

RH: Interactive cues and spring phenology

## **Limiting cues: How spring warming, winter chilling and daylength will shape climate change responses**

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## Abstract

**[1 Feb 2021: Abstract is not yet updated!]** Climate change has shifted plant phenology globally, with average shifts of 4-6 days per ° C and some species shifting much more. Globally, such shifts have been some of the most reported and most predictable biological impacts of climate change. This predictability comes from decades of research, which have outlined the major cues that drive most studied plant phenology: temperatures (including spring warming and winter chilling) and daylength. Further simplifying predictions, spring temperatures are often the dominant cue in nature, making linear models of heat sums often excellent at predicting interannual variation in phenology. Yet as climate change has marched on, new research has uncovered possible failures to predict the current observed changes; increasingly, phenological shifts appear more muted over recent decades, or in certain locations. Here we argue that some of these inaccurate predictions are due to simple models that neglect to consider other major cues—especially winter chilling and daylength, which moderate and shape plant phenological responses to spring warming. We highlight how over 70 years of research in controlled environments can improve predictions for when, where and how the interactive effects of other cues will impact simple linear predictions. Finally, we discuss how a new generation of controlled environment experiments could rapidly improve our predictive capacity for woody plant phenology in coming decades.

*Keywords:* phenology, climate change, spring warming, chilling, forcing, daylength, photoperiod, non-linear responses, leafout, budburst

# 1 Main text

Shifts in spring plant phenology are one of the most reported and most predictable changes with climate change. Decades of research have documented advancing budburst, leafout and flowering across systems (Delpierre *et al.*, 2009; Yu *et al.*, 2010; Ellwood *et al.*, 2013; Jochner *et al.*, 2013; Hereford *et al.*, 2017), especially in temperate systems where long-term records highlight how humans have altered the timing of spring (Schwartz, 1997; Menzel *et al.*, 2003, 2006). Recently, however, these advances have appeared to slow (Fu *et al.*, 2015) or even reverse in some places (Yu *et al.*, 2010)—failing to match simple predictions of an advancing spring with continued warming (Ellwood *et al.*, 2013). The main hypothesis for this failure is that spring warming—which most observational studies focus on—is no longer the only environmental cue that matters to predicting responses to warming (Chuine *et al.*, 2016; Gauzere *et al.*, 2019).

Despite the focus of much spring phenology research on spring warm temperatures, increasing evidence suggests the underlying physiology of spring phenology is more complicated for most temperate species (e.g., Zohner *et al.*, 2016; Gauzere *et al.*, 2019; Ettinger *et al.*, 2020). For many species three major cues drive spring phenology: forcing (warm temperatures, generally occurring in the late winter and early spring), chilling (cool temperatures, generally occurring in the fall and winter), and photoperiod (daylength).

Together, forcing, chilling and photoperiod cues may produce non-linear responses that many current methods do not predict (e.g., Ellwood *et al.*, 2013). Predicting these non-linearities is a common goal in plant phenology research today (Güsewell *et al.*, 2017; Martinez-Luscher *et al.*, 2017; Gauzere *et al.*, 2019; Chen *et al.*, 2019; Keenan *et al.*, 2020), but has been slowed by data gaps and the underlying complexity of spring phenology.

The first step towards improved phenological predictions is robust measurements of chilling, forcing and photoperiod cues. Recently, much effort has focused on estimating these cues from long-term observational data. Yet observational data may often fail to robustly estimate any of the three major cues due to two types of statistical issues. First, in most observational data these cues are correlated: forcing increases alongside longer days (Elmendorf & Ettinger, 2020), and chilling and photoperiod cues both yield similar predictions (i.e., both cues predict later spring phenology with warming). Other approaches that attempt to break some of these correlations, such as leveraging elevational or latitudinal gradients, may run afoul of other correlations—for example, gradients in local adaptation that mean cues shifts along these gradients in complex ways (Tansey *et al.*, 2017). Second, most observational studies focus on linear models of each cue, often without interactions between cues.

Using simple linear models with observational data may make sense as phenological responses to most cues are expected to be linear except at the extremes. Natural conditions often see only a small slice of the range of values of each cue that are possible—and those values often appear to be in the middle linear range (Gauzere *et al.*, 2017; Ettinger *et al.*, 2020). Further, given that interactions between cues are difficult to estimate—more so when those cues are highly correlated in nature—focusing on main effects of cues (which integrates over any interactions, Gelman &

Hill, 2006) may provide more robust estimates from observational data.

In contrast to the limitations of observational studies, one method is designed to measure the complexity of cues: controlled environment (e.g., growth chamber) studies (Nagano *et al.*, 2012; Satake *et al.*, 2013). Such studies have been conducted for over 70 years and are specifically designed to understand non-linearities both in individual cues and produced by interactions between cues. In contrast to observational studies, controlled environment studies can manipulate all three cues, extend to other cues that may be important in some species or biomes (e.g., humidity, drought conditions, light spectra), and can tease out interactions between cues by experimentally decoupling them.

Despite the prevalence of controlled environment studies on spring phenological cues, they have rarely been reviewed. Perhaps more surprisingly, they are often poorly integrated into the current phenological literature on climate change. This includes in debates where they are critical—such as about the importance of photoperiod (e.g., Fu *et al.*, 2015; Richardson *et al.*, 2018).

Here we aim to integrate the long-term literature on growth chamber studies into current phenological research on climate change more fully. We begin by outlining how the three major phenological cues—forcing, chilling and photoperiod—can produce non-linearities and how they will shift in coming decades with anthropogenic climate change. We then review controlled environment studies to understand how much of the cue-space (possible natural range of each cue and interactions across cues) has been studied and how experimental treatments compare to shifts in cues caused by climate change. Based on this, we discuss how controlled environment studies can be best designed to build more robust predictions.

Given our aim to improve understanding of current trends and forecasts we focus on early vegetative phases (budburst and leafout) of wild species, which are critical to plant growth and thus to models of carbon uptake and storage, and which have shifted most with climate change (Cleland *et al.*, 2007; IPCC, 2014). We touch on other areas of research, which have been important to our understanding of the cues underlying phenology. In particular, research has been especially strong in model systems (e.g., *Arabidopsis*, *Populus*) and crops (Cesaraccio *et al.*, 2004)—with the exact phenophase of interest varying (potentially by a species’ life history: more focus on germination and flowering in *Arabidopsis*, and more on leafout and budset in *Populus*). Given our focus on budburst and leafout, our review concentrates on woody species phenology, where most research has been conducted. Most of our conclusions and suggested approaches, however, could be adapted to non-woody species and/or other phenophases with similar underlying interactive cues.

## 1.1 How do phenological cues produce non-linear responses?

Forcing, chilling and photoperiod cues together determine budburst each year for woody species in many temperate species (e.g., Chuine & Regniere, 2017; Ettinger *et al.*, 2020). Forcing and

chilling cues are generally understood to be accumulation processes, where plants must integrate chilling and forcing experienced over time to meet a sum threshold value at which they can budburst, leafout or flower (Chuine, 2000). In contrast, photoperiod is generally not considered an integral cue, but one evaluated daily (Singh *et al.*, 2017). In practice, these two types of processes are often abstracted into the effects of average experienced values (mean temperature or daylength), either over some window in long-term data (e.g., Wolkovich *et al.*, 2012; Fu *et al.*, 2015), or through controlled environments that hold temperatures and light regimes more constant (e.g., Worrall & Mergen, 1967; Heide, 1993a,b; Skuterud & Dietrichson, 1994).

Controlled environment studies show two major ways these cues can produce non-linear response—each cue alone, or through interactions between cues (Figs. 1-2). Each cue alone may produce a non-linear phenological response when examined across a sufficiently wide range of values (Fig. 1). Cues may be linear in the mid-range of values, while extremely high or low values of some cues may produce alternative response (Gauzere *et al.*, 2017). For example, at very low photoperiod (short days) plants often will budburst erratically (Heide, 1993a; Partanen *et al.*, 1998; Singh *et al.*, 2017; Rinne *et al.*, 2018), similarly maximum growth may occur at sufficiently long photoperiods, meaning photoperiods longer than some threshold will have no additional effect on budburst timing (e.g., >18 hours for several crop species Major, 1980). Similarly, extremely cool or very hot temperatures may limit forcing as plant developmental processes slow (Parent & Tardieu, 2012). Such extreme values of cues, however, are likely less common than interactions between cues that can produce non-linearities.

More commonly research has focused on how the interaction of cues may produce non-linearities. For example, multiple studies now show that the threshold of forcing needed for budburst depends on the sum of chilling over the fall and winter and by the photoperiod while forcing is accumulating in the spring (e.g., Zohner & Renner, 2014; Flynn & Wolkovich, 2018). Higher forcing is generally needed given lower chilling (Fig. 3) and short photoperiods (Basler & Körner, 2014; Fu *et al.*, 2019)—producing generally a subadditive effect of forcing x chilling and forcing x photoperiod (i.e., both cues together produce a more muted response than the addition of each cue’s effect alone). This interaction of cues produces a non-linearity in environments where levels of cues are correlated over time or space—for example, if chilling declines are correlated with greater forcing (Fig. 2)—and may be critical to accurate forecasts with climate change.

## 1.2 How will chilling, forcing and photoperiod shift with climate change?

Translating when or if these non-linearities may be triggered by warming first requires understanding how climate change alters each of the three cues. All three cues are expected to shift with climate change, though the shifts will vary substantially across space and time. Most notably to date, warming increases the forcing plants experience each day, with more rapid shifts—and thus also greater shifts—at higher elevations and in the arctic (IPCC, 2014). Daily minima (generally night-time temperature) generally have and will warm more than maxima temperatures (though this effect varies spatially Alexander *et al.*, 2006), making efforts to understand whether plants accumulate temperatures differently in the night or day more critical

(Prasad *et al.*, 2008; Shen *et al.*, 2018).

Warming across seasons is also variable (Alexander *et al.*, 2006), meaning warming’s impact on forcing (generally accumulating in the late winter and spring) may not be equivalent to impacts on chilling (generally accumulating in the late fall through winter). Warming should translate into important shifts in chilling, which long-term observational studies have repeatedly suggested may already be occurring (Fu *et al.*, 2015; Piao *et al.*, 2017). Our poor understanding of chilling, however, makes current and predicted shifts in chilling complicated (Chaine *et al.*, 2016).

Research to date suggests chilling only accumulates in a certain range of temperatures with low (e.g.,  $<0^{\circ}\text{C}$ ) temperatures generally not contributing to chilling accumulations and higher temperatures (e.g.,  $>12^{\circ}\text{C}$ ) potentially decreasing previously accumulated chilling (see Fig. 4 and Richardson, 1974; Fishman *et al.*, 1987). Long-term studies generally focus on the warmer part of this chilling accumulation curve, suggesting that chilling should decrease with warming (Fu *et al.*, 2015; Piao *et al.*, 2017; Gauzere *et al.*, 2019). However, major shifts in accumulated chilling would be also predicted where temperature regimes that were previously too low to accumulate chilling in many months of the winter warm such that chilling begins to accumulate in those months (Guy, 2014). Areas with this shift would then expect much earlier budburst with warming, potentially far earlier than last frost dates.

Unfortunately, these predictions are based on models developed almost solely for agricultural crops (but see Harrington & Gould, 2015), especially stone fruits, and have rarely been robustly adapted to forest trees. While the development of classic models of chilling for peaches and related fruit trees benefited from data on these species being planted far outside their range into regions with extremely low or potentially no chilling, equivalent data on forest trees is almost never available (Dennis, 2003). Thus chilling models to date generally use limited observational and experimental data from forest trees to try to re-parametrize the basic stone fruit models (Chaine, 2000). This in turn makes any current observations of shifts in chilling—and all forecasts with warming—uncertain. Thus we believe is especially important to consider both increases and decreases as potential outcomes of warming (Fig. 2, 4).

Shifts in chilling and forcing with warming have been studied far more than shifts in photoperiod (but see Saikkonen *et al.*, 2012; Way & Montgomery, 2015). While an environment’s photoperiod does not shift with climate change, the relevant photoperiod a plant experiences at critical physiological points may change dramatically with warming. In particular, increases in chilling and/or forcing, which could alone produce much earlier budburst, may be offset by short photoperiods that delay budburst (Gauzere *et al.*, 2019). Similarly, long photoperiods can lead to budburst sooner than predicted by solely low chilling or forcing conditions (Nienstaedt, 1966; Myking & Heide, 1995; Partanen *et al.*, 1998). Thus, changes in chilling and/or forcing correspond to changes in the relevant photoperiod with climate change.

These shifts—in forcing, chilling and photoperiod experienced near the time of an event (henceforth ‘experienced photoperiod’)—can produce non-linearities when they push a single cue across

a critical threshold or inflection point in its effect. For example, if some species have a critical photoperiod for budburst and warming means forcing cues are met before the critical threshold, then we would expect incomplete or highly delayed budburst (Singh *et al.*, 2017; Rinne *et al.*, 2018). Alternatively, the threshold could be crossed in the other direction. For example, if pre-climate change conditions generally caused budburst to occur at the extremes of some cues and climate change has now pushed budburst into periods where these cues are at the more linear part. This is often the mechanism suggested for declining responses to warming in some temperate trees (Fu *et al.*, 2015; Piao *et al.*, 2017; Gauzere *et al.*, 2019), specifically that plants previously accumulated sufficient chilling for a minimal effect of chilling—making forcing the dominant cue—whereas warming has now reduced chilling such that more forcing is needed for budburst (producing an overall muted effect when estimated with current methods). As this example highlights, however, changes in a single cue are unlikely to occur without additional effects on other cues—complicating how well we can understand them in long-term data without robust understanding of the exact cue requirements from experimental studies.

We expect most non-linearities from climate change will come from the effects of interactive cues, as in the previous example where one cue pushed beyond an inflection point triggers shifts in other cues, and due to other covarying shifts the cues caused by environmental change. While simple linear interactions between cues may not alone produce non-linearities (Fig. 2), they quickly become non-linear when changes occur together—for example if increased forcing also occurs in step with shorter experienced photoperiods (Fig. 2). Predicting these non-linearities, however, requires a refined understanding of the interaction and whether there are critical inflection points that may be crossed with continued warming. These complexities highlight how difficult predictions may be without careful efforts to tease out how each cue works alone and interactively.

### 1.3 Forecasting non-linear responses

Controlled environment (generally growth chamber) studies can help predict non-linear responses by allowing researchers to examine the effects of one cue with the others held constant, and examine interactive effects, given the appropriate study design. Such experiments may be especially useful for forecasting if they contain enough variation in treatments to capture precisely where non-linearities occur, and are designed in a range relevant to current versus future conditions. Indeed, one of the major advantages of experiments is that they allow treatments outside of the historical range—an option long-term observational data cannot provide.

We reviewed controlled environment studies over the last seven decades to understand the range of treatments already available, and how they compare to current and future conditions. We note that these studies were rarely conducted for climate change research, and most often done for fundamental science or other areas of applied science (e.g., horticulture or forestry). Yet they are some of the best available data for how plants respond to the environment and thus a critical resource for climate change research today.

### How studies and their experimental treatments vary globally

Controlled environment studies have been conducted across 227 species across the globe, with the majority of papers report research occurring in Europe (54 of 85 papers), followed by North America (23, Fig. 5). Most studies manipulate one cue (Fig. 6), though studies of two or three cues have occurred in almost every decade. Forcing and photoperiod were the most commonly studied cues (56% manipulated forcing; 55% manipulated photoperiod), with chilling being studied in only a third of all studies (33% manipulated chilling). The actual cues studied varied across latitude with a general trend toward examining more extreme values at higher latitudes. Thus, forcing and chilling treatments decline  $0.1^{\circ}\text{C}$  per  $1^{\circ}$  latitude (for forcing, min is  $-0.12$ , for max it's  $-0.08$ , see Fig 7; for chilling it's  $-0.1$  for min and  $-0.07$  for max); and the maximum studied photoperiod increases with latitude ( $0.08$  hr per degree  $^{\circ}$  latitude). These shifts across space appear related to differences in extremes across latitudes (higher latitudes experience colder temperatures and longer photoperiods), but introduce a bias in results as any comparisons of studies from lower and higher latitudes are also comparing a different range of cues.

### How studies manipulate cues

Studies can be broadly categorized as manipulating one, two or (rarely) three cues at once. Single cue studies were the most common (ADDINFO). While valuable for defining potential non-linearities in one cue, single cue studies prevent understanding interactions among cues or comparisons of which cues dominate phenological responses; studies of multiple cues can overcome these challenges.

Of the studies manipulating at least one cue, half additionally manipulated another cue. Study designs most often allowed examining whether cues were interactive (that is, whether the effect of one cue depends on the level of the other cue), with the most studies testing for interactions between photoperiod and forcing (21 studies), followed by studies that examined the effects of photoperiod (13 studies) and forcing (12 studies) across the fall-winter. Such studies follow the design generally attributed to Weinberger *et al.* (1950) where tissue (e.g., cuttings) are taken progressively across the fall and/or winter seasons then exposed to controlled environment conditions. These studies often equate tissue removed later from the field as having received more chilling and thus often treat 'time of cutting' as interchangeable with 'chilling,' though forcing and photoperiod conditions also change. Studies examining photoperiod or forcing crossed with experimental chilling treatments (either through changes in temperature or days of chilling) were much less common (8 studies each for photoperiod and forcing).

Studies examining three cues directly were very rare: we identified only two studies examining all three cues at once, and both were on *Picea abies* (Worrall & Mergen, 1967; Sogaard *et al.*, 2008). A slightly larger set of studies (5 studies) examined three cues indirectly—manipulating photoperiod and forcing in controlled environments but equating chilling with sequential removal of tissue from the field—for 11 species (Schnabel & Wample, 1987; Heide, 1993a; Partanen *et al.*, 1998; Basler & Körner, 2014).



The paucity of studies examining multiple cues limits our fundamental understanding of each cue, as well as how—when combined—they will determine future leafout with continued warming. Because the cues are all known to be interactive, estimates of any one cue are influenced by the level of each other cue. Knowing the level of each other cue is difficult both because they are often not reported, and also because they are somewhat impossible to know given our current understanding of endodormancy (when we understand chilling is accumulated) and ecodormancy (when we understand forcing is accumulated). Authors may use the terms ‘chilling’ and ‘forcing’ for their treatments, but they rarely have physiological evidence that these are the actual conditions plants experience. Studies using sequential removal from the field to estimate chilling are at perhaps the greatest disadvantage to estimate the cues applied: chilling must rely on field estimates from models that are currently only hypotheses of actual chilling (Dennis, 2003), and forcing and photoperiod treatments are most probably a mix conditions in the field and conditions applied in controlled environments. Though such studies also have the advantage of the most natural chilling conditions.

#### *How relevant are treatments to current and future conditions?*

The utility of controlled environment studies to forecasting also depends on how relevant treatments are to current and future conditions. Estimating such relevance is difficult as it depends on a species’ range and projections considered. However, a simple analysis of two widely studied species, *Fagus sylvatica* and *Betula pendula*, suggests experiments have generally bracketed the range of projected temperatures (Fig. 9). Projected changes in maximum temperatures generally fit within the range of temperature differences conducted within forcing treatments in experiments (e.g., an experiment with both 16°C and 20°C forcing treatments would have a 4°C difference), and similarly matched differences in minimum temperatures in chilling treatments. As we noted above, however, there is a paucity of chilling studies that directly manipulate chilling temperature—and thus allow a comparison of how differences in chilling temperatures impact phenology. Indeed, we found no studies with multiple chill temperatures tested for *Fagus sylvatica*, even though it is one of the most well-studied species.

Experimental shifts were generally larger than expected shifts due to climate change. This makes sense from an experimental-statistical perspective: if the goal of an experiment is to identify if a cue is present then larger treatment differences should yield larger effect sizes and thus higher statistical power. But such large shifts may be risky to extrapolate to smaller shifts due to warming. Further, experimental studies vary from natural settings in myriad ways. Different studies have ameliorated some of these differences. For example, most studies (34 of the 48 that manipulated forcing) have constant day/night temperatures, but some vary day and night temperatures (26) with nights generally being cooler, while some have even introduced ramped temperature through the day and across an experiment’s length (e.g., Basler & Körner, 2012; Laube *et al.*, 2014). Such ramped conditions are generally introduced across all treatments in experiments and thus provide little insight on how much such experimental artifacts matter (but see Erwin & Heins, 1995). This means extrapolating from controlled environment studies should be done with care, and highlights a need for future experiments designed to improve forecasting effects of climate change.

## 1.4 Paths forward

We argue that controlled environment experiments will be critical for accurate predictions of phenology given future warming. How accurate such predictions are will depend on the design of future experiments, breakthroughs in our physiological understanding of the major cues, and how well these two areas can be integrated with long-term data to improve models.

### *Improving controlled environment studies*

We expect the most useful future experiments will be designed to improve models. In particular, experiments designed to identify threshold effects and optimal temperatures/photoperiods, and non-linearities from interactive cues may be most useful. Identifying threshold effects and optimal temperatures or photoperiods generally requires many different levels of a single cue, which can make such experiments difficult to cross with other cues. Yet, understanding if findings are consistent across varying levels of other cues should be a follow-up step to confirm that findings can be applied across levels of other cues. Studies manipulating more than one cue also test for non-linearities due to interactive cues, as long as they are fully-crossed (i.e., every combination of levels is present in treatments). Such experiments can quickly require a large number of controlled environments, but provide critical information for models and to connect to long-term findings. As growing experimental results support that all cues are dependent on the level of other cues (Stearns & Olson, 1958; Flynn & Wolkovich, 2018) and long-term data hint at multiple cues (Fu *et al.*, 2015), we believe this should be a major research aim.

Controlled environment studies may also be more readily applied to forecasting by exploring more realistic conditions. While identifying thresholds, optima and non-linearities may involve considering informative extremes in levels of cues, most changes in cues due to climate change are and will be on a (relatively) smaller scale (Fig. 9). Thus, when designing studies to contribute to improved forecasting of particular species, experimentalists should examine cues within the current and projected future range of species. In most species distribution models, species are expected to remain in the same climatic conditions, suggesting there may be minimal changes—assuming such models of species distribution are accurate and that species track perfectly. Most evidence, however, suggests species will lag in their spatial responses (Loarie *et al.*, 2009), meaning shifts in cues in the current range may be important to the fate of trailing edge populations (Bertrand *et al.*, 2011; Lenoir & Svenning, 2015; Savage & Vellend, 2015).

Beyond the absolute level of cues, controlled environment studies need more work on what attributes of the design are more or less critical for replicating responses from the field. For example, controlled environment studies have shown differing day/night temperatures are important for some species (Heuvelink, 1989; Abrol & Ingram, 1996; Thingnaes *et al.*, 2003; Pressman *et al.*, 2006), but comparison studies have not been conducted for most species. Equally, a few studies have attempted to replicate certain aspects of the environment, such as fluctuating temperatures, ramped temperatures and light throughout the day, the coincidence of temperature and sunrise (Erwin, 1998), but these are by no means widespread enough to understand how important these conditions are for extrapolation to models.

342 *Understanding the physiology of phenology*

343 Even with all the suggested above improvements, controlled environment studies will still be  
344 fundamentally limited in their utility for prediction without an improved understanding of how  
345 major phenological cues act physiologically. This problem is most apparent with chilling, but  
346 translates also to forcing—as the two are both defined by physiological phases of dormancy that  
347 are not easily measured.

348  
349 Chilling is defined as what leads to break of endodormancy, after which plants enter ecodormancy,  
350 when accumulated forcing then leads to budburst (Chuine *et al.*, 2016). Measuring  
351 endodormancy and its transition into ecodormancy, however, is notoriously difficult. Thus, in  
352 practice, most phenology studies use the terms ‘chilling’ and ‘forcing’ to mean ‘cool temper-  
353 atures’ (often either in the fall and winter or applied in experimental conditions) and ‘warm  
354 temperatures’ (often either in the spring or applied after sufficient chilling) and generally hope  
355 they correspond to endo- and eco-dormancy—without any evidence or tests of this hoped-for  
356 correspondence. Some studies use the sequential transfer of cuttings to warm conditions to es-  
357 timate the transition from endo- to eco-dormancy, with rapid and full (e.g., >90% of buds on a  
358 cutting) budburst generally meaning a plant is ecodormant (e.g., Junttila & Hänninen, 2012),  
359 but given that this is labor- and space-intensive few studies of chilling include this.

360  
361 Physiologists have long recognized this issue and recent breakthroughs provide new insights into  
362 what causes dormancy at the cellular level (van der Schoot *et al.*, 2014). Research suggests  
363 endodormancy may break when enzymes sufficiently remove the sugar (callose) that blocks  
364 plasmodesmata in bud cells (reviewed in Chang *et al.*, 2021), but work thus far has relied gen-  
365 erally on cellular staining methods tested on a very limited subset of species (Rinne *et al.*, 2011;  
366 Singh *et al.*, 2019), making extrapolation to other species difficult. Such results, however, hold  
367 promise for a much improved physiological understanding of endodormancy release in the future.

368  
369 An improved physiological understanding of endodormancy release could revolutionize models of  
370 chilling, and in turn, estimates of forcing. Forcing in controlled environment experiments is gen-  
371 erally defined simply as warm temperatures (or warm temperatures after cool temperatures),  
372 future estimates could be accurately defined simply as temperatures during ecodormancy—  
373 assuming tractable tests of endo- and eco-dormancy and the uptake of such tests in controlled  
374 environment studies. With these experiment studies in hand though, researchers could quickly  
375 build improved models of chilling, and forcing and—for the first time—provide accurate predic-  
376 tions of how chilling will shift with climate change.

377  
378 *Improving integration of controlled environment and physiological studies with long-term data*

379 A major need currently is improved integration between long-term observational, physiological  
380 and controlled environment studies. With important exceptions (e.g., Gauzere *et al.*, 2017),  
381 studies of long-term observational phenology data have moved forward independently from ad-  
382 vances in our physiological understanding and from controlled environment studies. Similarly,  
383 controlled environment studies, as we have reviewed here, generally do not use long-term data  
384 to help interpret results or define treatments.

385

386 While most studies of long-term data and controlled environments generally ignore one another,  
 387 attempts to integrate the two provide a useful path forward that can happen now (Caffarra *et al.*,  
 388 2011; Nagano *et al.*, 2012; Satake *et al.*, 2013; Ford *et al.*, 2016; Chuine & Regniere, 2017), while  
 389 we await physiological breakthroughs in defining endo- and eco-dormancy. Experiments that test  
 390 for thresholds and the presence of important interactions have helped re-design models (Caf-  
 391 farra *et al.*, 2011; Chuine & Regniere, 2017), while other studies have used experiments to test  
 392 extremes (e.g., extremely low chilling) combined with data from long-term provenance studies  
 393 to understand how growth and phenology will combine to determine future ranges (Ford *et al.*,  
 394 2016). Further, some work has used controlled environments to test model predictions, especially  
 395 in future climate scenarios where non-linearities are predicted (see Nagano *et al.*, 2012). Such  
 396 work underlies progress towards model development that relies continuously on a back-and-forth  
 397 process between developing models based on both long-term data and experiments, then testing  
 398 predictions with new experiments and as newer observational data are generated (i.e., more  
 399 years and also data from new locations) (Nagano *et al.*, 2012; Satake *et al.*, 2013). Such efforts  
 400 of continual development take extensive data and thus have only been carried out for a very few  
 401 species (e.g., *Arabidopsis thaliana*, *Oryza sativa* (rice), *Arabidopsis halleri*, Wilczek *et al.*, 2009;  
 402 Nagano *et al.*, 2012; Satake *et al.*, 2013).

403

#### 404 *Building species-rich predictions*

405 Given the efforts and data involved in models for a single species, building up to multi-species  
 406 predictions may appear daunting, but multi-species models are crucial for accurate forecasts that  
 407 can apply to diverse regions and large-scale vegetation models. Addressing this issue requires, of  
 408 course, more data. Long-term data is generally more species-rich than controlled environment  
 409 studies. For example long-term observational data in the PEP725 and NECTAR databases  
 410 together have multi-site data on more than 2500 species, while our review of controlled environ-  
 411 ment studies found most studies focused on only one species with data on a total of 227 species.  
 412 Thus, more diverse controlled environment studies may be the current major data limitation.  
 413 Beyond data, however, new modeling approaches can help integrate current and future data  
 414 more powerfully.

415

416 Bayesian hierarchical models are specifically designed for analysis of diverse datasets. With  
 417 the right information and sufficient data, they can attribute variation across studies to the  
 418 species studied, the cues (i.e., chilling, forcing and photoperiod levels in studies) and remaining  
 419 unmeasured variation in studies (i.e., differences in chamber design may be captured by including  
 420 a parameter to estimate a ‘study’ effect). Such models are extremely powerful for building  
 421 species-rich predictions as they leverage data across all species into one model designed to  
 422 capture both the cross-species and cross-study overall effects as well as species-level differences.  
 423 Yet, like all models, they are more robust with more data. In particular, attributing variation  
 424 due to study versus species requires the same species to be studied across several studies, which  
 425 is currently not the case for most species, according to our literature review (over 80% of the 227  
 426 species in our dataset appear in only one study, 26 species, or 11.4%, appear in more than two  
 427 studies and only 10 species, or 4.4%, appear in more than three studies). Thus, these models

will be most useful given greater efforts to publish data. Given proper data reporting (i.e., all cue conditions must be defined, even when not manipulated, and controlled environment conditions should be fully described including relative humidity and irradiance) all studies—whether designed to improve models or forecasting, or not—can be included in such models.

## 1.5 Right now: It's your tomorrow

Research on phenology had been conducted for centuries before anthropogenic climate change caused earlier budburst and leafout across much of the globe (Sparks & Carey, 1995). Decades of controlled environment studies contributed to our fundamental understanding of the drivers of spring plant phenology. Today, climate change requires leveraging these decades and centuries of research for more accurate predictions that can help humans adapt to warming.

We have outlined how researchers could better harness the power of controlled environment experiments to transform our fundamental understanding of phenology and advance forecasting. Controlled environment studies can critically rule out, or support, hypotheses to explain observed discrepancies in long-term data and open up new pathways to use long-term data to understand current trends, helping the field move beyond trying to tease out cues using only long-term data where cues are inherently correlated. While understanding, modeling and predicting interactions among cues and their effects on phenology is challenging, advances would yield more accurate predictions, with valuable implications to more realistically assess the effects of climate change on plant biodiversity, including agricultural and forest species.

## 2 References

- Abrol, Y.P. & Ingram, K.T. (1996) Effects of higher day and night temperatures on growth and yields of some crop plants. *Global climate change and agricultural production: Direct and indirect effects of changing hydrological, pedological and plant physiological processes* pp. 123–140.
- Alexander, L.V., Zhang, X., Peterson, T.C., Caesar, J., Gleason, B., Tank, A., Haylock, M., Collins, D., Trewin, B., Rahimzadeh, F., Tagipour, A., Kumar, K.R., Revadekar, J., Griffiths, G., Vincent, L., Stephenson, D.B., Burn, J., Aguilar, E., Brunet, M., Taylor, M., New, M., Zhai, P., Rusticucci, M. & Vazquez-Aguirre, J.L. (2006) Global observed changes in daily climate extremes of temperature and precipitation. *Journal of Geophysical Research-Atmospheres* **111**.
- Basler, D. & Körner, C. (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology* **165**, 73–81.
- Basler, D. & Körner, C. (2014) Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. *Tree Physiology* **34**, 377–388.
- Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.C. & Gégout, J.C. (2011) Changes in plant community composition lag behind climate warming in lowland forests. *Nature* **479**, 517.
- Caffarra, A., Donnelly, A. & Chuine, I. (2011) Modelling the timing of *Betula pubescens* bud-burst. II. Integrating complex effects of photoperiod into process-based models. *Climate Research* **46**, 159–170.
- Cesaraccio, C., Spano, D., Snyder, R.L. & Duce, P. (2004) Chilling and forcing model to predict bud-burst of crop and forest species. *Agricultural and Forest Meteorology* **126**, 1–13.
- Chang, C.Y.Y., Brautigam, K., Huner, N.P.A. & Ensminger, I. (2021) Champions of winter survival: cold acclimation and molecular regulation of cold hardiness in evergreen conifers. *New Phytologist* **229**, 675–691.
- Chen, L., Huang, J.G., Ma, Q.Q., Hanninen, H., Tremblay, F. & Bergeron, Y. (2019) Long-term changes in the impacts of global warming on leaf phenology of four temperate tree species. *Global Change Biology* **25**, 997–1004.
- Chuine, I. (2000) A unified model for budburst of trees. *Journal of Theoretical Biology* **207**, 337–347.
- Chuine, I., Bonhomme, M., Legave, J.M., García de Cortázar-Atauri, I., Charrier, G., Lacointe, A. & Améglio, T. (2016) Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. *Global Change Biology* **22**, 3444–3460.

- 483 Chuine, I. & Regniere, J. (2017) Process-based models of phenology for plants and animals.  
484 *Annual Review of Ecology, Evolution, and Systematics* **48**, 159–182.
- 485 Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant  
486 phenology in response to global change. *Trends in Ecology & Evolution* **22**, 357–365.
- 487 Delpierre, N., Dufrene, E., Soudani, K., Ulrich, E., Cecchini, S., Boe, J. & Francois, C. (2009)  
488 Modelling interannual and spatial variability of leaf senescence for three deciduous tree species  
489 in France. *Agricultural and Forest Meteorology* **149**, 938–948.
- 490 Dennis, F. (2003) Problems in standardizing methods for evaluating the chilling requirements  
491 for the breaking of dormancy in buds of woody plants. *HortScience* **38**, 347–350.
- 492 Ellwood, E.R., Temple, S.A., Primack, R.B., Bradley, N.L. & Davis, C.C. (2013) Record-  
493 breaking early flowering in the eastern united states. *Plos One* **8**, ellwood, Elizabeth R.  
494 Temple, Stanley A. Primack, Richard B. Bradley, Nina L. Davis, Charles C.
- 495 Elmendorf, S.C. & Ettinger, A.K. (2020) Is photoperiod a dominant driver of secondary growth  
496 resumption? *Proceedings of the National Academy of Sciences of the United States of America*  
497 **117**, 32861–32864.
- 498 Erwin, J.E. (1998) Temperature and light effects on stem elongation. *Journal of the Japanese*  
499 *Society for Horticultural Science* **67**, 1113–1120.
- 500 Erwin, J.E. & Heins, R.D. (1995) Thermomorphogenic responses in stem and leaf development.  
501 *Hortscience* **30**, 940–949.
- 502 Ettinger, A., Chamberlain, C., Morales-Castilla, I., Buonaiuto, D., Flynn, D., Savas, T.,  
503 Samaha, J. & Wolkovich, E. (2020) Winter temperatures predominate in spring phenolog-  
504 ical responses to warming. *Nature Climate Change* pp. 1–6.
- 505 Fishman, S., Erez, A. & Couvillon, G. (1987) The temperature dependence of dormancy break-  
506 ing in plants: mathematical analysis of a two-step model involving a cooperative transition.  
507 *Journal of Theoretical Biology* **124**, 473–483.
- 508 Flynn, D.F.B. & Wolkovich, E.M. (2018) Temperature and photoperiod drive spring phenology  
509 across all species in a temperate forest community. *New Phytologist* **219**, 1353–1362.
- 510 Ford, K.R., Harrington, C.A., Bansal, S., Gould, Peter, J. & St. Clair, J.B. (2016) Will changes  
511 in phenology track climate change? A study of growth initiation timing in coast Douglas-fir.  
512 *Global Change Biology* **22**, 3712–3723.
- 513 Fu, Y.H., Piao, S., Zhou, X., Geng, X., Hao, F., Vitasse, Y. & Janssens, I.A. (2019) Short  
514 photoperiod reduces the temperature sensitivity of leaf-out in saplings of *Fagus sylvatica* but  
515 not in horse chestnut. *Global Change Biology* **25**, 1696–1703.
- 516 Fu, Y.S.H., Zhao, H.F., Piao, S.L., Peaucelle, M., Peng, S.S., Zhou, G.Y., Ciais, P., Huang, M.T.,  
517 Menzel, A., Uelas, J.P., Song, Y., Vitasse, Y., Zeng, Z.Z. & Janssens, I.A. (2015) Declining  
518 global warming effects on the phenology of spring leaf unfolding. *Nature* **526**, 104–107.

519 Gauzere, J., Delzon, S., Davi, H., Bonhomme, M., de Cortazar-Atauri, I.G. & Chuine, I. (2017)  
520 Integrating interactive effects of chilling and photoperiod in phenological process-based mod-  
521 els. A case study with two European tree species: *Fagus sylvatica* and *Quercus petraea*.  
522 *Agricultural and Forest Meteorology* **244**, 9–20.

523 Gauzere, J., Lucas, C., Ronce, O., Davi, H. & Chuine, I. (2019) Sensitivity analysis of tree phe-  
524 nology models reveals increasing sensitivity of their predictions to winter chilling temperature  
525 and photoperiod with warming climate. *Ecological Modelling* **441**, 108805.

526 Gelman, A. & Hill, J. (2006) *Data analysis using regression and multilevel/hierarchical models*.  
527 Cambridge University Press.

528 Güsewell, S., Furrer, R., Gehrig, R. & Pietragalla, B. (2017) Changes in temperature sensitivity  
529 of spring phenology with recent climate warming in Switzerland are related to shifts of the  
530 preseason. *Global Change Biology* **23**, 5189–5202.

531 Guy, R.D. (2014) The early bud gets to warm. *New Phytologist* **202**, 7–9.

532 Harrington, C.A. & Gould, P.J. (2015) Tradeoffs between chilling and forcing in satisfying  
533 dormancy requirements for pacific northwest tree species. *Frontiers in Plant Science* **6**, 120.

534 Heide, O. (1993a) Daylength and thermal time responses of budburst during dormancy release  
535 in some northern deciduous trees. *Physiologia Plantarum* **88**, 531–540.

536 Heide, O. (1993b) Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and  
537 long days. *Physiologia Plantarum* **89**, 187–191.

538 Hereford, J., Schmitt, J. & Ackerly, D.D. (2017) The seasonal climate niche predicts phenology  
539 and distribution of an ephemeral annual plant, *mollugo verticillata*. *Journal of Ecology* **105**,  
540 1323–1334.

541 Heuvelink, E. (1989) Influence of day and night temperature on the growth of young tomato  
542 plants. *Scientia Horticulturae* **38**, 11–22.

543 IPCC (2014) *Climate Change 2014: Impacts, Adaptation, and Vulnerability*. Cambridge Univer-  
544 sity Press, Cambridge, United Kingdom and New York, NY, USA.

545 Jochner, S., Caffarra, A. & Menzel, A. (2013) Can spatial data substitute temporal data in  
546 phenological modelling? a survey using birch flowering. *Tree Physiology* **33**, 1256–1268.

547 Junttila, O. & Hänninen, H. (2012) The minimum temperature for budburst in *Betula* depends  
548 on the state of dormancy. *Tree physiology* **32**, 337–345.

549 Keenan, T.F., Richardson, A.D. & Hufkens, K. (2020) On quantifying the apparent temperature  
550 sensitivity of plant phenology. *New Phytologist* **225**, 1033–1040.

551 Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2014) Chilling  
552 outweighs photoperiod in preventing precocious spring development. *Global Change Biology*  
553 **20**, 170–182.



554 Lenoir, J. & Svenning, J.C. (2015) Climate-related range shifts—a global multidimensional syn-  
555 thesis and new research directions. *Ecography* **38**, 15–28.

556 Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The  
557 velocity of climate change. *Nature* **462**, 1052–U111.

558 Major, D.J. (1980) Photoperiod response characteristics controlling flowering of 9 crop species.  
559 *Canadian Journal of Plant Science* **60**, 777–784.

560 Martinez-Luscher, J., Hadley, P., Ordidge, M., Xu, X.M. & Luedeling, E. (2017) Delayed chilling  
561 appears to counteract flowering advances of apricot in southern uk. *Agricultural and Forest*  
562 *Meteorology* **237**, 209–218.

563 Menzel, A., Jakobi, G., Ahas, R., Scheifinger, H. & Estrella, N. (2003) Variations of the climato-  
564 logical growing season (1951–2000) in Germany compared with other countries. *International*  
565 *Journal of Climatology* **23**, 793–812.

566 Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kuebler, K. *et al.*  
567 (2006) European phenological response to climate change matches the warming pattern. *Global*  
568 *Change Biology* **12**, 1969–1976.

569 Myking, T. & Heide, O. (1995) Dormancy release and chilling requirement of buds of latitudinal  
570 ecotypes of *Betula pendula* and *B. pubescens*. *Tree Physiology* **15**, 697–704.

571 Nagano, A.J., Sato, Y., Mihara, M., Antonio, B.A., Motoyama, R., Itoh, H., Nagamura, Y.  
572 & Izawa, T. (2012) Deciphering and prediction of transcriptome dynamics under fluctuating  
573 field conditions. *Cell* **151**, 1358–1369.

574 Nienstaedt, H. (1966) Dormancy and dormancy release in white spruce. *Forest Science* **12**,  
575 374–384.

576 Parent, B. & Tardieu, F. (2012) Temperature responses of developmental processes have not  
577 been affected by breeding in different ecological areas for 17 crop species. *New Phytologist*  
578 **194**, 760–774.

579 Partanen, J., Koski, V. & Hänninen, H. (1998) Effects of photoperiod and temperature on the  
580 timing of bud burst in Norway spruce (*Picea abies*). *Tree Physiology* **18**, 811–816.

581 Piao, S., Liu, Z., Wang, T., Peng, S., Ciais, P., Huang, M., Ahlstrom, A., Burkhardt, J.F.,  
582 Chevallier, F., Janssens, I.A. *et al.* (2017) Weakening temperature control on the interannual  
583 variations of spring carbon uptake across northern lands. *Nature climate change* **7**, 359.

584 Prasad, P.V.V., Pisipati, S.R., Ristic, Z., Bukovnik, U. & Fritz, A.K. (2008) Impact of nighttime  
585 temperature on physiology and growth of spring wheat. *Crop Science* **48**, 2372–2380.

586 Pressman, E., Shaked, R. & Firon, N. (2006) Exposing pepper plants to high day temperatures  
587 prevents the adverse low night temperature symptoms. *Physiologia Plantarum* **126**, 618–626.

- 588 Richardson, A.D., Hufkens, K., Milliman, T., Aubrecht, D.M., Furze, M.E., Seyednasrollah, B.,  
589 Krassovski, M.B., Latimer, J.M., Nettles, W.R., Heiderman, R.R., Warren, J.M. & Hanson,  
590 P.J. (2018) Ecosystem warming extends vegetation activity but heightens vulnerability to cold  
591 temperatures. *Nature* **560**, 368–+.
- 592 Richardson, E. (1974) A model for estimating the completion of rest for ‘Redhaven’ and ‘Elberta’  
593 peach trees. *HortScience* **9**, 331–332.
- 594 Rinne, P.L.H., Paul, L.K. & van der Schoot, C. (2018) Decoupling photo- and thermoperiod by  
595 projected climate change perturbs bud development, dormancy establishment and vernaliza-  
596 tion in the model tree populus. *Bmc Plant Biology* **18**.
- 597 Rinne, P.L.H., Welling, A., Vahala, J., Ripel, L., Ruonala, R., Kangasjarvi, J. & van der Schoot,  
598 C. (2011) Chilling of dormant buds hyperinduces FLOWERING LOCUS T and recruits GA-  
599 Inducible 1,3-beta-Glucanases to reopen signal conduits and release dormancy in *Populus*.  
600 *Plant Cell* **23**, 130–146.
- 601 Saikkonen, K., Taulavuori, K., Hyvönen, T., Gundel, P.E., Hamilton, C.E., Vänninen, I., Nissi-  
602 nen, A. & Helander, M. (2012) Climate change-driven species’ range shifts filtered by pho-  
603 toperiodism. *Nature Climate Change* **2**, 239.
- 604 Satake, A., Kawagoe, T., Saburi, Y., Chiba, Y., Sakurai, G. & Kudoh, H. (2013) Forecasting  
605 flowering phenology under climate warming by modelling the regulatory dynamics of flowering-  
606 time genes. *Nature Communications* **4**.
- 607 Savage, J. & Vellend, M. (2015) Elevational shifts, biotic homogenization and time lags in  
608 vegetation change during 40 years of climate warming. *Ecography* **38**, 546–555.
- 609 Schnabel, B.J. & Wample, R.L. (1987) Dormancy and cold hardiness in *Vitis vinifera* L. cv.  
610 White Riesling as influenced by photoperiod and temperature. *American Journal of Enology*  
611 *and Viticulture* **38**, 265–272.
- 612 Schwartz, M.D. (1997) Spring index models: An approach to connecting satellite and surface  
613 phenology. *Phenology in Seasonal Climates I* (eds. H. Lieth & M.D. Schwartz), pp. 22–38,  
614 Backhuys Publisher, Leiden, The Netherlands.
- 615 Shen, X.J., Liu, B.H., Henderson, M., Wang, L., Wu, Z.F., Wu, H.T., Jiang, M. & Lu, X.G.  
616 (2018) Asymmetric effects of daytime and nighttime warming on spring phenology in the  
617 temperate grasslands of china. *Agricultural and Forest Meteorology* **259**, 240–249.
- 618 Singh, R.K., Miskolczi, P., Maurya, J.P. & Bhalerao, R.P. (2019) A tree ortholog of short  
619 vegetative phase floral repressor mediates photoperiodic control of bud dormancy. *Current*  
620 *Biology* **29**, 128–+.
- 621 Singh, R.K., Svystun, T., AlDahmash, B., Jönsson, A.M. & Bhalerao, R.P. (2017) Photoperiod-  
622 and temperature-mediated control of phenology in trees—a molecular perspective. *New Phy-*  
623 *tologist* **213**, 511–524.

- 624 Skuterud, R. & Dietrichson, J. (1994) Budburst in detached birch shoots (*Betula pendula*) of  
625 different varieties winter-stored in darkness at three different temperatures. *Silva Fennica* **28**,  
626 223–224.
- 627 Søgaaard, G., Johnsen, Ø., Nilsen, J. & Junttila, O. (2008) Climatic control of bud burst in young  
628 seedlings of nine provenances of norway spruce. *Tree Physiology* **28**, 311–320.
- 629 Sparks, T.H. & Carey, P.D. (1995) The responses of species to climate over two centuries - an  
630 analysis of the Marsham phenological record, 1736-1947. *Journal of Ecology* **83**, 321–329.
- 631 Stearns, F. & Olson, J. (1958) Interactions of photoperiod and temperature affecting seed ger-  
632 mination in *Tsuga canadensis*. *American Journal of Botany* **45**, 53–58.
- 633 Tansey, C.J., Hadfield, J.D. & Phillimore, A.B. (2017) Estimating the ability of plants to plas-  
634 tically track temperature-mediated shifts in the spring phenological optimum. *Global Change*  
635 *Biology* **23**, 3321–3334.
- 636 Thingnaes, E., Torre, S., Ernstsén, A. & Moe, R. (2003) Day and night temperature responses  
637 in arabidopsis: Effects on gibberellin and auxin content, cell size, morphology and flowering  
638 time. *Annals of Botany* **92**, 601–612.
- 639 van der Schoot, C., Paul, L.K. & Rinne, P.L.H. (2014) The embryonic shoot: a lifeline through  
640 winter. *Journal of Experimental Botany* **65**, 1699–1712.
- 641 Way, D.A. & Montgomery, R.A. (2015) Photoperiod constraints on tree phenology, performance  
642 and migration in a warming world. *Plant, Cell & Environment* **38**, 1725–1736.
- 643 Weinberger, J.H. *et al.* (1950) Chilling requirements of peach varieties. *Proceedings. American*  
644 *Society for Horticultural Science*, vol. 56, pp. 122–28.
- 645 Wilczek, A.M., Roe, J.L., Knapp, M.C., Cooper, M.D., Lopez-Gallego, C., Martin, L.J., Muir,  
646 C.D., Sim, S., Walker, A., Anderson, J., Egan, J.F., Moyers, B.T., Petipas, R., Giakountis, A.,  
647 Charbit, E., Coupland, G., Welch, S.M. & Schmitt, J. (2009) Effects of genetic perturbation  
648 on seasonal life history plasticity. *Science* **323**, 930–934.
- 649 Wolkovich, E.M., Cook, B.I., Allen, J.M., Crimmins, T.M., Betancourt, J.L., Travers, S.E.,  
650 Pau, S., Regetz, J., Davies, T.J., Kraft, N.J.B., Ault, T.R., Bolmgren, K., Mazer, S.J.,  
651 McCabe, G.J., McGill, B.J., Parmesan, C., Salamin, N., Schwartz, M.D. & Cleland, E.E.  
652 (2012) Warming experiments underpredict plant phenological responses to climate change.  
653 *Nature* **485**, 494–497.
- 654 Worrall, J. & Mergen, F. (1967) Environmental and genetic control of dormancy in *Picea abies*.  
655 *Physiologia Plantarum* **20**, 733–745.
- 656 Yu, H.Y., Luedeling, E. & Xu, J.C. (2010) Winter and spring warming result in delayed spring  
657 phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences of the*  
658 *United States of America* **107**, 22151–22156.

- 659 Zohner, C.M., Benito, B.M., Svenning, J.C. & Renner, S.S. (2016) Day length unlikely to  
660 constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate*  
661 *Change* **6**, 1120–1123.
- 662 Zohner, C.M. & Renner, S.S. (2014) Common garden comparison of the leaf-out phenology  
663 of woody species from different native climates, combined with herbarium records, forecasts  
664 long-term change. *Ecology Letters* **17**, 1016–1025.

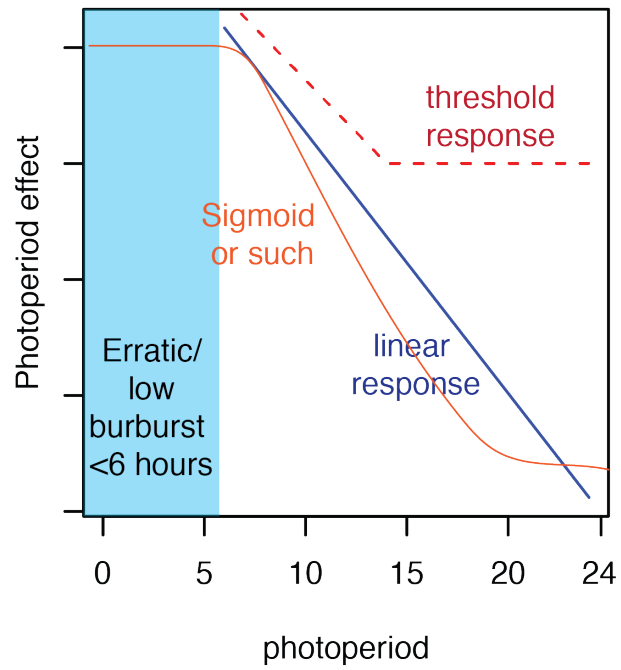


Figure 1: Draft of one-cue figure showing various types of non-linearities possible in a single cue. Do we need? Or combine with interaction figure?

### 665 3 Figures

How cue response shapes budburst with warming...

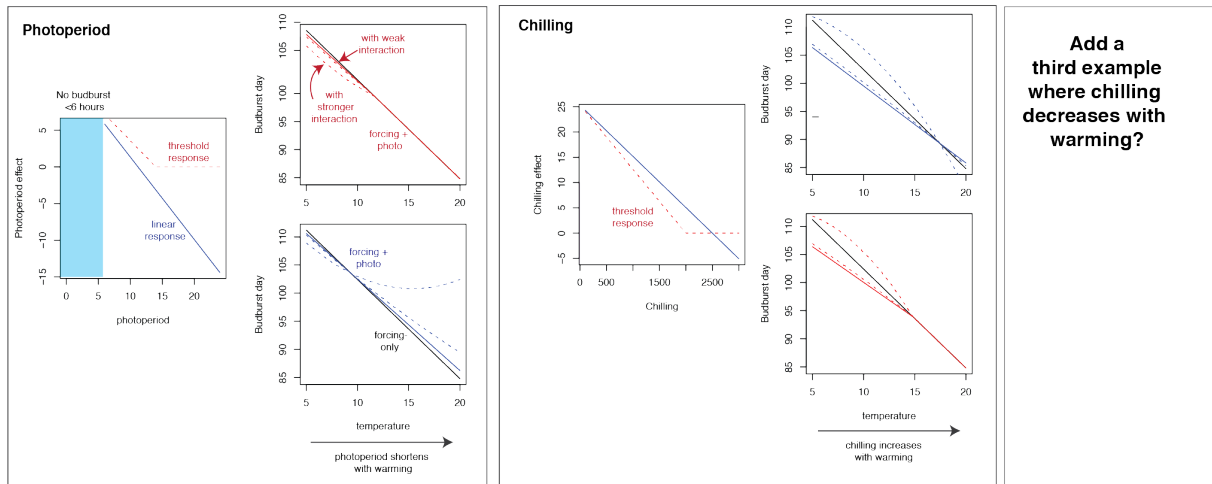


Figure 2: Interactions in linear models can produce nonlinearities, even in simple linear models if there are correlated shifts in cues. Here we show an example considering a forcing x photoperiod interaction (left) and forcing x chilling (right), considering both a linear effect of photoperiod or chilling (in blue) or a threshold effect (in red) versus an effect of forcing only (black line).

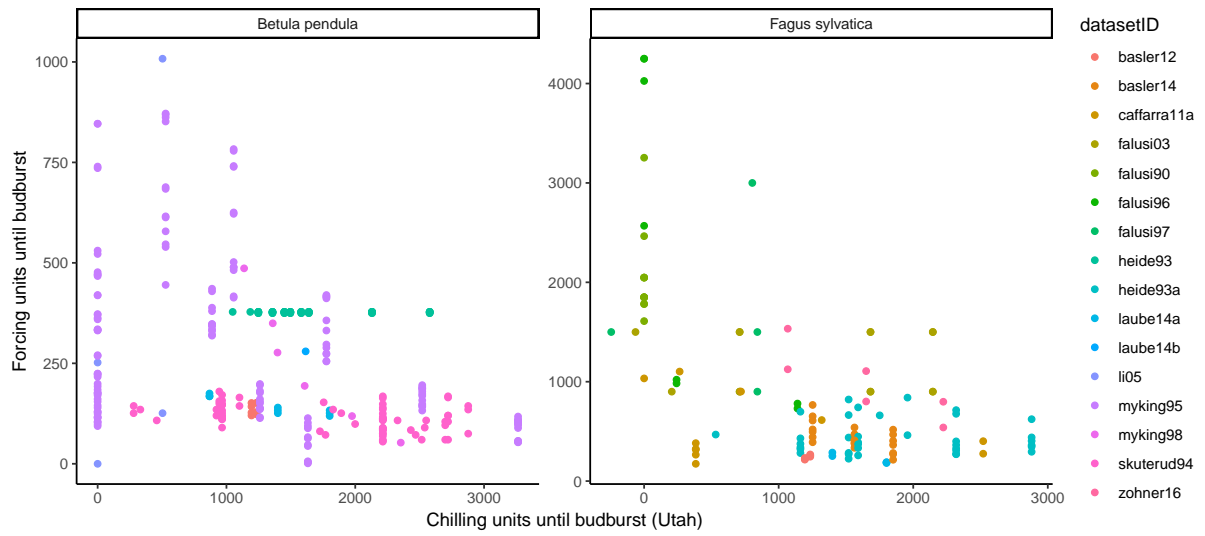


Figure 3: A common example of how one cue can modify another is experiments that show how the amount of chilling units effects of the amount of forcing units needed for budburst. Here, I show this from the BB analysis of OSPREE. But I can clean up some by limiting to the same photoperiod and only studies that vary chilling ... if we decide to keep it.

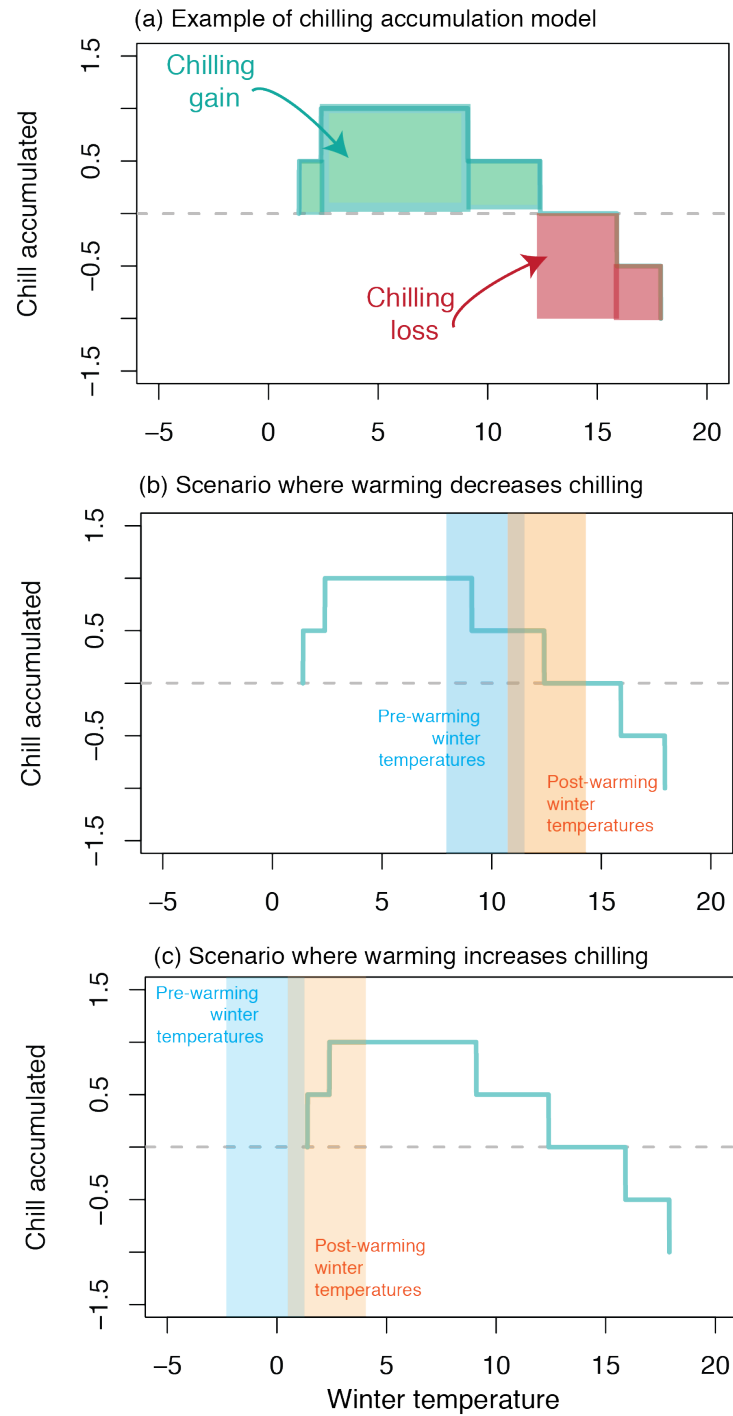
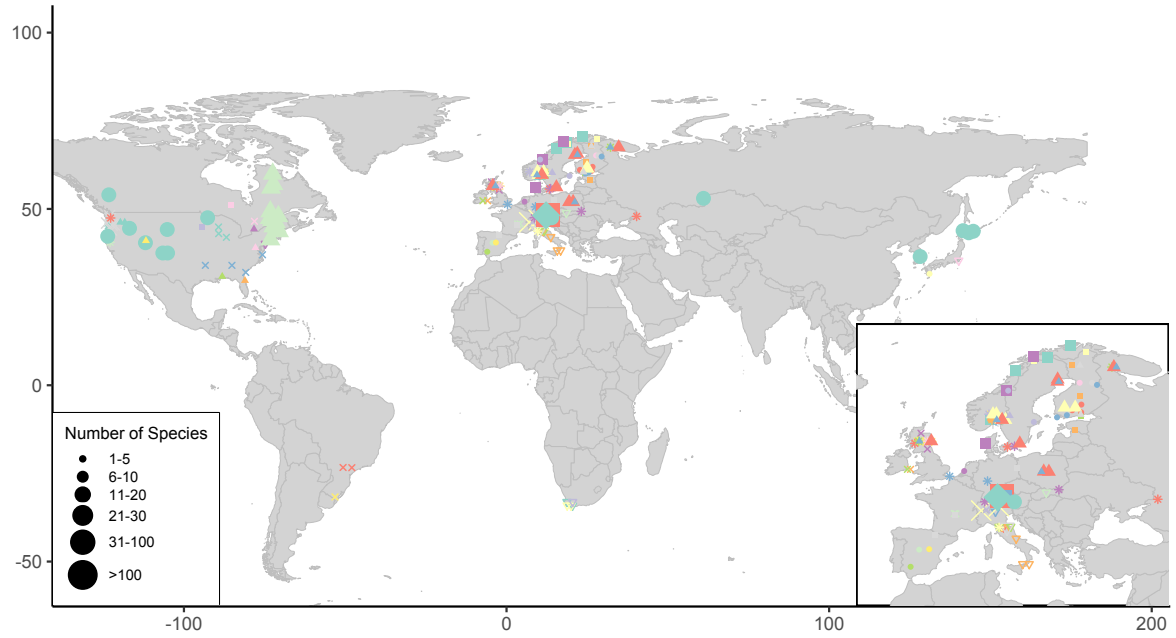


Figure 4: Chilling is complicated. Here we explain with a conceptual figure using a common version of the Utah model (top) and showing two scenarios of how warming may affect chilling accumulated over the winter.





DatasetID			
ashby62 ; 3	gansert02 ; 1	lamb37 ; 1	ruesink98 ; 1
basler12 ; 28	ghelardini10 ; 6	laube14a ; 36	Sanz-Perez09 ; 2
basler14 ; 4	gianfagna85 ; 1	laube14b ; 9	sanzperez10 ; 3
biasi12 ; 2	gomory15 ; 2	li05 ; 3	schnabel87 ; 2
boyer ; 4	granhus09 ; 1	linkosalo06 ; 1	skuterud94 ; 6
caffarra11a ; 4	guak98 ; 1	man10 ; 1	sogaard08 ; 1
caffarra11b ; 1	guerriero90 ; 1	morin10 ; 3	sonsteby13 ; 8
calme94 ; 3	Heide03 ; 3	myking95 ; 6	sonsteby14 ; 5
campbell75 ; 6	heide05 ; 4	myking97 ; 1	spann04 ; 1
cannell83 ; 2	heide08 ; 5	myking98 ; 3	spiers74 ; 1
charrier11 ; 3	heide11 ; 3	nienstaedt66 ; 14	swartz81 ; 1
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cronje03 ; 1	heide93a ; 5	partanen98 ; 3	yazdaniha64 ; 1
falusi03 ; 1	howe95 ; 2	pettersen71 ; 1	zohner16 ; 144
falusi90 ; 1	jones12 ; 3	ramos99 ; 1	
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Figure 5: Overview of the data across space.

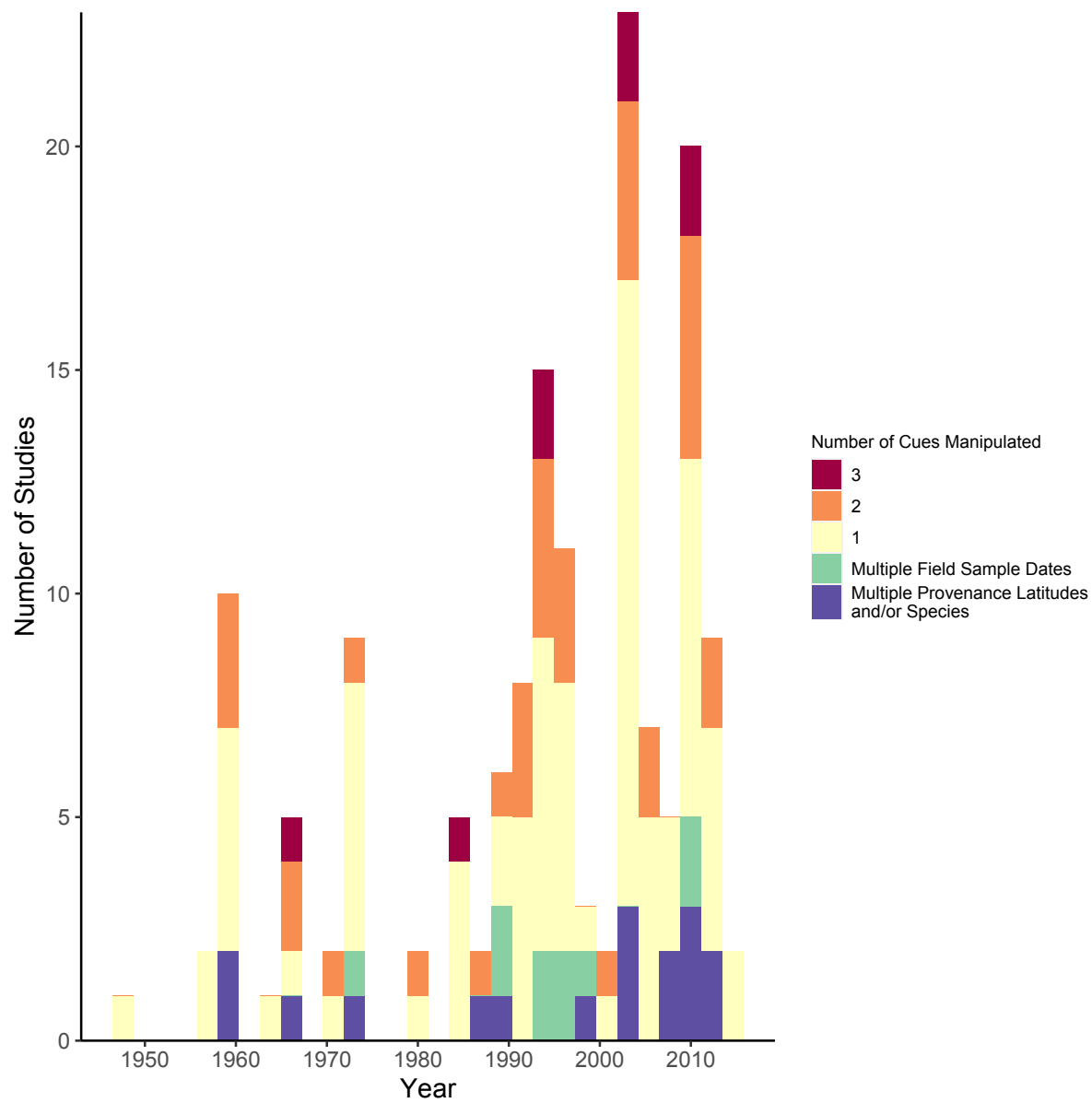


Figure 6: Cues manipulated over time.

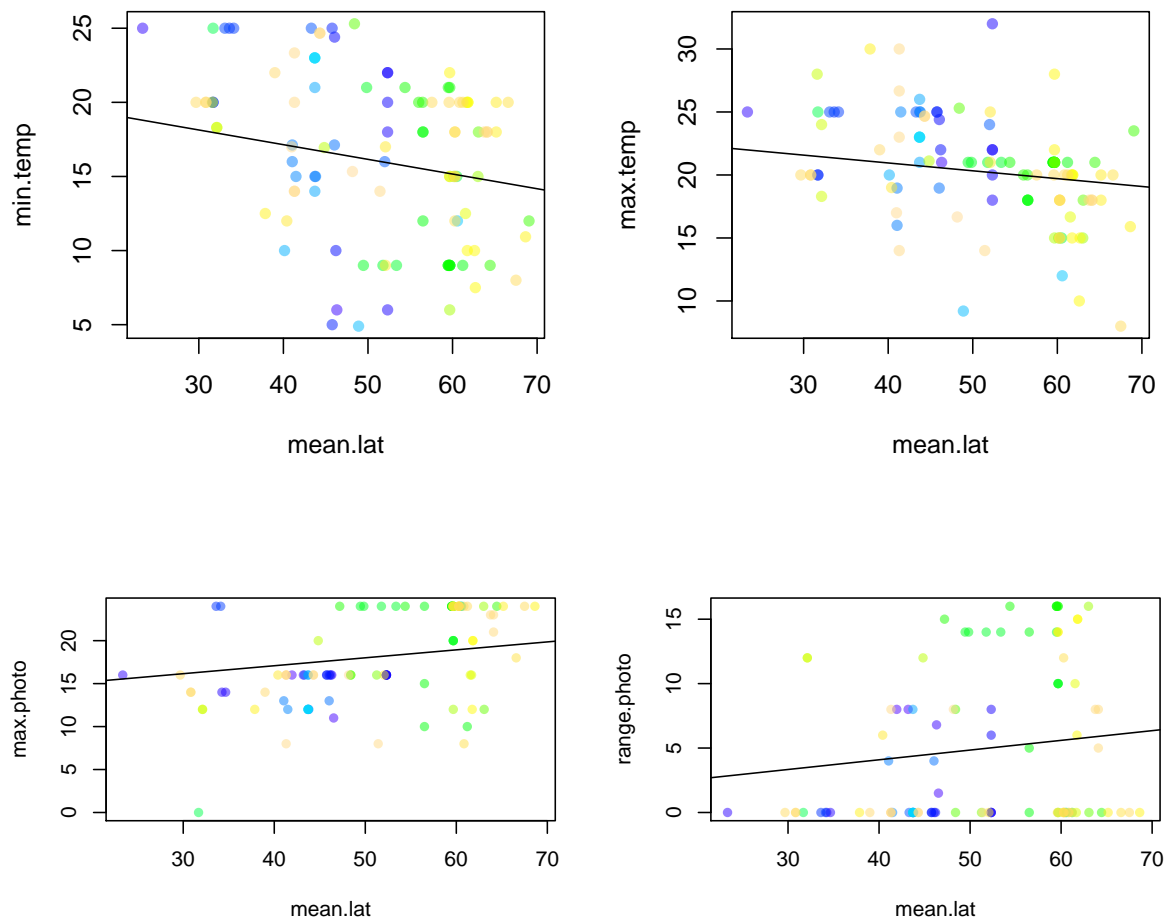


Figure 7: One correlation with latitude plot ... I think we could move to Supplement

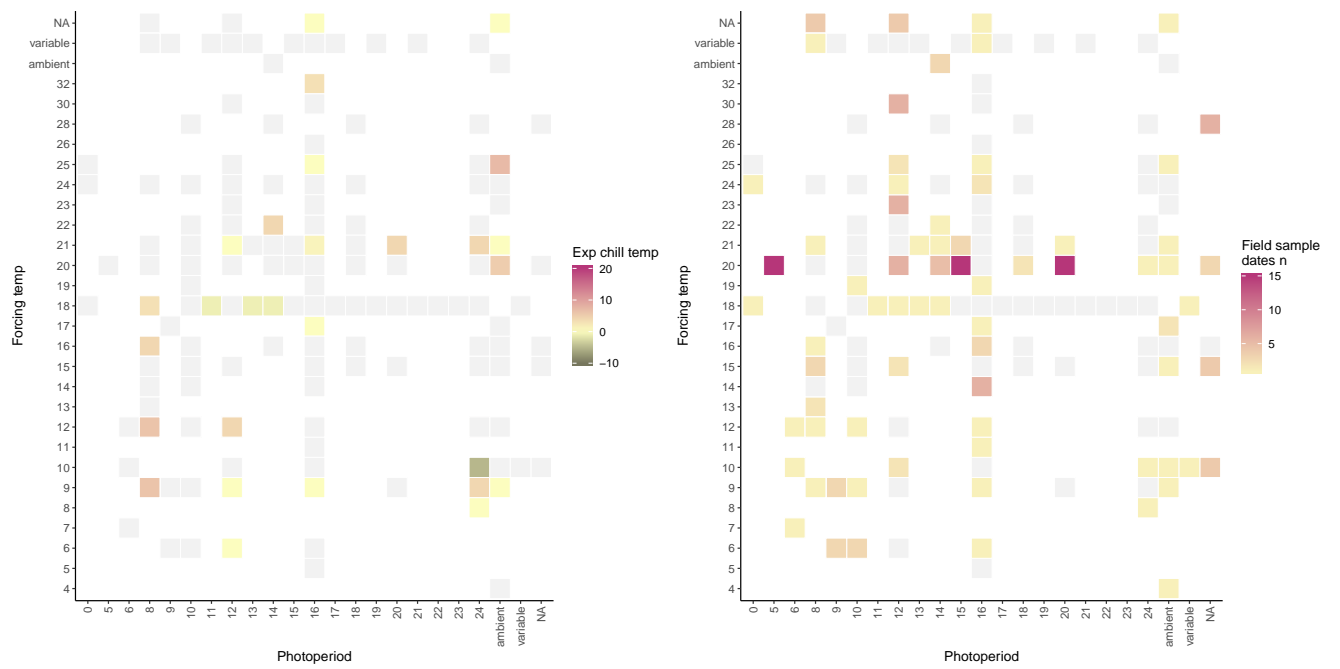


Figure 8: Heat maps of all data showing how few studies manipulate chilling experimentally (left); most use field sampling dates (right).

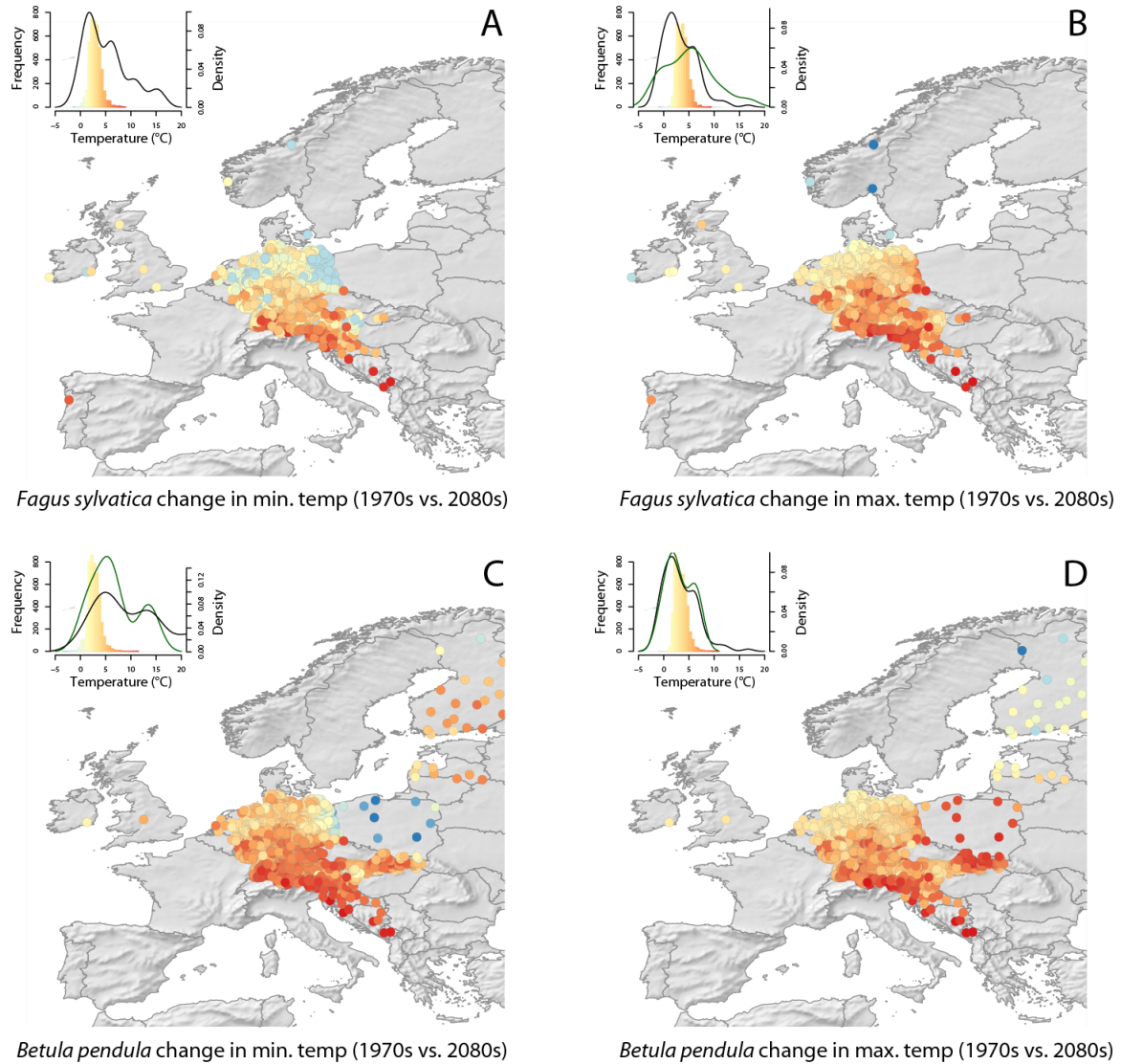


Figure 9: Predicted changes in temperatures relevant to chilling (A, C) and forcing (B, D) compared to a 1970s baseline shown for two species: *Fagus sylvatica* (A-B) and *Betula pendula*. Points represent a PEP725 site with XX data. Inlay plots in the upper left-hand corner of each plot show a histogram of the predicted changes in temperature overlaid with densities of the chilling (A, C) and forcing (B, D) treatments (green lines show the treatments for that exact species, while black lines show across all species; note that for *Fagus sylvatica* there are no chilling treatments of differing temperatures).