The ARNOLD ARBORETUM of HARVARD UNIVERSITY

1300 Centre Street
Boston, MA, 20131

February 17, 2020

Dear Editors:

Please consider our paper, entitled "Spatial and temporal shifts in photoperiod with climate change" as a Review & Synthesis in *Ecology Letters*. This manuscript is a revised version of manuscript ELE-01441-2019. We have incorporated the suggestions of the referees and editor, as detailed in the enclosed point-by-point response.

As you may remember, our paper addresses an urgent ecological question: What are the implications of the altered photoperiod that plants and animals experience as they shift their ranges and seasonal activities with climate change? The two most-observed biological impacts of climate change are shifts in space (range shifts) and time (phenological shifts). Both alter experienced photoperiod, which could dramatically affect performance and fitness. However, the magnitude of effects from shifts in photoperiod with climate change are unknown or unquantified for the vast majority of species. We address this need by synthesizing the large body of controlled climate experiments that test effects of temperature and photoperiod on spring phenology in plants *(1)*. Our review differs from previous work *(e.g., 2)* in that it quantifies expected changes in experienced photoperiod due to shifts in space versus time. Though we include a detailed discussion of woody plants, our review is broadly relevant, as photoperiod acts as a cue for the spring emergence and migration timing of diverse species, and altered photoperiod can affect development, growth, and fitness for plants, insects, fish, and mammals, among other organisms.

All three reviewers felt our review addressed an interesting and important topic. Beyond that, there were some differences in opinion. Reviewer 2 felt our manuscript is a good review of what is known about the effects of photoperiod in the context of climate change, with clear ideas, good discussion, relevant literature, and useful figures. Reviewer 1, on the other hand, felt that our manuscript was difficult to follow, in part because the figures were poorly explained, and that it should focus on autumn rather than spring phenology. The reviewers also made some suggestions for additional topics that should be better integrated into the manuscript: Reviewer 2 noted that the previous version of the manuscript was mostly plant (and tree) oriented, and suggested some areas in the text where additional emphasis could be placed on the relevance to animals. We have followed the suggestions of this reviewer, and added text and several new animal references about effects of photoperiod on reproduction. Reviewer 3 felt that we should more fully discuss the need for improvements to experiments, and specifically that the need for additional plant physiological experiments should be emphasized. To address these concerns, we have substantially modified the manuscript by adding text about animals and better explaining our choice to focus on spring phenology, modifying the figure legends to improve clarity, and adding references, in particular those suggested by the reviewers.

Please see our detailed, point-by-point response below for more information on the changes.

Sincerely,

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

References in cover letter

1. Wolkovich, E.M., et al. 2019. Observed Spring Phenology Responses in Experimental Environments (OSPREE). Knowledge Network for Biocomplexity. urn:uuid:b2ab2746-b830-4
2. Saikkonen, K., et al. 2012. Climate change-driven species' range shifts filtered by photoperiodism. *Nature Climate Change*, 2:239.

Response to Reviewers

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

Reviewer #1 (Comments for the Authors)

I am happy to review this manuscript as a Reviews and Synthesis paper to Ecology Letters. Basically, this paper aims at answering the three questions: 1. How will climate change alter the photoperiod experienced by organisms? 2. What are the implications of altered photoperiods for biological responses to climate change? 3. Can research apply data from experiments that alter photoperiod to aid in forecasting biological implications of climate change? Absolutely, these three questions are very important for understanding the changes of photoperiods and its impacts to biological phenophases. However, it is pity that I found very limited new knowledge by reading this paper, and many places are very difficulty to follow. I have several major concerns as followings.

We thank the reviewer for taking the time to review our paper and provide detailed comments. We appreciate that the reviewer agrees the questions on which we focus in our paper are very important. We have modified the manuscript to address the reviewer's concerns. In particular, we have worked to more clearly articulate the goals of our paper. As a Review paper, this manuscript does not present new data; rather, the primary goals of this manuscript are to synthesize previous studies, call attention to new research needs, and suggest novel approaches for future work. For example, in the abstract we have modified the text to clarify that our work is a review in the following places:

- Line 4, we have added "of reviewed studies" so that the sentence now says: "As photoperiod is a common trigger of seasonal biological responses (e.g., affecting plant phenology in 84% of reviewed studies that manipulated photoperiod), such shifts in experienced photoperiod may have important implications for future distributions and fitness of many species.
- Line 7, we have added "we synthesize published studies" so that the phrase says: "Here we synthesize published studies to show that impacts on experienced photoperiod from temporal shifts.."

HELP NEEDED: I would love additional ideas about how to address Reviewr 1's comments, both here and below!

1. The authors seem to focus on the responses of spring phenophases to photoperiods, but it may be a wrong direction. There is obvious asymmetry of radiation and temperature on seasonal changes. The peak of radiation is always earlier than that of temperature, and which means the limited environmental variable in Spring is temperature not radiation. Therefore, the photoperiod is not important for plant phenology in Spring. On contrary, in autumn, the radiation or daylength is very low when the temperature keeps still very high. However, I did not find some reviews on the changes in autumn phenophases in response to photoperiod.

The reviewer is correct that our work focuses on spring, not autumn, phenology; we agree that a review on autumn plant phenology responses would also be interesting and useful. We chose to focus on the intersection of photoperiod with spring phenology in part because, the role of photoperiod has received far more detailed attention for end-of-season activities, such as growth cessation in the fall, than for spring activities. In addition, this topic has received growing interest (e.g., Chamberlain et al 2019, Fu et al 2019, Richardson et a 2018), given recent studies highlighting declining responses of spring budburst to warming (e.g., Fu et al 2019, Güsewell et al 2017, Yu et al 2010). One possible cause of these declines in sensitivity could be photoperiod thresholds. Though photoperiod cues dominate in the fall for many organisms, as the reviewer suggests, fall phenology responses to climate change have been muted. In contrast, spring phenology responds strongly to temperature and thus has advanced substantially with warming—causing cascading, and generally unexplored, effects on photoperiod experienced at the start of spring. Thus, we wish to shine a light on the potential implications to spring phenology of altered photoperiod cues with climate change. We also suggest that there are many opportunities for additional research in this field, given the wealth of data from growth chamber experiments on woody plant spring phenology.

We have added a new subsection entitled 'Focal examples from spring woody plant phenology" in which we more full explain our choice to focus on spring phenology. For example, in Lines 74-78 we write: "We focus on spring events, as phenology during this time is one of the most widely observed and rapidly changing biological responses to climate change (Parmesan, 2006). In addition, the role of photoperiod is less well-understood in spring phenology compared with autumn phenophases, but recent studies showing declines in responses of spring budburst to warming (e.g., Fu et al., 2019; Güsewell et al., 2017; Yu et al., 2010) suggest that photoperiod constraints may be imminent."

We have also added a sentence to address the need for future research on experienced photoperiod shifts in autumn phenophases to the 'Future directions' section (Lines 227-229), where we write: "We have focused here on spring phenology, but future work could also address the sensitivity of model outcomes to shifts in experienced photoperiod at the end of the growing season (i.e., autumn phenology)."

2. the abstract is very week because it fails to summarize the main content of this review manuscript. The authors are going to review the study progresses on photoperiods and its impacts, therefore, the abstract should also focus on the three key scientific questions. However, the current abstract does not highlight the key results and conclusions but repeat the background.

We have modified the abstract, so that it includes a sentence addressing each of the three key scientific questions. (Due to word limits, we did not add the questions themselves).

To address question 1 ("How will climate change alter the photoperiod experienced by organisms?") the abstract includes the following sentence (Lines 7-9): "We synthesize published studies to show that impacts on experienced photoperiod from temporal shifts could be orders of magnitude larger than from spatial shifts (e.g., 1.6 hours of change for expected temporal versus only one minute for latitudinal shifts)."

To address question 2 ("What are the implications of altered photoperiods for biological responses to climate change?"), we have added the following sentence (Lines 9-10)"'For woody plant phenology, for example, shifts in experienced photoperiod may increasingly constrain their ability to respond to additional warming."

To address question 3 ("Can research apply data from experiments that alter photoperiod to aid in forecasting biological implications of climate change?"), the abstract states the following (Lines 11-13): "Incorporating these effects into forecasts is possible by leveraging existing experimental data; for example, growth chamber experiments on woody plant spring phenology often have data relevant for climate change impacts."

3. The introduction starts from the impacts of climate warming on phenophases (the first paragraph). I would like to read the importance of photoperiods first, and then to know the connections between temperature and photoperiods.

We have restructured the beginning of the introduction as the reviewer suggests, so that the paper now begins with a paragraph on photoperiod (Lines 16-26), followed by a paragraph on interactive effects of temperature and photoperiod (Lines 27-37).

HELP NEEDED: I personally do not like this restructuring but felt we needed to address Reviewer 1's comments. I would appreciate your feedback and suggestions for improvement!

4. Line 36: these two references did not support your statement "Some studies suggest that, with additional warming, photoperiod will limit phenological shifts of certain species such that they will not track rising temperatures (e.g., by leaf out earlier in the spring, Körner and Basler, 2010; Way and Montgomery, 2015)." These two papers are review papers, and both describe the contrary conclusion with the authors. For example, the first paper states "However, no study has demonstrated that photoperiod is more dominant than temperature when predicting leaf senescence (1), leafing, or flowering" The authors should double check and be cautious for all conclusions in the manuscript. Therefore, I doubt the main topic in this review paper as I mentioned before that the impacts of photoperiods is very limited to phenophases in Spring.

In this comment, the reviewer has made statements that we feel misrepresent our work. The reviewer incorrectly attributes a quote to Körner and Basler (2010b) ("However, no study has demonstrated that photoperiod is more dominant than temperature when predicting leaf senescence." This quote is from a "Response" to Körner and Basler (2010a), written by Isabelle Chuine, Xavier Morin, and Harald Bugmann (Chuine et al 2010). Chuine et al (2010) make important points in their response to Körner and Basler (2010a), but we did not reference their writing in our manuscript. The reviewer seems to suggest that we have misquoted the two references we cite (Körner and Basler, 2010b; Way and Montgomery, 2015). We disagree. These two references are examples of writing that describe the idea that, with future warming, photoperiod cues may limit plant responses to temperature. Both references we cite do this; they do not describe conclusions that are contrary to ours, as the reviewer states. Please see below for direct quotes from these two citations. We encourage the reviewer and editor to consult the references directly to confirm the accuracy of our summary of the authors' statements:

- From Körner and Basler (2010b): "Warm temperatures are most effective in promoting budburst only after the photoperiod requirement of adequately chilled buds is met (3, 6). This process prevents trees from sprouting before the risk of freezing damage is over. Photoperiodism in trees has been known for almost 100 years (7, 8), but is an often ignored environmental cue when predicting the effects of a future climate."
- From Way and Montgomery (2015): "Here, we discuss how day length may limit the ability of tree species to respond to climate warming in situ, focusing on the implications of photoperiodic sensing for extending the growing season and affecting plant phenology and growth, as well as the potential role of photoperiod in controlling carbon uptake and water fluxes in forests."
- From Way and Montgomery (2015): "Organisms that rely on photoperiodic cues for sensing the arrival of spring

and the approach of winter may have constrained responses to warming, which would limit expected extensions of the growing season in mid- and high latitude forests (Saikkonen et al. 2012).

- From Way and Montgomery (2015): “There is also evidence for direct photoperiodic sensitivity of bud burst in some species (e.g. F. sylvatica; Heide 1993a): at shorter photoperiods, it takes longer for buds to burst than at long photoperiods, indicating that long photoperiods enhance dormancy release (Heide 1993a,b). Tree species that fall into this category are likely to be strongly limited in their ability to respond to warmer springs by breaking bud earlier.”
- From Way and Montgomery (2015): “A reliance on photoperiod as a seasonal cue for growth and physiological activity may either constrain forest productivity, via limitations on photosynthetic capacity, migration potential or growing season length, or permit longer growing seasons and greater tree growth in individuals that migrate to higher latitudes.”

We do agree with the reviewer that our characterization of the papers as “studies” may have been misleading, as the referenced articles are not experiments. One is review paper summarizing many observational and experimental studies (Way and Montogmery 2015). The other (Basler and Körner 2010b) is a response to a response to a perspective (Basler and Körner 2010a). It was not our intention to be misleading. To address this, we have removed the original Körner and Basler citation (Körner and Basler 2010b) , and added instead references to a long-term observational study (Fu et al 2015), growth chamber/common garden experiments (Fudickar et al 2016, Basler & Körner 2012), and a perspective (Körner, C. Basler 2010a), in addition to the review paper we originally cited (Way and Montgomery 2015). We have also modified the text slightly. The new phrase says: “It has been suggested that, with additional climate change, photoperiod will limit phenological shifts of certain species such that they will not track rising temperatures (Fudickar et al 2016, Fu et al 2015, Way and Montgomery 2015, Basler & Körner 2012, Körner& Basler 2010).”

HELP NEEDED: Is the above response ok?

5. Figure 1 and 2 are two the most important results in this review paper. However, the authors fail to introduce their importance clearly. Figure 1 only shows the temporal changes of daylength at two locations, and I have no idea about other information in the figure. Figure 2 is very low level greenness map, and I did not find any useful information at all. In addition, these two figures can not support the conclusion in the text very well. For example, how can the authors arrive at this conclusion "A general pattern of longer photoperiod at green-up toward the poles is consistent across years (Fig. 2b) and green-up does not appear to occur at daylengths less than 10 hours."? (Line 82-83)

We thank the reviewer for pointing out that our explanations of the figures were unclear in the previous version. In this new version, we have adjusted the Figure legends to improve clarity, including adding units to the legends (e.g. "minutes" of change in daylength for Figure 1, "hours" change in daylength at greenup for Figure 2).

Figure 1 legend now says: “Temporal shifts in activity yield larger changes in experienced photoperiod compared to spatial (latitudinal) shifts on the same day of year, due to patterns in photoperiod variation with latitude and by day of year. Here, we show this variation at two latitudes (22.5°, 45°), using hypothetical spatial and temporal shifts. These shifts are based on observed rates with recent global warming: 6-17 kilometers per decade, or approximately 0.5-1.5 degrees in 100 years, for spatial shifts (Parmesan and Yohe 2003,Parmesan 2006, and 2-3 days per decade, or 30 days in 100 years, for temporal shifts (**??**)). They highlight the greater magnitude in daylength changes in the early spring, close to the vernal equinox (e.g., day of year 91), versus close to the summer solstice (e.g., day of year 182).”

HELP NEEDED FOR FIGURE !: Have I made enough changes to the figure legend? How else could I improve this? I tried a version of the figure adding the numerical changes in daylength to the figure but I don’t think this reviewer would find this helpful. (sent via email).

HELP NEEDED FOR FIGURE 2: NACHO: Could you please add "hours of daylength" underneath the color ramps in panels a and b and "hours" under the ramp in panel c? Do you have other ideas for how to address this comment?

6. the authors fail to summarize the knowledge on "How will climate change alter the photoperiod experienced by organisms?" I only get very limited knowledge on current conditions of photoperiods experiences by organisms and future changes. In addition, these information focus on the local scale, no global pattern shown. I do not think this kind review can promote science advances. Same feelings for other two sections.

We are sorry that the reviewer feels that we present limited knowledge on current conditions of photoperiods experienced by organisms and future changes. Part of the challenge is that, to our knowledge, there are limited data and few modelling studies on which to draw for our review. We have tried to present global patterns in Figure 2, using green-up date as an example; we wish that there were additional global phenology datasets available to use as examples. We are also unclear about what additional information the reviewer would like to see included. Does the reviewer wish to see quantification of the range of experienced photoperiods in current conditions and under future projected conditions? We have done this for two species included in OSPREE, in Figure 5, as an example. We do not believe it would be possible to expand this to a global scope because of a lack of phenology modelling studies that incorporate photoperiod in this way. Indeed, part of our goal in writing this manuscript is to highlight the need for additional research attention in this area.

HELP NEEDED! I'M NOT REALLY SURE WHAT ELSE TO SAY HERE OR WHAT WOULD HELP THIS REVIEWER. SHOULD I REACH OUT TO THE EDITOR? Do you think what they want is something like a table of current experienced photoperiod (for a range of species) and expected future experienced photoperiods? There may be a handful of studies that do projections and would allow for this to be done (e.g., Phenofit studies, Grevstad and Coop. 2015)

7. Figure 3 and 5 are results derived from OSPREE database, but it is very hard to understand how the experiments have been conducted and if the conclusions are reliable because the authors did not introduce them adequately.

Thank you for sharing the need for a more full explanation of the experiments in our OSPREE database. We have added a new subsection to the manuscript, prior to addressing our three main questions, entitled “Focal examples from spring woody plant phenology” (Lines 72-92). This section provides some details on the OSPREE database, as well as references for where additional details can be found.

HELP NEEDED: Is the above response ok? We could also add a figure, similar to what we did in the main OSPREE paper, but focused around photoperiod....

8. There are too many conclusions no evidence supported to list them all.

We have done our best to list references and/or our own figures to support our conclusions, where relevant. We welcome more detailed feedback on what specific statements, if any, are in need of additional evidence.

HELP NEEDED: Is the above response ok?

Reviewer #2 (Comments for the Authors)

Manuscript is a good review of what is known about the effects of photoperiod in the context of climate change. Although the title doesn't make this clear, it's mostly plant (and tree) oriented. I think I made a few notes about places where relevance to animals could be included. It's pretty well written, although I've flagged some editorial issues on the PDF. I think the relevant literature is cited, and the figures are useful and clear. The ideas are presented clearly and the discussion is good. See a few other comments on the PDF.

We thank the reviewer for these comments. We have incorporated the relevance to animals in places where the reviewer suggested (e.g., by mentioning the affect of photoperiod on reproduction in animals, and by adding additional references focused on photoperiod effects on animals). We feel this has strengthened the manuscript by demonstrating the broad range of taxa affected by photoperiod. We have also addressed the editorial issues noted in the pdf, which are summarized below:

Do you mean latitudinal shifts?

Yes! We have replaced “spatial” with “latitudinal” to be more specific. The phrase now says “(e.g., 1.6 hours of change for expected temporal shifts versus only one minute for latitudinal shifts).”

Line 21: We replaced ”climate change induced” with ”climate change-induced” as suggested by the reviewer.

Line 41: *cues? The cues won't change. maybe 'responses'?*

We thank the reviewer for pointing out a lack of clarity here. We have rewritten the phrase, as suggested, which now reads: “The extent to which daylength constrains phenology will depend in part on how rapidly photoperiod responses can acclimate or adapt to new environmental conditions, which remains poorly understood (Grevstad and Coop, 2015).”

Line 52-53 *Do you mean this to include reproduction? If not, add reproduction to that list.*

We have added reproduction to the list, which now reads: “...since daylength can affect the timing of development (Grevstad and Coop, 2015; Muir et al., 1994), migration (Dawbin, 1966), reproduction (Dunn, 2019; Dardente, 2012; Ben-David, 1997), and other important responses. ”

Line 62: We have replaced “research” with “researchers” as suggested by the reviewer.

Line 114: We have replaced "if" with "whether" as suggested by the reviewer.

Line 121-125: We have added reproduction to the list of animal responses affected by daylength, as suggested by the reviewer. This section now says: "Daylength can play a role in controlling critical biological functions, including vegetative growth, cell elongation, budburst, and flowering in plants (Heide and Sonsteby, 2012; Heide, 2011; Hsu et al., 2011; Sidaway-Lee122et al., 2010; Mimura and Aitken, 2007; Linkosalo and Lechowicz, 2006; Erwin, 1998; Ashby et al., 1962) and growth rate, maturation, reproduction, migration, and diapause in animals (Dunn, 2019; Zydlewski et al.,2014; Dardente, 2012; Tobin et al., 2008; Bradshaw and Holzapfel, 2006; Ben-David, 1997; Muir et al., 1994; Saunders and Henderson, 1970; Dawbin, 1966)."

Lines 156-157: We have added hyphens, as suggested, so that the phrase now reads: "slower-growing or later-emerging ones"

Line 168: We have added a semi-colon, as suggested.

Line 182: We have replaced "if" with "whether", as suggested.

Line 199: We have added a hyphen, as suggested, changing "fine scale" to "fine-scale".

Lines 233-257 (Glossary): We have ensured that all definitions end with periods, to be consistent, as suggested by the reviewer.

Line 290: We have made the suggested change to our wording. The phrase now reads: "..some species demonstrated a response to photoperiod opposite to that typically observed..."

Line 333: We have added the published of this book to the reference, as suggested by the reviewer. Thank you for noticing this error!

Line 359: We have capitalized the genus name, and italicized the genus, species, and variety names. Thank you for noticing this error!

Line 407: We have italicized the genus and species names. Thank you for noticing this error!

Figure 1: We have replaced "Spatial shift" with "Latitudinal shift" in the figure legend, as suggested.

Reviewer #3 (Comments for the Authors)

The shifts of photoperiod is not only the result of phenology changes, such as earlier in spring leaf-out and geographic shifts in species distribution, but also the reason/driver of phenology change, for example the shortening photoperiod associating with earlier leaf-out reduced the temperature sensitivity. I do think this is an interesting review in the photoperiod shifts, although many papers have discussed such photoperiod effect on phenology, and agree that the photoperiod effect should be coupled into the phenology modeling, especially considering the larger uncertainty of phenology modeling in the global carbon simulations. One major issue is that, although the importance of photoperiod has been addressed by many papers, such as Körner and Basler 2010 science paper, as well as papers the authors cited, how the photoperiod plays its role during the phenology processes is still largely unclear. For example, the interactive effect among photoperiod, chilling and forcing in the spring leaf-out processes, and the relative importance among these drivers for phenological processes. In one recently study, the authors proposed a framework that the photoperiod interacts with chilling and forcing (GDD) to modify the leaf-out dates to ensure the tree leaf out at the right time, and further suggested that the photoperiod plays its role depending on the phenology dates, i.e. whether or not the phenological dates filling into its optimal periods, see Fu et al, gcb (daylength helps the ..).based on such framework, the species-specific difference, as well as spatial difference in photoperiod effect could be explained. Anyway, such integrative effect need to be reviewed clearly.

We thank the reviewer for noting that our review is interesting, and for suggesting the need to more clearly review that effects of photoperiod are interactive with temperature for many species. We discuss the interactions of photoperiod and temperature in detail in Box 1, and have added some additional references to this box in the main text (see below). We have also added the following text to more clearly review the integrative nature of phenology, including adding relevant references such as the one the reviewer mentions:

- Lines 27-29: "For many organisms, the timing of spring events– i.e., phenology, including flowering, bird arrival, egg hatching and myriad other biological activities– is thought to be determined by photoperiod interactively with temperature (Fu et al., 2019; Winkler et al., 2014; see also Box 1)."
- Lines 134-138: "Daylength, often in combination with temperature, can play a role in controlling critical biological

functions, including vegetative growth, cell elongation, budburst, and flowering in plants (Fu et al 2019; Heide and Snsteby, 2012; Heide, 2011; Hsu et al., 2011; Sidaway-Lee et al., 2010; Mimura and Aitken, 2007; Linkosalo and Lechowicz, 2006; Erwin, 1998; Ashby et al., 1962) and growth rate, maturation, reproduction, migration, and diapause in animals (Dunn, 2019; Winkler et al 2014; Zydlewski et al., 2014; Dardente, 2012; Tobin et al., 2008; Bradshaw and Holzapfel, 2006; Ben-David, 1997; Muir et al., 1994; Saunders and Henderson, 1970; Dawbin, 1966).

- Lines 142-144: "The direction and magnitude of responses will vary, however, because of variation in photoperiod sensitivity, and because photoperiod often interacts with other environmental drivers, such as temperature, to affect phenology (Box 1)."

In addition, the authors suggested that the experimental results could be coupled into the modelling approaches, however the phenological experimental studies might be underestimated, comparing to its natural response, see Wolkovich et al, 2012 nature, how to improve the experimental study to be more reliable and reality is thus important, rather only suggesting couples the experimental results into the modeling approaches. In the review paper in Hänninen et al, 2019, Trends in plant science, in which the authors suggested even the processed-based modeling is still unreliable, because the key sub-processes are omitted during the experiments and thus physiological experiments are needed, for example controlling the dates of end endodormancy (Chine et al, 2016 gcb).

Hänninen H, Kramer K, Tanino K, et al. Experiments are necessary in process-based tree phenology modelling[J]. Trends in plant science, 2019, 24(3): 199-209.

Fu, Y H. et al. Daylength helps temperate deciduous trees to leaf-out at the optimal time[J]. Global change biology, 2019, 25(7), 2410-2418.

Chuine, I. et al. Can phenological models predict tree phenology accurately in the future? the unrevealed hurdle of endodormancy break. Glob. Change Biol. 2016, 22, 3444-3460

We thank the reviewer for pointing out some important challenges and needs in phenology research! We have added text to our manuscript suggesting the need for additional experimental research, in addition to incorporating these results into modelling approaches. We have also added some text to emphasize some of the physiological research needed, as the reviewer suggests, and we have added citations to the suggested references. Below we summarize the additions we have made:

- Lines 28-30: We have added the Fu et al 2019 reference: "For many organisms, the timing of spring events—i.e., phenology, including flowering, bird arrival, egg hatching and myriad other biological activities— is thought to be determined by photoperiod interactively with temperature (Fu et al., 2019; Winkler et al., 2014, see also Box 1)."
- Lines 75-77: We have added the Fu et al 2019 reference: "In addition, the role of photoperiod is less well-understood in spring phenology compared with autumn phenophases, but recent studies showing declines in responses of spring budburst to warming (e.g. Fu et al.,2019.."
- Lines 138-139: We have added the Fu et al 2019 reference: "Daylength, often in combination with temperature, can play a role in controlling critical biological functions,including vegetative growth, cell elongation, budburst, and flowering in plants (Fu et al., 2019;..."
- Lines 151-152: We have added the Fu et al 2019 reference: "The climate change-induced trend toward ever earlier springs means that experienced photoperiod may increasingly approach threshold photoperiod for many species, constraining their ability to respond to additional warming (Fu et al., 2019.."
- Lines 239-241: We have added the following text citing the Chuine et al 2016 and Hänninen et al 2019 references: "For many species, additional experimental physiological research239is necessary, since the dormancy-breaking processes that photoperiod a ects often require microscopy and240detailed physiological approaches to observe (Hanninen et al., 2019; Chuine et al 2016)."

Line 7-9, Larger spatial photoperiod shifts than temporal shifts was reported... does it suggest the local climate is more important than air temperature? or the interactive effect among environmental cues plays more important role than air temperature only?

We thank the reviewer for pointing out that this wording may have been unclear. We do not believe that our findings can be used to infer anything about the relative importance of local climate versus air temperature. Our finding that temporal shifts result in larger changes in experienced photoperiod are a result of the way that photoperiod varies with latitude and seasonally, from winter to spring (as shown in Figure 1). We have reworded this sentence slightly to try to make this more clear. The sentence (Lines 7-9) now reads: "We synthesize published studies to show that impacts on experienced photoperiod from temporal shifts could be orders of magnitude larger than from spatial shifts (e.g., 1.6 hours of change for expected temporal versus only one minute for latitudinal shifts)."

L152-153, yes, but the rate of frost damage may also increase...

The reviewer , who refers to our statement (now Lines 152-153) that "For example, a species or population that is relatively insensitive to photoperiod can take advantage of warmer springs by having an earlier start to its growing season, " makes an excellent point. We now mention this in explicitly in Lines 25-27, where we write: "For example, relying on a threshold photoperiod (seeGlossary), rather than temperature alone, may prevent woody plants from leafing out during 'false spring' events and experiencing frost damage (unusually warm periods during winter that are followed by a return of cold temperatures (Gu et al 2008)."

L158-159, also identifying the species-specific photoperiod sensitivity is important...

The reviewer makes an excellent point! We have incorporated this idea, so the statement now reads (Lines 180-182): "To identify where, when, and how communities may be altered, quantifying species-specific photoperiod sensitivity and developing methods for incorporating photoperiod into forecasting future phenology are critical."

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Editor's comments to the author(s):

Please consider the serious concerns of the referees, especially those of referee 1

We thank the editor for considering this manuscript.

References included in responses to reviewers

Chamberlain, C.J., et al. 2019. Rethinking false spring risk. *Global Change Biology.*

Fu, Y.H., et al. 2019. Daylength helps temperate deciduous trees to leaf-out at the optimal time. *Global change biology.*

Fu YH, Zhao H, Piao S, Peaucelle M, Peng S, Zhou G, Ciais P, Huang M, Menzel A, Peuelas J, Song Y. Declining global warming effects on the phenology of spring leaf unfolding. Nature. 2015 Oct;526(7571):104-7.

Fudickar AM, Greives TJ, Atwell JW, Stricker CA, Ketterson ED. Reproductive allochrony in seasonally sympatric populations maintained by differential response to photoperiod: implications for population divergence and response to climate change. The American Naturalist. 2016 Apr 1;187(4):436-46.

Güsewell S, Furrer R, Gehrig R, Pietragalla B. Changes in temperature sensitivity of spring phenology with recent climate warming in Switzerland are related to shifts of the preseason. Global change biology. 2017 Dec;23(12):5189-202.

Körner, C, Basler D. Phenology under global warming. Science. 2010a. 327(5972):1461-2.

Körner, C, Basler D. Warming, photoperiods, and tree phenology response. Science. 2010b. 329:278278.

Richardson, A.D., et al. 2018. Ecosystem warming extends vegetation activity but heightens vulnerability to cold temperatures. *Nature*, 560: 368.

Yu H, Luedeling E, Xu J. Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. Proceedings of the National Academy of Sciences. 2010 Dec 21;107(51):22151-6.