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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 Soviet Union. 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 falls 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.

Main text

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] – i.e. 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

208 phenology in terrestrial areas has advanced by a global average of 2.3 to 2.8 days/decade[2,8,13], some
209 studies have suggested changes as fast as 30 days per decade[14]. Higher rates of advance are possibly
210 associated with lower trophic levels[3,12], as perhaps reflecting not only different sensitivity to
211 different drivers among trophic layers, but also different responses in terms of physiological
212 development[3]. 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[15]. On top of species-specific variation, there is also considerable site-specific
215 variation in phenological advance[16]. 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[16,17].

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[5], 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[6]. 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[18–20]. Such local and regional variation in
225 drivers[19,21,22] and sensitivity towards them[18,20] can be reflected in spatiotemporal variation in
226 phenological shifts[4,8,15,23,24]. While the few studies analyzing geographically extensive datasets on
227 phenology have observed spatial variation in temporal trends of phenological responses (e.g. [25,26])
228 and their main abiotic drivers[5,27–29], the question remains whether patterns of change and response
229 follow major environmental gradients in latitude, photoperiod or temperature[15,16,30].

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

231 Evaluating to what extent shifts in phenological events vary over space[31], with their annual
232 timing[3,11,12] or with trophic level[16,32] requires consistently sampled, community-wide data which are
233 both long-term and spatially extensive[3,12,16,32]. Such data may also give insights on whether local
234 phenology is influenced by biotic interactions beyond abiotic cues[7,33,34]. Unfortunately, systematic
235 community-wide data sets are still uncommon, hampering progress in understanding large-scale
236 taxonomic and geographic patterns in phenological change[35]. The few existing exceptions (e.g.
237 [2,4,8,15,36,37]) are built on sparse data and/or combining individual studies using variable methods
238 (e.g.[38]). 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[2,4,39]. 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[40].

243 Here, we draw on a uniquely comprehensive, long-term database established using uniform
244 protocols across northern Eurasia[41–43]. 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

variables)? When combined, these questions allow us to characterize how different components of the ecosystem have shifted their phenologies over the last 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[41] 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 (i.e., mean annual temperature, mean annual chilling sum, photoperiod, or latitude), with a separate model fitted for each descriptor (see below). Additionally, in order 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; e.g. 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; Table S1) versus biotic events (n= 82; e.g. 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; Table S1), 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; Table S1). To evaluate how the multivariate response (i.e. 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. 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[41,43]. 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[5,6,8]. 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

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; i.e. 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.

Additionally, 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 which have actually shifted later at cold sites but earlier at warm sites, we 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 e.g. 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 within autumn events, but negatively associated between spring and autumn events (Fig. 4a); i.e., at any given site, spring events tended to occur particularly early while all autumn events 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; see 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 which is only partly captured by simple environmental gradients (for potential explanations, see below). 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 (i.e. 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 unexplicable 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. While 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. The strong effect of site beyond the effect of mean temperature (as shown by the overall partitioning of variance in our model; Figs. 2 and Extended Data Fig. 2) importantly qualifies the expectation of a strong and general pattern of phenology change along latitudinal or other environmental gradients [17]. Yet, it is consistent with our previous work[17] showing that phenological plasticity is constrained by local differentiation in reaction norms to temperature cues[44], i.e., by local adaptation (see also[18,45]). 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, 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 suggested by the overall effect of year. The strong dominance of positive residual associations between event-pairs at the random sample level (Figs. 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[41,43]. It is also worth noting that beyond biotic interactions, this result is likely to partly reflect the synchronizing effect of abiotic conditions which affect multiple events, as well as the fact that different phenophases within one and the same species are interconnected with each other (e.g 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 dependencies, we note that while we scored two or more separate phenological events in several species (Supplementary Information, Table S1), 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 of evidence for an imprint of biotic interactions on community-level phenology[7,33,34].

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

As proposed by Burrows et al.[17,52], 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[3,17,18,22,53–56]. Mismatches between the velocity of climate change and realised seasonal shifts may help identify regions of concern, e.g. 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[1,11,56] and potentially affect community structure and persistence. Importantly, 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 (e.g. [35]).

Accumulated negative effects of rapid seasonal shifts across many species may threaten biodiversity[14,57,58]. Surprisingly enough, our current findings suggest that phenological shifts during the last 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, i.e. 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 [21]. 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 a first attempt in this direction, and will hopefully inspire more work to come.

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Methods

We used data from Ovaskainen et al.[59], who compiled dates of phenological events (for concrete examples, see Supplementary Information, Table T1.1) 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 (e.g., ice formation and first day of snowfall). The data were curated by EarthCape[60] and published on Zenodo[59]. 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 four types of meteorological events (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.

The sampling units consist of (site, year) pairs. We denote by y_{ij} the date on which the phenological event *j* took place in sampling unit i. These are combined in the data matrix $\mathbf{Y} = \{y_{ij}\}$ with $j = 1, \dots, n_s = 110$ events recorded in $i = 1, \dots, n_y = 2789$ sampling units. The data consist of 70,709 dates, so that 77% of the entries in the **Y** matrix are missing (NA) due to not all events being recorded in all sites and in all years. To these data, we fitted Hierarchical Modeling of Species Communities (HMSC) models[41,43]. HMSC is a multivariate Bayesian generalized linear 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[41–43]. Additionally, HMSC allows including trait information to inform species-level
585 responses to model covariates[41] – 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 alternatives variables based
594 on [29], 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[61] and other biogeographic analyses[62]. 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)[63,64].
606 To calculate the photoperiod, we used the daylength function of the R-package geosphere[65].

To examine how the shifts and their dependency on the climatic conditions co-varied among different types of phenological events, we also included event-level predictors (i.e., species traits in the HMSC framework): (1) the mean timing of each event (calculated as the mean day of the year over the entire data set); 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 (i.e. year-site pairs). All of these were modelled at the community-level, using the latent variable approach of HMSC[41,43]. 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, we refer the reader to [41–43].

We fitted the models with package Hmsc[42] in R[66] assuming the default prior distributions (see[42,43]). 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 (β –parameters) and the random effects (Ω-parameters), equivalent to the Gelman-Rubin statistic[67].

Overall, we note that 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 [40,59], 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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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.

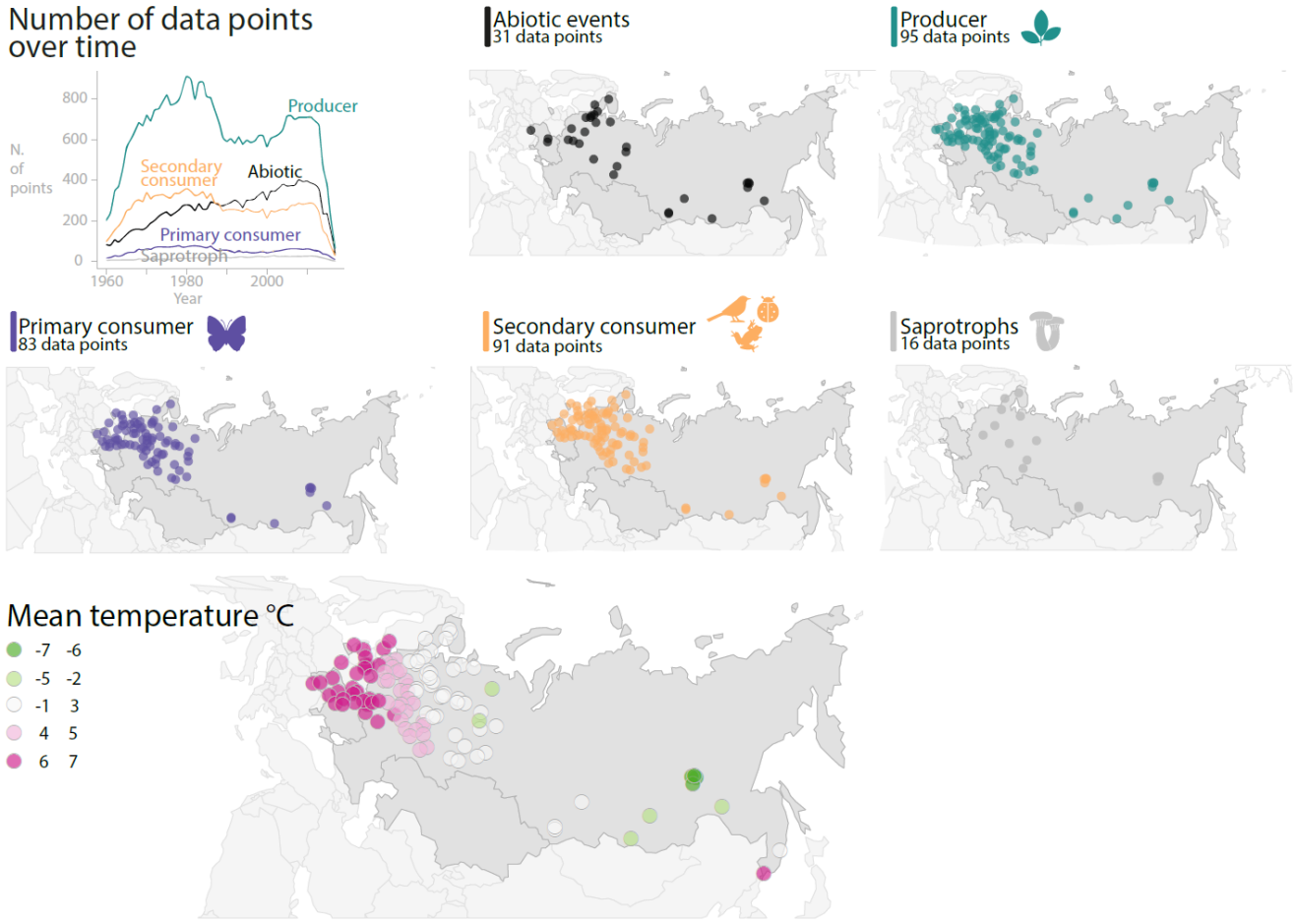
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697 **Competing Interests**

698 The authors declare no competing interests.

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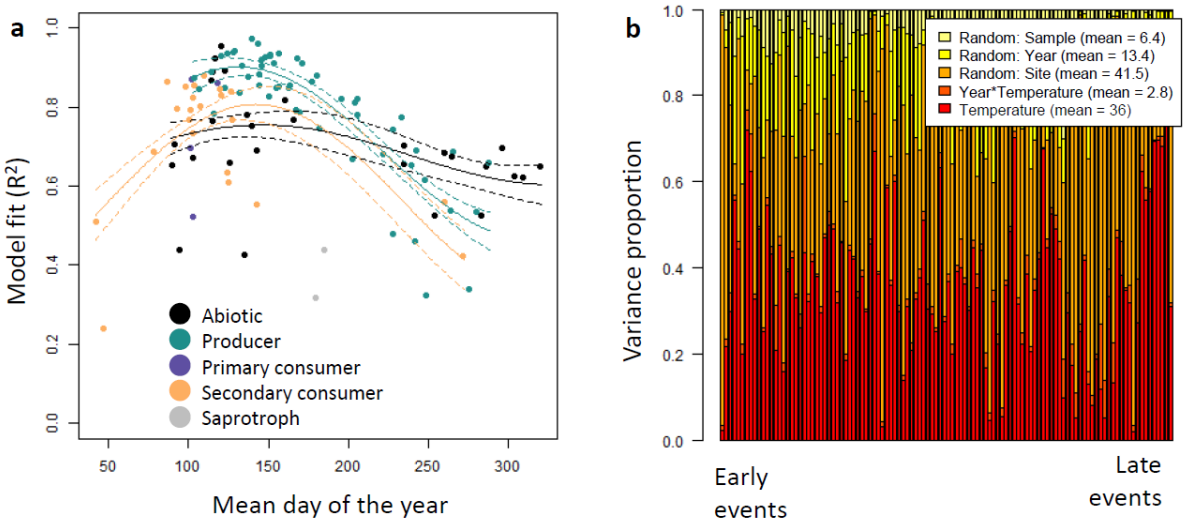
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701

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).

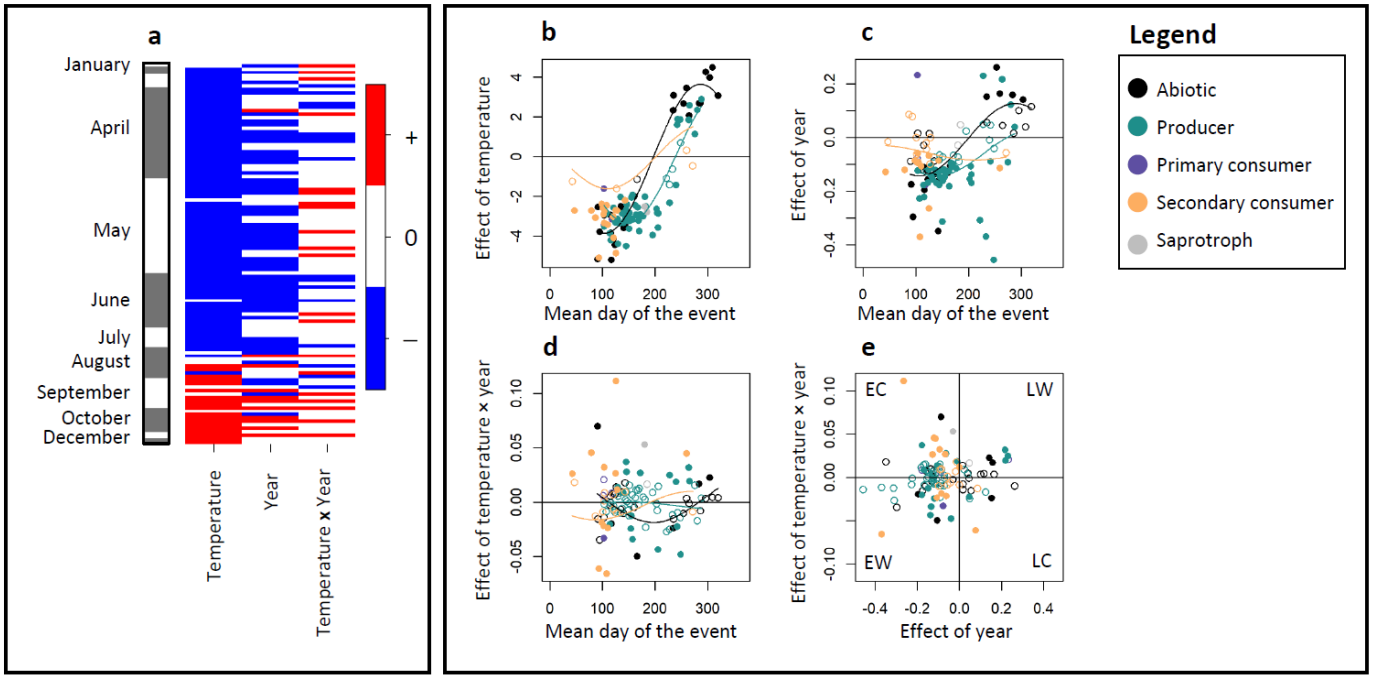
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710

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 ±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).

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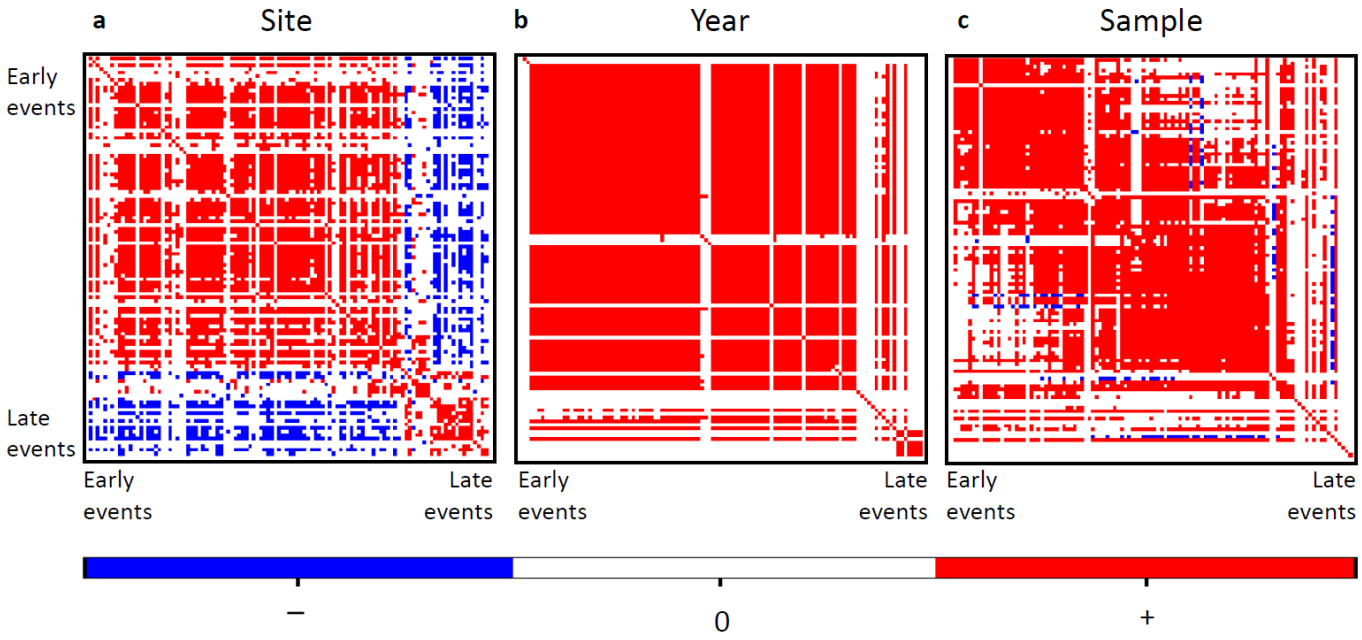


720

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.

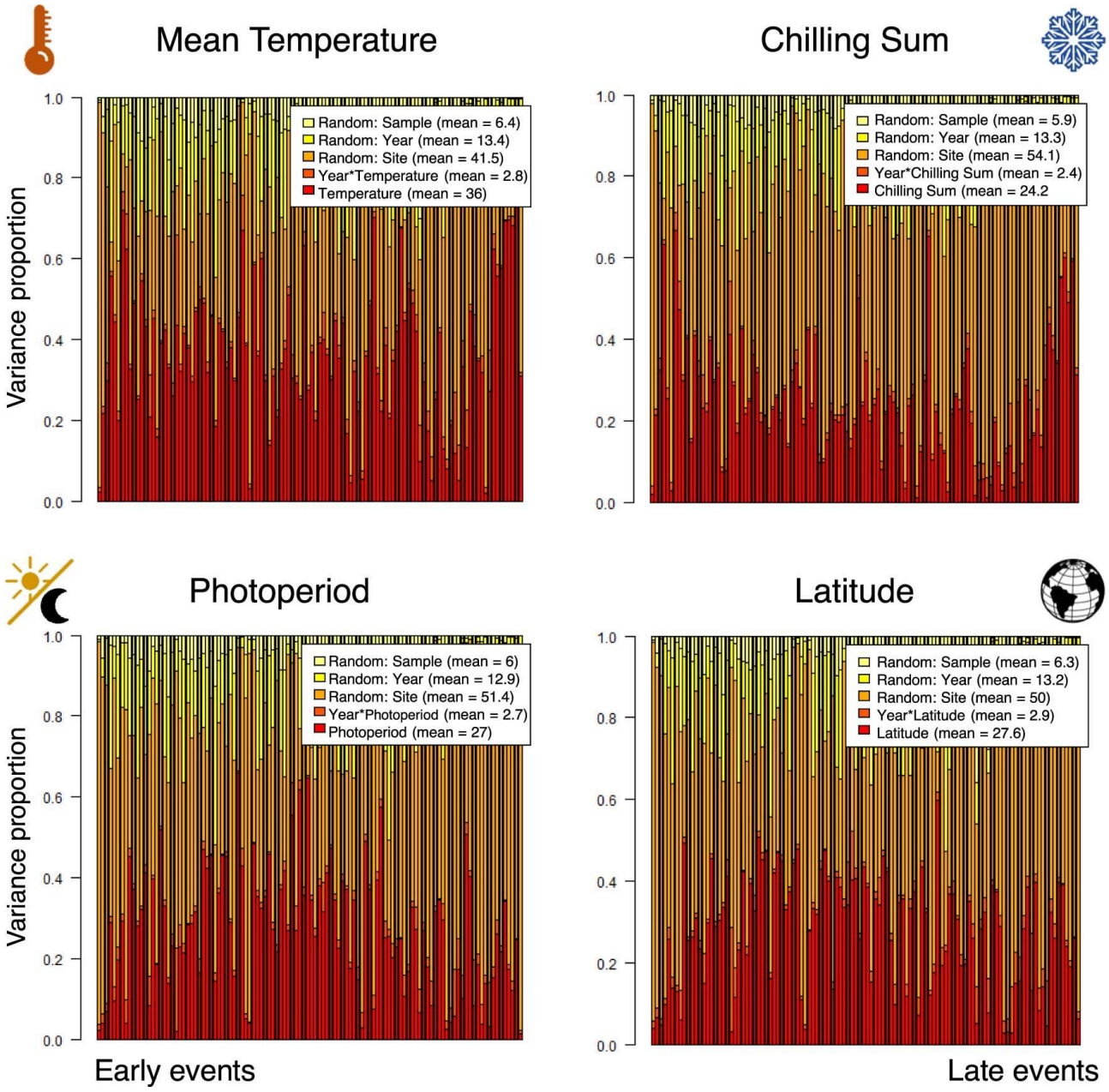
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739

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×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.

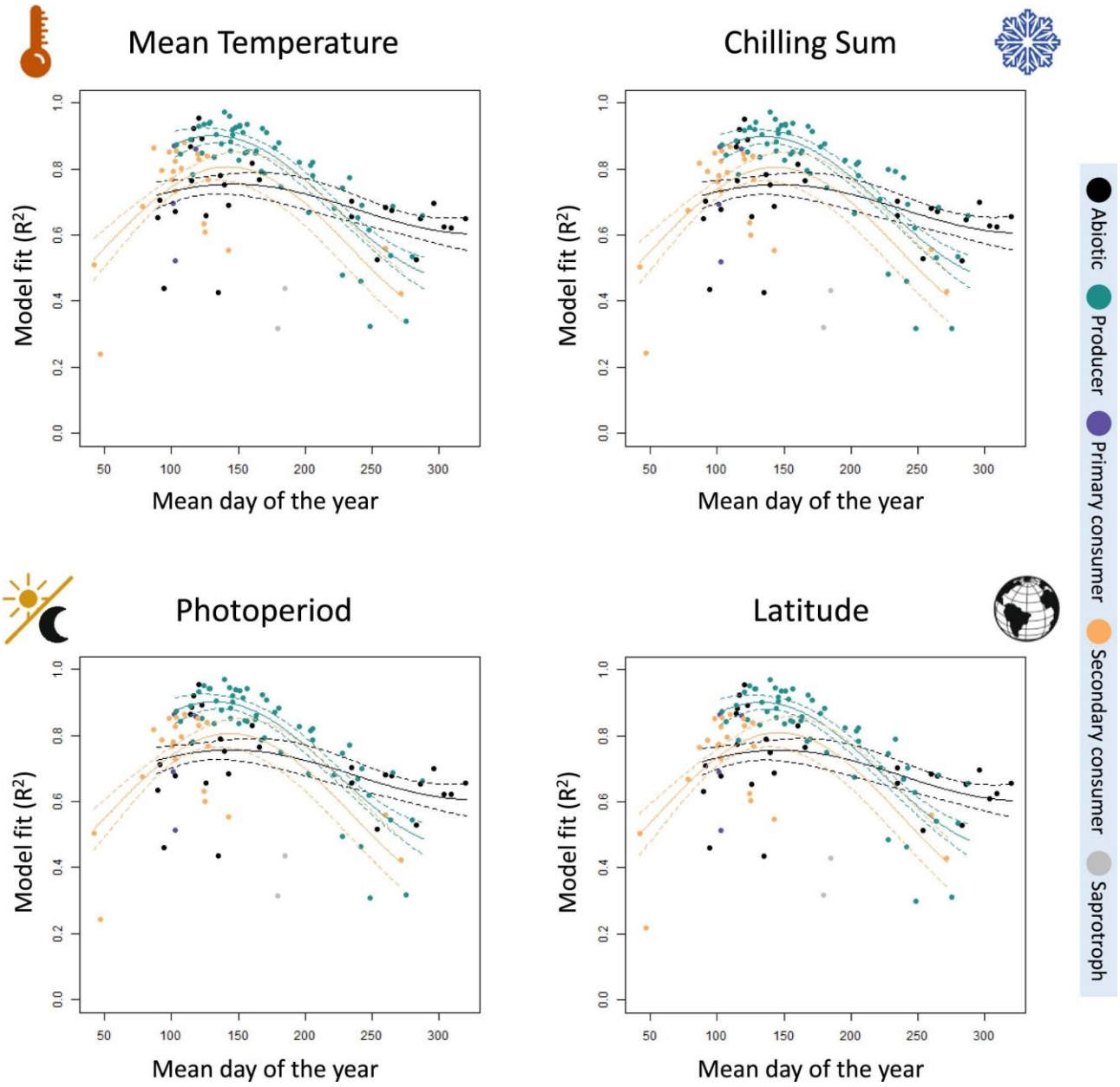
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747

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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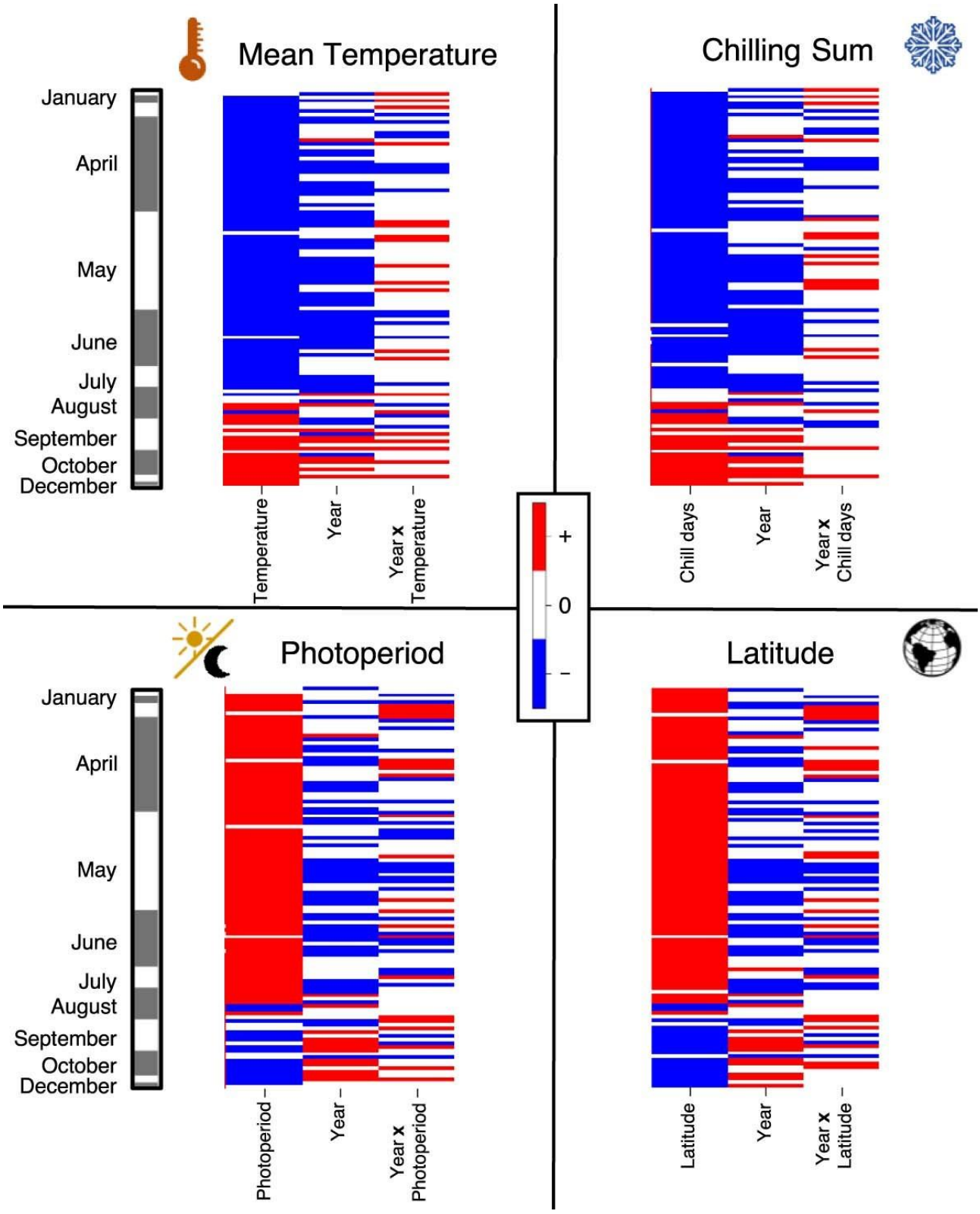
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755 **Extended Data Fig. 2: Explanatory power of alternative HMSC-models.** Plots show the degree
756 of determination (R2) as a function of the timing of the event (mean day of the year when the event
757 occurs) and the trophic level of the organism 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 ± 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.

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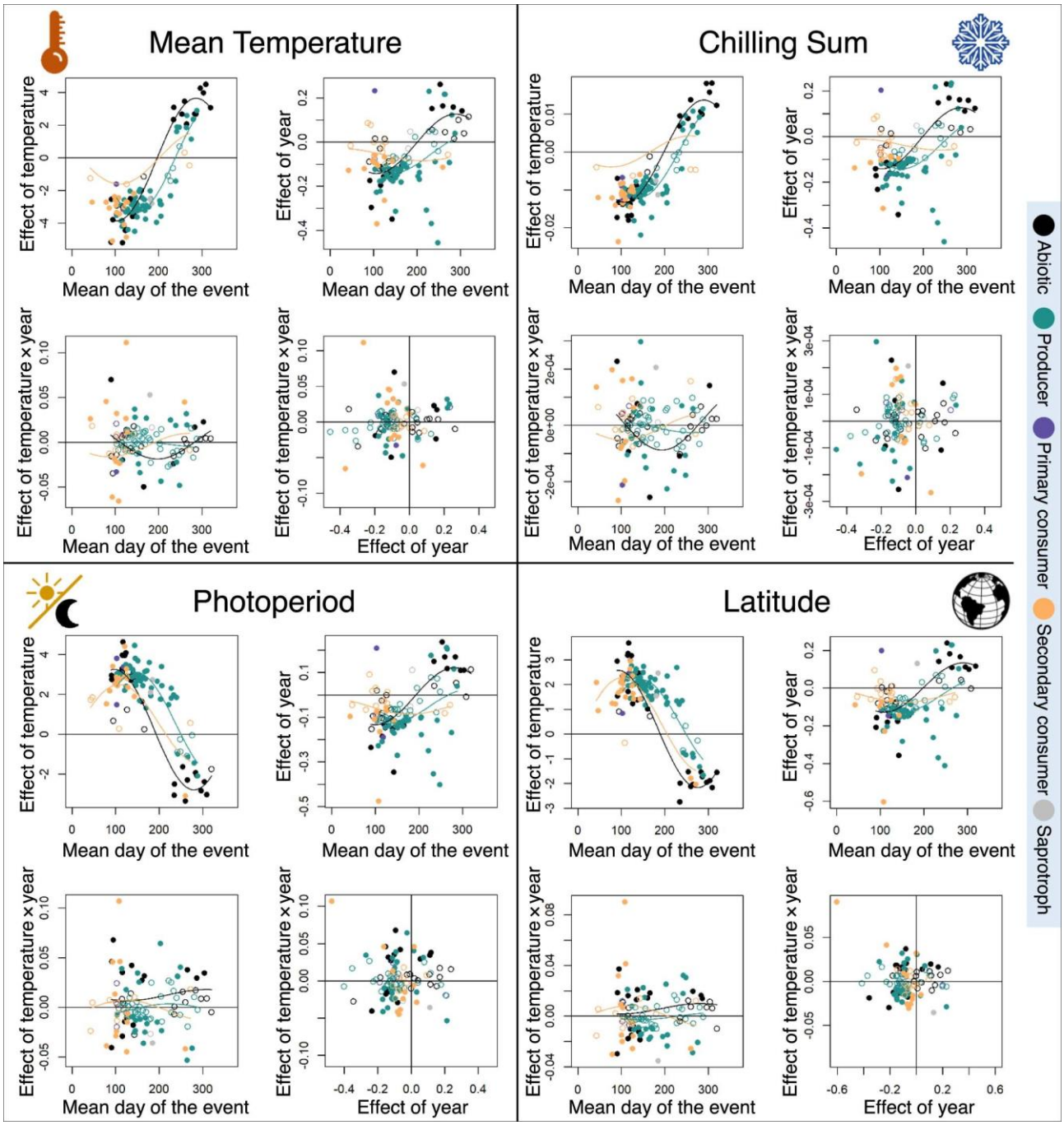
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765 **Extended Data Fig. 3: The sign of responses of phenological events to the fixed effects**

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

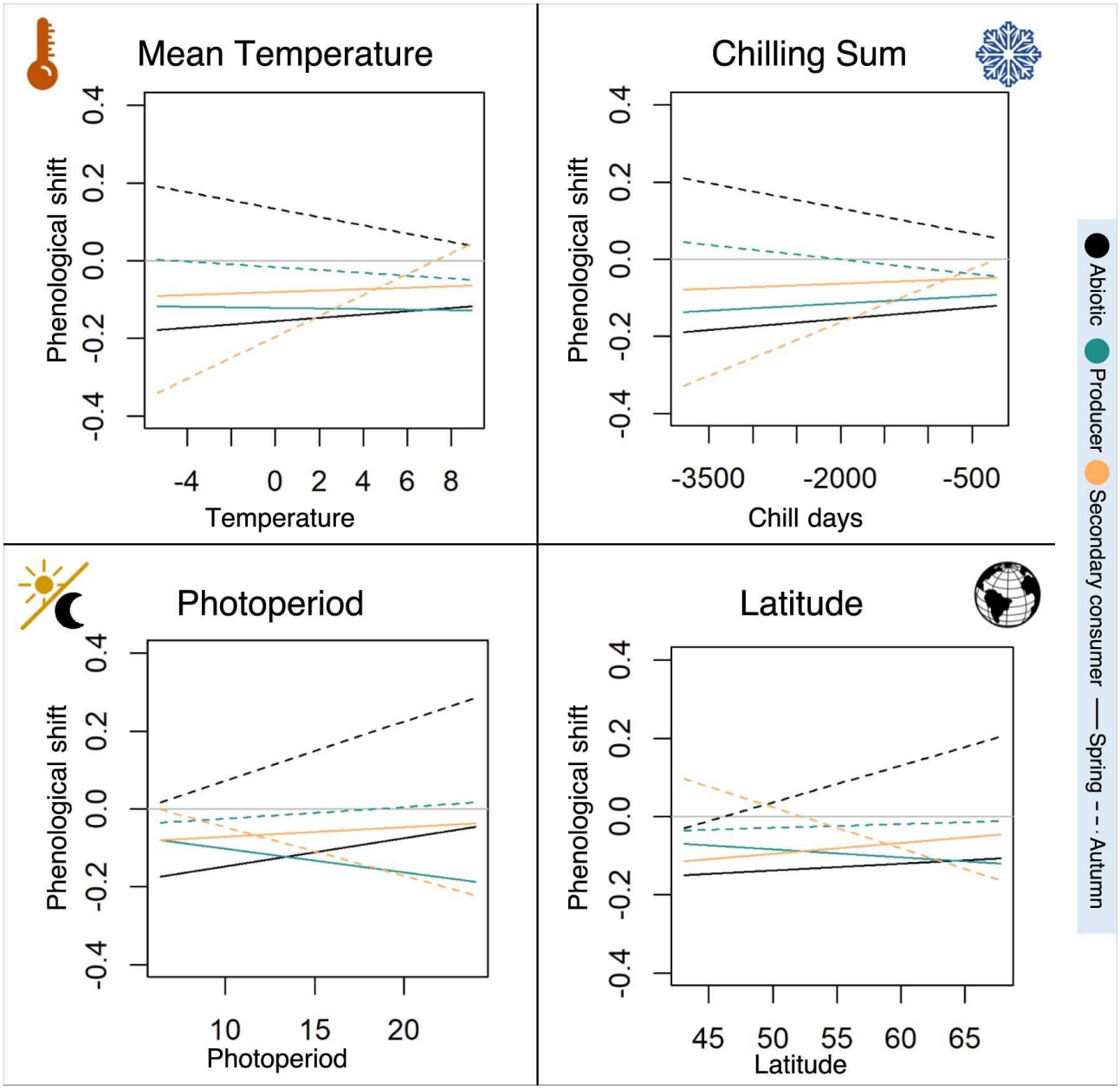


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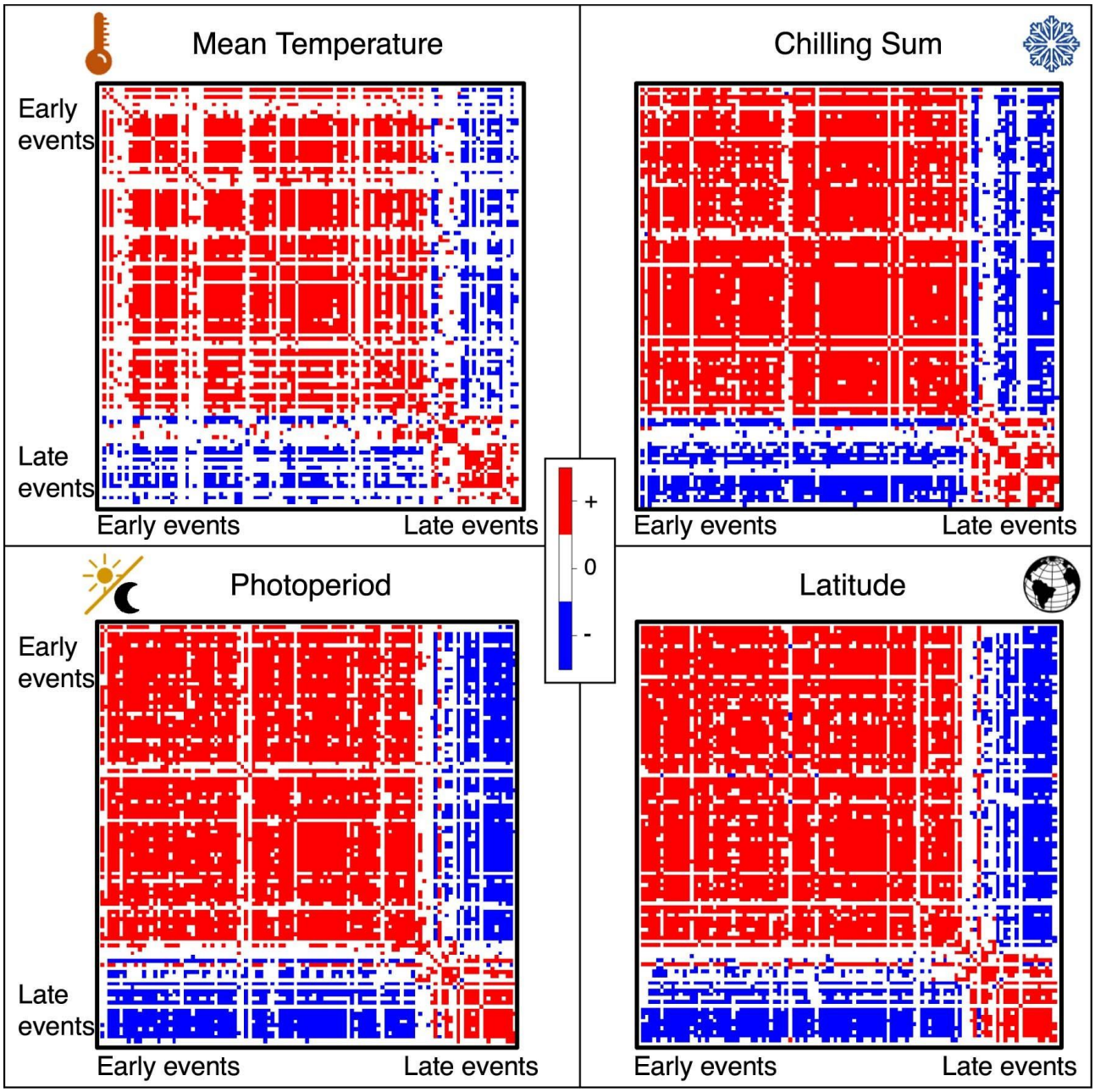
776 **Extended Data Fig. 4: Dependency of event-specific responses on phenological timing and on**
777 **the trophic level of the organism expressing the event**. Individual sections show results for
778 models with identical structure but using alternative climatic descriptors of the sampling sites; 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 × 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.

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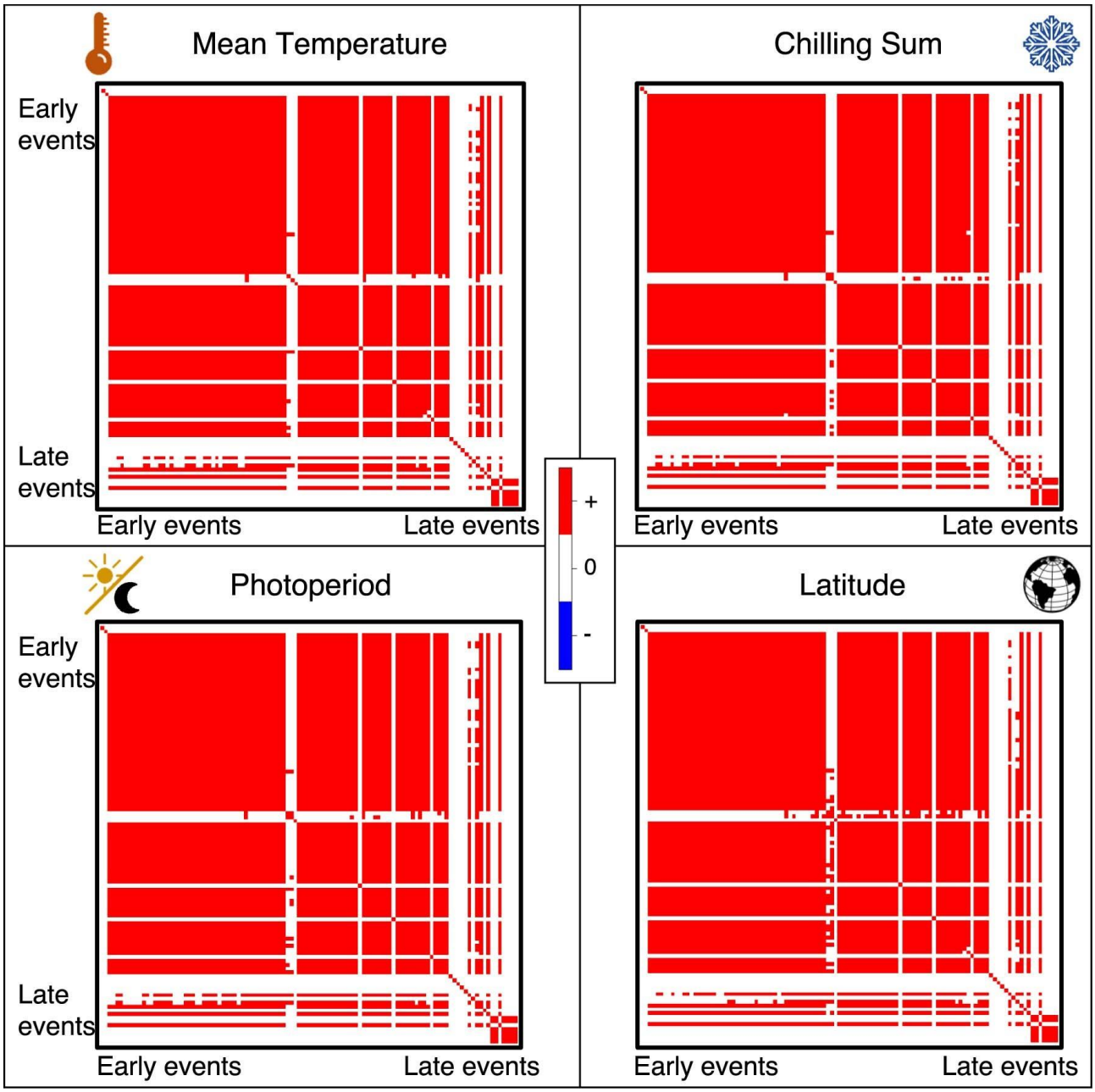


Extended Data Fig. 5: Estimated shift in the phenological timing of events occurring in the spring versus autumn as functions of the average climate descriptors of the site. Plots show the estimated shift in the phenological timing (days per year) among events occurring in the spring (solid line, showing 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.



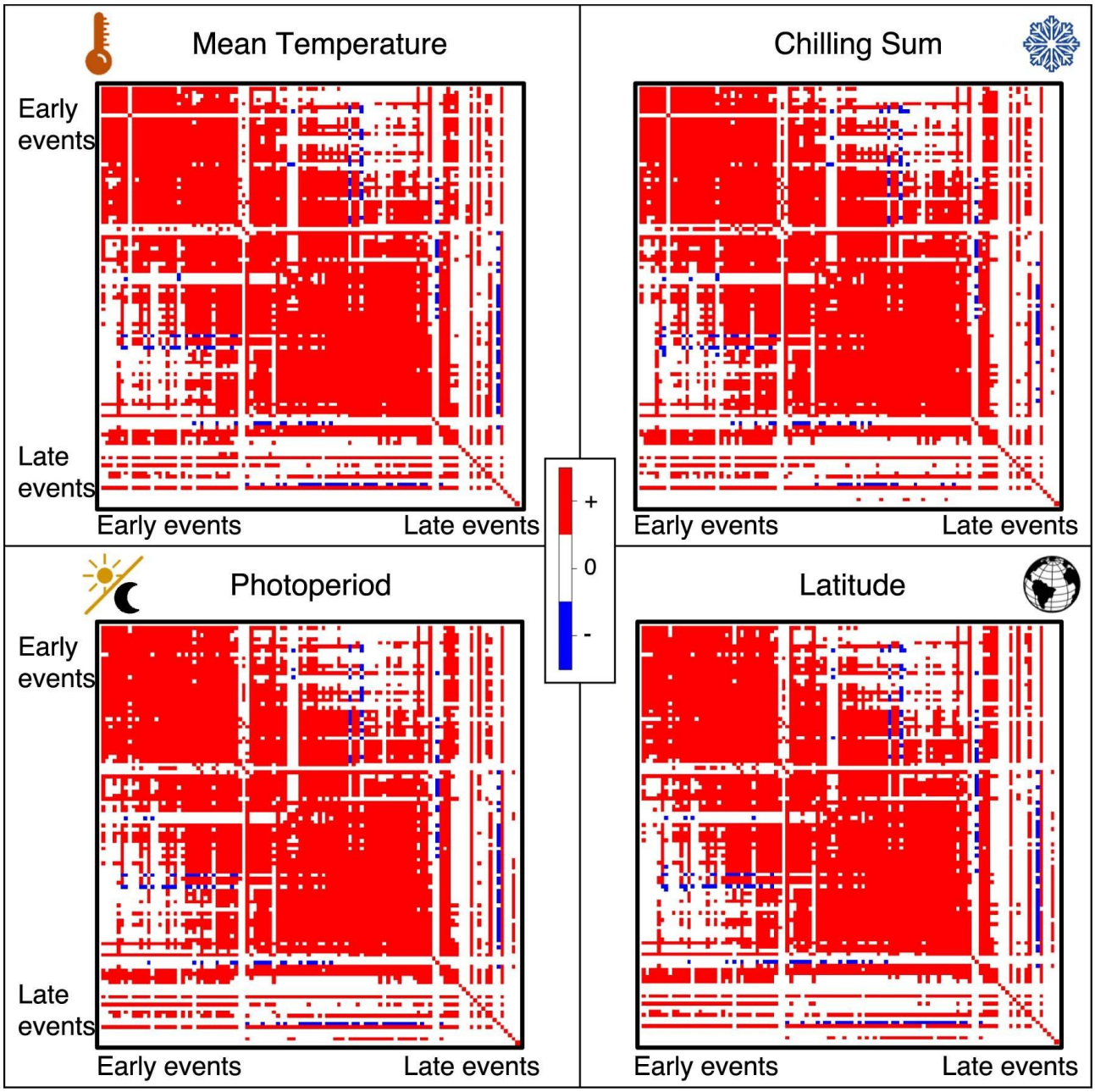
Extended Data Fig. 6: Residual associations among events related to the random effects of the site. Plots show the estimates of associations among events measured by residual correlation at the site level. The events have been ordered according to their mean date (increasing from left to right, and from 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

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 holometaboulous 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[1]. 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**
AVES			
Alaudidae			
Alauda arvensis	Secondary consumer	1st song*	93.14
Anatidae			
Anas crecca	Secondary consumer	1st occurrence	119.73
Anas platyrhyncos	Secondary consumer	1st occurrence*	101.64
Cygnus cygnus	Secondary consumer	1st occurrence	107.42
Bucephala clangula	Secondary consumer	1st occurrence	109.81
Apodidae			
Apus apus	Secondary consumer	1st occurrence*	142.78
Charadriidae			
Vanellus vanellus	Secondary consumer	1st occurrence	100.43
Corvidae			
Corvus frugilegus	Secondary consumer	1st occurrence	78.54
Cuculidae			
Cuculus canorus	Secondary consumer	1st song*	127.64
Fringillidae			
Fringilla coelebs	Secondary consumer	1st occurrence*	98.12
Gruidae			
Grus grus	Secondary consumer	1st occurrence	103.00
Hirundinidae			
Hirundo rustica	Secondary consumer	1st occurrence*	124.57
		Last occurrence	259.44
Motacillidae			
Motacilla alba	Secondary consumer	1st occurrence*	103.11
		Last occurrence	271.23

Muscicapidae			
Luscinia luscinia	Secondary consumer	1st song	125.15
Paridae			
Parus major	Secondary consumer	1st song	42.33
Picidae			
Dendrocopos major	Secondary consumer	Start of drumming	46.91
Sturnidae			
Sturnus vulgaris	Secondary consumer	1st occurrence	86.51

FUNGUS			
Boletaceae			
Leccinum aurantiacum	Saprotroph	1st occurrence	179.67
Leccinum scabrum	Saprotroph	1st occurrence	184.60

INSECTA			
Apidae			
Bombus sp	Primary consumer	1st occurrence	118.04
Culicidae			
Culicidae sp	Secondary consumer	1st occurrence	126.78
Formicidae			
Formica rufa	Secondary consumer	Livening up	103.83
Nymphalidae			
Aglais urticae	Primary consumer	1st occurrence	101.22
Pieridae			
Gonepteryx rhamni	Primary consumer	1st occurrence	102.30

MAMMALIA			
Ursidae			
Ursus arctos	Secondary consumer	Awakening	102.49

PLANTAE			
Asparagaceae			
Convallaria majalis	Producer	Onset of blooming	144.47
Maianthemum bifolium	Producer	Onset of blooming	167.92
Astaraceae			
Leucanthemum vulgare	Producer	Onset of blooming	169.79
Taraxacum officinale	Producer	Onset of blooming	131.87
Tussilago farfara	Producer	Onset of blooming	106.95
Betulaceae			
Betula pendula	Producer	Onset of sap bleeeding	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
Caprifoliaceae			
Lonicera caerulea		Onset of blooming	150.41
Ericaceae			
Oxycoccus palustris	Producer	Onset of blooming*	163.29
Ledum palustre	Producer	Onset of blooming	156.75
Vaccinium myrtillus	Producer	Onset of blooming	145.35

		Onset of fruiting (ripe)*	195.23
		Mass fruiting	204.14
Vaccinium vitis-idaea	Producer	Onset of blooming*	162.31
		Onset of fruiting (ripe)	227.44
		Mass fruiting	239.47
Fabaceae			
Caragana arborescens	Producer	Onset of blooming	148.28
Grossulariaceae			
Ribes nigrum	Producer	Onset of blooming*	145.99
		Onset of fruiting (ripe)	205.27
Malvaceae			
Tilia cordata	Producer	Onset of leaf unfolding	129.07
		Onset of blooming*	181.85
Oleaceae			
Syringa vulgaris	Producer	Onset of blooming	150.87
Onagraceae			
Epilobium angustifolium	Producer	Onset of blooming	180.06
Pinaceae			
Pinus sylvestris	Producer	onset of blooming*	153.18
Ranunculaceae			
Caltha palustris	Producer	Onset of blooming	133.70
Trollius europaeus	Producer	Onset of blooming	150.87
Rosaceae			
Fragaria vesca	Producer	Onset of blooming*	144.48
		Onset of fruiting (ripe)	176.94
Prunus padus	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
Rosa acicularis	Producer	Onset of blooming	171.34
Rubus chamaemorus	Producer	Onset of blooming*	154.64
Rubus idaeus	Producer	Onset of blooming*	166.83
		Onset of fruiting (ripe)	205.81
Sorbus aucuparia	Producer	Onset of blooming*	156.06
		Onset of fruiting (ripe)	227.55
Salicaceae			
Salix caprea	Producer	Onset of blooming*	123.08
Populus tremula	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
REPTILIA			
Squamata			
Zootoca vivipara	Secondary consumer	1st occurrence	120.50
METEO			

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	114.60
		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[2,3]. HMSC was primarily developed for community ecology, so that in a typical application the response matrix (**Y**) contains species occurrences or abundances on a set of sampling units (e.g. spatial locations), the environmental predictor matrix (**X**) contains e.g. climatic conditions in those sampling units, and the species trait matrix (**T**) includes species-level traits such as body size. HMSC allows to ask how species occurrences depend on environmental conditions (how **Y** depends on **X**), and how the species responses to environmental variation depend on their traits (how **T** modulates the mapping from **X** to **Y**). Additionally, HMSC includes community-level random effects implemented through latent variables; these allow the modelling of residual (not accounted for species responses to **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 **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 **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 **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 $y_{i\cdot}$, where the dot notation stands for the vector of y_{ij} values for all indices j, thus $y_{i\cdot}$ 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, β_{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 [2], 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), η_{sk}^s is the latent variable k for site s, and λ_{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 λ_{kj}^s as $\Omega_{j_1 j_2}^s = \sum_{h=1}^{n_f^s} \lambda_{hj_1}^s \lambda_{hj_2}^s$; see [2].
- Concerning the residual, we assume a linear model, so $\varepsilon_{ij} \sim N(0, \sigma_j^2)$, where σ_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 $\mu_{kj} = \mathrm{E}[\beta_{kj}]$ 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 saprotophs.

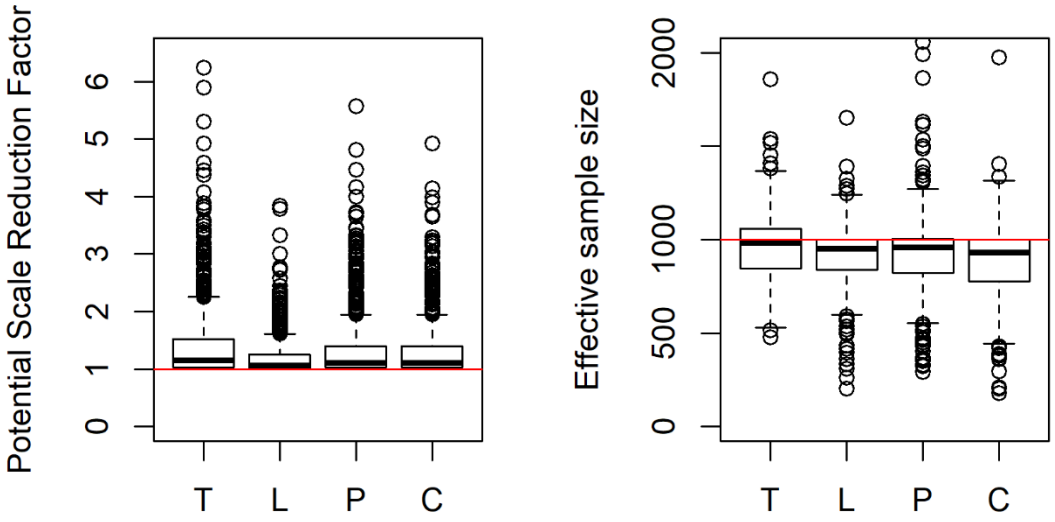
We fitted the models with R-package Hmsc[4] assuming the default prior distribution. For a technical description of the default prior distribution we refer to [4], whereas for an ecological motivation of the default prior distribution we refer to [2]. We performed posterior sampling for four Markov Chain 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 (β –parameters) and the random effects (Ω-parameters), equivalent to the Gelman-Rubin statistic[5].

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*thin iterations, out of which 125*thin were discarded as transient, and the remaining 250*thin iterations were then evenly thinned to yield 250 samples. We applied 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[4], 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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