

Spatial and temporal shifts in photoperiod with climate change

A.K. Ettinger, D. Buonaiuto, C. Chamberlain, I. Morales-Castilla, E. Wolkovich

May 14, 2019

Summary

Climate change drives species to undergo both temporal and geographic shifts that affect the daylength that they experience. Although photoperiod is a common trigger of seasonal biological responses (e.g., effects in 84% of studies that manipulated photoperiod in woody plant species), it has not been a focus of climate change forecasting to date. Here we address the potential for current knowledge and data to incorporate photoperiod into attempts at forecasting the spatial-temporal distribution of biodiversity. Impacts on experienced photoperiod due to temporal shifts will be orders of magnitude larger than impacts due to spatial shifts. We find that, for woody plant spring phenology, 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. Finally, 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 some 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 (Bradley et al., 1999; Parmesan and Yohe, 2003; Root et al., 2003) or 1.3 to 5.6 days earlier per °C of warming (Wolkovich et al., 2012; Polgar et al., 2013). Indeed, early spring phenology is shifting more rapidly than later season phenology in many cases (Bradley et al., 1999; Menzel et al., 2006), 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., Howe et al., 1996; Flynn and Wolkovich, 2018; Solbakken et al., 1994; Mcallan et al., 2006; Lagercrantz, 2009). Photoperiod is used to synchronize 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 woody 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).

Recent studies offer inconsistent views about whether photoperiod may eventually restrict spring phenology in a warmer world. Some studies suggest that with additional warming, photoperiod will limit phenology and certain species will be unable to track rising temperatures, e.g., by leafing out earlier in the spring (Koerner

and Basler, 2010; Way and Montgomery, 2015). Instead, these species will increasingly become constrained by daylength, since photoperiod sensitivity is primarily genetically controlled (Bradshaw and Holzapfel, 2008). Other studies, however, suggest that photoperiod is unlikely to constrain responses to warming for most species (Zohner et al., 2016; Chuine et al., 2010).

Perhaps because of these variable responses photoperiod is often not included in forecasts of biological responses to climate change, even though it is known to be an important cue for biological activity (but see Duputié et al., 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; Peñuelas and Boada, 2003)), 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 (Figure 1). Altered photoperiods may have cascading effects on species' performance, since daylength can affect development time (?), migration timing (?), and other critical responses.

The implications of potential climate-change induced shifts in experienced photoperiod are unclear, since the magnitude of potential shifts has not been described. Effects of photoperiod shifts may be relatively minor, especially because there can be substantial year-to-year 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. 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 experiments altering photoperiod be applied to forecasting biological implications of climate change?

These questions are broadly relevant for diverse species. We use a case study of woody plant spring phenology to illustrate our points (Box 1). Woody species are a useful focal group 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 plants, 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 (Richardson et al., 2013). We use studies included in OSPREE, a new database of plant growth chamber studies that manipulate photoperiod and temperature to measure plant phenology responses, including budburst and flowering (cite OSPREE database on knb).

How will climate change alter the photoperiod experienced by organisms?

Species experience different photoperiod regimes depending on their location on Earth, the seasonal timing of their activity, and with inter-annual variation in climate. 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 green-up date, which occurs earlier toward the equator and later toward the north pole, strongly driven by climatic differences that affect phenology, and in part because of latitudinal variation in photoperiod (e.g., at the north pole, the daylength at the summer solstice is 24 hours). A general pattern of longer photoperiod at green-up toward the poles is consistent across years (Figure 2b) and green-up 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., years with “early” versus “late” green-up) are considered (Figure 2c). Experienced photoperiod at green-up can vary by as much as two to three hours, across years, in the same location (Figure 2c). Though green-up date corresponds to plant phenology, we expect that spatiotemporal patterns of variation in spring phenology would be similar for other organisms (??).

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 1). Elevational shifts, on the other hand, would cause minimal changes in the range of 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., Saikkonen et al., 2012; Way and Montgomery, 2015). Shifting phenology will also alter experienced photoperiod, because of the seasonal patterns of daylength (Figure 1). To understand the magnitude of change in experienced photoperiod with spatial versus temporal shifts in organisms’ activities, we compared photoperiod across latitudes and dates that differed at relevant scales, given observed shifts in species’ ranges and phenology (Parmesan and Yohe, 2003; Chen et al., 2011).

Despite a focus on range shifts, current data suggest that temporal shifts are likely to yield much bigger changes in experienced photoperiod than spatial shifts (Figure 1). For example, consider an insect at latitude 45° that emerges from diapause, 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. (This 1.6 hour decrease in daylength is equivalent to moving up 28.5° in latitude on this day of year.) However, if the same insect 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. 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 in trees (Table S1).

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. Part of this lack of clarity stems from the fact that phenology (e.g., the day of year that an 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.

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

Daylength can play a role in controlling critical biological functions, including vegetative growth, cell elongation, budburst, and flowering in plants (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) and growth rate, maturation, and diapause in animals (Bradshaw and Holzapfel, 2006; ?; ?). 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 (Box 1, ?).

Over the past century, spring phenology has shifted earlier in diverse species (Menzel, 2000; ?; ?; Polgar et al., 2013), a pattern that, to date, can be largely explained by warming spring 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 become limiting, the average trend of earlier phenology with warming may stop abruptly, because photoperiod sensitivity is thought to be a threshold response, for plants (Box S1) and animals (??). This may in turn affect performance under climate change, since the ability to advance phenology with warming has been linked with increased growth, abundance, and fitness (?Cleland et al., 2012; Willis et al., 2010).

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 may be explained by different combinations of ambient temperature and photoperiod, because temperature cues can override photoperiod requirements under certain conditions (e.g., Tanino et al., 2010). In such cases, climate change induced phenological shifts may occur at different rates than past shifts with warming. However, 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)).

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 or later emerging ones that are limited by photoperiod and thus not able to take advantage of longer growing season conditions. To identify where, when, and how communities may be altered, methods for incorporating photoperiod into forecasting future phenology are critical.

Future directions: outstanding questions and incorporating photoperiod into forecasting

Incorporating photoperiod into forecasting is complex, since future rates of phenological shifts are unlikely be a straightforward extrapolation from current and past rates and because experienced photoperiod is both a driver and an effect of phenological shifts. Approaches for forecasting 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 phenology to climate change. First, statistical models generally assume linear relationships between species' responses and environmental variables (e.g., Flynn and Wolkovich, 2018; ?; ?), whereas process-based models incorporate nonlinear threshold relationships as well (e.g. Chuine and Beaubien, 2001; Morin and Thuiller, 2009; ?). Second, statistical models of phenology under climate change have typically ignored photoperiod, focusing instead on seasonal or annual temperature (e.g., ??Diez et al. (2012), but see Richardson et al. (2013) whereas process-based models of phenology are more likely to incorporate photoperiod, along with temperature (Duputié et al., 2015; Morin and Thuiller, 2009; ?; ?). The challenge of process-based models is that they require detailed data that is often not readily available (e.g., daily climate data, nonlinear biological responses to fine-scale changes in temperature). Perhaps because of this challenge, statistical models remain more commonly used in climate change forecasts of biological responses (e.g., Basler and Körner, 2012; ?; ?; ?; ?; Diez et al., 2012).

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 S1). Researchers can use these data to first learn if their species (or a closely related species) shows a photoperiod effect and, ideally, what its critical photoperiod is and how it varies by population, ecotype, or other factors (Bradshaw and Holzapfel, 2006; ?; ?). 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 6). Given the large change in experienced photoperiod with temporal shifts (Figure 1), 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 growth and fitness (Duputié et al., 2015), and alter community composition.

For some species, experimental data can be immediately used in forecasting because experiments manipulate photoperiod at relevant scales (e.g., Basler and Körner (2014); Heide and Sonstebj (2015), Figures 4, 5 A, Table S1). For example, photoperiod treatments from growth chamber experiments with *Fagus sylvatica* span the variation in both current and expected future ranges (here based on forecasts using the Phenofit model (Duputié et al., 2015), Figure 5) and may allow identification of critical photoperiod levels (Figure 6). 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. For example, photoperiod treatments from existing experiments of *Quercus robur* are missing many experienced photoperiods so finescale projections at many latitudes may be difficult, even for this relatively well-studied species. In such cases, the process of incorporating experimental data into more process-based models identifies critical knowledge gaps. Many experiments manipulate photoperiod much more dramatically than will occur with climate change (Figures 4, 5). Although these studies are useful for understanding mechanistically how photoperiod responses work, extrapolating these findings to climate change models may not be reasonable.

Photoperiod is not fully integrated into most current forecasts of biological responses to climate change (but see ?), and it is unclear how this omission affects accuracy of forecasts. Forecasts from ecosystem models often incorporate photoperiod, along with other variables such as evaporative demand and temperature (e.g., ED Jolly et al., 2005; Medvigy et al., 2013), but photoperiod is rarely included in species distribution models (e.g., Morin and Thuiller, 2009; ?). The sensitivity of model outcomes to assumptions made about photoperiod, critical photoperiod, and photoperiod responses needs further study, for example, across ecosystems, species, populations, and lifestages.

As we seek to more fully integrate photoperiod into forecasting, a critical area of further research is *how* photoperiod acts as a cue. Photoperiod seems to interact with temperature to affect phenology (e.g., ?); this would explain the divergent effects of photoperiod observed across studies in woody plants (e.g., Figure 3). However, exactly how it interacts with temperature, 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 (Boxes 1, S1).

Another important area of research is identifying mechanistic patterns in variation of photoperiod responses across species and populations, as well as the consequences of this variation. Understanding the extent to which this variation is predictable will be particularly beneficial for forecasting. For example, what traits are associated with photoperiod sensitivity and does variation in photoperiod sensitivity have a strong genetic component? If so, are species or populations from some locations or lineages more likely than others to be constrained by photoperiod in their responses to climate change?

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 addressed how an altered photoperiod may affect woody plant budburst (Table S1, Figure 4). 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 (Bradshaw and Holzapfel, 2006; Linn et al., 1996) and salmon (Solbakken et al., 1994; Taranger et al., 2003) to birds (Dawson et al., 2001) and marsupials (McCallan et al., 2006; Solbakken et al., 1994). Given what we know, incorporating photoperiod into forecasting of climate change responses should improve model accuracy, and is likely to highlight additional experiments needed to improve our mechanistic understanding of photoperiod as a critical cue to diverse biological responses.

Glossary

- chilling: the intensity and duration of winter temperature; critical chilling is the required amount of hours or days of cold temperature, defined by a specific critical temperature (e.g., 4 °C add citation), 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, and during which individuals can break dormancy with appropriate weather conditions, such as a warm spell.
- endodormancy: dormancy brought about by internal (rather than environmental) conditions, and during which individuals cannot break dormancy due to weather conditions, such as a warm spell.
- forcing: warm spring temperatures, critical forcing is the required amount of hours or days above a specific temperature, 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 biologist Erwin BÅijnnig; 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 is 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 behavior, physiology, growth, development or reproduction.

Box 1. Are photoperiod effects widespread? A case study of woody plant phenology

Photoperiod responses are 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 woody plant phenology: chilling, the prolonged exposure to cold temperatures after growth cessation in the fall, is required to initiate budburst; and forcing, prolonged exposure to warm temperatures, is required for budburst to occur. Thus, chilling and forcing treatments 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 main osprey bb paper), revealing that photoperiod sensitivity is widespread, though with wide variation across studies and species. Growth chamber experiments in OSPREE suggest that the dominant photoperiod response in woody plant species is earlier and more rapid budburst with longer days (e.g., Caffarra and Donnelly, 2011). 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, across XX species (Table S1). Main effects included responses such as growth (e.g., higher growth rates with longer days Ashby et al., 1962), budset (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 highlight that responses to photoperiod vary depending on temperature conditions. For example, more rapid advancement of budburst was observed under long versus short days with low chilling, than with high chilling in *Betula papyrifera* (Hawkins and Dhar, 2012) (Figure 3). Frequently, long photoperiods can compensate for low amounts of chilling during winter dormancy, resulting in enhanced cell growth (Heide, 1993a; Myking and Heide, 1995; Caffarra et al., 2011).

Woody plant growth chamber experiments also demonstrate that, though photoperiod responses are common, they are variable (Figure 3). Responses to photoperiod differ by species (e.g., Heide, 1993b; Howe et al., 1996; Basler and Körner, 2012, 2014; Zohner et al., 2016; Flynn and Wolkovich, 2018). For example, with longer chilling treatments some species seem insensitive to daylength (e.g., *Hammamelis* spp., *Prunus* spp. Zohner et al., 2016), whereas others (e.g. *Fagus* spp., Figure 5A) seem to be highly sensitive to daylength, even with long chilling treatments (Zohner et al., 2016). In addition, some species demonstrated an opposing response to photoperiod than typically observed: *Tilia*, for example, showed delayed budburst with longer daylengths (Figure 3, (Ashby et al., 1962)) Photoperiod sensitivity also varies by population and ecotype (e.g., Partanen et al., 2005) (Figure 3). For example, photoperiod effects on budburst were more significant for lower latitude populations of *Betula pendula* and *B. pubescens* (Partanen et al., 2005).

Supplement: Box S1. Dominant models of how photoperiod affects spring woody plant phenology

The molecular mechanisms and pathways underlying photoperiod sensitivity are poorly understood for most organisms, even in relatively well-studied phenophases such as spring budburst in woody plants (Ding and Nilsson, 2016). Spring budburst in woody plants is thought to be controlled by three main cues: chilling, forcing, and photoperiod, as well as interactions between them (Flynn and Wolkovich, 2018; Heide, 2008; Zohner et al., 2016). Our understanding of how plants interpret photoperiod comes largely from studies of flowering in the model plant *Arabidopsis thaliana* (e.g., Suárez-López et al., 2001) and budset in woody plant species (e.g., Howe et al., 1996). Similar pathways may underlie budburst phenology in woody plants (Lagercrantz, 2009; Ding and Nilsson, 2016).

Plants sense light inputs by blue light receptors and phytochromes, which have been found in nearly all organs throughout the plant. 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 (e.g., warm days), a response is induced (Lagercrantz, 2009). 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 (Davis, 2002; Petterle et al., 2013; Bastow and Dean, 2002; Kobayashi and Weigel, 2007; Andrés and Coupland, 2012; Singh et al., 2017). 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.

Little is known about the genetic pathways responsible for the light-sensing apparatuses involved in budburst, and how they may vary across species or populations. Some genes have been identified that play a role in coordinating budburst in poplar (*Populus* spp.), and may occur in other woody species as well. Many similarities exist between the proposed regulatory networks of vegetative growth in *Populus* and those controlling floral initiation in *Arabidopsis*, Ding and Nilsson (2016). For example, vegetative growth and inhibition of budset are promoted by the FLOWERING LOCUS T2 (FT2) gene, a homolog of *Arabidopsis thaliana* gene FLOWERING LOCUS (FT). Promotion occurs in response to warm temperatures and long days, marking the onset of the growing season (Hsu et al., 2011). FT2 expression appears to be controlled by a pathway that is effective in long days. Its loss of expression in autumn, when the days are getting shorter, is associated with the onset of dormancy (Glover, 2014).

There are large gaps in our understanding of how photoperiod sensing pathways affect budburst, the genetics behind these pathways, and the extent of species- and population-level genetic variation. Questions also remain about how photoperiod sensing interacts with temperature sensing to affect responses. For example, Figure 3 shows the most detailed data we were able to find of budburst responses across different photoperiod and chilling treatments. These data highlight how variable responses to photoperiod are, across species and populations, and with different chilling treatments. Additional growth chamber studies will be required to address the molecular mechanisms and genetic controls underlying this dramatic variation in budburst responses to photoperiod.

To do:

1. Add more methods to supplement

References

- Andrés, F., and G. Coupland. 2012. The genetic basis of flowering responses to seasonal cues. *Nature reviews. Genetics* 13:627.
- Ashby, W., et al. 1962. Germination capacity in american basswood [*tilia americana*]. *Transactions of the Illinois State Academy of Science* 55:120–3.
- Basler, D., and C. Körner. 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology* 165:73–81.
- . 2014. Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. *Tree physiology* 34:377–388.
- Bastow, R., and C. Dean. 2002. The molecular basis of photoperiodism. *Developmental cell* 3:461–462.
- Bradley, N. L., A. C. Leopold, J. Ross, and W. Huffaker. 1999. Phenological changes reflect climate change in wisconsin. *Proceedings of the National Academy of Sciences* 96:9701–9704.
- Bradshaw, H., and R. F. Stettler. 1995. Molecular genetics of growth and development in populus. iv. mapping qtls with large effects on growth, form, and phenology traits in a forest tree. *Genetics* 139:963–973.

- Bradshaw, W. E., and C. M. Holzapfel. 2006. Evolutionary response to rapid climate change. *Science*(Washington) 312:1477–1478.
- . 2008. Genetic response to rapid climate change: it’s seasonal timing that matters. *Molecular ecology* 17:157–166.
- Caffarra, A., and A. Donnelly. 2011. The ecological significance of phenology in four different tree species: effects of light and temperature on bud burst. *International journal of Biometeorology* 55:711–721.
- Caffarra, A., A. Donnelly, I. Chuine, and M. B. Jones. 2011. Modelling the timing of *betula pubescens* bud-burst. i. temperature and photoperiod: A conceptual model. *Climate Research* 46:147.
- Campbell, R. K., and A. I. Sugano. 1975. Phenology of bud burst in douglas-fir related to provenance, photoperiod, chilling, and flushing temperature. *Botanical Gazette* pages 290–298.
- Chen, I.-C., J. K. Hill, R. Ohlemueller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026.
- Chuine, I., and E. G. Beaubien. 2001. Phenology is a major determinant of tree species range. *Ecology Letters* 4:500–510.
- Chuine, I., X. Morin, and H. Bugmann. 2010. Warming, photoperiods, and tree phenology. *Science* 329:277–278.
- Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta, and E. M. Wolkovich. 2012. Phenological tracking enables positive species responses to climate change. *Ecology* 93:1765–1771.
- Davis, S. J. 2002. Photoperiodism: the coincidental perception of the season. *Current Biology* 12:R841–R843.
- Dawson, A., V. M. King, G. E. Bentley, and G. F. Ball. 2001. Photoperiodic control of seasonality in birds. *Journal of biological rhythms* 16:365–380.
- Diez, J. M., I. Ibáñez, A. J. Miller-Rushing, S. J. Mazer, T. M. Crimmins, M. A. Crimmins, C. D. Bertelsen, and D. W. Inouye. 2012. Forecasting phenology: from species variability to community patterns. *Ecology Letters* 15:545–553.
- Ding, J., and O. Nilsson. 2016. Molecular regulation of phenology in trees– because the seasons they are a-changin. *Current opinion in plant biology* 29:73–79.
- Duputié, A., A. Rutschmann, O. Ronce, and I. Chuine. 2015. Phenological plasticity will not help all species adapt to climate change. *Global change biology* 21:3062–3073.
- Erwin, J. E. 1998. Temperature and light effects on stem elongation (plant growth regulation by physical and mechanical stimuli, for further development of horticulture in east asia). *Journal of the Japanese Society for Horticultural Science* 67:1113–1120.
- Falusi, M., and R. Calamassi. 1990. Bud dormancy in beech (*fagus sylvatica* l.). effect of chilling and photoperiod on dormancy release of beech seedlings. *Tree physiology* 6:429–438.
- Flynn, D. F. B., and E. M. Wolkovich. 2018. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist* 0.
- Gauzere, J., S. Delzon, H. Davi, M. Bonhomme, I. G. de Cortazar-Atauri, and I. Chuine. 2017. Integrating interactive effects of chilling and photoperiod in phenological process-based models. a case study with two european tree species: *Fagus sylvatica* and *quercus petraea*. *Agricultural and Forest Meteorology* 244:9–20.
- Glover, B. 2014. *Understanding flowers and flowering* second edition. OUP Oxford.

- Gu, L., P. J. Hanson, W. M. Post, D. P. Kaiser, B. Yang, R. Nemani, S. G. Pallardy, and T. Meyers. 2008. The 2007 Eastern US spring freeze: Increased cold damage in a warming world. *BioScience* 58:253.
- Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? a global meta-analysis of treeline response to climate warming. *Ecology Letters* 12:1040–1049.
- Hawkins, C. D., and A. Dhar. 2012. Spring bud phenology of 18 *Betula papyrifera* populations in British Columbia. *Scandinavian Journal of Forest Research* 27:507–519.
- Heide, O. 1993a. Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physiologia Plantarum* 88:531–540.
- . 1993b. Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days. *Physiologia Plantarum* 89:187–191.
- Heide, O. M. 1977. Photoperiod and temperature interactions in growth and flowering of strawberry. *Physiologia Plantarum* 40:21–26.
- Heide, O. M. 2008. Interaction of photoperiod and temperature in the control of growth and dormancy of *Prunus* species. *Scientia Horticulturae* 115:309–314.
- . 2011. Temperature rather than photoperiod controls growth cessation and dormancy in *Sorbus* species. *Journal of experimental botany* page err213.
- Heide, O. M., and A. Sønsteby. 2012. Floral initiation in black currant cultivars (*Ribes nigrum* L.): Effects of plant size, photoperiod, temperature, and duration of short day exposure. *Scientia Horticulturae* 138:64–72.
- Heide, O. M., and A. Sønsteby. 2015. Simultaneous dormancy induction interferes with short day floral induction in black currant (*Ribes nigrum* L.). *Scientia Horticulturae* 185:228–232. Times Cited: 0 Heide, Ola M. Sønsteby, Anita O.
- Howe, G. T., G. Gardner, W. P. Hackett, and G. R. Furnier. 1996. Phytochrome control of short-day-induced bud set in black cottonwood. *Physiologia Plantarum* 97:95–103.
- Howe, G. T., W. P. Hackett, G. R. Furnier, and R. E. Klevorn. 1995. Photoperiodic responses of a northern and southern ecotype of black cottonwood. *Physiologia Plantarum* 93:695–708.
- Hsu, C.-Y., J. P. Adams, H. Kim, K. No, C. Ma, S. H. Strauss, J. Drnevich, L. Vandervelde, J. D. Ellis, B. M. Rice, et al. 2011. Flowering locus 1 duplication coordinates reproductive and vegetative growth in perennial poplar. *Proceedings of the National Academy of Sciences* 108:10756–10761.
- Jolly, W. M., R. Nemani, and S. W. Running. 2005. A generalized, bioclimatic index to predict foliar phenology in response to climate. *Global Change Biology* 11:619–632.
- Keller, S. R., R. Y. Soolanayakanahally, R. D. Guy, S. N. Silim, M. S. Olson, and P. Tiffin. 2011. Climate-driven local adaptation of ecophysiology and phenology in balsam poplar, *Populus balsamifera* L. (Salicaceae). *American Journal of Botany* 98:99–108.
- Kobayashi, Y., and D. Weigel. 2007. Move on up, it's time for change—mobile signals controlling photoperiod-dependent flowering. *Genes & development* 21:2371–2384.
- Koerner, C., and D. Basler. 2010. Warming, photoperiods, and tree phenology response. *Science* 329:278–278.
- Lagercrantz, U. 2009. At the end of the day: a common molecular mechanism for photoperiod responses in plants? *Journal of experimental botany* 60:2501–2515.
- Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* 20:170–182.

- Linkosalo, T., and M. J. Lechowicz. 2006. Twilight far-red treatment advances leaf bud burst of silver birch (*Betula pendula*). *Tree physiology* 26:1249–1256.
- Linn, C. E., M. G. Campbell, K. R. Poole, W.-Q. Wu, and W. L. Roelofs. 1996. Effects of photoperiod on the circadian timing of pheromone response in male *Trichoplusia ni*: relationship to the modulatory action of octopamine. *Journal of Insect Physiology* 42:881–891.
- McAllan, B. M., C. R. Dickman, and M. S. Crowther. 2006. Photoperiod as a reproductive cue in the marsupial genus *Antechinus*: ecological and evolutionary consequences. *Biological Journal of the Linnean Society* 87:365–379.
- Medvigy, D., S.-J. Jeong, K. L. Clark, N. S. Skowronski, and K. V. Schäfer. 2013. Effects of seasonal variation of photosynthetic capacity on the carbon fluxes of a temperate deciduous forest. *Journal of Geophysical Research: Biogeosciences* 118:1703–1714.
- Menzel, A. 2000. Trends in phenological phases in Europe between 1951 and 1996. *International journal of biometeorology* 44:76–81.
- Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aasa, R. Ahas, K. Alm-Kuebler, et al. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12:1969–1976.
- Mimura, M., and S. Aitken. 2007. Adaptive gradients and isolation-by-distance with postglacial migration in *Picea sitchensis*. *Heredity* 99:224.
- Morin, X., J. Roy, L. Sonié, and I. Chuine. 2010. Changes in leaf phenology of three European oak species in response to experimental climate change. *New Phytologist* 186:900–910.
- Morin, X., and W. Thuiller. 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology* 90:1301–1313.
- Myking, T., and O. Heide. 1995. Dormancy release and chilling requirement of buds of latitudinal ecotypes of *Betula pendula* and *B. pubescens*. *Tree physiology* 15:697–704.
- Nienstaedt, H. 1966. Dormancy and dormancy release in white spruce. *Forest Science* 12:374–384.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology and Systematics* 37:637–669.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37.
- Partanen, J., H. Hänninen, and R. Häkkinen. 2005. Bud burst in Norway spruce (*Picea abies*): preliminary evidence for age-specific rest patterns. *Trees* 19:66–72.
- Peñuelas, J., and M. Boada. 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biology* 9:131–140.
- Petterle, A., A. Karlberg, and R. P. Bhalerao. 2013. Daylength mediated control of seasonal growth patterns in perennial trees. *Current Opinion in Plant Biology* 16:301–306.
- Polgar, C. A., R. B. Primack, E. H. Williams, S. Stichter, and C. Hitchcock. 2013. Climate effects on the flight period of Lycaenid butterflies in Massachusetts. *Biological Conservation* 160:25–31.
- Richardson, A. D., T. F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag, and M. Toomey. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* 169:156–173.

- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60.
- Saikkonen, K., K. Taulavuori, T. Hyvönen, P. E. Gundel, C. E. Hamilton, I. Vänninen, A. Nissinen, and M. Helander. 2012. Climate change-driven species’ range shifts filtered by photoperiodism. *Nature Climate Change* 2:239.
- Sanz-Perez, V., P. Castro-Diez, and F. Valladares. 2009. Differential and interactive effects of temperature and photoperiod on budburst and carbon reserves in two co-occurring mediterranean oaks. *Plant Biol (Stuttg)* 11:142–51.
- Sidaway-Lee, K., E.-M. Josse, A. Brown, Y. Gan, K. J. Halliday, I. A. Graham, and S. Penfield. 2010. *Spatula* links daytime temperature and plant growth rate. *Current biology* 20:1493–1497.
- Singh, R. K., T. Svystun, B. AlDahmash, A. M. Jönsson, and R. P. Bhalerao. 2017. Photoperiod-and temperature-mediated control of phenology in trees—a molecular perspective. *New Phytologist* 213:511–524.
- Solbakken, V. A., T. Hansen, and S. O. Stefansson. 1994. Effects of photoperiod and temperature on growth and parr-smolt transformation in atlantic salmon (*salmo salar* l.) and subsequent performance in seawater. *Aquaculture* 121:13–27.
- Spann, T. M., J. G. Williamson, and R. L. Darnell. 2004. Photoperiod and temperature effects on growth and carbohydrate storage in southern highbush blueberry interspecific hybrid. *Journal of the American Society for Horticultural Science* 129:294–298.
- Suárez-López, P., K. Wheatley, F. Robson, H. Onouchi, F. Valverde, and G. Coupland. 2001. *CONSTANS* mediates between the circadian clock and the control of flowering in *arabidopsis*. *Nature* 410:1116.
- Tanino, K. K., L. Kalcsits, S. Silim, E. Kendall, and G. R. Gray. 2010. Temperature-driven plasticity in growth cessation and dormancy development in deciduous woody plants: a working hypothesis suggesting how molecular and cellular function is affected by temperature during dormancy induction. *Plant molecular biology* 73:49–65.
- Taranger, G., E. Vikingstad, U. Klenke, I. Mayer, S. Stefansson, B. Norberg, T. Hansen, Y. Zohar, and E. Andersson. 2003. Effects of photoperiod, temperature and GnRH treatment on the reproductive physiology of atlantic salmon (*salmo salar* l.) broodstock. *Fish Physiology and Biochemistry* 28:403–406.
- Viherä-Aarnio, A., R. Häkkinen, and O. Junttila. 2006. Critical night length for bud set and its variation in two photoperiodic ecotypes of *betula pendula*. *Tree physiology* 26:1013–1018.
- Vitasse, Y., and D. Basler. 2013. What role for photoperiod in the bud burst phenology of european beech. *European Journal of Forest Research* 132:1–8.
- Wareing, P. 1956. Photoperiodism in woody plants. *Annual Review of Plant Physiology* 7:191–214.
- Way, D. A., and R. A. Montgomery. 2015. Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, Cell & Environment* 38:1725–1736.
- Weih, M. 2004. Intensive short rotation forestry in boreal climates: present and future perspectives. *Canadian Journal of Forest Research* 34:1369–1378.
- Willis, C. G., B. R. Ruhfel, R. B. Primack, A. J. Miller-Rushing, J. B. Losos, and C. C. Davis. 2010. Favorable climate change response explains non-native species’ success in Thoreau’s woods. *Plos One* 5:e8878.
- Wolkovich, E. M., B. I. Cook, J. M. Allen, T. M. Crimmins, J. L. Betancourt, S. E. Travers, S. Pau, et al. 2012. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485:494–497.
- Zohner, C. M., B. M. Benito, J. C. Svenning, and S. S. Renner. 2016. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* .

Figures

<https://esajournals-onlinelibrary-wiley-com.ezp-prod1.hul.harvard.edu/doi/full/10.1890/14-2071.1>

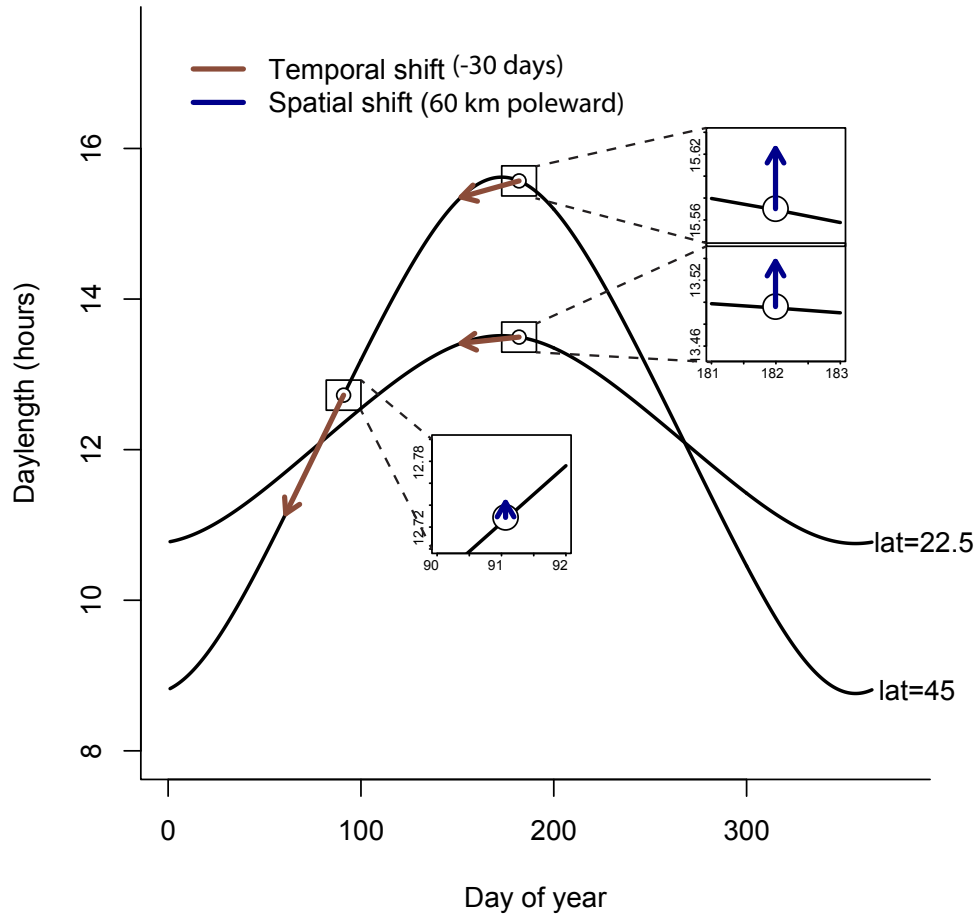


Figure 1: **Photoperiod varies with latitude and throughout the year**, such that temporal shifts in activity yield larger changes in experienced photoperiod compared with spatial shifts. Here, we show this variation at two latitudes (22.5°, 45°), using hypothetical of spatial and temporal shifts. These shifts, which are similar to observed average rates with recent global warming (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 solstice (e.g., DOY 182).

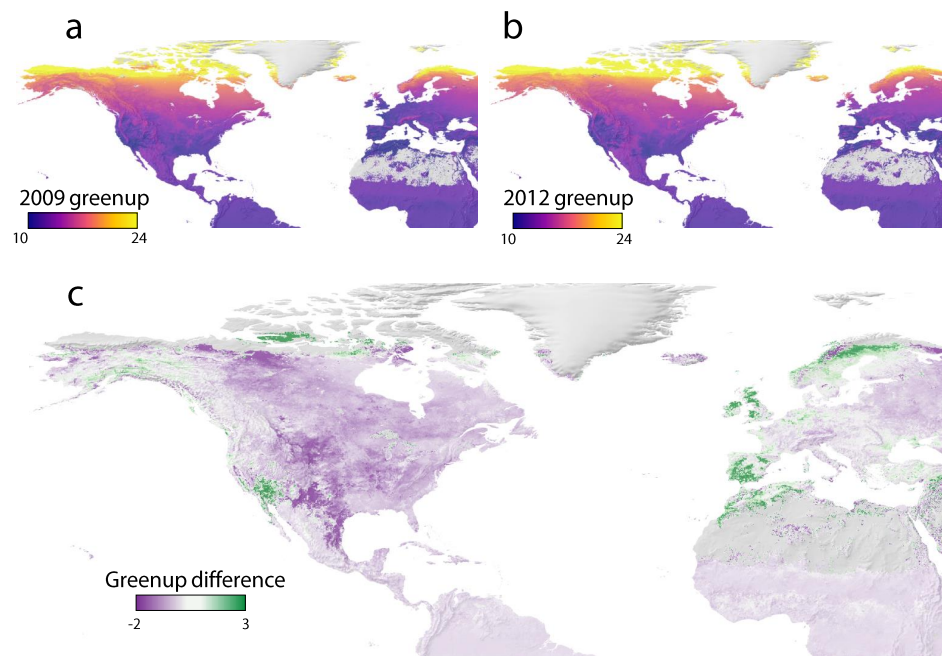


Figure 2: **Photoperiod on the "green-up" date (i.e., start of spring) varies over space and among years.** Hours of daylight on the date of spring green-up from MODIS satellite data across North America and Europe for an average (2009, a) and early (2012,b) North American start of spring. The differences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

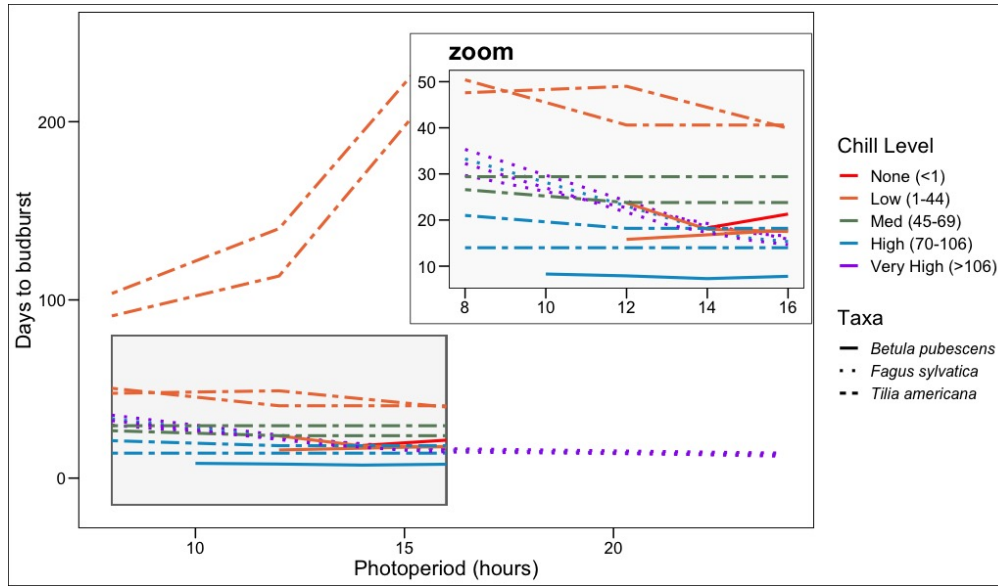


Figure 3: **Nonlinearities in the phenological response to daylength** are apparent in woody plant budburst experiments from the OSPREE database, in which three or more photoperiod treatment levels were applied. The shape of the response curves for *Betula pubescens* (Caffarra et al., 2011), *Fagus sylvatica* (Heide, 1993b) and *Tilia americana* (Ashby et al., 1962) differ depending on the amount of chilling recieved (in Chill portions). Species and chilling levels with multiple lines represent plant material from different populations.

A)

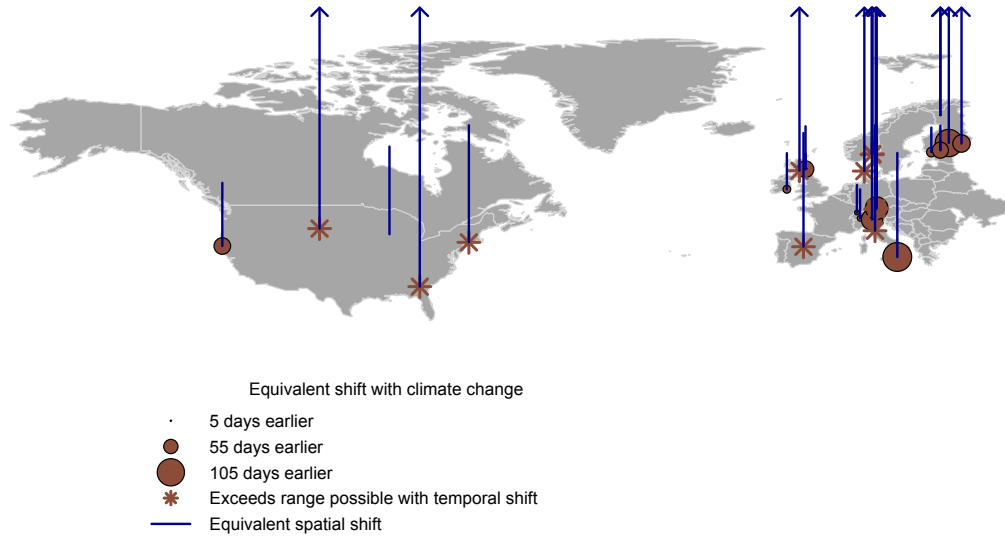


Figure 4: **Experimental photoperiod treatments and their equivalent spatial and temporal shifts** for experiments in the OSPREE database that manipulate photoperiod. To calculate the required spatial (blue lines) or temporal (pink circles/stars) shifts for each experiment, we used observed rates with recent warming: 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).

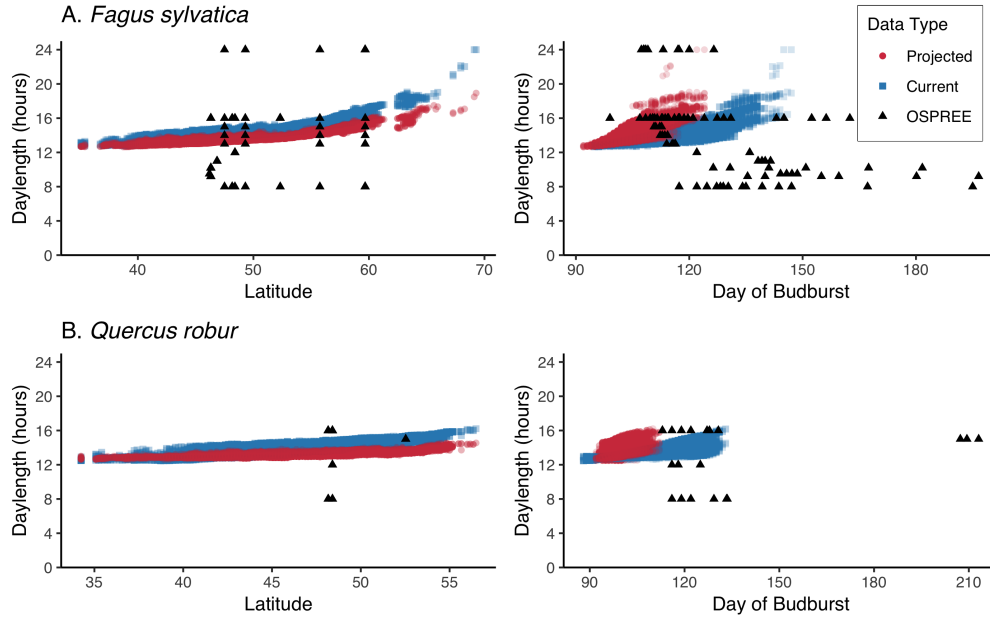


Figure 5: **Experimental treatments of daylength as it varies by latitude (left panels) and by day of budburst (right panels)** for *Fagus sylvatica* (A) and *Quercus robur* (B). For comparison, we show the daylength when budburst occurs in its current and projected ranges. We took current budburst data (1981-2000) and model projections for budburst (2081-2100) using the A1Fi Phenofit scenario (Duputié et al., 2015) for the two species and compared these points to data obtained from the OSPREE dataset. The OSPREE data points were collected from experiments and days of budburst were calculated from the start of the experiment, rather than from the start of the year. In order to render these points comparable to the current observations and the model projections, we scaled the days to budburst by adding the day of budburst from the first Phenofit observation to all of the OSPREE data points. We only used Phenofit data that had both current and projected data. In panel (B) for *Quercus robur*, we explored the 15 OSPREE data points that have later day to budburst times than the current or projected days to budburst. The majority of those points had 5-8 hours shorter photoperiods than is biologically possible and the last few points had little or no experimental chilling.

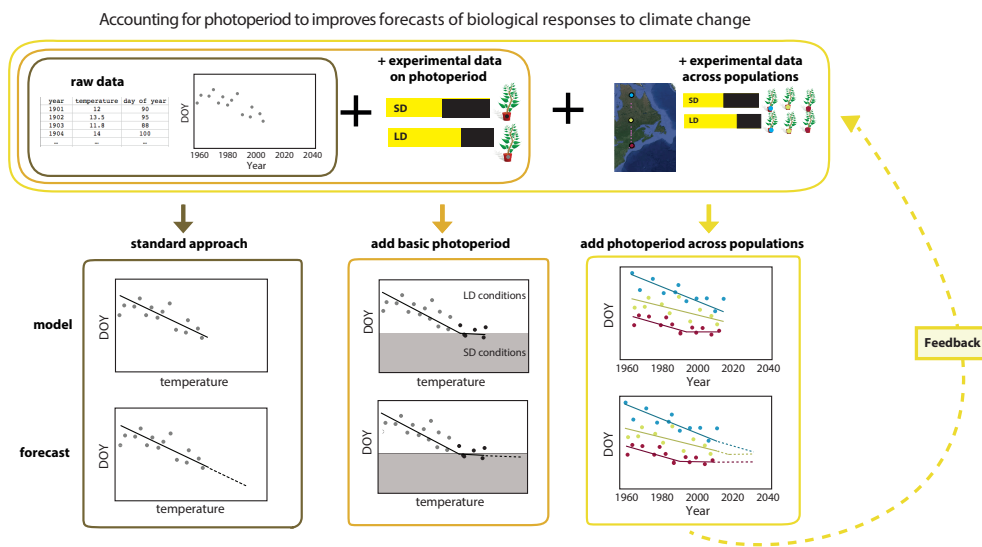


Figure 6: Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change.