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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 ($\bar{\beta} = -0.318$ (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

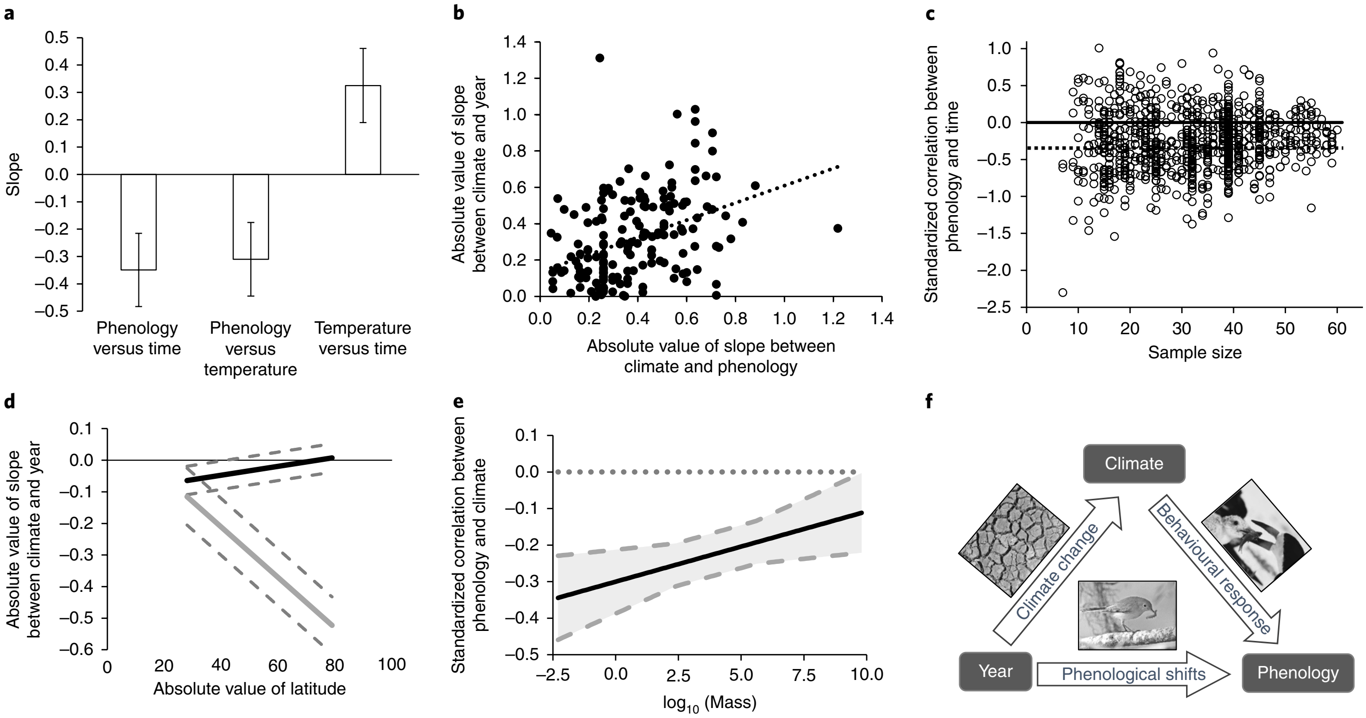

Fig. 1 | Improving how we understand advancements in phenology due to climate change. a, Across 1,011 time series, phenology occurred earlier through time as temperature increased and the increases in temperature were negatively correlated with phenology (see Supplementary Fig. 3 for precipitation). 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

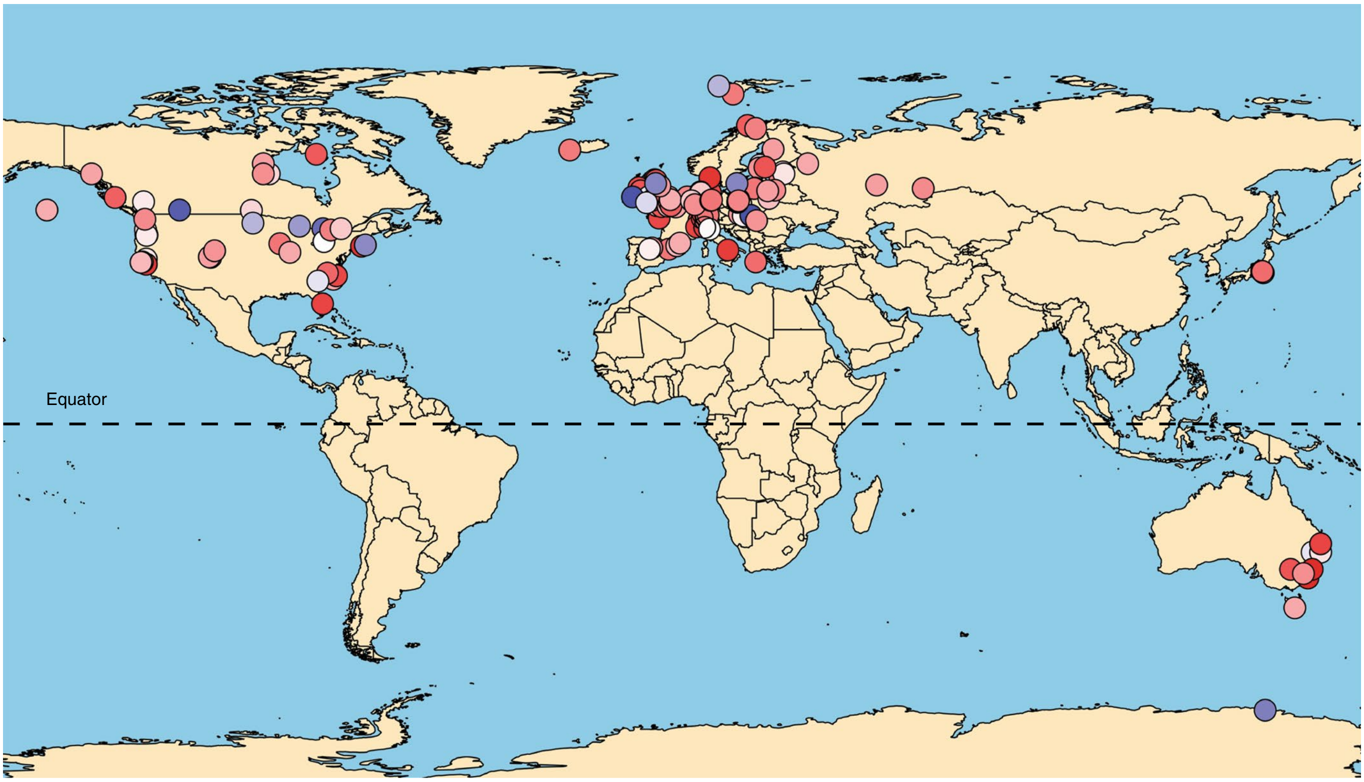

Fig. 2 | The uneven global distribution of published studies exploring the phenology of animals. There are hundreds of published phenological time series from North America and Europe, but much less is known about phenology on the other five continents with particularly large gaps in the tropics and 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).

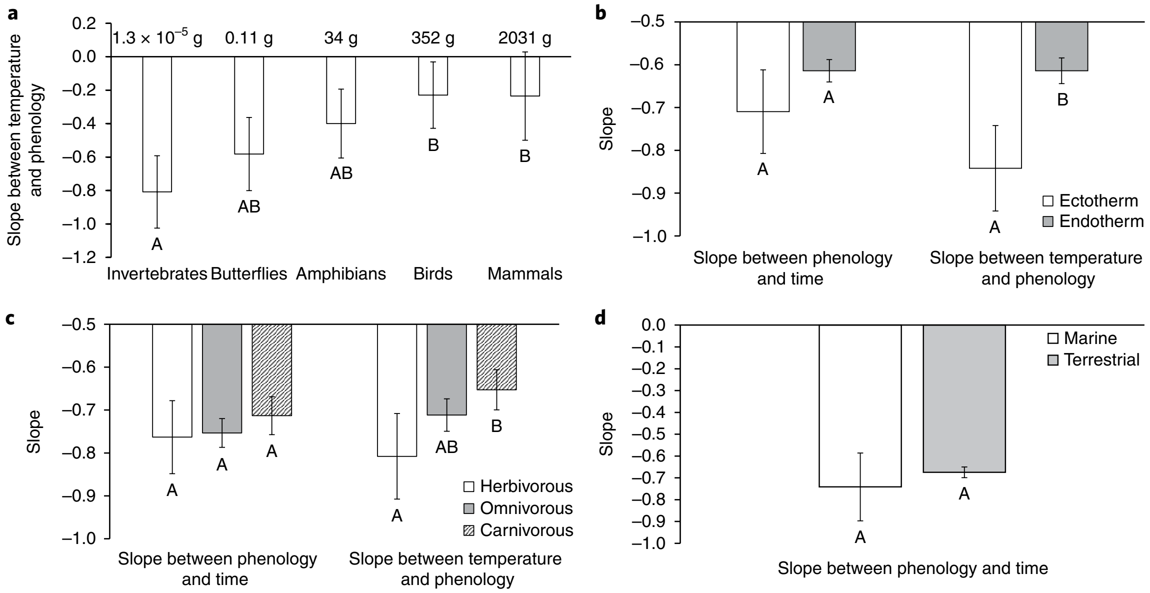

Fig. 3 | The ability of phenology to track temperature varies among taxonomic classes of animals, ecto- or endothermy, and trophic level. a–b, In models including body size and ecto- or endothermy as covariates, smaller taxa (**a**) and ectotherms (**b**) tracked temperature closer than larger animals 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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References

1. Thackeray, S. J. et al. Phenological sensitivity to climate across taxa and trophic levels. *Nature* **535**, 241–245 (2016).
2. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003).
3. Root, T. L. et al. Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60 (2003).
4. Walther, G. R. et al. Ecological responses to recent climate change. *Nature* **416**, 389–395 (2002).
5. Ge, Q. S., Wang, H. J., Rutishauser, T. & Dai, J. H. Phenological response to climate change in China: a meta-analysis. *Glob. Chang. Biol.* **21**, 265–274 (2015).
6. While, G. M. & Uller, T. Quo vadis amphibia? Global warming and breeding phenology in frogs, toads and salamanders. *Ecography* **37**, 921–929 (2014).
7. Brown, C. J. et al. Ecological and methodological drivers of species' distribution and phenology responses to climate change. *Glob. Chang. Biol.* **22**, 1548–1560 (2016).
8. Rosenzweig, C. et al. Attributing physical and biological impacts to anthropogenic climate change. *Nature* **453**, 353–357 (2008).
9. Menzel, A. et al. European phenological response to climate change matches the warming pattern. *Glob. Chang. Biol.* **12**, 1969–1976 (2006).
10. Barbraud, C. & Weimerskirch, H. Antarctic birds breed later in response to climate change. *Proc. Natl Acad. Sci. USA* **103**, 6248–6251 (2006).
11. Both, C. et al. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proc. R. Soc. B* **277**, 1259–1266 (2010).
12. Hegland, S. J., Nielsen, A., Lazaro, A., Bjerknes, A. L. & Totland, O. How does climate warming affect plant-pollinator interactions? *Ecol. Lett.* **12**, 184–195 (2009).
13. Lane, J. E., Kruuk, L. E. B., Charmantier, A., Murie, J. O. & Dobson, F. S. Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature* **489**, 554–557 (2012).
14. Visser, M. E. & Holleman, L. J. M. Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc. R. Soc. B* **268**, 289–294 (2001).
15. McKinney, A. M. et al. Asynchronous changes in phenology of migrating broad-tailed hummingbirds and their early-season nectar resources. *Ecology* **93**, 1987–1993 (2012).
16. Mas-Coma, S., Valero, M. A. & Bargues, M. D. Climate change effects on trematodiases, with emphasis on zoonotic fascioliasis and schistosomiasis. *Vet. Parasitol.* **163**, 264–280 (2009).
17. Yu, H. Y., Luedeling, E. & Xu, J. C. Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proc. Natl Acad. Sci. USA* **107**, 22151–22156 (2010).
18. Wolkovich, E. M., Cook, B. I. & Davies, T. J. Progress towards an interdisciplinary science of plant phenology: Building predictions across space, time and species diversity. *New Phytol.* **201**, 1156–1162 (2014).
19. Lajeunesse, M. J. On the meta-analysis of response ratios for studies with correlated and multi-group designs. *Ecology* **92**, 2049–2055 (2011).
20. van Houwelingen, H. C., Arends, L. R. & Stijnen, T. Advanced methods in meta-analysis: multivariate approach and meta-regression. *Stat. Med.* **21**, 589–624 (2002).
21. Inouye, D. W., Barr, B., Armitage, K. B. & Inouye, B. D. Climate change is affecting altitudinal migrants and hibernating species. *Proc. Natl Acad. Sci. USA* **97**, 1630–1633 (2000).
22. Lawrimore, J. H. et al. An overview of the global historical climatology network monthly mean temperature data set, version 3. *J. Geophys. Res. Atmos.* **116**, D19121 (2011).
23. Lajeunesse, M. J. Meta-analysis and the comparative phylogenetic method. *Am. Nat.* **174**, 369–381 (2009).
24. Field, C. B. & Van Aalst, M. *Climate Change 2014: Impacts, Adaptation, and Vulnerability* Section 1 (eds Field, C. B. et al.) (IPCC, Cambridge Univ. Press, 2014).
25. Paternoster, R., Brame, R., Mazerolle, P. & Piquero, A. Using the correct statistical test for the equality of regression coefficients. *Criminology* **36**, 859–866 (1998).
26. Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M. & Charnov, E. L. Effects of size and temperature on metabolic rate. *Science* **293**, 2248–2251 (2001).
27. Ovaskainen, O. et al. Community-level phenological response to climate change. *Proc. Natl Acad. Sci. USA* **110**, 13434–13439 (2013).
28. Lehikoinen, E., Sparks, T. H. & Zalakevicius, M. Arrival and departure dates. *Adv. Ecol. Res.* **35**, 1–31 (2004).
29. Gordo, O. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Clim. Res.* **35**, 37–58 (2007).

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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:

$$\mathbf{z} = \mathbf{MW}\boldsymbol{\beta} + \boldsymbol{\varepsilon} + \mathbf{Mu} + \sigma^2_{\mathbf{P}}\mathbf{PJ}, \qquad (1)$$

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× $(p+1)$ 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:

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

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 **ε** matrix used as weights for meta-analysis (as done in a previous study[19]). This **ε** 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):

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

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:

$$\begin{aligned}&\mathrm{cov}(Z_{(t,p)},\ Z_{(t,c)})\\&=\frac{\rho_{pc}(1-\rho_{t,p}^2-\rho_{t,c}^2+0.5\times\rho_{t,p}\times\rho_{t,c}\times\rho_{p,c})-0.5(\rho_{t,p}\times\rho_{t,c})(1-\rho_{t,p}^2+\rho_{t,c}^2)}{(n-3)(1-\rho_{t,p}^2(1-\rho_{t,c}^2))}\end{aligned} \tag{4}$$

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:

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

The matrices for each ith study were then stacked diagonally into a single matrix for meta-analysis (**ε**). 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.

References

30. IPCC *Climate Change 2014: Synthesis Report* (eds Core Writing Team, Pachauri, R. K. & Meyer L. A.) (Cambridge Univ. Press, 2015).
31. Viechtbauer, W. Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.* **36**, 1–48 (2010).
32. Dunning, J. B. Jr *CRC Handbook of Avian Body Masses* (CRC, Boca Raton, Florida, 1992).
33. Dell, A. I., Pawar, S. & Savage, V. M. Systematic variation in the temperature dependence of physiological and ecological traits. *Proc. Natl Acad. Sci. USA* **108**, 10591–10596 (2011).
34. Garcia-Barros, E. Body size, egg size, and their interspecific relationships with ecological and life history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea). *Biol. J. Linn. Soc.* **70**, 251–284 (2000).
35. Karlsson, B. Resource allocation and mating systems in butterflies. *Evolution* **49**, 955–961 (1995).
36. Trochet, A. et al. A database of life-history traits of European amphibians. *Biodivers. Data J.* **2**, e4123 (2014).
37. Brose, U. Body sizes of consumers and their resources: Ecological archives E086-135. *Ecology* **86**, 2545–2545 (2005).
38. Jones, K. E. et al. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. *Ecology* **90**, 2648–2648 (2009).
39. Myers, P. et al. *The Animal Diversity Web* (2016); http://animaldiversity.org
40. Williams, R. N. & MacGowan, B. J. in *Proc. Indiana Acad. Sci.* (eds Hay, O. P. et al.) 147–150 (1891).
41. Chown, S. L. et al. Scaling of insect metabolic rate is inconsistent with the nutrient supply network model. *Funct. Ecol.* **21**, 282–290 (2007).
42. Hódar, J. The use of regression equations for the estimation of prey length and biomass in diet studies of insectivore vertebrates. *Miscell. Zool.* **20**, 1–10 (1997).
43. Wickham, H. *ggplot2: Elegant Graphics for Data Analysis* (Springer, New York, 2009).
44. Viechtbauer, W. Conducting meta-analyses in with the metafor package. *J. Statistical Softw.* **36**, 3 (2010).
45. Olkin, I. & Finn, J. D. Correlations redux. *Psychol. Bull.* **118**, 155–164 (1995).
46. Becker, B. J. in *Handbook of Applied Multivariate Statistics and Mathematical Modeling* (eds Tinsley, H. & Brown, S.) 499–526 (Academic, Cambridge, MA, 2000).
47. Higham, N. J. Computing the nearest correlation matrix—A problem from finance. *IMA J. Numer. Anal.* **22**, 329–343 (2002).
48. Paradis, E., Claude, J. & Strimmer, K. APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290 (2004).
49. Grafen, A. The phylogenetic regression. *Phil. Trans. R. Soc. B* **326**, 119–157 (1989).
50. Hedges, S. B., Dudley, J. & Kumar, S. TimeTree: a public knowledge-base of divergence times among organisms. *Bioinformatics* **22**, 2971–2972 (2006).
51. Betancur-R, R. et al. The tree of life and a new classification of bony fishes. *PLOS Current. Tree Life* https://doi.org/10.1371/currents.tol.53ba26640df0ccaee75bb165c8c26288 (2013).
52. Meredith, R. W. et al. Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* **334**, 521–524 (2011).
53. Shaffer, H. B. & McKnight, M. L. The polytypic species revisited: Genetic differentiation and molecular phylogenetics of the tiger salamander *Ambystoma tigrinum* (Amphibia: Caudata) complex. *Evolution* **50**, 417–433 (1996).

54. Moriarty, E. C. & Cannatella, D. C. Phylogenetic relationships of the North American chorus frogs (*Pseudacris*: Hylidae). *Mol. Phylogenet Evol.* **30**, 409–420 (2004).
55. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444–448 (2012).
56. Podar, M., Haddock, S. H. D., Sogin, M. L. & Harbison, G. R. A molecular phylogenetic framework for the phylum Ctenophora using 18S rRNA genes. *Mol. Phylogenet Evol.* **21**, 218–230 (2001).
57. Regier, J. C. et al. A large-scale, higher-level, molecular phylogenetic study of the insect order Lepidoptera (moths and butterflies). *PLoS ONE* **8**, e58568 (2013).
58. Trautwein, M. D., Wiegmann, B. M., Beutel, R., Kjer, K. M. & Yeates, D. K. Advances in insect phylogeny at the dawn of the postgenomic era. *Annu. Rev. Entomol.* **57**, 449–44 (2012).
59. Wahlberg, N. et al. Synergistic effects of combining morphological and molecular data in resolving the phylogeny of butterflies and skippers. *Proc. R. Soc. B* **272**, 1577–1586 (2005).
60. Freitas, A. V. L. & Brown, K. S. Phylogeny of the Nymphalidae (Lepidoptera). *Syst. Biol.* **53**, 363–383 (2004).
61. Dumont, H. J., Vierstraete, A. & Vanfleteren, J. R. A molecular phylogeny of the Odonata (Insecta). *Syst. Entomol.* **35**, 6–18 (2010).

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SUPPLEMENTARY INFORMATION

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A global synthesis of animal phenological responses to climate change

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Title: A global synthesis of animal phenological responses to climate change

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Supplementary Information Guide:

Supplementary Discussion

Supplementary Figures S1-S6

Supplementary Tables S1-S8

Supplementary Code

Supplementary References

PRISMA Checklist

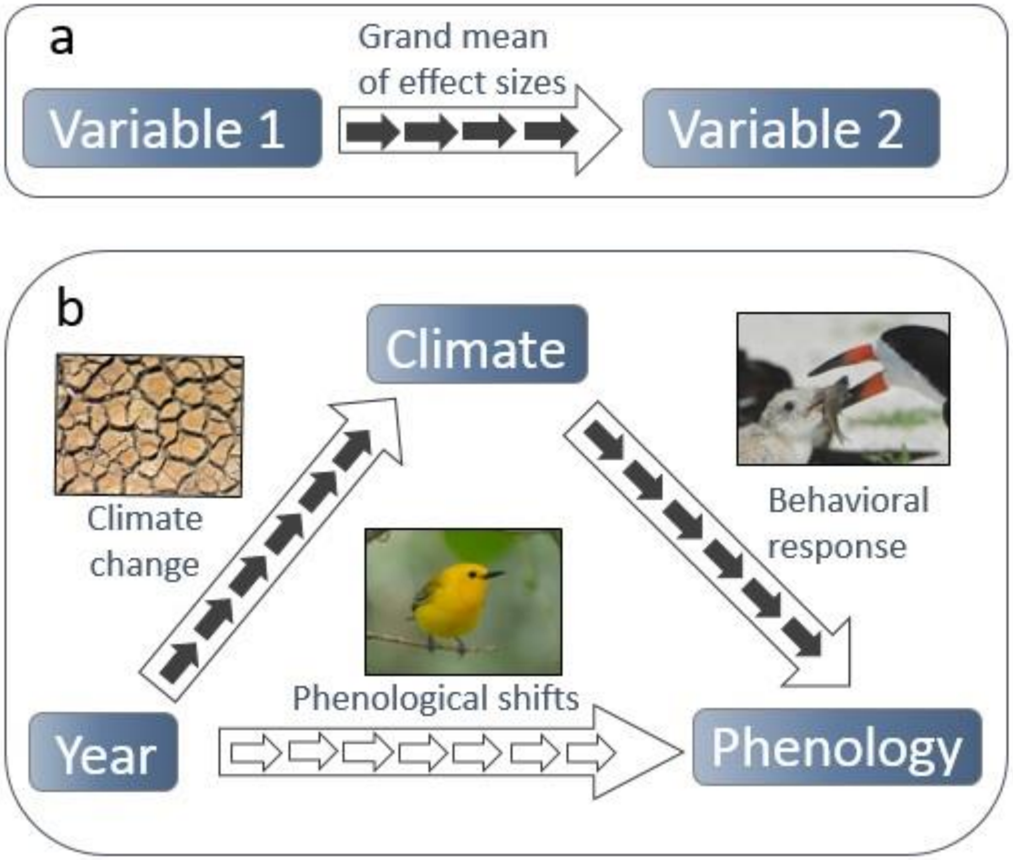
Supplementary Discussion

Use of annual climate data in models. For each phenological time series, we originally extracted both mean annual climate data and mean climate data for the month prior to the average phenological date in the time series (seasonal data). We chose to use annual, rather than seasonal, climate data because we did not want to bias the models with climate from the specific month that the phenology of a given species was measured. For example, insect phenology might be routinely measured later in the year than avian phenology because of different methodological approaches by different researchers or different measured phenological activities. In this scenario, climate data from cooler seasons may be disproportionately represented in conjunction with avian time series and imply that they are responding to different conditions than insects. Further, we were comfortable using annual climate data in our models because it correlates strongly with spring data ($R^2=0.93$, $p<0.00001$ across our time series; Extended Data Fig. 6). Finally, our effect sizes are based on inter-annual trends in phenology—finer scale monthly phenological data are not consistently available across species and thus would drastically reduce our sample sizes.

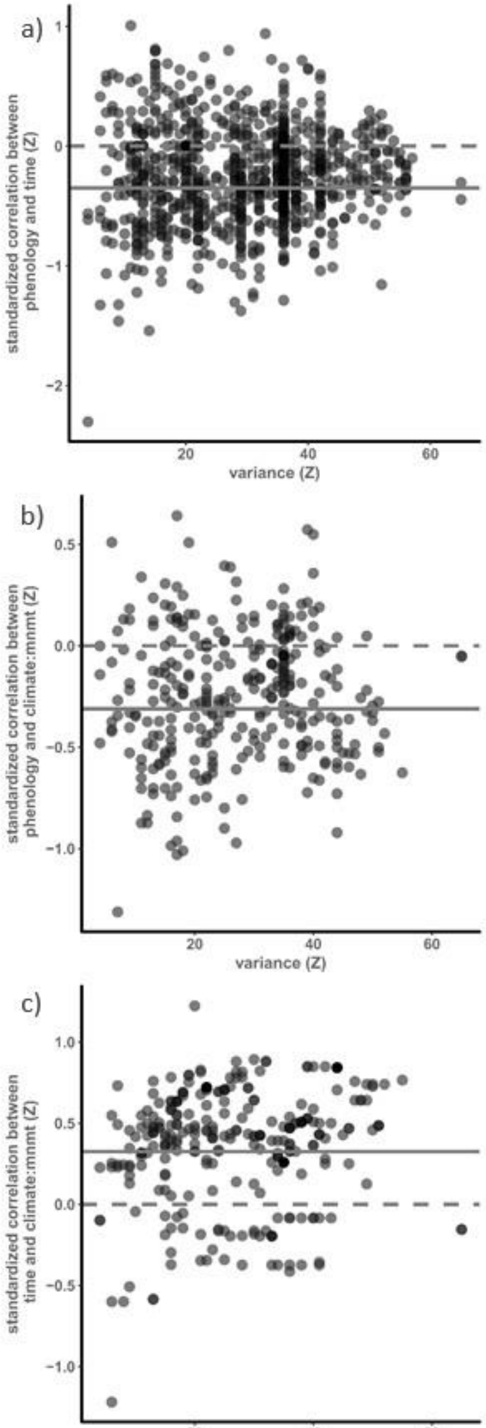
Future analyses should also explore effects of intra-annual trends. However, when approaching analyses at this finer scale, it requires a detailed understanding of how short-term variability influences long-term variability—however, identifying the mechanisms for these fine-scale sources of variability across many phenological datasets can be challenging. Presently, by examining inter-annual trends, we were able to focus on broad-scale sources of variability, such as climate change and geographic variability in effects of climate change.

Use of animal phenological data. The primary question that initially motivated the meta-analysis concerned the nature of the relationship between phenological shifts and body size, given that there is evidence that small organisms acclimate to new conditions faster than larger organisms[1,2]. However, body size questions are challenging to address using plants because below-ground mass is often difficult or impossible to quantify and some plants grow clonally, making the definition of an individual unclear. Other questions, such as the influence of thermoregulation on phenology, also could not be addressed using plants because none are endothermic. Thus, we initially created our dataset with animal records of phenological shifts only.

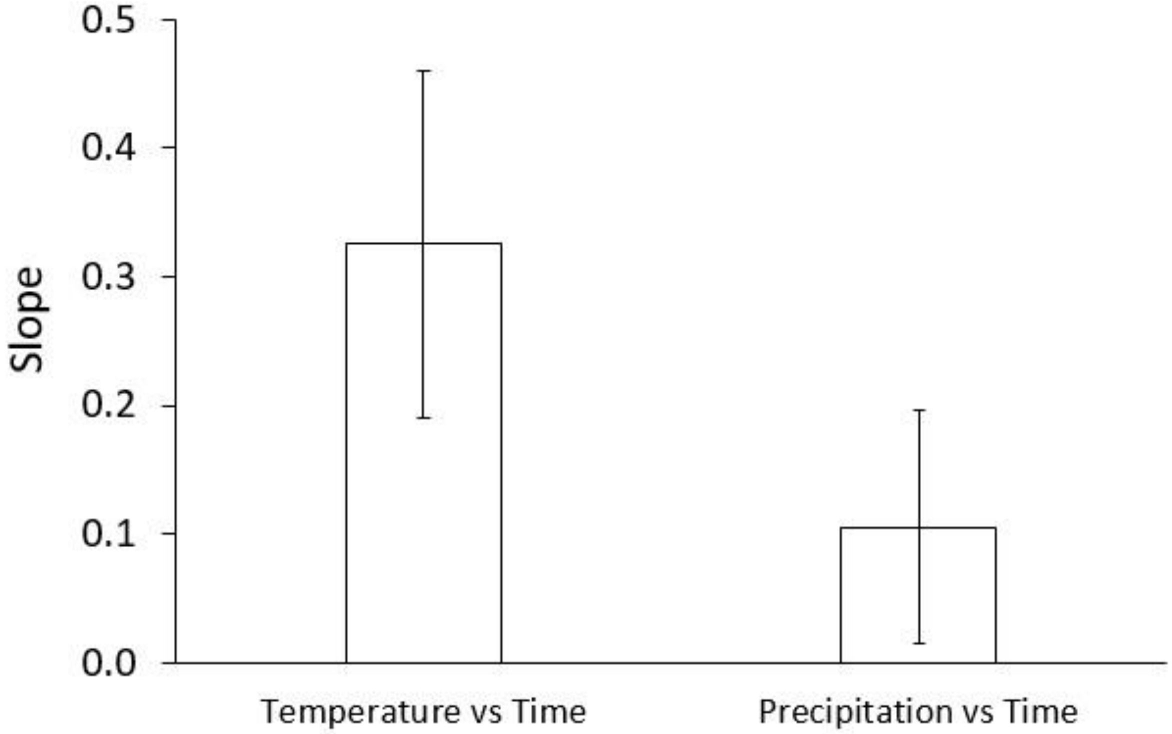
Supplementary Figures



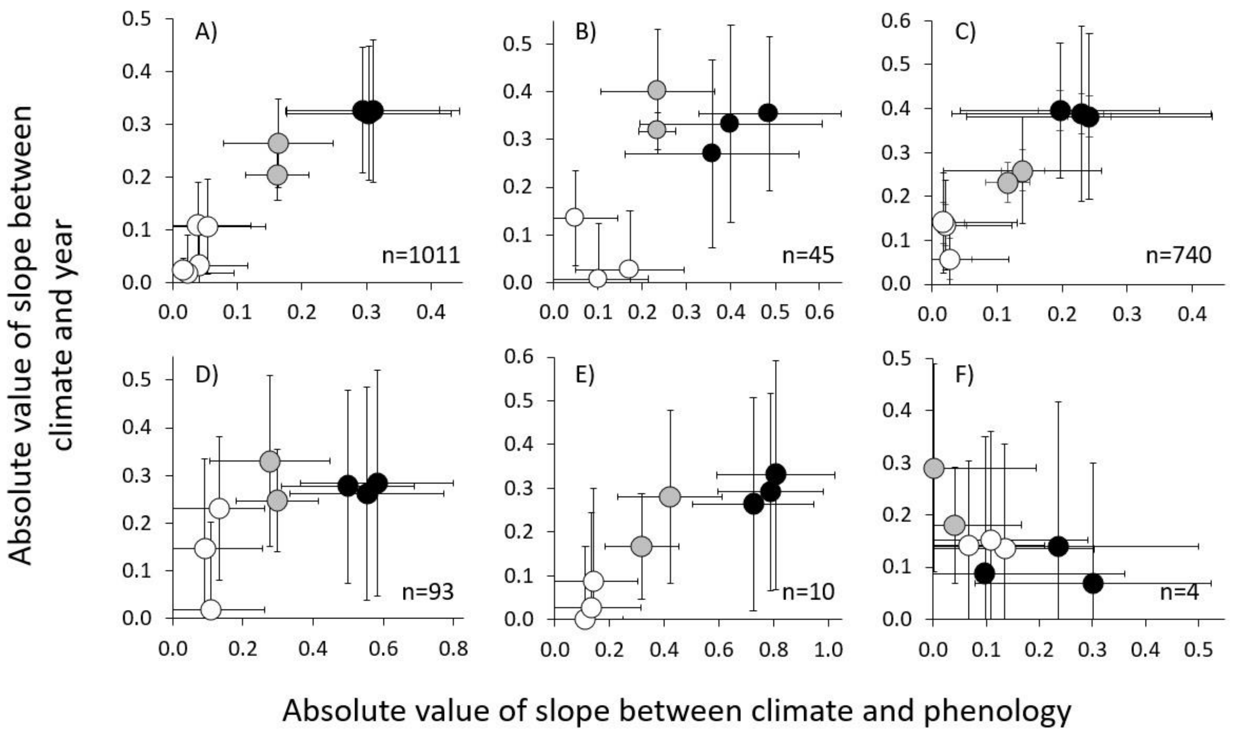
Supplementary Figure 1. Structure of trivariate meta-analysis examining the relationship between phenology, climate, and year. Conceptual schema contrasting the structure of (a) a typical (univariate) meta-analysis summarizing the relationship (correlation) between two variables using the grand mean of one effect size (large arrows) composed of many effect sizes reported in the literature (small arrows) and (b) the trivariate meta-analysis used in this study which summarizes the relationship among three variables using three effect sizes (standardized correlations). Filled arrows represent direct effects (i.e., the effect of climate on phenology) and open arrows represent indirect effects (i.e., the effect of year on phenology). This trivariate meta-analysis allowed us to jointly analyze the three effect sizes quantifying the pairwise relationships between phenology, time, and climate. Further, it enabled us to account for the correlations within the three non-independent effect sizes (because of common sampling variability), while also explicitly accounting for any existing correlations among them (via a multivariate random-effects model). See Methods for further details.


a)
standardized correlation between phenology and time (Z)
1
0
-1
-2
20
40
60
variance (Z)
b)
standardized correlation between phenology and climate:mnmt (Z)
0.5
0.0
-0.5
-1.0
20
40
60
variance (Z)
c)
standardized correlation between time and climate:mnmt (Z)
1.0
0.5
0.0
-0.5
-1.0

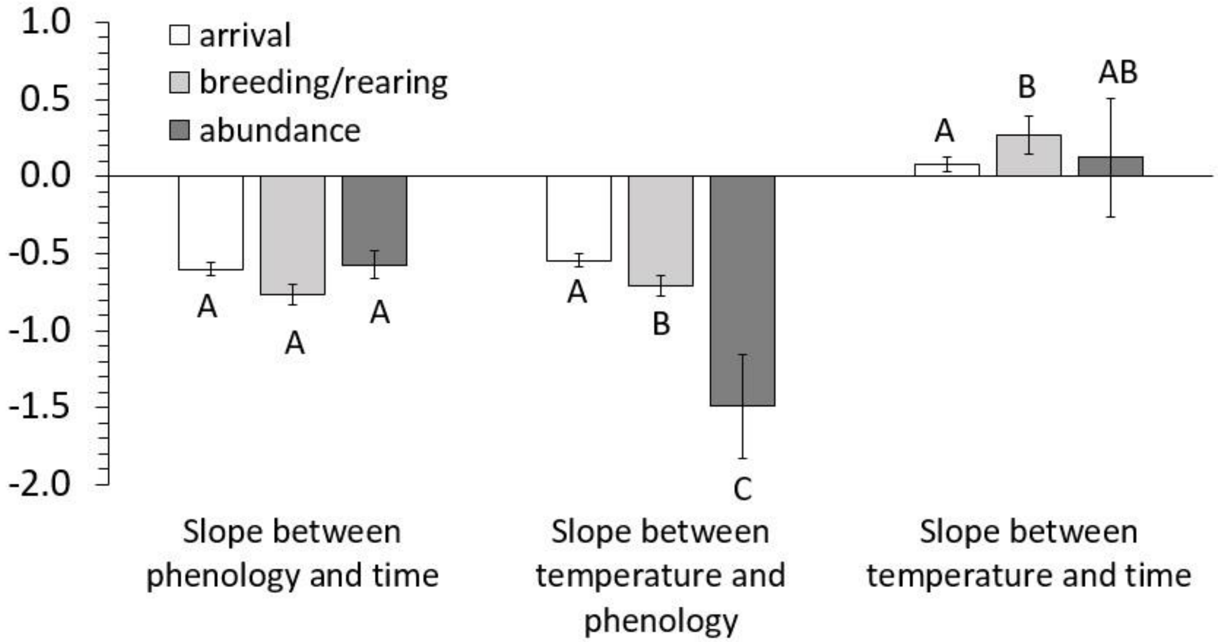
Supplementary Figure 2. Funnel plots of the three effect size datasets used in the trivariate meta-analysis. Depicted are variance and z-scores of the correlation coefficients describing the relationships between (a) phenology and year, (b) phenology and annual mean temperature, and (c) year and annual mean temperature. Dashed lines are the null effect (0.0) and solid lines are the grand mean effect sizes from a trivariate meta-analysis corrected for phylogenetic history.



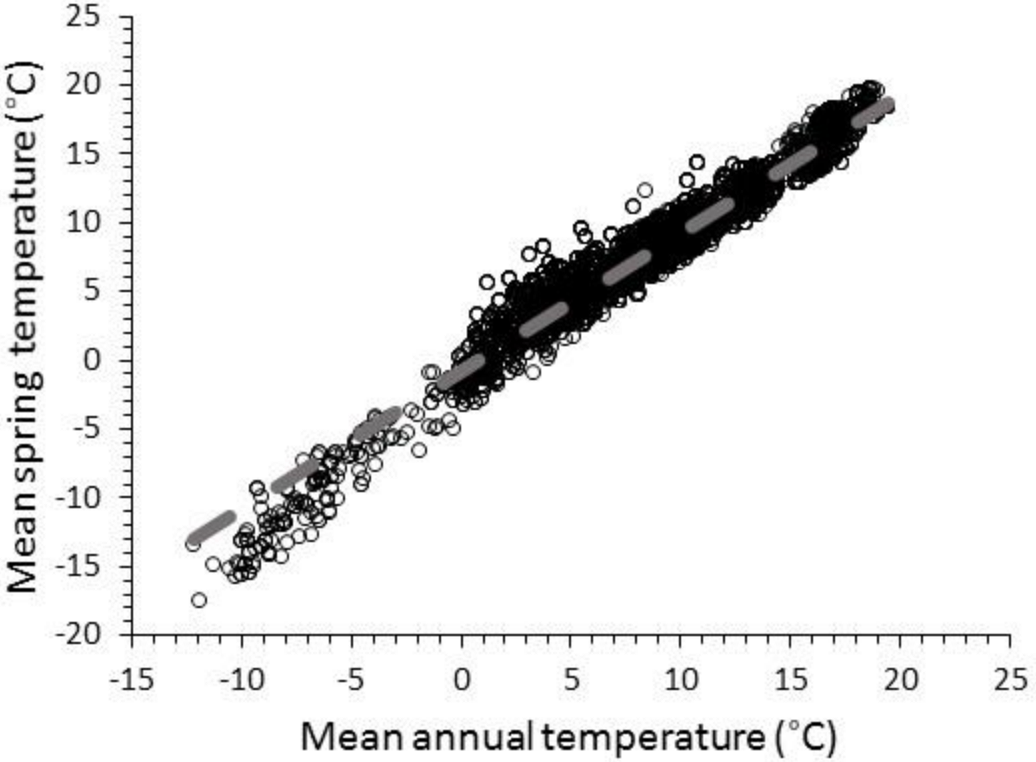
Supplementary Figure 3. Shifts in climate variables over time. In the locations of the time series in this study, mean temperature and total precipitation both increased over time, but temperature increased more than precipitation. Because recent major shifts in temperature have occurred alongside phenological advancements, the two phenomena have been closely associated with each other. Error bars represent standard errors.



Supplementary Figure 4. Generality of climatic conditions influencing changes in phenology. Absolute values of grand means of slopes between phenology and climate (x-axis) and between climate and time (y-axis) for the ten climatic variables used in the analysis (points). Variables that changed over time and were predictive of animal phenology appear in the upper right-hand corner, while variables that did not change much over time and did not match animal phenology well appear in the lower-left corner. Error bars represent standard errors for the regression slope parameters. We plotted absolute values to highlight the magnitude (rather than the direction) of the effect, because different climate variables affect phenology in different directions. We found a strong relationship between temperature variables (black circles) and phenology for (a) all taxa, (b) amphibians, (c) birds, and (d) butterflies. Relationships between temperature and phenology for (e) non-insect invertebrates and (f) mammals are presented as well. Meanwhile, relationships between phenology and precipitation variables (white circles) and precipitation and time were generally weaker than relationships between phenology and temperature variables and temperature and time, respectively. Of all the taxonomic groups, only amphibians had a significant relationship between precipitation (white circles) and phenology, but precipitation was still a weaker predictor of amphibian phenology than temperature. Gray circles represent variables derived from temperature (see methods for a list of variables in each category).



Supplementary Figure 5. Different types of phenological events respond differently to climate change. We categorized phenological events as associated with either “arrival” (migration), “breeding/rearing” (calling, nesting, laying, hatching, weaning), or “abundance” (time of peak abundance). Controlling for body size, abundance phenology tracked temperature change more closely than arrival or breeding/rearing endpoints. Breeding/rearing phenology was more closely tied to temperature than arrival phenology, possibly because arrival phenology is dependent on the climatic conditions in the region from where the species was overwintering, which were not included in the analyses. Error bars represent standard errors for the slope parameters.



Supplementary Figure 6. Relationship between spring and annual climate data. Mean annual temperature (used in our analyses) correlates strongly with mean spring temperature (mean of three months following three consecutive coldest months) across all of the time points in our dataset (R^2=0.93, p<0.00001). We used annual data in our analyses for several reasons outlined in the Supplementary Discussion.

Supplementary Tables

Table S1. List of studies and time-series collected for meta-analysis. Papers were included in the meta-analysis if they satisfied the basic requirements detailed in Methods and provided raw time-series data on phenological date. Papers were included in the trivariate meta-analysis (including climate in models) if they were at specific sites with locally corresponding terrestrial NOAA climate data (papers not included are denoted with *). N indicates the number of time-series in the paper. The shift column indicates the median days-per-decade shift among papers in the study.

Paper	Event	N	Class	Country	Time Span	Shift
Abraham and Sydeman 2004 [3]	breeding	1	Aves	USA	1973-2001	5.17
Adamik and Pietruszkova 2008* [4]	arrival	1	Aves	Czech Republic	1964-2004	-2.02
Adamik and Pietruszkova 2008* [4]	arrival	1	Aves	Czech Republic	1964-2004	-2.64
Ahas et al 1999 [5]	arrival	1	Aves	Estonia	1952-1996	-2.89
Ahola et al 2004 [6]	arrival	1	Aves	Finland	1970-2002	-2.66
Ahola et al 2004 [6]	arrival	1	Aves	Finland	1970-2002	-1.16
Ahola et al 2004 [6]	breeding	1	Aves	Finland	1970-2002	0.35
Anthes 2004 [7]	arrival	1	Aves	Germany	1969-2002	-2.95
Askeyev et al 2007 [8]	arrival	4	Aves	Russia	1957-2004	-0.46
Askeyev et al 2009a [9]	arrival	1	Aves	Russia	1950-2008	-1.49
Askeyev et al 2009b [10]	arrival	4	Aves	Russia	1957-2008	-0.94
Barbraud and Weimerskirch 2006 [11]	arrival	9	Aves	Antarctica	1951-2005	2.48
Barbraud and Weimerskirch	breeding	5	Aves	Antarctica	1953-	0.24

2006 [11]					2001	
Barett 2002 [12]	arrival	2	Aves	Norway	1978-2000	-0.35
Bauer et al 2010 [13]	breeding	2	Aves	Czech Republic	1961-2007	-1.89
Bauer et al 2010 [13]	arrival	1	Insecta	Czech Republic	1961-2007	-1.61
Beaumont et al 2006 [14]	arrival	16	Aves	Australia	1960-2004	-7.25
Beebee 1995a [15]	arrival	6	Amphibia	England	1978-1994	-1.78
Beebee 1995b [16]	arrival	1	Amphibia	England	1978-1994	-2.02
Bertram et al 2001 [17]	breeding	4	Aves	Canada	1975-1999	-11.44
Blaustein et al 2001 [18]	arrival	7	Amphibia	North America	1967-1999	-0.58
Both and Visser 2001 [19]	arrival	1	Aves	Netherlands	1980-2000	2.8
Both and Visser 2001 [19]	breeding	1	Aves	Netherlands	1980-2000	-4.03
Both et al 2005a [20]	breeding	1	Aves	Netherlands	1950-2003	-1.83
Both et al 2009 [21]	breeding	5	Aves	Netherlands	1985-2005	-3.15
Both et al 2009 [21]	abundance	1	Insecta	Netherlands	1985-2005	-7.60
Bradley et al 1999 [22]	arrival	4	Aves	USA	1977-1998	-0.98
Carroll et al 2009* [23]	arrival	1	Amphibia	UK	1998-2007	4.79
Chadwick et al 2006 [24]	arrival	2	Amphibia	England	1981-2005	-6.43
Chadwick et al 2006 [24]	arrival	2	Amphibia	England	1981-2005	-8.47
Corn and Muths 2002 [25]	arrival	1	Amphibia	USA	1986-	-3.35

					2001	
Costello et al 2006* [26]	arrival	1	Maxillopoda	USA	1951-2003	2.85
Costello et al 2006* [26]	arrival	1	Tentaculata	USA	1950-2003	-14.4
Cotton 2003 [27]	arrival	1	Aves	England	1972-2000	-6.71
Cresswell and McCleery 2003 [28]	breeding	1	Aves	England	1960-1999	-2.4
Cresswell and McCleery 2003 [28]	breeding	1	Aves	England	1960-1999	-1.91
Crick and Sparks 1999* [29]	breeding	1	Aves	UK	1950-1995	0.61
Crick et al 1997* [30]	arrival	3	Aves	UK	1971-1995	-6.67
Croxton et al 2006 [31]	arrival	10	Aves	England	1959-2005	-2.79
D'Alba et al 2010 [32]	breeding	1	Aves	Iceland	1977-2006	-2.86
Dell et al 2005 [33]	arrival	1	Insecta	Switzerland	1982-2002	-8.27
Dufour et al 2010* [34]	arrival	2	Actinopterygii	France/Spain	1967-2005	-5.82
Dufour et al 2010* [34]	arrival	2	Actinopterygii	France/Spain	1967-2005	-3.32
Dunn and Winkler 1999* [35]	arrival	1	Aves	USA	1959-1991	-2.86
Dyrcz and Halupka 2009 [36]	breeding	1	Aves	Poland	1970-2007	-3.08
Elliot 1996 [37]	arrival	1	Insecta	England	1966-1995	-1.90
Elliot 1996 [37]	arrival	1	Insecta	England	1966-1995	-1.50
Forister and Shapiro 2003 [38]	arrival	1	Insecta	USA	1972-2002	-1.18
Gaston et al 2009 [39]	breeding	1	Aves	Canada	1990-	-2.71

					2007	
Gillet and Quentin 2006* [40]	arrival	1	Actinopterygii	France	1983-2001	-10.4
Gordo and Sanz 2005 [41]	arrival	5	Aves	Spain	1950-2004	-3.16
Gordo and Sanz 2006* [42]	arrival	5	Aves	Spain	1950-2004	-0.8
Gordo and Sanz 2006* [42]	arrival	2	Insecta	Spain	1952-2004	0.57
Gordo et al 2005 [43]	arrival	6	Aves	Spain	1952-2003	1.49
Halupka et al 2008 [44]	breeding	1	Aves	Poland	1970-2006	-4.23
Harrington et al 2007* [45]	arrival	1	Insecta	Europe	1965-2000	-7.19
Huppop and Huppop 2003 [46]	arrival	6	Aves	Germany	1960-2000	-2.19
Hussell 2003 [47]	breeding	3	Aves	Canada	1969-2001	-1.66
Inouye et al 2000 [48]	arrival	1	Aves	USA	1974-1999	-4.26
Inouye et al 2000 [48]	arrival	1	Mammalia	USA	1976-1999	-10.2
Jarvinen 1989 [49]	breeding	1	Aves	Finland	1966-1987	-3.10
Jenkins and Watson 2000 [50]	arrival	2	Aves	Scotland	1974-1999	-10.12
Kanuscak et al 2004 [51]	arrival	1	Aves	Slovakia	1963-2003	-0.19
Kennedy and Crozier 2010* [52]	abundance	1	Actinopterygii	Ireland	1978-2008	-4.72
Kobori et al 2012 [53]	arrival	6	Aves	Japan	1986-2007	2.54
Koppman-Rumpf et al 2003 [54]	arrival	1	Mammalia	Germany	1972-1999	-14.3
Kusano and Inoue 2008 [55]	arrival	4	Amphibia	Japan	1976-	-2.44

					2007	
Laaksonen et al 2006 [56]	breeding	1	Aves	Finland	1950-2003	0.35
Lane et al 2012 [57]	arrival	1	Mammalia	Canada	1992-2011	4.78
Lappalainen et al 2008 [58]	arrival	2	Aves	Finland	1952-2005	-3.65
Lappalainen et al 2008 [58]	arrival	1	Amphibia	Finland	1952-2005	-1.44
Lehikonen et al 2004 [59]	arrival	6	Aves	Finland	1965-2003	-3.32
Ludwichowski 1997 [60]	breeding	1	Aves	Germany	1979-1995	-8.3
MacInnes et al 1990 [61]	breeding	3	Aves	Canada	1959-1986	-3.35
MacInnes et al 1990 [61]	breeding	3	Aves	Canada	1959-1986	-4.07
Mackas et al 1998* [62]	abundance	1	Maxillopoda	Canada	1975-1996	-4.37
Mazaris et al 2008* [63]	breeding	1	Reptilia	Greece	1984-2002	-7.12
McCleery and Perrins 1998 [64]	breeding	1	Aves	England	1950-1997	-1.18
Miller-Rushing et al 2008 [65]	arrival	2	Aves	USA	1970-2002	0.9
Miller-Rushing et al 2008 [65]	arrival	2	Aves	USA	1970-2002	-0.96
Mills 2005 [66]	arrival	4	Aves	Canada	1975-2000	-3.84
Mills 2005 [66]	arrival	2	Aves	Canada	1975-2000	-3.35
Mitrus et al 2005 [67]	arrival	1	Aves	Poland	1973-2002	-2.76
Moe et al 2009 [68]	breeding	2	Aves	Sweden	1963-2008	0.06
Murphy-Klassen et al 2005 [69]	arrival	4	Aves	Canada	1950-	-1.02

					2001	
Nielsen and Moller 2006 [70]	breeding	6	Aves	Denmark	1970-2004	-3.31
Ozgul et al 2010 [71]	breeding	1	Mammalia	USA	1976-2008	-1.88
Peintinger and Schuster 2006 [72]	arrival	8	Aves	Germany	1970-2003	-4.93
Penuelas et al 2002 [73]	arrival	1	Aves	Spain	1952-2000	3.03
Penuelas et al 2002 [73]	arrival	1	Insecta	Spain	1953-2000	-2.42
Phillipart et al 2003* [74]	arrival	1	Bivalvia	Netherlands	1973-2001	-4.39
Ptaszyk et al 2003 [75]	arrival	1	Aves	Poland	1983-2002	-5.49
Ptaszyk et al 2003 [75]	arrival	1	Aves	Poland	1983-2002	-0.89
Reading 1998 [76]	arrival	1	Amphibia	England	1980-1998	-8.12
Reed et al 2009 [77]	breeding	1	Aves	USA	1972-2005	-1.87
Rubolini et al 2007b [78]	arrival	4	Aves	Italy	1982-2006	-1.23
Rubolini et al 2007b [78]	breeding	4	Aves	Italy	1982-2006	-1.94
Sanz et al 2003 [79]	breeding	2	Aves	Spain	1984-2001	-3.15
Schiegg et al 2002 [80]	breeding	2	Aves	USA	1980-1998	-3.16
Schluter et al 2010* [81]	arrival	2	Tentaculata	Germany	1975-2004	-18.3
Schluter et al 2010* [81]	arrival	1	Nuda	Germany	1975-2004	-6.60
Schluter et al 2010* [81]	arrival	1	Maxillopoda	Germany	1975-2004	-7.00
Scott et al 2008 [82]	arrival	9	Amphibia	England	1994-	-9.53

					2005	
Sergio 2003 [83]	breeding	1	Aves	Italy	1994-2002	-11.33
Sims et al 2004* [84]	abundance	1	Actinopterygii	UK	1954-1965	-30.4
Slater 1999 [85]	breeding	1	Aves	Wales	1957-1997	-1.47
Sokolov and Gordienko 2008 [86]	arrival	6	Aves	Russia	1971-2005	0.01
Sokolov and Gordienko 2008 [86]	arrival	3	Aves	Russia	1971-2005	0.62
Sokolov et al 1998 [87]	arrival	34	Aves	Russia	1959-1996	-1.01
Sparks 1999 [88]	arrival	2	Aves	England	1954-1996	-2.8
Sparks and Braslavska 2001 [89]	arrival	1	Aves	Slovakia	1961-2000	2.41
Sparks and Mason 2001 [90]	arrival	2	Aves	England	1950-1998	-1.84
Sparks and Yates 1997 [91]	arrival	1	Insecta	Ireland	1976-1993	-1.52
Sparks et al 2005 [92]	arrival	9	Aves	Europe	1959-2002	-2.73
Sparks et al 2005 [92]	arrival	9	Aves	Europe	1959-2002	-3.51
Sparks et al 2007b [93]	breeding	2	Aves	Europe	1978-2004	-6.89
Sparks et al 2007b [93]	arrival	3	Amphibia	UK	1978-2004	-3.47
Sparks et al 2010 [94]	arrival	1	Insecta	Poland	1985-2009	-13.4
Strode 2003 [95]	arrival	16	Aves	USA	1950-2002	-0.607
Taylor 2008* [96]	arrival	1	Actinopterygii	USA (Alaska)	1972-2005	-2.43
Todd et al 2011 [97]	arrival	10	Amphibia	USA	1979-	1.00

					2008	
Tryjanowski 2001 [98]	arrival	1	Aves	Poland	1983-2000	-3.4
Tryjanowski et al 2003 [99]	arrival	2	Amphibia	Poland	1978-2002	-3.34
Visser et al 1998 [100]	breeding	1	Aves	Netherlands	1973-1995	-1.52
Visser et al 1998 [100]	abundance	1	Insecta	Netherlands	1973-1995	-3.74
Waite and Strickland 2006 [101]	breeding	1	Aves	Canada	1980-2005	-3.23
Wang et al 2002 [102]	breeding	1	Aves	USA	1975-1998	-3.63
Wanless et al 2009 [103]	breeding	13	Aves	UK	1971-2006	0.72
Wanless et al 2009 [103]	arrival	5	Aves	UK	1971-2006	-3.03
Wanless et al 2009 [103]	breeding	2	Aves	UK	1979-2006	-1.57
Weatherhead 2002 [104]	breeding	1	Aves	Canada	1974-2000	-0.78
Weishampel et al 2004* [105]	breeding	1	Reptilia	USA	1989-2003	-6.18
Wesolowski and Maziarz 2009 [106]	arrival	1	Aves	Poland	1976-2005	-1.46
Wesolowski and Maziarz 2009 [106]	breeding	1	Aves	Poland	1976-2005	-2.23
Wiebe and Gerstmar 2010 [107]	breeding	1	Aves	Canada	1998-2009	-0.56
Winder and Schindler et al 2004* [108]	abundance	1	Eurotifera	USA	1962-1995	-6.61
Winder and Schindler et al 2004* [108]	abundance	1	Branchiopoda	USA	1977-2002	7.23
Winkel and Hudde 1996 [109]	breeding	2	Aves	Germany	1970-1995	-2.45
Winkel and Hudde 1997 [110]	breeding	2	Aves	Germany	1970-	-2.61

1995

Table S2. List of studies and time-series collected to calculate days-per-decade shift. Papers were included in our calculation of days-per-decade shift (in addition to the papers in Table S1) if they satisfied the basic requirements detailed in Methods. N indicates the number of time-series in the paper. The shift column indicates the median days-per-decade shift among papers in the study.

Paper	Event	n	Class	Country	Time Span	Shift
Ahas et al 1999 [5]	arrival	1	Aves	Estonia	1952-1996	1.14
Crick and Sparks 1999 [29]	breeding	7	Aves	England	1950-1995	NA
Jenkins and Watson 2000 [50]	arrival	32	Aves	Scotland	1974-1999	NA
Browne and Aebischer 2003 [111]	arrival	6	Aves	England	1963-2000	-0.05
Huppop and Huppop 2003 [46]	arrival	18	Aves	Germany	1960-2000	-1.41
Stervander et al 2005 [112]	arrival	36	Aves	Sweden	1952-2002	-0.34
Mills 2005 [66]	arrival	9	Aves	Canada	1975-2000	-2.38
Mills 2005 [66]	arrival	9	Aves	Canada	1975-2000	-0.21
Murphy-Klassen et al 2005 [69]	arrival	92	Aves	Canada	1950-2001	-0.68
Both et al 2005b [113]	breeding	1	Aves	Netherlands	1960-2003	NA
Lehikonen et al 2006 [114]	arrival	1	Aves	Finland	1979-2004	NA
Lehikonen et al 2006 [114]	arrival	1	Aves	Finland	1979-2004	NA
Zalakevicius et al 2006 [115]	arrival	40	Aves	Lithuania	1971-2004	-2.81
Beaumont et al 2006 [14]	arrival	29	Aves	Australia	1960-2004	-1.2
Jonzen et al 2006 [116]	arrival	9	Aves	Italy	1980-2004	-2.39

Jonzen et al 2006 [116]	arrival	9	Aves	Italy	1980-2004	-2.28
MacMynowski et al 2007 [117]	arrival	45	Aves	USA	1969-2003	-2.22
Zalakevicius et al 2007 [118]	arrival	20	Aves	Lithuania	1966-2000	-4.61
Sokolov and Gordienko 2008 [86]	arrival	7	Aves	Russia	1971-2005	-1.58
Vegvari et al 2010 [119]	arrival	117	Aves	Hungary	1969-2007	-3.42
Neveu 2009 [120]	arrival	1	Amphibia	France	1984-2007	NA
Ahas et al 1999 [5]	arrival	2	Actinopterygii	Estonia	1952-1996	-1.59
Hawkes et al 2007 [121]	breeding	1	Reptilia	USA	1980-2005	NA
Telemeco et al 2009 [122]	breeding	1	Reptilia	Australia	1997-2006	NA
Pollard 1991 [123]	arrival	1	Insecta	UK	1976-1989	NA
Sparks and Yates 1997 [91]	arrival	9	Insecta	Ireland	1976-1993	NA
Roy and Sparks 2000 [124]	abundance	35	Insecta	England	1976-1998	-1.66
Forister and Shapiro 2003 [38]	arrival	23	Insecta	USA	1972-2002	-1.68
Stefanescu et al 2003 [125]	arrival	18	Insecta	Spain	1988-2002	NA
Stefanescu et al 2003 [125]	arrival	18	Insecta	Spain	1988-2002	NA
Hassall et al 2007 [126]	arrival	25	Insecta	England	1960-2004	NA
Doi 2008 [127]	arrival	1	Insecta	Japan	1953-2005	4.69
Lappalainen et al 2008 [58]	arrival	5	Insecta	Finland	1953-2005	-0.83

Diamond et al 2011 [128]	arrival	44	Insecta	England	1976-2008	-3.92
Ellwood et al 2012 [129]	arrival	14	Insecta	Japan	1961-2004	0.74
Brown et al 1999 [130]	breeding	1	Aves	USA	1971-1998	-3.76
Penuelas et al 2002 [73]	arrival	4	Aves	spain	1952-2000	3.31
Tryjanowski et al 2002 [131]	arrival	16	Aves	Poland	1970-1996	-4.18
Sanz 2002 [132]	breeding	12	Aves	Spain	1955-2000	-6.53
Howell and Gardali 2003 [133]	arrival	1	Aves	USA	1980-2000	0.07
Visser et al 2003 [134]	breeding	24	Aves	Europe	1979-2008	-3.31
Cotton 2003 [27]	arrival	19	Aves	England	1971-2000	-2.21
Both et al 2004 [135]	breeding	25	Aves	Europe	1980-2002	-1.64
Chambers 2005 [136]	arrival	5	Aves	Australia	1984-2003	-5.28
Torti and Dunn 2005 [137]	breeding	2	Aves	North America	1951-2000	0.02
Tottrup et al 2006 [138]	arrival	25	Aves	Denmark	1976-1997	-4.17
Tottrup et al 2006 [138]	arrival	25	Aves	Denmark	1976-1997	-1.57
Croxton et al 2006 [31]	arrival	15	Aves	England	1959-2005	-0.92
Peintinger and Schuster 2006 [72]	arrival	95	Aves	Germany	1970-2003	-3.12
Jonzen et al 2006 [116]	arrival	34	Aves	Scandanavia	1980-2004	-1.37
Jonzen et al 2006 [116]	arrival	34	Aves	Scandanavia	1980-2004	-0.71

Hoye et al 2007 [139]	breeding	3	Aves	Greenland	1996-2005	-6.57
Saino et al 2007 [140]	arrival	9	Aves	Italy	1981-2004	-1.81
Sparks et a 2007a [141]	arrival	108	Aves	England	1973-2002	-2.58
Miller-Rushing et al 2008 [65]	arrival	30	Aves	USA	1970-2002	0.11
Miller-Rushing et al 2008 [65]	arrival	30	Aves	USA	1970-2002	-0.77
Lappalainen et al 2008 [58]	arrival	15	Aves	Finland	1952-2005	-0.19
Adamik and Pietruszkova 2008 [4]	arrival	3	Aves	Czech Republic	1964-2005	-4.87
Adamik and Pietruszkova 2008 [4]	arrival	3	Aves	Czech Republic	1964-2005	-2.47
Swanson and Palmer 2009 [142]	arrival	88	Aves	USA	1964-2005	-1.99
van Buskirk et al 2009 [143]	arrival	58	Aves	USA	1961-2006	-0.94
van Buskirk et al 2009 [143]	arrival	58	Aves	USA	1961-2006	-0.69
Foster et al 2010 [144]	arrival	6	Aves	USA	1978-2005	2.21
Schneider et al 2010 [145]	arrival	12	Actinopterygii	USA	1966-2007	-2.14
Schneider et al 2010 [145]	abundance	12	Actinopterygii	USA	1966-2007	-1.45
Moyes et al 2011 [146]	breeding	1	Mammalia	Scotland	1980-2007	-2.6
Hoye et al 2007 [139]	arrival	3	Arachnida	Greenland	1996-2005	-7.77
Hoye et al 2007 [139]	arrival	1	Entognatha	Greenland	1996-2005	3.62
Hoye et al 2007 [139]	arrival	8	Insecta	Greenland	1996-2005	-17.6

Table S3. Results of meta-analysis testing the shift in phenology over time independent of climate. We calculated the slope coefficient between phenology and time (p_t) across all time series. SE indicates standard error. The model was controlled for phylogeny and study.

	Coefficient	SE	z-value	p-value
p_t	-0.3175	0.1258	-2.5228	0.0116

Table S4. Results of models testing the influence of climate variables on phenology across all taxa. We calculated the slope coefficient between different climate variables (mean temperature and total precipitation) and both phenology and time. Correlation coefficients for three effect sizes (p_t = phenology-time, p_c = phenology-climate, t_c = time-climate) are reported. SE indicates standard error. The models were controlled for phylogeny and study.

Temperature	Coefficient	SE	z-value	p-value
p_t	-0.3497	0.1339	-2.6109	0.0090
p_c	-0.3102	0.1347	-2.3037	0.0212
t_c	0.3251	0.1355	2.3994	0.0164

Precipitation	Coefficient	SE	z-value	p-value
p_t	-0.3016	0.0887	-3.4002	0.0007
p_c	-0.0544	0.0898	-0.6056	0.5448
t_c	0.1057	0.0905	1.1681	0.2428

Table S5. Results of models testing how the correlation between climate variables and phenology changes with latitude. We examined whether the slopes between different climate variables (temperature and days with heavy (>1 inch) precipitation) and phenology differ as latitude increased using trivariate meta-analysis models. Interactions are between one of three effect sizes (p_t = phenology-time correlation, p_c = phenology-climate correlation, t_c = time-climate correlation) and latitude. SE indicates standard error. The models were controlled for phylogeny and study.

Temperature	Coefficient	SE	z-value	p-value
intercept	-0.1086	0.1234	-0.8803	0.3787
p_t:Latitude	-0.0053	0.0005	-11.1918	<0.0001
p_c:Latitude	-0.0050	0.0005	-10.5132	<0.0001
t_c:Latitude	0.0069	0.0006	12.3861	<0.0001

Heavy Precip Days	Coefficient	SE	z-value	p-value
intercept	-0.0833	0.0735	-1.1325	0.2574
p_t:Latitude	-0.0037	0.0003	-10.7796	<0.0001
p_c:Latitude	0.0004	0.0003	1.2241	0.2209
t_c:Latitude	0.0014	0.0003	4.4480	<0.0001

Table S6. Results of models testing how individual taxa match their phenology to temperature and precipitation. We calculated the slope coefficient between different climate variables (temperature and precipitation) and both phenology and time for individual taxa. Interactions are between one of three effect sizes (p_t = phenology-time correlation, p_c = phenology-climate correlation, t_c = time-climate correlation) and latitude. SE indicates standard error. The models were controlled for phylogeny and study.

Temperature	Coefficient	SE	z-value	p-value
p_t:amphibians	-0.3144	0.2089	-1.5052	0.1323
p_c:amphibians	-0.3999	0.2058	-1.9429	0.0520
t_c:amphibians	0.3329	0.2076	1.6037	0.1088
p_t:birds	-0.2920	0.1986	-1.4708	0.1414
p_c:birds	-0.2296	0.1989	-1.1544	0.2483
t_c:birds	0.3884	0.1994	1.9482	0.0514
p_t:butterflies	-0.3067	0.1827	-1.6788	0.0932
p_c:butterflies	-0.5823	0.2188	-2.6608	0.0078
t_c:butterflies	0.2838	0.2369	1.1981	0.2309
p_t:dragonflies	-0.1663	0.1914	-0.8688	0.3849
p_t:fish	-0.3991	0.2449	-1.6298	0.1031
p_t:invertebrates	-0.3680	0.1655	-2.2236	0.0262
p_c:invertebrates	-0.8084	0.2167	-3.7303	0.0002
t_c:invertebrates	0.3298	0.2623	1.2572	0.2087

p_t:mammals	-0.3585	0.2910	-1.2320	0.2180
p_c:mammals	-0.2356	0.2639	-0.8926	0.3721
t_c:mammals	0.1391	0.2785	0.4994	0.6175
p_t:reptiles	-0.5401	0.3013	-1.7927	0.0730

Precipitation	Coefficient	SE	z-value	p-value
p_t:amphibians	-0.3863	0.1277	-3.0259	0.0025
p_c:amphibians	-0.1717	0.1216	-1.4117	0.1580
t_c:amphibians	0.0265	0.1250	0.2124	0.8318
p_t:birds	-0.2725	0.1129	-2.4136	0.0158
p_c:birds	-0.0168	0.1134	-0.1478	0.8825
t_c:birds	0.1395	0.1140	1.2228	0.2214
p_t:butterflies	-0.2098	0.1154	-1.8176	0.0691
p_c:butterflies	-0.0910	0.1656	-0.5493	0.5828
t_c:butterflies	0.1472	0.1887	0.7800	0.4354
p_t:dragonflies	-0.1154	0.1287	-0.8970	0.3697
p_t:fish	-0.3829	0.1797	-2.1307	0.0331
p_t:invertebrates	-0.3533	0.1263	-2.7983	0.0051

p_c:invertebrates	-0.1344	0.1798	-0.7479	0.4545
t_c:invertebrates	0.0275	0.2156	0.1275	0.8985
p_t:mammals	-0.3384	0.2315	-1.4615	0.1439
p_c:mammals	0.1082	0.1836	0.5893	0.5557
t_c:mammals	0.1524	0.2072	0.7354	0.4621
p_t:reptiles	-0.5254	0.2470	-2.1274	0.0334

Table S7. Results of models testing associations between organismal traits and phenological shifts. We examined whether the slopes between temperature, phenology and time differ between organisms that differ in thermy, trophic level, habitat, or whether they were vertebrates or invertebrates. Interactions are between one of three effect sizes (p_t = phenology-time correlation, p_c = phenology-climate correlation, t_c = time-climate correlation) and traits. SE indicates standard error. The models were controlled for phylogeny and study.

Temperature	Coefficient	SE	z-value	p-value
intercept	0.4861	0.1537	3.1624	0.0016
log(Mass)	-0.0165	0.0073	-2.2800	0.0226
p_c:ThermalEctotherm	-0.8420	0.1000	-8.4192	<0.0001
p_t:ThermalEctotherm	-0.7096	0.0977	-7.2593	<0.0001
t_c:ThermalEctotherm	-0.1050	0.1053	-0.9978	0.3184
p_c:ThermalEndotherm	-0.6140	0.0300	-20.484	<0.0001
p_t:ThermalEndotherm	-0.6776	0.0262	-25.8241	<0.0001

Temperature	Coefficient	SE	z-value	p-value
intercept	0.5152	0.1568	3.2853	0.0010
log(Mass)	-0.0132	0.0075	-1.7668	0.0773
p_c:Trophiccarnivorous	-0.6527	0.0468	-13.9478	<0.0001
p_t:Trophiccarnivorous	-0.7131	0.0444	-16.0438	<0.0001

t_c:Trophiccarnivorous	-0.1234	0.0505	-2.4438	0.0145
p_c:Trophicherbivorous	-0.8079	0.0997	-8.1003	<0.0001
p_t:Trophicherbivorous	-0.7631	0.0852	-8.9528	<0.0001
t_c:Trophicherbivorous	-0.1923	0.1090	-1.7645	0.0777
p_c:Trophicomnivorous	-0.7115	0.0378	-18.8196	<0.0001
p_t:Trophicomnivorous	-0.7534	0.0334	-22.5389	<0.0001

Temperature	Coefficient	SE	z-value	p-value
intercept	0.4424	0.1508	2.9343	0.0033
log(Mass)	-0.0158	0.0074	-2.1347	0.0328
p_t:Habitatmarine	-0.7414	0.1553	-4.7756	<0.0001
p_t:Habitatterrestrial	-0.6744	0.0247	-27.2527	<0.0001

Table S8. Results of models testing associations between seasonal behaviors and phenological shifts. We examined whether the slopes between temperature, phenology and time differ between different seasonal behaviors measured by researchers. Interactions are between one of three effect sizes (p_t = phenology-time correlation, p_c = phenology-climate correlation, t_c = time-climate correlation) and traits. SE indicates standard error. The model was controlled for phylogeny and study.

Temperature	Coefficient	SE	z-value	p-value
intercept	0.3709	0.1295	2.8648	0.0042
log(Mass)	-0.0096	0.0069	-1.3896	0.1646
p_c:arrival	-0.5436	0.0472	-11.5105	<0.0001
p_t:arrival	-0.6006	0.0460	-13.0444	<0.0001
t_c:arrival	0.0760	0.0495	1.5343	0.1249
p_c:peakabundance	-1.4912	0.3365	-4.4316	<0.0001
p_t:peakabundance	-0.5744	0.0894	-6.4261	<0.0001
t_c:peakabundance	0.1213	0.3863	0.3141	0.7535
p_c:rearing	-0.7118	0.0646	-11.0102	<0.0001
p_t:rearing	-0.7690	0.0672	-11.441	<0.0001

Supplementary Code

Code for trivariate meta-analysis. Example code for constructing variance-covariance matrices, phylogenetic and study-level random effects and fitting mixed-effects trivariate meta-analysis models.

```
# clear workspace and set working directory
rm(list = ls())

# remove current version and install custom metafor package by MJL that ignores positive definite errors
remove.packages("metafor")
install.packages("metafor_1.9-2_MJL.tar.gz", repos = NULL, type="source")

# get entire concatenated dataset with all climate variables
allData <- read.csv(file="phenology.csv", header=TRUE)

# remove rows with no effect size data
allData <- allData[which(!is.na(allData$z)),]

# parse dataset by climate variable and keep original order
climateDataList <- split(allData,
                   factor(allData$climate, levels=unique(allData$climate)))

# parallelized rma.mv function
rma.parallel <- function(aClimateData,
                       theRegressionModel,
                       modelFileName)
{
  # collect only complete cases for specified regression model
  determineCompleteCases <- aClimateData[,c(labels(terms(theRegressionModel)))]
  aClimateData <- aClimateData[which(complete.cases(determineCompleteCases)),]

  # load phylogeny and convert to phylogenetic correlation matrix
  phyloMatrix <- vcv(phy=read.tree(file="cohen_final_phylogeny_72214.tre"), corr=TRUE)
  phyloMatrix <- forceSymmetric(phyloMatrix)

  # construct VCV matrix for multivariate effect sizes and correct for positive definiteness
  getV <- function(someData) {
    dataList <- split(someData[,c("p_t", "p_c", "t_c")], someData$effect_ID)
    theVList <- lapply(dataList,
                     function(x) ifelse(nrow(x) == 1, return(as.matrix(x$p_t)), return(as.matrix(x))))
    theVList_PosDef_fixed <- lapply(theVList, force_Positive_Definiteness)
    return(as.matrix(bdiag(theVList_PosDef_fixed)))
```

```
  }


  # multi(tri)variate, multi-factor, mixed-model, meta-regression
  theResults <- rma.mv(yi = z,
                     V = getV(aClimateData),
                     mods = update(theRegressionModel, ~ . + cor_ID),
                     random = c(~ cor_ID | study_ID, ~ 1 | Genus_Species_NEWICK),
                     R = list(Genus_Species_NEWICK = phyloMatrix),
                     struct = "UN",
                     data = aClimateData,
                     control = list(optimizer = "nlminb"))

  # save results and notify analysis completion
  fileName <- paste(gsub("/", "//", getwd(), fixed = TRUE),
                    "// results//", modelFileName, aClimateData$climate[1], ".rda", sep = "")
  save(theResults, file = fileName)
  return(theResults)
}

# parallelize meta-regressions among the 12 climate variables
library("parallel")
cl <- makeCluster(detectCores(logical = TRUE))
clusterEvalQ(cl,
             { lapply(c("Matrix", "MASS", "corpcor", "metafor", "ape"), library, character.only = T); source("metaGear_v1_beta.r"); })


# available factors: VertInvert + Trophic + Thermal + Latitude + Longitude + Altitude + Habitat + TypeNEW
theRegressionModel <- ~ VertInvert + Trophic + Thermal + Latitude + Longitude + Altitude + Habitat + TypeNEW
modelFileName <- "all_factors_"
parLapply(cl, climateDataList, rma.parallel, theRegressionModel, modelFileName)

theRegressionModel <- ~ VertInvert + Trophic + Thermal + Latitude + Longitude + Altitude + Habitat + TypeNEW - 1
modelFileName <- "all_factors_noIntercept_"
parLapply(cl, climateDataList, rma.parallel, theRegressionModel, modelFileName)

stopCluster(cl)
```

NEWICK (text) version of phylogenetic tree used for phylogenetic analyses. The relationships between species in this tree were used to control for phylogeny in all mixed-effects meta-analyses because related species are non-independent because of their shared evolutionary history. The taxonomic composition of our meta-analytic dataset was broad and included 475 species, 289 genera, 119 families, 45 orders, 12 classes, and 5 phyla. For details concerning the methodology behind the compilation of the tree, see Methods. The following pages include the full NEWICK (text) version of this tree.

```
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):60,Platichthys_flesus:120):87):43):204.6,(((Hynobius_tokyoensis:217.5,(((Triturus_alpestris:84,Triturus_cristatus:84)
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120):237);
```

Supplementary References

1 Rohr, J. *et al.* Thermal acclimation capacity of ectotherms is determined by body size, latitude, and methodology and predicts risk from climate change *Ecology Letters* (in review).

2 Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M. & Charnov, E. L. Effects of size and temperature on metabolic rate. *Science* **293**, 2248-2251, doi:DOI 10.1126/science.1061967 (2001).

3 Abraham, C. L. & Sydeman, W. J. Ocean climate, euphausiids and auklet nesting: inter-annual trends and variation in phenology, diet and growth of a planktivorous seabird, Ptychoramphus aleuticus. *Mar Ecol Prog Ser* **274**, 235-250, doi:DOI 10.3354/meps274235 (2004).

4 Adamik, P. & Pietruszkova, J. Advances in spring but variable autumnal trends in timing of inland wader migration. *Acta Ornithol* **43**, 119-128, doi:10.3161/000164508x395225 (2008).

5 Ahas, R. Long-term phyto-, ornitho- and ichthyophenological time-series analyses in Estonia. *Int J Biometeorol* **42**, 119-123, doi:DOI 10.1007/s004840050094 (1999).

6 Ahola, M. *et al.* Variation in climate warming along the migration route uncouples arrival and breeding dates. *Global Change Biol* **10**, 1610-1617, doi:DOI 10.1111/j.1365-2486.2004.00823.x (2004).

7 Anthes, N. Long-distance migration timing of Tringa sandpipers adjusted to recent climate change. *Bird Study* **51**, 203-211 (2004).

8 Askeyev, O. V., Sparks, T. H., Askeyev, I. V. & Tryjanowski, P. Is earlier spring migration of Tatarstan warblers expected under climate warming? *Int J Biometeorol* **51**, 459-463, doi:10.1007/s00484-007-0085-8 (2007).

9 Askeyev, O. V., Sparks, T. H. & Askeyev, I. V. Earliest recorded Tatarstan skylark in 2008: non-linear response to temperature suggests advances in arrival dates may accelerate. *Clim Res* **38**, 189-192, doi:10.3354/cr00788 (2009).

10 Askeyev, O. V., Sparks, T. H., Askeyev, I. V. & Tryjanowski, P. Spring migration timing of Sylvia warblers in Tatarstan (Russia) 1957-2008. *Cent Eur J Biol* **4**, 595-602, doi:10.2478/s11535-009-0046-9 (2009).

11 Barbraud, C. & Weimerskirch, H. Antarctic birds breed later in response to climate change. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 6248-6251, doi:10.1073/pnas.0510397103 (2006).

12 Barrett, R. T. The phenology of spring bird migration to north Norway. *Bird Study* **49**, 270-277 (2002).

13 Bauer, Z. *et al*. Changing climate and the phenological response of great tit and collared flycatcher populations in floodplain forest ecosystems in Central Europe. *Int J Biometeorol* **54**, 99-111, doi:10.1007/s00484-009-0259-7 (2010).

14 Beaumont, L. J., McAllan, I. A. W. & Hughes, L. A matter of timing: changes in the first date of arrival and last date of departure of Australian migratory birds. *Global Change Biol* **12**, 1339-1354, doi:10.1111/j.1365-2486.2006.01171.x (2006).

15 Beebee, T. J. C. Amphibian Breeding and Climate. *Nature* **374**, 219-220, doi:DOI 10.1038/374219a0 (1995).

16 Beebee, T. J. C. Ever-earlier breeding migrations by alpine newts (Triturus alpestris) living wild in Britian *British Herpetological Society Bulletin* **51**, 5-6 (1995).

17 Bertram, D. F., Mackas, D. L. & McKinnell, S. M. The seasonal cycle revisited: interannual variation and ecosystem consequences. *Prog Oceanogr* **49**, 283-307, doi:Doi 10.1016/S0079-6611(01)00027-1 (2001).

18 Blaustein, A. R. *et al.* Amphibian breeding and climate change. *Conserv Biol* **15**, 1804-1809, doi:DOI 10.1046/j.1523-1739.2001.00307.x (2001).

19 Both, C. & Visser, M. E. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**, 296-298, doi:Doi 10.1038/35077063 (2001).

20 Both, C., Piersma, T. & Roodbergen, S. P. Climatic change explains much of the 20th century advance in laying date of Northern Lapwing Vanellus vanellus in The Netherlands. *Ardea* **93**, 79-88 (2005).

21 Both, C., van Asch, M., Bijlsma, R. G., van den Burg, A. B. & Visser, M. E. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J Anim Ecol* **78**, 73-83, doi:10.1111/j.1365-2656.2008.01458.x (2009).

22 Bradley, N. L., Leopold, A. C., Ross, J. & Huffaker, W. Phenological changes reflect climate change in Wisconsin. *P Natl Acad Sci USA* **96**, 9701-9704, doi:DOI 10.1073/pnas.96.17.9701 (1999).

23 Carroll, E. A., Sparks, T. H., Collinson, N. & Beebee, T. J. C. Influence of temperature on the spatial distribution of first spawning dates of the common frog (Rana temporaria) in the UK. *Global Change Biol* **15**, 467-473, doi:10.1111/j.1365-2486.2008.01726.x (2009).

24 Chadwick, E. A., Slater, F. M. & Ormerod, S. J. Inter- and intraspecific differences in climatically mediated phenological change in coexisting Triturus species. *Global Change Biol* **12**, 1069-1078, doi:10.1111/j.1365-2486.2006.01156.x (2006).

25 Corn, P. S. & Muths, E. Variable breeding phenology affects the exposure of amphibian embryos to ultraviolet radiation. *Ecology* **83**, 2958-2963, doi:Doi 10.2307/3071830 (2002).

26 Costello, J. H., Sullivan, B. K. & Gifford, D. J. A physical-biological interaction underlying variable phenological responses to climate change by coastal zooplankton. *J Plankton Res* **28**, 1099-1105, doi:10.1093/plankt/fbl042 (2006).

27 Cotton, P. A. Avian migration phenology and global climate change. *P Natl Acad Sci USA* **100**, 12219-12222, doi:10.1073/pnas.1930548100 (2003).

28 Cresswell, W. & McCleery, R. How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *J Anim Ecol* **72**, 356-366, doi:DOI 10.1046/j.1365-2656.2003.00701.x (2003).

29 Crick, H. Q. P. & Sparks, T. H. Climate change related to egg-laying trends. *Nature* **399**, 423-424, doi:Doi 10.1038/20839 (1999).

30 Crick, H. Q. P., Dudley, C., Glue, D. E. & Thomson, D. L. UK birds are laying eggs earlier. *Nature* **388**, 526-526, doi:Doi 10.1038/41453 (1997).

31 Croxton, P. J., Sparks, T. H., Cade, M. & Loxton, R. G. Trends and temperature effects in the arrival of spring migrants in Portland (United Kingdom) 1959-2005. *Acta Ornithol* **41**, 103-111 (2006).

32 D'Alba, L., Monaghan, P. & Nager, R. G. Advances in laying date and increasing population size suggest positive responses to climate change in Common Eiders Somateria mollissima in Iceland. *Ibis* **152**, 19-28 (2010).

33 Dell, D., Sparks, T. H. & Dennis, R. L. H. Climate change and the effect of increasing spring temperatures on emergence dates of the butterfly Apatura iris (Lepidoptera : Nymphalidae). *Eur J Entomol* **102**, 161-167 (2005).

34 Dufour, F., Arrizabalaga, H., Irigoien, X. & Santiago, J. Climate impacts on albacore and bluefin tunas migrations phenology and spatial distribution. *Prog Oceanogr* **86**, 283-290, doi:10.1016/j.pocean.2010.04.007 (2010).

35 Dunn, P. O. & Winkler, D. W. Climate change has affected the breeding date of tree swallows throughout North America. *P Roy Soc B-Biol Sci* **266**, 2487-2490 (1999).

36 Dyrcz, A. & Halupka, L. The response of the Great Reed Warbler Acrocephalus arundinaceus to climate change. *J Ornithol* **150**, 39-44, doi:10.1007/s10336-008-0315-9 (2009).

37 Elliot, J. M. Temperature-related fluctuations in the timing of emergence and pupation of Windermere alder-flies over 30 years. *Ecological Entomology* **21**, 241-247 (1996).

38 Forister, M. L. & Shapiro, A. M. Climatic trends and advancing spring flight of butterflies in lowland California. *Global Change Biol* **9**, 1130-1135, doi:DOI 10.1046/j.1365-2486.2003.00643.x (2003).

39 Gaston, A. T., Gilchrist, H. G., Mallory, M. L. & Smith, P. A. Changes in Seasonal Events, Peak Food Availability, and Consequent Breeding Adjustment in a Marine Bird: A Case of Progressive Mismatching. *Condor* **111**, 111-119, doi:10.1525/cond.2009.080077 (2009).

40 Gillet, C. & Quetin, P. Effect of temperature changes on the reproductive cycle of roach in Lake Geneva from 1983 to 2001. *J Fish Biol* **69**, 518-534, doi:10.1111/j.1095-8649.2006.01123.x (2006).

41 Gordo, O. & Sanz, J. J. Phenology and climate change: a long-term study in a Mediterranean locality. *Oecologia* **146**, 484-495, doi:10.1007/s00442-005-0240-z (2005).

42 Gordo, O. & Sanz, J. J. Temporal trends in phenology of the honey bee Apis mellifera (L.) and the small white Pieris rapae (L.) in the Iberian Peninsula (1952-2004). *Ecological Entomology* **31**, 261-268, doi:DOI 10.1111/j.1365-2311.2006.00787.x (2006).

43 Gordo, O., Brotons, L., Ferrer, X. & Comas, P. Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? *Global Change Biol* **11**, 12-21, doi:10.1111/j.1365-2486.2004.00875.x (2005).

44 Halupka, L., Dyrcz, A. & Borowiec, M. Climate change affects breeding of reed warblers Acrocephalus scirpaceus. *J Avian Biol* **39**, 95-100, doi:10.1111/j.2008.0908-8857.04047.x (2008).

45 Harrington, R. *et al.* Environmental change and the phenology of European aphids. *Global Change Biol* **13**, 1550-1564, doi:10.1111/j.1365-2486.2007.01394.x (2007).

46 Huppop, O. & Huppop, K. North Atlantic Oscillation and timing of spring migration in birds. *P Roy Soc B-Biol Sci* **270**, 233-240, doi:10.1098/rspb.2002.2236 (2003).

47 Hussell, D. J. T. Climate change, spring temperatures, and timing of breeding of tree swallows (Tachycineta bicolor) in southern Ontario. *Auk* **120**, 607-618, doi:Doi 10.1642/0004-8038(2003)120[0607:Ccstat]2.0.Co;2 (2003).

48 Inouye, D. W., Barr, B., Armitage, K. B. & Inouye, B. D. Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 1630-1633, doi:DOI 10.1073/pnas.97.4.1630 (2000).

49 Jarvinen, A. Patterns and Causes of Long-Term Variation in Reproductive Traits of the Pied Flycatcher Ficedula-Hypoleuca in Finnish Lapland. *Ornis Fennica* **66**, 24-31 (1989).

50 Jenkins, D. & Watson, A. Dates of first arrival and song of birds during 1974-99 in mid-Deeside, Scotland (vol 47, pg 249, 2000). *Bird Study* **47**, 377-377 (2000).

51 Kanuscak, P., Hromada, M., Tryjanowski, P. & Sparks, T. Does climate at different scales influence the phenology and phenotype of the River Warbler Locustella fluviatilis? *Oecologia* **141**, 158-163, doi:10.1007/s00442-004-1646-8 (2004).

52 Kennedy, R. J. & Crozier, W. W. Evidence of changing migratory patterns of wild Atlantic salmon Salmo salar smolts in the River Bush, Northern Ireland, and possible associations with climate change. *J Fish Biol* **76**, 1786-1805, doi:10.1111/j.1095-8649.2010.02617.x (2010).

53 Kobori, H., Kamamoto, T., Nomura, H., Oka, K. & Primack, R. The effects of climate change on the phenology of winter birds in Yokohama, Japan. *Ecol Res* **27**, 173-180, doi:10.1007/s11284-011-0891-7 (2012).

54 Koppmann-Rumpf, B., Heberer, C. & Schmidt, K. H. Long term study of the reaction of the edible dormouse Glis glis (Rodentia : Gliridae) to climatic changes and its interactions with hole-breeding passerines. *Acta Zool Acad Sci H* **49**, 69-76 (2003).

55 Kusano, T. & Inoue, M. Long-Term Trends toward Earlier Breeding of Japanese Amphibians. *J Herpetol* **42**, 608-614, doi:Doi 10.1670/08-002r1.1 (2008).

56 Laaksonen, T., Ahola, M., Eeva, T., Vaisanen, R. A. & Lehikoinen, E. Climate change, migratory connectivity and changes in laying date and clutch size of the pied flycatcher. *Oikos* **114**, 277-290, doi:DOI 10.1111/j.2006.0030-1299.14652.x (2006).

57 Lane, J. E., Kruuk, L. E. B., Charmantier, A., Murie, J. O. & Dobson, F. S. Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature* **489**, 554-+, doi:Doi 10.1038/Nature11335 (2012).

58 Lappalainen, H. K., Linkosalo, T. & Venalainen, A. Long-term trends in spring phenology in a boreal forest in central Finland. *Boreal Environ Res* **13**, 303-318 (2008).

59 Lehikoinen, E., Sparks, T. H. & Zalakevicius, M. Arrival and departure dates. *Adv Ecol Res* **35**, 1-31, doi:Doi 10.1016/S0065-2504(04)35001-4 (2004).

60 Ludwichowski, I. Long-term changes of wing-length, body mass and breeding parameters in first-time breeding females of Goldeneyes (Buchepala clangula clangula) in Northern Germany. *Vogelwarte* **39**, 103-116 (1997).

61 Macinnes, C. D., Dunn, E. H., Rusch, D. H., Cooke, F. & Cooch, F. G. Advancement of Goose Nesting Dates in the Hudson-Bay Region, 1951-1986. *Can Field Nat* **104**, 295-297 (1990).

62 Mackas, D. L., Goldblatt, R. & Lewis, A. G. Interdecadal variation in developmental timing of Neocalanus plumchrus populations at Ocean Station P in the subarctic North Pacific. *Can J Fish Aquat Sci* **55**, 1878-1893, doi:DOI 10.1139/cjfas-55-8-1878 (1998).

63 Mazaris, A. D., Kallimanis, A. S., Sgardelis, S. P. & Pantis, J. D. Do long-term changes in sea surface temperature at the breeding areas affect the breeding dates and reproduction performance of Mediterranean loggerhead turtles? Implications for climate change. *J Exp Mar Biol Ecol* **367**, 219-226, doi:10.1016/j.jembe.2008.09.025 (2008).

64 McCleery, R. H. & Perrins, C. M. ... temperature and egg-laying trends. *Nature* **391**, 30-31, doi:Doi 10.1038/34073 (1998).

65 Miller-Rushing, A. J., Lloyd-Evans, T. L., Primack, R. B. & Satzinger, P. Bird migration times, climate change, and changing population sizes. *Global Change Biol* **14**, 1959-1972, doi:10.1111/j.1365-2486.2008.01619.x (2008).

66 Mills, A. M. Changes in the timing of spring and autumn migration in North American migrant passerines during a period of global warming. *Ibis* **147**, 259-269, doi:DOI 10.1111/j.1474-919X.2005.00380.x (2005).

67 Mitrus, C., Sparks, T. H. & Tryjanowski, P. First evidence of phenological change in a transcontinental migrant overwintering in the Indian sub-continent: the Red-breasted Flycatcher Ficedula parva. *Ornis Fennica* **82**, 13-19 (2005).

68 Moe, B. Marine ecosystems, climate and phenology: impacts on top predators. *Mar Ecol Prog Ser* **393**, 185-301 (2009).

69 Murphy-Klassen, H. M., Underwood, T. J., Sealy, S. G. & Czyrnyj, A. A. Long-term trends in spring arrival dates of migrant birds at Delta Marsh, Manitoba, in relation to climate change. *Auk* **122**, 1130-1148, doi:Doi 10.1642/0004-8038(2005)122[1130:Ltisad]2.0.Co;2 (2005).

70 Nielsen, J. T. & Moller, A. P. Effects of food abundance, density and climate change on reproduction in the sparrowhawk Accipiter nisus. *Oecologia* **149**, 505-518, doi:10.1007/s00442-006-0451-y (2006).

71 Ozgul, A. *et al.* Coupled dynamics of body mass and population growth in response to environmental change. *Nature* **466**, 482-U485, doi:10.1038/nature09210 (2010).

72 Peintinger, M. Changes in first arrival dates of common migratory bird species in southwestern Germany. *Vogelwarte* **43**, 161-170 (2006).

73 Penuelas, J., Filella, I. & Comas, P. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biol* **8**, 531-544, doi:DOI 10.1046/j.1365-2486.2002.00489.x (2002).

74 Philippart, C. J. M. *et al.* Climate-related changes in recruitment of the bivalve Macoma balthica. *Limnol Oceanogr* **48**, 2171-2185 (2003).

75 Ptaszyk, J., Kosicki, J., Sparks, T. H. & Tryjanowski, P. Changes in the timing and pattern of arrival of the White Stork (Ciconia ciconia) in western Poland. *Journal Fur Ornithologie* **144**, 323-329, doi:DOI 10.1046/j.1439-0361.2003.03011.x (2003).

76 Reading, C. J. The effect of winter temperatures on the timing of breeding activity in the common toad Bufo bufo. *Oecologia* **117**, 469-475, doi:DOI 10.1007/s004420050682 (1998).

77 Reed, T. E. *et al.* Timing is everything: flexible phenology and shifting selection in a colonial seabird. *J Anim Ecol* **78**, 376-387, doi:10.1111/j.1365-2656.2008.01503.x (2009).

78 Rubolini, D. *et al.* Long-term trends in first arrival and first egg laying dates of some migrant and resident bird species in northern Italy. *Int J Biometeorol* **51**, 553-563, doi:10.1007/s00484-007-0094-7 (2007).

79 Sanz, J. J., Potti, J., Moreno, J., Merino, S. & Frias, O. Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Global Change Biol* **9**, 461-472, doi:DOI 10.1046/j.1365-2486.2003.00575.x (2003).

80 Schiegg, K., Pasinelli, G., Walters, J. R. & Daniels, S. J. Inbreeding and experience affect response to climate change by endangered woodpeckers. *P Roy Soc B-Biol Sci* **269**, 1153-1159, doi:10.1098/rspb.2002.1966 (2002).

81 Schluter, M. H. *et al.* Phenological shifts of three interacting zooplankton groups in relation to climate change. *Global Change Biol* **16**, 3144-3153, doi:10.1111/j.1365-2486.2010.02246.x (2010).

82 Scott, W. A., Pithart, D. & Adamson, J. K. Long-term United Kingdom trends in the breeding phenology of the Common Frog, Rana temporaria. *J Herpetol* **42**, 89-96, doi:Doi 10.1670/07-022.1 (2008).

83 Sergio, F. Relationship between laying dates of black kites Milvus migrans and spring temperatures in Italy: rapid response to climate change? *J Avian Biol* **34**, 144-149, doi:DOI 10.1034/j.1600-048X.2003.03104.x (2003).

84 Sims, D. W., Wearmouth, V. J., Genner, M. J., Southward, A. J. & Hawkins, S. J. Low-temperature-driven early spawning migration of a temperate marine fish. *J Anim Ecol* **73**, 333-341, doi:DOI 10.1111/j.0021-8790.2004.00810.x (2004).

85 Slater, F. M. First-egg date fluctuations for the Pied Flycatcher Ficedula hypoleuca in the woodlands of mid-Wales in the twentieth century. *Ibis* **141**, 497-499 (1999).

86 Sokolov, L. V. & Gordienko, N. S. Has recent climate warming affected the dates of bird arrival to the Il'men Reserve in the Southern Urals? *Russ J Ecol+* **39**, 56-62, doi:10.1134/S1067413608010098 (2008).

87 Sokolov, L. V. Long-term trends in the timing of spring migration of passerines on the Courish Spit of the Baltic Sea. *Avian Ecology and Behaviour* **1**, 1-21 (1998).

88 Sparks, T. H. Phenology and the changing pattern of bird migration in Britain. *Int J Biometeorol* **42**, 134-138, doi:DOI 10.1007/s004840050096 (1999).

89 Sparks, T. H. & Braslavska, O. The effects of temperature, altitude and latitude on the arrival and departure dates of the swallow Hirundo rustica in the Slovak Republic. *Int J Biometeorol* **45**, 212-216, doi:DOI 10.1007/s004840100095 (2001).

90 Sparks, T. Dates of arrivals and departures of spring migrants taken from essex bird reports 1950-1998. *Essex Bird Report* **1999** (2001).

91 Sparks, T. H. & Yates, T. J. The effect of spring temperature on the appearance dates of British butterflies 1883-1993. *Ecography* **20**, 368-374, doi:DOI 10.1111/j.1600-0587.1997.tb00381.x (1997).

92 Sparks, T. H. *et al.* Examining the total arrival distribution of migratory birds. *Global Change Biol* **11**, 22-30, doi:10.1111/j.1365-2486.2004.00887.x (2005).

93 Sparks, T., Tryjanowski, P., Cooke, A., Crick, H. & Kuzniak, S. Vertebrate phenology at similar latitudes: temperature responses differ between Poland and the United Kingdom. *Clim Res* **34**, 93-98, doi:DOI 10.3354/cr034093 (2007).

94 Sparks, T. H. *et al.* Advances in the timing of spring cleaning by the honeybee Apis mellifera in Poland. *Ecological Entomology* **35**, 788-791, doi:10.1111/j.1365-2311.2010.01226.x (2010).

95 Strode, P. K. Implications of climate change for North American wood warblers (Parulidae). *Global Change Biol* **9**, 1137-1144, doi:DOI 10.1046/j.1365-2486.2003.00664.x (2003).

96 Taylor, S. G. Climate warming causes phenological shift in Pink Salmon, Oncorhynchus gorbuscha, behavior at Auke Creek, Alaska. *Global Change Biol* **14**, 229-235, doi:10.1111/j.1365-2486.2007.01494.x (2008).

97 Todd, B. D., Scott, D. E., Pechmann, J. H. K. & Gibbons, J. W. Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. *P Roy Soc B-Biol Sci* **278**, 2191-2197, doi:10.1098/rspb.2010.1768 (2011).

98 Tryjanowski, P. & Sparks, T. H. Is the detection of the first arrival date of migrating birds influenced by population size? A case study of the red-backed shrike Lanius collurio. *Int J Biometeorol* **45**, 217-219, doi:DOI 10.1007/s00484-001-0112-0 (2001).

99 Tryjanowski, P., Rybacki, M. & Sparks, T. Changes in the first spawning dates of common frogs and common toads in western Poland in 1978-2002. *Ann Zool Fenn* **40**, 459-464 (2003).

100 Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. Warmer springs lead to mistimed reproduction in great tits (Parus major). *Proceedings of the Royal Society B-Biological Sciences* **265**, 1867-1870 (1998).

101 Waite, T. A. & Strickland, D. Climate change and the demographic demise of a hoarding bird living on the edge. *P Roy Soc B-Biol Sci* **273**, 2809-2813, doi:10.1098/rspb.2006.3667 (2006).

102 Wang, G. M. *et al.* Relationships between climate and population dynamics of white-tailed ptarmigan Lagopus leucurus in Rocky Mountain National Park, Colorado, USA. *Clim Res* **23**, 81-87, doi:DOI 10.3354/cr023081 (2002).

103 Wanless, S., Frederiksen, M., Walton, J. & Harris, M. P. Long-term changes in breeding phenology at two seabird colonies in the western North Sea. *Ibis* **151**, 274-285, doi:10.1111/j.1474-919X.2008.00906.x (2009).

104 Weatherhead, P. J. Effects of climate variation on timing of nesting, reproductive success, and offspring sex ratios of red-winged blackbirds. *Oecologia* **144**, 168-175, doi:10.1007/s00442-005-0009-4 (2005).

105 Weishampel, J. F., Bagley, D. A. & Ehrhart, L. M. Earlier nesting by loggerhead sea turtles following sea surface warming. *Global Change Biol* **10**, 1424-1427, doi:10.1111/j.1365-2486.2004.00817.x (2004).

106 Wesolowski, T. & Maziarz, M. Changes in breeding phenology and performance of Wood Warblers Phylloscopus sibilatrix in a primeval forest: a thirty-year perspective. *Acta Ornithol* **44**, 69-80, doi:10.3161/000164509x464902 (2009).

107 Wiebe, K. L. & Gerstmar, H. Influence of Spring Temperatures and Individual Traits on Reproductive Timing and Success in a Migratory Woodpecker. *Auk* **127**, 917-925, doi:10.1525/auk.2010.10025 (2010).

108 Winder, M. & Schindler, D. E. Climate change uncouples trophic interactions in an aquatic system (vol 85, pg 2100, 2004). *Ecology* **85**, 3178-3178 (2004).

109 Winkel, W. & Hudde, H. Long-term changes of breeding parameters of Nuthatches Sitta europaea in two study areas of northern Germany. *Journal Fur Ornithologie* **137**, 193-202, doi:Doi 10.1007/Bf01653634 (1996).

110 Winkel, W. & Hudde, H. Long-term trends in reproductive traits of tits (Parus major, P-caeruleus) and pied flycatchers Ficedula hypoleuca. *J Avian Biol* **28**, 187-190, doi:Doi 10.2307/3677313 (1997).

111 Browne, S. J. & Aebischer, N. J. Temporal changes in the migration phenology of turtle doves Streptopelia turtur in Britain, based on sightings from coastal bird observatories. *J Avian Biol* **34**, 65-71, doi:DOI 10.1034/j.1600-048X.2003.03060.x (2003).

112 Stervander, M., Lindstrom, K., Jonzen, N. & Andersson, A. Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and the significance of different migration routes. *J Avian Biol* **36**, 210-221, doi:DOI 10.1111/j.0908-8857.2005.03360.x (2005).

113 Both, C., Bijlsma, R. G. & Visser, M. E. Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher Ficedula hypoleuca. *J Avian Biol* **36**, 368-373, doi:DOI 10.1111/j.0908-8857.2005.03484.x (2005).

114 Lehikoinen, A., Kilpi, M. & Ost, M. Winter climate affects subsequent breeding success of common eiders. *Global Change Biol* **12**, 1355-1365, doi:10.1111/j.1365-2486.2006.01162.x (2006).

115 Zalakevicius, M., Bartkeviciene, G., Raudonikis, L. & Janulaitis, J. Spring arrival response to climate change in birds: a case study from eastern Europe. *J Ornithol* **147**, 326-343, doi:10.1007/s10336-005-0016-6 (2006).

116 Jonzen, N. *et al.* Rapid advance of spring arrival dates in long-distance migratory birds. *Science* **312**, 1959-1961, doi:10.1126/science.1126119 (2006).

117 Macmynowski, D. P., Root, T. L., Ballard, G. & Geupel, G. R. Changes in spring arrival of Nearctic-Neotropical migrants attributed to multiscalar climate. *Global Change Biol* **13**, 2239-2251, doi:DOI 10.1111/j.1365-2486.2007.01448.x (2007).

118 Zalakevicius, M. The response of spring arrival dates of non-passerine migrants to climate change: a case study from eastern baltic. *Acta Zoologica Lituanica* **19** (2007).

119 Vegvari, Z., Bokony, V., Barta, Z. & Kovacs, G. Life history predicts advancement of avian spring migration in response to climate change. *Global Change Biol* **16**, 1-11, doi:10.1111/j.1365-2486.2009.01876.x (2010).

120 Neveu, A. Incidence of climate on common frog breeding: Long-term and short-term changes. *Acta Oecol* **35**, 671-678, doi:10.1016/j.actao.2009.06.012 (2009).

121 Hawkes, L. A., Broderick, A. C., Godfrey, M. H. & Godley, B. J. Investigating the potential impacts of climate change on a marine turtle population. *Global Change Biol* **13**, 923-932, doi:10.1111/j.1365-2486.2007.01320.x (2007).

122 Telemeco, R. S., Elphick, M. J. & Shine, R. Nesting lizards (Bassiana duperreyi) compensate partly, but not completely, for climate change. *Ecology* **90**, 17-22, doi:Doi 10.1890/08-1452.1 (2009).

123 Pollard, E. Changes in the Flight Period of the Hedge Brown Butterfly Pyronia-Tithonus during Range Expansion. *J Anim Ecol* **60**, 737-748, doi:Doi 10.2307/5411 (1991).

124 Roy, D. B. & Sparks, T. H. Phenology of British butterflies and climate change. *Global Change Biol* **6**, 407-416, doi:DOI 10.1046/j.1365-2486.2000.00322.x (2000).

125 Stefanescu, C., Penuelas, J. & Filella, I. Effects of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biol* **9**, 1494-1506, doi:DOI 10.1046/j.1365-2486.2003.00682.x (2003).

126 Hassall, C., Thompson, D. J., French, G. C. & Harvey, I. F. Historical changes in the phenology of British Odonata are related to climate. *Global Change Biol* **13**, 933-941, doi:10.1111/j.1365-2486.2007.01318.x (2007).

127 Doi, H. Delayed phenological timing of dragonfly emergence in Japan over five decades. *Biol Letters* **4**, 388-391, doi:10.1098/rsbl.2008.0234 (2008).

128 Diamond, S. E., Frame, A. M., Martin, R. A. & Buckley, L. B. Species' traits predict phenological responses to climate change in butterflies. *Ecology* **92**, 1005-1012 (2011).

129 Ellwood, E. R. *et al.* Disentangling the paradox of insect phenology: are temporal trends reflecting the response to warming? *Oecologia* **168**, 1161-1171, doi:10.1007/s00442-011-2160-4 (2012).

130 Brown, J. L., Li, S. H. & Bhagabati, N. Long-term trend toward earlier breeding in an American bird: A response to global warming? *P Natl Acad Sci USA* **96**, 5565-5569, doi:DOI 10.1073/pnas.96.10.5565 (1999).

131 Tryjanowski, P., Kuzniak, S. & Sparks, T. Earlier arrival of some farmland migrants in western Poland. *Ibis* **144**, 62-68, doi:DOI 10.1046/j.0019-1019.2001.00022.x (2002).

132 Sanz, J. J. Climate change and breeding parameters of great and blue tits throughout the western Palaearctic. *Global Change Biol* **8**, 409-422, doi:DOI 10.1046/j.1365-2486.2002.00496.x (2002).

133 Howell, S. N. G. & Gardali, T. Phenology, sex ratios, and population trends of Selasphorus hummingbirds in central coastal California. *J Field Ornithol* **74**, 17-25 (2003).

134 Visser, M. E. *et al.* Variable responses to large-scale climate change in European Parus populations. *P Roy Soc B-Biol Sci* **270**, 367-372, doi:10.1098/rspb.2002.2244 (2003).

135 Both, C. *et al.* Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society B-Biological Sciences* **271**, 1657-1662, doi:DOI 10.1098/rspb.2004.2770 (2004).

136 Chambers, L. E. Migration dates at Eyre Bird Observatory: links with climate change? *Clim Res* **29**, 157-165, doi:DOI 10.3354/cr029157 (2005).

137 Torti, V. M. & Dunn, P. O. Variable effects of climate change on six species of North American birds. *Oecologia* **145**, 486-495, doi:10.1007/s00442-005-0175-4 (2005).

138 Tottrup, A. P., Thorup, K. & Rahbek, C. Patterns of change in timing of spring migration in North European songbird populations. *J Avian Biol* **37**, 84-92, doi:DOI 10.1111/j.0908-8857.2006.03391.x (2006).

139 Hoye, T. T., Post, E., Meltofte, H., Schmidt, N. M. & Forchhammer, M. C. Rapid advancement of spring in the High Arctic. *Curr Biol* **17**, R449-R451, doi:DOI 10.1016/j.cub.2007.04.047 (2007).

140 Saino, N. *et al.* Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds. *Clim Res* **35**, 123-134, doi:10.3354/cr00719 (2007).

141 Sparks, T. H. *et al.* How consistent are trends in arrival (and departure) dates of migrant birds in the UK? *J Ornithol* **148**, 503-511, doi:10.1007/s10336-007-0193-6 (2007).

142 Swanson, D. L. & Palmer, J. S. Spring migration phenology of birds in the Northern Prairie region is correlated with local climate change. *J Field Ornithol* **80**, 351-363, doi:10.1111/j.1557-9263.2009.00241.x (2009).

143 van Buskirk, J. Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. *Global Change Biol* **15**, 760-771 (2009).

144 Foster, C. R., Amos, A. F. & Fuiman, L. A. Phenology of Six Migratory Coastal Birds in Relation to Climate Change. *Wilson J Ornithol* **122**, 116-125, doi:Doi 10.1676/09-054.1 (2010).

145 Schneider, K. N., Newman, R. M., Card, V., Weisberg, S. & Pereira, D. L. Timing of Walleye Spawning as an Indicator of Climate Change. *T Am Fish Soc* **139**, 1198-1210, doi:10.1577/T09-129.1 (2010).

146 Moyes, K. *et al.* Advancing breeding phenology in response to environmental change in a wild red deer population. *Global Change Biol* **17**, 2455-2469, doi:10.1111/j.1365-2486.2010.02382.x (2011).

Section/topic	#	Checklist item	Reported in…
TITLE			
Title	1	Identify the report as a systematic review, meta-analysis, or both.	Main text
ABSTRACT			
Structured summary	2	Provide a structured summary including, as applicable: background; objectives; data sources; study eligibility criteria, participants, and interventions; study appraisal and synthesis methods; results; limitations; conclusions and implications of key findings; systematic review registration number.	Main text
INTRODUCTION			
Rationale	3	Describe the rationale for the review in the context of what is already known.	Main text
Objectives	4	Provide an explicit statement of questions being addressed with reference to participants, interventions, comparisons, outcomes, and study design (PICOS).	Main text
METHODS			
Protocol and registration	5	Indicate if a review protocol exists, if and where it can be accessed (e.g., Web address), and, if available, provide registration information including registration number.	Supplement - Methods
Eligibility criteria	6	Specify study characteristics (e.g., PICOS, length of follow-up) and report characteristics (e.g., years considered, language, publication status) used as criteria for eligibility, giving rationale.	Supplement - Methods
Information sources	7	Describe all information sources (e.g., databases with dates of coverage, contact with study authors to identify additional studies) in the search and date last searched.	Supplement - Methods
Search	8	Present full electronic search strategy for at least one database, including any limits used, such that it could be repeated.	Supplement - Methods
Study selection	9	State the process for selecting studies (i.e., screening, eligibility, included in systematic review, and, if applicable, included in the meta-analysis).	Supplement - Methods
Data collection process	10	Describe method of data extraction from reports (e.g., piloted forms, independently, in duplicate) and any processes for obtaining and confirming data	Supplement - Methods

		from investigators.	
Data items	11	List and define all variables for which data were sought (e.g., PICOS, funding sources) and any assumptions and simplifications made.	Supplement - Methods
Risk of bias in individual studies	12	Describe methods used for assessing risk of bias of individual studies (including specification of whether this was done at the study or outcome level), and how this information is to be used in any data synthesis.	Supplement - Methods
Summary measures	13	State the principal summary measures (e.g., risk ratio, difference in means).	Supplement - Methods
Synthesis of results	14	Describe the methods of handling data and combining results of studies, if done, including measures of consistency (e.g., I^2) for each meta-analysis.	Supplement - Methods
Risk of bias across studies	15	Specify any assessment of risk of bias that may affect the cumulative evidence (e.g., publication bias, selective reporting within studies).	Supplement - Methods
Additional analyses	16	Describe methods of additional analyses (e.g., sensitivity or subgroup analyses, meta-regression), if done, indicating which were pre-specified.	Supplement - Methods
RESULTS			
Study selection	17	Give numbers of studies screened, assessed for eligibility, and included in the review, with reasons for exclusions at each stage, ideally with a flow diagram.	Main text
Study characteristics	18	For each study, present characteristics for which data were extracted (e.g., study size, PICOS, follow-up period) and provide the citations.	Supplement - Tables
Risk of bias within studies	19	Present data on risk of bias of each study and, if available, any outcome level assessment (see item 12).	Main text and Supplement - Tables
Results of individual studies	20	For all outcomes considered (benefits or harms), present, for each study: (a) simple summary data for each intervention group (b) effect estimates and confidence intervals, ideally with a forest plot.	Supplement - Tables
Synthesis of results	21	Present results of each meta-analysis done, including confidence intervals and measures of consistency.	Supplement - Tables
Risk of bias across studies	22	Present results of any assessment of risk of bias across studies (see Item 15).	Supplement - Tables

Additional analysis	23	Give results of additional analyses, if done (e.g., sensitivity or subgroup analyses, meta-regression [see Item 16]).	Supplement – Supplementary Results
DISCUSSION			
Summary of evidence	24	Summarize the main findings including the strength of evidence for each main outcome; consider their relevance to key groups (e.g., healthcare providers, users, and policy makers).	Main text
Limitations	25	Discuss limitations at study and outcome level (e.g., risk of bias), and at review-level (e.g., incomplete retrieval of identified research, reporting bias).	Main text and Supplementary Discussion
Conclusions	26	Provide a general interpretation of the results in the context of other evidence, and implications for future research.	Main text
FUNDING			
Funding	27	Describe sources of funding for the systematic review and other support (e.g., supply of data); role of funders for the systematic review.	Main text - Acknowledgments