



Dear Dr. Buckley,

Please consider our revised manuscript "Differences between flower and leaf phenological responses to environmental variation drive shifts in spring phenological sequences of temperate woody plants" as a research article in *Journal of Ecology*.

Phenological sequences are a major driver of plant fitness, and for temperate woody plants, the relative timing of flower and leaf emergence, or flower-leaf sequence (FLS), may be particularly important for reproductive and physiological performance in many species. Observed shifts in the timing and duration of FLSs in the last several decades due to anthropogenic climate change indicate that this phenological sequences can be substantially altered by climatic variation, but exactly how the environment determines FLS variation is not well understood. We present data from a full factorial experiment of the major environmental cues for spring phenology for 10 temperate woody plant species to characterize the relationship between FLSs and environmental variation. The results of our multi-species experiment showed that two competing hypotheses about the drivers of FLS variation can be explained by one mechanism, and identified several functional traits (flowering-first FLS and wind-pollination) that may predispose certain species to maladaptive FLS shifts with climate change.

Comments from the Associate Editor and two reviewers suggested our manuscript was generally well written and our analyses thorough and robust, but pointed out several areas for improvement regarding the framing of our manuscript and the presentation of our results. Based on their comments, we have revised the structure of the manuscript to discuss the implications of FLS shifts in wind- and biotically- pollinated taxa separately, and amended our figures substantially to more clearly demonstrate our findings. We have also reworked our manuscript to more explicitly address several concerns about our multi-species approach including phylogenetic relatedness and co-variation with other functional traits.

Reviewers also raised important points about the specific phenological phases we presented. To address these concerns, we have added an additional analysis using a later vegetative phenological stage in addition the our original stages, and re-made all relevant figures to present this comparison.

We feel that the editor's and reviewers' input has helped shape a new submission that is much improved, and we detail our specific changes in the following pages with reviewer comments in *italics* and our responses in regular text.

Our current submission is 5,144 words in length and it contains 4 figures. As before, it is co-authored by E.M. Wolkovich is not under consideration elsewhere. We hope that you will find it suitable for publication in *Journal of Ecology*, and look forward to hearing from you.

Best,

A handwritten signature in black ink, appearing to read "D Buonaiuto". The signature is fluid and cursive, with the first letter "D" being large and prominent.

Daniel Buonaiuto

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

## Handling Editor Comments for Authors:

*Both reviewers felt this ms has merit, and I agree that this is an interesting study. However, I also agree with Reviewer 1 that the current text could do much more to motivate the examination of variation in flower-leaf sequences. In particular, Reviewer 1 notes that the importance of flower-leaf sequences is much less obvious for insect-pollinated species (which constitute 6 of the 10 species analyzed, with only 2 being strictly wind-pollinated and the other 2 being both wind- and insect-pollinated). Reviewer 2 offers several suggestions to improve the figures and presentation of results.*

We thank the Editor and both Reviewers for their feedback and are pleased that they found our manuscript interesting and valuable. Based on their suggestions, we have made significant adjustments to the manuscript and figures to elaborate on the complexities of and caveats for the functional significance of FLS variation, with a particular focus on how this function may differ depending on pollinator syndrome. We detail these changes further below.

*I would also like to see the authors address the phylogenetic non-independence of their study species, several of which are congeners. My understanding is that using species as a “grouping factor” accounts for the non-independence of observations of the same species but does not account for phylogenetic relatedness.*

We appreciate the Editor’s concerns on this issue, as it has been demonstrated that FLSs can be strongly influenced by phylogeny (Buonaiuto *et al.*, 2021; Gougherty & Gougherty, 2018). When including congeners in the study, we chose species specifically to avoid issues with phylogenetic non-independence. As phylogenetic non-independence is primarily an issue when a trait (in this case FLS) is inherited from a common ancestor we chose specific congeners that have different FLSs, suggesting each species’ FLS evolved independently (Revell, 2010). Thus our use of congeners was meant to be a strength of the study design, but we failed to explain this in our original submission, and we think that many readers will (and should) share the Editor’s concerns about phylogenetic non-independence! We have thus added text in the Methods (line 197-199) to clarify our selection criteria, and appreciate the editor pointing this out.

To triple check that phylogenetic non-independence was not impacting the inference of our analyses, we have also calculated the phylogenetic signal for mean FLS interphase among species using a phylogeny pruned from Zanne *et al.* (2013) and the R package “phytools” (Revell, 2012). With the species in our study, the phylogenetic signal for the trait “mean FLS interphase” was low ( $\lambda=0.129$ ) suggesting that for our species assemblage, phylogenetic non-independence is not influencing our results. We did not include this analysis in the manuscript, but would be happy to add it if the Editor thinks it would be helpful for readers.

*Finally, I have a few additional suggestions to clarify aspects of the Abstract:L5-6: Unclear why ob-*

*served variation in FLS (among species, populations, individuals) indicates that the relative timing of these events is important. Couldn't such variation also suggest relative timing is unimportant; otherwise, why would variation persist?*

We are grateful to the Editor for helping us fine tune our Abstract and found these suggestions very helpful. We agree that variation does not inherently indicate functional importance of a trait. We were basing this assertion on previous work in the literature rather than first principles, and have adjusted the language accordingly (line 5).

*L8: Here it is asserted that anticipating the extent of these shifts is key, but why is it key? I did not feel this had been demonstrated by the preceding text.*

We agree with the Editor that this point was unclear. We have re-worked this sentence, merging it with the preceding sentence to make the connection between potential impacts of changes in FLS on reproduction, recruitment and survival of individuals and species performance clearer (line 9).

*L16: Please clarify here if flower and leaf buds respond with differential sensitivity within species/among species/both.*

We have altered this sentence to clarify the intra- and inter-specific differences in FLS responses (line 16-23).

*L22: Unclear why expectation is that these taxa will experience reproductive declines; please explain briefly.*

We have elaborated and clarified this assertion. This portion of the Abstract now reads:

“Simple projections of FLS shifts with climate change, based on our results, showed large shifts in wind-pollinated species that flower before leafing, with flower-leaf interphases substantially shortened. This shorter interphase would reduce the time period for efficient pollen transfer, and thus raises the possibility that wind-pollinated taxa especially may experience reproductive declines due to FLS shifts in the decades to come.”

## **Reviewer: 1**

### *COMMENTS FOR THE AUTHOR*

*I think this paper takes an intriguing approach to considering the phenology of leaves and flowers by examining whether they share similar or different cues. It makes a strong argument for why wind-pollinated species that flower first might be more strongly impacted by climate change and has an interesting discussion of mechanisms that could drive FLS. Overall, I don't have much to comment on about the analyses and data, but I do have some questions about how things were framed.*

*I outlined two main points of consideration and some minor comments below.*

We thank the Reviewer for their thoughtful comments on our manuscript and glad they found our work interesting. We appreciated the Reviewer’s point about the framing of the paper, and have made a number of adjustments that we detail below.

*In general, I would like to see a stronger argument for why FLS matters or have the paper focus more on just wind pollination (see below) or on differences between vegetative and reproductive phenology (not the interval). The argument that FLS matters to wind pollinated plants seems reasonable (and less complicated) but for insect-pollinated plants seems less clear. Are there more citations that support its importance to insect pollination? Savage 2019 doesn't show this (even though it is cited here). Janzen does suggest this but in the middle of a longer list and only suggests that it “may” matter. In the context of the current study, FLS is between budburst and flowering, and for many species the overlap would only be with young leaves. Would this be enough to claim visibility issues? Would this even matter depending on the non-visual cues for pollinator attraction? It also seems that when discussing climate change and insect-pollinated flowers, it becomes tricky without tracking changes in the insects. There are so many things that impact insect-pollinated flowers (that are well-studied) including what other species are flowering (how likely is a plant to get pollen from the right species?), the size of floral displays and synchrony. I am left wondering whether FLS matters for insect-pollinated flowers. Is the presence of flowering first in the early spring more about flowering early instead of the coordination of leaves and flowers? I may be wrong and there might be a stronger argument out there for FLS, but I did not feel that it came across well in this paper at least for insect-pollinated species. I think it is important to take the time to build the argument of why FLS matters in general or the papers should focus more on wind-pollination and talk about insect-pollination by comparison (or set insect-pollination up as more questionable).*

We thank the Reviewer for this valuable point and agree fully that the function of FLS variation may be of less importance in insect pollinated species, and have in fact, addressed this issue in some of our previous work (Buonaiuto *et al.*, 2021). We felt that the Reviewer’s points merited a more in depth discussion in our manuscript, and have added several paragraphs to the Introduction, Methods and Discussion to more explicitly address the nuances of FLS function across species.

Beginning at line 54 we now discuss the function of FLS variation in wind-pollinated and insect-pollinated taxa separately so that we can more accurately present the uncertainty surrounding the function of FLS variation for insect pollinated species. We also qualify in lines 72-79 that even shifts of the same magnitude will likely have different impacts in wind vs. insect pollinated species given the role of FLS variation in each of these groups.

At the same time, we have also added two more citations that we feel are better evidence for the insect-visibility hypothesis. We agree with the Reviewer that this hypothesis remains largely speculative. Further, it is complicated by the fact that the overlap between flower and leafing may occur when leaves are small and it remains unknown at what stage any impact to pollination might occur. Because this is also an issue for the wind-pollination efficiency hypothesis, we have added a more explicit treatment of this issue in lines 473-479.

As the reviewer suggested, we have tried to more clearly demarcate our discussion of FLS variation in wind-pollinated and insect-pollinated taxa, focusing more on the contrasts between them and highlighting that the role of FLS variation in insect-pollinated species is more uncertain. We feel this comparative approach appropriately leverages our data (which contains mostly insect pollinated species) while providing a more nuanced and realistic framing for the role of FLS shifts in forest communities. We thank the Reviewer for guiding us to this shift in approach, and feel that the manuscript is much improved because of it.

*I think that “bud type” needs to be brought up and addressed earlier. It is first mentioned in the methods with no explanation with what it refers to (line 164) and then was mentioned to be important to the results with no reference to the analysis and how it was relevant (lines 283-284). It seems to me that bud type is very important. Whether the flower and leaf bud are united should determine whether it is possible for a plant to flower before it has leaves. As seen in the summary table, most of the species that flower before they produce leaves have separate buds. Separate buds have the flexibility to have different leaf and flower phenology in a way that mixed buds likely do not (physically and physiologically). I think it would be good if the paper included a brief explanation of bud type and their implications to the plasticity of FLS in the introduction. This would make the discussion of bud type in the discussion clearer and not seem tangential.*

We agree with the Reviewer on this point as well. Our initial omission of the discussion of physical constraints on phenological shifts was a missed opportunity to address a factor that is likely important to our specific questions and to the study of phenology and climate change in general. To address this we now explicitly introduce and define bud type, as well as several other physical constraints in lines 93-101. Additionally, we have added to our Methods a more explicit statement about why we included multiple bud types in this study (line 195). We agree that presenting information about bud types earlier in the manuscript makes our treatment of them in the Discussion feel more relevant to the paper as a whole.

*Smaller comments:*

*Line 150 I assume dormancy is when plants lose their leaves? There are multiple stages of dormancy in buds and it might be simpler to explain this in terms of the visual cue you are talking about instead of using the term dormancy.*

We agree with the Reviewer and have made this change in line 181.

*Line 166 It is not really “preventing” cavitation by cutting. It can minimize embolism in the stem by cutting off the end.*

Thanks to the Reviewer for providing more precise language for this methodological step. We have adjusted the sentence accordingly (now line 202).

*Line 177 This would be more clear if you said “leaf budburst”. I am a bit confused why two similar stages were not picked for flowers and leaf buds. Why not pick a more equivalent budburst stage for flowers instead of open flowers or a leaf unfolding stage more similar to open flowers? This doesn't matter much but did confuse me a bit when reading the paper because of terminology. For example, on line 274, it says “leaf and flower bud phenological responses”. This made me stop for a second and double check that bud phenology was not measured for flowers. I realize this is a small point, but it might be clearer to write “leaf bud and flower phenological responses”. I noticed this in several places in the paper.*

We thank the Reviewer for this point and their suggestion that we clarify our description of these phenological stages. We based our phenological observations on the BBCH scale, choosing BBCH 07 which is the first of the 6 stages describing leaf expansion and BBCH 60, which is the first of the 7 stages that describe the progression of flowering (Finn *et al.*, 2007). Because each stage is first of its respective sequence (flowering or vegetative) we feel these stages do reflect some equivalency between them. We agree with the Reviewer that without an in depth knowledge of the BBCH scale, our descriptions may confuse readers and have clarified our language throughout the manuscript now referring to budburst as “leaf budburst” throughout the manuscript.

Additionally, we did observe a later stage of leaf development (BBCH 15 or “leafout”) in our experiment. In light of the the Reviewer’s feedback and the fact that the functional hypothesis for FLS and wind-pollination efficiency hinges on developing leaves being sufficiently large, we expanding our models and climate projection to include this additional stage in our analyses. We have re-created all relevant figures (Fig. 2, Fig. 4, Fig. S3) to display these results along with our previous analyses, and in the main text we now report and discuss the sensitivity of leafout to environmental cues in addition to the other two phases, and explain our rationale for this at line 214.

*Lines 357-358. What are the implications for this mismatch for insect-pollinated species? Does it result in changes in flower synchrony, which could be a bigger problem than changes in FLS because of the ability of plants to outcross? The next paragraph seems primarily tied to wind-pollination. Are you just talking about wind-pollinated species here?*

Here, we also agree with the Reviewer that this point may primarily apply to wind-pollinated species. We have clarified this in the manuscript in line 413 and added a sentence addressing this population level shifts in FLSs for biotically-pollinated species (line 419) to further the contrast of FLS functions among these two functional groups and emphasize the uncertainty and need for more research regarding how FLS variation impacts biotic pollination.

*lines 408-409. I still wonder how much this is the case. It would be nice to see leaf out instead of bud burst because open buds will not interfere with pollen dispersal (or minimally). How much later is leaf expansion in these species? Is there ever a reversal of leaf expansion and flowering? I know this likely cannot be addressed with the current data but would be worth discussing. Do you know anything of the time frame of flowering? Would the predicted shifts likely interfere with pollen and/or shorten the effective pollen dispersal window?*

We thank the reviewer for this point. We believe the Reviewer is correct that the early stages of leaf expansion that we measured would not alter the structure of the canopy much and such impacts would be expected at later stages of leafout, but it is unclear at exactly what point in leaf development expanding leaves would become a barrier to pollen transport. Based on this, as mentioned above, we incorporated models and climate change projections for leafout (“BBCH 15”) to our analyses and Discussion, explicitly addressing the idea that leaves must be a certain size before they would be expected to impact canopy structure in lines 473-490.

*Line 413 I agree with this fully, but this is the first time this is really said in the paper. There is lots of hand waving about insect-pollination. Is that needed or can you frame things more strongly in terms of wind pollination?*

We have tried to more strongly differentiate the implications of FLS shifts for wind vs. insect pollinated taxa. We hope that the Reviewer feels that our revised submission appropriately addresses the importance of FLS shifts for wind-pollinated species throughout the manuscript.

## **Reviewer: 2**

### *COMMENTS FOR THE AUTHOR*

*Buonaiuto and Wolkovich present a study of how three factors affect the relative phenology of leaves (budburst) and flowers (first opening). This was an experimental study conducted in a growth chamber, conducted on ten woody plant species found in the New England study site. They used their fully factorial study design to test two competing hypotheses regarding what drives differences in leaf and flower phenology. The authors took the work one step further and attempted to project how relative phenology will change under different future climate scenarios.*

*Across the conditions they tested, the authors found that the factors associated with temperature (chilling, forcing) were more influential than photoperiod. The study design allows for compelling evaluation of the “DSH” and “FHH”, and the conclusions they reach are convincing. The manuscript has many strengths, including the presentation of the competing hypotheses, the study design, statistical analysis, the test of whether the FHH is a special case of the DSH, reconciling seemingly contradictory findings from previously published articles, and the careful consideration of what this work means for species of with different life history characteristics. I would especially like to commend the authors on the section ‘Hypotheses for FLS variation’, which is written in a style that I appreciate and that I associate with the work of Wolkovich.*

We thanks the Reviewer for their time and feedback on this manuscript and are pleased that they identified several strengths in our initial submission and enjoyed our writing style.

*There are some changes required before the manuscript is ready for publication. Below I go through critiques and suggested edits that I breakdown into categories: major, intermediate, and minor/optional. All of these critiques can be addressed with the data already analyzed and presented.*

We thank the Reviewer for their feedback and suggestions, and agree that the changes they suggested strongly improve the presentation of our findings. The changes we have made to the manuscript are detailed below.

*MAJOR COMMENTS:*

*In general, there are elements of the figures and tables that are presented too informally.*

We have made several change to the figures and tables to improve them. Specifically, we now use more technical language to describe the relevant phenological phases (leaf budburst, leafout and flowering instead of “leaf” vs. “flower”) and describe our environmental treatments more precisely.

*Some labels are inconsistent with the wording used in the text. In Figure 2, the term ‘light’ is used when it should be ‘photoperiod’ (as in the text) or ‘photo’ (as in Figure 1).*

We have changed the labels to “Photo” for consistency with the rest of the paper.

*Figure 4, the names of the different scenarios should be more consistent with the variables being modeled (especially ‘warming only’)*

We agree with the Reviewer that these labels were confusing. We now describe the scenarios based on the treatment levels that we applied to simulate each scenario.

*Table S2, I do not understand the reference to the ‘Utah model’*

We think this is a good point, and in our original submission we did not adequately reference the three major models used to calculate chilling (the Utah Model is one of them). We have added a citation that is a comprehensive review of the three different models to the caption and adjusted the language of the caption accordingly.

*Figure S1, why is the word ‘scenario’ included in the x-axis label? Also, for Fig S1, an 89% credible interval should not be presented, as the 50% interval is used elsewhere.*

We thank the reviewer for pointing out this inconsistency. We have adjusted the figure to portray the 50% credible interval and removed the x-axis label, which was printed unintentionally in a previous version of figure.

*Figure S2, an explanation of the labels on the x-axis is needed in the figure caption.*

We agree with the Reviewer that these labels do not clearly describe the climate scenarios we are projecting in this figure. As this figure is reflecting the same projections as Fig. 4 in the main text but grouped by species rather than FLS type, in the new version of this we have adopted



similar labels that Reviewer 2 recommended for Fig. 4 above. We hope this change clarifies the interpretation of this plot.

*It is my understanding that all of the data presented are standardized values. It would be valuable to have summaries of the unstandardized values presented at least once, even if it is in the supplement. An unstandardized version of Table S5 would be great.*

We are very grateful to the Reviewer for addressing this issues as it helped us identify a larger issue in our manuscript. In our preliminary analyses, we ran our models several times both with unscaled variables (that is, in natural units, such as ‘days’) and using several different methods of standardization (e.g., z-scores) to make sure our results were robust (which they were). The results that we ended up reporting in the paper are in fact not standardized—this sentence in our Methods description should have been removed, and we thank the Reviewer for catching this error.

All of our results and figures are, in fact, in regular units scaled by the treatment levels. We have added these units to our reporting in the Results section and changed the captions of all relevant figures and tables to explicitly define sensitivity as “ $\Delta$  day of phenological event/  $\Delta$  environmental cue; 30 days chilling/6°C forcing/4 hours photoperiod”. We hope this clarifies our results, and apologize for the confusion in our original submission.

*INTERMEDIATE COMMENTS:*

*I spent some time staring at the figures of this manuscript wondering if it would be helpful to present the graphical results in terms of the length of the FLS as a single variable. This is especially true for Fig 2, and somewhat for Fig 4. The information is available as the gap between the triangles and the circles, but with so may pairs it is hard to follow. An additional panel, figure, or supplemental figure showing the FLS value would be helpful.*

We agree with the Reviewer that we should also use our data to visualize the differences in the sensitivity among phases. We have added additional panels for Fig. 4 and Fig. S3, and created an alternative version of Fig. 2 that displays the response differences between phases (gaps between the shapes) for the Supporting Information (Fig. S2) to aide with this interpretation (we can move this figure to the main text if requested).

*For Fig 1, I might prefer presenting the panels in a different order: FHH, DSH, and the combination*

Agreed, we have made this change.

*Id like a bit more emphasis on results in the Abstract. Nothing too long, for example I recommend highlighting consistency of results across species.*

We thank the Reviewer for this idea and have incorporated their suggestion at line 18.

*Line 266 and elsewhere. When discussing the photoperiod treatment, the language of “increasing” photoperiod is a bit awkward or counter-intuitive. In terms of departing from the historic natural conditions, the treatment (and possible expectation with climate change) is that photoperiod will “decrease”. I understand the point from a statistical perspective, and I don’t dispute it. But because it is not intuitive, the reader might be helped with some guidance/reminders.*

We think this is a good point the Reviewer makes, and in our revised manuscript we tried to strike a better balance between consistency with the statistical orientation of our figures and the intuitive understanding many readers have about how photoperiod impacts phenology. We have removed references to “increasing photoperiod” throughout the manuscript, replacing it with simply “longer” or “shorter” photoperiod where appropriate (see lines 312-318).

MINOR/OPTIONAL COMMENTS: *When I first read the title, I was not sure if “Differences” referred to the different bud types or the different species. A slight re-wording might be in order.*

We have changed the title to more precisely reflect our study:  
“Differences between flower and leaf phenological responses to environmental variation drive shifts in spring phenological sequences of temperate woody plants”.

*Line 63-67, the authors state that a decrease in FLS interphase could harm reproduction in wind-pollinated species. Is there any reason to believe that an increase could also be harmful?*

We thank the Reviewer for raising this interesting point. We think this is an important point to consider and have added a paragraph to the manuscript to discuss it in greater detail from lines 484-490.

*Line 125, change ‘with’ to ‘will’*

We have made this change.

*Line 133, 353, and elsewhere. The authors make the point that under the DSH, shifts in FLS could be quite local. I would expect that they would be more “regional” than “local”. The latter seems a too-narrow scale. Perhaps this perspective is shaped by the very flat, elevationally homogeneous places I’ve lived.*

We agree with the Reviewer that it is difficult to clearly predict the geographic scale at which FLS differences will occur. We now qualify this in the manuscript by suggesting that there may be:

“strongly localized or regional effects of climate change on FLSs.” (line 163).

*Line 186, change ‘standardized’ to ‘standardize’*

As mentioned above, this line was included in the original submission in error and has been removed in this version of the manuscript.

*Line 224, the authors refer to a 5 deg C increase in temperature although their study design uses a 6 deg increase. Is this an error? Do they mean that climate projections predict a 5 deg increase for the study site?*

This was a typo in the original submission, which we apologize for and have fixed (the projection is indeed a 6°increase).

*The authors do a good job of explaining how the implications of their findings may differ for wind-pollinated versus insect-pollinated species, and for flowering-first versus leafing-first species. I would like to see them (briefly) consider tree versus shrub.*

We thank the Reviewer for this point, and we now explicitly mention the possible differences between tree and shrubs in line 98. We think this is an important comparison and designed our study in hopes to address it more fully. Due to low flowering of two species, however, our final analysis consisted of far more shrub species than trees (seven shrubs, two under story trees and only one canopy tree). Thus, further analysis of this difference is now beyond the scope of our data.

*Line 281, change ‘showed’ to ‘show’*

We have made this change.

*Line 304-307, although a point is made later, I think it is worth mentioning here that both species shrubs, flowering-first, and wind-pollinated*

We have added this information in this line (line 356).

*Line 347, missing a comma after ‘temperatures’ (optional)*

We added this comma.

*Line 372-374, another supporting point may be that photoperiod had less of an effect.*

We think this is a strong point and have added this to the manuscript in line 431.

*Line 413, delete ‘which is of little relevance to abiotically pollinated taxa’*

We have removed this line.

*Supplemental Methods Line 13, change the wording of “In this scenario we let increased both chilling...”*

We have clarified this sentence (line 13).

## References

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