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## Phenological shifts of abiotic events, producers and consumers across a continent

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# 1 Phenological shifts of abiotic events, producers and consumers 2 across a continent

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157 Mari El Republic, Zvenigovsky District, Krasnogorsky Settlement, Tsentralnaya Street, 73, Russian  
158 Federation, <sup>85</sup>State Nature Reserve Vishersky, 618590, Perm region, Krasnovishersk, Gagarina  
159 street 36B, Russian Federation, <sup>86</sup>State Nature Reserve Olekminsky, 678100, Republic Sakha,  
160 Olekminsk, Filatova 6, Russian Federation, <sup>87</sup>Crimea Nature Reserve, 298514, Alushta,  
161 Partizanskaya, 42, Republic of Crimea, <sup>88</sup>Forest Research Institute Karelian Research Centre  
162 Russian Academy of Sciences, 185910, Karelia, Petrozavodsk, Pushkinskaya 11, Russian  
163 Federation, <sup>89</sup>Black Sea Biosphere Reserve, 75600, Khersons'ka oblast, Hola Prystan', Mikhail  
164 Lermontov 1, Ukraine, <sup>90</sup>Institute of Physicochemical and Biological Problems in Soil Sciences  
165 Russian Academy of Science, 142290, Moscow Region, Pushchino, Institutskaya 2, Russian  
166 Federation, <sup>91</sup>State Nature Reserve Nurgush, 610002, Kirov, Lenina street, 129a, Russian  
167 Federation, <sup>92</sup>Caucasian State Biosphere Reserve of the Ministry of Natural Resources, 385000,  
168 Adygea Republik, Maykop, Sovetskaya str. 187, Russian Federation, <sup>93</sup>National Nature Park



169 Vyzhnytskiy, 59200, Chernivtsi Region, Vyzhnytsya District, Berehomet, Street Central 27 a,  
170 Ukraine, <sup>94</sup>National Park Khvalynsky, 412780, Region Saratov, Khvalynsk Sity, Oktyberskya  
171 Street, 2b, Russian Federation, <sup>95</sup>State Research Center Arctic and Antarctic Research Institute,  
172 199397, Saint Petersburg, Bering st. 38, Russian Federation, <sup>96</sup>Information-Analytical Centre for  
173 Protected Areas, 123242, Moscow, Kapranova side-street 3, <sup>97</sup>State Nature Reserve Malaya Sosva,  
174 628242, Tjumen region, Sovetskiy, Lenina str., 46, Russian Federation, <sup>98</sup>Krasnoyarsk State  
175 Medical University named after Prof. V.F.Voino-Yasenetsky, 660022, Krasnoyarsk region,  
176 Krasnoyarsk, Partizana Zhelezniaka, 1, Russian Federation, <sup>99</sup>Surhanskiy State Nature Reserve,  
177 191404, Surhandarja region, Sherabad, Agahi, 1, Uzbekistan, <sup>100</sup>Mordovia State Nature Reserve,  
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184

185 **Ongoing climate change can shift organism phenology in ways that vary depending on species,**  
186 **habitats, and climate factors studied. To probe for large-scale patterns in associated**  
187 **phenological change, we use 70,709 observations from six decades of systematic monitoring**  
188 **across the former Soviet Union. Among 110 phenological events related to plants, birds,**  
189 **insects, amphibians and fungi, we find a mosaic of change, defying simple predictions of**  
190 **earlier springs, later falls and stronger changes at higher latitudes and elevations. Site mean**  
191 **temperature emerged as a strong predictor of local phenology, but the magnitude and**  
192 **direction of change varied with trophic level and the relative timing of an event. Beyond**  
193 **temperature-associated variation, we uncover high variation among both sites and years, with**  
194 **some sites being characterized by disproportionately long seasons and others by short ones.**  
195 **Our findings emphasize concerns regarding ecosystem integrity and highlight the difficulty of**  
196 **predicting climate change outcomes.**

197

## 198 **Main text**

199 Climate change is restructuring biodiversity across the globe<sup>1</sup>. Among key responses to spatial and  
200 seasonal changes in ambient temperature are changes in phenology<sup>2,3</sup> – i.e. changes in season-  
201 related life cycle events. At mid- to high latitudes in the northern hemisphere, spring events are  
202 generally occurring earlier, whereas autumn events are occurring later, mostly due to rising  
203 temperatures<sup>2,4</sup>. Overall, responses are expected to be faster and more pronounced the higher the  
204 latitude or elevation, that is, the lower the average temperatures<sup>5-7</sup>.

205 Despite rough consensus regarding these general trends and expectations, there are substantial  
206 differences in the observed magnitude and direction of phenological responses to climate change  
207 among individual species<sup>8-10</sup>, different taxonomic groups and trophic levels<sup>3,11,12</sup>. Where spring

208 phenology in terrestrial areas has advanced by a global average of 2.3 to 2.8 days/decade<sup>2,8,13</sup>, some  
209 studies have suggested changes as fast as 30 days per decade<sup>14</sup>. Higher rates of advance are possibly  
210 associated with lower trophic levels<sup>3,12</sup>, as perhaps reflecting not only different sensitivity to  
211 different drivers among trophic layers, but also different responses in terms of physiological  
212 development<sup>3</sup>. Another factor which may accelerate phenological advance relates to the mean  
213 timing of an event within the season: spring-time events may be advancing at higher rates than  
214 autumn events<sup>15</sup>. On top of species-specific variation, there is also considerable site-specific  
215 variation in phenological advance<sup>16</sup>. Such variation among sites and populations may arise from a  
216 combination of factors, including changes in temperature and other climatic variables, population  
217 sizes, genetic differences, phenotypic plasticity, and land use<sup>16,17</sup>.

218 A general reason for variability in phenological responses is that patterns of climate change vary  
219 substantially across the globe. As the climate of different regions and biomes are changing in  
220 somewhat different ways<sup>5</sup>, uniform responses to climate change are hardly to be expected. Regional  
221 variation in climate change concern patterns in e.g. overall warming, precipitation and in the  
222 seasonal distribution of change<sup>6</sup>. Thus, changes in phenology can be expected to track local changes  
223 in the timing of abiotic or climatically-driven events, within the constraints set by the utilization of  
224 and sensitivity to cues of the regional species assemblage<sup>18-20</sup>. Such local and regional variation in  
225 drivers<sup>19,21,22</sup> and sensitivity towards them<sup>18,20</sup> can be reflected in spatiotemporal variation in  
226 phenological shifts<sup>4,8,15,23,24</sup>. While the few studies analyzing geographically extensive datasets on  
227 phenology have observed spatial variation in temporal trends of phenological responses (e.g. <sup>25,26</sup>)  
228 and their main abiotic drivers<sup>5,27-29</sup>, the question remains whether patterns of change and response  
229 follow major environmental gradients in latitude, photoperiod or temperature<sup>15,16,30</sup>.

230 **Spatially extensive, long-term data across northern Eurasia**

231 Evaluating to what extent shifts in phenological events vary over space<sup>31</sup>, with their annual  
232 timing<sup>3,11,12</sup> or with trophic level<sup>16,32</sup> requires consistently sampled, community-wide data which are  
233 both long-term and spatially extensive<sup>3,12,16,32</sup>. Such data may also give insights on whether local  
234 phenology is influenced by biotic interactions beyond abiotic cues<sup>7,33,34</sup>. Unfortunately, systematic  
235 community-wide data sets are still uncommon, hampering progress in understanding large-scale  
236 taxonomic and geographic patterns in phenological change<sup>35</sup>. The few existing exceptions (e.g.  
237 <sup>2,4,8,15,36,37</sup>) are built on sparse data and/or combining individual studies using variable methods  
238 (e.g.<sup>38</sup>). However, for such data, both noise and bias may affect the overall pattern detected.  
239 Regarding seasonality, most datasets come with a particular bias, since much more interest has been  
240 invested in spring- than in autumn-time events<sup>2,4,39</sup>. This is a problem, since where data are  
241 available, phenological events occurring during different times of the year have oftentimes been  
242 found to shift differently<sup>40</sup>.

243 Here, we draw on a uniquely comprehensive, long-term database established using uniform  
244 protocols across northern Eurasia<sup>41-43</sup>. As this monitoring effort encompassed the timing of multiple  
245 seasonal events as characterizing both climatic variation and a wealth of taxa (plants, birds, insects,  
246 amphibians, reptiles and fungi; Fig. 1), it allows us to quantify large-scale patterns in phenological  
247 responses over six decades. Specifically, we ask: 1) Has the timing of different phenological events  
248 shifted similarly across this vast geographic range, measured in terms of the rate and direction  
249 (advance or delay) of change?; 2) To what extent does variation in the rate and direction of change  
250 follow major biogeographic gradients, such as latitude, photoperiod, temperature or chilling-degree-  
251 days?; 3) To what extent can variation in the rate and direction of change be linked to the relative  
252 seasonal timing of the event (early versus late), or to the species' trophic level?; and 4) To what  
253 extent does variation in the timing of different events covary locally in ways not attributable to  
254 overall patterns, suggesting an effect of biotic interactions (and/or joint responses to unmeasured

255 variables)? When combined, these questions allow us to characterize how different components of  
256 the ecosystem have shifted their phenologies over the last few decades of climate change, which  
257 environmental gradients can explain variation on a large spatial scale, and whether events occurring  
258 during different parts of the season or for different taxa keep pace with each other.

259 To quantify phenological shifts across events, trophic levels and environmental gradients, we fitted  
260 a joint species distribution model<sup>41</sup> treating the dates of the phenological events as the multivariate  
261 response variable. To capture linear shifts in the timing of events, we included year as a fixed  
262 covariate, and to account for phenology varying with environmental or spatial gradients, we  
263 included the linear effect of four environmental descriptors of each study site (i.e., mean annual  
264 temperature, mean annual chilling sum, photoperiod, or latitude), with a separate model fitted for  
265 each descriptor (see below). Additionally, in order to quantify to what extent shifts in phenology  
266 differ along the environmental gradient, we included an interaction term between year and the  
267 environmental descriptor. Variation among sites beyond that explained by the environmental  
268 descriptor was captured by including site as a random factor, and similarly year-to-year variation  
269 beyond any linear trend was modelled by including year as a random factor. All events were  
270 grouped into abiotic (n=28; e.g. the transition of daily average temperatures above a given  
271 threshold, the melt of snow cover, or the breakup of ice on a given water body; Table S1) versus  
272 biotic events (n= 82; e.g. the first occurrence of a fungus species, the onset of blooming in a plant  
273 species, or the end of leaf fall for a tree species; Table S1), with the latter further split according to  
274 the species trophic level, yielding five “trophic levels” (producers, n=54; primary consumers, n=4;  
275 secondary consumers, n=22; and saprotrophs, n=2; Fig. 1; Table S1). To evaluate how the  
276 multivariate response (i.e. dates of the phenological events) varies within year for each trophic  
277 level, we further included as explanatory variables the trophic level, the mean timing of the event  
278 across all sites, and their interaction. Since we treated the phenological events as the “species” of

279 our joint species distribution model, we treated their characteristics (i.e. the trophic level or the  
280 mean timing of the event) as its “traits”, just as one would model e.g. the body size or feeding guild  
281 of a species as its traits<sup>41,43</sup>. Thus, the explanatory variables were allowed to affect how the events  
282 respond to the fixed effects of year, the environmental descriptor (i.e., mean annual temperature,  
283 mean annual chilling sum, photoperiod, or latitude), and their interaction<sup>5,6,8</sup>. The periodic nature of  
284 seasons over time was captured by including the mean timing of the event as the linear effects of its  
285 cosine and sine transformations (see Methods for more details).

286 To examine the impact of different descriptors of climatic conditions at each site, we fitted four  
287 alternatives models to the data. Each model was identical in structure, but used an alternative  
288 climatic descriptor of the sampling sites. The specific metrics used were (1) the mean annual  
289 temperature in each study location, (2) the mean annual chilling sum (sum of degree days for those  
290 days for which the temperature is below zero), (3) the photoperiod (measured as the difference  
291 between the longest and shortest days of the year), and (4) the latitude of the site, with data sources  
292 for (1)–(3) identified in the Methods section. We fitted four separate models, rather than including  
293 all drivers into a single model, because all four drivers are highly correlated. Thus, their  
294 simultaneous inclusion in a single model would be of limited added value (in terms of variation  
295 “accounted for”), whereas it would compromise the interpretability of the results.

## 296 **How phenology is shifting across a continent**

297 All models provided adequate descriptions of the data, as evidenced by a high mean explanatory  
298 power: averaged over the events  $R^2$  was 74% for the model with latitude and 75% for all other  
299 models. We note that the reason why all models had similarly high explanatory power was that the  
300 part of the site-specific variation not explained by the climatic descriptor of the site was captured by  
301 the random effect of the site. The proportion of explained variation attributed to the climatic  
302 descriptor was 36% for the mean annual temperature of the site, 24% for the chilling sum, 27% for

303 the photoperiod, and 28% for the latitude (Extended Data Fig 2). Because mean annual temperature  
304 was the best predictor in the sense of explaining the most variation, we report the results of that  
305 model in the main text. All four models yielded qualitatively consistent results (Extended Data Figs.  
306 1-8).

307 The explanatory power was greater for spring events than for autumn events, except for abiotic  
308 events (see Table S1) where it was consistently high (Fig. 2a for the model with mean temperature;  
309 Extended Data Figure 1 for other models). Averaged over the different events, 36.0% of the  
310 explained variance was attributed to the site mean temperature, 2.8% to the linear effect of year and  
311 its interaction with the temperature, 41.5% to the random effect of the site (i.e. variation among  
312 sites not explained by mean temperature), 13.4% to the random effect of the year (i.e. variation  
313 among years not explained by linear trends), and 6.4% to the random effect of the sample (i.e.  
314 synchronous variation at the level of site-year combinations; Fig. 2b).

315 Spring events tend to occur earlier and autumn events tend to occur later at warmer (typically lower  
316 latitude or elevation) sites, creating a longer activity period or growing season, as reflected by a  
317 strong negative effect of temperature on spring event timing and strong positive effect for autumn  
318 event timing (Fig. 3a, b). For a large proportion (54%) of all events, we found strong statistical  
319 support (at least 95% posterior probability) for a shift towards an earlier date, whereas fewer events  
320 (10%) showed strong statistical support for a shift towards a later date (Fig. 3a). As examples of  
321 events shifting towards an earlier date, we find the break of ice cover, the first blooming of many  
322 plants (from Tussilago, *Tussilago farfara*, to the Lily of the valley, *Convallaria majalis*), the first  
323 flight of bumblebees, *Bombus*, and the first occurrence of a range of bird species (ranging from the  
324 swift *Apus apus* to the crane *Grus grus*). Among events shifting towards a later date, we find the  
325 formation of snow and ice cover, the timing of autumn colours and leaf fall in several trees (from  
326 aspen *Populus tremula* to birch *Betula pendula*), and – perhaps oddly enough – the spring-time

327 awakening of the brown bear, *Ursus arctos*. Specifically, spring events showed the strongest shift  
328 towards earlier dates, whereas autumn events showed the strongest shifts towards later dates (Fig.  
329 3c). This was particularly evident for primary producers, which overall showed stronger shifts in  
330 both directions; i.e. plants advanced early or delayed late events faster than did higher trophic  
331 levels. By comparison, the abiotic events showed even stronger shifts in both directions for both  
332 temperature and year effects. Thus, abiotic change, consumers and producers slide apart as springs  
333 shift earlier and autumns later.

334 Additionally, shifts were more positive at warmer sites for some events (18% showed strong  
335 statistical support; Fig. 3d), but more negative for others (15%; Fig. 3d), with no clear pattern over  
336 time or across trophic levels. Among those events that showed a strong statistical support for an  
337 overall shift to earlier, 17% showed a strong statistical support for shifting to earlier especially in  
338 cold sites and 16% in warm sites (Fig. 3e). Among those events that showed a strong statistical  
339 support for an overall shift to later, 11% showed a strong statistical support for shifting to later  
340 especially in cold sites and 22% in warm sites (Fig. 3e). As concrete examples of events which have  
341 actually shifted later at cold sites but earlier at warm sites, we find the first spring rain, the onset of  
342 blooming in Scots pine (*Pinus sylvestris*) and Marsh Labrador tea (*Rhododendron tomentosum*, syn.  
343 *Ledum palustre*), and the first song of the skylark (*Alauda arvensis*). Among events shifting earlier  
344 at cold sites but later at warm sites, we find e.g. the arrival of the rook (*Corvus frugilegus*), and the  
345 ripening of blueberry (*Vaccinium myrtillus*) and lingonberry (*Vaccinium vitis-idaea*).

346 The random effect of site was positively associated both within spring and within autumn events,  
347 but negatively associated between spring and autumn events (Fig. 4a); i.e., at any given site, spring  
348 events tended to occur particularly early while all autumn events particularly late, or vice versa,  
349 after accounting for the effect of site mean temperature. This pattern remained qualitatively  
350 unchanged when replacing mean temperature with other environmental descriptors (mean chilling



351 sums, photoperiod or latitude; see Extended Data Fig. 6). Thus, summer – in the sense of the  
352 biologically active period – tends to be particularly long at some sites and particularly short at other  
353 sites, a pattern which is only partly captured by simple environmental gradients (for potential  
354 explanations, see below). The random effect of year was positively correlated among events overall,  
355 but especially among spring events, meaning that some years are characterized by early spring  
356 phenology and others by late spring phenology across all events and trophic levels (Fig. 4b).  
357 Perhaps most interestingly, though, the random effect at the level of the sampling unit (i.e. the site-  
358 by-year combination) showed positive association among most phenological events. Thus, a large  
359 majority of all phenological events within a given site in a given year tended to be consistently  
360 “early” or “late” to an extent unexplicable by the effect of the year as such (Fig. 4c) – a pattern  
361 suggesting that some other factor may be orchestrating the relative timing of events at the level of  
362 the local community.

### 363 **Striking variation over space, species and trophic levels**

364 Our results highlight considerable spatial, seasonal and trophic heterogeneity in the magnitude and  
365 direction of shifts in phenological timing. While much of the large-scale variation can be attributed  
366 to a simple environmental gradient, phenological responses to ongoing climate change can  
367 idiosyncratically cause advance or delay over time within regions, and among sites and trophic  
368 levels. The strong effect of site beyond the effect of mean temperature (as shown by the overall  
369 partitioning of variance in our model; Figs. 2 and Extended Data Fig. 2) importantly qualifies the  
370 expectation of a strong and general pattern of phenology change along latitudinal or other  
371 environmental gradients<sup>17</sup>. Yet, it is consistent with our previous work<sup>17</sup> showing that phenological  
372 plasticity is constrained by local differentiation in reaction norms to temperature cues<sup>44</sup>, i.e., by  
373 local adaptation (see also<sup>18,45</sup>). Under such a scenario, we would indeed expect site-specific  
374 variation in phenology beyond patterns attributable to average temperature or its change over time.

375 However, it is worth noting that different abiotic events (such as snowmelt, ice formation and ice  
376 break) likewise vary differently with mean temperature, change differently over time, and remain  
377 cross-correlated even when temperature has been accounted for (Figs. 3, 4). In other words, early  
378 sites tend to remain early, and late sites tend to remain late, both with respect to the biotic and  
379 abiotic components of the local ecosystems. Most interestingly, the overall timing of events tends to  
380 be more synchronized than suggested by the overall effect of year. The strong dominance of  
381 positive residual associations between event-pairs at the random sample level (Figs. 4c and  
382 Extended Data Fig. 8) implies that an early date of one given event is associated with an earlier date  
383 in another *beyond* the advance expected by the overall earliness of the year. Residual covariance at  
384 this level could potentially be interpreted as a sign of a synchronizing effect of biotic interactions  
385 among species. In doing so, we should naturally exercise the same caution as whenever statistically  
386 observed associations are interpreted as biotic interactions<sup>41,43</sup>. It is also worth noting that beyond  
387 biotic interactions, this result is likely to partly reflect the synchronizing effect of abiotic conditions  
388 which affect multiple events, as well as the fact that different phenophases within one and the same  
389 species are interconnected with each other (e.g a migratory bird species cannot breed without first  
390 arriving, so the timing of breeding is constrained by the timing of arriving). Regarding the latter  
391 type of dependencies, we note that while we scored two or more separate phenological events in  
392 several species (Supplementary Information, Table S1), such repeated measures concerned far too  
393 few species to account for the vast predominance of positive residual associations observed overall.  
394 Thus, the pattern observed may be seen as suggestive, but clearly inconclusive of evidence for an  
395 imprint of biotic interactions on community-level phenology<sup>7,33,34</sup>.

396 Overall, strong phenological shifts over time occur not in lieu of but on top of the imprints of  
397 environmental gradients of mean temperature, photoperiod and latitude<sup>5,6,8</sup>. That is, strong added  
398 imprints of site on local phenology change might stem from spatial variation in additional factors

399 varying more idiosyncratically in space, rather than as smooth gradients. Species respond to  
400 multiple climatic dimensions over time<sup>46,47</sup>, and the effects of climate on phenology may further  
401 vary with habitat<sup>48</sup>, urbanization<sup>49,50</sup>, and precipitation<sup>5,6</sup>. Thus, an anthropogenic-induced shift in  
402 the macroclimate<sup>4,5,15,32</sup>, potentially leading to large-scale environmental changes along latitudes<sup>51</sup>  
403 or other geographical gradients, may be further modified by the local changes that species are  
404 responding to customized by the local conditions that they have adapted to. Such added impacts  
405 could limit the scope for space-for-time substitutions<sup>16</sup>, and leads us to warn against uncritical  
406 extrapolation of trends observed among sites, trophic levels, or from one region to another<sup>5</sup>.

407 As proposed by Burrows et al.<sup>17,52</sup>, the observed patterns of shifts in phenology should be compared  
408 to patterns in the velocity and seasonal shift of climate change. In this context, we note that our  
409 current data include both abiotic climate-related events and biotic responses, with the former  
410 shifting more than the latter. These disparities between the rates of change in the abiotic  
411 environment and species responses match previous observations that current phenological plasticity  
412 is not keeping pace with variation in climatic conditions<sup>3,17,18,22,53–56</sup>. Mismatches between the  
413 velocity of climate change and realised seasonal shifts may help identify regions of concern, e.g.  
414 where phenology change is lagging behind species thermal niches.

#### 415 **Ecosystem integrity imperilled yet understudied**

416 Our findings emphasize concerns regarding ecosystem integrity, as the velocity of change in space  
417 and time differed between interacting trophic levels. Combined with different responses among  
418 events over different parts of the season, this variation can lead to temporal mismatches between  
419 species<sup>1,11,56</sup> and potentially affect community structure and persistence. Importantly, a shift in the  
420 timing of an event related to one life-stage may propagate to another, but our current dataset holds  
421 limited resolution towards resolving such knock-on effects. To establish whether the stability and  
422 persistence of natural systems is ultimately affected by the loss of phenological synchrony at one

423 stage, or within food webs, we need a much-improved understanding of the interplay between  
424 spatial, trophic, species- and event-specific patterns in phenological responses (e.g. <sup>35</sup>).

425 Accumulated negative effects of rapid seasonal shifts across many species may threaten  
426 biodiversity<sup>14,57,58</sup>. Surprisingly enough, our current findings suggest that phenological shifts during  
427 the last few decades may differ between warmer and colder locations across our study area. In this  
428 context, we stress that our estimates concern absolute, not relative, rates of change. Counter-  
429 weighing the interpretation of stronger shifts at warmer (thus more southern or lower elevations)  
430 sites is the fact that phenology is naturally constrained by the overall length of the season. At high  
431 latitudes, i.e. in colder regions, a shift of a few days may amount to a considerable part of the full  
432 growing season. As polar areas warm at faster rates, resident organisms might lose major parts of  
433 their phenological niches <sup>21</sup>. In contrast, areas of slower seasonal shifts, and smaller relative shifts,  
434 may be important repositories for both biodiversity and ecosystem integrity<sup>5</sup>. Our current study  
435 provides a first attempt in this direction, and will hopefully inspire more work to come.

436

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561

## 562 **Methods**

563 We used data from Ovaskainen *et al.*<sup>59</sup>, who compiled dates of phenological events (for concrete  
564 examples, see Supplementary Information, Table T1.1) systematically recorded for multiple  
565 taxonomic groups in 471 localities across the Russian Federation, Ukraine, Uzbekistan, Belarus and  
566 Kyrgyzstan. In addition, the database includes dates on climatic events recorded at each locality  
567 (e.g., ice formation and first day of snowfall). The data were curated by EarthCape<sup>60</sup> and published  
568 on Zenodo<sup>59</sup>. From this set, we selected events for which there were at least 100 data points in total,  
569 and at least 10 data points from at least 10 sites. Further, we only included sites that were at least 25  
570 km apart, and sampling units for which there were at least 10 events recorded. All anthropogenic  
571 events, such as dates for sowing and harvest, were excluded from this analysis. This process yielded  
572 70,709 phenological observations for 110 events across 113 locations (Fig. 1). The data included 52  
573 taxa and four types of meteorological events (Supplementary Info, Table S1.1), and covered the  
574 period between 1960-2017 (earlier records were excluded), spanning 43.08°–67.82° latitude and  
575 21.15°–136.15° longitude.

576 The sampling units consist of (site, year) pairs. We denote by  $y_{ij}$  the date on which the  
577 phenological event  $j$  took place in sampling unit  $i$ . These are combined in the data matrix  $\mathbf{Y} = \{y_{ij}\}$   
578 with  $j = 1, \dots, n_s = 110$  events recorded in  $i = 1, \dots, n_y = 2789$  sampling units. The data consist  
579 of 70,709 dates, so that 77% of the entries in the  $\mathbf{Y}$  matrix are missing (NA) due to not all events  
580 being recorded in all sites and in all years. To these data, we fitted Hierarchical Modeling of  
581 Species Communities (HMSC) models<sup>41,43</sup>. HMSC is a multivariate Bayesian generalized linear  
582 mixed modelling framework, which allowed us to account for both correlation among the



583 phenological events included in the models, as well as for the spatio-temporal structure of the study  
584 design<sup>41-43</sup>. Additionally, HMSC allows including trait information to inform species-level  
585 responses to model covariates<sup>41</sup> – in our case, event-level responses. Here, we summarize our  
586 rationale and inference, while an in-depth description of the HMSC model fitted is provided in  
587 Supplementary Information, Text S2.

588 As predictors related to each sampling unit  $i$ , we included the linear effect of year of the sampling,  
589 aimed to capture temporal shifts in phenology which are the main focus of this study. To account  
590 for phenological variation due to climatic conditions, as well as to capture any systematic variation  
591 in the phenological shifts as a function of climatic conditions, we also included a variable  
592 describing the overall (not year-specific) climatic conditions at each study site, and its interaction  
593 with the linear effect of year. As climatic descriptor, we considered four alternative variables based  
594 on<sup>29</sup>, who identified the three most important factors controlling phenology in primary producers as  
595 the degree of winter chilling, photoperiod (day length relative to night length), and temperature. We  
596 thus derived descriptors of spatial variation in each of these three variables, and showed that our  
597 main results were upheld across each (Extended Data Figs. 1-8). Specifically, these were (1) the  
598 mean annual temperature, (2) the mean annual chilling sum (calculated as the sum of degree days  
599 for those days for which the temperature is below zero), and (3) the photoperiod measured as the  
600 difference between the longest and shortest days of the year, for each site. In addition, we  
601 considered (4) the absolute latitude of the site, as a standard descriptor of space as such in both  
602 phenological<sup>61</sup> and other biogeographic analyses<sup>62</sup>. We note that photoperiod is a function of  
603 latitude, but that the two are non-linearly related to each other. For this reason, we included latitude  
604 *per se* as a separate, potential climatic descriptor. To compute the mean annual temperature and the  
605 mean annual chilling sum, we used the ERA5-Land data (representing the period 1979-2019)<sup>63,64</sup>.  
606 To calculate the photoperiod, we used the daylength function of the R-package geosphere<sup>65</sup>.

607 To examine how the shifts and their dependency on the climatic conditions co-varied among  
608 different types of phenological events, we also included event-level predictors (i.e., species traits in  
609 the HMSC framework): (1) the mean timing of each event (calculated as the mean day of the year  
610 over the entire data set); and (2) the trophic level of the species for which the phenological event  
611 was recorded (classified as producers, primary consumers, secondary consumers, and saprotrophs, or  
612 abiotic events). To account for the periodic nature of seasons over time, we included the mean  
613 timing of each event as the linear effect of its cosine and sine transformations. To account for the  
614 nature of the study design and to evaluate co-variation among the phenological events, we included  
615 three random effects for the site, the year, and the sampling unit (i.e. year-site pairs). All of these  
616 were modelled at the community-level, using the latent variable approach of HMSC<sup>41,43</sup>. This  
617 allowed us to assess the relationships among phenological events that could not be explained by  
618 responses to the main covariates, and for each of the three random effect levels included in our  
619 models. For a more technical description of the HMSC model, we refer the reader to <sup>41-43</sup>.

620 We fitted the models with package `Hmsc`<sup>42</sup> in R<sup>66</sup> assuming the default prior distributions (see<sup>42,43</sup>).  
621 We performed posterior sampling for four Markov Chain Monte Carlo (MCMC) chains, each of  
622 which we sampled for 375,000 iterations, out of which we discarded the first 125,000 as a transient  
623 and thinned the remaining by 1000, thus yielding 250 samples per chain and 1000 samples in total.  
624 To evaluate MCMC convergence, we examined the distributions of the potential scale reduction  
625 factor over the parameters related to the fixed effects ( $\beta$  –parameters) and the random effects ( $\Omega$ -  
626 parameters), equivalent to the Gelman-Rubin statistic<sup>67</sup>.

627 Overall, we note that our aim is to quantify spatial variation in the rates (slope) of phenological  
628 change over time, not to identify the specific drivers of the timing of each individual event. To  
629 emphasize this point, we stress that we regressed phenological timing on year and on descriptors of  
630 each site's position in physical (latitude) or environmental space (average temperature, average sum

631 of chilling degree days or photoperiod), not on year-to-year variation in some specific driver. What  
632 our analyses show is thus that trophic level and seasonal timing of an event affect how it has shifted  
633 over time, and that the rate of shift is further affected by its position along the biogeographic  
634 gradient, whereas the exact descriptor of this gradient has little impact on the results (Extended Data  
635 Figs. 1–8).

636

### 637 **Reporting summary**

638 Reporting summary. Further information on research design is available in Nature Research  
639 Reporting Summary linked to this article.

640

### 641 **Data availability**

642 The data that support the findings of this study are available in <sup>40,59</sup>, with the exact subset of the data  
643 used in the present analyses available at <https://doi.org/10.5281/zenodo.3774386>.

644

### 645 **Code availability**

646 The code needed to replicate the current analyses, from data extraction to parameter estimates  
647 presented, is available at <https://doi.org/10.5281/zenodo.3774386>.

648

### 649 **References**

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- 668

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685 Mirsaitov, M. Nanynets, L. Ovcharenko, L. Rassohina, E. Romanova, A. Shelekhov, N. Shirshova,  
686 D. Sizhko, I. Sorokin, H. Subota, V. Syzhko, G. Talanova, P. Valizer and A. Zakusov.

687

### 688 **Author Contributions**

689 The data were collected by the 195 authors starting from Marina Abadonova and ending with  
690 Tatyana Zubina in the author list. Juri Kurhinen, Evgeniy Meyke, Coong Lo, Gleb Tikhonov and  
691 Eliezer Gurarie contributed to the establishment and coordination of the collaborative network and  
692 to the compilation and curation of the resulting dataset. Tomas Roslin, Otso Ovaskainen, Laura  
693 Antão, Maria Hällfors, and Maria del Mar Delgado conceived of the idea behind the current study  
694 and wrote the first draft of the paper, with Otso Ovaskainen conducting the analyses. All authors  
695 provided useful comments on earlier drafts.

696

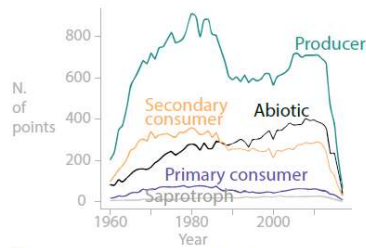
### 697 **Competing Interests**

698 The authors declare no competing interests.

699

700

### Number of data points over time



Abiotic events  
31 data points



Producer  
95 data points



Primary consumer  
83 data points



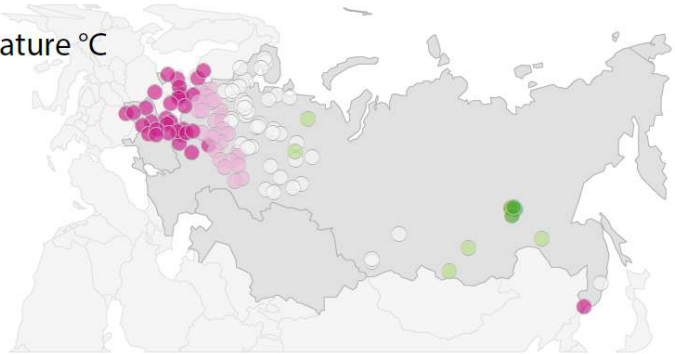
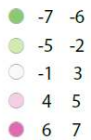
Secondary consumer  
91 data points



Saprotrophs  
16 data points



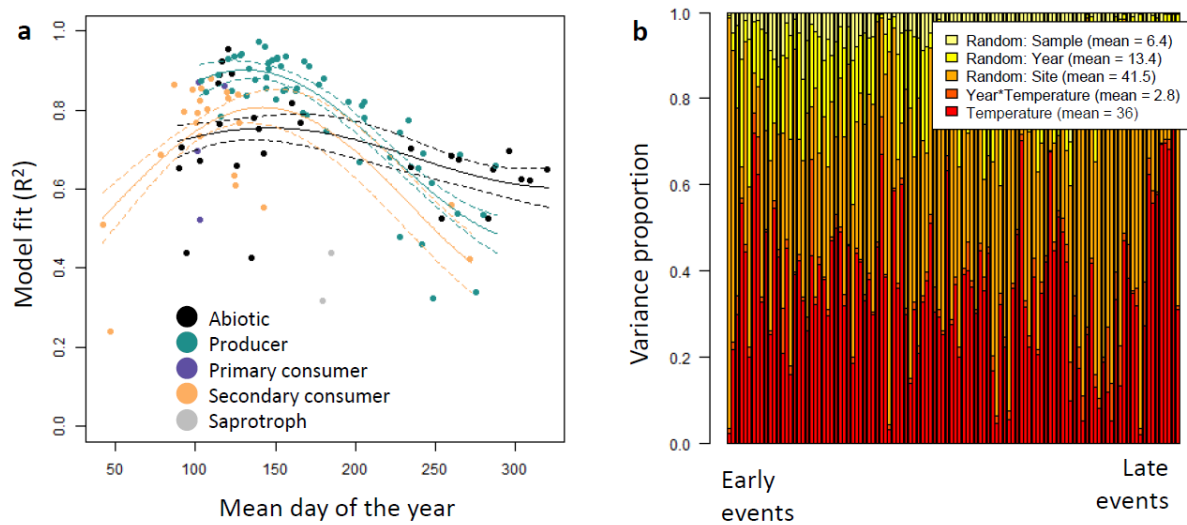
### Mean temperature °C



701

702 **Figure 1. Illustration of the study design and the extent of data.** Individual panels show **top-left:**  
 703 the amount of phenological data per year included in the study; **top and middle:** the spatial  
 704 provenance of data of each type; and **bottom:** mean annual temperature for each sampling location.  
 705 All events were classified into four trophic levels according to the organism expressing the event:  
 706 primary producers (plants), primary consumers (herbivorous insects), secondary consumers  
 707 (predatory insects, amphibians, birds, mammals), and saprotrophs (fungi, as commonly feeding on  
 708 the remains of multiple other levels).

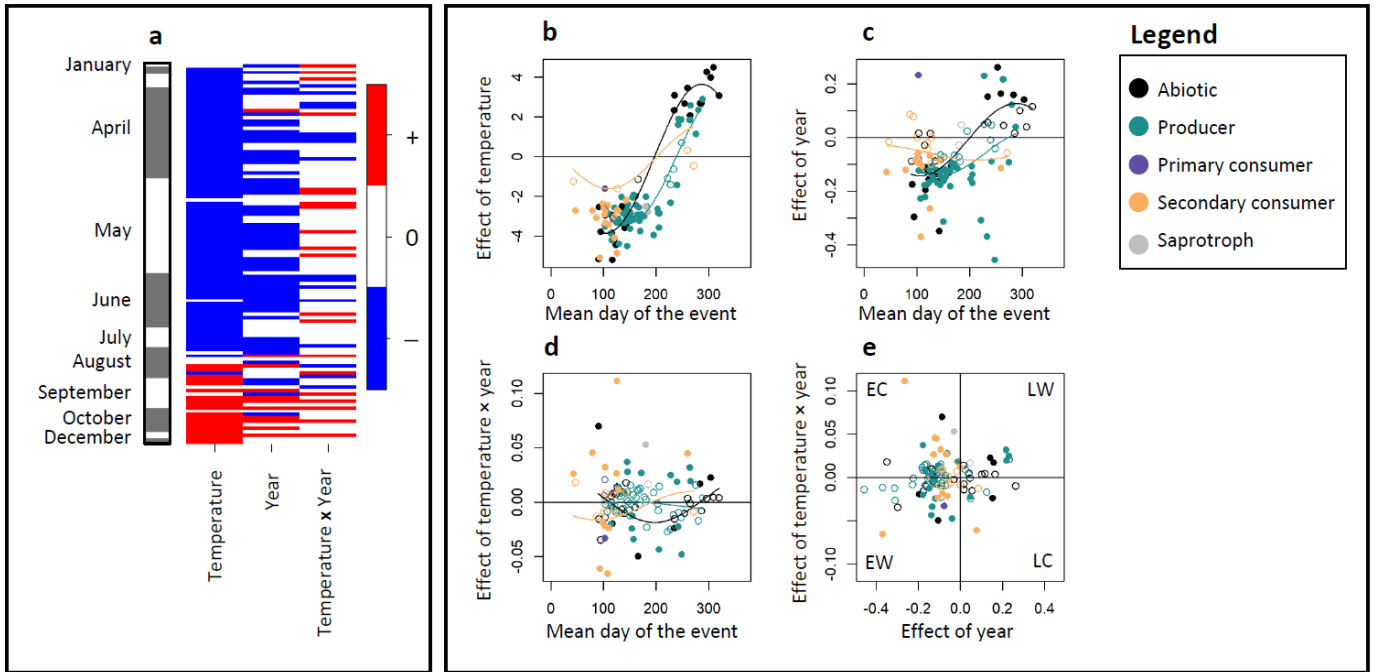
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710

711 **Figure 2. Explanatory power (a) and variance partitioning (b) of the HMSC-model with mean**  
 712 **annual temperature as explanatory variable. a,** Degree of determination ( $R^2$ ) as a function of the  
 713 timing of the event (mean day of the year when the event occurs) and of the trophic level of the  
 714 organism expressing the event (shown by curves in different colours). Here, curves show second-  
 715 order models fitted to groups with at least 5 events; continuous lines show mean model prediction  
 716 and dashed lines  $\pm 1$  standard error. **b,** Partitioning of the overall variance of the data into the  
 717 different model components. Here, individual events have been sorted from the earliest to the latest  
 718 (left to right along abscissa).

719



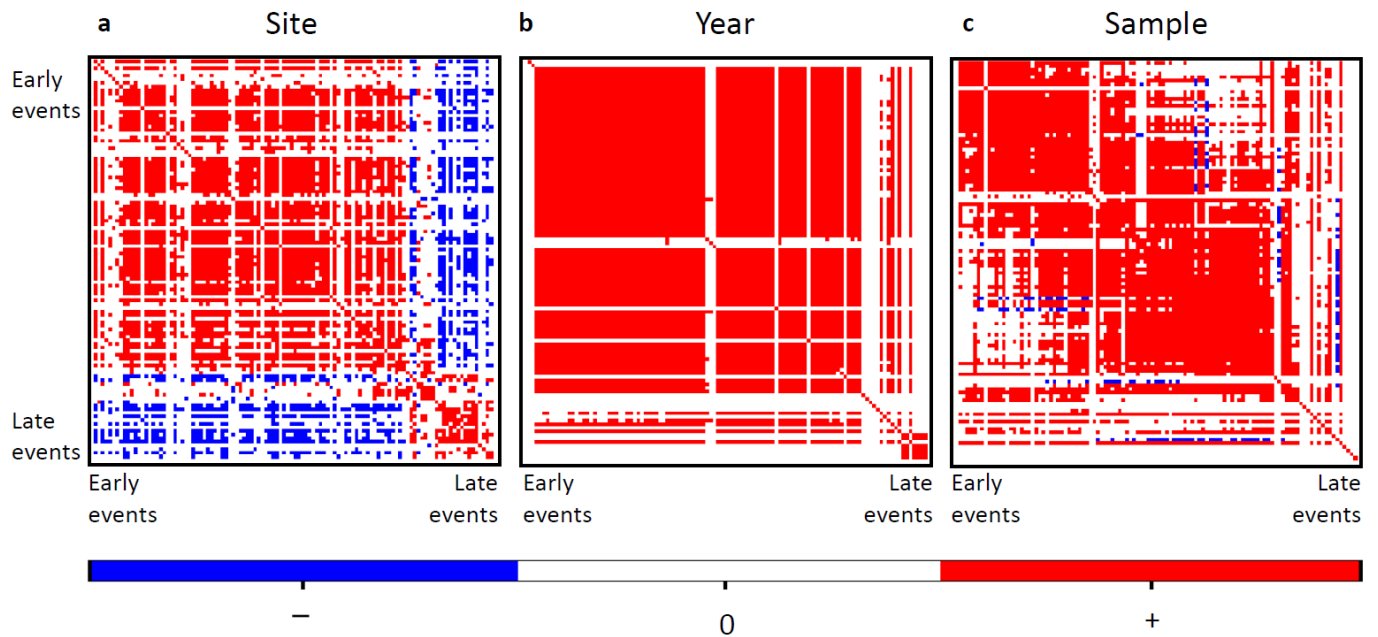
720

721 **Figure 3. Responses of the events to the fixed effects of mean temperature and year. a,** Cases  
 722 for which the response is positive (red) or negative (blue) with at least 95% posterior probability,  
 723 with the events ordered according to their mean date (increasing from top to bottom). The  
 724 covariates year and temperature have been normalized to have zero mean, so the main effect of the  
 725 year relates to a site with average temperature, and the main effect of temperature relates to data  
 726 points collected at the middle of the study period. **b, c, d** Dependency of event-specific responses  
 727 on phenological timing (mean day of the year when the event occurs) and on the trophic level of the  
 728 organism expressing the event (shown by curves in different colours for those groups with at least 5  
 729 events). **e,** Dependency of the response to year x temperature on the response to year. The four  
 730 quadrats correspond to events that have shifted to earlier especially at cold sites (EC), shifted to  
 731 earlier especially at warm sites (EW), shifted to later especially at cold sites (LC), and shifted to  
 732 later especially at warm sites (LW). Filled symbols indicate cases that are either positive or negative  
 733 with at least 95% posterior probability. For the effect of year, we show responses in days per year,  
 734 so that a value of -0.2 represents a shift of two days earlier per decade. For the effect of



735 temperature, the unit is days per degree Celsius, so that a value of -4 means that the event takes  
736 place 8 days earlier in a location with mean temperature 4°C compared to a location with mean  
737 temperature of 2°C.

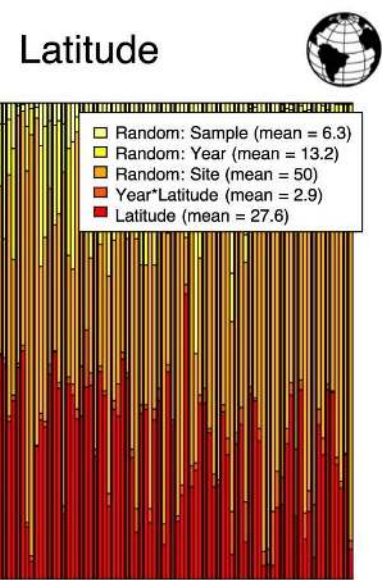
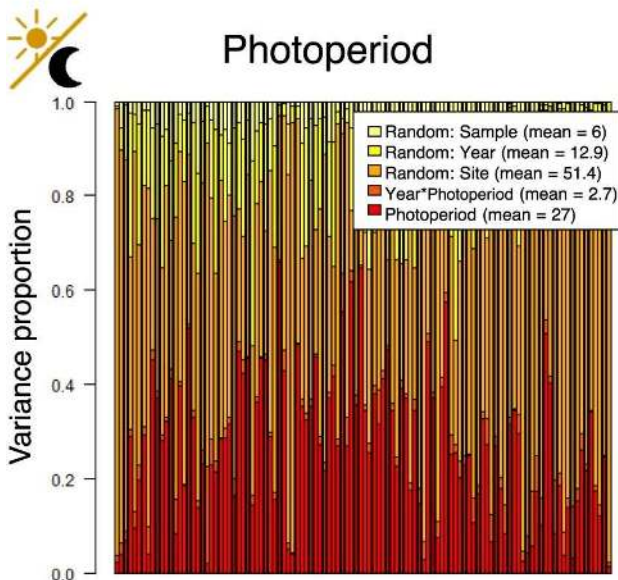
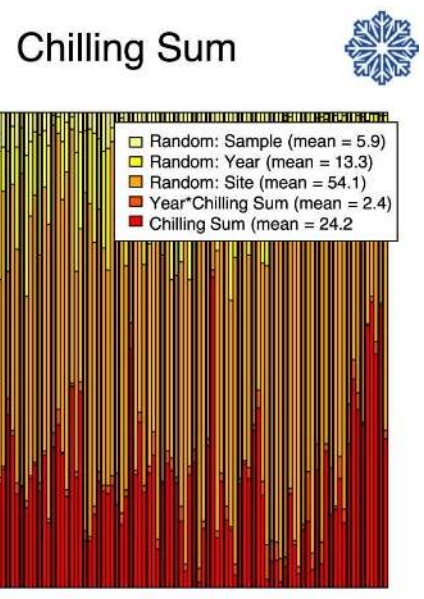
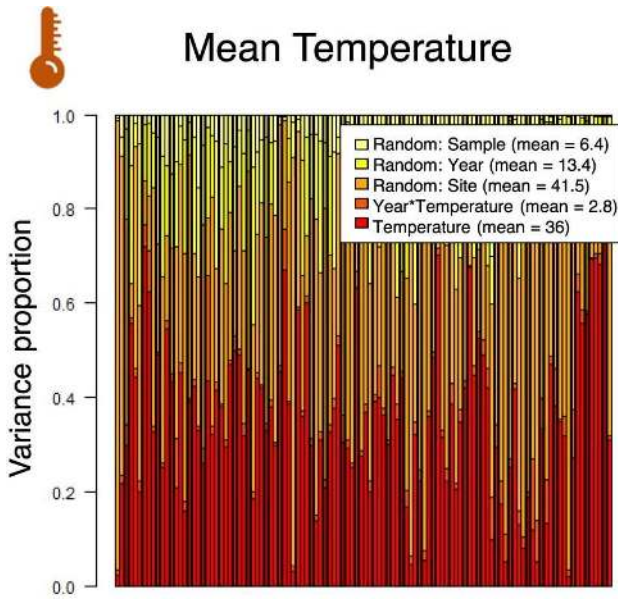
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739

740 **Figure 4. Residual associations among events related to random effects. a,b,c** Associations at  
 741 the level of the site (a), the year (b) and the sample (site $\times$ year; c) The events have been ordered  
 742 according to their mean date (increasing from left to right, and from top to bottom), and estimates of  
 743 events associations are measured by residual correlation. Shown in colour are associations showing  
 744 a positive (red) or negative (blue) association with at least 95% posterior probability, with  
 745 remaining cases indicated in white.

746



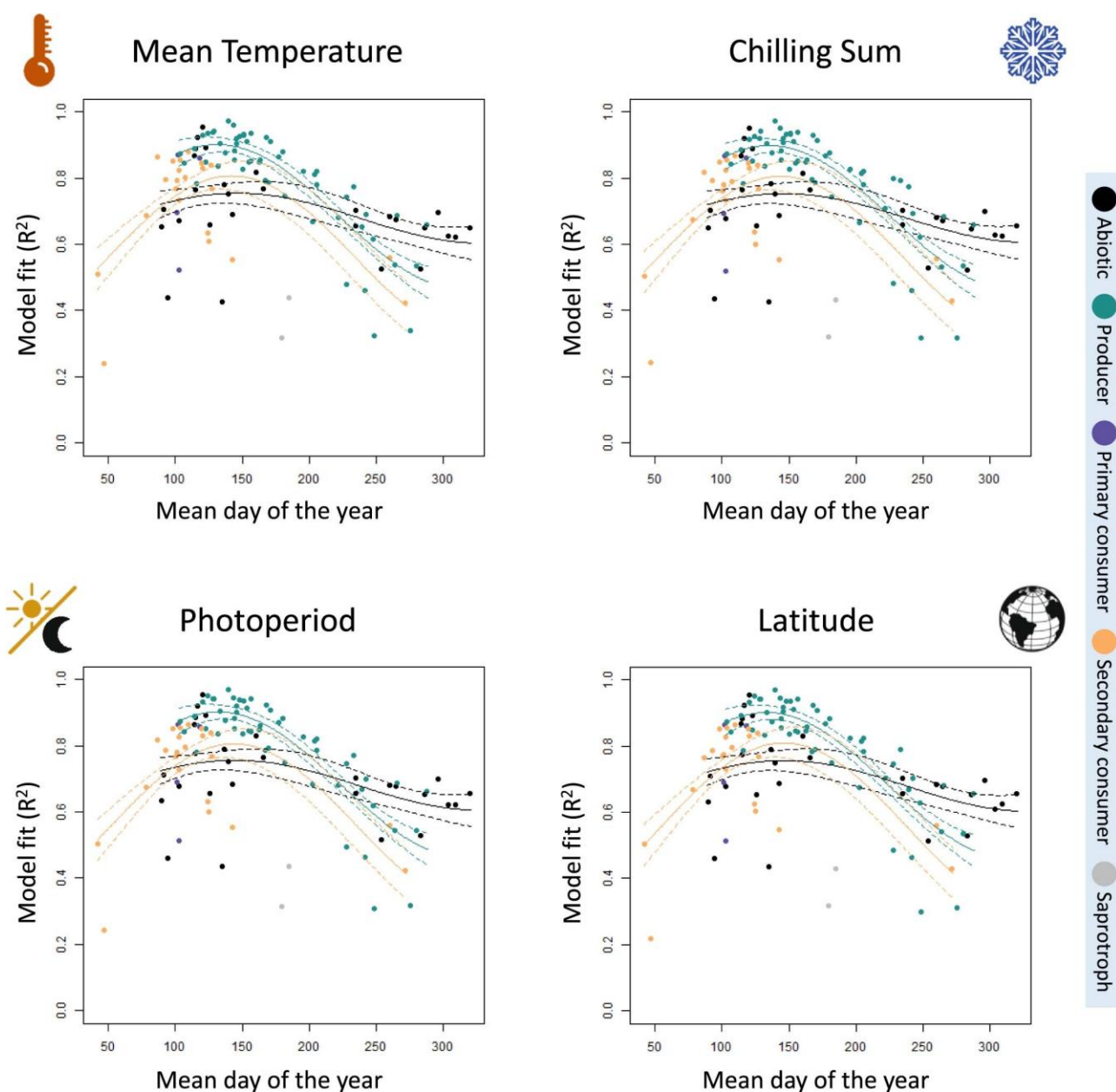
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Early events

Late events

748 **Extended Data Fig. 1: Variance partitioning of alternative HMSC-models.** Plots show the  
 749 partitioning of the overall variance of the data into the model components identified in the figure  
 750 legend. Individual panels show results for models with identical structure but using alternative  
 751 climatic descriptors of the sampling sites; note that the top-left panel corresponds to Fig. 2b of the  
 752 main text. Silhouettes adapted from <https://thenounproject.com>.

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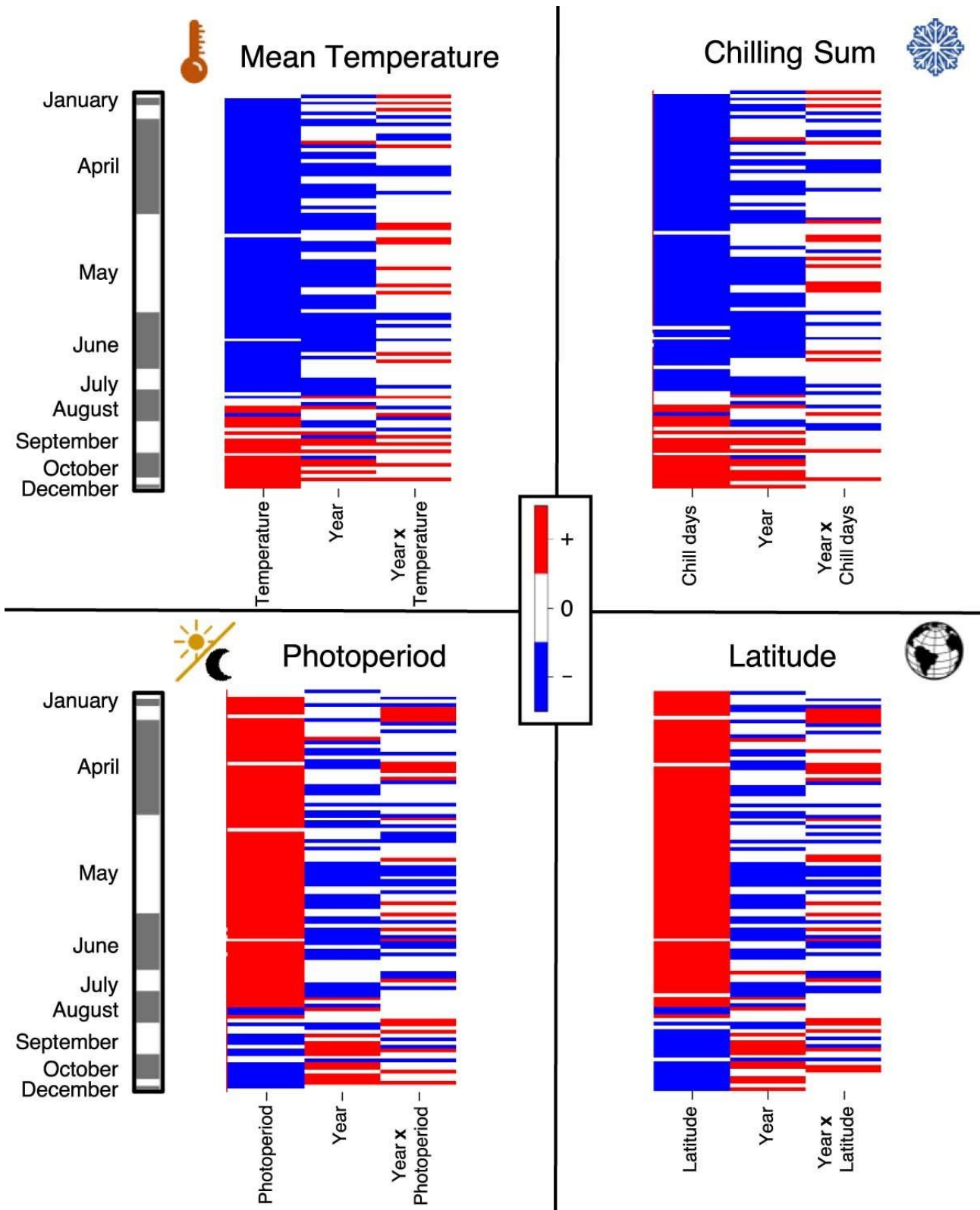
754

755 **Extended Data Fig. 2: Explanatory power of alternative HMSC-models.** Plots show the degree  
 756 of determination ( $R^2$ ) as a function of the timing of the event (mean day of the year when the event  
 757 occurs) and the trophic level of the organism expressing the event (different colours). Curves show  
 758 second-order models fitted to groups with at least 5 events; continuous lines show mean model  
 759 prediction and dashed lines  $\pm$  one standard error. Individual panels show results for models with  
 760 identical structure but using alternative climatic descriptors of the sampling sites; note that the top-

761 left panel corresponds to Fig. 2a of the main text. Silhouettes adapted from

762 <https://thenounproject.com>.

763



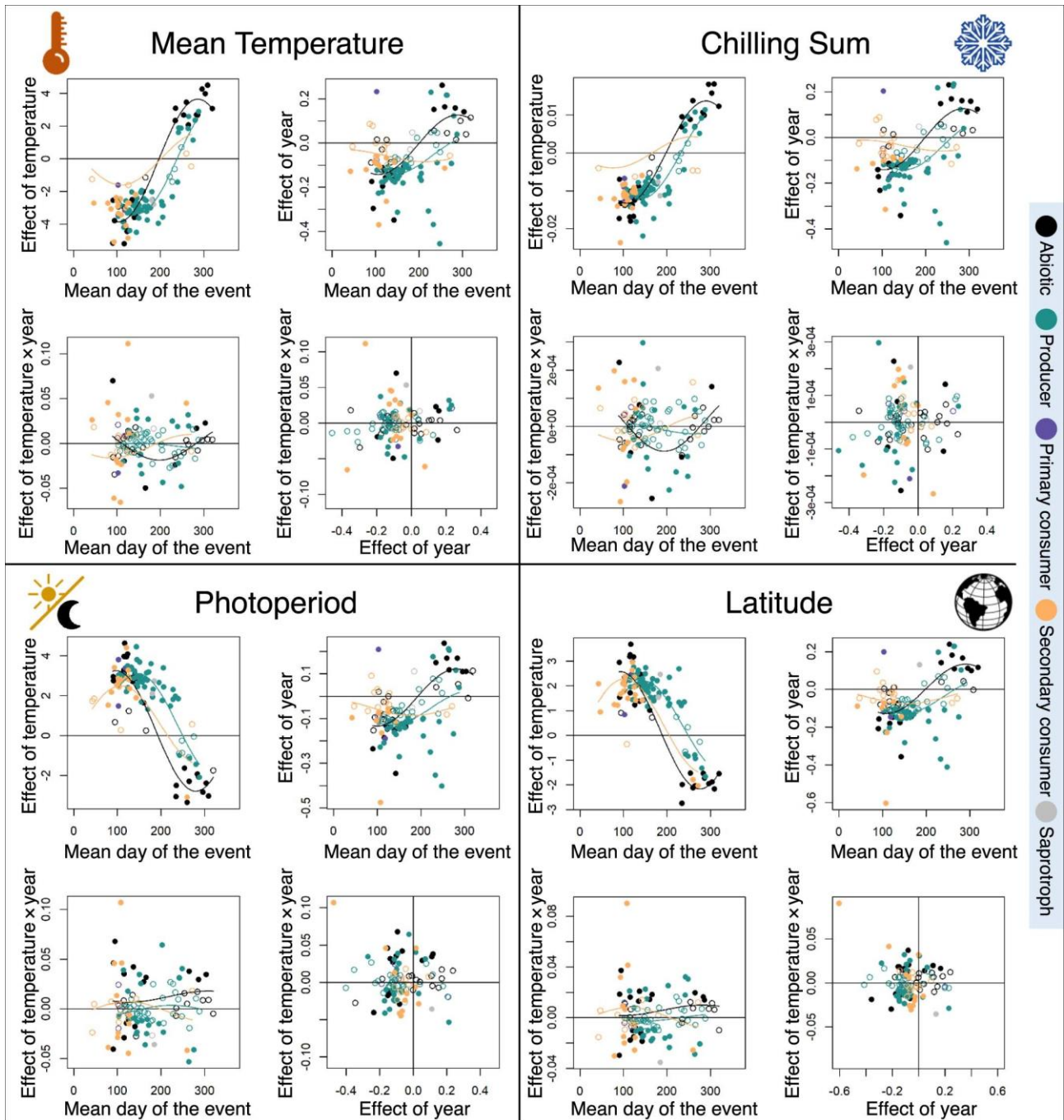
764

765 **Extended Data Fig. 3: The sign of responses of phenological events to the fixed effects**

766 **included in the HMSC model.** Plots show cases for which the response is positive (red) or

767 negative (blue) with at least 95% posterior probability. Events have been ordered according to their  
768 mean date (increasing from top to bottom). The covariates have been normalized to have zero mean,  
769 so that the main effect of the climatic descriptor relates to a data point collected at the middle of the  
770 study period, and the main effect of the year relates to a site with an average value of the climatic  
771 descriptor. Individual panels show results for models with identical structure but using alternative  
772 climatic descriptors of the sampling sites; note that the top-left panel corresponds to Fig. 3a of the  
773 main text. Silhouettes adapted from <https://thenounproject.com>.

774



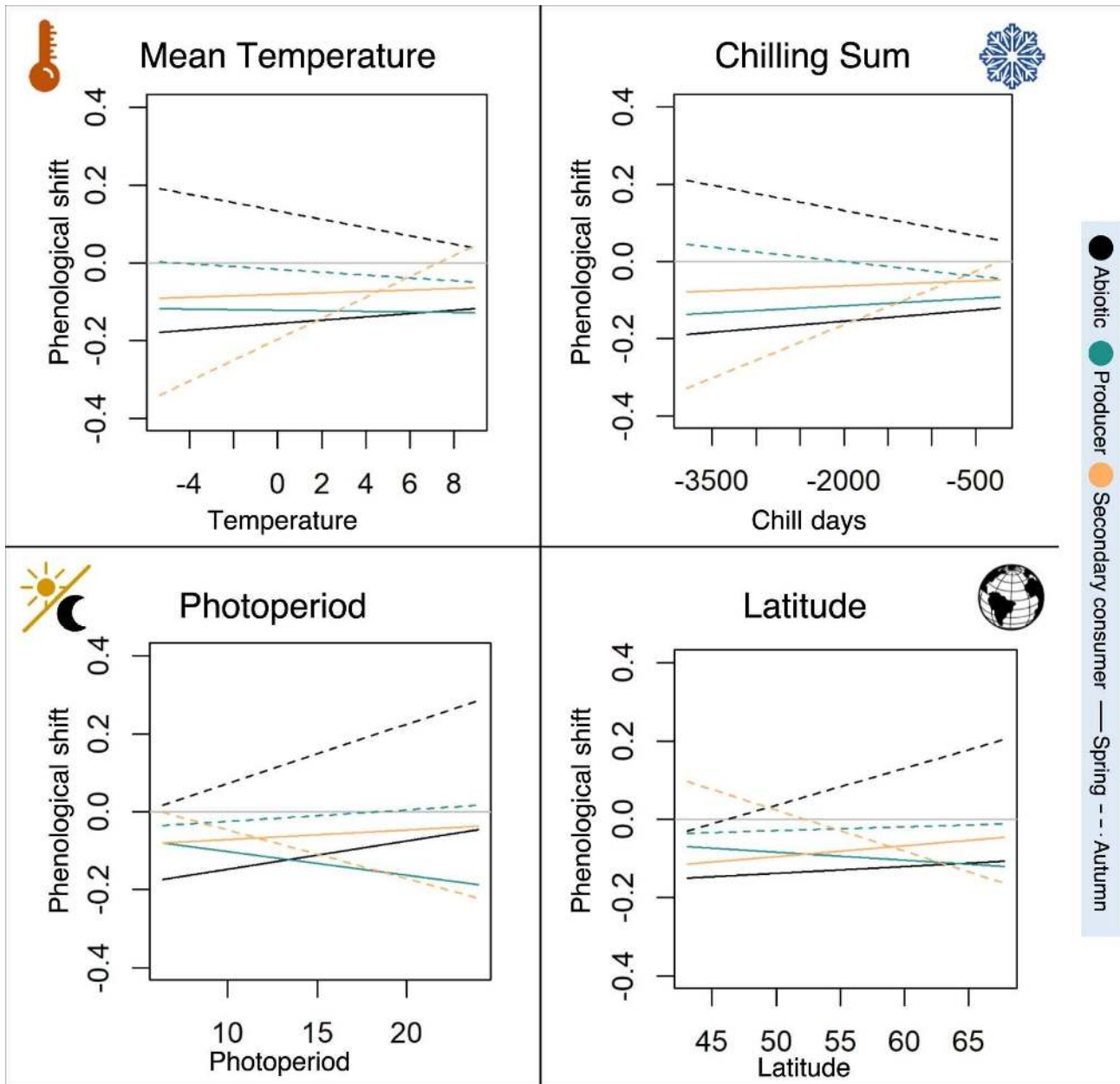
775

776 **Extended Data Fig. 4: Dependency of event-specific responses on phenological timing and on**  
 777 **the trophic level of the organism expressing the event.** Individual sections show results for  
 778 models with identical structure but using alternative climatic descriptors of the sampling sites; note  
 779 that the top-left section corresponds to Fig. 3b–e of the main text. Within each section, that is for  
 780 each model, individual panels show the dependency of event-specific responses on phenological



781 timing (mean day of the year when the event occurs) and on the trophic level of the organism  
782 expressing the event (shown by curves in different colours for those groups with at least 5 events).  
783 The covariates have been normalized to have zero mean, so that the main effect of the climatic  
784 descriptor relates to a data point collected at the middle of the study period, and the main effect of  
785 the year relates to a site with an average value of the climatic descriptor. In the bottom-right figure  
786 within each quadrat, we show the dependency of the response to year  $\times$  temperature on the response  
787 to year; here, the four quadrats within the panel correspond to events that have shifted to earlier  
788 especially at cold sites (EC), shifted to earlier especially at warm sites (EW), shifted to later  
789 especially at cold sites (LC), and shifted to later especially at warm sites (LW). Filled symbols  
790 indicate cases that are either positive or negative with at least 95% posterior probability. Silhouettes  
791 adapted from <https://thenounproject.com>.

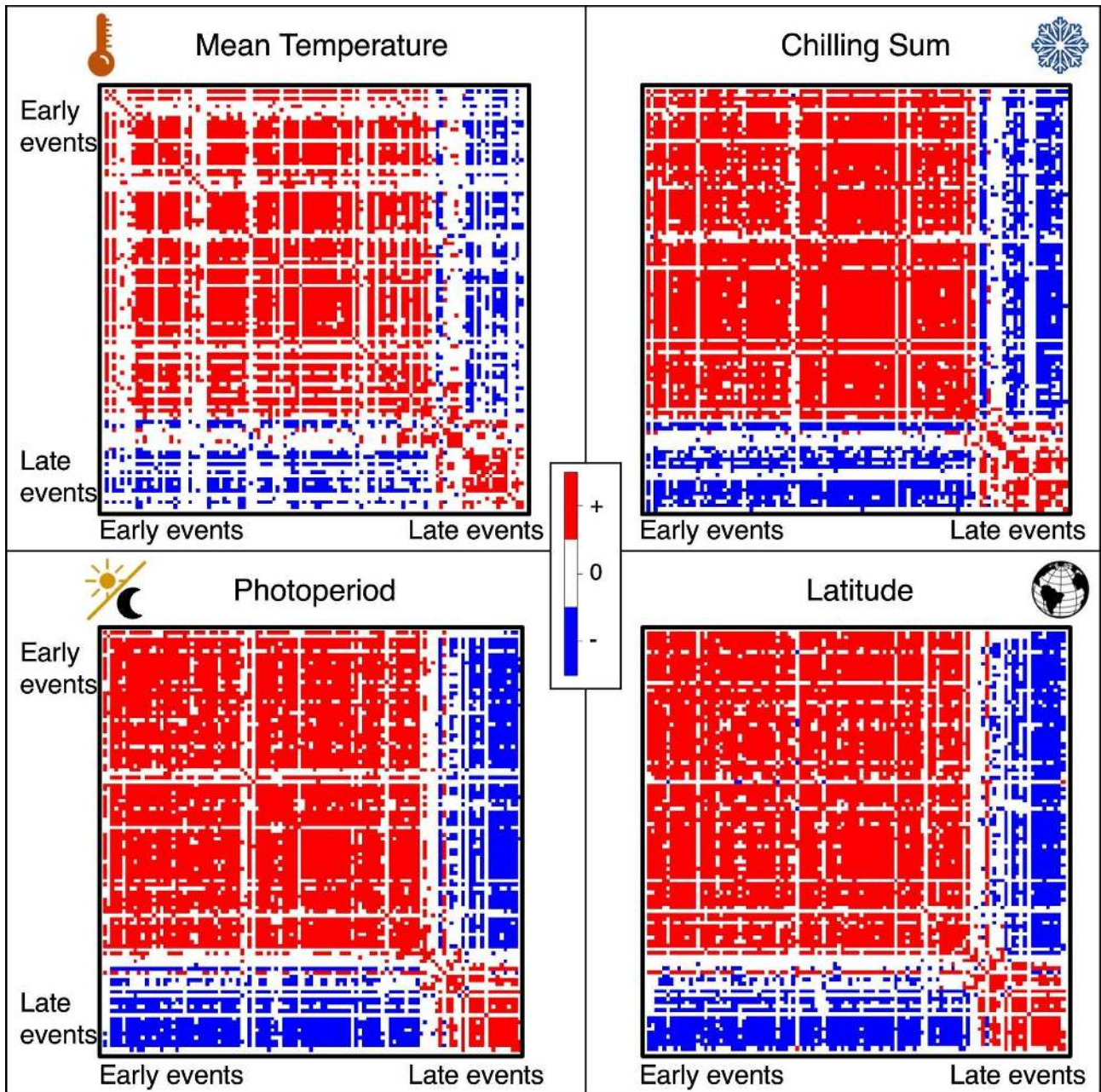
792



793

794 **Extended Data Fig. 5: Estimated shift in the phenological timing of events occurring in the**  
 795 **spring versus autumn as functions of the average climate descriptors of the site.** Plots show the  
 796 estimated shift in the phenological timing (days per year) among events occurring in the spring  
 797 (solid line, showing predictions for Day of Year (DOY) 100, that is April 10) versus autumn (dotted  
 798 line, showing DOY250, that is September 7), plotted against the average climate descriptors of the  
 799 site. The colours of the lines identify the trophic level of the organism expressing the event.

800 Silhouettes adapted from <https://thenounproject.com>.

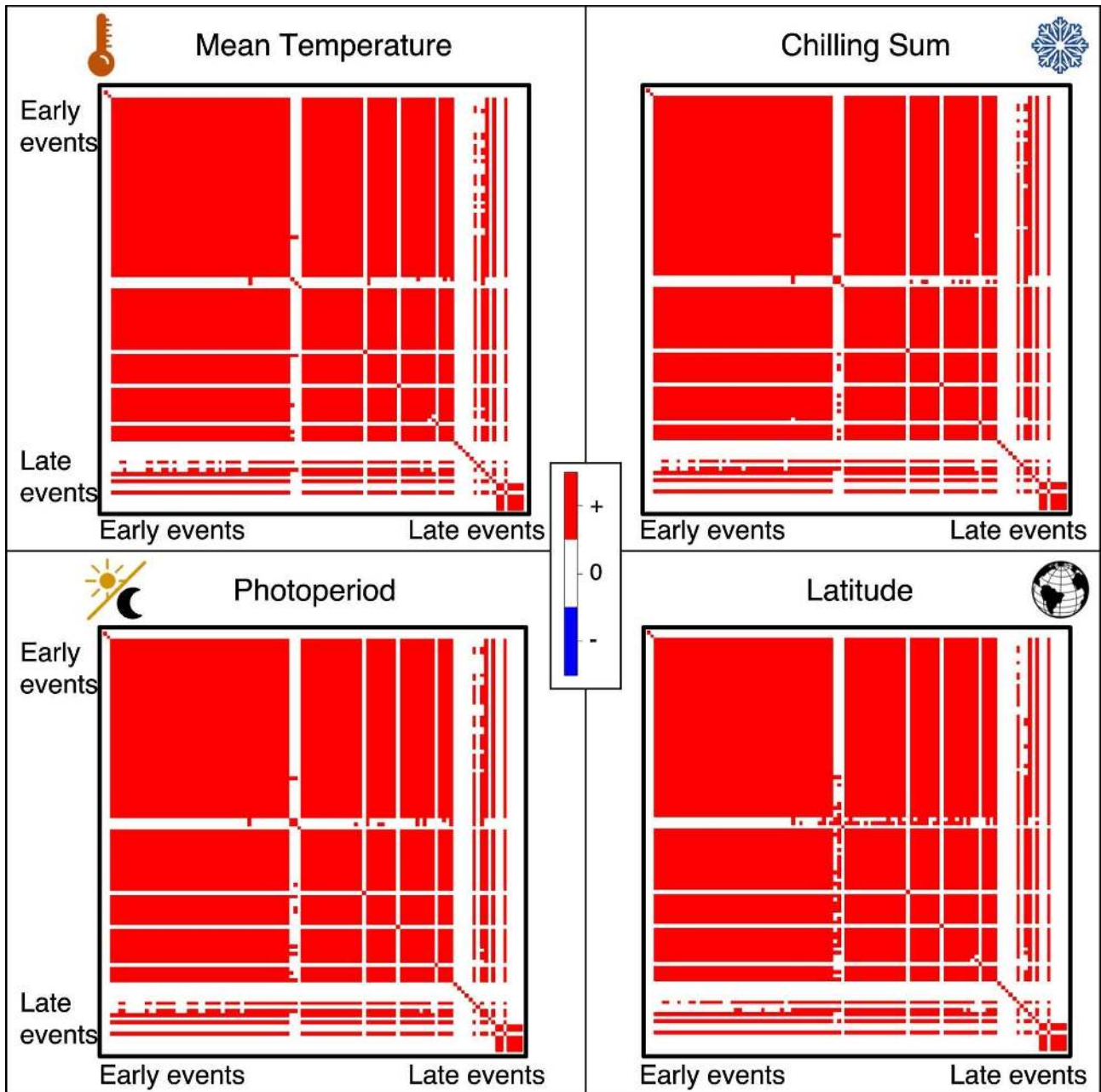


801

802 **Extended Data Fig. 6: Residual associations among events related to the random effects of the**  
 803 **site.** Plots show the estimates of associations among events measured by residual correlation at the  
 804 site level. The events have been ordered according to their mean date (increasing from left to right,  
 805 and from top to bottom). Event-to-event association matrices identify pairs showing a positive (red)  
 806 or negative (blue) association, shown only if association has either sign with at least 95% posterior

807 probability (the remaining cases are shown in white). Note that the top-left panel corresponds to  
808 Fig. 4a of the main text. Silhouettes adapted from <https://thenounproject.com>.

809

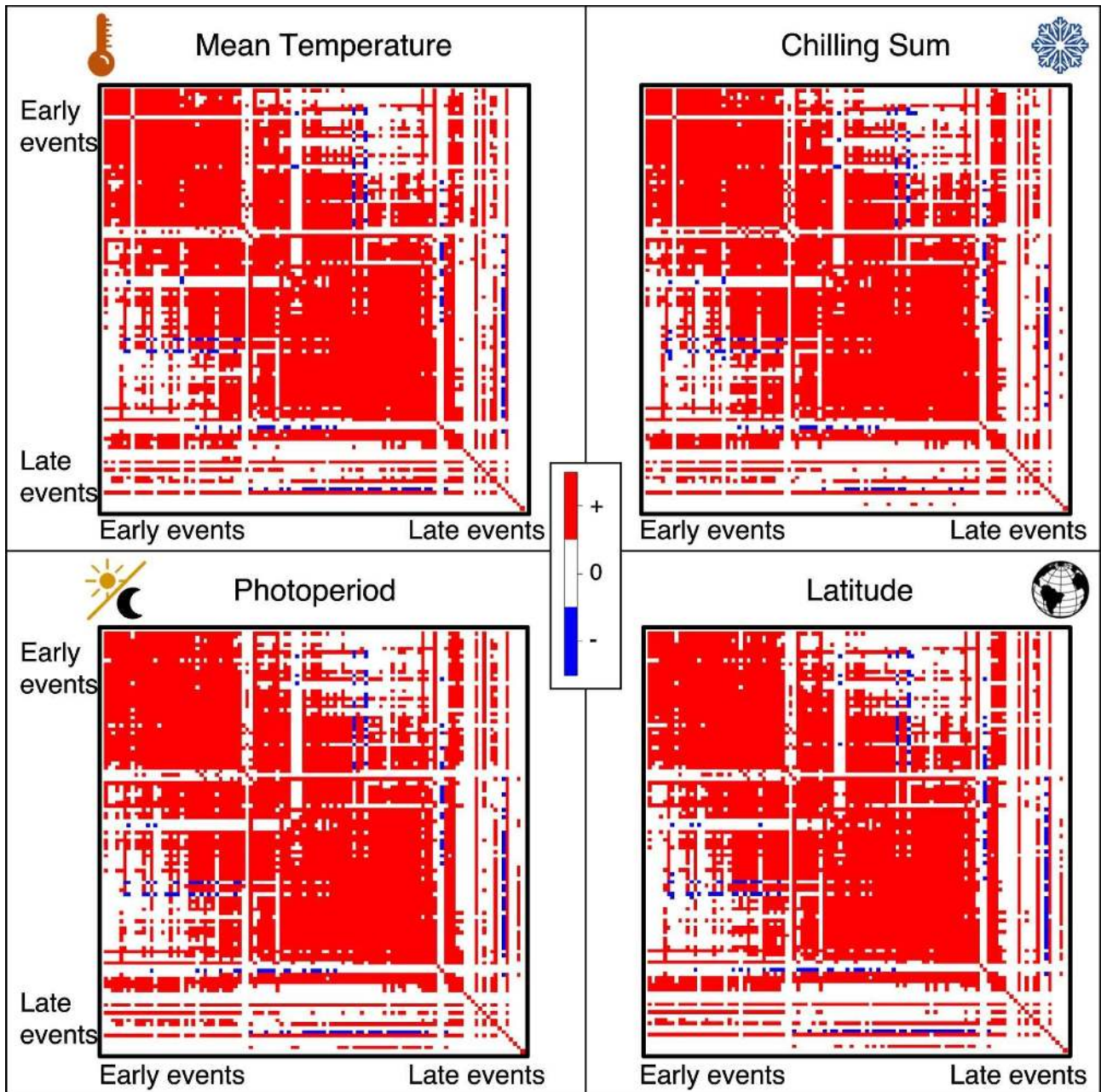


810

811 **Extended Data Fig. 7: Residual associations among events related to the random effects of the**  
 812 **year.** Plots show the estimates of associations between events measured by residual correlation at  
 813 the year level. The events have been ordered according to their mean date (increasing from left to  
 814 right, and from top to bottom). Event-to-event association matrices identify pairs showing a positive  
 815 (red) or negative (blue) association, shown only if association has either sign with at least 95%

816 posterior probability (the remaining cases are shown in white). Note that the top-left panel  
817 corresponds to Fig. 4b of the main text. Silhouettes adapted from <https://thenounproject.com>.

818



819

820 **Extended Data Fig. 8: Residual associations among events related to the random effects of the**  
 821 **year-site pair.** Plots show the estimates of associations among events measured by residual  
 822 correlation at the level of samples, that is year×site combinations. The events have been ordered  
 823 according to their mean date (increasing from left to right, and from top to bottom). Event-to-event  
 824 association matrices identify pairs showing a positive (red) or negative (blue) association, shown  
 825 only if association has either sign with at least 95% posterior probability (the remaining cases are

826 shown in white). Note that the top-left panel corresponds to Fig. 4c of the main text. Silhouettes  
827 adapted from <https://thenounproject.com>.



# Supporting online material for Phenological shifts of abiotic events, producers and consumers across a continent

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# Text S1. Classification of phenological events

All events were classified into four trophic levels according to the organism expressing the event: primary producers (plants), primary consumers (herbivorous insects) and secondary consumers (predatory insects, amphibians, birds, mammals). Saprotrophs (fungi) were included as a separate level, as commonly feeding on the remains of multiple other levels, and abiotic events as a separate category. Species classification was based on the basic biology of the juvenile stage. For holometabolous organisms (such as insects undergoing full metamorphosis), the juvenile stage is typically the one consuming the most resources for growth, and the same applies for birds. Specifically, in classifying all birds as secondary consumers, we note that while some species may be mainly herbivorous as adults, their young are dependent on protein-rich arthropods for growth<sup>1</sup>. Since we expect breeding-time resources to be more decisive for these species' phenology than the needs of the adults, we have used the diet of the young for our trophic classification.

**Table S1. Classification of events by taxonomic and trophic position**

The table shows the identity of the species and events included in the analyses, with their taxonomic position, trophic level and relative timing (here expressed as the mean Day of the Year when the phenological event first occurred; mean DOY).

Taxon (+ meteo events)	Trophic level	Event scored	Mean DOY
<b>AVES</b>			
<b>Alaudidae</b>			
<i>Alauda arvensis</i>	Secondary consumer	1st song*	93.14
<b>Anatidae</b>			
<i>Anas crecca</i>	Secondary consumer	1st occurrence	119.73
<i>Anas platyrhynchos</i>	Secondary consumer	1st occurrence*	101.64
<i>Cygnus cygnus</i>	Secondary consumer	1st occurrence	107.42
<i>Bucephala clangula</i>	Secondary consumer	1st occurrence	109.81
<b>Apodidae</b>			
<i>Apus apus</i>	Secondary consumer	1st occurrence*	142.78
<b>Charadriidae</b>			
<i>Vanellus vanellus</i>	Secondary consumer	1st occurrence	100.43
<b>Corvidae</b>			
<i>Corvus frugilegus</i>	Secondary consumer	1st occurrence	78.54
<b>Cuculidae</b>			
<i>Cuculus canorus</i>	Secondary consumer	1st song*	127.64
<b>Fringillidae</b>			
<i>Fringilla coelebs</i>	Secondary consumer	1st occurrence*	98.12
<b>Gruidae</b>			
<i>Grus grus</i>	Secondary consumer	1st occurrence	103.00
<b>Hirundinidae</b>			
<i>Hirundo rustica</i>	Secondary consumer	1st occurrence*	124.57
		Last occurrence	259.44
<b>Motacillidae</b>			
<i>Motacilla alba</i>	Secondary consumer	1st occurrence*	103.11
		Last occurrence	271.23

<b>Muscicapidae</b>			
<i>Luscinia luscinia</i>	Secondary consumer	1st song	125.15
<b>Paridae</b>			
<i>Parus major</i>	Secondary consumer	1st song	42.33
<b>Picidae</b>			
<i>Dendrocopos major</i>	Secondary consumer	Start of drumming	46.91
<b>Sturnidae</b>			
<i>Sturnus vulgaris</i>	Secondary consumer	1st occurrence	86.51
<b>FUNGUS</b>			
<b>Boletaceae</b>			
<i>Leccinum aurantiacum</i>	Saprotroph	1st occurrence	179.67
<i>Leccinum scabrum</i>	Saprotroph	1st occurrence	184.60
<b>INSECTA</b>			
<b>Apidae</b>			
<i>Bombus sp</i>	Primary consumer	1st occurrence	118.04
<b>Culicidae</b>			
<i>Culicidae sp</i>	Secondary consumer	1st occurrence	126.78
<b>Formicidae</b>			
<i>Formica rufa</i>	Secondary consumer	Livening up	103.83
<b>Nymphalidae</b>			
<i>Aglais urticae</i>	Primary consumer	1st occurrence	101.22
<b>Pieridae</b>			
<i>Gonepteryx rhamni</i>	Primary consumer	1st occurrence	102.30
<b>MAMMALIA</b>			
<b>Ursidae</b>			
<i>Ursus arctos</i>	Secondary consumer	Awakening	102.49
<b>PLANTAE</b>			
<b>Asparagaceae</b>			
<i>Convallaria majalis</i>	Producer	Onset of blooming	144.47
<i>Maianthemum bifolium</i>	Producer	Onset of blooming	167.92
<b>Astaraceae</b>			
<i>Leucanthemum vulgare</i>	Producer	Onset of blooming	169.79
<i>Taraxacum officinale</i>	Producer	Onset of blooming	131.87
<i>Tussilago farfara</i>	Producer	Onset of blooming	106.95
<b>Betulaceae</b>			
<i>Betula pendula</i>	Producer	Onset of sap bleeding	103.36
		Onset of budburst	120.20
		Onset of leaf unfolding	128.36
		Onset of autumn colouring	242.07
		Onset of leaf fall	247.69
		Full autumn colouring of leaves	264.94
		Leaf fall end	287.69
<b>Caprifoliaceae</b>			
<i>Lonicera caerulea</i>		Onset of blooming	150.41
<b>Ericaceae</b>			
<i>Oxycoccus palustris</i>	Producer	Onset of blooming*	163.29
<i>Ledum palustre</i>	Producer	Onset of blooming	156.75
<i>Vaccinium myrtillus</i>	Producer	Onset of blooming	145.35

		Onset of fruiting (ripe)*	195.23
		Mass fruiting	204.14
<i>Vaccinium vitis-idaea</i>	Producer	Onset of blooming*	162.31
		Onset of fruiting (ripe)	227.44
		Mass fruiting	239.47
<b>Fabaceae</b>			
<i>Caragana arborescens</i>	Producer	Onset of blooming	148.28
<b>Grossulariaceae</b>			
<i>Ribes nigrum</i>	Producer	Onset of blooming*	145.99
		Onset of fruiting (ripe)	205.27
<b>Malvaceae</b>			
<i>Tilia cordata</i>	Producer	Onset of leaf unfolding	129.07
		Onset of blooming*	181.85
<b>Oleaceae</b>			
<i>Syringa vulgaris</i>	Producer	Onset of blooming	150.87
<b>Onagraceae</b>			
<i>Epilobium angustifolium</i>	Producer	Onset of blooming	180.06
<b>Pinaceae</b>			
<i>Pinus sylvestris</i>	Producer	onset of blooming*	153.18
<b>Ranunculaceae</b>			
<i>Caltha palustris</i>	Producer	Onset of blooming	133.70
<i>Trollius europaeus</i>	Producer	Onset of blooming	150.87
<b>Rosaceae</b>			
<i>Fragaria vesca</i>	Producer	Onset of blooming*	144.48
		Onset of fruiting (ripe)	176.94
<i>Prunus padus</i>	Producer	Onset of budburst	114.10
		Onset of leaf unfolding	124.06
		Onset of blooming*	139.22
		Onset of mass blooming	143.10
		Onset of fruiting (ripe)	202.32
		Onset of autumn colouring	221.38
		Onset of leaf fall	232.95
		Leaf fall end	275.01
<i>Rosa acicularis</i>	Producer	Onset of blooming	171.34
<i>Rubus chamaemorus</i>	Producer	Onset of blooming*	154.64
<i>Rubus idaeus</i>	Producer	Onset of blooming*	166.83
		Onset of fruiting (ripe)	205.81
<i>Sorbus aucuparia</i>	Producer	Onset of blooming*	156.06
		Onset of fruiting (ripe)	227.55
<b>Salicaceae</b>			
<i>Salix caprea</i>	Producer	Onset of blooming*	123.08
<i>Populus tremula</i>	Producer	Onset of blooming	115.70
		Onset of leaf unfolding	137.18
		Onset of autumn colouring	241.60
		Onset of leaf fall	248.20
		Full autumn colouring of leaves	263.45
		Leaf fall end	280.00
<b>REPTILIA</b>			
<b>Squamata</b>			
<i>Zootoca vivipara</i>	Secondary consumer	1st occurrence	120.50
<b>METEO</b>			



Thaw		1st thawed patches to an earth surface around trunks of trees	90.00
		1st thawed patches on open places	103.11
Temperature		Daily average air temperature - transition above 0	91.23
		Daily average air temperature - transition above +5	115.19
		Daily average air temperature - transition above +10	136.45
		Frost; last	139.86
		Frost; soil; last	142.44
		Daily average air temperature - transition above +15	160.29
		Daily minimal air temperature - transition above +10	165.44
		Daily average air temperature - transition more low +15	234.26
		Daily minimal air temperature - transition more low +10	234.83
		Frost; soil; 1st	253.34
		Frost; 1st	259.51
		Daily average air temperature - transition more low +10	264.52
		Daily average air temperature - transition more low +5	285.69
		Daily average air temperature - transition more low 0	303.48
	Snow		Snow cover melted
		Snow cover melted; open spaces	115.25
		Snow cover melted; forest	123.08
		Snowfall; last	125.66
		Snow cover formation; 1st	295.66
		Snow cover formation; permanent	308.57
		Snowfall; 1st	283.16
Ice		Ice cover melting; breakup	116.33
		Ice cover melted	120.27
		Ice formation; definitive	319.39
Others		Rain; 1st	94.58
		Thunderstorm; 1st	134.92

## Text S2. Description of the HMSC model

Hierarchical Modelling of Species Communities (HMSC) is a multivariate generalized linear mixed modelling framework<sup>2,3</sup>. HMSC was primarily developed for community ecology, so that in a typical application the response matrix ( $\mathbf{Y}$ ) contains species occurrences or abundances on a set of sampling units (e.g. spatial locations), the environmental predictor matrix ( $\mathbf{X}$ ) contains e.g. climatic conditions in those sampling units, and the species trait matrix ( $\mathbf{T}$ ) includes species-level traits such as body size. HMSC allows to ask how species occurrences depend on environmental conditions (how  $\mathbf{Y}$  depends on  $\mathbf{X}$ ), and how the species responses to environmental variation depend on their traits (how  $\mathbf{T}$  modulates the mapping from  $\mathbf{X}$  to  $\mathbf{Y}$ ). Additionally, HMSC includes community-level random effects implemented through latent variables; these allow the modelling of residual (not accounted for species responses to  $\mathbf{X}$ ) species associations at different spatiotemporal levels.

Here, we apply HMSC to phenological data, so that instead of species occurrences we include in the response matrix  $\mathbf{Y}$  the dates of the phenological events. In other words, phenological events (e.g. the first arrival of a given bird species) here play the role of “species”. In the predictor matrix  $\mathbf{X}$ , we include the climatic conditions of the study locations, as well as the year of the observation, with the latter capturing the trends over time that are the main focus of this paper. In the species trait matrix  $\mathbf{T}$ , we include key characteristics of the phenological events: the mean timing of the event (e.g. to distinguish spring events from autumn events), and the type of event (e.g. to distinguish abiotic from biotic events).

We call a given site-year pair as “sampling unit”, and denote by  $y_{ij}$  the date at which the phenological event  $j$  took place in sampling unit  $i$ . Each data point is then the vector  $y_i$ , where the dot notation stands for the vector of  $y_{ij}$  values for all indices  $j$ , thus  $y_i$  consisting of the dates at which all phenological events took place for the site-year pair  $i$ . We modelled the data with the multivariate hierarchical linear mixed model defined as:

$$y_{ij} = \sum_k x_{ik} \beta_{kj} + a_{s(i)j} + b_{t(i)j} + c_{ij} + \varepsilon_{ij}.$$

- Concerning the fixed effects,  $\beta_{kj}$  is the effect of the covariate  $k$  on the phenological event  $j$ . The covariates included for each sampling unit  $i$  were the year, the climatic descriptor of the site, and the interaction between these two. Additionally the model includes the intercept, so  $x_{1i} = 1$  for all  $i$ .
- Concerning the community-level random effects,  $s(i)$  denotes the site and  $t(i)$  denotes the year of the sampling unit  $i$ . Thus  $a_{s(i)j}$  is the random effect of the site,  $b_{t(i)j}$  is the random effect of the year, and  $c_{ij}$  is the random effect of the sampling unit. Each of these is modelled through the latent variable model described in detail in <sup>2</sup>, so that e.g.  $a_{sj} = \sum_{h=1}^{n_f^s} \lambda_{hj}^s \eta_{hs}^s$ , where  $n_f^s$  is the number of factors included at the site level (as indicated by the superscript  $s$ ),  $\eta_{sk}^s$  is the latent variable  $k$  for site  $s$ , and  $\lambda_{kj}^s$  is the loading of phenological event  $j$  for factor  $k$ . We note that the association matrix among the phenological events can be constructed from the loadings  $\lambda_{kj}^s$  as  $\Omega_{j_1 j_2}^s = \sum_{h=1}^{n_f^s} \lambda_{h j_1}^s \lambda_{h j_2}^s$ ; see <sup>2</sup>.
- Concerning the residual, we assume a linear model, so  $\varepsilon_{ij} \sim N(0, \sigma_j^2)$ , where  $\sigma_j^2$  is the residual variance of phenological event  $j$ .

The responses of the phenological events to the covariates were further modelled with a linear regression, using the traits of the events as predictors. The expected response  $\mu_{kj} = E[\beta_{kj}]$  was modelled as  $\mu_{kj} = \sum_l t_{jl} \gamma_{kl}$  and the realized response with the multivariate normal model as

$\beta_{.j} \sim N(\mu_{k.}, \mathbf{V})$ . As the trait predictors  $t_{jh}$ , we included the intercept, the mean day of the phenological event, the type of the phenological event, and the interaction between them. To account for the periodic nature of the day of the year, the mean day of the phenological event  $d$  was modelled with the predictors  $\cos(2\pi d/356)$  and  $\sin(2\pi d/356)$ . The type of event was implemented as a factor, with the levels of abiotic events, producers, primary consumers, secondary consumers, and saprotrophs.

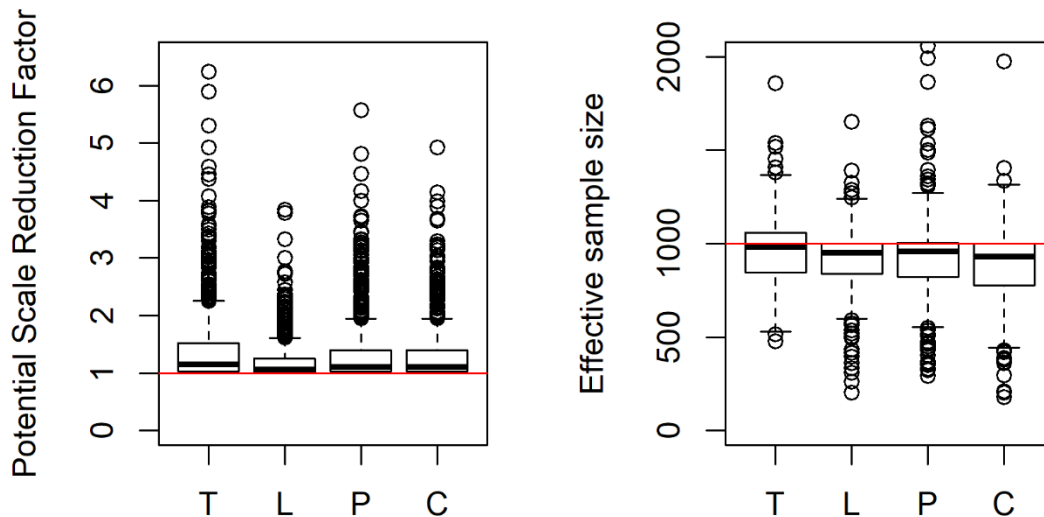
We fitted the models with R-package `Hmsc`<sup>4</sup> assuming the default prior distribution. For a technical description of the default prior distribution we refer to <sup>4</sup>, whereas for an ecological motivation of the default prior distribution we refer to <sup>2</sup>. We performed posterior sampling for four Markov Chain Monte Carlo (MCMC) chains, each of which we sampled for 375,000 iterations, out of which we discarded the first 125,000 as a transient and thinned the remaining by 1000, thus yielding 250 samples per chain and 1000 samples in total. To evaluate MCMC convergence, we examined the distributions of the potential scale reduction factor over the parameters related to the fixed effects ( $\beta$  –parameters) and the random effects ( $\Omega$ -parameters), equivalent to the Gelman-Rubin statistic<sup>5</sup>.

# Text S3. Convergence of the Markov chain Monte Carlo (MCMC) scheme used for posterior sampling

For each model we obtained 250 samples for each of the four MCMC chains, and thus in total 1000 samples. The 250 samples for each chain were obtained by running the MCMC for  $375 \times \text{thin}$  iterations, out of which  $125 \times \text{thin}$  were discarded as transient, and the remaining  $250 \times \text{thin}$  iterations were then evenly thinned to yield 250 samples. We applied  $\text{thin}=1, 10, 100, 1000$  to check which level of thinning was sufficient to ensure satisfactory convergence. We assessed MCMC convergence by computing the effective number of samples and the potential scale reduction factor. These are shown in Fig. S3 for the beta-parameters of the HMSC model<sup>4</sup>, which parameters measure the responses of the species to the included covariates. As the majority of the potential scale reduction factors are close to one and the effective sample size is close to the actual sample size of 1000, we conclude the MCMC convergence was satisfactory.

## Figure S1. MCMC convergence statistics, measured as potential scale reduction factors and effective sample sizes.

Each boxplot shows the distribution of values over the species-specific beta-parameters for models that include the mean annual temperature (T), latitude (L), photoperiod (P) or chilling sum (C) as the climatic predictor.



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