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Tritrophic phenological match-mismatch in space and time

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Temperature influences the phenology of plants, insects and birds and thus increasing temperatures associated with climate change has the potential to disrupt previously synchronous trophic interactions^{1,2}. Most work on the phenology of interacting organisms focuses on temporal trends^{1,3}, whereas spatial trends have largely been neglected. Spatial variation in the degree of trophic synchrony may give rise to variation in demography⁴, including the potential for phenological buffering, where some populations are matched while others are mismatched⁵. Here, using extensive phenological data from across Britain, we show that across both space and years the spring timings of oak first leaf are positively correlated with those of peak caterpillar biomass, which are in turn correlated with first egg dates in forest insectivorous passerine birds. Phenology of all species delayed with increasing latitude, with the latitudinal slope for oak significantly steeper than for other species, implying a shortening interval between oak and caterpillar phenology further North. Peak caterpillar timing varies less over space than years with no evidence of spatial variation in the timing of peak bird nestling demand relative to peak caterpillar availability. In late (cold) years the peak nestling demand of the two resident bird species approximately coincides with peak caterpillar availability, with asynchrony

increasing in earlier (warmer) years. The migratory bird species has later egg laying phenology, with nestling demand after peak resource in every year, becoming more mismatched in early springs. Given projections of continued spring warming⁶, we predict that temperate forest birds will become increasingly mismatched with peak caterpillar timing, and that geographic variation in mismatch is unlikely to serve as a demographic buffer.

Rising temperatures are impacting phenology⁷, leading to concern that once synchronous trophic interactions may become disrupted with negative impacts on consumer fitness and demography^{8,9}. Asynchrony or trophic mismatch appears to be most prevalent in the food webs of seasonal habitats, such as deciduous forests and aquatic systems¹⁰, where resource peaks are ephemeral. Most of our insights into natural variation in mismatch and its impacts on the fitness and demography of terrestrial consumers have focused on year to year variation and temporal trends. However, it is also possible for mismatch to vary in space ^{***}, if interacting species differ in their degree of local adaptation or respond with differing plasticity or to different cues. Few studies have considered the spatial dimension of variation in mismatch⁵, despite the potential for it to impact on demography and evolution at the metapopulation level. For instance, if mismatch impacts negatively on demography and is in the same direction everywhere then consumer populations may decline, but (assuming there is additive variance for phenology and populations exchange individuals) these same conditions may facilitate evolutionary rescue¹¹. Whereas, if mismatch varies in its direction over space, then in the short term and at the metapopulation level, the demographic consequences of mismatch at one location may be buffered by match at another location⁵. However, over longer periods spatial variation in the direction of selection will hamper evolutionary rescue¹¹. The spatial relationship between mismatch and its consequences remains largely unstudied, but 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 earlier⁴.

The scarcity of studies addressing spatial variation in mismatch means that we have little evidence on which to judge whether mismatch estimates from one site can be extrapolated to others. 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. Studies show the phenology of these three trophic levels advance with warmer spring temperatures, though birds typically advance by less than trees or caterpillars^{12,13}, causing bird-caterpillar mismatch to be most pronounced in warm springs and exerting strong directional selection for earlier laying¹.

We estimate the spatial (latitudinal) and temporal (among year) trends in relative phenology of oaks and caterpillars, and the synchronicity of 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 from the UK Phenology Network. The timing of peak arboreal caterpillar community biomass was inferred from frass captured in traps set beneath oak trees at x sites across Britain for the period 2008-2016¹⁴ (trap:years = 696). Bird phenology was calculated using first egg dates (FED)

from across Britain for the period 1960-2016 using data from the BTO Nest Record Scheme, comprising 36839 blue tit (*Cyanistes caeruleus*), 24427 great tit (*Parus major*) and 23813 pied flycatcher (*Ficedula hypoleuca*) nests. The phenology of oak¹⁵ and all three bird species¹⁶ have been shown to correlate negatively with mean spring temperatures over time and space, implying that temperature plays a key role as the proximate or ultimate phenological cue. Here we show that frass timing exhibits similar trends, correlating negatively with temperature over time and space, albeit non-significantly in the case of the latter (supplementary materials).

Our focus is on the relationship between the phenology of interacting species¹². Where timing changes more in one species than another, this is indicative of spatial/temporal variation in the direction or magnitude of mismatch, which may imply a buffering of the impacts of mismatch at the meta-population scale⁵. In Britain latitude is a major spatial axis of phenological variation, therefore to examine spatial trends in mismatch we estimate the latitudinal trends in relative phenology of species pairs. We also estimate the relationship between the timing of the consumer and resource as the major axis (MA) slope over space (i.e. among 50km grid cells after de-trending for the latitudinal gradient in the phenology of each species) and time (years), with a slope $\neq 1$ indicative of spatial/temporal variation in relative timing. For the bird – caterpillar interaction we have an estimate of the timing of peak consumer demand and peak resource availability and we can estimate the absolute departure from synchrony (demand earlier or later than supply).

Starting at the base of this food chain, at the average latitude (52.63°N) and year in our dataset, there is a roughly 28-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, Table S2a), resulting in a reduction of the predicted interval to 22 days at 56°N. The de-trended spatial relationship between these species is poorly estimated (Table 1) and the timing of caterpillar phenology varies much more over time than space (Table S2). Among years, the timing of oak and caterpillar is strongly positively correlated (Table 1a) and the MA slope does not depart significantly from 1 (Fig. 2b, Table 1b), consistent with the caterpillar consumer perfectly tracking the timing of the resource over time, but no evidence that this varies across space. The relationship between oak and caterpillar is thus unlikely to be disrupted by future warming, as both 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 north⁵ which still allows tracking the timing of the resource.

In the average year and at the average latitude, FEDs of blue tits (posterior mean day 118.31 [95% credible interval = 116.82 – 119.75], Table S2b) and great tits (day 118.95, [117.24 – 120.61], Table S2c) are approximately one month earlier than peak caterpillar availability (~day 148). However, peak demand is when nestlings are around 14 days old^{38,39}, 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 = 7.22 [-2.35 – 11.82] days in blue tits and 6.3

[0.09 – 12.32] days in great tits. Pied flycatchers also lay earlier (day 135.04 [133.59–136.49, Table S2d) than the peak caterpillar biomass, but predicted peak nestling demand occurs 16.41 [10.49 – 22.12] days behind peak caterpillar availability, suggesting substantial trophic mismatch in the average UK environment.

With increasing latitude the phenology of both birds and caterpillars is delayed by 1.2 – 1.9 days per 50km grid cell (Tables S2b-d) and, while the slope for birds is marginally steeper than for caterpillars, the slope differences are non-significant, meaning that we have no evidence for a latitudinal trend in mismatch (Fig. 3a-c). Indeed, the point estimate of the magnitude of change in relative phenology over the latitudinal range of our data is <5 days in each case. After de-trending for the latitudinal relationship between the phenology of birds and caterpillars, we find that among 50km grid cell correlations and MA slopes between bird and caterpillar phenology are poorly estimated (Table 1).

Across years, the timing of the caterpillar peak date and FED is strongly and significantly positively correlated for all three birds (Table 1a), which implies a strong correlation between the environments that determine development and selection, as required for plasticity to evolve¹⁸. The MA slope is significantly <1, meaning that among years FED varies by less than the timing of the resource peak (Table 1b, Fig. 3d-f), which generates year-to-year variation in the degree of mismatch. For every 10-day advance in the caterpillar peak, the corresponding advance by the birds is estimated to be 5.1, 5.2 and 3.5 days in blue tit, great tit and pied flycatcher, respectively. In late springs (i.e. under cold 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 (Fig. 3d-f). When caterpillar phenology is earlier (i.e. warm 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. The patterns of temporal variation in mismatch we identify for these species are very similar to those reported for great tits in the UK¹⁹ and all three species in the Netherlands¹² and result from the timing of caterpillar resources being relatively more phenologically plastic in response to spring temperatures (supplementary materials). Warmer conditions also produce shorter duration food peaks¹⁴, that may exert stronger 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 incubation²⁰⁻²³.

One of our key findings is that, within any year, there is little latitudinal variation in the amount of caterpillar-bird mismatch. Therefore, meso-scale geographic variation in mismatch is unlikely to buffer metapopulations from the negative consequences of mismatch, or explain spatial variation in population trends. However, it should be easier for connected populations to evolve in response to spatially consistent selection pressures¹¹. This also has the practical implication that insights into the degree of mismatch in one location are likely to generalize to trends elsewhere in the UK. In the average year, 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 optimum

conditions as they vary in space. Of course spatial variation in mismatch may still arise if there is substantial year by site variation in spring temperatures.

In agreement with other European studies on temperate insectivorous passerines¹², we find that the degree of mismatch varies year-to-year. Of the three bird species, migratory pied flycatchers showed the greatest mismatch with caterpillar availability, the predicted peak nestling period being later and mismatched with caterpillars in all but the coldest conditions. This may arise because arrival dates to breeding grounds cannot advance sufficiently, being mediated by African conditions²⁴⁻²⁶ or constraints en-route²⁷, despite UK pied flycatcher FEDs correlating with spring temperatures on the breeding grounds²⁸. Pied flycatchers also showed the shallowest temporal MA slope, which might mean that warm springs are especially detrimental to breeding success and demography. However, pied flycatchers provision nestlings with fewer caterpillars compared to blue tit and great tit²⁹ so may be less dependent on seasonal caterpillar peaks, and there may also be benefits of warmer conditions on arrival³⁰.

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). 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 buffer populations on a local scale. The residual variance for each taxon, which corresponds to variance within a year and site, is >30 (Table S2), and this value corresponds to 95% of individuals being in the range ± 10.74 days of the population mean. All three of our focal birds are able to inhabit woodland types other than oak and such habitats may differ in the timing or ephemerality of the caterpillar resource³¹, which may affect spatial variation in demography and fitness.

While phenological mismatch is frequently raised as a potential impact of climate change, there is an urgent need to compile evidence on the demographic consequences of mismatch and how these interactions play out in realistic spatial or ecological (e.g., habitat generalist) settings. Here we make a first step towards this goal. We find no evidence for spatial variation in mismatch between birds and their caterpillar resource. We do find a latitudinal trend in the interval between oak leafing and the caterpillar peak, but we have no evidence to suggest that the caterpillars are mismatched.

Methods

Phenology data. We obtained pedunculate oak first leafing dates from the UK Phenology Network (<http://www.naturescalendar.org.uk/>). As a quality control step we excluded outliers ($60 \leq \text{leafing date} \leq 155$) and retained only observations made by individuals who submitted records in multiple years.

Arboreal caterpillar biomass was monitored by collecting frass fall from traps set beneath oak trees at 47 sites across Britain¹⁴. 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 $\text{g m}^{-2} \text{ day}^{-1}$. For traps where frass had been collected on at least five occasions in a year we identified the period over which the rate of frass fall was highest by identifying the start and end of this interval. Where the highest rate was found over two or more separate periods then

we allowed the interval to span the combined period. At Wytham Woods the timing of peak frass was estimated statistically³². For these estimates we assumed that uncertainty in the timing of the peak was ± 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^{16,33}. 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. We excluded observations where the interval between minimum and maximum FED exceeded 10 days. We treated the minimum and maximum FED dates as an interval censored Gaussian response.

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 R³⁴. 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 model³⁵ with the phenology of the two interacting species included as a bivariate (and, with the exception of oak, interval censored – meaning that an event was considered to be equally likely to occur at any time within a given interval³⁶) Gaussian response^{5,37}. 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, although we assumed no residual covariance. For caterpillars we also included trap as a random effect. Our ability to estimate covariances between species depends principally on the replication of grid cells or years for which we have data for both species. However, locations where we have data for one species still inform our estimates of latitudinal trends and spatial variance in that species. Similarly, years for which we have data for only a single species still inform our estimates of year variance for that species. Precise estimates of variances improve our ability to estimate relationships between the phenology of species 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 100,000 iterations, with 10,000 iterations removed as burnin. We assessed model convergence on the basis of visual inspection of the posterior distribution trace plots and we ensured that effective sample sizes for all focal parameters exceeded 400 (they were usually in excess of 1000). We provide an example R-code in the supplementary materials.

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, we ignore correlations among 5km grid cells as we have

insufficient replication) and year, respectively. We estimated the major axis rather than type I regression slope³⁸, 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 obtained by summing the predicted FED with mean clutch size, incubation duration (both from BTO nest record scheme, <http://app.bto.org/birdfacts/results/>) and 14 days^{39,40}. 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.

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Author contributions

M.D.B., A.B.P. and K.W.S. conceived the study. A.B.P. and M.D.B. analyzed and interpreted the data and wrote the manuscript. M.D.B., K.W.S., K.B., J.C. K.L.E, C.dF., R.N., B.C.S, J.S.R.C.W. and S.G.W collected frass data and D.L and J.W.P-H. provided bird data. All authors commented on and edited the manuscript.

Additional information

Supplementary materials are available in the online version of the paper. Correspondence and requests for materials should be addressed to M.D.B.

Competing financial interests

The authors declare no competing financial interests.

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

(a)

| | Oak leafing | Peak caterpillar | Blue tit FED | Great tit FED | Pied flycatcher FED |
|---------------------|------------------------|------------------------|-----------------------|-----------------------|-----------------------|
| Oak leafing | - | 0.74 (0.275 - 0.964) | 0.788 (0.541 - 0.924) | 0.839 (0.644 - 0.949) | 0.771 (0.416 - 0.949) |
| Peak caterpillar | 0.475 (-0.101 - 0.986) | - | 0.8 (0.475 - 0.95) | 0.717 (0.243 - 0.939) | 0.911 (0.663 - 0.986) |
| Blue tit FED | 0.677 (0.465 - 0.855) | 0.532 (-0.046 - 0.95) | - | - | - |
| Great tit FED | 0.718 (0.477 - 0.912) | 0.599 (0.02 - 0.987) | - | - | - |
| Pied flycatcher FED | 0.57 (0.175 - 0.928) | 0.398 (-0.504 - 0.974) | - | - | - |

(b)

| | Oak leafing | Peak caterpillar | Blue tit FED | Great tit FED | Pied flycatcher FED |
|---------------------|--------------------------|------------------------|-----------------------|-----------------------|---------------------|
| Oak leafing | - | 1.556 (0.558 - 4.466) | 0.663 (0.417 - 0.949) | 0.717 (0.489 - 0.992) | 0.42 (0.25 - 0.64) |
| Peak caterpillar | 1.613 (-12.025 - 18.936) | - | 0.51 (0.236 - 0.77) | 0.515 (0.109 - 0.904) | 0.348 (0.21 - 0.49) |
| Blue tit FED | 1.097 (0.701 - 1.616) | 0.559 (-0.577 - 3.687) | - | - | - |
| Great tit FED | 1.109 (0.66 - 1.625) | 0.591 (-0.505 - 2.525) | - | - | - |
| Pied flycatcher FED | 0.946 (0.173 - 2.632) | 0.375 (-3.348 - 4.387) | - | - | - |

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Figure 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.

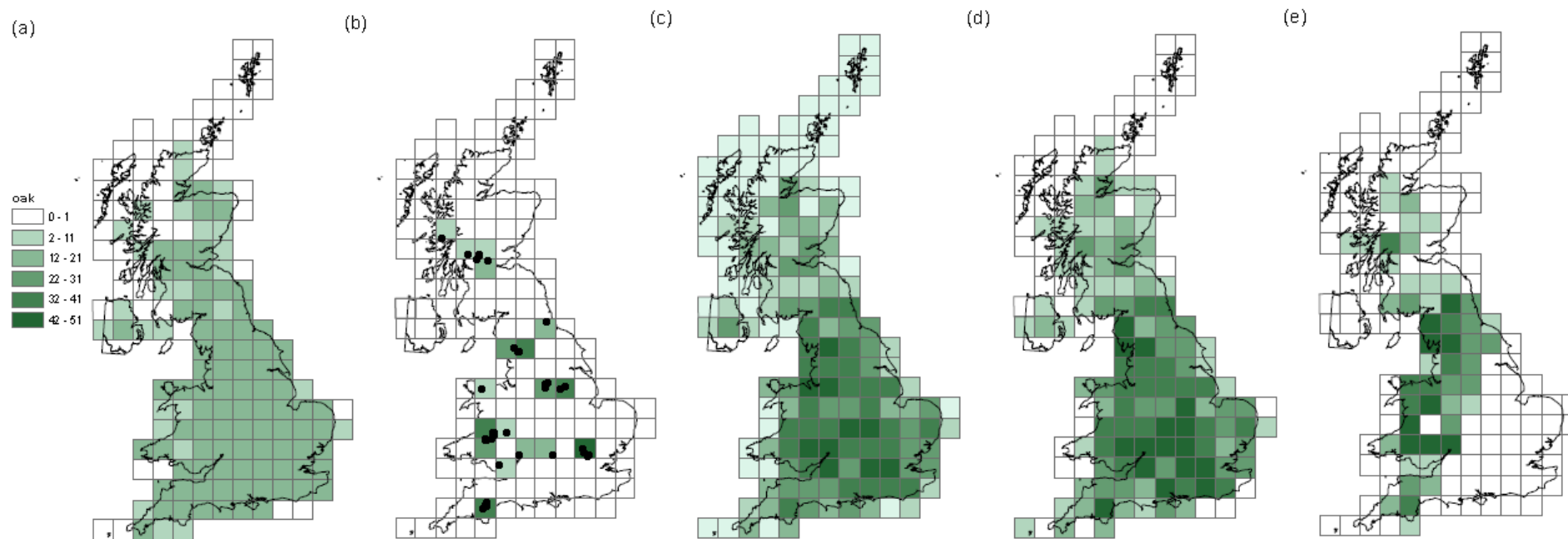


Figure 2| The relationship between latitude and the phenology of oak and caterpillar (a) and the among year relationship between the timing of the two taxa (b). In both panels the black line corresponds to then mean prediction and the grey lines correspond to the posterior distribution of predictions under a ordinary (a) or major axis regression (b). In b, data points represent the posterior means for the best linear unbiased predictions for years that have observations for both species. Dashed line corresponds to unity.

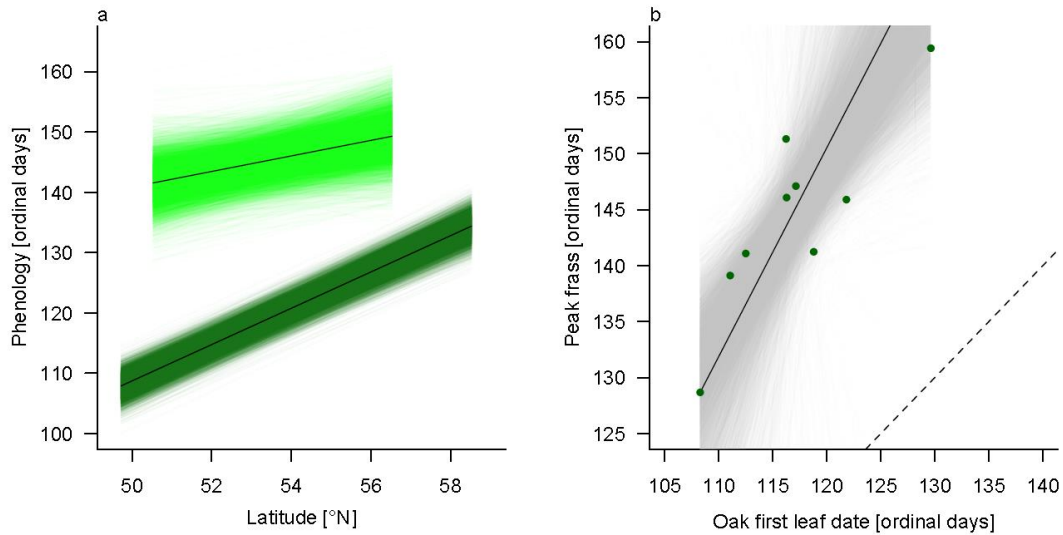


Figure 3| The relationship between latitude and mismatch (a – c) and the timing of peak frass versus first egg date among years (d – f), with a and d for blue tits, b and e for great tits and c and f pied flycatchers. In panels a – c mismatch is defined as the timing of peak avian demand minus the timing of peak frass availability. A prediction of peak nestling demand is obtained from predicted first egg date plus the sum of average UK clutch size, incubation duration and 10 days. In panels d – f datapoints represent the posterior medians for the best linear unbiased predictions for years that have observations for both trophic levels. Dashed line corresponds to unity. The red line indicates the predicted relationship between peak resource availability and peak demand. In all panels the solid lines correspond to the mean slopes (linear regression in a – c and major axis in d – f), with shaded areas representing the posterior distribution of predictions.

