

1 **Tritrophic phenological match-mismatch in space and** 2 **time**

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

51

52 Temperature changes are impacting phenology¹, prompting concern that previously
53 synchronous trophic interactions may be disrupted and lead to negative impacts on
54 consumer fitness and demography²⁻⁴. Trophic asynchrony or mismatch appears to be
55 most prevalent in the food webs of seasonal habitats, such as deciduous forests and

56 aquatic systems⁵, where resource peaks are ephemeral. Most studies of natural variation
57 in mismatch and its impacts on the fitness and population trends of terrestrial
58 consumers are on temporal data. However, it is also possible for mismatch to vary in
59 space, if species respond differently via plasticity or local adaptation to geographic
60 variation in cues. The scarcity of studies addressing the spatial dimension of variation in
61 mismatch⁶ means that we have little evidence as to whether the insights into mismatch
62 estimated at one site can be extrapolated to others.

63

64 The degree to which mismatch varies in space has the potential to impact on both
65 population trends and evolution of consumer species on a meso-scale (Supplementary
66 Table 1). Consider the following latitudinal trends in the phenology of a consumer and a
67 resource, assuming that latitudinal variation in consumer phenology has a plastic basis⁷.
68 If all consumer populations, regardless of their latitude, experience the same magnitude
69 and direction of mismatch (Supplementary Table 1b), which impacts negatively on vital
70 rates, all consumer populations may decline in the short term. If populations of the
71 consumer possess additive variance for phenology, over longer time periods spatially
72 consistent directional selection arising from directional mismatch may facilitate
73 adaptation to reduce mismatch⁸, although the rate of evolutionary change will also
74 depend on the effect of mismatch on population size and the standing genetic variation.
75 In a second example (Supplementary Table 1c), if the consumer phenology varies less
76 over space than the resource phenology⁹, and this generates spatial variation in the
77 direction of mismatch, then in the short term there may be spatial buffering that limits
78 population declines. In this case the consequences of mismatch on one population may
79 be buffered by dispersal from a matched population elsewhere⁶. With gene flow, spatial
80 variation in the direction of selection may oppose the adaption of mismatched
81 populations to their local optima⁸.

82 Here, we use the well-studied tri-trophic deciduous tree–caterpillar–passerine bird food
83 chain, a highly seasonal system, to identify the extent to which consumer phenology
84 tracks resource phenology over time and space. The phenology of these three trophic
85 levels advance with warmer spring temperatures, though birds typically advance by less
86 than trees or caterpillars^{10,11}, causing bird-caterpillar mismatch to be most pronounced
87 in warm springs and associated with strong directional selection for earlier laying¹².

88

89 We estimate the spatial (latitudinal) and temporal (among year) trends in relative
90 phenology of consumer (caterpillar) and primary resource (oak) species, and the
91 synchrony of secondary consumer (bird) peak nestling demand and peak caterpillar
92 resource availability. Fig. 1 shows the distribution of sampling across Britain and among
93 years. We used 10073 observations of pedunculate oak (*Quercus robur*) first leafing for
94 the period 1998-2016. The timing of peak arboreal caterpillar community biomass was
95 inferred from frass captured in traps set beneath oak trees at sites across Britain for the
96 period 2008-2016¹³ (trap:years = 696). Bird phenology was calculated using first egg
97 dates (FED) from across Britain for the period 1960-2016, comprising 36839 blue tit
98 (*Cyanistes caeruleus*), 24427 great tit (*Parus major*) and 23813 pied flycatcher (*Ficedula*
99 *hypoleuca*) nests. The phenology of oak¹⁴ and all three bird species⁷ have been shown to
100 respond negatively to mean spring temperatures over time and space, in a manner that
101 suggests plasticity is responsible for the majority of the spatiotemporal variation and
102 that temperature may be the proximate or ultimate phenological cue. Here we show that
103 frass timing exhibits similar trends, correlating negatively with temperature over time
104 and space, albeit more shallowly and non-significantly over space (supplementary
105 materials).

106

107 Our focus is on the relationship between the phenology of interacting species¹⁵. Where
108 timing changes more in one species than the other, this is indicative of spatial or
109 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

137 represent an adaptation of the life cycle of Lepidoptera species to the shorter spring and
138 summer period in the north⁶.

139

140 In the average year and at the average latitude, FEDs of blue tits (posterior mean ordinal
141 day 118.30 [95% credible interval = 116.83 – 119.85], Supplementary Table 3b) and
142 great tits (day 118.95, [117.20 – 120.61], Supplementary Table 3c) are approximately
143 one month earlier than peak caterpillar availability (~day 148). However, peak demand
144 is when nestlings are around 10 days old^{18,19}, and once we allow for average clutch sizes
145 and incubation durations (see methods), we find that peak demand occurs soon after
146 peak resource availability, with mean peak demand–mean peak resource = 3.39 [–6.63 –
147 8.86] days in blue tits and 2.01 [–3.99 – 7.71] days in great tits. Pied flycatchers also lay
148 earlier (day 135.04 [133.55–136.53, Supplementary Table 3d) than the peak caterpillar
149 biomass, but predicted peak nestling demand occurs 12.87 [6.69 – 19.40] days later
150 than peak caterpillar availability, suggesting substantial trophic mismatch in the
151 average UK environment.

152

153 With increasing latitude the phenology of caterpillars is delayed by ~ 1.3 days $^{\circ}\text{N}^{-1}$ and
154 the point estimates for the equivalent latitudinal trend in birds are from 1.67 – 1.93 days
155 $^{\circ}\text{N}^{-1}$ (Supplementary Tables 3b-d). While the slope for birds is marginally steeper than
156 for caterpillars, such that birds in the north are slightly more mismatched, we have no
157 evidence for a significant latitudinal trend in mismatch (Fig. 3a-c). Moreover, the effect
158 size of any latitudinal trend in mismatch is small, as the point estimate of the magnitude
159 of change in the relative phenology of consumer – resource over the latitudinal range of
160 our data (50 – 57°N) is < 5 days in each case.

161

162 Across years, the timing of the caterpillar peak date and bird FED is strongly and
163 significantly positively correlated for all three bird species (Table 1a). The MA slope is
164 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

193 populations when selection pressures are spatially consistent compared to being
194 spatially variable⁸. This result also has the practical implication that insights into the
195 degree of mismatch in one location can be generalized to trends at different latitudes. In
196 the average spring, the timing of blue tit and great tit nestling demand is quite
197 synchronous with the peak resource, which is consistent with birds being able to track
198 spatial variation in optimal timing. Spatial variation in mismatch will still occur if there
199 is substantial year by site variation in spring temperatures, as would arise if the rate of
200 warming varies spatially.

201

202 Of the three bird species, migratory pied flycatchers showed the greatest mismatch with
203 caterpillar availability, the predicted peak nestling period being consistently later than
204 peak caterpillar timing. If pied flycatcher migration times are mediated by African
205 conditions²⁶⁻²⁸ or constraints en-route²⁹, this may limit their ability to advance their
206 arrival times, even if once they have arrived they are able to respond to spring
207 temperatures on breeding grounds³⁰. However, pied flycatchers provision nestlings
208 with fewer caterpillars and more winged invertebrates compared to blue tit and great
209 tit³¹, so may be less dependent on seasonal caterpillar peaks.

210

211 Our study focuses on mismatch judged from population means within a year and site (or
212 in the case of oak leafing the first date in a population – see methods). There is of course
213 potential for some individuals within a population to be matched even when population
214 means are mismatched, and this could serve to reduce effects of mismatch on local
215 populations³². The residual variance for caterpillars and birds, which corresponds to
216 variance within a year and site, is >30 (Supplementary Table 3), which corresponds to
217 95% of individuals within a 5km grid cell and year being in the range ± 10.74 days of the
218 population mean. All three of our focal bird species are able to inhabit woodland types
219 other than oak and such habitats may differ in the timing or ephemerality of the

220 caterpillar resource³³, which may have further impacts on spatial variation in
221 demography and selection.
222
223 While phenological mismatch is frequently raised as a potential impact of climate
224 change, there is an urgent need to compile evidence on the consequences of mismatch
225 for population trends across realistic spatial or ecological (e.g., habitat generalist)
226 settings. A Dutch study on pied flycatchers found that population declines were greater
227 in areas where the caterpillar peak (assumed to be a proxy for mismatch) was earlier³⁴,
228 but the spatial relationship between mismatch and population trends remains largely
229 unstudied³⁵. Our study presents the first assessment of whether latitudinal variation in
230 mismatch exists, as is sometimes proposed as a mechanism whereby the adverse
231 impacts of climate change might be buffered, for example, more northern populations
232 being less adversely affected by spring warming compared to southern populations³⁶.
233 The lack of evidence we find for latitudinal variation in mismatch between birds and
234 their caterpillar resource suggests mismatch is unlikely to be a driver of spatially
235 varying population trends found in avian secondary consumers³⁷.

236

237 **Methods**

238

239 **Phenology data.** We obtained pedunculate oak first leafing dates from the UK
240 Phenology Network (<https://naturescalendar.woodlandtrust.org.uk/>). As a quality
241 control step we excluded outliers (ordinal day $60 \leq$ leafing date ≥ 155) and retained only
242 observations from individuals who submitted records in multiple years. Our data for oak
243 leafing differ from the other trophic levels in that they are of first dates within local
244 populations. First dates will be earlier than mean dates, but would only be biased if
245 there is a trend (latitudinal or correlating with year earliness) in sampling effort,
246 population abundance or variance. We suggest that the first two are unlikely to pose a
247 problem^{14,38}, but we do not have the data to rule out the third source of bias.

248

249 Arboreal caterpillar biomass was monitored by collecting frass fall from traps set
250 beneath oak trees at 47 sites across Britain¹³. Frass was collected, sorted and the dry
251 weight obtained approximately every 5 days (mean = 4.63) during spring up until day
252 180 at the latest, from which we calculated a frass fall rate in g square m⁻¹ day⁻¹. For
253 traps where frass had been collected on at least five occasions during a spring we
254 identified the sampling period over which the rate of frass fall was highest and then
255 identified the start and end of this interval. Where the highest rate was found over two
256 or more separate periods then we allowed the peak frass interval to span the combined
257 period. At one site, Wytham Woods, the timing of peak frass was estimated
258 statistically³². For these estimates we assumed that the interval was the peak date \pm 3
259 days.

260

261 First egg dates (FED) for blue tit, great tit and pied flycatcher were obtained from nests
262 monitored across Britain for the BTO Nest Record Scheme^{7,39}. Few nests were visited
263 daily, and so a minimum FED was calculated by combining information collected over
264 repeated visits before and after laying, including the date of previous visits with no eggs
265 present, clutch size, laying rate and incubation period. A maximum FED was calculated
266 as the date on which eggs were first observed minus the product of the number of eggs
267 and the maximum laying rate, i.e. one egg per day. We excluded observations where the
268 interval between minimum and maximum FED exceeded 10 days.

269

270 We imposed a 'population' structure on all observations by dividing Britain into 50km x
271 50km grid cells. To spatially match observations at a finer scale within these
272 'populations' and to address some of the spatial pseudoreplication of observations we
273 generated a smaller grid structure corresponding to 5km x 5km.

274

275 **Analysis.** All analyses were conducted in R⁴⁰. We assessed the degree to which
276 consumer species were able to track the phenology of resource/primary producer
277 species across space and time using a generalized linear mixed model⁴¹ with the
278 phenology of the two interacting species included as a bivariate Gaussian response^{6,42}.
279 With the exception of oak, the response was interval censored, meaning that an event
280 was considered to be equally likely to occur at any time within the given interval⁴³. The
281 model included the intercept and latitude as the only fixed effects for each of the
282 response variables, and 50km grid cell, 5km grid cell, year and residual as random
283 effects. For each random term we estimated the (co)variance components, with the
284 exception of the residual term for which we estimated variances but not covariance. For
285 caterpillars we also included trap as a random effect. Our ability to estimate covariances
286 between trophic levels depends principally on the replication of grid cells or years for
287 which we have data for both trophic levels. However, locations where we have data for
288 one trophic level inform our estimates of latitudinal trends, among grid cell variance and
289 year means for that level. Similarly, years for which we have data for only a single
290 trophic level inform our estimates of among year variance and grid cell means or that
291 level. Precise estimates of these means and variances inform our estimates of
292 relationships between the phenology of trophic level pairs.
293
294 We used parameter expanded priors for (co)variances across years and grid cells and
295 inverse-Wishart priors for the residual term. Models were run for 440,000 iterations,
296 with 40,000 iterations removed as burnin and sampling every 100. We assessed model
297 convergence via visual inspection of the posterior distribution trace plots and by
298 running a second chain and ensuring that the multivariate potential scale reduction
299 factor for fixed effects on the two chains was < 1.1 ⁴⁴. The effective sample sizes for all
300 focal parameters exceeded 1000.
301

302 The model intercepts estimate the mean phenology of each species at the average
303 latitude in the average year. We used the (co)variance components estimated for grid
304 cells and years to obtain correlation estimates between the two species over space
305 (50km grid cells only) and years, respectively. We estimated the major axis rather than
306 type I regression slope⁴⁵, because we were interested in the degree of phenological
307 tracking, rather than the degree to which the phenology of one species predicts the
308 phenology of another.

309

310 We considered the following bivariate models: (i) peak caterpillar date versus oak first
311 leafing date, (ii) each of the three bird species FED versus peak caterpillar date, and (iii)
312 each bird FED with oak first leafing date. For the bird versus caterpillar we compared
313 the predicted peak resource availability to the predicted peak consumer demand, which
314 we calculated as the predicted FED across latitudes or years plus mean clutch size which
315 varies little at the scale of our study⁴⁶, and incubation duration (both from BTO nest
316 record scheme <http://app.bto.org/birdfacts/results/>) and the 10 day duration between
317 hatching and peak nestling food demand^{47,48}. While the tree versus bird comparisons are
318 not trophic interactions, we consider them here because we anticipate that oak leafing
319 may be a proxy for peak caterpillar date, with the spatiotemporal replication of first
320 leafing observations greatly exceeding those of peak caterpillar.

321

322 **Data availability**

323

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

328

329 **Code availability**

330

331 Example R code is available at the following repository:

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

333

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335

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343

344 **Author contributions**

345

346 M.D.B., A.B.P. and K.W.S. conceived the study. M.D.B led and coordinated the study, A.B.P.
347 analyzed the data and M.D.B and A.B.P wrote the manuscript with K.L.E. making
348 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.,
349 J.S.R.C.W. and S.G.W collected frass data, K.L. provided oak leafing data, and D.L and
350 J.W.P-H. provided bird data. All authors commented on and edited the manuscript.

351

352 **Competing financial interests**

353

354 The authors declare no competing financial interests.

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513
514

515

516 **Figure legends**

517

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

521

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

532

533 **Fig. 3 | The relationship between latitude and mismatch (a – c) and the timing of**
534 **peak frass versus first egg date among years (d – f),** with **a** and **d** for blue tits, **b** and **e**
535 for great tits and **c** and **f** pied flycatchers. In panels a – c mismatch is defined as the
536 timing of peak avian demand minus the timing of peak frass availability, with peak
537 nestling demand calculated as being when nestlings are predicted to be 14 days old (see
538 methods). In panels d – f datapoints represent the posterior means for the best linear
539 unbiased predictions for years that have observations for both birds and caterpillars.

540 Dashed line corresponds to unity. In d – f the black line is the among year mean major
 541 axis slope and the red line is the predicted relationship between peak resource
 542 availability and peak demand. Transparent gray lines represent the posterior
 543 distribution of predictions.

544

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

548

549 (a)

	Oak leafing	Peak caterpillar	Blue tit FED	Great tit FED	Pied flycatcher FED
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)	-	-	-

550

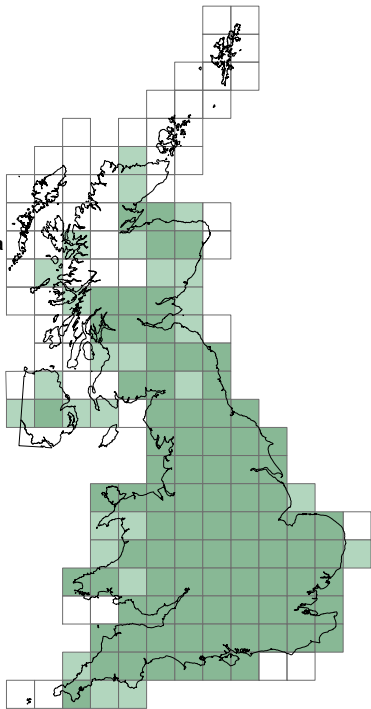
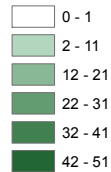
551 (b)

	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)	-	-	-

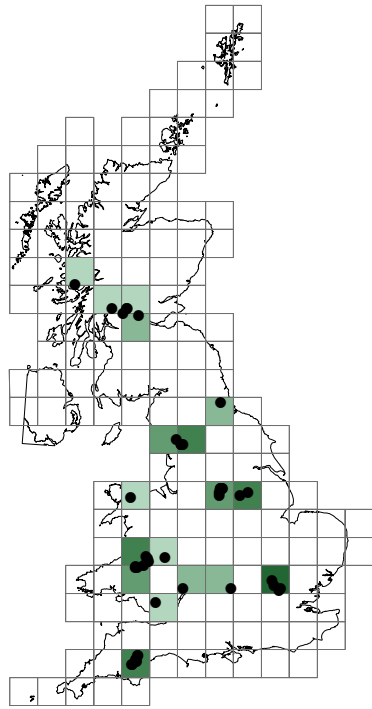
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(a)

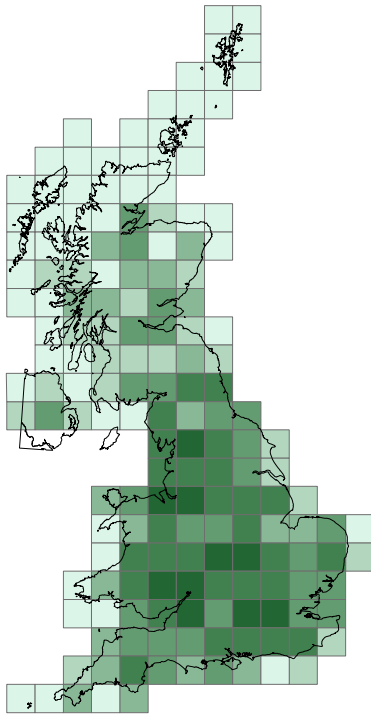
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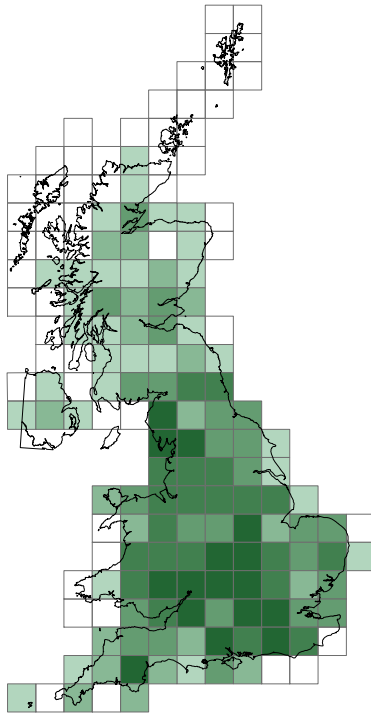
(b)



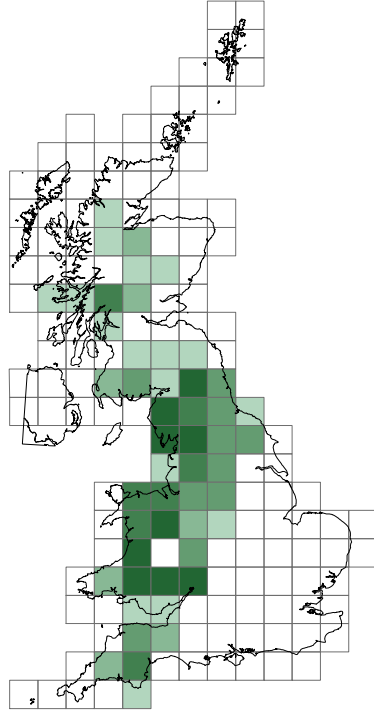
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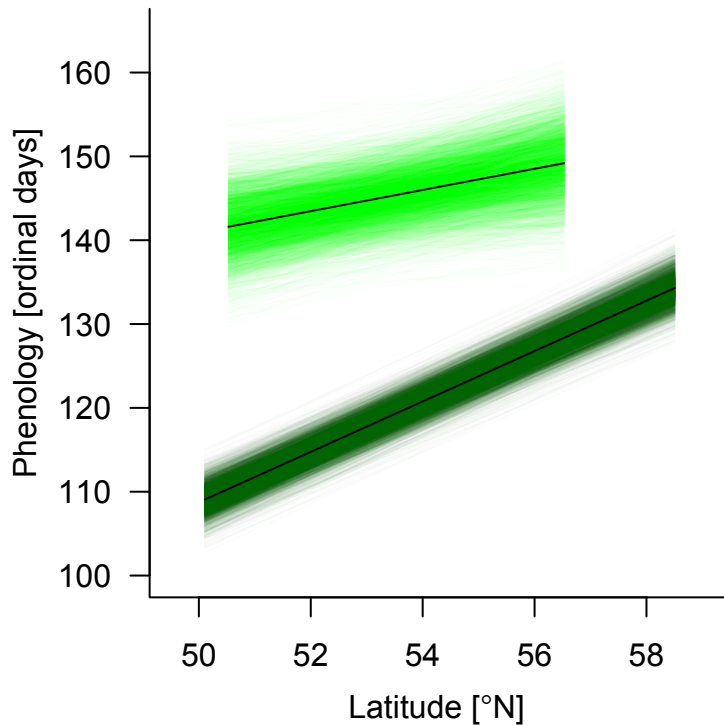
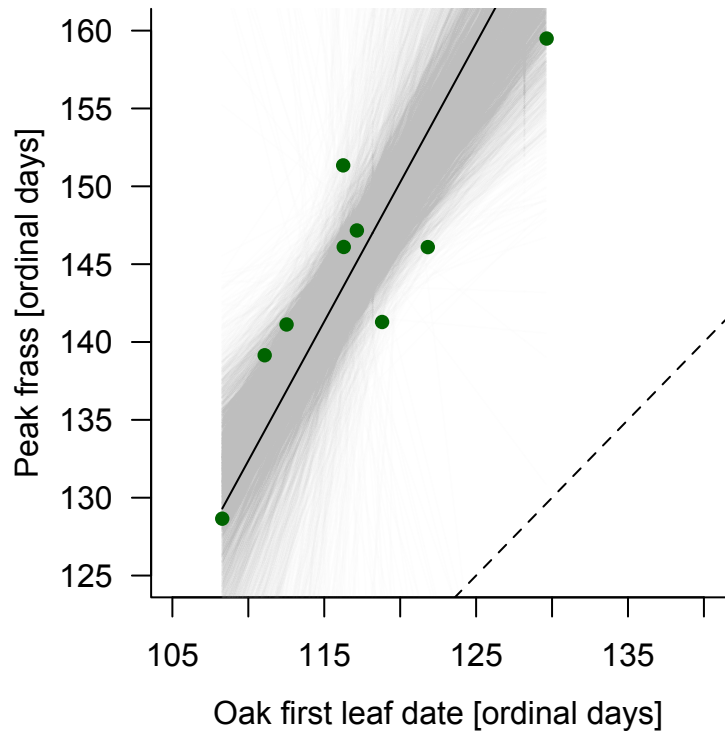


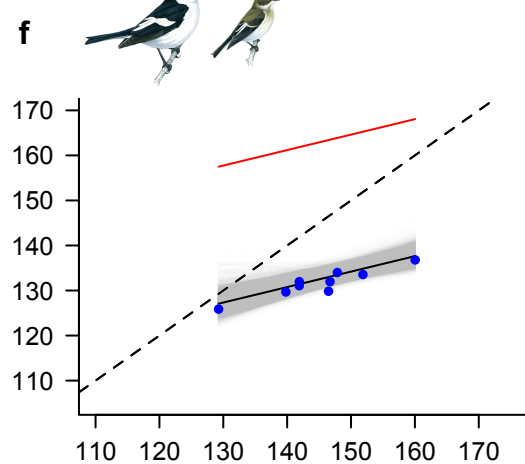
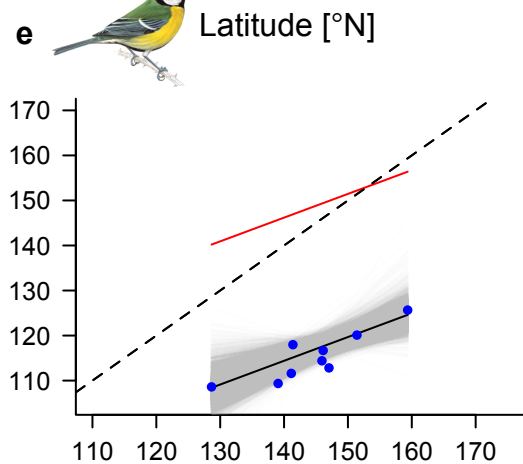
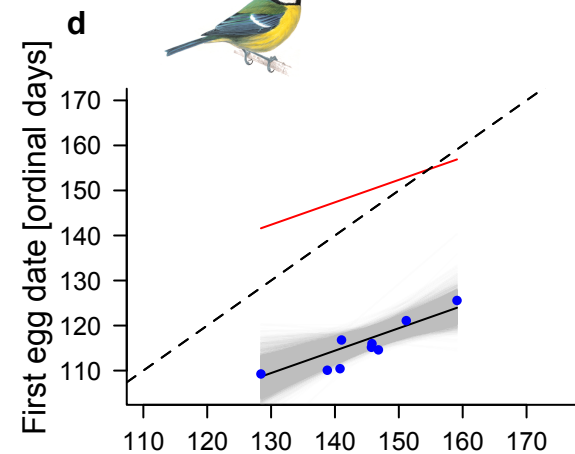
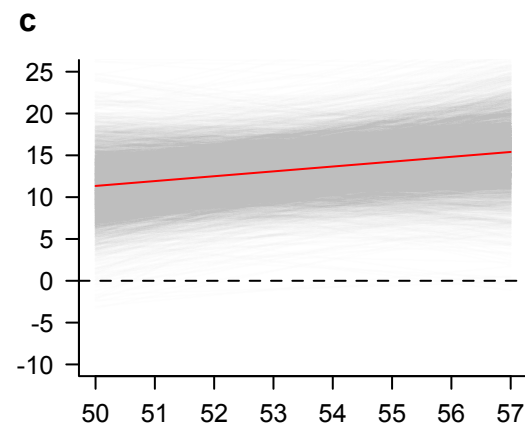
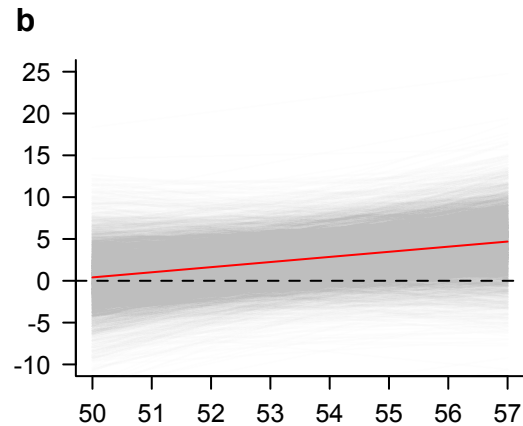
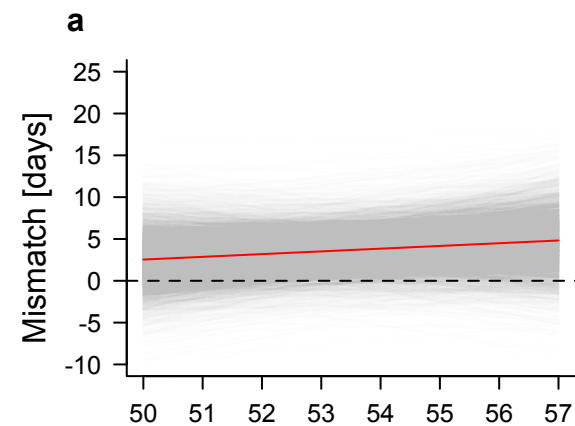
(d)



(e)



a**b**



Peak frass date [ordinal days]