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## Predicting insect phenology across space and time

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## Predicting insect phenology across space and time

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Keywords:	climate change, emergence time, latitude, growing degree days, phenotypic plasticity, adaptation, butterfly monitoring scheme, lepidoptera
Abstract:	<p>Many species appear to be undergoing shifts in phenology, arising from climate change. To predict the direction and magnitude of future changes requires an understanding of how phenology depends on climatic variation. Species show large-scale spatial variation in phenology (affected by differentiation among populations) as well as variation in phenology from year-to-year at the same site (affected predominantly by local plasticity). Teasing apart spatial and temporal variation in phenology should allow improved predictions of phenology under climate change. This study is the first to quantify large-scale spatial and temporal variation in the entire emergence pattern of species, and to test the relationships found by predicting future data. We use data from up to 33 years of permanent transect records of butterflies in the UK to fit and test models for 15 butterfly species. We use generalised additive models (GAMs) to model spatial and temporal variation in the distribution of adult butterflies over the season, allowing us to capture changes in the timing of emergence peaks, relative sizes of peaks and/or number of peaks in a single analysis. We develop these models using data for 1973-2000, and then use them to predict phenologies from 2001-2006. For 6 of our study species, a model with only spatial variation in phenology is the best predictor of the future, implying that these species have limited plasticity. For the remaining 9 species, the best predictions come from a model with both spatial and temporal variation in phenology; for 4 of these, growing-degree-days have similar effects over space and</p>

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	time, implying high levels of plasticity. The results show that statistical phenology models can be used to predict phenology shifts in a second time period, suggesting that it should be feasible to project phenologies under climate change scenarios, at least over modest time scales



For Review Only

# Predicting insect phenology across space and time

**Running title:** predicting insect phenology

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**Keywords:** climate change; emergence time; latitude; growing degree days; phenotypic plasticity; adaptation; butterfly monitoring scheme; lepidoptera

18 ***Abstract***

19 Many species appear to be undergoing shifts in phenology, arising from climate change. To  
20 predict the direction and magnitude of future changes requires an understanding of how  
21 phenology depends on climatic variation. Species show large-scale spatial variation in  
22 phenology (affected by differentiation among populations) as well as variation in phenology  
23 from year-to-year at the same site (affected predominantly by local plasticity). Teasing apart  
24 spatial and temporal variation in phenology should allow improved predictions of phenology  
25 under climate change. This study is the first to quantify large-scale spatial and temporal  
26 variation in the entire emergence pattern of species, and to test the relationships found by  
27 predicting future data. We use data from up to 33 years of permanent transect records of  
28 butterflies in the UK to fit and test models for 15 butterfly species. We use generalised  
29 additive models (GAMs) to model spatial and temporal variation in the distribution of adult  
30 butterflies over the season, allowing us to capture changes in the timing of emergence peaks,  
31 relative sizes of peaks and/or number of peaks in a single analysis. We develop these models  
32 using data for 1973-2000, and then use them to predict phenologies from 2001-2006. For 6 of  
33 our study species, a model with only spatial variation in phenology is the best predictor of the  
34 future, implying that these species have limited plasticity. For the remaining 9 species, the  
35 best predictions come from a model with both spatial and temporal variation in phenology; for  
36 4 of these, growing-degree-days have similar effects over space and time, implying high  
37 levels of plasticity. The results show that statistical phenology models can be used to predict  
38 phenology shifts in a second time period, suggesting that it should be feasible to project  
39 phenologies under climate change scenarios, at least over modest time scales.

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## ***Introduction***

42 Many species appear to be undergoing shifts in phenology as a result of climate change  
43 (Sparks & Carey 1995; Crick *et al.* 1997; Menzel & Fabian 1999; Roy & Sparks 2000;  
44 Stefanescu *et al.* 2003), and phenological changes constitute a high proportion of all of the  
45 evidence that species are responding to climate change (Walther *et al.* 2002; IPCC 2007).  
46 Thanks to comprehensive biological recording, butterflies have become a model group in  
47 detecting the impacts of climate change, including impacts on phenology (Sparks & Yates  
48 1997; Roy & Sparks 2000; Forister & Shapiro 2003; Stefanescu *et al.* 2003; Dell *et al.* 2005;  
49 Gordo & Sanz 2006; Menzel *et al.* 2006). However, understanding and predicting these  
50 changes remains more of a challenge (Visser 2008). The climate change literature is replete  
51 with statements about the potential detrimental effects of phenology shifts because they could  
52 lead to significant changes in population growth rates and in community interactions (van  
53 Asch *et al.* 2007; Doi *et al.* 2008). For example, temporal mismatches between plants and  
54 their pollinators could reduce seed set in plants (including crops) and reduce food availability  
55 for the pollinators (Memmott *et al.* 2007). To predict whether such issues will become greater  
56 in the future demands an ability to predict phenology shifts, based on climatic variation.

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58 In insects, a variety of life history parameters (e.g. induction of diapause, size at pupation,  
59 maternal investments, etc.) may evolve in order to maximize fitness under the prevailing  
60 climate and the historic range of variability of that climate (Davidson 1944; Lees 1950; Manly  
61 1974; Visser 2008). Insects respond to very specific cues which, over their evolutionary  
62 history, have helped them to stay in synchrony with important seasonal events, such as the  
63 bud burst of trees (van Asch *et al.* 2007). Temperature and day length (photoperiod) may both

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3 64 be used as cues (Bale *et al.* 2002). Because different species have evolved to use different  
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5 65 cues, and because climate change affects temperature but not day length, this could lead to  
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8 66 maladaptive responses (Doi *et al.* 2008).  
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12 68 A number of studies have used year-to-year variation in phenology (usually earliest  
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15 69 emergence or mean emergence date) regressed on yearly climate to predict future changes  
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17 70 (e.g. Roy & Sparks 2000; Gordo & Sanz 2006). As well as temporal changes, many species  
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20 71 also show spatial variation in phenology (e.g. Zhou *et al.* 1995; Langvatn *et al.* 1996; White *et*  
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22 72 *al.* 1997), but a given climate variable may have different effects over space and over time  
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25 73 (Pollard 1991; Rock *et al.* 1993; Thompson & Clark 2006; Doi *et al.* 2008; Doi & Takahashi  
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27 74 2008; Forkner *et al.* 2008). For example, the leafing date of japanese trees varies less with the  
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30 75 gradient of temperature over space than it does with changes in temperature over time at a  
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32 76 single site (Doi & Takahashi 2008). If phenology varies to different extents in space and in  
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34 77 time this implies that species do not simply respond physiologically to temperature cues.  
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36 78 Instead they are likely to be, in part, locally adapted and/or responsive to spatially fixed cues,  
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38  
39 79 such as daylength (Bradshaw & Holzapfel 2001; Visser 2008).  
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43 81 Teasing apart the spatial variation in phenology, which is affected by local differentiation of  
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46 82 populations, and the temporal variation, which is affected by phenotypic plasticity within a  
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49 83 population, should allow much better predictions of phenology under climate change than  
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51 84 looking at one (space/time) dimension in isolation. However, few studies have considered  
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53 85 both spatial and temporal variation in phenology (Rock *et al.* 1993; Doi *et al.* 2008; Doi &  
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55 86 Takahashi 2008), and none of these has explicitly attempted to predict the future.  
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3 88 In this study we use data from up to 33 years of permanent transect records of butterflies in  
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5 89 the UK to fit and test models of the phenology of 15 butterfly species, modelling both spatial  
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7 90 and temporal variation in relation to the climate. We use generalised additive models (GAMs)  
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9 91 (Wood 2006) to model the distribution of adult butterflies over the season, independently of  
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11 92 the overall abundance at a particular site and year, allowing us to capture changes in the  
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13 93 timing of emergence peaks, relative sizes of peaks and/or number of peaks in a single  
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15 94 analysis. We develop these models using data for the time period 1973-2000, and then use  
16  
17 95 each model to predict phenologies for the period 2001-2006. The testing data enables us to  
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19 96 assess our ability to predict detailed phenological patterns into the future. Furthermore, the  
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21 97 relative predictive power of alternative models that have different predictor variables allows  
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23 98 us to make inferences about the factors that regulate phenology in different species.  
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4 99 **Methods**  
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8 100 **Butterfly data**  
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10 101 We used butterfly abundance data from UK Butterfly Monitoring Scheme (collected and  
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12 102 maintained by Butterfly Conservation and the Centre for Ecology and Hydrology; Pollard &  
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14 103 Yates 1993; Asher *et al.* 2001). Butterflies of all species are recorded along a permanent  
15  
16 104 transect at weekly intervals between April and September at a network of sites across the  
17  
18 105 country. The number of sites taking part in the scheme has increased from 1 in 1973 to 750 in  
19  
20 106 2006. In order to fit models to roughly half the data, and use the other half to test model  
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22 107 predictions, we split the data set into 1973-2000 and 2001-2006 periods.  
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29 109 We focused on the 15 species that are known to have multiple generations per year in at least  
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31 110 part of their British range, since these have the most complex phenological patterns and might  
32  
33 111 be expected to be the most difficult to model and predict future changes. We ran all the  
34  
35 112 analyses separately for each species, using only sites where the species was found at a  
36  
37 113 reasonable frequency (usually using the condition that the median count over all weeks and  
38  
39 114 years should be greater than one, but this condition had to be relaxed for 4 species that were  
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41 115 particularly rare and/or temporally variable: holly blue, wall brown, small blue and wood  
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43 116 white; common English and Latin names are given in Table 2).  
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50 118 **Climate data**  
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52 119 We used historical monthly mean temperature data at the 10 km grid resolution, from  
53  
54 120 averages of the 5 km grid resolution data available from the Met Office (“UKCP09” data,  
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56 121 Met\_Office 2009). We decided to use growing degree days above 5° Celsius (henceforth  
57  
58 122 “GDD5”) as a measure of the warmth available for development and reproduction that is  
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3 123 relevant to all butterfly species (even though there will also be various effects of winter  
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5 124 minima, summer maxima, rainfall, cloudiness, etc.) (Romo & Eddleman 1995; Bryant *et al.*  
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7 125 2002). From the monthly mean temperatures we calculated the GDD5 for each UKBMS site  
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9 126 (henceforth actual GDD5) in each year; defining “year” as the months between October of the  
10  
11 127 previous year (just after the previous transect season finished) and September (when the  
12  
13 128 transect season in question finished). Across the UK, GDD5 has been increasing in the time  
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15 129 period of this study, but there is also considerable year-to-year variation (Fig. 1). The average  
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17 130 increase in GDD5 between the period 1973-2000 and the period 2001-2006 is c.200, which is  
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19 131 nearly half of the inter-annual variation (variation in medians among years), and 10% of the  
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21 132 spatial variation in GDD5 that exists across all British 10km grid squares within a single year  
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23 133 (Fig. 1).  
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32 135 Because we wanted to separate the effects of spatial variation in the climate from temporal  
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34 136 variation in the climate, we also calculated (a) mean GDD5 for each site over the period 1973-  
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36 137 2000 (henceforth “site GDD5”), and (b) the difference between each site’s actual GDD5 in  
37  
38 138 each year and the site mean (henceforth “GDD5 differential”). Hence each site and year has 3  
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40 139 interrelated GDD5 measures:  $(\text{actual GDD5})_t = (\text{site GDD5}) + (\text{GDD5 differential})_t$  where  $t$   
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43 140 indexes years.  
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## 48 142 **Statistical analyses**

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50 143 We used generalised additive models (GAMs) with a negative binomial error structure to  
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52 144 model the emergence pattern as a flexible, smooth function of the time of year (measured as  
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54 145 weeks from the first week in April). By using 2-D and 3-D smooths, we could represent the  
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56 146 fact that emergence pattern would change gradually with the climate over space and/or time.  
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58 147 We used the GAM implementation in the mgcv package in R (Wood 2003; Wood 2008;  
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3 148 R\_Development\_Core\_Team 2009) with the extension to negative binomial family in the  
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5 149 MASS package (Venables & Ripley 2002). Because the data consisted of butterfly counts (of  
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8 150 a certain species at a given site, week and year), but we wanted to investigate the emergence  
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10 151 pattern independently of the overall abundance of butterflies, we always included the average  
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12 152 abundance for the site and year as a linear covariate in the GAM. Specifically, this linear  
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15 153 covariate was calculated as:  $\text{mean}[\ln(\text{count}_i + 1/27)]$  where  $i$  indexes the week, and there are  
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17 154 usually 26 weeks (sometimes fewer because of missed surveys). The mean is calculated in log  
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19 155 space because the negative-binomial GAM has a log link function, and a constant  $1/27$  is  
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21 156 added to the count because zeros cannot be logged. Using this average abundance as a  
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23 157 covariate means that the variation remaining to be explained is the distribution of individuals  
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25 158 among the weeks of a given year – which is the main quantity of interest – and that the  
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27 159 observation error structure relevant to such count data is retained.  
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34 161 We fitted 7 GAMs, representing different hypotheses about the drivers of phenology, to each  
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36 162 species' data for the early time period (1973-2000). We evaluated the GAMs on their ability to  
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38 163 predict the later time period (2001-2006). Details of the 7 models used are given in Table 1.  
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40 164 The spatial component of climate is represented either by site GDD5 or by site northing: the  
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42 165 latter should be a better predictor of phenology if the species responds more to day length  
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44 166 than temperature. The temporal component is represented by GDD5 differential. If the basic  
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46 167 responses to temperature are the same everywhere (i.e. different populations are not adapted  
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48 168 to the climate differently) then the actual GDD5 experienced by each site in each year might  
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51 169 be the best predictor of phenology.  
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## 57 171 **Model comparison**

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3 172 The exact likelihood of each observation ( $x$ ) given our model can be calculated as the  
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5 173 probability density at  $x$  of the negative binomial distribution with mean given by the GAM  
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8 174 prediction (according to the explanatory variables specific to that observation), and shape  
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10 175 parameter as fitted by the GAM (the same shape parameter for all observations under a given  
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12 176 model). Taking logs of these probabilities and summing over all observations (either  
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15 177 observations in the fitting period, or observations in the testing period) gave us the log  
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17 178 likelihood,  $L$ . The proportion of deviance “explained” was taken to be how far  $L$  lies between  
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19 179  $L_{\text{null}}$  (likelihood under model 00, see Table 1) and  $L_{\text{sat}}$ .  $L_{\text{sat}}$  is the maximum likelihood  
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21 possible for those data: that which would occur under a model where predictions are exactly  
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23 180 the same as observations (i.e. a saturated model) and where a Poisson distribution (no  
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25 181 overdispersion) is assumed. So proportion deviance explained =  $1 - (L - L_{\text{sat}}) / (L_{\text{null}} - L_{\text{sat}})$ .  
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31 184 Our results focus on comparing the log likelihood of the testing (2001-2006) data under each  
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33 185 GAM. Using a separate test data set effectively penalizes overfitted models, and the model  
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35 186 with the highest log likelihood can be said to be the best model (i.e., no GAM parameters  
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37 187 were estimated for any model using the testing data). We can also use  $-2L$  to calculate Akaike  
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39 188 weights (Burnham & Anderson 2002) to give us a “degree of belief” in a certain model  
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41 189 compared to others. However, the Akaike weighting is strongly dependent on the assumption  
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43 190 that observations are independent – an assumption that was not really tenable for our data,  
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45 191 where there were multiple observations from exactly the same site. To show which of our  
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47 192 conclusions are robust to this assumption, we report raw model weights, and weights where  
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49 193 each observation only counts as 1/12 of a degree of freedom ( $L$  becomes  $L/12$ ). The factor 12  
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51 194 was chosen based on the autocorrelation of residuals in the testing data. Residuals from  
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53 195 consecutive weeks at the same site and the same year had rank correlation coefficients  $>0.5$ ,  
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55 196 but correlation dropped quickly with lag  $> 1$  week, so roughly every other week’s data could  
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3 197 be considered a pseudoreplicate. Residuals from the same week at the same site for different  
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5 198 years had rank correlation coefficients  $>0.5$ , irrespective of the time lag in years – suggesting  
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8 199 that of 6 years of data, 5 may be pseudoreplicates. Dividing by 2 for non-independent weeks  
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10 200 and by 6 for non-independent years resulted in the factor 12. Although this “correction factor”  
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12 201 is crude, it should be noted that there is no perfect way of assessing independence, and that  
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15 202 the main results in this paper are robust to quite large changes in the weighting.  
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For Review Only

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5 203 ***Results***  
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8 204 For all species except the small tortoiseshell, the GAMs predict 15-30% of the deviance in the  
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10 205 testing data (Table 2). The amount of deviance explained is only slightly lower in the testing  
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12 206 than in the training data (Table 2), showing relatively good explanatory performance of the  
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14 207 models. There is strong support for at least some spatiotemporal variability in phenology for  
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16 208 all the species (i.e., models incorporating variation in space and/or time perform consistently  
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18 209 and significantly better than “null” week-only models; final two columns in Table 2).  
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24 211 For 6 species, phenologies are spatially variable but seem little affected by year-to-year  
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26 212 changes in temperature; a model with only spatial variation in phenology is the best predictor  
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28 213 of the “future” 2001-2006 dynamics (model 1 or 2 have the best fit: Table 2, Fig. 2). Of these  
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30 214 6 species, latitude alone is the best predictor for 5 species (common blue, speckled wood,  
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32 215 brown argus, small blue, wood white), whereas for the remaining one (holly blue) the site’s  
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34 216 average GDD5 is the best predictor. This implies that, for these 6 species, phenology is  
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36 217 relatively fixed at a given site (or that it responds to climate variables that are not correlated  
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38 218 with GDD5).  
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44  
45 220 The best-fitting models for the remaining 9 species suggest that they exhibit some temporal  
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47 221 variation in their phenology, depending on the thermal conditions from year to year and site to  
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49 222 site. For 4 of these species (small white, large white, Adonis blue, wall brown), the model  
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51 223 based on actual GDD5 (the GDD5 experienced in year X at site Y, model 3) is the best at  
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53 224 predicting the future - their phenologies appear entirely flexible with respect to GDD5 (Table  
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55 225 2, Fig. 2). For the remaining 5 species (green-veined white, small tortoiseshell, small heath,  
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57 226 small copper, comma), fixed spatial variables (northing or average site GDD5) combine with  
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3 227 responses to annual variation in GDD5 to determine observed emergence patterns (model 4 or  
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5 228 5 best; Table 2, Fig. 2). For these 5 species, the model based on actual GDD5 (model 3) still  
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8 229 outperforms purely spatial models (models 1-2, Table 2, Fig. 2). This demonstrates that, even  
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10 230 though there may not be perfect space-for-time equivalence, there is a degree of consistency  
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12 231 in the response to temperature in different places (Table 2, Fig. 2).

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17 233 For 9 species, northing is a consistently better spatial covariate than site average GDD5, i.e.  
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19 234 the Akaike weight of models with northing versus those with GDD5 is close to 1 (Table 2).  
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22 235 This suggests that day length could play a role in determining their phenologies, without  
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24 236 necessarily implying site-specific local adaptation. For 6 species, the opposite is true (low  
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27 237 weight of models with northing, compared to site average GDD5; Table 2); this suggests that  
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29 238 phenological changes are triggered by cues that are correlated with the average GDD5 of each  
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31 239 site, and this could potentially include population-specific photoperiod responses. Hypotheses  
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33 240 about population and species differences in photoperiod responses remain to be tested  
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36 241 experimentally.

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41 243 There is great variation between species in exactly how phenology varies over space and time.  
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43 244 The number of emergence peaks appears to change in space and/or time for 7 out of the 15  
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45 245 species (Fig. 3, Fig. 4, Fig. S2). Six of these species show a greater number of peaks in the  
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47 246 southern (hotter) parts of their ranges than in the north (common blue (Fig. 3a), wood white,  
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49  
50 247 small blue, small tortoiseshell, small copper, small heath (Fig S2)). Two of these species  
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52 248 show an increased tendency to produce an extra peak in the south in relatively hot years  
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54 249 (small copper (Fig. 4a-b), small heath (Fig S2)). The speckled wood (Fig 3b) appears to be an  
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57 250 exception in that there are fewer emergence peaks in the far south (2) than further north (3).  
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3 251 However, because of the complex life cycle of this species, fewer peaks might not imply  
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5 252 fewer generations per year (see discussion).  
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10 254 For other species, the number of peaks does not seem to change, but the relative sizes of the  
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12 255 different peaks do change. The holly blue (Fig 3c), green veined white, and large white (Fig  
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14 256 S2), show higher late summer peaks in the south than in the north. The brown argus (Fig. 3d)  
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16 257 shows a higher first peak in the south. In the comma butterfly, the relative size of the middle  
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18 258 peak is larger in the south than in the north (Fig 4c-d). Finally, for some species the timing of  
19  
20 259 the peaks changes, with earlier emergences in the south and in hotter years (e.g. wall brown,  
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22 260 green-veined white, large white, Fig. S2).  
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## 261 *Discussion*

262 This is the first study to quantify large-scale spatial and temporal variation in the entire  
263 emergence pattern of species, and to test the relationships found by predicting future data.  
264 Even though a large proportion of the deviance remained unexplained, predictions from our  
265 models were surprisingly robust (similar amounts of deviance were explained in the testing as  
266 in the training data). Because the data we fitted consisted of transect counts in particular  
267 weeks and sites, which are inherently variable for many reasons, we would never expect  
268 predictions to have a very high precision, but this should not prevent them from predicting  
269 large-scale trends. The results show that statistical phenology models can be used to predict  
270 phenology shifts in a second time period, suggesting that it should be feasible to project  
271 phenologies under climate change scenarios, at least over modest time scales.

272  
273 Our method isolates “phenology” in the sense of the distribution of adults over the season,  
274 independently of the overall abundance in a particular site or year. This is a desirable first step  
275 to understanding the underlying biology: it is more meaningful than other commonly used  
276 metrics such as the date of first observation, mean date or date range, which can be biased by  
277 changes in overall abundance or changes in voltinism. The entire pattern of emergence is  
278 relevant to the interactions between species, such as between herbivores and plants or  
279 between plants and pollinators. Observing the distribution of adults over the season in relation  
280 to habitat and climate factors also permits fuller consideration of how climate change alters  
281 the interactions among species, and how it might change selection pressures.

282  
283 **The variety of phenological patterns observed**

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3 284 One of the desirable features of our GAM modelling approach is its flexible ability to  
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5 285 represent the variety of phenological patterns seen in butterflies, especially multivoltine  
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7 286 butterflies. The patterns of emergence peaks in the GAMs (Fig. 3-4 and S2) are largely what  
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9 287 we would expect given what is known about the voltinism of these species. For example, the  
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11 288 common blue was already known to have univoltine populations in the north and bivoltine  
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13 289 ones in the south and this is picked up very clearly in the GAM (Fig. 3a). The northern peak is  
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15 290 timed midway between the two southern peaks, suggesting that it would not be simple for a  
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17 291 population to switch between the two modes over time, and thus is not surprising that the  
18  
19 292 northing-only model predicted best for this species.  
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26 293  
27 294 The speckled wood also shows a complex pattern, broadly consistent with what is known  
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29 295 about its phenology. This species has a complex life cycle, overwintering in both larval and  
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31 296 pupal stages (Nylin *et al.* 1995; Blakeley 1997). The pupae emerge somewhat before the  
32  
33 297 larvae in spring, producing two small peaks in the first half of the flight season (Fig. 3b).  
34  
35 298 Going from north to south, the two small peaks overlap more and more until they appear as  
36  
37 299 one extended peak. So we do not think this decrease in number of emergence peaks represents  
38  
39 300 a decrease in the numbers of generations the speckled wood achieves in a year – in fact it may  
40  
41 301 represent an increase. There could be 2 generations per year in the south but only 3  
42  
43 302 generations per 2 years in the north (the 3<sup>rd</sup> peak being the offspring of the 1<sup>st</sup> peak and the 2<sup>nd</sup>  
44  
45 303 peak being the offspring of the 3<sup>rd</sup> peak in the previous year). It is a little surprising that the  
46  
47 304 northing-only model gave the best predictions for this species, because it has been observed  
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49 305 elsewhere that development times are very dependent on temperature, and that the flight  
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51 306 period can be extended (start earlier and finish later) in relatively warm years at a single site  
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53 307 (Shreeve 1986). This highlights the potential for more detailed species-specific models to  
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3 308 explain more of the observed variation by including additional climatic and other variables  
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5 309 (see below).  
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10 311 For other species, the GAMs pick up changes in the relative sizes of the different peaks. The  
11  
12 312 holly blue (Fig 3c), green veined white, and large white (Fig S2), show higher late summer  
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14  
15 313 peaks in the south than in the north. For the holly blue and the green-veined white, the second  
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17 314 peak in the north is smaller than the first, and may represent only a partial second generation.  
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19 315 For the large white the second peak is always substantially bigger than the first, so it seems  
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21 316 more reasonable to assume that there are 2 complete generations per year, but that high  
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23 317 breeding success and/or survival during summer are higher in the warm south. The brown  
24  
25 318 argus (Fig. 3d) shows a higher first peak in the south, seemingly because the first adult peak is  
26  
27 319 extremely small in northern locations rather than because summer breeding success is  
28  
29 320 increased in the north (although the latter is possible because of reduced parasitism in the  
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31 321 north; Menendez *et al.* 2008). In the comma butterfly, the relative size of the middle peak is  
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33 322 larger in the south than in the north (Fig 4c-d). Two types of comma adults are produced in  
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35 323 the mid-summer peak: bright orange, active individuals that breed again in the same year,  
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37 324 with their offspring emerging in late summer; and darker, less active individuals that will  
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39 325 overwinter directly as adults and that will not breed until the following year (Nylin 1989;  
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41 326 1992). Therefore, the shift most likely reflects an increase in the frequency of two  
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43 327 generations per year in the south.  
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### 51 329 **Insight into the drivers of phenology**

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53 330 Our statistical models can potentially capture the net effects of phenological adaptations (the  
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55 331 average and slope of the reaction norms) that differ between populations, and make successful  
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57 332 predictions without necessarily knowing what the climate triggers are. It is likely, as has been  
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3 333 shown for many insects, that phenological events are triggered by a combination of  
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5 334 temperature and day-length cues. For example, the developmental pathways of the comma  
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8 335 butterfly, for which model 5 (indicating an interaction effect of latitude and GDD5  
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10 336 differential) was the best predictor, are known to be affected by both photoperiod and  
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12 337 temperature (Nylin 1989; 1992). Any ongoing evolution of the reaction norms will cause  
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14  
15 338 mismatches between our models and future data. To predict this evolution is a very difficult  
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17 339 task, and would require more detailed knowledge of the traits that underlie the realised  
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19 340 phenology (Visser 2008). However, our results suggest testable predictions about which  
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21 341 species respond to which triggers.  
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26  
27 343 The relative performance of our 5 alternative models suggest that different species currently  
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29 344 have different amounts of regional adaptation of phenology, and different levels of plasticity  
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31 345 in phenology. Some species show quite flexible space-for-time substitution (i.e., the  
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33 346 phenology can simply be predicted by knowing the temperature accumulated in a given  
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35 347 site/year), but others show patterns of emergence that are less flexible over time. Six out of  
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37 348 the 15 species' phenologies were best fit solely by fixed spatial effects (latitude or average  
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39 349 GDD5 of a site), four species showed flexible space-for-time substitution, while five species  
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41 350 showed complex patterns that were best fitted by an interaction between spatial and temporal  
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43  
44 351 variation in phenology (i.e. change in phenology over time was dependent on the spatial  
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46 352 location of the site). Species with fixed spatial effects have, *prima facie*, no plasticity and  
47  
48 353 therefore may only respond to climate change gradually, through evolutionary changes (for  
49  
50 354 example evolution of critical photoperiods that induce diapause, Bradshaw & Holzapfel  
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52 355 2001). When species exhibit space-for-time equivalence this suggests that reaction norms are  
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54 356 the same in all populations, and that no evolution is required to respond to moderate climate  
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56 357 change. Therefore we may expect these species to “keep up” with climate change, and we  
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3 358 might also have greater confidence in the predictions of our models for future years for these  
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5 359 species. When species exhibit space-time interactions, this suggests that reaction norms are  
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7 360 different in different geographic areas. Therefore we may expect these species to show an  
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10 361 intermediate rate of response to climate change, or to respond in some geographic areas but  
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12 362 not others. It is not clear whether year-to-year plasticity necessarily increases fitness,  
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15 363 compared to a fixed phenology strategy – presumably this would also depend on the  
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17 364 phenological responses of the resources, mutualists and natural enemies of the species under  
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19 365 consideration.  
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### 23 24 367 **Limitations**

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27 368 We have focused on how the GDD5 summed over a whole year affects the entire sequence of  
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29 369 emergence, and in doing so we have inevitably glossed over many of the climatic and  
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31 370 biological details that underlie these phenomena. Better fits could undoubtedly be obtained in  
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33 371 future studies by including additional climate variables, particularly those that show little  
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35 372 correlation with GDD5. The small tortoiseshell in particular could be an interesting subject  
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37 373 for further study because so much variation was left unexplained by temperature or nothing.  
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39 374 The speckled wood deserves further consideration because its phenology responds to early  
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41 375 and late season temperatures (Shreeve 1986) that were not fully encapsulated within our  
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43 376 GDD5 approach, and the same may be true for additional species. It may be argued that better  
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45 377 predictions of the future would be obtained from a mechanistic model of the species'  
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48 378 development, life-history and population dynamics. In several experimental studies it has  
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50 379 been shown that degree-days have quite a direct relationship to the development rate of each  
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52 380 larval instar of insects (Manel & Debouzie 1997; Gu & Novak 2006; Thompson & Clark  
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54 381 2006; Raworth 2007; Trnka *et al.* 2007). These relationships are often used to build  
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56 382 sophisticated models of the phenology of certain well-known species, such as crop pests (e.g.  
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3 383 Collier & Finch 1985; Trnka *et al.* 2007). However, such models usually need to be calibrated  
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5 384 differently for different geographic areas, reflecting the variability of development conditions  
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8 385 in the field relative to laboratory conditions, microclimate differences among sites and  
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10 386 individuals, and the genetic differentiation of populations (Collier & Finch 1985; Bryant *et al.*  
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12 387 2002; Trnka *et al.* 2007). Because physiological data will be required for large numbers of  
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15 388 populations of every species, it is unlikely to be feasible to parameterize such models for the  
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17 389 majority of species for which we would like to predict phenological responses.  
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22 391 Whilst our model projections performed well in testing data, the predictions were only for a  
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24 392 relatively short testing period (2001-2006), immediately following the model training period  
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26 393 (1973-2000), and the climate during the testing period remained largely within the bounds of  
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29 394 conditions experienced during the training period (Fig. 1). As such, the testing data were  
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31 395 independent, but we remain cautious about the capacity of such models (or other models) to  
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33 396 project phenologies far into the future. Reaction norms may evolve, especially once the new  
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35 397 climate falls outside the range of the conditions previously experienced by those populations,  
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37 398 and cause future phenologies to deviate systematically from model projections. This would  
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39 399 be true even for species that already have high levels of phenotypic plasticity in phenology.  
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42 400 For multivoltine species, such as these butterflies, extra generations may be observed under  
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44 401 future, hotter climates, which could accelerate the pace of demographic and evolutionary  
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46 402 responses.  
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53 404 Although we remain cautious about long-term projections, the approach we have taken  
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55 405 appears suitable to model and predict short-term phenology patterns in space and time. The  
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57 406 statistical models presented here can be parameterized from the sort of phenology data that  
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59 407 are regularly collected by volunteer recorders, and this approach can straightforwardly be

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3 408 applied to large numbers of species. The models have a predictive power which is reasonably  
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6 409 high and surprisingly consistent across species. We see this as an important step towards  
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8 410 anticipating which species might be threatened as a result of phenological mismatches as the  
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10 411 climate changes.  
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For Review Only

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551 **Tables**

552 Table 1: summary of 7 GAM models fitted to each species' data

Code number	Model variables†	Max. # of parameters	Interpretation
00	abundance	2	No climate effects and no seasonality
0	00+ smooth(week)	12	No climate effects
1	00+ smooth(week * site gdd5)	25	Spatial variation only (suggests response to fixed site-specific cues that are correlated with site temperature; possibly local photoperiod adaptation)
2	00+ smooth(week * northing)	25	Spatial variation only (suggests response to fixed cues that are correlated with latitude; probably photoperiod)
3	00+ smooth(week * actual gdd5)	25	Space-for-time substitution (suggests plastic response to temperature)
4	00+ smooth(week * site gdd5 * gdd5 diff )	41	Different spatial & temporal effects (suggests site-specific responses, as in model 1, combined with flexible temperature responses)
5	00+ smooth(week * northing * gdd5 diff)	41	Different spatial & temporal effects (suggests likely photoperiod response, as in model 2, combined with flexible temperature response)

† each site and year has 3 interrelated GDD5 measures:  $(\text{actual GDD5})_t = (\text{site GDD5}) + (\text{GDD5 differential})_t$ . Site GDD5 is the mean GDD5 for the site for the period 1973-2000.

553 Table 2: summary of results for each species

species common English name	Latin name	no. observations in 1973-2000 period	no. observations in 2001-2006 period	best % explained in fitting data (1973-2000)	best % explained in testing data (2001-2006)	best model at predicting testing data	second best model at predicting testing data	Akaike weight of model 3 relative to 1 & 2*	Akaike weight of 3 with df correction*	Akaike weight of the models with northing vs. those with site GDD5*	Akaike weight of models with northing with df correction*	Akaike weight of model 0 relative to all others*	Akaike weight of 0 with df correction*
Holly blue	<i>Celastrina argiolus</i>	38157	33980	18	15	1	0	0.00000	0.00003	0.00000	0.00260	0.08465	0.08465
Common blue	<i>Polyommatus icarus</i>	21900	17347	23	23	2	5	0.00000	0.00000	1.00000	1.00000	0.00000	0.00000
Speckled wood	<i>Pararge aegeria</i>	42782	33303	18	16	2	3	0.00000	0.00299	1.00000	0.99998	0.00000	0.00000
Brown argus	<i>Aricia agestis</i>	2488	2151	24	22	2	0	0.00000	0.00011	1.00000	0.88283	0.12504	0.12504
Small blue	<i>Cupido minimus</i>	877	933	37	30	2	5	0.00001	0.18354	0.99999	0.76765	0.06272	0.06272
Wood white	<i>Leptidea sinapis</i>	911	803	37	23	2	3	0.08686	0.31741	0.99784	0.53666	0.07144	0.07144
Small white	<i>Pieris rapae</i>	29420	20736	20	19	3	4	1.00000	1.00000	0.00000	0.25855	0.00000	0.00000



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Large white	<i>Pieris brassicae</i>	20281	15059	20	20	3	4	1.00000	1.00000	0.04052	0.43445	0.00000	0.00000
Adonis blue	<i>Polyommatus bellargus</i>	1030	591	36	27	3	1	0.99997	0.60770	0.00000	0.18239	0.05358	0.05358
Wall brown	<i>Lasiommata megera</i>	35070	15463	25	20	3	5	1.00000	0.99991	1.00000	0.99950	0.00000	0.00000
Green-veined white	<i>Pieris napi</i>	35484	20578	20	19	4	5	1.00000	1.00000	0.00000	0.00000	0.00000	0.00000
Small tortoiseshell	<i>Aglais urticae</i>	14272	8252	10	4	4	3	1.00000	0.99984	0.00000	0.00000	0.00000	0.00000
Small heath	<i>Coenonympha pamphilus</i>	20111	12892	22	21	5	4	0.99988	0.64557	1.00000	0.93065	0.00000	0.00000
Small copper	<i>Lycaena phlaeas</i>	7184	3087	22	18	5	4	1.00000	0.90559	1.00000	0.91856	0.00001	0.00001
Comma	<i>Polygonia c-album</i>	2021	2538	21	18	5	3	1.00000	0.77540	1.00000	0.75212	0.00335	0.00335

\*model weights are by definition between 0 and 1, but are only shown to 5 decimal places

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5 554 *Figure legends*  
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10 556 Figure 1: the distribution of GDD5 across all 10 km squares in the UK (boxplots of the  
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12 557 median, interquartile range and extremes) in each of the 33 years of the study. Red lines show  
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14 558 the overall mean for the period of fitting data (1973-2000) and the period of testing data  
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16 559 (2001-2006).  
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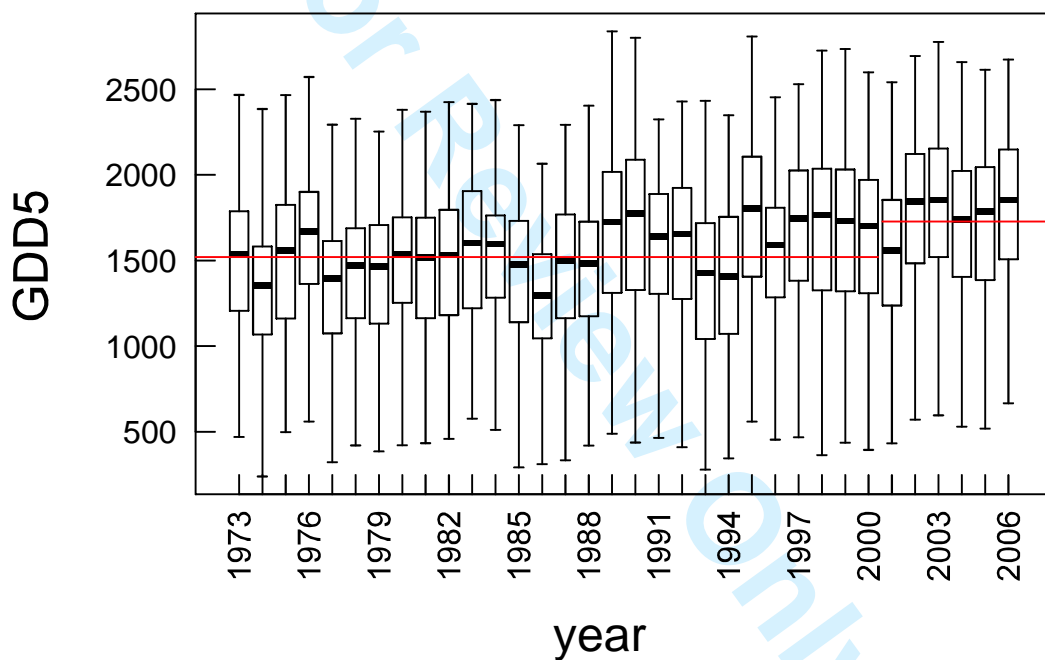
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3 560 Figure 2: Comparison of deviance in an independent test dataset explained by GAMs 1-5  
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5 561 compared to GAM 0 (where phenology is a smooth function of week of the year, with no  
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8 562 spatial or temporal variation). Bars are shaded to aid the comparison of similar models: light  
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10 563 grey when site GDD5 is the spatial covariate, dark grey when northing is the spatial covariate,  
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12 564 and white when actual GDD5 is the covariate (combining both spatial and temporal  
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15 565 variation). For the absolute amounts of deviance explained, see supplementary material, Fig.  
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3 567 Figure 3: Spatio-temporal variation in phenology of selected species where the best-predicting  
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5 568 GAM included only spatial variation. In each panel, the unlogged, GAM-fitted distribution of  
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7 569 butterflies across the 26 weeks of transect surveys is shown by lines, standardized so that the  
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10 570 sum of all weeks equals 1. Different lines represent different values of Northing: equally-  
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12 571 spaced steps between the southernmost (red) and the northernmost (blue) parts of the species'  
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14 572 data (the range, in British National Grid 10 km squares is also printed in the panel). For  
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17 573 example, the common blue shows one peak in the north and two in the south. Equivalent  
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20 574 figures for all other species are given in supplementary material, Fig. S2.  
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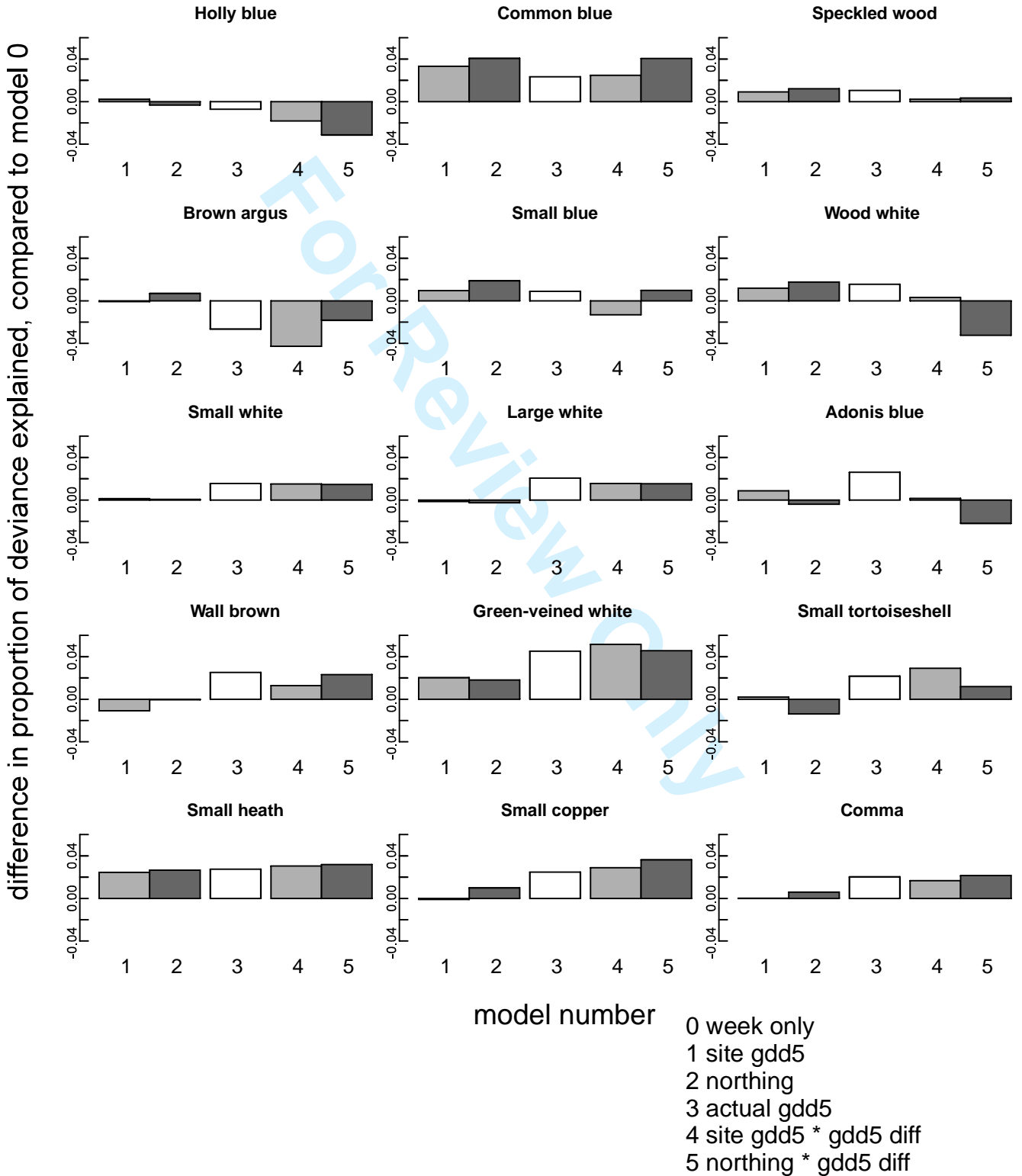
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3 576 Figure 4: Spatio-temporal variation in phenology of selected species where the best-predicting  
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5 577 GAM included temporal as well as spatial variation. In each panel, the unlogged, GAM-fitted  
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8 578 distribution of butterflies across the 26 weeks of transect surveys is shown by lines,  
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10 579 standardized so that the sum of all weeks equals 1. Different lines represent different values of  
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12 580 Northing: equally-spaced steps between the southernmost (red) and the northernmost (blue)  
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15 581 parts of the species' data (the range, in British National Grid 10 km squares is also printed in  
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17 582 the panel). To illustrate temporal variation, predictions for an average year (GDD5  
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19 583 differential= 0) and a hot year (GDD5 differential= 200), are shown in adjacent panels. For  
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21 584 example, the small copper exhibits two distinct peaks in mid-late summer in the hot south, but  
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23 585 only in hot years. Equivalent figures for all other species are given in supplementary material,  
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27 586 Fig. S2.  
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Figure 1



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# Figure 2



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## Figure 3

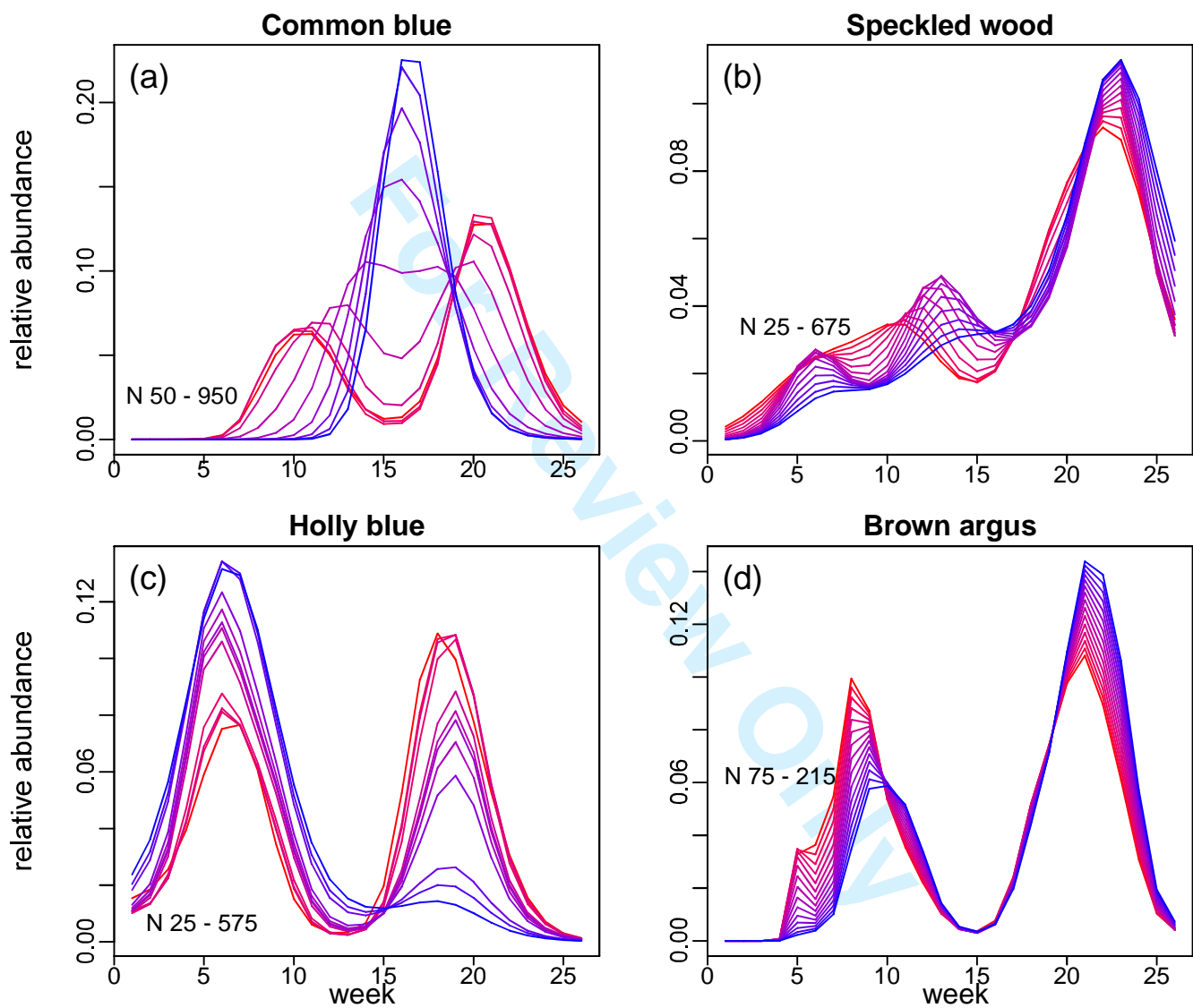




Figure 4

