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Climate warming explains half of the magnitude of temporal changes in life-history traits

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Abstract

Many wild populations are showing changes in phenotypic traits. However, the common assumption that such changes are driven by climate change relies on three conditions: that local climate is changing over time, that trait(s) are sensitive to climate variability, and that other causal agents are not also changing. We used long-term datasets on 60 bird species to test these conditions and to quantify the contribution of warming temperatures to changes in three important life-history traits. Across species, approximately half of the magnitude of changes in traits could be attributed to a single temperature window, with averages of 50% for laying date, 40% for body condition and 56% for offspring numbers. Thus, although warming temperatures were a key driver of change, other unknown factors contributed substantially to temporal trends (typically reinforcing change). Further analyses showed that these non-temperature-driven contributions explained most of the inter-specific variation in trait changes.

Introduction

Given the widespread evidence for ongoing temporal change in life-history traits of wild animal and plant populations, a key challenge facing ecology today is to understand the role of our rapidly changing climate in driving these phenotypic changes. Many studies have correlated the responses of traits (such as phenology or reproduction) to climatic variables, which is arguably the most direct means of understanding the sensitivities of species to climate. However, much of the literature simply considers changes in traits over time and makes the implicit assumption that temporal trends reflect responses to climate change; this approach is probably most prevalent in large-scale meta-analyses and comparative studies. Although the approach has benefits, whether attributing phenotypic change solely or largely to climate change is justifiable is rarely considered, let alone quantitatively tested.

To attribute temporal trends in phenotypic traits to effects of climate change alone, three conditions must be met (Fig. 1): (1) the climate experienced by the population is changing over time; (2) the trait is sensitive to climate variability; and (3) phenotypic change is not due to other causes, i.e. that other non-climatic aspects of the environment with causal effects on the trait are also not changing over time. Even though many studies acknowledge one or more of these conditions when interpreting their results, these three conditions are rarely explicitly checked simultaneously. It therefore remains an open question as to what extent observed trait changes over time are due to climate change, as opposed to being caused by other environmental or evolutionary drivers that are concurrently changing. There is thus a need for a quantitative decomposition of the relative importance of temperature versus other causes of temporal trends, and how this differs among species and traits.
**Figure 1 The components of trait change over time.** The combined strengths of (1) the rate of change in climate and (2) the focal trait’s sensitivity to climate, determine a ‘climate pathway’, or the change in the trait over time due to climate. The combined impact of both the climate pathway (1,2) and (3) the non-climatic effects determines the total change in the trait over time. This path-diagram shows a visual representation of the structural equation model used and how the terminology in Equation 1 relate, where we use ‘$d$’ and ‘$\partial$’ to distinguish full and partial regression coefficients, respectively.

The three conditions needed to attribute trait changes over time to climate will not necessarily always be met. Firstly, although changes in the global climate system are unequivocal, the rate of climate change (Fig 1 component 1) varies seasonally, among locations, and may be absent over short time periods. Traits may be climate sensitive, but if there is no change in climate over the study period then temporal trends in traits will be independent of climate. For example, breeding time of British ring ouzels (Turdus torquatus) advances in wetter springs, but precipitation has not changed over the study period, and therefore nor has breeding time. Secondly, even if organisms experience high rates of climate change, climate will not drive temporal trends if traits are insensitive or only mildly sensitive to climate (Fig 1 component 2). For instance, Robinson et al. found that juvenile survival was insensitive to climate in 5 out of 10 passerine species. Third, non-climatic factors that drive trait change can also change over time (Fig 1 component 3). These could include changes in habitat loss, pollution, spread of invasive species or diseases, loss of keystone species or overexploitation. The diversity of human impacts on wild populations implies that attributing changes over time to a single causal driver may be overly simplistic, even if that single driver is as prominent as climate change.

We also have little understanding of how the contribution of climatic and non-climatic factors to phenotypic change differs among traits. We consider here three traits that have received much attention in studies of wild animals, and have long-term datasets: reproductive timing, body condition, 

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**Equation 1**

\[
\frac{\partial \text{Trait}}{\partial \text{Clim}} = \frac{d\text{Clim}}{d\text{Year}}
\]
and reproductive success. Timing of reproduction can be influenced not only by temperature, but also large-scale changes in land use, urban expansion, or nutritional state linked to, for example, habitat degradation or population density. Body condition is sensitive to changes in food availability, predation, selective harvesting and habitat degradation. There are also many non-climatic variables that are known to impact reproductive success such as predation, parasitism or diseases. Despite these non-climatic effects being known to be important, we currently have little understanding of how strongly they contribute to temporal trends or how this varies for different traits in wild populations, mainly because they are challenging to quantifying. It is also not clear whether non-climatic factors generate trait change in the same direction as those of climate change, reinforcing its effects, or if they instead counteract them.

Using two long-term datasets on common bird species from the United Kingdom and the Netherlands for three important life-history traits (laying date, body condition, and offspring productivity), we investigate to what extent changes over time can be assumed to be due to increasing temperatures, a key component of climate change. Therefore, we first identify the temperature windows (periods) that best describe associations between traits and temperature. We then use structural equation modelling to quantify the conditions needed to attribute trait changes over time to climate: the rate of change of temperature, the sensitivity of traits to temperature, and the rate of change in traits due to other unknown drivers that are changing concurrently. Finally, we ask three questions: (1) what proportion of trait changes over time are due to temperature, (2) are the combined effects of temperature and other factors counteracted or reinforced, and (3) does the contribution of temperature vary among different traits and species.

**Methods**

**Biological Data**
To get a general understanding of the extent that changes over time can be assumed to be due to warming temperatures, we looked at three commonly studied traits: the timing of egg laying ('laying date'), body condition and the number of fledglings produced per breeding attempt/brood (termed FPBA, a standard measure of breeding success). We used two long-term datasets on common bird species, one from the United Kingdom (UK) and another from the Netherlands (NL). Laying date and FPBA were calculated from the dataset from the UK, which consisted of records of 35 common British bird species over 48 years recorded as part of the British Trust for Ornithology’s Nest Record Scheme (1966–2013; see Table S1 for sample sizes; British Trust for Ornithology 2015). Body condition was calculated from the dataset from the Netherlands, which consisted of ringing records for 47 common bird species recorded as part of the Dutch Constant Effort Site (CES) program over 21 years (1994-
Due to data availability, the UK dataset consisted of national averages for each species, while the NL dataset consisted of data from multiple sites for each species (range 39-68 sites; see Fig. S1 for map and Table S1 for site details).

For both laying date and FPBA, we used annual mean estimates and their standard errors; these data thus consisted of a single estimate per species per year, for both traits (35 species x 48 years = 1680 samples). Laying dates were recorded from March to July and were derived by back-calculating from the date and stage (still egg-laying, incubating, hatchling of certain age) of when the nest was found. FPBA estimates were derived from maximum recorded brood size and egg and chick stage nest failure rates in each year (for details see ). As a result, partial brood losses were not taken into account and so breeding success could be underestimated. However, we had no reason to assume that this underestimation is dependent on the climate in any given year or that it has changed over time.

We calculated the average adult body condition per species per site per year and its standard error (i.e. population annual averages based on 160,550 captures; see Appendix for details). From the 13th April until the 14th August every year birds were captured, and body mass (grams), wing length (maximum chord measurement), sex and age-class (juvenile or adult) were all recorded. Birds were considered adults after their first calendar year in all species. We calculated body condition as the residuals of body mass on size (wing length), while correcting for age, sex and moment of capture (Appendix S1). To make body condition comparable across species of different sizes, we expressed changes in body condition as a percentage relative to a species’ mean body mass.

We used daily mean temperature records from the Central England Temperature dataset (Parker et al. 1992) and from the Royal Netherlands Meteorological Institute (KNMI; www.knmi.nl). As we used only single laying date and FPBA estimates for the whole of the United Kingdom (rather than site-level estimates), we used a single measure of climate taken from the Central England Temperature dataset. Dutch temperature data from 37 weather stations across the Netherlands were used, with biological data from each Dutch CES site matched with the closest weather station (mean distance 17 km; Table S3).

We performed ‘sliding window’ analyses for each species and trait (laying date, body condition and FPBA) to identify the time period in each year during which mean temperature best explained the variation in annual trait values for each species. Using the R package climwin, we systematically explored all possible combinations of consecutive weeks for the previous two years (from the 1st and
15th of August for the UK and NL datasets, respectively) to identify the ‘best’ possible temperature window. Consequently, a mean annual trait value from 2009 in the UK would consider weather over the dates 01/08/2007-01/08/2009. This meant that potential climate windows could differ in their periods across species, for instance from recent spring temperatures to previous year conditions. All analyses fitted linear temperature relationships and assumed Gaussian distributions for the response variables. For all three response variables, the climwin analysis weighted values by the inverse of the standard errors of the estimates, such that uncertain estimates contributed less. We selected the best model based on Akaike’s Information Criterion modified for small samples (AICc).

When testing so many climate window models, the chances of spurious results are high. Randomisation techniques were therefore used to assess the likelihood that the best time window might occur by chance. For each species we performed 50 randomisations using the randwin function and calculated the chance that the best window was a true positive using the inbuilt function pvalue within climwin ($P_{true \ positive} = 1 - P_c$, see). We considered there to be a temperature signal present if the best window had more than a 50% chance that it was a true positive. Species were therefore categorised as either temperature sensitive or insensitive depending on whether a reliable temperature window could be identified.

Although our timeseries are at least two decades long, species with smaller sample sizes could still be more likely to be categorised as insensitive. Therefore, we conducted a generalised linear model with binary errors with the average number of individuals per site per year as the explanatory variable and temperature sensitivity (sensitive or insensitive) as the response variable. Our ability to detect a climate window did not depend on sample size for any of the three traits (Table S6, Fig S7).

**Structural Equation Models**

After identifying the climate windows for which temperature explained most variation in the traits for each species, we used structural equation models (SEMs) to quantify the importance of temperature in mediating trait changes over time. For each species that was found to be temperature sensitive, we constructed a structural equation model using the R-package piecewiseSEM (See appendix for R code). Figure 1 shows the path-diagram of the SEM, with three individual path estimates being calculated: the effect of year on temperature, the effect of temperature on the trait and the direct effect of year on the trait. The association between year and trait was therefore decomposed into two pathways, the ‘Temperature Pathway’ which is the indirect effect on the trait mediated by temperature (i.e. changes over time due to the effects of temperature; Fig 1 components 1 & 2) and the ‘Other Pathway’ which is the direct effect on the trait due to all other drivers (i.e. not due to the effects of the identified temperature window; Fig 1 component 3). By assessing the partial regression
of a trait on both temperature and year, we effectively ask the question whether temperature explains
temporal trait variation beyond any shared directional temporal trends in trait and temperature (i.e.
do year-to-year fluctuations around any shared temporal trend also covary?). Because the Other
Pathway captures the change in the trait over time unrelated to the identified temperature window,
it effectively incorporates effects of other drivers of trait change that have changed directionally over
time. The Other pathway is thus likely composed of many drivers. Although we refer to the first
pathway as the ‘Temperature Pathway’, we note there could in theory also be additional effects of
temperature in other window periods outside of the ‘best’ windows selected in our climwin analysis
that would contribute to the ‘Other Pathway’.

Temperature was mean centred for each species to ensure that the relationships would reflect within-
population associations, all response variables had Gaussian distributions and were weighted by the
inverse of the standard error. Species for which there was no evidence of a reliable temperature
window (‘insensitive’ species) were excluded from SEM analyses.

Our model was ‘saturated’ as all path estimates were needed to answer our questions. This meant
that the usual model fit statistics could not be calculated. In order to check that the estimates from
our SEMs were likely to be reasonable, we checked the fits of each of the individual path estimates
and made sure the residuals were normally distributed, and the standard errors were not extremely
large or close to zero. All models satisfied these assumptions.

**Temperature and Total Pathways**

The Temperature and Total Pathways for each species and trait were calculated from the three
individual path estimates previously calculated in each SEM (Fig 1 components 1, 2 & 3). Following the
rules of path tracing, the Total Pathway — or the total change in a trait over time — is determined
by each of the underlying linear relationships between year, trait and climate:

\[
\frac{dd_{\text{Trait}}}{d\text{Year}} = \frac{dd_{\text{Temp}}}{d\text{Year}} \times \frac{\partial_{\text{Trait}}}{\partial_{\text{Temp}}} + \frac{\partial_{\text{Trait}}}{\partial_{\text{Year}}} \quad \text{(eq. 1)}
\]

(where we use ‘d’ and ‘∂’ to distinguish full and partial regression coefficients, respectively). Equation
1 could be read as the Total Pathway \(\frac{dd_{\text{Trait}}}{d\text{Year}}\) being equal to the sum of the Temperature Pathway
\(\frac{dd_{\text{Temp}}}{d\text{Year}} \times \frac{\partial_{\text{Trait}}}{\partial_{\text{Temp}}}\) and the Other Pathway \(\frac{\partial_{\text{Trait}}}{\partial_{\text{Year}}}\). Where, the Temperature Pathway was calculated as
the product of the effect of year on temperature \(\frac{dd_{\text{Temp}}}{d\text{Year}}\) with the effect of temperature on the trait
\(\frac{\partial_{\text{Trait}}}{\partial_{\text{Temp}}}\) (Fig 1 components 1 & 2). As the individual path coefficients from the SEM each have
estimates of associated uncertainty, we applied a bootstrapping technique to calculate 95%
confidence intervals for the compound Temperature and Total Pathways (Appendix 1).
Percentage of change over time explained by temperature

For each species and trait, we calculated the percentage of change over time due to the Temperature Pathway as:

$$\% \text{trend due to temperature} = \frac{|\text{Temperature Pathway}|}{|\text{Other Pathway}| + |\text{Temperature Pathway}|} \times 100 \quad \text{(eq. 2)}$$

where $|..|$ denotes the absolute value. Equation 2 denotes the percent contribution of the Temperature Pathway to the Total Pathway, irrespective of sign or counteracting effects. For example, if a species had a Total Path estimate of a rate of change in laying date of 4 days per year, a Temperature Path estimate of 2 days per year, and an Other Path estimate of 2 days per year, then the Temperature Pathway explains 50% of the total change. If there are counteracting effects, where the Total Path estimate is zero days per year, the Temperature Path estimate is -1 days per year and the Other Path estimate is +1 days per year, then the Temperature Pathway would again explain 50% of the total change. Thus, our metric of eq. 2 is insensitive to the sign of the single pathways and the magnitude of the Total Pathway, see also Fig. 2 for a graphical example on the great tit and reed bunting data-sets from the UK. The percent contribution of the Temperature Pathway will be underestimated due to any error in the estimates of the temperature indices (temperatures collected at weather stations may differ from the temperatures experienced by birds at their study sites), which will lead to regression dilution. Consequently, the estimates of the Temperature Path contribution will be lower than in reality, and the estimate of the Other Pathway will increase correspondingly (as the two sum to produce the total change). In summary, our estimate of the Temperature Pathway contribution will be a conservative measure.

Figure 2 Example diagrams illustrating temporal trends in lay date and the contribution of the different pathways. Points represent the average laying date in each year. In (a) we show a real example of the reinforced effects in great tits in the UK, with negative slopes for both the Temperature Pathway (orange) and the Other Pathway (blue), resulting in a stronger overall change in laying date over time (i.e. the Total Pathway). Plot (b) shows a real example of counteracted
effects in reed buntings in the UK, with a negative slope for the Temperature Pathway and a positive slope for the Other Pathway, resulting in a weaker overall change in laying date over time (i.e. the Total Pathway). Plot (c) shows how the slopes in (a) and (b) relate to the structural equation model.

**Results**

**Conditions for attributing trait changes to climate**

To test whether temporal trends can be attributed to warming temperatures, we decomposed trait changes into the three key underlying conditions: change in temperature over time, sensitivity of traits to temperature and impacts of other drivers over time.

In support of the first condition, mean temperature (during the windows over which the trait was sensitive) increased over time in both countries over the study period (Fig 3a-c). The second condition was not always met, as traits were not always sensitive to temperature. Laying date was sensitive to temperature in 77% of species (27/35 species in the UK dataset), with the relevant temperature windows occurring around March-May in spring (Figure S5, Table S4). Body condition was sensitive to temperature in 47% of species (22/47 species in the Netherlands dataset), with many temperature windows occurring around early May to mid-July in spring-early summer (Table S5). FPBA was sensitive to temperature in 34% of species (12/35 UK species; Table S4). For the temperature-sensitive species, warming was associated with advances in laying date (2.3 days/°C on average; Fig 3a), decreases in body condition (0.22% /°C on average; Fig 3b), and highly variable effects on FPBA (decreased for 6 species and increased for the other 6 species such that there was no change on average; FigS4b).

For the third condition, effects other than the identified temperature window were often associated with traits. On average, birds significantly advanced laying by 0.07±0.02 days/year and FBPA increased by 0.005±0.002 fledglings/year due to other effects changing over time (the ‘Other Pathway’; Fig 3a,c). Body condition did not show a clear trait change due to other effects (Fig 3c), but this was mainly caused by one species (Jays) showing a strong change in the direction opposite to almost all other species showing decreasing body condition (fig. 3b).
Figure 3 Estimates of path coefficients averaged across species and displayed for each species. The plots in the left column (a-c) show the graphical representations of the structural equation models and the averaged path estimates (± standard error) across all species found to be sensitive to temperature. The leftmost blue and yellow arrows show the full SEM and the individual path estimates for each pathway, while the middle yellow arrow shows the change in trait over time due to temperature (the Temperature Pathway, calculated as the product of the year-to-temperature and the temperature-to-trait path estimates). The rightmost black arrow shows the total change in the trait over time due to all variables, and is calculated as the Temperature Pathway summed with the Other Pathway. Solid arrows indicate the 95% confidence interval did not cross zero, while the dashed arrows indicate it did cross zero. The plots in the right column (d-f) show the path estimates (+/- SEs) for the Total (black), Temperature (yellow) and Other (blue) Pathways. In general, the Temperature Pathway coefficients varied less across species than the Other and Total Pathways. In most cases, the Total path estimate was larger than the two others because the Temperature and Other Pathways reinforced one another. However in some cases, the Total Pathway was closer to zero when the Temperature and Other Pathways counteracted each other’s effects.

Temperature-driven trait change

On average across the three traits, half (49%) of the changes in traits over time was due to the Temperature Pathway. There was some variation among the traits, with an average of 50% of temporal changes in lay date attributed to the temperature window, an average of 40% for body condition and an average of 56% for FPBA (Fig 4). However, there were large differences among species in the percentage explained, with values ranging from 9% to 86% for lay date (Fig 4a), from 8% to 74% for body condition (Fig 4b) and from 23% to 91% for FPBA (Fig 4c).

In most cases the Temperature and Other Pathways had the same sign and reinforced each other (85% for laying date, 77% for body condition and 75% for FPBA; Fig 3d-f). Consequently, the total changes in traits over time were mostly greater than the changes due to temperature alone.
Figure 4 Percentage of temporal trait trends due to increasing temperature. Percentage of the trend in life-history traits over time that is due to the Temperature Pathway for each of the three traits across all species. The separate value listed as ‘All Species’ shows the average value across all species for that trait and the horizontal dotted line shows this same average for reference. Error bars reflect 95% confidence intervals.
Interspecific variation

There was a significant difference in the changes in laying date over time between temperature-sensitive versus insensitive species. Temperature sensitive species advanced their laying dates by three times as much as insensitive species on average (−0.15±0.04 SE days/year sensitive vs. 0.05±0.06 SE days/year insensitive; Fig S6a; Linear regression with Total path coefficient as response and temperature sensitivity [sensitive/insensitive] as the explanatory variable df=33, p=0.008). However, there were no significant differences in trait changes over time between temperature-sensitive versus -insensitive species for body condition (−0.060±0.049 SE days/year insensitive vs. 0.010±0.056 SE days/year sensitive) or FPBA (0.006±0.003 SE days/year insensitive vs. 0.003±0.004 SE days/year sensitive) (Fig S6b & c).

Of the temperature-sensitive species, the Temperature Pathway and Other Pathway estimates were positively correlated for laying date (r=0.64 95% CI=0.35, 0.82, n=27) and FPBA (r=0.72 95% CI=0.24, 0.91, n=12), but not for body condition (r=0.13 95% CI=−0.31, 0.52, n=22) (Fig 5a-c).

Responses to temperature were more consistent compared to responses to other effects, which varied substantially across species. Variation among species in the total trait change over time (due to both temperature and other effects) appeared to be mainly due to the varying effects of the Other Pathway, even though temperature explained on average about half of the total temporal change within a species (Fig 3d-f). Specifically, for all traits, the Other Pathway better explained variation in the total change in trait over time among species ($r^2_{\text{Laydate}}=0.94$, $r^2_{\text{Condition}}=0.94$, $r^2_{\text{FPBA}}=0.89$) than the Temperature Pathway ($r^2_{\text{Laydate}}=0.70$, $r^2_{\text{Condition}}=0.66$, $r^2_{\text{FPBA}}=0.84$; Fig. 5d-f).
Figure 5 Interspecific comparison of path estimates. The left panels (a-c) show the correlation between the Temperature and the Other Pathway for all temperature-sensitive species, where each point represents a species and bars showing 95% confidence intervals. The dark shaded areas indicate when the Temperature and Other Pathways had reinforced effects. The right panel (d-f) shows the relationships between the Total change in trait over time (calculated as the Temperature Pathway summed with the Other Pathway) compared to the change over time due to ‘Temperature’ (yellow) and ‘Other’ (blue) Pathway. The x-axis is the path estimate for either the Temperature or Other Pathway. The dotted diagonal Y=X is plotted to emphasize that points that fall closer to this line are more similar to the Total Pathway.
The notion that changes in traits through time reflect responses to climate warming relies on three conditions being met: climatic conditions are changing, traits are sensitive to climate, and no alternative drivers of change occur. By using two long-term datasets on three life-history traits in common European bird species, we show that (1) temperatures generally increased over time, (2) traits were not always sensitive to temperature and (3) there were additional temporal trends in traits unrelated to temperature. Our results can be viewed as both glass-half-full and glass-half-empty scenarios. The fact that, on average, half of trait changes over time could be attributed to a single temperature window across all species is remarkable for any ecological study, and clearly underlines the impact that global warming has on natural populations. However, our analysis shows that temporal trends in traits should not be solely ascribed to increasing temperature. The non-temperature effects mostly reinforced temperature effects and differences in temporal trends among species were more likely to be due to non-temperature factors than warming, as temperature impacted species fairly consistently. This suggests that comparative studies should be cautious of attributing differences in temporal trends to underlying species differences in sensitivity or exposure to climate change.

Temporal trends predominantly, but not solely due to warming

The Temperature Pathway explained about half (49%) of temporal changes across all traits and species. This suggests that temperature is likely the single most important contributor to temporal trends given that the Other Pathway is likely comprised of many factors (such as habitat degradation or predation levels), while the Temperature Pathway is driven by one single factor. Yet, other factors were also associated with trait changes over time, suggesting that other drivers outside of our temperature windows must also be influencing traits in European birds. Parmesan & Yohe³ argue that, although competing explanations in the form of non-climatic causal agents could have impacts, it is unlikely that such factors would produce a consistent pattern of impact over space and time. Yet our results, and those of Crick & Sparks¹⁶ who found that only 37% of temporal trends in phenology could be statistically accounted for by changes in spring temperature and rainfall (though their paper does not explain how they arrived at this percentage), suggest that trends over time can be quite strongly determined by non-temperature effects. Furthermore, we found that many species were insensitive to temperature, suggesting that any trait changes over time in these species were solely due to non-climatic effects, or other unidentified climatic effects (i.e. rainfall).

The finding that changes in temperature ‘only’ contributed on average 49% to changes in laying date could be viewed as somewhat unexpected. Many studies have shown that laying date is closely

Discussion
associated with mean spring temperatures\textsuperscript{16,36–38}. This relationship is considered to be predominantly driven by the need to reduce mismatches with their food supplies, whose timing of peak abundance vary with temperature\textsuperscript{37,39}. However, because the total change in laying date was substantially earlier than would be expected due to increased temperatures alone, other climatic (rainfall\textsuperscript{38}) or non-climatic factors (urbanisation, land-use\textsuperscript{16,17,40}) may play a stronger role than previously thought and deserve more attention.

Increasing temperature was also the main driver for changes in body condition and FPBA (offspring productivity), contributing on average 40\% and 56\% to temporal changes, respectively. Yet, changes in factors other than increasing temperatures still contributed substantially to trends in FPBA and body condition over time. Although it is becoming clearer that body condition and mass are impacted by warming temperatures\textsuperscript{34,41–43}, our understanding of the mechanisms driving temporal changes are still limited\textsuperscript{44}. Similarly, warming temperatures can influence offspring success via heat stress on young or indirectly affect resources\textsuperscript{21}, yet many other variables are known to be important including predation, disease\textsuperscript{20} and rainfall\textsuperscript{21}. Future studies are now needed to confirm whether this dominant role of temperature is a general pattern in other taxa, traits and regions. Our simple quantitative framework provides a straightforward way to perform such comparative studies with the main prerequisite being long time series on traits (as our framework does not rely on data of potential other drivers).

**Interspecific variation in trait change**

Interspecific variation in trait changes over time depended more on the impact of non-temperature drivers, rather than reflecting thermal sensitivity. Interspecific variation was better explained by the Other Pathway than the Temperature Pathway, largely because of considerable variation in the sensitivity of traits to non-temperature effects across species (Fig 5). For instance, changes in laying date from warming were fairly consistent across species (Fig 3d), while the total change in laying date differed substantially across species due to non-temperature factors. Part of this high interspecific variability might be due to the Other Pathway being comprised of multiple drivers. Different drivers might act upon species differently depending on their sensitivities. For example, increased urbanisation might cause earlier egg laying in some species (e.g. magpie\textsuperscript{16}), while rural species may be more affected by agricultural changes.

**Effects of temperature mostly reinforced by other effects**

The effects of increasing temperatures on traits were reinforced by the Other Pathway in 82\% of cases, suggesting that ‘disturbance-sensitive’ species may be sensitive to both global warming as well as various (unknown) environmental drivers. Other studies on population dynamics and biodiversity show combined non-climatic and climatic effects increased overall species declines\textsuperscript{12,45}. Our results
thus echo the idea of a ‘deadly anthropogenic cocktail’ of climate change and other effects like habitat
destruction\textsuperscript{11,45,46}. Reinforcing effects are important to recognise because if changes over time are
assumed to reflect effects of warming (as in most large-scale meta-analyses), they would be
overestimated. Additionally, counteracted effects were not uncommon (18% of cases), where the
effects of increasing temperatures were dampened or buffered by other factors. Several single species
studies on population growth have shown that counteracting effects occur\textsuperscript{15,47}, suggesting that
identifying these other factors could improve management actions to help buffer the effects of climate
change.

Quantitative framework for estimating contributions to change

Our simple framework to decompose the contribution of temperature to phenotypic change is
conceptually similar to methods used to account for shared trends (i.e. year-detrending\textsuperscript{48}), but our
multivariate structural equation model also specifically allows for decomposing the contribution of
climatic and other pathways on the trait change over time.

Several decisions were made that could be important when interpreting results. Firstly, because we
selected only the best average temperature window, our temperature measure is a proxy of global
warming and is thus a minimum estimate of the impact of climate change more generally. However,
we have shown that this proxy is potentially the single most important contributor to trait changes
over time. Secondly, this means that we compare temperature across different periods which may
have different underlying mechanisms for different species. Here, we were not primarily interested in
the mechanisms, but instead focused on identifying correlations. Thirdly, we compared two datasets
with different scales of information. The national UK temperatures are potentially a poorer proxy of
local temperatures. A consequence of having less reliable temperature data could be weaker
estimates of climate sensitivity due to regression dilution, but we note that temperatures are usually
strongly spatially autocorrelated.

Implications for comparative climate change ecology

Our study illustrates that although increasing temperatures contribute greatly to changes in life-
history traits, temporal trends cannot be assumed to be due solely to the effects of warming
temperatures. Because temperature-unrelated factors contribute to trends over time and differences
in trends may more reflect a species sensitivity and exposure to non-temperature drivers, we caution
whether studies should be considering trends over time to be solely due to global warming. As
comparative studies typically aim to identify species characteristics that make some species more
vulnerable to climate change, focussing on trend data thus runs the risk of identifying the species
characteristics that make them either sensitive to non-climatic drivers, or to environmental change in
general. Clearly, for identifying the species most at risk from climate change, and for developing predictive models and appropriate conservation management strategies it is important to attribute changes to the correct drivers\(^3,49\). We acknowledge the challenges in quantifying climatic sensitivity directly for multiple species, that meta-analyses rely on information available in the literature (mostly temporal trends) and climate sensitivities are quantified using various methods and different climate variables are hard to compare\(^50\). Further studies are needed that decompose the contributions of climate to trait changes to help identify general patterns in other taxa, traits and regions. Decomposing changes over time due to other specific climate variables such as rain and humidity, and non-climatic variables such as pollution or habitat fragmentation, would substantially improve our understanding of their contributions to temporal trends. Our framework provides a much-needed quantitative means to assess the relative contributions of different drivers to change.

References


30. Lefcheck, J. S. *piecewiseSEM*: Piecewise structural equation modelling in r for ecology,


47. Cleasby, I. R. *et al.* Climatic conditions produce contrasting influences on demographic traits


The components of trait change over time. The combined strengths of (1) the rate of change in climate and (2) the focal trait’s sensitivity to climate, determine a ‘climate pathway’, or the change in the trait over time due to climate. The combined impact of both the climate pathway (1,2) and (3) the non-climatic effects determines the total change in the trait over time. This path-diagram shows a visual representation of the structural equation model used and how the terminology in Equation 1 relate, where we use ‘d’ and ‘∂’ to distinguish full and partial regression coefficients, respectively.
Figure 2

Example diagrams illustrating temporal trends in lay date and the contribution of the different pathways. Points represent the average laying date in each year. In (a) we show a real example of the reinforced effects in great tits in the UK, with negative slopes for both the Temperature Pathway (orange) and the Other Pathway (blue), resulting in a stronger overall change in laying date over time (i.e. the Total Pathway). Plot (b) shows a real example of counteracted effects in reed buntings in the UK, with a negative slope for the Temperature Pathway and a positive slope for the Other Pathway, resulting in a weaker overall change in laying date over time (i.e. the Total Pathway). Plot (c) shows how the slopes in (a) and (b) relate to the structural equation model.
Estimates of path coefficients averaged across species and displayed for each species. The plots in the left column (a-c) show the graphical representations of the structural equation models and the averaged path estimates (± standard error) across all species found to be sensitive to temperature. The leftmost blue and yellow arrows show the full SEM and the individual path estimates for each pathway, while the middle yellow arrow shows the change in trait over time due to temperature (the Temperature Pathway, calculated as the product of the year-to-temperature and the temperature-to-trait path estimates). The rightmost black arrow shows the total change in the trait over time due to all variables, and is calculated as the Temperature Pathway summed with the Other Pathway. Solid arrows indicate the 95% confidence interval did not cross zero, while the dashed arrows indicate it did cross zero. The plots in the right column (d-f) show the path estimates (+/- SEs) for the Total (black), Temperature (yellow) and Other (blue) Pathways. In general, the Temperature Pathway coefficients varied less across species than the Other and Total Pathways. In most cases, the Total path estimate was larger than the two others because the Temperature and Other Pathways reinforced one another. However in some cases, the Total Pathway was closer to zero when the Temperature and Other Pathways counteracted each other's effects.
Figure 4

Percentage of temporal trait trends due to increasing temperature. Percentage of the trend in life-history traits over time that is due to the Temperature Pathway for each of the three traits across all species. The separate value listed as ‘All Species’ shows the average value across all species for that trait and the horizontal dotted line shows this same average for reference. Error bars reflect 95% confidence intervals.
Figure 5

Interspecific comparison of path estimates. The left panels (a-c) show the correlation between the Temperature and the Other Pathway for all temperature-sensitive species, where each point represents a species and bars showing 95% confidence intervals. The dark shaded areas indicate when the Temperature and Other Pathways had reinforced effects. The right panel (d-f) shows the relationships between the Total change in trait over time (calculated as the Temperature Pathway summed with the
Other Pathway) compared to the change over time due to ‘Temperature’ (yellow) and ‘Other’ (blue) Pathway. The x-axis is the path estimate for either the Temperature or Other Pathway. The dotted diagonal Y=X is plotted to emphasize that points that fall closer to this line are more similar to the Total Pathway.

**Supplementary Files**

This is a list of supplementary files associated with this preprint. Click to download.

- Appendix.doc