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A global synthesis of animal phenological responses to climate change

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Shifts in phenology are already resulting in disruptions to the timing of migration and breeding, and asynchronies between interacting species[1–5]. Recent syntheses have concluded that trophic level[1], latitude[6] and how phenological responses are measured[7] are key to determining the strength of phenological responses to climate change. However, researchers still lack a comprehensive framework that can predict responses to climate change globally and across diverse taxa. Here, we synthesize hundreds of published time series of animal phenology from across the planet to show that temperature primarily drives phenological responses at mid-latitudes, with precipitation becoming important at lower latitudes, probably reflecting factors that drive seasonality in each region. Phylogeny and body size are associated with the strength of phenological shifts, suggesting emerging asynchronies between interacting species that differ in body size, such as hosts and parasites and predators and prey. Finally, although there are many compelling biological explanations for spring phenological delays, some examples of delays are associated with short annual records that are prone to sampling error. Our findings arm biologists with predictions concerning which climatic variables and organismal traits drive phenological shifts.

Global climate change has important ecological consequences[4,8] and perhaps the best studied are advancements in the timing of seasonal activities, or phenology, of organisms[1–3,5,7,9–13]. Understanding the factors that influence phenological shifts is critical because these shifts can impact the fitness of organisms by altering the availability of resources[2–4]. In addition, phenological shifts can cause species declines by generating asynchronies or 'mismatches' between plants and pollinators[12], plants and herbivores[14], migrant birds and their prey[11] or floral resources[15], and hosts and parasites[16]. Several recent syntheses have made inroads to understanding how the phenology of species is shifting with climate change[1,5–7,13]. For example, primary consumers were demonstrated to be shifting their phenology faster than other species in the UK[1], species are shifting their phenology faster in spring than in autumn in China[5], and the strength of phenological responses to climate change is dependent on the way responses are measured (for example, by the types of behaviour observed or the number of observations[7]).

Despite these insights, several critical knowledge gaps preclude accurate predictions of the sensitivity of organisms to climate change on a global level. First, although many phenological syntheses assume climate change as an important driver, few explicitly test for the effects of climate (but there are exceptions[1,5,6]), and among those that do, climate data have rarely been standardized across studies to confirm the link between changes in phenology and climate. Therefore, it remains unclear which climatic variables, such as temperature or precipitation, are driving shifts in phenology, and whether the broad geographical heterogeneity in these climate variables impacts their power to explain and predict ecological trends. Second, recent syntheses have relied on country-level data, and no synthesis in over a decade has addressed phenological responses to climate change across the globe. Global analyses are important because they cover a greater extent of climatic conditions than local or regional analyses. For example, global syntheses are critical to test broad-scale latitudinal hypotheses about phenological shifts, such as the hypothesis that the climatic factors driving seasonality across latitudes also drive phenological changes. Third, it is unclear why some species show delayed spring phenologies despite an overall trend towards advancement[10,17]. Finally, it is also unclear whether certain ecologically important characteristics of organisms are predictive of strong phenological responses. For example, phylogeny or body size may be an important factor in determining the magnitude of phenological response to climate change because smaller organisms acclimate more quickly to changing conditions than larger organisms (J.R.R., manuscript in preparation). In addition, ectotherms may exhibit stronger phenological responses than endotherms because they cannot thermoregulate independently of their environments and are therefore more sensitive to changes in environmental conditions. Because of these knowledge gaps, a general global framework is still missing for predicting the direction and magnitude of phenological shifts based on ecological context and organismal traits.

To address these gaps, we conducted a global synthesis of animal phenological time series from 127 studies (Supplementary Tables 1 and 2), spanning 5 continents and 15 classes of animals including insects, mammals, reptiles and birds. We focused on spring phenological events in animals because phenological responses to climate change in plants have recently been synthesized[18], some of our primary questions could only be answered using animal data, and the evidence for advancement in animal phenology is more conflicting and controversial than it is for plants[9] (see Supplementary Information). Here, we synthesized the multivariate effects of climate change on phenology, as well as testing predictors of this complex phenomenon (such as latitude, endo- or ectothermy), with a unique meta-analysis approach that jointly modelled phenological shifts, the effects of climate on phenology and climate change (the 50 yr correlation between climate and year) using a trivariate mixed-effects model[19,20] (see Supplementary Fig. 1; see Methods). Unlike previous univariate meta-analyses that strictly synthesize phenological shifts[2,3], our trivariate approach assessed whether phenology is dependent on climate and climate change and whether the magnitude and direction of these relationships is dependent on 10 climate variables (for example, mean, minimum and maximum temperature, precipitation, snowfall[21], see Methods). All climate variables were standardized across all time series by accessing a single source of historical point-based climate data (the National Oceanic and

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Atmospheric Administration (NOAA) NCDC-3 data[22]) with data that were specific to the region and time of each study, reliably allowing us to identify which aspects of climate were driving phenological shifts. Importantly, this approach facilitated evaluation of whether climate change, rather than just long-term climate means, was associated with changes in phenology. Further, our trivariate mixed-effects meta-analysis also accounted for dependencies of effects among related taxa due to their shared phylogenetic history[23] (see Supplementary Code). We were able to compare relationships between phenology and year for 1,011 time series and relationships among phenology, year and climate for a subset of these including 321 time series.

The meta-analysis revealed that, on average, animals have advanced their phenology significantly since 1950 ($\overline{\beta} = -0.318$ (mean slope), d.f. = 937, $P = 0.01$; Fig. 1a; Supplementary Table 3), advancing by 2.88 days per decade. Across all species and sites, mean temperature increased significantly over time (Fig. 1a; Supplementary Table 4). The meta-analysis also revealed that temperature is closely related to phenological date independent of year, and that phenology is more closely linked with mean temperature in areas that have experienced more climate change (Fig. 1b), suggesting that climate change is indeed the driver of these shifts (Fig. 1a; Supplementary Table 4). Phenological shifts were not heavily biased by the phylogenetic history of taxa, which accounted for only about 4.5% of the variance (phylogenetic τ^2) between phenology and year, and 0–6% between phenology and climate (Supplementary Tables 3–8). Between-study variance accounted for 8–9% of the total variance accounted for in all models (Supplementary Tables 3–8).

The direction of phenological shifts may differ among taxa, with some species showing delays rather than advances of spring phenology[5,10,13,17,18]—such as delays in seabird egg-laying as a consequence of reduced sea ice[10] or delays in phenology (flowering, for example) after short winters that fail to induce vernalization[17]. To test whether a phenomenon similar to vernalization might be responsible for phenological delays among animals (positive relationships between phenological date and year), we examined whether the magnitude of the delay could be predicted by the increase in winter temperatures (defined here as the relationship between year and average temperature during the year's three coolest consecutive months), controlling for latitude. We found no support for the hypothesis that winter temperatures predicted phenological delays, instead finding that they predicted advancements ($\beta = -0.296$ (slope), d.f. = 321, $P < 0.001$ in models with all time series) or were not significantly predictive ($\beta = -0.125$, d.f. = 68, $P = 0.32$ among time series with delays only). In fact, winter temperatures were positively correlated with spring temperatures that are well

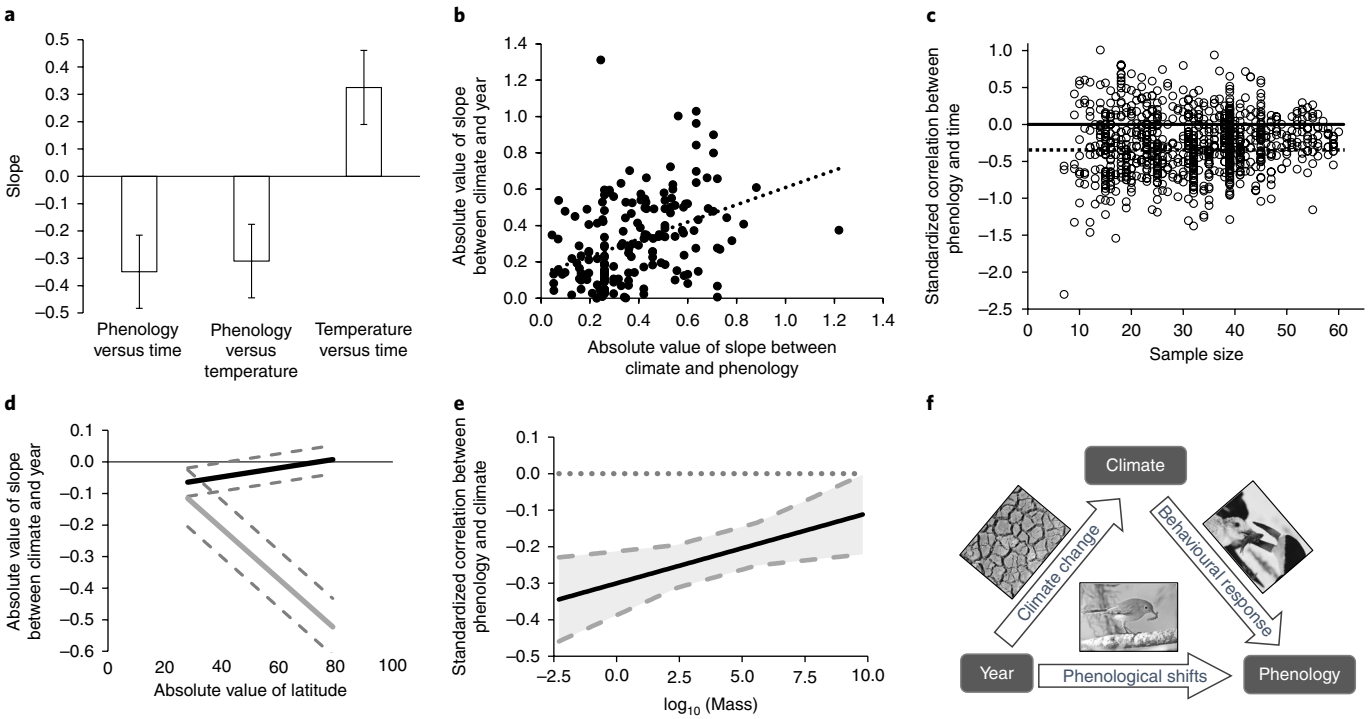

Fig. 1 | Improving how we understand advancements in phenology due to climate change. a, Across 1,011 time series, phenology occurred earlier through time as temperature increased and the increases in temperature were negatively correlated with phenology (see Supplementary Fig. 3 for precipitation). Error bars represent s.e.m. **b**, Phenology was more closely linked with mean temperature (*x* axis) in areas with more climate change (*y* axis; $R^2 = 0.152$, d.f. = 175, $P < 0.0001$). **c**, A funnel plot comparing sample sizes (total years in time series) with standardized effect sizes (correlation between phenology and time quantified via Fisher's z effect sizes (standard score)) reveals that studies with small samples sizes have large variation with both the positive and negative shifts, suggesting that species that appear to delay their phenology in spring might sometimes be spurious products of sampling error. The solid line is the zero line and the dotted line represents the grand mean effect size (−0.349). **d**, Precipitation becomes more important in driving phenological responses (that is, more negative values) as one moves towards the Equator from temperate regions (orange line with 95% confidence band), whereas temperature becomes important as one moves away from the Equator towards temperate regions (blue line with 95% confidence band; test for different slopes: $P < 0.0001$). Data on time series of phenological shifts close to the equator are unfortunately unavailable. **e**, The slope between log-transformed body mass and the correlation between phenological date and mean temperature is positive in a non-phylogenetically controlled trivariate meta-analysis model, suggesting that smaller organisms might track their phenology with temperature more closely than larger organisms. Data points are not shown to reduce clutter and 95% confidence intervals are provided in grey. **f**, Conceptual figure explaining the meaning of the slope and correlation terms on the other panels, which represent relationships betwen year, climate and phenology.

documented as drivers of phenological advancements ($\beta = 0.298$, d.f. = 321, $P < 0.0001$ for all time series, $\beta = 0.202$, d.f. = 68, $P = 0.03$ among delays). Alternatively, many apparent spring delays might be sampling artifacts of short annual records. Indeed, a funnel plot revealed that many studies based on short time series (small sample sizes) had both delays and strong advances in phenology, but when sample sizes were large, phenology advanced more uniformly (Flinger–Killeen test for homoscedasticity: $\chi^2 = 112.72$, $P < 0.0001$; Fig. 1c; see Extended Data Fig. 2 for comparisons of effect sizes with variance). In addition, there was no evidence of funnel plot asymmetry (Egger's test: $z = -0.724$, $P = 0.47$), suggesting that the representation of phenological delays in our dataset does not differ from what would be expected by chance. While this result does not exclude true and biologically relevant spring delays in phenology (see examples above), it suggests that reports of delays are probably sensitive to sampling error; in fact, the duration of time series has previously been found to influence observed phenological trends in marine species[7].

We also hypothesized that phenological shifts would be associated with the climatic variables that drive seasonality locally—such as temperature at mid-latitudes (that is, temperate zones) and precipitation at low latitudes (that is, tropical and subtropical zones). Moreover, because climate change is resulting in greater changes in temperature than precipitation[24], we hypothesized greater phenological shifts in temperate than tropical zones. In support of these hypotheses, as the absolute value of latitude increased, changes to temperature became more predictive of the magnitude of phenological shifts, and as latitude decreased, precipitation became a more important predictor of phenology (test for different slopes[25]: $t = 7.89$, d.f. = 1650, $P < 0.0001$; Fig. 1d; Supplementary Table 5). Further, there was a greater increase in temperature than precipitation through time (Extended Data Fig. 3), and the correlation between phenology and temperature in the temperate zones was stronger than the correlation between phenology and precipitation near the tropics (Fig. 1d). These results indicate that different climatic variables are triggering phenology in temperate and tropical regions. While past syntheses have hypothesized that species should shift their phenology faster at higher latitudes in response to greater warming in these regions[2,3,6], low-latitude species may also be shifting their phenology in response to changes in rainfall. Given that the majority of phenological studies are from northern temperate climates[7] (especially North America and Europe; Fig. 2), and emphasize temperature over precipitation, additional phenological time series from low latitudes are needed to quantify the full effects of precipitation shifts on tropical phenology. However, the effects of precipitation on phenology may be less closely associated with latitude than the effects of temperature simply because latitude is more strongly correlated with temperature than precipitation.

Given that temperature and precipitation drive phenology unequally across the globe and particular taxa exhibit differential sensitivities to extreme temperatures and moisture levels, we hypothesized that the phenology of specific taxonomic groups might be more strongly associated with temperature or precipitation. For example, we expected amphibians to respond to precipitation more strongly than any other taxonomic group because of their considerable reliance on moist conditions for survival and reproduction. However, across all taxa synthesized, phenology was associated more strongly with temperature than with precipitation (temperature, $\overline{\beta} = -0.310$, d.f. = 1579, $P = 0.02$; precipitation, $\overline{\beta} = -0.054$, d.f. = 1579, $P = 0.54$; Extended Data Fig. 4; Supplementary Table 4), and different components of temperature (mean, minimum and maximum) did not significantly differ from one another at predicting phenology. As

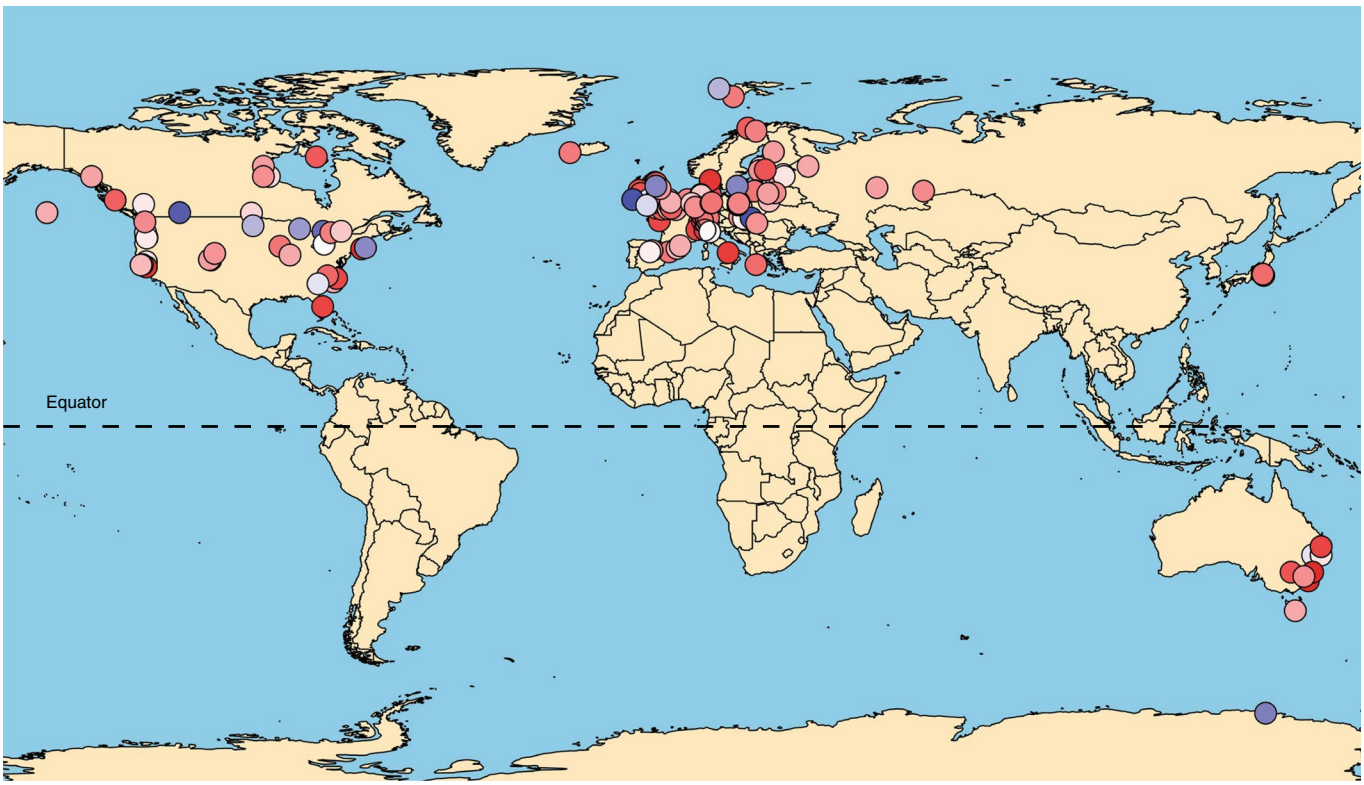

Fig. 2 | The uneven global distribution of published studies exploring the phenology of animals. There are hundreds of published phenological time series from North America and Europe, but much less is known about phenology on the other five continents with particularly large gaps in the tropics and marine systems. Red points indicate advancements in phenology over time and blue points indicate delays. The strength of the color indicates the magnitude of the relationship between phenology and time (as quantified with a Fisher's z effect size).

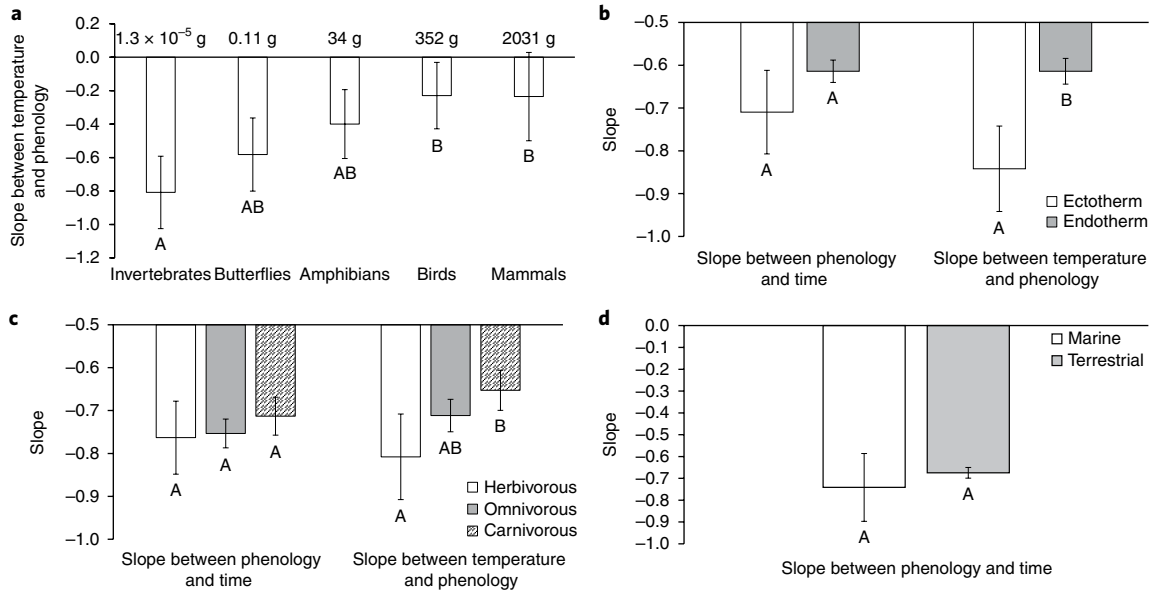

Fig. 3 | The ability of phenology to track temperature varies among taxonomic classes of animals, ecto- or endothermy, and trophic level. a–b, In models including body size and ecto- or endothermy as covariates, smaller taxa (**a**) and ectotherms (**b**) tracked temperature closer than larger animals and endotherms. Generally, taxa with smaller body sizes shifted at faster rates than larger taxa (mean body sizes are reported above bars). **c**, Herbivores had a greater association between temperature and phenology than carnivores, possibly because herbivores were reacting to shifts in plant phenology associated with temperature. **d**, However, we did not observe a difference in phenological response between terrestrial and marine organisms. We report relationships between phenology and both temperature and time (except in **d**, because we lack climate data for marine organisms) to highlight that even if groups are apparently advancing their phenology at similar rates, they could be responding to changing climates at dissimilar rates if they come from regions that are experiencing different rates of climate change. Error bars represent the s.e.m. for the slope parameters from trivariate mixed-model meta-regressions. Different letters denote statistically significant differences in effect sizes.

predicted, amphibians exhibited the strongest association between precipitation and phenology among all taxa ($\overline{\beta} = -0.172$, d.f. = 1564, $P = 0.16$; Extended Data Fig. 4b; Supplementary Table 6). Although Thackery et al. found that amphibian phenology was not sensitive to precipitation in the UK[1], this might only be the case at high latitudes where the effects of precipitation are less pronounced.

Next, we sought to identify general ecologically important characteristics of taxa that might predict the strength of phenological responses to climate change. Here, we hypothesized that ectotherms and smaller organisms should be more sensitive to shifts in climate than endotherms and larger organisms (because thermal inertia is positively associated with body size[26]; J.R.R., manuscript in preparation). When we tested for the effects of body size in a phylogenetically controlled model, there was no significant effect of body size, at least partly because body size is correlated with phylogeny (for example, almost all birds have greater mass than all insects). However, smaller invertebrate groups advanced their phenology faster than larger vertebrates (Fig. 3a; Supplementary Table 7); non-insect invertebrates (mean body mass: 5.3×10^{-6} g) advanced their phenology 4.93 days per decade, insects (0.15 g) advanced 4.15 days per decade, amphibians (34 g) advanced 3.23 days per decade and birds (352 g) advanced 2.24 days per decade. In addition, body size was a significant predictor of phenological shifts in a model without phylogenetic controls ($\beta = 0.0544$, d.f. = 921, $P < 0.01$), suggesting that it may be a factor influencing the strength of phenological shifts. As predicted, the phenology of ectotherms was more strongly correlated with temperature than the phenology of endotherms (Fig. 3b; Supplementary Table 7), even when controlling for phylogeny. Finally, herbivore phenology tracked temperature more closely than carnivore phenology (Fig. 3c; Supplementary Table 7), possibly because herbivores are also responding to shifts in the timing of plant phenology[27], and supporting similar conclusions by Thackeray et al. in the UK[1]. Additionally, we did not observe a difference between the phenological responses of terrestrial and aquatic species (Fig. 3d; Supplementary Table 7), although there are admittedly few aquatic species in the dataset (18 total) and all are marine.

Finally, we posited that the type of phenological responses, such as peak seasonal abundance, arrival (migration) and breeding/rearing (calling, nesting, laying, hatching or weaning), may differ in their sensitivities to climate change, as recently concluded by a synthesis on marine systems[7]. We predicted that arrival would be least correlated with climatic factors because migrants are probably reacting to climatic conditions where they left from rather than conditions where they are arriving[28]. Phenological responses related to arrival tracked climate the most poorly (Extended Data Fig. 5; Supplementary Table 8), and those based on peak abundance tracked temperature changes the most closely—possibly because peak abundance is more often documented with smaller invertebrates that phenologically respond strongly to climate. Unfortunately, because there are very few phenological time series from equatorial regions, and arriving species often come from multiple departure locations, we could not test whether the timing of departures for spring migrations tracked temperature better than arrivals (but see ref. [29]).

Our findings add to the growing evidence of direct ecological consequences of climate change on ecological systems and provide strong evidence linking climate change to phenological shifts.

Our synthesis unveiled previously unidentified generality in the phenological responses of organisms to climate, indicating that the phenology of species at high latitudes most strongly responds to temperature, while species at lower latitudes are responding to temperature and precipitation equally; thus, different components of climate drive phenology in different regions of the globe. We also found that different taxa respond to the same climatic signals but do so at different rates, and that the strength of these phenological shifts may be predictable based on two easily measured traits: thermoregulation and body size. As climate change intensifies in the next century, our results suggest that advances in phenology are likely to become more exaggerated, potentially further desynchronizing interactions between species that vary considerably in their body sizes, such as mutualistic, predator–prey, and host–parasite interactions. However, the synthesis presented here now equip climate biologists with knowledge regarding the specific components of climate and the traits of interacting species that can drive phenological shifts, providing new opportunities to forecast mismatches and mitigate their adverse effects.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available at https://doi.org/10.1038/s41558-018-0067-3.

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Author contributions

J.M.C., M.J.L., and J.R.R. contributed ideas and devised the analyses. J.M.C. assembled the database of phenological time-series and collected climate data. M.J.L. designed and conducted the analyses. J.M.C., M.J.L. and J.R.R. wrote the paper.

Competing interests

The authors declare no competing interests

Additional information

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Methods

Literature survey and data requirements. We conducted a literature search in September 2012 on Web of Science for the term 'phenology AND climate' within the following fields: environmental sciences and ecology, zoology, developmental biology, reproductive biology, life sciences (other), entomology, behavioural sciences, physiology, biodiversity and conservation, fisheries, evolutionary biology, parasitology, marine and freshwater biology, infectious diseases and oceanography. This search generated 6,989 studies that were examined for phenological time series. References in these papers and the USA National Phenology Network (https://usanpn.org) database were also examined for time series. Time series were not used if they: (1) contained data spanning <10 yr; (2) contained data for fewer than seven individual years; (3) described autumn migrations; or (4) described data that were redundant with data we had already compiled from another paper. We also eliminated raw data from before 1950, because this is considered to be before significant global climate change[30]. Our exclusion criteria are similar to those from previous meta-analyses[1,2].

Data extractions. We extracted raw time series data from figures plotting day of year of phenological event (including date of first or median arrival, first calling, nesting, laying, peak abundance, oestrus, or weaning) against year using Datathief III Version 1.6 (Bas Tummers). Correlation coefficients between phenological date and year, standard errors or surrogates, and slopes were also calculated for each time series when they were not reported in the original text (all analyses were conducted in R 3.1.0; stats package, glm function). Correlation coefficients (r) and standard deviations were available for 1,011 of these time series (representing 127 studies) that were used in the meta-analysis examining the relationship between phenology and year. Approximately 400 time series from about 100 papers provided raw data and were used in the meta-analyses examining the relationships between phenology, year and climate (the actual numbers varied between different climate variables because some variables were not available at certain geographic locations). Sampling variances (used as weights) were derived from all correlation coefficients, and coefficients and variances were standardized using Fisher's z-transformation before all meta-analysis modelling.

External climate data. Climate data were obtained from the NOAA National Climatic Data Center (NCDC; www.ncdc.noaa.gov) worldwide database of monthly observational data corresponding to the nearest location (within 100 km) and all years in every time series that provided raw data and geographic coordinates. Ten climate variables were obtained for each site and year (see Extended Data Fig. 4) and they generally were related to temperature or precipitation. Climate variables were used individually in models instead of as covariates (see below). Yearly averages of climate variables were compiled for all variables in all locations and for the years in all time series only when data were available for all 12 months. Within each time series, correlation coefficients and standard errors were compiled for all correlations between all annual climate variables year, all climate variables and phenology, and phenology and year (stats package, glm function). We did not have any climate data for marine species and did not include these time series in any analyses testing the effects of climate.

Independent fixed-effects variables. Independent variables collected for each time series included taxonomic classification of the focal species, absolute value of latitude, elevation, form of thermoregulation (ectothermy or endothermy), trophic level, habitat (terrestrial or marine), country (to control for geography), log-transformed body mass (see below) and type of phenological event (endpoint measured). Taxonomic classification was assessed to the class level. Elevation specific to the locations where time series were observed was extracted from Worldclim elevation rasters (www.worldclim.org) (raster package, extract function). Trophic levels were assigned categorically as 'herbivore', 'omnivore', or 'carnivore. If a species typically eats plants and animals it was designated an omnivore, but if it mostly relies on either prey or plants and only occasionally ate the other, it was assigned to 'carnivore' or 'herbivore' respectively. Phenological events were categorized as either 'arrival' (migrations), 'breeding/rearing' (calling, nesting, laying, hatching, or weaning) or 'peak abundance' (peak population abundance).

Meta-analysis models. A trivariate mixed-effects meta-analysis was used to analyse three effect sizes per study that jointly quantify the pairwise relationships among phenology, time and a single climate variable (Fig. 1f). Preserving the trivariate structure of effect sizes has the advantage of accounting for the correlations within the three non-independent effect sizes (because of sampling variability and covariances), while also explicitly accounting for any existing correlations among these three effect size groups (via a multivariate random-effects model). Our overall model had a hierarchical structure in which we modelled the sampling variances and covariances among the three effect sizes (within-study weighting to account for study sampling error), between-study random-effects for each effect size triplicate that were allowed to be correlated but differ among groups (that is, a multivariate version of the between-study variance component typically included in traditional random-effects meta-analysis) and finally an unstructured random-effect modeling the phylogenetic correlations among taxa (see Supplementary Code). For all models, the *rma.mv* function from the R package *metafor*[31] was used, with the variance–covariance matrix as the variance–covariance matrix of the sampling errors, and all random effects (trivariate between-study variances, and phylogenetic) were based on restricted maximum likelihood estimator using a nlminb numerical optimizer. However, we did not include phylogenetic random-effects in our initial analysis of the relationship between phenology and body size because phylogeny and body size are highly correlated and thus controlling for phylogeny also indirectly eliminates much of the body size variation. See Supplementary Code for the R script used in these analyses.

Species-level body mass data. We collected species-level body masses from several existing datasets and sources[32–40]. We calculated mass based on body length for some insects as described by previous studies[41,42], when we could not find published estimates of body mass. For species for which we could not obtain or calculate reliable body mass data (including several amphibian and invertebrate species), we estimated mass by taking the mean of the mass of species in the lowest taxonomic level occupied by that species. Although this method is relatively coarse, we were not concerned about obtaining highly specific values of mass because across the organisms in our dataset mass varied by >10 orders of magnitude and mass was log-transformed in our analyses. To plot the relationship between body mass and phenology, we used the ggplot2 package[43], ggplot function.

Trivariate mixed-effects meta-regression model. In matrix notation, our trivariate and phylogenetic mixed-effects meta-analysis can be described with this regression model:

$$\mathbf{z} = \mathbf{MW}\boldsymbol{\beta} + \varepsilon + \mathbf{Mu} + \sigma_p^2\mathbf{PJ}, \quad (1)$$

where $\mathbf{z}$ denotes a $(k \times 1)$ column vector containing all of the k number of effect sizes. For each ith of m number of studies there can be three effect sizes (specifically Fisher's Z transformed correlation coefficients): the standardized correlation ($Z_{t,p}$) between time (t) and phenology (p), the correlation ($Z_{t,c}$) between time and the climate variable (c) and the correlation between phenology and the climate variable ($Z_{p,c}$). Therefore $\mathbf{z}$ can have length $k = m \times 3$. However, for some climate variables, data were incomplete such that $Z_{t,c}$ and $Z_{p,c}$ could not be calculated. The indicator matrix $\mathbf{M}$ models this availability of effect sizes among studies. It has a block diagonal design with its main diagonal defined by $\mathbf{I}_i$; a vector whose ith elements are either a 3×3 identity matrix when the three effect sizes are available or a 1×1 identity matrix when otherwise (for example, designating studies with only $\delta_{t,p}$ available). The second matrix in equation (1) ($\mathbf{W}$) is the regression design matrix of $m \times (p+1)$ size, with p number of covariates, and where the first column of $\mathbf{W}$ contains only ones (for example, the model intercept). The regression coefficient of this model is defined by $\boldsymbol{\beta}$ which is a column vector of size $(p+1) \times 3$. Because covariates (predictors) are included in our model and are treated as fixed effects, our meta-analysis model can also be described as a trivariate mixed-effects meta-regression.

The within-study sampling error and sampling covariances (further defined below in the Within study sampling error of trivariate effect sizes section) among the effect sizes is modelled as a block diagonal matrix $\boldsymbol{\varepsilon}$, which on its main diagonal contains the elements of an $m \times 1$ column vector of sampling variance–covariance matrices. The $\boldsymbol{\varepsilon}$ matrix models the weighting of effect sizes based on their sampling error, and models the non-independence of the trivariate effects that share common dependent variables. Also, as assumed by all random-effects meta-analysis, a between-study variance τ^2 component is estimated; however, here our among-study variance component (as well as covariance) is estimated for each of the three main underlying effects. For simplicity, it is assumed that the main effects have the following multivariate normal (MVN) between-study random-effects distribution:

$$\begin{bmatrix} u_{t,p} \\ u_{t,c} \\ u_{p,c} \end{bmatrix} \sim MVN\left(0 = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, u = \begin{bmatrix} \tau^2_{t,p} & \tau(t,p),\ (t,c) & \tau(t,p),(t,c) \\ sym & \tau^2_{t,c} & \tau(t,c),(p,c) \\ & & \tau^2_{p,c} \end{bmatrix}\right) \quad (2)$$

Where u is a 3×3 variance–covariance matrix defining the trivariate between-study variance. Multivariate among-study variance components are estimated via maximum likelihood using the *ram.mv* function in the *metafor R* package. In addition to the multivariate among-study random affects, the phylogenetic effects are modelled as random factor with an unstructured multivariate distribution $\sigma^2_{\mathbf{P}}\mathbf{PJ}$. Here $\sigma^2_{\mathbf{P}}$ is the estimated phylogenetic variance, and following ref. [44], $\mathbf{J}$ is a secondary indicator matrix that links the phylogenetic correlations ($\mathbf{P}$) to individual effect sizes and when multiple effect sizes are derived from single species it specifies their shared covariance to one. Finally, $\mathbf{P}$ is the phylogenetic correlation matrix; details about $\mathbf{P}$ are described below under the Non-independence due to shared evolutionary history among taxa section.

Marginally, this trivariate and phylogenetic mixed-effects meta-regression model can be described as:

$$z_i \sim MVN(\mathbf{MW}\boldsymbol{\beta},\ \boldsymbol{\varepsilon}+\mathrm{M}u+\sigma_p^2 PJ)$$

Within-study sampling error of trivariate effect sizes. We accounted for the non-independence that occurs when combining and comparing multiple effect sizes that share common variables (phenology, climate and year) by including their estimated sampling covariances in the off-diagonals of the variance–covariance $\boldsymbol{\varepsilon}$ matrix used as weights for meta-analysis (as done in a previous study[19]). This $\boldsymbol{\varepsilon}$ matrix has a block-diagonal design, where each block can represent a 1×1 matrix containing the sampling variance of an effect size (cases where only $Z_{t,p}$ was available for a study), or a 3×3 matrix where its main diagonal contains the sampling variances (var) of each of three Fisher's Z transformed correlation (effect size):

$$\mathrm{var}\left(Z_{t,p}=\mathrm{var}\left(Z_{t,c}\right)=\mathrm{var}\left(Z_{p,c}\right)=\frac{1}{n-3}\right), \quad (3)$$

where each variance is the predicted sampling variance of the pairwise Fisher's Z transformed correlation for three variables (t, p and c). All correlations share a common sample size (n). The covariance between two Z correlations, for example $Z_{t,p}$ and $Z_{t,c}$, is $\mathrm{cov}(Z_{t,p}, Z_{t,c})$, where $Z_{t,p}$ is the effect size for a correlation between variables time and phenology, and $Z_{t,c}$ is the effect size for the correlation between time and climate. Further, the raw correlations (Pearson product moment correlation coefficient) are needed to estimate these covariances, where for example between t and p the correlation will be $\rho_{t,p}$. Following two previous studies[45,46], the covariance between two Fisher's Z effect sizes with a t common dependent variable, $\mathrm{cov}(Z_{t,p}, Z_{t,c})$, is estimated as:

$$\mathrm{cov}\left(Z_{(t,p)},\ Z_{(t,c)}\right) = \frac{\rho_{pc}\left(1-\rho_{t,p}^2-\rho_{t,c}^2+0.5\times\rho_{t,p}\times\rho_{t,c}\times\rho_{p,c}\right)-0.5\left(\rho_{t,p}\times\rho_{t,c}\right)\left(1-\rho_{t,p}^2+\rho_{t,c}^2\right)}{(n-3)\left(1-\rho_{t,p}^2\left(1-\rho_{t,c}^2\right)\right)} \quad (4)$$

The covariance was estimated for all pairwise correlations among the phenology, time and climate variables. For example, the variance–covariance matrix for ith of the effect size triplicates can be described with this symmetric matrix:

$$\begin{bmatrix} \mathrm{var}\left(Z_{t,p}\right) & \mathrm{cov}\left(Z_p, Z_{t,c}\right) & \mathrm{cov}\left(Z_{t,p}, Zp, c\right) \\ & \mathrm{var}\left(Z_{t,c}\right) & \mathrm{cov}\left(Z_{t,c}, Z_{p,c}\right) \\ & & \mathrm{var}\left(Z_{p,c}\right) \end{bmatrix} \quad (5)$$

The matrices for each ith study were then stacked diagonally into a single matrix for meta-analysis ($\boldsymbol{\varepsilon}$). When needed, individual matrices described in equation (5) that were not positive definite were fixed following an earlier work[47].

Testing for impacts of shorter winters on spring phenological delays. We examined whether the magnitude of a phenological delay could be positively predicted by an increase in winter temperatures (defined as the relationship between year and average temperature during the year's three coolest consecutive months), controlling for latitude (glm function, stats package). We tested this using the full dataset and a subset containing only time series with delayed phenology (positive relationships between phenology and year). We also tested whether winter warming correlated with spring warming (change in average temperature in three months following 'winter' over time), also controlling for latitude.

Funnel plot statistics. To evaluate our funnel plot (Fig. 1b) for asymmetry in effect sizes (slopes of phenology versus year), we conducted an Egger's regression test for funnel plot asymmetry (*regtest* function, *metafor* package). To test whether the variance in effect sizes decreased with increasing sample size, we conducted a Fligner–Killeen test of homogeneity of variances (*fligner.test* function, *stats* package).

Non-independence due to shared evolutionary history among taxa. To account for the correlational structures among taxa due to their shared evolutionary history[23], we treated the phylogenetic correlations (**P**) derived from a composite phylogenetic tree of all taxa in our study (see equation (1)) as an unstructured random-effect in our trivariate meta-regressions. These phylogenetic correlations in **P** were extracted from an ultrametric tree using the *vcv* function of the *ape* package in R[48], and explicitly assume trait evolution via Brownian motion[49]. Our composite phylogeny of all 475 species used the topology and internode divergence times from published sources when available. The deep divergence times among phyla were based on ref. [50]. Among vertebrates, the topology and estimated divergence times among fish were compiled from ref. [51], mammals from ref. [52], and amphibians from refs [53,54]. The topology and divergence times among birds were derived from a random sample of the Bayesian tree pool provided by the online avian phylogeny generating tool[55]. Among invertebrates, the topology and divergence times among hexapods, calanoids and branchiopods were based two previous studied[56,57]. The topology and divergence times among insect orders were compiled using an earlier work[58]. However, within insect orders topologies were only available for moths and butterflies[57,59,60], and dragonflies and damselflies[61]. Because the divergence times within Lepidoptera and Odonata were unavailable, we arbitrarily scaled branch-lengths distances using a published method[49] while assuming ρ to the power of 1.0 to create divergence times fitting a Brownian motion model of evolution.

Code availability. The code used to generate trivariate model results is available as Supplementary Code.

Data availability. The data that support the findings of this study are available from the corresponding author upon request.

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