

# Tritrophic phenological match-mismatch in space and time

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**Increasing temperatures associated with climate change may generate phenological mismatches that disrupt previously synchronous trophic interactions. Most work on mismatch has focused on temporal trends, whereas spatial variation in the degree of trophic synchrony has largely been neglected, even though the degree to which mismatch varies in space has implications for meso-scale population dynamics and evolution. Here we quantify latitudinal trends in phenological mismatch, using phenological data on an oak-caterpillar-bird system from across the UK. Increasing latitude delays phenology of all species, but more so for oak, resulting in a shorter interval between leaf emergence and peak caterpillar biomass at northern locations. Asynchrony found between peak caterpillar biomass and peak nestling demand of blue tits, great tits and pied flycatchers increases in earlier (warm) springs. There is no evidence of spatial variation in the timing of peak nestling demand relative to peak caterpillar biomass for any species. Phenological mismatch alone is thus unlikely to explain spatial variation in population trends. Given projections of continued spring warming, we predict that temperate forest birds will become increasingly mismatched with peak caterpillar timing. Latitudinal invariance in the direction of mismatch may act as a double-edged sword that presents no opportunities for spatial buffering from the effects of mismatch on population size, but generates spatially consistent directional selection on timing, which could facilitate rapid evolutionary change.**

Temperature changes are impacting phenology<sup>1</sup>, prompting concern that previously synchronous trophic interactions may be disrupted and lead to negative impacts on consumer fitness and demography<sup>2–4</sup>. Trophic asynchrony or mismatch appears to be most prevalent in the food webs of seasonal habitats, such as deciduous forests and aquatic systems<sup>5</sup>, where resource peaks are ephemeral. Most studies of natural variation in mismatch and its impacts on the fitness and population trends of terrestrial consumers are on temporal data. However, it is also possible for mismatch to vary in space if species respond differently via plasticity or local adaptation to geographic variation in cues. The scarcity of studies addressing the spatial dimension of variation in mismatch<sup>6</sup> means we have little evidence on whether the insights into mismatch estimated at one site can be extrapolated to others.

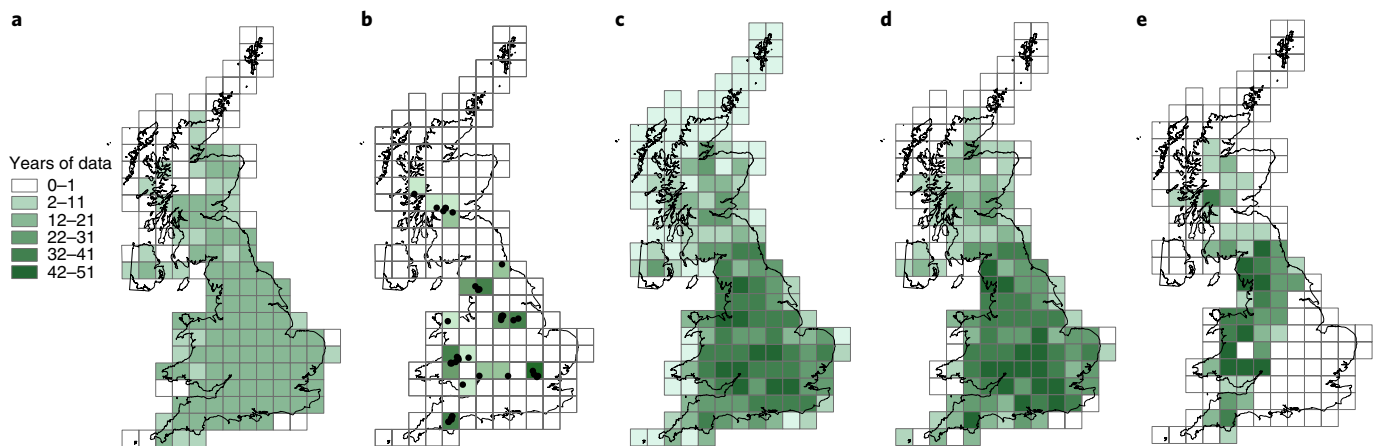
The degree to which mismatch varies in space has the potential to impact on both population trends and the evolution of consumer species on a meso-scale (Supplementary Table 1). Consider the following latitudinal trends in the phenology of a consumer and a resource, assuming that latitudinal variation in consumer phenology has a plastic basis<sup>7</sup>. If all consumer populations, regardless of their latitude, experience the same magnitude and direction of mismatch (Supplementary Table 1b), which impacts negatively on vital rates, all consumer populations may decline in the short term. If populations of the consumer possess additive variance for

phenology, over longer time periods spatially consistent directional selection arising from directional mismatch may facilitate adaptation to reduce mismatch<sup>8</sup>, although the rate of evolutionary change will also depend on the effect of mismatch on population size and the standing genetic variation. In a second example (Supplementary Table 1c), if the consumer phenology varies less over space than the resource phenology<sup>9</sup>, and this generates spatial variation in the direction of mismatch, in the short term there may be spatial buffering that limits population declines. In this case, the consequences of mismatch on one population may be buffered by dispersal from a matched population elsewhere<sup>6</sup>. With gene flow, spatial variation in the direction of selection may oppose the adaption of mismatched populations to their local optima<sup>8</sup>.

Here, we use the well-studied tritrophic deciduous tree-caterpillar-passerine-bird food chain—a highly seasonal system—to identify the extent to which consumer phenology tracks resource phenology over time and space. The phenologies of these three trophic levels advance with warmer spring temperatures, although birds typically advance by less than trees or caterpillars<sup>10,11</sup>, causing bird-caterpillar mismatch to be most pronounced in warm springs and associated with strong directional selection for earlier laying<sup>12</sup>.

We estimated the spatial (latitudinal) and temporal (among-year) trends in relative phenology of consumer (caterpillar) and primary resource (oak) species, and the synchrony of secondary consumer

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**Fig. 1 | Number of years of data for each 50 km grid cell used for each trophic level and bird species. a, Oak. b, Frass, with trapping locations indicated by dots. c, Blue tit. d, Great tit. e, Pied flycatcher.**

(bird) peak nestling demand and peak caterpillar resource availability. Fig. 1 shows the distribution of sampling across the UK and among years. We used 10,073 observations of pedunculate oak (*Quercus robur*) first leafing for the period 1998–2016. The timing of peak arboreal caterpillar community biomass was inferred from frass captured in traps set beneath oak trees at sites across the UK for the period 2008–2016 (ref. <sup>13</sup>) (696 trap years). Bird phenology was calculated using first egg dates (FEDs) from across the UK for the period 1960–2016, comprising 36,839 blue tit (*Cyanistes caeruleus*), 24,427 great tit (*Parus major*) and 23,813 pied flycatcher (*Ficedula hypoleuca*) nests. The phenologies of oak<sup>14</sup> and all three bird species<sup>7</sup> have been shown to respond negatively to mean spring temperatures over time and space in a manner that suggests plasticity is responsible for the majority of the spatiotemporal variation and that temperature may be the proximate or ultimate phenological cue. Here, we show that frass timing exhibits similar trends, correlating negatively with temperature over time and space, albeit more shallowly and non-significantly over space (Supplementary Materials).

Our focus was on the relationship between the phenologies of interacting species<sup>15</sup>. Where timing changed more in one species than the other, this was indicative of spatial or temporal variation in the magnitude—and potentially the direction—of mismatch. In the UK, latitude provides a major temperature cline along which phenology varies at large scales; therefore, the spatial component of our study addresses latitudinal trends in the relative phenology of species pairs. We also considered the relationship between the timing of the consumer and resource as the major axis slopes estimated over time (years) and space (that is, among 50 km grid cells after de-trending for the latitudinal gradient in the phenology of each species). For the bird–caterpillar interaction, we can derive predictions in the timing of peak consumer demand and peak resource availability, which enables us to estimate the absolute departure from synchrony (demand earlier or later than supply).

## Results and discussion

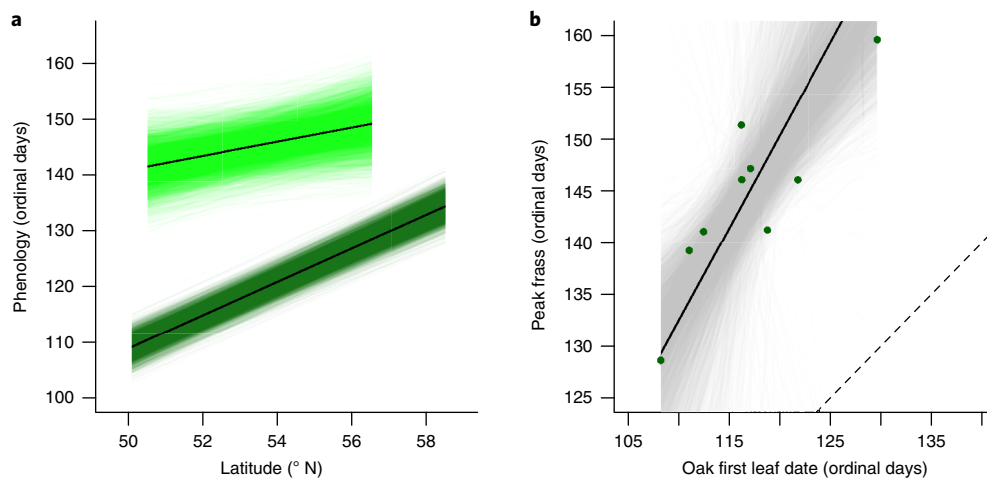
Starting at the base of this food chain, for the average latitude (52.63°N) and year (in terms of phenology) in our dataset, there is a 27.6 day interval between oak first leaf and peak caterpillar biomass. With increasing latitude, the delay in oak leafing is significantly steeper than that of the caterpillar peak (Fig. 2a and Supplementary Table 3a). This results in a reduction of the predicted interval to 22 days at 56°N. After de-trending for latitudinal effects, the spatial relationship between the phenologies of these species is poorly estimated (Table 1) and caterpillar phenology varies more over time than space (Supplementary Table 3). Among years, the timing of

oaks and caterpillars is strongly positively correlated (Table 1a) and the major axis slope does not depart significantly from 1 (Fig. 2b and Table 1b). This result is consistent with the caterpillar consumer perfectly tracking the timing of the resource over time. This is consistent with earlier work showing that oaks and one of their main caterpillar consumers—the winter moth, *Operophtera brumata*—are similarly sensitive to temperature<sup>16</sup>. The shortening of the time between first leaf and peak caterpillar availability as latitude increases may result from the action of a third variable, such as photoperiod, acting on one or both species. Alternatively, it may represent an adaptation of the life cycle of Lepidoptera species to the shorter spring and summer period in the north<sup>6</sup>.

In the average year and at the average latitude, FEDs of blue tits (posterior mean ordinal day: 118.30 (95% credible interval: 116.83 to 119.85); Supplementary Table 3b) and great tits (day 118.95 (117.20 to 120.61); Supplementary Table 3c) were approximately one month earlier than peak caterpillar availability (around day 148). However, peak demand was when nestlings were around 10 days old<sup>17,18</sup>, and once we allowed for average clutch sizes and incubation durations (see Methods), we found that peak demand occurred soon after peak resource availability, with mean peak demand–mean peak resource = 3.39 (−6.63 to 8.86) days in blue tits and 2.01 (−3.99 to 7.71) days in great tits. Pied flycatchers also lay earlier (day 135.04 (133.55 to 136.53); Supplementary Table 3d) than the peak caterpillar biomass, but predicted peak nestling demand occurred 12.87 (6.69 to 19.40) days later than peak caterpillar availability, suggesting substantial trophic mismatch in the average UK environment.

With increasing latitude, the phenology of caterpillars was delayed by ~1.3 days °N<sup>−1</sup> and the point estimates for the equivalent latitudinal trend in birds were from 1.67–1.93 days °N<sup>−1</sup> (Supplementary Tables 3b–d). While the slope for birds is marginally steeper than for caterpillars, such that birds in the north are slightly more mismatched, we have no evidence for a significant latitudinal trend in mismatch (Fig. 3a–c). Moreover, the effect size of any latitudinal trend in mismatch is small, as the point estimate of the magnitude of change in the relative phenologies between consumer and resource over the latitudinal range of our data (50–57°N) is <5 days in each case.

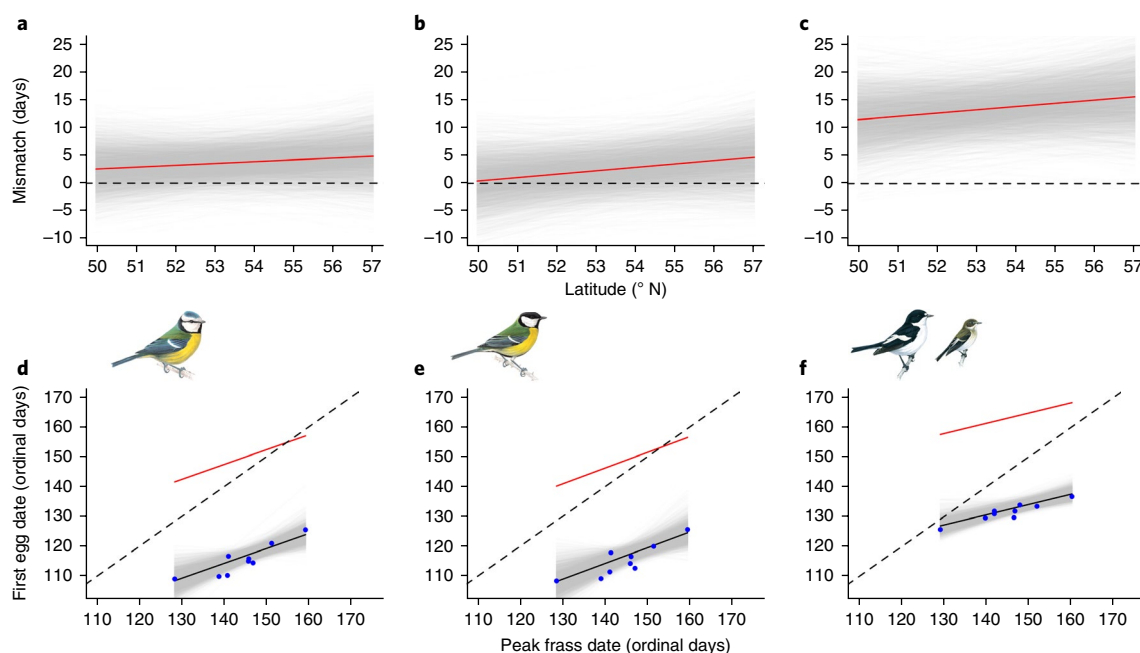
Across years, the timing of the caterpillar peak date and FED is strongly and significantly positively correlated for all three bird species (Table 1a). The major axis slope is significantly <1 for all three bird species. This means that among years, FED varied by less than the timing of the caterpillar resource peak (Table 1b and Fig. 3d–f), which gave rise to year-to-year variation in the degree of mismatch. For every 10 day advance in the caterpillar peak, the corresponding bird advance is estimated to be 5.0, 5.3 and 3.4 days for blue tits,



**Fig. 2 | Latitudinal effects on phenology, and the relationship between oak first leaf dates and peak frass. a**, Relationship between latitude and oak leafing (dark green) and peak caterpillar abundance (light green). **b**, Among-year relationship between the timings of oak first leaf date and peak frass. Data points represent the posterior means for the best linear unbiased predictions for years that have observations for both trophic levels. The dashed line corresponds to unity, which is plotted to illustrate the relative slopes. An offset intercept is expected owing to the growth and development of caterpillars. In **a** and **b**, the solid lines correspond to the mean prediction. The shaded areas correspond to the posterior distribution of predictions under type I regression (**a**) and major axis regression (**b**).

great tits and pied flycatchers, respectively. In late springs (that is, under colder conditions) peak demand from blue tit and great tit nestlings is expected to coincide with the peak resource availability, whereas pied flycatcher peak demand occurs soon after the resource peak (Fig. 3d–f). When caterpillar phenology is earlier (that is, warmer springs), the peak demand of nestlings is predicted to be substantially later than peak resource availability, rendering the

nestlings of all three species mismatched, and pied flycatchers most mismatched. For example, in the earliest year for which we have caterpillar data (2011), at the average latitude, the peak demand of the nestling birds is predicted to occur 17.78, 11.74 and 27.03 days, respectively, after the peak availability of caterpillars. The patterns of temporal variation in mismatch we identify for these species are very similar to those reported for great tits in the UK<sup>19</sup> and all three



**Fig. 3 | Relationships between latitude and mismatch, and the timing of peak frass and first egg date in three avian species. a–f**, Relationship between latitude and mismatch (**a–c**) and timing of peak frass versus first egg date among years (**d–f**) for blue tits (**a** and **d**), great tits (**b** and **e**) and pied flycatchers (**c** and **f**). In **a–c**, mismatch is defined as the timing of peak avian demand minus the timing of peak frass availability, with peak nestling demand calculated as when nestlings were predicted to be 10 days old (see Methods). In **d–f**, data points represent the posterior means for the best linear unbiased predictions for years that have observations for both birds and caterpillars, black lines are the among-year mean major axis slope. In all panels, red lines are the predicted relationship between peak resource availability and peak demand, dashed lines correspond to unity and grey shading represents the posterior distribution of predictions. Bird drawings reproduced with permission from Mike Langman, RSPB.

**Table 1 | Correlations and major axis slopes for the phenology of the higher trophic level on the lower trophic level in time and de-trended space**

	Oak leafing	Peak caterpillar	Blue tit FED	Great tit FED	Pied flycatcher FED
<b>(a) Correlations</b>					
Oak leafing	–	<b>0.69 (0.295 to 0.963)</b>	<b>0.754 (0.537 to 0.918)</b>	<b>0.808 (0.62 to 0.95)</b>	<b>0.719 (0.409 to 0.934)</b>
Peak caterpillar	0.415 (–0.153 to 0.945)	–	<b>0.724 (0.388 to 0.949)</b>	<b>0.691 (0.297 to 0.951)</b>	<b>0.834 (0.54 to 0.984)</b>
Blue tit FED	0.665 (0.463 to 0.86)	0.485 (–0.028 to 0.963)	–	–	–
Great tit FED	0.713 (0.49 to 0.907)	0.534 (–0.012 to 0.966)	–	–	–
Pied flycatcher FED	0.547 (0.147 to 0.913)	0.306 (–0.498 to 0.959)	–	–	–
<b>(b) Major axis slopes</b>					
Oak leafing	–	<b>1.788 (0.497 to 3.896)</b>	<b>0.667 (0.409 to 0.935)</b>	<b>0.744 (0.485 to 1.023)</b>	<b>0.413 (0.228 to 0.621)</b>
Peak caterpillar	3.008 (–13.635 to 20.407)	–	<b>0.498 (0.189 to 0.775)</b>	<b>0.527 (0.154 to 0.88)</b>	<b>0.343 (0.2 to 0.521)</b>
Blue tit FED	1.126 (0.675 to 1.626)	1.061 (–0.55 to 3.452)	–	–	–
Great tit FED	1.128 (0.7 to 1.639)	0.778 (–0.391 to 2.905)	–	–	–
Pied flycatcher FED	1.113 (0.174 to 2.814)	2.471 (–3.121 to 5.03)	–	–	–

Values in time are shown in bold (top right) and values in de-trended space are shown in roman type (bottom left). 95% credible intervals are shown in parentheses.

species in the Netherlands<sup>15</sup>, and are likely to result from the caterpillars being more phenologically plastic in response to spring temperatures (see Supplementary Materials). Warmer conditions also produce shorter-duration food peaks<sup>13</sup>, which may strengthen the selection against mismatched individuals. It is also possible that bird populations may advance timings in response to temperature cues experienced after the FED by varying clutch size, laying interruptions or the initiation and duration of incubation<sup>20–23</sup>.

One of our key findings is that in the average year there is little latitudinal variation in the magnitude of caterpillar–bird mismatch. Therefore, meso-scale geographic variation in mismatch in the average year is unlikely to buffer metapopulations from the negative consequences of mismatch, or explain spatial variation in population trends. Thus, more negative declines in population trends of insectivorous birds in southern UK, driven by low productivity<sup>24</sup>, do not appear to be caused by greater mismatch in the south than the north. Directional adaptive evolution is expected to be more rapid for connected populations when selection pressures are spatially consistent compared with being spatially variable<sup>8</sup>. This result also has the practical implication that insights into the degree of mismatch in one location can be generalized to trends at different latitudes. In the average spring, the timing of blue tit and great tit nestling demand is quite synchronous with the peak resource, which is consistent with birds being able to track spatial variation in optimal timing. Spatial variation in mismatch will still occur if there is substantial year-by-site variation in spring temperatures, as would arise if the rate of warming varies spatially.

Of the three bird species, migratory pied flycatchers show the greatest mismatch with caterpillar availability, the predicted peak nestling period being consistently later than peak caterpillar timing. If pied flycatcher migration times are mediated by African conditions<sup>25–27</sup> or constraints en-route<sup>28</sup>, this may limit their ability to advance their arrival times, even if once they have arrived they are able to respond to spring temperatures on breeding grounds<sup>29</sup>. However, pied flycatchers provision nestlings with fewer caterpillars and more winged invertebrates compared with blue tits and great tits<sup>30</sup>, so may be less dependent on seasonal caterpillar peaks.

Our study focuses on mismatch judged from population means within a year and site (or in the case of oak leafing, the first date in a population; see Methods). There is of course potential for some individuals within a population to be matched even when population

means are mismatched, and this could serve to reduce the effects of mismatch on local populations<sup>31</sup>. The residual variance for caterpillars and birds, which corresponds to variance within a year and site, is >30 (Supplementary Table 3), which corresponds to 95% of individuals within a 5 km grid cell and year being in the range  $\pm 10.74$  days of the population mean. All three of our focal bird species are able to inhabit woodland types other than oak, and such habitats may differ in the timing or ephemerality of the caterpillar resource<sup>32</sup>, which may have further impacts on spatial variation in demography and selection.

While phenological mismatch is frequently raised as a potential impact of climate change, there is an urgent need to compile evidence on the consequences of mismatch for population trends across realistic spatial or ecological (for example, habitat generalist) settings. A Dutch study on pied flycatchers found that population declines were greater in areas where the caterpillar peak (assumed to be a proxy for mismatch) was earlier<sup>33</sup>, but the spatial relationship between mismatch and population trends remains largely unstudied<sup>34</sup>. Our study presents an assessment of whether latitudinal variation in mismatch exists, as it is sometimes proposed as a mechanism for the buffering of the adverse impacts of climate change (for example, more northern populations being less adversely affected by spring warming compared with southern populations<sup>35</sup>). The lack of evidence we find for latitudinal variation in mismatch between birds and their caterpillar resource suggests mismatch is unlikely to be a driver of spatially varying population trends found in avian secondary consumers<sup>36</sup>.

## Methods

**Phenology data.** We obtained pedunculate oak first-leafing dates from the UK Phenology Network (<https://naturescalendar.woodlandtrust.org.uk/>). As a quality control step, we excluded outliers (that is, ordinal days  $\leq 60$  or  $\geq 155$ ) and retained only observations from individuals who submitted records in multiple years. Our data for oak leafing differ from the other trophic levels in that they are of first dates within local populations. First dates are earlier than mean dates, but are only biased if there is a trend (latitudinal or correlating with year earliness) in the sampling effort, population abundance or variance. We suggest that sampling effort and population abundance are unlikely to pose a problem<sup>14</sup>, but we do not have the data to rule out variance as a source of bias.

Arboreal caterpillar biomass was monitored by collecting frass fall from traps set beneath oak trees at 47 sites across the UK<sup>13</sup>. Frass was collected and sorted, and the dry weight obtained approximately every 5 days (mean = 4.63) during spring until day 180 at the latest, from which we calculated a frass fall rate in  $\text{g m}^{-2} \text{day}^{-1}$ .



For traps where frass had been collected on at least five occasions during a spring, we identified the sampling period over which the rate of frass fall was highest and then identified the start and end of this interval. Where the highest rate was found over two or more separate periods, we allowed the peak frass interval to span the combined period. At one site (Wytham Woods), the timing of peak frass was estimated statistically<sup>31</sup>. For these estimates, we assumed that interval was the peak date  $\pm 3$  days.

FEDs for blue tits, great tits and pied flycatchers were obtained from nests monitored across the UK for the British Trust for Ornithology (BTO) Nest Record Scheme<sup>7,37</sup>. Few nests were visited daily, so a minimum FED was calculated by combining information collected over repeated visits before and after laying, including the date of previous visits with no eggs present, clutch size, laying rate and incubation period. A maximum FED was calculated as the date on which eggs were first observed minus the product of the number of eggs and the maximum laying rate; that is, one egg per day. We excluded observations where the interval between the minimum and maximum FED exceeded ten days.

We imposed a 'population' structure on all observations by dividing the UK into 50 km  $\times$  50 km grid cells. To spatially match observations at a finer scale within these 'populations' and to address some of the spatial pseudoreplication of observations, we generated a smaller grid structure corresponding to 5 km  $\times$  5 km.

**Analysis.** All analyses were conducted in R (ref. <sup>38</sup>). We assessed the degree to which consumer species were able to track the phenology of resource/primary producer species across space and time using a generalized linear mixed model<sup>39</sup> with the phenology of the two interacting species included as a bivariate Gaussian response<sup>40</sup>. With the exception of oak, the response was interval-censored, meaning that an event was considered to be equally likely to occur at any time within the given interval<sup>41</sup>. The model included the intercept and latitude as the only fixed effects for each of the response variables, and 50 km grid cell, 5 km grid cell, year and residual as random effects. For each random term, we estimated the (co)variance components, with the exception of the residual term for which we estimated variances but not covariance. For caterpillars, we also included trap as a random effect. Our ability to estimate covariances between trophic levels depends principally on the replication of grid cells or years for which we have data for both trophic levels. However, locations where we have data for one trophic level inform our estimates of latitudinal trends, among-grid-cell variance and year means for that level. Similarly, years for which we have data for only a single trophic level inform our estimates of among-year variance and grid cell means for that level. Precise estimates of these means and variances inform our estimates of relationships between the phenology of trophic-level pairs.

We used parameter expanded priors for (co)variances across years and grid cells and inverse-Wishart priors for the residual term. Models were run for 440,000 iterations, with 40,000 iterations removed as burn-in and sampling every 100. We assessed model convergence via visual inspection of the posterior distribution trace plots and by running a second chain and ensuring that the multivariate potential scale reduction factor for fixed effects on the two chains was  $<1.1$  (ref. <sup>42</sup>). The effective sample sizes for all focal parameters exceeded 1,000.

The model intercepts estimate the mean phenology of each species at the average latitude in the average year. We used the (co)variance components estimated for grid cells and years to obtain correlation estimates between the two species over space (50 km grid cells only) and years, respectively. We estimated the major axis rather than the type I regression slope<sup>43</sup> because we were interested in the degree of phenological tracking, rather than the degree to which the phenology of one species predicts the phenology of another.

We considered the following bivariate models: (1) peak caterpillar date versus oak first-leafing date, (2) each of the three bird species' FED versus peak caterpillar date and (3) each bird species' FED versus oak first-leafing date. For the bird versus caterpillar model, we compared the predicted peak resource availability with the predicted peak consumer demand, which we calculated as the predicted FED across latitudes or years plus mean clutch size, which varies little at the scale of our study<sup>44</sup>, and incubation duration (both from the BTO Nest Record Scheme; <http://app.bto.org/birdfacts/results/>) and the ten day duration between hatching and peak nestling food demand<sup>45,46</sup>. While the tree versus bird comparisons are not trophic interactions, we consider them here because we anticipate that oak leafing may be a proxy for peak caterpillar date, with the spatiotemporal replication of first-leafing observations greatly exceeding those of peak caterpillar observations.

**Reporting Summary.** Further information on experimental design is available in the Nature Research Reporting Summary linked to this article.

**Code availability.** Example R code is available at the following repository: [https://github.com/allyphillimore/birds\\_frass\\_oak](https://github.com/allyphillimore/birds_frass_oak).

**Data availability.** The data that support the findings of this study are available at the following DataShare repository: <http://dx.doi.org/10.7488/ds/2215>.

Received: 30 June 2016; Accepted: 22 March 2018;  
Published online: 23 April 2018

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### Acknowledgements

We thank the many contributors of the UK Phenology Network and BTO Nest Record Scheme, as well as J. Hadfield for statistical advice and J. Shutt for helpful discussion. The UK Phenology Network is coordinated by the Woodland Trust. The Nest Record Scheme is a partnership jointly funded by the BTO, the Joint Nature Conservation Committee and the fieldworkers themselves. A.B.P. was funded by a Natural Environment Research Council Advanced Fellowship (Ne/I020598/1).

### Author contributions

M.D.B., A.B.P. and K.W.S. conceived the study. M.D.B. led and coordinated the study. A.B.P. analysed the data. M.D.B. and A.B.P. wrote the manuscript with significant contributions from K.L.E. M.D.B., K.W.S., C.J.B., K.B., J.R.C., K.L.E., C.R.dE, R.G.N., B.C.S., J.A.S., R.C.W. and S.G.W. collected the frass data. K.L. provided the oak leafing data. D.L. and J.W.P.-H. provided the bird data. All authors commented on and edited the manuscript.

### Competing interests

The authors declare no competing interests.

### Additional information

**Supplementary information** is available for this paper at <https://doi.org/10.1038/s41559-018-0543-1>.

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### ► Experimental design

#### 1. Sample size

Describe how sample size was determined.

All sample sizes and justification for them are included in methods section.

#### 2. Data exclusions

Describe any data exclusions.

Inclusion/exclusion criteria are included in methods section. All data exclusions were quality control steps; we excluded outliers in the tree phenology data (ordinal day  $60 \leq$  leafing date  $\geq 155$ ) and retained only observations from individuals who submitted records in multiple years, and we excluded First Egg Date observations where the interval between minimum and maximum FED exceeded 10 days. Criteria was not pre-established.

#### 3. Replication

Describe the measures taken to verify the reproducibility of the experimental findings.

Our study was not experimental and so no replication was required.

#### 4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

Our study was not experimental and so did not include any experimental groups.

#### 5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

Our study was not experimental and so did not include any group allocation.

Note: all in vivo studies must report how sample size was determined and whether blinding and randomization were used.

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For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

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- ☒ ☐ The exact sample size ( $n$ ) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
- ☒ ☐ A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
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- ☐ ☒ The statistical test(s) used and whether they are one- or two-sided  
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- ☐ ☒ A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
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See the web collection on [statistics for biologists](#) for further resources and guidance.

## ► Software

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### 7. Software

Describe the software used to analyze the data in this study.

All analysis was run in the open software R (version 3.4.1), using the "MCMCglmm" package. The data used is available from a datashare repository at <http://dx.doi.org/10.7488/ds/2215> and example R code at [https://github.com/allyphillimore/birds\\_frass\\_oak](https://github.com/allyphillimore/birds_frass_oak).

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## ► Materials and reagents

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### 8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a third party.

No unique materials were used for our study.

### 9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

No antibodies were used in our study.

### 10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

No eukaryotic cell lines were used in our study.

b. Describe the method of cell line authentication used.

No eukaryotic cell lines were used in our study.

c. Report whether the cell lines were tested for mycoplasma contamination.

No eukaryotic cell lines were used in our study.

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by [ICLAC](#), provide a scientific rationale for their use.

No eukaryotic cell lines were used in our study.

## ► Animals and human research participants

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### 11. Description of research animals

Provide all relevant details on animals and/or animal-derived materials used in the study.

No laboratory animals were used in our study. The nests of wild birds (of Blue tit, Great tit and Pied flycatcher) were observed in the wild but no bird captures were made for this study. Nests were monitored following the methods and guidelines of the British Trust for Ornithology's Nest Record Scheme.

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### 12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

No human research participants were used for this study.



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