

November 13, 2019

Dear Dr. Findlay:

Please consider our paper, entitled “Winter temperatures dominate spring phenological responses to warming” for publication as a “Letter” in *Nature Climate Change*. This manuscript is a revised version of an earlier submission (NCLIM-19081773). We include a point-by-point response to reviewer comments.

As you may recall, our manuscript utilizes an extensive new, extensive, global database to address a research topic of critical relevance to a broad swath of *Nature Climate Change* readers: the timing of spring phenology (e.g., budburst, leafout) in woody plants. Spring phenology impacts plant fitness, shapes plant and animal communities, and affects wide-ranging ecosystem services from crop productivity to carbon sequestration. Our work is groundbreaking in its synthesis of four decades of research across 72 experiments to quantify the relative importance of three environmental cues critical to phenology. We estimate overall chilling, forcing and photoperiod responses for 203 species from around the globe.

The three reviewers recognized the potential of our work to influence future research, as well as its interest to *Nature Climate Change* readers. They also highlighted some concerns. Reviewer 1 suggested that additional details and clarification of methods would be beneficial for a fuller evaluation of the study. Reviewer 2 felt unconvinced that the experimental methods synthesized in our meta-analysis could be reliably applied to natural systems. Reviewer 3 had reservations about the validity of the results given the data and modeling approaches used.

We have substantially modified the manuscript to address the concerns expressed by reviewers and the issues mentioned by the Editor after the initial submission. Specifically, we have added new text and analyses to the main manuscript, including two new models testing for effects of continent and life stage and as well as applying a recently published modelling approach for estimating temperature sensitivity (sliding windows), as suggested by the reviewer. We have also created a new figure, and modified previous figures in the main text to address reviewer concerns. We have also added substantially to the online ‘Methods’ section, which adheres to the new guidelines of *Nature Climate Change*.

Upon acceptance for publication, the database will be freely available at KNB (7; currently meta-data are there); the full database is available to reviewers and editors upon request. This work is a meta-analysis, so data have been previously published; however, the synthesis of these data and the tables, figures, models, and materials presented in this manuscript have not been previously published nor are they under consideration for publication elsewhere.

Sincerely,



Ailene Ettinger

Quantitative Ecologist, The Nature Conservancy- Washington Field Office Visiting Fellow, Arnold Arboretum of Harvard University

Reviewer Comments are in *italics*. Author responses are in plain text.

Reviewer 1 (*Remarks to the Author*)

The relative importance of forcing, chilling and photoperiod as cues for budburst is a fascinating one, with clear implications for predicting how species will respond to climate change. Here the authors leverage an exceptional dataset arising from experimental studies using sophisticated statistical analyses and arrive at the surprising conclusion that plants are generally more sensitive to chilling than forcing. I think this study has the potential to make a really valuable contribution that will be of broad interest to readers of this journal. However, I have quite a lot of criticisms/concerns of the study as it stands.

We thank the reviewer for the recognition that the OSPREE dataset is exceptional and that our study can make a valuable contribution to *Nature Climate Change* readers. We have revised the original manuscript substantially to address the reviewer's concerns, as detailed below.

(1) Models: The STAN modelling approach is sophisticated but I think the model is rather incomplete and this could affect the inferences that are reached. For instance why aren't terms included to allow the intercepts and slopes to vary across studies within species?

We completely agree with the reviewer that, ideally, our models would account for both variation in budburst responses among species and among studies. This was our aim in building the OSPREE database and using Bayesian models that can allow complex models to converge. During our data and model development, however, we found studies were generally confounded with species. This is a common problem in this area of research and other meta-analyses have faced similar issues (e.g., Kharouba et al 2019). Without strong priors to help differentiate what variation should load onto the study versus species, it is difficult to fit both variables. Indeed, we evaluated models that included studies within species and studies crossed with species but both models were found to be unstable (e.g., estimates varied widely across model runs, model estimates had wide credible intervals, chains frequently did not converge).

To address this we worked to present a main model that only included species for which we had multiple treatments across multiple studies. We combined species found in only one study into "complexes" at the level of genera, such that each taxonomic unit we use in our model occurs across multiple studies (and treatments). Thus our taxonomic units of analysis are "species complexes," which are either species represented in ≥ 1 dataset or complexes combining multiple species within a genus that are each singly represented in the dataset. Species represented in only one dataset with no con-generics in other datasets were excluded from most of our analyses. We do include a model fit to all species and report these results in the supplement (Tables S3 and S4); we refer to this model as the 'all species' model.

We realize now we should have made these issues more clear. We now write on Lines 62-67 in the main manuscript: 'Some species are often only represented in one dataset in the OSPREE database, making it impossible to statistically differentiate between species, study, and treatment effects for these taxa. To address this, we combined species found in only one study into "complexes" at the level of genera—such that each taxonomic unit we use in our model occurs across multiple studies (and treatments, see the *The Observed Spring Phenology Responses in Experimental Environments (OSPREE)* database section in the Supplemental Materials for details.'

Also, I would have thought there is very likely a geographic effect on the effects, and I suggest that you test whether the results are sensitive to inclusion of a spatial random term across which slopes and intercepts vary.

The reviewer makes an excellent point that budburst responses to temperature and photoperiod may vary due to the spatial location of studies or the geographic origin of plant material. In particular, budburst responses are expected to vary by latitude (Zohner, et al 2016; Gauzere et al. 2017; Saikkonen et al 2012). We address variation in space primarily by including a latitude model, which we now discuss on lines XX in the main manuscript. We focus on the spatial effect of latitude because there is strong evidence that there can be latitudinal differences in budburst responses, for example via interactions between latitude and photoperiod sensitivity and interactions with chilling responses (XX CITATIONS). In this new version, we have also added a model that includes continent. This new continent model includes photoperiod, forcing, and a random effect of continent on the intercept, as well as species-level random effects (as in the main budburst model). This new model is described on page X in the supplement, with results summarized in Table SX. Note that we do not include chilling in this new model because the climate data used to estimate chilling is only available for two continents (North America and Europe). We find that variation by continent XXXX

(2) Meta-analysis: The analysis is described as a meta-analysis, but falls short of being a formal meta-analysis as it seems as though measurement error in the response variable is not incorporated. This should be straightforward to incorporate and I was surprised that it hadn't been given the complexity of the analyses. Also, please report the extent to which the approach followed recommendations made in the PRISMA checklist

This is a good point; we now review the PRISMA checklist point-by-point in the Supplement (page 1, first paragraph). Many of the checklist items are done by our data publication, and we feel this addition greatly strengthens the paper and appreciate the reviewer suggesting it.

(3) Methods: The methods seem to be missing from the main ms, and I kept flicking forward to consult a section that does not exist. I thought the Nature letter format does allow a methods section and I found it really to the detriment of the readability of the ms that there wasn't one.

We appreciate the reviewer's concern that methods are not easy to find; this was a concern of multiple reviewers so clearly something we needed to improve. We have worked to now more clearly embed key methods in the text. We now have included a more full model description and the model equation (Lines 66- 74), and .

We also provide a separate Methods section with full details of the data and are analyses. This section will be available online, should our manuscript be accepted for publication in *Nature climate change*, following the journal's requirements.

(4) Chilling, forcing and photoperiod: In order for a reader to reach a conclusion about the robustness of the inferences it is vital that the method for quantifying cues is easily understandable. Currently in the main ms it is not (last paragraph of page 3). For instance, we are told the minimum temperature for chilling but not maximum, we are not informed as to when the chilling and forcing periods are and no discussion is given as to how the effect of photoperiod is modeled. It's also unclear in the main ms what a 'standard unit' (I see it is described in the supplement) is and this leaves the reader disconnected with what the analyses are doing. A simple remedy for this would be to include a schematic (as figure 1) that identifies the information used to quantify each cue and relate it to the response. In general the main ms does a very poor job of explaining what was done (the data used, how cues were inferred and vital details about what the models were estimating), instead referring the reader repeatedly to supplementary materials. While the supplementary materials are generally good I still felt disconnected from the data and how the cues were actually quantified. This could be addressed by taking some example datasets and working through in detail how the different metrics were calculated. Without knowing what was done I find it very hard to judge whether the main conclusions are robust.

We thank the reviewer for pointing out that important details on the chilling, forcing, and photoperiod estimates used in our analysis were unclear in the original version. We have added a new schematic figure (the new Figure 1), as the reviewer suggested, which we hope clarifies how the chilling, forcing, and photoperiod estimates were obtained from the original studies for use in our meta-analytical work. We have added relevant details on chilling, forcing, and photoperiod to the main text in the following locations:

We also provide full descriptions, including the upper and lower thresholds for chilling, in the online methods section (NEED TO ADD THIS).

(5) Chilling: I think it's important to know whether the inferences are robust to an alternative model of chilling, e.g., the sequential model that is widely used. From the supplementary materials it is clear that some effort has been made to consider alternatives (chilling portions) but given this analysis underlies the main conclusion of the paper I'd like to see alternative hypotheses considered.

This is an excellent point as our earlier version did not adequately compare results with the Utah model to results with the other chilling model we evaluated, Chill Portions. Now we more clearly compare them in the main text (lines xx-xx), where we write:. [GIVE QUOTE of main text].

Based on our understanding and in consultation with Isabelle Chuine the sequential model usually refers only to process-based models thus we are unsure how to apply it in our framework; if the reviewer has specific modeling suggestions or other chilling model he would like applied we would be happy to test them.

(6) Estimates: It is surprising to see point estimates repeatedly reported throughout the ms without 95% credible intervals, this needs to be rectified. Also at present there is no formal test of whether the chilling response is significantly stronger than the forcing response, though this would be easy to do using the posteriors.

We thank the reviewer for this suggestion and have added 95% credible intervals to all estimates presented in the main text (e.g., Lines 79-91) . In figures, we show 50% credible intervals, and in the supplemental tables we present both 50% and 95% credible intervals.

Statistical artefact with linear regression (Page 5): That application of linear regression to data arising from a growing degree model can lead to biased estimates is a fascinating insight. However, in the supplementary materials it is not clear to me how the temperature sensitivity window for linear regression (for B. pendula or the simulations) is calculated/defined. How much can the issue of an advancing period of sensitivity be addressed by allowing the sliding window to shift over time? This issue is discussed in Simmonds, E. G., Cole, E. F., & Sheldon, B. C. (2019). Cue identification in phenology: a case study of the predictive performance of current statistical tools. Journal of Animal Ecology.

We thank the reviewer for highlighting the need for additional methodological details, and for this insightful question about the shifting window approach. The window we used was 1 March through 30 April, which we are now stated in the online Methods, section *Applying our model to Central European data*, (Page 6, paragraph 2).

To address the reviewers question, we applied the shifting window approach to the same dataset and compared the temperature sensitivities pre-and post- warming. These sensitivities show the same pattern: higher sensitivity pre-warming compared with post-warming. We have added these analyses to a new section in the “Methods and Supplemental Materials” entitled *Applying the sliding windows approach to Central European data*.

Minor comments

Page 2. I suggest changing 'high unexplained variation across' to 'substantial variation among'.

We thank the reviewer for this suggestion and have made the recommended change (now Lines 22-23).

Page 3. All three cues are not generally correlated in longitudinal studies; photoperiod and forcing are, but neither is usually very correlated with chilling.

We thank the reviewer for pointing out that our writing was not clear in this section. In our earlier version of the manuscript, we mentioned correlations between cues but did not specify clearly whether we meant correlations across space or time, nor were we clear about the scale or window at which these cues can be correlated. Though the reviewer states that chilling is often not correlated longitudinally, we have found that it can be correlated (ADD FIGURE OR JUST r/r^2 showing this?). In addition, chilling and forcing are frequently negatively correlated in space (sites that have experience high chilling tend to have low forcing, ADD FIGURE OR JUST r/r^2 showing this). In this new version of the manuscript, we have clarified our writing, which now says (Lines XX): “XX”

Page 3. Last sentence of paragraph 2. This is hyperbole. The mean is not expected to shift far beyond historical bounds, though the extremes clearly will.

The reviewer appears to have concerns about the following phrase from the previous version of our manuscript: “... continued warming pushes climate into environmental regimes far beyond historical bounds.” We thank the reviewer for highlighting this phrase, which is a bit vague in its reference to ‘environmental regimes’ and for which we clearly should have included citations to support. We now cite the IPCC forecasts that climate change is expected to push temperatures to XXX, well beyond the historical bounds. We adjusted the sentence to be more clear and have added references so that it now says (Lines XX): “Resolving these discrepancies is critical to accurate predictions of spring phenology, especially as continued climate change will yield warmer temperatures than has been experienced in at least 150 years and warming will occur at a rapid pace (Ohlemuller et al 2006, Williams et al 2007, Williams et al 2007b, IPCC 2013, Xu et al 2018).

Page 3. Fourth line from bottom. Is interactions the correct term?

We apologize that this was unclear. We have now adjusted this sentence (lines xx-xx), which now reads “Our model averages over interactive effects of predictors, as it includes only main effects; it estimates both species-level responses...”

Reviewer 2 (Remarks to the Author):

Spring leaf-out phenology plays a key role in terrestrial carbon and water flux, but the underlying processes are still unclear, especially how the environmental cues, including chilling, photoperiod, and spring warm temperatures, interact and determine the leaf-out processes is still unclear, although most of the phenologist agreed that these three cues are all important. Therefore, quantify the relative importance are

valuable and might be important for the phenology modeling and dynamics vegetation models. I carefully read this meta-analysis and found this is an interesting study, but I'm wondering, given the results were reliable, whether the meta-analysis results across experimental studies could reflect the natural plants' response? Or could we rely these experimental results that may inaccurate reflect underlying mechanisms? Because, according to the author (E.M. Wolkovich) previous study, the phenology under warming experiments could not reflect the natural observations (Wolkovich et al, 2012 nature, warming experiments underpredict plant phenological responses to climate change), which might arise from complex interactions among multiple drivers and remediable artefacts in the experiments that result in lower irradiance and drier soils.

We thank the reviewer for pointing out that there are limits to the controlled environment studies synthesized in our meta-analysis. We agree that there are many ways in which experimental conditions differ from observational conditions and we were not clear about this in our previous version. The reviewer's comment also highlights that the previous version did not adequately describe the experimental methods used in controlled environment studies.

To address these comments, we have added a new figure (Figure 1) to show the experimental design of the controlled environment studies in our synthesis. In this new version, we also discuss these issues in the following places:

1. Lines 42-47: "In contrast to observational studies, controlled environment experiments can break down correlations between the cues. Note that controlled environment studies differ from field warming experiments, which are designed to test higher temperatures in natural conditions, because they are designed to create conditions less often seen in nature, but which can critically help researchers identify cues. These experiments—most often conducted in growth chambers or similar systems to control temperature and light (Fig.1)—have been conducted for decades and their accurate representation of phenology in the natural world has been tested (Vitasse and Basler 2014). "
2. Supplement Pages 5-6, *Applying our model to Central European data* : "We also wished to understand how our findings may apply to conditions more commonly found in nature, where conditions often vary dramatically from those applied in controlled environment experiments. For example, very low amounts of chilling can be applied in experiments compared to the natural chilling found in many temperate areas (Fig. S5). Additionally, chilling temperature and total chilling are more correlated in nature than in experimental conditions (Fig. S5). Further, given the importance of chilling and forcing combined with the fact that seasons do not always warm uniformly with climate change (17; 18), we also wished to understand how warming in the winter, spring, or both seasons would shift budburst timing."

We hope that these changes clarify that the controlled environment studies in the present paper differ from the field-based warming experiments in Wolkovich et al 2012. Controlled environment studies are typically designed to tease apart the role of different cues (chilling, photoperiod, forcing), rather than to replicate current or future natural conditions (the warming studies synthesized in Wolkovich et al 2012 are typically designed to replicate natural conditions).

Furthermore, I'm not convinced that the chilling overweight forcing, and the effect of chilling, photoperiod and forcing might be quantified across more than 200 species based on the various manipulative experiments and MCMC-based Bayesian method, especially considering most of these experimental studies conducted only one year or less than 3 years. The main reasons come from: 1) most of these experimental studies conducted with very different settings, such as using saplings vs. mature tree's cuttings, how the ontogenetic effects play a role or impacts the results? Arbitrary controls in lights/photoperiod length/intensity vs. greenhouse natural light; in addition, for many experimental studies, the temperature and photoperiod were set under extreme climates. I would say this is a response to extreme climate. All of these factors might substantially affect the results.

We agree with the reviewer that there are many factors, not included in our main model, that could explain variation in budburst responses to chilling, photoperiod, and forcing (e.g., ontogeny). In this version we have tried to more strongly indicate this, as well as state that separating chilling from forcing requires more physiological research. For example, please see Lines XXX, where we state: ""

In addition, in this new version we include a new model to directly test for ontogenetic effects on budburst by adding a predictor of "life stage" (juvenile vs. adult) to the main budburst model. We found that material from juvenile trees (seedlings or saplings) burst, on average, 3.6 days later than material from

adult trees. We have added this model and a table summarizing its results to the supplemental materials.

We believe that there are many additional potential questions and avenues of research to better understand how woody plant phenology responds to different cues, at varying life stages, and in different contexts. Our database and analyses provide a critical step in pushing this work forward by providing the first comprehensive meta-analysis quantifying responses to chilling, photoperiod, and forcing; it is our hope that our analyses, as well as the freely available OSPREE database, stimulates future experiments and analyses to test additional hypotheses.

2) the interact between chilling, photoperiod and forcing is complicated, and there are still unclear in many important facts. For example, the temperature thresholds of chilling and forcing estimation, and its species-specific values, are largely unknown. For some boreal or alps plants, they may budburst even when air temperature around freezing points, but the temperate trees are still dormancy even air $T \geq 15$ degree; the correlations between eco- and endo-dormancy, corresponding the chilling and forcing, whether they are a parallel or a sequential pattern between chilling and forcing? When/how the photoperiod plays its role during the two phase dormancy? Once the endo-dormancy break, continuous chilling accumulation, for example a cold span during spring, is still active? Or entirely depending on the forcing? All these questions are still not figured out; 3) except chilling, forcing and photoperiod, other cues are also involved with the leaf-out processes, for example air humidity, see Laube et al, 2014 (but recently, Zohner et al, 2019 New phytologist deny this effect) and soil moisture and snow cover. Under manipulative conditions, these effect might be largely ignored as argued in Wolkovich et al, 2012 as well.

We completely agree with the reviewer that the interaction between chilling, photoperiod and forcing is complicated, as we note on lines xx-xx, where we write: “A caveat to our estimates is that there are likely complex interactions between chilling, photoperiod, and forcing that we were not able to quantify in this meta-analysis; indeed, very few experimental studies test for interactions between all three cues (but see Flynn et al 2018)”. We have also tried to present some of the complexities in our new Figure 1. We note, however, that our results are strong (e.g., 95% credible intervals for estimates of chilling, photoperiod, and forcing do not overlap zero) and suggest that, despite these complexities, consistent effects emerge.

(No third point listed by the reviewer) *4) species-specific response to chilling, photoperiod and forcing. This has been well reported, for example the pioneer species are opportunistic and photoperiod-insensitive, in contrast the late successional species are sensitive to photoperiod and higher forcing requirements, see the papers, as the authors cited, Krner & Basler 2010;2014; Laube et al, 2014; Zohner et al, 2016 and other studies. Across so large dataset/many species, the mean values, for example chilling effect is 2 times larger than forcing and photoperiod as well as its sensitivity, hold large uncertainty and are no sense.*

We completely agree with the reviewer that species-specific differences are important. Indeed our modeling approach is designed to help examine across-species effects but also species-level differences. We now clarify this on Lines 62-65, where we write “

One of the main conclusions is that chilling is over-weight forcing and recent advanced leaf-out is mainly associated with spring warming. However, this is inconsistent with recent study that found the spring phenology did not significantly change during the global warming hiatus, see its figure 1 in Wang et al, 2019 Nature comm, but the spring T is still significantly increase and winter getting colder over the Eurasian (Li, Stevens and Marotzke 2015 GRL)). It seems that increasing chilling and forcing could not explain the dynamics in spring phenology? How to explain this inconsistency?

We thank the reviewer for thinking critically about how our paper may contrast with previous work, and seeking to understanding the implications of our work. We now cite these two papers in Lines XX and We believe the reviewer is suggesting that, if winters got cooler (and chilling therefore increases), as the Reviewer suggests Li, Stevens and Marotzke (2015) find, one might expect spring phenology to advance, given our hypothesis and findings. However, this is not what was found according to Wang et al (2019). We wish to point out to the reviewer that a decrease in temperature is not necessarily equivalent to an increase in temperature, given the thresholds involved in estimating chilling. For example, in this paper we find that warming actually increases chilling in many locations (Supp Fig). Thus, cooling might be decreasing chilling estimates and could sto; be consistent with the Wang et al paper, as well as our findings.

Minor commons Line numbers are needed;

We thank the reviewer for this suggestion and have added line numbers.

In methods, the study yielded data from 72 studies across 39 yrs... this is misleading, because for many experimental studies, table S1, the data only for one year, and most less than 3 yrs.

We thank the reviewer for pointing this out. To address this concern, we have added the phrase ‘with most studies lasting one year’ so that the phrase now says (Line 51): ‘...yielding data from 72 studies across 39 years and 203 species (with most studies lasting one year, Fig....’

More description is needed of Bayesian hierarchical model in the main text;

We thank the reviewer for pointing out the need for more detail on our model. We now describe the model in more detail and include the equation for our main budburst model (Lines 61-77).

In the results sections, chilling has greater effect on budburst than forcing?. I would suggest providing the conditions, i.e. under future climate warming, due to the fact that these results come from experimental studies that simulated future warming,

We have added a phrase to clarify that the scope of our results applies to controlled environment studies by saying (Lines 95-97): “Our results, however, suggest that, across 203 species and 72 controlled environment studies around the world, chilling has a greater effect on budburst than forcing”

In the results sections as well, the chilling only occur at warming above 4C? interesting, but does it occur across species? and locations?

We thank the reviewer calling our attention to the need for more detail and nuance here. We have modified the sentence so that it now says (Lines XX-XX): “..our results suggest that delays due to decreased chilling only occur at warming above at least 4°C for most sites, though responses vary by species (Fig. 4, S6, S9).”

Zohner, Constantin M., et al. “Rising air humidity during spring does not trigger leaf-out timing in temperate woody plants.” New Phytologist (2019). Wang, Xufeng, et al. “No trends in spring and autumn phenology during the global warming hiatus.” Nature communications 10.1 (2019): 2389. Li, Chao, Bjorn Stevens, and Jochem Marotzke. “Eurasian winter cooling in the warming hiatus of 1998-2012.” Geophysical Research Letters 42.19 (2015): 8131-8139. -cite these in main ms -could add humidity when to main text- Reviewer 3 (Remarks to the Author):

This manuscript addresses the relative importance of the environmental determinants of plant phenology using a meta-analytical approach. Specifically, the authors combine the experimental results of 72 studies and 203 species to estimate the effects of day length, winter chilling, and forcing on spring phenology, using hierarchical Bayesian models. The main finding is that almost all species respond to all three cues, with chilling having the largest, day length the smallest effect. Furthermore, the results suggest that, while all cues are important under experimental conditions, spring forcing will remain the dominant driver of spring phenology over the coming decades. The manuscript is well written and addresses a clear question. However, I have reservations as to the overall importance and validity of these results. That chilling is more important than day length has been shown by previous multi-species studies addressing this (e.g., Laube et al. 2014, Zohner et al. 2016). -true! other studies have looked at this. this is a meta-analytic approach. also, none of these studies attempted to look at 3 cues as the reviewer points out But forcing is usually considered to be the most important!

Furthermore, the model output seems to suggest that all three cues (day length, chilling, and forcing) affect phenology in almost all species, leading the authors to conclude that their results contrast with the extensive literature [Zohner et al. 2016, Körner & Basler 2010] suggesting photoperiod is an unimportant cue for many species. [page 4]? Yet, when looking at Table S2, most of the species-level data they use are taken from Zohner et al. (2016) [Zohner16 database]. In fact, 173 (85%) of the 203 species included in this study were already investigated in Zohner et al. (2016). Given that in Zohner et al. (2016), 112 (65%) out of 173 studied species did not react to daylength at all, it is surprising that day length is reported as a relevant, consistent cue across species. This makes me wonder whether their hierarchical Bayesian model is confounded (e.g., giving too much weight to certain species ?complexes?) and thus not suitable for exploring the relative importance of the different environmental drivers of spring phenology.*

-interesting point about species differences. this is why we focus on the but compare only really abundance species: betula, fagus, quercus and - not sure what the reviewer means when s/he says that “most of the species-level data” are from Zohner. The Zohner dataset comprised 864/7459 (11%) rows in OSPREE. It's true that the Zohner dataset includes 144 out of 203 species in the full OSPREE budburst database. However, we include in the main model interpreted and presented in the figures only species that were across multiple studies. - To make this more clear, we have added a column to S2 which lists models included in? -many Zohner species excluded from main budburst model. in model that includes all species

(Table S3)- estimated effect of photoperiod does weaken (forcing estimate gets stronger, chilling is about the same) -add comparison between all species and single model -look at Zohner methods- could analyze this alone? could be because we estimated. - add something about partial pooling.- the reviewer seems to not understand this.

Körner & Basler 2010 clearly is an inadequate reference here, please delete

In our original submission, we cited two papers by Körner & Basler 2010: a 'Perspective' in *Science* (Körner & Basler 2010, *Science* 327, 1461) and a response to a critique of this perspective (Körner & Basler 2010, *Science* 329, 278). We believe that the reviewer is referring to the response and we agree that this reference is inadequate. We thank the reviewer for this comment, and have removed the reference from our manuscript.

Apart from that, I take issue with the estimation of the importance of forcing and the attempt to estimate the relative importance of day length, chilling, and forcing. First, I don't see how the effect of forcing can be disentangled from the effects of chilling. This would require knowledge on which temperature ranges are adequate to satisfy chilling and forcing requirements. Yet, as correctly stated in the Supplementary information (page 2), current models of chilling are hypotheses and likely to be inaccurate for many species. Similarly, the effective temperature ranges to fulfill forcing requirements are not known. As such, when comparing the relative importance of winter chilling versus spring warming both factors are likely to be confounded. Also, if a study uses two different forcing temperatures that both lie within the range of optimal forcing conditions, one would see no effect between the treatments and the authors would thus infer that forcing didn't affect phenology, when in fact, forcing has a huge effect, not detected by the study design. Given these considerations, I don't think that a multivariate model, such as the one presented in this study, can adequately disentangle the relative importance of the three main phenological cues.

-great point! impossible to disentangle. much more info needed at species level. in absence of this...what is approach? one motivation for this paper is to highlight the need for additional work. -we rely on the original researchers to separate forcing from chilling conditions- these were the treatments that they imposed. we therefore assume that they used a range of treatments that are relevant for their focal species. -the reviewer does not suggest an alternative approach....

-cite new schematic figure - one of the findings of our paper- is that we need more work to accurately separate chilling and forcing - the perceptive reviewer has highlighted a general problem of the field...and yet...our models has been extremely predictive. Supplementary material

p.2: What do you mean by 'we included only studies with at least 49.5% budburst?' This is not correct for most of the studies included in your OSPREE dataset. E.g., Heide (1993) and Zohner et al. (2016) defined budburst as the date when 1-3 buds on a twig had opened. Please clarify.

We thank the reviewer for pointing out that we were not clear about our methods in the earlier version. What now have adjusted text on lines xx-xx to read as follows, ". As what we meant was [explain in greater detail, also ref our table about this from Cat! We actually did work on this and should clarify it in the text and for the reviewer.'

p. 3: Total chilling ranged from -1304 to 4724 Utah units? The Utah model allows for negative chilling units? What's the biological justification for that?

We agree with the reviewer that the Utah model, as well as other chilling models, are non-intuitive and biological justifications may not be immediately apparent. We now describe this model, as well as the other chilling model we used, Chill portions, on Lines XX. We could also add a little more discussion of this to supp.] -the biological justification, as described by the developer of the original model (Richardson) is ...

We have also tried to make clear that in the main text that all chilling models are hypotheses. [

We used the Utah model to report chilling because that allowed us to include the greatest amount of studies from the OSPREE database (i.e., because many studies used this model to estimate chilling).

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 (31) and chill portions (36), 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 (37).

p. 4: Latitude model: This model doesn't make sense to me. What is the latitude you refer to here? The location where the experiment took place? You refer to provenance locations, I doubt these are available for most of the studies, especially the ones conducted in botanical gardens or other collections.

We thank the reviewer for highlighting the need for greater clarity and methodological details about this model. In the initial submission, we did not adequately clarify what was meant by latitude. The latitude in our model refers to the latitude where plant material was growing at the time of collection, prior to being placed in experimental conditions. We referred to this as 'provenance latitude' in our previous version of the manuscript, and realize now that this may have been confusing. For example, for the Zohner et al (2016) study, which was conducted at a botanical garden with specimen trees grown from source material, the 'provenance latitude' refers to the location of the botanical garden where cuttings were collected from adult trees; we recognize now that the term 'provenance' in this context may be misleading, so have removed it from this new version, and instead have added details about the meaning of 'latitude' in our model. For some studies, the latitude at which plant material was growing refers equivalently to the location where the experiment took place, as the reviewer suggests. This is not always the case, however; for other studies plant material was collected at one or more latitudes and then taken to a different latitude where the controlled chamber experiment was conducted. We have attached the full database for reviewers to investigate these details for each study included in our analyses; this database will be made freely available at the time of publication on KNB ().

1. Lines 93-95 in the main text: we now say '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; 5)—instead we found it was surprisingly large, even when accounting for its interaction with latitude (i.e., the latitude from which plant material was collected prior to being placed in experimental conditions; see Supplemental Materials for details, especially Figs. S3, S11, Table S5).'
2. Supplemental Materials, Page 4: in the description of the Latitude Model, we now say: 'we examined the effect of including latitude in a model similar to our main one, but designed to estimate latitude effects. This model estimated the effects of each phenological cue (chilling, forcing, photoperiod) on days to budburst (as in the main model), in addition to the effect of collection latitude (i.e., the latitude from which plant material was collected prior to being placed in experimental conditions) and the interaction of photoperiod and latitude. We include this interaction because photoperiod effects are expected to vary by latitude...' and later in this paragraph we now say '...then subsetted the species and species complexes to include only those that had multiple collection locations across different latitudes.'
3. Supplemental Materials, Caption for Table S5: We have replaced 'latitude' with 'collection latitude' so that the caption now reads: 'Using a model with Utah chilling units and testing the effects of collection latitude plus the interaction between latitude and photoperiod results in slightly muted effects...'
4. Supplemental Materials, Caption for Figure S3: We have replaced 'latitude' with 'collection latitude' so that the title of the caption now reads: 'Estimates for effects of chilling exceeded estimates for forcing, photoperiod, collection latitude, and the interaction between latitude and photoperiod, for most species...'

Figures: Figs. 2 and 3, showing a 3-dimensional illustration of the interplay between winter chilling and spring warming, are very hard to read. I would prefer a simpler illustration.

We appreciate the Reviewer's perspective. We have shown both simpler 2-dimensional versions of these figures and the more complex 3-dimensional versions to a number of scientists and found opinions to be split on preferences for 2d versus 3d versions. To address this reviewer's concern, we have moved the 3-dimensional version of the manuscript to the supplemental materials, and now include 2 dimensional versions of Figure 2 and 3 in the main text.

References cited 11. J. Gauzere, et al., *Agricultural and Forest Meteorology* 244, 9 (2017). 12. K. Saikkonen, et al., *Nature Climate Change* 2, 239 (2012). 13. D. A. Way, R. A. Montgomery, *Plant, Cell & Environment* 38, 1725 (2015).