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 and fall senescence, as well as spatial shifts in species' distributions. These 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, so additional testing of the importance of photoperiod to phenology and adding it to forecasts of biological shifts should be major goals. We find that, though many experiments impose photoperiod treatments well outside current and expected future conditions, there is a substantial resource of studies 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 phenology.

Introduction

Photoperiod is a critical cue for plants, signalling changes to their activities, such as photosynthesis, growth, reproduction, dormancy, and senescence (e.g., Howe et al., 1996; Lagercrantz, 2009). Photoperiod is used by plants to synchronize their activities with seasonal climatic changes (e.g., Hsu et al., 2011; Singh et al., 2017; Basler and Körner, 2012) because it is consistent across years, especially compared to other seasonal cues such as temperature and precipitation (Saikkonen et al., 2012). For example, relying on photoperiod, rather than temperature alone, may prevent plants from leafing out during "false spring" events (unusually warm periods during winter that are followed by a return of cold temperatures Gu et al., 2008))).

We know that photoperiod is an important cue for spring budburst phenology, largely through growth chamber experiments. 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 break dormancy within the bud; 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., Campbell and Sugano, 1975; HEIDE, 1977; Falusi and Calamassi, 1990; Spann et al., 2004; Laube et al., 2014). 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.

Recent studies offer conflicting evidence about the extent to which photoperiod may control spring phenology in a warmer world. Some studies suggest that certain species, such as late successional taxa, will be unable

to track climate warming, i.e., by leafing out earlier in the spring and senescing later in the fall (Koerner and Basler, 2010) (Any Other studies with similar ideas?). Instead, these species will increasingly become constrained by daylength, since photoperdio sensitivity is primarily genetically controlled (Koerner and Basler, 2010). Other studies, however, suggest that photoperiod is unlikely to constrain responses to warming for most species (Zohner et al., 2016) (others?).

Perhaps because of these conflicting views, photoperiod is often not included in forecasts of biological responses to climate change even though it is known to be an important cue for platn activity Duputié et al. (but see 2015). 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 Parmesan, 2006; Chen et al., 2011; Harsch et al., 2009))), and/or shifted their activity earlier in the year (i.e., phenological shifts Parmesan, 2006; Wolkovich et al., 2012). 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 2). Alternatively, photoperiod may begin to constrain species responses to climate change (Koerner and Basler, 2010).

Here, we ask:

1. Do results from growth chamber experiments suggest that photoperiod responses are widespread in woody plants?

2. How will climate change alter the photoperiod experienced by organisms, given observed climate change-induced biological shifts, both spatially and temporally?

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 for 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.

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 1). Main effects included responses such as growth (e.g., higher growth rates with longer days Ashby et al., 1962), onset of dormancy (e.g., more rapid induction of budset with shorter days Howe et al., 1995), and reproduction (e.g., increased flowering with longer days Heide and Sønsteby, 2012).

Growth chamber experiments demonstrate that, though photoperiod responses are common, they are variable (Figure 1). Responses to photoperiod commonly differ by species (e.g., Heide, 1993; Howe et al., 1996; Basler

and Körner, 2012, 2014; Zohner et al., 2016; Flynn and Wolkovich, 2018). 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 to break dormancy, even with long chilling treatments (Zohner et al., 2016). Photoperiod sensitivity also varies by populations and ecotypes (e.g., Partanen et al., 2005; Flynn and Wolkovich, 2018). For example, photoperiod effects on budburst were more significant for lower latitude populations of *Betula pendula* and *B. pubescens* (Partanen et al., 2005).

In addition to the variation among species and populations, growth chamber experiments highlight that responses to photoperiod vary 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 (Hawkins and Dhar, 2012).

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 2a). This is in part because of latitudinal variation in both photoperiod and green-up date, which occurrs earlier toward the equator and later toward the poles. Athough the general pattern is consistent across years (Figure 2b), there is strong spatiotemporal variation in experienced photoperiod (Figure 2c).

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 3). 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 (Saikkonen et al., 2012) (other citations?). Shifting phenology will also alter experienced photoperiod, because of the seasonal patterns of daylength (Figure 3). To understand the magnitude of change in experienced photoperiod with spatial versus temporal shifts in organisms activity, we compared photoperiods across latitudes and days that differed at relevant scales, given observed shifts in species' ranges and phenology (Parmesan and Yohe, 2003; Chen et al., 2011).

We found that temporal shifts are actually likely to yield bigger changes in experienced photoperiod than spatial shifts (Figure 3). 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 (Parmesan and Yohe, 2003, 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 (Parmesan and Yohe, 2003; Chen et al., 2011)), it will experience a daylength that differs by less than a minute on the same DOY. Importantly, growth chamber studies demonstrate that the magnitudes of daylength shifts we can expect with climate change (i.e. 1-2 hours difference in daylength with temporal shifts over the next century) are substantial enough to alter phenology(cite new 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 (Howe et al., 1996; Saikkonen et al., 2012; Partanen et al., 2005; Viherä-Aarnio et al., 2006; Caffarra et al., 2011; Gauzere et al., 2017), 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.

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

Daylength plays a role in controling critical plant functions, including vegetative growth, cell elongation, budburst, and flowering (Linkosalo and Lechowicz, 2006; Erwin, 1998; Sidaway-Lee et al., 2010; Hsu et al., 2011; Heide, 2011; Ashby et al., 1962; Heide and Sønsteby, 2012; Mimura and Aitken, 2007). 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, budburst has shifted earlier in diverse woody species (CITES), 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 (Koerner and Basler, 2010; Vitasse and Basler, 2013; Morin et al., 2010; Nienstaedt, 1966). Interactions between photoperiod and temperature may therefore result in muted phenological shifts, compared to what would be expected based on temperature change alone (Wareing, 1956; Mimura and Aitken, 2007; Koerner and Basler, 2010). If photoperiod does becomes limiting, phenology may shift abruptly, not gradually, because photoperiod sensitivity is thought to be a theshold response (Box 1).

A challenge in understanding biological responses to shifts in photoperiod is the wide range of sensitivity observed across species (Sanz-Perez et al., 2009; Zohner et al., 2016; Flynn and Wolkovich, 2018), populations (Tanino et al., 2010), and ecotypes(Howe et al., 1995). Some of this variation is likely due to underlying genetic differences, because photoperiod responses are thought to be under strong genetic control Bradshaw and Stettler (1995); Weih (2004); Keller et al. (2011). This variation may also be explained by different combinations of ambient temperature and photoperiod, because temperature cues can override photoperiod requirements under certain conditions (e.g., during growth cessation Tanino et al., 2010). In such cases, climate change induced phenological shifts may occur at different rates than past shifts with warming.

Future rates of phenological shifts are unlikely to be a straightforward extrapolation from current and past rates. Predicting future shifts is further complicated by the spatial and temporal variation in experienced photoperiod, and by varying sensitivity to photoperiod across species and populations. Methods for incoporating photoperiod into forecasting future phenology and other biological responses would therefore be incredibly useful.

Future directions: outstanding questions and incorporating photoperiod into forecasting

Approaches to forecasting biological responses to climate change 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.,), whereas process-based models incorporate nonlinear/threshold relationships as well (e.g., PhenoFit). Second, statistical models of phenology under climate change have typically ignored photoperiod and focus instead on seasonal or annual temperature,whereas process-based models are more likely to incorporate photoperiod, along with forcing and chilling, accumulated daily. The challenge of process-based models is that they often 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 (I think this is true, but need data/citation to back this up!).

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 4, Table 1). Researchers can use these data to first learn if their species (or a closely related species) shows a photoperiod effect, and, ideally, how it varies by population, ecotype, or other factors. If there is evidence of a photoperiod response, as for many species, daylength should be added to forecasting models (Figure 6).

In many cases, experimental data can be immediately used in forecasting because experiments manipulate photoperiod at relevant scales (e.g., Basler and Körner (2014); Heide and Sonsteby (2015), Figures 4, 5, Table 1). The available data can inform critical non-linearities and variations across species, and/or populations (Figure 6. Adding photoperiod and variable responses to forecasts could fundamentally alter the future species and communities we expect.

Models ideally will then guide 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 knowlege gaps will be identified. For example, many experiments manipulate photoperiod much more dramatically than will occur with climate change (Figures 4, 5,**??**. Extrapolating these findings with models may be difficult.

Even the excercize of thinking about how to incorporate photoperiod into forecasts of future phenology higlights that there is a great need to better understand many aspects of photoperiod and photoperiod responses. Some areas of further research include:

1. How does photoperiod act as a cue? The divergent effects of photoperiod observed across studies (e.g., Figure 1) 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 break dormancy, as well as the type of response it ellicits (e.g., linear versus threshold) is not well-defined for many species.

2. What are the causes and consequences of species- and population-level variation in photoperiod sensitivy? For example, 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 climte change?

3. Does incorporating photoperiod responses alter forecasting outcomes, at population, commnity, and ecosystem scales? Photoperiod is incorporated into foreacasts, along with other variables such as evaporative demand, and temperature, in many ecosytem models (e.g. ED Jolly et al., 2005; Medvigy et al., 2013). The sensitivity of model outcomes to assumptions made about photoperiod and photoperiod responses should be more widely tested, e.g. in different ecosystems, and across different species and populations.

4. How much does model accuracy (process-based or statistical) improve when we include photoperiod responses and changes in photoperiod, in addition to forecasted temperature shifts?

Conclusions

Organisms may undergo large changes to the photoperiod they experience, with climate change, even if they do not shift their ranges spatially. An altered photoperiod is likely to have implications for a variety of plant responses, as well as responses in animals and other organisms, given the diverse species for which daylength affects activities (e.g., Taranger et al., 2003; Bradshaw and Holzapfel, 2006; Mcallan et al., 2006; Linn et al.,

1996; **?**; Solbakken et al., 1994). 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

1. * <u>chilling</u>: 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 to break dormancy

2. * <u>endodormancy</u>

3. * <u>ectodormancy</u>

4. * <u>forcing</u>: arequired amount of hours or days above some specific critical temperatures, that must be experienced before budburst or flowering can occur.

5. * <u>vernalization</u>

1   Box 1. How do plants interpret photoperiod?

Here we focus on spring budburst responses to photoperiod. However, our understanding of how plants interpet photoperiod comes largely from studies of flowering in the model plant *Arabidopsis thaliana* and budset in woody plant species. Budburst phenology is assumed (thought?) to sense photoperiod through similar pathways, though this is not known.

Plants interpret photoperiod through a coordinated response to light in relation to the time of day. The "external coincidence model," which has been widely studied in *Arabidopsis*, is thought to be a relevant mechanism for photoperiod responses in diverse perennial and woody plant species as well (Davis, 2002; Petterle et al., 2013; Bastow and Dean, 2002; Kobayashi and Weigel, 2007; Andrés and Coupland, 2012; Singh et al., 2017). (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.

if it is its own box, need to add to this something about arabidopsis model versus populalus or other woody species and how much is transferable

questions to address by looking at literature:

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 (buds?)

3. look at papers on budset and photoperiod

4. add something about how there is a lot of photoperiod research done for other phenophases

5. talk about circadian rhythm and gate keeper instead of external coincidence model (but mention this term in the glossery)

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

4. Add a box for are external coincidence model (i.e. that responses to photoperiod are nonlinear) Also, we can see this in Figure 1 .

Random notes that may be useful to work in somewhere:

1. Bradshaw and Holzapfel (2001) showed that the pitcher plant mosquito, Wyeomyia smithii, has evolved a shorter critical photoperiod in association with a longer growing season. Northern populations of this mosquito now use a shorter day-length cue to enter winter diapause, doing so later in the fall than they did 24 years ago.

2. Decreasing day-length is the main environmental cue inducing growth cessation and bud set in many perennial plants, including poplar

   (a) Lagercrantz U: At the end of the day: a common molecular mechanism for photoperiod responses in plants?. J Exp Bot. 2009, 60: 2501-2515. 10.1093/jxb/erp139. (lagercrantz2009

   (b) Howe GT, Gardner G, Hackett WP, Furnier GR: Phytochrome control of short-day-induced bud set in black cottonwood. Physiol Plant. 1996, 97: 95-103. 10.1111/j.1399-3054.1996.tb00484.x. (Howe: 1996)

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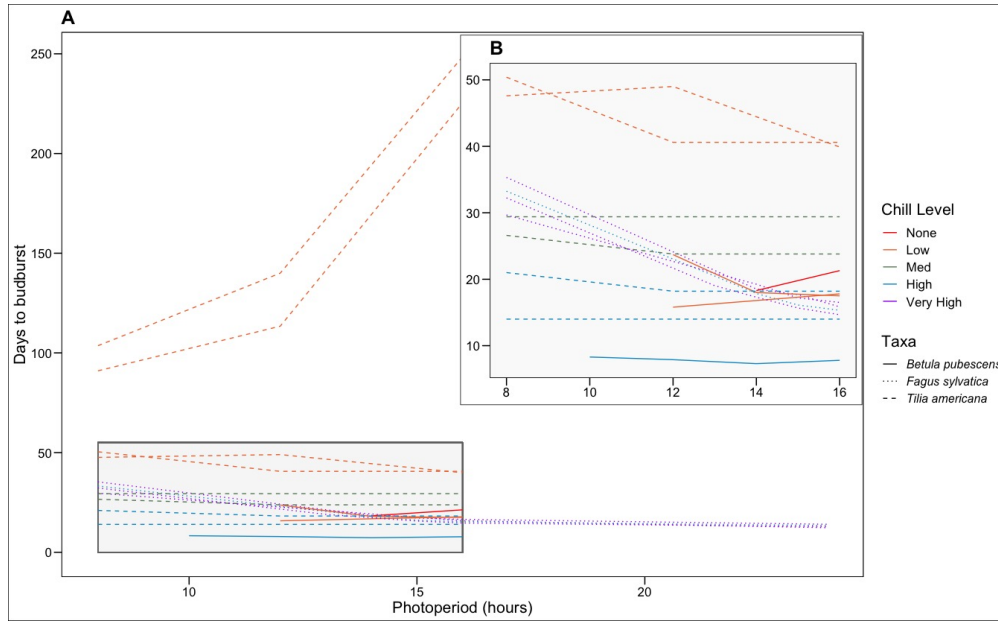
Figure 1: **Plant responses to changes in daylength vary across species and populations, and with the amount of chilling recieved**.
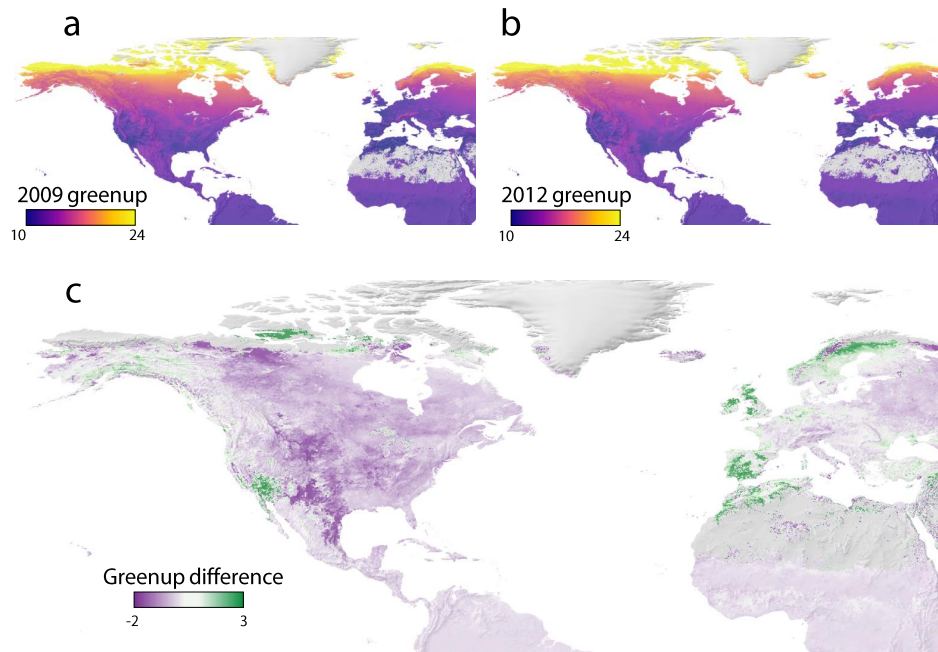

Figure 2: **The photoperiod on the green up date (start of spring) varies over space** and among years. Hours of daylight on the date of spring green up from MODIS satilite data across North America and Europe for an average (2009, a) and early (2012,b) North American start of spring. The differences between the years are shown in (c).
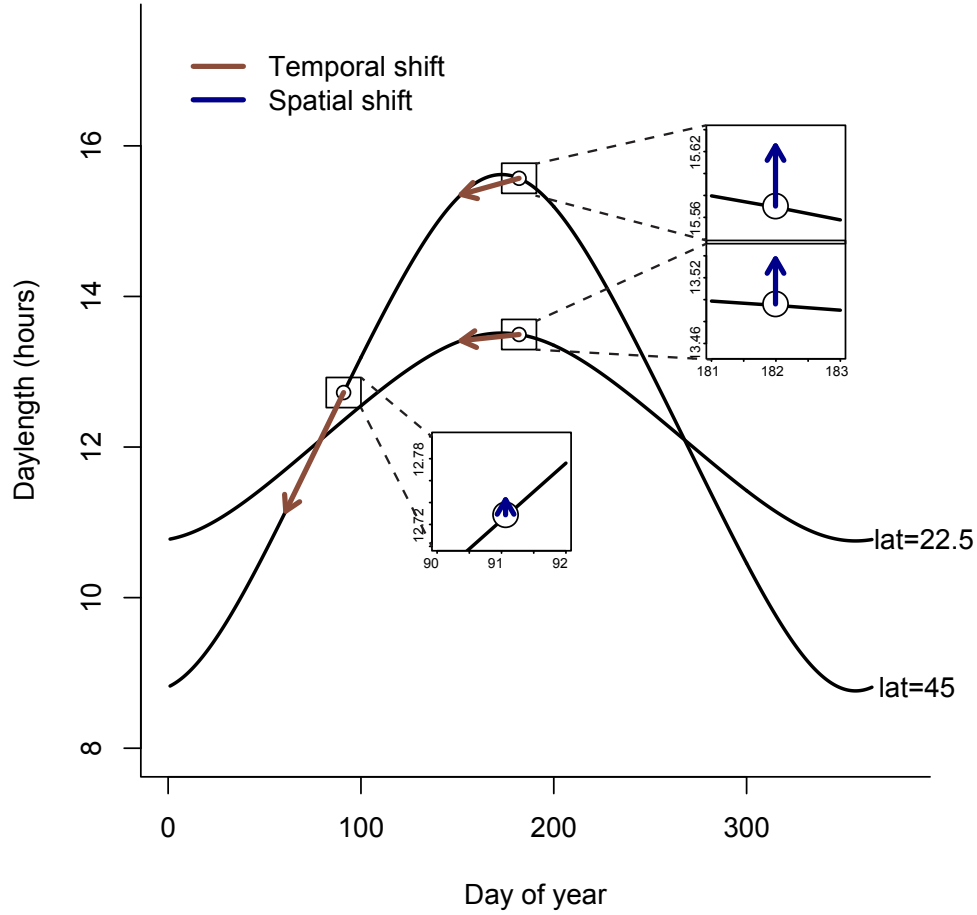
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Figure 3: **Photoperiod varies with latitude and throughout the year**, such that temporal shifts in activity yield larger changes in experienced photoperiod compared with spatial shifts. Here, we show this variation at two latitudes, using hypothetical 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., Parmesan, 2006; Chen et al., 2011), highlight the greater magnitude in daylength changes close to the equinox (e.g., DOY 91), versus close to the summer solcstice (e.g., DOY 182).
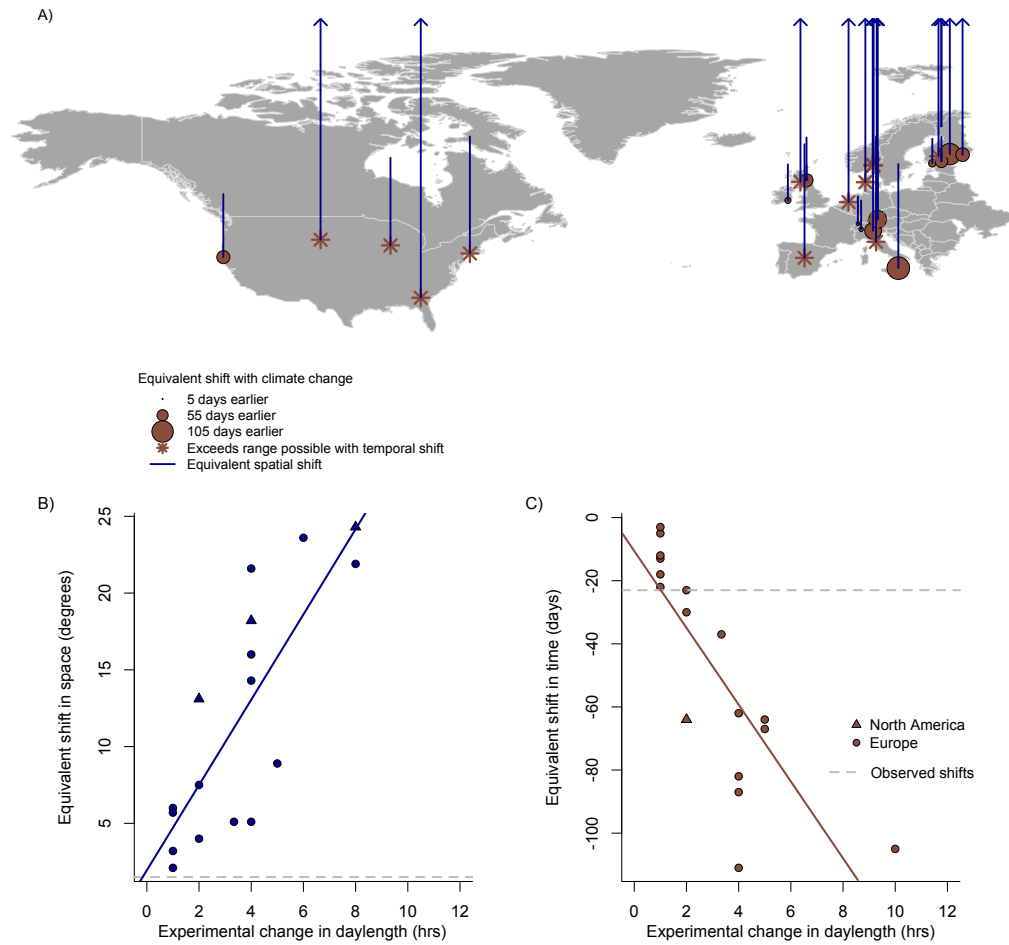
Figure 4: **OSPREE experiments that manipulate photoperiod**, and their equivalent spatial and temporal shifts, mapped (A), and graphed (B-C). Observed rates (dashed gray lines) 16.9 kilometers per decade (or approximately 1.5 degrees in 100 years) for spatial shifts (Chen et al. 2011) and 2.3 days per decade (or 23 days in 100 years) for temporal shifts (Parmesan and Yohe 2003).
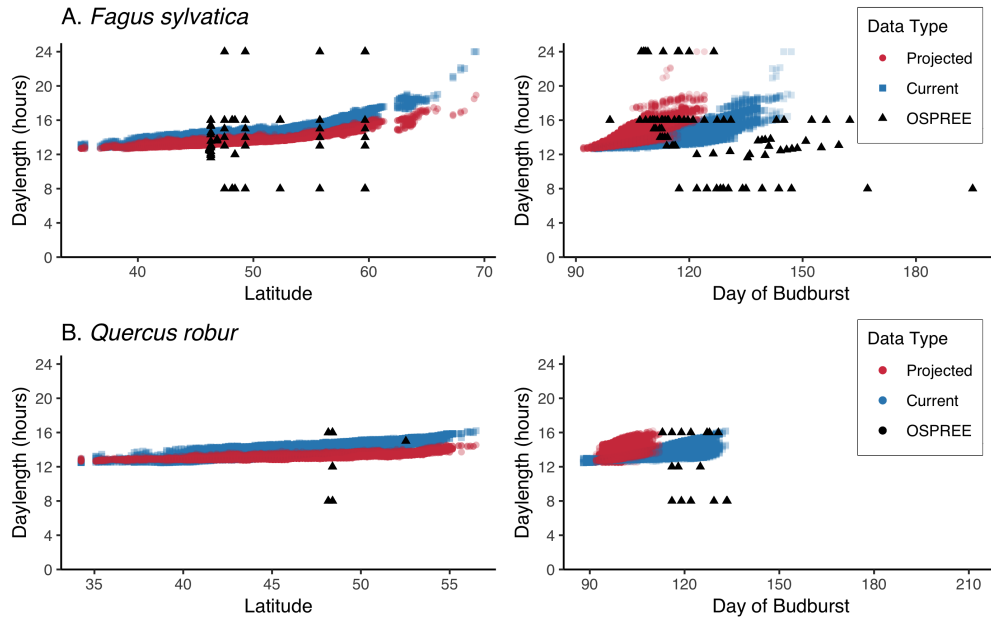
Figure 5: **Experimental treatments of daylength in the OSPREE database** for *Fagus sylvatica* (A) and *Quercus robur* (B). For comparison, we show the daylength when budburst occurs in its current and projected ranges (left panels) and in its current range only, with expected shifts in phenology (right panels). Estimates and projections are from Phenofit (Duputié et al., 2015)
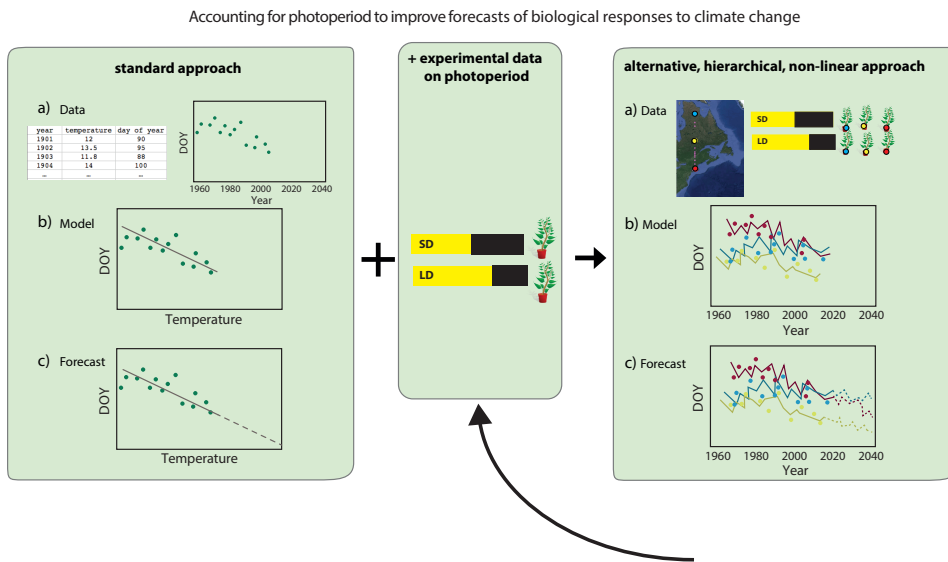

Figure 6: **Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change**.