

1    **Phenological sensitivity to climate across taxa and trophic levels**

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3    **Among-species differences in phenological responses to climate change can**  
4    **desynchronise ecological interactions, threatening ecosystem function. To assess these**  
5    **threats, we must quantify the relative impact of climate change on species at different**  
6    **trophic levels. Here, we apply a novel Climate Sensitivity Profile approach to 10,003**  
7    **terrestrial and aquatic phenological data sets, spatially-matched to temperature and**  
8    **precipitation data, quantifying variation in climate sensitivity. The direction, magnitude**  
9    **and timing of climate sensitivity varied markedly among organisms within taxonomic**  
10    **and trophic groups. Despite this, we detected systematic variation in the direction and**  
11    **magnitude of phenological climate sensitivity. Secondary consumers showed**  
12    **consistently lower climate sensitivity than other groups. Based upon mid-century**  
13    **climate change projections, we estimate that the timing of phenological events could**  
14    **change more for primary consumers than for other trophic levels (6.2 versus 2.5 - 2.9**  
15    **days earlier on average), with substantial taxonomic variation (1.1 - 14.8 days earlier on**  
16    **average).**

17

18    Numerous long-term ecological changes have been attributed to climate change<sup>1</sup>. Shifts in the  
19    seasonal timing of recurring biological events such as reproduction and migration (i.e.  
20    phenological changes) are especially well documented<sup>2,3</sup>. Long-term ecosystem studies<sup>4-7</sup> and  
21    global meta-analyses<sup>2,3,8</sup> have demonstrated that many spring and summer phenological  
22    events now occur earlier in the year. Substantial among-species variation in responses has  
23    fuelled concerns that key seasonal species interactions may desynchronise over time, with  
24    potentially severe consequences for wild populations and, hence, for ecosystem functioning<sup>9</sup>.

25

26 Identifying systematic taxonomic and trait-based differences in phenological climate  
27 sensitivity (i.e. change in seasonal timing per unit change in climatic conditions) would have  
28 significant socio-ecological implications. This would afford some predictability to future  
29 ecological outcomes and would identify species that represent effective sentinels of climate  
30 impact, facilitating the development of indicators and estimates of vulnerability for  
31 conservation and national adaptation programmes<sup>10–12</sup>. Unfortunately, such generalisations  
32 are currently elusive.

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#### 34 **Analytical approach and data sets**

35 Among-species differences in phenological change may arise from two aspects of climate  
36 sensitivity. Firstly, variation may reflect differences in physiological and behavioural  
37 responses, microclimate use, and the importance of non-climate related cues, such as  
38 photoperiod<sup>13</sup> or resource availability<sup>14</sup>. Therefore, even when species have the same seasonal  
39 period (window) for which they are most sensitive to climate change, they show different  
40 phenological responses to a given climatic change. Secondly, co-occurring species may vary  
41 in their seasonal periods of climate sensitivity, each typified by different levels of directional  
42 climate change<sup>15–17</sup>. We conceptualise these two aspects of phenological responses as  
43 species- (or population-) specific Climate Sensitivity Profiles (CSPs, Fig. 1). The CSP  
44 approach differs fundamentally from attempts to identify single “critical” seasonal periods  
45 within which climatic change most strongly affects seasonal events<sup>17</sup>, by quantifying the full  
46 range of phenological responses to seasonal climatic change. We ask “*How sensitive are*  
47 *phenological events to temperature and precipitation change at different times of year?*”. By  
48 applying this approach to a large, taxonomically-diverse national-scale data set, we discern

49 coherent patterns within a multitude of idiosyncratic biological climate-responses. We assess  
50 whether systematic differences in climate sensitivity underpin differences in phenological  
51 change among taxonomic and trophic groups in the UK<sup>8</sup>.

52

53 We elected against using published climate responses that may be biased in favour of species  
54 showing an effect. Instead, we analysed 10,003 long-term ( $\geq 20$  year) phenological time series  
55 for 812 marine, freshwater and terrestrial taxa over the period 1960-2012. Our data set  
56 aggregates many of the UK's foremost long-term biological monitoring schemes  
57 (Supplementary Table 1), including phenological information on amphibians (spawning),  
58 birds (egg laying, migration), planktonic crustaceans (population peaks), fish (spawning,  
59 migration), insects (flight periods), mammals (birth dates), phytoplankton (population peaks)  
60 and plants (flowering, fruiting, leafing). These taxa represent three broad trophic levels:  
61 primary producers (phytoplankton, plants), primary consumers (granivorous birds,  
62 herbivorous insects, mammals, planktonic crustaceans) and secondary consumers (predatory  
63 amphibians, birds, fish, insects, mammals, planktonic crustaceans). We spatially-matched all  
64 10,003 phenological time series with local temperature and precipitation data from a 5×5km  
65 resolution gridded data set, before statistically modelling the relationship between seasonal  
66 timing and climatic variables. Between 1960 and 2012 mean UK air temperatures increased  
67 in all months, and mean precipitation increased in most months (Fig. 2a).

68

69 Spatial variability in climatic change (Fig. 2b,c), necessitates local matching of phenological  
70 and climatic datasets rather than the use of regionally-averaged climate data (e.g. Central  
71 England Temperatures) or large-scale climatic indicators (e.g. North Atlantic Oscillation).  
72 We did not make the restrictive assumption that biological events would be related to annual

73 mean climatic conditions, or to conditions within periods based upon calendar months. Our  
74 CSP approach identified seasonal periods within which climatic change has its most positive  
75 and negative correlations with phenology (hereafter referred to as upper and lower limits of  
76 climate sensitivity, respectively). We could identify, for each phenological series, up to two  
77 seasonal periods within which climatic variation had a significant correlation with seasonal  
78 timing. The method was flexible enough to 1) allow situations in which climatic variation  
79 within only a single period had a significant correlation, and 2) identify seasonal windows  
80 ranging from a few days to a whole year in length. Our analysis captured the idiosyncrasies  
81 of phenological responses, allowed their categorisation into generic types of climate  
82 response, and is consistent with current biological understanding of climate-phenology  
83 relationships<sup>15,16</sup>.

84

## 85 **Climate response-types in the UK**

86 CSPs fall into three categories. The qualitative type of climate-phenology correlation  
87 (positive or negative) may remain consistent, irrespective of when in the year climatic change  
88 occurs. In this case only the magnitude of the phenological response differs with the time of  
89 year at which climatic variables change. The climate-phenology correlation may be  
90 consistently negative (CSP type I, Fig. 1, red curve) or positive (CSP type III, Fig. 1, blue  
91 curve). Alternatively, opposing correlations between seasonal climatic change and the timing  
92 of biological events may exist i.e. the direction and magnitude of the phenological response  
93 varies (CSP type II, Fig. 1, orange curve). We determined CSPs for responses to temperature  
94 ( $CSP_{temp}$ ) and precipitation ( $CSP_{precip}$ ).

95

96 Focusing on temperature, CSP type II was most common (Extended Data Table 1, 69.7 % of  
97 phenological series): seasonal events were advanced by (i.e. negatively correlated with)  
98 warming during one period of the year, and delayed by (i.e. positively correlated with)  
99 warming in another period. After multiple testing correction, 44.8% of the observed  
100 phenological advances (but only 1.0% of delays) with warming were statistically significant  
101 ( $P < 0.05$ ). CSP type I was the next most common response-type: warming in different  
102 seasonal windows was consistently correlated with earlier seasonal events (i.e. negative  
103 correlations, 24.7% of series). In this case the lower and upper limits of CSPs represent the  
104 “strongest” and “weakest” phenological advances with warming, respectively, and 58.1% of  
105 the “strongest” responses were statistically significant ( $P < 0.05$ , correcting for multiple  
106 testing).

107

108 Phenological events most commonly demonstrated opposing (Fig. 1, CSP type II, 53.0% of  
109 series) or consistently positive (Fig. 1, CSP type III, 28.0% of phenological series)  
110 correlations with increasing seasonal precipitation. Though delayed phenological events may  
111 commonly be associated with higher precipitation (81.0% of events show this type of  
112 response), few of these associations were significant (Extended Data Table 1).

113

#### 114 **Climate sensitivity at the UK-scale**

115 We matched each phenological series with four climate variables: mean temperature during  
116 the seasonal windows at the upper and lower limits of  $CSP_{temp}$ , and similarly-averaged  
117 precipitation data for the seasonal windows at the upper and lower limits of  $CSP_{precip}$ . We  
118 then combined all 10,003 phenological series and their matched climate data, and modelled

the relationships between seasonal timing and climate variables using linear mixed effects (LME) models. Initially we fitted a “global” model to quantify upper and lower limits of temperature and precipitation sensitivity, averaged across all phenological events. Marine plankton data were excluded at this stage, due to a lack of precipitation data.

Most phenological events occurred earlier with seasonal warming (average rate  $-2.6 \text{ days } ^\circ\text{C}^{-1}$ , Fig. 3a, Extended Data Table 2). Variation in the strength of this correlation was similar among sites and species (random-effects variances in site and species level seasonal timing – temperature slopes were 2.1 and 1.9, respectively). Some phenological events occurred later with seasonal warming (Fig. 3a) though, in other cases, the upper limit of  $\text{CSP}_{\text{temp}}$  was in fact a “weak” advance with warming. The upper limit of temperature sensitivity was more variable among species than sites (random effects variances in species and site level seasonal timing – temperature slopes were 2.3 and 0.4, respectively). Averaged across species and populations, temperature responses were most consistent with CSP type II.

Most phenological events showed opposing responses to increasing seasonal precipitation (Fig. 1, CSP type II). The tendency for delays with rising precipitation was greatest: the average upper limit of  $\text{CSP}_{\text{precip}}$  exceeded the lower limit ( $1.4 \text{ days mm}^{-1}$  and  $-0.4 \text{ days mm}^{-1}$ , respectively, Fig. 3b, Extended Data Table 2). The upper limit of  $\text{CSP}_{\text{precip}}$  was more variable among species than sites (species and site level random-effects variances in the seasonal timing – precipitation slopes were 1.9 and 1.2, respectively). The fitted climate-phenology model was better supported by the data than a year-only model with the same random effects structure (delta-AIC 293,516). This indicates the presence of real associations between climate and seasonality, rather than purely spurious correlations due to shared temporal

trends. Average sensitivity to temperature was very similar in the model that included marine plankton data, but excluded precipitation effects (Supplementary Discussion, Extended Data Fig. 1).

### **Taxonomic and trophic group sensitivity**

We tested the hypothesis that the limits of seasonal climate sensitivity differ coherently among taxonomic groups by including a fixed-effect interaction between taxonomic group and each climatic variable (Fig. 4, Extended Data Table 2). The lower limit of  $CSP_{temp}$  was negative for all groups (“earliness” with warming), the strongest responses being found for plants, freshwater phytoplankton, insects and amphibians (4.3, 4.1, 3.7 and 3.4 days earlier  $^{\circ}C^{-1}$ , respectively). Upper limits of  $CSP_{temp}$  indicated that freshwater phytoplankton and mammals experienced the greatest phenological delays with seasonal warming (2.9 and 2.0 days later  $^{\circ}C^{-1}$ , respectively) but that plants showed little evidence of such delays. The strongest phenological delays with rising seasonal precipitation were found for freshwater phytoplankton and insects (2.5 and 2.2 days later  $mm^{-1}$ , respectively), while freshwater phytoplankton also exhibited the strongest phenological advances with rising precipitation during other seasonal windows (1.1 days earlier  $mm^{-1}$ ). Average temperature and precipitation responses were consistent with a CSP type II in most cases. There was considerable within-group variability in sensitivity.

We examined trophic-level differences in climate sensitivity by including this in interaction with each climate variable in the global model. The lower limit of  $CSP_{temp}$  showed greater systematic variation among trophic levels than the upper limit (Fig. 3c,e). The tendency

towards “earliness” with seasonal warming was strongest at lower trophic levels (-4.1, -3.7 and -1.9 days °C<sup>-1</sup> for primary producers, primary consumers and secondary consumers, respectively, Extended Data Table 2), consistent with observations of more rapid phenological changes at lower trophic levels, in the UK<sup>8</sup>. Conversely, the lower limit of CSP<sub>precip</sub> varied less among trophic levels than the upper limit (Fig. 3d,f). The tendency for later seasonal events with higher seasonal precipitation was greater for primary producers and primary consumers (1.8 and 2.2 days mm<sup>-1</sup> on average, respectively) than for secondary consumers (1.0 days mm<sup>-1</sup>). Variations in climate sensitivity were described more parsimoniously by taxonomic groups than by trophic levels (AICs of taxonomic and trophic-level models 3237611 and 3238061, respectively).

Results were little-affected when analysing only pre- and post-1980 data, to minimise among-group variation in time series length, and after Monte Carlo re-sampling to assess the potential effects of taxonomic bias (Supplementary Discussion, Extended Data Figs. 2-4). The same qualitative trophic-level differences in climate sensitivity were apparent when including marine plankton data in a temperature-only LME model (Supplementary Discussion, Extended Data Fig. 1). In contrast to trophic-level differences in the magnitude of sensitivity, there was little evidence of similar variation in the seasonal timing of climate sensitivity (Supplementary Discussion, Extended Data Figs. 5-7).

## **Estimating future change**

Overall, “net”, phenological responses to climatic change combine potentially-opposing responses to conditions in different seasonal periods. We estimated “net” responses by the



2050s by applying our fitted models to UKCP09 probabilistic projections (bias-corrected relative to a 1961-90 baseline) of temperature and precipitation change under low, medium and high emissions scenarios. Rather than predicting the *absolute* timing of future phenological events, we contrasted possible *changes* in seasonal timing among organism groups based upon established climate scenarios and contemporary patterns of climate sensitivity. Estimated average phenological changes for primary producers and secondary consumers were less than those for primary consumers (Fig. 5a). This occurred because, averaged across species, the opposing climate responses of primary producers and secondary consumers are more similar in magnitude than are those for primary consumers (Fig. 3), effectively “cancelling each other out”. Our models suggest greater average advances for crustacea, fish and insects than for other groups, such as freshwater phytoplankton, birds and mammals (Fig. 5b). However, response-variation is high for crustacea (Fig. 5b).

## Discussion

In the UK, phenological climate sensitivity varies greatly, suggesting effects of locally-varying non-climatic drivers such as population structure<sup>18</sup>, resource availability<sup>19</sup> and adaptation<sup>20</sup>. This is relevant to the use of phenological change as a tangible climate change indicator<sup>1,21</sup>. Mediators of phenological climate sensitivity are only known locally for some of the groups in our data set e.g. nutrient availability (freshwater phytoplankton)<sup>22</sup>. However, for others, the climate sensitivity of different biological traits is known to be mediated by alternative drivers<sup>23,24</sup>. High climate-response variability necessitates wide site and species coverage in long-term monitoring schemes aiming to develop robust aggregate indicators of change<sup>21</sup>. Since climatic conditions are more spatially-variable across broader geographic domains, site-level replication of phenological monitoring is particularly important when

interpreting phenology at continental to global scales. In the UK, average responses for fish and insects appear to provide climate-indicator potential. These groups show consistently strong phenological advances with seasonal warming, and only weak opposing responses, resulting in relatively large (net) changes in seasonal timing. Interpretation of phenological changes for other groups is more complex. For example, freshwater phytoplankton show strong evidence of opposing phenological responses to climatic variation at different times of year and these are near-equivalent in magnitude, such that estimated net changes are negligible. This highlights that long-term observations represent the net effect of potentially-opposing biological responses<sup>25</sup>. To fully capitalise on the indicator potential of phenological change, we must advance mechanistic understanding of responses to potentially opposing climate and non-climate drivers.

Despite this variability, we identified coherent patterns in climate sensitivity among the idiosyncratic responses of many wild plant and animal populations. For the first time we show that, on average, trophic levels differ in the magnitude of seasonal climate sensitivity, but not the time-of-year within which climatic change has its most pronounced effects. This may be a key mechanism underpinning observations of trophic level differences in phenological change in the UK<sup>8</sup>. Lower trophic levels demonstrated more pronounced variation in their sensitivity to changing temperature and precipitation at different times of year, and stronger phenological responses to climatic change during defined (taxon- and population-specific) seasonal periods.

In response to climatic changes projected for the 2050s, relative changes in seasonal timing are likely to be greatest for primary consumers, particularly in the terrestrial environment.

The difference in magnitude between opposing climate responses is greatest for primary consumers, resulting in greater “net” change. Our approach makes the simplifying assumption that climatic change has the overriding influence upon seasonality. Nevertheless, this suggests that systematic differences in climate sensitivity could result in widespread phenological desynchronisation. However, factors that shape phenological climate-responses introduce uncertainty into projections of future phenological change. These results should catalyse research to improve predictive capacity in the face of multiple environmental and demographic drivers that not only mediate rates of change, but might also confer resilience to desynchronisation e.g. population density-dependence<sup>26</sup>, compensatory range shifts<sup>27</sup>, and the formation of novel inter-specific interactions<sup>28,29</sup>. These findings also underscore the importance of developing our capacity to manage ecosystems within a “safe operating space” with respect to the likely impacts of projected climate change<sup>30</sup>.

**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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## **Author Contributions**

SJT and SW conceived and co-ordinated the study, and led writing of the manuscript. PAH developed the analysis routine and wrote statistical code to be applied to all data sets. DH extracted all climatic and sea surface temperature data. IDJ and EBM calculated water temperatures for lakes and streams, respectively. SJT, JRB, MSB, SB, PH, TTH, DJ, DIL, EBM and DM led analysis of specific data sets using code from PAH. SA, PJB, TMB, LC, THC-B, CD, ME, JME, SJGH, RH, JWP-H, LEBK, JMP, THS, PMT, IW and IJW derived phenological data for analysis, advised on interpretation, and assisted in assigning species traits. All co-authors commented on the manuscript.

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## METHODS

### Data sets

We integrated data from many major UK biological monitoring schemes (Supplementary Table 1), resulting in 10,003 long-term (at least 20-years between 1960 and 2012) phenological series for 812 marine, freshwater and terrestrial taxa. The amassed data sets included records for plants, phytoplankton, zooplankton, insects, amphibians, fish, mammals and birds (379,081 individual phenological observations). For each study we used a single population-level phenological measure per year (Supplementary Table 1). Since the sampling resolution for the marine plankton data was monthly, prior to analysis we re-scaled these data into units of days. Trophic level, taxonomic Class and environmental affinity were assigned to each taxon, to permit analyses of correlations between these attributes and climate sensitivity.

Daily air temperature and precipitation data were extracted from the Met Office National Climate Information Centre (NCIC) 5km-resolution gridded data set<sup>31</sup> for the spatial locations of all biological monitoring sites across the UK land surface. If available, recorded water temperatures from the same site were used in place of air temperatures, for phenological time series representing obligate aquatic taxa (freshwater plankton and fish). Water temperatures were interpolated onto a daily time-step prior to analysis<sup>32</sup>. If these data were not available, daily water temperature data were estimated from air temperatures using a

fitted empirical site-specific relationship between air and water temperature. For the sea trout (*Salmo trutta*) data, an existing linear relationship<sup>33</sup> was used, while for the Atlantic salmon (*Salmo salar*) data, a non-linear relationship<sup>34</sup> was calculated for a nearby river, the Tarland Burn, and applied to air temperatures from the sampling site. For the marine plankton, mean monthly sea surface temperatures were extracted from the Met Office Hadley Centre Sea Ice and Sea Surface Temperature (HadISST) data set<sup>35</sup> for each of the Standard Areas<sup>36</sup> in which phenological data were available. Precipitation data were not available for marine Standard Areas.

## **Statistics**

Our analysis was conducted in two distinct phases (Supplementary Notes). Firstly, the CSP for each phenological series was estimated using generalized linear models to quantify associations between the timing of seasonal events and mean temperature and precipitation (within defined seasonal time windows) at the same location. Secondly, the phenological time series were aggregated and a single linear mixed effects (LME) model was run, capturing upper and lower limits of climate sensitivity across many species. CSPs for precipitation were not estimated for marine plankton data (see above), and so the second-phase LME models were run twice: once to examine correlations with temperature and precipitation for all but the marine plankton phenological series (9,800 series), and once to examine only correlations with temperature for the whole data set (10,003 series).

### ***Phase 1: Estimating Climate Sensitivity Profiles (CSPs) for each time series***

We used consistent methods to “screen” all phenological events with respect to their climate sensitivity, finding periods of the year in which temperature and precipitation have their most positive and negative correlations with seasonal timing (the upper and lower limits of climate sensitivity). This approach was flexible enough to detect when these limits represented opposing correlations between temperature or precipitation and seasonality, depending upon the seasonal timing of climatic change e.g. spring warming may advance budburst, but winter warming may delay it<sup>37</sup> (Fig. 1, CSP type II). It could also detect when the direction of the correlation between climatic variables and seasonal timing was consistent irrespective of the seasonal timing of climatic change, with only the magnitude of the correlation varying between the limits of the CSP (Fig. 1, CSP types I and III).

For each phenological time series, we calculated the day of year by which 95% of the recorded seasonal events had occurred ( $do_{y95}$ ). Inter-annual variations in seasonal timing were statistically modelled as a function of daily mean temperatures on  $do_{y95}$  each year. Then, a series of 365 statistical models was run that used instead daily mean temperatures on  $do_{y95}-1$  to  $do_{y95}-365$  as predictors. Slope coefficients and  $R^2$  values for the temperature terms in these models were collated, capturing seasonal variations in the sign and magnitude of the phenology-temperature relationship (i.e. the CSP, Fig. 1). Generalized Linear Models (GLMs) were used.

For two data sets (BTO Nest Record Scheme and PTES National Dormouse Monitoring Scheme, Supplementary Table 1) we modified the above analytical framework. In both of these schemes, the precise location of the biological observations changed among years (*cf* other schemes where monitoring sites are static over time). We extracted matching climatic

data for each specific location in each year, as for all other schemes, but then grouped the phenological and climatic data at county level (mean area = 3,440 km<sup>2</sup>). Then, for each taxon in each county we used the fixed-effect slope parameters and R<sup>2</sup> values from a series of LME models, instead of GLMs, as a basis for estimating CSPs. In these models, we included fixed effects of temperature on *doy*<sub>95</sub> to *doy*<sub>95-365</sub> as before, and included a year random effect to account for replicate phenological records for each taxon in each county in each year. For the SAHFOS marine plankton data set, we modified our iterative approach to analyse seasonal timing-temperature relationships at monthly, instead of daily, time steps (the temporal resolution of the sea surface temperature data).

As a final step in estimating the CSP for each series, temporal variation in the sign and magnitude of the seasonal timing-temperature correlation was itself modelled (Extended Data Fig. 8). This was done by fitting Generalized Additive Models (GAMs, Gamma error distribution) to the time series of slope coefficients and R<sup>2</sup> values from the models described above. By smoothing these time series, the GAMs identified periods of the year in which slope coefficients were consistently negative (i.e. warming advances seasonal timing), or consistently positive (i.e. warming delays seasonal timing), and during which the climate-phenology models generating the slope estimates had a their highest goodness-of-fit.

Seasonal “windows” in which the upper and lower limits of temperature sensitivity occurred were identified as periods during which 1) the 95% confidence interval for the GAM fitted to the slope coefficients surpassed the limits of the 2.5 and 97.5 percentiles of the original slope coefficients and 2) the 95% confidence interval for the GAM fitted to the R<sup>2</sup> values surpassed the 97.5 percentile of the original R<sup>2</sup> values. This ensured that seasonal windows were

defined by periods combining the greatest climate effect size and relatively strong predictive power (determined by  $R^2$ ). Using this framework, we identified the lower limit of  $CSP_{temp}$ : the period of the year in which an advancing effect of increasing temperature upon seasonal timing was most likely. This was estimated by determining when the 95% confidence interval of the GAM intersected the *lower* percentile of the seasonal timing-temperature slope coefficients, by “tracking” the most *negative* coefficients (Extended Data Fig. 8). In addition, we identified the upper limit of  $CSP_{temp}$  by determining when the 95% confidence interval of the GAM intersected the *upper* percentile of the seasonal timing-temperature slope coefficients, by “tracking” the most *positive* (or least negative) coefficients. Excluding the marine plankton data, the whole modelling process was repeated with precipitation as a predictor instead of air temperature, culminating in the estimation of seasonal periods capturing the limits of phenological responses to changing precipitation.

After this process, temperature and precipitation were each averaged within the two seasonal windows in which the limits of phenological sensitivity occurred. With the exception of the marine plankton data, the final seasonal timing-climate model for each series was then fitted using a GLM with Gamma error distribution including four predictors: inter-annual variations in 1) mean temperature during the period at the lower limit of  $CSP_{temp}$ , 2) mean temperature during the period at the upper limit of  $CSP_{temp}$ , 3) mean precipitation during the period at the lower limit of  $CSP_{precip}$ , 4) mean precipitation during the period at the upper limit of  $CSP_{precip}$ . For the marine plankton data, only the first two terms were fitted. For the BTO Nest Records and PTES National Dormouse Monitoring Scheme data sets we implemented these final models in a mixed effects framework with a random effect of year, as before. Therefore, although we modelled changes in statistical parameters (which are not estimated without error) to identify seasonal periods, this step was only used to find the original climatic data to

be used in subsequent modelling. Inferences were not, therefore, directly based upon statistical modelling of uncertain parameter estimates. We categorised the results of all 10,003 CSPs according to three broad response-types (CSP types I–III, Fig. 1), and retained P values for each fitted model term to infer which of the modelled climatic effects were statistically significant. We examined the evidence for trophic-level differences in the mean seasonal timing of climate sensitivity by modelling the relationship between the start date, end date and duration of the seasonal windows capturing the upper and lower limits of phenological sensitivity to temperature and rainfall as a function of trophic level (fixed effect), with random effects of phenological metric, within species, within site. Analyses were conducted using the *base*, *mgcv* and *lme4* packages in R<sup>38–40</sup>.

## ***Phase 2: “Global” models of phenological climate sensitivity***

We estimated the upper and lower limits of phenological climate sensitivity at a multi-species scale by “matching” each phenological series with data on mean temperature and precipitation, during the seasonal windows characterising the CSP for that series (Phase 1, above). We aggregated all 10,003 of these matched phenology-climate data sets. To quantify the average, multi-species, upper and lower limits of climate sensitivity we constructed a linear mixed effects (LME) model, in which phenology (day of year) was modelled as a function of mean temperature and precipitation within the seasonal windows of the amassed CSPs (fixed effects) with random effects of phenological metric, within species, within site. These random effects were necessary since our data could not be considered independent. The timing of events for the same species are more likely to be similar than for different species. Likewise for different sites and the phenological metric-types used to describe the events (e.g. first flight time or seasonal peak abundance). Random slopes and intercepts were

544 allowed to ensure that each phenological event, for a species at a site, was allowed a different  
545 rate of climate response.

546

547 For some species, more than one phenological event was recorded in the same year, at the  
548 same site. For example, butterflies may have more than one flight period in the same year,  
549 and plankton populations may be characterised by more than one seasonal abundance peak.  
550 As climate responses are unlikely to be the same for the first event of the year, and  
551 subsequent events, we introduced a voltinism factor in the analysis. This allowed us to  
552 distinguish between data representing the first/only events of each year (e.g. a spring  
553 plankton bloom or butterfly generation) and second events in each year (e.g. the subsequent  
554 summer plankton bloom or butterfly generation). This distinction captured all possibilities  
555 within our data set.

556

557 For site  $i$ , species  $j$ , voltmetric  $k$  (where voltmetric is a unique combination of voltinism class  
558 and the metric-type used to identify the event) the corresponding day of year ( $DOY$ ) of a  
559 particular seasonal event is modelled as:

560

561 
$$DOY_{ijk} = \alpha_0 + \beta_1 TL_{ijk} + \beta_2 TU_{ijk} + \beta_3 PL_{ijk} + \beta_4 PU_{ijk} + \varepsilon_{ijk}$$

562 where  $\varepsilon_{ijk} \sim \mathcal{N}(0, \sigma^2)$  and the model includes temperature at the upper limit of each CSP ( $TU$ ),  
563 temperature at the lower limit of each CSP ( $TL$ ), precipitation at the upper limit of each CSP  
564 ( $PU$ ) and precipitation at the lower limit of each CSP ( $PL$ ). Due to the non-independence  
565 within the data, we allow the intercepts and coefficients corresponding to all four covariates

to vary by site, species and voltmetric. Preserving the natural nesting of a metric for a species at a particular site, this gives:

$$\alpha_0 = \gamma_0 + \mu_{0,ijk} + \mu_{0,ij,k} + \mu_{0,i,jk}$$

$$\beta_1 = \gamma_1 + \mu_{1,ijk} + \mu_{1,ij,k} + \mu_{1,i,jk}$$

$$\beta_2 = \gamma_2 + \mu_{2,ijk} + \mu_{2,ij,k} + \mu_{2,i,jk}$$

$$\beta_3 = \gamma_3 + \mu_{3,ijk} + \mu_{3,ij,k} + \mu_{3,i,jk}$$

$$\beta_4 = \gamma_4 + \mu_{4,ijk} + \mu_{4,ij,k} + \mu_{4,i,jk}$$

where each of the  $\mu$  terms is a random effect following:  $\mu \sim N(0, \delta^2)$

This nesting of random effects is most conservative in terms of inference at the global level and is as flexible as possible, allowing each time series to have its own set of model parameters. This permits a high degree of biological realism since each distinct phenological event, for a given species, at a given site, is permitted to have a different slope for the effects of temperature and precipitation i.e. a different climate sensitivity.

In this model framework we are specifically testing the null hypotheses that each of the climate variables show no relation with seasonal timing of biological events. Because of this, and the fact that each parameter is estimated directly, without distributional form assumed *a priori* or as the target distribution, we follow a frequentist approach to analysis. However,



because the exact degrees of freedom cannot be evaluated when using restricted maximum likelihood, hence no exact P-value, we present full summaries of all the parameters estimated at species level (as given by:  $\gamma + \mu_{ij,k} + \mu_{i,jk}$ , above). Approximate P-values could be presented based on taking conservative estimates of the degrees of freedom though, given the volume of data available, this will typically lead to the detection of many statistically-significant results that may not be biologically significant. Examining the full range of estimated coefficients across the random effects levels ensures that we present the full range of variation around global parameters and can make more informed inference. In this way we encourage the reader to interpret our results by using biological insight, not by depending upon P-values alone.

To examine high-level differences in climate sensitivity among trophic levels and taxonomic groups we re-fitted the LME model with these attributes as fixed-effect factors, interacting with the fixed-effect climate variables. The fixed-effect slopes from the resulting models allowed us to compare differences in phenological climate sensitivity among these broad organism groups, averaged across all taxa within each group. Supplementary Table 2 shows the number of phenological series, sites and distinct taxa that contributed data to each of these groups. All models were run twice: once to examine correlations with both temperature and precipitation excluding marine plankton data (9,800 time series), and once to examine only temperature-phenology correlations for the whole data set (10,003 time series).

## **Potential biases**

609 Data availability differed among taxonomic groups. To assess the extent to which mean  
610 responses were biased by data inequality we conducted Monte Carlo re-sampling, iteratively  
611 selecting 5, 20, 50 and 100 phenological series from each taxonomic group and re-fitting  
612 climate-phenology models with these sampled data sets. For taxonomic groups with less data  
613 than the larger sample sizes, we retained all available data (Supplementary Discussion). This  
614 allowed us to compare taxonomic group and trophic level responses based upon sampled and  
615 all data, to fully investigate potential bias.

616

617 Another potential bias in our analysis is that phenological time series length is variable,  
618 affecting the length of time over which climate-phenology correlations are assessed. In order  
619 to assess the extent to which differences in mean trophic level and taxonomic group  
620 responses are biased by variable time series length, we also re-fitted our models but based  
621 only on pre- and post-1980 data. All models were run in the *lme4* package in  $R^{38,40}$ .

622

### 623 **Estimating future change**

624 To estimate potential future “net” effects of temperature and precipitation change, we  
625 compared predictions of seasonal timing under baseline conditions, and under established  
626 climate change scenarios. Firstly, estimates of seasonal timing (day of year) were obtained  
627 for the same baseline period used in the UKCP09 projections (long term average 1961-1990),  
628 using modelled correlations between phenology, temperature and precipitation (from Phase  
629 1). Having obtained these baseline estimates, we applied our models to projected changes in  
630 monthly temperature and precipitation for the 2050s (UK Climate Projections, UKCP09,  
631 <http://ukclimateprojections.metoffice.gov.uk/>). We used 10<sup>th</sup>, 50<sup>th</sup> and 90<sup>th</sup> percentile changes

under low, medium and high emissions scenarios (relative to the 1961-90 baseline). The spatial location of each phenological series was matched to climate projection data for the 25 × 25km grid square in which it occurred, and temporally matched to climatic data from the months-of-year in which its respective climate sensitivity windows occurred. Relative changes in timing, in response to climatic change of the magnitude projected to occur by the 2050s, were summarised by trophic levels and taxonomic groups.

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663

**FIGURE LEGENDS**

**Figure 1 | Climate Sensitivity Profiles (CSPs).** Climate sensitivity is the change in seasonal timing per unit change in temperature ( $\text{days } ^\circ\text{C}^{-1}$ ) or precipitation ( $\text{days mm}^{-1}$ ). Irrespective of the date, increasing temperature/precipitation may always correlate with earlier (red curve, CSP type I) or later (blue curve, CSP type III), biological events, but sensitivity to climate variation (correlation magnitude) differs (*cf* w1 and w2, w5 and w6). In contrast, opposing climate-phenology correlations may occur, depending on the date at which climate changes (orange curve, w3 and w4, CSP type II). Panels show hypothetical relationships for seasonal windows w1-w6.

**Figure 2 | Climatic change in the UK, 1960-2012.** a) Long-term changes in air temperature and precipitation are the differences between 1960 and 2012 monthly means of these variables, derived from a regression fitted through each monthly time series. Error bars indicate the standard deviation of linearly-detrended climatological data, as an indication of inter-annual variation around each trend. b) and c) Examples of spatial variation in the extent of long-term climatic changes are shown for March air temperatures and February precipitation.

**Figure 3 | Upper and lower limits of phenological climate sensitivity.** Sensitivity is the slope of the relationship between seasonal timing (day of year) and climatic variables. All-taxa upper and lower limits in a) temperature ( $^\circ\text{C}$ ) and b) precipitation ( $\text{mm day}^{-1}$ ) sensitivity are summarised. Lower (c, d) and upper (e, f) limits of temperature (c, e) and precipitation (d, f) sensitivity are shown by trophic level. Inverted triangles indicate average sensitivity.

Curves are kernel density plots: estimates of the probability density distribution of species-level climate sensitivity i.e. the relative likelihood of different levels of climate sensitivity within each species group ( $n = 370,725$ ).

**Figure 4 | Upper and lower limits of phenological climate sensitivity for broad taxonomic groups.** Lower (blue) and upper (red) limits of the sensitivity of phenological events to seasonal temperature (a) and precipitation (b) change are shown. Coloured circles indicate the median response, and bars show the 5<sup>th</sup>-to-95<sup>th</sup> percentile responses for each group. Sensitivity is quantified by summarising the species-level (random effects) responses from a mixed effects model including data for all taxa, and with taxonomic group as a fixed effect ( $n = 370,725$ ).

**Figure 5 | Estimated phenological shifts by the 2050s.** Modelled responses to projected temperature and precipitation change, assuming contemporary climate sensitivity, for trophic levels (a) and taxonomic groups (b). Projected median shifts in seasonal timing are shown. Change estimates are based on low, medium and high emissions climate scenarios. Bars represent median responses to 50<sup>th</sup> percentile climate change projections under each scenario, while extremes of whiskers represent median responses to 10<sup>th</sup> and 90<sup>th</sup> percentile projected climatic changes under each scenario. Standard deviations indicate variation in projected responses for each group under the 50<sup>th</sup> percentile of the medium emissions scenario.

**EXTENDED DATA FIGURE AND TABLE LEGENDS**

710

711 **Extended Data Figure 1 | Limits of phenological temperature sensitivity inclusive of**  
712 **marine plankton data.** Upper and lower limits of phenological temperature sensitivity are  
713 quantified as the slope of the relationship between seasonal timing (day of year) and  
714 temperature (°C) variation within specific seasonal periods. Limits in temperature sensitivity  
715 are shown for all taxa (a) and by trophic level (lower limit b, upper limit c). Inverted triangles  
716 indicate average sensitivity for all species in each group and curves are probability density  
717 plots of species-level variation in sensitivity.

718

719 **Extended Data Figure 2 | Limits of phenological climate sensitivity for taxonomic**  
720 **groups (top) and trophic levels (bottom), after Monte-Carlo resampling.** Lower (blue)  
721 and upper (red) limits of the sensitivity of phenological events to seasonal temperature (a)  
722 and precipitation (b) change. Coloured circles: responses based upon the full data set. Bars:  
723 2.5<sup>th</sup>-to-97.5<sup>th</sup> percentile responses for each group, based upon 100 draws from the full data  
724 set. Data were sampled so that 5, (dotted bar), 20 (solid bar), 50 (dashed bar) and 100 (dot-  
725 dashed bar) phenological time series were drawn from each taxonomic group.

726

727 **Extended Data Figure 3 | Climate sensitivities, based on different time periods (top: all**  
728 **data, middle: pre-1980 data, bottom: post-1980 data).** Sensitivity is the slope of the  
729 relationship between seasonal timing (day of year) and temperature (°C), or precipitation  
730 (mm day<sup>-1</sup>). Limits of a) temperature and b) precipitation sensitivity are summarised for all  
731 taxa. Lower (c, d) and upper (e, f) limits of temperature (c, e) and precipitation (d, f)  
732 sensitivity are shown by trophic level. Inverted triangles: average sensitivity for all species (a,

b) or trophic levels (c-f). Curves: kernel density plots: probability density distributions of species-level climate sensitivity i.e. the relative likelihood of different climate sensitivities within each species group.

**Extended Data Figure 4 | Limits of phenological climate sensitivity for broad taxonomic groups (top: all data, bottom: post-1980 data only).** Lower (blue) and upper (red) limits of the sensitivity of phenological events to seasonal temperature (a) and precipitation (b) change are shown. Coloured circles indicate the median response, and bars show the 5<sup>th</sup>-to-95<sup>th</sup> percentile responses for each group. Sensitivity is quantified by summarising the species-level (random effects) responses from a mixed effects model including data for all taxa, and with taxonomic group as a fixed effect.

**Extended Data Figure 5 | Seasonal windows for Climate Sensitivity Profiles (CSPs).** Estimated climatic sensitivity at the lower (a, c) and upper (b, d) limits of CSPs for 10,003 phenological series. Grey lines are seasonal time periods (x axis) within which climatic variables have their most positive/negative correlations with the seasonal timing of each phenological event. The y-axis indicates the slope coefficient for each of these correlations; a measure of climate sensitivity (days change °C<sup>-1</sup>, or mm<sup>-1</sup>). Shown are the lower/upper limits of CSP<sub>temp</sub> (a, b, respectively) and the lower/upper limits of CSP<sub>precip</sub> (c, d, respectively). Inset histograms show seasonal time window length (days).

**Extended Data Figure 6 | Time lags between phenological events and seasonal windows of climate sensitivity.** Frequency histograms showing the time lag (in days) between the



mean timing of each phenological event and the end of seasonal windows corresponding to the lower and upper limits of  $CSP_{temp}$  (a, b, respectively) and the lower and upper limits of  $CSP_{precip}$  (c, d, respectively). Peaks at lags of around 1 year are where windows were identified that ended at the mean seasonal timing of an event, but in the previous year, due to temporal autocorrelation in climate data.

**Extended Data Figure 7 | Seasonal windows for Climate Sensitivity Profiles (CSPs) by trophic level.** Estimated climatic sensitivity at the lower and upper limits of CSPs for taxa at each of three trophic levels. Formatting is the same as in Extended Data Figure 5. Shown are the lower and upper limits of  $CSP_{temp}$  (a, b, respectively) and the lower and upper limits of  $CSP_{precip}$  (c, d, respectively).

**Extended Data Figure 8 | Example Climate Sensitivity Profile (CSP).** Temperature sensitivity ( $CSP_{temp}$ ) for alderfly (*Sialis lutaria*) emergence from Windermere, UK. Solid black line: sensitivity of first emergence to water temperature on different days of the year (days change  $^{\circ}C^{-1}$ ). Grey horizontal lines: 2.5 and 97.5 percentiles of these sensitivity values. Solid orange curve: GAM smoother fitted through the sensitivity values with associated confidence intervals (dashed orange curves). Horizontal bars indicate where GAM confidence intervals exceed the percentiles of the original sensitivity values, indicating seasonal windows at the limits of the climate sensitivity profile.

**Extended Data Table 1 | Modelled relationships between seasonal timing and climate variables for n=10,003 phenological time series.** Climate Sensitivity Profiles (CSPs) fall

within three broad response-types; events always advance with increases in the climate variable irrespective of the seasonal timing of climate change (CSP Type I, Fig. 1 - red curve), events are always delayed by increases in the climate variable irrespective of the seasonal timing of climate change (CSP Type III, Fig. 1 - blue curve), and events may be advanced or delayed by increases in the climate variable, depending on the seasonal timing of climate change (CSP Type II, Fig. 1 - orange curve). Shown are the percentage of series that fall in each Type (% series), the percentage of effects that are statistically significant at  $P < 0.05$  after multiple testing correction (% effects significant). □ Based only on freshwater and terrestrial taxa, for which precipitation data were available. † NA indicates effect not evaluated, due to lack of precipitation data for marine taxa

**Extended Data Table 2 | Parameter estimates and test statistics from climate-phenology mixed-effects models.** Presented are fixed-effect parameter estimates from each model; the intercept and slope for each climatic predictor. Following R convention, absolute parameter estimates are provided for an assigned “baseline” group within each model (*b*), and remaining estimates are given as differences from this baseline ( $\Delta b$ ). Each estimate has an associated standard error and *t* statistic in parentheses (standard error, *t*). Climatic predictors include mean temperature and precipitation in seasonal windows at the upper and lower limit of the climate sensitivity profile for each phenological series. The number of observations, *n*, is 370,725. □ Models were re-run including the marine plankton data, and excluding precipitation effects (see text). In these models the number of observations, *n* = 379,081









