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 change[1]. 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 studies[4–7] 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 functioning[9].

25

Identifying systematic taxonomic and trait-based differences in phenological climate

sensitivity (i.e. change in seasonal timing per unit change in climatic conditions) would have

significant socio-ecological implications. This would afford some predictability to future

ecological outcomes and would identify species that represent effective sentinels of climate

impact, facilitating the development of indicators and estimates of vulnerability for

conservation and national adaptation programmes[10–12]. Unfortunately, such generalisations

are currently elusive.

33

Analytical approach and data sets

Among-species differences in phenological change may arise from two aspects of climate

sensitivity. Firstly, variation may reflect differences in physiological and behavioural

responses, microclimate use, and the importance of non-climate related cues, such as

photoperiod[13] or resource availability[14]. Therefore, even when species have the same seasonal

period (window) for which they are most sensitive to climate change, they show different

phenological responses to a given climatic change. Secondly, co-occurring species may vary

in their seasonal periods of climate sensitivity, each typified by different levels of directional

climate change[15–17]. We conceptualise these two aspects of phenological responses as

species- (or population-) specific Climate Sensitivity Profiles (CSPs, Fig. 1). The CSP

approach differs fundamentally from attempts to identify single "critical" seasonal periods

within which climatic change most strongly affects seasonal events[17], by quantifying the full

range of phenological responses to seasonal climatic change. We ask "*How sensitive are*

phenological events to temperature and precipitation change at different times of year?". By

applying this approach to a large, taxonomically-diverse national-scale data set, we discern

2

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[8].

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 days °C$^-$

125   ^{1}, 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 CSP_{precip} exceeded the lower limit (1.4 days mm^{-1} and -0.4 days mm^{-1},

137   respectively, Fig. 3b, Extended Data Table 2). The upper limit of CSP_{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

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    $°C^{-1}$, 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 $°C^{-1}$, 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

7

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 UK[8]. 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 structure[18], resource availability[19] and

205 adaptation[20]. 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 change[21]. 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 responses[25]. 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 UK[8]. 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-dependence[26], compensatory range shifts[27], 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 change[30].

249

250 **Supplementary Information** is linked to the online version of the paper at

251 www.nature.com/nature.

252

253 **Acknowledgements**

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.

275

276   Author Information

277   *Stephen J. Thackeray[1], Peter A. Henrys[1], Deborah Hemming[2], James R. Bell[3], Marc S.*

278   *Botham[4], Sarah Burthe[5], Pierre Helaouet[6], David Johns[6], Ian D. Jones[1], David I. Leech[7],*

279   *Eleanor B. Mackay[1], Dario Massimino[7], Sian Atkinson[8], Philip J. Bacon[9], Tom M.*

280   *Brereton[10], Laurence Carvalho[5], Tim H. Clutton-Brock[11], Callan Duck[12], Martin Edwards[6],*

281   *J. Malcolm Elliott[13], Stephen J. G. Hall[14], Richard Harrington[3], James W. Pearce-Higgins[7],*

Toke T. Høye[15], Loeske E. B. Kruuk[16,17], Josephine M. Pemberton[16], Tim H. Sparks[18,19], Paul M. Thompson[20], Ian White[21], Ian J. Winfield[1] & Sarah Wanless[5]

1. Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster, Lancashire, LA1 4AP, UK.

2. Met Office, FitzRoy Road, Exeter, Devon, EX1 3PB, UK.

3. Rothamsted Research, West Common, Harpenden, Hertfordshire, AL5 2JQ, UK.

4. Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire, OX10 8BB, UK.

5. Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian, EH26 0QB, UK.

6. The Sir Alister Hardy Foundation for Ocean Science, The Laboratory, Citadel Hill, Plymouth, Devon, PL1 2PB, UK.

7. British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK.

8. The Woodland Trust, Kempton Way, Grantham, Lincolnshire, NG31 6LL, UK.

9. Futtie Park, Banchory, Aberdeen, AB31 4RX, UK.

10. Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset, BH20 5QP, UK.

11. Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK.

12. Sea Mammal Research Unit, Scottish Oceans Institute, East Sands, University of St Andrews, St Andrews, Fife, KY16 8LB, UK.

13. The Freshwater Biological Association, The Ferry Landing, Far Sawrey, Ambleside, Cumbria, LA22 0LP, UK.

14. University of Lincoln, Riseholme Hall, Riseholme Park, Lincoln, Lincolnshire, LN2 2LG, UK.

306   15. Aarhus Institute of Advanced Studies, Department of Bioscience and Arctic Research

307   Centre, Aarhus University, Høegh-Guldbergs Gade 6B, DK-8000 Aarhus C, Denmark.

308   16. Institute of Evolutionary Biology, School of Biological Sciences, University of

309   Edinburgh, Edinburgh, EH9 3FL, UK.

310   17. Research School of Biology, The Australian National University, ACT 2612 Australia.

311   18.   Faculty of Engineering and Computing, Coventry University, Priory Street, Coventry,

312   CV1 5FB, UK.

313   19. Institute of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71C, 60-625

314   Poznań, Poland.

315   20.   University of Aberdeen, Lighthouse Field Station, George Street, Cromarty, Ross-shire,

316   IV11 8YJ, UK.

317   21.   People's Trust for Endangered Species, 15 Cloisters House, 8 Battersea Park Road,

318   London SW8 4BG, UK.

319

324

References

326   1.   IPCC. *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global*
327   *and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment*
328   *Report of the Intergovernmental Panel on Climate Change [Field, C.B., V.R. Barros,*
329   *D.J. Dokken, K.J.* 1132 (Cambridge University Press, 2014).

2.	Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421,** 37–42 (2003).

3.	Root, T. L. *et al.* Fingerprints of global warming on wild animals and plants. *Nature* **421,** 57–60 (2003).

4.	Both, C., van Asch, M., Bijlsma, R. G., van den Burg, A. B. & Visser, M. E. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J. Anim. Ecol.* **78,** 73–83 (2009).

5.	Visser, M. E., Holleman, L. J. M. & Gienapp, P. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* **147,** 164–172 (2006).

6.	Burthe, S. *et al.* Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web. *Mar. Ecol. Ser.* **454,** 119–133 (2012).

7.	Jonsson, T. & Setzer, M. A freshwater predator hit twice by the effects of warming across trophic levels. *Nat. Commun.* (2015). doi:doi:10.1038/ncomms6992

8.	Thackeray, S. J. *et al.* Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Glob. Chang. Biol.* **16,** 3304–3313 (2010).

9.	Visser, M. E. & Both, C. Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc. London Ser. B-Biological Sci.* **272,** 2561–2569 (2005).

10.	Walpole, M. *et al.* Ecology. Tracking progress toward the 2010 biodiversity target and beyond. *Science* **325,** 1503–1504 (2009).

11.	Butchart, S. H. M. *et al.* Global biodiversity: indicators of recent declines. *Science* **328,** 1164–1168 (2010).

12.	Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A. & Langham, G. Towards an Integrated Framework for Assessing the Vulnerability of Species to Climate Change. *PLoS Biol.* **6,** 2621–2626 (2008).

13.	Post, E. & Forchhammer, M. C. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philos. Trans. R. Soc. B Biol. Sci.* **363,** 2367–2373 (2008).

14.	Thackeray, S. J., Jones, I. D. & Maberly, S. C. Long-term change in the phenology of spring phytoplankton: species-specific responses to nutrient enrichment and climatic change. *J. Ecol.* **96,** 523–535 (2008).

15.	Doi, H., Gordo, O. & Katano, I. Heterogeneous intra-annual climatic changes drive different phenological responses at two trophic levels. *Clim. Res.* **36,** 181–190 (2008).

15

364 16. Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. Warmer
365   springs lead to mistimed reproduction in great tits (Parus major). *Proc. R. Soc. B-*
366   *Biological Sci.* **265,** 1867–1870 (1998).

367 17. Van de Pol, M. & Cockburn, A. Identifying the Critical Climatic Time Window That
368   Affects Trait Expression. *Am. Nat.* **177,** 698–707 (2011).

369 18. Ohlberger, J., Thackeray, S., Winfield, I., Maberly, S. & Vøllestad, L. When
370   phenology matters: age–size truncation alters population response to trophic mismatch.
371   *Proc. R. Soc. B-Biological Sci.* **281,** 20140938
372   http://dx.doi.org/10.1098/rspb.2014.0938 (2014).

373 19. Thackeray, S. J., Henrys, P. A., Jones, I. D. & Feuchtmayr, H. Eight decades of
374   phenological change for a freshwater cladoceran: what are the consequences of our
375   definition of seasonal timing? *Freshw. Biol.* **57,** 345–359 (2012).

376 20. Phillimore, A. B., Hadfield, J. D., Jones, O. R. & Smithers, R. J. Differences in
377   spawning date between populations of common frog reveal local adaptation. *Proc.*
378   *Natl. Acad. Sci. U. S. A.* **107,** 8292–8297 (2010).

379 21. Amano, T., Smithers, R. J., Sparks, T. H. & Sutherland, W. J. A 250-year index of first
380   flowering dates and its response to temperature changes. *Proc. Biol. Sci.* **277,** 2451–
381   2457 (2010).

382 22. Feuchtmayr, H. *et al.* Spring phytoplankton phenology - are patterns and drivers of
383   change consistent among lakes in the same climatological region? *Freshw. Biol.* **57,**
384   331–344 (2012).

385 23. Nussey, D. H., Clutton-Brock, T. H., Albon, S. D., Pemberton, J. & Kruuk, L. E. B.
386   Constraints on plastic responses to climate variation in red deer. *Biol. Lett.* (2015).
387   doi:doi:10.1098/rsbl.2005.0352

388 24. Van Emden, H. F. & Harrington, R. *Aphids as Crop Pests*. 717 (CABI, 2007).

389 25. Cook, B. I., Wolkovich, E. M. & Parmesan, C. Divergent responses to spring and
390   winter warming drive community level flowering trends. *Proc. Natl. Acad. Sci.* **109,**
391   9000–9005 (2012).

392 26. Reed, T. E., Grøtan, V., Jenouvrier, S., Sæther, B.-E. & Visser, M. E. Population
393   growth in a wild bird is buffered against phenological mismatch. *Science* **340,** 488–91
394   (2013).

395 27. Amano, T. *et al.* Links between plant species' spatial and temporal responses to a
396   warming climate. *Proc. Biol. Sci.* **281,** 20133017 (2014).

397 28. Miller-Rushing, A. J., Hoye, T. T., Inouye, D. W. & Post, E. The effects of
398   phenological mismatches on demography. *Philos. Trans. R. Soc. B-Biological Sci.* **365,**
399   3177–3186 (2010).

400 29. Nakazawa, T. & Doi, H. A perspective on match/mismatch of phenology in
401   community contexts. *Oikos* **121,** 489–495 (2012).

402 30. Scheffer, M. *et al.* Creating a safe operating space for iconic ecosystems. *Science (80-.*
403   *).* **347,** 1317–1319 (2015).

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 set[31] 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 analysis[32]. 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 relationship[33] was used, while for the Atlantic salmon

427　(*Salmo salar*) data, a non-linear relationship[34] 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 set[35] for each of the Standard Areas[36] 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*

18

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 it[37] (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 (doy_{95}). Inter-annual variations in seasonal timing

460   were statistically modelled as a function of daily mean temperatures on doy_{95} each year. Then,

461   a series of 365 statistical models was run that used instead daily mean temperatures on doy_{95}-

462   1 to doy_{95}-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 km^2). Then, for each taxon

473   in each county we used the fixed-effect slope parameters and R^2 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 R^2 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 R^2 values surpassed

494   the 97.5 percentile of the original R^2 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    $DOY_{ijk} = \alpha_0 + \beta_1 TL_{ijk} + \beta_2 TU_{ijk} + \beta_3 PL_{ijk} + \beta_4 PU_{ijk} + \varepsilon_{ijk}$

562   where $\varepsilon_{ijk} \sim N(0,\sigma^2)$ 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 $\alpha_0 = \gamma_0 + \mu_{0;ijk} + \mu_{0;ij,k} + \mu_{0;i,jk}$

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

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

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

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

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

REFERENCES

640   31.   Perry, M. & Hollis, D. The generation of monthly gridded data sets for a range of
641   climatic variables over the UK. *Int. J. Climatol.* **25,** 1041–1054 (2005).

642   32.   Jones, I. D., Winfield, I. J. & Carse, F. Assessment of long-term changes in habitat
643   availability for Arctic charr (*Salvelinus alpinus*) in a temperate lake using oxygen
644   profiles and hydroacoustic surveys. *Freshw. Biol.* **53,** 393–402 (2008).

645   33.   Elliott, J. Numerical changes and population regulation in young migratory trout
646   Salmo trutta in a Lake District stream, 1966-83. *J. Anim. Ecol.* **53,** 327–350 (1984).

647   34.   Mohseni, O., Stefan, H. G. & Erickson, T. R. A nonlinear regression model for weekly
648   stream temperatures. *Water Resour. Res.* **34,** 2685–2692 (1998).

649   35.   Rayner, N. A. *et al.* Global analyses of sea surface temperature, sea ice, and night
650   marine air temperature since the late nineteenth century. *J. Geophys. Res.* **108,** 4407,
651   doi:10.1029/2002JD002670, (2003).

652   36.   Reid, P. C., Colebrook, J. M., Matthews, J. B. L. & Aiken, J. The Continuous Plankton
653   Recorder: concepts and history, from Plankton Indicator to undulating recorders. *Prog.*
654   *Oceanogr.* **58,** 117–173 (2003).

655   37.   Pope, K. S. *et al.* Detecting nonlinear response of spring phenology to climate change
656   by Bayesian analysis. *Glob. Chang. Biol.* **19,** 1518–1525 (2013).

657   38.   R Development Core Team. R: A language and environment for statistical computing.
658   (2011).

659   39.   Wood, S. N. Stable and efficient multiple smoothing parameter estimation for
660   generalized additive models. *J. Am. Stat. Assoc.* **99,** 673–686 (2004).

661   40.   Bates, D., Maechler, M. & Bolker, B. lme4: Linear mixed-effects models using S4
662   classes. (2011).

663

FIGURE LEGENDS

665 **Figure 1 | Climate Sensitivity Profiles (CSPs).** Climate sensitivity is the change in seasonal

666 timing per unit change in temperature (days $°C^{-1}$) 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 (°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

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

718

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

726

Extended Data Figure 3 | Climate sensitivities, based on different time periods (top: all data, middle: pre-1980 data, bottom: post-1980 data). Sensitivity is the slope of the relationship between seasonal timing (day of year) and temperature (°C), or precipitation (mm day^{-1}). Limits of a) temperature and b) precipitation sensitivity are summarised for all taxa. Lower (c, d) and upper (e, f) limits of temperature (c, e) and precipitation (d, f) 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 5th-to-95th 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 $°C^{-1}$, or mm^{-1}). Shown are the lower/upper limits of CSP_{temp} (a, b, respectively) and the lower/upper limits of CSP_{precip} (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

32

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

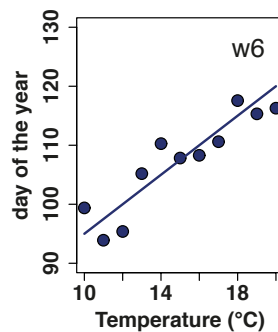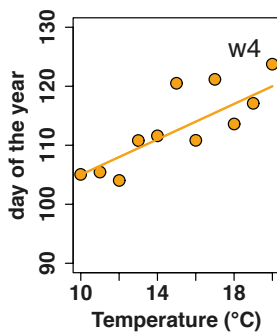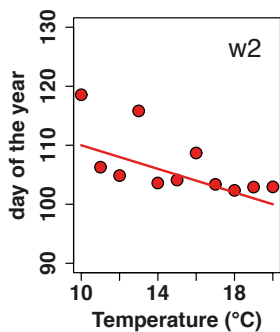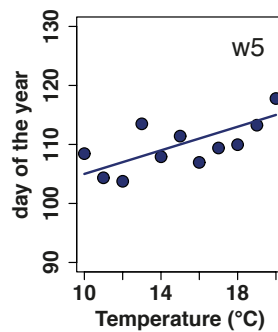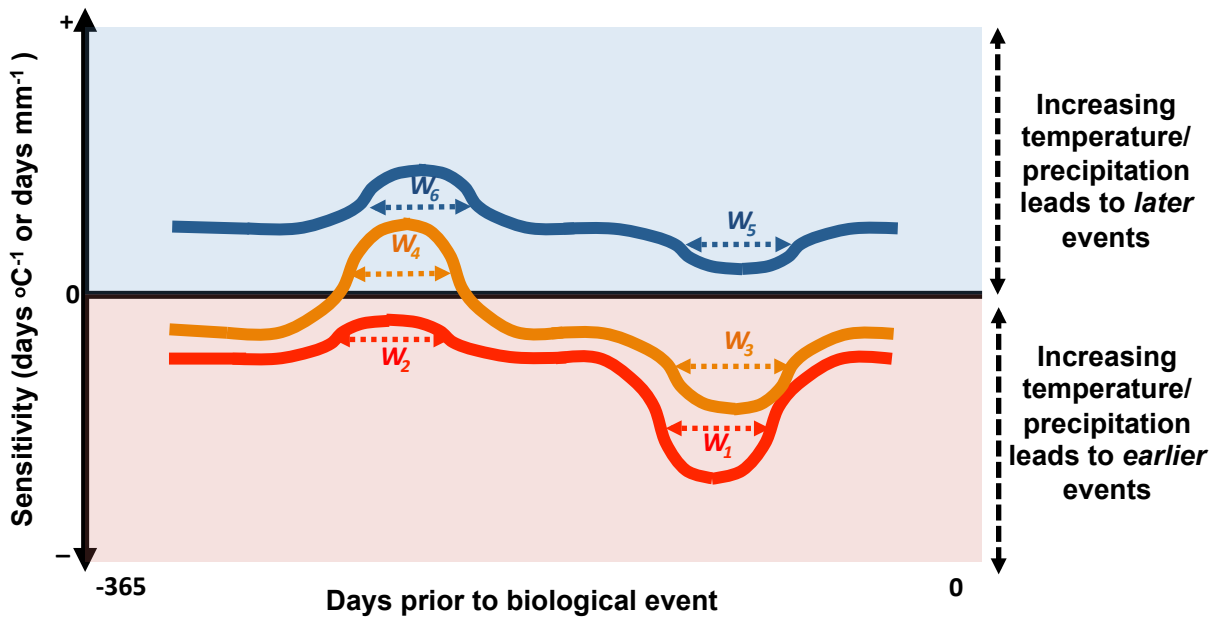775   seasonal windows at the limits of the climate sensitivity profile.
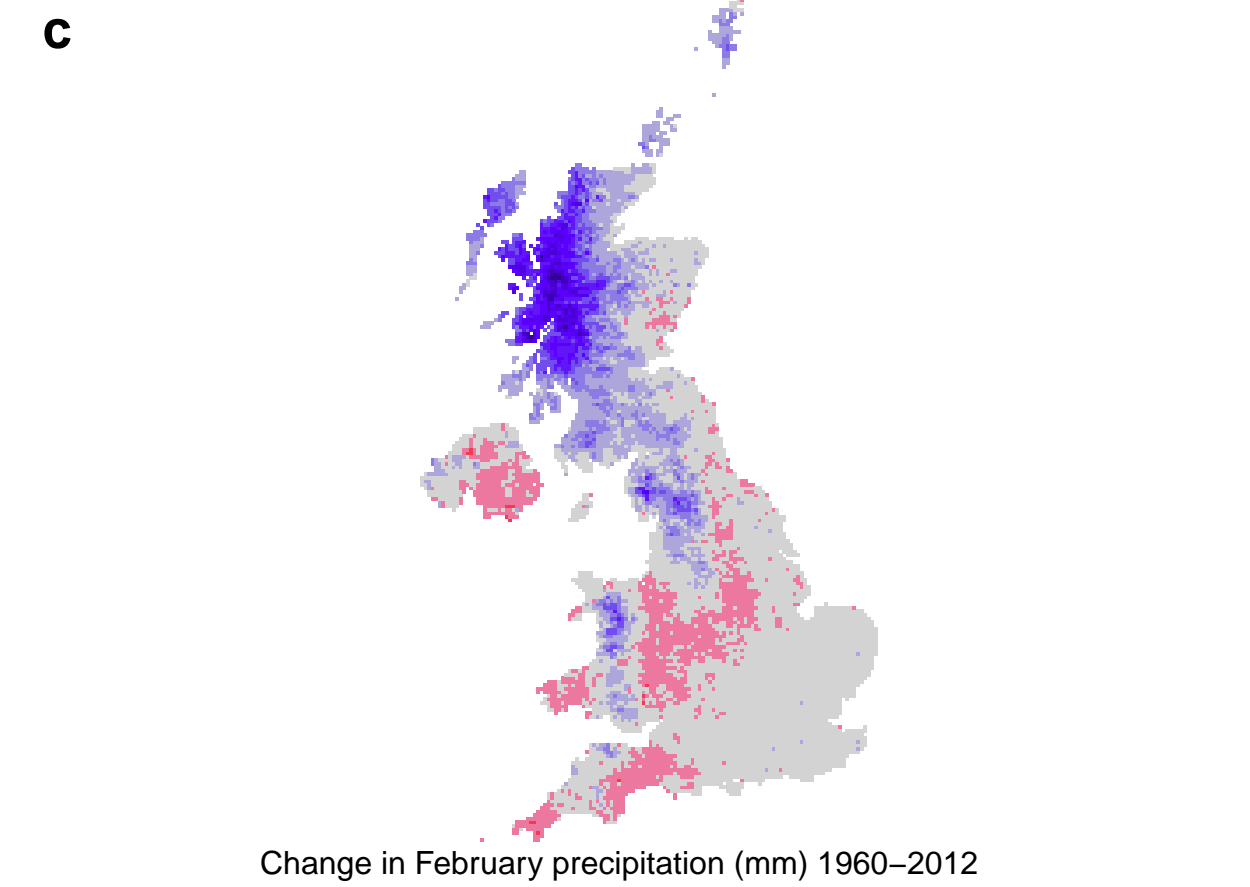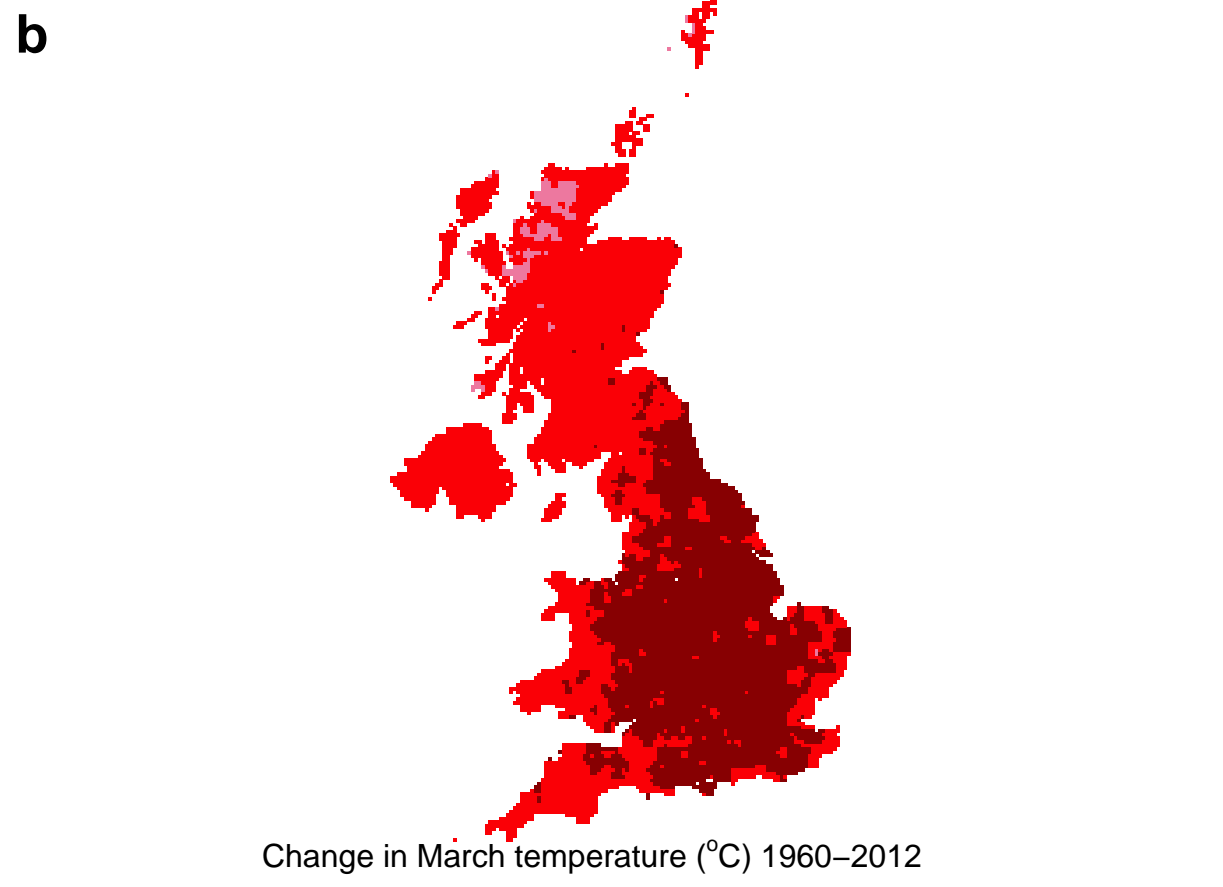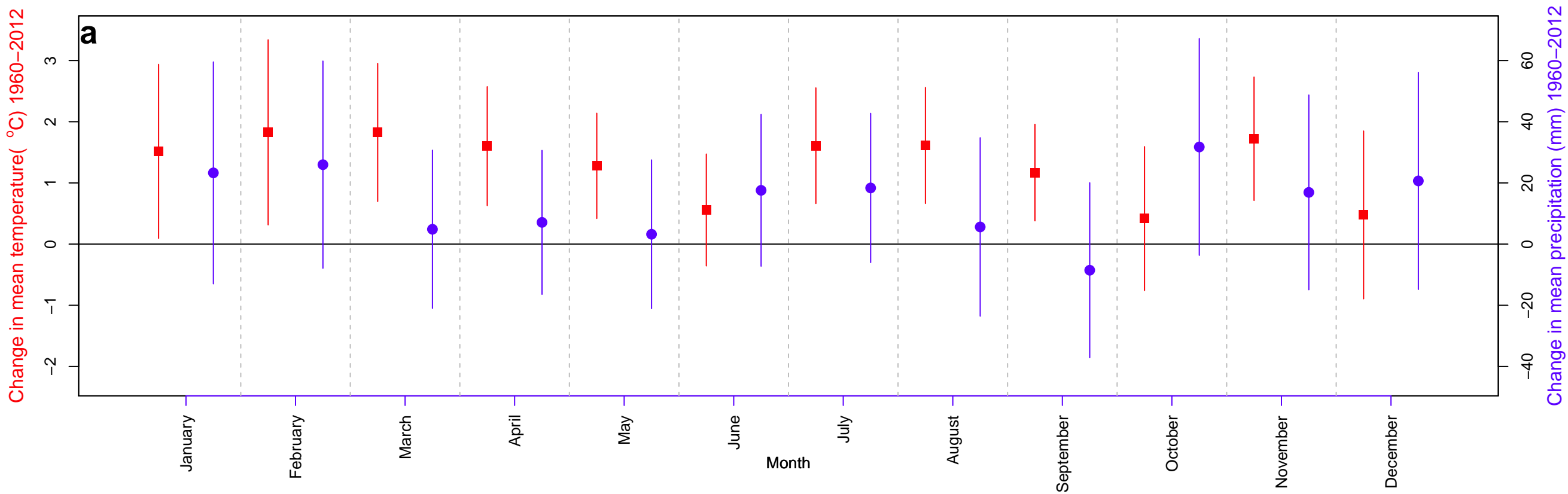
776

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
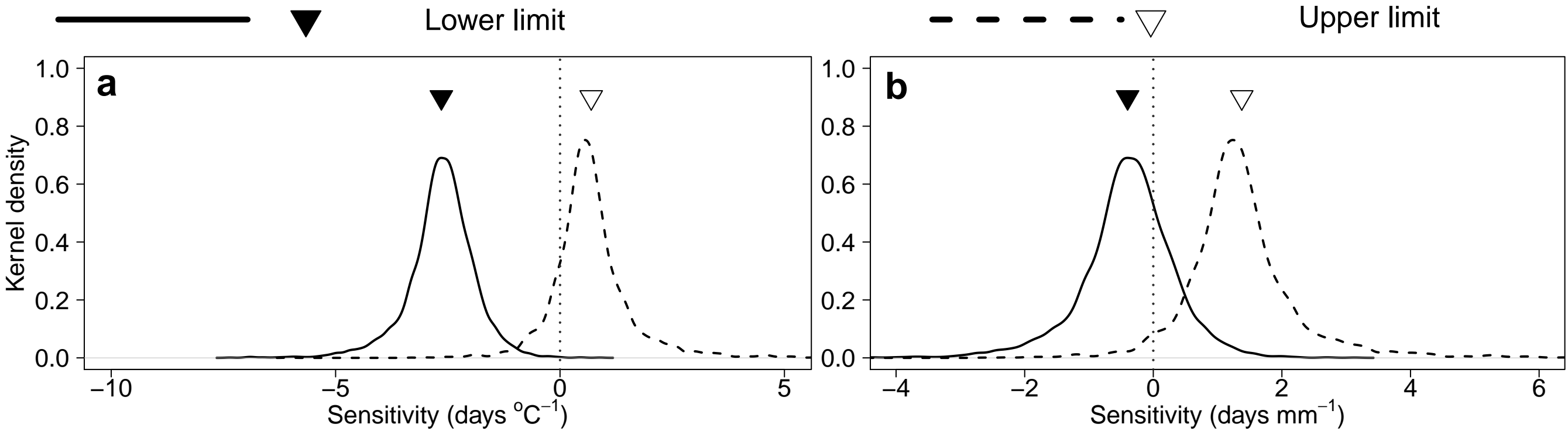
33

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

Sensitivity (days °C⁻¹ or days mm⁻¹)

W_6 W_5
W_4
W_2 W_3
W_1

Increasing temperature/ precipitation leads to *later* events

Increasing temperature/ precipitation leads to *earlier* events

-365   0

Days prior to biological event

w1   w3   w5

w2   w4   w6

day of the year

Temperature (°C)

a

b

Change in March temperature (°C) 1960−2012

c

Change in February precipitation (mm) 1960−2012