

Warming temperatures drive at least half of the magnitude of long-term trait changes in European birds

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Many wild populations are experiencing temporal changes in life-history and other phenotypic traits, and these changes are frequently assumed to be driven by climate change rather than nonclimatic drivers. However, this assumption relies on three conditions: that local climate is changing, traits are sensitive to climate variability, and other drivers are not also changing over time. Although many studies acknowledge one or more of these conditions, all three are rarely checked simultaneously. Consequently, the relative contribution of climate change to trait change, and the variation in this contribution across traits and species, remain unclear. We used long-term datasets on 60 bird species in Europe to test the three conditions in laying date, offspring number, and body condition and used a method that quantifies the contribution of warming temperatures to changes in traits relative to other effects. Across species, approximately half of the magnitude of changes in traits could be attributed to rising mean temperature, suggesting that increasing temperatures are likely the single most important contributor to temporal trends and emphasizes the impact that global warming is having on natural populations. There were also substantial nontemperature-related temporal trends (presumably due to other changes such as urbanization), which generally caused trait change in the same direction as warming. Attributing temporal trends solely to warming thus overestimates the impact of warming. Furthermore, contributions from nontemperature drivers explained most of the interspecific variation in trait changes, raising concerns about comparative studies that attribute differences in temporal trends to species differences in climate-change sensitivity.

global warming | phenotypic trait | birds

Given the widespread evidence for ongoing temporal changes in traits of wild animal and plant populations, a key challenge facing ecology today is to understand the role of the rapidly changing climate in driving these changes. Many studies have correlated temporal variation in phenotypic traits, such as phenology, morphophysiology, and life history (offspring number, survival/longevity), with changes in climatic variables, which is arguably the most direct means of understanding species' sensitivities to climate (see ref. 1 for review of approaches). However, much of the literature simply considers changes in climate-sensitive traits over time—as such information is most widely available—and makes the implicit assumption that temporal trends largely reflect responses to climate change. This approach is probably most prevalent in large-scale meta-analyses and comparative studies (e.g., refs. 2–4). Although it has its merits, whether attributing trait change solely or largely to effects of climate change is justifiable is rarely considered, let alone quantitatively tested.

To attribute temporal trends in traits to effects of climate change alone, three conditions must be met (Fig. 1A): 1) The climate experienced by the population is changing over time; 2) the trait is sensitive to climate variability [i.e., the mean population value of a trait covaries with a climate variable across years, likely reflecting the average phenotypically plastic response of all individuals, a microevolutionary response or changes to the population composition (5)]; and 3) phenotypic change is not due to other causes/stressors, i.e., other nonclimatic 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 primarily by other environmental drivers that are concurrently changing. There is thus a need for a quantitative decomposition of the relative importance

Significance

Climate change is impacting wild populations, but its relative importance compared to other causes of change is still unclear. Many studies assume that changes in traits primarily reflect effects of climate change, but this assumption is rarely tested. We show that in European birds global warming was likely the single most important contributor to temporal trends in laying date, body condition, and offspring number. However, nontemperature factors were also important and acted in the same direction, implying that attributing temporal trends solely to rising temperatures overestimates the impact of climate warming. Differences among species in the amount of trait change were predominantly determined by these nontemperature effects, suggesting that species differences are not due to variation in sensitivity to temperature.

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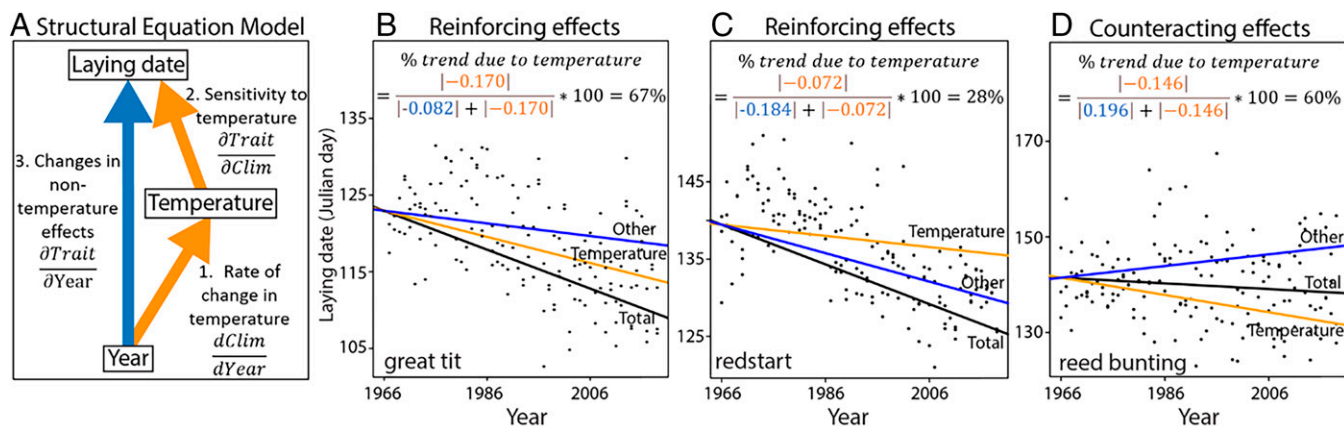


Fig. 1. The components of trait change over time and examples illustrating temporal trends in lay date and the contribution of the different pathways. In A this path diagram shows a visual representation of the structural equation model used with terminology as in Eq. 1 (d and ∂ to distinguish full and partial regression coefficients, respectively). The combined strengths of (1) the rate of change in temperature, (2) the trait's sensitivity to temperature, determine a temperature pathway, or the change in the trait over time due to temperature. The combined impact of both the Temperature Pathway (1 and 2) and (3) the nontemperature (Other) effects determines the total change in the trait over time. In B we show a real example of reinforcing effects on great tit laying date in the UK, with negative slopes for both the Temperature Pathway (orange) and the Other Pathway (blue), resulting in a stronger overall advance in laying date over time (i.e., the Total Pathway in black). C shows another example of reinforcing effects in redstart laying date, but the Temperature Pathway is much weaker than the Other Pathway, and so the percent trend due to temperature is much lower. D shows an example of counteracting effects in Reed bunting laying date, with a negative slope for the Temperature Pathway and a positive slope for the Other Pathway, resulting in little overall change in laying date over time (i.e., the Total Pathway). The calculations for the percentage of the trend over time due to temperature are also displayed. Points represent the average laying date in each year in each of the three latitudinal bands.

of temperature versus other causes of temporal trends and how this differs among species and traits.

The three conditions needed to attribute trait changes over time to climate will not necessarily always be met. First, although changes in the global climate system are unequivocal (6), the rate of change in particular aspects of climate (Fig. 1A, component 1) will vary seasonally and geographically and may even be absent over short study periods (7). Traits may be climate-sensitive, but if there is no directional change in climate over the study period then temporal trends in traits are not being driven by climate. For example, breeding advanced in wetter springs for British ring ouzels (*Turdus torquatus*), but precipitation had not increased or decreased over the study period (only annual variation with no temporal trend), and therefore breeding time did not become earlier in recent years either (8). Second, 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. 1A, component 2). For instance, Robinson et al. (9) found that juvenile survival was insensitive to climate in 5 of 10 British bird species. Third, nonclimatic factors that drive trait change can also change over time (Fig. 1A, component 3). These could include changes in urbanization, habitat loss, pollution, invasive species, diseases, loss of keystone species, or overexploitation (10–15). 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.

To date, we have little understanding of how the contribution of climatic and nonclimatic factors to phenotypic change differs among traits. We consider three traits that have received much attention in studies of wild animals and for which long-term datasets are available: reproductive timing, body condition, and offspring number. Timing of reproduction can be influenced not only by temperature but also by large-scale changes in land use, urban expansion, or nutritional state linked to habitat degradation or population density (16, 17). Changes in morphology (body condition, mass, and size) have been noted as another of the major responses to climate across the globe

(18, 19). Hotter temperatures are often associated with decreased body mass or condition (20–23), although it is still unclear whether this is a detrimental consequence from poorer foraging or heat stress or if it provides some advantage through lowered energy expenditure or improved agility (24). Body condition is also sensitive to nonclimatic factors like changes in food availability, predation, selective harvesting, and habitat degradation (25–27). Offspring number can be influenced by warming temperatures via heat stress directly affecting young or indirectly affecting resources (28), yet many nonclimatic variables are also known to impact this trait, such as predation, parasitism, or diseases (29). However, despite both climatic and nonclimatic stressors being known to be important for all these traits, we currently have little understanding of how strongly they contribute to temporal trends, or how the contributions vary for different traits in wild populations, mainly because they are challenging to quantify. It is also not clear whether nonclimatic factors generate trait change in the same direction as those of climate change, reinforcing its effects (12, 28), or if they instead counteract them (15, 30).

Using two long-term datasets on 60 common bird species from the United Kingdom and The Netherlands for the three traits of laying date, body condition, and offspring productivity, we investigate here to what extent changes over time can be assumed to be due to increasing mean temperatures, a key component of, and our index for, climate warming. Therefore, we first identify the temperature periods (or “windows”) that best describe associations between traits and temperature. We present a method based on path analysis (31) that can quantify the parameters involved in attributing 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, using our simple method we answer three questions: Of those species sensitive to temperature, 1) what proportion of trait changes over time are due to warming, 2) do the effects of warming and other drivers counteract or reinforce each other, and 3) does the contribution of warming vary among different traits and species?

Methods

Data. To quantify the extent of trait changes attributable to warming temperatures, we analyzed the timing of egg laying ("laying date"), body condition, and the number of fledglings produced per breeding attempt ("offspring number"). We used two long-term datasets on common bird species, one from the United Kingdom (UK) and one from The Netherlands (NL).

The dataset from the UK was part of the British Trust for Ornithology's Nest Record Scheme (32), which was used to investigate laying date and offspring number (36 species, 1966 to 2019; *SI Appendix, Table S1*). Data are not collected at distinct sites but rather are opportunistic throughout the region. We grouped the UK data into three latitudinal bands (*SI Appendix, Fig. S2*) and calculated annual averages and SEs within these to account for possible latitudinal gradients (*SI Appendix, Fig. S2*). The UK data therefore consisted of an estimate of the average value for each species in each year for each of the three latitudinal bands for each trait (36 species, 54 y, and 3 bands, giving 5,185 laying date and 5,222 offspring number estimates). We used daily mean temperature records from the European Climate Assessment and Dataset (33) for the UK. Temperature was averaged within the three latitudinal bands to account for any latitudinal differences in climate windows (see *SI Appendix* for details).

The dataset from NL was part of the site-specific Dutch Constant Effort Site program (collected from April to August) and was used to analyze changes in body condition (47 species, 86 sites, 1994 to 2014; *SI Appendix, Table S2*). Adult body condition was calculated as the residuals from the linear regression of body mass on wing length, age, sex, and capture timing for each individual. Average adult body condition and its SE were then calculated per species per site per year (i.e., population annual averages based on 193,028 individual captures from 47 species, 86 sites, and 30 y, giving 11,568 average condition estimates; not all species/site/year combinations were available; see *SI Appendix*). We used daily mean temperature records from the Royal Netherlands Meteorological Institute for NL (see *SI Appendix* for details).

Statistical Analysis.

Climate windows. We performed "sliding window" analyses to identify the time period during which mean temperature best explained the variation in annual trait values for each trait and species. Thus, we used the mean temperature within the relevant time window as our index for global warming. To identify this "best" possible temperature window, we used the R package *climwin* (34) and systematically explored all possible combinations of consecutive weeks for the previous two years. Consequently, species' climate windows can differ in both duration and timing, for instance ranging from periods in recent springs to periods in the previous year (*SI Appendix, Fig. S3*). For the UK specifically, the best temperature window was identified for each of the three latitudinal bands to account for any latitudinal differences in climate windows (see *SI Appendix* for details). The NL data were not broken up by latitude, and so the best temperature window identified was for each species across the whole (small) country. All analyses fitted linear temperature relationships and assumed Gaussian distributions for the response variables.

When testing so many climate window models, the chances of spurious results are high (1). Randomization techniques were used to assess the likelihood that the best window occurred by chance (34). Species were categorized as either temperature-sensitive or -insensitive depending on whether a reliable temperature window could be identified (see *SI Appendix* for details). Although our time series are at least two decades long, species with smaller sample sizes could still be more likely to be categorized as insensitive. However, we checked that the ability to detect a climate window did not depend on sample size for any traits (see *SI Appendix, Table S6*).

Path analysis using structural equation models. We used path analyses within structural equation models (SEMs) to quantify the importance of temperature in mediating trait changes over time (31). SEMs are a generalization of path models that *inter alia* allow for the inclusion of random effects. We constructed a SEM for each species that was found to be temperature-sensitive. Fig. 1A shows the path diagram of the SEM, with three individual path estimates being calculated: 1) the effect of year on temperature, 2) the effect of temperature on the trait, and 3) the direct effect of year on the trait. We used the R-package *piecewiseSEM* (35) (see *SI Appendix* for code). Temperature was mean-centered for each species to ensure that the relationships would reflect within-population associations (36), and all response variables had Gaussian distributions and were weighted by the inverse of the SE to account for differences in precision within time series. Site (for the NL) or band (for the UK) were included as a random intercept term for each response variable.

The association between year and trait was decomposed into two pathways: the "Temperature Pathway," which is the indirect effect on the trait mediated by temperature (i.e., trait changes over time due to the effects of

the identified temperature window; Fig. 1A, components 1 and 2), and the "Other Pathway," which is the direct net effect on the trait due to all other drivers combined (i.e., not due to the effects of mean temperature—instead, due to any other drivers changing directionally over time, such as habitat degradation; Fig. 1A, component 3) (37). Consequently, the Temperature Pathway gives the change in trait due to increasing mean temperature per year, and the Other Pathway gives the change in trait over time due to nontemperature drivers.

This method aims to isolate temperature effects from other covarying impacts similarly changing over time. Because the Other Pathway captures changes over time unrelated to the temperature window, it separates out the effects of all other, nontemperature drivers of trait change over time from the Temperature Pathway. 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 (38). The Other Pathway is likely composed of many drivers. Theoretically, there could also be effects of temperature from other window periods outside of the "best" windows selected that would contribute to the Other Pathway (see *Discussion*), but we assumed that multiple uncorrelated temperature signals are rare and therefore did not consider them separately.

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 (37). 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 SEs were not extremely large or close to zero. All models satisfied these assumptions.

Temperature and Total Pathway calculations. The Temperature and Total Pathways for each SEM were calculated from the three individual path estimates (Fig. 1A, components 1, 2, and 3). Following the rules of path tracing (31), 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 (23):

$$\begin{aligned} \text{Total Pathway} &= \text{Temperature Pathway} + \text{Other Pathway} \\ \frac{d\text{Trait}}{d\text{Year}} &= \frac{d\text{Temp}}{d\text{Year}} * \frac{\partial\text{Trait}}{\partial\text{Temp}} + \frac{\partial\text{Trait}}{\partial\text{Year}} \end{aligned} \quad [1]$$

(where we use d and ∂ to distinguish full and partial regression coefficients, respectively). The Total Pathway ($\frac{d\text{Trait}}{d\text{Year}}$) is equal to the sum of the Temperature Pathway ($\frac{d\text{Temp}}{d\text{Year}} * \frac{\partial\text{Trait}}{\partial\text{Temp}}$) and the Other Pathway ($\frac{\partial\text{Trait}}{\partial\text{Year}}$). The Temperature Pathway was calculated as the product of the effect of year on temperature ($\frac{d\text{Temp}}{d\text{Year}}$) with the effect of temperature on trait ($\frac{\partial\text{Trait}}{\partial\text{Temp}}$) [Fig. 1A, components 1 and 2 (37)]. We classify species where the Temperature and Other Pathways are in the same direction (Fig. 1B) as "reinforced effects" and in opposite directions (Fig. 1C) as "counteracted effects." We applied a bootstrapping technique to calculate 95% CIs for the compound Temperature and Total Pathways (see *SI Appendix*).

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

$$\begin{aligned} \% \text{ trend due to warming} &= \frac{|\text{Temperature Pathway}|}{|\text{Other Pathway}| + |\text{Temperature Pathway}|} \\ &\quad * 100, \end{aligned} \quad [2]$$

where $|\cdot|$ denotes the absolute value. Eq. 2 denotes the percent contribution of the Temperature Pathway to the Total Pathway. Because the Temperature Pathway gives the change in trait due to increasing mean temperature per year, this metric gives the percent trend due to warming temperatures. Our metric is insensitive to the sign of the single pathways (i.e., allows for comparing counteracting and reinforcing effects) and the magnitude of the Total Pathway (see *SI Appendix* for rationale). Fig. 1B–D shows graphical examples.

Results

Conditions for Attributing Trait Changes to Climate. To understand whether temporal trends can be attributed to warming temperatures, we tested for 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 "best windows" identified for each species–trait combination) increased over time for all traits and species except three which experienced decreasing mean temperature (3/119; Reed bunting, Blackbird,

and Chiffchaff for body condition; *SI Appendix*, Figs. S5C, S6C, and S7C).

The degree to which the second condition (trait sensitivity to climate) was met varied across traits. Laying date was sensitive to mean temperature in 86% of species (31/36 species; *SI Appendix*, Table S4), with the relevant temperature windows occurring around March to June in spring (*SI Appendix*, Fig. S3). Body condition was sensitive to temperature in 32% of species (15/47 of NL species; *SI Appendix*, Table S5), with many temperature windows occurring around early May to mid-July in spring to early summer in that year and the previous year. Offspring number was sensitive to temperature in 31% of species (11/35 of UK species; *SI Appendix*, Table S4). The three temperature-sensitive species with decreasing temperatures were removed from further analyses, as we were interested in the contribution of warming. For the temperature-sensitive species, warming was associated with advances in laying date (3.2 d/°C on average; Fig. 2A), decreases in body condition (0.45%/°C on average; Fig. 2B), and highly variable effects on offspring number (negative for seven species and positive for the other four species, such that there was on average no change across species; *SI Appendix*, Fig. S7B). Temperature-insensitive species were removed from further analyses, but we note that there were no significant differences in trait changes over time between temperature-sensitive versus -insensitive species (*SI Appendix*, Fig. S4).

For the third condition (no impacts of other drivers over time), trait changes due to effects other than the identified mean temperature window were common and often strong. On average, laying date and body condition had a consistent nontemperature-related trend across species that advanced laying date by 0.06 ± 0.01 d/y and decreased body condition by $0.03 \pm 0.007\%/y$. For offspring number, other effects contributed strongly to temporal trends in individual species, but the direction/sign was not consistent across species (the “Other Pathway”; Fig. 2A–C).

Trait Change over Time Due to Warming. Across all temperature-sensitive species and traits, over half (52%) of the change in traits over time was due to the Temperature Pathway. However, there was some variation among the traits, with an average of 57% of temporal changes in laying date attributed to the temperature window (Fig. 3A), an average of 44% for body condition (Fig. 3B), and an average of 48% for offspring number (Fig. 3C).

Relationship between Temperature and Other Pathways. The Temperature and Other Pathways tended to have the same sign and thus reinforced each other (same sign pathways in 83% of species for body condition, 82% for offspring number, and 68% for laying date; Fig. 2D–F). The magnitude of the Temperature and Other Pathway estimates were positively correlated for offspring number ($r = 0.85$ 95% CI = 0.51, 0.96, $n = 11$) but uncorrelated for body condition ($r = 0.39$ 95% CI = -0.28, 0.80, $n = 11$) and laying date ($r = -0.02$ 95% CI = -0.39, 0.35, $n = 28$) (Fig. 4A–C).

Interspecific Variation. The percentage of the overall trend in a trait attributed to warming differed substantially among species, with values ranging from 28 to 82% for laying date, from 13 to 71% for body condition, and from 17 to 71% for offspring number (Fig. 3). Notably, variation among species in the total trait change over time (the Total Pathway) appeared to be mainly due to variation in the Other Pathway (explained interspecific variation in Total Pathways by Other Pathway: $r^2_{\text{laydate}} = 0.75$, $r^2_{\text{condition}} = 0.77$, $r^2_{\text{offspring}} = 0.96$; Fig. 4D–F) rather than in the Temperature Pathway ($r^2_{\text{laydate}} = 0.11$, $r^2_{\text{condition}} = 0.30$, $r^2_{\text{offspring}} = 0.88$), even though temperature explained on

average almost half of the total temporal change within a species (Fig. 3). This is likely because changes in traits due to the Temperature Pathway were more consistent among species compared to changes due to the Other Pathway for all traits.

Discussion

The assumption that changes in phenotypic traits through time reflect responses to climate warming relies on three conditions being met: changing local climate, traits being sensitive to climate, and no alternative drivers of change occurring. By using our simple method with long-term datasets on three traits in 60 common bird species in Europe, we show here that 1) mean temperatures generally increased over time, 2) laying date was sensitive to mean temperature for most species, but sensitivity of body condition and offspring number could only be detected in about a third of the species, and 3) other unknown drivers contributed strongly to temporal trends. On average across all three traits, 44 to 57% of trait changes over the past decades could be attributed to warming in temperature-sensitive species. Parmesan and Yohe (2) have argued that although competing explanations in the form of nonclimatic causal agents could have impacts, it is unlikely that such drivers would produce a consistent pattern of impact over space and time. Our study suggests that this proposition, which is also a crucial—but rarely explicitly mentioned—assumption in many other studies, may not generally hold, and that other drivers in addition to temperature change may also have a strong and consistent effect on phenotypic trends. Such a conclusion should possibly not be surprising in a world where humans are rapidly altering the environment in multiple ways, of which anthropogenic climate warming is only one.

Importance of Global Warming for Trait Change. Our analysis thus shows that temporal trends in traits cannot always be solely ascribed to increasing temperature. However, the fact that a single temperature variable can explain around 50% of the temporal trends across all species is remarkable for any ecological study and clearly underlines the impact that global warming is having on natural populations. Increasing temperatures were still likely the single most important contributor to temporal trends in all traits, even though less than half of temporal trends were due to warming for body condition and offspring number. This is because the Other Pathway is likely composed of many drivers such as habitat degradation or predation. Despite this, the Other Pathway strongly determined trait changes over time, suggesting that unknown drivers outside of our temperature windows were also heavily influencing these traits in European birds. Furthermore, similar changes in traits over time in species that were insensitive to temperature (i.e., more than half of the bird species considered), were solely due to nonclimatic effects, or other climatic effects that were not considered (e.g., rainfall).

The total change in laying date was substantially earlier than would be expected due to increased temperatures alone. Many studies have shown that laying date is closely associated with mean spring temperatures (16, 39–41). 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 (40, 42). Consequently, it was somewhat surprising that 43% of changes in laying date over time were due to the Other Pathway. Our study strongly suggests that temperature only tells part of the story for changes in laying date and that changes in other climatic [e.g., rainfall (41)] or nonclimatic factors [e.g., urbanization and land use (16, 17, 43)] may play a more prominent role than previously thought, and hence may deserve more attention.

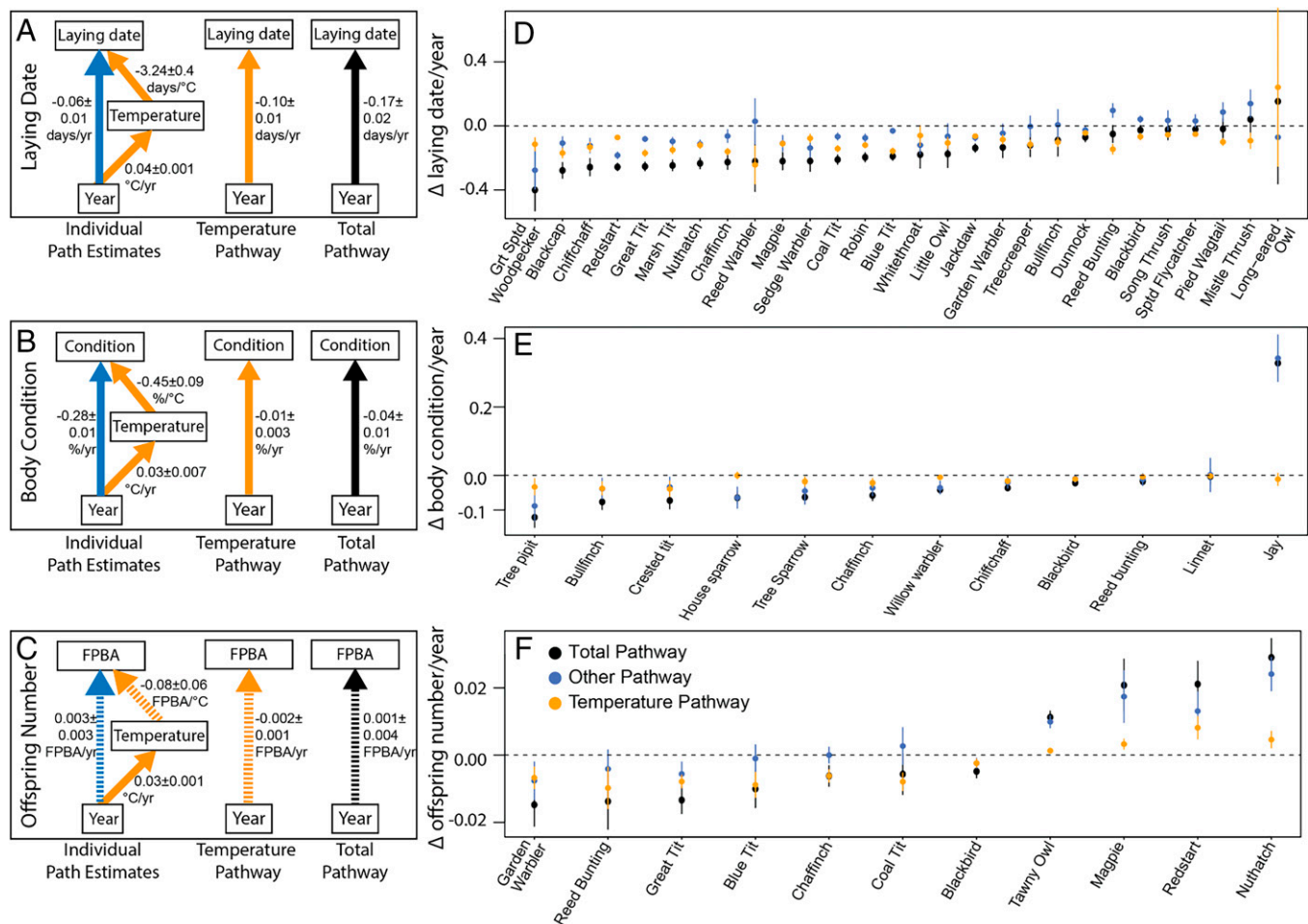


Fig. 2. Estimates of path coefficients averaged across species and displayed for each species. The plots in the left column (A–C) show the graphical representations of the structural equation models and the averaged path estimates (\pm SE) across all species found to be sensitive to temperature. The 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% CI 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 (\pm SEs) for the Total (black), Temperature (yellow), and Other (blue) Pathways for all temperature-sensitive species. In general, the Temperature Pathway coefficients varied less across species than the Other and Total Pathways. Note that the Jay has been removed from the average body condition estimates as it was a substantial outlier, although its removal did not change the estimates but did lower the 95% CI.

Overall, warming only tells us a part of the story of why these traits are changing. Future work is now needed to determine whether this extends to other species and traits. It will be important to identify the key ecological driver(s) that make up the Other Pathway, and the path analysis method we presented here is amenable to explicitly including additional climatic and nonclimatic drivers as alternative mediating pathways to explore this in a quantitative way. Thus, the method used here provides a framework for further work on identifying and quantifying these other ecological drivers.

Reinforcing Climatic and Nonclimatic Drivers. We found that attributing trait changes solely to climate warming is not only imprecise but actually results in systematic overestimation of its impact because temperature effects were mostly reinforced by nontemperature effects for all three traits. Reinforcement among pathways also suggests that species which are sensitive to warming are also sensitive to other changes in the environment, thereby providing support for the idea of “disturbance-

sensitive” species [a concept raised in the field of population dynamics and biodiversity (12, 44)] and emphasizes that different aspects of global change may accumulate on wildlife. In the case of body condition, trait change due to warming and other drivers typically resulted in lowered body condition, which has previously been suggested as a maladaptive impact of climatic change (24). However, for offspring numbers some species increased their productivity while other species decreased their productivity over time due to both pathways, and the positive correlation among both pathways further suggested that there are likely winners and losers among European birds from ongoing environmental change. Additionally, advances in laying date are typically considered plastic responses that should allow species to track temperature-mediated variation in optimum conditions (45). Our large-scale analysis provides the insight that these reinforcements may be common, but whether this is of concern will depend strongly on the ecological context of the trait (directionality of change and whether this is maladaptive or not).

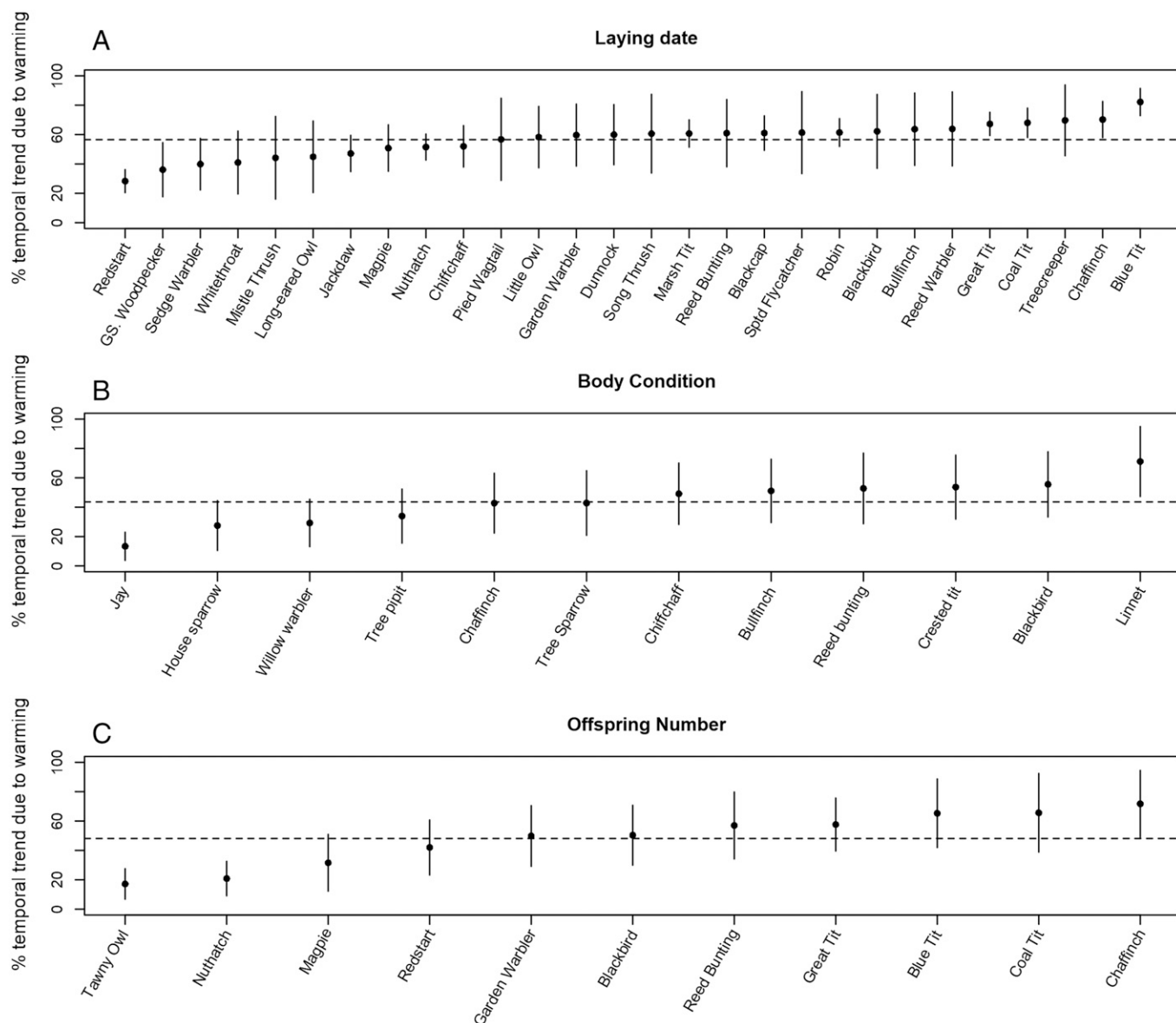


Fig. 3. Percentage of temporal trait trends due to increasing temperature. Percentage of the trend in life-history traits over time that is due to the Temperature Pathway for (A) laying date, (B) body condition, and (C) offspring number across all species sensitive to temperature. The horizontal dotted line in each panel shows the average value across all species for that trait. Error bars indicate 95% CIs.

Identifying What Makes a Species Sensitive to Climate Change.

Among-species differences in temporal trends were driven primarily by drivers other than warming. This appeared to be because warming had a more consistent effect on species compared to nontemperature effects. Nontemperature effects on species varied more, which drove the variation in total trait change over time across species. This implies that comparative studies should be cautious of attributing differences in temporal trends to underlying species differences in sensitivity (or exposure) to climate change, as they may actually more reflect sensitivity to other changes in the environment. For instance, comparative studies typically aim to identify species characteristics (e.g., allometry, longevity, specialization, and dispersal capacity) that make some species more vulnerable or sensitive to climate change (potentially including not “keeping up” enough in the case of phenology), but basing these analyses on responses over time runs the risk of identifying species characteristics that make them sensitive to nonclimatic drivers. Such potential misidentification is of

concern, as species characteristic are increasingly used to extrapolate climate vulnerabilities to data-deficient species to prioritize conservation strategies across taxa and countries (46–48). Instead, improving our understanding of exactly which species or habitat characteristics can explain a species’ sensitivity to rising temperatures versus other nontemperature effects will provide a better understanding of species’ vulnerabilities to climatic changes over time. Identifying such species or habitat characteristics will also generate hypotheses about what other nontemperature drivers might be important, and why the Temperature Pathway might be more or less important for different species.

Method for Estimating Contributions to Change. Our simple quantitative method to decompose the contribution of climate warming to trait change is conceptually similar to statistical methods used to account for shared trends [i.e., year detrending (38)]. However, our method can decompose the contributions of

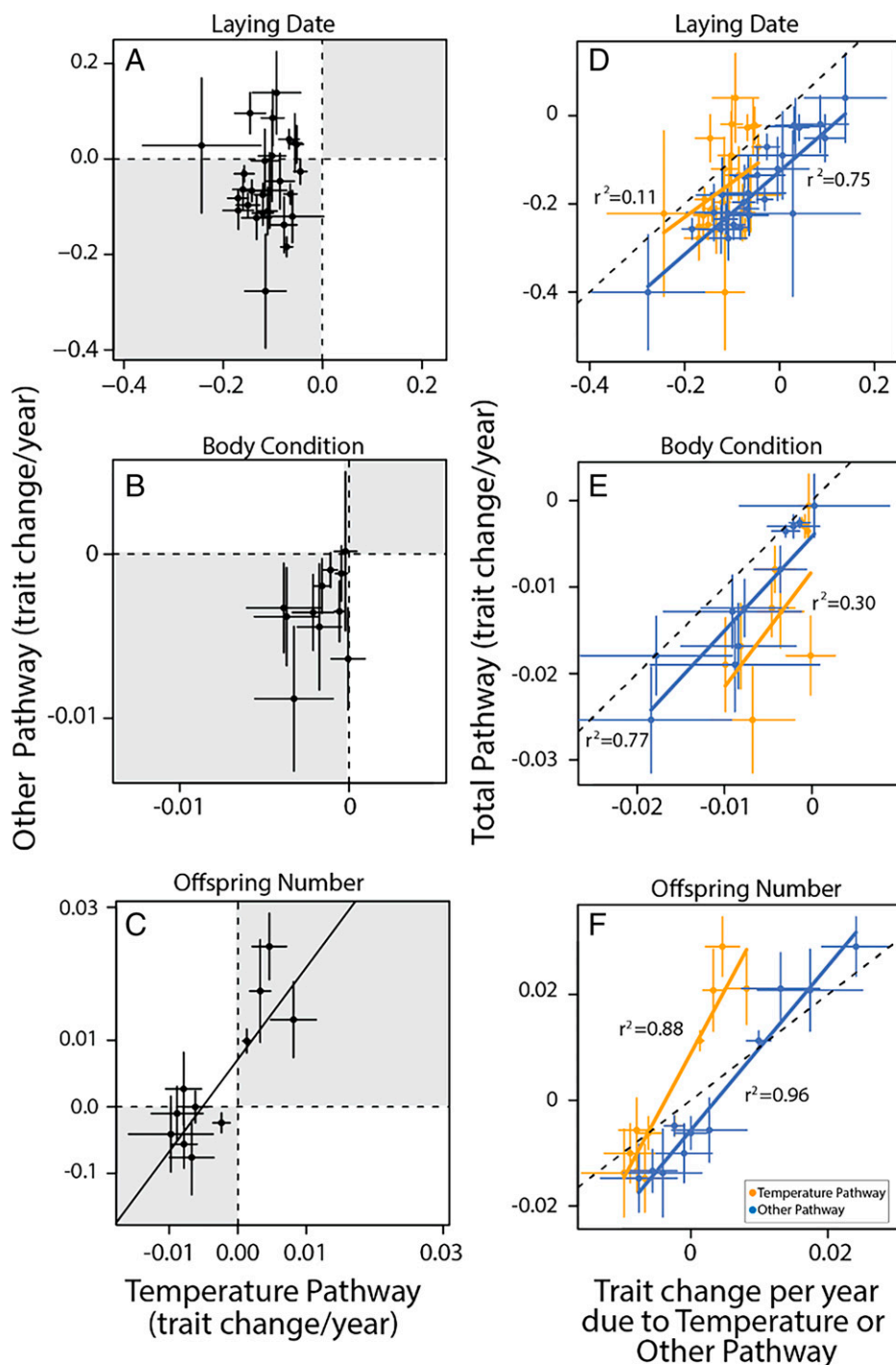


Fig. 4. Interspecific comparison of path estimates. The left panels (A–C) show the correlation between the Temperature and the Other Pathway for all temperature-sensitive species, where each point represents a species. The dark shaded areas indicate the Temperature and Other Pathways having “reinforced” effects. The right panels (D–F) show the relationships between the Total Pathway (the 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) Pathways. 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 long-eared owl was removed from the laying date estimates and figures as it was an outlier with substantial uncertainty surrounding path estimates. Error bars show 95% CIs.

climatic and other pathways to trait change over time. Thus, we aim to investigate whether it is likely that temperature causes trait variation, or whether instead they are only correlated due to something else changing over time (see [SI Appendix](#) for details). Our key metric “percentage of trend due to warming” should be

viewed as a conservative (minimum) estimate for two reasons. First, the strength of the temperature sensitivity—and consequently also of the Temperature Pathway—could be underestimated (biased toward zero) due to measurement error surrounding the temperatures that the birds experience (causing regression dilution).

Although temperatures at weather stations will have little measurement error, they can be imperfect proxies of the causal microclimates that organisms experience at study sites. We note that mean temperatures at the nearest weather station are likely to be highly correlated with the mean temperature at the study site because mean temperatures typically exhibit strong spatial autocorrelation and their proximities were close in both countries due to their high density of weather stations. A second reason for our key metric to be conservative is that we selected only the “best” mean temperature window, and thus our temperature measure is only an index of global warming, or climate change more generally. Additional periods in other parts of the year, or other temperature measures (e.g., number of hot days) could also be influential (see *SI Appendix* for further discussion). Other dimensions of warming or climate change outside of the temperature windows identified here may have been captured by the Other Pathway, but only if 1) sensitivity to such alternative aspects of climate change exist, 2) these climate variables are also changing over time, and 3) they are uncorrelated to the focal climate aspect (mean temperature here). We have shown that our mean temperature index is likely the single most important contributor to trait changes over time and note that different aspects of climate change are often highly intercorrelated. Our method is amenable to including additional climate variables to explore hypotheses about effects of other variables.

Conclusion. Although it is clear that warming is having large impacts on natural populations and that rising temperatures appear to be a main driver of changes in traits over time, we have shown here that temporal trends in phenotypic traits cannot always be assumed to be driven entirely by rising temperatures. Identifying the contributions of key climatic and nonclimatic drivers to trait changes over time will be vital for developing appropriate conservation management strategies as the specific actions to mitigate impacts or promote adaptation will differ substantially for different drivers (2, 49). As we increase our understanding of how changes in climate directly impact species and how nonclimatic variables simultaneously drive changes, we can better identify those species or populations most at risk from climate change.

Data Availability. Some study data are available. Previously published data were used for this work. The data from The Netherlands are already available online with previous publications, found here: <https://datadryad.org/stash/dataset/doi:10.5061/dryad.8r882> and <https://datadryad.org/stash/dataset/doi:10.5061/dryad.zs7h4j56>.

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