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

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

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

Climate change is restructuring biodiversity across the globe[1]. Among key responses to spatial and seasonal changes in ambient temperature are changes in phenology[2,3]—that is, changes in season-related life cycle events. At mid to high latitudes in the Northern Hemisphere, spring events are generally occurring earlier, whereas autumn events are occurring later, mostly due to rising temperatures[2,4]. Overall, responses are expected to be faster and more pronounced the higher the latitude or elevation, that is, the lower the average temperatures[5–7].

Despite rough consensus regarding these general trends and expectations, there are substantial differences in the observed magnitude and direction of phenological responses to climate change among individual species[8–10], different taxonomic groups and trophic levels[3,11,12]. Where spring phenology in terrestrial areas has advanced by a global average of 2.3 to 2.8 days per decade[2,8,13], some studies have suggested changes as fast as 30 days per decade[14]. Higher rates of advance are possibly associated with lower trophic levels[3,12], perhaps reflecting not only different sensitivity to different drivers among trophic layers, but also varying responses in terms of physiological development[3]. Another factor that may accelerate phenological advance relates to the mean timing of an event within the season: spring-time events may be advancing at higher rates than autumn events[2,4]. On top of species–specific variation, there is also considerable site-specific variation in phenological advance[15,16]. Such variation among sites and populations may arise from a combination of factors, including changes in temperature and other climatic variables, population sizes, genetic differences, phenotypic plasticity and land use[16,17].

A general reason for variability in phenological responses is that patterns of climate change vary substantially across the globe. As the climate of different regions and biomes is changing in somewhat different ways[5], uniform responses to climate change are hardly to be expected. Regional variation in climate change concerns patterns in, for example, overall warming, precipitation and the seasonal distribution of change[6]. Thus, changes in phenology can be expected to track local changes in the timing of abiotic or climatically driven events, within the constraints set by the utilization of and sensitivity to cues of the regional species assemblage[18–20]. Such local and regional variation in drivers[19,21,22] and sensitivity towards them[18,20] can be reflected in spatiotemporal variation in phenological shifts[4,8,15,23,24]. Although the few studies analysing geographically extensive datasets on phenology have observed spatial variation in temporal trends of phenological responses (for example, refs. [13,25]) and their main abiotic drivers[5,26–28], the question remains whether patterns of change and response follow major environmental gradients in latitude, photoperiod or temperature[15,16,29].

Spatially extensive long-term data across northern Eurasia

Evaluating to what extent shifts in phenological events vary over space[15,16], with their annual timing[30] or with trophic level[3,11,12] requires consistently sampled, community-wide data that are both long-term and spatially extensive[3,12,16,31]. Such data may also give insights on whether local phenology is influenced by biotic interactions beyond abiotic cues[7,32,33]. Unfortunately, systematic community-wide datasets are still uncommon, hampering progress in understanding large-scale taxonomic and geographic patterns in phenological change[34]. The few existing exceptions (for example, refs. [2,4,8,15,35,36]) are built on sparse data and/or combining individual studies using variable methods. However, for such data, both noise and bias may affect the overall pattern detected. Regarding seasonality, most datasets come with a particular bias, as much more interest has been invested in spring- than in autumn-time events[37]. This is a problem, because where data are available, phenological events occurring during different times of the year have often been found to shift differently[2,4].

Here, we draw on a uniquely comprehensive, long-term database established using uniform protocols across northern Eurasia[38,39]. As this monitoring effort encompassed the timing of multiple seasonal events as characterizing both climatic variation and a wealth of taxa (plants, birds, insects, amphibians, reptiles and fungi; Fig. 1), it allows us to quantify large-scale patterns in phenological responses over six decades. Specifically, we ask: (1) Has the timing of different phenological events shifted similarly across this vast geographic range, measured in terms of the rate and direction (advance or delay) of change? (2) To what extent does variation in the rate and direction of change follow major biogeographic gradients, such as latitude, photoperiod, temperature or chilling degree days? (3) To what extent can variation in the rate and direction of change be linked to the relative seasonal timing of the event (early versus late), or to the species' trophic level? (4) To what extent does variation in the timing of different events covary locally in ways not attributable to overall patterns, suggesting an effect of biotic interactions

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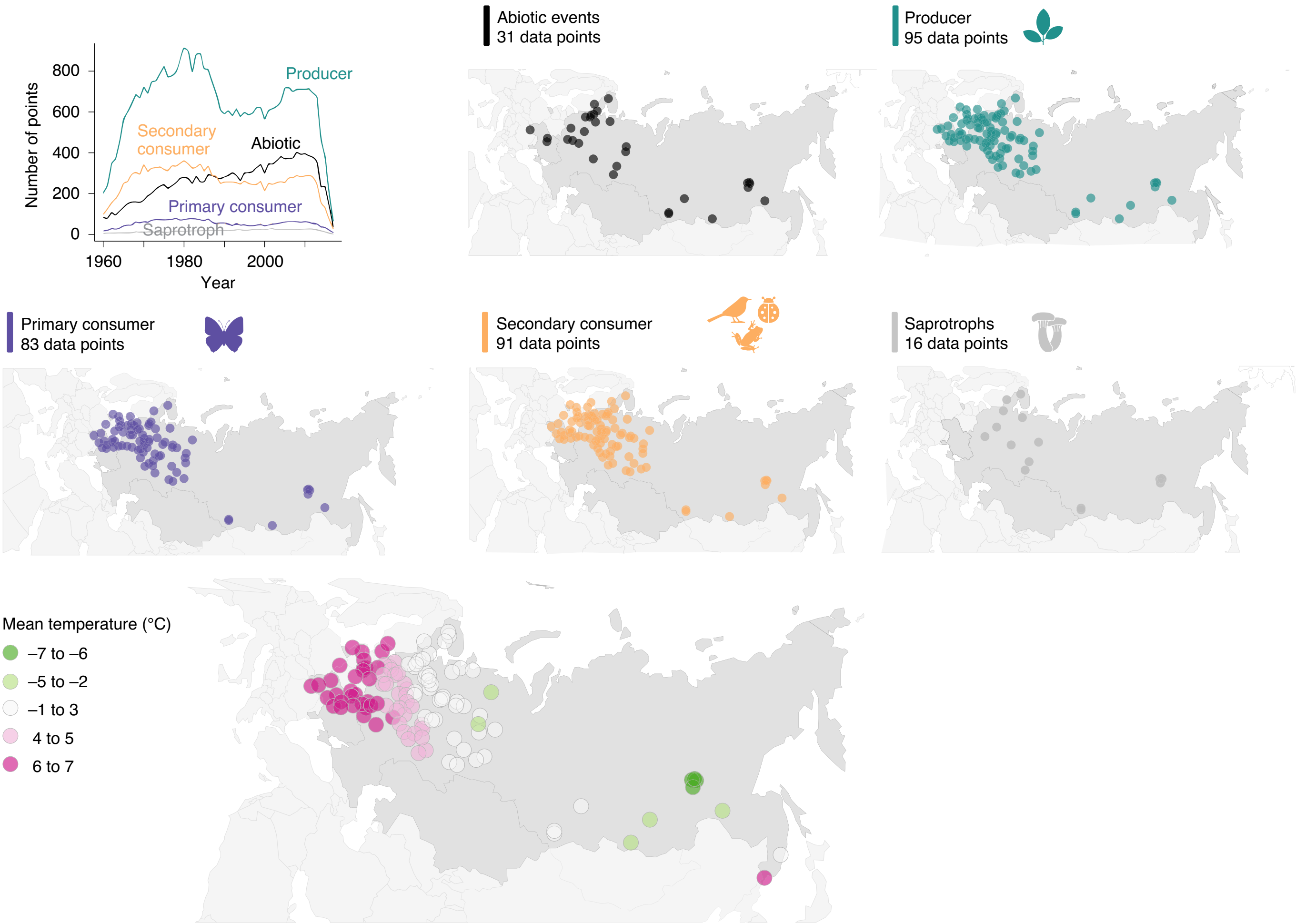

Fig. 1 | Illustration of the study design and the extent of data. Individual panels show the amount of phenological data per year included in the study (top left), the spatial provenance of data of each type (top and middle) and mean annual temperature for each sampling location (bottom). All events were classified into four trophic levels according to the organism expressing the event: primary producers (plants), primary consumers (herbivorous insects), secondary consumers (predatory insects, amphibians, birds, mammals) and saprotrophs (fungi, as commonly feeding on the remains of multiple other levels). Silhouettes adapted from https://thenounproject.com.

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

To quantify phenological shifts across events, trophic levels and environmental gradients, we fitted a joint species distribution model[40–42] treating the dates of the phenological events as the multivariate response variable. To capture linear shifts in the timing of events, we included year as a fixed covariate, and to account for phenology varying with environmental or spatial gradients, we included the linear effect of four environmental descriptors of each study site (that is, mean annual temperature, mean annual chilling sum, photoperiod, or latitude) with a separate model fitted for each descriptor (see below). Additionally, to quantify to what extent shifts in phenology differ along the environmental gradient, we included an interaction term between year and the environmental descriptor. Variation among sites beyond that explained by the environmental descriptor was captured by including site as a random factor, and similarly year-to-year variation beyond any linear trend was modelled by including year as a random factor. All events were grouped into abiotic ($n=28$; for example, the transition of daily average temperatures above a given threshold, the melt of snow cover, or the breakup of ice on a given water body; Supplementary Table 1) versus biotic events ($n=82$; for example, the first occurrence of a fungus species, the onset of blooming in a plant species, or the end of leaf fall for a tree species; Supplementary Table 1), with the latter further split according to the species trophic level, yielding five 'trophic levels' (producers, $n=54$; primary consumers, $n=4$; secondary consumers, $n=22$; and saprotrophs, $n=2$; Fig. 1 and Supplementary Table 1). To evaluate how the multivariate response (that is, dates of the phenological events) varies within year for each trophic level, we further included as explanatory variables the trophic level, the mean timing of the event across all sites, and their interaction. As we treated the phenological events as the 'species' of our joint species distribution model, we treated their characteristics (that is, the trophic level or the mean timing of the event) as its 'traits', just as one would model, for example, the body size or feeding guild of a species as its traits[40,42]. Thus, the explanatory variables were allowed to affect how the events respond to the fixed effects of year, the environmental descriptor (that is, mean annual temperature, mean annual chilling sum, photoperiod, or latitude) and their interaction. The periodic nature of seasons over time was captured by including the mean timing of the event as the linear effects of its cosine and sine transformations (see Methods for more details).

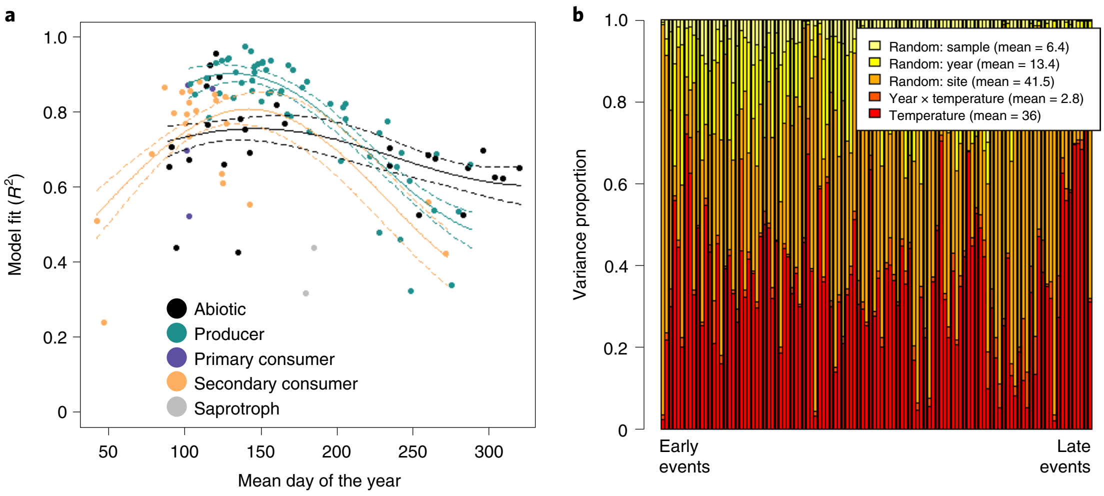

Fig. 2 | Explanatory power and variance partitioning of the HMSC model with mean annual temperature as explanatory variable. a, Degree of determination (R^2) as a function of the timing of the event (mean day of the year when the event occurs) and of the trophic level of the organism expressing the event (shown by curves in different colours). Here, curves show second-order models fitted to groups with at least five events; continuous lines show mean model prediction and dashed lines ±1 s.e. **b**, Partitioning of the overall variance of the data into the different model components. Here, individual events have been sorted from the earliest to the latest (left to right along abscissa).

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

How phenology is shifting across a continent

All models provided adequate descriptions of the data, as evidenced by a high mean explanatory power: averaged over the events, R^2 was 74% for the model with latitude and 75% for all other models. We note that the reason why all models had similarly high explanatory power was that the part of the site-specific variation not explained by the climatic descriptor of the site was captured by the random effect of the site. The proportion of explained variation attributed to the climatic descriptor was 36% for the mean annual temperature of the site, 24% for the chilling sum, 27% for the photoperiod and 28% for the latitude (Extended Data Fig. 1). Because mean annual temperature was the best predictor in the sense of explaining the most variation, we report the results of that model here. All four models yielded qualitatively consistent results (Extended Data Figs. 1–8).

The explanatory power was greater for spring events than for autumn events, except for abiotic events (Supplementary Table 1) where it was consistently high (Fig. 2a for the model with mean temperature and Extended Data Fig. 2 for other models). Averaged over the different events, 36.0% of the explained variance was attributed to the site mean temperature, 2.8% to the linear effect of year and its interaction with the temperature, 41.5% to the random effect of the site (that is, variation among sites not explained by mean temperature), 13.4% to the random effect of the year (that is, variation among years not explained by linear trends) and 6.4% to the random effect of the sample (that is, synchronous variation at the level of site–year combinations; Fig. 2b).

Spring events tend to occur earlier and autumn events later at warmer (typically lower latitude or elevation) sites, creating a longer activity period or growing season, as reflected by a strong negative effect of temperature on spring event timing and strong positive effect on autumn event timing (Fig. 3a,b). For a large proportion (54%) of all events, we found strong statistical support (at least 95% posterior probability) for a shift towards an earlier date, whereas fewer events (10%) showed strong statistical support for a shift towards a later date (Fig. 3a). As examples of events shifting towards an earlier date, we find the break of ice cover, the first blooming of many plants (from Tussilago, *T. farfara*, to lily of the valley, *Convallaria majalis*), the first flight of bumblebees, *Bombus*, and the first occurrence of a range of bird species (ranging from the swift, *Apus apus*, to the crane, *Grus grus*). Among events shifting towards a later date, we find the formation of snow and ice cover, the timing of autumn colours and leaf fall in several trees (from aspen, *Populus tremula*, to birch, *Betula pendula*) and—perhaps oddly enough—the spring-time awakening of the brown bear, *Ursus arctos*. Specifically, spring events showed the strongest shift towards earlier dates, whereas autumn events showed the strongest shifts towards later dates (Fig. 3c). This was particularly evident for primary producers, which overall showed stronger shifts in both directions; that is, plants advanced early or delayed late events faster than did higher trophic levels. By comparison, the abiotic events showed even stronger shifts in both directions for both temperature and year effects. Thus, abiotic change, consumers and producers slide apart as springs shift earlier and autumns later.

Furthermore, shifts were more positive at warmer sites for some events (18% showed strong statistical support; Fig. 3d), but more negative for others (15%; Fig. 3d), with no clear pattern over time or across trophic levels. Among those events that showed a strong statistical support for an overall shift to earlier, 17% showed a strong statistical support for shifting to earlier especially in cold sites and 16% in warm sites (Fig. 3e). Among those events that showed a strong statistical support for an overall shift to later, 11% showed a strong statistical support for shifting to later especially in cold sites and 22% in warm sites (Fig. 3e). As concrete examples of events that have actually shifted later at cold sites but earlier at warm sites, we

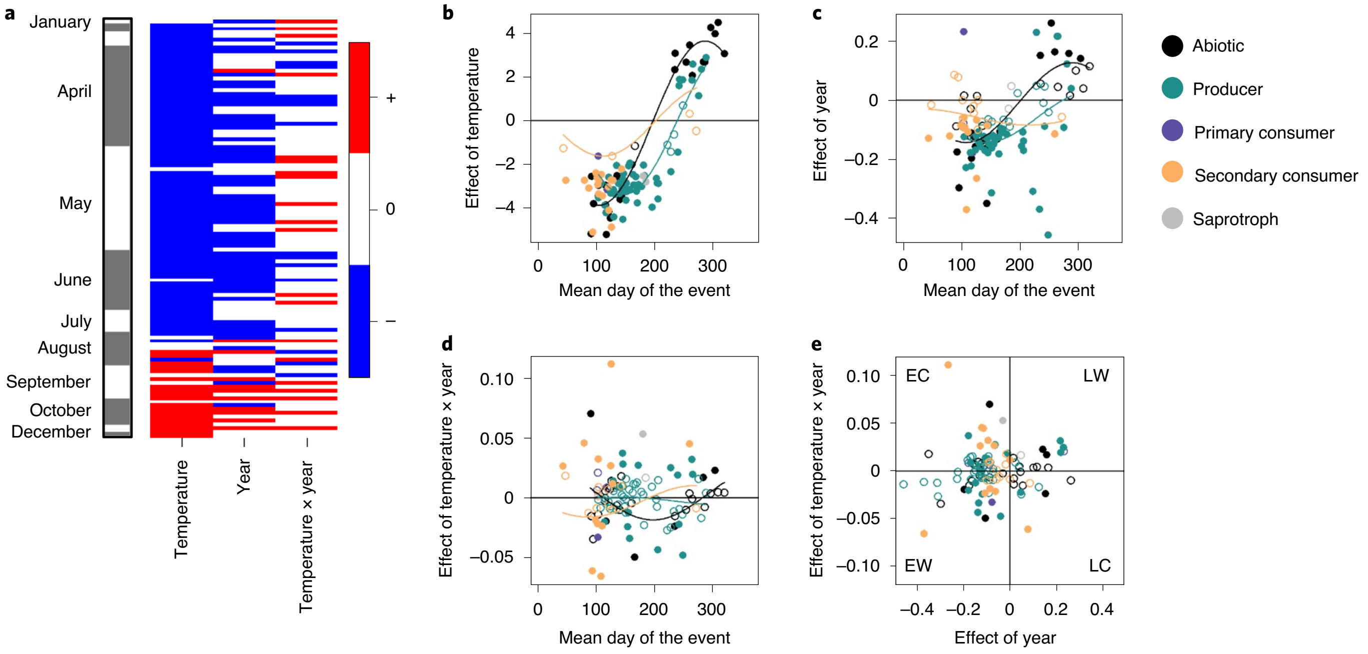

Fig. 3 | Responses of the events to the fixed effects of mean temperature and year. a, Cases for which the response is positive (red) or negative (blue) with at least 95% posterior probability, with the events ordered according to their mean date (increasing from top to bottom). The covariates year and temperature have been normalized to have zero mean, so the main effect of the year relates to a site with average temperature, and the main effect of temperature relates to data points collected at the middle of the study period. **b–d**, Dependency of event-specific responses to site-specific mean annual temperature (**b**), year (**c**) and year × temperature (**d**) on phenological timing (mean day of the year when the event occurs) and on the trophic level of the organism expressing the event (shown by curves in different colours for those groups with at least five events). **e**, Dependency of the response to year × temperature on the response to year. The four quadrats correspond to events that have shifted to earlier especially at cold sites (EC), shifted to earlier especially at warm sites (EW), shifted to later especially at cold sites (LC) and shifted to later especially at warm sites (LW). Filled symbols indicate cases that are either positive or negative with at least 95% posterior probability. For the effect of year, we show responses in days per year, so that a value of −0.2 represents a shift of 2 days earlier per decade. For the effect of temperature, the unit is days per degree Celsius, so that a value of −4 means that the event takes place 8 days earlier in a location with mean temperature 4 °C compared with a location with mean temperature 2 °C.

find the first spring rain, the onset of blooming in Scots pine (*Pinus sylvestris*) and marsh Labrador tea (*Rhododendron tomentosum*, syn. *Ledum palustre*), and the first song of the skylark (*Alauda arvensis*). Among events shifting earlier at cold sites but later at warm sites, we find, for example, the arrival of the rook (*Corvus frugilegus*), and the ripening of blueberry (*Vaccinium myrtillus*) and lingonberry (*Vaccinium vitis-idaea*).

The random effect of site was positively associated both within spring and autumn events, but negatively associated between spring and autumn events (Fig. 4a); that is, at any given site, spring events tended to occur particularly early, whereas all autumn events occurred particularly late, or vice versa, after accounting for the effect of site mean temperature. This pattern remained qualitatively unchanged when replacing mean temperature with other environmental descriptors (mean chilling sums, photoperiod or latitude; Extended Data Fig. 6). Thus, summer—in the sense of the biologically active period—tends to be particularly long at some sites and particularly short at other sites, a pattern that is only partly captured by simple environmental gradients (for potential explanations, see section titled 'Striking variation over space, species and trophic levels'). The random effect of year was positively correlated among events overall, but especially among spring events, meaning that some years are characterized by early spring phenology and others by late spring phenology across all events and trophic levels (Fig. 4b). Perhaps most interestingly, though, the random effect at the level of the sampling unit (that is, the site-by-year combination) showed positive association among most phenological events. Thus, a large majority of all phenological events within a given site in a given year tended to be consistently 'early' or 'late' to an extent inexplicable by the effect of the year as such (Fig. 4c)—a pattern suggesting that some other factor may be orchestrating the relative timing of events at the level of the local community.

Striking variation over space, species and trophic levels

Our results highlight considerable spatial, seasonal and trophic heterogeneity in the magnitude and direction of shifts in phenological timing. Although much of the large-scale variation can be attributed to a simple environmental gradient, phenological responses to ongoing climate change can idiosyncratically cause advance or delay over time within regions, and among sites and trophic levels. Notably, the strong effect of site beyond the effect of mean temperature (as shown by the overall partitioning of variance in our model; Fig. 2 and Extended Data Fig. 1) qualifies the expectation of a strong and general pattern of phenology change along latitudinal or other environmental gradients[5,6,8]. Yet it is consistent with our previous work showing that phenological plasticity is constrained by local differentiation in reaction norms to temperature cues[17], that is, by local adaptation (see also ref. [43]). Under such a scenario, we would indeed expect site-specific variation in phenology beyond patterns attributable to average temperature or its change over time. However, it is worth noting that different abiotic events (such as snowmelt, ice formation and ice break) likewise vary differently with mean temperature, change differently over time and remain cross-correlated even when temperature has been accounted for (Figs. 3 and 4). In other words, early sites tend to remain early and late sites tend to remain late, both with respect to the biotic and abiotic components of the local ecosystems. Most interestingly, the overall timing of events tends to be more synchronized than

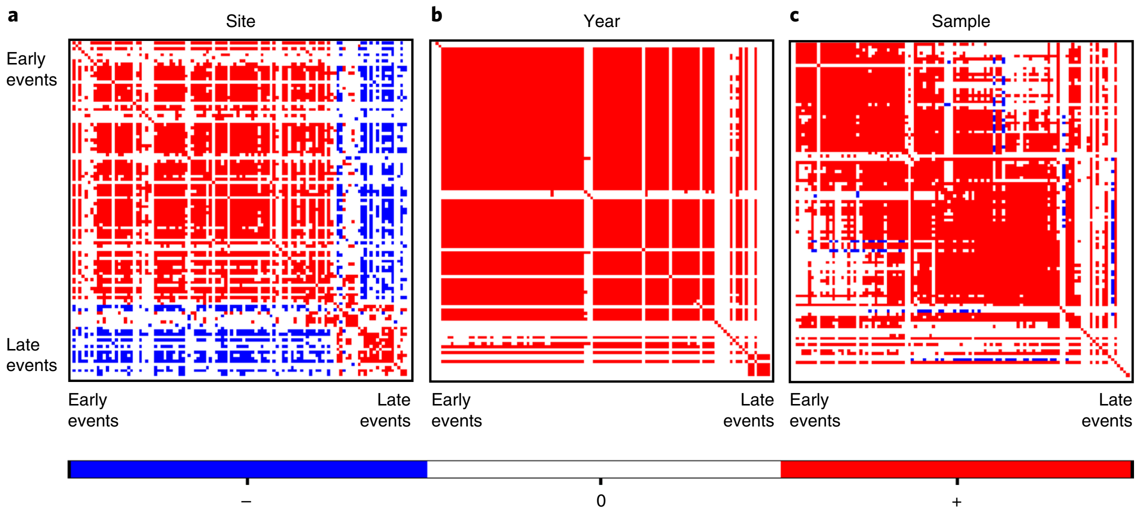

Fig. 4 | Residual associations among events related to random effects. a–c, Associations at the level of the site (**a**), the year (**b**) and the sample (site × year; **c**) The events have been ordered according to their mean date (increasing from left to right and from top to bottom) and estimates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

suggested by the overall effect of year. The strong dominance of positive residual associations between event pairs at the random sample level (Fig. 4c and Extended Data Fig. 8) implies that an early date of one given event is associated with an earlier date in another beyond the advance expected by the overall earliness of the year. Residual covariance at this level could potentially be interpreted as a sign of a synchronizing effect of biotic interactions among species. In doing so, we should naturally exercise the same caution as whenever statistically observed associations are interpreted as biotic interactions[40,42]. It is also worth noting that beyond biotic interactions, this result is likely to partly reflect the synchronizing effect of abiotic conditions that affect multiple events, as well as the fact that different phenophases within one and the same species are interconnected (for example, a migratory bird species cannot breed without first arriving, so the timing of breeding is constrained by the timing of arriving). Regarding the latter type of dependency, we note that although we scored two or more separate phenological events in several species (Supplementary Information and Supplementary Table 1), such repeated measures concerned far too few species to account for the vast predominance of positive residual associations observed overall. Thus, the pattern observed may be seen as suggestive, but clearly inconclusive evidence for an imprint of biotic interactions on community-level phenology[7,32,33].

Overall, strong phenological shifts over time occur not in lieu of but on top of the imprints of environmental gradients of mean temperature, photoperiod and latitude[5,6,8]. That is, strong added imprints of site on local phenology change might stem from spatial variation in additional factors varying more idiosyncratically in space, rather than as smooth gradients. Species respond to many climatic dimensions over time[44], and the effects of climate on phenology may further vary with habitat[45,46], urbanization[47] and precipitation[48,49]. Thus, an anthropogenic-induced shift in the macroclimate[5,6], potentially leading to large-scale environmental changes along latitudes[4,5,15,31] or other geographical gradients, may be further modified by the local changes that species are responding to being customized by the local conditions that they have adapted to. Such added impacts could limit the scope for space-for-time substitutions[50], and leads us to warn against uncritical extrapolation of trends observed among sites, trophic levels, or from one region to another[16].

As previously proposed[5], the observed patterns of shifts in phenology should be compared to patterns in the velocity and seasonal shift of climate change. In this context, we note that our current data include both abiotic climate-related events and biotic responses, with the former shifting more than the latter. These disparities between the rates of change in the abiotic environment and species responses match previous observations that current phenological plasticity is not keeping pace with variation in climatic conditions[17,51]. Mismatches between the velocity of climate change and realized seasonal shifts may help identify regions of concern, for example, where phenology change is lagging behind species' thermal niches.

Ecosystem integrity imperilled yet understudied

Our findings emphasize concerns regarding ecosystem integrity, as the velocity of change in space and time differed between interacting trophic levels. Combined with different responses among events over different parts of the season, this variation can lead to temporal mismatches between species[3,17,18,22,52–55] and potentially affect community structure and persistence. Notably, a shift in the timing of an event related to one life stage may propagate to another, but our current dataset holds limited resolution towards resolving such knock-on effects. To establish whether the stability and persistence of natural systems is ultimately affected by the loss of phenological synchrony at one stage, or within food webs, we need a much-improved understanding of the interplay between spatial, trophic, species- and event-specific patterns in phenological responses (for example, ref. [34]).

Accumulated negative effects of rapid seasonal shifts across many species may threaten biodiversity[1]. Surprisingly enough, our current findings suggest that phenological shifts during the past few decades may differ between warmer and colder locations across our study area. In this context, we stress that our estimates concern absolute, not relative, rates of change. Counter-weighing the interpretation of stronger shifts at warmer (thus more southern or lower elevations) sites is the fact that phenology is naturally constrained by the overall length of the season. At high latitudes, that is, in colder regions, a shift of a few days may amount to a considerable part of the full growing season. As polar areas warm at faster rates, resident organisms might lose major parts of their phenological niches[14,56,57]. In contrast, areas of slower seasonal shifts, and smaller relative shifts, may be important repositories for both biodiversity and ecosystem integrity[5]. Our current study provides an attempt in this direction and will hopefully inspire more work to come.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-020-00967-7.

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Tomas Roslin[1,2] ✉, **Laura Antão**[2], **Maria Hällfors**[2], **Evgeniy Meyke**[3], **Coong Lo**[2],
Gleb Tikhonov[4], **Maria del Mar Delgado**[5], **Eliezer Gurarie**[6], **Marina Abadonova**[7],
Ozodbek Abduraimov[8], **Olga Adrianova**[9], **Tatiana Akimova**[10], **Muzhigit Akkiev**[11], **Aleksandr Ananin**[12,13],
Elena Andreeva[14], **Natalia Andriychuk**[15], **Maxim Antipin**[16], **Konstantin Arzamascev**[17],
Svetlana Babina[18], **Miroslav Babushkin**[19], **Oleg Bakin**[20], **Anna Barabancova**[21], **Inna Basilskaja**[22],
Nina Belova[23], **Natalia Belyaeva**[24], **Tatjana Bespalova**[25], **Evgeniya Bisikalova**[26], **Anatoly Bobretsov**[27],
Vladimir Bobrov[28], **Vadim Bobrovskyi**[29], **Elena Bochkareva**[30,31], **Gennady Bogdanov**[32],
Vladimir Bolshakov[33], **Svetlana Bondarchuk**[34], **Evgeniya Bukharova**[12,102], **Alena Butunina**[25],
Yuri Buyvolov[35], **Anna Buyvolova**[36], **Yuri Bykov**[37], **Elena Chakhireva**[20], **Olga Chashchina**[38],
Nadezhda Cherenkova[39], **Sergej Chistjakov**[40], **Svetlana Chuhontseva**[10], **Evgeniy A. Davydov**[30,41],
Viktor Demchenko[42], **Elena Diadicheva**[42], **Aleksandr Dobrolyubov**[43], **Ludmila Dostoyevskaya**[44],
Svetlana Drovnina[39], **Zoya Drozdova**[37], **Akynaly Dubanaev**[45], **Yuriy Dubrovsky**[46], **Sergey Elsukov**[34],
Lidia Epova[47], **Olga Ermakova**[23], **Olga S. Ermakova**[48], **Elena Ershkova**[49,50], **Aleksandra Esengeldenova**[25],
Oleg Evstigneev[51], **Irina Fedchenko**[52], **Violetta Fedotova**[44], **Tatiana Filatova**[53], **Sergey Gashev**[54],
Anatoliy Gavrilov[55], **Irina Gaydysh**[9], **Dmitrij Golovcov**[56], **Nadezhda Goncharova**[14], **Elena Gorbunova**[10],
Tatyana Gordeeva[57,103], **Vitaly Grishchenko**[58], **Ludmila Gromyko**[34], **Vladimir Hohryakov**[59],
Alexander Hritankov[14], **Elena Ignatenko**[60], **Svetlana Igosheva**[61], **Uliya Ivanova**[62], **Natalya Ivanova**[63],
Yury Kalinkin[10], **Evgeniya Kaygorodova**[51], **Fedor Kazansky**[64], **Darya Kiseleva**[65], **Anastasia Knorre**[14,66],
Leonid Kolpashikov[55], **Evgenii Korobov**[67], **Helen Korolyova**[10], **Natalia Korotkikh**[25], **Gennadiy Kosenkov**[59],
Sergey Kossenko[51], **Elvira Kotlugalyamova**[68], **Evgeny Kozlovsky**[69], **Vladimir Kozsheechkin**[14],
Alla Kozurak[15], **Irina Kozyr**[23], **Aleksandra Krasnopevtseva**[23], **Sergey Kruglikov**[51], **Olga Kuberskaya**[29],
Aleksey Kudryavtsev[43], **Elena Kulebyakina**[70], **Yuliia Kulsha**[58], **Margarita Kupriyanova**[62],
Murad Kurbanbagamaev[27], **Anatoliy Kutenkov**[71], **Nadezhda Kutenkova**[71], **Nadezhda Kuyantseva**[38,72],
Andrey Kuznetsov[19], **Evgeniy Larin**[25], **Pavel Lebedev**[44,73], **Kirill Litvinov**[74], **Natalia Luzhkova**[12],
Azizbek Mahmudov[8], **Lidiya Makovkina**[75], **Viktor Mamontov**[70], **Svetlana Mayorova**[37],
Irina Megalinskaja[27], **Artur Meydus**[76,77], **Aleksandr Minin**[78,79], **Oleg Mitrofanov**[10], **Mykhailo Motruk**[80],
Aleksandr Myslenkov[75], **Nina Nasonova**[81], **Natalia Nemtseva**[19], **Irina Nesterova**[34], **Tamara Nezdoliy**[62],
Tatyana Niroda[82], **Tatiana Novikova**[61], **Darya Panicheva**[64], **Alexey Pavlov**[20], **Klara Pavlova**[60],
Sergei Podolski[60], **Natalja Polikarpova**[83], **Tatiana Polyanskaya**[84], **Igor Pospelov**[28], **Elena Pospelova**[55],
Ilya Prokhoro[36], **Irina Prokosheva**[85], **Lyudmila Puchnina**[52], **Ivan Putrashyk**[82], **Julia Raiskaya**[76],
Yuri Rozhkov[86], **Olga Rozhkova**[86], **Marina Rudenko**[87], **Irina Rybnikova**[19], **Svetlana Rykova**[52],
Miroslava Sahnevich[10], **Alexander Samoylov**[39], **Valeri Sanko**[42], **Inna Sapelnikova**[22],
Sergei Sazonov[88,104], **Zoya Selyunina**[89], **Ksenia Shalaeva**[59], **Maksim Shashkov**[63,90],
Anatoliy Shcherbakov[71], **Vasyl Shevchyk**[58], **Sergej Shubin**[91], **Elena Shujskaja**[67], **Rustam Sibgatullin**[24],
Natalia Sikkila[9], **Elena Sitnikova**[51], **Andrei Sivkov**[52,105], **Nataliya Skok**[62], **Svetlana Skorokhodova**[71],
Elena Smirnova[34], **Galina Sokolova**[35], **Vladimir Sopin**[76], **Yurii Spasovski**[92], **Sergei Stepanov**[67],
Vitaliy Stratiy[93], **Violetta Strekalovskaya**[55], **Alexander Sukhov**[71], **Guzalya Suleymanova**[94],
Lilija Sultangareeva[68], **Viktorija Teleganova**[57], **Viktor Teplov**[27,106], **Valentina Teplova**[27], **Tatiana Tertitsa**[27],
Vladislav Timoshkin[14], **Dmitry Tirski**[86], **Andrej Tolmachev**[21], **Aleksey Tomilin**[95,96], **Ludmila Tselishcheva**[91],
Mirabdulla Turgunov[8], **Yurij Tyukh**[82], **Polina Van**[29], **Vladimir Van**[29], **Aleksander Vasin**[97],
Aleksandra Vasina[97], **Anatoliy Vekliuk**[15], **Lidia Vetchinnikova**[88], **Vladislav Vinogradov**[98],
Nikolay Volodchenkov[23], **Inna Voloshina**[75], **Tura Xoliqov**[99], **Eugenia Yablonovska-Grishchenko**[58],

Vladimir Yakovlev[10,107], Marina Yakovleva[71], Oksana Yantser[62], Yurij Yarema[82], Andrey Zahvatov[100], Valery Zakharov[38], Nicolay Zelenetskiy[19], Anatolii Zheltukhin[67], Tatyana Zubina[10], Juri Kurhinen[2,88] and Otso Ovaskainen[2,101]

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[1]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden. [2]University of Helsinki, Helsinki, Finland. [3]EarthCape OY, Helsinki, Finland. [4]Department of Computer Science, Aalto University, Espoo, Finland. [5]Research Unit of Biodiversity (UMIB, UO-CSIC-PA), Oviedo University, Mieres, Spain. [6]3237 Biology-Psychology Building, University of Maryland, College Park, MD, USA. [7]National Park Orlovskoe Polesie, Oryol, Russian Federation. [8]Institute of Botany, Academy of Sciences of the Republic of Uzbekistan, Tashkent, Uzbekistan. [9]Kostomuksha Nature Reserve, Kostomuksha, Russian Federation. [10]Altai State Nature Biosphere Reserve, Gorno-Altaysk, Russian Federation. [11]Kabardino-Balkarski Nature Reserve, Kashkhatau, Russian Federation. [12]FSE Zapovednoe Podlemorye, Ust-Bargizin, Russian Federation. [13]Institute of General and Experimental Biology, Siberian Branch, Russian Academy of Sciences, Ulan-Ude, Russian Federation. [14]State Nature Reserve Stolby, Krasnoyarsk, Russian Federation. [15]Carpathian Biosphere Reserve, Rakhiv, Ukraine. [16]Nizhne-Svirsky State Nature Reserve, Lodeinoe Pole, Russian Federation. [17]State Nature Reserve Prisursky, Cheboksary, Russian Federation. [18]Zapovednoe Pribajkalje (Bajkalo-Lensky State Nature Reserve, Pribajkalsky National Park), Irkutsk, Russian Federation. [19]Darwin Nature Biosphere Reserve, Borok, Russian Federation. [20]Volzhsko-Kamsky National Nature Biosphere Rezerve, Sadovy, Russian Federation. [21]FGBU National Park Shushenskiy Bor, Shushenskoe, Russian Federation. [22]Voronezhsky Nature Biosphere Reserve, Voronezh, Russian Federation. [23]Baikalsky State Nature Biosphere Reserve, Tankhoy, Russian Federation. [24]Visimsky Nature Biosphere Reserve, Kirovgrad, Russian Federation. [25]Kondinskie Lakes National Park named after L. F. Stashkevich, Sovietsky, Russian Federation. [26]FSBI United Administration of the Kedrovaya Pad' State Biosphere Nature Reserve and Leopard's Land National Park, Vladivostok, Russian Federation. [27]Pechoro-Ilych State Nature Reserve, Yaksha, Russian Federation. [28]A. N. Severtsov Institute of Ecology and Evolution, Moscow, Russian Federation. [29]Komsomolskiy Department, FGBU Zapovednoye Priamurye, Komsomolsk-on-Amur, Russian Federation. [30]Tigirek State Nature Reserve, Barnaul, Russian Federation. [31]Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences, Novosibirsk, Russian Federation. [32]State Nature Reserve Bolshaya Kokshaga, Yoshkar-Ola, Russian Federation. [33]Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Ekaterinburg, Russian Federation. [34]Sikhote-Alin State Nature Biosphere Reserve named after K. G. Abramov, Terney, Russian Federation. [35]FSBI Prioksko-Terrasniy State Reserve, Danky, Russian Federation. [36]Lomonosov Moscow State University, Moscow, Russian Federation. [37]National Park Meshchera, Gus-Hrustalnyi, Russian Federation. [38]South Urals Federal Research Center of Mineralogy and Geoecology, Ilmeny State Reserve, Ural Branch, Russian Academy of Sciences, Miass, Russian Federation. [39]FGBU National Park Kenozersky, Arkhangelsk, Russian Federation. [40]FGBU GPZ Kologrivskij les im. M.G. Sinicina, Kologriv, Russian Federation. [41]Altai State University, Barnaul, Russian Federation. [42]Pryazovskyi National Nature Park, Melitopol', Ukraine. [43]State Nature Reserve Privolzhskaya Lesostep, Penza, Russian Federation. [44]Komarov Botanical Institute, Russian Academy of Sciences, Saint Petersburg, Russian Federation. [45]Sary-Chelek State Nature Reserve, Aksu, Kyrgyzstan. [46]Institute for Evolutionary Ecology NAS Ukraine, Kiev, Ukraine. [47]FGBU State Nature Reserve Kuznetsk Alatau, Mezhdurechensk, Russian Federation. [48]Kerzhenskiy State Nature Biosphere Reserve, Nizhny Novgorod, Russian Federation. [49]FSBI United Administration of the Mordovia State Nature Reserve and National Park Smolny, Republic of Mordovia, Saransk, Russian Federation. [50]Ogarev Mordovia State University, Saransk, Russian Federation. [51]Bryansk Forest Nature Reserve, Nerussa, Russian Federation. [52]Pinezhsky State Nature Reserve, Pinega, Russian Federation. [53]The Central Chernozem State Biosphere Nature Reserve named after Professor V.V. Alyokhin, Kurskiy, Russian Federation. [54]Tyumen State University, Tyumen, Russian Federation. [55]Reserves of Taimyr, Norilsk, Russian Federation. [56]Chatkalski National Park, Toshkent, Uzbekistan. [57]National Park Ugra, Kaluga, Russian Federation. [58]Kaniv Nature Reserve, Kaniv, Ukraine. [59]Smolenskoe Poozerje National Park, Przhevalskoe, Russian Federation. [60]FSBI Zeya State Nature Reserve, Zeya, Russian Federation. [61]Polistovsky State Nature Reserve, Pskov, Russian Federation. [62]Ural State Pedagogical University, Yekaterinburg, Russian Federation. [63]Institute of Mathematical Problems of Biology RAS—the Branch of the Keldysh Institute of Applied Mathematics, Russian Academy of Sciences, Pushchino, Russian Federation. [64]Kronotsky Federal Nature Biosphere Reserve, Yelizovo, Russian Federation. [65]Zhiguli Nature Reserve, P. Bakhilova Polyana, Russian Federation. [66]Institute for Ecology and Geography, Siberian Federal University, Krasnoyarsk, Russian Federation. [67]Central Forest State Nature Biosphere Reserve, Tver, Russian Federation. [68]National Park Bashkirija, Nurgush, Russian Federation. [69]State Nature Reserve Kurilsky, Juzhno-Kurilsk, Russian Federation. [70]Vodlozersky National Park, Karelia, Petrozavodsk, Russian Federation. [71]State Nature Reserve Kivach, Kondopoga, Russian Federation. [72]South-Ural Federal University, Miass, Russian Federation. [73]Saint-Petersburg State Forest Technical University, St. Petersburg, Russian Federation. [74]Astrakhan Biosphere Reserve, Astrakhan, Russian Federation. [75]FSBI United Administration of the Lazovsky State Reserve and National Park Zov Tigra, Lazo, Russian Federation. [76]State Nature Reserve Tungusskiy, Krasnoyarsk, Russian Federation. [77]Krasnoyarsk State Pedagogical University named after V.P. Astafyev, Krasnoyarsk, Russian Federation. [78]Institute of Geography, Russian Academy of Sciences, Moscow, Russian Federation. [79]Koltzov Institute of Developmental Biology, Russian Academy of Sciences, Moscow, Russian Federation. [80]Carpathian National Nature Park, Yaremche, Ukraine. [81]State Environmental Institution National Park Braslav lakes, Braslav, Belarus. [82]National Park Synevyr, Synevyr-Ostriki, Ukraine. [83]Pasvik State Nature Reserve, Nikel, Russian Federation. [84]Mari Chodra National Park, Krasnogorsky, Russian Federation. [85]State Nature Reserve Vishersky, Krasnovishersk, Russian Federation. [86]State Nature Reserve Olekminsky, Olekminsk, Russian Federation. [87]Crimea Nature Reserve, Alushta, Republic of Crimea. [88]Forest Research Institute Karelian Research Centre, Russian Academy of Sciences, Petrozavodsk, Russian Federation. [89]Black Sea Biosphere Reserve, Hola Prystan', Ukraine. [90]Institute of Physicochemical and Biological Problems in Soil Sciences, Russian Academy of Sciences, Pushchino, Russian Federation. [91]State Nature Reserve Nurgush, Kirov, Russian Federation. [92]Caucasian State Biosphere Reserve of the Ministry of Natural Resources, Maykop, Russian Federation. [93]National Nature Park Vyzhnytskiy, Berehomet, Ukraine. [94]National Park Khvalynsky, Khvalynsk, Russian Federation. [95]State Research Center Arctic and Antarctic Research Institute, Saint Petersburg, Russian Federation. [96]Information-Analytical Centre for Protected Areas, Moscow, Russian Federation. [97]State Nature Reserve Malaya Sosva, Sovetskiy, Russian Federation. [98]Krasnoyarsk State Medical University named after Prof. V.F.Voino-Yasenetsky, Krasnoyarsk, Russian Federation. [99]Surhanskiy State Nature Reserve, Sherabad, Uzbekistan. [100]Mordovia State Nature Reserve, Pushta, Russian Federation. [101]Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway. [102]Deceased: Evgeniya Bukharova. [103]Deceased: Tatyana Gordeeva. [104]Deceased: Sergei Sazonov. [105]Deceased: Andrei Sivkov. [106]Deceased: Viktor Teplov. [107]Deceased: Vladimir Yakovlev. ✉e-mail: tomas.roslin@slu.se

Methods

We used data from a previous study[38], which compiled dates of phenological events (for concrete examples see Supplementary Information and Supplementary Table 1.1) systematically recorded for multiple taxonomic groups in 471 localities across the Russian Federation, Ukraine, Uzbekistan, Belarus and Kyrgyzstan. In addition, the database includes dates on climatic events recorded at each locality (for example, ice formation and first day of snowfall). The data were curated by EarthCape[58] and published on Zenodo[39]. From this set, we selected events for which there were at least 100 data points in total, and at least 10 data points from at least 10 sites. Further, we only included sites that were at least 25 km apart, and sampling units for which there were at least 10 events recorded. All anthropogenic events, such as dates for sowing and harvest, were excluded from this analysis. This process yielded 70,709 phenological observations for 110 events across 113 locations (Fig. 1). The data included 52 taxa and 4 types of meteorological event (Supplementary Information and Supplementary Table 1.1), and covered the period between 1960 and 2017 (earlier records were excluded), spanning 43.08°–67.82° N latitude and 21.15°–136.15° E longitude.

The sampling units consist of year–site pairs. We denote by $y_{i,j}$ the date on which the phenological event j took place in sampling unit i. These are combined in the data matrix $Y=\{y_{i,j}\}$ with $j=1,\ldots,n_s=110$ events recorded in $i=1,\ldots,n_y=2{,}789$ sampling units. The data consist of 70,709 dates, so that 77% of the entries in the Y matrix are missing due to not all events being recorded in all sites and in all years. To these data, we fitted hierarchical modelling of species communities (HMSC) models[40,42]. HMSC is a multivariate Bayesian generalized linear mixed modelling framework that allowed us to account for both correlation among the phenological events included in the models, as well as for the spatiotemporal structure of the study design[40–42]. Additionally, HMSC allows inclusion of trait information to inform species-level responses to model covariates[40]—in our case, event-level responses. Here, we summarize our rationale and inference; an in-depth description of the HMSC model fitted is provided in the Supplementary Information and Supplementary Text 2.

As predictors related to each sampling unit i, we included the linear effect of year of the sampling, aimed to capture temporal shifts in phenology, which are the main focus of this study. To account for phenological variation due to climatic conditions, as well as to capture any systematic variation in the phenological shifts as a function of climatic conditions, we also included a variable describing the overall (not year-specific) climatic conditions at each study site, and its interaction with the linear effect of year. As climatic descriptor, we considered four alternatives variables based on ref. [28], which identified the three most important factors controlling phenology in primary producers as the degree of winter chilling, photoperiod (day length relative to night length) and temperature. We thus derived descriptors of spatial variation in each of these three variables and showed that our main results were upheld across each (Extended Data Figs. 1–8). Specifically, these were: (1) the mean annual temperature; (2) the mean annual chilling sum (calculated as the sum of degree days for those days for which the temperature is below zero); and (3) the photoperiod measured as the difference between the longest and shortest days of the year, for each site. In addition, we considered (4) the absolute latitude of the site as a standard descriptor of space as such in both phenological[59] and other biogeographic analyses[60]. We note that photoperiod is a function of latitude, but that the two are non-linearly related to each other. For this reason, we included latitude per se as a separate, potential climatic descriptor. To compute the mean annual temperature and the mean annual chilling sum, we used the ERA5-Land data (representing the period 1979–2019)[61,62]. To calculate the photoperiod, we used the day length function of the R-package geosphere[63].

To examine how the shifts and their dependency on the climatic conditions co-varied among different types of phenological event, we also included event-level predictors (that is, species traits in the HMSC framework): (1) the mean timing of each event (calculated as the mean day of the year over the entire dataset); and (2) the trophic level of the species for which the phenological event was recorded (classified as producers, primary consumers, secondary consumers and saprotophs, or abiotic events). To account for the periodic nature of seasons over time, we included the mean timing of each event as the linear effect of its cosine and sine transformations. To account for the nature of the study design and to evaluate co-variation among the phenological events, we included three random effects for the site, the year and the sampling unit (that is, year–site pairs). All of these were modelled at the community level using the latent variable approach of HMSC[40,42]. This allowed us to assess the relationships among phenological events that could not be explained by responses to the main covariates, and for each of the three random effect levels included in our models. For a more technical description of the HMSC model, see refs. [40–42].

We fitted the models with package HMSC[41] in R[64] assuming the default prior distributions (see refs. [41,42]). We performed posterior sampling for four Markov chain Monte Carlo 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 remainder by 1,000, thus yielding 250 samples per chain and 1,000 samples in total. To evaluate Markov chain Monte Carlo convergence, we examined the distributions of the potential scale reduction factor over the parameters related to the fixed effects (β parameters) and the random effects (Ω parameters), equivalent to the Gelman–Rubin statistic[65].

Overall, our aim is to quantify spatial variation in the rates (slope) of phenological change over time, not to identify the specific drivers of the timing of each individual event. To emphasize this point, we stress that we regressed phenological timing on year and on descriptors of each site's position in physical (latitude) or environmental space (average temperature, average sum of chilling degree days or photoperiod), not on year-to-year variation in some specific driver. What our analyses show is thus that trophic level and seasonal timing of an event affect how it has shifted over time, and that the rate of shift is further affected by its position along the biogeographic gradient, whereas the exact descriptor of this gradient has little impact on the results (Extended Data Figs. 1–8).

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

Data availability

The data that support the findings of this study are available in refs. [38,39], with the exact subset of the data used in the present analyses available at https://doi.org/10.5281/zenodo.3774386.

Code availability

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

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Author contributions

The data were collected by the 195 authors starting from M.A. and ending with T.Z. in the author list. J.K., E.M., C.L., G.T. and E.G. contributed to the establishment and coordination of the collaborative network and to the compilation and curation of the resulting dataset. T.R., O.O., L.A., M.H. and M.d.M.D. conceived the idea behind the current study and wrote the first draft of the paper, with O.O. conducting the analyses. All authors provided useful comments on earlier drafts.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41558-020-00967-7.

Supplementary information is available for this paper at https://doi.org/10.1038/s41558-020-00967-7.

Correspondence and requests for materials should be addressed to T.R.

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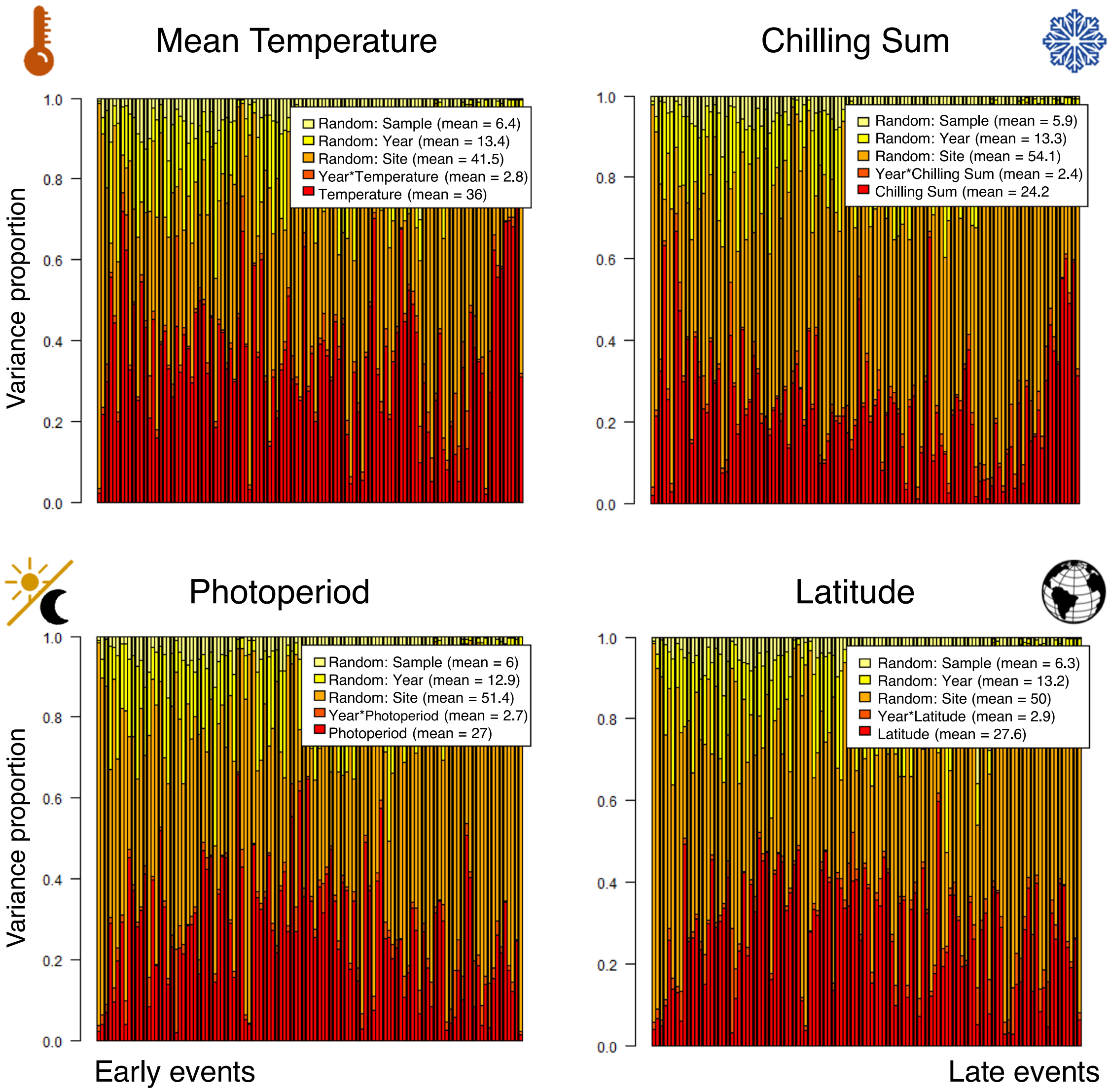
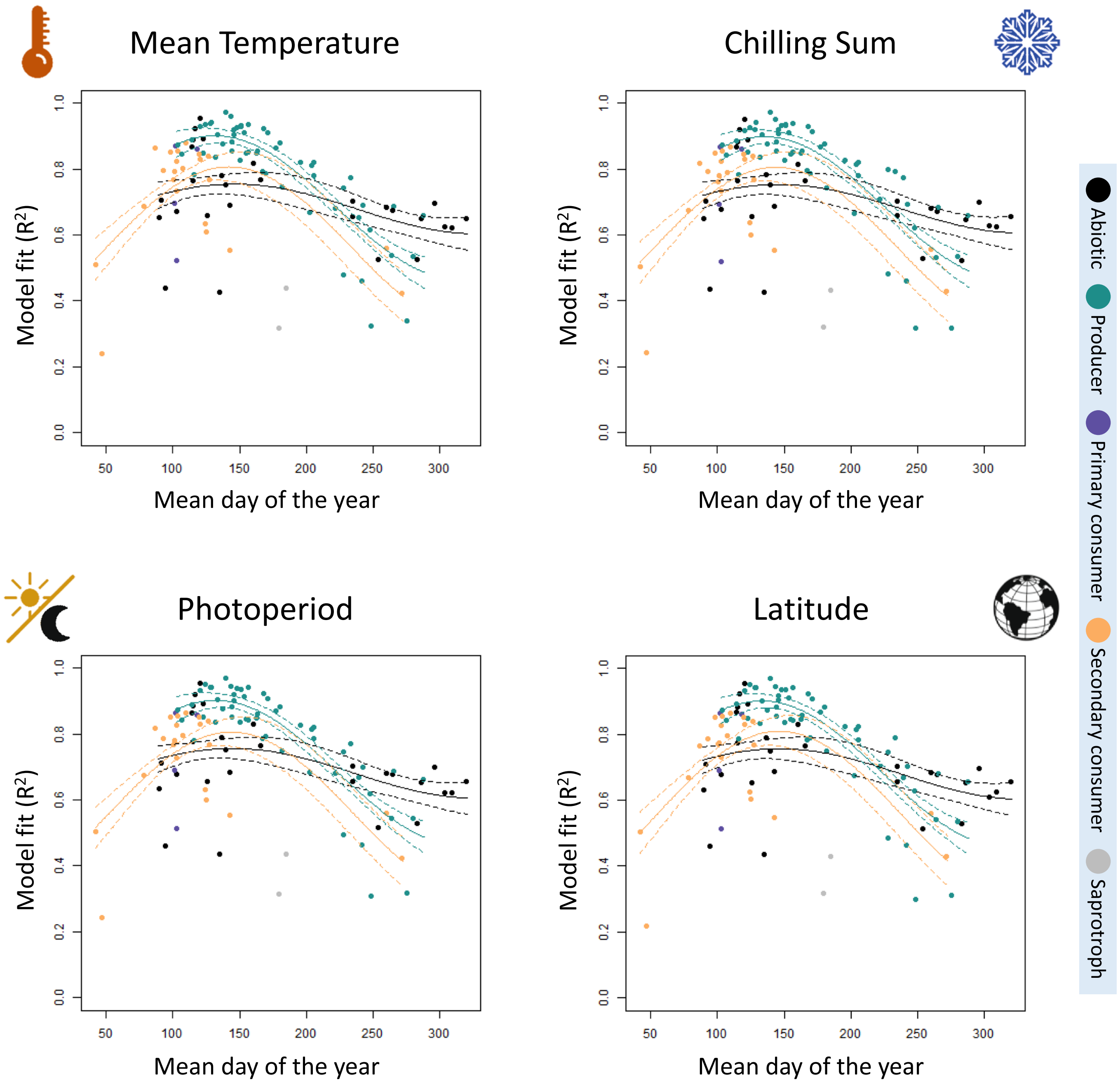
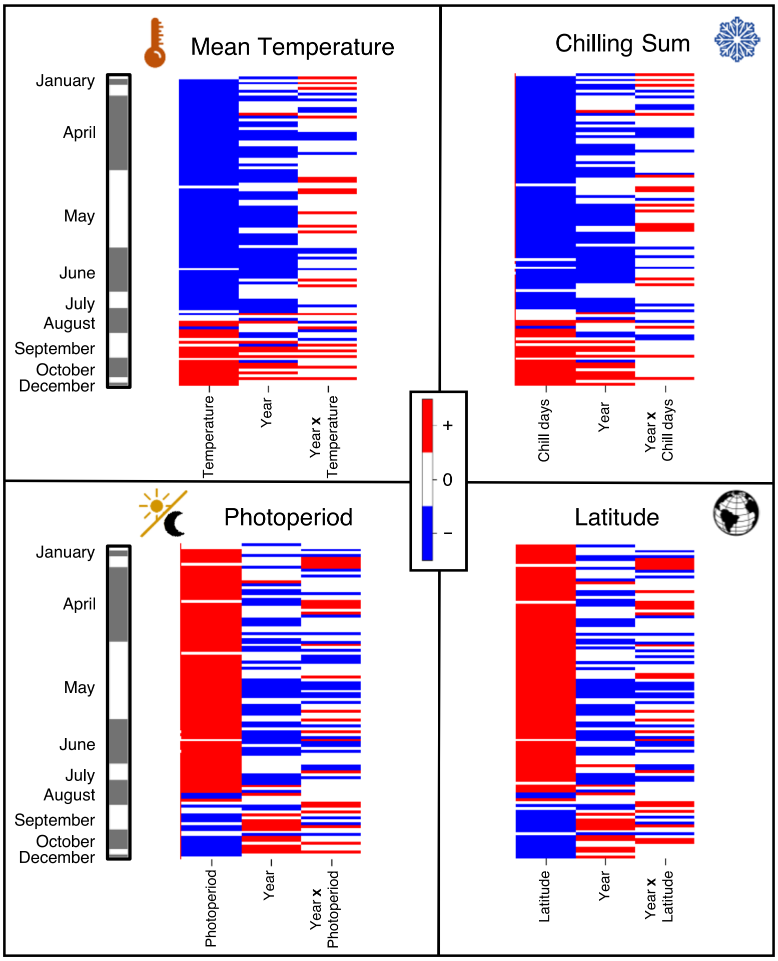


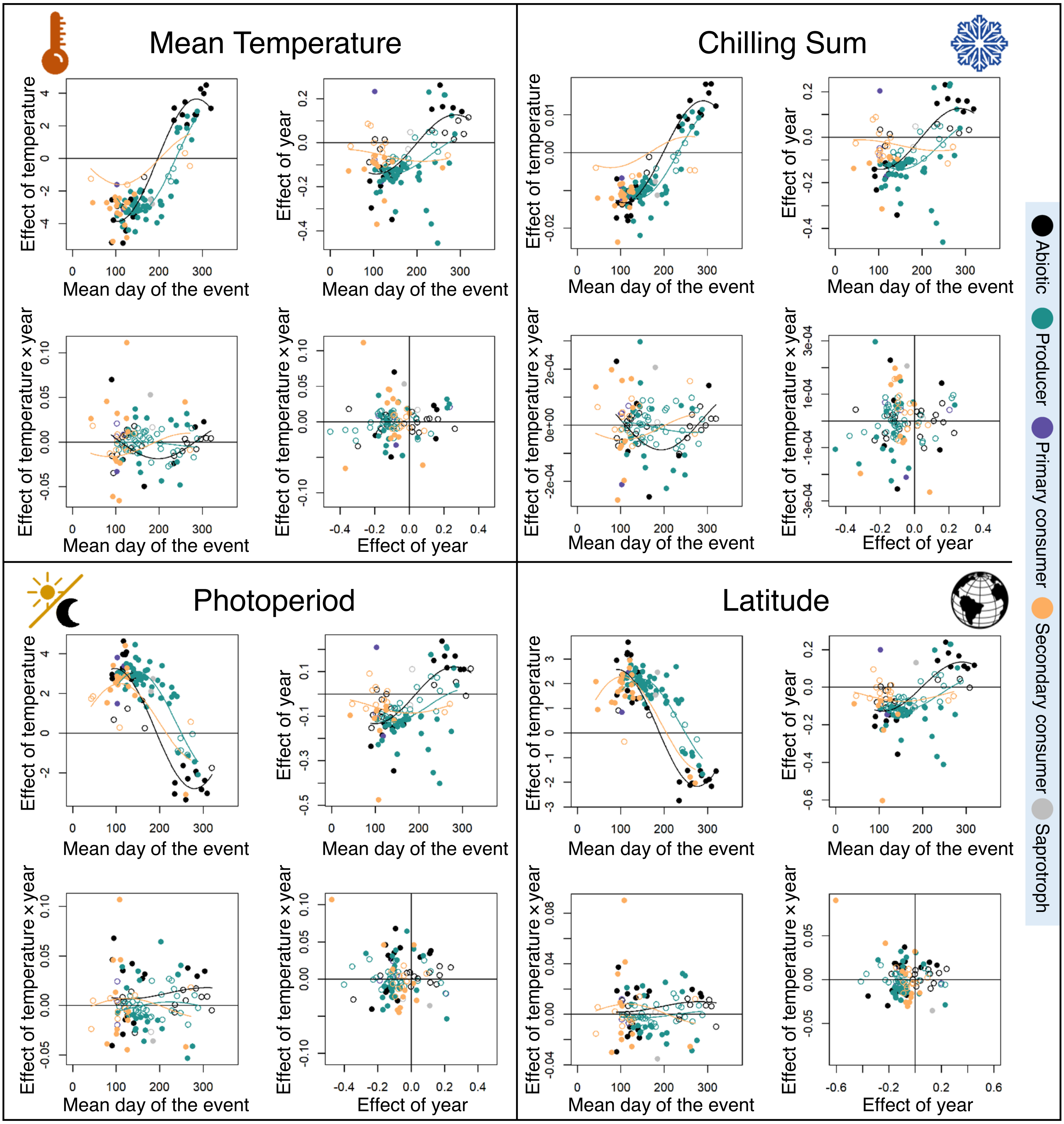
Extended Data Fig. 1 | Variance partitioning of alternative HMSC-models. Plots show the partitioning of the overall variance of the data into the model components identified in the figure legend. Individual panels show results for models with identical structure but using alternative climatic descriptors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



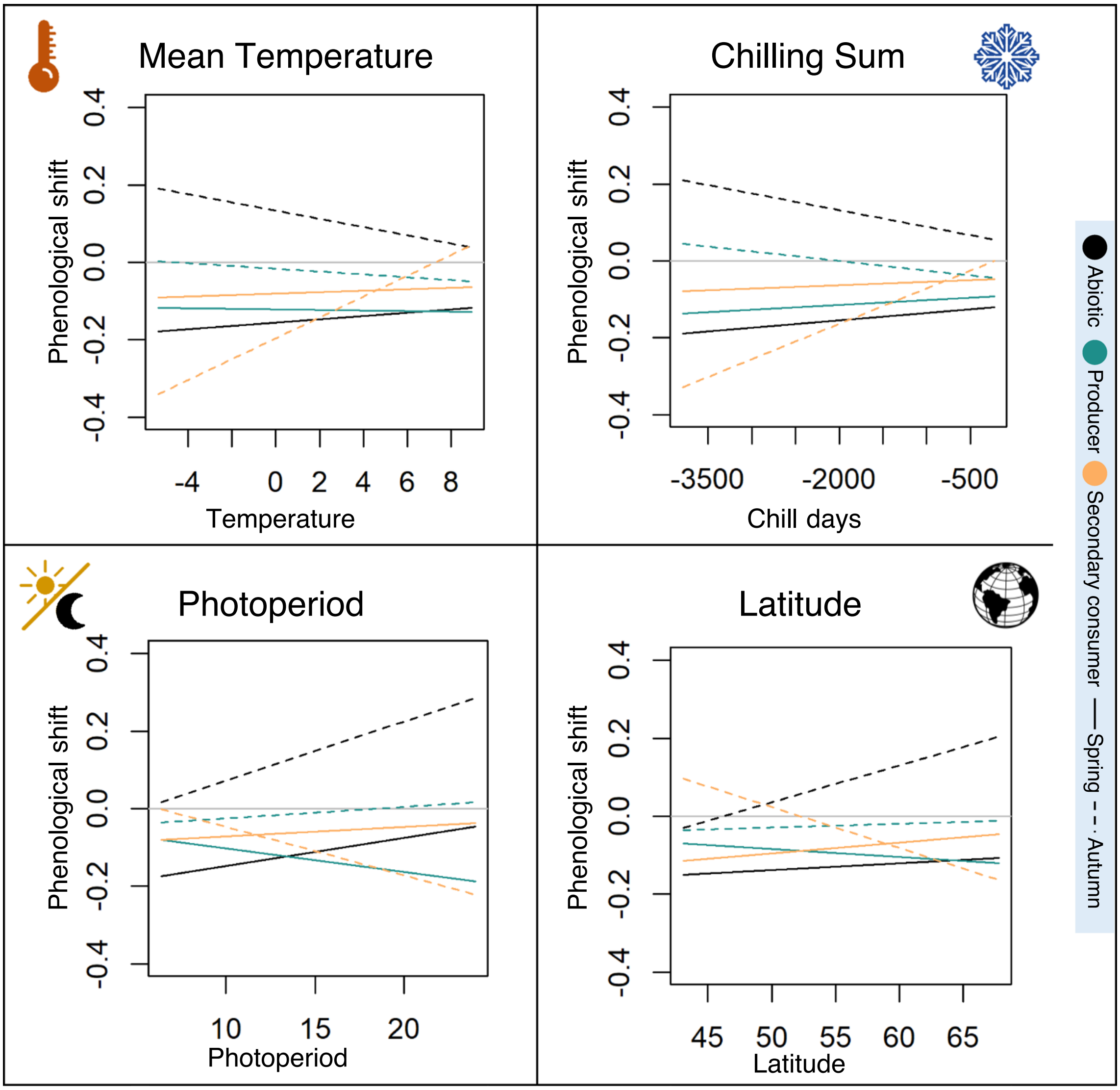
Extended Data Fig. 2 | Explanatory power of alternative HMSC-models. Plots show the degree of determination (R^2) as a function of the timing of the event (mean day of the year when the event occurs) and the trophic level of the organism expressing the event (different colours). Curves show second-order models fitted to groups with at least 5 events; continuous lines show mean model prediction and dashed lines ± one standard error. Individual panels show results for models with identical structure but using alternative climatic descriptors of the sampling sites; note that the top-left panel corresponds to Fig. 2a of the main text. Silhouettes adapted from https://thenounproject.com.



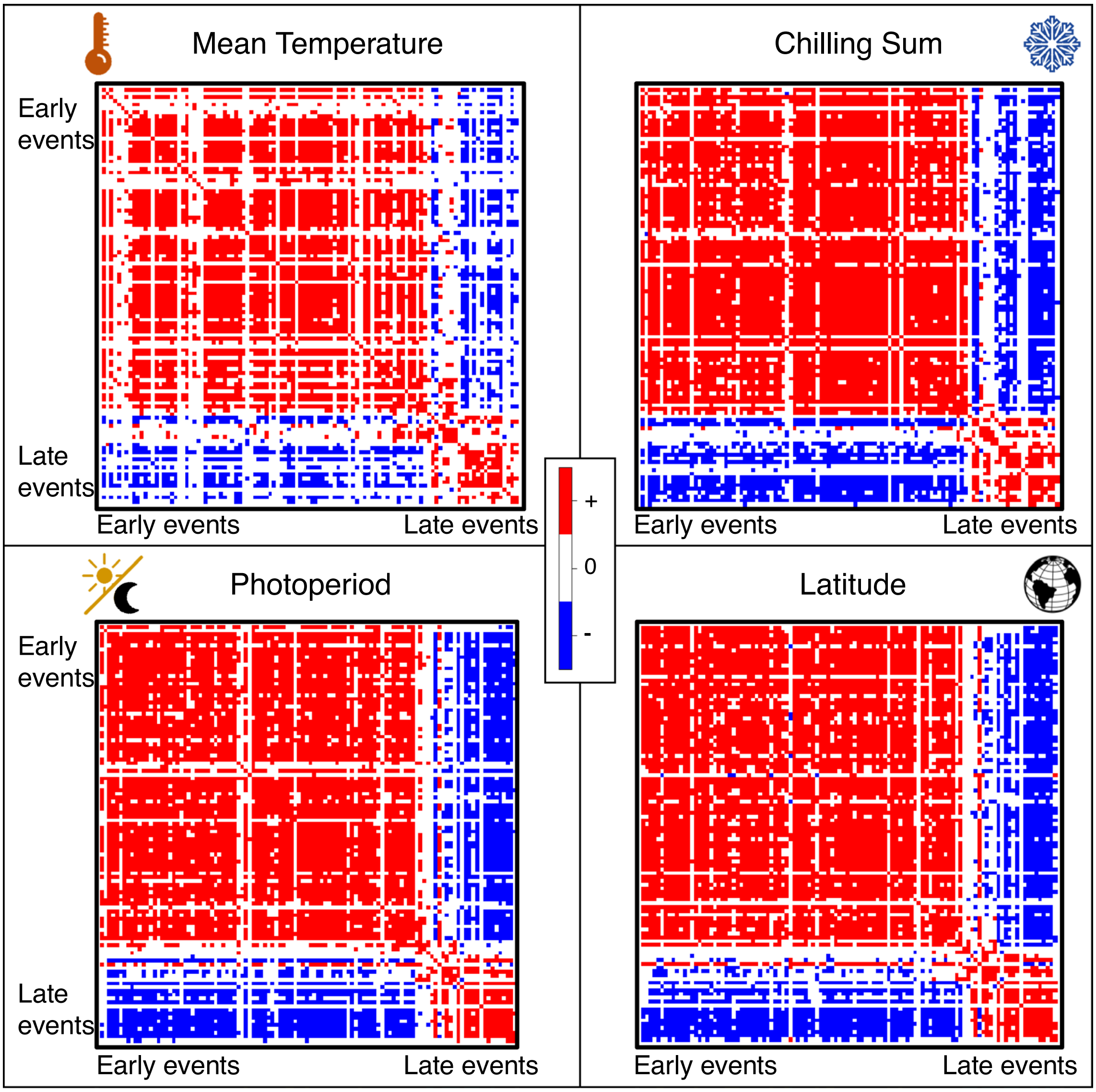
Extended Data Fig. 3 | The sign of responses of phenological events to the fixed effects included in the HMSC model. Plots show cases for which the response is positive (red) or negative (blue) with at least 95% posterior probability. Events have been ordered according to their mean date (increasing from top to bottom). The covariates have been normalized to have zero mean, so that the main effect of the climatic descriptor relates to a data point collected at the middle of the study period, and the main effect of the year relates to a site with an average value of the climatic descriptor. Individual panels show results for models with identical structure but using alternative climatic descriptors of the sampling sites; note that the top-left panel corresponds to Fig. 3a of the main text. Silhouettes adapted from https://thenounproject.com.



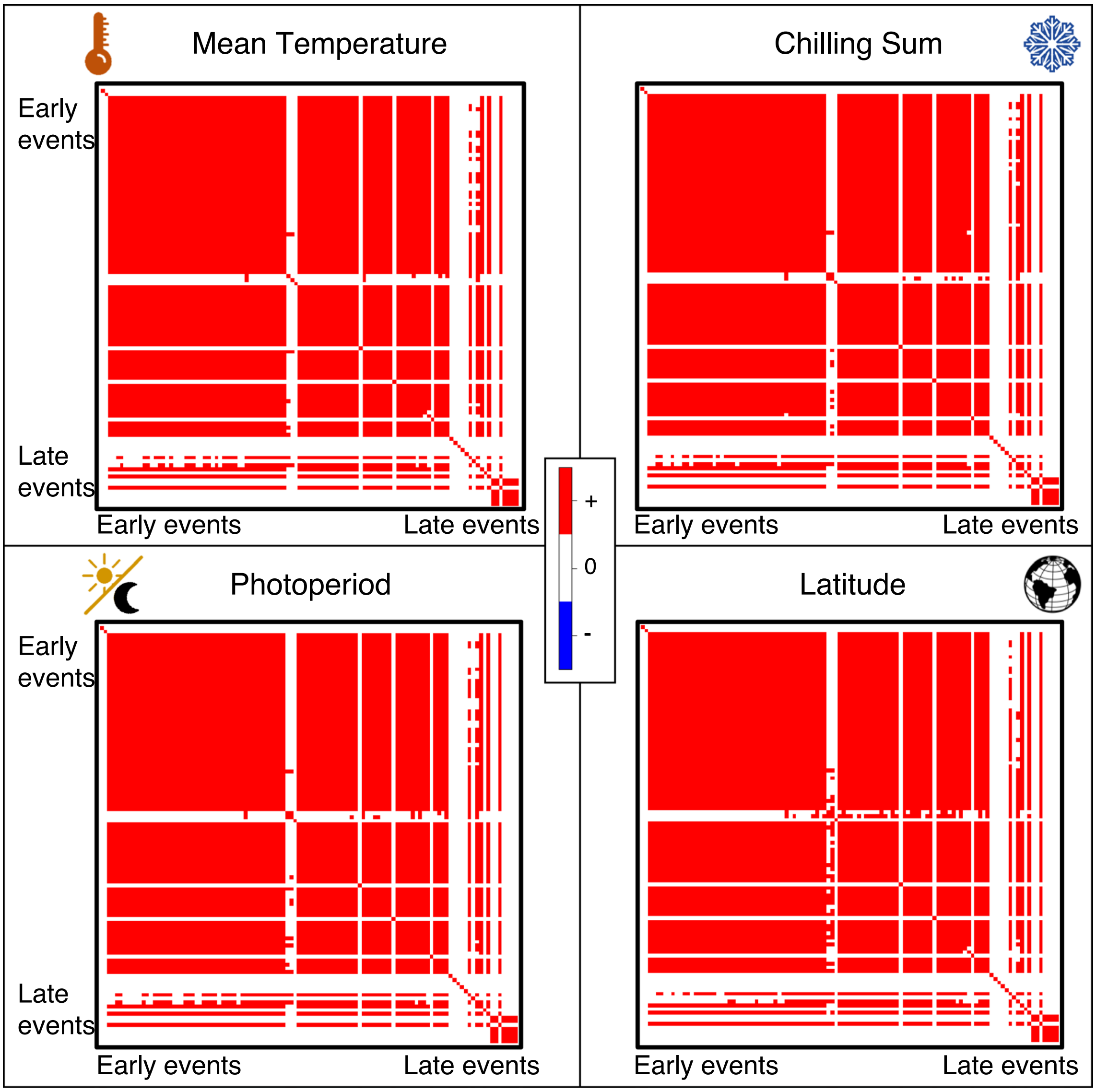
Extended Data Fig. 4 | Dependency of event-specific responses on phenological timing and on the trophic level of the organism expressing the event. Individual sections show results for models with identical structure but using alternative climatic descriptors of the sampling sites; note that the top-left section corresponds to Fig. 3b–e of the main text. Within each section, that is for each model, individual panels show the dependency of event-specific responses on phenological timing (mean day of the year when the event occurs) and on the trophic level of the organism expressing the event (shown by curves in different colours for those groups with at least 5 events). The covariates have been normalized to have zero mean, so that the main effect of the climatic descriptor relates to a data point collected at the middle of the study period, and the main effect of the year relates to a site with an average value of the climatic descriptor. In the bottom-right figure within each quadrat, we show the dependency of the response to year × temperature on the response to year; here, the four quadrats within the panel correspond to events that have shifted to earlier especially at cold sites (EC), shifted to earlier especially at warm sites (EW), shifted to later especially at cold sites (LC), and shifted to later especially at warm sites (LW). Filled symbols indicate cases that are either positive or negative with at least 95% posterior probability. Silhouettes adapted from https://thenounproject.com.



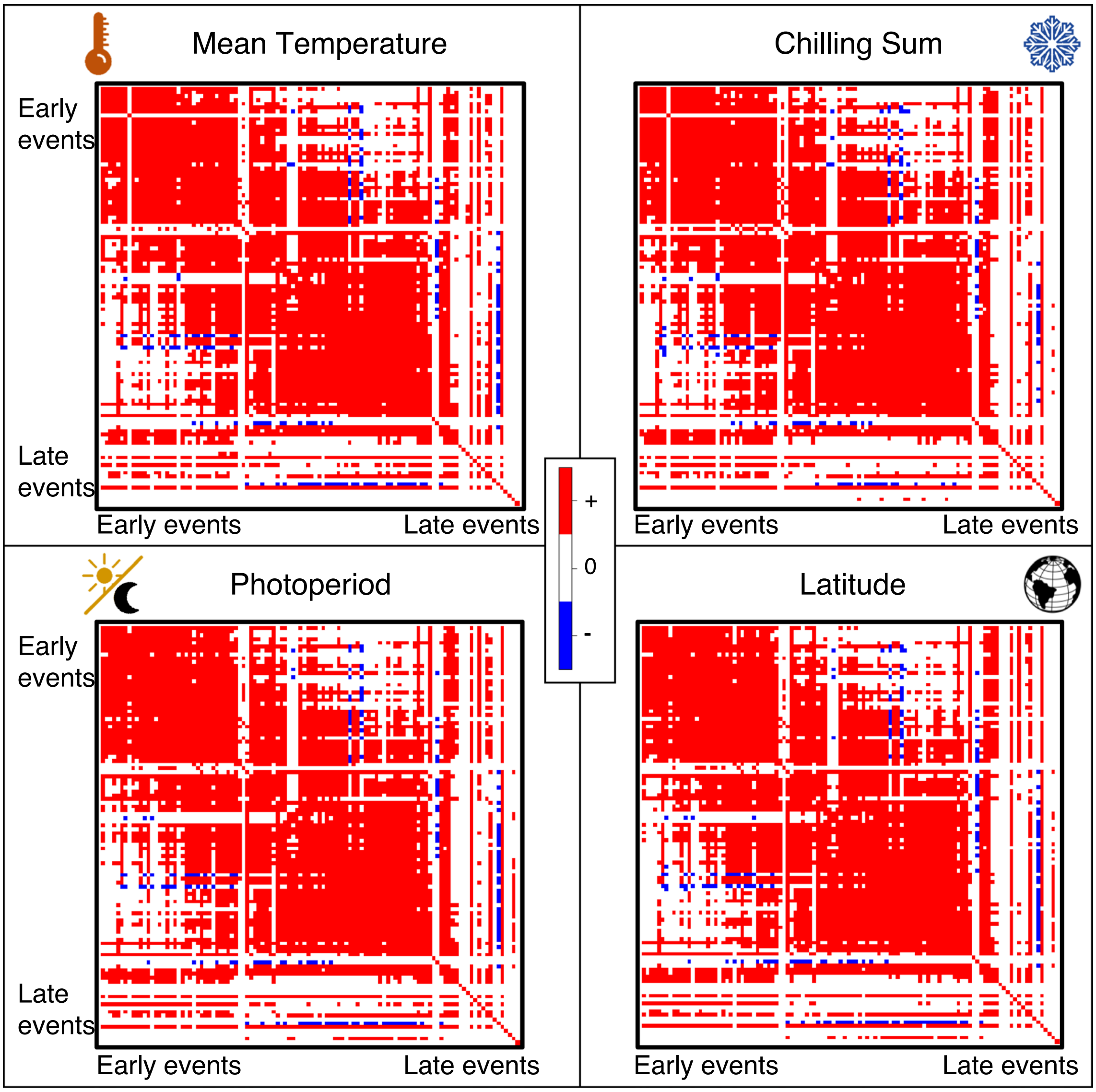
Extended Data Fig. 5 | Estimated shift in the phenological timing of events occurring in the spring versus autumn as functions of the average climate descriptors of the site. Plots show the estimated shift in the phenological timing (days per year) among events occurring in the spring (solid line, showing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



Extended Data Fig. 6 | Residual associations among events related to the random effects of the site. Plots show the estimates of associations among events measured by residual correlation at the site level. The events have been ordered according to their mean date (increasing from left to right, and from top to bottom). Event-to-event association matrices identify pairs showing a positive (red) or negative (blue) association, shown only if association has either sign with at least 95% posterior probability (the remaining cases are shown in white). Note that the top-left panel corresponds to Fig. 4a of the main text. Silhouettes adapted from https://thenounproject.com.



Extended Data Fig. 7 | Residual associations among events related to the random effects of the year. Plots show the estimates of associations between events measured by residual correlation at the year level. The events have been ordered according to their mean date (increasing from left to right, and from top to bottom). Event-to-event association matrices identify pairs showing a positive (red) or negative (blue) association, shown only if association has either sign with at least 95% posterior probability (the remaining cases are shown in white). Note that the top-left panel corresponds to Fig. 4b of the main text. Silhouettes adapted from https://thenounproject.com.



Extended Data Fig. 8 | Residual associations among events related to the random effects of the year-site pair. Plots show the estimates of associations among events measured by residual correlation at the level of samples, that is year×site combinations. The events have been ordered according to their mean date (increasing from left to right, and from top to bottom). Event-to-event association matrices identify pairs showing a positive (red) or negative (blue) association, shown only if association has either sign with at least 95% posterior probability (the remaining cases are shown in white). Note that the top-left panel corresponds to Fig. 4c of the main text. Silhouettes adapted from https://thenounproject.com.

Corresponding author(s): Tomas Roslin

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used for data collection
Data analysis	R3.6.2 was used for data analysis. The code needed to replicate the current analyses, from data extraction to parameter estimates presented, is available at https://doi.org/10.5281/zenodo.3774386

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

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The data that support the findings of this study are described in Ovaskainen et al. 2020. Chronicles of nature calendar, a long-term and large-scale multitaxon database on phenology. Scientific Data 7, 47 and freely available through Ovaskainen, O. et al. (2020) Chronicles of Nature Calendar, a long-term and large-scale multitaxon database on phenology. Zenodo https://doi.org/10.5281/zenodo.3607556. The exact subset of the data used in the present analyses is available at https://doi.org/10.5281/zenodo.3774386.

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Data used in this study were extracted from an extensive, large-scale, long-term and multitaxon database on phenological and climatic variation, involving 506,186 observation dates acquired in 471 localities in Russian Federation, Ukraine, Uzbekistan, Belarus and Kyrgyzstan. The data cover the period 1890–2018, with 96% of the data being from 1960 onwards. The database is rich in plants, birds and climatic events, but also includes insects, amphibians, reptiles and fungi. The data were acquired using standardized methods by permanent staff of national parks and nature reserves (87% of the data) and members of a phenological observation network (13% of the data). The full data set is described in Ovaskainen et al. 2020. Chronicles of nature calendar, a long-term and large-scale multitaxon database on phenology. Scientific Data 7, 47 and freely available through Ovaskainen, O. et al. (2020) Chronicles of Nature Calendar, a long-term and large-scale multitaxon database on phenology. Zenodo https://doi.org/10.5281/zenodo.3607556.
Research sample	We used existing datasets as described above.
Sampling strategy	The sample size in this study was not pre-determined but essentially driven by the availability of data. Using the data exclusion criteria documented below, we retained 70,709 phenological observations for 110 events across 113 locations.
Data collection	The data were collected by a number of observers For a description of data collection procedures , see Ovaskainen et al. 2020. Chronicles of nature calendar, a long-term and large-scale multitaxon database on phenology. Scientific Data 7, 47. The data on climatic variables were derived by GT and OO. To compute the mean annual temperature and the mean annual chilling sum, we used the ERA5-Land data (representing the period 1979-2019). To calculate the photoperiod, we used the daylength function of the R-package geosphere.
Timing and spatial scale	The data included 52 taxa and four types of meteorological events (see Supplementary Info, Table S1.1), and covered the period between 1960-2017 (earlier records were excluded), spanning 43.08°–67.82° latitude and 21.15°–136.15° longitude. For a map of the spatial extent, see Fig. 1 in the paper.
Data exclusions	From the original data set of Ovaskainen et al (2020, described above), we selected events for which there were at least 100 data points in total, and at least 10 data points from at least 10 sites. Further, we only included sites that were at least 25 km apart, and sampling units for which there were at least 10 events recorded. All anthropogenic events, such as dates for sowing and harvest, were excluded from this analysis. The exact subset of the data used in the present analyses available at https://doi.org/10.5281/zenodo.3774386
Reproducibility	Our study is not based on experiments. We provided data sources and R codes for reproducibility
Randomization	In the analyses we used as many species and survey sites as possible, based on the criteria described above. The key analyses were repeated using four different climatic descriptors, with the Results documented in Extended Data Fig. 1-8.
Blinding	Blinding is not relevant to our study as we did not use any experiments.

Did the study involve field work? ☐ Yes ☒ No

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Materials & experimental systems

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☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	This study did not involve laboratory animals
Wild animals	We used observation data on phenological events (with details shown in Supplementary Data Table S1). Sex and age were not recorded in the surveys.
Field-collected samples	This study did not involve samples collected from the field.
Ethics oversight	No ethical approval was required because this study is based on observation data. The species and events observed were not disturbed or otherwise affected by the observers.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

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