

Phenology varies with phylogeny but not by trophic level with climate change

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Shifts in phenology with climate change can lead to asynchrony between interacting species, with cascading impacts on ecosystem services.

Previous meta-analyses have produced conflicting results on whether asynchrony has increased in recent decades, but the underlying data have also varied—including in species composition, interaction types and whether studies compared data grouped by trophic level or compared shifts in known interacting species pairs. Here, using updated data from previous studies and a Bayesian phylogenetic model, we found that species have advanced an average of 3.1 days per decade across 1,279 time series across 29 taxonomic classes. We found no evidence that shifts vary by trophic level: shifts were similar when grouped by trophic level, and for species pairs when grouped by their type of interaction—either as paired species known to interact or as randomly paired species. Phenology varied with phylogeny ($\lambda = 0.4$), suggesting that uneven sampling of species may affect estimates of phenology and potentially phenological shifts. These results could aid forecasting for well-sampled groups but suggest that climate change has not yet led to widespread increases in phenological asynchrony across interacting species, although substantial biases in current data make forecasting for most groups difficult.

Early research on the biological impacts of climate change emphasized the globally coherent fingerprint seen in phenological shifts, with the majority of species advancing the timing of major life history events in step with rising temperatures^{1–5}. As more data accumulated, however, concerns over how this phenological variability impacts species interactions started to receive more attention^{6,7}. Shifts across species that lead to phenological asynchrony (as illustrated by Fig. 1) may be especially concerning. Assuming that phenological synchrony was optimal historically⁸, shifts in synchrony may disrupt ecosystem services, such as pollination and carbon and nutrient cycling^{9–12}.

There is debate, however, on how widespread asynchrony is with climate change. Finding consistent trends, even for well-studied species—such as *Parus major* and its caterpillar prey—has proven

challenging, with trends varying by site^{13,14} and changing as researchers gathered more years of data¹⁵. Previous meta-analyses across diverse species in the UK¹⁶ and animals globally¹⁷ have found evidence for asynchrony, with greater phenological advances with climate change in lower trophic levels and for ectothermic species. But another study found no change in synchrony in slightly over half of the species pairs observed¹⁸. Taken together, these results make it difficult to predict the impact of continued changes in climate on ecological communities and ecosystems.

One potential explanation for these diverging results is that they span different groups of species. Previous studies have focused on different subsets of species, with some well-studied lineages—such as birds or insects—being highly over-represented in certain studies.

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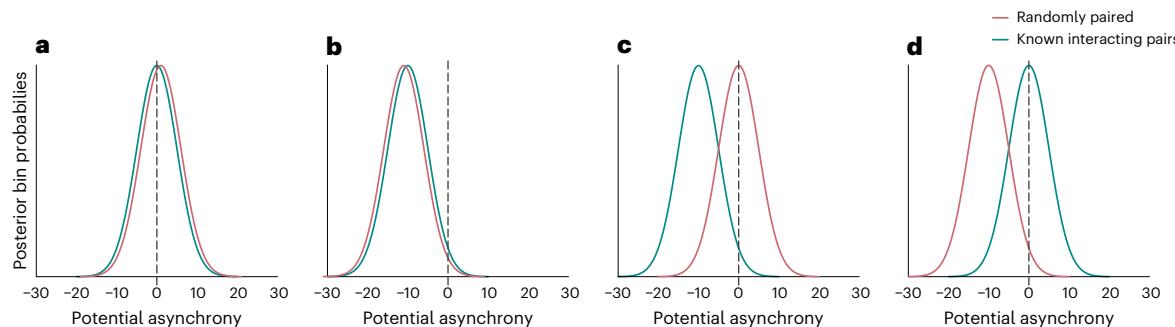


Fig. 1 | Estimating shifts in synchrony may—or may not—vary between known interacting species or randomly paired species (where data come from single-species time series that were often not collected originally for questions of synchrony). **a,b**, We show two cases where estimated shifts are the same regardless of the underlying data: there is no change in species synchrony regardless of whether species are known to interact ('known interacting pairs', blue lines) or not ('randomly paired', red lines), and thus

the difference in paired phenologies would be centred at 0 (**a**); interactions are increasingly asynchronous, and thus the difference in the interacting and random species pairs would be off-zero (but distributions would still overlap) (**b**). **c,d**, Alternatively, results may vary depending on whether they are using single or paired species data to estimate shifts in synchrony: asynchrony (Extended Data Fig. 1a) occurs only for the interacting species pair (**c**), or asynchrony occurs only for the randomly paired species (**d**).

As different evolutionary lineages may have different phenological triggers¹⁹, they could also vary in their phenology, and thus the species composition of different datasets could produce differing results. Data for some asynchrony studies come from single-species time series that were not collected to test questions of synchrony^{20,21}. As such, studies often make inferences across single-species data grouped to trophic level^{16,17}. Other studies, by contrast, have focused on species pairs known to interact¹⁸. As selection can drive interacting species to use similar environmental cues²², studies of known species pairs could find less asynchrony with climate change because both species respond to the same changing environmental cues. We may then predict that ecosystem services dependent on species interactions will be maintained—potentially until climate shifts exceed historical variation.

To understand shifts in synchrony with climate change and improve predictions requires methods that account for species-level differences and oversampling of certain taxonomic lineages and allow estimates of both trends across trophic groups and paired interacting species. To this aim, we combined a new phenological database with cutting-edge Bayesian models that include species' shared evolutionary history via phylogeny. Our new, more global and species-rich database includes most data from previous meta-analyses^{16–18}—updated through recent years when possible—with added information on interaction type and trophic levels, allowing us to test for shifting synchrony and potential drivers of variation in responses. Furthermore, our modelling approach allows under-sampled species within a lineage to partially pool (or 'shrink') to closely related taxa (or not, depending on the data). This approach is a major advance from previous analyses, which treated all species as completely exchangeable, which would thus pool ('shrink') towards the most well-sampled and least variable species.

Results and discussion

After combining and updating the studies from previous meta-analyses of trophic asynchrony^{16–18}, our final dataset included time series with 5 or more years of data of 19 phenological events for 1,200 unique species, across 29 taxonomic classes (Fig. 2 and Extended Data Fig. 2). Data spanned from 1933 to 2020, with an average year of 1986, and included a total of 42,510 individual observations. On average, time series spanned 33 years and ranged from 5 to 65 years. In our dataset, (1) the majority of the data are from single-species observations, which have been commonly grouped by trophic level in past meta-analyses to test for evidence of asynchrony^{16,17}, and (2) data are from 177 species pairs with four interaction types (pollination, competition, herbivory and predation)—a 328% increase in the number of interactions compared to Kharouba et al.¹⁸. Almost all data are point estimates (for example,

phenology represented by one date per year) giving limited insight into how the overlap of species annual phenological distributions may change⁸; however, point estimates are by far the most common type of data collected to date.

Across species, we estimated phenological shifts of −3.1 days per decade (−5.2, −0.9; we present all results as means with 90% posterior uncertainty intervals following in parentheses; see Methods for more details) from our Bayesian phylogenetic model. Carrying through uncertainty, we then used these estimates to test for variation across trophic levels and types of interaction. We found that phenological shifts showed no differences when grouped by trophic level (Fig. 3a), with shifts overlapping highly across trophic levels (furthermore, all had 90% posterior uncertainty intervals that overlapped 0). Primary producers shifted −3.8 (−13.5, 5.8) days per decade, while primary consumers shifted −2.6 (−14.2, 7.6) days per decade, and secondary consumers shifted −6.0 (−26.7, 4.7) days per decade. Tertiary consumers, which were rare in these data (with only 6 time series), shifted −2.7 (−12.5, 8.1) days per decade (Fig. 3a).

We also did not find evidence of consistent differences in phenological trends when considering paired species, which tended to shift at similar rates for both pairs of known interacting species and randomly paired species (Fig. 4). Using our unique database with extensive species information, we assigned all species to a consumer level and to a type of interaction (for example, pollination, competition, herbivory and predation; see Methods for more details); we then simulated random—but biologically sensible—species pairings to test whether estimates of asynchrony over time were influenced by using data from known interacting pairs of species, comparing within types of species interaction. From this approach, we found that differences in species phenological shifts centred around 0 for both known interacting and random species pairs—suggesting pairs shift at similar rates (see the high degree of overlap between the distributions; Fig. 4 and Extended Data Fig. 3). Embedded in these results is a diversity of interaction types and habitats, including terrestrial or aquatic (results were similar for pairings within these two groups, compared to our less restricted simulations; Extended Data Fig. 4).

Our results include variation from apparently synchronous to asynchronous shifts, including capturing well-known cases of diverging trends over time for interacting species (for example, between *P. major* and its caterpillar prey; Extended Data Fig. 5). This highlights that there are cases of asynchrony, but they are relatively rare (80.1% of species within a pair shift in the same direction). Furthermore, they were not predicted by interaction type or other variables we considered. We also did not find differences in phenological shifts across types

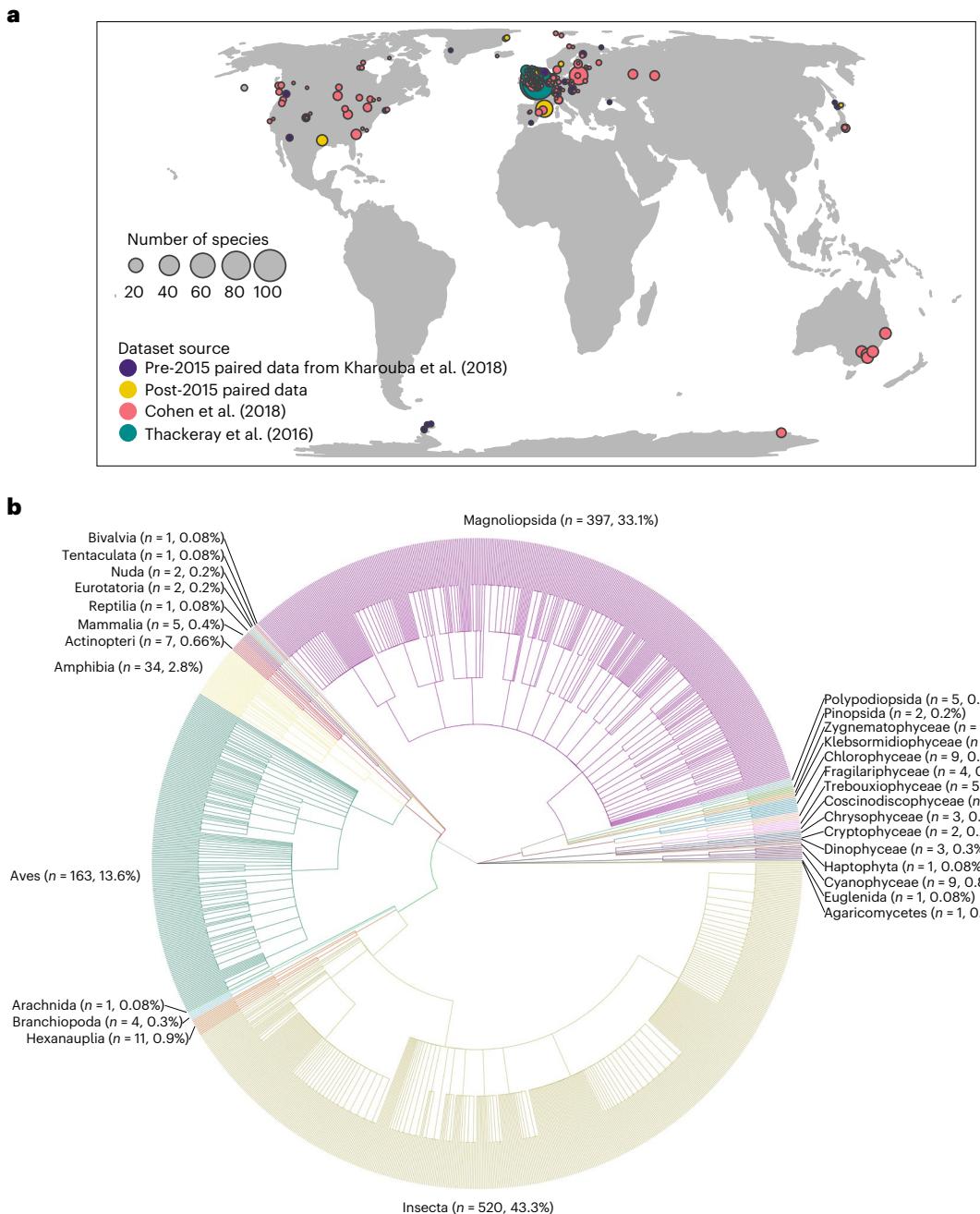


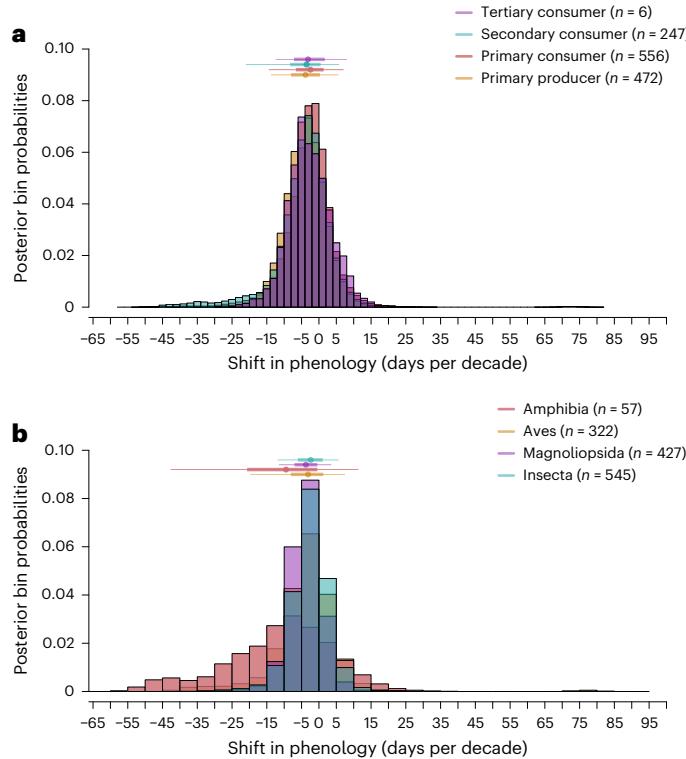
Fig. 2 | Time series analysis includes globally distributed and spanning the tree of life. **a**, Combining three previous meta-analyses with newly available data yielded 1,279 time series of species phenological events for 1,200 unique species, biased towards Europe and North America. **b**, In addition, the diversity of species sampled exhibit a overrepresentation of species from four lineages: birds (Aves),

amphibians (Amphibia), insects (Insecta) and flowering plants (Magnoliopsida). Phylogenetic effects were modelled based on a dated phylogenetic tree. This tree was based on divergence time data from the Timetree database and constructed using the TreePL software.

of phenological event (Extended Data Fig. 6d). Taken together, these results suggest that the phenological data we currently collect and/or our conceptual models, for example, the Cushing match–mismatch hypothesis^{7,23,24}, are insufficient to predict asynchrony. In addition to a lack of data on the underlying distribution of phenological events⁸, only 10.0% of species data were collected as part of a paired species study. Most data were from single species and events related to species abundance and appearance, which may not accurately reflect the key life history events that shape species synchrony⁷.

We found considerable variation in phenology across the 1,200 species we examined (Extended Data Table 1), some of which was explained by shared evolutionary history (through phylogeny). Our

model, spanning across all data (1,279 time series), showed that phylogeny somewhat explains the variation in the timing of phenological events among species ($\lambda = 0.4; 0.2, 0.6$; Pagel's λ is a scaling parameter related to phylogenetic signal²⁵). However, shifts in phenologies showed much weaker phylogenetic correlations (which was not distinguishable from no signal: $\lambda = 0.1; 0.0, 0.3$), suggesting that evolutionary history does not explain how species respond to climate change, at least at the phylogenetic scale of this analysis. These data, however, while capturing the diversity within previous meta-analyses together, still capture only a tiny subset of the relevant tree of life. Furthermore, they include a highly diverse assemblage of species spanning deep evolutionary time (for example, between jellyfish and marmots) and may not



be representative of the phylogenetic structure in phenological shifts at more recent evolutionary scales²⁶. To explore the variability of phenology across evolutionary scales, we conducted additional analyses for the four most well-sampled lineages in our data—amphibians (2.9% of all species), birds (16.5%), insects (41.4%) and flowering plants (32.8%; Extended Data Fig. 7).

We found similar estimates from models of each group individually (amphibians, birds, insects and plants) and from our model using the full phylogeny, but estimates of whether phylogeny predicts phenological timing or phenological shifts varied. In contrast to the model of all species, we found that the timing of phenological events were only weakly structured by phylogeny within each of these four lineages (and not distinguishable from no phylogenetic signal, for plants ($\lambda = 0.1; 0.0, 0.2$), insects ($\lambda = 0.1; 0.0, 0.3$), birds ($\lambda = 0.1; 0.0, 0.2$) and amphibians ($\lambda = 0.3; 0.0, 0.6$)) (Extended Data Table 1). Instead, phylogenetic effects were greater on the phenological shifts, especially for plants ($\lambda = 0.2; 0.1, 0.4$) and amphibians ($\lambda = 0.3; 0.1, 0.5$). Effects for birds were also stronger ($\lambda = 0.2; 0.0, 0.4$), although for both birds and insects ($\lambda = 0.1; 0.0, 0.3$) they were still not distinguishable from no signal (Extended Data Table 1).

These phylogenetic correlations support the overlapping but varied phenological responses we found for these four lineages (Fig. 3b), which also strongly co-varied with trophic level and thus could impact current estimates across varying datasets. The lowest trophic level, flowering plants (Magnoliopsida, all primary producers), had the second largest shift in phenology, advancing by 4.1 (3.3, 4.9) days per decade on average (Extended Data Table 1). By contrast, insects had the smallest phenological response, advancing on average by 2.2 (4.1, 0.2) days per decade (with 99.4% of insects being primary consumers and

0.2% secondary and tertiary consumers; Extended Data Table 1 and Extended Data Fig. 7), and amphibians, a relatively higher trophic level of only secondary consumers (Extended Data Table 1 and Extended Data Fig. 7), were most responsive, advancing by 12.8 (23.8, 2.2) days per decade (Extended Data Table 1). Last, birds (our only endothermic group with sufficient data) had a more moderate response shifting earlier by 3.4 (5.9, 1.0) days per decade on average (Extended Data Table 1; with 8% of birds being primary consumers, 90.2% secondary consumers and 2.5% tertiary consumers; Extended Data Table 1 and Extended Data Fig. 7). The covariation of our sampled insects, birds and amphibians species with trophic level likely reflects a limitation of currently available phenological data, as these lineages have far greater trophic diversity than captured by these data (for example, refs. 27,28). For instance, parasitoids (which are tertiary consumers) are estimated to be a widespread and important group²⁹, constituting possibly 20% of all insect species³⁰, but our dataset included only one parasitoid species.

The phylogenetic structuring of phenology we found suggests one or more latent traits underlie phenological shifts³¹. These latent traits may be related to physiology, as many physiological traits are critical to how species respond to warming—including phenological sensitivity to temperature, light and other cues—and can vary by taxonomic group^{22,32}. To date, however, these traits are poorly understood for most taxa, making it difficult to test whether they are related to the phylogenetic structuring we observed. Phylogeny could additionally capture multiple traits, including habitat use, thermal tolerances and behaviour, which can all impact responses to climate change^{19,33–36}. Our results—although of varying signal on the timing of phenology or shift in phenology—suggest we are limited by data to robustly identify these traits. Thus, new insights will likely require efforts to sample more species and more evenly, which is important for robust forecasting. Currently, the over-representation of flowering plants, insects and bird species in phenological records hinders accurate predictions for understudied—and potentially more vulnerable—species.

Trends in phenology may also vary with warming across space—with greater shifts in phenology expected in areas of greater warming—and/or across latitude, which correlates with gradients in photoperiod, winter intensities or seasonality^{37–39}. But we found similar phenological responses regardless of site latitude (-0.4 ($-1.3, 0.3$) days per degree latitude; Extended Data Fig. 2) and the rate of local temperature varied from warming of 0.6 ($0.2, 1.0$) °C in Europe to 0.3 ($0.1, 0.5$) °C per decade in the UK for the 3 month window spanning the phenological event (Extended Data Fig. 8).

The lack of trends with temperature or latitude might seem surprising, but high interannual variability in annual phenology could mask these relationships. Many species adapt to interannual variability in climate (which is high in the areas towards which our data are biased; Fig. 2b) via plasticity in phenology—adjusting their arrival or reproduction each year and allowing them to withstand changes across years in their interactions. Our models estimated fairly high variation in measured annual phenology (Extended Data Table 1) and suggest that most species have not been pushed beyond their pre-1980 threshold of phenological variation (Fig. 5), which may explain the low occurrences of species asynchrony we found. For these thresholds to be crossed, phenological shifts would need to be five times greater for most species or twice as great for species with shifts above the 75th percentile of estimates (Fig. 5). These estimates, however, come from data highly biased towards northern temperate latitudes where interannual variability is high.

Twenty years following reports of a globally coherent fingerprint of climate change, our results highlight the variability of responses that underlie a single mean value. While some species interactions have clearly shifted with warming^{40–42}, our results—spanning 87 years and the tree of life, from *Microcystis* (cyanobacteria) to *Marmota flaviventris* (yellow-bellied marmot)—suggest widespread asynchrony

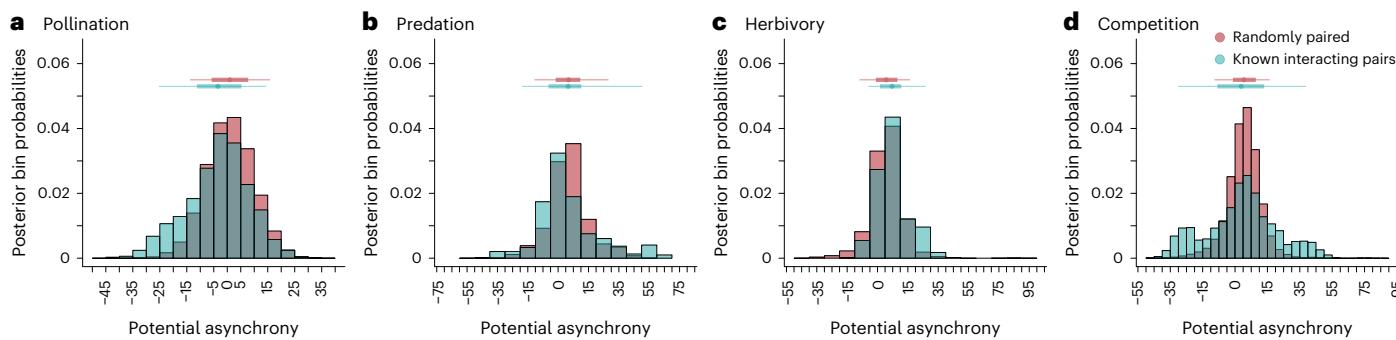


Fig. 4 | Changes in phenological synchrony were similar across known interacting pairs of species (shown in blue, with n given) and randomly paired species (shown in red) across different interaction types.
a–d, For pollination ($n = 47$) (a), predation ($n = 37$) (b), herbivory ($n = 20$) (c) and competitive ($n = 72$) (d) interactions the distribution of the posterior estimates

are normalized by counts and depict the full distribution. The lines above the figure depict the uncertainty intervals, with thinner lines representing the 90% interval and thicker lines the 50% interval, and the point the mean. See Extended Data Fig. 3 for illustration of how synchrony is calculated. Results are in line with those shown in conceptual Fig. 1a.

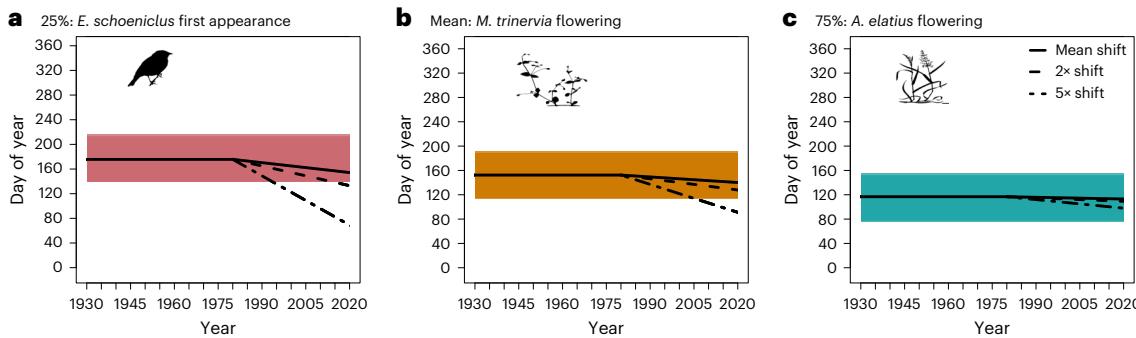


Fig. 5 | Current estimated shifts in phenology, as represented by the solid lines, suggest most species have not been pushed beyond their pre-1980 variation in phenology (solid lines do not exceed their pre-existing variation, the 95% range of the quantile of which is represented by the coloured bands). a–c, The dashed and dotted lines depict hypothetical changes in the

magnitude of phenological shifts: two times and five times current rates. To visualize the breadth in these trends, we show species with shifts closest to the 25th percentile, *Emberiza schoeniclus* (common reed bunting) (a), closest to the mean, *Moehringia trinervia* (three-veined sandwort) (b) and closest to the 75th percentile, *Arrhenatherum elatius* (tall oat grass) (c).

is uncommon. Instead, most species' responses appear within the range of pre-climate change variability. Our results suggest predicting responses before critical thresholds are crossed may still be possible, especially given evolutionary differences that could aid forecasts. However, the current taxonomic, temporal and geographical biases in most phenological data may prevent us from accurately predicting and mediating impacts on some of the most vulnerable species.

Methods

Data collection

For our analyses, we obtained data from previous meta-analyses and updated a literature search of paired studies. Our dataset includes diverse types of phenological data from 147 unique studies and monitoring schemes. This includes the full datasets used in Cohen et al.¹⁷ (from 173 species) and Kharouba et al.¹⁸ (from 86 species). We received permission to use 66.5% of the data used by Thackeray et al.¹⁶ (from 540 species), in addition to independently gaining access to two of the long-term monitoring schemes used in this study: Rothamsted Insect Survey (484 species from 1933 to 2017) and Woodland Trust Nature's Calendar data (452 species from 1960 to 2020). We subsetted the data from the Rothamsted Insect Survey to exclude rare species (fewer than 10 individuals). Finally, using the same search terms and criteria as Kharouba et al.¹⁸, we found ten additional datasets of paired species data published up until 2020 (Extended Data Table 2). In addition to our phenological time series, we also collected data on the natural history of each species, using information on species prey and food to assign

species to one of four trophic levels, one of six consumer types and one of nine different habitat types (Extended Data Fig. 6).

In total, our dataset includes observations for 1,200 species. Of these, we have observations of multiple types of phenological event for 103 species, resulting in 1,279 unique phenological time series. Similar to previous analyses, each type of phenological event for a given species was independently modelled. These time series come from 263 unique sites (Fig. 2a), although 33 (22.3%) of our studies, as well as the Rothamsted Insect Survey and Woodland Trust Nature's Calendar datasets, collect phenological data for a single species at multiple sites. For each study in which a species had multiple time series collected across more than one site, we followed methods of previous analyses and averaged the timing of phenological events across sites for a given year. Overall, these methods of collating the data are similar to the methods used in previous meta-analyses^{17,18}. Results are reported in days per decades, as this is a commonly used unit in the literature, including by both Kharouba et al.¹⁸ and Cohen et al.¹⁷.

Phylogenetic tree methods

We verified all species names using The Plant List (TPL) function in the Taxonstand package (v. 2.4)⁴³ and obtained data for each taxonomic level possible from the Integrated Taxonomic Information System (ITIS) and National Center for Biotechnology Information (NCBI) databases using the tax_name function in the taxize package (v. 0.9.99)⁴⁴. We then constructed an undated, Linnaean tree in R using the phytools (v. 0.7-47) and ape (v. 5.5) packages^{45,46}. We calibrated a dated phylogeny

using the TreePL program (v.1.0)⁴⁷ combining our tree with divergence dates for each node from molecular sequence data available in Time-tree (v. 4)⁴⁸; this approach allowed us to estimate divergence times of species using penalized likelihoods and apply an approach specifically designed for large phylogenies such as ours⁴⁷. We included as many branch lengths as possible, although data limitations prevented dated genus level divergences for several algae and moth species (Fig. 2).

Statistical analyses

Our modelling approach addresses the challenges inherent when combining phenological time series from different studies and species (including time series length, start dates, observation frequencies, hierarchical structure and resolution of taxonomy). We incorporated the effects of phylogeny into a hierarchical model that allowed variation in both the mean (intercept) and shifts (slopes) for each observation of a phenological event, y_i (where i denotes an individual observation), for a given species (sp), and assumed a normal distribution:

$$y_i \sim \text{normal}(\hat{y}_i, \sigma_e^2). \quad (1)$$

We used a linear model with a hinge in the baseline phenology at 1980. This commonly used method allows us to account for the considerable trends in warming in recent decades as well as species' non-stationary responses to changes in temperature and climate change impacts^{49,50}. Our model thus included the day of year a phenological event occurred (\hat{y}_i), year as the year of an observation since 1980, the shift in phenology as β_{sp} , the species-specific intercept as α_{sp} and the remaining variability, σ_e :

$$\hat{y}_i = \alpha_{sp} + \beta_{sp} \times h(\text{year}_i - 1980), \quad (2)$$

where the hinge function, $h(x)$, if defined as:

$$h(x) = \begin{cases} x, & x > 0 \\ 0, & x \leq 0 \end{cases}. \quad (3)$$

We included a phylogenetic variance–covariance matrix in the parameterization of the normal random vectors:

$$\boldsymbol{\alpha}_{sp} = [\alpha_1, \dots, \alpha_n]^T \text{ such that } \boldsymbol{\alpha} \sim \text{multi-normal}(\mu_\alpha, \mathbf{V}), \quad (4)$$

$$\boldsymbol{\beta}_{sp} = [\beta_1, \dots, \beta_n]^T \text{ such that } \boldsymbol{\beta} \sim \text{multi-normal}(\mu_\beta, \mathbf{V}). \quad (5)$$

The means (μ) of the multivariate normal distributions are root values, reflecting phenology before evolution along the phylogenetic tree. In this model the \mathbf{V} are $n \times n$ phylogenetic variance–covariance matrices with the general matrix specification as:

$$\begin{bmatrix} \sigma_i^2 & \lambda_i \times \sigma_i \times \rho_{12} & \dots & \lambda_i \times \sigma_i \times \rho_{1n} \\ \lambda_i \times \sigma_i \times \rho_{21} & \sigma_i^2 & \dots & \lambda_i \times \sigma_i \times \rho_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ \lambda_i \times \sigma_i \times \rho_{n1} & \lambda_i \times \sigma_i \times \rho_{n2} & \dots & \sigma_i^2 \end{bmatrix} \quad (6)$$

where σ_i^2 is the rate of evolution across a tree (assumed to be constant along all branches) and λ_i is a branch-length scaling parameter (and a measure of phylogenetic signal²⁵). The phylogenetic correlation between species x and y is ρ_{xy} , or the fraction of the tree shared by two species on α_{sp}, β_{sp} . See Morales-Castilla, et al.⁵¹ for additional details regarding this modeling approach. To explore differences in the phenological shifts of lineages and groups—including trophic levels, phenological events and across species habitats—we extracted and compared the posterior distributions for species across the different groups. We present results as means and 90% posterior uncertainty

intervals from our Bayesian phylogenetic models with a precision to one decimal place, which we consider most relevant to our data⁵². We consider trends as different when 90% intervals do not overlap (for example, across trophic levels or with 0 for changes with climate change), but for λ , which is often reported without error, we report all estimates, although we refer to trends as weak when they overlap with 0 and always further mention that such trends are 'not distinguishable from no signal.'

In addition to our main analysis, we performed individual analyses of the four major lineages most represented in our dataset. For these analyses, we ran the same phylogenetic mixed effects models using subsets of our full dataset for species of Aves, Insecta, Magnoliopsida and Amphibia. In performing this analysis using both data from across the evolutionary tree and individual lineages, we could consider responses across all species and within individual lineages.

This modelling approach is a major advance in phylogenetic analyses and produces better estimates of variability across species and variably sampled data. This approach addresses several major biases and potential drivers of variation in the data—specifically, taxonomic diversity, time series length and start year. Most of the species in our dataset are represented by only one single time series, with 56.4% of species from the UK and 28.6% from continental Europe, making it challenging to accurately estimate parameters related to study-level and geographic variability.

Our model included semi-informative priors for each parameter, and model code was validated using test data before analysis. Given the complexity of our posterior geometry and the inferential aims of our study, models were deemed sufficient if they produced \hat{R} values below 1.1. However, our main model generated \hat{R} values close to 1, with well-mixed chains, and values of n_{eff} greater than 10% of the model iterations. We wrote our models in the Stan programming language for Bayesian models using the rstan package⁵³, using R version 4.1.2⁵⁴.

In addition to phenological data, we recorded site coordinates for all studies in which they were reported (95.3% of studies). For all terrestrial species (1,075 species), we extracted monthly temperature data from the WorldClim database for both the full year and the mean 3 month period that spanned the month before an event occurred to the month after an event occurred⁵⁵. Averaging across the minimum and maximum monthly temperatures, we obtained the monthly average temperature of each month for each year and site at which phenological events were recorded. For each continent, the rate of temperature change at each site was estimated using a modified linear mixed effect model with partial pooling across site coordinates for both the intercept and slope. The effect of the temperature model's mean posterior estimates were then modelled against the mean estimated phenological shift for each species phenological event using a simple linear model. Similarly, we used a similar approach to test the relationship between latitude and species phenological shifts.

Simulations of paired versus single-species data

To determine whether the finding that species synchrony is largely preserved with climate change as a result of using paired species data¹⁸, we compared the changes in synchrony of paired species datasets to changes in randomly paired single-species datasets. We assigned both species from the single-species data as either a consumer or resource, and to one of the five following interaction types: competition, herbivory, predation, pollination or parasitism. Our dataset only included one parasitic species, so this interaction was not included in our analyses. We assigned interaction level and type to the single-species data based on the classification of species within the same genus or taxonomic classes in the paired datasets. For each suite of interactions of both the known interacting and randomly paired species, we extracted 1,000 iterations of the posterior draws and calculated the difference in the mean shift in phenology for these iterations, estimating the change in species synchrony (potential asynchrony). Simulations were

performed both across all species within a suite of interactions and for species within terrestrial and aquatic species separately. To visualize the high degree of overlap between the posterior bin probabilities, and generally in our visualizations throughout the manuscript, we used overlapping transparent histograms.

To examine the degree of interannual variation in phenological events (as in Fig. 5), we simulated the extent of naturally occurring variation in phenological events before climate change within each location. Using only time series with a minimum of 5 years of observations before 1980 ($n = 918$), we extracted 500 posterior estimates for each species intercept from our phylogenetic mixed model and added the estimated variability (σ_e^2) for that posterior draw. We then compared this to the shifts in phenological events for a given species, as well as higher shifts (two times and five times current rates).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data we scraped is available through the Knowledge Network for Biocomplexity (<https://doi.org/10.5063/F12J69B2>)⁵⁶.

Code availability

Code developed for this analysis is available through the Knowledge Network for Biocomplexity (<https://doi.org/10.5063/F12J69B2>)⁵⁶.

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Author contributions

Conceptualization: D.L. and E.M.W.; methodology: D.L., E.M.W., G.L., S.J. and M.B.; critical insights: D.L., E.M.W., G.L., S.J. and M.B.; writing—original draft: D.L. and E.M.W.; writing—review and editing: D.L., E.M.W., H.M.K., G.L., S.J. and M.B.

Competing interests

The authors declare no competing interests.

Additional information

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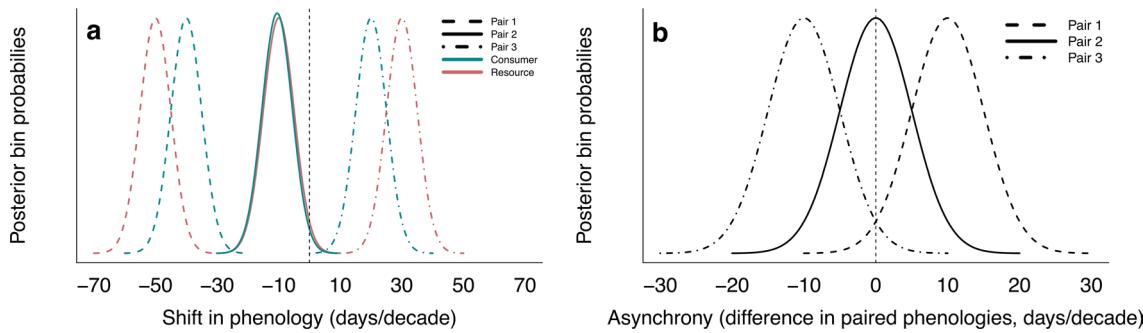
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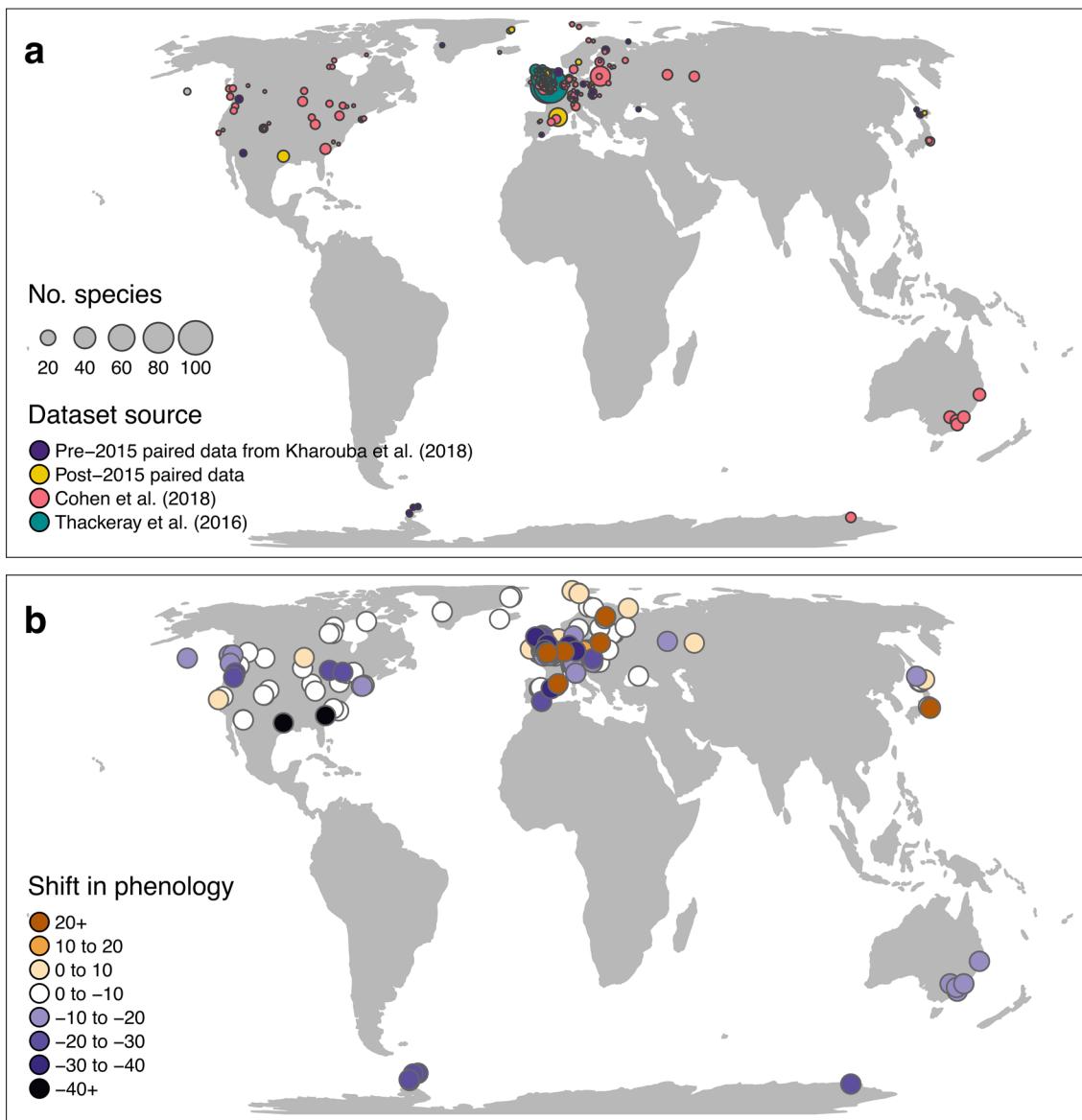
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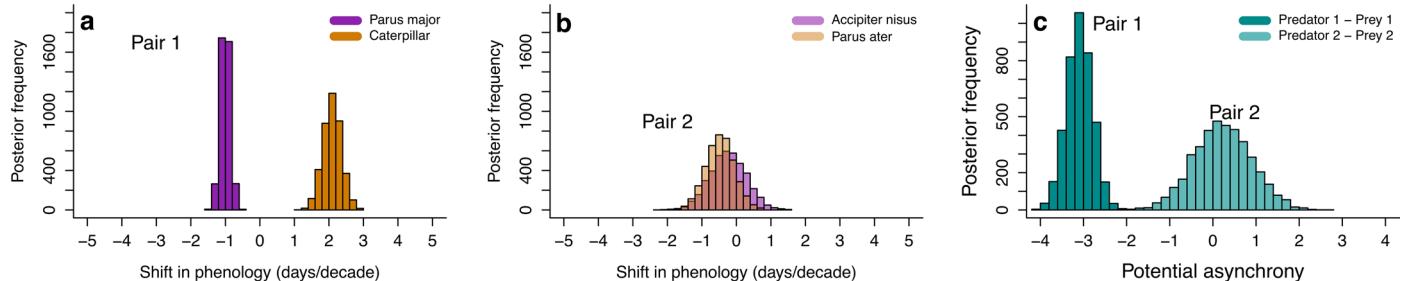
Extended Data Fig. 1 | Conceptual diagram of how phenological shifts by interacting species pairs effect species synchrony. A conceptual diagram of how species within an interacting pair may differ in their phenological shifts and the resulting effects on species synchrony. **a**, Within an interacting pair, illustrated here using a consumer and resource species (shown in blue and red respectively) as an example (though our data includes five types of

interactions), the resource species may shift at a greater, lesser, or equal rate than their consumer. **b**, This results in different synchrony responses, with negative asynchrony occurring when the consumers phenology shifts earlier (dotdash line), positive asynchrony occurring when the resources phenology shifts earlier relative to the consumer (dashed line), and no change when both species shift at the same rate (solid line).



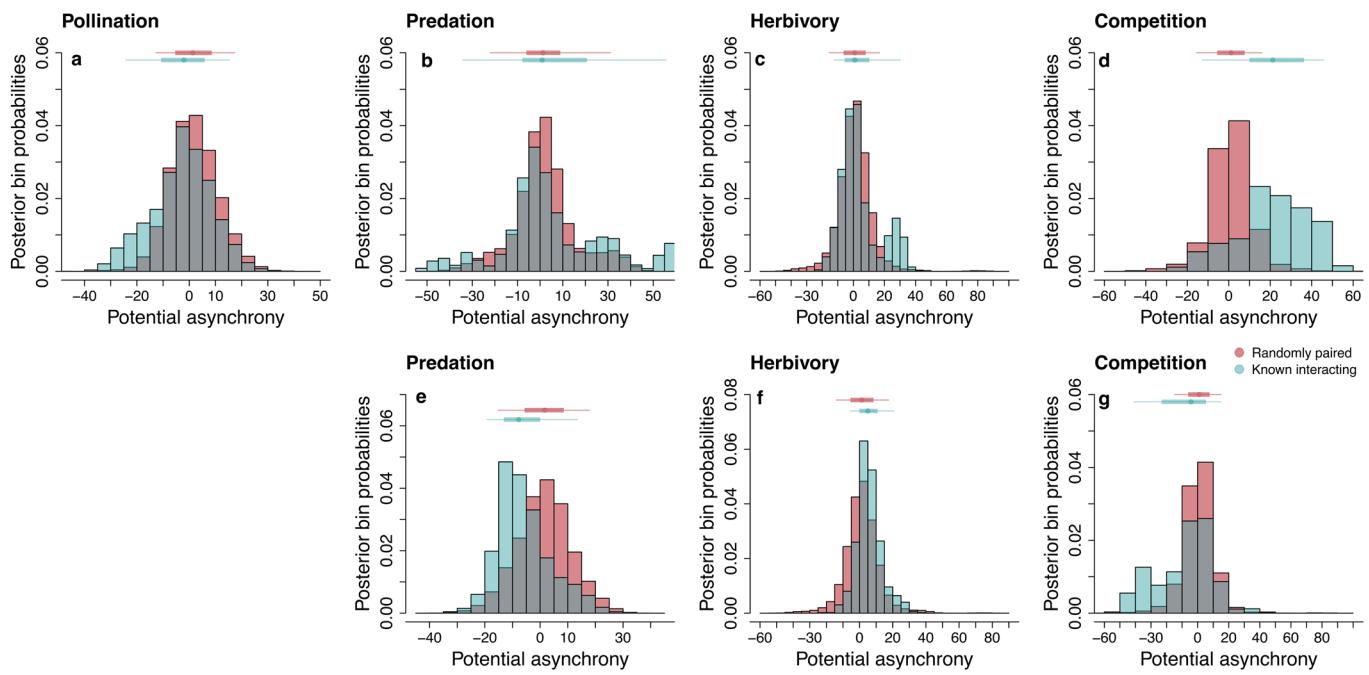
Extended Data Fig. 2 | The global distribution of our phenological time-series and lack of variation with latitudinal gradients. Species time-series were observed across the globe, but with strong biases towards certain regions, **a**, with point colour representing the original source of the dataset and point

size the number of species within a dataset. **b**, The observed trends in species phenological shifts do not vary with latitude despite spanning latitudinal gradients across temperate ecosystems (Table ED1), as shown using points coloured to depict the magnitude of species shift per decade.



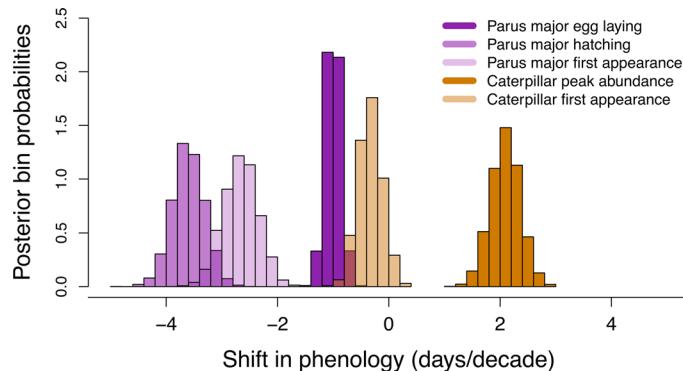
Extended Data Fig. 3 | Species pairs exhibiting variable shifts in phenology and the resulting changes in synchrony. To assess how pairs of species differ in their phenological shifts and synchrony, we randomly sampled 1000 posterior estimates from both the high and low-level species within each interaction, as shown here for two sets of species pairs. **a**, Some pairs differ in their phenological

shifts, as shown for the interaction between *Parus major* and its caterpillar prey, **b**, while others shift at similar rates, shown here for *Accipiter nisus* and *Parus ater*. **c**, Changes in synchrony are calculated as the differences between the high-level species, shown here as predators, and the low-level species, or prey.



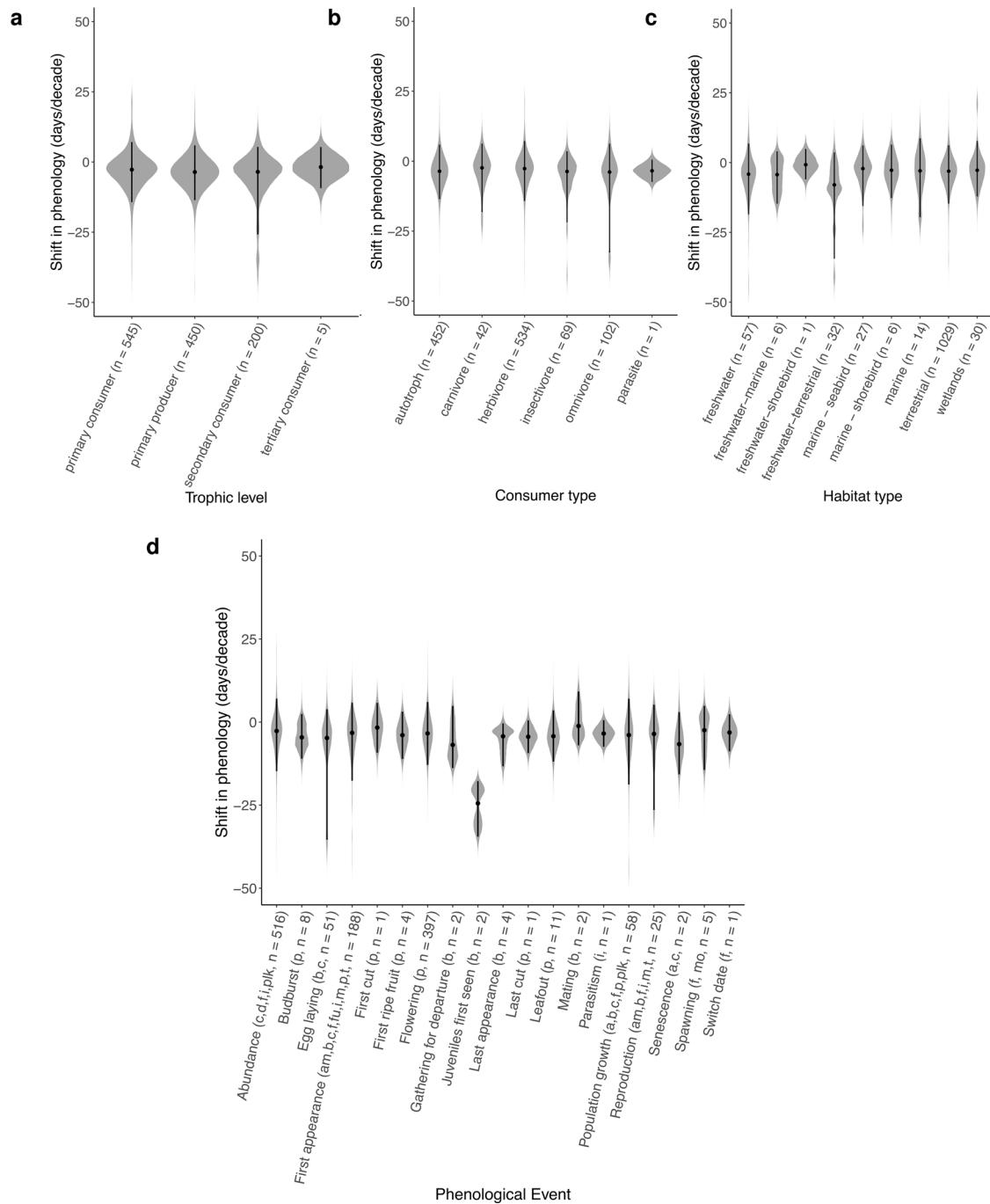
Extended Data Fig. 4 | Species phenological synchrony across suites of interactions when simulated for terrestrial and aquatic interactions separately. Species phenological synchrony across **a**, pollination ($n=47$), **b**, predation ($n=24$), **c**, herbivory ($n=10$), and **d**, competitive ($n=18$) interactions amongst terrestrial species (**a–c**), in comparison to **e**, predation ($n=13$), **f**, herbivory ($n=10$), and **g**, competitive ($n=54$) interactions amongst aquatic species (**e–g**), showed no differences in the distributions of posterior estimates

of consumer or resource species phenological shifts for pairs of known interacting species (in blue) and randomly paired species (in red) for any of the four types of interactions. Plots are normalized by counts, with the x-axis spanning the total density distribution. Above the figures, the two lines depict the 90% uncertainty intervals (thinner line) and 50% interval (thicker line), and the point the median.



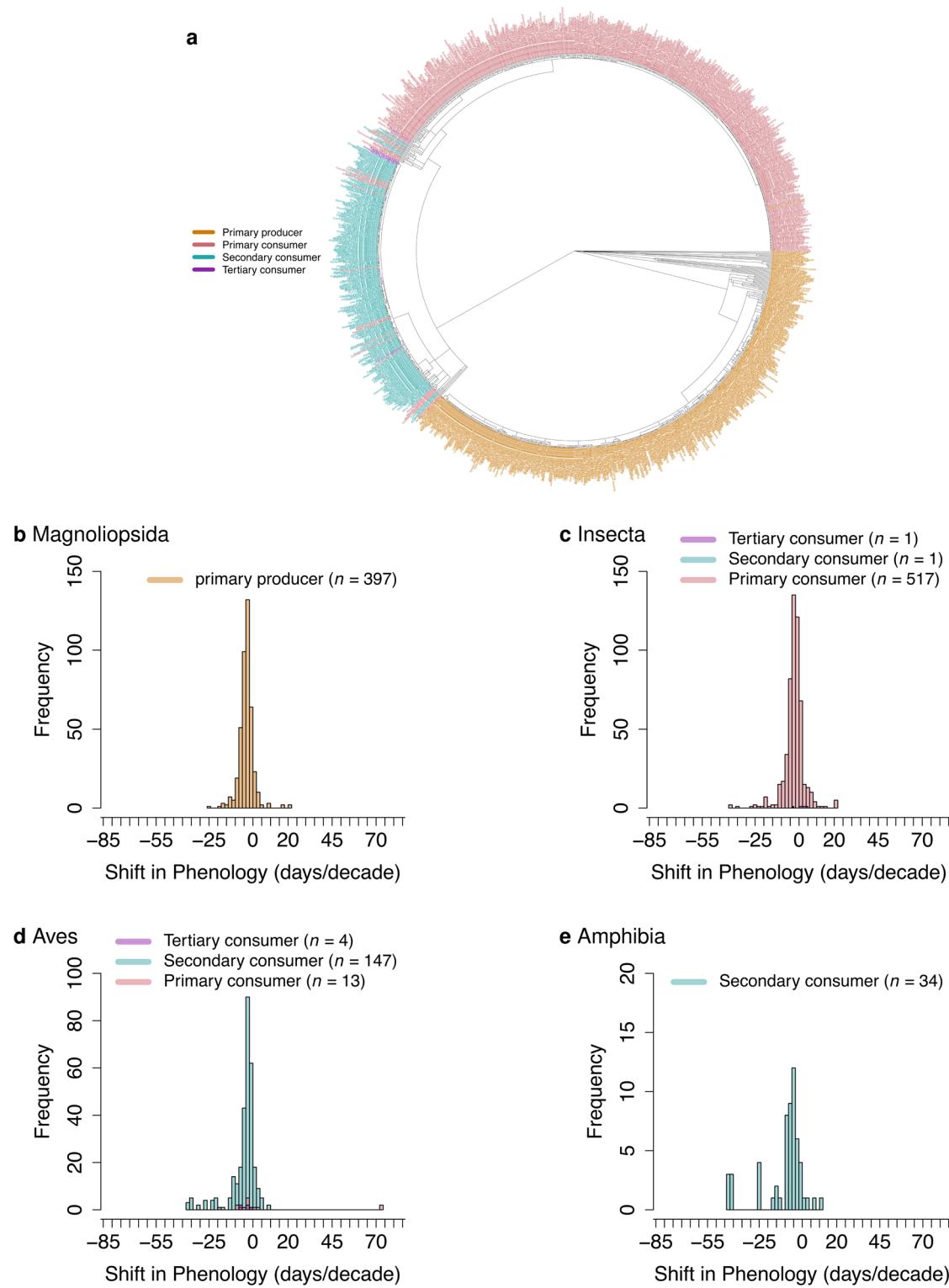
Extended Data Fig. 5 | Estimated phenological shifts of the well-studied interaction between *Parus major* and caterpillars. Our model replicates the strong asynchronies found in interactions of well studied species pairs.

Illustrated here is the classic example of the estimated phenological shifts of *Parus major* and caterpillars, shown across each type of phenological event represented in our dataset.



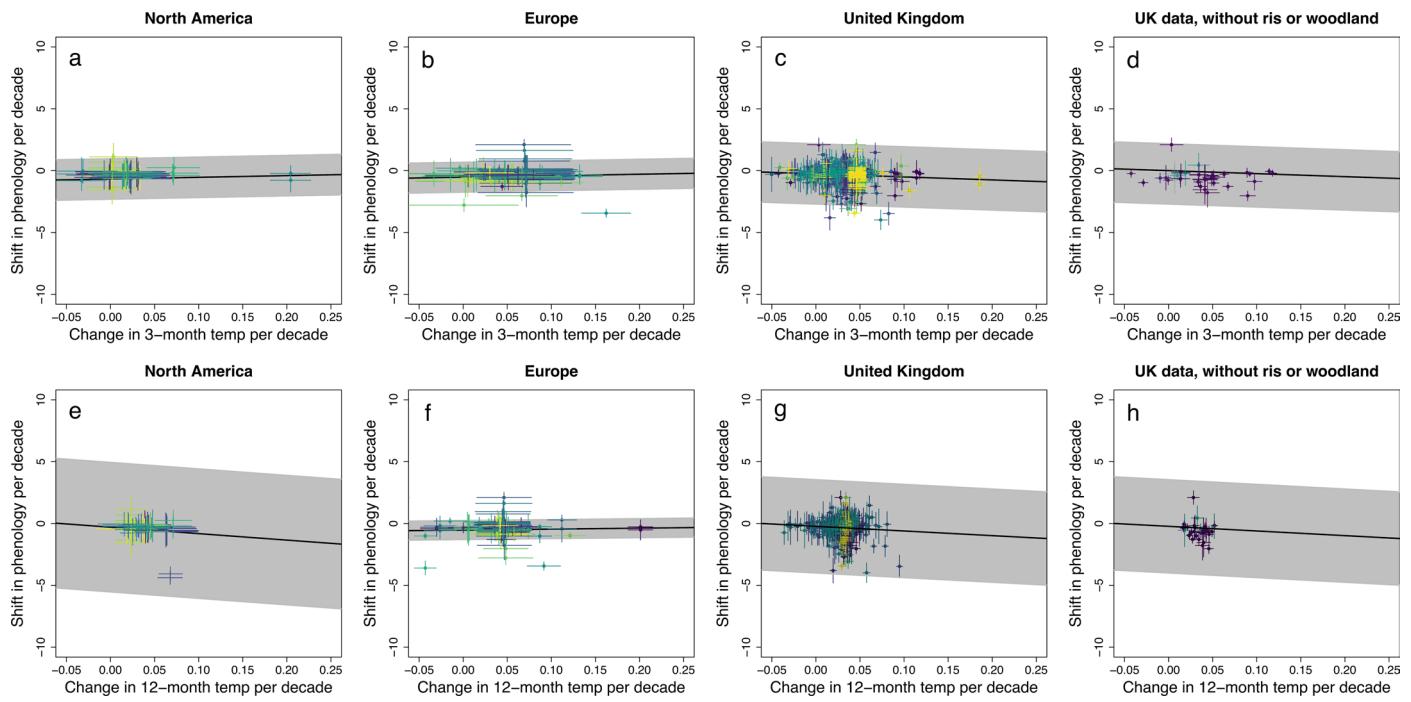
Extended Data Fig. 6 | Species phenological shifts across trophic levels, consumer types, habitats, and types of phenological events. Shifts in species phenology are similar across several grouping factors, including: **a**, trophic levels, **b**, consumer types, and **c**, habitat types. **d**, We also observed similar shifts across phenological events, with the exception of juvenile bird first appearance. Eye-plots of the posterior estimates from our full phylogeny model (including

phylogenetic effects, Table ED1) include a gray distribution as the density of the posteriors, black circles for the median value, thick dark lines depict the 50% quantile interval, and thin black lines depict the 90% quantile interval. Letters denote groups of species – f = fish, mo = mollusc, a = arachnids, am = amphibians, b = birds, c = copepod, d = diatom, f = fish, fu = fungi, i = insects, m = mammals, p = plants, plk = plankton, t = turtle.



Extended Data Fig. 7 | Trophic level differences across our species phylogeny and well-studied evolutionary lineages. **a**, Within our highly diverse and global dataset, species trophic level is highly confounded with phylogeny, limiting our ability to model trophic level directly. This is further illustrated for the four most

well-sampled evolutionary lineages in our dataset, each of which map strongly to certain trophic levels, **b**, as all plants are primary producers, **c**, while most insects are primary consumers, **c**, the majority of birds (aves) secondary consumers, **d**, and all of amphibia are secondary consumers.



Extended Data Fig. 8 | Species phenological shifts with temperature change across study sites. Shifts in species phenology show no strong relationships to the rate of temperature change at each site of observation across a & e, North America ($n = 42$ sites), b & f, Europe ($n = 109$ sites), c & g, the United Kingdom ($n = 98$ sites), d & h, or independent studies in the United Kingdom, not including

data from RIS or the Woodland trust (n sites = 14). Analyses were replicated for both the three month period around which an event occurred (a–d) and for the annual monthly temperatures (e–h). Gray bands represent the 50% quantile interval and crosses the 50%.

Extended Data Table 1 | Summary of model outputs from our phylogenetic model, latitudinal model, and models of well-sample evolutionary lineages

Model	Variable	Mean	25%	75%	n_eff	Rhat
Main	α	173.55	163.40	183.91	7177.03	1.00
	λ_α	0.39	0.31	0.47	5949.33	1.00
	μ_{sp}	-0.31	-0.39	-0.23	5057.54	1.00
	λ_β	0.11	0.05	0.15	3720.85	1.00
	σ_{λ_α}	72.92	68.00	77.21	6885.79	1.00
	σ_{λ_β}	0.77	0.74	0.79	3604.46	1.00
	σ_{doy}	19.14	19.10	19.19	5861.51	1.00
	α	-0.48	-0.51	-0.46	4454	1.00
Latitude	$\mu_{latitude}$	0.00	0.00	0.00	4279	1.00
	σ	0.66	0.65	0.67	4152	1.00
	α	135.45	120.91	149.54	1109.15	1.00
Amphibia	λ_α	0.31	0.16	0.43	8131.95	1.00
	μ_{sp}	-1.28	-1.68	-0.88	13517.40	1.00
	λ_β	0.26	0.15	0.36	14272.34	1.00
	σ_{λ_α}	71.30	64.89	76.85	11668.76	1.00
	σ_{λ_β}	1.77	1.54	1.96	8847.29	1.00
	σ_{doy}	30.20	29.68	30.69	21057.70	1.00
Aves	α	143.56	139.10	148.45	118.11	1.02
	λ_α	0.08	0.03	0.11	2065.25	1.00
	μ_{sp}	-0.34	-0.44	-0.25	13079.24	1.00
	λ_β	0.20	0.12	0.27	9924.23	1.00
	σ_{λ_α}	67.50	65.04	69.75	8729.92	1.00
	σ_{λ_β}	1.06	1.01	1.10	10437.31	1.00
Insecta	σ_{doy}	21.36	21.26	21.46	19840.64	1.00
	α	202.11	197.26	207.02	57.83	1.09
	λ_α	0.09	0.02	0.13	577.54	1.01
	μ_{sp}	-0.22	-0.29	-0.15	13797.50	1.00
	λ_β	0.14	0.07	0.18	9662.33	1.00
	σ_{λ_α}	52.75	50.91	54.17	891.74	1.01
Magnoliopsida	σ_{λ_β}	0.59	0.56	0.62	4908.87	1.00
	σ_{doy}	20.73	20.64	20.81	22811.61	1.00
	α	145.40	142.91	147.85	56.28	1.01
	λ_α	0.12	0.08	0.16	1215.21	1.00
	μ_{sp}	-0.41	-0.44	-0.38	9683.58	1.00
	λ_β	0.19	0.13	0.24	6610.99	1.00
	σ_{λ_α}	43.77	42.59	44.82	7331.78	1.00
	σ_{λ_β}	0.50	0.48	0.52	5576.54	1.00
	σ_{doy}	12.70	12.64	12.76	11360.82	1.00

Summary of model outputs from our phylogenetic model using all species and phenological event data (n = 1279), our latitudinal model testing for latitudinal relationships with phenology (across n = 263 sites), and models of lineages. Results are reported in days per year.

Extended Data Table 2 | Bibliographic information of recent studies added to the database for 2015 to 2020

Source	Species name	Phenophase	Taxonomic class	No. years
Burgess <i>et al.</i> ⁴²	Caterpillar	abundance	insecta	9
Burgess <i>et al.</i> ⁴²	<i>Quercus robur</i>	leafout	dicotyledon	19
Carter <i>et al.</i> ⁵⁶	<i>Acrid crepitans</i>	first appearance	amphibia	6
Carter <i>et al.</i> ⁵⁶	<i>Bufo valliceps</i>	first appearance	amphibia	12
Carter <i>et al.</i> ⁵⁶	<i>Bufo valliceps</i>	first appearance	amphibia	12
Carter <i>et al.</i> ⁵⁶	<i>Bufo woodhousei</i>	first appearance	amphibia	12
Carter <i>et al.</i> ⁵⁶	<i>Bufo woodhousei</i>	first appearance	amphibia	12
Carter <i>et al.</i> ⁵⁶	<i>Gastrophryne carolinensis</i>	first appearance	amphibia	13
Carter <i>et al.</i> ⁵⁶	<i>Gastrophryne carolinensis</i>	first appearance	amphibia	13
Carter <i>et al.</i> ⁵⁶	<i>Hyla cinerea</i>	first appearance	amphibia	12
Carter <i>et al.</i> ⁵⁶	<i>Hyla cinerea</i>	first appearance	amphibia	12
Carter <i>et al.</i> ⁵⁶	<i>Hyla versicolor</i>	first appearance	amphibia	13
Carter <i>et al.</i> ⁵⁶	<i>Hyla versicolor</i>	first appearance	amphibia	13
Carter <i>et al.</i> ⁵⁶	<i>Pseudacris crucifer</i>	first appearance	amphibia	15
Carter <i>et al.</i> ⁵⁶	<i>Pseudacris crucifer</i>	first appearance	amphibia	15
Carter <i>et al.</i> ⁵⁶	<i>Pseudacris triseriata</i>	first appearance	amphibia	13
Carter <i>et al.</i> ⁵⁶	<i>Pseudacris triseriata</i>	first appearance	amphibia	13
Carter <i>et al.</i> ⁵⁶	<i>Rana catesbeiana</i>	first appearance	amphibia	12
Carter <i>et al.</i> ⁵⁶	<i>Rana catesbeiana</i>	first appearance	amphibia	12
Carter <i>et al.</i> ⁵⁶	<i>Rana clamitans</i>	first appearance	amphibia	13
Carter <i>et al.</i> ⁵⁶	<i>Rana clamitans</i>	first appearance	amphibia	13
Carter <i>et al.</i> ⁵⁶	<i>Rana palustris</i>	first appearance	amphibia	6
Carter <i>et al.</i> ⁵⁶	<i>Rana sphenocephala</i>	first appearance	amphibia	15
Carter <i>et al.</i> ⁵⁶	<i>Rana sphenocephala</i>	first appearance	amphibia	15
Davies ⁵⁷	<i>Alliaria petiolata</i>	flowering	dicotyledon	12
Davies ⁵⁷	<i>Anthocharis cardamines</i>	first appearance	insecta	17
Davies ⁵⁷	<i>Cardamine pratensis</i>	flowering	dicotyledon	17
Donoso <i>et al.</i> ⁵⁸	<i>Ballota nigra</i>	flowering	dicotyledon	17
Donoso <i>et al.</i> ⁵⁸	<i>Brassica nigra</i>	flowering	dicotyledon	17
Donoso <i>et al.</i> ⁵⁸	<i>Celastrina argiolus</i>	abundance	insecta	13
Donoso <i>et al.</i> ⁵⁸	<i>Coenonympha pamphilus</i>	abundance	insecta	17
Donoso <i>et al.</i> ⁵⁸	<i>Colias croceus</i>	abundance	insecta	16
Donoso <i>et al.</i> ⁵⁸	<i>Cynthia cardui</i>	abundance	insecta	12
Donoso <i>et al.</i> ⁵⁸	<i>Diplotaxis erucoides</i>	flowering	dicotyledon	13
Donoso <i>et al.</i> ⁵⁸	<i>Ditrichia viscosa</i>	flowering	dicotyledon	16
Donoso <i>et al.</i> ⁵⁸	<i>Helminthotheca echioides</i>	flowering	dicotyledon	16
Donoso <i>et al.</i> ⁵⁸	<i>Lamium hybridum</i>	flowering	dicotyledon	13
Donoso <i>et al.</i> ⁵⁸	<i>Leptotes pirithous</i>	abundance	insecta	13
Donoso <i>et al.</i> ⁵⁸	<i>Limonium vulgare</i>	flowering	dicotyledon	14
Donoso <i>et al.</i> ⁵⁸	<i>Lotus corniculatus</i>	flowering	dicotyledon	17
Donoso <i>et al.</i> ⁵⁸	<i>Lycena phlaeas</i>	abundance	insecta	14
Donoso <i>et al.</i> ⁵⁸	<i>Lythrum salicaria</i>	flowering	dicotyledon	17
Donoso <i>et al.</i> ⁵⁸	<i>Melanargia lachesis</i>	abundance	insecta	15
Donoso <i>et al.</i> ⁵⁸	<i>Ochrodes venata</i>	abundance	insecta	17
Donoso <i>et al.</i> ⁵⁸	<i>Pieris hieracioides</i>	flowering	dicotyledon	16
Donoso <i>et al.</i> ⁵⁸	<i>Pieris napi</i>	abundance	insecta	17
Donoso <i>et al.</i> ⁵⁸	<i>Pieris rapae</i>	abundance	insecta	17
Donoso <i>et al.</i> ⁵⁸	<i>Plebejus argus</i>	abundance	insecta	17
Donoso <i>et al.</i> ⁵⁸	<i>Polygonatum icarus</i>	abundance	insecta	17
Donoso <i>et al.</i> ⁵⁸	<i>Prunus spinosa</i>	flowering	dicotyledon	13
Donoso <i>et al.</i> ⁵⁸	<i>Ranunculus sardous</i>	flowering	dicotyledon	13
Donoso <i>et al.</i> ⁵⁸	<i>Rubus ulmifolius</i>	flowering	dicotyledon	17
Donoso <i>et al.</i> ⁵⁸	<i>Sonchus aquatilis</i>	flowering	dicotyledon	15
Donoso <i>et al.</i> ⁵⁸	<i>Taraxacum campylodes</i>	flowering	dicotyledon	16
Donoso <i>et al.</i> ⁵⁸	<i>Trifolium fragiferum</i>	flowering	dicotyledon	16
Donoso <i>et al.</i> ⁵⁸	<i>Trifolium pratense</i>	flowering	dicotyledon	17
Kudo & Cooper ⁵⁹	<i>Bombyx hypocrita</i>	first appearance	insecta	19
Kudo & Cooper ⁵⁹	<i>Corydalis ambigua</i>	flowering	dicotyledon	19
Regnier <i>et al.</i> ⁶⁰	<i>Ammodytes marinus</i>	abundance	actinopterygi	7
Regnier <i>et al.</i> ⁶⁰	<i>Calanus finmarchicus</i>	egg laying	hexanauplii	7
Regnier <i>et al.</i> ⁶⁰	<i>Calanus helgolandicus</i>	egg laying	maxillopoda	7
Reneerkens <i>et al.</i> ⁶¹	<i>Arenaea</i>	abundance	arachnida	15
Reneerkens <i>et al.</i> ⁶¹	<i>Cnidiris alba</i>	reproduction	aves	7
Reneerkens <i>et al.</i> ⁶¹	<i>Diptera</i>	abundance	insecta	17
Reneerkens <i>et al.</i> ⁶¹	<i>Hemiptera</i>	abundance	insecta	15
Reneerkens <i>et al.</i> ⁶¹	<i>Hymenoptera</i>	abundance	insecta	17
Reneerkens <i>et al.</i> ⁶¹	<i>Lepidoptera</i>	abundance	insecta	15
Reneerkens <i>et al.</i> ⁶¹	<i>Thysanoptera</i>	abundance	insecta	12
Senior <i>et al.</i> ⁶²	<i>Acer pseudoplatanus</i>	budburst	dicotyledon	20
Senior <i>et al.</i> ⁶²	<i>Drepanosiphum platanoidis</i>	first appearance	insecta	20
Senior <i>et al.</i> ⁶²	<i>Drepanosiphum platanoidis</i>	first appearance	insecta	20
Senior <i>et al.</i> ⁶²	Parasitoids	parasitism	insecta	20
Senior <i>et al.</i> ⁶²	<i>Periphyllus testudinaceus</i>	first appearance	insecta	20
Senior <i>et al.</i> ⁶²	<i>Periphyllus testudinaceus</i>	first appearance	insecta	20
Shutt <i>et al.</i> ⁶³	<i>Betula</i>	budburst	dicotyledon	5
Shutt <i>et al.</i> ⁶³	<i>Cyanistes caeruleus</i>	egg laying	aves	5
Wegge & Rolstad ⁶⁴	<i>Tetrao tetrix</i>	reproduction	aves	38
Wegge & Rolstad ⁶⁴	<i>Tetrao urogallus</i>	reproduction	aves	38
Wegge & Rolstad ⁶⁴	<i>Vaccinium myrtillus</i>	population growth	dicotyledon	38

Bibliographic information for recent studies added to the database for 2015 to 2020, including details for phenological events recorded within a time-series, and their characteristics.

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our [Editorial Policies](#) and the [Editorial Policy Checklist](#).

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a Confirmed

- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
- A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- The statistical test(s) used AND whether they are one- or two-sided
Only common tests should be described solely by name; describe more complex techniques in the Methods section.
- A description of all covariates tested
- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
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- For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
Give P values as exact values whenever suitable.
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection No software was used

Data analysis We used code written in the R (version 4.1.2) and Stan (version 2.19.3) programming languages, both of which are free, open source softwares. We also used TreePL package to build our phylogenetic tree, which is also free and open source.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

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All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
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All data we scraped and Stan code for this study will be made available online at the Knowledge Network for Biocomplexity prior to publication.

Research involving human participants, their data, or biological material

Policy information about studies with [human participants or human data](#). See also policy information about [sex, gender \(identity/presentation\), and sexual orientation](#) and [race, ethnicity and racism](#).

Reporting on sex and gender	NA
Reporting on race, ethnicity, or other socially relevant groupings	NA
Population characteristics	NA
Recruitment	NA
Ethics oversight	NA

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences Behavioural & social sciences Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We performed a meta-analysis using phenological time-series data for 1200 species spanning the tree of life, testing for trends in phenological shifts and changes in synchrony. Data was analyzed using a novel Bayesian phylogenetic model that allowed us to incorporate evolutionary history.
Research sample	We obtained data from 147 existing studies and long-term monitoring programs. A large portion of our data was obtained from three existing meta-analyses. We also added updated data from a literature review using the same search terms as one of the previous meta-analyses.
Sampling strategy	We used existing datasets with diverse sampling strategies.
Data collection	We used existing datasets and obtained data through data requests and a standardized literature review.
Timing and spatial scale	Our data reflects the global distribution of available data. To ensure our ability to detect changes in phenology, we excluded studies with less than five years of data. Our datasets include phenological observations spanning from 1933 to 2020.
Data exclusions	Data was only excluded for species with fewer than five years of phenological observations.
Reproducibility	In sharing our model code and the datasets we created, including the additional information we compiled for species life history traits, promotes the reproducibility of our work.
Randomization	We allocated species into groups based on their natural history and ecological constraints, such as being terrestrial versus aquatic. Since we are using existing datasets, we were not able to control the randomization of individuals or observations.
Blinding	Blinding is not relevant to our study as we were using existing data and our aim was to include as diverse and globally distributed data as possible.

Did the study involve field work? Yes No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
<input checked="" type="checkbox"/>	Antibodies
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<input checked="" type="checkbox"/>	Animals and other organisms
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<input checked="" type="checkbox"/>	Plants

Methods

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Plants

Seed stocks

Report on the source of all seed stocks or other plant material used. If applicable, state the seed stock centre and catalogue number. If plant specimens were collected from the field, describe the collection location, date and sampling procedures.

Novel plant genotypes

Describe the methods by which all novel plant genotypes were produced. This includes those generated by transgenic approaches, gene editing, chemical/radiation-based mutagenesis and hybridization. For transgenic lines, describe the transformation method, the number of independent lines analyzed and the generation upon which experiments were performed. For gene-edited lines, describe the editor used, the endogenous sequence targeted for editing, the targeting guide RNA sequence (if applicable) and how the editor was applied.

Authentication

Describe any authentication procedures for each seed stock used or novel genotype generated. Describe any experiments used to assess the effect of a mutation and, where applicable, how potential secondary effects (e.g. second site T-DNA insertions, mosaicism, off-target gene editing) were examined.