

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 Photoperiod (daylength) is a critical cue for the onset of spring in plants and animals, signaling changes in
¹⁸ growth, migration, and reproduction across diverse species (e.g., Flynn and Wolkovich, 2018; Lagercrantz,
¹⁹ 2009; Bradshaw and Holzapfel, 2007; McCallan et al., 2006; Howe et al., 1996; Solbakken et al., 1994; Barker
²⁰ and Herman, 1976; Farner, 1964). Photoperiod is a useful cue for diverse species to synchronize activities
²¹ with seasonal climatic changes (e.g., Singh et al., 2017; Basler and Körner, 2012; Hsu et al., 2011) because it
²² is consistent across years, especially compared to other seasonal cues such as temperature and precipitation
²³ (Saikkonen et al., 2012). In addition to being consistent over time, photoperiod reflects annual cycles at a
²⁴ broad spatial scale, filtering out noise in local conditions (Winkler et al., 2014).

²⁵ For many organisms, spring phenology—i.e., the timing of spring events, including flowering, bird arrival, egg
²⁶ hatching and myriad other biological activities—is thought to be determined by photoperiod interactively
²⁷ with temperature (Fu et al., 2019; Winkler et al., 2014, see also Box 1). The strong role of temperature
²⁸ is apparent in recent advances in spring phenology. Across taxa, from plants and insects to mollusks and
²⁹ mammals, spring phenology is occurring earlier as temperatures warm, with average shifts of 1.2 to 5.1 days
³⁰ earlier per decade (Bradley et al., 1999; Parmesan and Yohe, 2003; Poloczanska et al., 2013; Root et al.,
³¹ 2003) or 1.3 to 5.6 days earlier per °C of warming (Polgar et al., 2013; Wolkovich et al., 2012). These changes
³² are some of the largest climate change-induced shifts observed, with early spring phenology shifting more
³³ rapidly than later season phenology in most cases (Bradley et al., 1999; Menzel et al., 2006). These shifts
³⁴ occur while, at a given location on Earth, annual patterns in photoperiod have not changed as climates have
³⁵ warmed.

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

⁴³ will depend in part on how rapidly photoperiod responses can acclimate or adapt to new environmental
⁴⁴ conditions, which remains poorly understood (Grevstad and Coop, 2015; Bradshaw and Holzapfel, 2007).

⁴⁵ Perhaps because of these variable and uncertain responses, photoperiod is often not included in forecasts of
⁴⁶ biological responses to climate change, especially in the spring, even though it is known to be an important
⁴⁷ cue for biological activity (but see Duputié et al., 2015; Grevstad and Coop, 2015; Caffarra et al., 2011a).

⁴⁸ The exclusion of photoperiod may be problematic: although photoperiod itself is stable over time, the
⁴⁹ photoperiod that species *experience*, as they undergo climate change-induced shifts in space and time, is
⁵⁰ likely to be much less stable. In addition to shifting activity earlier with recent warming, many species have
⁵¹ shifted their distributions poleward and upward in elevation (i.e., range shifts, Chen et al., 2011; Harsch et al.,
⁵² 2009; Parmesan, 2006; Peñuelas and Boada, 2003). These spatial and temporal shifts alter the photoperiod
⁵³ experienced by organisms (Fig. 1); altered photoperiods may have cascading effects on species' performance,
⁵⁴ since daylength can affect the timing of development (Grevstad and Coop, 2015; Muir et al., 1994; Tauber
⁵⁵ and Tauber, 1975), migration (Dawbin, 1966), reproduction (Dunn, 2019; Dardente, 2012; Ben-David, 1997),
⁵⁶ and other important responses.

⁵⁷ The implications of potential climate change-induced shifts in experienced photoperiod are unclear, as the
⁵⁸ magnitudes of potential shifts have not been described. Effects of photoperiod shifts may be relatively
⁵⁹ minor, especially because there can be substantial year-to-year variation in experienced photoperiod (Fig.
⁶⁰ 2). Alternatively, photoperiod may begin to constrain species' responses to climate change (Fu et al., 2015;
⁶¹ Way and Montgomery, 2015; Basler and Körner, 2012; Körner and Basler, 2010a).

⁶² Here, we ask:

- ⁶³ 1. How will climate change alter the photoperiod experienced by organisms?
- ⁶⁴ 2. What are the implications of altered photoperiods for biological responses to climate change?
- ⁶⁵ 3. Can researchers apply data from experiments that alter photoperiod to aid in forecasting biological
⁶⁶ implications of climate change?

⁶⁷ We focus on spring events, as phenology during this time is one of the most widely observed and rapidly
⁶⁸ changing biological responses to climate change (Parmesan, 2006). In addition, the role of photoperiod is

69 less understood in spring phenology compared with autumn phenophases (reviewed in, e.g., Azeez and Sane,
70 2015; Gallinat et al., 2015; Lagercrantz, 2009; Allona et al., 2008), but recent studies showing declines in
71 responses of spring budburst to warming (e.g., Fu et al., 2019; Güsewell et al., 2017; Yu et al., 2010) suggest
72 that photoperiod constraints may be imminent. While our questions are broadly relevant for diverse species,
73 we use a case study of spring woody plant phenology to illustrate some of our points (Boxes 1, 2).

74 **How will climate change alter the photoperiod experienced by or- 75 ganisms?**

76 Species experience different photoperiod regimes depending on their location on Earth, the seasonal timing
77 of their activity, and inter-annual variation in climate (Fig. 1, 2). Consider, as an example, the daylength
78 experienced by plants on the date that spring “green-up” occurs. Spring green-up varies with latitude (Fig.
79 2a), in part because latitudinal variation in green-up date, which occurs earlier toward the equator and later
80 toward the poles, is strongly driven by climatic differences that affect phenology, and in part because of
81 latitudinal variation in photoperiod (e.g., at the poles, the daylength at the summer solstice is 24 hours; see
82 also Fig. 1).

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

87 Despite these consistent broad-scale patterns, there is also strong spatiotemporal variation in experienced
88 photoperiod across years. Comparing the photoperiod at green-up in an “early” versus an “average” year (Fig.
89 2) shows that experienced photoperiod at green-up can vary by two to three hours from one year to the next
90 in the same location (Fig. 2c). We use green-up date as an example here because it is an available dataset
91 and represents an important biological event, signalling the start of the growing season. Though green-up
92 date corresponds to plant phenology, we expect that spatiotemporal patterns are similarly heterogeneous in
93 spring phenology of other organisms (Ovaskainen et al., 2013; Peñuelas et al., 2002).

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

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

105 Despite a focus on range shifts, current data suggest that temporal shifts will yield much larger changes in
106 experienced photoperiod than latitudinal shifts (Fig. 1). Consider an insect that emerges from diapause or
107 a tree that bursts its buds at latitude 45° , on average around day of year 91 (April 2), when daylength is
108 12.8 hours. If the organism's phenology shifts 30 days earlier over the next century (i.e., a rate of 3 days
109 per decade, as has been observed, Parmesan and Yohe, 2003), it will experience a daylength that is 1.6 hours
110 shorter. This 1.6 hour decrease in daylength is equivalent to moving up 28.5° in latitude on this day of year.
111 However, if the same species shifts its range up in latitude 0.5° (i.e., 60 km over the next century, comparable
112 to observed rates, Chen et al., 2011; Parmesan and Yohe, 2003), it will experience a daylength that differs
113 by less than a minute on the same day of year.

114 In many cases organisms may shift both their ranges and their phenology simultaneously (i.e., due to new
115 climatic conditions, Duputié et al., 2015; Grevstad and Coop, 2015). In addition, photoperiod sensitivity
116 (see *Glossary*) can vary with latitude, likely due to population-level differences in sensitivity (Gauzere et al.,
117 2017; Saikkonen et al., 2012; Caffarra et al., 2011b; Bradshaw and Holzapfel, 2007; Viherä-Aarnio et al., 2006;
118 Partanen et al., 2005; Howe et al., 1996). With future climate change, it is unclear how these complexities
119 will affect the photoperiod experienced by organisms and whether these shifts in photoperiod will have im-
120 portant implications for biological responses. This lack of clarity stems, in part, from the fact that phenology
121 both affects and is affected by experienced photoperiod: climate change-induced shifts in phenology alter

¹²² experienced photoperiod, which in turn affects phenology.

¹²³ **What are the implications of altered photoperiods for biological
124 responses to climate change?**

¹²⁵ Daylength, often in combination with temperature, can play a role in controlling critical biological functions,
¹²⁶ including vegetative growth, cell elongation, budburst, and flowering in plants (Fu et al., 2019; Heide and
¹²⁷ Sønsteby, 2012; Heide, 2011; Hsu et al., 2011; Sidaway-Lee et al., 2010; Mimura and Aitken, 2007; Linkosalo
¹²⁸ and Lechowicz, 2006; Erwin, 1998; Ashby et al., 1962) and growth rate, maturation, reproduction, migration,
¹²⁹ and diapause in animals (Dunn, 2019; Winkler et al., 2014; Zydlowski et al., 2014; Dardente, 2012; Tobin
¹³⁰ et al., 2008; Bradshaw and Holzapfel, 2006; Ben-David, 1997; Muir et al., 1994; Saunders and Henderson, 1970;
¹³¹ Dawbin, 1966). Climate change-induced shifts in photoperiod are therefore likely to alter these functions.
¹³² Indeed, growth chamber studies demonstrate that the magnitude of daylength shifts we can expect with
¹³³ climate change (i.e., 1-2 hours of difference in daylength with temporal shifts over the next century) are
¹³⁴ substantial enough to affect spring phenology in trees (Table S1). The direction and magnitude of responses
¹³⁵ will vary, however, because of variation in photoperiod sensitivity, and because photoperiod often interacts
¹³⁶ with other environmental drivers, such as temperature, to affect phenology (Box 1).

¹³⁷ The climate change-induced trend toward ever-earlier springs means that experienced photoperiod may in-
¹³⁸ creasingly approach threshold photoperiods (see *Glossary*) for many species, constraining their ability to
¹³⁹ respond to additional warming (Fu et al., 2019; Vitasse and Basler, 2013; Körner and Basler, 2010a; Morin
¹⁴⁰ et al., 2010; Nienstaedt, 1966). Interactions between photoperiod and temperature may therefore result in
¹⁴¹ muted phenological shifts, compared to what would be expected based on temperature change alone (Körner
¹⁴² and Basler, 2010a; Mimura and Aitken, 2007; Wareing, 1956). If photoperiod does become limiting, the
¹⁴³ average trend of earlier phenology with warming (Ovaskainen et al., 2013; Polgar et al., 2013; Peñuelas et al.,
¹⁴⁴ 2002; Menzel, 2000) may stop.

¹⁴⁵ A challenge in understanding the implications of altered photoperiods under climate change, and for forecast-
¹⁴⁶ ing whether and when the trend of earlier phenology with warming may slow or stop abruptly, is the wide

¹⁴⁷ range of observed photoperiod sensitivity across species (Flynn and Wolkovich, 2018; Zohner et al., 2016;
¹⁴⁸ Sanz-Perez et al., 2009), populations (Tanino et al., 2010), and ecotypes (Howe et al., 1995). How much
¹⁴⁹ genotype versus environment explain this variation is an active area of research (e.g., Fréjaville et al., 2019;
¹⁵⁰ Franks et al., 2014; Gould et al., 2010; Mimura and Aitken, 2010). Environmental conditions clearly play a
¹⁵¹ role, since different combinations of ambient temperature and photoperiod may explain some of this variation
¹⁵² and because temperature cues can override photoperiod requirements under certain conditions (e.g., Tanino
¹⁵³ et al., 2010). In such cases, climate change-induced phenological shifts may occur at different rates than past
¹⁵⁴ shifts with warming. On the other hand, some of this variation may be due to underlying genetic differences,
¹⁵⁵ because photoperiod responses can be under strong genetic control (Bradshaw and Stettler, 1995; Keller
¹⁵⁶ et al., 2011; Weih, 2004, see also Boxes 1, 2). Teasing out the relative roles of genetics versus environmental
¹⁵⁷ conditions will be critical to accurate forecasts of future phenology under climate change.

¹⁵⁸ Species- and population-level variation in photoperiod sensitivity may result in altered communities as climate
¹⁵⁹ change progresses. For example, a species or population that is relatively insensitive to photoperiod can take
¹⁶⁰ advantage of warmer springs by having an earlier start to its growing season. Indeed, phenological tracking of
¹⁶¹ temperature (e.g., earlier flowering, leafout, migration with warming) has been linked with higher performance
¹⁶² in plants and animals (Cleland et al., 2012; Muir et al., 1994; Willis et al., 2010). Species or populations
¹⁶³ that are sensitive to temperature but relatively insensitive to photoperiod may therefore outcompete slower-
¹⁶⁴ growing or later-emerging ones that are limited by photoperiod and thus cannot take advantage of longer
¹⁶⁵ growing season conditions. Not all studies, however, find links between performance and high sensitivity
¹⁶⁶ to temperature (e.g., Block et al., 2020), and early-season species in most temperature zones risk losing to
¹⁶⁷ tissue to frost (Sakai and Larcher, 1987). Thus, the advantages of tracking warming may depend on how
¹⁶⁸ quickly mean temperatures versus last frost dates shift (e.g., Inouye et al., 2002), such that in some systems
¹⁶⁹ photoperiod cues could prevent species from starting growth or reproduction too early and thus losing their
¹⁷⁰ investments in new tissue or offspring. To identify where, when, and how communities may be altered thus
¹⁷¹ requires quantifying species-specific temperature and photoperiod sensitivities, and developing methods that
¹⁷² incorporate both photoperiod and environmental events that impact fitness (such as frosts).

¹⁷³ Future directions: outstanding questions and incorporating pho-
¹⁷⁴ toperiod into forecasting

¹⁷⁵ Incorporating photoperiod into forecasting is complex for a few major reasons. Future rates of phenological
¹⁷⁶ shifts are unlikely to be straightforward extrapolations from past and current rates. In addition, an organism's
¹⁷⁷ experienced photoperiod is both a driver and an effect of phenological shifts.

¹⁷⁸ Approaches for forecasting can be grouped into two broad categories: statistical models and process-based
¹⁷⁹ models. These two modelling paradigms differ in how they relate phenology to climate change. Statistical
¹⁸⁰ models relating phenology to climate change generally assume linear relationships between species' responses
¹⁸¹ and environmental variables (e.g., Flynn and Wolkovich, 2018; Ibáñez et al., 2010; Van Belle et al., 2007),
¹⁸² whereas process-based models often incorporate nonlinear threshold relationships (e.g. Chuine and Beaubien,
¹⁸³ 2001; Morin and Thuiller, 2009; Xie and Hsieh, 1989). Further, statistical models of phenology under climate
¹⁸⁴ change have typically ignored photoperiod, focusing instead on seasonal or annual temperature (e.g. Diez
¹⁸⁵ et al., 2012; Ibáñez et al., 2010; Van Belle et al., 2007, but see Richardson et al. (2013)), whereas process-
¹⁸⁶ based models of phenology more frequently incorporate photoperiod, along with temperature (Lundell et al.,
¹⁸⁷ 2020; Duputié et al., 2015; Zhao et al., 2013; Morin and Thuiller, 2009; Xie and Hsieh, 1989). Process-based
¹⁸⁸ models may thus seem superior for integrating photoperiod, but they can be challenging to develop, requiring
¹⁸⁹ detailed data that are often not readily available (e.g., daily climate data, nonlinear biological responses to
¹⁹⁰ fine-scale changes in temperature). Perhaps because of this, statistical models remain more commonly used
¹⁹¹ in climate change forecasts of biological responses (e.g., García-Valdés and Morales-Castilla, 2016; Basler and
¹⁹² Körner, 2012; Diez et al., 2012; Zhu et al., 2012; Ibáñez et al., 2010; Van Belle et al., 2007).

¹⁹³ Future modelling of spring woody plant phenology can incorporate photoperiod by leveraging the large
¹⁹⁴ amount of experimental data on photoperiod responses (e.g., Fig. 3, Table S1, Box 2), especially when
¹⁹⁵ process-based approaches are used. Researchers can use these data to first learn whether the study species
¹⁹⁶ (or a phylogenetically closely related species) shows a photoperiod effect and, ideally, identify its threshold
¹⁹⁷ photoperiod and how it varies by population, ecotype, or other factors (Tobin et al., 2008; Bradshaw and
¹⁹⁸ Holzapfel, 2006; Gwinner, 1996). If there is evidence of a photoperiod response (e.g., *Fagus grandifolia*,
¹⁹⁹ or *Tilia americana* with low chilling in Fig. 4), daylength should be added to forecasting models, using

200 the threshold photoperiod to define short-day and long-day conditions (Fig. 6). Given the large change in
201 experienced photoperiod with temporal shifts (Fig. 1), this may be particularly important for phenological
202 forecasting. Since spatial shifts are associated with smaller changes in experienced photoperiod, it may be less
203 important for distribution forecasts. Many species, however, may shift in *both* space and time simultaneously.
204 Thus, even though experienced photoperiod changes little as species distributions shift in space, phenology
205 may be altered significantly.

206 For some species, experimental data can be immediately used in forecasting because experiments manipulate
207 photoperiod at relevant scales (e.g., Heide and Sonsteby, 2015; Basler and Körner, 2014, Figs. 3, 5A, Table
208 S1). For example, photoperiod treatments from growth chamber experiments with *Fagus sylvatica* span
209 the variation in both current and expected future ranges (Fig. 5A, Duputié et al., 2015), and may allow
210 identification of threshold photoperiods (Fig. 6). In other cases, attempting to incorporate photoperiod
211 into forecasts of future phenology will reveal gaps in our understanding of many aspects of photoperiod
212 responses. For example, photoperiod treatments from existing experiments of *Quercus robur* do not accurately
213 represent experienced photoperiods from current or future estimates (Fig. 5B), making fine-scale projections
214 difficult, even for this relatively well-studied species. This gap extends to many species, as most experiments
215 manipulate photoperiod much more dramatically than will occur with climate change (Figs. 3, 5). Although
216 these studies can be useful for understanding mechanistically how photoperiod responses work, extrapolating
217 them to climate change models may not be reasonable.

218 Photoperiod is not fully integrated into most current forecasts of biological responses to climate change (but
219 see Tobin et al., 2008), an omission that could affect the accuracy of forecasts. Forecasts from ecosystem mod-
220 els often incorporate photoperiod, along with other variables such as evaporative demand and temperature
221 (e.g., the Ecosystem Demography model Jolly et al., 2005; Medvigy et al., 2013), but photoperiod is rarely
222 included in species distribution models (e.g., Morin and Thuiller, 2009; Zhu et al., 2012). The sensitivity of
223 model outcomes to assumptions made about experienced photoperiod and threshold responses to photope-
224 riod needs further study, including understanding how variation in photoperiod responses across ecosystems,
225 species, populations, and life stages impacts forecasts.

226 As researchers more fully integrate photoperiod into forecasting, a critical area of further study is understand-
227 ing *how* photoperiod acts as a cue. Photoperiod seems to interact with temperature to affect phenology (e.g.,

228 Box 1, Zydlewski et al., 2014); this would explain the divergent effects of photoperiod observed across studies
229 in woody plants (Box 1, Fig. 4). However, exactly how it interacts with temperature is not well-defined for
230 most species or populations. For many species, additional experimental and physiological research is nec-
231 essary, since the dormancy-breaking processes that photoperiod affects often require detailed physiological
232 approaches to observe (Box 2, Hänninen et al., 2019; Chuine et al., 2016). Understanding the drivers, as
233 well as the consequences, of variations in photoperiod responses across species and populations will be par-
234 ticularly beneficial for forecasting. For example, what traits are associated with photoperiod sensitivity and
235 does variation in photoperiod sensitivity or related traits have a strong genetic component? If so, are species
236 or populations from some locations or lineages more likely than others to be constrained by photoperiod in
237 their responses to climate change?

238 Conclusions

239 Organisms may undergo large changes to the photoperiod they experience with climate change, even if they
240 do not shift their ranges spatially. Here we have shown that these altered photoperiods may result in stalled
241 future advances of spring phenology with warming (e.g., Table S1, Fig. 5, Fu et al., 2019; Güsewell et al.,
242 2017; Yu et al., 2010), with cascading effects on growth, fitness, and community composition due to the
243 large variation in photoperiod responses across species and populations (Fig. 4). Shifts in photoperiod with
244 climate change have implications for a variety of plant and animal responses, given that daylength affects
245 critical activities for diverse species from insects (Bradshaw and Holzapfel, 2006; Linn et al., 1996) and salmon
246 (Taranger et al., 2003; Solbakken et al., 1994) to birds (Dawson et al., 2001) and marsupials (McCallan et al.,
247 2006; Solbakken et al., 1994). Given what we know, incorporating photoperiod into forecasting of climate
248 change responses should improve model accuracy (Fig. 6), and will illuminate additional experiments that
249 could improve our mechanistic understanding of photoperiod as a critical cue for diverse biological responses.

250 Glossary

- 251 • budburst: when one or more leaf buds have visible green tips.

- 252 ● chilling: the intensity and duration of winter temperature, often a certain sum of chilling that is required
253 (e.g., some amount of hours or days of cold temperatures, defined by a specific critical temperature or
254 range of temperatures, such as between 0 and 7.2 °C, Richardson, 1974), that must be experienced for
255 budburst to occur.
- 256 ● daylength: the period of time during a 24-hour period during which an organism receives light.
- 257 ● diapause: period of suspended development or growth, usually used to describe invertebrates during
258 unfavorable environmental conditions such as winter.
- 259 ● dormancy: halted or reduced growth or activity, usually used to describe plants.
- 260 ● forcing: warm spring temperatures, often a certain sum of forcing that is required (e.g., some amount
261 of hours or days above a specific temperature) for budburst or flowering can occur.
- 262 ● green-up: The beginning of a new cycle of plant growth, usually evaluated at the landscape scale.
- 263 ● phenology: the timing of life cycle events in organisms
- 264 ● photoperiod: the daily duration of light (daylength) and dark to which an organism is exposed; often
265 used synonymously with daylength.
- 266 ● photoperiod sensitivity: the degree to which phenology is controlled by daylength; may be a nonlinear,
267 or “threshold”, response in plants (Box 2) and animals (Grevstad and Coop, 2015; Tobin et al., 2008).
- 268 ● photoperiodism: the ability to assess the length of day or night to regulate behavior, physiology, growth,
269 development or reproduction.
- 270 ● threshold photoperiod: length of day that causes an organism to switch from a short- to a long-day
271 response (or vice versa). For example, in European larch (*Larix decidua*), budburst development may
272 be constrained under short-day conditions, when daylengths are less than a threshold photoperiod of
273 10-11 hours (Migliavacca et al., 2008). Above this threshold photoperiod, the long-day response of
274 unconstrained budburst development can occur.

²⁷⁵ **Box 1. Are photoperiod effects widespread? A case study of woody**

²⁷⁶ **plant spring phenology**

²⁷⁷ Photoperiod responses are particularly well-studied in woody plant phenology, making this a useful case study
²⁷⁸ to consider climate change-induced shifts in photoperiod. Spring woody plant phenology in particular has
²⁷⁹ critical implications for global carbon cycling and feedbacks to the climate system (Richardson et al., 2013),
²⁸⁰ and has been at the center of an important and controversial debate on the relative effects of photoperiod
²⁸¹ versus temperature on phenology (e.g., Fu et al., 2019; Chuine et al., 2010; Körner and Basler, 2010*a,b*).

²⁸² Experimental growth chamber studies have shown that photoperiod is an important cue for spring budburst
²⁸³ phenology in woody plants (e.g., Flynn and Wolkovich, 2018; Basler and Körner, 2014; Heide, 1993*b*). These
²⁸⁴ experiments often manipulate photoperiod in combination with temperature to address basic questions about
²⁸⁵ how these two environmental conditions act as biological cues. Temperature has a dual role in regulating
²⁸⁶ woody plant phenology: chilling—the prolonged exposure to cold temperatures after growth cessation in the
²⁸⁷ fall—is required to initiate budburst; and forcing—prolonged exposure to warm temperatures—is required
²⁸⁸ for budburst to occur. Different photoperiod treatments are typically applied during the forcing treatment
²⁸⁹ phase in growth chamber experiments (e.g., Laube et al., 2014; Spann et al., 2004; Falusi and Calamassi,
²⁹⁰ 1990; Heide, 1977; Campbell and Sugano, 1975).

²⁹¹ Woody plant growth chamber studies have been conducted for decades, but have only recently been syn-
²⁹² thesized to show that photoperiod sensitivity is widespread, with large variation across studies and species.
²⁹³ These studies have been synthesized in Observed Spring Phenology Responses in Experimental Environments
²⁹⁴ (OSPREE), a new database of plant growth chamber studies that manipulate photoperiod and temperature
²⁹⁵ to measure plant phenological responses, including budburst and flowering (Wolkovich et al., 2019). The
²⁹⁶ database includes studies that manipulate photoperiod (by applying treatments with different daylength du-
²⁹⁷ rations, applying long-day versus short-day conditions for different lengths of time, and/or applying varying
²⁹⁸ versus constant photoperiods) and temperature (by imposing different chilling and/or forcing treatments).
²⁹⁹ The OSPREE database spans 201 woody plant species; all experiments in the database use dormant plant
³⁰⁰ tissue (grown in greenhouses or taken directly from the field) exposed to experimental conditions (Wolkovich
³⁰¹ et al., 2019) for which we could identify forcing, photoperiod, and chilling treatments quantitatively. See

³⁰² Supplemental Methods and Wolkovich et al. (2019) for details.

³⁰³ Growth chamber experiments in OSPREE suggest that the dominant photoperiod response in woody plant
³⁰⁴ species is earlier and more rapid budburst with longer days (e.g., Caffarra and Donnelly, 2011). Thirty-one
³⁰⁵ of the 85 studies in the OSPREE database included two or more different photoperiod treatments. Of these,
³⁰⁶ 26 (84%) found significant photoperiod main effects or significant interactive effects with temperature (i.e.,
³⁰⁷ photoperiod x temperature effects), across 176 species (Table S1). Main effects included responses such as
³⁰⁸ growth (e.g., higher growth rates with longer days Ashby et al., 1962) and reproduction (e.g., increased
³⁰⁹ flowering with longer days Heide and Sønsteby, 2012).

³¹⁰ Growth chamber experiments highlight that responses to photoperiod vary depending on temperature con-
³¹¹ ditions. For example, more rapid advancement of budburst was observed under long versus short days with
³¹² low chilling, than with high chilling in *Betula payrifera* (Hawkins and Dhar, 2012) (Fig. 4). Similarly, across
³¹³ species, as chilling accumulates from winter to spring, sensitivity to forcing and photoperiod sensitivity can
³¹⁴ decrease (Malyshev et al., 2018). Frequently, long photoperiods can compensate for low amounts of chilling,
³¹⁵ resulting in enhanced cell growth (Caffarra et al., 2011b; Myking and Heide, 1995; Heide, 1993a).

³¹⁶ Woody plant growth chamber experiments also demonstrate that, though photoperiod responses are common,
³¹⁷ they are variable (Fig. 4). Responses to photoperiod differ by species (e.g., Flynn and Wolkovich, 2018;
³¹⁸ Zohner et al., 2016; Basler and Körner, 2014, 2012; Howe et al., 1996; Heide, 1993b). For example, with
³¹⁹ longer chilling treatments some species seem insensitive to daylength (e.g., *Hammamelis* spp., *Prunus* spp.,
³²⁰ Zohner et al., 2016), whereas others seem to be highly sensitive to daylength (e.g. *Fagus* spp., Fig. 5A),
³²¹ even with long chilling treatments (Zohner et al., 2016). In addition, some species demonstrate a response
³²² to photoperiod opposite to that typically observed: *Tilia*, for example, showed delayed budburst with longer
³²³ daylengths (Fig. 4, Ashby et al., 1962). Photoperiod sensitivity also varies by population and ecotype (e.g.,
³²⁴ Fig. 4). For example, photoperiod effects on budburst were more significant for lower latitude populations
³²⁵ of *Betula pendula* and *B. pubescens* (Partanen et al., 2005).

³²⁶ **Box 2. Dominant models of how photoperiod affects spring woody**

³²⁷ **plant phenology**

³²⁸ The cues and molecular pathways underlying photoperiod sensitivity are poorly understood for most organ-
³²⁹ isms, even in relatively well-studied phenophases and taxa, such as spring budburst in woody plants (Ding
³³⁰ and Nilsson, 2016). Decades of growth chamber experiments suggest three main cues—chilling, forcing, and
³³¹ photoperiod—control spring budburst for many woody species (Flynn and Wolkovich, 2018; Zohner et al.,
³³² 2016; Heide, 2008), with many models suggesting a dominant role of forcing in most natural conditions. Forc-
³³³ ing requirements, however, appear to increase given shorter photoperiods or lower chilling (Caffarra et al.,
³³⁴ 2011a; Chuine et al., 2010). Research has yet to fully tease out effects of these three cues, their interactions,
³³⁵ and their prevalence, and photoperiod responses appear variable across species and populations, and with
³³⁶ different chilling treatments (see Fig. 4). Not surprisingly, then, there is currently little agreement on the
³³⁷ underlying model for how photoperiod affects spring phenology for most species (Chuine et al., 2016; Hänni-
³³⁸ nen et al., 2019). More physiological research will likely be necessary for major advances, as understanding
³³⁹ the exact cellular pathways through which chilling, forcing, and photoperiod act appears increasingly critical
³⁴⁰ to accurate models (van der Schoot et al., 2014; Hänninen et al., 2019).

³⁴¹ Additional cellular and molecular studies may quickly advance understanding and scale up to improved
³⁴² photoperiod models. While our understanding of how plants interpret photoperiod at the molecular-level
³⁴³ comes from fewer species, largely from studies of flowering in the model plant *Arabidopsis thaliana* (e.g.,
³⁴⁴ Suárez-López et al., 2001) and fall budset in woody plant species (e.g., Howe et al., 1996), these studies have
³⁴⁵ proved useful across other species. For example, the “external coincidence model” (where plants sense light
³⁴⁶ via blue light receptors and phytochromes, then interpret photoperiod through a coordinated response to
³⁴⁷ light in relation to the time of day, see Lagercrantz, 2009) has been most widely studied in *Arabidopsis*, but
³⁴⁸ appears to be a relevant mechanism for photoperiod responses in diverse perennial and woody plant species
³⁴⁹ (Singh et al., 2017; Petterle et al., 2013; Andrés and Coupland, 2012; Kobayashi and Weigel, 2007; Davis,
³⁵⁰ 2002; Bastow and Dean, 2002; Bünning, 1936). The model proposes the existence of a circadian rhythm of
³⁵¹ light sensitivity, in which the night-phase is sensitive to light and the day-phase is insensitive to light. As days
³⁵² get longer in the spring, daylight illuminates the light sensitive phase, triggering a response. This provides a

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

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

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

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675 **Figures**

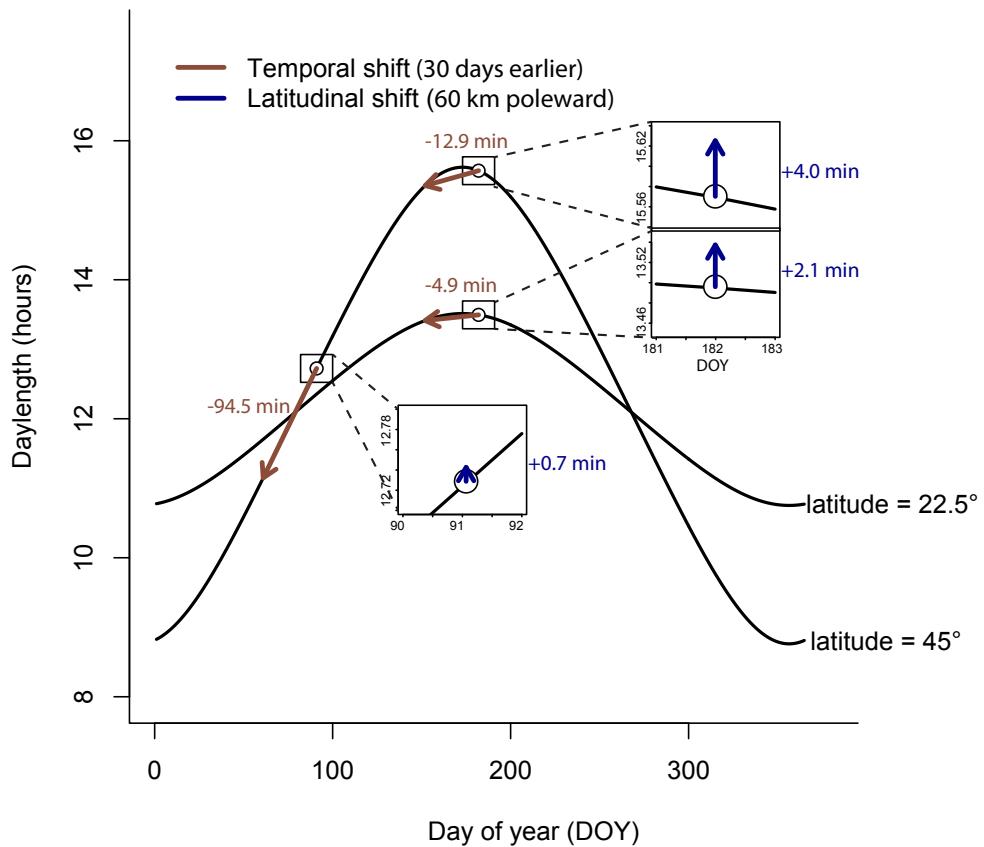


Figure 1: **Temporal (i.e., phenological) shifts in activity yield larger changes in experienced photoperiod compared to spatial (i.e., latitudinal) shifts** on the same day of year, due to patterns in photoperiod variation with latitude and by day of year. Here, we show this variation at two latitudes (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).

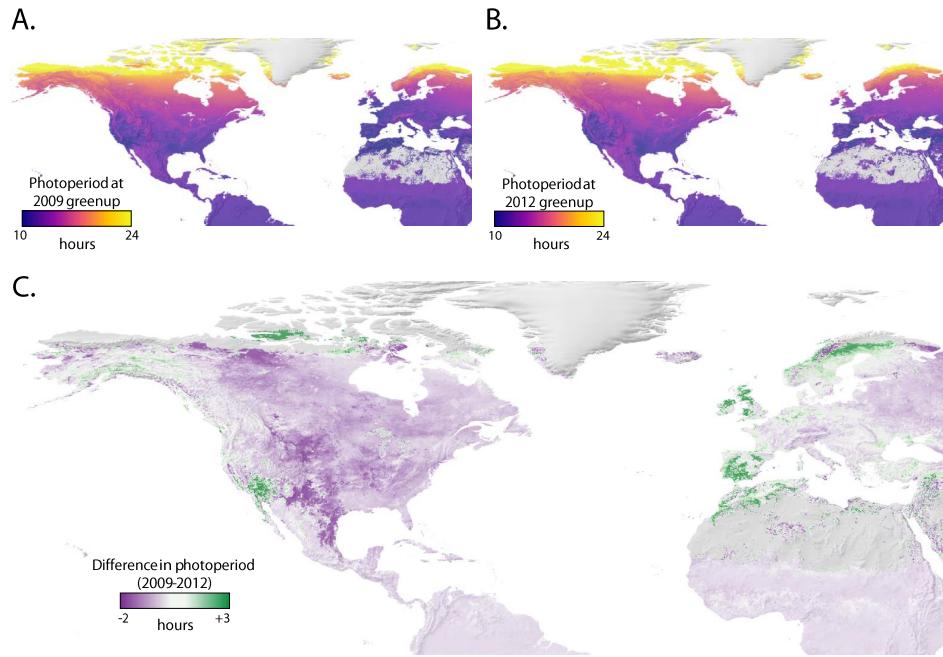


Figure 2: Photoperiod on “green-up” date varies over space and between years “Green-up” date is the beginning of seasonal greening, identified by satellite remote sensing measurements taken regularly throughout the year of the concentrations of green leaf vegetation. Hours of daylight on the date of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

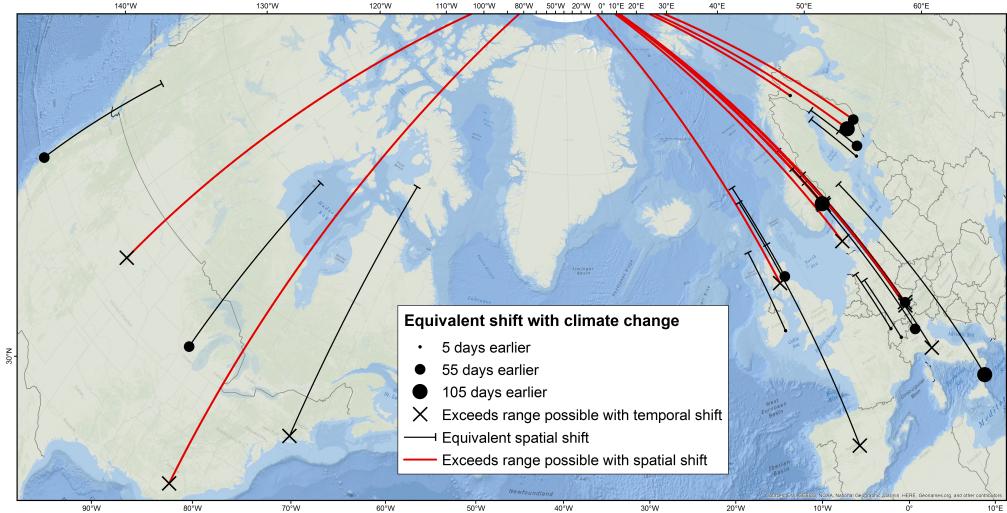


Figure 3: Experimental photoperiod treatments and their equivalent spatial and temporal shifts for experiments in the OSPREE database that manipulated photoperiod (see Box 1). See ‘Mapping temporal and spatial shifts in space and time’ in the Supplemental Materials for details on how we calculated the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

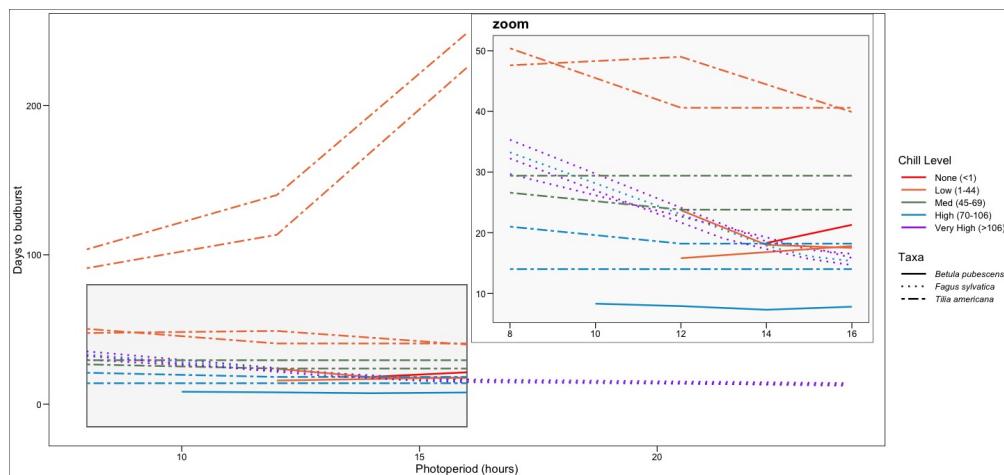


Figure 4: Nonlinearities in phenological responses to daylength are apparent in spring woody plant phenology experiments (from the OSPREE database, described in Box 1) in which three or more photoperiod treatment levels were applied. The shape of the response curves for *Betula pubescens* (Caffarra et 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.

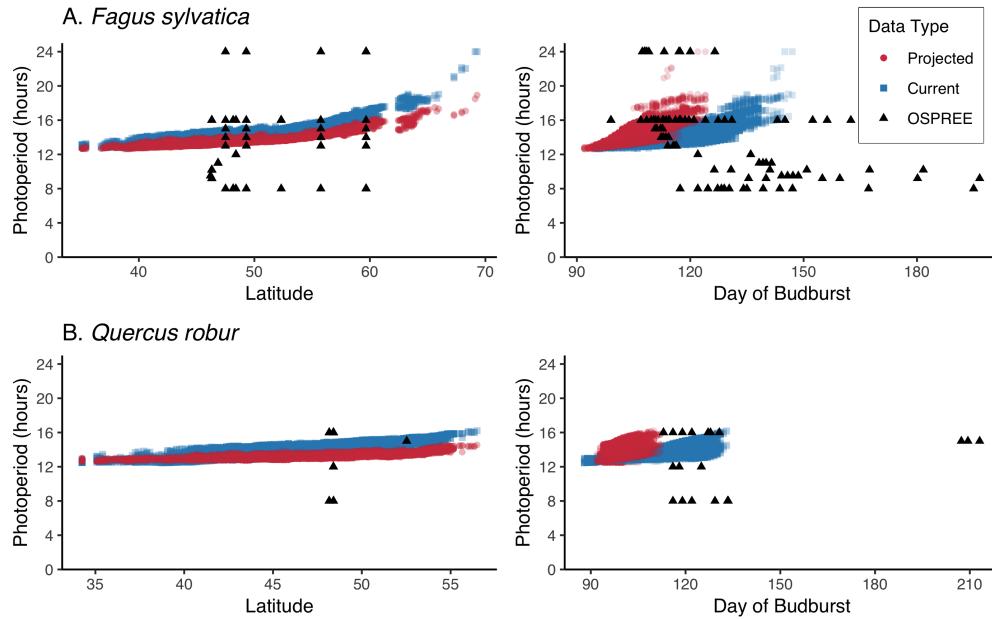


Figure 5: Experienced photoperiods in growth chamber experiments differ from those in the natural world, shown here by latitude (left panels) and by day of budburst (right panels) for *Fagus sylvatica* (A, upper panels) and *Quercus robur* (B, lower panels). Triangles show experimental treatments of photoperiod in the OSPREE database (Box 1). 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

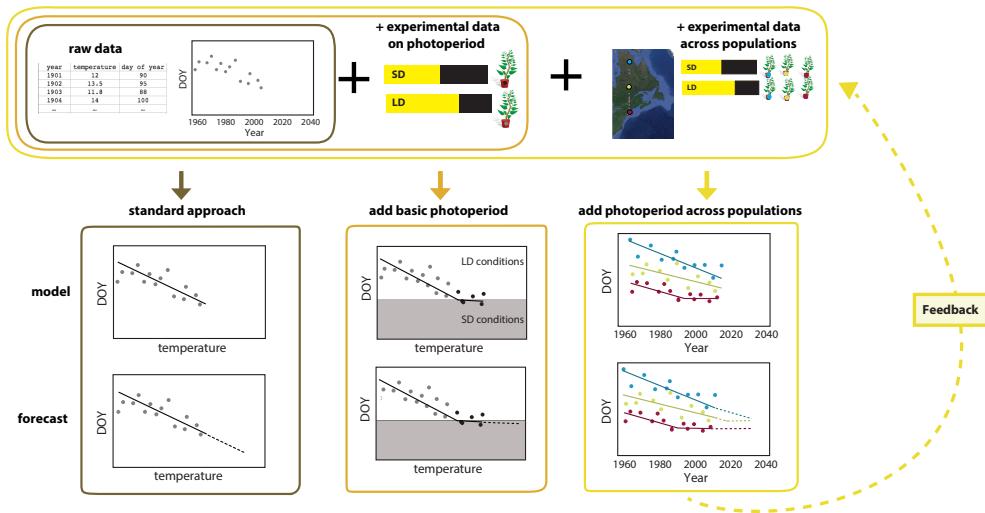


Figure 6: **Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change.** Current approaches for forecasting spring phenology with climate change frequently rely on linear relationships between historical temperature data and observed dates of spring phenology (left panels). Adding responses to photoperiod, which commonly operate as threshold responses to short days (SD) versus long days (LD, 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).