

Supplemental materials for Chilling outweighs photoperiod and forcing cues for temperate trees in experiments, but not in natural systems

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May need to move back to main text ...

The paucity of studies directly manipulating chilling—which our results suggest has the greatest effect on budburst—suggests a major gap in current research. While many studies (X out of Y here) directly manipulated forcing, far fewer directly manipulated chilling (Z out of Y). Our model highlights how the choice of chill units can affect model estimates and associated forecasts (reference supplemental figure with Utah units vs chill portions in main manuscript). Given the limited manipulation of chilling in studies, we estimated chilling for all studies by combining chilling from the field (i.e., chilling before plants were sampled) and experimental chilling into two widely used metrics of chilling: Utah and Chill portions (Dennis, 2003). We found the effects of chilling and other cues remain qualitatively consistent across the two chilling units, though chilling and photoperiod estimates were slightly lower using chill portions compared to Utah (cite supplemental table comparing estimates with both units).

An additional important limitation is the rarity of studies designed to test interactions. Interactions between these cues are widely expected (cites) and, when examined, often found (cites), we were unable to estimate interactions in our meta-analysis because very few studies design experiments to test for interactions between chilling, forcing, and photoperiod (cite table with number of interactions from coding challenge!). 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 (cites, Tables, figs). Our estimated effects average over interactions (Gelman and Hill, 2006), but identifying them in future research will be critical to understanding and predicting budburst. For example, the most commonly observed interaction between chilling and forcing—that lower amounts of chilling increases forcing requirements for budburst (cite papers in the osprey database that interact chilling and forcing)—is the hypothesized cause of declining sensitivities in European trees (Fu et al., 2015; ?). As more data become available, it would allow additional tests of important interactions, such as how responses vary across latitudes (ref latitude figure).

Things we'd like to discuss in main paper but don't have room for

Photothermoperiodicity, for example, is an ongoing challenge: chamber studies may seek to replicate patterns in nature, pairing daylength and temperature treatments such that night temperatures are always cooler than day temperatures (e.g., cite studies that do this). This results in daylength treatments that differ in temperature conditions (and therefore chilling and forcing treatments) as well, however.

Chilling: Current common models for chilling (i.e., Utah which was developed for XX species, chill portions which was developed for XX species) are *hypotheses* for how chilling may accumulate to affect the process of dormancy release, but are likely to be inaccurate for many species. Our model highlights how the choice of chill units can affect model estimates and associated forecasts (Figures 1,???, 2).

Supplemental Methods

1. Data: search terms, etc
2. Species complex description
3. Equation of our model
4. Quick review of what standardized units are (We used a standardized scale to allow comparisons of the three cues ...)
5. Forecasting with the OSPREE model: We selected sites in Germany where temperature and budburst have been monitored since the 1950s. We extracted mean temperature data from 1951 through 1961 (pre warming time period) and used these values as baseline data. We then investigated model predictions of budburst given different levels of warming (from 1-7 °C) above this baseline, including altered chilling and forcing as well as potential declines in photoperiod due to advancing phenology. We did this for one common European species: *Betula pendula* (silver birch) at all lat/longs included in the PEP database between 1951 and 1961. We also did this for another common European species, *Fagus sylvatica*, for a subset of sites where it occurred with *B. pendula*, in order to compare budburst responses of these two species when they experience the same baseline climate and warming levels.
6. To understand how experimental temperature, photoperiod, and budburst sensitivity compares to past and current conditions in nature, we used data from the PEP database (cite). We summarized forcing, chilling, and budburst day for two common species: *Betula pendula* (silver birch) and *Fagus sylvatica* (European beech) during a pre-warming time-period (1950-1980) and post-warming period (1981-2014?).

Supplemental Results/Discussion

1. Surprising species-specific responses:
 - (a) Positive Responses to chilling for Tilia and Salix. have positive response to chilling with chill portions model. T
 - (b) Positive responses to forcing: Acer-complex, Fraxinus complex, Cornus alba.

Supplemental Tables

1. Table 1S: Species included in OSPREE, with the reference(s) of studies they are included in, the range of forcing, chilling, and photoperiod treatments in these studies, and perhaps the range of latitudes.
2. Table 2S: model estimates for 4 models: Utah z (used in main text Figure 1), Utah uncentered, Chill portions z, Chill portions uncentered

3. Table 3S: a table that goes with Figure 3 (the 4-paneled 3D forecasting figure) that includes the mean budburst day of year, chilling estimates, mean winter temperature, and spring (forcing) temperatures for the 4 sites with no warming and with the 7 levels of warming.

Supplemental figures

1. Map of study locations, shading or symbol coding for number of cues (Lizzie)
2. Map of species forecasting to justify sites
3. Heat maps for the main data associated, including by actual study design and by calculated chilling (our calculations)
4. Photoperiod x latitude effects figure
5. Maps of current and forecasted budburst and chilling for PEP sites (heat maps)

Understanding declines in temperature sensitivity in European long-term data

As our model results (when applied to realistic forcing, chilling and photoperiod conditions in Europe) do not predict a dramatic decline temperature sensitivity, we tested whether observed declines could instead be due to a statistical artifact of the method commonly used to estimate temperature sensitivity (a linear regression of annual budburst date versus mean or other aggregated metrics of spring temperature yielding estimates in days/°C). If warming produces systematically warmer daily temperatures this method will inherently estimate lower sensitivities, because the ‘days’ unit will effectively have increased in the thermal time it represents.

To test this hypothesis we compared observed trends with simulations. First, we collated PEP 725 (CITE) data for *Betula pendula* for all sites with leafout data each year from two 10-year time-periods: 1950-1960, which represented a period before significant anthropogenic warming (citeIPCC) and 2000-2010, a period with significant warming. We used leafout data (BBCH=XX) instead of budburst (BBCH=XX) 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 simply assumed budburst occurred after a certain summation of heat, 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 showed here we used a GDD 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 daily temperatures. Across the sites studied here we estimated a decline of 0.9 ± 0.3 days/°C (comparing 2000-2010 and 1950-1960) and 1.1°C warming; this estimate was very similar to simulations given constant cues and 1°C warming (Fig. 8). Additionally, in both the real and simulated data variance in leafout date declined, as 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 57%, 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 ± 31 Utah units in 1950-1960, compared to 2236 ± 20 Utah units in 2000-2010), 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. fig:pepgddchill).

Reference list

A few categories:

Papers about contrasting results over what cues matter from growth chamber studies: Basler and Körner (2012, 2014); Caffarra et al. (2011a); Caffarra and Donnelly (2011); Caffarra et al. (2011b); Heide and Prestud (2005); Koerner and Basler (2010); Laube et al. (2014); Vitasse and Basler (2013); Zohner et al. (2016). Get Nanninga *et al.* 2017: 'Increased exposure to chilling advances the time to budburst in North American tree species' and maybe Malyshev *et al.* 2018 'Temporal photoperiod sensitivity and forcing requirements for budburst in temperate tree seedlings.'

Papers about declining sensitivities (Ailene will update this list): Rutishauser et al. (2008); Fu et al. (2015). Also look for a Wang *et al.* article 'Impacts of global warming on phenology of spring leaf unfolding remain stable in the long run.' Vitasse paper on declining variation across elevation gradient. See Yu et al. (2010), but this is not temperate trees.

Papers about chilling units paper (Lizzie gets a list): Fu 2012 from OSPREE. Harrington and Gould (2015)Luedeling et al. (2011); Luedeling and Brown (2011); Luedeling et al. (2013)

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section* Figures

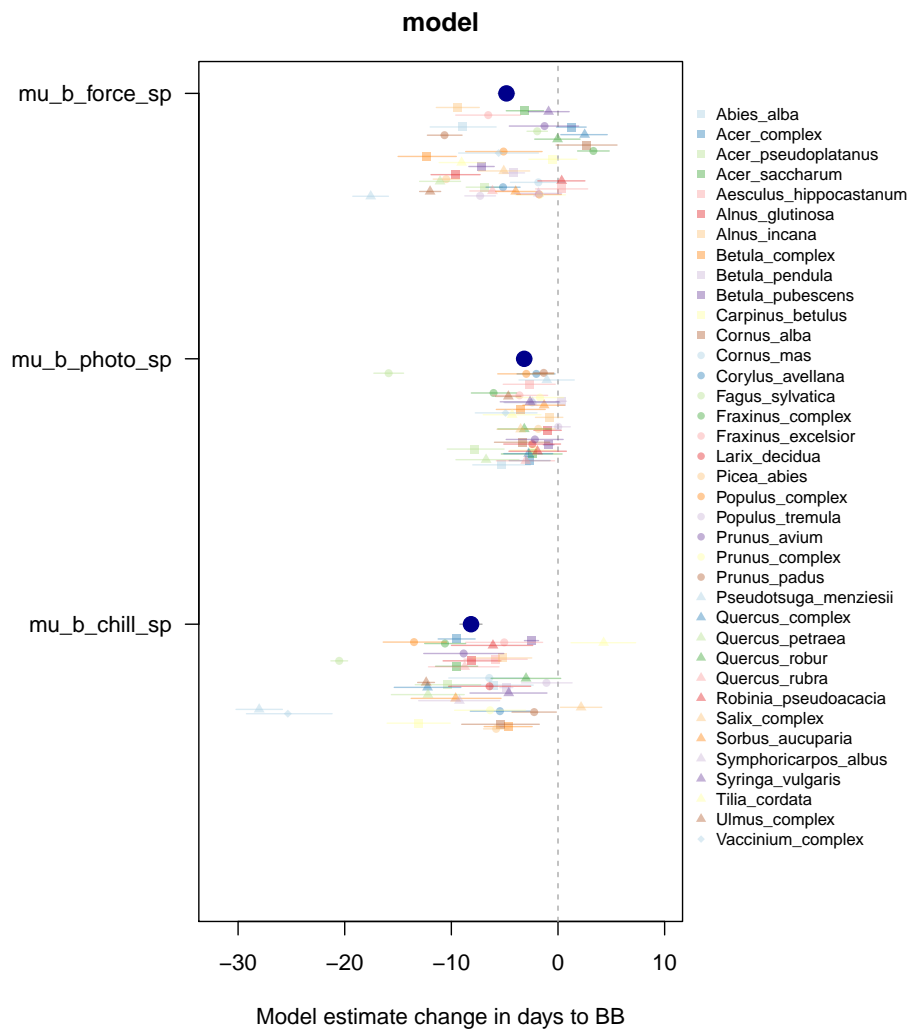


Figure 1: *Estimates for effects of chilling, forcing, and photoperiod from the model fit with Chill Portions*, with centered data, enabling comparisons of effect sizes across predictors. Coefficients were qualitatively similar to those in the model with Utah and can be found in the main text. Convert this into a table and combine with below figure!

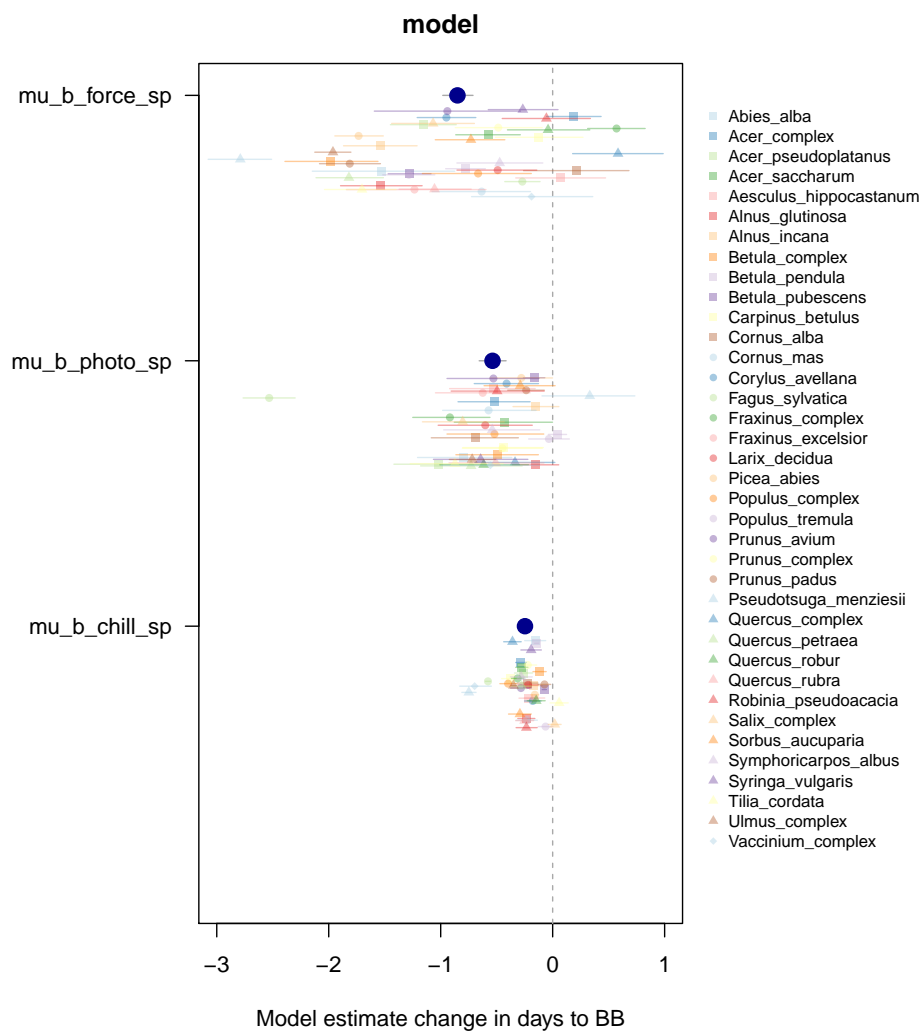


Figure 2: Estimates for effects of chilling, forcing, and photoperiod from the models fit with uncentered predictors using Chill Portions. Convert this into a table and combine with above figure!

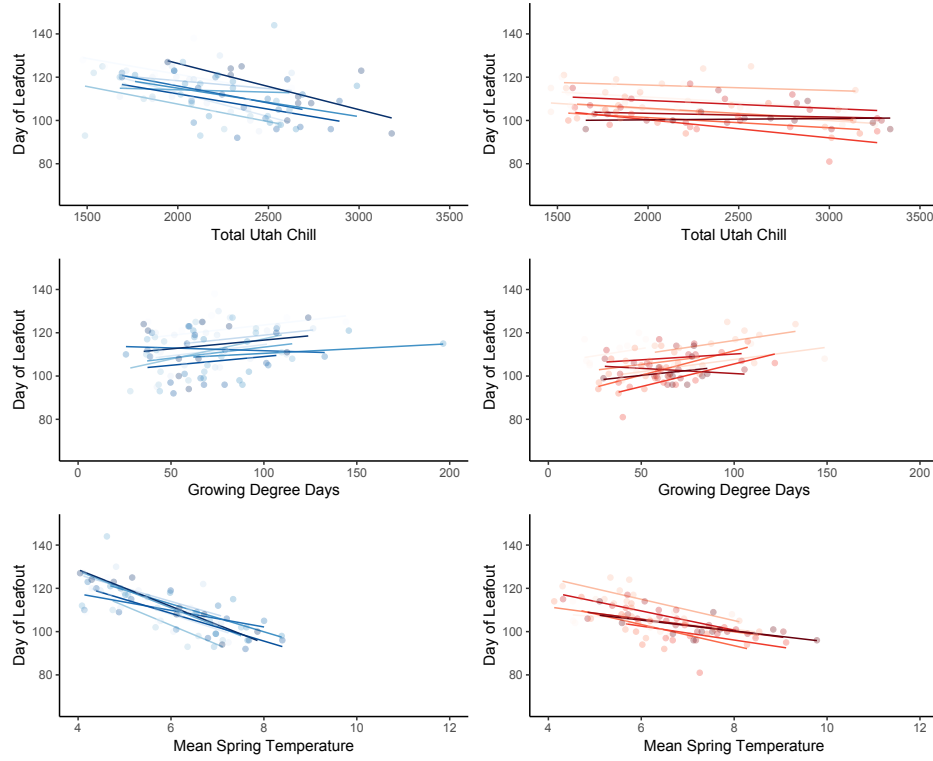


Figure 3: Day of leaf out versus chilling, growing degree-days, and mean spring temperature pre- (left panels, 1951-1961) and post- warming (right panels, 1981-1991) for PEP sites in Germany where *Betula pendula* phenology has been monitored for decades.

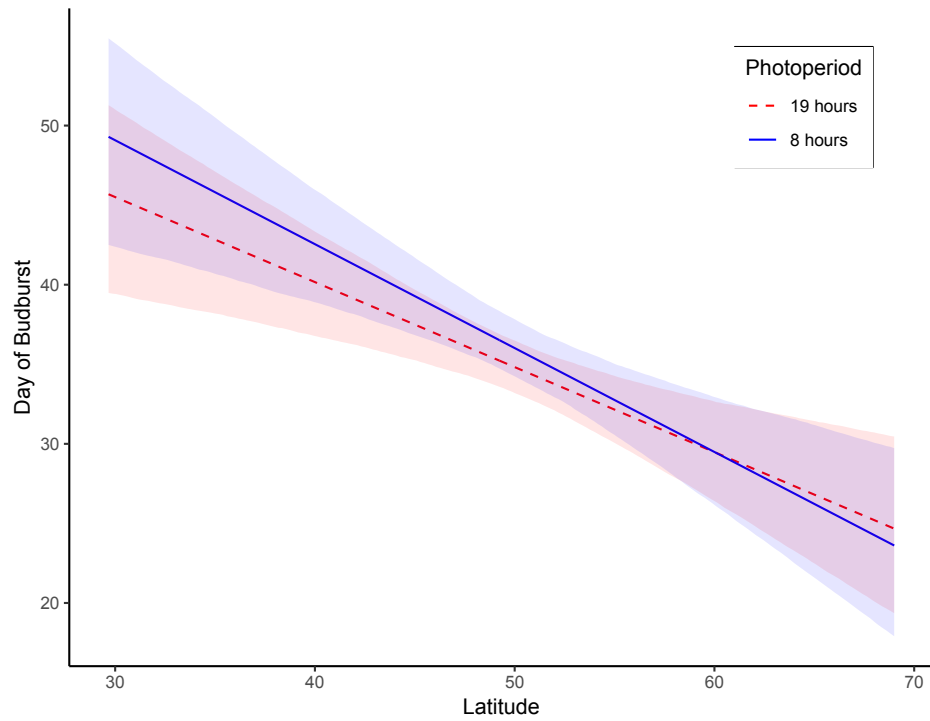


Figure 4: Latitude model. Cat: Could you make a muplot that is similar to those in the main text? Should we keep this plot, or something similar as a second panel?

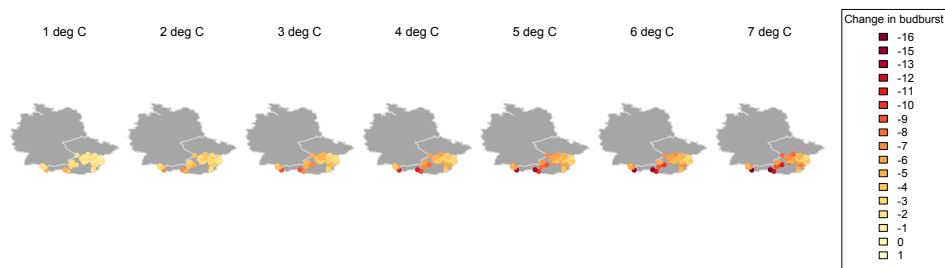


Figure 5: Forecasted chilling and budburst, in PEP areas. Ailene will update this.

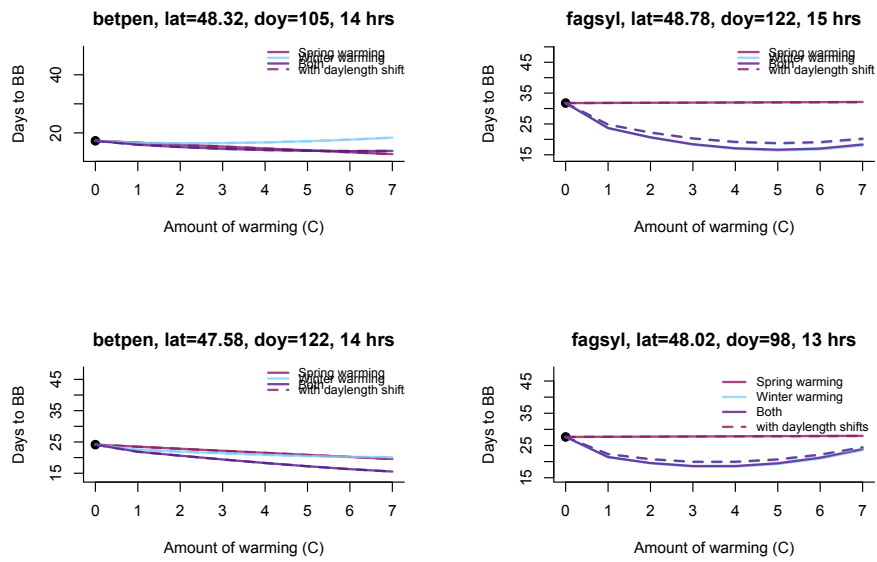
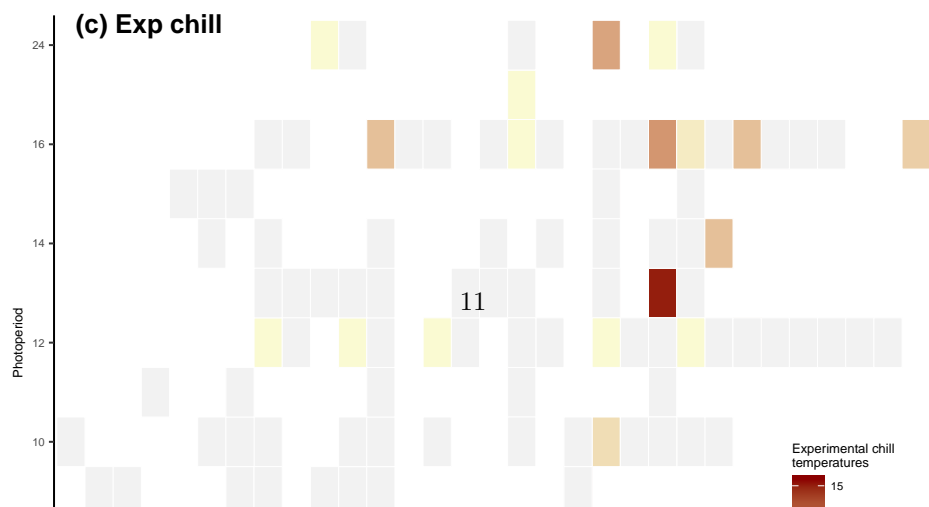
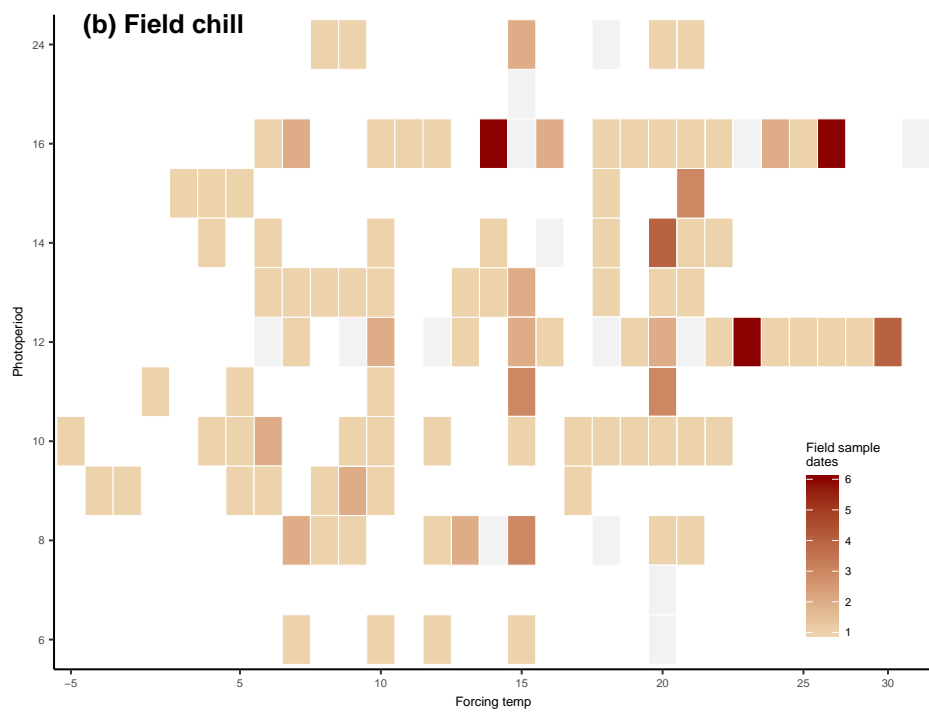
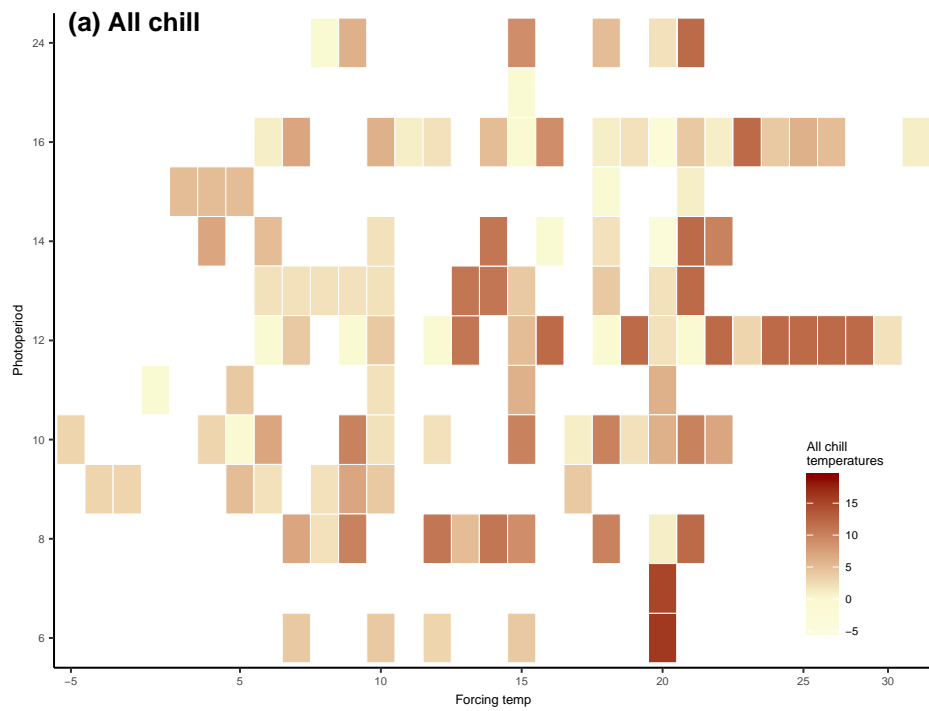


Figure 6: Forecasted



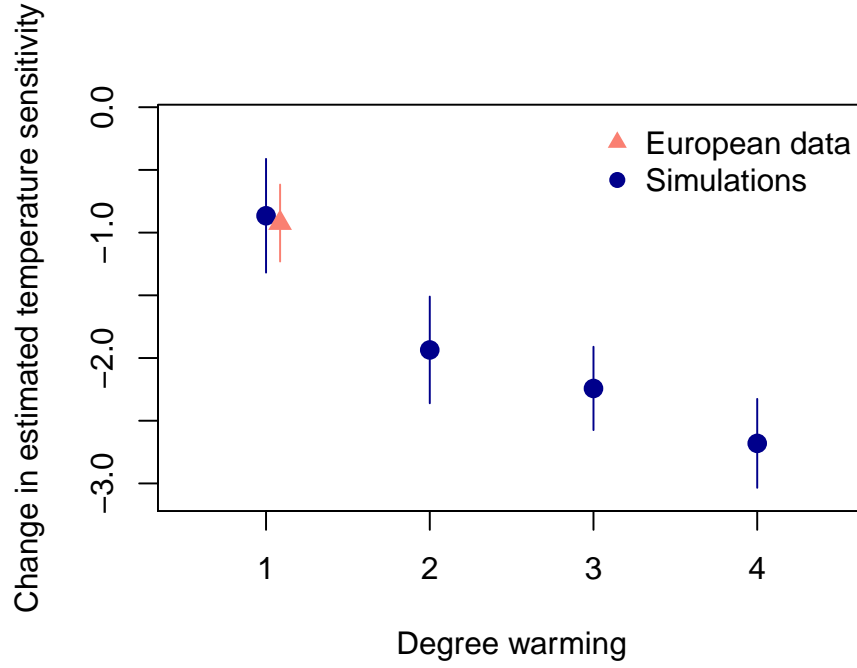


Figure 8: Declining sensitivities observed in long-term European data for a suite of common trees may be explained by a statistical artifact. We compared the sensitivity estimated from linear regressions of day of leafout versus mean spring temperature (estimated thus as days/°C) from PEP 725 data for *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* in Supplement for further details.

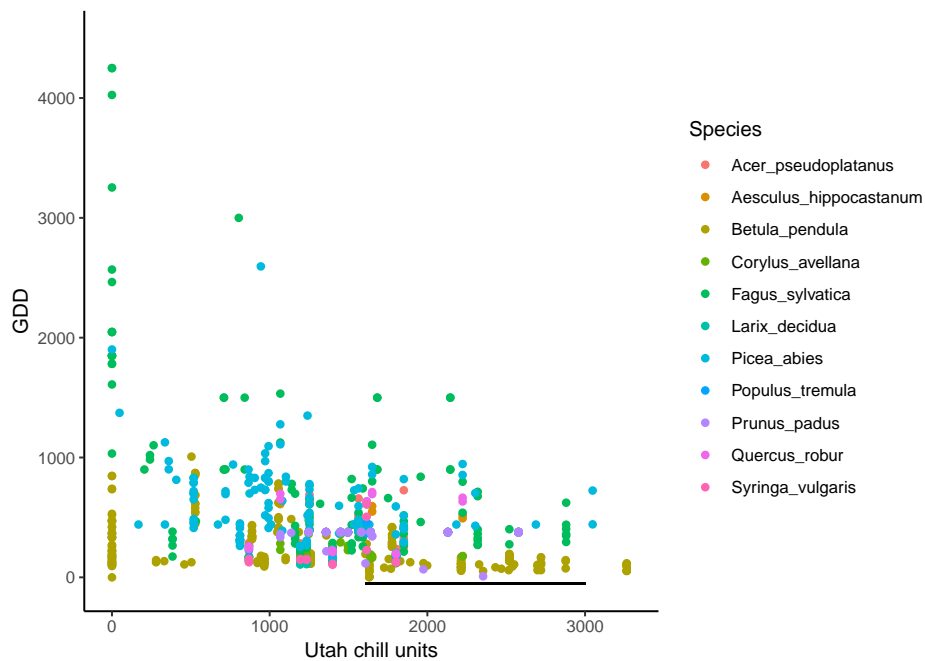


Figure 9: GDD (growing degree days) versus chill units at the time of budburst from the OSPREE database for common species in the PEP 725 long-term phenological database. The black line shows the range of chilling (10-90% quantiles) accumulated from 1 September to 1 March for 45 sites for *Betula pendula* (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.