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 Britain. 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 was 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\textsuperscript{1}, prompting concern that previously synchronous trophic interactions may be disrupted and lead to negative impacts on consumer fitness and demography\textsuperscript{2-4}. Trophic asynchrony or mismatch appears to be most prevalent in the food webs of seasonal habitats, such as deciduous forests and
aquatic systems, 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 means that we have little evidence as to 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 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. 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, 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, and this generates spatial variation in the direction of mismatch, then 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. With gene flow, spatial variation in the direction of selection may oppose the adaption of mismatched populations to their local optima.
Here, we use the well-studied tri-trophic 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 phenology of these three trophic
levels advance with warmer spring temperatures, though birds typically advance by less
than trees or caterpillars\textsuperscript{10,11}, causing bird-caterpillar mismatch to be most pronounced
in warm springs and associated with strong directional selection for earlier laying\textsuperscript{12}.

We estimate 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 (bird) peak nestling demand and peak caterpillar
resource availability. Fig. 1 shows the distribution of sampling across Britain and among
years. We used 10073 observations of pedunculate oak (\textit{Quercus robur}) first leaing 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 Britain for the
period 2008-2016\textsuperscript{13} (trap\texttimes years = 696). Bird phenology was calculated using first egg
dates (FED) from across Britain for the period 1960-2016, comprising 36839 blue tit
\textit{(Cyanistes caeruleus)}, 24427 great tit \textit{(Parus major)} and 23813 pied flycatcher \textit{(Ficedula}
\textit{hypoleuca)} nests. The phenology of oak\textsuperscript{14} and all three bird species\textsuperscript{7} 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 is on the relationship between the phenology of interacting species\textsuperscript{15}. Where
timing changes more in one species than the other, this is indicative of spatial or
temporal variation in the magnitude, and potentially direction, of mismatch. In Britain
latitude provides a major temperature cline along which phenology varies at large scales\textsuperscript{16}, therefore, the spatial component of our study addresses latitudinal trends in relative phenology of species pairs. We also consider the relationship between the timing of the consumer and resource as the major axis (MA) slopes estimated over time (years) and space (i.e. among 50km 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 the peak caterpillar biomass. With increasing latitude the delay in oak leafing is significantly steeper than that of the caterpillar peak (Fig. 2a, 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 phenology 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 MA slope does not depart significantly from 1 (Fig. 2b, 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 – are similarly sensitive to temperature\textsuperscript{17}. 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.

In the average year and at the average latitude, FEDs of blue tits (posterior mean ordinal day 118.30 [95% credible interval = 116.83 - 119.85], Supplementary Table 3b) and great tits (day 118.95, [117.20 - 120.61], Supplementary Table 3c) are approximately one month earlier than peak caterpillar availability (~day 148). However, peak demand is when nestlings are around 10 days old, and once we allow for average clutch sizes and incubation durations (see methods), we find that peak demand occurs soon after peak resource availability, with mean peak demand–mean peak resource = 3.39 [-6.63 - 8.86] days in blue tits and 2.01 [-3.99 - 7.71] days in great tits. Pied flycatchers also lay earlier (day 135.04 [133.55 - 136.53, Supplementary Table 3d] than the peak caterpillar biomass, but predicted peak nestling demand occurs 12.87 [6.69 - 19.40] days later than peak caterpillar availability, suggesting substantial trophic mismatch in the average UK environment.

With increasing latitude the phenology of caterpillars is delayed by ~ 1.3 days °N⁻¹ and the point estimates for the equivalent latitudinal trend in birds are from 1.67 – 1.93 days °N⁻¹ (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 phenology of consumer–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 bird FED is strongly and significantly positively correlated for all three bird species (Table 1a). The MA slope is significantly <1 for all three bird species. This means that among years FED varies by
less than the timing of the caterpillar resource peak (Table 1b, Fig. 3d-f), which gives 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 in blue tit, great tit and pied flycatcher respectively. In late springs (i.e. under colder conditions) peak demand from blue tit and great tit nestlings is expected to coincide with the peak resource availability, and pied flycatcher peak demand occurs soon after the resource peak (Fig. 3d-f). When caterpillar phenology is earlier (i.e. 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 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 and all three species in the Netherlands and are likely to result from the caterpillars being more phenologically plastic in response to spring temperatures (supplementary materials).

Warmer conditions also produce shorter duration food peaks, 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 first lay date by varying clutch size, laying interruptions or the initiation and duration of incubation.

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 populations 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 Britain, driven by low productivity, 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 to being spatially variable. 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 showed 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 or constraints en-route, 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. However, pied flycatchers provision nestlings with fewer caterpillars and more winged invertebrates compared to blue tit and great tit, 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 effects of mismatch on local populations. 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 5km grid cell and year being in the range ±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, 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 (e.g., 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, but the spatial relationship between mismatch and population trends remains largely unstudied. Our study presents the first assessment of whether latitudinal variation in mismatch exists, as is sometimes proposed as a mechanism whereby the adverse impacts of climate change might be buffered, for example, more northern populations being less adversely affected by spring warming compared to southern populations. 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.

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 (ordinal day 60 ≤ leafing date ≥ 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 will be earlier than mean dates, but would only be biased if there is a trend (latitudinal or correlating with year earliness) in sampling effort, population abundance or variance. We suggest that the first two are unlikely to pose a problem, but we do not have the data to rule out the third source of bias.
Arboreal caterpillar biomass was monitored by collecting frass fall from traps set beneath oak trees at 47 sites across Britain. Frass was collected, sorted and the dry weight obtained approximately every 5 days (mean = 4.63) during spring up until day 180 at the latest, from which we calculated a frass fall rate in g square m\(^{-1}\) 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 then we allowed the peak frass interval to span the combined period. At one site, Wytham Woods, the timing of peak frass was estimated statistically. For these estimates we assumed that the interval was the peak date ± 3 days.

First egg dates (FED) for blue tit, great tit and pied flycatcher were obtained from nests monitored across Britain for the BTO Nest Record Scheme. Few nests were visited daily, and 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, i.e. one egg per day. We excluded observations where the interval between minimum and maximum FED exceeded 10 days.

We imposed a 'population' structure on all observations by dividing Britain into 50km x 50km 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 5km x 5km.
Analysis. All analyses were conducted in R\textsuperscript{40}. 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\textsuperscript{41} with the phenology of the two interacting species included as a bivariate Gaussian response\textsuperscript{6,42}. 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\textsuperscript{43}. The model included the intercept and latitude as the only fixed effects for each of the response variables, and 50km grid cell, 5km 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 or 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 burnin 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 \textsuperscript{44}. The effective sample sizes for all focal parameters exceeded 1000.
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 (50km grid cells only) and years, respectively. We estimated the major axis rather than type I regression slope\(^4\), 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: (i) peak caterpillar date versus oak first leafing date, (ii) each of the three bird species FED versus peak caterpillar date, and (iii) each bird FED with oak first leafing date. For the bird versus caterpillar we compared the predicted peak resource availability to 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\(^4\), and incubation duration (both from BTO nest record scheme http://app.bto.org/birdfacts/results/) and the 10 day duration between hatching and peak nestling food demand\(^4\),\(^8\). 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.

**Data availability**

Supplementary materials are available in the online version of the paper. The data that support the findings of this study are available at the following datashare repository: http://dx.doi.org/10.7488/ds/2215. Correspondence and requests for materials and data should be addressed to M.D.B.

**Code availability**
Example R code is available at the following repository:


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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. analyzed the data and M.D.B and A.B.P wrote the manuscript with K.L.E. making significant contributions. M.D.B., K.W.S., C.J.B., K.B., J.C., K.L.E., C.d.F., R.G.N., B.C.S., J.A.S., J.S.R.C.W. and S.G.W collected frass data, K.L. provided oak leafing data, and D.L and J.W.P-H. provided bird data. All authors commented on and edited the manuscript.

Competing financial interests

The authors declare no competing financial interests.

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**Figure legends**

**Fig. 1 | Number of years of data for each 50km grid cell used for each trophic level and bird species.** a for oak, b for frass, with trapping locations indicated by dots, c for blue tit, d for great tit and e for pied flycatcher.

**Fig. 2 | The relationship between latitude and the phenology of oak leafing and peak caterpillar abundance (a) and the among year relationship between the timing of the two trophic levels (b).** In both panels the solid lines correspond to the mean prediction and the shaded areas correspond to the posterior distribution of predictions under type I regression (a) and major axis regression (b). In a, dark green shaded area shows oak leafing and light green shaded area shows the caterpillar peak. In b, data points represent the posterior means for the best linear unbiased predictions for years that have observations for both trophic levels. Dashed line corresponds to unity; this is plotted to illustrate the relative slopes. An offset intercept is expected owing to the growth and development of caterpillars.

**Fig. 3 | The relationship between latitude and mismatch (a – c) and the timing of peak frass versus first egg date among years (d – f),** with a and d for blue tits, b and e for great tits and c and f pied flycatchers. In panels 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 being when nestlings are predicted to be 14 days old (see methods). In panels d – f datapoints represent the posterior means for the best linear unbiased predictions for years that have observations for both birds and caterpillars.
Dashed line corresponds to unity. In d – f the black line is the among year mean major axis slope and the red line is the predicted relationship between peak resource availability and peak demand. Transparent gray lines represent the posterior distribution of predictions.

**Table 1 | Correlation (a) and major axis slopes (b) of the phenology of higher trophic level on lower trophic level in time (bold, upper right) and de-trended space (lower left). 95% credible intervals in parentheses.**

### (a)

<table>
<thead>
<tr>
<th></th>
<th>Oak leafing</th>
<th>Peak caterpillar</th>
<th>Blue tit FED</th>
<th>Great tit FED</th>
<th>Pied flycatcher FED</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oak leafing</td>
<td>-</td>
<td>0.69 (0.295 - 0.963)</td>
<td>0.754 (0.537 - 0.918)</td>
<td>0.808 (0.62 - 0.95)</td>
<td>0.719 (0.409 - 0.934)</td>
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<td>Peak caterpillar</td>
<td>0.415 (-0.153 - 0.945)</td>
<td>-</td>
<td>0.724 (0.388 - 0.949)</td>
<td>0.691 (0.297 - 0.951)</td>
<td>0.834 (0.54 - 0.984)</td>
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<td>Blue tit FED</td>
<td>0.665 (0.463 - 0.86)</td>
<td>0.485 (-0.028 - 0.963)</td>
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<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Great tit FED</td>
<td>0.713 (0.49 - 0.907)</td>
<td>0.534 (-0.012 - 0.966)</td>
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<td>-</td>
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<tr>
<td>Pied flycatcher FED</td>
<td>0.547 (0.147 - 0.913)</td>
<td>0.306 (-0.498 - 0.959)</td>
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### (b)

<table>
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<th>Great tit FED</th>
<th>Pied flycatcher FED</th>
</tr>
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<td>Oak leafing</td>
<td>-</td>
<td>1.788 (0.497 - 3.896)</td>
<td>0.667 (0.409 - 0.935)</td>
<td>0.744 (0.485 - 1.023)</td>
<td>0.413 (0.228 - 0.621)</td>
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<td>3.008 (-13.635 - 20.407)</td>
<td>-</td>
<td>0.498 (0.189 - 0.775)</td>
<td>0.527 (0.154 - 0.88)</td>
<td>0.343 (0.2 - 0.521)</td>
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<td>Blue tit FED</td>
<td>1.126 (0.675 - 1.826)</td>
<td>1.061 (-0.55 - 3.452)</td>
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<td>-</td>
<td>-</td>
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<tr>
<td>Great tit FED</td>
<td>1.128 (0.7 - 1.639)</td>
<td>0.778 (-0.391 - 2.905)</td>
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<td>-</td>
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<tr>
<td>Pied flycatcher FED</td>
<td>1.113 (0.174 - 2.814)</td>
<td>2.471 (-3.121 - 5.03)</td>
<td>-</td>
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