

Spatial and temporal shifts in photoperiod with climate change

A. K. Ettinger (ailene.ettinger@tnc.org)^{1,2,a}, D. M. Buonaiuto
(dbuonaiuto@g.harvard.edu)^{2,3}, C. J. Chamberlain (cchamberlain@g.harvard.edu)^{2,3}, I.
Morales-Castilla (ignacio.moralesc@uah.es)^{2,3,4,5}, and E. M. Wolkovich
(e.wolkovich@ubc.ca)^{2,3,6}

¹The Nature Conservancy, Seattle, Washington, USA

²Arnold Arboretum of Harvard University, Boston, Massachusetts, USA

³Department of Organismic and Evolutionary Biology, Harvard University, Cambridge,
Massachusetts, USA

⁴Department of Life Sciences, University of Alcalà CTRA N-II, KM., 33,600, 28802, Alcalà
de Henares, Spain

⁵Department of Environmental Science and Policy, George Mason University, Fairfax,
Virginia, USA

⁶Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia,
Vancouver, British Columbia, Canada

^aCorresponding author; phone: 781-296-4821; mailing address: 74 Wall Street, Seattle, WA
98121 USA

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Data Accessibility Should the manuscript be accepted in Ecology Letters, the data supporting our results will be archived in an appropriate public repository. The full OSPREE database will be publicly archived at KNB, doi:10.5063/F1QV3JQR (Wolkovich et al., 2019).

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

¹⁶ Introduction

¹⁷ Photoperiod is a critical cue for the onset of spring in plants and animals, signaling changes in growth,
¹⁸ migration, and reproduction across diverse species (e.g., Flynn and Wolkovich, 2018; Howe et al., 1996;
¹⁹ Lagercrantz, 2009; Bradshaw and Holzapfel, 2007; Mcallan et al., 2006; Solbakken et al., 1994; Barker and
²⁰ Herman, 1976; Farner, 1964). Photoperiod is a useful cue for diverse species to synchronize activities with
²¹ seasonal climatic changes (e.g., Singh et al., 2017; Basler and Körner, 2012; Hsu et al., 2011) because it is
²² 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, some of the most widely documented signals of climate
²⁹ change. At a given location on Earth, annual patterns in photoperiod have not changed as climates have
³⁰ warmed. Yet, across taxa, from plants and insects to mollusks and mammals, spring phenology is occurring
³¹ earlier as temperatures warm, with average shifts of 1.2 to 5.1 days earlier per decade (Bradley et al., 1999;
³² Parmesan and Yohe, 2003; Poloczanska et al., 2013; Root et al., 2003) or 1.3 to 5.6 days earlier per °C of
³³ warming (Polgar et al., 2013; Wolkovich et al., 2012). These changes are some of the largest climate change-
³⁴ induced shifts observed, with early spring phenology shifting more rapidly than later season phenology in
³⁵ most cases (Bradley et al., 1999; Menzel et al., 2006).

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

⁴³ constrains phenology will depend in part on how rapidly photoperiod responses can acclimate or adapt to
⁴⁴ new environmental conditions, which remains poorly understood (Grevstad and Coop, 2015; Bradshaw and
⁴⁵ Holzapfel, 2007).

⁴⁶ Perhaps because of these variable and uncertain responses, photoperiod is often not included in forecasts of
⁴⁷ biological responses to climate change, especially in the spring, even though it is known to be an important
⁴⁸ cue for biological activity (but see Duputié et al., 2015; Grevstad and Coop, 2015; Caffarra et al., 2011a).
⁴⁹ The exclusion of photoperiod may be problematic: although photoperiod itself is stable over time, the
⁵⁰ photoperiod that species *experience*, as they undergo climate change-induced shifts in space and time, is
⁵¹ likely to be much less stable. In addition to shifting activity earlier with recent warming, many species have
⁵² shifted their distributions poleward and upward in elevation (i.e., range shifts, Chen et al., 2011; Harsch et al.,
⁵³ 2009; Parmesan, 2006; Peñuelas and Boada, 2003). These spatial and temporal shifts alter the photoperiod
⁵⁴ experienced by organisms (Fig. 1); altered photoperiods may have cascading effects on species' performance,
⁵⁵ since daylength can affect the timing of development (Grevstad and Coop, 2015; Muir et al., 1994; Tauber
⁵⁶ and Tauber, 1975), migration (Dawbin, 1966), reproduction (Dunn, 2019; Dardente, 2012; Ben-David, 1997),
⁵⁷ and other important responses.

⁵⁸ The implications of potential climate change-induced shifts in experienced photoperiod are unclear, as the
⁵⁹ magnitude of potential shifts has not been described. Effects of photoperiod shifts may be relatively mi-
⁶⁰ nor, especially because there can be substantial year-to-year variation in experienced photoperiod (Fig. 2).
⁶¹ Alternatively, photoperiod may begin to constrain species' responses to climate change (Körner and Basler,
⁶² 2010b).

⁶³ Here, we ask:

- ⁶⁴ 1. How will climate change alter the photoperiod experienced by organisms?
- ⁶⁵ 2. What are the implications of altered photoperiods for biological responses to climate change?
- ⁶⁶ 3. Can researchers apply data from experiments that alter photoperiod to aid in forecasting biological
⁶⁷ implications of climate change?

⁶⁸ We focus on spring events, as phenology during this time is one of the most widely observed and rapidly

69 changing biological responses to climate change (Parmesan, 2006). In addition, the role of photoperiod is less
70 understood in spring phenology compared with autumn phenophases, 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. Our questions are broadly relevant for diverse species; to
73 illustrate some of our points, we use a case study of spring woody plant phenology (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. Compare the photoperiod at green-up in an “early” versus an “average” year (Fig.
89 2): experienced photoperiod at green-up can vary by two to three hours from one year to the next in the
90 same location (Fig. 2c). We use green-up date as an example here because it is an available dataset and
91 represents an important biological event, signalling the start of the growing season. Though green-up date
92 corresponds to plant phenology, we expect that spatiotemporal patterns are similarly heterogeneous in spring
93 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, where the scientific literature has addressed shifts in photoperiod with climate change, the focus has
102 been on how spatial range shifts will affect photoperiod (e.g., Saikkonen et al., 2012; Way and Montgomery,
103 2015). However, shifting phenology—especially the large changes seen in spring phenology—will also alter
104 experienced photoperiod, 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 photoperiod (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, 2010b; 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, 2010b; 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 force-
¹⁴⁶ casting whether and when the trend of earlier phenology with warming may slow or stop abruptly, is the

¹⁴⁷ wide range of observed photoperiod sensitivity across species (Flynn and Wolkovich, 2018; Sanz-Perez et al.,
¹⁴⁸ 2009; Zohner et al., 2016), 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., Franks et al., 2014;
¹⁵⁰ Gould et al., 2010; Mimura and Aitken, 2010; Fréjaville et al., 2019). 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 et al.,
¹⁵⁶ 2011; Weih, 2004, see also Box 1). Teasing out the relative roles of genetics versus environmental conditions
¹⁵⁷ 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. To identify where, when, and how communities may be altered, quantifying
¹⁶⁶ species-specific photoperiod sensitivity and developing methods for incorporating photoperiod into forecasting
¹⁶⁷ future phenology are critical.

¹⁶⁸ Future directions: outstanding questions and incorporating pho- ¹⁶⁹ toperiod into forecasting

¹⁷⁰ Incorporating photoperiod into forecasting is complex for a few major reasons. Future rates of phenological
¹⁷¹ shifts are unlikely to be straightforward extrapolations from past and current rates. In addition, an organism's
¹⁷² experienced photoperiod is both a driver and an effect of phenological shifts.

173 Approaches for forecasting can be grouped into two broad categories: statistical models and process-based
174 models. These two modelling paradigms differ in at least two ways, in terms of relating phenology to climate
175 change. First, statistical models relating phenology to climate change generally assume linear relationships
176 between species' responses and environmental variables (e.g., Flynn and Wolkovich, 2018; Van Belle et al.,
177 2007; Ibáñez et al., 2010). Process-based models often incorporate nonlinear threshold relationships (e.g.
178 Chuine and Beaubien, 2001; Morin and Thuiller, 2009; Xie and Hsieh, 1989). Second, statistical models of
179 phenology under climate change have typically ignored photoperiod, focusing instead on seasonal or annual
180 temperature (e.g. Diez et al., 2012; Ibáñez et al., 2010; Van Belle et al., 2007, but see Richardson et al.
181 (2013)). whereas process-based models of phenology more frequently incorporate photoperiod, along with
182 temperature (Lundell et al., 2020; Duputié et al., 2015; Zhao et al., 2013; Morin and Thuiller, 2009; Xie
183 and Hsieh, 1989). A challenge of process-based models is that they require detailed data that are often not
184 readily available (e.g., daily climate data, nonlinear biological responses to fine-scale changes in temperature).
185 Perhaps because of this challenge, statistical models remain more commonly used in climate change forecasts
186 of biological responses (e.g., García-Valdés and Morales-Castilla, 2016; Basler and Körner, 2012; Diez et al.,
187 2012; Zhu et al., 2012; Ibáñez et al., 2010; Van Belle et al., 2007).

188 Future modelling of spring woody plant phenology can incorporate photoperiod by leveraging the large
189 amount of experimental data on photoperiod responses (e.g., Fig. 3, Table S1, Box 2), especially when
190 process-based approaches are used. Researchers can use these data to first learn whether the study species
191 (or a phylogenetically closely related species) shows a photoperiod effect and, ideally, identify its threshold
192 photoperiod and how it varies by population, ecotype, or other factors (Tobin et al., 2008; Bradshaw and
193 Holzapfel, 2006; Gwinner, 1996). If there is evidence of a photoperiod response (e.g., *Fagus grandifolia*,
194 or *Tilia americana* with low chilling in Fig. 4), daylength should be added to forecasting models, using
195 the threshold photoperiod to define short-day and long-day conditions (Fig. 6). Given the large change in
196 experienced photoperiod with temporal shifts (Fig. 1), this may be particularly important for phenological
197 forecasting. Since spatial shifts are associated with smaller changes in experienced photoperiod, it may be less
198 important for distribution forecasts. Many species, however, may shift in *both* space and time simultaneously.
199 Thus, even though experienced photoperiod changes little as species distributions shift in space, phenology
200 may be altered significantly.

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

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

221 As researchers more fully integrate photoperiod into forecasting, a critical area of further study is under-
222 standing *how* photoperiod acts as a cue. Photoperiod seems to interact with temperature to affect phenology
223 (e.g., Zydlewski et al., 2014); this would explain the divergent effects of photoperiod observed across studies
224 in woody plants (e.g., Fig. 4). However, exactly how it interacts with temperature is not well-defined for most
225 species or populations (Boxes 1, 2). For many species, additional experimental and physiological research
226 is necessary, since the dormancy-breaking processes that photoperiod affects often require microscopy and
227 detailed physiological approaches to observe (Hänninen et al., 2019; Chuine et al., 2016). Understanding the
228 drivers, as well as the consequences, of variations in photoperiod responses across species and populations

²²⁹ will be particularly beneficial for forecasting. For example, what traits are associated with photoperiod sen-
²³⁰ sitivity and does variation in photoperiod sensitivity or related traits have a strong genetic component? If
²³¹ so, are species or populations from some locations or lineages more likely than others to be constrained by
²³² photoperiod in their responses to climate change?

²³³ Conclusions

²³⁴ Organisms may undergo large changes to the photoperiod they experience with climate change, even if they
²³⁵ do not shift their ranges spatially. Here we have shown that these altered photoperiods may result in stalled
²³⁶ future advances of woody plant phenology with warming (e.g., Table S1, Fig. 5, Fu et al., 2019; Güsewell
²³⁷ et al., 2017; Yu et al., 2010), with cascading effects on growth, fitness, and community composition due to the
²³⁸ large variation in photoperiod responses across species and populations (Fig. 4). Shifts in photoperiod with
²³⁹ climate change have implications for a variety of plant and animal responses, given that daylength affects
²⁴⁰ critical activities for diverse species from insects (Bradshaw and Holzapfel, 2006; Linn et al., 1996) and
²⁴¹ salmon (Taranger et al., 2003; Solbakken et al., 1994) to birds (Dawson et al., 2001) and marsupials (McAllan
²⁴² et al., 2006; Solbakken et al., 1994). Given what we know, incorporating photoperiod into forecasting of
²⁴³ climate change responses should improve model accuracy, and will illuminate additional experiments that
²⁴⁴ could improve our mechanistic understanding of photoperiod as a critical cue for diverse biological responses.

²⁴⁵ Glossary

- ²⁴⁶ • budburst: when one or more leaf buds have visible green tips.
- ²⁴⁷ • chilling: the intensity and duration of winter temperature, often a certain sum of chilling that is required
²⁴⁸ (e.g., some amount of hours or days of cold temperatures, defined by a specific critical temperature or
²⁴⁹ range of temperatures, such as between 0 and 7.2 °C, Richardson, 1974), that must be experienced for
²⁵⁰ budburst to occur.
- ²⁵¹ • daylength: the period of time during a 24-hour period during which an organism receives light.

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

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

272 **Focal examples from spring woody plant phenology**

273 Photoperiod responses are particularly well-studied in woody plant phenology, making this a useful focal
274 system in which to consider climate change-induced shifts in photoperiod. Decades of experimental growth

chamber studies have shown that photoperiod is an important cue for spring budburst phenology in woody plants (e.g., Flynn and Wolkovich, 2018; Basler and Körner, 2014; Heide, 1993b). These experiments often manipulate photoperiod in combination with temperature to address basic questions about how these two environmental conditions act as biological cues. Temperature has a dual role in regulating woody plant phenology: chilling—the prolonged exposure to cold temperatures after growth cessation in the fall—is required to initiate budburst; and forcing—prolonged exposure to warm temperatures—is required for budburst to occur. Different photoperiod treatments are typically applied during the forcing treatment phase in growth chamber experiments (e.g., Laube et al., 2014; Spann et al., 2004; Falusi and Calamassi, 1990; Heide, 1977; Campbell and Sugano, 1975). We also focus on spring woody plant phenology because it is at the center of an important and controversial debate on the relative effects of photoperiod versus temperature on phenology, and because the length of the growing season has critical implications for global carbon cycling and feedbacks to the climate system (Richardson et al., 2013).

Woody plant growth chamber studies have been conducted for decades, but have only recently been synthesized, revealing that photoperiod sensitivity is widespread, though with wide variation across studies and species. These studies were synthesized in Observed Spring Phenology Responses in Experimental Environments (OSPREE), a new database of plant growth chamber studies that manipulate photoperiod and temperature to measure plant phenological responses, including budburst and flowering (Wolkovich et al., 2019). The database includes studies that manipulate photoperiod (by applying treatments with different daylength durations, applying long-day versus short-day conditions for different lengths of time, and/or applying varying vs constant photoperiods) and temperature (by imposing different chilling and/or forcing treatments). The OSPREE database spans 201 woody plant species; all experiments in the database use dormant plant tissue (grown in greenhouses or taken directly from the field) exposed to experimental conditions (Wolkovich et al., 2019) for which we could identify forcing, photoperiod, and chilling treatments quantitatively. See Supplemental Methods and Wolkovich et al. (2019) for details.

Growth chamber experiments in OSPREE suggest that the dominant photoperiod response in woody plant species is earlier and more rapid budburst with longer days (e.g., Caffarra and Donnelly, 2011). Thirty-one of the 85 studies in the OSPREE database included two or more different photoperiod treatments. Of these, 26 (84%) found significant photoperiod main effects or significant interactive effects with temperature (i.e.,

³⁰³ photoperiod x temperature effects), across 176 species (Table S1). Main effects included responses such as
³⁰⁴ growth (e.g., higher growth rates with longer days Ashby et al., 1962) and reproduction (e.g., increased
³⁰⁵ flowering with longer days Heide and Sønsteby, 2012).

³⁰⁶ Growth chamber experiments highlight that responses to photoperiod vary depending on temperature con-
³⁰⁷ ditions. For example, more rapid advancement of budburst was observed under long versus short days with
³⁰⁸ low chilling, than with high chilling in *Betula payrifera* (Hawkins and Dhar, 2012) (Fig. 4). Similarly, across
³⁰⁹ species, as chilling accumulates from winter to spring, sensitivity to forcing and photoperiod sensitivity can
³¹⁰ decrease (Malyshev et al., 2018). Frequently, long photoperiods can compensate for low amounts of chilling,
³¹¹ resulting in enhanced cell growth (Caffarra et al., 2011b; Myking and Heide, 1995; Heide, 1993a).

³¹² Woody plant growth chamber experiments also demonstrate that, though photoperiod responses are common,
³¹³ they are variable (Fig. 4). Responses to photoperiod differ by species (e.g., Flynn and Wolkovich, 2018;
³¹⁴ Zohner et al., 2016; Basler and Körner, 2014, 2012; Howe et al., 1996; Heide, 1993b). For example, with
³¹⁵ longer chilling treatments some species seem insensitive to daylength (e.g., *Hammamelis* spp., *Prunus* spp.,
³¹⁶ Zohner et al., 2016), whereas others seem to be highly sensitive to daylength (e.g. *Fagus* spp., Fig. 5A),
³¹⁷ even with long chilling treatments (Zohner et al., 2016). In addition, some species demonstrate a response
³¹⁸ to photoperiod opposite to that typically observed: *Tilia*, for example, showed delayed budburst with longer
³¹⁹ daylengths (Fig. 4, Ashby et al., 1962). Photoperiod sensitivity also varies by population and ecotype (e.g.,
³²⁰ Partanen et al., 2005) (Fig. 4). For example, photoperiod effects on budburst were more significant for lower
³²¹ latitude populations of *Betula pendula* and *B. pubescens* (Partanen et al., 2005).

³²² **Box 2. Dominant models of how photoperiod affects spring woody 323 plant phenology**

³²⁴ The molecular mechanisms and pathways underlying photoperiod sensitivity are poorly understood for most
³²⁵ organisms, even in relatively well-studied phenophases such as spring budburst in woody plants (Ding and
³²⁶ Nilsson, 2016). Spring budburst in woody plants is thought to be controlled by three main cues: chilling,
³²⁷ forcing, and photoperiod, as well as interactions between them (Flynn and Wolkovich, 2018; Heide, 2008;

328 Zohner et al., 2016). Our understanding of how plants interpret photoperiod comes largely from studies of
329 flowering in the model plant *Arabidopsis thaliana* (e.g., Suárez-López et al., 2001) and fall budset in woody
330 plant species (e.g., Howe et al., 1996).

331 Plants sense light inputs by blue light receptors and phytochromes, which have been found in nearly all
332 organs throughout the plant. Plants are thought to interpret photoperiod through a coordinated response
333 to light in relation to the time of day. When the internal circadian rhythm coincides with an external signal
334 (light) under certain conditions (e.g., warm days), a response is induced (Lagercrantz, 2009). This “external
335 coincidence model” has been most widely studied in *Arabidopsis*, and is thought to be a relevant mechanism
336 for photoperiod responses in diverse perennial and woody plant species (Bünning, 1936; Davis, 2002; Bastow
337 and Dean, 2002; Kobayashi and Weigel, 2007; Andrés and Coupland, 2012; Petterle et al., 2013; Singh et al.,
338 2017). The model proposes the existence of a circadian rhythm of light sensitivity, in which the night-phase
339 is sensitive to light and the day-phase is insensitive to light. As days get longer in the spring, daylight
340 illuminates the light sensitive phase, triggering a response.

341 Little is known about the genetic pathways responsible for the light-sensing apparatuses involved in spring
342 budburst, and how they may vary across species or populations. Some genes have been identified that play
343 a role in coordinating budburst in poplar (*Populus* spp.), and may occur in other woody species as well.
344 Many similarities exist between the proposed regulatory networks of vegetative growth in *Populus* and those
345 controlling floral initiation in *Arabidopsis*, (Ding and Nilsson, 2016). For example, vegetative growth and
346 inhibition of budset are promoted by the FLOWERING LOCUS T2 (FT2) gene, a homolog of *Arabidopsis*
347 *thaliana* gene FLOWERING LOCUS (FT). FT2 expression appears to be controlled by a pathway that is
348 effective in long days and warm temperatures, marking the onset of the growing season (?). Its loss of
349 expression in autumn, when the days are getting shorter, is associated with the onset of dormancy (Glover,
350 2014).

351 There are large gaps in our understanding of how photoperiod sensing pathways affect budburst, the genetics
352 behind these pathways, and the extent of species- and population-level genetic variation. Questions also
353 remain about how photoperiod sensing interacts with temperature sensing to affect responses. For example,
354 Figure 4 shows the most detailed data we were able to find of budburst responses across different photoperiod
355 and chilling treatments. These data underscore how variable responses to photoperiod are, across species

356 and populations, and with different chilling treatments.

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365 References

- 366 Andrés, F., and G. Coupland. 2012. The genetic basis of flowering responses to seasonal cues. *Nature reviews. Genetics* 13:627.
- 367 Ashby, W., et al. 1962. Germination capacity in American Basswood *Tilia americana*. *Transactions of the Illinois State Academy of Science* 55:120–3.
- 368 Barker, J. F., and W. S. Herman. 1976. Effect of photoperiod and temperature on reproduction of the monarch butterfly, *danaus plexippus*. *Journal of Insect Physiology* 22:1565–1568.
- 369 Basler, D., and C. Körner. 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology* 165:73–81.
- 370 ———. 2014. Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. *Tree Physiology* 34:377–388.
- 371 Bastow, R., and C. Dean. 2002. The molecular basis of photoperiodism. *Developmental cell* 3:461–462.
- 372 Ben-David, M. 1997. Timing of reproduction in wild mink: the influence of spawning Pacific salmon. *Canadian Journal of Zoology* 75:376–382.

- 379 Bradley, N. L., A. C. Leopold, J. Ross, and W. Huffaker. 1999. Phenological changes reflect climate change
380 in Wisconsin. *Proceedings of the National Academy of Sciences* 96:9701–9704.
- 381 Bradshaw, H., and R. F. Stettler. 1995. Molecular genetics of growth and development in *Populus*. IV.
382 Mapping QTLs with large effects on growth, form, and phenology traits in a forest tree. *Genetics* 139:963–
383 973.
- 384 Bradshaw, W. E., and C. M. Holzapfel. 2006. Evolutionary response to rapid climate change. *Science*
385 312:1477–1478.
- 386 ———. 2007. Evolution of animal photoperiodism. *Annu. Rev. Ecol. Evol. Syst.* 38:1–25.
- 387 Büning, E. 1936. Endogenous daily rhythms as the basis of photoperiodism. *Ber Deut Bot Ges* 54:590–607.
- 388 Caffarra, A., and A. Donnelly. 2011. The ecological significance of phenology in four different tree species:
389 effects of light and temperature on bud burst. *International Journal of Biometeorology* 55:711–721.
- 390 Caffarra, A., A. Donnelly, and I. Chuine. 2011a. Modelling the timing of *Betula pubescens* budburst. II.
391 Integrating complex effects of photoperiod into process-based models. *Climate Research* 46:159–170.
- 392 Caffarra, A., A. Donnelly, I. Chuine, and M. B. Jones. 2011b. Modelling the timing of *Betula pubescens*
393 bud-burst. I. Temperature and photoperiod: A conceptual model. *Climate Research* 46:147.
- 394 Campbell, R. K., and A. I. Sugano. 1975. Phenology of bud burst in Douglas-fir related to provenance,
395 photoperiod, chilling, and flushing temperature. *Botanical Gazette* pages 290–298.
- 396 Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species
397 associated with high levels of climate warming. *Science* 333:1024–1026.
- 398 Chuine, I., and E. G. Beaubien. 2001. Phenology is a major determinant of tree species range. *Ecology*
399 Letters 4:500–510.
- 400 Chuine, I., M. Bonhomme, J.-M. Legave, I. García de Cortázar-Atauri, G. Charrier, A. Lacointe, and
401 T. Améglio. 2016. Can phenological models predict tree phenology accurately in the future? The un-
402 revealed hurdle of endodormancy break. *Global Change Biology* 22:3444–3460.

- 403 Chuine, I., X. Morin, and H. Bugmann. 2010. Warming, photoperiods, and tree phenology. *Science* 329:277–
404 278.
- 405 Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta, and E. M.
406 Wolkovich. 2012. Phenological tracking enables positive species responses to climate change. *Ecology*
407 93:1765–1771.
- 408 Dardente, H. 2012. Melatonin-dependent timing of seasonal reproduction by the pars tuberalis: pivotal roles
409 for long daylengths and thyroid hormones. *Journal of Neuroendocrinology* 24:249–266.
- 410 Davis, S. J. 2002. Photoperiodism: the coincidental perception of the season. *Current Biology* 12:R841–R843.
- 411 Dawbin, W. H. 1966. The seasonal migratory cycle of humpback whales, pages 145–170. University of
412 California Press Berkeley.
- 413 Dawson, A., V. M. King, G. E. Bentley, and G. F. Ball. 2001. Photoperiodic control of seasonality in birds.
414 *Journal of Biological Rhythms* 16:365–380.
- 415 Diez, J. M., I. Ibáñez, A. J. Miller-Rushing, S. J. Mazer, T. M. Crimmins, M. A. Crimmins, C. D. Bertelsen,
416 and D. W. Inouye. 2012. Forecasting phenology: from species variability to community patterns. *Ecology*
417 Letters 15:545–553.
- 418 Ding, J., and O. Nilsson. 2016. Molecular regulation of phenology in trees— because the seasons they are
419 a-changin. *Current Opinion in Plant Biology* 29:73–79.
- 420 Dunn, P. O. 2019. Changes in timing of breeding and reproductive success in birds. *Effects of Climate Change*
421 on Birds page 108.
- 422 Duputié, A., A. Rutschmann, O. Ronce, and I. Chuine. 2015. Phenological plasticity will not help all species
423 adapt to climate change. *Global Change Biology* 21:3062–3073.
- 424 Erwin, J. E. 1998. Temperature and light effects on stem elongation. *Journal of the Japanese Society for*
425 *Horticultural Science* 67:1113–1120.
- 426 Falusi, M., and R. Calamassi. 1990. Bud dormancy in beech (*Fagus sylvatica* L.). Effect of chilling and
427 photoperiod on dormancy release of beech seedlings. *Tree Physiology* 6:429–438.

- 428 Farner, D. S. 1964. The photoperiodic control of reproductive cycles in birds. American Scientist 52:137–156.
- 429 Fishman, S., A. Erez, and G. Couvillon. 1987. The temperature dependence of dormancy breaking in plants:
430 mathematical analysis of a two-step model involving a cooperative transition. Journal of Theoretical
431 Biology 124:473–483.
- 432 Flynn, D. F. B., and E. M. Wolkovich. 2018. Temperature and photoperiod drive spring phenology across all
433 species in a temperate forest community. New Phytologist 219:1353–1362.
- 434 Franks, S. J., J. J. Weber, and S. N. Aitken. 2014. Evolutionary and plastic responses to climate change in
435 terrestrial plant populations. Evolutionary Applications 7:123–139.
- 436 Fréjaville, T., B. Fady, A. Kremer, A. Ducouso, and M. Benito Garzón. 2019. Inferring phenotypic plasticity
437 and population responses to climate across tree species ranges using forest inventory data. Global Ecology
438 and Biogeography 28:1259–1271.
- 439 Fu, Y. H., S. Piao, X. Zhou, X. Geng, F. Hao, Y. Vitasse, and I. A. Janssens. 2019. Short photoperiod
440 reduces the temperature sensitivity of leaf-out in saplings of *Fagus sylvatica* but not in horse chestnut.
441 Global Change Biology 25:1696–1703.
- 442 Fu, Y. S. H., H. F. Zhao, S. L. Piao, M. Peaucelle, S. S. Peng, G. Y. Zhou, P. Ciais, M. T. Huang, A. Menzel,
443 J. P. Uelas, Y. Song, Y. Vitasse, Z. Z. Zeng, and I. A. Janssens. 2015. Declining global warming effects on
444 the phenology of spring leaf unfolding. Nature 526:104–107.
- 445 García-Valdés, R., and I. Morales-Castilla. 2016. Efectos del cambio climático en los ecosistemas forestales:
446 integrando inventarios y modelos. Ecosistemas 25:51–59.
- 447 Gauzere, J., S. Delzon, H. Davi, M. Bonhomme, I. G. de Cortazar-Atauri, and I. Chuine. 2017. Integrating
448 interactive effects of chilling and photoperiod in phenological process-based models. A case study with
449 two European tree species: *Fagus sylvatica* and *Quercus petraea*. Agricultural and Forest Meteorology
450 244:9–20.
- 451 Glover, B. 2014. Understanding flowers and flowering, Second edition. OUP Oxford.

- 452 Gould, P. J., C. A. Harrington, and J. B. St. Clair. 2010. Incorporating genetic variation into a model of
453 budburst phenology of coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). Canadian journal of forest
454 research 41:139–150.
- 455 Grevstad, F. S., and L. B. Coop. 2015. The consequences of photoperiodism for organisms in new climates.
456 Ecological Applications 25:1506–1517.
- 457 Güsewell, S., R. Furrer, R. Gehrig, and B. Pietragalla. 2017. Changes in temperature sensitivity of spring
458 phenology with recent climate warming in switzerland are related to shifts of the preseason. Global Change
459 Biology 23:5189–5202.
- 460 Gwinner, E. 1996. Circadian and circannual programmes in avian migration. Journal of Experimental Biology
461 199:39–48.
- 462 Hänninen, H., K. Kramer, K. Tanino, R. Zhang, J. Wu, and Y. H. Fu. 2019. Experiments are necessary in
463 process-based tree phenology modelling. Trends in Plant Science 24:199–209.
- 464 Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global
465 meta-analysis of treeline response to climate warming. Ecology Letters 12:1040–1049.
- 466 Hawkins, C. D., and A. Dhar. 2012. Spring bud phenology of 18 *Betula papyrifera* populations in British
467 Columbia. Scandinavian Journal of Forest Research 27:507–519.
- 468 Heide, O. 1993a. Daylength and thermal time responses of budburst during dormancy release in some
469 northern deciduous trees. Physiologia Plantarum 88:531–540.
- 470 ———. 1993b. Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days.
471 Physiologia Plantarum 89:187–191.
- 472 Heide, O. M. 1977. Photoperiod and temperature interactions in growth and flowering of strawberry. Physi-
473 ologia Plantarum 40:21–26.
- 474 ———. 2008. Interaction of photoperiod and temperature in the control of growth and dormancy of *Prunus*
475 species. Scientia Horticulturae 115:309–314.
- 476 ———. 2011. Temperature rather than photoperiod controls growth cessation and dormancy in *Sorbus*
477 species. Journal of Experimental Botany 62:5397–5404.

- 478 Heide, O. M., and A. Sønsteby. 2012. Floral initiation in black currant cultivars (*Ribes nigrum* L.): Effects of
479 plant size, photoperiod, temperature, and duration of short day exposure. *Scientia Horticulturae* 138:64–72.
- 480 Heide, O. M., and A. Sonsteby. 2015. Simultaneous dormancy induction interferes with short day floral
481 induction in black currant (*Ribes nigrum* L.). *Scientia Horticulturae* 185:228–232.
- 482 Howe, G. T., G. Gardner, W. P. Hackett, and G. R. Furnier. 1996. Phytochrome control of short-day-induced
483 bud set in black cottonwood. *Physiologia Plantarum* 97:95–103.
- 484 Howe, G. T., W. P. Hackett, G. R. Furnier, and R. E. Klevorn. 1995. Photoperiodic responses of a northern
485 and southern ecotype of black cottonwood. *Physiologia Plantarum* 93:695–708.
- 486 Hsu, C.-Y., J. P. Adams, H. Kim, K. No, C. Ma, S. H. Strauss, J. Drnevich, L. Vandervelde, J. D. Ellis, B. M.
487 Rice, et al. 2011. FLOWERING LOCUS T duplication coordinates reproductive and vegetative growth in
488 perennial poplar. *Proceedings of the National Academy of Sciences* 108:10756–10761.
- 489 Ibáñez, I., R. B. Primack, A. J. Miller-Rushing, E. Ellwood, H. Higuchi, S. D. Lee, H. Kobori, and J. A.
490 Silander. 2010. Forecasting phenology under global warming. *Philosophical Transactions of the Royal
491 Society B-Biological Sciences* 365.
- 492 Jolly, W. M., R. Nemani, and S. W. Running. 2005. A generalized, bioclimatic index to predict foliar
493 phenology in response to climate. *Global Change Biology* 11:619–632.
- 494 Keller, S. R., R. Y. Soolanayakanahally, R. D. Guy, S. N. Silim, M. S. Olson, and P. Tiffin. 2011. Climate-
495 driven local adaptation of ecophysiology and phenology in balsam poplar, *Populus balsamifera* L. (Salicaceae). *American Journal of Botany* 98:99–108.
- 496 Kobayashi, Y., and D. Weigel. 2007. Move on up, it's time for change—mobile signals controlling photoperiod-
497 dependent flowering. *Genes & Development* 21:2371–2384.
- 498 Körner, C., and D. Basler. 2010a. Phenology under global warming. *Science* 327:1461–1462.
- 499 ———. 2010b. Warming, photoperiods, and tree phenology response. *Science* 329:278–278.
- 500 Lagercrantz, U. 2009. At the end of the day: a common molecular mechanism for photoperiod responses in
501 plants? *Journal of Experimental Botany* 60:2501–2515.

- 503 Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs
504 photoperiod in preventing precocious spring development. *Global Change Biology* 20:170–182.
- 505 Linkosalo, T., and M. J. Lechowicz. 2006. Twilight far-red treatment advances leaf bud burst of silver birch
506 (*Betula pendula*). *Tree Physiology* 26:1249–1256.
- 507 Linn, C. E., M. G. Campbell, K. R. Poole, W.-Q. Wu, and W. L. Roelofs. 1996. Effects of photoperiod on
508 the circadian timing of pheromone response in male *trichoplusia ni*: relationship to the modulatory action
509 of octopamine. *Journal of Insect Physiology* 42:881–891.
- 510 Lundell, R., H. Hänninen, T. Saarinen, H. Åström, and R. Zhang. 2020. Beyond rest and quiescence (endodormancy
511 and ecodormancy): A novel model for quantifying plant–environment interaction in bud dormancy
512 release. *Plant, Cell & Environment* 43:40–54.
- 513 Malyshev, A. V., H. A. Henry, A. Bolte, M. A. A. Khan, and J. Kreyling. 2018. Temporal photoperiod
514 sensitivity and forcing requirements for budburst in temperate tree seedlings. *Agricultural and Forest
515 Meteorology* 248:82–90.
- 516 Mcallan, B. M., C. R. Dickman, and M. S. Crowther. 2006. Photoperiod as a reproductive cue in the
517 marsupial genus *Antechinus*: ecological and evolutionary consequences. *Biological Journal of the Linnean
518 Society* 87:365–379.
- 519 Medvigy, D., S.-J. Jeong, K. L. Clark, N. S. Skowronski, and K. V. Schäfer. 2013. Effects of seasonal variation
520 of photosynthetic capacity on the carbon fluxes of a temperate deciduous forest. *Journal of Geophysical
521 Research: Biogeosciences* 118:1703–1714.
- 522 Menzel, A. 2000. Trends in phenological phases in Europe between 1951 and 1996. *International Journal of
523 Biometeorology* 44:76–81.
- 524 Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aasa, R. Ahas, K. Alm-Kuebler, et al. 2006. European
525 phenological response to climate change matches the warming pattern. *Global Change Biology* 12:1969–
526 1976.
- 527 Migliavacca, M., E. Cremonese, R. Colombo, L. Busetto, M. Galvagno, L. Ganis, M. Meroni, E. Pari,
528 M. Rossini, C. Siniscalco, et al. 2008. European larch phenology in the Alps: can we grasp the role

- 529 of ecological factors by combining field observations and inverse modelling? International Journal of
530 Biometeorology 52:587–605.
- 531 Mimura, M., and S. Aitken. 2007. Adaptive gradients and isolation-by-distance with postglacial migration
532 in *Picea sitchensis*. Heredity 99:224.
- 533 ———. 2010. Local adaptation at the range peripheries of Sitka spruce. Journal of evolutionary biology
534 23:249–258.
- 535 Morin, X., J. Roy, L. Sonié, and I. Chuine. 2010. Changes in leaf phenology of three European oak species
536 in response to experimental climate change. New Phytologist 186:900–910.
- 537 Morin, X., and W. Thuiller. 2009. Comparing niche-and process-based models to reduce prediction uncertainty
538 in species range shifts under climate change. Ecology 90:1301–1313.
- 539 Muir, W. D., W. S. Zaugg, A. E. Giorgi, and S. McCutcheon. 1994. Accelerating smolt development and
540 downstream movement in yearling chinook salmon with advanced photoperiod and increased temperature.
541 Aquaculture 123:387–399.
- 542 Myking, T., and O. Heide. 1995. Dormancy release and chilling requirement of buds of latitudinal ecotypes
543 of *Betula pendula* and *B. pubescens*. Tree Physiology 15:697–704.
- 544 Nienstaedt, H. 1966. Dormancy and dormancy release in white spruce. Forest Science 12:374–384.
- 545 Ovaskainen, O., S. Skorokhodova, M. Yakovleva, A. Sukhov, A. Kutenkov, N. Kutenkova, A. Shcherbakov,
546 E. Meyke, and M. del Mar Delgado. 2013. Community-level phenological response to climate change.
547 Proceedings of the National Academy of Sciences 110:13434–13439.
- 548 Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of
549 Ecology Evolution and Systematics 37:637–669.
- 550 Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural
551 systems. Nature 421:37.
- 552 Partanen, J., H. Hänninen, and R. Häkkinen. 2005. Bud burst in Norway spruce (*Picea abies*): preliminary
553 evidence for age-specific rest patterns. Trees 19:66–72.

- 554 Peñuelas, J., and M. Boada. 2003. A global change-induced biome shift in the Montseny mountains (NE
555 Spain). *Global Change Biology* 9:131–140.
- 556 Peñuelas, J., I. Filella, and P. Comas. 2002. Changed plant and animal life cycles from 1952 to 2000 in the
557 Mediterranean region. *Global Change Biology* 8:531–544.
- 558 Petterle, A., A. Karlberg, and R. P. Bhalerao. 2013. Daylength mediated control of seasonal growth patterns
559 in perennial trees. *Current Opinion in Plant Biology* 16:301–306.
- 560 Polgar, C. A., R. B. Primack, E. H. Williams, S. Stichter, and C. Hitchcock. 2013. Climate effects on the
561 flight period of Lycaenid butterflies in Massachusetts. *Biological Conservation* 160:25–31.
- 562 Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D. S. Schoeman, P. J. Moore, K. Brander,
563 J. F. Bruno, L. B. Buckley, M. T. Burrows, et al. 2013. Global imprint of climate change on marine life.
564 *Nature Climate Change* 3:919.
- 565 Richardson, A. D., T. F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag, and M. Toomey. 2013. Climate
566 change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural
567 and Forest Meteorology* 169:156–173.
- 568 Richardson, E. 1974. A model for estimating the completion of rest for ‘Redhaven’ and ‘Elberta’ peach trees.
569 *HortScience* 9:331–332.
- 570 Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints
571 of global warming on wild animals and plants. *Nature* 421:57–60.
- 572 Saikkonen, K., K. Taulavuori, T. Hyvönen, P. E. Gundel, C. E. Hamilton, I. Vänninen, A. Nissinen, and
573 M. Helander. 2012. Climate change-driven species’ range shifts filtered by photoperiodism. *Nature Climate
574 Change* 2:239.
- 575 Sanz-Perez, V., P. Castro-Diez, and F. Valladares. 2009. Differential and interactive effects of temperature
576 and photoperiod on budburst and carbon reserves in two co-occurring Mediterranean oaks. *Plant Biology*
577 11:142–51.
- 578 Saunders, R. L., and E. B. Henderson. 1970. Influence of photoperiod on smolt development and growth of
579 Atlantic salmon (*Salmo salar*). *Journal of the Fisheries Board of Canada* 27:1295–1311.

- 580 Sidaway-Lee, K., E.-M. Josse, A. Brown, Y. Gan, K. J. Halliday, I. A. Graham, and S. Penfield. 2010.
581 SPATULA links daytime temperature and plant growth rate. *Current Biology* 20:1493–1497.
- 582 Singh, R. K., T. Svystun, B. AlDahmash, A. M. Jönsson, and R. P. Bhalerao. 2017. Photoperiod-and
583 temperature-mediated control of phenology in trees—a molecular perspective. *New Phytologist* 213:511–
584 524.
- 585 Solbakken, V. A., T. Hansen, and S. O. Stefansson. 1994. Effects of photoperiod and temperature on growth
586 and parr-smolt transformation in Atlantic salmon (*Salmo salar* L.) and subsequent performance in seawater.
587 *Aquaculture* 121:13–27.
- 588 Spann, T. M., J. G. Williamson, and R. L. Darnell. 2004. Photoperiod and temperature effects on growth
589 and carbohydrate storage in southern highbush blueberry interspecific hybrid. *Journal of the American
590 Society for Horticultural Science* 129:294–298.
- 591 Suárez-López, P., K. Wheatley, F. Robson, H. Onouchi, F. Valverde, and G. Coupland. 2001. CONSTANS
592 mediates between the circadian clock and the control of flowering in *Arabidopsis*. *Nature* 410:1116.
- 593 Tanino, K. K., L. Kalcsits, S. Silim, E. Kendall, and G. R. Gray. 2010. Temperature-driven plasticity in
594 growth cessation and dormancy development in deciduous woody plants: a working hypothesis suggesting
595 how molecular and cellular function is affected by temperature during dormancy induction. *Plant Molecular
596 Biology* 73:49–65.
- 597 Taranger, G., E. Vikingstad, U. Klenke, I. Mayer, S. Stefansson, B. Norberg, T. Hansen, Y. Zohar, and
598 E. Andersson. 2003. Effects of photoperiod, temperature and GnRHa treatment on the reproductive
599 physiology of Atlantic salmon (*Salmo salar* L.) broodstock. *Fish Physiology and Biochemistry* 28:403–406.
- 600 Tauber, M. J., and C. A. Tauber. 1975. Natural daylengths regulate insect seasonality by two mechanisms.
601 *Nature* 258:711–712.
- 602 Tobin, P. C., S. Nagarkatti, G. Loeb, and M. C. Saunders. 2008. Historical and projected interactions between
603 climate change and insect voltinism in a multivoltine species. *Global Change Biology* 14:951–957.
- 604 Van Belle, J., J. Shamoun-Baranes, E. Van Loon, and W. Bouten. 2007. An operational model predicting
605 autumn bird migration intensities for flight safety. *Journal of Applied Ecology* 44:864–874.

- 606 Viherä-Aarnio, A., R. Häkkinen, and O. Junntila. 2006. Critical night length for bud set and its variation in
607 two photoperiodic ecotypes of *Betula pendula*. *Tree Physiology* 26:1013–1018.
- 608 Vitasse, Y., and D. Basler. 2013. What role for photoperiod in the bud burst phenology of European beech.
609 *European Journal of Forest Research* 132:1–8.
- 610 Wareing, P. 1956. Photoperiodism in woody plants. *Annual Review of Plant Physiology* 7:191–214.
- 611 Way, D. A., and R. A. Montgomery. 2015. Photoperiod constraints on tree phenology, performance and
612 migration in a warming world. *Plant, Cell & Environment* 38:1725–1736.
- 613 Weih, M. 2004. Intensive short rotation forestry in boreal climates: present and future perspectives. *Canadian
614 Journal of Forest Research* 34:1369–1378.
- 615 Willis, C. G., B. R. Ruhfel, R. B. Primack, A. J. Miller-Rushing, J. B. Losos, and C. C. Davis. 2010. Favorable
616 climate change response explains non-native species' success in Thoreau's woods. *Plos One* 5:e8878.
- 617 Winkler, D. W., C. Jørgensen, C. Both, A. I. Houston, J. M. McNamara, D. J. Levey, J. Partecke, A. Fudickar,
618 A. Kacelnik, D. Roshier, et al. 2014. Cues, strategies, and outcomes: how migrating vertebrates track
619 environmental change. *Movement Ecology* 2:10.
- 620 Wolkovich, E. M., B. I. Cook, J. M. Allen, T. M. Crimmins, J. L. Betancourt, S. E. Travers, S. Pau,
621 J. Regetz, T. J. Davies, N. J. B. Kraft, T. R. Ault, K. Bolmgren, S. J. Mazer, G. J. McCabe, B. J. McGill,
622 C. Parmesan, N. Salamin, M. D. Schwartz, and E. E. Cleland. 2012. Warming experiments underpredict
623 plant phenological responses to climate change. *Nature* 485:494–497.
- 624 Wolkovich, E. M., A. K. Ettinger, D. Flynn, T. Savas, C. Chamberlain, D. Buonaiuto, and
625 J. Samaha. 2019. Observed Spring Phenology Responses in Experimental Environments (OSPREE).
626 doi:10.5063/F1QV3JQR.
- 627 Xie, L., and W. W. Hsieh. 1989. Predicting the return migration routes of the Fraser River sockeye salmon
628 (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 46:1287–1292.
- 629 Yu, H. Y., E. Luedeling, and J. C. Xu. 2010. Winter and spring warming result in delayed spring phenology
630 on the Tibetan Plateau. *Proceedings of the National Academy of Sciences of the United States of America*
631 107:22151–22156.

- 632 Zhao, M., C. Peng, W. Xiang, X. Deng, D. Tian, X. Zhou, G. Yu, H. He, and Z. Zhao. 2013. Plant
633 phenological modeling and its application in global climate change research: overview and future challenges.
634 Environmental Reviews 21:1–14.
- 635 Zhu, K., C. W. Woodall, and J. S. Clark. 2012. Failure to migrate: lack of tree range expansion in response
636 to climate change. Global Change Biology 18:1042–1052.
- 637 Zohner, C. M., B. M. Benito, J. C. Svenning, and S. S. Renner. 2016. Day length unlikely to constrain
638 climate-driven shifts in leaf-out times of northern woody plants. Nature Climate Change 6:1120–1123.
- 639 Zydlowski, G. B., D. S. Stich, and S. D. McCormick. 2014. Photoperiod control of downstream movements
640 of Atlantic salmon *Salmo salar* smolts. Journal of Fish Biology 85:1023–1041.

₆₄₁ **Figures**

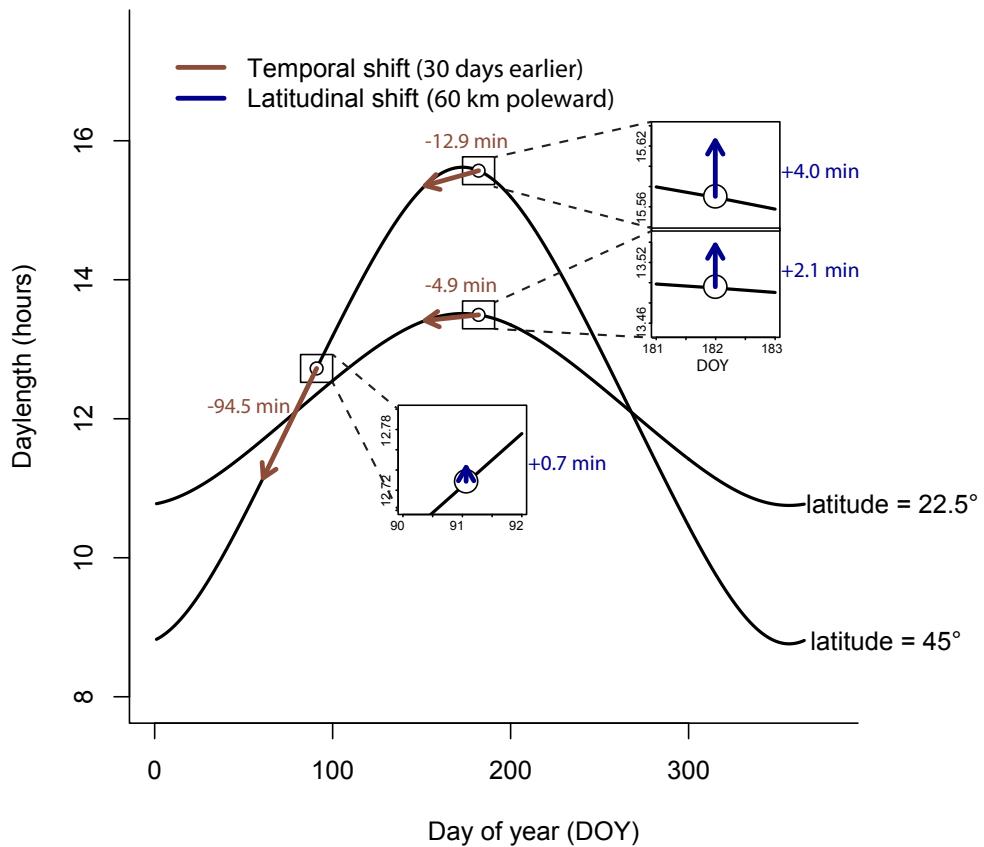


Figure 1: **Temporal (i.e., phenological) shifts in activity yield larger changes in experienced photoperiod compared to spatial (i.e., latitudinal) shifts** on the same day of year, due to patterns in photoperiod variation with latitude and by day of year. Here, we show this variation at two latitudes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

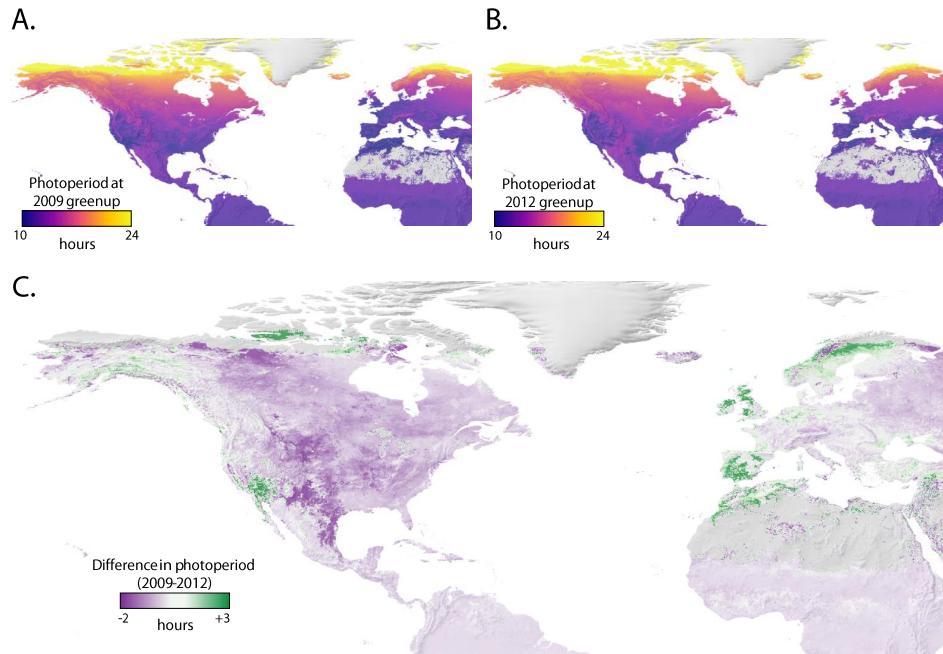


Figure 2: Photoperiod on the “green-up” date varies over space and between years “Green-up” date is the beginning of seasonal greening, identified by satellite remote sensing measurements taken regularly throughout the year of the concentrations of green leaf vegetation. Hours of daylight on the date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

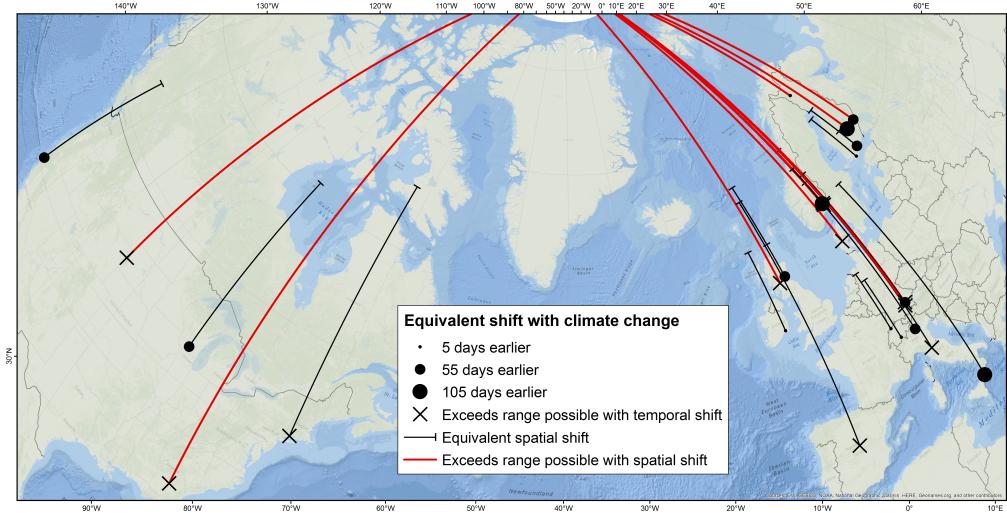


Figure 3: Experimental photoperiod treatments and their equivalent spatial and temporal shifts for experiments in the OSPREE database that manipulated photoperiod (see Box 2). See ‘Mapping temporal and spatial shifts in space and time’ in the Supplemental Materials for details on how we calculated the required spatial (lines) or temporal (circles and Xes) shifts to be equivalent to photoperiod treatments in each experiment.

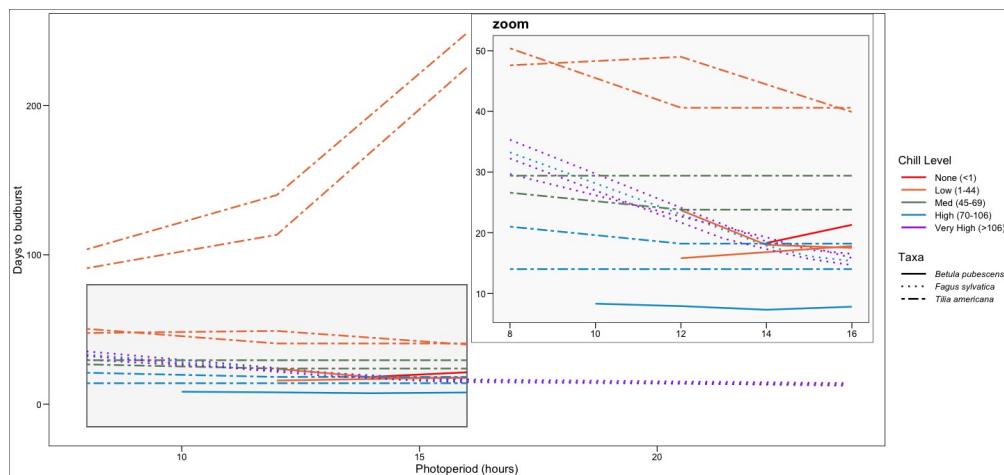


Figure 4: Nonlinearities in phenological responses to daylength are apparent in spring woody plant phenology experiments (from the OSPREE database, described in Box 2) in which three or more photoperiod treatment levels were applied. The shape of the response curves for *Betula pubescens* (Caffarra et 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.

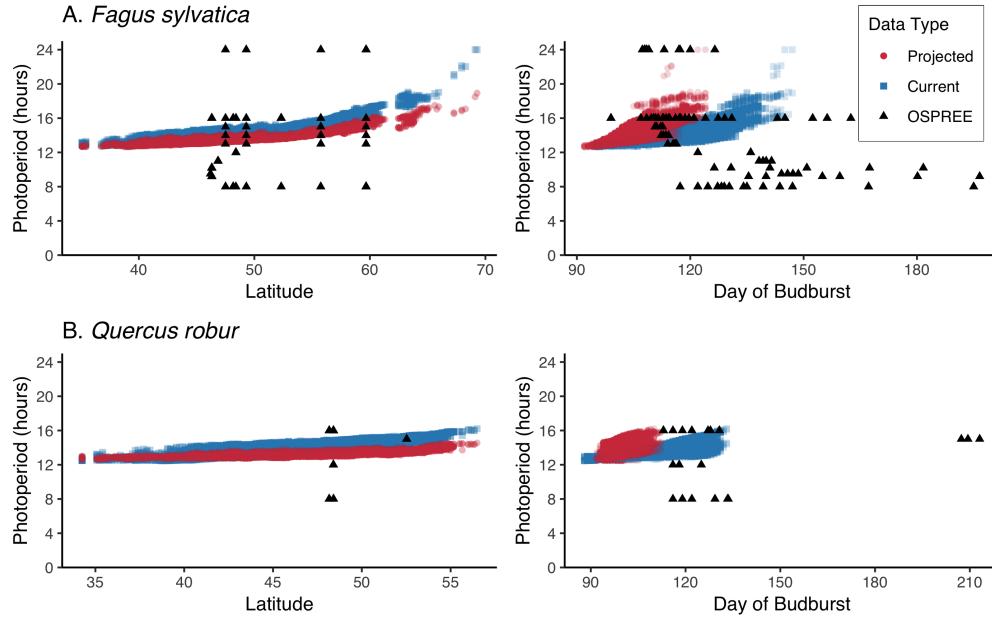


Figure 5: Experienced photoperiods in growth chamber experiments differ from those in the natural world, shown here by latitude (left panels) and by day of budburst (right panels) for *Fagus sylvatica* (A, upper panels) and *Quercus robur* (B, lower panels). Triangles show experimental treatments of photoperiod in the OSPREE database (Box 2). 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

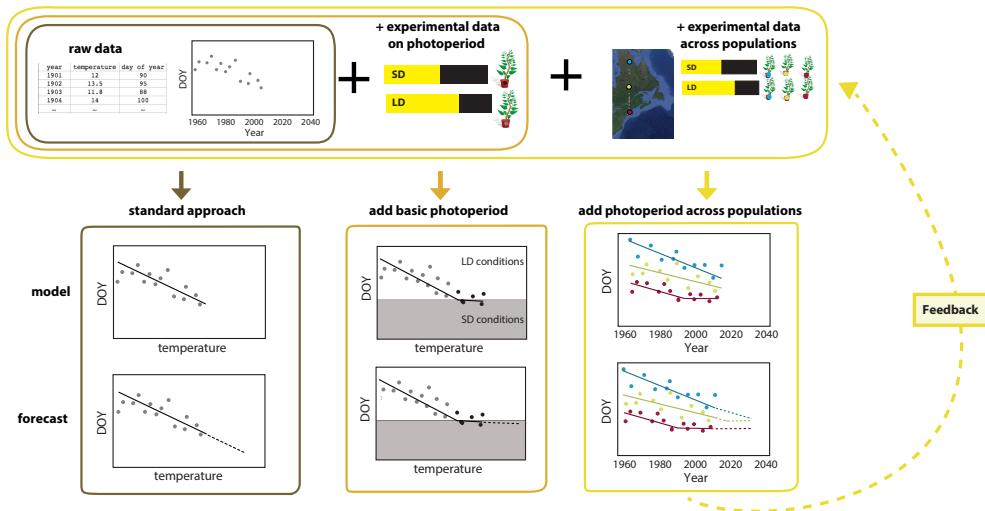


Figure 6: **Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change.** Current approaches for forecasting spring phenology with climate change frequently rely on linear relationships between historical temperature data and observed dates of spring phenology (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*), 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).