

Spatial and temporal shifts in photoperiod with climate change

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Summary

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

Introduction

Shifts in the timing of spring events—i.e., phenology, including flowering, bird arrival, egg hatching and myriad other biological activities—are some of the most widely documented 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). These changes are some of the largest average shifts observed with warming, with early spring phenology shifting more rapidly than later season phenology in most cases (Bradley et al., 1999; Menzel et al., 2006), and suggest temperature is a major driver of spring phenophases.

Spring phenology is not controlled solely by temperature, however. Photoperiod is also a critical cue for plants and animals, signaling changes in growth, mating, and reproduction across diverse species (e.g., Howe et al., 1996; Flynn and Wolkovich, 2018; Solbakken et al., 1994; McCallan et al., 2006; Lagercrantz, 2009). Photoperiod is often 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 a threshold photoperiod (see Glossary), 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). With current rapid warming photoperiod may also potentially slow the observed trend of advancing spring phenology.

Recent studies offer inconsistent views about whether photoperiod may eventually restrict advances in spring

phenology in a warmer world. Some studies suggest that, with additional warming, photoperiod will limit phenological shifts of certain species such that they will not track rising temperatures (e.g., by leafing out earlier in the spring, Koerner and Basler, 2010; Way and Montgomery, 2015). Instead, these species' responses will increasingly become constrained by daylength. Other studies, however, suggest that photoperiod will not constrain responses to warming for most species (Zohner et al., 2016; Chuine et al., 2010). The extent to which daylength constrains responses will depend in part on how rapidly threshold photoperiod can acclimate or adapt to new environmental conditions, which remains an open question (Grevstad and Coop, 2015).

Perhaps because of these variable and uncertain responses, photoperiod is often not included in forecasts of biological responses to climate change, especially in the spring, even though it is known to be an important cue for biological activity (but see Duputié et al., 2015; Caffarra et al., 2011a; Grevstad and Coop, 2015). The exclusion of photoperiod may be problematic: 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 the timing of development (Muir et al., 1994; Grevstad and Coop, 2015), migration (Dawbin, 1966), and other important responses.

When a population is moved to a new location with even a slight difference in climate, latitude, or seasonal timing, the genetically based photoperiod response is likely to be maladapted, leading to a life cycle that is asynchronous with resources or that includes too many or too few generations for the season duration (Danilevskii 1965). Models that ignore photoperiod responses in their forecasts are effectively assuming that the threshold photoperiod changes instantaneously with new conditions (Grevstad and Coop, 2015).

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 research apply experiments that alter photoperiod to forecasting biological implications of climate change?

These questions are broadly relevant for diverse species. Here, we use a case study of spring woody plant phenology to illustrate our points (Box 1). We focus on spring events, as phenology during this time is one of the most widely observed and rapidly changing biological responses to climate change (Parmesan, 2006). Woody species are a useful focal group because they have been the subject of decades of growth chamber experiments, are the focus of an important and controversial debate on the relative effects of photoperiod versus temperature on their phenology, and because forecasting effects of climate change on their 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 Observed Spring Phenology Responses in Experimental Environments (OSPRE), a new database of plant growth chamber studies that manipulate photoperiod and temperature to measure plant phenological responses, including budburst and flowering (Wolkovich et al., 2019).

How will climate change alter the photoperiod experienced by organisms?

Species experience different photoperiod regimes depending on their location on earth (Fig. 2), the seasonal timing of their activity, and inter-annual variation in climate. The daylength experienced by plants on the date that spring "green-up" occurs, 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, is 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 (Fig. 2b) and green-up does not appear to occur at daylengths less than 10 hours. There is strong spatiotemporal variation in experienced photoperiod across years (e.g., years with "early" versus "late" green-up, Figure 2c), and experienced photoperiod at green-up can vary two to three hours from one year to the next 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 (Ovaskainen et al., 2013; Peñuelas et al., 2002).

Against this existing background variation, climate change will cause 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, in contrast, cause minimal changes in the range of daylength throughout the year.

To date, much 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—especially the large changes seen in spring 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 will yield much larger changes in experienced photoperiod than spatial shifts (Figure 1). For example, consider an insect that emerges from diapause or a tree that bursts its buds at latitude 45°, on average, around day of year 91 (April 2, when daylength is 12.8 hours). If the organism's 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 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 day of year.

In many cases organisms may shift both their ranges and their phenology simultaneously (i.e., due to new climatic conditions, Duputié et al., 2015; Grevstad and Coop, 2015). In addition, photoperiod sensitivity, or the degree to which phenology is controlled by daylength, can vary with latitude, likely due to population-level differences in sensitivity (Howe et al., 1996; Saikkonen et al., 2012; Partanen et al., 2005; Viherä-Aarnio et al., 2006; Caffarra et al., 2011b; Gauzere et al., 2017). With future climate change, it is unclear how these complexities will affect the photoperiod experienced by organisms and if these shifts in photoperiod will have important implications for biological responses. This lack of clarity stems, in part, from the fact that phenology 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, migration, and diapause in animals (Muir et al., 1994; Bradshaw and Holzapfel, 2006; Saunders and Henderson, 1970; Tobin et al., 2008; Zydlewski et al., 2014). Climate change-induced shifts in photoperiod are therefore likely to alter these functions. Indeed, growth chamber studies demonstrate that the magnitude 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). The direction and magnitude of responses will vary, however, because of variation in photoperiod sensitivity, and because photoperiod often interacts with other environmental drivers, such as temperature, to affect phenology (Box 1).

Threshold photoperiods may increasingly constrain 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 (Menzel, 2000; Ovaskainen et al., 2013; Peñuelas et al., 2002; Polgar et al., 2013) may stop abruptly, because photoperiod sensitivity is thought to be a threshold response in plants (Box S1) and animals (Tobin et al., 2008; Grevstad and Coop, 2015). 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 (Muir et al., 1994; 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 may be 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 threshold for photoperiod effects, even with climate change) can take advantage of warmer springs by having an earlier start to its growing season. Indeed, phenological tracking of temperature (i.e., earlier flowering or leafout with warming) has been linked with higher performance in plants (Cleland et al., 2012). Species or populations that are sensitive to temperature but relatively insensitive to photoperiod may therefore outcompete slower growing or later emerging ones that are limited by photoperiod and thus cannot 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 for a few major reasons. Future rates of phenological shifts are unlikely to be straightforward extrapolations from past and current rates. In addition, an organism's 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 paradigms 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; Van Belle et al., 2007; Ibáñez et al., 2010), whereas process-based models often incorporate nonlinear threshold relationships as well (e.g. Chuine and Beaubien, 2001; Morin and Thuiller, 2009; Xie and Hsieh, 1989). Second, statistical models of phenology under climate change have typically ignored photoperiod, focusing instead on seasonal or annual temperature (Van Belle et al. (e.g. 2007); Ibáñez et al. (e.g. 2010); Diez et al. (e.g. 2012), but see Richardson et al. (2013)). whereas process-based models of phenology more frequently incorporate photoperiod, along with temperature (Duputié et al., 2015; Morin and Thuiller, 2009; Xie and Hsieh, 1989; Zhao et al., 2013). 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; Zhu et al., 2012; García-Valdés and Morales-Castilla, 2016; Van Belle et al., 2007; Ibáñez et al., 2010; Diez et al., 2012).

Future modelling can incorporate photoperiod by leveraging the large amount of experimental data on photoperiod responses (Figure 4, Table S1), especially when process-based approaches are used. Researchers can use these data to first learn if the study species (or a closely related species) shows a photoperiod effect and, ideally, what its threshold photoperiod is and how it varies by population, ecotype, or other factors (Bradshaw and Holzapfel, 2006; Gwinner, 1996; Tobin et al., 2008). If there is evidence of a photoperiod response (e.g., *Tilia americana* with low chilling in Fig. 3), daylength should be added to forecasting models, using the threshold 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 phenological forecasting. Since spatial shifts are associated with smaller changes in experienced photoperiod, it may be less important for distribution forecasts. Many species, however, may 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 Sonstebø (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 from Duputié et al. (2015), Figure 5) and may allow identification of threshold photoperiod levels (Figure 6). In other cases, attempting to incorporate photoperiod into forecasts of future phenology will reveal gaps in our understanding of many aspects of photoperiod responses. For example, photoperiod treatments from existing experiments of *Quercus robur* lack many experienced photoperiods from current or future estimates, making fine scale projections difficult, even for this relatively well-studied species. This gap extends to many species, as 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 them 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 Tobin et al., 2008), an omission that could affect the accuracy of forecasts. Forecasts from ecosystem mod-

els 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; Zhu et al., 2012). The sensitivity of model outcomes to assumptions made about experienced photoperiod and threshold responses to photoperiod needs further study, including understanding how variation in photoperiod responses across ecosystems, species, populations, and life stages impacts forecasts.

As researchers more fully integrate photoperiod into forecasting, a critical area of further study is understanding *how* photoperiod acts as a cue. Photoperiod seems to interact with temperature to affect phenology (e.g., Zydlewski et al., 2014); 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 threshold photoperiods, are not well-defined for most species (Boxes 1, S1).

Another important area of research is quantifying patterns in variation of photoperiod responses across species and populations. Understanding the drivers, as well as the consequences, of this variation 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 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 will illuminate additional experiments that could improve our mechanistic understanding of photoperiod as a critical cue to diverse biological responses.

Glossary

- budburst: the emergence of new leaves on a plant at the beginning of the growing season.
- 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.
- diapause: period of suspended development or growth, usually used to describe invertebrates during unfavorable environmental conditions such as winter
- dormancy: halted or reduced growth or activity, usually used to describe plants
- 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.
- green-up: The beginning of a new cycle of plant growth, usually evaluated at the landscape scale

- phenology: the timing of life cycle events in organisms
- photoperiod: the daily duration of light (daylength) and dark to which an organism is exposed; often used synonymously with daylength
- photoperiodism: the ability to assess the length of day or night to regulate behavior, physiology, growth, development or reproduction.
- threshold photoperiod: length of day that causes an individual to switch from a long- to a short-day response (or vice versa).

Box 1. Are photoperiod effects widespread? A case study of woody plant spring 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 (e.g., Heide, 1993b; Basler and Körner, 2014; Flynn and Wolkovich, 2018). These experiments often manipulate photoperiod in combination with temperature to address basic questions about how these two environmental conditions act as biological cues. 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).

Woody plant growth chamber studies have been conducted for decades, but have only recently been synthesized (cite main ospree 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 (i.e., photoperiod x temperature effects), across 176 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 paynifera* (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., 2011b).

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).

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Figures

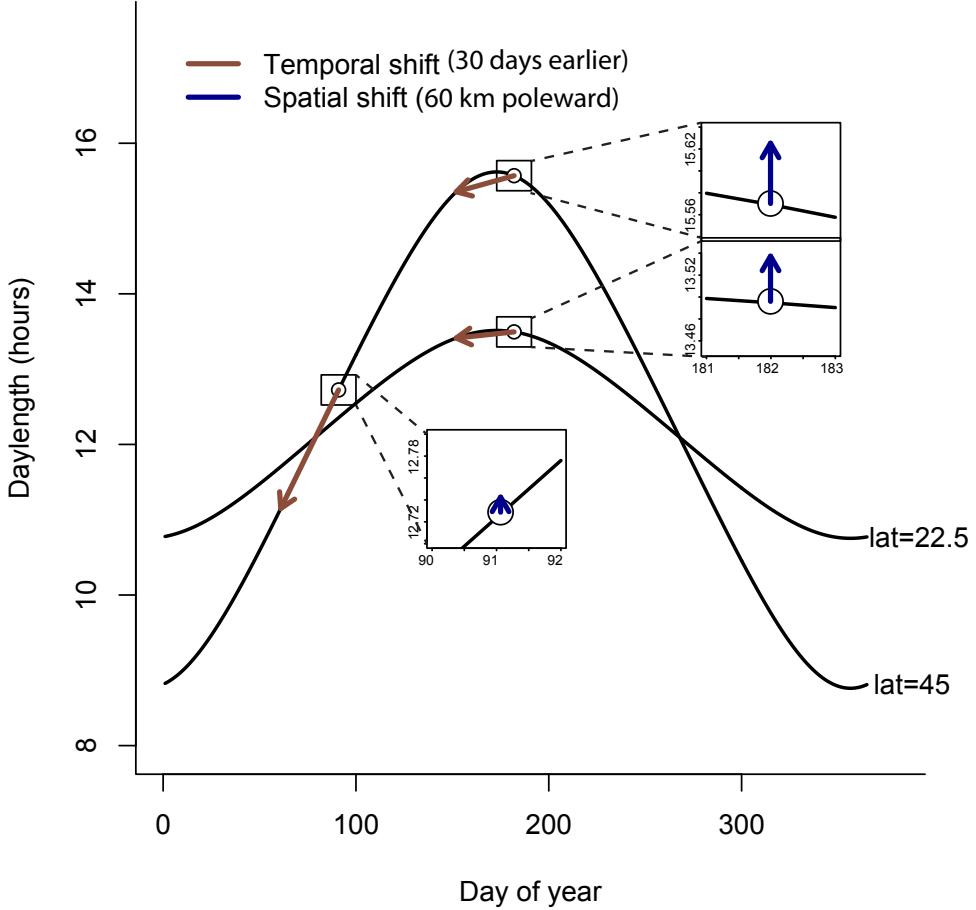


Figure 1: **Photoperiod varies with latitude and by day of year**, such that temporal shifts in activity yield larger changes in experienced photoperiod compared with spatial shifts. Here, we show this variation at two latitudes (22.5° , 45°), using hypothetical spatial and temporal shifts. These shifts, based on observed average rates with recent global warming ((e.g., 16.9 kilometers per decade (or approximately 1.5 degrees in 100 years) for spatial shifts Parmesan, 2006), and (e.g., 3 days per decade, or 23 days in 100 years, for temporal shifts Chen et al., 2011)), highlight the greater magnitude in daylength changes close to the equinox (e.g., day of year 91), versus close to the summer solstice (e.g., day of year 182).

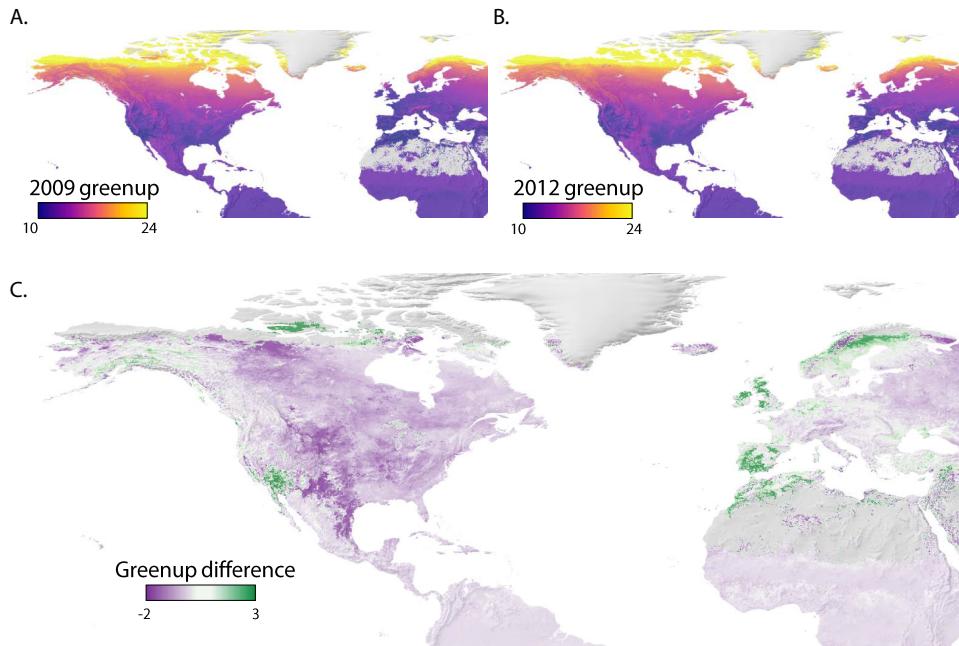


Figure 2: Photoperiod on the “green-up” date varies over space and between years “Green-up” is the beginning of seasonal greening, identified by satellite remote sensing measurements (here using MODIS) taken regularly throughout the year of the concentrations of green leaf vegetation. Hours of daylight 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). See “Quantifying and mapping differences in green-up across the United States and Europe” in the Supplemental Materials for more details. A negative difference signifies earlier green-up in 2012 versus 2009; a positive difference is the result of later green-up in 2012 compared with 2009.

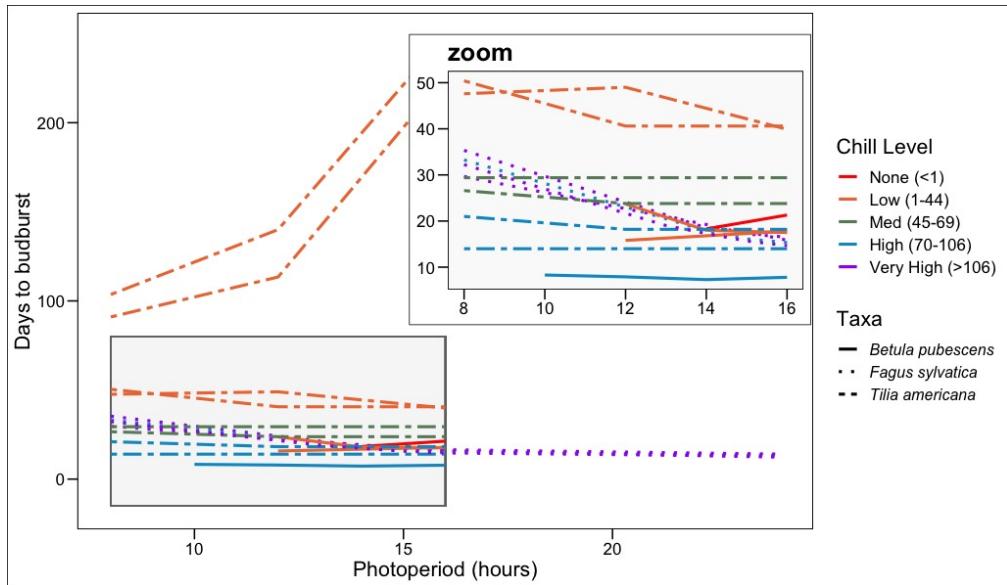


Figure 3: **Nonlinearities in phenological responses to daylength** are apparent in spring woody plant phenology experiments (from the OSPREE database) in which three or more photoperiod treatment levels were applied. The shape of the response curves for *Betula pubescens* (Caffarra et al., 2011b), *Fagus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

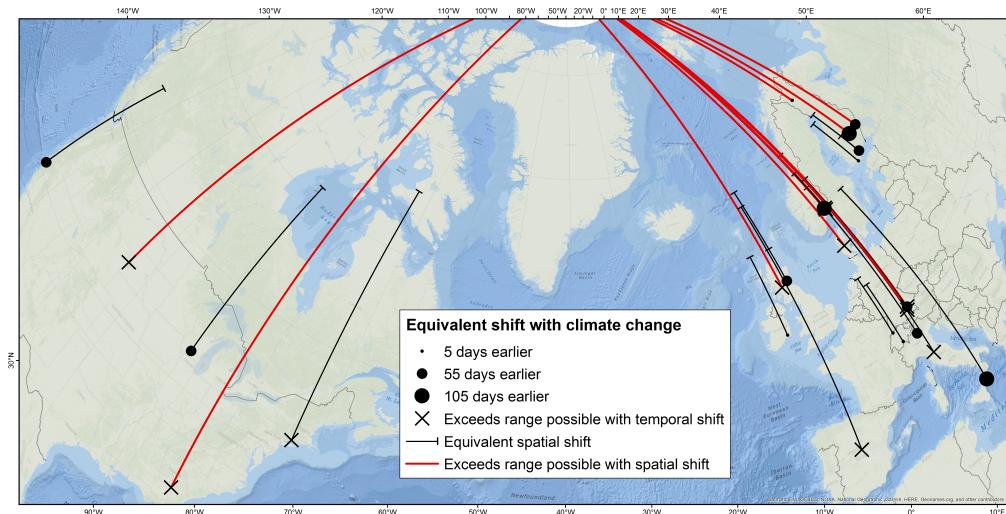


Figure 4: **Experimental photoperiod treatments and their equivalent spatial and temporal shifts** for experiments in the OSPREE database that manipulated photoperiod. See ‘Mapping temporal and spatial shifts in space and time’ in the Supplemental Materials for details on how we calculated the required spatial (lines) or temporal (circles and Xes) shifts to be equivalent to photoperiod treatments in each experiment.

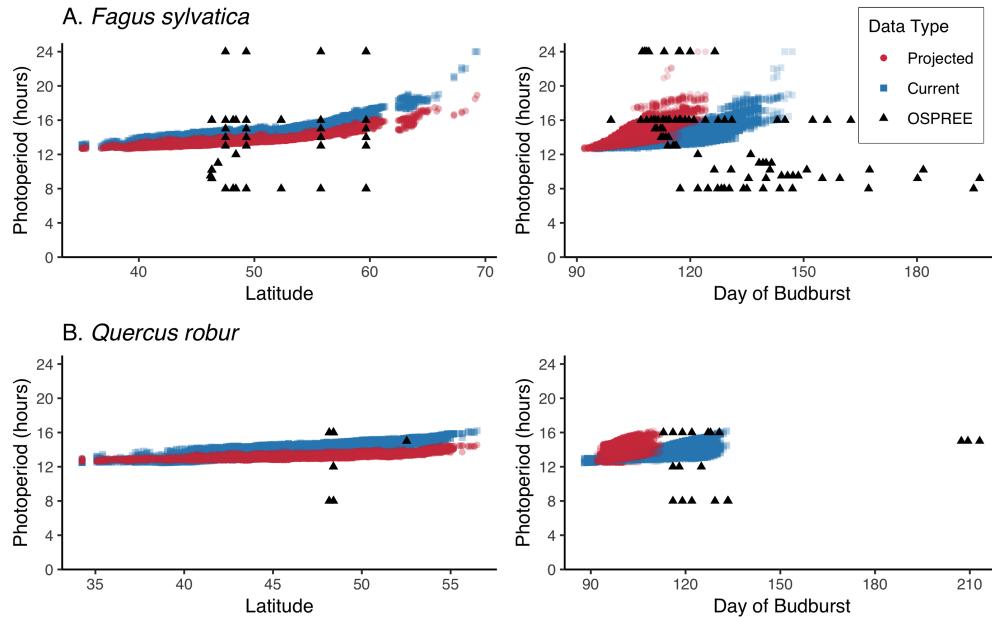


Figure 5: Experienced photoperiods in experiments differ than those in the natural world, shown here by latitude (left panels) and by day of budburst (right panels) for *Fagus sylvatica* (A, upper panels) and *Quercus robur* (B, lower panels). Triangles show experimental treatments of photoperiod in the OSPREE database. To illuminate potential gaps between experiments and the natural world, we show the photoperiod when budburst occurs in its current (1981-2000) and projected ranges, (2081-2100, using the A1Fi Phenofit scenario, see Duputié et al., 2015). We scaled the days to budburst for all OSPREE data points by adding the day of budburst from the first Phenofit observation. See Supplemental Materials and Duputié et al. (2015) for additional details.

Accounting for photoperiod to improve forecasts of biological responses to climate change

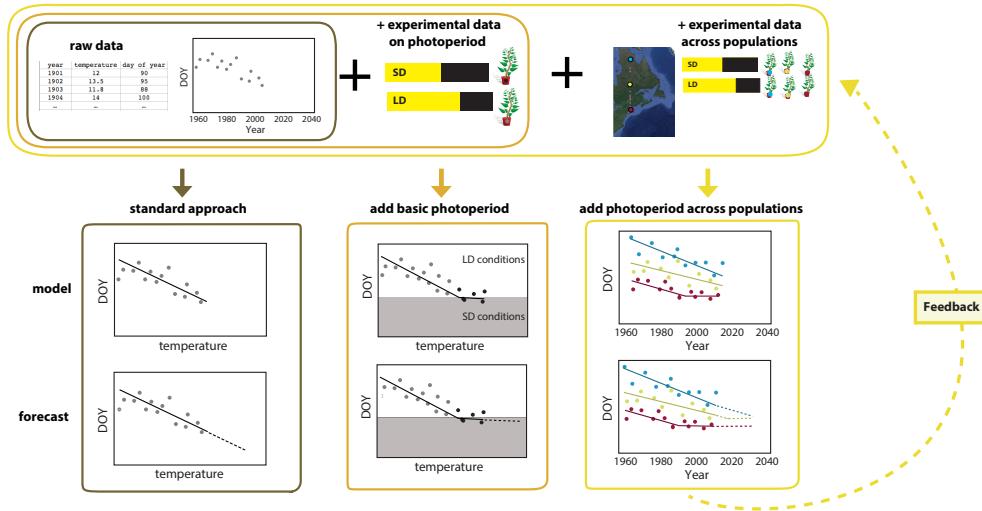


Figure 6: **Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change.** Current approaches for forecasting spring phenology with climate change frequently rely on linear relationships between historical temperature data and observed dates of spring phenology (left panels). Adding responses to photoperiod, which commonly operate as threshold responses to short days (SD) versus long days (LD), will alter these forecasts (center panel) in ways that differ across species that differ in their respective threshold photoperiods. Other factors that interact with photoperiod, such as population-level variation in photoperiod responses, can be incorporated into forecasts to further improve their accuracy (right panel).