

# Spatial and temporal shifts in photoperiod with climate change

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## Summary

Recent warming temperatures have brought about temporal shifts in biological activity, such as spring budburst, as well as spatial shifts in species' distributions. Both temporal and spatial shifts are expected to continue with future warming, and will alter the photoperiod experienced by diverse species. To date, photoperiod has not been a focus of climate change forecasting, despite the fact that photoperiod responses are common (observed in 26/31 or 84% of studies that manipulated photoperiod in woody plant species). We argue that temporal shifts are expected to have a major impact on experienced photoperiod. Thus, improving our mechanistic understanding of the role of photoperiod in spring phenology and adding incorporating photoperiod into forecasts of biological shifts should be major goals. We find that there already exists a substantial resource of growth chamber experiments with relevant treatments that could be used to forecast implications of photoperiod shifts with climate change. We highlight outstanding questions that are in need of additional research and modelling approaches to improve predictions of when, where, and how much photoperiod is likely to affect future spring phenology.

## Introduction

Shifts in the timing of spring events, including flowering, bird arrival, egg hatching and myriad other activities, are one of the most widely documented biological signals of climate change. Across taxa from plants and insects to mollusks and mammals, spring phenology is occurring earlier as temperatures warm, with average shifts of 1.2 to 5.1 days earlier per decade (???) or 1.3–5.6 days earlier /°C of warming(?). Indeed, early spring phenology appears to be shifting more rapidly than later season phenology in many cases (??), suggesting strong temperature sensitivity of spring phenophases.

Spring phenology is not controlled solely by temperature, however. Photoperiod is also a critical cue for plants and animals, signalling changes in growth, mating, and reproduction across diverse species (e.g., ?????). Photoperiod is used to synchronize activities with seasonal climatic changes (e.g., ???) because it is consistent across years, especially compared to other seasonal cues such as temperature and precipitation (?). For example, relying on photoperiod, rather than temperature alone, may prevent woody plants from leafing out during “false spring” events (unusually warm periods during winter that are followed by a return of cold temperatures ?)).

Recent studies offer inconsistent views about whether photoperiod may eventually restrict spring phenology in a warmer world. Some studies suggest that certain species will be unable to track climate warming, i.e., by leafing out earlier in the spring (?). Instead, these species will increasingly become constrained by daylength, since photoperiod sensitivity is primarily genetically controlled (?). Other studies, however, suggest that photoperiod is unlikely to constrain responses to warming for most species (?).

Interactions between temperature and photoperiod have been particularly well studied in woody plant phenology. Decades of experimental growth chamber studies have shown that photoperiod is an important cue for spring budburst phenology in woody plants. These experiments often manipulate photoperiod in combination with temperature to address basic questions about how these two environmental drivers act as biological cues. Air temperature has a dual role in regulating phenology: chilling, the prolonged exposure to cold temperatures after growth cessation in the fall, that is required to initiate budburst; and forcing, prolonged exposure to warm temperatures, that is required for budburst to occur. Thus, chilling and forcing temperatures are often altered in addition to photoperiod in growth chamber experiments (e.g., ????). Growth chamber studies have been conducted for decades, but have only recently been synthesized (cite our paper). This synthesis reveals wide variation in sensitivity to photoperiod across species and populations.

Perhaps because of these conflicting views across both experimental and observational studies, photoperiod is often not included in forecasts of biological responses to climate change even though it is known to be an important cue for plant activity ?. The exclusion of photoperiod may be problematic because, although photoperiod itself is stable over time, the photoperiod that species *experience*, as they undergo climate change-induced shifts in space and time, is likely to be much less stable. With recent warming, many species have shifted their distributions poleward and upward in elevation (i.e., range shifts ???), and/or shifted their activity earlier in the year (i.e., phenological shifts ??). These spatial and temporal shifts will alter the photoperiod regime experienced by organisms.

The implications of potential climate-change induced shifts in experienced photoperiod are unclear, since the magnitude of potential shifts has not been described. Shifts may be relatively minor, especially because there can be substantial year-to-year background variation in experienced photoperiod (Figure ??). Alternatively, photoperiod may begin to constrain species responses to climate change (?).

Here, we ask:

1. How will climate change alter the photoperiod experienced by organisms, given observed climate change-induced biological shifts, both spatially and temporally?
2. Are photoperiod responses widespread in woody plants?
3. What are the implications of altered photoperiods for biological responses to climate change?
4. Can data from growth chamber experiments altering photoperiod be applied to forecasting biological implications of climate change (i.e., do they occur at the appropriate scale)?

We address these questions using a new database of plant growth chamber studies that manipulate photoperiod and temperature and measure plant responses, including budburst, flowering, and growth. We focus on woody species because plant growth chamber experiments using woody plant material have been conducted for decades, because the importance of photoperiod versus temperature effects on phenology remain controversial in woody species, and because forecasting effects of climate change on woody plant phenology (i.e., the length of the growing season) has critical implications for global carbon cycling and feedbacks to the climate system.

## How will climate change alter the photoperiod experienced by organisms?

Species experience different photoperiod regimes depending on their location in space and the seasonal timing of their activity. The daylength experienced by plants on spring green-up date, for example, varies with latitude (Figure ??a). This is in part because of latitudinal variation in green-up date, which occurs earlier

toward the equator and later toward the north pole, likely driven by climatic differences, and in part because of latitudinal variation in photoperiod. A general pattern of longer photoperiod at greenup toward the poles is consistent across years (Figure ??b) and greenup does not appear to occur at daylengths less than 10 hours. However, there is strong spatiotemporal variation in experienced photoperiod when differences across years (e.g., “early” versus “late” years) are considered: experienced photoperiod at greenup can vary by as much as two to three hours in the same location (Figure ??c).

Against this existing background variation, climate change is likely to cause average shifts in experienced photoperiod, as species respond to warming temperatures. Spatial shifts in species’ ranges and temporal shifts in phenology will alter the photoperiods experienced by organisms with future climate change. The magnitude of these alterations will vary depending on the organism’s location and the type of shift(s) it undergoes. For example, poleward shifts in species’ ranges cause organisms to experience a wider range of daylength throughout the year (Figure ??). Elevational shifts, on the other hand, would cause minimal changes in daylength throughout the year.

To date, most of the scientific literature has focused on how spatial range shifts linked to climate change will affect photoperiod (e.g., ??). Shifting phenology will also alter experienced photoperiod, because of the seasonal patterns of daylength (Figure ??). To understand the magnitude of change in experienced photoperiod with spatial versus temporal shifts in organisms’ activities, we compared photoperiod across latitudes and days that differed at relevant scales, given observed shifts in species’ ranges and phenology (??).

We found that temporal shifts are actually likely to yield bigger changes in experienced photoperiod than spatial shifts (Figure ??). For example, consider a tree at latitude 45° that completes spring budbursts, on average, around DOY 91 (April 2, when daylength is 12.8 hours). If its phenology shifts 30 days earlier over the next century (i.e., a rate of 3 days per decade, as has been observed), it will experience a daylength that is 1.6 hours shorter. However, if the same tree species shifts its range up in latitude 0.5° (i.e., 60 km over the next century, comparable to observed rates (??)), it will experience a daylength that differs by less than a minute on the same DOY. Growth chamber studies demonstrate that the magnitudes of daylength shifts we can expect with climate change (i.e., 1-2 hours of difference in daylength with temporal shifts over the next century) are substantial enough to affect spring phenology (Table ??).

In many cases organisms may shift both their geographic ranges and their phenology simultaneously. In addition, photoperiod sensitivity, or the degree to which phenology is controlled by daylength, can vary with latitude (?????), perhaps because of population-level differences in sensitivity. With future climate change, it is unclear how these complications will affect the photoperiod experienced by organisms and if these shifts in photoperiod will have important implications for biological responses. Part of this lack of clarity stems from the fact that phenology (e.g., the day of year that a plant bursts its buds) both affects and is affected by experienced photoperiod: climate change-induced shifts in phenology alter experienced photoperiod, which in turn affects phenology.

## Are photoperiod responses common in woody plants?

Growth chamber experiments suggest that photoperiod responses are common in woody plant species. Thirty-one of the 85 studies in the OSPREE database included two or more different photoperiod treatments. Of these, 26 (84%) found significant photoperiod main effects or significant interactive effects with temperature (Table ??). Main effects included responses such as growth (e.g., higher growth rates with longer days ?), budset (e.g., more rapid induction of budset with shorter days ?), and reproduction (e.g., increased flowering with longer days ?).

Growth chamber experiments demonstrate that, though photoperiod responses are common, they are variable (Figure ??). Responses to photoperiod commonly differ by species (e.g., ?????). For example, with long chilling treatments some species seem insensitive to daylength (e.g., Cat- could you add a sp or 2 from zohner),

whereas others (e.g. *Fagus* spp.) seem to have daylength requirements for budburst, even with long chilling treatments (?). Photoperiod sensitivity also varies by populations and ecotypes (e.g., ??). For example, photoperiod effects on budburst were more significant for lower latitude populations of *Betula pendula* and *B. pubescens* (?).

In addition to the variation among species and populations, growth chamber experiments highlight that responses to photoperiod vary within an individual depending on the temperature. For example, more rapid advancement of budburst was observed under long versus short days with low chilling, than with high chilling in *Betula papyrifera* (?).

## What are the implications of altered photoperiods for biological responses to climate change?

Daylength plays a role in controlling critical plant functions, including vegetative growth, cell elongation, budburst, and flowering (????????). Climate change-induced shifts in photoperiod are therefore likely to alter these functions. The direction and magnitude of such alterations will vary, however, because of variation in photoperiod sensitivity, and because photoperiod often interacts with other environmental drivers, such as temperature, to affect phenology.

Over the past century, spring phenology has shifted earlier in diverse woody species (?), a pattern that, to date, can be largely explained by warming temperatures. Photoperiod may eventually become a limiting factor, however, constraining the ability of species to respond to additional warming (????). Interactions between photoperiod and temperature may therefore result in muted phenological shifts, compared to what would be expected based on temperature change alone (???). If photoperiod does become limiting, the average trend of earlier phenology with warming may stop abruptly, because photoperiod sensitivity is thought to be a threshold response (Box 1).

A challenge in understanding biological responses to shifts in photoperiod is the wide range of sensitivity observed across species (???), populations (?), and ecotypes(?). Some of this variation may be explained by different combinations of ambient temperature and photoperiod, because temperature cues can override photoperiod requirements under certain conditions ( at least during growth cessation ?). In such cases, climate change induced phenological shifts may occur at different rates than past shifts with warming. However, a large portion of this variation is likely due to underlying genetic differences, because photoperiod responses are thought to be under strong genetic control ???.

Species- and population-level variation in sensitivity to photoperiod may result in altered communities as climate change progresses. For example, a species or population that is relatively insensitive to photoperiod (or whose experienced photoperiod does not approach its critical photoperiod, even with climate change) will be able to take advantage of warmer springs by having an earlier start to its growing season. Such species (or populations) may therefore be able to outcompete slower growing ones that are limited by photoperiod and thus not able to take advantage of longer growing season conditions. In this way, sensitivity to photoperiod could act as a critical filter that alters plant communities with future climate change.

## Future directions: outstanding questions and incorporating photoperiod into forecasting

Methods for incorporating photoperiod into forecasting future phenology would be incredibly useful, especially since future rates of phenological shifts are unlikely to be a straightforward extrapolation from current and past rates and because phenological shifts may result in altered communities of species. Approaches for including

photoperiod into forecasts can be grouped into two broad categories: statistical models and process-based models. These two modelling extremes differ in at least two ways, in terms of relating plant phenology to climate change. First, statistical models generally assume linear relationships between species' responses and environmental variables (e.g., OTHER EXAMPLES ?), whereas process-based models incorporate nonlinear threshold relationships as well (e.g. ??). Second, statistical models of phenology under climate change have typically ignored photoperiod, focusing instead on seasonal or annual temperature, whereas process-based models are more likely to incorporate photoperiod, along with forcing and chilling. The challenge of process-based models is that they require detailed data (e.g., daily climate data, nonlinear biological responses). Perhaps because of this challenge, statistical models remain more commonly used in climate change forecasts of biological responses (e.g., ?).

Whether statistical or process-based approaches are used, future modelling can incorporate photoperiod by leveraging the large amount of experimental data on photoperiod responses (Figure ??, Table ??). Researchers can use these data to first learn if their species (or a closely related species) shows a photoperiod effect, what its critical photoperiod is, and, ideally, how it varies by population, ecotype, or other factors. If there is evidence of a photoperiod response, daylength should be added to forecasting models, using the critical photoperiod to define short-day and long-day conditions (Figure ??). Given the large change in experienced photoperiod with temporal shifts (Figure ??), this may be particularly important for phenology forecasting. Since spatial shifts are associated with smaller changes in experienced photoperiod, it may be less important for distribution forecasts. That being said, species are likely to shift in *both* space and time simultaneously. Thus, even though experienced photoperiod changes little as species distributions shift in space, phenology may be altered significantly, and have cascading effects on plant growth and fitness(?).

In many cases, experimental data can be immediately used in forecasting because experiments manipulate photoperiod at relevant scales (e.g., ??, Figures ??, ??, Table ??). The available data can facilitate identifying critical photoperiod levels and variations in critical photoperiod across species, and/or populations (Figure ??). Adding photoperiod and variable responses to it to forecasts could fundamentally alter the future species and communities we expect, as discussed above.

In other cases, attempting to incorporate photoperiod into forecasts of future phenology will highlight that there is a great need to better understand many aspects of photoperiod responses. Thus, modelling efforts may inspire additional experiments to test some of the critical predictions and assumptions that they make, and address outstanding questions in the field. Through the process of incorporating experimental data into more process-based models, it is likely that knowledge gaps will be identified. For example, many experiments manipulate photoperiod much more dramatically than will occur with climate change (Figures ??, ??,??). Although these studies are useful for understanding mechanistically how photoperiod responses work, extrapolating these findings to climate change models may be difficult.

Additional areas of further research to improve our understanding of the effects of shifts in photoperiod with climate change include:

1. How does photoperiod act as a cue? The divergent effects of photoperiod observed across studies (e.g., Figure ??) suggests that photoperiod interacts with other environmental drivers, such as chilling and forcing, to affect phenology and other activities. However, exactly how it interacts with temperature to initiate budburst, as well as the type of response it elicits (e.g., linear versus threshold) and population- and species-specific critical photoperiods, are not well-defined for many species.
2. Are there predictable mechanistic patterns in variation of photoperiod responses across species and populations? What traits are associated with photoperiod sensitivity and does this variation have a strong genetic component? If so, are species or populations from some locations more likely than others to be constrained by photoperiod in their responses to climate change?
3. How inaccurate are current forecasts of biological responses to climate change, given that photoperiod not fully integrated into forecasts? Photoperiod is incorporated into forecasts, along with other variables such as evaporative demand, and

temperature, in many ecosystem models (e.g. ED ??), but is rarely included in species distribution models. The sensitivity of model outcomes to assumptions made about photoperiod, critical photoperiod, and photoperiod responses needs further study, for example, across ecosystems, species, and populations.

## Conclusions

Organisms may undergo large changes to the photoperiod they experience, with climate change, even if they do not shift their ranges spatially. Here, we have focused on how an altered photoperiod will affect woody plant budburst. Shifts in photoperiod with climate change are likely to have implications for a variety of plant and animal responses, given that daylength affects critical activities for diverse species from insects (??) and salmon (??) to birds (?) and marsupials (??). Incorporating photoperiod into forecasting of climate change responses may improve model accuracy, and is likely to highlight additional experiments needed to improve our mechanistic understanding of photoperiod as a cue to diverse biological responses.

## Glossary

- chilling: a required amount hours or days of cold temperature, defined by a specific critical temperature (e.g., 0 °C- or what is most common?), that must be experienced for budburst to occur.
- daylength: the period of time during a 24-hour period during which an organism receives light.
- ecodormancy: dormancy (e.g., halted or reduced growth) brought about by external conditions, such as cold temperatures or drought conditions.
- endodormancy: dormancy brought about by internal (rather than environmental) conditions.
- forcing: required amount of hours or days above some specific critical temperatures, that must be experienced before budburst or flowering can occur.
- external coincidence model: a model for how light sensing occurs in plants, first proposed by German biology Erwin Bünning; it proposes the existence of a circadian rhythm of photoperiodic photosensitivity in which the night-phase is sensitive to light and the day-phase is insensitive to light.
- vernalization: exposure of plants or seeds to low temperatures, often in order to stimulate flowering or to enhance seed production; analogous to chilling.
- photoperiod: the daily duration of light (daylength) and dark to which an organism is exposed; often used synonymously with daylength.
- critical photoperiod: the length of day that causes an individual to switch from a long- to a short-day response (or vice versa).
- photoperiodism: the ability to assess the length of day or night to regulate behaviour, physiology, growth, development or reproduction.

## 1 Box 1. Dominant models of how photoperiod affects spring phenology

Here we focus on spring budburst in woody plants, which is thought to be controlled by three main cues: chilling, forcing, and photoperiod, as well as interactions between them (???). However, our understanding

of how plants interpret photoperiod comes largely from studies of flowering in the model plant *Arabidopsis thaliana* (citations) and budset in woody plant species (?) (add more citations). Budburst phenology in woody plants may sense photoperiod through similar pathways, though this is not known (?) (other citations comparing Populus to Arabidopsis?).

Plants are thought to interpret photoperiod through a coordinated response to light in relation to the time of day. When the internal circadian rhythm coincides with an external signal (light) under certain conditions, the response is induced (?). This “external coincidence model” has been most widely studied in *Arabidopsis*, and is thought to be a relevant mechanism for photoperiod responses in diverse perennial and woody plant species as well (??????). (add Bunning 1936). The model proposes the existence of a circadian rhythm of light sensitivity, in which the night-phase is sensitive to light and the day-phase is insensitive to light. As days get longer in the spring, daylight illuminates the light sensitive phase, triggering a response.

Other things to consider adding to this box:

1. what parts of the Arabidopsis photoperiod sensing mechanism is maintained in Populus or other woody species?
2. what part of wood plants senses light (phytochrome, particular tissues- buds)
3. talk about photoperiod as a gate keeper to other cues and responses?

## To do:

1. Update table/map to fix 2 studies have a max NA and a min NA- these look reasonable so add them with an \*
2. Make lines thicker/darker in Figure 2 (looks a bit washed out)
3. Work Figures 5 and 6 more explicitly into the paper

## Tables



Table 1: **Growth chamber experiments and their photoperiod treatments.** We note whether or not photoperiod had a significant effect (‘effect’ column) and compared treatments to the spatial and temporal shifts required for organisms to experiments photoperiod changes equivalent to those treatments. For shifts in space, ‘ER’ indicates that the photoperiod treatments exceeds the change of photoperiod from moving up to 40 degrees latitudinally on June 21. For shifts in time, ‘ER’ indicates that the range of photoperiod treatments exceeds the change in daylengths at that latitude during the entire year. ‘max NA’ indicates that the maximum daylength treatment does not exist at that latitude; ‘min NA’ indicates that the minimum daylength treatment does not exist at that latitude.

idstudy	continent	lat	long	effect	day_range	delta	space	time
ashby62_exp1	north america	42.99	-89.41	Y	8-16	4.00	18.2	min NA (9)
basler14_exp1	europe	46.31	8.27	Y	9.2-16	1.00	6	-22
caffarra11b_exp2	europe	52.32	-6.93	Y	10-16	2.00	7.5	-30
falusi90_exp1	europe	46.03	10.75	N	9-13	4.00	16	-82
falusi96_exp3	europe	38.27	15.99	Y	9-13	4.00	21.6	-111
ghelardini10_exp1	europe	43.72	11.37	N	8-16	8.00	21.9	ER
heide05_exp1	europe	56.18	-4.32	Y/N	10-24	14.00	ER	ER
heide08_exp1	europe	48.40	11.72	Y	10-24	14.00	ER	ER
heide11_exp1	europe	59.67	10.67	N	10-20	10.00	ER	max NA (18.7)
heide12_exp1	europe	56.50	-3.06	Y	10-24	5.00	8.9	-64
heide15_exp2	europe	56.50	-3.06	Y	10-15	1.00	3.2	-13
heide93_exp1	europe	59.50	10.77	Y	8-24	16.00	ER	ER
heide93a_exp1	europe	59.67	10.83	Y	8-24	16.00	ER	ER
heide93a_exp3	europe	47.50	7.60	Y	13-16	1.00	5.7	-18
howe95_exp1	north america	40.55	-124.10	Y	9-24	2.00	13.1	-64
laube14a_exp1	europe	48.40	11.71	N	8-16	4.00	14.3	-87
myking95_exp1	europe	56.10	9.15	Y	8-24	16.00	ER	ER
nienstaedt66_exp1	north america	44.17	-103.92	Y	8-20	12.00	ER	ER
okie11_exp1	north america	32.12	-83.12	Y	0-12	12.00	ER	ER
partanen01_exp1	europe	61.93	26.68	Y	6-16	10.00	ER	-105
partanen05_exp1	europe	61.82	29.32	Y	5-20	5.00	ER	-67
partanen98_exp1	europe	60.03	23.05	Y	8.66-12	3.34	5.1	-37
pettersen71_exp1	europe	59.66	10.77	N	10-24	2.00	4	-23
Sanz-Perez09_exp1	europe	40.40	-3.48	Y	10-16	6.00	23.6	ER
viheraaarnio06_exp1	europe	60.45	24.93	Y	16-17	1.00	2.1	-12
viheraaarnio06_exp1	europe	67.73	24.93	Y	20-21	1.00	ER	-5
viheraaarnio06_exp2	europe	60.45	24.93	Y	15-19	4.00	5.1	-62
viheraaarnio06_exp2	europe	67.73	24.93	Y	22-23	1.00	ER	-3
worrall67_exp 3	north america	41.31	-72.93	Y	8-16	8.00	24.3	ER
zohner16_Exp1	europe	48.16	11.50	Y	8-16	8.00	ER	ER
hawkins12_				Y				

## Figures



Figure 1: **Plant responses to changes in daylength vary across species and populations, and with the amount of chilling received.**



/Users/aileneettinger/Documents/GitHub/osprey/docs/photoperiod/figures/Greenup\_corr.pdf

Figure 2: **The photoperiod on the green up date (start of spring) varies over space** and among years. Hours of daylight on the date of spring green up from MODIS satellite data across North America and Europe for an average (2009, a) and early (2012,b) North American start of spring. The differences between the years are shown in (c).



Figure 3: **Photoperiod varies with latitude and throughout the year**, such that temporal shifts in activity yield larger changes in experienced photoperiod compared with spatial shifts. Here, we show this variation at two latitudes, using hypothetical rates of spatial and temporal shifts: 30 days earlier for temporal shifts, and 0.5 degrees poleward for spatial shifts. These shifts, which are similar to observed average rates (e.g., ??), highlight the greater magnitude in daylength changes close to the equinox (e.g., DOY 91), versus close to the summer solstice (e.g., DOY 182).



/Users/aileneettinger/Documents/GitHub/ospree/analyses/photoperiod/figures/ospree\_photopmap.pdf

Figure 4: **OSPREE experiments that manipulate photoperiod**, and their equivalent spatial and temporal shifts, mapped (A), and graphed (B-C). Observed rates (dashed gray lines) 16.9 kilometers per decade (or approximately 1.5 degrees in 100 years) for spatial shifts (Chen et al. 2011) and 2.3 days per decade (or 23 days in 100 years) for temporal shifts (Parmesan and Yohe 2003).

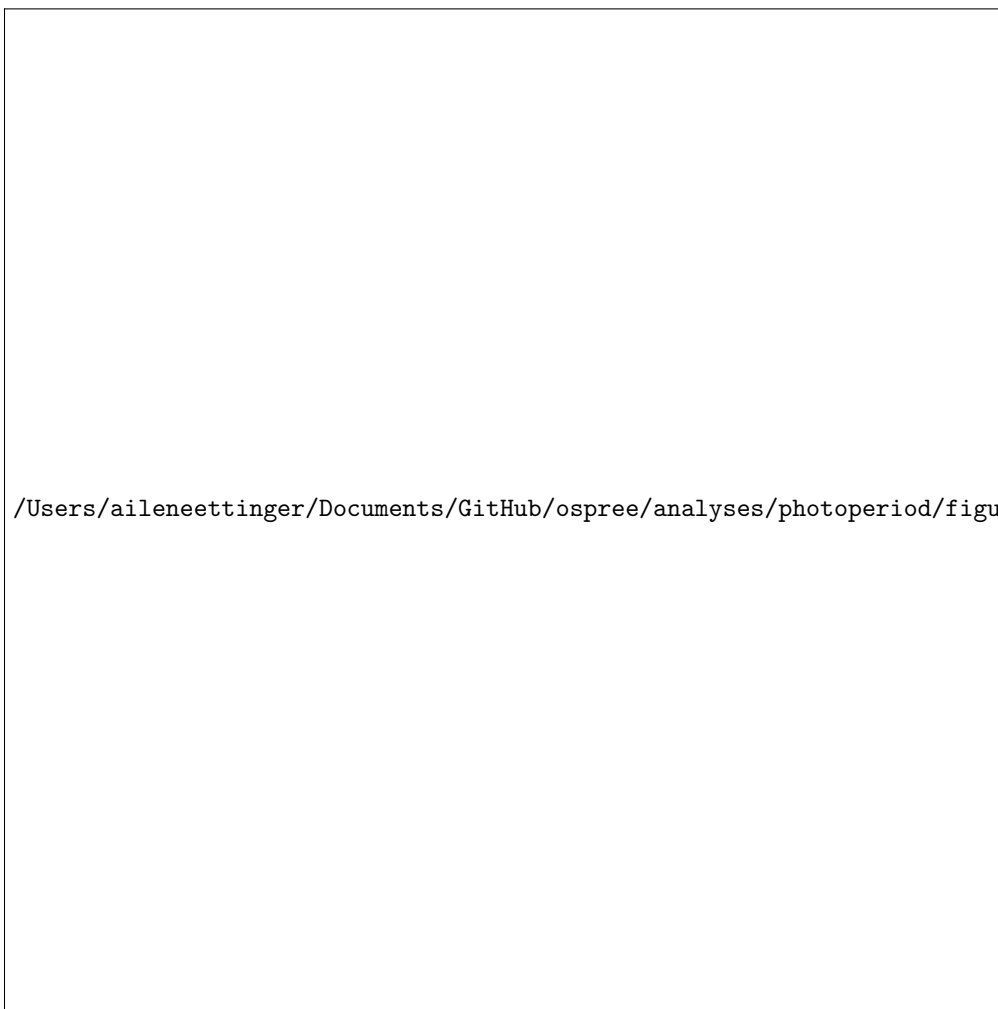


Figure 5: **Experimental treatments of daylength in the OSPREE database** for *Fagus sylvatica* (A) and *Quercus robur* (B). For comparison, we show the daylength when budburst occurs in its current and projected ranges (left panels) and in its current range only, with expected shifts in phenology (right panels). Estimates and projections are from Phenofit (?)



/Users/aileneettinger/Documents/GitHub/osprey/analyses/photoperiod/figures/photocondiag6.pdf

**Figure 6: Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change.**