

# Supplemental materials: Winter temperatures dominate spring phenological responses to warming

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## Observed Spring Phenology Responses in Experimental Environments (OSPREE) database

We searched the literature for research papers which experimentally addressed controls of temperature, chilling, and/or photoperiod requirements on the spring phenology of woody plant species. To identify phenological experiments that manipulated chilling, forcing, and/or photoperiod, we searched both ISI Web of Science and Google Scholar with the following terms:

1. TOPIC = (budburst OR leaf-out) AND (photoperiod or daylength) AND temperature\*, which yielded 85 publications
2. TOPIC = (budburst OR leaf-out) AND dormant\*, which yielded 193 publications

The initial searches yielded 201 papers, which we reviewed and assessed for inclusion in the database using the following criteria: focusing on woody plants in temperate ecosystems, and testing for at least photoperiod or temperature effects on budburst, leafout or flowering.

Although all studies measured days to budburst, many communicated results differently (e.g. days to budburst, degree-days to budburst, percent budburst, number of leaves etc). We standardized papers to common units whenever possible (details below) and further restricted studies to those for which forcing, chilling, and photoperiod treatments could be quantitatively identified. For this paper, we focus on studies measuring days to budburst. This subset of OSPREE includes data across 72 experiments (in 49 papers, Table S1), 39 years, and 203 species (Table S2, Fig. S1).

Some species are only represented in one dataset in the OSPREE database, making it impossible to statistically differentiate between species, study, and treatment effects for these taxa. To address this, we combined species found in only one study into “complexes” at the level of genera—such that each taxonomic unit we use in our model occurs across multiple studies (and treatments). Thus our taxonomic units of analysis are “species complexes,” which are either species represented in >1 dataset or complexes combining multiple species within a genus that are each singly represented in the dataset. Species represented in only one dataset with no congeners in other datasets were excluded from our analysis.

### *Defining budburst*

Most studies defined budburst as initial “green tips” (33/49 papers). Select studies defined budburst as a specific increment of growth (e.g., “0.5cm of new growth”) or as bud swell, leaf emergence, leaf unfolded, open bud scales, or petiole emerged. The remaining papers (4/49) did not include a definition of budburst. The

majority of papers using the above definitions (34/49) required only one bud to have met the defined criteria of budburst, however, the remaining studies implemented specific thresholds to be met (i.e., 10-100% of all buds on an individual needed to have bursted bud). We only included studies with at least 49.5% budburst. For studies with multiple measurements of percent budburst over time, we used the days to budburst when percent budburst was closest to 90%.

### *Estimating chilling*

Chilling was reported far less in the OSPREE database than forcing and photoperiod. Although not all studies applied multiple treatments of forcing and/or photoperiod they generally all maintained and explicitly defined their forcing temperatures and daylengths. In contrast, we found that most studies did not experimentally apply chilling by manipulating duration or temperature of chilling in controlled environments, nor did most quantify the total chilling imposed in their experiment. We therefore calculated the total chilling imposed by all studies, as it would otherwise have been impossible to provide estimates with only experimental chilling given the rarity of such study designs (Fig S2).

To estimate total chilling we combined chilling from the field (i.e., chilling before plant material was brought into controlled environment conditions) and experimental chilling (i.e., chilling that plant material experienced in controlled environment conditions) into two widely used metrics of chilling: Utah units and dynamic chill portions (Dennis, 2003). We used the *chillR* package (version 0.70.17) in R (R Development Core Team, 2017; ?), version 3.6.0, to calculate both positive Utah units and dynamic chill portions from timeseries of hourly temperature data. To estimate field chilling, we generated hourly time series from a European-wide gridded climate dataset (Cornes et al., 2018), from which we extracted daily minimum and maximum temperature from the grid cells and dates during which experiments were conducted. For experimental chilling, we used reported chilling treatments to generate timeseries of hourly temperature data.

In the formulation we used, Utah chilling units accumulated the most at temperatures between 2.4-9.1°C but slightly less at temperatures between 1.4-2.4°C and from 9.1-12.4°C. Utah units were reduced when temperatures fell below or exceeded this range. Chill portions accumulated when temperatures were between 0 and 7.2°C. We note that these models for chilling (both of which were originally developed for peach species) are *hypotheses* for how chilling may accumulate to affect the process of endodormancy release, but are likely to be inaccurate for many species. These models are, however, some of our current best approximations, and versions of them are routinely applied to forest trees (e.g., Harrington et al., 2010). We found the effects of chilling and other cues remained qualitatively consistent across the two methods of estimating total chilling, though total chilling and photoperiod estimates were slightly lower using chill portions compared to Utah units (Table S3).

We wished to explore model predictions across a wide range of experimental temperature conditions (i.e., chilling and forcing temperatures) applied by studies included in the OSPREE database (Fig. 2). To do this, we needed to convert chilling temperature to total chilling units, which could be input into our model. There is no straightforward conversion between chilling temperature and total chilling, since the duration a temperature is applied affects chilling (Fig. S5). We therefore made these conversions using two alternative approaches and we present both. For one approach, we generated daily time series of a range of experimental chilling temperatures for a range of durations spanning those in the OSPREE database (from -10 to 16 °C for 7 to 240 days). We averaged across the range of durations for each temperature to get one chilling estimate per chilling temperature (Fig. S8). For the alternative approach, we used historical climate data from a gridded climate dataset (EOBs, Cornes et al., 2018) to estimate chilling, and used these historical relationships between mean winter temperature and total chilling to convert chilling temperature to a representative amount of total chilling (Fig. 2). We present this alternative approach in the main text as it is more closely related to field chilling conditions, which was by far the most common type of chilling across experiments.

### *Estimating forcing & photoperiod*

Our studies included a diversity of designs for applying forcing and/or photoperiod experimentally, including

studies that imposed constant forcing temperatures and forcing temperatures that varied between day and night. Additionally several studies applied forcing or photoperiod using a “ramped” design, such that treatments increased or decreased gradually over time throughout the duration of the application. For all studies we used the daylength of light as our photoperiod estimate (e.g., a study with 8 hours of light and 16 hours of dark was recorded as ‘8’). For forcing, we used the temperature applied when forcing temperatures were constant (i.e., the same temperature was applied 24 hours per day)- if forcing varied with photoperiod, we estimated the mean daily temperature weighted by the hours that temperature was applied. Similarly, for studies that ramped forcing, we calculated a weighted average of forcing temperature over the period from when forcing treatments were applied until budburst day. For studies that ramped photoperiod, we used the photoperiod individuals initially experienced (e.g., studies with photoperiod lengthening from 6 hours until budburst, we recorded as ‘6’). When forcing and photoperiod treatments were reported as ambient, we used the E-OBs dataset to estimate mean forcing temperature and the R package ‘geosphere’ to get daylength associated with each date and latitude (Cornes et al., 2018).

## Models

We fit three overall models: the main budburst model, fit to all studies in OSPREE that measured days to budburst; the latitude model, which included only studies that had provenance latitude information, and a model to examine how the design of chilling treatments affects estimated effects. Given the complexity of our meta-analytic data we fit each model separately, and present the main model in the main text as it was designed to best estimate chilling, forcing and photoperiod cues (our primary goal here). The other two models represent subsets of the data in the main model that allow more direct tests of relevant, related questions.

As our primary goal was to directly compare the effects of chilling, forcing and photoperiod we standardized these predictor variables (Gelman and Hill, 2006). This was necessary because the range and scale of each predictor varied widely (total chilling ranged from -1304 to 4724 Utah units; forcing ranged from -5.2 to 32 °C, photoperiod ranged from 6 to 24 hours). We followed well-established methods of subtracting the mean and dividing by the standard deviation (Gelman and Hill, 2006) to yield ‘z-score’ values for all predictor variables (total chilling units, forcing temperatures, and photoperiods in the experiments). In addition to these models with standardized predictors (Table S3), we also fit models in which predictors were not standardized (Table S4) so that estimates could be more easily interpreted on their natural scales. For all figures in which predictors are shown on their natural scales, we use estimates from models in which predictors were not standardized.

All models were fit using the programming languages **Stan** (Carpenter et al., 2017)([www.mc-stan.org](http://www.mc-stan.org)), accessed via the *rstan* package (version 2.18.0) in R (R Development Core Team, 2017; Stan Development Team, 2018), version 3.6.0. Stan provides efficient MCMC sampling via a No-U-Turn Hamiltonian Monte Carlo approach (more details can be found in Gelman et al. (2014) and in Carpenter et al. (2017)). We validated that our models using test data, then fit the following models described below. In all models  $i$  represents each unique observation,  $sp$  is the species or species complex grouping,  $\alpha$  terms represent intercepts while  $\beta$  terms represent slope estimates,  $y$  is the days to budburst since forcing conditions were applied.

### 1. Main budburst model:

$$y_i = \alpha_{sp[i]} + \beta_{forcing_{sp[i]}} + \beta_{photoperiod_{sp[i]}} + \beta_{chilling_{sp[i]}} + \epsilon_i, \epsilon_i \sim N(0, \sigma_y^2)$$

The  $\alpha$  and each of the three  $\beta$  coefficients were modeled at the species level, as follows:

$$\begin{aligned}\alpha_{sp} &\sim N(\mu_{\alpha}, \sigma_{\alpha}) \\ \beta_{forcing_{sp}} &\sim N(\mu_{forcing}, \sigma_{forcing}) \\ \beta_{photoperiod_{sp}} &\sim N(\mu_{photoperiod}, \sigma_{photoperiod}) \\ \beta_{chillingsp} &\sim N(\mu_{chilling}, \sigma_{chilling})\end{aligned}$$

We applied this model to both a dataset with 203 species, as well as with 67 species, Tables S3, S4). We present estimates from the model fit to the reduced dataset in the main text (and for Fig. 1-3 in the main text) as it represents species that were more well-represented across multiple papers and study designs, and thus are likely to be more accurate estimates (more details above in section describing the OSPREE database). Based on our modeling approach, species from fewer studies will be pooled towards the overall mean. The reduced dataset model also excluded studies which reported only 'ambient' forcing and photoperiod; these studies were included in the dataset with 203 species.

2. Latitude model: Given continuing debate over the role of photoperiod on budburst timing across a species' latitudinal range (e.g., Zohner et al., 2016; Gauzere et al., 2017), we examined the effect of including latitude in a model similar to our main one, but designed to estimate latitude effects. This model estimated the effects of each phenological cue (chilling, forcing, photoperiod) on days to budburst (as in the main model), in addition to the effect of latitude and the interaction of photoperiod by latitude. We include this interaction because photoperiod effects are expected to vary by latitude and this interaction may have important implications under climate change (Saikkonen et al., 2012; Way and Montgomery, 2015; Gauzere et al., 2017).

We followed the guidelines above for including species or species complex (see *Observed Spring Phenology Responses in Experimental Environments (OSPREE) database* section above), then subsetted the species and species complexes to include only those that had multiple provenance locations. This yielded the following model:

$$y_i = \alpha_{sp[i]} + \beta_{forcing_{sp[i]}} + \beta_{photoperiod_{sp[i]}} + \beta_{chilling_{sp[i]}} + \beta_{latitude_{sp[i]}} + \beta_{photoperiod:latitude_{sp[i]}} + \epsilon_i, \\ \epsilon_i \sim N(0, \sigma_y^2)$$

The  $\alpha$  and each of the five  $\beta$  coefficients were modeled at the species level, as follows:

$$\begin{aligned}\alpha_{sp} &\sim N(\mu_{\alpha}, \sigma_{\alpha}) \\ \beta_{forcing_{sp}} &\sim N(\mu_{forcing}, \sigma_{forcing}) \\ \beta_{photoperiod_{sp}} &\sim N(\mu_{photoperiod}, \sigma_{photoperiod}) \\ \beta_{chillingsp} &\sim N(\mu_{chilling}, \sigma_{chilling}) \\ \beta_{latitudesp} &\sim N(\mu_{latitude}, \sigma_{latitude}) \\ \beta_{photoperiod:latitudesp} &\sim N(\mu_{photoperiod:latitude}, \sigma_{photoperiod:latitude})\end{aligned}$$

3. Chilling study design model: As we found chilling to be the strongest cue, and given how few studies directly manipulate it (Fig S2), we also used a subset of our data to estimate how a study's experimental design for chilling impacts model estimates. For this, we included only species or species complexes used in both experiments that employed the Weinberger method (in this method plant tissue is sequentially removed from the field and then exposed to 'forcing' conditions, with the assumption that tissues collected later experience more field chilling Weinberger et al., 1950) and those that experimentally manipulated chilling (i.e., by varying chilling temperatures and/or the duration of chilling conditions).

We defined Weinberger studies as those with two or more field sample dates, each two or more weeks apart, that did not otherwise manipulate chilling. The chilling study-design model was thus:

$$y_i = \alpha_{sp[i]} + \beta_{forcing} + \beta_{photoperiod} + \beta_{chilling} + \beta_{chillmethod} + \\ \beta_{forcing:chillmethod} + \beta_{photoperiod:chillmethod} + \beta_{chilling:chillmethod} + \epsilon_i, \\ \epsilon_i \sim N(0, \sigma_y^2)$$

The  $\alpha$  coefficients were modeled at the species level, as follows:

$$\alpha_{sp} \sim N(\mu_\alpha, \sigma_\alpha)$$

For all models, we chose weakly informative priors; increasing the priors three-fold did not change the model results.

We ran four chains simultaneously, each with 1 500 warm-up iterations followed by 2 500 sampling iterations, yielding 4 000 posterior samples for each parameter. We assessed model performance through  $\hat{R}$  close to 1 and high  $n_{eff}$  (4 000 for most parameters, but as low as 713 for a few parameters in the latitude model), as well as visual consideration of chain convergence and posteriors (Gelman et al., 2014).

In our figures we show means  $\pm$  50% credible intervals from our models (Fig. 1, S3 - S4), because our focus here is on the most likely value for each parameter (e.g., estimated response to forcing) and because they are computationally stable (Gelman et al., 2014; Carpenter et al., 2017). See Tables S3- S6 for 95% credible intervals.

#### *Modeling limitations based on experimental designs*

An ideal model to predict budburst would potentially include (but is not limited to): interactions between cues, sigmoidal or other non-linearities to assess potential threshold effects, provenance location, methodological details (e.g., if tissue was seedlings versus twigs, or whether temperatures were constant or varied each day, etc). As with all models, though, we were limited in how many parameters we could estimate given available data. Thus we focused on species differences and used additional models to assess some of the potentially largest other effects (latitude, methods of estimating chilling). We were unable to estimate interactions between cues in our meta-analysis because very few studies design experiments to test for interactions between chilling, forcing, and photoperiod (Table S7).

As our focus is on experiments, which—by design—often impose high variation in phenological cues, we expected a linear model for chilling, forcing, and photoperiod would be most appropriate. Non-linear models, however, are often most appropriate for phenological cues, especially in nature where chilling may always be very high or extremely short photoperiods are rare. Thus we tested a non-linear (sigmoidal) model on the OSPREE data (Chuine et al., 2013). As chilling was the least experimentally manipulated in our database, we examined whether a sigmoidal curve for chilling would be more appropriate, but found that it was a poorer fit than a comparable all-linear model (R-squared = 0.53 versus 0.57), did not dramatically alter estimates of forcing (-0.83 versus -0.85) or photoperiod (-0.25 versus -0.13) and led to non-biologically relevant estimates of chilling. Fitting non-linear models to experimental data may require more data, and/or data at very high and low chilling, forcing and photoperiod values, than currently available.

The few that do incorporate interactions generally use the Weinberger method, which is not designed to robustly tease out of the effects of multiple cues (Table S6, Fig. S7). Similarly we found variation in study material/tissue and variation in thermoperiodicity was too infrequent to test for effects with current data. Our estimated effects therefore average over interactions (Gelman and Hill, 2006), but identifying them in future research will be critical to understanding and predicting budburst. This will be particularly challenging for forcing and chilling, as a lack of information on endodormancy requirements makes disentangling forcing from chilling conditions impossible with current data (Chuine et al., 2016).

## Applying our model to Central European data

Our results integrate over a large range of chilling, forcing and photoperiod conditions (e.g., forcing treatment temperatures ranged from 0-32 °C and chilling temperatures ranged from -10-16 °C in experiments, as defined by the each study’s authors, Fig. 2, S4, S8). We also wished to understand how our findings may apply to conditions more commonly found in nature, where conditions often vary dramatically from those applied in controlled environment experiments. For example, very low amounts of chilling can be applied in experiments compared to the natural chilling found in many temperate areas (Fig. S5). Additionally, chilling temperature and total chilling are more correlated in nature than in experimental conditions (Fig. S5). Further, given the importance of chilling and forcing combined with the fact that seasons do not always warm uniformly with climate change (Vautard et al., 2014; Agency, 2019), we also wished to understand how warming in the winter, spring, or both seasons would shift budburst timing. Given these goals we focused on applying our model estimates to defined levels of warming layered onto historical climate. Alternative approaches, such as using climate projections from global circulation models, would have hindered our efforts to understand degrees of warming in different seasons. Further, we emphasize that our predictions are not designed to be accurate forecasts of future budburst dates, even for the locations for which we use historical climate and budburst data. They are designed, however, to provide insights into how natural conditions can differ from experimental conditions, and to provide guidance on how much varying effects of winter and spring warming together will shape future budburst timing.

We thus applied our model to Central Europe, a well-studied area for phenology, which has both relatively long-term daily temperature data and budburst data. We selected sites that are part of the Pan European Phenology Project (PEP 725, <http://www.pep725.eu>) and included data for two common European species that are prevalent in the OSPREE database: *Betula pendula* (silver birch) and *Fagus sylvatica* (European beech, Templ et al., 2018). We used a European-wide gridded climate dataset (E-OBs Cornes et al., 2018) to extract daily minimum and maximum temperature for the grid cells where observations of leafout for these two species were available. We extracted temperature data from 1951 through 1960 (selected as a pre-warming time period) and used these data to estimate annual values for total winter chilling (from 1 September through 30 April, in Utah units, using the R package *chillR*, see details above in *Estimating chilling* section) and mean spring forcing estimated as the mean temperature from 1 March through 30 April. We inputted these estimates for chilling and forcing into our main model, and set photoperiod to the daylength on the mean day of leafout across the PEP observations from 1951 through 1960. This yielded estimates of budburst under ‘pre-warming conditions,’ and we then investigated model predictions of budburst given different levels of warming (from 1-7 °C) above this baseline, including a full matrix of altered total chilling and forcing estimates (Fig. 3, S9, S10).

We applied our model at all latitudes and longitudes included in the PEP 725 database between 1951 and 1960 for *Betula pendula* (Fig. S6). We selected two of these sites for *Betula pendula*, as well as two sites where *Fagus sylvatica* occurs, to compare budburst responses across species that differ in their responses to chilling, forcing, and photoperiod, as well as sites that differ in baseline climate (Fig. 3, S6 - S10).

We also applied our latitude model to Central Europe, focusing on PEP sites where *Fagus sylvatica* leafout data were available from 1951-1960. We fit the model to three sites that differed in latitude, following the approach above for estimating baseline chilling and forcing for these sites (Fig. S11) and applying warming levels ranging from 1 to 7 °C. As above, we used the photoperiod on the mean day of leafout across the from 1951 through 1960 PEP observations as a baseline photoperiod. We then further estimated potential changes in photoperiod due to advancing phenology. To do this, we first estimated the shift in days to budburst as described above for Fig. 3. We then used this budburst date estimate the change in photoperiod between the day of year during the pre- and post-warming periods and then re-fit the model with this new photoperiod (Fig. S11)

Note that, as described above in *Models*, our days to budburst estimate is the days to budburst since forcing conditions were applied in the experiment (which we stress is not necessarily the days to budburst after the

start of ecodormancy, Chuine et al., 2016).

## Potential statistical artifacts in declines of temperature sensitivity in observational long-term data

As our model results do not predict a dramatic decline in temperature sensitivity in Central Europe, as has been observed (e.g., Fu et al., 2015), we tested whether observed declines could instead be due to a statistical artifact. Researchers today commonly estimate temperature sensitivity via a linear regression of annual budburst date versus mean or other aggregated metrics of spring temperature yielding estimates in days/°C. However, if warming produces systematically warmer daily temperatures this method will inherently estimate lower sensitivities with warming, because the ‘days’ unit will effectively have increased in the thermal sum it represents (that is the unit of ‘days’ is non-stationary in recent decades).

To test this hypothesis we compared observed trends with simple simulations. First, we collated PEP 725 data (Templ et al., 2018) for *Betula pendula* for all sites with leafout data each year from two 10-year time-periods: a period before significant anthropogenic warming (1951-1960) and a period with significant warming (2001-2010, see IPCC, 2014). We used leafout data (BBCH=11; which is defined as ‘leaf unfolding (first visible leaf stalk)’ in the PEP725 database) instead of budburst (BBCH=7; defined as “Beginning of sprouting”) as leafout data are far more common in the PEP 725 database. Next, we simulated budburst data with constant cues. For this, we did not include any chilling or photoperiod cues, but assumed budburst occurred after a certain thermal sum, estimated via growing degree days with a base temperature of 0°C. We then estimated temperature sensitivity (days/°C) and the difference in these estimates given different levels of spring warming. For the simulations shown here we used a GDD (growing degree day) requirement of 150, a base mean spring temperature of 6°C with a variance of 3°C, and estimated temperature sensitivity for 10-year periods for 45 simulated sites (these values were chosen to best match the PEP 725 data, but note that the general findings are robust to other combinations of these parameter values).

As expected temperature sensitivity estimates for *Betula pendula* from PEP 725 declined across the two time periods in step with warming. Across the sites studied here we estimated a decline of  $0.8 \pm 0.3$  days/°C (comparing 2001-2010 and 1951-1960) and  $1.1 \pm 0.2$ °C warming; this estimate was very similar to simulations given constant cues and 1°C warming (Fig. S12).

Additionally, several other metrics suggest declines may be more statistical than biological. Research suggests substantial declines in chilling that could lead to observed shifts in sensitivity to warming should increase variance in leafout timing (Ford et al., 2016). In contrast, in both the real and simulated data variance in leafout date declined over time—this would be expected if plants use a thermal sum threshold of forcing to leaf out and warming produces systematically warmer days. In the PEP 725 data we found a decline in leafout variance of 58% (in recent years, compared to earlier years), compared to a decline of 37% in the simulations. Additionally we found little change in accumulated chilling (1 September - 1 March of each year) in the PEP 725 data across the two time points ( $2247 \pm 31$  Utah units in 1951-1960, compared to  $2236 \pm 20$  Utah units in 2001-2010), further suggesting that shifts in chilling do not explain the declining sensitivities. Simple plots of the chilling and forcing required for budburst suggest very low chilling is often required to dramatically increase the forcing required for budburst (Fig. S13, S14).

This potential artifact adds to existing research that has documented the statistical challenges of accurately estimating temperature sensitivities from long-term data (Güsewell et al., 2017; Clark et al., 2014) and may be overcome by some methods. Research that measures sensitivity as a thermal sum or other temperature metric (e.g., GDD) until leafout should be less vulnerable to this artifact. Indeed, in the PEP 725 data we found little difference across the two time-periods in GDD ( $68.7 \pm 2.6$  in 1950-1960 versus  $61.5 \pm 2.0$  in 2000-2010 for GDD calculated from January 1st to leafout with a base temperature of 0°C; and a mean temperature in the 30 days before leafout of  $6.8^\circ\text{C} \pm 0.1$  in 1950-1960 versus  $6.6^\circ\text{C} \pm 0.1$ ). Methods such as these (that accumulate thermal temperatures until event date) are also vulnerable to other issues: as researchers must

select the day to start accumulating or averaging temperatures, these methods should work best when the start date is always after endodormancy break, when plants are most responsive to forcing (Chuine et al., 2016). As climate change may push endodormancy break later and later in some regions, this method could inaccurately attribute changes in other cues to shifts in forcing (Güsewell et al., 2017). Without measures of endodormancy break (Chuine et al., 2016), we suggest efforts to accurately estimate cues from long-term observational data may be difficult or impossible without additional physiological information from controlled environment experiments.

## References

- Agency, E. E. 2019. Global and european temperature.
- Basler, D., and C. Körner. 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology* 165:73–81.
- . 2014. Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. *Tree physiology* 34:377–388.
- Biasi, L., F. Zanette, and R. Carvalho. 2012. Dormancy dynamics of grape and kiwifruit buds in a region of low chill occurrence. Pages 507–512 *in* XXVIII International Horticultural Congress on Science and Horticulture for People (IHC2010): International Symposium on Plant 932.
- Caffarra, A., and A. Donnelly. 2011. The ecological significance of phenology in four different tree species: effects of light and temperature on bud burst. *International journal of Biometeorology* 55:711–721.
- Caffarra, A., A. Donnelly, I. Chuine, and M. B. Jones. 2011. Modelling the timing of *Betula pubescens* bud-burst. I. Temperature and photoperiod: A conceptual model. *Climate Research* 46:147.
- Calmé, S., F. J. Bigras, H. A. Margolis, and C. Hébert. 1994. Frost tolerance and bud dormancy of container-grown yellow birch, red oak and sugar maple seedlings. *Tree physiology* 14:1313–1325.
- Campbell, R. K., and A. I. Sugano. 1975. Phenology of bud burst in douglas-fir related to provenance, photoperiod, chilling, and flushing temperature. *Botanical Gazette* pages 290–298.
- Carpenter, B., A. Gelman, M. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. A. Brubaker, J. Guo, P. Li, and R. Allen. 2017. Stan: A probabilistic programming language. *Journal of Statistical Software* 76:10.18637/jss.v076.i01.
- Chavarria, G., F. G. Herter, M. d. C. B. Raseira, A. C. Rodrigues, C. Reisser, and J. B. d. Silva. 2009. Mild temperatures on bud breaking dormancy in peaches. *Ciência Rural* 39:2016–2021.
- Chuine, I., M. Bonhomme, J.-M. Legave, I. García de Cortázar-Atauri, G. Charrier, A. Lacointe, and T. Améglio. 2016. Can phenological models predict tree phenology accurately in the future? the unrevealed hurdle of endodormancy break. *Global change biology* 22:3444–3460.
- Chuine, I., I. Garcia de Cortazar Atauri, H. Hanninen, and K. Kramer. 2013. Plant development models, pages 275–293. Kluwer, Dordrecht, the Netherlands.
- Clark, J. S., J. Melillo, J. Mohan, and C. Salk. 2014. The seasonal timing of warming that controls onset of the growing season. *Global Change Biology* 20:1136–1145.
- Cook, C., and G. Jacobs. 2000. Progression of apple (*malus* × *domestica* borkh.) bud dormancy in two mild winter climates. *The Journal of Horticultural Science and Biotechnology* 75:233–236.



- Cornes, R. C., G. van der Schrier, E. J. van den Besselaar, and P. D. Jones. 2018. An ensemble version of the e-obs temperature and precipitation data sets. *Journal of Geophysical Research: Atmospheres* 123:9391–9409.
- Dennis, F. 2003. Problems in standardizing methods for evaluating the chilling requirements for the breaking of dormancy in buds of woody plants. *HortScience* 38:347–350.
- Falusi, M., and R. Calamassi. 1990. Bud dormancy in beech (*Fagus sylvatica* L.). Effect of chilling and photoperiod on dormancy release of beech seedlings. *Tree physiology* 6:429–438.
- . 1996. Geographic variation and bud dormancy in beech seedlings (*fagus sylvatica* l). Pages 967–979 in *Annales des Sciences forestières*. Vol. 53. EDP Sciences.
- . 1997. Bud dormancy in *fagus sylvatica* l. ii. the evolution of dormancy in seedlings and one-node cuttings. *Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology* 131:143–148.
- . 2003. Dormancy of *fagus sylvatica* l. buds iii. temperature and hormones in the evolution of dormancy in one-node cuttings. *Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology* 137:185–191.
- Ford, K. R., C. A. Harrington, S. Bansal, J. Gould, Peter, and J. B. St. Clair. 2016. Will changes in phenology track climate change? a study of growth initiation timing in coast douglasâ€™fir. *Global Change Biology* 22:3712–3723.
- Fu, Y. S. H., H. F. Zhao, S. L. Piao, M. Peaucelle, S. S. Peng, G. Y. Zhou, P. Ciais, M. T. Huang, A. Menzel, J. P. Uelas, Y. Song, Y. Vitasse, Z. Z. Zeng, and I. A. Janssens. 2015. Declining global warming effects on the phenology of spring leaf unfolding. *Nature* 526:104–107.
- Gauzere, J., S. Delzon, H. Davi, M. Bonhomme, I. G. de Cortazar-Atauri, and I. Chuine. 2017. Integrating interactive effects of chilling and photoperiod in phenological process-based models. A case study with two European tree species: *Fagus sylvatica* and *Quercus petraea*. *Agricultural and Forest Meteorology* 244:9–20.
- Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2014. *Bayesian Data Analysis*. 3rd ed. CRC Press, New York.
- Gelman, A., and J. Hill. 2006. *Data analysis using regression and multilevel/hierarchical models*. Cambridge university press.
- Ghelardini, L., A. Santini, S. Black-Samuelsson, T. Myking, and M. Falusi. 2010. Bud dormancy release in elm (*ulmus* spp.) clones—a case study of photoperiod and temperature responses. *Tree physiology* 30:264–274.
- Gianfagna, T., and S. Mehlenbacher. 1985. Importance of heat requirement for bud break and time of flowering in apple. *HortScience* 20:909–911.
- Gömöry, D., E. Foffová, R. Longauer, and D. Krajmerová. 2015. Memory effects associated with early-growth environment in norway spruce and european larch. *European Journal of Forest Research* 134:89–97.
- Guak, S., D. M. Olszyk, L. H. Fuchigami, and D. T. Tingey. 1998. Effects of elevated co2 and temperature on cold hardiness and spring bud burst and growth in douglas-fir (*pseudotsuga menziesii*). *Tree Physiology* 18:671–679.
- Guerriero, P., G. Scalabrelli, and G. Grazzini. 1990. Chilling effect on inhibition removal in kiwifruit dormant lateral buds. Pages 79–86 in *I International Symposium on Kiwifruit* 282.

- Güsewell, S., R. Furrer, R. Gehrig, and B. Pietragalla. 2017. Changes in temperature sensitivity of spring phenology with recent climate warming in Switzerland are related to shifts of the pre-season. *Global change biology* 23:5189–5202.
- Harrington, C. A., P. J. Gould, and J. B. St. Clair. 2010. Modeling the effects of winter environment on dormancy release of Douglas-fir. *Forest Ecology and Management* 259:798–808. Harrington, Constance A. Gould, Peter J. St. Clair, J. Bradley Conference on Adaptation of Forests and Forest Management to Changing Climate with Emphasis on Forest Health Aug 25-28, 2008 Umea, SWEDEN Si.
- Heide, O. 1993a. Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physiologia Plantarum* 88:531–540.
- . 1993b. Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days. *Physiologia Plantarum* 89:187–191.
- Heide, O. M., and A. Sønsteby. 2012. Floral initiation in black currant cultivars (*Ribes nigrum* L.): Effects of plant size, photoperiod, temperature, and duration of short day exposure. *Scientia Horticulturae* 138:64–72.
- IPCC. 2014. *Climate Change 2014: Impacts, Adaptation, and Vulnerability*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Jones, H., R. Hillis, S. Gordon, and R. Brennan. 2012. An approach to the determination of winter chill requirements for different ribes cultivars. *Plant Biology* 15:18–27.
- Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014a. Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* 20:170–182.
- Laube, J., T. H. Sparks, N. Estrella, and A. Menzel. 2014b. Does humidity trigger tree phenology? proposal for an air humidity based framework for bud development in spring. *New Phytologist* 202:350–355.
- Li, C., A. Welling, T. Puhakainen, A. Viherä-Aarnio, A. Ernstsén, O. Junttila, P. Heino, and E. T. Palva. 2005. Differential responses of silver birch (*Betula pendula*) ecotypes to short-day photoperiod and low temperature. *Tree physiology* 25:1563–1569.
- Linkosalo, T., and M. J. Lechowicz. 2006. Twilight far-red treatment advances leaf bud burst of silver birch (*Betula pendula*). *Tree physiology* 26:1249–1256.
- Man, R., and P. Lu. 2010. Effects of thermal model and base temperature on estimates of thermal time to bud break in white spruce seedlings. *Canadian journal of forest research* 40:1815–1820.
- Morin, X., J. Roy, L. Sonié, and I. Chuine. 2010. Changes in leaf phenology of three European oak species in response to experimental climate change. *New Phytologist* 186:900–910.
- Myking, T. 1997. Effects of constant and fluctuating temperature on time to budburst in *Betula pubescens* and its relation to bud respiration. *Trees* 12:107–112.
- . 1998. Interrelations between respiration and dormancy in buds of three hardwood species with different chilling requirements for dormancy release. *Trees* 12:224–229.
- Myking, T., and O. Heide. 1995. Dormancy release and chilling requirement of buds of latitudinal ecotypes of *Betula pendula* and *B. pubescens*. *Tree physiology* 15:697–704.
- Pagter, M., U. B. Andersen, and L. Andersen. 2015. Winter warming delays dormancy release, advances budburst, alters carbohydrate metabolism and reduces yield in a temperate shrub. *AoB plants* 7:plv024.
- Partanen, J., V. Koski, and H. Hänninen. 1998. Effects of photoperiod and temperature on the timing of bud burst in Norway spruce (*Picea abies*). *Tree physiology* 18:811–816.

- Partanen, J., I. Leinonen, and T. Repo. 2001. Effect of accumulated duration of the light period on bud burst in norway spruce (*picea abies*) of varying ages. *Silva Fennica* 35:111–117.
- R Development Core Team. 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ramos, A., and L. Rallo. 1999. Effect of the bearing condition of the tree, chilling and defoliation on the forced budburst of olive cuttings at different temperatures. Pages 251–254 in I. T. Metzidakis and D. G. Voyiatzis, eds. III International Symposium on Olive Growing 474.
- Rinne, P., H. Hänninen, P. Kaikuranta, J. Jalonen, and T. Repo. 1997. Freezing exposure releases bud dormancy in *betula pubescens* and *b. pendula*. *Plant, Cell & Environment* 20:1199–1204.
- Rinne, P., A. Saarelainen, and O. Junttila. 1994. Growth cessation and bud dormancy in relation to aba level in seedlings and coppice shoots of *betula pubescens* as affected by a short photoperiod, water stress and chilling. *Physiologia Plantarum* 90:451–458.
- Saikkonen, K., K. Taulavuori, T. Hyvönen, P. E. Gundel, C. E. Hamilton, I. Vänninen, A. Nissinen, and M. Helander. 2012. Climate change-driven species’ range shifts filtered by photoperiodism. *Nature Climate Change* 2:239.
- Sanz-Pérez, V., and P. Castro-Díez. 2010. Summer water stress and shade alter bud size and budburst date in three mediterranean quercus species. *Trees* 24:89–97.
- Sanz-Perez, V., P. Castro-Diez, and F. Valladares. 2009. Differential and interactive effects of temperature and photoperiod on budburst and carbon reserves in two co-occurring mediterranean oaks. *Plant Biol (Stuttg)* 11:142–51.
- Schnabel, B. J., and R. L. Wample. 1987. Dormancy and cold hardiness in *vitis vinifera* l. cv. white riesling as influenced by photoperiod and temperature. *American Journal of Enology and Viticulture* 38:265–272.
- Skuterud, R., J. Dietrichson, et al. 1994. Budburst in detached birch shoots (*betula pendula*) of different varieties winter-stored in darkness at three different temperatures. .
- Sønsteby, A., and O. M. Heide. 2014. Chilling requirements of contrasting black currant (*ribes nigrum* l.) cultivars and the induction of secondary bud dormancy. *Scientia Horticulturae* 179:256–265.
- Spann, T. M., J. G. Williamson, and R. L. Darnell. 2004. Photoperiod and temperature effects on growth and carbohydrate storage in southern highbush blueberry interspecific hybrid. *Journal of the American Society for Horticultural Science* 129:294–298.
- Spiers, J., and A. Draper. 1974. Effect of chilling on bud break in rabbiteye blueberry [cultivars]. *Journal American Society for Horticultural Science* .
- Stan Development Team. 2018. RStan: the R interface to Stan. R package version 2.17.3.
- Swartz, H., and L. Powell Jr. 1981. The effect of long chilling requirement on time of bud break in apple. Pages 173–178 in Symposium on Growth Regulators in Fruit Production 120.
- Templ, B., E. Koch, K. Bolmgren, M. Ungersböck, A. Paul, H. Scheifinger, T. Rutishauser, M. Busto, F.-M. Chmielewski, L. Hájková, S. Hodzić, F. Kaspar, B. Pietragalla, R. Romero-Fresneda, A. Tolvanen, V. Vučetić, K. Zimmermann, and A. Zust. 2018. Pan european phenological database (pep725): a single point of access for european data. *International Journal of Biometeorology* 62:1109–1113.
- Thielges, B., and R. Beck. 1976. Control of bud break and its inheritance in *populus deltoides*. *Tree Physiology and Yield Improvement* .

- Vautard, R., A. Gobiet, S. Sobolowski, E. Kjellström, A. Stegehuis, P. Watkiss, T. Mendlik, O. Landgren, G. Nikulin, C. Teichmann, et al. 2014. The european climate under a 2 c global warming. *Environmental Research Letters* 9:034006.
- Way, D. A., and R. A. Montgomery. 2015. Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, Cell & Environment* 38:1725–1736.
- Webb, D. P. 1977. Root regeneration and bud dormancy of sugar maple, silver maple, and white ash seedlings: effects of chilling. *Forest Science* 23:474–483.
- Weinberger, J. H., et al. 1950. Chilling requirements of peach varieties. Pages 122–28 *in* Proceedings. American Society for Horticultural Science. Vol. 56.
- Worrall, J., and F. Mergen. 1967. Environmental and genetic control of dormancy in picea abies. *Physiologia Plantarum* 20:733–745.
- Zohner, C. M., B. M. Benito, J. C. Svenning, and S. S. Renner. 2016. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* 6:1120–1123.

## Supplemental Tables

Table S1: Dataset names and references for papers in the OSPREE database.

Dataset	Reference
basler12	Basler and Körner (2012)
basler14	Basler and Körner (2014)
biasi12	Biasi et al. (2012)
caffarra11a	Caffarra and Donnelly (2011)
caffarra11b	Caffarra et al. (2011)
calme94	Calmé et al. (1994)
campbell75	Campbell and Sugano (1975)
chavarria09	Chavarria et al. (2009)
cook00b	Cook and Jacobs (2000)
falusi03	Falusi and Calamassi (2003)
falusi90	Falusi and Calamassi (1990)
falusi96	Falusi and Calamassi (1996)
falusi97	Falusi and Calamassi (1997)
ghelardini10	Ghelardini et al. (2010)
gianfagna85	Gianfagna and Mehlenbacher (1985)
gomory15	Gömöry et al. (2015)
guak98	Guak et al. (1998)
guerriero90	Guerriero et al. (1990)
heide12	Heide and Sønsteby (2012)
heide93	Heide (1993a)
heide93a	Heide (1993b)
jones12	Jones et al. (2012)
laube14a	Laube et al. (2014a)
laube14b	Laube et al. (2014b)
li05	Li et al. (2005)
linkosalo06	Linkosalo and Lechowicz (2006)
man10	Man and Lu (2010)
morin10	Morin et al. (2010)
myking95	Myking and Heide (1995)
myking97	Myking (1997)
myking98	Myking (1998)
pagter15	Pagter et al. (2015)
partanen01	Partanen et al. (2001)
partanen98	Partanen et al. (1998)
ramos99	Ramos and Rallo (1999)
rinne94	Rinne et al. (1994)
rinne97	Rinne et al. (1997)
Sanz-Perez09	Sanz-Perez et al. (2009)
sanzperez10	Sanz-Pérez and Castro-Díez (2010)
schnabel87	Schnabel and Wample (1987)
skuterud94	Skuterud et al. (1994)
sonsteby14	Sønsteby and Heide (2014)
spann04	Spann et al. (2004)
spiers74	Spiers and Draper (1974)
swartz81	Swartz and Powell Jr (1981)
thielges75	Thielges and Beck (1976)
webb78	Webb (1977)
worrall67	Worrall and Mergen (1967)
zohner16	Zohner et al. (2016)

Table S2: Species included in the OSPREE cdatabase. See Table S1 for reference associated with each dataset.

Species	Number of papers	Dataset
<i>Abies alba</i>	2	basler12, laube14a
<i>Abies homolepis</i>	1	laube14a
<i>Acer barbinerve</i>	1	zohner16

Table S2: **Species included in the OSPREE cdatabase.** See Table S1 for reference associated with each dataset.

Species	Number of papers	Dataset
<i>Acer campestre</i>	1	zohner16
<i>Acer ginnala</i>	1	zohner16
<i>Acer negundo</i>	1	laube14a
<i>Acer platanoides</i>	1	zohner16
<i>Acer pseudoplatanus</i>	3	basler12, basler14, laube14a
<i>Acer saccharinum</i>	1	webb78
<i>Acer saccharum</i>	3	calme94, laube14a, webb78
<i>Acer tataricum</i>	1	laube14a
<i>Actinidia deliciosa</i>	2	biasi12, guerriero90
<i>Aesculus flava</i>	1	zohner16
<i>Aesculus hippocastanum</i>	3	basler12, laube14a, zohner16
<i>Aesculus parviflora</i>	1	zohner16
<i>Alnus glutinosa</i>	2	heide93, myking98
<i>Alnus incana</i>	2	heide93, zohner16
<i>Alnus maximowiczii</i>	1	zohner16
<i>Amelanchier alnifolia</i>	1	zohner16
<i>Amelanchier florida</i>	1	zohner16
<i>Amelanchier laevis</i>	1	zohner16
<i>Amorpha fruticosa</i>	1	laube14a
<i>Aronia melanocarpa</i>	1	zohner16
<i>Berberis dielsiana</i>	1	zohner16
<i>Betula alleghaniensis</i>	1	calme94
<i>Betula lenta</i>	1	zohner16
<i>Betula nana</i>	1	zohner16
<i>Betula pendula</i>	10	heide93, li05, rinne97, basler12, laube14a, laube14b, linkosalo06, myking95, myking95, skuterud94
<i>Betula populifolia</i>	1	zohner16
<i>Betula pubescens</i>	6	heide93, rinne94, caffarra11a, caffarra11b, myking95, myking97, , , ,
<i>Buddleja albiflora</i>	1	zohner16
<i>Buddleja alternifolia</i>	1	zohner16
<i>Buddleja davidii</i>	1	zohner16
<i>Caragana pygmaea</i>	1	zohner16
<i>Carpinus betulus</i>	3	heide93a, laube14a, zohner16
<i>Carpinus laxiflora</i>	1	zohner16
<i>Carpinus monbeigiana</i>	1	zohner16
<i>Carya cordiformis</i>	1	zohner16
<i>Carya laciniosa</i>	1	zohner16
<i>Carya ovata</i>	1	zohner16
<i>Castanea sativa</i>	1	zohner16
<i>Cedrus libani</i>	1	zohner16
<i>Celtis caucasica</i>	1	zohner16
<i>Celtis laevigata</i>	1	zohner16
<i>Celtis occidentalis</i>	1	zohner16
<i>Cephalanthus occidentalis</i>	1	zohner16
<i>Cercidiphyllum japonicum</i>	1	zohner16
<i>Cercidiphyllum magnificum</i>	1	zohner16
<i>Cercis canadensis</i>	1	zohner16
<i>Cercis chinensis</i>	1	zohner16
<i>Cladrastis lutea</i>	1	zohner16
<i>Cornus alba</i>	2	laube14a, zohner16
<i>Cornus kousa</i>	1	zohner16
<i>Cornus mas</i>	2	laube14a, laube14b
<i>Corylopsis sinensis</i>	1	zohner16
<i>Corylopsis spicata</i>	1	zohner16
<i>Corylus avellana</i>	4	basler12, heide93, laube14a, zohner16
<i>Corylus heterophylla</i>	1	zohner16
<i>Corylus sieboldiana</i>	1	zohner16

Table S2: **Species included in the OSPREE cdatabase.** See Table S1 for reference associated with each dataset.

Species	Number of papers	Dataset
<i>Decaisnea fargesii</i>	1	zohner16
<i>Deutzia gracilis</i>	1	zohner16
<i>Deutzia scabra</i>	1	zohner16
<i>Elaeagnus ebbingei</i>	1	zohner16
<i>Eleutherococcus senticosus</i>	1	zohner16
<i>Eleutherococcus setchuenensis</i>	1	zohner16
<i>Eleutherococcus sieboldianus</i>	1	zohner16
<i>Euonymus europaeus</i>	1	zohner16
<i>Euonymus latifolius</i>	1	zohner16
<i>Fagus crenata</i>	1	zohner16
<i>Fagus engleriana</i>	1	zohner16
<i>Fagus orientalis</i>	1	zohner16
<i>Fagus sylvatica</i>	10	falusi03, falusi90, falusi96, falusi97, basler12, basler14, caffarra11a, heide93a, heide93a, zohner16
<i>Forsythia ovata</i>	1	zohner16
<i>Forsythia suspensa</i>	1	zohner16
<i>Fraxinus americana</i>	1	webb78
<i>Fraxinus chinensis</i>	1	laube14a
<i>Fraxinus excelsior</i>	2	basler12, laube14a
<i>Fraxinus latifolia</i>	1	zohner16
<i>Fraxinus ornus</i>	1	zohner16
<i>Fraxinus pennsylvanica</i>	1	laube14a
<i>Ginkgo biloba</i>	1	zohner16
<i>Hamamelis japonica</i>	1	zohner16
<i>Hamamelis vernalis</i>	1	zohner16
<i>Heptacodium miconioides</i>	1	zohner16
<i>Hibiscus syriacus</i>	1	zohner16
<i>Hydrangea arborescens</i>	1	zohner16
<i>Hydrangea involucrata</i>	1	zohner16
<i>Hydrangea serrata</i>	1	zohner16
<i>Juglans ailantifolia</i>	1	laube14a
<i>Juglans cinerea</i>	1	laube14a
<i>Juglans regia</i>	1	laube14a
<i>Larix decidua</i>	4	basler12, gomory15, laube14a, laube14b
<i>Larix gmelinii</i>	1	zohner16
<i>Larix kaempferi</i>	1	zohner16
<i>Ligustrum tschonoskii</i>	1	zohner16
<i>Liquidambar orientalis</i>	1	zohner16
<i>Liquidambar styraciflua</i>	1	zohner16
<i>Liriodendron tulipifera</i>	1	zohner16
<i>Lonicera alpigena</i>	1	zohner16
<i>Lonicera caerulea</i>	1	zohner16
<i>Lonicera maximowiczii</i>	1	zohner16
<i>Malus domestica</i>	3	cook00b, gianfagna85, swartz81
<i>Metasequoia glyptostroboides</i>	1	zohner16
<i>Nothofagus antarctica</i>	1	zohner16
<i>Oemleria cerasiformis</i>	1	zohner16
<i>Olea europaea</i>	1	ramos99
<i>Oriza japonica</i>	1	zohner16
<i>Ostrya carpinifolia</i>	1	zohner16
<i>Ostrya virginiana</i>	1	zohner16
<i>Paeonia rockii</i>	1	zohner16
<i>Parrotia persica</i>	1	zohner16
<i>Parrotiopsis jaquemontiana</i>	1	zohner16
<i>Photinia villosa</i>	1	zohner16



Table S2: **Species included in the OSPREE cdatabase.** See Table S1 for reference associated with each dataset.

Species	Number of papers	Dataset
<i>Picea abies</i>	9	basler12, basler14, gomory15, laube14a, laube14b, partanen01, partanen98, worrall67, worrall67, man10
<i>Picea glauca</i>	1	laube14a
<i>Pinus nigra</i>	1	laube14a
<i>Pinus strobus</i>	1	laube14a
<i>Pinus sylvestris</i>	1	laube14a
<i>Pinus wallichiana</i>	1	laube14a
<i>Populus deltoides</i>	1	thielges75
<i>Populus koreana</i>	1	zohner16
<i>Populus tremula</i>	3	heide93, laube14a, laube14b
<i>Prinsepia sinensis</i>	1	zohner16
<i>Prinsepia uniflora</i>	1	zohner16
<i>Prunus avium</i>	2	basler12, laube14a
<i>Prunus cerasifera</i>	1	zohner16
<i>Prunus padus</i>	3	heide93, myking98, zohner16
<i>Prunus persica</i>	1	chavarria09
<i>Prunus serotina</i>	1	laube14a
<i>Prunus serrulata</i>	1	zohner16
<i>Prunus tenella</i>	1	zohner16
<i>Pseudotsuga menziesii</i>	3	guak98, campbell75, laube14a
<i>Ptelea trifoliata</i>	1	zohner16
<i>Pyrus elaeagnifolia</i>	1	zohner16
<i>Pyrus pyrifolia</i>	1	zohner16
<i>Pyrus ussuriensis</i>	1	zohner16
<i>Quercus bicolor</i>	1	laube14a
<i>Quercus coccifera</i>	1	sanzperez10
<i>Quercus faginea</i>	2	Sanz-Perez09, sanzperez10
<i>Quercus ilex</i>	3	Sanz-Perez09, sanzperez10, morin10
<i>Quercus petraea</i>	2	basler12, basler14
<i>Quercus pubescens</i>	1	morin10
<i>Quercus robur</i>	4	laube14a, laube14b, morin10, zohner16
<i>Quercus rubra</i>	2	calme94, laube14a
<i>Quercus shumardii</i>	1	zohner16
<i>Rhamnus alpina</i>	1	zohner16
<i>Rhamnus cathartica</i>	1	zohner16
<i>Rhododendron canadense</i>	1	zohner16
<i>Rhododendron dauricum</i>	1	zohner16
<i>Rhododendron mucronulatum</i>	1	zohner16
<i>Ribes alpinum</i>	1	zohner16
<i>Ribes divaricatum</i>	1	zohner16
<i>Ribes glaciale</i>	1	zohner16
<i>Ribes nigrum</i>	4	jones12, heide12, pagter15, sonsteby14
<i>Robinia pseudoacacia</i>	2	laube14a, laube14b
<i>Rosa hugonis</i>	1	zohner16
<i>Rosa majalis</i>	1	zohner16
<i>Rubus idaeus</i>	1	heide93
<i>Salix gracilistyla</i>	1	zohner16
<i>Salix repens</i>	1	zohner16
<i>Salix smithiana</i>	1	caffarra11a
<i>Sambucus nigra</i>	1	zohner16
<i>Sambucus pubens</i>	1	zohner16
<i>Sambucus tigranii</i>	1	zohner16
<i>Sinowilsonia henryi</i>	1	zohner16
<i>Sorbus aria</i>	1	zohner16
<i>Sorbus aucuparia</i>	2	basler12, heide93
<i>Sorbus commixta</i>	1	zohner16
<i>Sorbus decora</i>	1	zohner16

Table S2: **Species included in the OSPREE cdatabase.** See Table S1 for reference associated with each dataset.

Species	Number of papers	Dataset
<i>Spiraea canescens</i>	1	zohner16
<i>Spiraea chamaedryfolia</i>	1	zohner16
<i>Spiraea japonica</i>	1	zohner16
<i>Stachyurus praecox</i>	1	zohner16
<i>Stachyurus sinensis</i>	1	zohner16
<i>Symphoricarpos albus</i>	2	laube14a, laube14b
<i>Syringa josikaea</i>	1	zohner16
<i>Syringa reticulata</i>	1	zohner16
<i>Syringa villosa</i>	1	zohner16
<i>Syringa vulgaris</i>	3	basler12, laube14a, laube14b
<i>Tilia cordata</i>	2	basler12, caffaral1a
<i>Tilia dasystyla</i>	1	zohner16
<i>Tilia japonica</i>	1	zohner16
<i>Tilia platyphyllos</i>	1	zohner16
<i>Toona sinensis</i>	1	zohner16
<i>Ulmus americana</i>	1	zohner16
<i>Ulmus glabra</i>	1	ghelardini10
<i>Ulmus laevis</i>	1	zohner16
<i>Ulmus macrocarpa</i>	1	ghelardini10
<i>Ulmus minor</i>	1	ghelardini10
<i>Ulmus parvifolia</i>	1	ghelardini10
<i>Ulmus pumila</i>	1	ghelardini10
<i>Ulmus villosa</i>	1	ghelardini10
<i>Vaccinium ashei</i>	1	spiers74
<i>Vaccinium corymbosum</i>	1	spann04
<i>Viburnum betulifolium</i>	1	zohner16
<i>Viburnum buddleifolium</i>	1	zohner16
<i>Viburnum carlesii</i>	1	zohner16
<i>Viburnum opulus</i>	1	zohner16
<i>Viburnum plicatum</i>	1	zohner16
<i>Vitis vinifera</i>	2	biasi12, schnabel87
<i>Weigela coraeensis</i>	1	zohner16
<i>Weigela florida</i>	1	zohner16
<i>Weigela maximowiczii</i>	1	zohner16

Table S3: **Estimates from model fit with standardized predictors.** The model we present in the main text uses Utah units for chilling and includes studies that experimentally manipulated forcing and photoperiod. Using instead a model with chilling in chill portions results in quantitatively different species-level and overall estimates, though the results are qualitatively similar to the Utah model. We also present coefficients from a model including all species (i.e., with crops) with all treatment types. We present posterior means, as well as 50 percent and 95 percent credible intervals from models in which the predictors have been standardized so that they are directly comparable.

	Utah units					chill portions					All species, Utah units				
	mean	25%	75%	2.5%	97.5%	mean	25%	75%	2.5%	97.5%	mean	25%	75%	2.5%	97.5%
$\mu_\alpha$	29.94	28.77	31.1	26.45	33.29	30.73	29.52	31.97	27.07	34.41	30.89	30.14	31.61	28.71	33.19
$\mu_{forcing}$	-4.36	-5.12	-3.61	-6.6	-2.1	-4.83	-5.64	-4.06	-7.1	-2.47	-6.17	-7.02	-5.29	-8.86	-3.64
$\mu_{photoperiod}$	-3.15	-3.97	-2.3	-5.53	-0.74	-3.18	-3.92	-2.42	-5.4	-0.96	-1.02	-1.44	-0.61	-2.2	0.25
$\mu_{chilling}$	-8.89	-9.93	-7.81	-12.03	-5.8	-8.2	-9.27	-7.19	-11.18	-5.07	-8	-8.55	-7.45	-9.62	-6.4
$\sigma_\alpha$	9.41	8.51	10.18	7.19	12.31	10.18	9.2	11.05	7.76	13.08	14.37	13.71	15	12.63	16.3
$\sigma_{forcing}$	5.67	4.99	6.29	4.01	7.75	6.05	5.34	6.66	4.31	8.2	8.73	7.94	9.44	6.73	11.06
$\sigma_{photoperiod}$	5.24	4.4	5.95	3.32	7.87	4.47	3.83	5	2.93	6.54	3.68	3.35	3.97	2.79	4.71
$\sigma_{chilling}$	7.36	6.48	8.1	5.3	10.07	7.89	7.02	8.67	5.69	10.57	6.29	5.73	6.82	4.69	8.06
$\sigma_y$	15.77	15.59	15.96	15.24	16.31	15.47	15.27	15.65	14.94	16.01	14.94	14.8	15.07	14.56	15.33
$N_{sp}$	37					37					203				

Table S4: **Estimates from models fit with predictors on their natural scales,** so that estimates can be readily interpreted in a meaningful way (e.g., change in days of budburst per degree C of warming for forcing temperature). The model we present in the main text uses Utah units for chilling. Here we also present coefficients from models included all species, including crops, and all treatment types. We present posterior means, as well as 50 percent and 95 percent credible intervals, from models.

	Utah units					chill portions					All species, Utah units				
	mean	25%	75%	2.5%	97.5%	mean	25%	75%	2.5%	97.5%	mean	25%	75%	2.5%	97.5%
$\mu_\alpha$	62.87	60.21	65.53	54.87	70.84	66.94	63.87	69.99	57.95	75.87	62.7	61.05	64.36	57.82	67.74
$\mu_{forcing}$	-0.79	-0.91	-0.67	-1.16	-0.41	-0.85	-0.99	-0.72	-1.25	-0.46	-1.03	-1.12	-0.94	-1.29	-0.77
$\mu_{photoperiod}$	-0.54	-0.67	-0.41	-0.93	-0.17	-0.53	-0.66	-0.41	-0.91	-0.17	-0.14	-0.22	-0.07	-0.35	0.07
$\mu_{chilling}$	-2.84	-3.13	-2.53	-3.73	-1.97	-0.25	-0.28	-0.22	-0.33	-0.17	-2.48	-2.63	-2.34	-2.91	-2.08
$\sigma_\alpha$	19.16	17.35	20.79	14.53	24.78	21.97	19.93	23.74	16.86	28.42	17.7	16.81	18.54	15.33	20.38
$\sigma_{forcing}$	0.91	0.8	1.01	0.63	1.26	0.99	0.87	1.09	0.69	1.35	0.72	0.66	0.77	0.57	0.89
$\sigma_{photoperiod}$	0.79	0.67	0.88	0.51	1.16	0.7	0.6	0.79	0.46	1.03	0.59	0.54	0.64	0.45	0.75
$\sigma_{chilling}$	2.07	1.82	2.28	1.47	2.83	0.21	0.18	0.23	0.14	0.3	1.24	1.13	1.34	0.95	1.58
$\sigma_y$	15.82	15.63	16	15.27	16.37	15.52	15.34	15.7	15	16.08	15.16	15.02	15.3	14.78	15.57
$N_{sp}$	37					37					203				

## Supplemental Figures

Table S5: **Estimates from latitude model fit with standardized predictors.** Using a model with Utah chilling units and testing the effects of latitude plus the interaction between latitude and photoperiod results in slightly muted effects for forcing, photoperiod and chilling, though the results are qualitatively similar. We present posterior means, as well as 50 percent and 95 percent credible intervals from models in which the predictors have been standardized so that they are directly comparable,

	mean	25%	75%	2.5%	97.5%
$\mu_{\alpha}$	29.13	27.85	30.49	25.09	32.93
$\mu_{forcing}$	-4.33	-5.15	-3.50	-6.80	-1.87
$\mu_{photoperiod}$	-2.28	-3.28	-1.31	-5.11	0.74
$\mu_{chilling}$	-8.18	-9.21	-7.15	-11.31	-5.05
$\mu_{latitude}$	-2.85	-4.34	-1.34	-7.43	1.60
$\mu_{photo:latitude}$	3.35	2.01	4.67	-0.62	7.42
$\sigma_{\alpha}$	8.86	7.77	9.80	6.23	12.34
$\sigma_{forcing}$	6	5.20	6.69	4.18	8.43
$\sigma_{photoperiod}$	5.34	4.45	6.09	3.33	8.11
$\sigma_{chilling}$	6.82	5.96	7.55	4.80	9.52
$\sigma_{latitude}$	8.1	6.44	9.50	4.21	13.30
$\sigma_{photo:latitude}$	6.79	5.37	7.95	3.63	11.19
$\sigma_y$	15.44	15.25	15.63	14.90	16.01
$N_{sp}$	36				

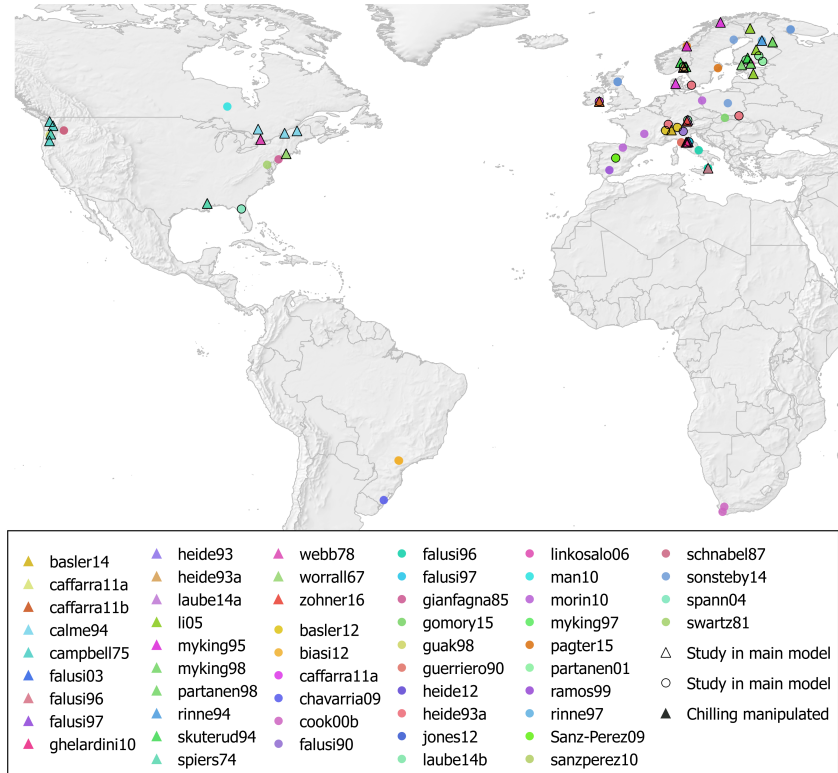


Figure S1: **Map of days to budburst experiments in the OSPREE database.** Legend shows each dataset included in the main OSPREE model with all species and treatments (S3, S4); symbols outlined in black represent datasets for which chilling was manipulated. See Table S1 for the reference associated with each dataset.

Table S6: **Estimates from chilling study design model fit with standardized predictors.** Using a model with Utah chilling units and testing the effects of the Weinberger method and the interaction between this method and the three main environmental cues show that budburst is generally later for Weinberger studies and the effect of chilling is muted while the effect of forcing is stronger. We present posterior means, as well as 50 percent and 95 percent credible intervals from models in which the predictors have been standardized so that they are directly comparable.

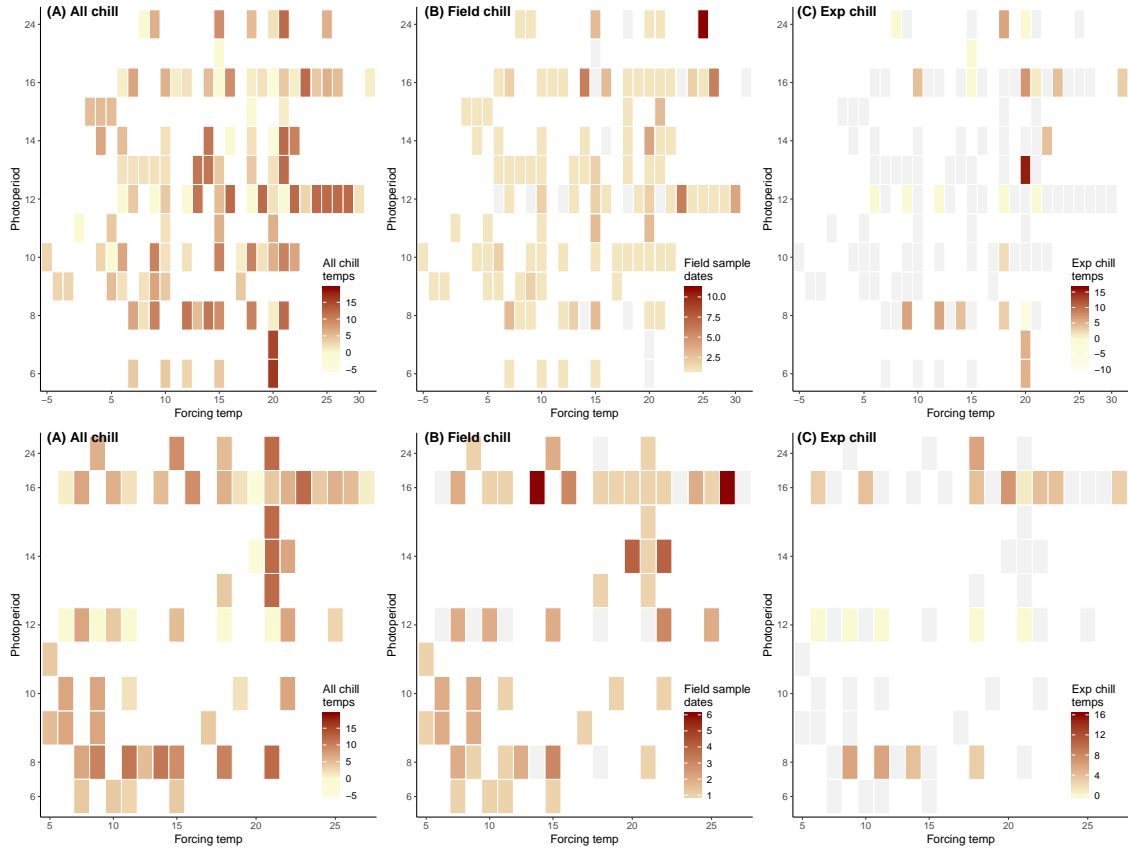
	mean	25%	75%	2.5%	97.5%
$\mu_{\alpha}$	32.46	29.65	35.32	23.73	40.75
$\beta_{forcing}$	-0.21	-1.08	0.66	-2.75	2.39
$\beta_{photoperiod}$	-1.92	-2.50	-1.34	-3.65	-0.31
$\beta_{chilling}$	-8.22	-8.76	-7.68	-9.80	-6.61
$\sigma_{\alpha}$	13.34	11.28	14.96	8.81	20.24
$\sigma_y$	20.58	20.23	20.91	19.64	21.55
$\beta_{chillmethod}$	4.24	3.09	5.40	0.93	7.59
$\beta_{chilling:chillmethod}$	1.74	0.35	3.15	-2.43	5.73
$\beta_{forcing:chillmethod}$	-3.24	-4.35	-2.15	-6.50	-0.03
$\beta_{photoperiod:chillmethod}$	0.63	-0.42	1.67	-2.39	3.68
$N_{sp}$	11				

Table S7: **Number of studies testing for interactions between chilling, forcing, and photoperiod treatments**, out of the 42 studies (across 30 papers) included in the main budburst model

treat1	treat2	n
photo	force	5
chilltemp	force	1
chilldays	force	5
chilltemp	photo	1
chilldays	photo	7
fieldsample.date	force	7
fieldsample.date	photo	10

Table S8: **Locations and pre-warming winter and spring conditions** for sites included in Fig. 3, S9, S10

Species	Latitude	Longitude	Spring Temp	Winter Temp
<i>Betula pendula</i>	46.82	12.80	0.69	-1.05
	48.32	15.82	7.13	4.31
<i>Fagus sylvatica</i>	48.78	15.40	4.76	2.25
	46.72	15.77	7.40	4.33



**Figure S2: The diversity of study designs used in analyses.** Heatmaps show the range and commonness of different forcing (x-axis in all panels) by photoperiod (y-axis in all panels) combinations and with which chilling they were combined. In (A, top and bottom) we show our estimated chill units, which integrate across field (B, top and bottom) and experimental chilling (C, top and bottom). The top row shows all data included in the full model with 203 species, while the bottom row shows the data included in the main model with a subset of species well-represented across treatments and studies. Gray squares indicate a treatment was not applied (i.e., the prevalence of gray squares in (C) highlights how few studies include experimental chilling). Field sample dates are counted as any reported sampling dates more than 14 days apart.

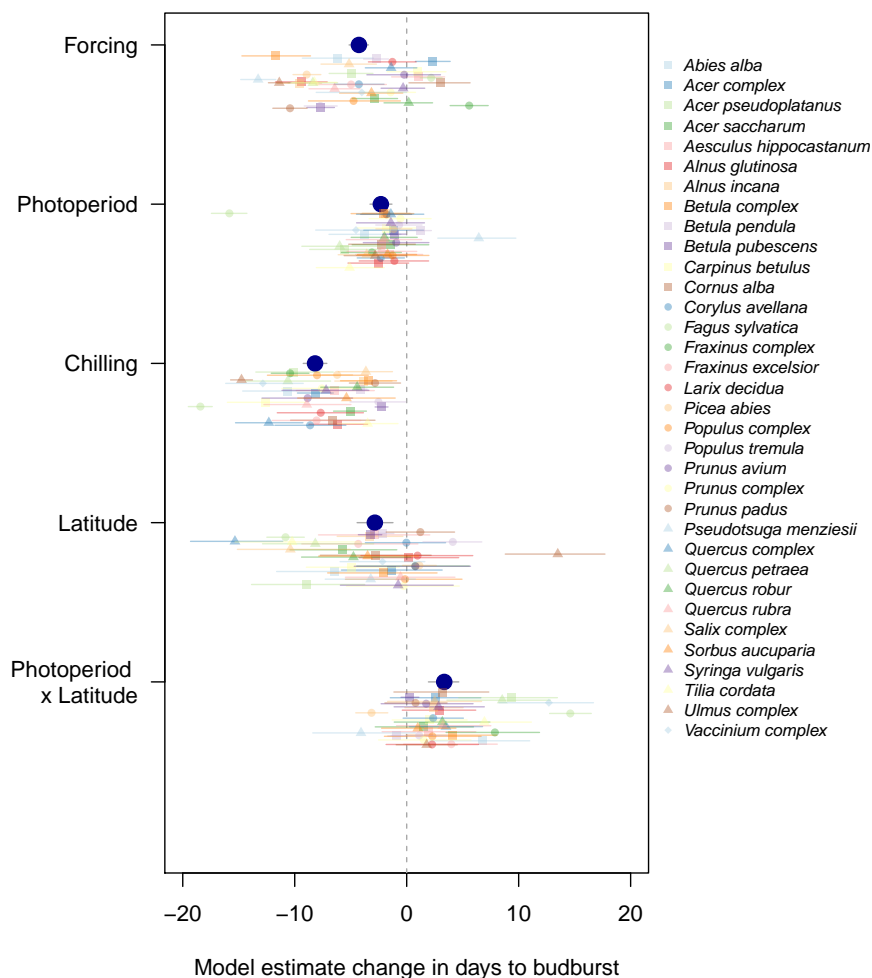


Figure S3: **Estimates for effects of chilling exceeded estimates for forcing, photoperiod, latitude, and the interaction between latitude and photoperiod, for most species, in the latitude budburst model, using Utah units (Table S5).** Using standardized units, which allow comparisons across cues, we show that, as with the main budburst model (Fig. 1), most species (smaller symbols) are responsive to most cues. Chilling is the strongest cue when considering overall estimates across species (larger, dark blue circles).

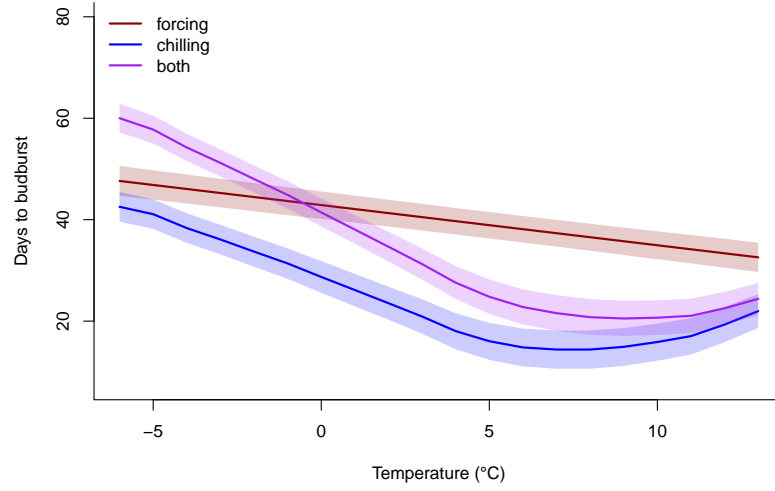


Figure S4: **Chilling and forcing temperatures affect budburst across a range of experimental conditions**, as shown here in a two-dimensional version of Fig. 2 in the main text. We predict budburst timing based on forcing temperature and estimated chilling (converted to a mean temperature, see *Estimating chilling*). Note that days to budburst is relative to experimental methods and thus not comparable to day of year in the field, shading represents 50% credible intervals. We show the effect of chilling temperature on budburst, with forcing kept at the mean level across all experiments (16 °C); the effect of forcing temperature with chilling kept at the mean level across all experiments (1324 chilling units), and the effect of varying both chilling and forcing temperatures simultaneously. Compare this to Fig. 2 in the main text, which shows all possible combinations of chilling and forcing temperatures in a three-dimensional diagram.



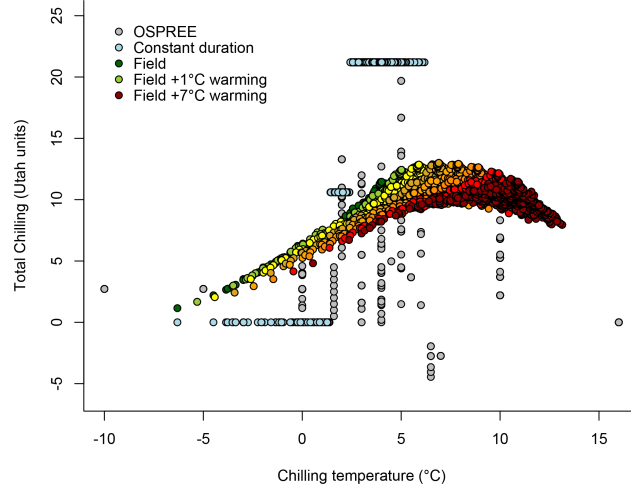


Figure S5: **Chilling accumulates differently in experiments with constant temperatures versus natural systems**, in which temperature is more strongly correlated with chilling. See *Estimating chilling* for a detailed description of 'Field' climate data, for which we use historical climate data from Europe. Fig. 2 and S4 use 'Field' relationships to convert chill temperature to total chilling, whereas Fig. S8 uses 'Constant duration' relationships.

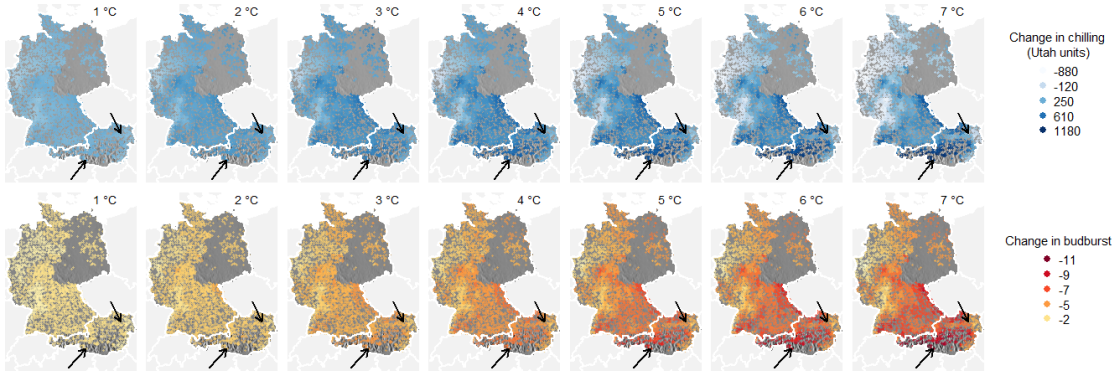


Figure S6: **Forecasted changes in chilling (top panel) and spring phenology for *Betula pendula* (bottom panel)**, in locations included in the PEP 725 database, where phenology dates are known for the pre-warming time period (1951-1960). Changes in chilling and budburst are calculated relative to the mean chilling and leafout dates during this pre-warming time period for each location. Arrows indicate sites shown in Fig. 3A (latitude = 46.8°N, longitude = 12.8°E, 659 m above sea level) and 3B (latitude = 48.3°N, longitude = 15.8°E, 210 m above sea level) in the main manuscript.

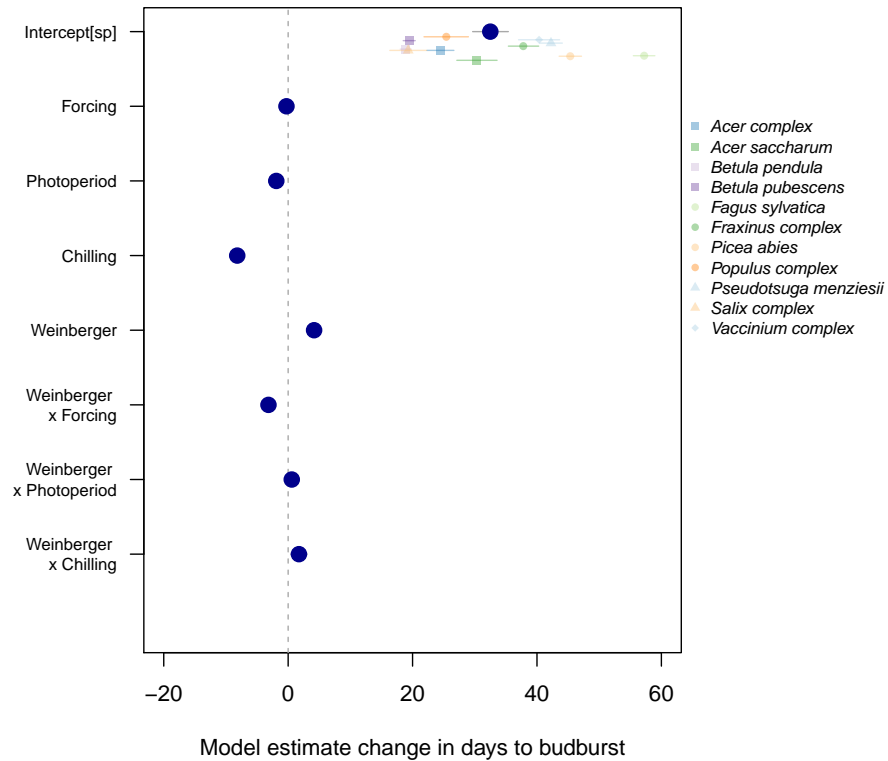


Figure S7: **Chilling study design affects estimates of major cues.** Studies using the ‘Weinberger’ method (sequential removal of tissue from field) had later budburst timing, stronger estimates of forcing (Weinberger x Forcing) and weaker estimates of chilling (Weinberger x Chilling) compared to studies that experimentally manipulated chilling directly. For an extended description of model and underlying data see *Chilling study design model*; for model summary see Table S6.

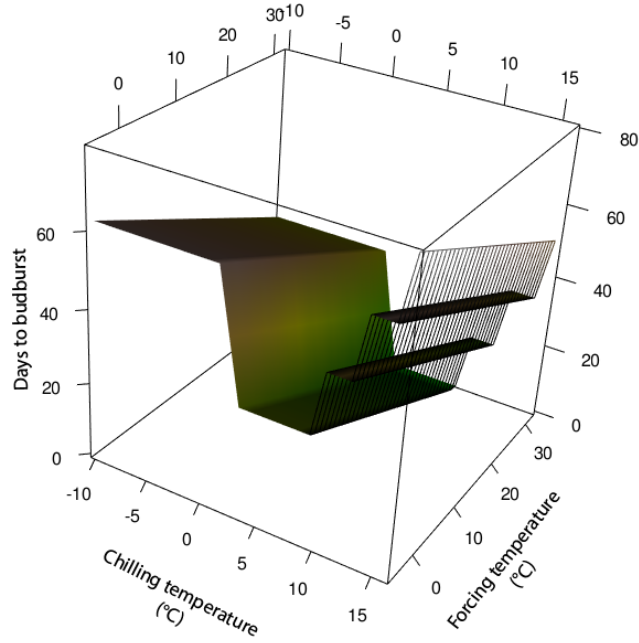


Figure S8: **Based on our model (see ‘main budburst model’ *Models* section), days to budburst decrease linearly with forcing temperature and vary nonlinearly with chilling temperature** due to the way that chilling is estimated (in this case, the Utah model). Forcing treatment temperatures in growth chamber experiments ranged from 0-32 °C and chilling temperatures ranged from -10-16 °C (see Table 2S for details). Budburst responses predicted by the main budburst model are shown across the full range of experimental conditions in the OSPREE database with chilling calculated as a constant temperature across a range of durations (as is commonly applied in experiments). Maximum advances in budburst occur at intermediate chilling temperatures (e.g., here at mean chilling temperatures between 3 and 9 °C) and the highest forcing temperatures (32 °C). Compare this to Fig. 2 in the main text, which uses field chilling at mean chilling temperatures.

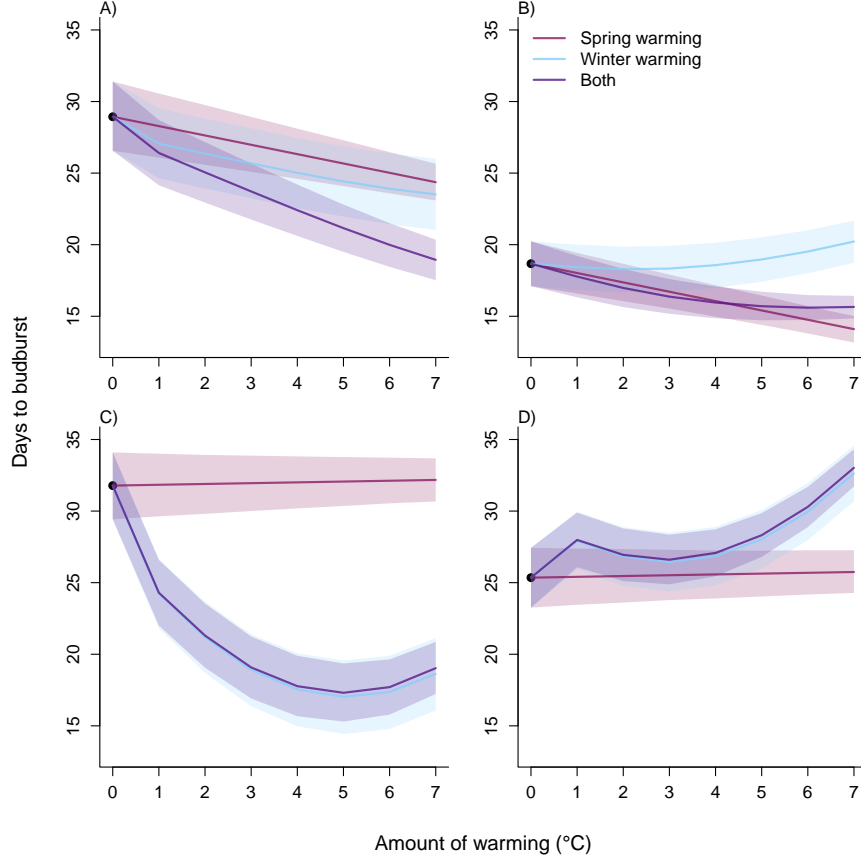


Figure S9: **Implications of warming on budburst timing varies across species and sites**, depending strongly on pre-warming climate conditions related to chilling for each site. Here we show species-level estimates from our model (see Fig. 1 in the main text) for the two most common species in the OSPREE database: *Betula pendula* (A,B) and *Fagus sylvatica* (C,D). We compare estimates of budburst assuming varying levels of winter warming (i.e., affecting chilling, Fig. S10), with forcing kept at the mean pre-warming level, to estimates assuming varying levels of spring warming (i.e. forcing) with chilling kept at mean pre-warming levels, to estimates with winter and spring warming occurring simultaneously. For sites in A (46.8°N, 12.8°E) and C (48.8°N, 15.4°E) chilling decreases with warming, leading to greater advances in budburst (compared to forcing alone). For the sites in B (48.3°N, 15.8°E) and D (46.7, 15.8°E), on the other hand, warming increases chilling, leading to smaller advances, and eventually, delays with substantial warming. Compare this to Fig. 3 in the main text, which shows all possible combinations of winter and spring warming in a three-dimensional diagram.

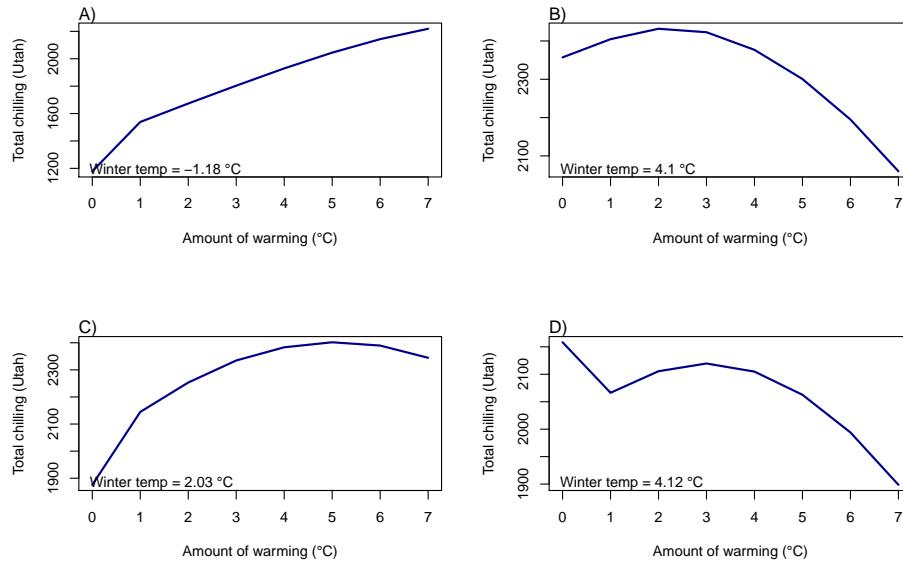


Figure S10: **Implications of global warming on chilling vary by site**, depending on pre-warming climate. At sites in A (46.8°N, 12.8°E) and C (48.8°N, 15.4°E), chilling increases with warming, whereas chilling decreases with warming for the sites in B (48.3°N, 15.8°E) and D (46.7, 15.8°E). Compare to Fig. S9 and Fig. 3 in the main text.

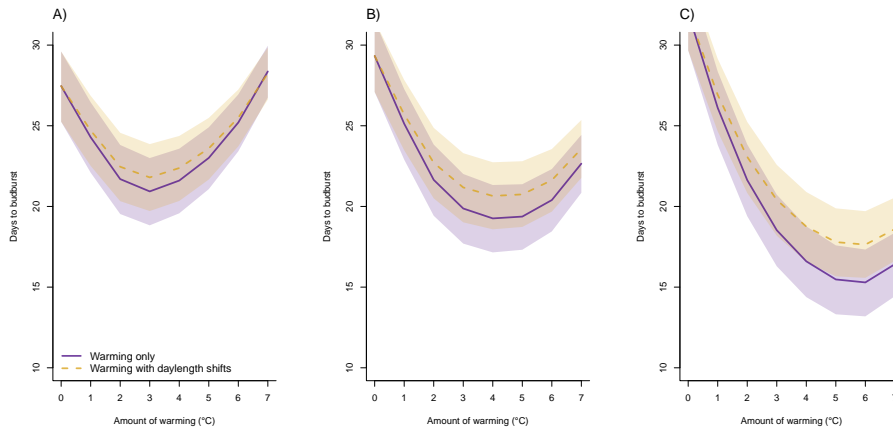


Figure S11: **Budburst is affected by climate-change induced shifts in photoperiod, especially at high latitudes**, though effects vary by site and are minor compared to effects of warming. We show forecasted effects of varying levels of warming on *Fagus sylvatica*, the most photoperiod-sensitive species in our database, across three latitudes within its range, as predicted by the latitude model. The low latitude site (A) is located at 46.8°N, 15.7°E; the mid-latitude site (B) is located at 47.7°N, 16.3°E; and the high-latitude (C) site is located at 48.8°N, 15.4°E.

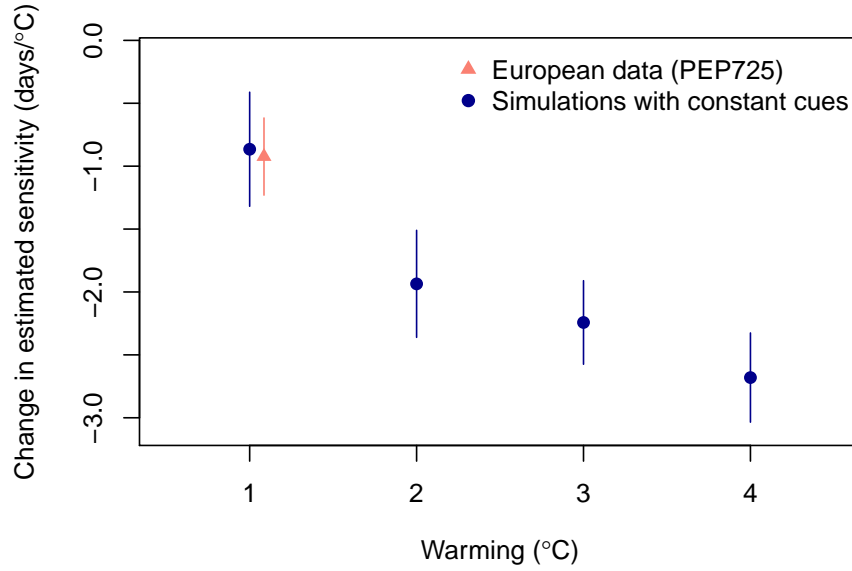


Figure S12: **Declining sensitivities observed in long-term European data for a suite of common trees may be explained by a statistical artifact.** We compared the sensitivity estimated from linear regressions of day of leafout versus mean spring temperature (estimated thus as days/°C) from PEP 725 data for *Betula pendula* from 45 sites ('European data') with estimated declines in simulations where the cues were held constant but spring temperatures warmed by 1-4°C ('Simulations') and found the estimated temperature sensitivity measured as days/°C declined even though the underlying cues had not changed, see *Understanding declines in temperature sensitivity in European long-term data* for further details.

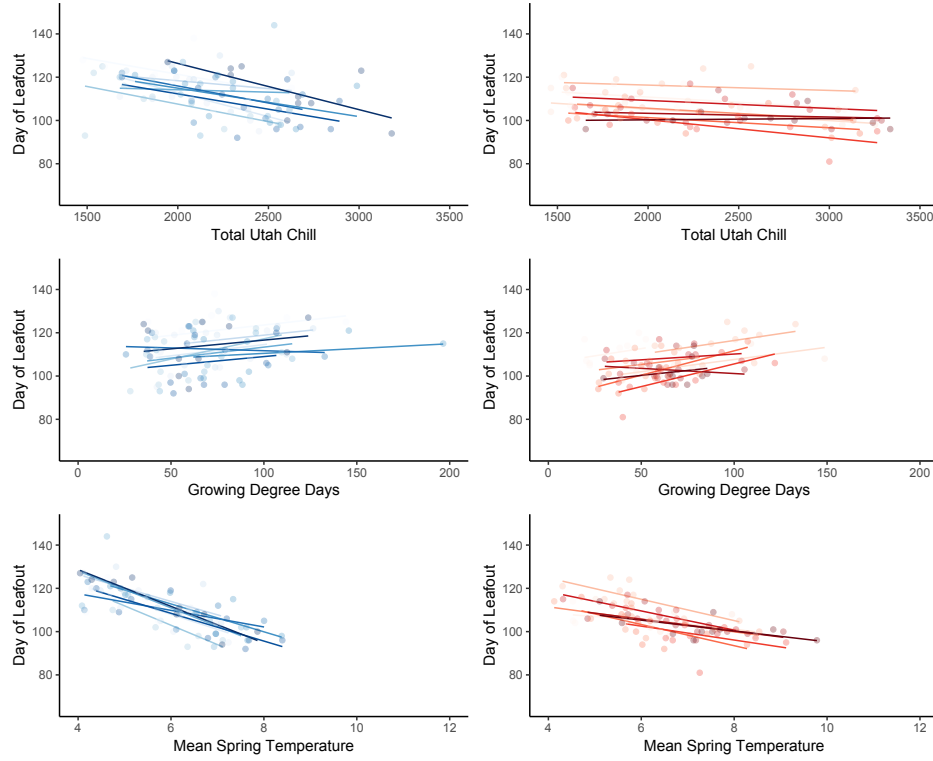


Figure S13: **Day of leaf out versus chilling, growing degree-days, and mean spring temperature** pre- (left panels, 1951-1960) and post- warming (right panels, 2000-2010) for PEP 725 sites in Germany where *Betula pendula* phenology has been monitored for decades.

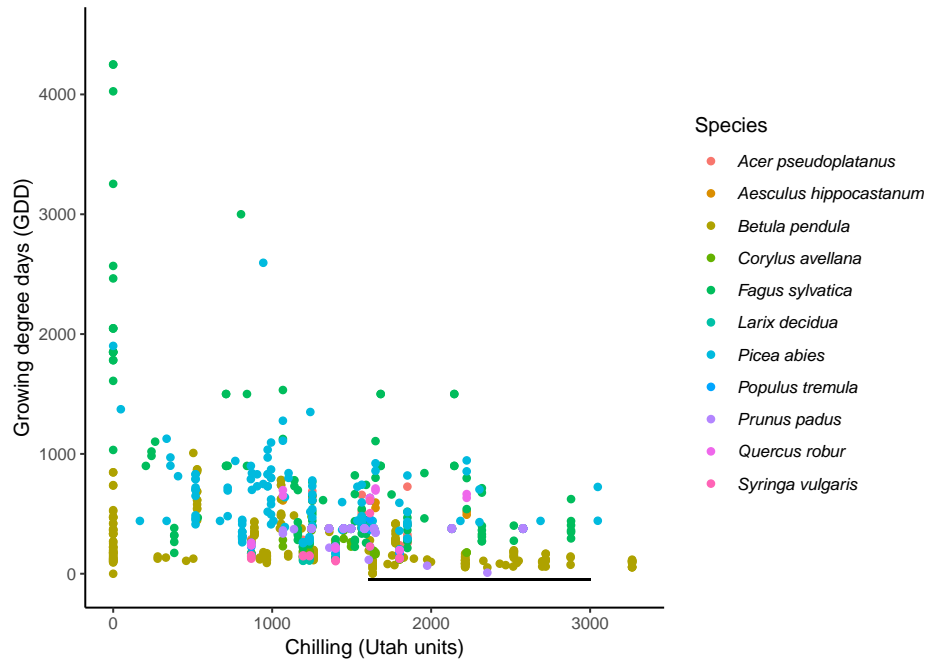


Figure S14: **Growing degree days (GDD) versus chill units at the time of budburst** from the OSPREE database for common species in the PEP 725 long-term phenological database. The black line shows the range of chilling (10-90% quantiles) accumulated from 1 September to 1 March for 45 sites for *Betula pendula* (see also *Understanding declines in temperature sensitivity in European long-term data*). We calculated GDD here as the average daily forcing temperature multiplied by days to budburst.