

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

2

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 change¹. Shifts in the
19 seasonal timing of recurring biological events such as reproduction and migration (i.e.
20 phenological changes) are especially well documented^{2,3}. Long-term ecosystem studies⁴⁻⁷ and
21 global meta-analyses^{2,3,8} 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 functioning⁹.

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 programmes¹⁰⁻¹². Unfortunately, such generalisations
32 are currently elusive.

33

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 photoperiod¹³ or resource availability¹⁴. 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 change¹⁵⁻¹⁷. 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 events¹⁷, 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 UK⁸.

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 (≥ 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^{15,16}.

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

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

123

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

133

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

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

146

147 **Taxonomic and trophic group sensitivity**

148 We tested the hypothesis that the limits of seasonal climate sensitivity differ coherently
149 among taxonomic groups by including a fixed-effect interaction between taxonomic group
150 and each climatic variable (Fig. 4, Extended Data Table 2). The lower limit of CSP_{temp} was
151 negative for all groups (“earliness” with warming), the strongest responses being found for
152 plants, freshwater phytoplankton, insects and amphibians (4.3, 4.1, 3.7 and 3.4 days earlier
153 $^{\circ}C^{-1}$, respectively). Upper limits of CSP_{temp} indicated that freshwater phytoplankton and
154 mammals experienced the greatest phenological delays with seasonal warming (2.9 and 2.0
155 days later $^{\circ}C^{-1}$, respectively) but that plants showed little evidence of such delays. The
156 strongest phenological delays with rising seasonal precipitation were found for freshwater
157 phytoplankton and insects (2.5 and 2.2 days later mm^{-1} , respectively), while freshwater
158 phytoplankton also exhibited the strongest phenological advances with rising precipitation
159 during other seasonal windows (1.1 days earlier mm^{-1}). Average temperature and
160 precipitation responses were consistent with a CSP type II in most cases. There was
161 considerable within-group variability in sensitivity.

162

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

166 towards “earliness” with seasonal warming was strongest at lower trophic levels (-4.1, -3.7
167 and -1.9 days °C⁻¹ for primary producers, primary consumers and secondary consumers,
168 respectively, Extended Data Table 2), consistent with observations of more rapid
169 phenological changes at lower trophic levels, in the UK⁸. Conversely, the lower limit of
170 CSP_{precip} varied less among trophic levels than the upper limit (Fig. 3d,f). The tendency for
171 later seasonal events with higher seasonal precipitation was greater for primary producers and
172 primary consumers (1.8 and 2.2 days mm⁻¹ on average, respectively) than for secondary
173 consumers (1.0 days mm⁻¹). Variations in climate sensitivity were described more
174 parsimoniously by taxonomic groups than by trophic levels (AICs of taxonomic and trophic-
175 level models 3237611 and 3238061, respectively).

176

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

185

186 **Estimating future change**

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

189 2050s by applying our fitted models to UKCP09 probabilistic projections (bias-corrected
190 relative to a 1961-90 baseline) of temperature and precipitation change under low, medium
191 and high emissions scenarios. Rather than predicting the *absolute* timing of future
192 phenological events, we contrasted possible *changes* in seasonal timing among organism
193 groups based upon established climate scenarios and contemporary patterns of climate
194 sensitivity. Estimated average phenological changes for primary producers and secondary
195 consumers were less than those for primary consumers (Fig. 5a). This occurred because,
196 averaged across species, the opposing climate responses of primary producers and secondary
197 consumers are more similar in magnitude than are those for primary consumers (Fig. 3),
198 effectively “cancelling each other out”. Our models suggest greater average advances for
199 crustacea, fish and insects than for other groups, such as freshwater phytoplankton, birds and
200 mammals (Fig. 5b). However, response-variation is high for crustacea (Fig. 5b).

201

202 **Discussion**

203 In the UK, phenological climate sensitivity varies greatly, suggesting effects of locally-
204 varying non-climatic drivers such as population structure¹⁸, resource availability¹⁹ and
205 adaptation²⁰. This is relevant to the use of phenological change as a tangible climate change
206 indicator^{1,21}. Mediators of phenological climate sensitivity are only known locally for some
207 of the groups in our data set e.g. nutrient availability (freshwater phytoplankton)²². However,
208 for others, the climate sensitivity of different biological traits is known to be mediated by
209 alternative drivers^{23,24}. High climate-response variability necessitates wide site and species
210 coverage in long-term monitoring schemes aiming to develop robust aggregate indicators of
211 change²¹. Since climatic conditions are more spatially-variable across broader geographic
212 domains, site-level replication of phenological monitoring is particularly important when

213 interpreting phenology at continental to global scales. In the UK, average responses for fish
214 and insects appear to provide climate-indicator potential. These groups show consistently
215 strong phenological advances with seasonal warming, and only weak opposing responses,
216 resulting in relatively large (net) changes in seasonal timing. Interpretation of phenological
217 changes for other groups is more complex. For example, freshwater phytoplankton show
218 strong evidence of opposing phenological responses to climatic variation at different times of
219 year and these are near-equivalent in magnitude, such that estimated net changes are
220 negligible. This highlights that long-term observations represent the net effect of potentially-
221 opposing biological responses²⁵. To fully capitalise on the indicator potential of phenological
222 change, we must advance mechanistic understanding of responses to potentially opposing
223 climate and non-climate drivers.

224

225 Despite this variability, we identified coherent patterns in climate sensitivity among the
226 idiosyncratic responses of many wild plant and animal populations. For the first time we
227 show that, on average, trophic levels differ in the magnitude of seasonal climate sensitivity,
228 but not the time-of-year within which climatic change has its most pronounced effects. This
229 may be a key mechanism underpinning observations of trophic level differences in
230 phenological change in the UK⁸. Lower trophic levels demonstrated more pronounced
231 variation in their sensitivity to changing temperature and precipitation at different times of
232 year, and stronger phenological responses to climatic change during defined (taxon- and
233 population-specific) seasonal periods.

234

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

237 The difference in magnitude between opposing climate responses is greatest for primary
238 consumers, resulting in greater “net” change. Our approach makes the simplifying
239 assumption that climatic change has the overriding influence upon seasonality. Nevertheless,
240 this suggests that systematic differences in climate sensitivity could result in widespread
241 phenological desynchronisation. However, factors that shape phenological climate-responses
242 introduce uncertainty into projections of future phenological change. These results should
243 catalyse research to improve predictive capacity in the face of multiple environmental and
244 demographic drivers that not only mediate rates of change, but might also confer resilience to
245 desynchronisation e.g. population density-dependence²⁶, compensatory range shifts²⁷, and the
246 formation of novel inter-specific interactions^{28,29}. These findings also underscore the
247 importance of developing our capacity to manage ecosystems within a “safe operating space”
248 with respect to the likely impacts of projected climate change³⁰.

249

250 **Supplementary Information** is linked to the online version of the paper at
251 www.nature.com/nature.

252

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265

266 **Author Contributions**

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

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404

405 **METHODS**

406 **Data sets**

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

417

418 Daily air temperature and precipitation data were extracted from the Met Office National
419 Climate Information Centre (NCIC) 5km-resolution gridded data set³¹ for the spatial
420 locations of all biological monitoring sites across the UK land surface. If available, recorded
421 water temperatures from the same site were used in place of air temperatures, for
422 phenological time series representing obligate aquatic taxa (freshwater plankton and fish).
423 Water temperatures were interpolated onto a daily time-step prior to analysis³². If these data
424 were not available, daily water temperature data were estimated from air temperatures using a

425 fitted empirical site-specific relationship between air and water temperature. For the sea trout
426 (*Salmo trutta*) data, an existing linear relationship³³ was used, while for the Atlantic salmon
427 (*Salmo salar*) data, a non-linear relationship³⁴ was calculated for a nearby river, the Tarland
428 Burn, and applied to air temperatures from the sampling site. For the marine plankton, mean
429 monthly sea surface temperatures were extracted from the Met Office Hadley Centre Sea Ice
430 and Sea Surface Temperature (HadISST) data set³⁵ for each of the Standard Areas³⁶ in which
431 phenological data were available. Precipitation data were not available for marine Standard
432 Areas.

433

434 **Statistics**

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

445

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

447 We used consistent methods to “screen” all phenological events with respect to their climate
448 sensitivity, finding periods of the year in which temperature and precipitation have their most
449 positive and negative correlations with seasonal timing (the upper and lower limits of climate
450 sensitivity). This approach was flexible enough to detect when these limits represented
451 opposing correlations between temperature or precipitation and seasonality, depending upon
452 the seasonal timing of climatic change e.g. spring warming may advance budburst, but winter
453 warming may delay it³⁷ (Fig. 1, CSP type II). It could also detect when the direction of the
454 correlation between climatic variables and seasonal timing was consistent irrespective of the
455 seasonal timing of climatic change, with only the magnitude of the correlation varying
456 between the limits of the CSP (Fig. 1, CSP types I and III).

457

458 For each phenological time series, we calculated the day of year by which 95% of the
459 recorded seasonal events had occurred (do_{y95}). Inter-annual variations in seasonal timing
460 were statistically modelled as a function of daily mean temperatures on do_{y95} each year. Then,
461 a series of 365 statistical models was run that used instead daily mean temperatures on $do_{y95}-$
462 1 to $do_{y95}-365$ as predictors. Slope coefficients and R^2 values for the temperature terms in
463 these models were collated, capturing seasonal variations in the sign and magnitude of the
464 phenology-temperature relationship (i.e. the CSP, Fig. 1). Generalized Linear Models
465 (GLMs) were used.

466

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

471 data for each specific location in each year, as for all other schemes, but then grouped the
472 phenological and climatic data at county level (mean area = 3,440 km²). Then, for each taxon
473 in each county we used the fixed-effect slope parameters and R² values from a series of LME
474 models, instead of GLMs, as a basis for estimating CSPs. In these models, we included fixed
475 effects of temperature on *doy*₉₅ to *doy*₉₅₋₃₆₅ as before, and included a year random effect to
476 account for replicate phenological records for each taxon in each county in each year. For the
477 SAHFOS marine plankton data set, we modified our iterative approach to analyse seasonal
478 timing-temperature relationships at monthly, instead of daily, time steps (the temporal
479 resolution of the sea surface temperature data).

480

481 As a final step in estimating the CSP for each series, temporal variation in the sign and
482 magnitude of the seasonal timing-temperature correlation was itself modelled (Extended Data
483 Fig. 8). This was done by fitting Generalized Additive Models (GAMs, Gamma error
484 distribution) to the time series of slope coefficients and R² values from the models described
485 above. By smoothing these time series, the GAMs identified periods of the year in which
486 slope coefficients were consistently negative (i.e. warming advances seasonal timing), or
487 consistently positive (i.e. warming delays seasonal timing), and during which the climate-
488 phenology models generating the slope estimates had a their highest goodness-of-fit.

489

490 Seasonal “windows” in which the upper and lower limits of temperature sensitivity occurred
491 were identified as periods during which 1) the 95% confidence interval for the GAM fitted to
492 the slope coefficients surpassed the limits of the 2.5 and 97.5 percentiles of the original slope
493 coefficients and 2) the 95% confidence interval for the GAM fitted to the R² values surpassed
494 the 97.5 percentile of the original R² values. This ensured that seasonal windows were

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

507

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

520 be used in subsequent modelling. Inferences were not, therefore, directly based upon
521 statistical modelling of uncertain parameter estimates. We categorised the results of all
522 10,003 CSPs according to three broad response-types (CSP types I–III, Fig. 1), and retained P
523 values for each fitted model term to infer which of the modelled climatic effects were
524 statistically significant. We examined the evidence for trophic-level differences in the mean
525 seasonal timing of climate sensitivity by modelling the relationship between the start date,
526 end date and duration of the seasonal windows capturing the upper and lower limits of
527 phenological sensitivity to temperature and rainfall as a function of trophic level (fixed
528 effect), with random effects of phenological metric, within species, within site. Analyses
529 were conducted using the *base*, *mgcv* and *lme4* packages in R^{38–40}.

530

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

532 We estimated the upper and lower limits of phenological climate sensitivity at a multi-species
533 scale by “matching” each phenological series with data on mean temperature and
534 precipitation, during the seasonal windows characterising the CSP for that series (Phase 1,
535 above). We aggregated all 10,003 of these matched phenology-climate data sets. To quantify
536 the average, multi-species, upper and lower limits of climate sensitivity we constructed a
537 linear mixed effects (LME) model, in which phenology (day of year) was modelled as a
538 function of mean temperature and precipitation within the seasonal windows of the amassed
539 CSPs (fixed effects) with random effects of phenological metric, within species, within site.
540 These random effects were necessary since our data could not be considered independent.
541 The timing of events for the same species are more likely to be similar than for different
542 species. Likewise for different sites and the phenological metric-types used to describe the
543 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

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

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

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

568

$$569 \quad \alpha_0 = \gamma_0 + \mu_{0,ijk} + \mu_{0,ij,k} + \mu_{0,i,jk}$$

$$570 \quad \beta_1 = \gamma_1 + \mu_{1,ijk} + \mu_{1,ij,k} + \mu_{1,i,jk}$$

$$571 \quad \beta_2 = \gamma_2 + \mu_{2,ijk} + \mu_{2,ij,k} + \mu_{2,i,jk}$$

$$572 \quad \beta_3 = \gamma_3 + \mu_{3,ijk} + \mu_{3,ij,k} + \mu_{3,i,jk}$$

$$573 \quad \beta_4 = \gamma_4 + \mu_{4,ijk} + \mu_{4,ij,k} + \mu_{4,i,jk}$$

574

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

576

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

582

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

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

597

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

607

608 **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 10th, 50th and 90th percentile changes

632 under low, medium and high emissions scenarios (relative to the 1961-90 baseline). The
633 spatial location of each phenological series was matched to climate projection data for the 25
634 × 25km grid square in which it occurred, and temporally matched to climatic data from the
635 months-of-year in which its respective climate sensitivity windows occurred. Relative
636 changes in timing, in response to climatic change of the magnitude projected to occur by the
637 2050s, were summarised by trophic levels and taxonomic groups.

638

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663

664 **FIGURE LEGENDS**

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

673

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

681

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

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

690

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

698

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

707

708 **EXTENDED DATA FIGURE AND TABLE LEGENDS**

709

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 2.5th-to-97.5th 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⁻¹). 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,

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

736

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

744

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

753

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

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

761

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

767

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

776

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

779 within three broad response-types; events always advance with increases in the climate
780 variable irrespective of the seasonal timing of climate change (CSP Type I, Fig. 1 - red
781 curve), events are always delayed by increases in the climate variable irrespective of the
782 seasonal timing of climate change (CSP Type III, Fig. 1 - blue curve), and events may be
783 advanced or delayed by increases in the climate variable, depending on the seasonal timing of
784 climate change (CSP Type II, Fig. 1 - orange curve). Shown are the percentage of series that
785 fall in each Type (% series), the percentage of effects that are statistically significant at
786 $P < 0.05$ after multiple testing correction (% effects significant). □ Based only on freshwater
787 and terrestrial taxa, for which precipitation data were available. † NA indicates effect not
788 evaluated, due to lack of precipitation data for marine taxa

789

790 **Extended Data Table 2 | Parameter estimates and test statistics from climate-phenology**
791 **mixed-effects models.** Presented are fixed-effect parameter estimates from each model; the
792 intercept and slope for each climatic predictor. Following R convention, absolute parameter
793 estimates are provided for an assigned “baseline” group within each model (*b*), and remaining
794 estimates are given as differences from this baseline (Δb). Each estimate has an associated
795 standard error and *t* statistic in parentheses (standard error, *t*). Climatic predictors include
796 mean temperature and precipitation in seasonal windows at the upper and lower limit of the
797 climate sensitivity profile for each phenological series. The number of observations, *n*, is
798 370,725. □ Models were re-run including the marine plankton data, and excluding
799 precipitation effects (see text). In these models the number of observations, $n = 379,081$









