

Spatial and temporal 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 shifts (e.g., range
3 expansion poleward) in species; these shifts affect the photoperiod experienced. As photoperiod is a common
4 trigger of seasonal biological responses—affecting plant phenology in 84% of reviewed studies that manipu-
5 lated photoperiod—shifts in experienced photoperiod may have important implications for future distribu-
6 tions and fitness. However, photoperiod has not been a focus of climate change forecasting to date, especially
7 for early-season ('spring') events often assumed to be driven by temperature. We synthesize published studies
8 to show that impacts on experienced photoperiod from temporal shifts could be orders of magnitude larger
9 than from spatial shifts (1.6 hours of change for expected temporal versus one minute for latitudinal shifts).
10 Incorporating these effects into forecasts is possible by leveraging existing experimental data. For example,
11 growth chamber experiments on woody plant spring phenology often have data relevant for climate change
12 impacts, and suggest that shifts in experienced photoperiod may increasingly constrain responses to addi-
13 tional warming. We highlight how combining modeling approaches and empirical work on when, where, and
14 how much photoperiod affects spring phenology could rapidly advance our understanding and predictions of
15 future spatio-temporal shifts from climate change.

¹⁶ Introduction

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

²⁵ Spring phenology is not controlled solely by temperature, however. Photoperiod is also a critical cue, signalling
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), and spring phenology is
²⁸ thought to be determined interactively by photoperiod and temperature (Fu et al., 2019, see also Box 1).

²⁹ Photoperiod is a useful cue to synchronize activities with seasonal climatic changes (e.g., Singh et al., 2017;
³⁰ Basler and Körner, 2012; Hsu et al., 2011) because it is consistent across years, especially compared to other
³¹ cues such as temperature and precipitation (Saikkonen et al., 2012). For example, relying on a threshold
³² photoperiod (see *Glossary*), rather than temperature alone, may prevent woody plants from leading out during
³³ “false spring” events (unusually warm periods during winter that are followed by a return to cold temperatures
³⁴ Gu et al., 2008).

³⁵ Recent studies suggest that photoperiod cues may eventually restrict advances in spring phenology in a warmer
³⁶ world. With additional climate change, photoperiod will limit phenological shifts of certain species such that
³⁷ they will not track rising temperatures (Fu et al., 2015; Way and Montgomery, 2015; Basler and Körner,
³⁸ 2012; Körner and Basler, 2010a). Instead, these species’ responses will increasingly become constrained by
³⁹ daylength and the trend of ever-earlier springs with warming may halt. The idea of photoperiod constraints is
⁴⁰ controversial, however, as other studies suggest that photoperiod will not constrain responses to warming for
⁴¹ most species (Chuine et al., 2010; Zohner et al., 2016). The extent to which daylength constrains phenology
⁴² will depend in part on how rapidly photoperiod responses can acclimate or adapt to new environmental

43 conditions, which remains poorly understood (Grevstad and Coop, 2015).

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

47 The exclusion of photoperiod may be problematic: although photoperiod itself is stable over time, the
48 photoperiod that species *experience*, as they undergo climate change-induced shifts in space and time, is
49 likely to be much less stable. In addition to shifting activity earlier with recent warming, many species have
50 shifted their distributions poleward and upward in elevation (i.e., range shifts, Chen et al., 2011; Harsch et al.,
51 2009; Parmesan, 2006; Peñuelas and Boada, 2003). These spatial and temporal shifts alter the photoperiod
52 experienced by organisms (Fig. 1).

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

58 Here, we ask:

59 1. How will climate change alter the photoperiod experienced by organisms?

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

61 3. Can researchers apply data from experiments that alter photoperiod to aid in forecasting biological
62 implications of climate change?

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

⁶⁹ we use a case study of spring woody plant phenology to illustrate some of our points (Boxes 1, 2).

⁷⁰ **How will climate change alter the photoperiod experienced by organisms?**

⁷² Species experience different photoperiod regimes depending on their location on Earth, the seasonal timing
⁷³ of their activity, and inter-annual variation in climate (Fig. 1, 2). Consider, as an example, the daylength
⁷⁴ experienced by plants on the date that spring “green-up” occurs. Spring green-up varies with latitude (Fig.
⁷⁵ 2a), in part because latitudinal variation in green-up date, which occurs earlier toward the equator and later
⁷⁶ toward the poles, is strongly driven by climatic differences that affect phenology, and in part because of
⁷⁷ latitudinal variation in photoperiod (e.g., at the poles, the daylength at the summer solstice is 24 hours; see
⁷⁸ also Fig. 1).

⁷⁹ Some consistent patterns in experienced photoperiod are apparent at a broad scale. Across years, photoperiod
⁸⁰ at green-up is longer toward the poles (i.e., on the day of year when green-up occurs close to the north pole,
⁸¹ daylength approaches 24 hours in both an average year, Fig. 2A, and in an early year, Fig. 2B). In addition,
⁸² green-up does not appear to occur at daylengths less than 10 hours, across North America and Europe.

⁸³ Despite these consistent broad-scale patterns, there is also strong spatiotemporal variation in experienced
⁸⁴ photoperiod across years. Comparing the photoperiod at green-up in an “early” versus an “average” year (Fig.
⁸⁵ 2) shows that experienced photoperiod at green-up can vary by two to three hours from one year to the next
⁸⁶ in the same location (Fig. 2C). We use green-up date as an example here because it is an available dataset
⁸⁷ and represents an important biological event, signalling the start of the growing season.

⁸⁸ Against this existing background variation, climate change will cause shifts in experienced photoperiod as
⁸⁹ species respond to warming temperatures. Spatial shifts in species’ ranges and temporal shifts in phenology
⁹⁰ will alter the photoperiods experienced by organisms with future climate change. The magnitude of these
⁹¹ alterations will vary depending on the organism’s location and the type of shift(s) it undergoes. For example,
⁹² poleward shifts in species’ ranges cause organisms to experience a wider range of daylength throughout the
⁹³ year (Fig. 1). Elevational shifts, in contrast, cause minimal change to the range of daylength throughout the

94 year.

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

99 Despite a focus on range shifts, current data suggest that temporal shifts will yield much larger changes
100 in experienced photoperiod than latitudinal shifts (Fig. 1). Consider a tree species that bursts its buds
101 at latitude 45° , on average around day of year 91 (April 2), when daylength is 12.8 hours. If the species'
102 phenology shifts 30 days earlier over the next century (i.e., a rate of 3 days per decade, as has been observed,
103 Parmesan and Yohe, 2003), it will experience a daylength that is 1.6 hours shorter. This 1.6 hour decrease
104 in daylength is equivalent to moving up 28.5° in latitude on this day of year. However, if the same species
105 shifts its range up in latitude 0.5° (i.e., 60 km over the next century, comparable to observed rates, Chen
106 et al., 2011; Parmesan and Yohe, 2003), it will experience a daylength that differs by less than a minute on
107 the same day of year.

108 In many cases organisms may shift both their ranges and their phenology simultaneously (i.e., due to new
109 climatic conditions, Duputié et al., 2015). In addition, photoperiod sensitivity (see *Glossary*) can vary with
110 latitude, likely due to population-level differences in sensitivity (Gauzere et al., 2017; Saikkonen et al., 2012;
111 Caffarra et al., 2011b; Bradshaw and Holzapfel, 2007; Viherä-Aarnio et al., 2006; Partanen et al., 2005; Howe
112 et al., 1996). With future climate change, it is unclear how these complexities will affect the photoperiod
113 experienced by organisms and whether these shifts in photoperiod will have important implications for biolog-
114 ical responses. This lack of clarity stems, in part, from the fact that phenology both affects and is affected by
115 experienced photoperiod: climate change-induced shifts in phenology alter experienced photoperiod, which
116 in turn affects phenology.

¹¹⁷ **What are the implications of altered photoperiods for biological
118 responses to climate change?**

¹¹⁹ Daylength, often in combination with temperature, can play a role in controlling critical biological functions,
¹²⁰ including vegetative growth, cell elongation, budburst, and flowering in plants (Fu et al., 2019; Heide and
¹²¹ Sønsteby, 2012; Heide, 2011; Hsu et al., 2011; Sidaway-Lee et al., 2010; Mimura and Aitken, 2007; Linkosalo
¹²² and Lechowicz, 2006; Erwin, 1998; Ashby et al., 1962) Climate change-induced shifts in photoperiod are
¹²³ therefore likely to alter these functions. Indeed, growth chamber studies demonstrate that the magnitude of
¹²⁴ daylength shifts we can expect with climate change (i.e., 1-2 hours of difference in daylength with temporal
¹²⁵ shifts over the next century) are substantial enough to affect spring phenology in trees (Table S1). The
¹²⁶ direction and magnitude of responses will vary, however, because of variation in photoperiod sensitivity,
¹²⁷ and because photoperiod often interacts with other environmental drivers, such as temperature, to affect
¹²⁸ phenology (Box 1).

¹²⁹ The climate change-induced trend toward ever-earlier springs means that experienced photoperiod may in-
¹³⁰ creasingly approach threshold photoperiods (see *Glossary*) for many species, constraining their ability to
¹³¹ respond to additional warming (Fu et al., 2019; Vitasse and Basler, 2013; Körner and Basler, 2010a; Morin
¹³² et al., 2010; Nienstaedt, 1966). Interactions between photoperiod and temperature may therefore result in
¹³³ muted phenological shifts, compared to what would be expected based on temperature change alone (Körner
¹³⁴ and Basler, 2010a; Mimura and Aitken, 2007; Wareing, 1956). If photoperiod does become limiting, the
¹³⁵ average trend of earlier phenology with warming (Polgar et al., 2013; Peñuelas et al., 2002; Menzel, 2000)
¹³⁶ may stop.

¹³⁷ A challenge in understanding the implications of altered photoperiods under climate change, and for forecast-
¹³⁸ ing whether and when the trend of earlier phenology with warming may slow or stop abruptly, is the wide
¹³⁹ range of observed photoperiod sensitivity across species (Flynn and Wolkovich, 2018; Zohner et al., 2016;
¹⁴⁰ Sanz-Perez et al., 2009), populations (Tanino et al., 2010), and ecotypes (Howe et al., 1995). How much
¹⁴¹ genotype versus environment explain this variation is an active area of research (e.g., Fréjaville et al., 2019;
¹⁴² Franks et al., 2014; Gould et al., 2010; Mimura and Aitken, 2010). Environmental conditions clearly play a
¹⁴³ role, since different combinations of ambient temperature and photoperiod may explain some of this variation

¹⁴⁴ and because temperature cues can override photoperiod requirements under certain conditions (e.g., Tanino
¹⁴⁵ et al., 2010). In such cases, climate change-induced phenological shifts may occur at different rates than past
¹⁴⁶ shifts with warming. On the other hand, some of this variation may be due to underlying genetic differences,
¹⁴⁷ because photoperiod responses can be under strong genetic control (Bradshaw and Stettler, 1995; Keller
¹⁴⁸ et al., 2011; Weih, 2004, see also Boxes 1, 2). Teasing out the relative roles of genetics versus environmental
¹⁴⁹ conditions will be critical to accurate forecasts of future phenology under climate change.

¹⁵⁰ Species- and population-level variation in photoperiod sensitivity may result in altered communities as climate
¹⁵¹ change progresses. For example, a species or population that is relatively insensitive to photoperiod can take
¹⁵² advantage of warmer springs by having an earlier start to its growing season. Indeed, phenological tracking of
¹⁵³ temperature (e.g., earlier flowering, leafout, migration with warming) has been linked with higher performance
¹⁵⁴ in plants and animals (Cleland et al., 2012; Muir et al., 1994; Willis et al., 2010). Species or populations
¹⁵⁵ that are sensitive to temperature but relatively insensitive to photoperiod may therefore outcompete slower-
¹⁵⁶ growing or later-emerging ones that are limited by photoperiod and thus cannot take advantage of longer
¹⁵⁷ growing season conditions. Not all studies, however, find links between performance and high sensitivity
¹⁵⁸ to temperature (e.g., Block et al., 2020), and early-season species in most temperature zones risk losing to
¹⁵⁹ tissue to frost (Sakai and Larcher, 1987). Thus, the advantages of tracking warming may depend on how
¹⁶⁰ quickly mean temperatures versus last frost dates shift (e.g., Inouye et al., 2002), such that in some systems
¹⁶¹ photoperiod cues could prevent species from starting growth or reproduction too early (when they risk losing
¹⁶² their investments in new tissue). To identify where, when, and how communities may be altered therefore
¹⁶³ requires quantifying species-specific temperature and photoperiod sensitivities, and developing methods that
¹⁶⁴ incorporate both photoperiod and environmental events that impact fitness (such as frosts).

¹⁶⁵ Future directions: outstanding questions and incorporating photoperiod into forecasting

¹⁶⁷ Incorporating photoperiod into forecasting is complex for a few major reasons. Future rates of phenological
¹⁶⁸ shifts are unlikely to be straightforward extrapolations from past and current rates. In addition, an organism's
¹⁶⁹ experienced photoperiod is both a driver and an effect of phenological shifts.

170 Approaches for forecasting can be grouped into two broad categories: statistical models and process-based
171 models. These two modelling paradigms differ in how they relate phenology to climate change. Statistical
172 models relating phenology to climate change often assume linear relationships between species' responses and
173 environmental variables (e.g., Flynn and Wolkovich, 2018; Ibáñez et al., 2010), whereas process-based models
174 often incorporate nonlinear threshold relationships (e.g. Chuine and Beaubien, 2001; Morin and Thuiller,
175 2009). Further, statistical models of phenology under climate change frequently ignore photoperiod, focusing
176 instead on seasonal or annual temperature (e.g. Diez et al., 2012; Ibáñez et al., 2010, but see Richardson et al.
177 (2013)), whereas process-based models of phenology more frequently incorporate photoperiod, along with
178 temperature (Lundell et al., 2020; Duputié et al., 2015; Zhao et al., 2013; Morin and Thuiller, 2009). Process-
179 based models may thus seem superior for integrating photoperiod, but they can be challenging to develop,
180 requiring detailed data that are often not readily available (e.g., daily climate data, nonlinear biological
181 responses to fine-scale changes in temperature). Perhaps because of this, statistical models remain more
182 commonly used in climate change forecasts of biological responses (e.g., García-Valdés and Morales-Castilla,
183 2016; Basler and Körner, 2012; Diez et al., 2012; Zhu et al., 2012; Ibáñez et al., 2010).

184 Future modelling of spring woody plant phenology can incorporate photoperiod by leveraging the large
185 amount of experimental data on photoperiod responses (e.g., Fig. 3, Table S1, Box 2), especially when
186 process-based approaches are used. Researchers can use these data to first learn whether the study species
187 (or a phylogenetically closely related species) shows a photoperiod effect and, ideally, identify its threshold
188 photoperiod and how it varies by population, ecotype, or other factors (Tobin et al., 2008; Bradshaw and
189 Holzapfel, 2006). If there is evidence of a photoperiod response (e.g., *Fagus grandifolia*, or *Tilia americana*
190 with low chilling shown in Box 1), daylength should be added to forecasting models, using the threshold
191 photoperiod to define short-day and long-day conditions (Fig. 4). Given the large change in experienced
192 photoperiod with temporal shifts (Fig. 1), this may be particularly important for phenological forecasting.
193 Since spatial shifts are associated with smaller changes in experienced photoperiod, it may be less important
194 for distribution forecasts. Many species, however, may shift in *both* space and time simultaneously. Even
195 though experienced photoperiod changes little as species distributions shift in space, phenology may be altered
196 significantly.

197 For some species, experimental data can be immediately used in forecasting because experiments manipulate

198 photoperiod at relevant scales (e.g., Heide and Sonsteby, 2015; Basler and Körner, 2014, Figs. 3, S1A, Table
199 S1). For example, photoperiod treatments from growth chamber experiments with *Fagus sylvatica* span the
200 variation in both current and expected future ranges (Fig. S1A, Duputié et al., 2015), and may allow
201 identification of threshold photoperiods (Fig. 4). In other cases, attempting to incorporate photoperiod
202 into forecasts of future phenology will reveal gaps in our understanding of many aspects of photoperiod
203 responses. For example, photoperiod treatments from existing experiments of *Quercus robur* do not accurately
204 represent experienced photoperiods from current or future estimates (Fig. S1B), making fine-scale projections
205 difficult, even for this relatively well-studied species. This gap extends to many species, as most experiments
206 manipulate photoperiod much more dramatically than will occur with climate change (Figs. 3, S1). Although
207 these studies can be useful for understanding mechanistically how photoperiod responses work, extrapolating
208 them to climate change models may not be reasonable.

209 Photoperiod is not fully integrated into most current forecasts of biological responses to climate change (but
210 see Tobin et al., 2008, for an example in insects); this omission could affect forecast accuracy. Forecasts from
211 ecosystem models often incorporate photoperiod, along with other variables such as evaporative demand
212 and temperature (e.g., the Ecosystem Demography model Jolly et al., 2005; Medvigy et al., 2013), but
213 photoperiod is rarely included in species distribution models (e.g., Morin and Thuiller, 2009; Zhu et al.,
214 2012). The sensitivity of model outcomes to assumptions made about experienced photoperiod and threshold
215 responses to photoperiod needs further study, including understanding how variation in photoperiod responses
216 across ecosystems, species, populations, and life stages impacts forecasts.

217 As researchers more fully integrate photoperiod into forecasting, a critical area of further study is under-
218 standing *how* photoperiod acts as a cue. Photoperiod seems to interact with temperature to affect phenology
219 (e.g., Box 1, Zydlewski et al., 2014); this would explain the divergent effects of photoperiod observed across
220 studies in woody plants (Box 1). However, exactly how it interacts with temperature is not well-defined for
221 most species or populations. For many species, additional experimental and physiological research is nec-
222 essary, since the dormancy-breaking processes that photoperiod affects often require detailed physiological
223 approaches to observe (Box 2, Hänninen et al., 2019; Chuine et al., 2016). Understanding the drivers, as
224 well as the consequences, of variations in photoperiod responses across species and populations will be par-
225 ticularly beneficial for forecasting. For example, what traits are associated with photoperiod sensitivity and

²²⁶ does variation in photoperiod sensitivity or related traits have a strong genetic component? If so, are species
²²⁷ or populations from some locations or lineages more likely than others to be constrained by photoperiod in
²²⁸ their responses to climate change?

²²⁹ Conclusions

²³⁰ Organisms may undergo large changes to the photoperiod they experience with climate change, even if they
²³¹ do not shift their ranges spatially. Here we have shown that these altered photoperiods may result in stalled
²³² future advances of spring phenology with warming (e.g., Table S1, Fig. S1, Fu et al., 2019; Güsewell et al.,
²³³ 2017; Yu et al., 2010), with cascading effects on growth, fitness, and community composition due to the large
²³⁴ variation in photoperiod responses across species and populations (Box 1). We have focused on woody plant
²³⁵ spring phenology, but shifts in photoperiod with climate change have implications for a variety of plant and
²³⁶ animal responses, given that daylength affects critical activities for diverse species from insects (Bradshaw and
²³⁷ Holzapfel, 2006) and salmon (Taranger et al., 2003) to birds (Dawson et al., 2001) and marsupials (McAllan
²³⁸ et al., 2006). Given what we know, incorporating photoperiod into forecasting of climate change responses
²³⁹ should improve model accuracy (Fig. 6), and will illuminate additional experiments that could improve our
²⁴⁰ mechanistic understanding of photoperiod as a critical cue for diverse biological responses.

²⁴¹ Glossary

- ²⁴² • budburst: when one or more leaf buds have visible green tips.
- ²⁴³ • chilling: the intensity and duration of winter temperature, often a certain sum of chilling that is required
²⁴⁴ (e.g., some amount of hours or days of cold temperatures, defined by a specific critical temperature or
²⁴⁵ range of temperatures, such as between 0 and 7.2 °C, Richardson, 1974), that must be experienced for
²⁴⁶ budburst to occur.
- ²⁴⁷ • daylength: the period of time during a 24-hour period during which an organism receives light.
- ²⁴⁸ • diapause: period of suspended development or growth, usually used to describe invertebrates during
²⁴⁹ unfavorable environmental conditions such as winter.

- 250 • dormancy: halted or reduced growth or activity, usually used to describe plants.
- 251 • forcing: warm spring temperatures, often a certain sum of forcing that is required (e.g., some amount
252 of hours or days above a specific temperature) for budburst or flowering can occur.
- 253 • green-up: The beginning of a new cycle of plant growth, usually evaluated at the landscape scale.
- 254 • phenology: the timing of life cycle events in organisms
- 255 • photoperiod: the daily duration of light (daylength) and dark to which an organism is exposed; often
256 used synonymously with daylength.
- 257 • photoperiod sensitivity: the degree to which phenology is controlled by daylength; may be a nonlinear,
258 or “threshold”, response in plants (Box 2) and animals (Grevstad and Coop, 2015; Tobin et al., 2008).
- 259 • photoperiodism: the ability to assess the length of day or night to regulate behavior, physiology, growth,
260 development or reproduction.
- 261 • threshold photoperiod: length of day that causes an organism to switch from a short- to a long-day
262 response (or vice versa). For example, in European larch (*Larix decidua*), budburst development may
263 be constrained under short-day conditions, when daylengths are less than a threshold photoperiod of
264 10-11 hours (Migliavacca et al., 2008). Above this threshold photoperiod, the long-day response of
265 unconstrained budburst development can occur.

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₅₄₃ **Figures**

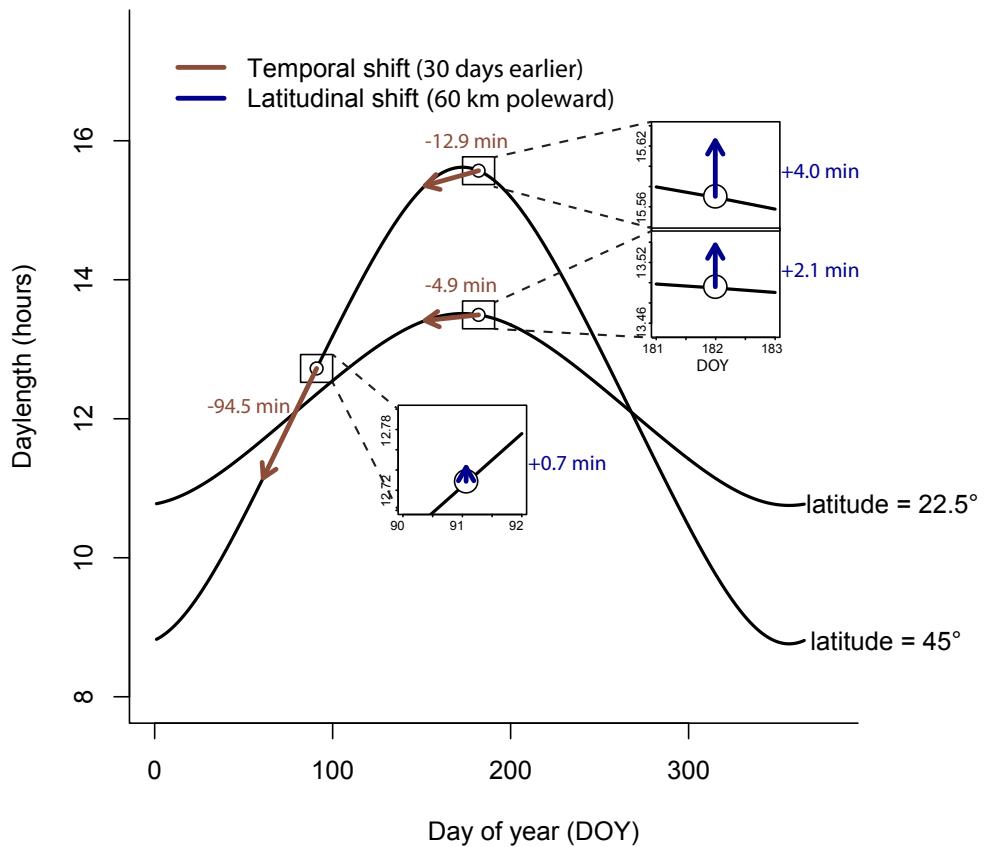


Figure 1: **Temporal (i.e., phenological) shifts in activity yield larger changes in experienced photoperiod compared to spatial (i.e., latitudinal) shifts** on the same day of year, due to patterns in photoperiod variation with latitude and by day of year. Here, we show this variation at two latitudes (22.5° , 45°), using hypothetical spatial and temporal shifts. These shifts are based on observed rates with recent global warming: 6-17 kilometers per decade, or approximately 0.5-1.5 degrees in 100 years, for spatial shifts (Parmesan and Yohe, 2003; Parmesan, 2006), and 2-3 days per decade, or 30 days in 100 years, for temporal shifts (Parmesan, 2006; Chen et al., 2011). They highlight the greater magnitude in daylength changes 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).

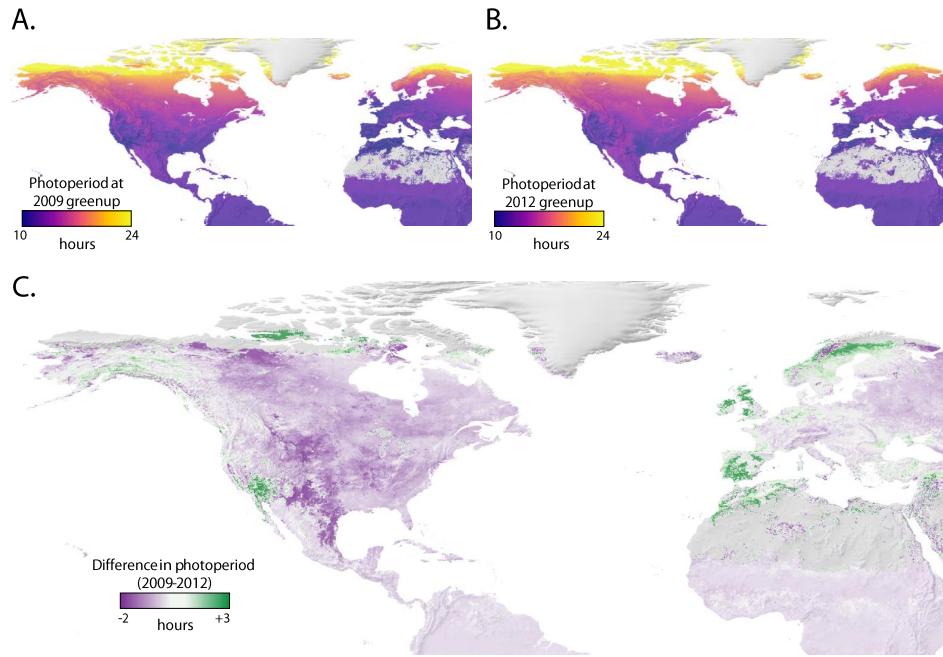


Figure 2: Photoperiod on “green-up” date varies over space and between years “Green-up” date is the beginning of seasonal greening, identified by satellite remote sensing measurements taken regularly throughout the year of the concentrations of green leaf vegetation. Hours of daylight on the date of 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 Materials for more details.

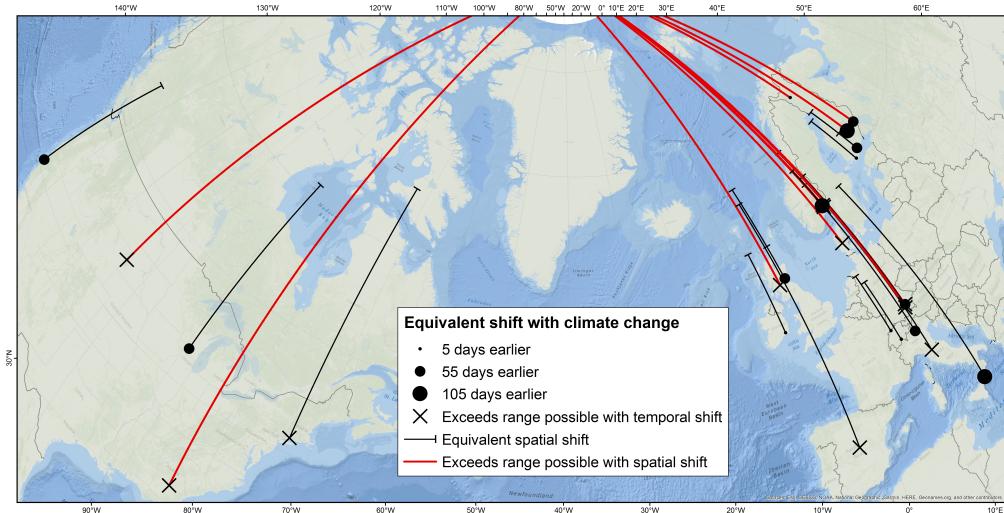


Figure 3: **Experimental photoperiod treatments and their equivalent spatial and temporal shifts** for experiments in the OSPREE database that manipulated photoperiod (see Box 1). See ‘Mapping temporal and spatial shifts in space and time’ in the Supplemental Materials for details on how we calculated the required spatial (lines) or temporal (circles and Xes) shifts to be equivalent to photoperiod treatments in each experiment.

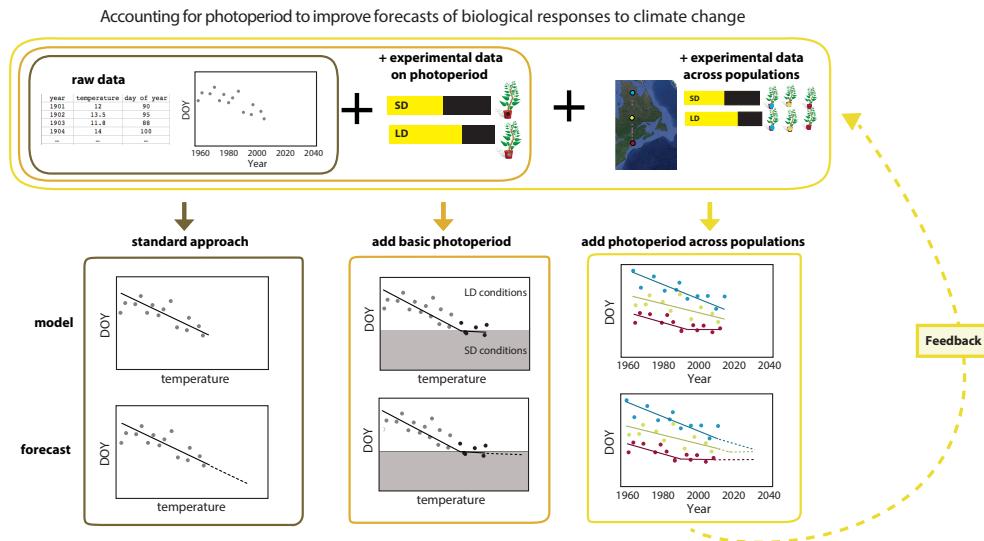


Figure 4: **Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change.** Current approaches for forecasting spring phenology with climate change frequently rely on linear relationships between historical temperature data and observed dates of spring phenology (left panels). Adding responses to photoperiod, which commonly 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).

544 **Box 1. Are photoperiod effects widespread? A case study of woody**

545 **plant spring phenology**

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

551 Experimental growth chamber studies have shown that photoperiod is an important cue for spring budburst
552 phenology in woody plants (e.g., Flynn and Wolkovich, 2018; Basler and Körner, 2014; Heide, 1993*b*). These
553 experiments often manipulate photoperiod in combination with temperature to address basic questions about
554 how these two environmental conditions act as biological cues. Temperature has a dual role in regulating
555 woody plant phenology: chilling—the prolonged exposure to cold temperatures after growth cessation in the
556 fall—is required to initiate budburst; and forcing—prolonged exposure to warm temperatures—is required
557 for budburst to occur. Different photoperiod treatments are typically applied during the forcing treatment
558 phase in growth chamber experiments (e.g., Laube et al., 2014; Spann et al., 2004; Falusi and Calamassi,
559 1990; Heide, 1977; Campbell and Sugano, 1975).

560 Woody plant growth chamber studies have been conducted for decades, but have only recently been syn-
561 thesized to show that photoperiod sensitivity is widespread, with large variation across studies and species.
562 These studies have been synthesized in Observed Spring Phenology Responses in Experimental Environments
563 (OSPREE), a new database of plant growth chamber studies that manipulate photoperiod and temperature
564 to measure plant phenological responses, including budburst and flowering (Wolkovich et al., 2019). The
565 database includes studies that manipulate photoperiod (by applying treatments with different daylength du-
566 rations, applying long-day versus short-day conditions for different lengths of time, and/or applying varying
567 versus constant photoperiods) and temperature (by imposing different chilling and/or forcing treatments).
568 The OSPREE database spans 201 woody plant species; all experiments in the database use dormant plant
569 tissue (grown in greenhouses or taken directly from the field) exposed to experimental conditions (Wolkovich
570 et al., 2019) for which we could identify forcing, photoperiod, and chilling treatments quantitatively. See

571 Supplemental Methods and Wolkovich et al. (2019) for details.

572 Growth chamber experiments in OSPREE suggest that the dominant photoperiod response in woody plant
573 species is earlier and more rapid budburst with longer days (e.g., Caffarra and Donnelly, 2011). Thirty-one
574 of the 85 studies in the OSPREE database included two or more different photoperiod treatments. Of these,
575 26 (84%) found significant photoperiod main effects or significant interactive effects with temperature (i.e.,
576 photoperiod x temperature effects), across 176 species (Table S1). Main effects included responses such as
577 growth (e.g., higher growth rates with longer days Ashby et al., 1962) and reproduction (e.g., increased
578 flowering with longer days Heide and Sønsteby, 2012).

579 Growth chamber experiments highlight that responses to photoperiod vary depending on temperature condi-
580 tions. For example, more rapid advancement of budburst was observed under long versus short days with low
581 chilling, than with high chilling in *Betula payrifera* (Hawkins and Dhar, 2012, see figure). Similarly, across
582 species, as chilling accumulates from winter to spring, sensitivity to both forcing and photoperiod sensitivity
583 can decrease (Malyshev et al., 2018). Frequently, long photoperiods can compensate for low amounts of
584 chilling (Caffarra et al., 2011b; Myking and Heide, 1995; Heide, 1993a).

585 Woody plant growth chamber experiments also demonstrate that, though photoperiod responses are com-
586 mon, they are variable, as shown in the figure. Responses to photoperiod differ by species (e.g., Flynn and
587 Wolkovich, 2018; Zohner et al., 2016; Basler and Körner, 2014, 2012; Howe et al., 1996; Heide, 1993b). For
588 example, with longer chilling treatments some species seem insensitive to daylength (e.g., *Hammamelis* spp.,
589 *Prunus* spp., Zohner et al., 2016), whereas others seem to be highly sensitive to daylength (e.g. *Fagus* spp.,
590 Fig. S1A, even with long chilling treatments (Zohner et al., 2016). In addition, some species demonstrate
591 a response to photoperiod opposite to that typically observed: *Tilia*, for example, showed delayed budburst
592 with longer daylengths (see figure, Ashby et al., 1962). Photoperiod sensitivity also varies by population
593 and ecotype (e.g., see figure). For example, photoperiod effects on budburst were more significant for lower
594 latitude populations of *Betula pendula* and *B. pubescens* (Partanen et al., 2005).

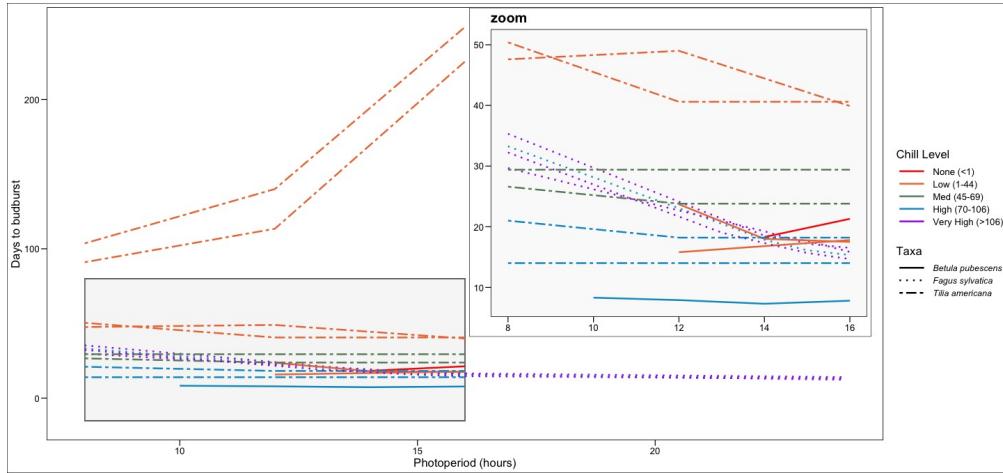


Figure: **Nonlinearities in phenological responses to daylength** are apparent in spring woody plant phenology experiments (from the OSPREE database) in which three or more photoperiod treatment levels were applied. The shape of the response curves for *Betula pubescens* (Caffarra et al., 2011b), *Fagus sylvatica* (Heide, 1993b) and *Tilia americana* (Ashby et al., 1962) differ depending on the amount of winter chilling received (measured in Chill portions Fishman et al., 1987). Species and chilling levels with multiple lines represent plant material from different populations.

595 Box 2. Dominant models of how photoperiod affects spring woody 596 plant phenology

597 The cues and molecular pathways underlying photoperiod sensitivity are poorly understood for most organ-
598 isms, even in relatively well-studied phenophases and taxa, such as spring budburst in woody plants (Ding
599 and Nilsson, 2016). Decades of growth chamber experiments suggest three main cues—chilling, forcing, and
600 photoperiod—control spring budburst for woody species (Flynn and Wolkovich, 2018; Zohner et al., 2016;
601 Heide, 2008), with many models suggesting a dominant role of forcing in most natural conditions. Forc-
602 ing requirements, however, appear to increase given shorter photoperiods or lower chilling (Caffarra et al.,
603 2011a; Chuine et al., 2010). Research has yet to fully tease out effects of these three cues, their interactions,
604 and their prevalence; photoperiod responses appear variable across species and populations, as well as with
605 different chilling treatments (see Box 1). Not surprisingly, then, there is currently little agreement on the un-
606 derlying model for how photoperiod affects spring phenology for most species (Chuine et al., 2016; Hänninen
607 et al., 2019). More physiological research will likely be necessary for major advances, as understanding the
608 exact cellular pathways through which chilling, forcing, and photoperiod act appears increasingly critical to
609 accurate models (van der Schoot et al., 2014; Hänninen et al., 2019).

610 Additional cellular and molecular studies may quickly advance understanding and scale up to improved
611 photoperiod models. While our understanding of how plants interpret photoperiod at the molecular-level
612 comes from fewer species, largely from studies of flowering in the model plant *Arabidopsis thaliana* (e.g.,
613 Suárez-López et al., 2001) and fall budset in woody plant species (e.g., Howe et al., 1996), these studies have
614 proved useful across other species. For example, the “external coincidence model” (where plants sense light
615 via blue light receptors and phytochromes, then interpret photoperiod through a coordinated response to
616 light in relation to the time of day, see Lagercrantz, 2009) has been most widely studied in *Arabidopsis*, but
617 appears to be a relevant mechanism for photoperiod responses in diverse perennial and woody plant species
618 (Singh et al., 2017; Petterle et al., 2013; Andrés and Coupland, 2012; Kobayashi and Weigel, 2007; Davis,
619 2002; Bastow and Dean, 2002; Bünning, 1936). The model proposes the existence of a circadian rhythm of
620 light sensitivity, in which the night-phase is sensitive to light and the day-phase is insensitive to light. As days
621 get longer in the spring, daylight illuminates the light sensitive phase, triggering a response. This provides a
622 clear mechanistic pathway to build into models (Burghardt et al., 2015).

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

634 Efforts to better map the genetic and cellular pathways of spring phenology combined with common garden
635 studies can provide a powerful method to test mechanistic understanding and improve models (e.g., Burghardt
636 et al., 2015; Fournier-Level et al., 2016). Here we have mainly outlined how to combine growth chamber studies
637 with long-term data to improve models and forecasting; a greater physiological understanding of at least a

⁶³⁸ few species will likely also be necessary for generating robust predictions with climate change.