The ARNOLD ARBORETUM
of HARVARD UNIVERSITY

December 3, 2019

Dear Dr. Chase and Dr. Hillebrand:

We propose a Review & Synthesis to address 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 would address this need by synthesizing the large body of controlled climate experiments that test effects of temperature and photoperiod on spring phenology *(1)*. Our review would differ from previous work *(e.g., 2)* in that it would quantify expected changes in experienced photoperiod due to shifts in space versus time. It would be 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. Thus, understanding these changes is critical for scientists studying basic ecology, as well as those who wish to forecast species responses to climate change and use forecasts to develop adaptation strategies. Yet, photoperiod has rarely been included in forecasts of climate change responses, and implications of climate-change-induced shifts in photoperiod are largely unexplored, especially for early-season spring events, where changes will be most dramatic.

This piece would be timely and important because of its focus on the intersection of photoperiod and spring phenology (similar to *3,4,5*)—this is an area of growing interest given recent studies suggesting that photoperiod may underlie declining responses to warming. To date, 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. Though photoperiod cues dominate in the fall for many organisms, 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. We demonstrate that incorporating photoperiod into forecasts is possible by leveraging existing experimental data: as an example, we show that growth chamber experiments on woody plant spring phenology often have data relevant for climate change impacts (e.g., Fig. 1). s

Our international team includes researchers well-versed in techniques of controlled climate experiments, having conducted such studies ourselves *(e.g., 6)*, as well as scientists with expertise in meta-analytical approaches *(e.g., 7,8)*. We expect our proposed Review & Synthesis will inspire innovative research to improve mechanistic understanding of photoperiod as a cue for diverse biological processes, as well as a deeper appreciation for the ways that experienced photoperiod may both affect and be affected by species responses to climate change; we hope you will consider it for *Ecology Letters*.

Sincerely,

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References in cover letter

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Spatial and temporal shifts in photoperiod with climate change

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Climate change causes both temporal and geographic shifts in species; these shifts in turn affect the daylength (photoperiod) that species experience. As photoperiod is a common trigger of seasonal biological responses (e.g., affecting plant phenology in 84% of studies that manipulated photoperiod), such shifts in experienced photoperiod may have important implications for future distributions and fitness of many species. However, photoperiod has not been a focus of climate change forecasting to date, especially for early-season ('spring') events—which are often assumed to be driven by temperature. Here we show that impacts on experienced photoperiod due to temporal shifts could be quite large and may be orders of magnitude larger than impacts due to spatial shifts (e.g., 1.6 hours of change for expected temporal shifts versus only one minute for spatial shifts). Incorporating these effects into forecasts may be possible by leveraging existing experimental data; for example, growth chamber experiments on woody plant spring phenology often have data relevant for climate change impacts. We highlight how combining novel modeling approaches and empirical work on when, where, and how much photoperiod affects spring phenology, could rapidly advance our understanding and predictions of future spatial-temporal shifts due to climate change.

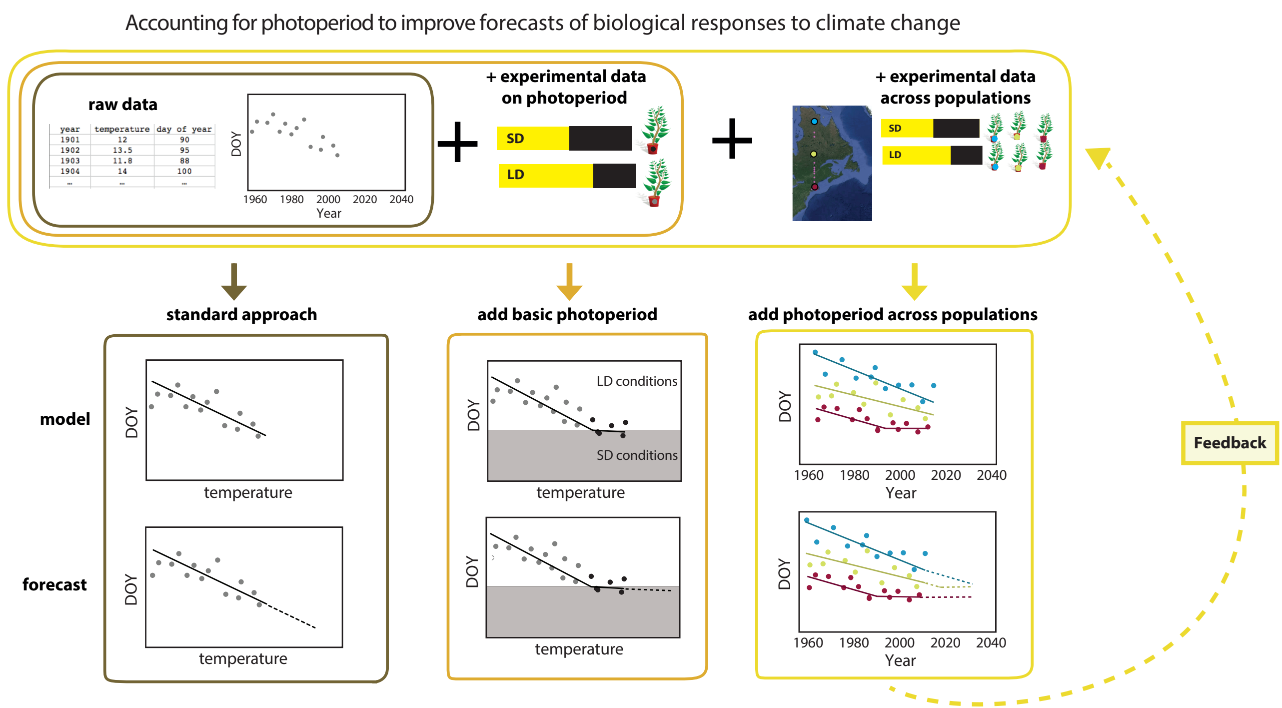

Figure 1. Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change. Current approaches for forecasting spring phenology with climate change frequently rely on linear relationships between historical temperature data and observed dates of spring phenology (left panels). Adding responses to photoperiod, which commonly operate as threshold responses to short days (SD) versus long days (LD, see "photoperiod sensitivity" in the *Glossary*), will alter these forecasts (center panel) in ways that differ across species with divergent threshold photoperiods. Other factors that interact with photoperiod, such as population-level variation in photoperiod responses, can be incorporated into forecasts to further improve their accuracy (right panel).