

Spatial and temporal shifts in photoperiod with climate change

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Running head Shifts in photoperiod with climate change

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1 Abstract

2 Climate change causes both temporal (e.g., advancing spring phenology) and geographic (e.g., range ex-
3 pansion poleward) species shifts, which affect the photoperiod experienced at critical developmental stages
4 ('experienced photoperiod'). As photoperiod is a common trigger of seasonal biological responses—affecting
5 woody plant spring phenology in 87% of reviewed studies that manipulated photoperiod—shifts in expe-
6 rienced photoperiod may have important implications for future plant distributions and fitness. However,
7 photoperiod has not been a focus of climate change forecasting to date, especially for early-season ('spring')
8 events, often assumed to be driven by temperature. Synthesizing published studies, we find that impacts on
9 experienced photoperiod from temporal shifts could be orders of magnitude larger than from spatial shifts (1.6
10 hours of change for expected temporal versus one minute for latitudinal shifts). Incorporating these effects
11 into forecasts is possible by leveraging existing experimental data; we show that results from growth chamber
12 experiments on woody plants often have data relevant for climate change impacts, and suggest that shifts
13 in experienced photoperiod may increasingly constrain responses to additional warming. Further, combining
14 modeling approaches and empirical work on when, where, and how much photoperiod affects phenology could
15 rapidly advance our understanding and predictions of future spatio-temporal shifts from climate change.

¹⁶ Introduction

¹⁷ Shifts in phenology—i.e., the timing of biological events, including budburst, leafout, and flowering in plants,
¹⁸ as well as bird arrival, egg hatching and myriad other biological activities—are some of the most widely
¹⁹ documented signals of climate change. Spring phenology in particular has shifted, occurring earlier as tem-
²⁰ peratures warm, with average shifts of 1.2 to 5.1 days earlier per decade (Bradley et al., 1999; Parmesan
²¹ and Yohe, 2003; Poloczanska et al., 2013; Root et al., 2003) or 1.3 to 5.6 days earlier per °C of warming
²² (Polgar et al., 2013; Wolkovich et al., 2012). These changes are some of the largest climate change-induced
²³ shifts observed, with early spring phenology shifting more rapidly than later season phenology in most cases
²⁴ (Bradley et al., 1999; Menzel et al., 2006).

²⁵ Phenology is not controlled solely by temperature, however. Photoperiod is also a critical cue, signaling
²⁶ changes in growth and reproduction across diverse species (e.g., Flynn and Wolkovich, 2018; Lagercrantz,
²⁷ 2009; Bradshaw and Holzapfel, 2007; Howe et al., 1996; Solbakken et al., 1994). Even spring phenology, which
²⁸ is highly temperature-sensitive, is thought to be determined interactively by photoperiod and temperature
²⁹ (Fu et al., 2019, see also Box 1). Photoperiod is a useful cue to synchronize activities with seasonal climatic
³⁰ changes (e.g., Singh et al., 2017; Basler and Körner, 2012; Hsu et al., 2011) because it is consistent across
³¹ years, especially compared to other cues such as temperature and precipitation (Saikkonen et al., 2012). For
³² example, relying on a threshold photoperiod (see *Glossary*), rather than temperature alone, may prevent
³³ woody plants from leafing out during ‘false spring’ events (unusually warm periods during winter and early
³⁴ spring that are followed by a return to cold temperatures, Gu et al., 2008).

³⁵ Recent studies suggest that photoperiod cues may eventually restrict phenology in a warmer world. With
³⁶ additional climate change, photoperiod may limit phenological shifts of certain species such that they will
³⁷ not track rising temperatures (Fu et al., 2015; Way and Montgomery, 2015; Basler and Körner, 2012; Körner
³⁸ and Basler, 2010a). The idea of photoperiod constraints is controversial, however, as other studies suggest
³⁹ that photoperiod will not slow responses to warming for most species (Chuine et al., 2010; Zohner et al.,
⁴⁰ 2016). Resolving this debate requires a greater understanding of the extent to which daylength constrains
⁴¹ phenology and how rapidly photoperiod responses can acclimate or adapt to new environmental conditions
⁴² (Grevstad and Coop, 2015).

⁴³ Perhaps because of these variable and uncertain responses, photoperiod is often not included in forecasts of
⁴⁴ biological responses to climate change, especially in the spring, even though it is known to be an important
⁴⁵ cue for biological activity (but see Duputié et al., 2015; Grevstad and Coop, 2015; Caffarra et al., 2011a).

⁴⁶ The exclusion of photoperiod may be problematic: although photoperiod itself is stable over time, the
⁴⁷ photoperiod that species *experience* at critical developmental stages (henceforth, ‘experienced photoperiod’),
⁴⁸ as they undergo climate change-induced shifts in space and time, is likely to be much less stable (Fig. 1).
⁴⁹ This shift in experienced photoperiod extends to distributional shifts due to climate change, as many species’
⁵⁰ distributions have moved poleward and upward in elevation (i.e., range shifts, Chen et al., 2011; Harsch et al.,
⁵¹ 2009; Parmesan, 2006; Peñuelas and Boada, 2003).

⁵² The implications of potential climate change-induced shifts in experienced photoperiod are unclear, as the
⁵³ magnitudes of potential shifts have not been described. Effects of photoperiod shifts may be relatively
⁵⁴ minor, especially compared to the substantial year-to-year variation in experienced photoperiod (Fig. 2).
⁵⁵ Alternatively, photoperiod may begin to constrain species’ responses to climate change (Huffeldt, 2020; Fu
⁵⁶ et al., 2015; Way and Montgomery, 2015; Basler and Körner, 2012; Körner and Basler, 2010a).

⁵⁷ Here, we ask:

- ⁵⁸ 1. How will climate change alter experienced photoperiod for plants?
- ⁵⁹ 2. What are the implications of altered experienced photoperiods for plant responses to climate change?
- ⁶⁰ 3. Can researchers apply data from experiments that alter photoperiod to improve forecasts of biological
⁶¹ implications of climate change?

⁶² Our questions are broadly relevant for diverse species and seasonal events. We use a case study of spring
⁶³ woody plant phenology to illustrate several of our points (Boxes 1 & 2). We focus on spring events, as
⁶⁴ phenology during this time is one of the most widely observed and rapidly changing biological responses to
⁶⁵ climate change (Parmesan, 2006). In addition, the role of photoperiod is less understood in spring phenology
⁶⁶ compared with autumn phenophases (reviewed in, e.g., Azeez and Sane, 2015; Gallinat et al., 2015; Gill
⁶⁷ et al., 2015; Lagercrantz, 2009; Allona et al., 2008), but recent studies showing declines in responses of spring
⁶⁸ budburst to warming (e.g., Fu et al., 2019; Güsewell et al., 2017; Yu et al., 2010) suggest that photoperiod
⁶⁹ constraints may be imminent.

70 How will climate change alter experienced photoperiod for plants?

71 Species experience different photoperiod regimes depending on their location on Earth, the seasonal timing
72 of their activity, and inter-annual variation in climate (Fig. 1). Consider, as an example, the daylength
73 experienced by plants on the date that spring ‘green-up’ occurs. We use green-up date as an example because
74 it represents an important spring event, signaling the start of the growing season, and global estimates are
75 available. Photoperiod on green-up date varies with latitude (Fig. 2A), in part because latitudinal variation
76 in green-up date, which occurs earlier toward the equator and later toward the poles, is strongly driven by
77 climatic differences that affect phenology, and in part because of latitudinal variation in photoperiod (e.g., at
78 the poles, the daylength at the summer solstice is 24 hours; see also Fig. 1). (See “Quantifying and mapping
79 differences in green-up across the United States and Europe” in the *Supplemental Methods* for additional
80 details of this analysis.)

81 Some consistent patterns in experienced photoperiod are apparent at a broad scale. Across years, photoperiod
82 at green-up is longer toward the poles (i.e., on the day of year when green-up occurs close to the north pole,
83 daylength approaches 24 hours in both an average year, Fig. 2A, and in an early year, Fig. 2B). In addition,
84 green-up does not appear to occur at daylengths less than 10 hours across North America and Europe.

85 Despite these consistent broad-scale patterns, there is also strong spatiotemporal variation in experienced
86 photoperiod across years. Comparing the photoperiod at green-up in an ‘early’ versus an ‘average’ year (Fig.
87 2A,B) shows that experienced photoperiod at green-up can vary by two to three hours from one year to the
88 next in the same location (Fig. 2C).

89 Against this existing background variation, climate change will cause shifts in experienced photoperiod as
90 species respond to warming temperatures. Spatial shifts in species’ ranges and temporal shifts in phenology
91 will alter the photoperiods experienced by organisms with future climate change. The magnitude of these
92 alterations will vary depending on the organism’s location and the type of shift(s) it undergoes. For example,
93 poleward shifts in species’ ranges cause plants to experience a wider range of daylength throughout the year
94 (Fig. 1), which may pose challenges to organisms undergoing temperature-induced poleward range shifts
95 (Huffeldt, 2020). Elevational shifts, in contrast, cause minimal change to the range of daylength throughout
96 the year.

⁹⁷ To date, most focus on shifts in photoperiod with climate change has centered on how spatial range shifts
⁹⁸ will affect photoperiod (e.g., Huffeldt, 2020; Way and Montgomery, 2015; Saikkonen et al., 2012). How-
⁹⁹ ever, shifting phenology—especially the large changes seen in spring phenology—will also alter experienced
¹⁰⁰ photoperiod, because of the seasonal patterns of daylength (Fig. 1).

¹⁰¹ Current data suggest that temporal shifts will yield much larger changes in experienced photoperiod than
¹⁰² latitudinal shifts (Fig. 1). Consider a tree species that bursts its buds at latitude 45° , on average around
¹⁰³ day of year 91 (April 2), when daylength is 12.8 hours. If the species' phenology shifts 30 days earlier over
¹⁰⁴ the next century (i.e., a rate of 3 days per decade, as has been observed, Parmesan and Yohe, 2003), it will
¹⁰⁵ experience a daylength that is 1.6 hours shorter. This 1.6 hour decrease in daylength is equivalent to moving
¹⁰⁶ 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.,
¹⁰⁷ 60 km over the next century, comparable to observed rates, Chen et al., 2011; Parmesan and Yohe, 2003), it
¹⁰⁸ will experience a daylength that differs by less than a minute on the same day of year.

¹⁰⁹ Temporal shifts in temperate areas are likely to yield larger changes in experienced photoperiod for autumn
¹¹⁰ phenology, as well. Consider again the tree at latitude 45° , which may senescence on day of year 300 (October
¹¹¹ 27), on average (Gill et al., 2015), when daylength is 10.5 hours. If senescence shifts 33 days later over the
¹¹² next century (i.e., a rate of 3.3 days per decade, as has been observed, Gill et al., 2015), it will experience,
¹¹³ at the end of the growing season, a daylength that is 1.3 hours shorter. This is equivalent to moving up 16°
¹¹⁴ in latitude on this day of year.

¹¹⁵ **What are the implications of altered photoperiods for plant re- 116 responses to climate change?**

¹¹⁷ Climate change alters the experienced photoperiod, but the implications of this change for plants are currently
¹¹⁸ unclear, in part, because phenology both affects and is affected by experienced photoperiod: climate change-
¹¹⁹ induced shifts in phenology alter experienced photoperiod, which in turn affects phenology. Daylength,
¹²⁰ often in combination with temperature, can play a role in controlling critical biological functions, including
¹²¹ vegetative growth, cell elongation, budburst, and flowering in plants (Fu et al., 2019; Heide and Sønsteby, 2012;

¹²² Heide, 2011; Hsu et al., 2011; Sidaway-Lee et al., 2010; Mimura and Aitken, 2007; Linkosalo and Lechowicz,
¹²³ 2006; Erwin, 1998; Ashby et al., 1962). Climate change-induced shifts in photoperiod are therefore likely to
¹²⁴ alter these functions.

¹²⁵ Growth chamber studies show that the magnitude of daylength shifts expected with climate change (i.e., 1-2
¹²⁶ hours of difference in daylength with temporal shifts over the next century) are substantial enough to affect
¹²⁷ spring phenology in trees (Table S1). The direction and magnitude of responses will vary, however, because
¹²⁸ of variation in photoperiod sensitivity, and because photoperiod often interacts with other environmental
¹²⁹ drivers, such as temperature, to affect phenology (Box 1).

¹³⁰ The climate change-induced trend toward ever-earlier springs means that experienced photoperiod may in-
¹³¹ creasingly approach threshold photoperiods (see *Glossary*) for many species, potentially constraining their
¹³² ability to respond to additional warming (Fu et al., 2019; Vitasse and Basler, 2013; Körner and Basler, 2010a;
¹³³ Morin et al., 2010; Nienstaedt, 1966). Interactions between photoperiod and temperature may therefore re-
¹³⁴ sult in muted phenological shifts, compared to what would be expected based on temperature change alone
¹³⁵ (Körner and Basler, 2010a; Mimura and Aitken, 2007; Wareing, 1956). This has been a topic of much interest
¹³⁶ in the climate change literature because it predicts that as photoperiod becomes limiting, average trends of
¹³⁷ earlier spring phenology (Polgar et al., 2013; Peñuelas et al., 2002; Menzel, 2000) and later autumn senescence
¹³⁸ (Gill et al., 2015; Richardson et al., 2018) with warming may stop.

¹³⁹ A challenge in predicting if or when the trends of shifting phenology with warming may slow or stop abruptly
¹⁴⁰ is the wide range of observed photoperiod sensitivity (see *Glossary*) across events (e.g., spring versus fall
¹⁴¹ events Mimura and Aitken, 2010), species (Flynn and Wolkovich, 2018; Zohner et al., 2016; Sanz-Perez
¹⁴² et al., 2009), latitudes (Ettinger et al., 2020; Partanen et al., 2005; Johnsen and Seiler, 1996), populations
¹⁴³ (Gauzere et al., 2017; Saikonen et al., 2012; Caffarra et al., 2011b; Bradshaw and Holzapfel, 2007; Viherä-
¹⁴⁴ Aarnio et al., 2006), and ecotypes (Howe et al., 1995). How much genotype versus environment explain
¹⁴⁵ this variation is an active area of research (e.g., Fréjaville et al., 2019; Franks et al., 2014; Gould et al.,
¹⁴⁶ 2010; Mimura and Aitken, 2010). Environmental conditions clearly play a role: different combinations of
¹⁴⁷ ambient temperature and photoperiod may explain some of this variation, and temperature cues can override
¹⁴⁸ photoperiod requirements under certain conditions (e.g., Tanino et al., 2010). In such cases, future climate
¹⁴⁹ change-induced phenological shifts may occur at different rates than past shifts with warming. On the other

hand, some of this variation may be due to underlying genetic differences driven by local adaptation, because photoperiod responses can be under strong genetic control (Keller et al., 2011; Weih, 2004; Bradshaw and Stettler, 1995, see also Boxes 1, 2). Differences in genetic control of photoperiod may be pronounced across spring versus fall events, as research suggests stronger local adaptation in photoperiod cues for budset than budburst (Mimura and Aitken, 2010), though to date much research focuses on spring or fall events separately, making a robust comparison difficult. Valuable advances to the field may be achieved by increased efforts to compare controls on phenological events across the growing season and how they may be connected, through carbon dynamics or other factors (Zani et al., 2020; Ettinger et al., 2018). Further teasing out the relative roles of genetics versus environmental conditions on phenology will be critical to accurate forecasts under climate change (Pau et al., 2011).

Species- and population-level variation in photoperiod sensitivity may scale up to alter communities as climate change progresses. For example, a species or population that is relatively insensitive to photoperiod can take advantage of warmer springs by having an earlier start to its growing season. Indeed, phenological tracking of temperature (e.g., earlier flowering, leafout or migration with warming) has been linked with higher performance in plants and animals (Cleland et al., 2012; Muir et al., 1994; Willis et al., 2010). 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. Not all studies, however, find links between performance and high sensitivity to temperature (e.g., Block et al., 2020), and early-season species in most temperate zones risk losing tissue to frost (Sakai and Larcher, 1987). Thus, the advantages of tracking warming may depend on how quickly mean temperatures versus last frost dates shift (e.g., Inouye et al., 2002), such that in some systems photoperiod cues could prevent species from starting growth or reproduction too early (when they risk losing their investments in new tissue). To identify where, when, and how communities may be altered therefore requires quantifying species- and potentially population-specific temperature and photoperiod sensitivities, and developing methods that incorporate both photoperiod and environmental events that impact fitness (such as frosts).

₁₇₆ Future directions: outstanding questions and incorporating pho-
₁₇₇ toperiod into forecasting

₁₇₈ The complexity of photoperiod effects on phenology and how warming alters experienced photoperiod high-
₁₇₉ lights that future rates of phenological shifts are unlikely to be straightforward extrapolations from past and
₁₈₀ current rates. Statistical and process-based models—the two broad categories of forecasting approaches—
₁₈₁ both acknowledge this difficulty, but differ importantly in how they relate phenology to climate change.
₁₈₂ Statistical models relating phenology to climate change typically assume linear relationships between species'
₁₈₃ responses and environmental variables (e.g., Flynn and Wolkovich, 2018; Ibáñez et al., 2010), whereas
₁₈₄ process-based models often incorporate nonlinear threshold relationships (e.g. Chuine and Beaubien, 2001;
₁₈₅ Morin and Thuiller, 2009). Further, statistical models of phenology under climate change often ignore pho-
₁₈₆ toperiod, focusing instead on seasonal or annual temperature (e.g. Diez et al., 2012; Ibáñez et al., 2010,
₁₈₇ but see Richardson et al. (2013)), whereas process-based models of phenology more frequently incorporate
₁₈₈ photoperiod, along with temperature (Lundell et al., 2020; Duputié et al., 2015; Zhao et al., 2013; Morin
₁₈₉ and Thuiller, 2009). Process-based models may thus seem superior for integrating photoperiod, but they
₁₉₀ can be challenging to develop, requiring detailed data that are often not readily available (e.g., daily climate
₁₉₁ data, nonlinear biological responses to fine-scale changes in temperature). Perhaps because of this, statistical
₁₉₂ models remain more commonly used in climate change forecasts of biological responses (e.g., García-Valdés
₁₉₃ and Morales-Castilla, 2016; Basler and Körner, 2012; Diez et al., 2012; Zhu et al., 2012; Ibáñez et al., 2010).

₁₉₄ Future modelling of spring plant phenology can incorporate photoperiod by leveraging the large amount of
₁₉₅ experimental data on photoperiod responses (e.g., for woody plants, see Fig. 3, Table S1, Box 1), especially
₁₉₆ when process-based approaches are used. Researchers can use these data to first learn whether the study
₁₉₇ species (or a phylogenetically closely related species) shows a photoperiod effect and, ideally, identify its
₁₉₈ threshold photoperiod and how it varies by population, ecotype, or other factors (Tobin et al., 2008; Bradshaw
₁₉₉ and Holzapfel, 2006). If there is evidence of a photoperiod response (e.g., *Fagus grandifolia*, or *Tilia americana*
₂₀₀ with low chilling, shown in Fig. Box 1-1), daylength should be added to forecasting models. We suggest
₂₀₁ initial models could use a threshold photoperiod to define short-day and long-day conditions (Fig. 4, Box 1),
₂₀₂ then test how much the addition alters forecasts. Given the large change in experienced photoperiod with

203 temporal shifts (Fig. 1), this may be particularly important for phenological forecasting. Since spatial shifts
204 are associated with smaller changes in experienced photoperiod, it may be less important for distribution
205 forecasts. Many species, however, may shift in *both* space and time simultaneously. Thus, even though
206 experienced photoperiod changes little as species distributions shift in space, phenology may be altered
207 significantly if the newly expanded portions of the range contain novel environmental conditions (e.g., Martin
208 et al., 2014).

209 For some species, experimental data can be immediately used in forecasting because experiments manipulate
210 photoperiod at relevant scales (e.g., Heide and Sonsteb, 2015; Basler and Körner, 2014, Fig. 3, Box 1,
211 Table S1). For example, photoperiod treatments from growth chamber experiments with *Fagus sylvatica*
212 span the variation in both current and expected future ranges (Box 1, Duputié et al., 2015), and may allow
213 identification of threshold photoperiods (Fig. 4). In other cases, attempting to incorporate photoperiod
214 into forecasts of future phenology will reveal gaps in our understanding of many aspects of photoperiod
215 responses. For example, photoperiod treatments from existing experiments of *Quercus robur* do not accurately
216 represent experienced photoperiods from current or future estimates (Box 1), making fine-scale projections
217 difficult, even for this relatively well-studied species. This gap extends to many species, as most experiments
218 manipulate photoperiod much more dramatically than will occur with climate change (Fig. 3, Box 1).
219 Although these studies can be useful for a mechanistic understanding of photoperiod responses, extrapolating
220 them to climate change models may not be reasonable.

221 Photoperiod is not fully integrated into most forecasts of biological responses to climate change (but see
222 Tobin et al., 2008, for an example in insects), an omission that could affect forecast accuracy. Photoperiod
223 is incorporated into some ecosystem models (e.g., the Ecosystem Demography model Jolly et al., 2005;
224 Medvigy et al., 2013) used for forecasting but not others (e.g., Richardson et al., 2012), and is rarely included
225 in species distribution models (e.g., Morin and Thuiller, 2009; Zhu et al., 2012). The sensitivity of model
226 outcomes to assumptions made about experienced photoperiod and threshold responses to photoperiod needs
227 further study, including understanding how variation in photoperiod responses across ecosystems, species,
228 populations, and life stages impacts forecasts. We have focused here on spring phenology, but future work
229 could also address the sensitivity of model outcomes to shifts in experienced photoperiod at the end of the
230 growing season (e.g., leaf senescence and onset of dormancy). Autumn photoperiod affects photosynthesis,

²³¹ growth, and budset in woody plant species, and photoperiod-induced declines in photosynthetic capacity may
²³² constrain carbon sequestration even if warming prolongs leaf senescence (Howe et al., 1996; Bauerle et al.,
²³³ 2012; Stinziano and Way, 2017).

²³⁴ As researchers more fully integrate experienced photoperiod into forecasting, a critical area of further study
²³⁵ is understanding *how* photoperiod acts as a cue. For some species, photoperiod responses are qualitative
²³⁶ (that is, there is a threshold photoperiod with long-day responses differing from short-day responses; see
²³⁷ *Glossary*), whereas other species appear to exhibit quantitative responses to photoperiod (Wareing, 1956).
²³⁸ Photoperiod seems to interact with temperature to affect phenology (e.g., Zydlewski et al., 2014); this would
²³⁹ explain the divergent effects of photoperiod observed across studies in woody plants (Box 1). However,
²⁴⁰ exactly how it interacts with temperature is not well-defined for most taxa. For many species, additional
²⁴¹ experimental and physiological research is necessary, since the dormancy-breaking processes that photoperiod
²⁴² affect require detailed physiological approaches to observe. Though the main ecophysiological processes
²⁴³ involved in regulating phenology of woody plants are relatively well-documented, a mechanistic understanding
²⁴⁴ of the physiological, molecular, and genetic bases of dormancy is lacking (Box 2, Hänninen et al., 2019; Chuine
²⁴⁵ et al., 2016). In addition, photoperiod and temperature cues can differentially affect the phenology of distinct
²⁴⁶ physiological processes in woody species, decoupling, for example, responses of growth or leaf development and
²⁴⁷ carbon uptake to warming (Stinziano and Way, 2017; Bauerle et al., 2012). Accounting for ecophysiological
²⁴⁸ effects of photoperiod can result in quantifiable declines on modeled global gross primary production (Bauerle
²⁴⁹ et al., 2012), suggesting that including temporal and spatial shifts in experienced photoperiod with climate
²⁵⁰ change may also alter global model estimates.

²⁵¹ Understanding the drivers, as well as the consequences, of variation in photoperiod responses within and across
²⁵² individuals, populations, and species will be critical for forecasting. Incorporating trait and/or phylogenetic
²⁵³ frameworks may provide useful avenues for improving forecasts (Buckley and Kingsolver, 2012). For example,
²⁵⁴ what traits are associated with photoperiod sensitivity and does variation in photoperiod sensitivity or related
²⁵⁵ traits have a strong genetic component? If so, are species or populations from some locations or lineages
²⁵⁶ more likely than others to be constrained by photoperiod in their responses to climate change? More accurate
²⁵⁷ forecasts will facilitate improved understanding of the implications of shifts in experienced photoperiod for
²⁵⁸ carbon sequestration under climate change at a global scale.

₂₅₉ **Conclusions**

₂₆₀ Organisms may undergo large changes to the photoperiod they experience with climate change, even if they
₂₆₁ do not shift their ranges spatially. Here we have highlighted that these altered photoperiods may stall
₂₆₂ phenological shifts with future warming (e.g., Table S1, Fu et al., 2019; Güsewell et al., 2017; Yu et al.,
₂₆₃ 2010), with cascading effects on growth, fitness, and community composition due to the large variation in
₂₆₄ photoperiod responses across species and populations (Box 1). We have focused on woody plant phenology,
₂₆₅ but shifts in photoperiod with climate change have implications for a variety of plant and animal responses,
₂₆₆ as daylength affects critical activities for species from insects (Bradshaw and Holzapfel, 2006) and salmon
₂₆₇ (Taranger et al., 2003) to birds (Dawson et al., 2001) and marsupials (McAllan et al., 2006). Given what we
₂₆₈ know, incorporating photoperiod into forecasting of climate change responses should improve model accuracy
₂₆₉ (Fig. 4), and will illuminate additional experiments that could improve our mechanistic understanding of
₂₇₀ photoperiod as a critical cue for diverse biological responses.

₂₇₁ **Glossary**

- ₂₇₂ • budburst: one or more leaf buds have visible green tips.
- ₂₇₃ • chilling: the intensity and duration of winter temperature, often a certain sum of chilling (e.g., amount
₂₇₄ of hours or days of cold temperatures, defined by a specific critical temperature or range of temperatures,
₂₇₅ such as between 0 and 7.2 °C, Richardson, 1974) that is required to initiate budburst.
- ₂₇₆ • daylength: the period of time during a 24-hour period during which an organism receives light.
- ₂₇₇ • dormancy: halted or reduced growth or activity.
- ₂₇₈ • forcing: warm spring temperatures, often a certain sum of forcing (e.g., amount of hours or days above
₂₇₉ a specific temperature) that is required before budburst can occur.
- ₂₈₀ • green-up: the beginning of a new cycle of plant growth, usually evaluated at the landscape scale.
- ₂₈₁ • phenology: the timing of life cycle events in organisms.

- 282 • photoperiod: the daily duration of light (daylength) and dark to which an organism is exposed; often
283 used synonymously with daylength.
- 284 • photoperiod sensitivity: the degree to which phenology is controlled by daylength; may be a nonlinear,
285 or ‘threshold’, response in plants (Box 2).
- 286 • photoperiodism: the ability of an organism to assess or respond to length of day or night in its behavior,
287 physiology, growth, development, or reproduction.
- 288 • threshold photoperiod: length of day that causes an organism to switch from a short- to a long-day
289 response (or vice versa). For example, in European larch (*Larix decidua*), budburst development may
290 be constrained under short-day conditions, when daylengths are less than a threshold photoperiod of
291 10-11 hours (Migliavacca et al., 2008). Above this threshold photoperiod, the long-day response of
292 unconstrained budburst development can occur.

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609 Figures

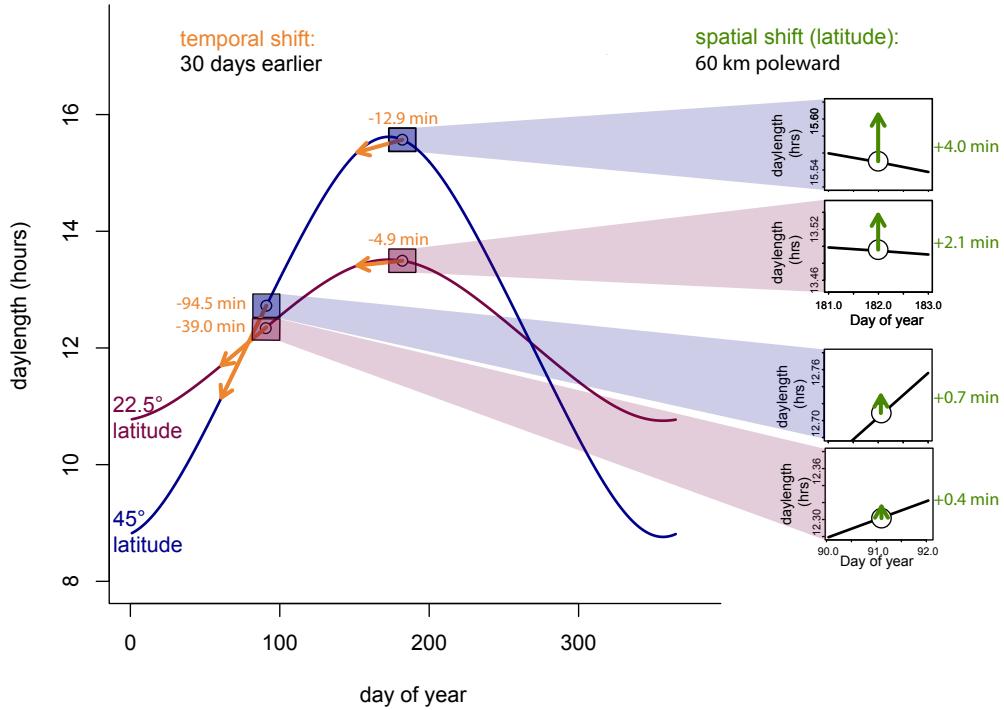


Figure 1: **Temporal (i.e., phenological) shifts in activity yield larger changes in experienced photoperiod compared to spatial (i.e., latitudinal) shifts** on the same day of year, due to patterns in photoperiod variation with latitude and by day of year. Here, we show this variation at two latitudes (22.5° , 45°), using hypothetical spatial and temporal shifts. These shifts are based on observed rates with recent global warming: for spatial shifts, 6–17 kilometers per decade, or approximately $0.5\text{--}1.5^\circ$ in 100 years (Parmesan and Yohe, 2003; Parmesan, 2006); for temporal shifts, 3 days per decade, or 30 days in 100 years (Parmesan, 2006; Chen et al., 2011). These potential, plausible shifts highlight the greater magnitude in daylength changes from temporal shifts in the early spring, close to the vernal equinox (e.g., day of year 91), versus close to the summer solstice (e.g., day of year 182) at temperate latitudes. It is also apparent that early spring temporal shifts at high latitudes result in more extreme changes in daylength than shifts at lower latitudes (e.g., a temporal shift 30 days earlier results in a reduction in daylength of 94.5 minutes at 45° versus 39.5 minutes at 22.5°).

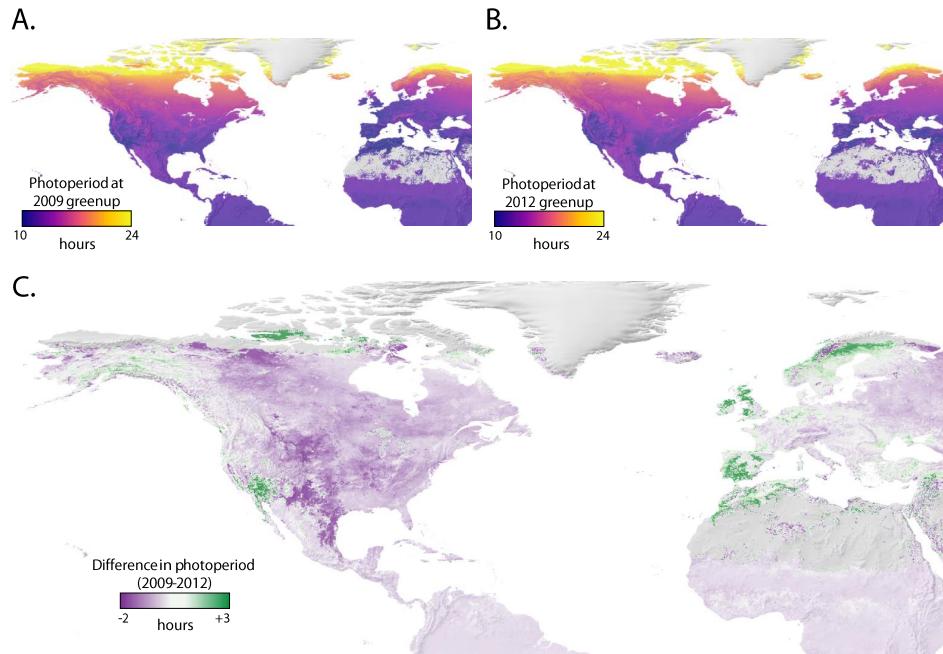


Figure 2: Photoperiod on ‘green-up’ date varies over space and between years ‘Green-up’ date is the beginning of seasonal greening, identified by satellite remote sensing measurements, taken regularly throughout the year, of concentrations of green leaf vegetation. Hours of daylight are shown on the date of spring green-up (here 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). 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. See “Quantifying and mapping differences in green-up across the United States and Europe” in the *Supplemental Methods* for additional details.

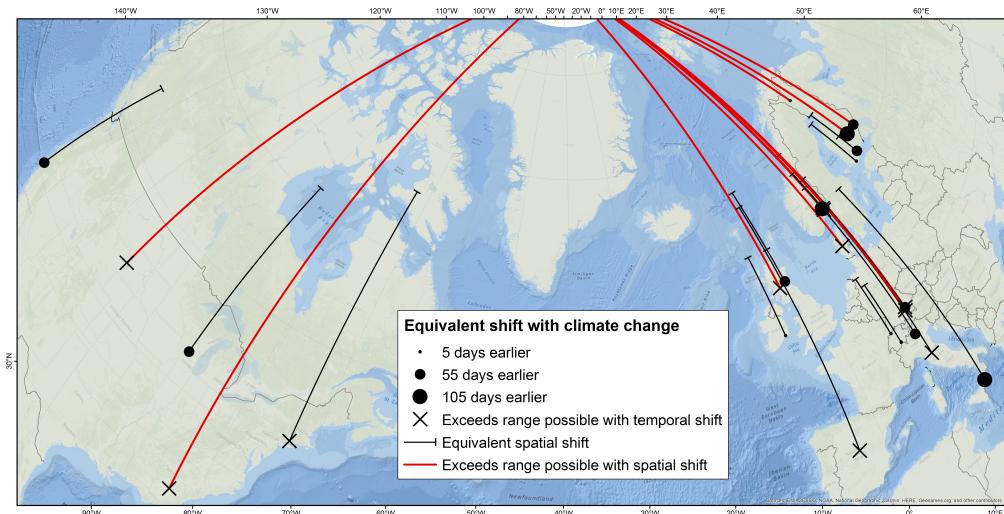


Figure 3: A map of experimental photoperiod treatments from a meta-analysis of woody plant spring phenology and their equivalent spatial and temporal shifts demonstrates that many experiments manipulate photoperiod more dramatically than will occur with climate change. Mapped points (circles and Xes) are locations of experiments in Wolkovich et al. (2019) that manipulated photoperiod (30 total experiments; see Box 1). In 11 out of 30 cases, the difference between experimental treatments exceeded the range in photoperiod experienced across the entire year at the study latitude (Xs; circles mark temporal shifts within a possible range). Note that many studies occur at high latitudes, which experience a wide range of photoperiod across the year. In 13 out of 30 cases, the experimental treatment differences exceeded the photoperiod change that would be experienced with a latitudinal shift of up to 40° (red lines; black lines represent spatial shifts within a possible range). See “Mapping temporal and spatial shifts in space and time” in the *Supplemental Methods* for additional details.

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

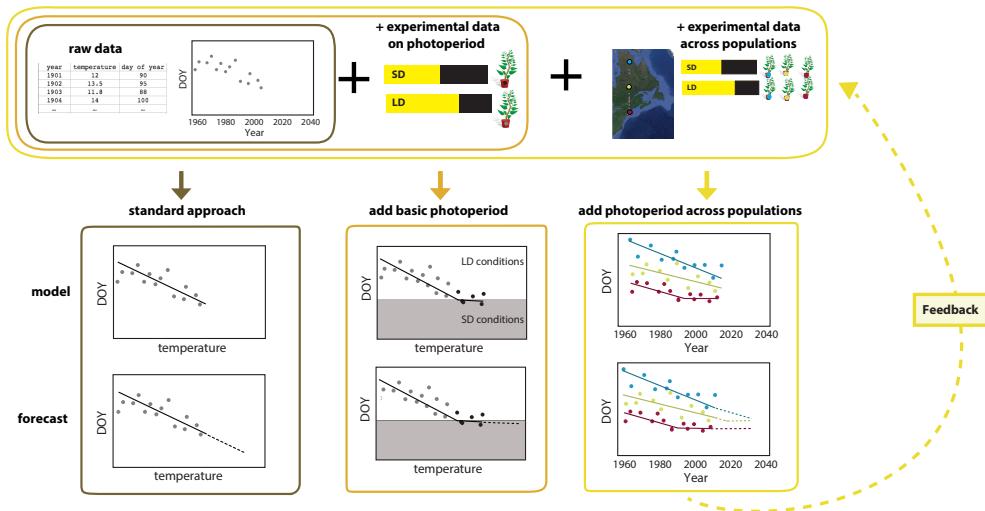


Figure 4: **Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change.** Current approaches for forecasting spring phenology with climate change frequently rely on linear relationships between historical temperature data and observed dates of spring phenology (left panels). Adding responses to photoperiod, which may operate as threshold responses to short days (SD) versus long days (LD, see ‘photoperiod sensitivity’ in the *Glossary* and Box 2 for details), will alter these forecasts (center panel) in ways that differ across species with divergent threshold photoperiods. Other factors that interact with photoperiod, such as population-level variation in photoperiod responses, can be incorporated into forecasts to further improve their accuracy (right panel).

610 **Box 1. Are photoperiod effects widespread? A case study of woody**
611 **plant spring phenology**

612 Photoperiod responses are well-studied in woody plant phenology, making this a useful case study to con-
613 sider climate change-induced shifts in photoperiod. Spring woody plant phenology in particular has critical
614 implications for global carbon cycling and feedbacks to the climate system (Richardson et al., 2013), and
615 has been at the center of an important and controversial debate on the relative effects of photoperiod versus
616 temperature on phenology (e.g., Fu et al., 2019; Chuine et al., 2010; Körner and Basler, 2010a,b).

617 Experimental growth chamber studies have shown that photoperiod is an important cue for spring budburst
618 phenology in woody plants (e.g., Flynn and Wolkovich, 2018; Basler and Körner, 2014; Heide, 1993b). These
619 experiments often manipulate photoperiod in combination with temperature to address basic questions about
620 how these two environmental conditions act as biological cues. Temperature has a dual role in regulating
621 woody plant phenology: chilling—the prolonged exposure to cold temperatures after growth cessation in the
622 fall—is required to initiate budburst, and forcing—prolonged exposure to warm temperatures—is required
623 for budburst to occur. Different photoperiod treatments are typically applied during the forcing treatment
624 phase in growth chamber experiments (e.g., Laube et al., 2014; Spann et al., 2004; Falusi and Calamassi,
625 1990; Heide, 1977; Campbell and Sugano, 1975).

626 Woody plant growth chamber studies have been conducted for decades, but have only recently been synthe-
627 sized to show that photoperiod sensitivity is widespread, with large variation across studies and species. These
628 studies were aggregated in Observed Spring Phenology Responses in Experimental Environments (OSPREE),
629 a new database of plant growth chamber studies that manipulate photoperiod and temperature to measure
630 plant phenological responses, such as budburst and flowering (Wolkovich et al., 2019). The database includes
631 studies that manipulate photoperiod (by applying treatments with different daylength durations, applying
632 long-day versus short-day conditions for different lengths of time, and/or applying varying versus constant
633 photoperiods) and temperature (by imposing different chilling and/or forcing treatments). The OSPREE
634 database spans 201 woody plant species; all experiments in the database use dormant plant tissue (grown
635 in greenhouses or taken directly from the field) exposed to experimental conditions for which we could iden-
636 tify forcing, photoperiod, and chilling treatments quantitatively. See *Supplemental Methods*, Ettinger et al.

637 (2020), and Wolkovich et al. (2019) for details.

638 Growth chamber experiments in OSPREE suggest that the dominant photoperiod response in woody plant
639 species is earlier and more rapid budburst with longer days (e.g., Caffarra and Donnelly, 2011). Thirty of
640 the 72 studies in the OSPREE database included two or more different photoperiod treatments. Of these,
641 26 (87%) found significant photoperiod main effects or significant interactive effects with temperature (i.e.,
642 photoperiod x temperature effects), across 176 species (Table S1). Main effects included responses such as
643 growth (e.g., higher growth rates with longer days Ashby et al., 1962) and reproduction (e.g., increased
644 flowering with longer days Heide and Sønsteby, 2012).

645 Growth chamber experiments highlight that responses to photoperiod vary depending on temperature condi-
646 tions. For example, an accelerated advance of budburst was observed under long versus short days with low
647 chilling, relative to budburst with high chilling in *Betula payrifera* (Hawkins and Dhar, 2012, see Fig. Box
648 1-1). Similarly, across species, as chilling accumulates from winter to spring, sensitivity to both forcing and
649 photoperiod sensitivity can decrease (Malyshev et al., 2018). Frequently, long photoperiods can compensate
650 for low amounts of chilling (Caffarra et al., 2011b; Myking and Heide, 1995; Heide, 1993a).

651 Woody plant growth chamber experiments also demonstrate that, though photoperiod responses are common,
652 they are variable, as shown in Fig. Box 1-1. Responses to photoperiod differ by species (e.g., Flynn and
653 Wolkovich, 2018; Zohner et al., 2016; Basler and Körner, 2014, 2012; Howe et al., 1996; Heide, 1993b). For
654 example, with longer chilling treatments some species seem insensitive to daylength (e.g., *Hammamelis* spp.,
655 *Prunus* spp., Zohner et al., 2016), whereas others seem to be highly sensitive to daylength (e.g. *Fagus*
656 spp., Fig. Box 1-2A), even with long chilling treatments (Zohner et al., 2016). In addition, some species
657 demonstrate a response to photoperiod opposite to that typically observed: *Tilia*, for example, showed delayed
658 budburst with longer daylengths (see Fig. Box 1-1, Ashby et al., 1962). Photoperiod sensitivity also varies
659 by population and ecotype (e.g., Fig. Box 1-1). For example, photoperiod effects on budburst were more
660 significant for lower latitude populations of *Betula pendula* and *B. pubescens* (Partanen et al., 2005).

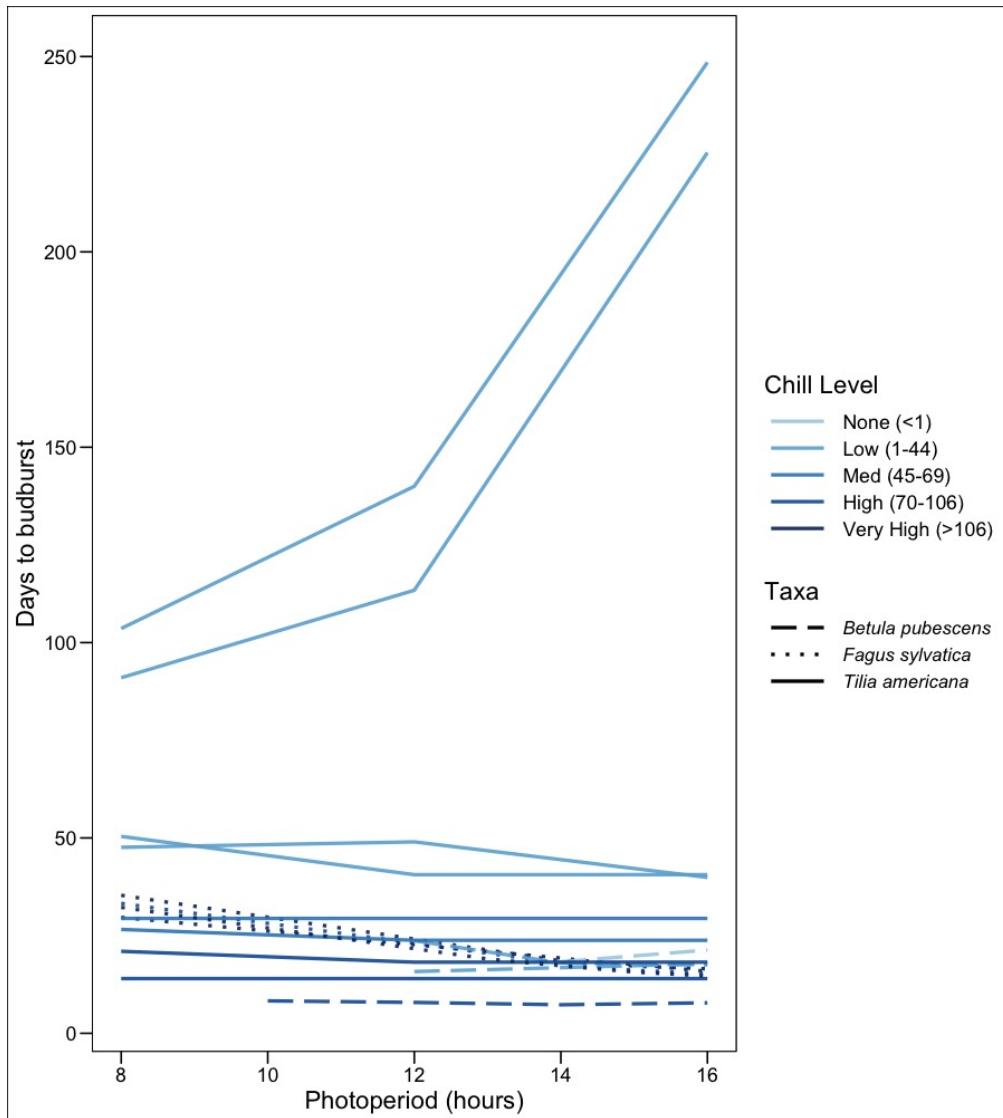


Figure Box 1-1: Nonlinearities in phenological responses to daylength are apparent in spring woody plant phenology experiments. Shown are responses from all experiments from Wolkovich et al. (2019) in which three or more photoperiod treatment levels were applied. The shape of the response curves for *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 Fishman et al., 1987, , with darker blue indicating more chilling). Species and chilling levels with multiple lines represent plant material from different populations. See “Nonlinearities in phenological responses to daylength” in the *Supplemental Methods* for additional details.

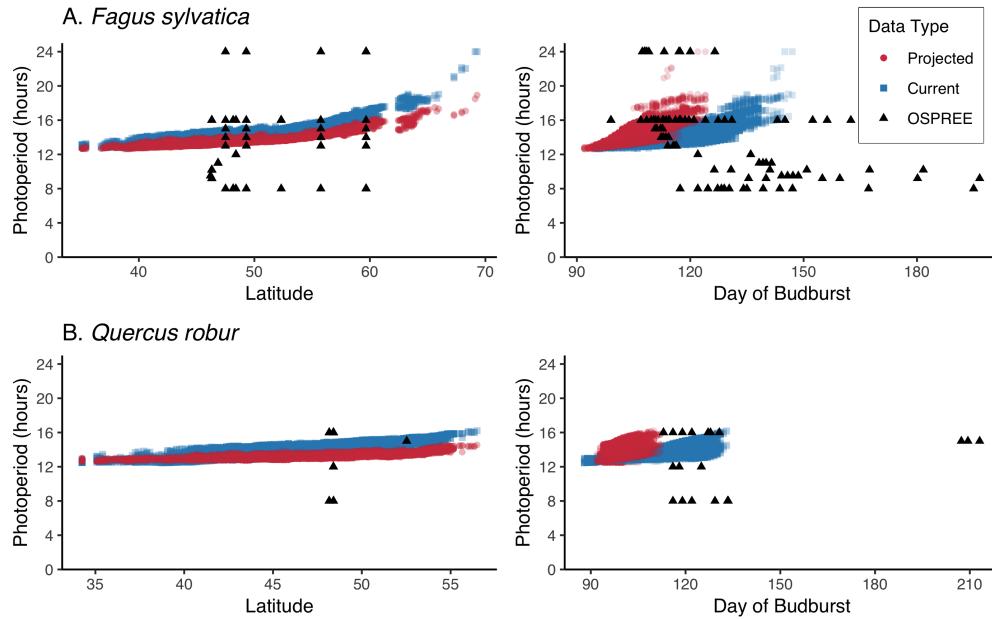


Figure Box 1-2: **Experienced photoperiods in growth chamber experiments differ from those in the natural world**, shown here by latitude (left panels) and by day of budburst (right panels) for *Fagus sylvatica* (A, upper panels) and *Quercus robur* (B, lower panels). Triangles show experimental treatments of photoperiod in Wolkovich et al. (2019). 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 data points in Wolkovich et al. (2019) by adding the day of budburst from the first Phenofit observation. See “Comparing shifts in experienced photoperiod in experiments to those in the natural world with climate change” in *Supplemental Methods* and Duputié et al. (2015) for additional details.

661 **Box 2. Dominant models of how photoperiod affects spring woody**

662 **plant phenology**

663 The cues and molecular pathways underlying photoperiod sensitivity are poorly understood for most organ-
664 isms, even in relatively well-studied phenophases and taxa, such as spring budburst in woody plants (Ding
665 and Nilsson, 2016). Decades of growth chamber experiments demonstrate that three main cues—chilling,
666 forcing, and photoperiod—control spring budburst for woody species (Flynn and Wolkovich, 2018; Zohner
667 et al., 2016; Heide, 2008), with many models suggesting a dominant role of forcing in most natural conditions.
668 Forcing requirements, however, appear to increase given shorter photoperiods or lower chilling (Caffarra et al.,
669 2011a; Chuine et al., 2010). Research has yet to fully tease out effects of these three cues, their interactions,
670 and their prevalence; photoperiod responses appear variable across species and populations, as well as with
671 different chilling treatments (see Box 1). Not surprisingly, there is currently little agreement on the under-
672 lying model for how photoperiod affects spring phenology for most species (Chuine et al., 2016; Hänninen
673 et al., 2019). More physiological research will likely be necessary for major advances, as understanding the
674 exact cellular pathways through which chilling, forcing, and photoperiod act appears increasingly critical to
675 accurate modelling (van der Schoot et al., 2014; Hänninen et al., 2019).

676 Additional cellular and molecular studies may quickly advance understanding and scale up to improved
677 photoperiod models. While our understanding of how plants interpret photoperiod at the molecular-level
678 comes from few species, largely from studies of flowering in the model plant *Arabidopsis thaliana* (e.g.,
679 Suárez-López et al., 2001) and fall budset in woody plant species (e.g., Howe et al., 1996), these studies have
680 proved useful across other species. For example, the ‘external coincidence model’ (where plants sense light
681 via blue light receptors and phytochromes, then interpret photoperiod through a coordinated response to
682 light in relation to the time of day, see Lagercrantz, 2009) has been most widely studied in *Arabidopsis*, but
683 appears to be a relevant mechanism for photoperiod responses in diverse perennial and woody plant species
684 (Singh et al., 2017; Petterle et al., 2013; Andrés and Coupland, 2012; Kobayashi and Weigel, 2007; Davis,
685 2002; Bastow and Dean, 2002; Bünning, 1936). The model proposes the existence of a circadian rhythm of
686 light sensitivity, in which the night-phase is sensitive to light and the day-phase is insensitive to light. As days
687 get longer in the spring, daylight illuminates the light sensitive phase, triggering a response. This provides a

688 clear mechanistic pathway to build into models (Burghardt et al., 2015).

689 We expect progress on spring phenology will benefit from similar physiological research that spans the molec-
690 ular to whole-plant levels. To date, little is known about the genetic pathways responsible for the light-sensing
691 apparatuses involved in spring budburst, and how they may vary across species or populations. Some genes
692 have been identified that play a role in coordinating budburst in poplar (*Populus* spp.), and may occur in
693 other woody species as well. Many similarities exist between the proposed regulatory networks of vegetative
694 growth in *Populus* and those controlling floral initiation in *Arabidopsis*, (Ding and Nilsson, 2016). For exam-
695 ple, vegetative growth and inhibition of budset are promoted by the FLOWERING LOCUS T2 (FT2) gene, a
696 homolog of *Arabidopsis thaliana* gene FLOWERING LOCUS (FT). FT2 expression appears to be controlled
697 by a pathway that is effective in long days and warm temperatures, marking the onset of the growing season
698 (Hsu et al., 2011). Its loss of expression in autumn, when the days are getting shorter, is associated with the
699 onset of dormancy (Glover, 2014).

700 Efforts to better map the genetic and cellular pathways of spring phenology combined with common garden
701 studies can provide a powerful method to test mechanistic understanding and improve models (e.g., Burghardt
702 et al., 2015; Fournier-Level et al., 2016). Here we have mainly outlined how to combine growth chamber studies
703 with long-term data to improve models and forecasting; a greater physiological understanding of at least a
704 few species will likely also be necessary for generating robust predictions with climate change.