# Winter temperatures dominate spring phenological responses to warming

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**Abstract**

Decades of fundamental research on woody plant species highlight three major cues that shape spring

phenological events: chilling, forcing, and photoperiod *(e.g., 1; 2; 3)*. Increasing research on the phenological impacts of climate change has led to debate over how common these cues are across species, and—if prevalent—whether chilling and/or photoperiod cues may be slowing phenological responses to warming in recent years *(4; 5; 6; 7)*. Here we use a global meta-analysis of all published controlled environment studies to test for the relative effects of these cues across 203 species. We find almost all species show strong responses to all three cues, with chilling being the strongest (2 times greater than forcing), and photoperiod the weakest (0.7 relative to forcing). Simple forecasts from our findings for a well-studied region (Central Europe) suggest that spring phenology will continue to advance. Stalling effects of chilling generally appear above 4°C warming for most locations, and thus are unlikely to underlie apparently slowing phenological responses. Our results unify both sides of the debate over phenological cues: while all species may respond to all cues strongly in experimental conditions, in current environmental conditions the dominant signal of climate change is from increased forcing.

# Main text

For decades, plant phenology has been one of the most reported and consistent biological imprints of climate change *(8)*: many temperate plants are leafing and flowering days to weeks earlier with rising temperatures *(9; 10)*. Understanding such shifts is important as phenology shapes community assembly and a suite of ecosystem services, including pollination and carbon sequestration, and scales up to impact projections of climate change itself *(11)*.

As research interest in phenology has progressed, critical discrepancies and uncertainties in our understanding have emerged. Though responses to warming are consistent on average, they show high unexplained variation across species and sites *(12)*. Furthermore, long-term observational studies provide increasing evidence that sensitivities of phenology to temperature are weakening in recent decades *(13; 14)*, especially in Europe, where researchers suggest that responses to multiple environmental cues underlie declining temperature sensitivities *(6)*.

Fundamental research in phenology outlines how three major environmental cues, chilling (cool temperatures, generally occurring in the fall and late winter), forcing (warm temperatures, generally occurring in the late winter and early spring), and photoperiod (daylength), provide multiple routes to budburst each spring, depending on the environment *(15)*. For example, in some species a cool winter will lower the amount of forcing required to trigger budburst, compared to a warmer winter *(16)*. Additionally, photoperiod may

trigger budburst, given low chilling and/or forcing *(7; 17; 18)*. Research suggests that all three cues may affect spring phenology for many temperate woody species *(3; 17; 19)*, which could have critical forecasting implications—predicting delays in spring phenology as increased warming reduces chilling in some areas *(20)* or where earlier budburst shortens the experienced photoperiod. However, there is strong debate, with some research suggesting some cues—such as photoperiod—may be effectively absent in some species, but dominate in others *(7; 21)*.

Resolving this debate requires overcoming major hurdles to estimate responses to each cue. Studies attempting to estimate cues using long-term observational data *(e.g., 7; 22)* generally fail to overcome the fundamental challenge that all three cues are strongly correlated in nature (*e.g.*, during the transition from winter to spring at temperate latitudes, forcing and photoperiod usually increase in step). In contrast to observational studies, controlled environment experiments can break down correlations between the cues. These experiments—most often conducted in growth chambers or similar systems to control temperature and light—have been conducted for decades. They have produced contrasting results, however, potentially due to differences in focal species or study sites *(7; 18; 23; 24; 25)*. Resolving these discrepancies is critical to accurate predictions of spring phenology, especially as continued warming pushes climate into environmental regimes far beyond historical bounds.

Here, we leverage nearly 40 years of controlled environment studies to understand how chilling, forcing, and photoperiod determine budburst timing in woody species. We reviewed 201 papers from controlled environment studies, then extracted data from all experiments that reported budburst responses, yielding data from 72 studies across 39 years and 203 species (Fig. S1, Tables S1, S2). The resulting Observed Spring Phenology Responses in Experimental Environments (OSPREE) database includes only studies for which we could identify forcing, photoperiod, and chilling treatments quantitatively and includes a mix of studies where plant tissue was grown in greenhouses or brought in from the field and exposed to experimental conditions. As chilling was rarely reported, we calculated chilling when possible, using a common but approximate method *(26)*, in which chilling does not accumulate below 1.4°C or at high temperatures (throughout the main text we use the term 'chill unit,' see Supplemental Materials for details). We estimated the effects of chilling, forcing, and photoperiod using a Bayesian hierarchical model. Our model averages over interactions between predictors to estimate both species-level responses (generally yielding more accurate estimates for well-studied species, such as *Fagus sylvatica* and *Betula pendula*), and the distribution from which they are drawn, yielding an estimate of the overall response across species (see Supplemental Materials).

Across studies, all cues—chilling, forcing, and photoperiod—advance budburst phenology (Fig. 1, Tables S3, S4). Chilling was the strongest cue (-2.84 days/standard unit or -8.89 days per chill unit), followed by forcing (-0.79 days/standard unit or -4.36 days per °C of warming), and photoperiod (-0.54 days/standard unit or -3.15 days per hour of daylight; Figs. 2, S4, S8; Tables S3, S4; see Supplemental Materials for more details). While photoperiod had the smallest effect among the three cues, our results contrast with the extensive literature suggesting photoperiod is an unimportant cue for many species *(7; 21)*—instead we found it was surprisingly large, even when accounting for its interaction with latitude (see Supplemental Materials for details, especially Figs. S3, S11, Table S5). It was also generally consistent across species, only deviating in *Fagus sylvatica*, a species well-known for having a large response to photoperiod (which we also found, Figs. 1, S3). Species responses to chilling were slightly more variable (variance = 7.36 days per chill unit in the standardized model, Fig. 1) than responses to forcing (variance = 5.67 days per forcing unit in the standardized model Fig. 1).

As temperature is fundamentally altered by climate change, our finding that different ends of the temperature spectrum—chilling and forcing—have the strongest effects on budburst suggests that understanding these cues will be critical for forecasting phenology with climate change. Many previous studies attribute advances in budburst to increased forcing *(10; 16; 17; 27)*. Our results, however, suggest that chilling has a greater effect on budburst than forcing (Figs. 1, S3, S7; Tables S3-S5). This has not been widely suggested previously, perhaps because little work has directly manipulated chilling, and the few studies that have were designed to compare chilling versus photoperiod effects *(e.g., 7; 17; 19; 23)*, not chilling versus forcing effects.

A simple interpretation of our results supports the hypotheses that chilling and photoperiod cues may underlie declining sensitivities to warming in long-term Central European data *(6; 13; 14)*. Under these hypotheses, warming increases forcing and thus advances budburst, but such advances become muted if warming also causes declines in chilling and shorter photoperiods experienced near the timing of budburst *(21)*. This basic agreement between our results and long-term observational trends integrates across experimental conditions that encompass more extreme scenarios than may be seen in nature (Fig. 2). A more robust comparison requires examining predictions under conditions closer to those found in nature.

Reinterpreting our model using climate and phenology data that have led to observations of declining temperature sensitivities in Central Europe suggests that chilling and photoperiod are unlikely to cause the observed declines in sensitivity. Our model predicts such declines only at extreme warming for most sites (see Supplemental Materials). In contrast to the common hypothesis that plants experience less chilling with

global warming, we found that—for many sites—total estimated chilling increased with warming (Fig. 3A, C), though this varied with local climate prior to warming (Figs. S6 - S10). Portions of Central Europe have experienced more dramatic warming in winter versus summer *(28)*; yet even if warming uniquely occurs in the winter, our results suggest that delays due to decreased chilling only occur at warming above 4°C for most sites (Fig. 3). At high warming, predicted declines in sensitivity were due to declines in chilling—photoperiod had comparatively little effect on budburst day of year, even for the photosensitive species *F. sylvatica* (Fig. S11).

Our predictions leave open the question of what underlies declining sensitivities across Europe, but one possibility is that it may be a statistical artifact of how temperature sensitivities are calculated. Physiologically, budburst is triggered by the accumulation of forcing temperatures during the spring *(15; 29)*. However, researchers today often estimate temperature sensitivities from long-term observational data using a linear regression of annual budburst date versus mean spring temperature, or other aggregated temperature metrics *(e.g., 12)*. This approach has the benefit of yielding an easily interpretable metric—days change per °C—but will estimate systematically lower sensitivities given warmer daily temperatures, even with no change in the underlying cues (Fig. S12). We found the declining sensitivities observed in European data are of the same magnitude as those predicted from a statistical artifact (sensitivity declines of 0.8±0.3 days/°C in European data versus 0.9±0.5 days/°C in simulations), and the data also show a related decline in leafout variance that would not be immediately predicted from shifting cues (see *Potential statistical artifacts in declines of temperature sensitivity in observational long-term data* in the Supplemental Materials and *30,* for further details). This statistical artifact is likely not confined to phenological studies; it should apply to any research using a similar days/°C metric to estimate an underlying thermal accumulation model where the thermal sum per day is non-stationary, as is the case with climate change.

A consistent result of our findings—across both the experimental and future in situ environmental conditions—is the importance of chilling. Yet chilling and its related physiological stage, endodormancy, are not well understood *(15)*. Models of how species accumulate chilling are poorly developed for forest trees, with few relevant tests evaluating the particular temperatures at which species do or do not accumulate chilling. Instead, researchers generally rely on models developed for perennial fruit trees (*i.e.,* Utah *(26)* and chill portions *(31)*, both of which were developed for peach species). These models are themselves *hypotheses* for how chilling may accumulate and produce dormancy release, but are likely to be inaccurate for many species *(32)*.

Progress on developing chilling models for wild species is especially slow, as only a small portion of studies (13 of the total 72 studies) manipulate chilling directly. Instead many studies estimate chilling effects through sequential removal of tissue from the field followed by exposure to 'forcing' conditions (25 out of 72; the remaining studies did not appear to manipulate chilling), with the assumption that tissues collected later experience more chilling *(33)*. This method benefits from more natural chilling conditions but introduces other challenges: first, chilling duration may not always co-vary with the magnitude of total accumulated chilling *(32)*, and, second, photoperiod and other factors also change over time. Indeed, we found that sequential-removal studies tended to result in later budburst, weaker effects of chilling and stronger effects of forcing compared to estimates from studies that directly manipulated chilling (Fig. S7, Table S6, *(33; 34)*), suggesting a study's design of chilling manipulation impacts both forcing and chilling estimates. An improved understanding of chilling could in turn alter our understanding of forcing. Although researchers often define 'chilling' and 'forcing' treatments based on temperatures, physiologically plants appear to accumulate forcing mainly after chilling requirements have been met, thus identifying processes that plants undergo when accumulating chilling versus forcing will be critical for the most accurate forecasts *(15)*.

Our results unify decades of experimental studies, which have shown the importance of chilling, forcing, and daylength to determining budburst timing, with long-term observational data, where forcing appears to dominate responses to recent warming. We do not find strong evidence for delaying budburst in the near future, and suggest that recent observed declines in temperature sensitivity may be related to statistical artifacts from estimating complex cues from observational data. Instead, our predictions suggest budburst will continue to advance in many well-studied European regions in the future. The most dramatic changes will come from regions where winter warming causes dramatic decreases in chilling, with implications for ecosystem services related to phenology.

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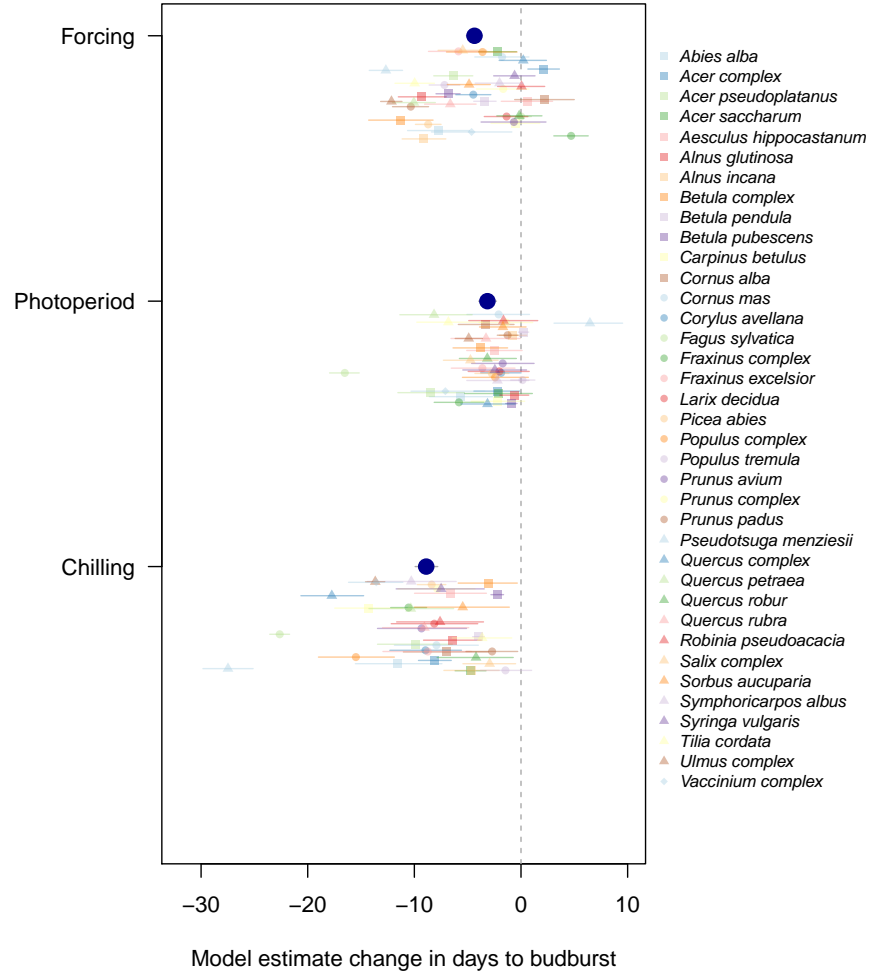
# Acknowledgements

# Figures

Figure 1: **Estimated effects of chilling, forcing, and photoperiod on budburst timing across 67 species in 42 controlled environment studies.** Using standardized units, which allow comparisons across cues, we show that most species (smaller symbols) are responsive to most cues, with chilling being the strongest cue when considering overall estimates across species (larger, dark blue circles). Overall estimates shown here were generally similar to other model formulations, including using data from 203 species, and using different methods for calculating chilling (Figs. S3, S7; Tables S3-S5). Lines represent 50% uncertainty intervals (other intervals provided in Tables S3-S5)
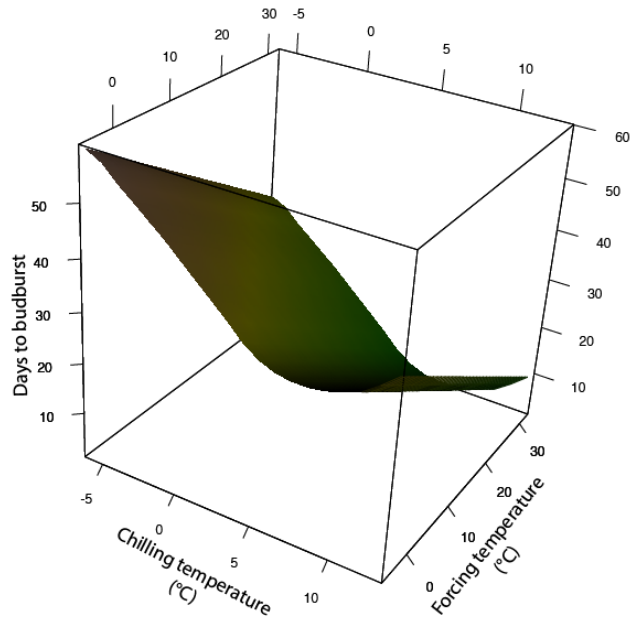
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Figure 2: **Estimates of budburst across a range of forcing temperatures and estimated chilling** (converted to a representative mean temperature, see *Estimating chilling* in the Supplemental Materials) based on overall estimates of chilling and forcing effects (Fig. 1). Maximum advances in budburst occur at intermediate chilling temperatures (*e.g.*, here at mean winter temperatures of 6-7°C) and the highest forcing (here at 32°C). We set photoperiod to eight hours, which is the most common photoperiod treatment in the database. Note that days to budburst is relative to experimental methods and thus is not comparable to day of year in the field; shading represents days to budburst.
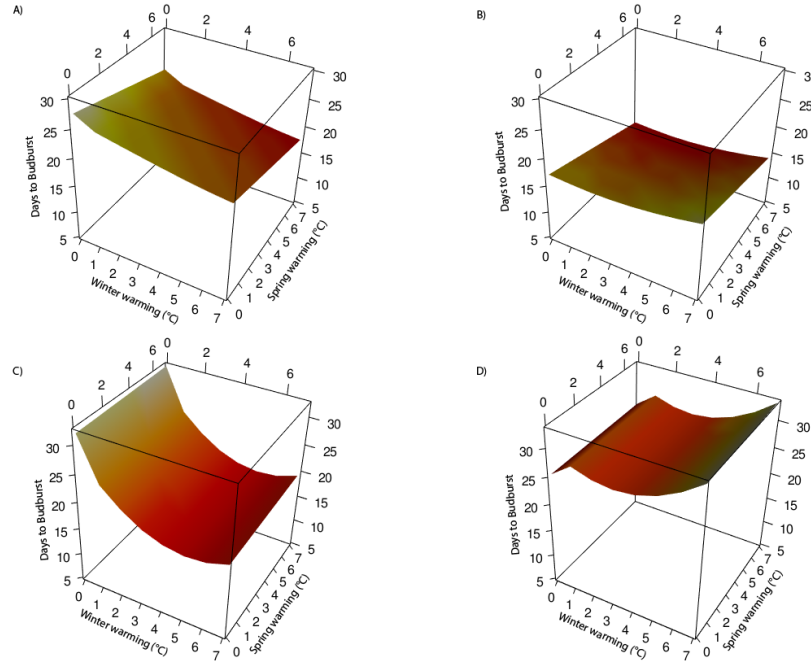
Figure 3: **Implications of warming on budburst timing varies across species and sites**, depending strongly on pre-warming climate conditions related to chilling for each site. Here we show species-level estimates from our model (Fig. 1) for the two most common species in the OSPREE database: *Betula pendula* (A, B) and *Fagus sylvatica* (C, D), for sites that highlight the diversity of possible budburst responses to warming (Fig. S6, which shows general trends across many sites in Central Europe). In some sites, warming increases total chilling estimates (A, C) leading to greater advances in budburst (compared to forcing alone), whereas warming decreases total chilling estimates in other sites (B, D), leading to smaller advances and, eventually, delays with substantial warming. See Supplemental Materials, especially Figs. S6 - S10, for details.

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