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology*, *20*(2), 495–503. https://doi.org/10.1111/gcb.12439

Schluter, D., & Grant, P. R. (1984). Determinants of morphological patterns in communities of Darwin's finches. *The American Naturalist*, *123*(2), 175–196. https://doi.org/10.1086/284196

Seddon, A. W., Macias-Fauria, M., Long, P. R., & Willis, K. J. (2016). Sensitivity of global terrestrial ecosystems to climate variability. *Nature*, *531*(7593), 229–232. https://doi.org/10.1038/nature16986

Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, *1*(8), 401–406. https://doi.org/10.1038/nclimate1259

Siepielski, A. M., Morrissey, M. B., Buoro, M., & MacColl, A. D. (2017). Precipitation drives global variation in natural selection. *Science*, *355*(6328), 959–962. https://doi.org/10.1126/science.aag2773

Stan Development Team. (2023). *Stan modeling language users guide and reference manual*. VERSION 2.37. https://mc-stan.org. Date accessed May 22, 2023.

Tattersall, G. J., Chaves, J. A., & Danner, R. M. (2018). Thermoregulatory windows in Darwin's finches. *Functional Ecology*, *32*(2), 358–368. https://doi.org/10.1111/1365-2435.12990

Tëmkin, I., & Eldredge, N. (2015). Networks and hierarchies: Approaching complexity in evolutionary theory. *Macroevolution: Explanation, Interpretation and Evidence*, 183–226.

Teplitsky, C., & Millien, V. (2014). Climate warming and Bergmann's rule through time: is there any evidence?. *Evolutionary Applications*, *7*(1), 156–168. https://doi.org/10.1111/eva.12129

Trueman, M., & d'Ozouville, N. (2010). Characterizing the Galápagos terrestrial climate in the face of global climate change. *Galápagos Research*, *67*, 26–37.

van Asch, M., Salis, L., Holleman, L. J., & Visser, M. E. (2013). Evolutionary response of the egg hatching date of an herbivorous insect under climate change. *Nature Climate Change*, *3*(3), 244–248. https://doi.org/10.1038/nclimate1717

Van Buskirk, J., Mulvihill, R. S., & Leberman, R. C. (2010). Declining body sizes in North American birds associated with climate change. *Oikos*, *119*(6), 1047–1055. https://doi.org/10.1111/j.1600-0706.2009.18349.x

Venables, W., & Ripley, B. D. (2002). *Modern applied statistics with S*(4th ed.) New York, NY: Springer.

Visser, M. E., Noordwijk, A. V., Tinbergen, J. M., & Lessells, C. M. (1998). Warmer springs lead to mistimed reproduction in great tits (Parus major). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*(1408), 1867–1870. https://doi.org/10.1098/rspb.1998.0514

Wilcox, R. C., Benson, T. J., Brawn, J. D., & Tarwater, C. E. (2024). Observed declines in body size have differential effects on survival and recruitment, but no effect on population growth in tropical birds. *Global Change Biology*, *30*(8), e17455. https://doi.org/10.1111/gcb.17455

Yom-Tov, Y., & Geffen, E. (2011). Recent spatial and temporal changes in body size of terrestrial vertebrates: probable causes and pitfalls. *Biological Reviews*, *86*(2), 531–541. https://doi.org/10.1111/j.1469-185X.2010.00168.x