

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 phenology¹, prompting concern that previously synchronous trophic interactions may be disrupted and lead to negative impacts on

consumer fitness and demography²⁻⁴. Trophic asynchrony or mismatch appears to be most prevalent in the food webs of seasonal habitats, such as deciduous forests and aquatic systems⁵, 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 mismatch⁶ 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 basis⁷. 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 mismatch⁸, 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 phenology⁹, 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 elsewhere⁶. With gene flow, spatial

variation in the direction of selection may oppose the adaption of mismatched populations to their local optima⁸.

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^{10,11}, causing bird-caterpillar mismatch to be most pronounced in warm springs and associated with strong directional selection for earlier laying¹².

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 (*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 Britain for the period 2008-2016¹³ (trap:years = 696). Bird phenology was calculated using first egg dates (FED) from across Britain for the period 1960-2016, comprising 36839 blue tit (*Cyanistes caeruleus*), 24427 great tit (*Parus major*) and 23813 pied flycatcher (*Ficedula hypoleuca*) nests. The phenology of oak¹⁴ and all three bird species⁷ 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 species¹⁵. 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 scales¹⁶, 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 temperature¹⁷. 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 north⁶.

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^{18,19}, 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 $^{\circ}\text{N}^{-1}$ and the point estimates for the equivalent latitudinal trend in birds are from 1.67 – 1.93 days $^{\circ}\text{N}^{-1}$ (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 $^{\circ}\text{N}$) 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 UK²⁰ and all three species in the Netherlands¹⁵ 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 peaks¹³, 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 incubation²¹⁻²⁴.

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 Britain, driven by low productivity²⁵, 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 variable⁸. 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 conditions²⁶⁻²⁸ or constraints en-route²⁹, 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 grounds³⁰. However, pied flycatchers provision nestlings with fewer caterpillars and more winged invertebrates compared to blue tit and great tit³¹, 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

populations³². 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 resource³³, 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 earlier³⁴, but the spatial relationship between mismatch and population trends remains largely unstudied³⁵. 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 populations³⁶. 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 consumers³⁷.

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 $60 \leq$ 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^{14,38}, 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 Britain¹³. 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 statistically³². For these estimates we assumed that the interval was the peak date \pm 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^{7,39}. 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 R⁴⁰. 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 model⁴¹ with the phenology of the two interacting species included as a bivariate Gaussian response^{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 interval⁴³. 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 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 slope⁴⁵, 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 study⁴⁶, 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^{47,48}. 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:

https://github.com/allyphillimore/birds_frass_oak.

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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.dF., 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)

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

(b)

	Oak leafing	Peak caterpillar	Blue tit FED	Great tit FED	Pied flycatcher FED
Oak leafing	-	1.788 (0.497 - 3.896)	0.667 (0.409 - 0.935)	0.744 (0.485 - 1.023)	0.413 (0.228 - 0.621)
Peak caterpillar	3.008 (-13.635 - 20.407)	-	0.498 (0.189 - 0.775)	0.527 (0.154 - 0.88)	0.343 (0.2 - 0.521)
Blue tit FED	1.126 (0.675 - 1.626)	1.061 (-0.55 - 3.452)	-	-	-
Great tit FED	1.128 (0.7 - 1.639)	0.778 (-0.391 - 2.905)	-	-	-
Pied flycatcher FED	1.113 (0.174 - 2.814)	2.471 (-3.121 - 5.03)	-	-	-

Fig. 1

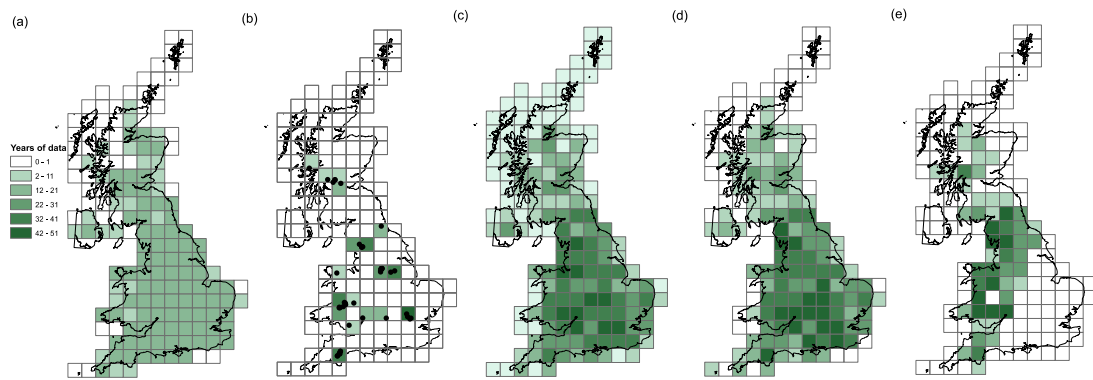


Fig. 2

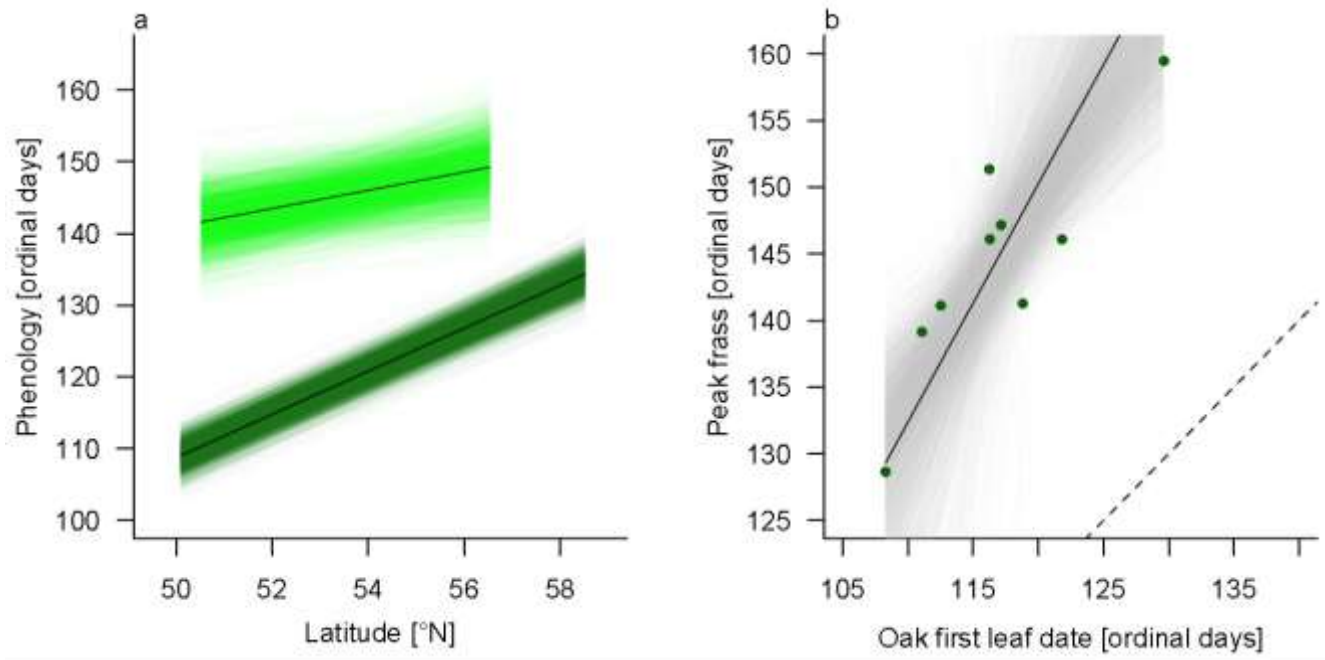
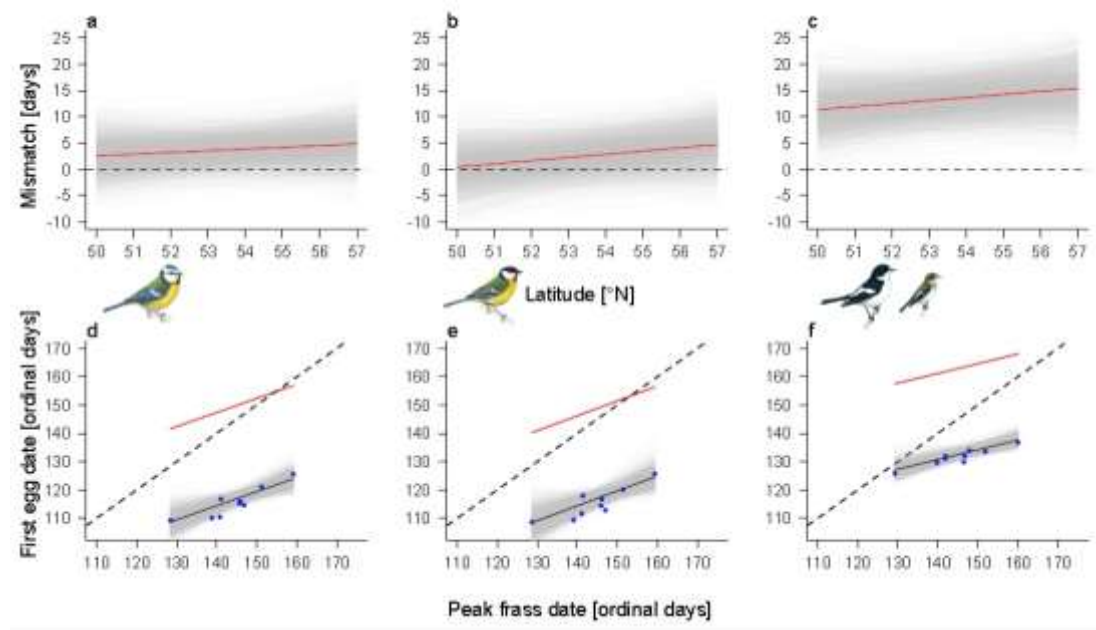


Fig. 3



Tritrophic phenological match-mismatch in space and time

Supplementary Information

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Temperature as a predictor of peak caterpillar abundance timing

For each peak frass estimate in each year we calculated the mean air temperature over ordinal days 75–140 for the appropriate 5km grid cell from Met Office daily interpolated temperatures for 2008–2016¹. We selected this time period within the year as it overlaps the windows of temperature sensitivity in relation to laying dates found for the three bird species².

Following the method described in³, we included phenology and temperature as a bivariate response and 50km grid cell, 10km grid cell, year, frass collection tray and residual as random effects in MCMCglmm⁴. For each random term we estimated the (co)variance components, though for frass tray we only estimated the phenological variance. We controlled for uncertainty in peak caterpillar dates by treating the time period over which the peak rate of frass fell on each tray as interval censored Gaussian data⁵. Priors were as described in main methods, and the model was run for 5040000 iterations, sampling every 500th iteration and removing the first 40000 as burnin.

Based on the (co)variance components (Table S2) we were able to estimate (i) the type I slope of phenology regressed on temperature and (ii) the correlation between the phenology and temperature over time and space³.

The timing of peak caterpillar availability was highly sensitive to spring temperature over time ($b = -5.98 \text{ days}^\circ\text{C}^{-1}$, 95% CI = -8.76 – -2.94, $r = -0.88$). This is a similar slope to that obtained for pedunculate oak leafing ($b = -5.65$)⁶ and steeper than slopes estimated for the bird species ($b \sim -4$ in blue and great tit and -2 in pied flycatcher)^{2,6}. This temporal slope is likely to be the result of multiple species' plastic responses and the magnitude is similar to estimates of the phenological plasticity of the winter moth (*Operophtera brumata*) from the Netherlands ⁷, which is one of the most abundant species in UK woodlands in spring⁸.

The point estimate of the spatial slope of timing of the caterpillar peak regressed on mean temperature is negative, though the relationship is non-significant ($b = -1.83$,

95% CI = $-4.74 - 0.70$, $r = -0.60$). Consistent with this finding we observe that the timing of peak frass varies much more over years than it does over grid cells (Table S2). The spatial slope is shallower than spatial slope estimates that have been obtained for the FEDs of the focal bird species² [ENREF 22](#) [ENREF 26](#) [ENREF 26](#).

The interpolated temperatures at one upland frass site (Pass of Leny) are 1.5°C below those obtained for any other site, which suggests that the grid centroid at which the temperature has been interpolated is at a high elevation. After excluding this site, we estimate a steeper temperature sensitivity over both time ($b = -7.99$ days°C⁻¹ 95% CI = $-11.95 - -4.72$, $r = -1.00$) and space ($b = -2.70$, 95% CI = $-5.98 - 0.89$, $r = -0.66$).

Bird first egg date in relation to oak first leafing dates

In the average year and at the average latitude blue tit and great tit FEDs occur at roughly the same time as oak first leafing, whereas pied flycatcher FED occurs about 13 days after leafing (Table S2e-g). The FEDs of all three bird species are strongly correlated ($r > 0.5$) with oak first leafing dates across space and time (Table 1a). As latitude increases, bird phenology delays significantly more slowly than that of oaks, such that blue tits and great tits FEDs switch from occurring after first leafing in the south to before first leafing in the north (Fig S1a,b). Pied flycatchers, which breed later, have a substantially shorter interval between oak first leafing and FED in the north than south (Fig S1c). After de-trending for latitude, there remained a significant positive correlation between bird and oak phenology among 50km grid cells and the MA slope was estimated to be close to 1 (Table 1a,b). In all cases the temporal MA slope is estimated to be <1 , and significantly less for blue tits and pied flycatchers (Fig. S1d-f, Table 1b). However, the bird:oak temporal MA slopes are slightly steeper (i.e. closer to 1) than those obtained for bird phenology regressed on caterpillar phenology.

Power analysis

We used simulations to assess the statistical power of our approach to detect the following relationships between consumer and resource phenology: (i) a difference in the slopes across latitudes, a correlation across (ii) space and (iii) time and a major axis slope that differs from 1 across (iv) space and (v) time. We conducted simulations for each of the bird versus caterpillar relationships and also the caterpillar versus oak relationship.

When simulating data we retained the sample sizes and structure of the original data, i.e. latitudinal, year and grid cell replication. At the 5km grid cell and residual levels we randomly sampled from a bivariate normal distribution using variance and covariance values estimated from the data. For the spatial (50km) and temporal random terms we also randomly drew from a bivariate normal distribution, but in these cases we selected the following values: spatial consumer variance = 10.25, spatial resource variance = 30, spatial consumer:resource covariance = 15.75, temporal consumer variance = 41, temporal resource variance = 120, temporal consumer:resource covariance = 63. These values were selected because they result in a correlation of 0.9 and major axis slope of 0.55, representing substantial effect sizes. The magnitude of the (co)variances was selected to be similar to those obtained from the data across space and time, respectively. For bird and oak latitudinal slopes we used the real estimates. For caterpillar latitudinal slopes we used the real data + or - 2 in the cases of birds and oak, respectively. We selected a slope difference of 2 between consumer and resource, as this is sufficient to generate a difference in relative phenology of around 14 days between our northernmost and southernmost points. Two differences between simulated and real data is that we did not simulate interval censored data for the birds or caterpillars and we did not simulate a tray effect for caterpillars.

For each consumer and resource combination we simulated data 100 times and applied a Bayesian bivariate mixed modeling approach, running each model for 100,000

iterations and removing the first 20,000 as burnin. Across the 100 simulations we assessed power by calculating the proportion of simulations for which the 95% credible intervals did not include 0 (or 1 in the case of the major axis slope) and that the direction of the slope was in the same direction that was simulated. R code is available from https://github.com/allyphillimore/birds_frass_oak.

Our power to detect a latitudinal slope difference of 2 was around 0.8 (Fig S2a). In comparison, while our power to detect a spatial correlation was adequate for the bird:caterpillar relationships (though not caterpillar:oak, Fig 2b), power to detect a detrended spatial major axis slope < 1 consistently below 0.8 (Fig. S2c), which is unsurprising given the broad credible intervals for these estimates reported in table 1b. We have good power to detect a positive temporal correlation between phenologies of consumer and resource species (Fig. 2d), whereas our power to detect a temporal major axis < 1 is just below 0.8 for blue and great tit versus caterpillars, but closer to 0.7 for the pied flycatcher comparison and the caterpillar:oak relationship.

Sensitivity of analyses to inclusion of shared years only


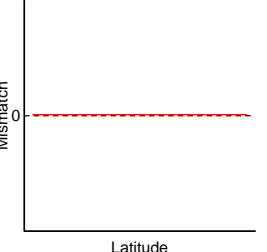
The time series we have for oak and caterpillars is much shorter than those for the bird species. While information about taxon covariances in phenology comes from instances where data exists for both taxa, our bivariate modeling approach also uses data arising from years where we only have phenology information for one taxon to inform the estimates of that taxon's phenological latitudinal trend, among grid cell variance and among year variance. To examine the sensitivity of our analyses to including only years for which we have data for both species, we re-ran all analyses excluding non-shared years.

The impact of excluding non-shared years on focal parameters and their credible intervals was quite minimal. Temporal correlations remained significant (Table S4a) and most of the major axis slope estimates were within 0.05 of those obtained with the

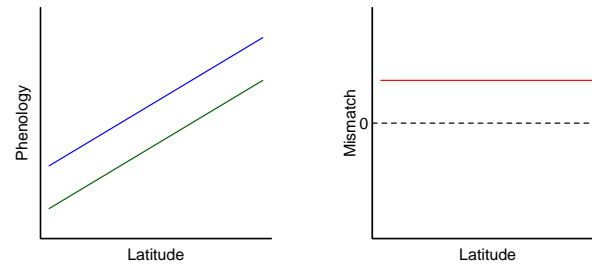
full dataset (Tables 1 and S4b), with the exception of the pied flycatcher and oak relationship, which was estimated to be even shallower. Estimates of differences in the latitudinal slope were also qualitatively unchanged (Table S5), remaining near zero and non-significant for bird-caterpillar comparisons and significant for all comparisons involving oaks. One notable difference between the models with (Table S3) and without (Table S5) non-shared year data is that for models including bird phenology intercepts were several days earlier in the latter, consistent with breeding phenology being earlier in the more recent years for which we have data on oak and caterpillar phenology.

Supplementary tables

Supplementary Table 1 | Potential consequences of four latitudinal patterns in resource and consumer phenology with regard to consumer populations' magnitude of mismatch, population size and selection pressures. We assume that mismatch impacts negatively on local population growth (via mean population fitness) and induces selection (via relative fitness). We assume that the latitudinal gradient is composed of many local populations that are connected and exchange individuals/genes. We consider two scenarios that represent ends of a continuum where the latitudinal slope in consumer phenology is due to (i) plasticity (populations are not divergent with regard to genetic control of phenology) and (ii) local adaptation (populations are divergent with regard to genetic control of phenology) with respect to an environmental cue (in our case spring temperatures). For the bird species studied here much of the spatial response to temperature seems likely to be attributable to temperature-mediated phenotypic plasticity². Predictions are for the average year, but the degree of mismatch and its latitudinal trend may vary from year to year depending on the phenological plasticity of the consumer relative to the resource.

	Latitudinal trend in phenology of consumer (blue line) and resource (green line)	Latitudinal trend in mismatch (dashed line corresponds to synchronous peak demand and peak resource, red line = timing of peak demand minus timing of peak resource)	Predicted short term consequences for consumer population sizes depending on whether the spatial slope is due to (i) plasticity or (ii) local adaptation	Predicted consequences for selection pressure on the consumer depending on whether the spatial slope is due to (i) plasticity or (ii) local adaptation, and the impacts of gene flow/movement of individuals.
a Both species share the same slope and intercept, so are well matched. This is likely to be the situation prior to marked climate change.			All else being equal, populations are predicted to be stable.	<p>(i) Plasticity: The phenology of the consumer tracks the optimum perfectly and is under stabilizing selection.</p> <p>(ii) Locally adapted: Gene flow from centre to periphery may perturb populations from the optimum and reduce the latitudinal slope of consumer phenology⁹.</p>

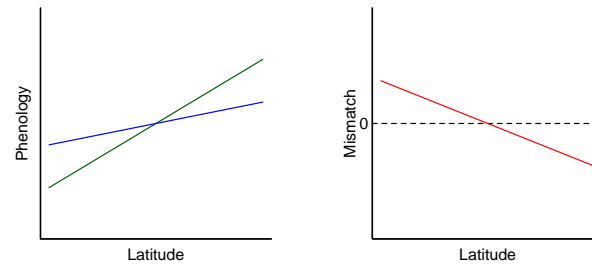
b Both species share the same slope but the consumer species intercept is later. This generates mismatch in the average year. This pattern may arise if there has been a shift in the mean cue (temperature) as compared with historic levels and consumer and resource has advanced by different amounts.



No spatial variation in population trends (i.e. spatial buffering). All populations are predicted to decline.

Spatially consistent directional selection.
 (i) Plasticity: If there is sufficient additive genetic variation, adaptive evolution may advance phenology by selecting for a temperature: phenology relationship with a steeper plastic slope or lower intercept. Adaptation may be accelerated if gene flow leads to sharing of beneficial alleles.
 (ii) Local adaptation: northwards gene flow and movement of individuals will reduce mismatch for northern populations.

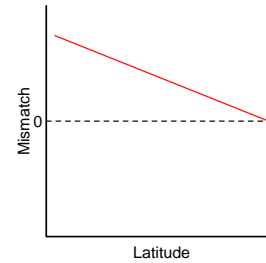
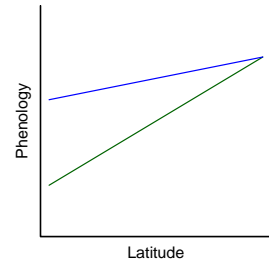
c The slope of the consumer species phenology on latitude is shallower than that of the resource. Such situations may arise as rates of phenological shifts in consumers in response to climate change are less than those of their resource. At intermediate latitudes both species are matched.



(i) Plasticity: Spatial buffering may arise as matched central populations act as a source for mismatched sink populations at high and low latitudes.
 (ii) Local adaptation: Central populations stable. Peripheral populations decline.

Spatially varying selection.
 (i) Plasticity: Selection will favour early individuals in the south and later individuals in the north. Peripheral populations may be subject to greater migration load, which opposes local adaptation, as individuals disperse from centre to periphery.
 (ii) Local adaptation: Selection would favour immigrants moving from periphery toward centre as such individuals would be more matched with the resource.

d The slope of the consumer species phenology on latitude is shallower than that of the resource. Such situations may arise where phenological shifts in consumers in response to recent climate change have been less pronounced than those of their resource. At northern latitudes both species are matched.



(i) Plasticity: Spatial buffering may arise if southward dispersal from matched northern sites acts as a source of colonists for mismatched sink populations further south.
 (ii) Local adaptation: The most northern populations are stable, but other populations decline.

Spatially varying selection.
 (i) Plasticity: selection favours earlier individuals in the south and centre. Migration load from individuals in the north may oppose adaptation in the north, resulting in overall evolutionary change < scenario b.
 (ii) Local adaptation: Selection would favour individuals that moved northwards, as such individuals would be more matched with the resource.

1 **Supplementary Table 2 | (Co)variance estimates from the bivariate mixed model**
 2 **of peak caterpillar and spring temperature**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	caterpillar	11.23 (0.00 – 29.30)
	caterpillar, temperature	-1.90 (-5.17 – 0.44)
	temperature	0.79 (0.08 – 1.60)
10km grid cells	caterpillar	15.05 (3.96 – 29.02)
	caterpillar, temperature	-1.32 (-2.86 – 0.04)
	temperature	0.24 (0.06 – 0.53)
Year	caterpillar	97.35 (24.85 – 212.93)
	caterpillar, temperature	-12.09 (-28.35 – -2.43)
	temperature	2.05 (0.51 -4.42)
Tray	caterpillar	0.36 (0.00 – 1.32)
Residual	caterpillar	33.98 (30.02 – 38.01)
	caterpillar, temperature	-0.15 (-0.27 – -0.05)
	temperature	0.05 (0.04 – 0.06)

3 Model intercepts: caterpillar = 145.70 (138.99 – 152.92), temperature = 8.15 (7.04 –
 4 9.19).

5 **Supplementary Table 3 | (Co)variance estimates from the bivariate mixed model**
6 **of the phenology of a) oak and caterpillar, b) caterpillar and blue tit, c) caterpillar**
7 **and great tit, d) caterpillar and pied flycatcher, e) oak and blue tit, f) oak and great**
8 **tit, and g) oak and pied flycatcher**

10 **a)**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	oak	5.19 (2.75 - 7.71)
	oak, caterpillar	2.9 (-1.82 - 7.83)
	caterpillar	11.48 (0 - 27.44)
5km grid cells	oak	24.82 (22.17 - 27.62)
	oak, caterpillar	1.48 (-12.02 - 14.33)
	caterpillar	7.23 (0 - 18.18)
Year	oak	43.8 (19.28 - 77.29)
	oak, caterpillar	43.14 (6.31 - 92.14)
	caterpillar	92.07 (24.91 - 187.18)
Tray	caterpillar	4.92 (0 - 11.63)
Residual	oak	54.8 (53.1 - 56.48)
	caterpillar	33.35 (29.72 - 37.41)

11 Fixed effects. Intercept: oak = 116.65 (113.63 - 119.53), caterpillar = 144.26 (138.48 -
12 149.8). Latitude slopes: oak = 3.01 (2.69 - 3.32), caterpillar = 1.26 (-0.03 - 2.48).
13 Latitudinal slope difference (consumer - resource) = -1.74 (-3 - -0.46).

15 **b)**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	caterpillar	11.95 (0 - 27.71)
	caterpillar, blue tit	3.68 (-0.91 - 9.05)
	blue tit	5.53 (3.78 - 7.71)
5km grid cells	caterpillar	5.96 (0 - 16.6)
	caterpillar, blue tit	-0.65 (-6.43 - 5.28)
	blue tit	10.18 (8.91 - 11.49)
Year	caterpillar	74.08 (27.63 - 143.78)
	caterpillar, blue tit	29.53 (9.79 - 52.73)
	blue tit	23.35 (14.68 - 33.65)
Tray	caterpillar	5.21 (0 - 12.08)
Residual	caterpillar	33.4 (29.74 - 37.62)
	blue tit	44.25 (43.57 - 44.98)

16 Fixed effects. Intercept: caterpillar = 147.85 (142.53 - 153.24), blue tit = 118.3 (116.83 -
17 119.85). Latitude slope: caterpillar = 1.35 (0.12 - 2.64), blue tit = 1.67 (1.42 - 1.94).
18 Latitudinal slope difference (consumer - resource) = 0.33 (-0.96 - 1.56).

20 **c)**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	caterpillar	12.74 (0 - 28.66)
	caterpillar, great tit	4.4 (-1.39 - 10.08)
	great tit	5.92 (3.55 - 8.61)
5km grid cells	caterpillar	6.56 (0 - 17.55)
	caterpillar, great tit	-2.64 (-13.44 - 6.25)
	great tit	17.42 (14.95 - 19.92)
Year	caterpillar	88.01 (25.48 - 175.98)
	caterpillar, great tit	35.14 (7.84 - 66.47)
	great tit	30.84 (19.64 - 44.75)
Tray	caterpillar	4.81 (0 - 11.07)

Residual caterpillar 33.36 (29.83 - 37.53)
 great tit

61.28 (60.1 - 62.46)

21 Fixed effects. Intercept: caterpillar = 148.73 (142.62 - 154.66), great tit = 118.96 (117.21
 22 - 120.61). Latitude slopes: caterpillar = 1.32 (0.08 - 2.68), great tit = 1.93 (1.64 - 2.21).
 23 Latitudinal slope difference (consumer - resource) = 0.61 (-0.67 - 1.97).
 24

25 **d)**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	caterpillar	15.37 (0 - 36.92)
	caterpillar, pied flycatcher	2.97 (-6.12 - 13.3)
	pied flycatcher	6.61 (2.08 - 12.26)
5km grid cells	caterpillar	5.75 (0 - 16.29)
	caterpillar, pied flycatcher	-0.37 (-3.5 - 2.39)
	pied flycatcher	3.13 (2.25 - 4.1)
Year	caterpillar	113.56 (36.89 - 211.79)
	caterpillar, pied flycatcher	35.14 (12.06 - 60.94)
	pied flycatcher	15.95 (10.45 - 22.75)
Tray	caterpillar	5.48 (0 - 12.29)
Residual	caterpillar	33.33 (29.64 - 37.3)
	pied flycatcher	44.68 (43.75 - 45.46)

26 Fixed effects. Intercept: caterpillar = 152.59 (145.82 - 159.03), pied flycatcher = 135.04
 27 (133.55 - 136.53). Latitude slopes: caterpillar = 1.15 (-0.19 - 2.48), pied flycatcher = 1.73
 28 (1.27 - 2.16). Latitudinal slope difference (consumer - resource) = 0.58 (-0.9 - 1.88).
 29

30 **e)**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	oak	5.12 (2.81 - 7.73)
	oak, blue tit	3.58 (1.86 - 5.41)
	blue tit	5.73 (3.65 - 7.74)
5km grid cells	oak	24.88 (22.19 - 27.64)
	oak, blue tit	1.95 (-0.24 - 4.32)
	blue tit	10.15 (8.95 - 11.49)
Year	oak	45.36 (21.34 - 75.6)
	oak, blue tit	24.42 (10.43 - 39.95)
	blue tit	23.12 (14.28 - 33.42)
Residual	oak	54.79 (53.04 - 56.36)
	blue tit	44.26 (43.57 - 44.91)

31 Fixed effects. Intercept: oak = 119.73 (116.87 - 122.64), blue tit = 118.34 (116.95 -
 32 119.93). Latitude slopes: oak = 2.99 (2.69 - 3.29), blue tit = 1.69 (1.42 - 1.94). Latitudinal
 33 slope difference (bird - tree) = -1.3 (-1.62 - -0.97).
 34

35 **f)**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	oak	5.05 (2.8 - 7.57)
	oak, great tit	3.81 (1.96 - 5.7)
	great tit	5.76 (3.44 - 8.31)
5km grid cells	oak	24.88 (22.21 - 27.61)
	oak, great tit	1.94 (-0.99 - 4.99)
	great tit	17.53 (15.11 - 20.05)
Year	oak	52.93 (24.69 - 90.11)
	oak, great tit	32.56 (15.23 - 52.97)

	great tit	30.63 (19.02 - 43.34)
Residual	oak	54.81 (53.22 - 56.55)
	great tit	61.3 (60.17 - 62.54)
36	Fixed effects. Intercept: oak = 120.92 (117.64 - 123.97), great tit = 118.99 (117.34 -	
37	120.7). Latitude slopes: oak = 2.98 (2.68 - 3.3), great tit = 1.95 (1.67 - 2.24). Latitudinal	
38	slope difference (bird - tree) = -1.03 (-1.35 - -0.68).	

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40 **g)**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	oak	5.33 (2.68 - 7.9)
	oak, pied flycatcher	2.78 (0.52 - 5.35)
	pied flycatcher	5.27 (1.62 - 9.81)
5km grid cells	oak	24.79 (22.19 - 27.74)
	oak, pied flycatcher	2.66 (-0.46 - 5.84)
	pied flycatcher	3.14 (2.23 - 4.1)
Year	oak	66.96 (24.57 - 124.6)
	oak, pied flycatcher	23.64 (6.52 - 42.89)
	pied flycatcher	15.98 (9.89 - 22.4)
Residual	oak	54.81 (53.16 - 56.46)
	pied flycatcher	44.67 (43.82 - 45.47)

41 Fixed effects. Intercept: oak = 121.97 (117.62 - 126.81), pied flycatcher = 134.73 (133.32

42 - 136.1). Latitude slopes: oak = 3.02 (2.69 - 3.32), pied flycatcher = 1.8 (1.4 - 2.23).

43 Latitudinal slope difference (bird - tree) = -1.22 (-1.68 - -0.72).

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45 **Supplementary Table 4 | Correlation (a) and major axis slopes (b) of the**
 46 **phenology of higher trophic level on lower trophic level in time (shaded, upper**
 47 **triangle) and de-trended space (unshaded, lower triangle) restricting analyses to**
 48 **years with data for both taxa. 95% credible intervals in parentheses.**

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a)

	Oak leafing	Peak caterpillar	Blue tit FED	Great tit FED	Pied flycatcher FED
Oak leafing	-	0.69 (0.296 - 0.981)	0.745 (0.514 - 0.926)	0.77 (0.565 - 0.933)	0.6 (0.29 - 0.859)
Peak caterpillar	0.157 (-0.464 - 0.868)	-	0.758 (0.405 - 0.978)	0.724 (0.357 - 0.976)	0.802 (0.473 - 0.993)
Blue tit FED	0.649 (0.43 - 0.835)	0.533 (0 - 0.973)	-	-	-
Great tit FED	0.657 (0.394 - 0.882)	0.487 (-0.071 - 0.981)	-	-	-
Pied flycatcher FED	0.559 (0.11 - 0.954)	0.206 (-0.562 - 0.888)	-	-	-

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b)

	Oak leafing	Peak caterpillar	Blue tit FED	Great tit FED	Pied flycatcher FED
Oak leafing	-	1.768 (0.44 - 3.964)	0.642 (0.376 - 0.933)	0.662 (0.4 - 0.932)	0.261 (0.086 - 0.427)
Peak caterpillar	4.327 (-27.483 - 28.712)	-	0.57 (0.172 - 0.985)	0.571 (0.161 - 1.006)	0.314 (0.135 - 0.49)
Blue tit FED	1.227 (0.725 - 1.769)	1.912 (-0.679 - 4.181)	-	-	-
Great tit FED	1.14 (0.614 - 1.746)	-5.947 (-2.087 - 6.216)	-	-	-
Pied flycatcher FED	0.569 (-0.112 - 1.431)	0.696 (-0.493 - 0.709)	-	-	-

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57 **Supplementary Table 5 | (Co)variance estimates from the bivariate mixed model**
 58 **of the phenology of a) oak and caterpillar, b) caterpillar and blue tit, c) caterpillar**
 59 **and great tit, d) caterpillar and pied flycatcher, e) oak and blue tit, f) oak and great**
 60 **tit, and g) oak and pied flycatcher restricted to years for which there are data for**
 61 **both taxa.**

62

63 **a)**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	oak	6.38 (2.93 - 10.45)
	oak, caterpillar	1.2 (-4.92 - 7.35)
	caterpillar	12.52 (0 - 30.64)
5km grid cells	oak	27.85 (23.98 - 32.06)
	oak, caterpillar	-1.36 (-16.26 - 11.88)
	caterpillar	7.28 (0 - 18.87)
Year	oak	56.56 (13.61 - 127.34)
	oak, caterpillar	52.33 (2.32 - 129.36)
	caterpillar	103 (26.32 - 229.95)
Tray	caterpillar	5.04 (0 - 12.2)
Residual	oak	60.38 (57.84 - 63.01)
	caterpillar	33.4 (29.7 - 37.37)

64 Fixed effects. Intercept: oak = 116.65 (111.83 - 122.15), caterpillar = 144.75 (137.89 -
 65 152.26). Latitude slopes: oak = 2.93 (2.51 - 3.3), caterpillar = 1.12 (-0.19 - 2.37).
 66 Latitudinal slope difference = -1.81 (-3.16 - -0.48).

67

68 **b)**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	caterpillar	12.17 (0 - 28.57)
	caterpillar, blue tit	4.57 (-1.3 - 10.55)
	blue tit	6.71 (4.15 - 9.57)
5km grid cells	caterpillar	6.09 (0 - 16.24)
	caterpillar, blue tit	-1.25 (-7.59 - 4.89)
	blue tit	11.64 (9.86 - 13.52)
Year	caterpillar	99.12 (26.16 - 216.54)
	caterpillar, blue tit	47.11 (4.77 - 110.33)
	blue tit	38.98 (9.64 - 86.02)
Tray	caterpillar	4.86 (0 - 11.34)
Residual	caterpillar	33.39 (29.71 - 37.22)
	blue tit	45.25 (44.36 - 46.06)

69 Fixed effects. Intercept: caterpillar = 144.08 (137.03 - 151.03), blue tit = 115.5 (111.29 -
 70 119.45). Latitude slope: caterpillar = 1.33 (0.11 - 2.6), blue tit = 1.71 (1.38 - 2.07).
 71 Latitudinal slope difference = 0.38 (-0.99 - 1.53).

72

73 **c)**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	caterpillar	11.52 (0 - 27.03)
	caterpillar, great tit	4.18 (-1.58 - 10.58)
	great tit	7.34 (4.21 - 11.1)
5km grid cells	caterpillar	7.53 (0 - 18.49)
	caterpillar, great tit	-5.25 (-15.45 - 4.84)
	great tit	20.21 (16.79 - 24.09)
Year	caterpillar	101.57 (25.76 - 224.49)
	caterpillar, great tit	46.86 (1.52 - 111.54)

	great tit	40.58 (9.02 - 87.87)
Tray	caterpillar	4.16 (0 - 10.01)
Residual	caterpillar	33.38 (29.37 - 37.21)
	great tit	

11.52 (0 - 27.03)

74 Fixed effects. Intercept: caterpillar = 144.32 (136.86 - 150.98), great tit = 115.1 (110.84 -
75 119.45). Latitude slopes: caterpillar = 1.29 (0.01 - 2.54), great tit = 1.79 (1.38 - 2.19).
76 Latitudinal slope difference = 0.51 (-0.74 - 1.82).

77

78 **d)**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	caterpillar	13.79 (0 - 32.39)
	caterpillar, pied flycatcher	0.82 (-2.64 - 4.36)
	pied flycatcher	1.34 (0 - 2.82)
5km grid cells	caterpillar	6.22 (0 - 16.55)
	caterpillar, pied flycatcher	-0.56 (-4.22 - 2.67)
	pied flycatcher	3.23 (2.06 - 4.51)
Year	caterpillar	97.48 (23.54 - 206.76)
	caterpillar, pied flycatcher	28.69 (5.28 - 67.71)
	pied flycatcher	13.07 (3.01 - 28.46)
Tray	caterpillar	5.07 (0 - 11.84)
Residual	caterpillar	33.36 (29.61 - 37.24)
	pied flycatcher	39.98 (38.76 - 41.25)

79 Fixed effects. Intercept: caterpillar = 144.78 (138.53 - 152.45), pied flycatcher = 131.08
80 (128.78 - 133.6). Latitude slopes: caterpillar = 1.11 (-0.27 - 2.41), pied flycatcher = 1.05
81 (0.68 - 1.49). Latitudinal slope difference = -0.06 (-1.38 - 1.35).

82

83 **e)**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	oak	5.27 (2.87 - 7.77)
	oak, blue tit	3.81 (2 - 5.84)
	blue tit	6.58 (4.21 - 9.15)
5km grid cells	oak	24.85 (22.08 - 27.51)
	oak, blue tit	3.19 (0.7 - 6.01)
	blue tit	10.86 (9.37 - 12.37)
Year	oak	42.86 (19.68 - 74.61)
	oak, blue tit	22.67 (8.01 - 41.79)
	blue tit	21.28 (9.07 - 36.62)
Residual	oak	54.8 (53.09 - 56.42)
	blue tit	43.86 (43.17 - 44.61)

84 Fixed effects. Intercept: oak = 116.89 (113.77 - 119.87), blue tit = 115.68 (113.5 -
85 117.83). Latitude slopes: oak = 3.01 (2.69 - 3.33), blue tit = 1.79 (1.49 - 2.09). Latitudinal
86 slope difference = -1.22 (-1.59 - -0.88).

87

88 **f)**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	oak	5.07 (2.87 - 7.71)
	oak, great tit	3.5 (1.65 - 5.61)
	great tit	5.71 (3.16 - 8.4)
5km grid cells	oak	24.88 (22.22 - 27.82)
	oak, great tit	1.8 (-1.68 - 5.53)
	great tit	18.32 (15.26 - 21.43)

Year	oak	42.62 (17.75 - 72.92)
	oak, great tit	23.67 (8.2 - 43.06)
	great tit	21.88 (9.31 - 36.92)
Residual	oak	54.79 (53.19 - 56.47)
	great tit	59.17 (57.91 - 60.44)

89 Fixed effects. Intercept: oak = 116.79 (113.82 - 119.98), great tit = 115.07 (112.99 -
90 117.42). Latitude slopes: oak = 3.01 (2.69 - 3.32), great tit = 1.87 (1.56 - 2.2). Latitudinal
91 slope difference = -1.13 (-1.52 - -0.74).

92

93 **g)**

Term	Response	Mean (co)variance (95% CI)
50km grid cells	oak	5.24 (2.94 - 8.09)
	oak, pied flycatcher	1.88 (0.11 - 3.87)
	pied flycatcher	2.55 (0.33 - 5.82)
5km grid cells	oak	24.75 (22.08 - 27.62)
	oak, pied flycatcher	2.18 (-1.34 - 5.36)
	pied flycatcher	3.62 (2.48 - 4.97)
Year	oak	44.96 (18.05 - 77.69)
	oak, pied flycatcher	10.48 (2.34 - 21.5)
	pied flycatcher	6.7 (2.98 - 11.94)
Residual	oak	54.79 (53.17 - 56.44)
	pied flycatcher	41.67 (40.69 - 42.76)

94 Fixed effects. Intercept: oak = 116.65 (113.67 - 119.67), pied flycatcher = 130.81 (129.42
95 - 132.15). Latitude slopes: oak = 3 (2.71 - 3.33), pied flycatcher = 1.37 (0.94 - 1.79).
96 Latitudinal slope difference = -1.63 (-2.12 - -1.14).

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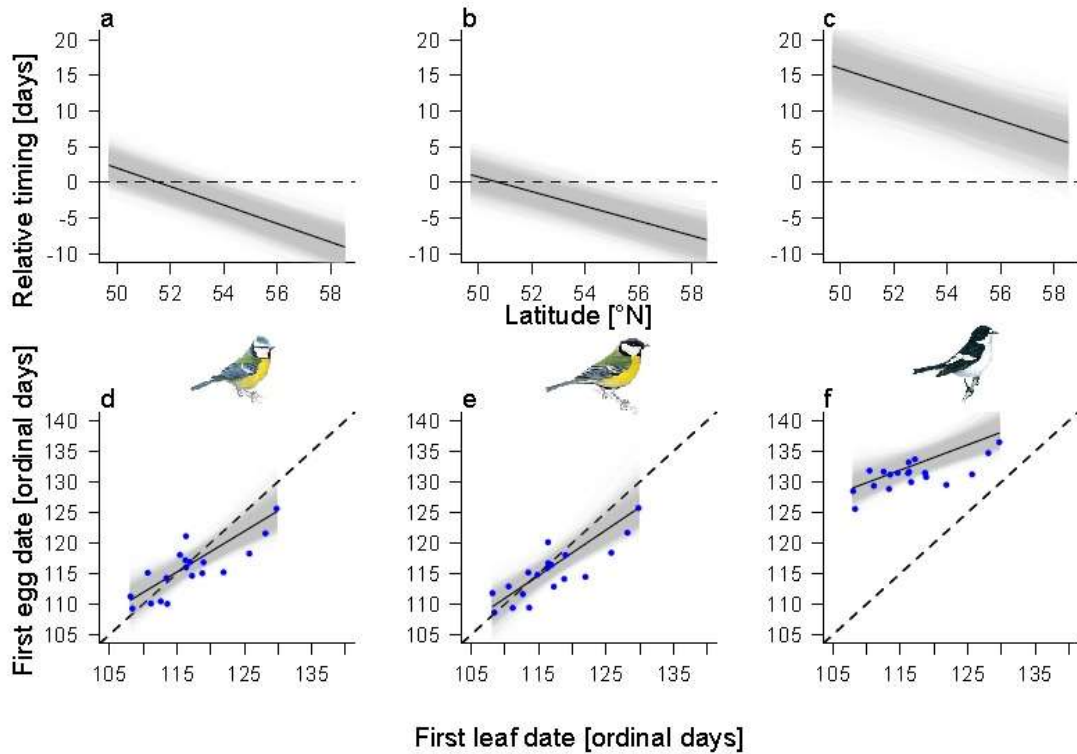
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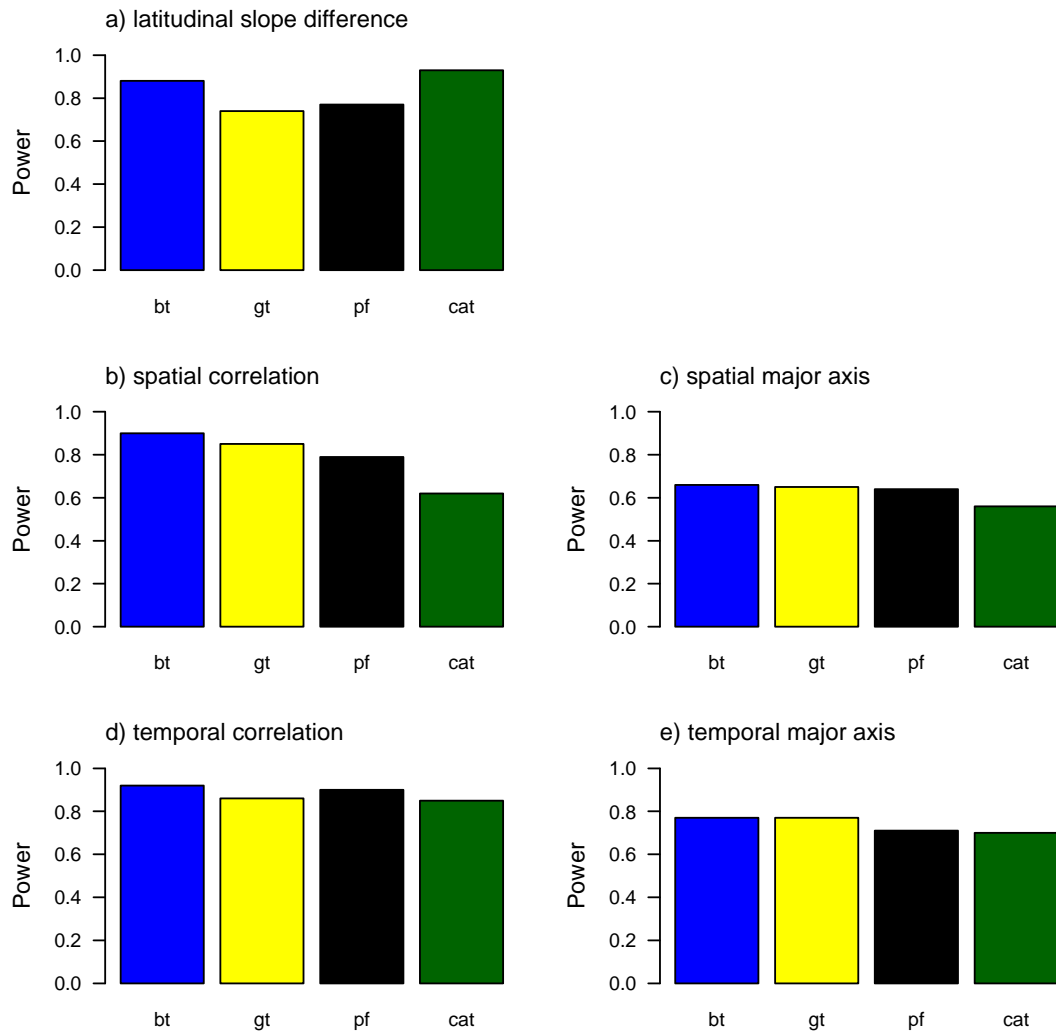
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122 **Supplementary Figure 1 | The relationship between latitude and first egg date**
 123 **relative to oak leafing (a – c) and variation in relative timing among years (d – f),**
 124 **with a and d for blue tits, b and e for great tits and c and f pied flycatchers.** In all panels
 125 the black lines corresponds to the mean slopes (linear regression in a – c and major axis
 126 in d – f), with transparent gray lines representing the posterior distribution of
 127 predictions. In panels a – c relative timing is defined as the predicted first egg date
 128 minus predicted first leaf date. In panels d – f datapoints represent the posterior means
 129 for the best linear unbiased predictions for years that have observations for both
 130 trophic levels. Dashed line corresponds to unity.



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133 **Supplementary Figure 2 | Power to reject the null hypothesis for a)** the
 134 **latitudinal slope difference, b)** spatial correlation, **c)** spatial major axis slope, **d)**
 135 **temporal correlation and e)** temporal major axis slope. Consumer:resource
 136 relationships are bt = blue tit and caterpillar, gt =great tit and caterpillar, pf =
 137 pied flycatcher and caterpillar and cat = caterpillar and oak.
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