

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

¹⁶ Introduction

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

²⁵ Spring phenology is not controlled solely by temperature, however. Photoperiod is also a critical cue, signaling
²⁶ changes in growth and reproduction across diverse species (e.g., Flynn and Wolkovich, 2018; Lagercrantz,
²⁷ 2009; Bradshaw and Holzapfel, 2007; Howe et al., 1996; Solbakken et al., 1994), and spring phenology is
²⁸ thought to be determined interactively by photoperiod and temperature (Fu et al., 2019, see also Box 1).

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

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

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

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

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

⁵⁷ Here, we ask:

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

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

69 How will climate change alter the photoperiod experienced by or-
70 ganisms?

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

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

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

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

93 To date, most focus on shifts in photoperiod with climate change has been centered on how spatial range
94 shifts will affect photoperiod (e.g., Saikkonen et al., 2012; Way and Montgomery, 2015). However, shifting

⁹⁵ phenology—especially the large changes seen in spring phenology—will also alter experienced photoperiod,
⁹⁶ because of the seasonal patterns of daylength (Fig. 1).

⁹⁷ Current data suggest that temporal shifts will yield much larger changes in experienced photoperiod than
⁹⁸ latitudinal shifts (Fig. 1). Consider a tree species that bursts its buds at latitude 45°, on average around
⁹⁹ day of year 91 (April 2), when daylength is 12.8 hours. If the species' phenology shifts 30 days earlier over
¹⁰⁰ the next century (i.e., a rate of 3 days per decade, as has been observed, Parmesan and Yohe, 2003), it will
¹⁰¹ experience a daylength that is 1.6 hours shorter. This 1.6 hour decrease in daylength is equivalent to moving
¹⁰² up 28.5° in latitude on this day of year. However, if the same species shifts its range up in latitude 0.5° (i.e.,
¹⁰³ 60 km over the next century, comparable to observed rates, Chen et al., 2011; Parmesan and Yohe, 2003), it
¹⁰⁴ will experience a daylength that differs by less than a minute on the same day of year.

¹⁰⁵ **What are the implications of altered photoperiods for biological ¹⁰⁶ responses to climate change?**

¹⁰⁷ Climate change alters the experienced photoperiod, but the implications of this change for plants is currently
¹⁰⁸ unclear, in part, because phenology both affects and is affected by experienced photoperiod: climate change-
¹⁰⁹ induced shifts in phenology alter experienced photoperiod, which in turn affects phenology. Daylength,
¹¹⁰ often in combination with temperature, can play a role in controlling critical biological functions, including
¹¹¹ vegetative growth, cell elongation, budburst, and flowering in plants (Fu et al., 2019; Heide and Sønsteby,
¹¹² 2012; Heide, 2011; Hsu et al., 2011; Sidaway-Lee et al., 2010; Mimura and Aitken, 2007; Linkosalo and
¹¹³ Lechowicz, 2006; Erwin, 1998; Ashby et al., 1962) Climate change-induced shifts in photoperiod are therefore
¹¹⁴ likely to alter these functions.

¹¹⁵ Growth chamber studies show that the magnitude of daylength shifts expected with climate change (i.e., 1-2
¹¹⁶ hours of difference in daylength with temporal shifts over the next century) are substantial enough to affect
¹¹⁷ spring phenology in trees (Table S1). The direction and magnitude of responses will vary, however, because
¹¹⁸ of variation in photoperiod sensitivity, and because photoperiod often interacts with other environmental
¹¹⁹ drivers, such as temperature, to affect phenology (Box 1).

120 The climate change-induced trend toward ever-earlier springs means that experienced photoperiod may in-
121 creasingly approach threshold photoperiods (see *Glossary*) for many species, constraining their ability to
122 respond to additional warming (Fu et al., 2019; Vitasse and Basler, 2013; Körner and Basler, 2010a; Morin
123 et al., 2010; Nienstaedt, 1966). Interactions between photoperiod and temperature may therefore result in
124 muted phenological shifts, compared to what would be expected based on temperature change alone (Körner
125 and Basler, 2010a; Mimura and Aitken, 2007; Wareing, 1956). This has been a topic of much interest in
126 the climate change literature because it predicts that as photoperiod becomes limiting, the average trend of
127 earlier phenology with warming (Polgar et al., 2013; Peñuelas et al., 2002; Menzel, 2000) may stop.

128 A challenge in predicting if or when the trend of earlier phenology with warming may slow or stop abruptly
129 is the wide range of observed photoperiod sensitivity (see *Glossary*) across species (Flynn and Wolkovich,
130 2018; Zohner et al., 2016; Sanz-Perez et al., 2009), populations (Gauzere et al., 2017; Saikkonen et al., 2012;
131 Caffarra et al., 2011b; Bradshaw and Holzapfel, 2007; Viherä-Aarnio et al., 2006; Partanen et al., 2005), and
132 ecotypes (Howe et al., 1995). How much genotype versus environment explain this variation is an active
133 area of research (e.g., Fréjaville et al., 2019; Franks et al., 2014; Gould et al., 2010; Mimura and Aitken,
134 2010). Environmental conditions clearly play a role, since different combinations of ambient temperature
135 and photoperiod may explain some of this variation and because temperature cues can override photoperiod
136 requirements under certain conditions (e.g., Tanino et al., 2010). In such cases, climate change-induced
137 phenological shifts may occur at different rates than past shifts with warming. On the other hand, some of
138 this variation may be due to underlying genetic differences driven by local adaptation, because photoperiod
139 responses can be under strong genetic control (Bradshaw and Stettler, 1995; Keller et al., 2011; Weih, 2004,
140 see also Boxes 1, 2). Teasing out the relative roles of genetics versus environmental conditions will be critical
141 to accurate forecasts of future phenology under climate change.

142 Species- and population-level variation in photoperiod sensitivity may scale up to alter communities as climate
143 change progresses. For example, a species or population that is relatively insensitive to photoperiod can take
144 advantage of warmer springs by having an earlier start to its growing season. Indeed, phenological tracking of
145 temperature (e.g., earlier flowering, leafout, migration with warming) has been linked with higher performance
146 in plants and animals (Cleland et al., 2012; Muir et al., 1994; Willis et al., 2010). Species or populations
147 that are sensitive to temperature but relatively insensitive to photoperiod may therefore outcompete slower-

¹⁴⁸ growing or later-emerging ones that are limited by photoperiod and thus cannot take advantage of longer
¹⁴⁹ growing season conditions. Not all studies, however, find links between performance and high sensitivity
¹⁵⁰ to temperature (e.g., Block et al., 2020), and early-season species in most temperature zones risk losing to
¹⁵¹ tissue to frost (Sakai and Larcher, 1987). Thus, the advantages of tracking warming may depend on how
¹⁵² quickly mean temperatures versus last frost dates shift (e.g., Inouye et al., 2002), such that in some systems
¹⁵³ photoperiod cues could prevent species from starting growth or reproduction too early (when they risk losing
¹⁵⁴ their investments in new tissue). To identify where, when, and how communities may be altered therefore
¹⁵⁵ requires quantifying species-specific temperature and photoperiod sensitivities, and developing methods that
¹⁵⁶ incorporate both photoperiod and environmental events that impact fitness (such as frosts).

¹⁵⁷ Future directions: outstanding questions and incorporating photoperiod into forecasting

¹⁵⁹ The complexity of photoperiod effects on phenology and how warming alters experienced photoperiod high-light that future rates of phenological shifts are unlikely to be straightforward extrapolations from past and
¹⁶⁰ current rates. Statistical and process-based models—the two broad categories of forecasting approaches—
¹⁶¹ both acknowledge this difficulty, but differ importantly in how they relate phenology to climate change.
¹⁶² Statistical models relating phenology to climate change often assume linear relationships between species'
¹⁶³ responses and environmental variables (e.g., Flynn and Wolkovich, 2018; Ibáñez et al., 2010), whereas
¹⁶⁴ process-based models often incorporate nonlinear threshold relationships (e.g. Chuine and Beaubien, 2001;
¹⁶⁵ Morin and Thuiller, 2009). Further, statistical models of phenology under climate change frequently ignore
¹⁶⁶ photoperiod, focusing instead on seasonal or annual temperature (e.g. Diez et al., 2012; Ibáñez et al., 2010,
¹⁶⁷ but see Richardson et al. (2013)), whereas process-based models of phenology more frequently incorporate
¹⁶⁸ photoperiod, along with temperature (Lundell et al., 2020; Duputié et al., 2015; Zhao et al., 2013; Morin
¹⁶⁹ and Thuiller, 2009). Process-based models may thus seem superior for integrating photoperiod, but they
¹⁷⁰ can be challenging to develop, requiring detailed data that are often not readily available (e.g., daily climate
¹⁷¹ data, nonlinear biological responses to fine-scale changes in temperature). Perhaps because of this, statistical
¹⁷² models remain more commonly used in climate change forecasts of biological responses (e.g., García-Valdés
¹⁷³

174 and Morales-Castilla, 2016; Basler and Körner, 2012; Diez et al., 2012; Zhu et al., 2012; Ibáñez et al., 2010).

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

188 For some species, experimental data can be immediately used in forecasting because experiments manipulate
189 photoperiod at relevant scales (e.g., Heide and Sonsteby, 2015; Basler and Körner, 2014, Figs. 3& S1A,
190 Table S1). For example, photoperiod treatments from growth chamber experiments with *Fagus sylvatica*
191 span the variation in both current and expected future ranges (Fig. S1A, Duputié et al., 2015), and
192 may allow identification of threshold photoperiods (Fig. 4). In other cases, attempting to incorporate
193 photoperiod into forecasts of future phenology will reveal gaps in our understanding of many aspects of
194 photoperiod responses. For example, photoperiod treatments from existing experiments of *Quercus robur*
195 do not accurately represent experienced photoperiods from current or future estimates (Fig. S1B), making
196 fine-scale projections difficult, even for this relatively well-studied species. This gap extends to many species,
197 as most experiments manipulate photoperiod much more dramatically than will occur with climate change
198 (Figs. 3, S1). Although these studies can be useful for a mechanistic understanding of photoperiod responses,
199 extrapolating them to climate change models may not be reasonable.

200 Photoperiod is not fully integrated into most current forecasts of biological responses to climate change (but
201 see Tobin et al., 2008, for an example in insects); this omission could affect forecast accuracy. Photoperiod

202 is incorporated into some ecosystem models (e.g., the Ecosystem Demography model Jolly et al., 2005;
203 Medvigy et al., 2013) used for forecasting but not others (e.g., Richardson et al., 2012), and is rarely included
204 in species distribution models (e.g., Morin and Thuiller, 2009; Zhu et al., 2012). The sensitivity of model
205 outcomes to assumptions made about experienced photoperiod and threshold responses to photoperiod needs
206 further study, including understanding how variation in photoperiod responses across ecosystems, species,
207 populations, and life stages impacts forecasts.

208 As researchers more fully integrate experienced photoperiod into forecasting, a critical area of further study
209 is understanding *how* photoperiod acts as a cue. Photoperiod seems to interact with temperature to affect
210 phenology (e.g., Box 1, Zydlewski et al., 2014); this would explain the divergent effects of photoperiod observed
211 across studies in woody plants (Box 1). However, exactly how it interacts with temperature is not well-
212 defined for most species or populations. For many species, additional experimental and physiological research
213 is necessary, since the dormancy-breaking processes that photoperiod affects require detailed physiological
214 approaches to observe (Box 2, Hänninen et al., 2019; Chuine et al., 2016). Understanding the drivers, as well
215 as the consequences, of variation in photoperiod responses across species and populations will be particularly
216 beneficial for forecasting. For example, what traits are associated with photoperiod sensitivity and does
217 variation in photoperiod sensitivity or related traits have a strong genetic component? If so, are species or
218 populations from some locations or lineages more likely than others to be constrained by photoperiod in their
219 responses to climate change?

220 Conclusions

221 Organisms may undergo large changes to the photoperiod they experience with climate change, even if they
222 do not shift their ranges spatially. Here we have shown that these altered photoperiods may result in stalled
223 future advances of spring phenology with warming (e.g., Table S1, Fig. S1, Fu et al., 2019; Güsewell et al.,
224 2017; Yu et al., 2010), with cascading effects on growth, fitness, and community composition due to the large
225 variation in photoperiod responses across species and populations (Box 1). We have focused on woody plant
226 spring phenology, but shifts in photoperiod with climate change have implications for a variety of plant and
227 animal responses, given that daylength affects critical activities for diverse species from insects (Bradshaw and

²²⁸ Holzapfel, 2006) and salmon (Taranger et al., 2003) to birds (Dawson et al., 2001) and marsupials (McAllan
²²⁹ et al., 2006). Given what we know, incorporating photoperiod into forecasting of climate change responses
²³⁰ should improve model accuracy (Fig. 4), and will illuminate additional experiments that could improve our
²³¹ mechanistic understanding of photoperiod as a critical cue for diverse biological responses.

²³² Glossary

- ²³³ • budburst: one or more leaf buds has visible green tips.
- ²³⁴ • chilling: the intensity and duration of winter temperature, often a certain sum of chilling that is required
²³⁵ (e.g., some amount of hours or days of cold temperatures, defined by a specific critical temperature or
²³⁶ range of temperatures, such as between 0 and 7.2 °C, Richardson, 1974), that must be experienced for
²³⁷ budburst to occur.
- ²³⁸ • daylength: the period of time during a 24-hour period during which an organism receives light.
- ²³⁹ • dormancy: halted or reduced growth or activity.
- ²⁴⁰ • forcing: warm spring temperatures, often a certain sum of forcing that is required (e.g., some amount
²⁴¹ of hours or days above a specific temperature) before budburst or flowering can occur.
- ²⁴² • green-up: the beginning of a new cycle of plant growth, usually evaluated at the landscape scale.
- ²⁴³ • phenology: the timing of life cycle events in organisms.
- ²⁴⁴ • photoperiod: the daily duration of light (daylength) and dark to which an organism is exposed; often
²⁴⁵ used synonymously with daylength.
- ²⁴⁶ • photoperiod sensitivity: the degree to which phenology is controlled by daylength; may be a nonlinear,
²⁴⁷ or ‘threshold’, response in plants (Box 2).
- ²⁴⁸ • photoperiodism: the ability of an organism to assess or respond to length of day or night in its behavior,
²⁴⁹ physiology, growth, development, or reproduction.
- ²⁵⁰ • threshold photoperiod: length of day that causes an organism to switch from a short- to a long-day
²⁵¹ response (or vice versa). For example, in European larch (*Larix decidua*), budburst development may

252 be constrained under short-day conditions, when daylengths are less than a threshold photoperiod of
253 10-11 hours (Migliavacca et al., 2008). Above this threshold photoperiod, the long-day response of
254 unconstrained budburst development can occur.

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263 References

- 264 Allona, I., A. Ramos, C. Ibáñez, A. Contreras, R. Casado, and C. Aragoncillo. 2008. Molecular control of
265 winter dormancy establishment in trees: a review. Spanish Journal of Agricultural Research 6:201–210.
- 266 Andrés, F., and G. Coupland. 2012. The genetic basis of flowering responses to seasonal cues. Nature reviews.
267 Genetics 13:627.
- 268 Ashby, W., et al. 1962. Germination capacity in American Basswood *Tilia americana*. Transactions of the
269 Illinois State Academy of Science 55:120–3.
- 270 Azeez, A., and A. P. Sane. 2015. Photoperiodic growth control in perennial trees. Plant signaling & behavior
271 10:e1087631.
- 272 Basler, D., and C. Körner. 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree species.
273 Agricultural and Forest Meteorology 165:73–81.

- 274 ———. 2014. Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest
275 tree species. *Tree Physiology* 34:377–388.
- 276 Bastow, R., and C. Dean. 2002. The molecular basis of photoperiodism. *Developmental cell* 3:461–462.
- 277 Block, S., J. Alexander, and J. M. Levine. 2020. Phenological plasticity is a poor predictor of subalpine plant
278 population performance following experimental climate change. *Oikos* 129:184–193.
- 279 Bradley, N. L., A. C. Leopold, J. Ross, and W. Huffaker. 1999. Phenological changes reflect climate change
280 in Wisconsin. *Proceedings of the National Academy of Sciences* 96:9701–9704.
- 281 Bradshaw, H., and R. F. Stettler. 1995. Molecular genetics of growth and development in *Populus*. IV.
282 Mapping QTLs with large effects on growth, form, and phenology traits in a forest tree. *Genetics* 139:963–
283 973.
- 284 Bradshaw, W. E., and C. M. Holzapfel. 2006. Evolutionary response to rapid climate change. *Science*
285 312:1477–1478.
- 286 ———. 2007. Evolution of animal photoperiodism. *Annu. Rev. Ecol. Evol. Syst.* 38:1–25.
- 287 Büning, E. 1936. Endogenous daily rhythms as the basis of photoperiodism. *Ber Deut Bot Ges* 54:590–607.
- 288 Burghardt, L. T., C. J. E. Metcalf, A. M. Wilczek, J. Schmitt, and K. Donohue. 2015. Modeling the influence
289 of genetic and environmental variation on the expression of plant life cycles across landscapes. *American
290 Naturalist* 185:212–227.
- 291 Caffarra, A., and A. Donnelly. 2011. The ecological significance of phenology in four different tree species:
292 effects of light and temperature on bud burst. *International Journal of Biometeorology* 55:711–721.
- 293 Caffarra, A., A. Donnelly, and I. Chuine. 2011a. Modelling the timing of *Betula pubescens* budburst. II.
294 Integrating complex effects of photoperiod into process-based models. *Climate Research* 46:159–170.
- 295 Caffarra, A., A. Donnelly, I. Chuine, and M. B. Jones. 2011b. Modelling the timing of *Betula pubescens*
296 bud-burst. I. Temperature and photoperiod: A conceptual model. *Climate Research* 46:147.
- 297 Campbell, R. K., and A. I. Sugano. 1975. Phenology of bud burst in Douglas-fir related to provenance,
298 photoperiod, chilling, and flushing temperature. *Botanical Gazette* pages 290–298.

- 299 Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species
300 associated with high levels of climate warming. *Science* 333:1024–1026.
- 301 Chuine, I., and E. G. Beaubien. 2001. Phenology is a major determinant of tree species range. *Ecology*
302 Letters 4:500–510.
- 303 Chuine, I., M. Bonhomme, J.-M. Legave, I. García de Cortázar-Atauri, G. Charrier, A. Lacointe, and
304 T. Améglio. 2016. Can phenological models predict tree phenology accurately in the future? The un-
305 revealed hurdle of endodormancy break. *Global Change Biology* 22:3444–3460.
- 306 Chuine, I., X. Morin, and H. Bugmann. 2010. Warming, photoperiods, and tree phenology. *Science* 329:277–
307 278.
- 308 Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta, and E. M.
309 Wolkovich. 2012. Phenological tracking enables positive species responses to climate change. *Ecology*
310 93:1765–1771.
- 311 Davis, S. J. 2002. Photoperiodism: the coincidental perception of the season. *Current Biology* 12:R841–R843.
- 312 Dawson, A., V. M. King, G. E. Bentley, and G. F. Ball. 2001. Photoperiodic control of seasonality in birds.
313 *Journal of Biological Rhythms* 16:365–380.
- 314 Diez, J. M., I. Ibáñez, A. J. Miller-Rushing, S. J. Mazer, T. M. Crimmins, M. A. Crimmins, C. D. Bertelsen,
315 and D. W. Inouye. 2012. Forecasting phenology: from species variability to community patterns. *Ecology*
316 Letters 15:545–553.
- 317 Ding, J., and O. Nilsson. 2016. Molecular regulation of phenology in trees— because the seasons they are
318 a-changin. *Current Opinion in Plant Biology* 29:73–79.
- 319 Duputié, A., A. Rutschmann, O. Ronce, and I. Chuine. 2015. Phenological plasticity will not help all species
320 adapt to climate change. *Global Change Biology* 21:3062–3073.
- 321 Erwin, J. E. 1998. Temperature and light effects on stem elongation. *Journal of the Japanese Society for*
322 *Horticultural Science* 67:1113–1120.
- 323 Falusi, M., and R. Calamassi. 1990. Bud dormancy in beech (*Fagus sylvatica* L.). Effect of chilling and
324 photoperiod on dormancy release of beech seedlings. *Tree Physiology* 6:429–438.

- 325 Fishman, S., A. Erez, and G. Couvillon. 1987. The temperature dependence of dormancy breaking in plants:
326 mathematical analysis of a two-step model involving a cooperative transition. *Journal of Theoretical*
327 *Biology* 124:473–483.
- 328 Flynn, D. F. B., and E. M. Wolkovich. 2018. Temperature and photoperiod drive spring phenology across all
329 species in a temperate forest community. *New Phytologist* 219:1353–1362.
- 330 Fournier-Level, A., E. O. Perry, J. A. Wang, P. T. Braun, A. Migneault, M. D. Cooper, C. J. E. Metcalf,
331 and J. Schmitt. 2016. Predicting the evolutionary dynamics of seasonal adaptation to novel climates in
332 *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences of the United States of America*
333 113:E2812–E2821.
- 334 Franks, S. J., J. J. Weber, and S. N. Aitken. 2014. Evolutionary and plastic responses to climate change in
335 terrestrial plant populations. *Evolutionary Applications* 7:123–139.
- 336 Fréjaville, T., B. Fady, A. Kremer, A. Ducousoo, and M. Benito Garzón. 2019. Inferring phenotypic plasticity
337 and population responses to climate across tree species ranges using forest inventory data. *Global Ecology*
338 and Biogeography
- 339 Fu, Y. H., S. Piao, X. Zhou, X. Geng, F. Hao, Y. Vitasse, and I. A. Janssens. 2019. Short photoperiod
340 reduces the temperature sensitivity of leaf-out in saplings of *Fagus sylvatica* but not in horse chestnut.
341 *Global Change Biology* 25:1696–1703.
- 342 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,
343 J. P. Uelas, Y. Song, Y. Vitasse, Z. Z. Zeng, and I. A. Janssens. 2015. Declining global warming effects on
344 the phenology of spring leaf unfolding. *Nature* 526:104–107.
- 345 Gallinat, A. S., R. B. Primack, and D. L. Wagner. 2015. Autumn, the neglected season in climate change
346 research. *Trends in Ecology & Evolution* 30:169–176.
- 347 García-Valdés, R., and I. Morales-Castilla. 2016. Efectos del cambio climático en los ecosistemas forestales:
348 integrando inventarios y modelos. *Ecosistemas* 25:51–59.
- 349 Gauzere, J., S. Delzon, H. Davi, M. Bonhomme, I. G. de Cortazar-Atauri, and I. Chuine. 2017. Integrating
350 interactive effects of chilling and photoperiod in phenological process-based models. A case study with

- 351 two European tree species: *Fagus sylvatica* and *Quercus petraea*. Agricultural and Forest Meteorology
352 244:9–20.
- 353 Glover, B. 2014. Understanding flowers and flowering, Second edition. OUP Oxford.
- 354 Gould, P. J., C. A. Harrington, and J. B. St. Clair. 2010. Incorporating genetic variation into a model
355 of budburst phenology of coast Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). Canadian Journal of
356 Forest Research 41:139–150.
- 357 Grevstad, F. S., and L. B. Coop. 2015. The consequences of photoperiodism for organisms in new climates.
358 Ecological Applications 25:1506–1517.
- 359 Gu, L., P. J. Hanson, W. M. Post, D. P. Kaiser, B. Yang, R. Nemani, S. G. Pallardy, and T. Meyers. 2008.
360 The 2007 Eastern US spring freeze: Increased cold damage in a warming world. BioScience 58:253.
- 361 Güsewell, S., R. Furrer, R. Gehrig, and B. Pietragalla. 2017. Changes in temperature sensitivity of spring
362 phenology with recent climate warming in Switzerland are related to shifts of the preseason. Global Change
363 Biology 23:5189–5202.
- 364 Hänninen, H., K. Kramer, K. Tanino, R. Zhang, J. Wu, and Y. H. Fu. 2019. Experiments are necessary in
365 process-based tree phenology modelling. Trends in Plant Science 24:199–209.
- 366 Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global
367 meta-analysis of treeline response to climate warming. Ecology Letters 12:1040–1049.
- 368 Hawkins, C. D., and A. Dhar. 2012. Spring bud phenology of 18 *Betula papyrifera* populations in British
369 Columbia. Scandinavian Journal of Forest Research 27:507–519.
- 370 Heide, O. 1993a. Daylength and thermal time responses of budburst during dormancy release in some
371 northern deciduous trees. Physiologia Plantarum 88:531–540.
- 372 ———. 1993b. Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days.
373 Physiologia Plantarum 89:187–191.
- 374 Heide, O. M. 1977. Photoperiod and temperature interactions in growth and flowering of strawberry. Physi-
375 ologia Plantarum 40:21–26.

- 376 ———. 2008. Interaction of photoperiod and temperature in the control of growth and dormancy of *Prunus*
377 species. *Scientia Horticulturae* 115:309–314.
- 378 ———. 2011. Temperature rather than photoperiod controls growth cessation and dormancy in *Sorbus*
379 species. *Journal of Experimental Botany* 62:5397–5404.
- 380 Heide, O. M., and A. Sønsteby. 2012. Floral initiation in black currant cultivars (*Ribes nigrum* L.): Effects of
381 plant size, photoperiod, temperature, and duration of short day exposure. *Scientia Horticulturae* 138:64–72.
- 382 Heide, O. M., and A. Sonsteby. 2015. Simultaneous dormancy induction interferes with short day floral
383 induction in black currant (*Ribes nigrum* L.). *Scientia Horticulturae* 185:228–232.
- 384 Howe, G. T., G. Gardner, W. P. Hackett, and G. R. Furnier. 1996. Phytochrome control of short-day-induced
385 bud set in black cottonwood. *Physiologia Plantarum* 97:95–103.
- 386 Howe, G. T., W. P. Hackett, G. R. Furnier, and R. E. Klevorn. 1995. Photoperiodic responses of a northern
387 and southern ecotype of black cottonwood. *Physiologia Plantarum* 93:695–708.
- 388 Hsu, C.-Y., J. P. Adams, H. Kim, K. No, C. Ma, S. H. Strauss, J. Drnevich, L. Vandervelde, J. D. Ellis, B. M.
389 Rice, et al. 2011. FLOWERING LOCUS T duplication coordinates reproductive and vegetative growth in
390 perennial poplar. *Proceedings of the National Academy of Sciences* 108:10756–10761.
- 391 Ibáñez, I., R. B. Primack, A. J. Miller-Rushing, E. Ellwood, H. Higuchi, S. D. Lee, H. Kobori, and J. A.
392 Silander. 2010. Forecasting phenology under global warming. *Philosophical Transactions of the Royal
393 Society B-Biological Sciences* 365.
- 394 Inouye, D. W., M. A. Morales, and G. J. Dodge. 2002. Variation in timing and abundance of flowering by
395 *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Niña, in the context of
396 climate change. *Oecologia* 130:543–550. Inouye, David/C-2997-2011 Inouye, David/0000-0003-2076-7834.
- 397 Jolly, W. M., R. Nemani, and S. W. Running. 2005. A generalized, bioclimatic index to predict foliar
398 phenology in response to climate. *Global Change Biology* 11:619–632.
- 399 Keller, S. R., R. Y. Soolanayakanahally, R. D. Guy, S. N. Silim, M. S. Olson, and P. Tiffin. 2011. Climate-
400 driven local adaptation of ecophysiology and phenology in balsam poplar, *Populus balsamifera* L. (Salicaceae). *American Journal of Botany* 98:99–108.

- 402 Kobayashi, Y., and D. Weigel. 2007. Move on up, it's time for change—mobile signals controlling photoperiod-
403 dependent flowering. *Genes & Development* 21:2371–2384.
- 404 Körner, C., and D. Basler. 2010a. Phenology under global warming. *Science* 327:1461–1462.
- 405 ———. 2010b. Warming, photoperiods, and tree phenology response. *Science* 329:278–278.
- 406 Lagercrantz, U. 2009. At the end of the day: a common molecular mechanism for photoperiod responses in
407 plants? *Journal of Experimental Botany* 60:2501–2515.
- 408 Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs
409 photoperiod in preventing precocious spring development. *Global Change Biology* 20:170–182.
- 410 Linkosalo, T., and M. J. Lechowicz. 2006. Twilight far-red treatment advances leaf bud burst of silver birch
411 (*Betula pendula*). *Tree Physiology* 26:1249–1256.
- 412 Lundell, R., H. Hänninen, T. Saarinen, H. Åström, and R. Zhang. 2020. Beyond rest and quiescence (endodorm-
413 ency and ecodormancy): A novel model for quantifying plant–environment interaction in bud dormancy
414 release. *Plant, Cell & Environment* 43:40–54.
- 415 Malyshev, A. V., H. A. Henry, A. Bolte, M. A. A. Khan, and J. Kreyling. 2018. Temporal photoperiod
416 sensitivity and forcing requirements for budburst in temperate tree seedlings. *Agricultural and Forest
417 Meteorology* 248:82–90.
- 418 Mcallan, B. M., C. R. Dickman, and M. S. Crowther. 2006. Photoperiod as a reproductive cue in the
419 marsupial genus *Antechinus*: ecological and evolutionary consequences. *Biological Journal of the Linnean
420 Society* 87:365–379.
- 421 Medvigy, D., S.-J. Jeong, K. L. Clark, N. S. Skowronski, and K. V. Schäfer. 2013. Effects of seasonal variation
422 of photosynthetic capacity on the carbon fluxes of a temperate deciduous forest. *Journal of Geophysical
423 Research: Biogeosciences* 118:1703–1714.
- 424 Menzel, A. 2000. Trends in phenological phases in Europe between 1951 and 1996. *International Journal of
425 Biometeorology* 44:76–81.

- 426 Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aasa, R. Ahas, K. Alm-Kuebler, et al. 2006. European
427 phenological response to climate change matches the warming pattern. *Global Change Biology* 12:1969–
428 1976.
- 429 Migliavacca, M., E. Cremonese, R. Colombo, L. Busetto, M. Galvagno, L. Ganis, M. Meroni, E. Pari,
430 M. Rossini, C. Siniscalco, et al. 2008. European larch phenology in the Alps: can we grasp the role
431 of ecological factors by combining field observations and inverse modelling? *International Journal of
432 Biometeorology* 52:587–605.
- 433 Mimura, M., and S. Aitken. 2007. Adaptive gradients and isolation-by-distance with postglacial migration
434 in *Picea sitchensis*. *Heredity* 99:224.
- 435 ———. 2010. Local adaptation at the range peripheries of Sitka spruce. *Journal of Evolutionary Biology*
436 23:249–258.
- 437 Morin, X., J. Roy, L. Sonié, and I. Chuine. 2010. Changes in leaf phenology of three European oak species
438 in response to experimental climate change. *New Phytologist* 186:900–910.
- 439 Morin, X., and W. Thuiller. 2009. Comparing niche-and process-based models to reduce prediction uncertainty
440 in species range shifts under climate change. *Ecology* 90:1301–1313.
- 441 Muir, W. D., W. S. Zaugg, A. E. Giorgi, and S. McCutcheon. 1994. Accelerating smolt development and
442 downstream movement in yearling chinook salmon with advanced photoperiod and increased temperature.
443 *Aquaculture* 123:387–399.
- 444 Myking, T., and O. Heide. 1995. Dormancy release and chilling requirement of buds of latitudinal ecotypes
445 of *Betula pendula* and *B. pubescens*. *Tree Physiology* 15:697–704.
- 446 Nienstaedt, H. 1966. Dormancy and dormancy release in white spruce. *Forest Science* 12:374–384.
- 447 Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of
448 Ecology Evolution and Systematics* 37:637–669.
- 449 Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural
450 systems. *Nature* 421:37.

- 451 Partanen, J., H. Hänninen, and R. Häkkinen. 2005. Bud burst in Norway spruce (*Picea abies*): preliminary
452 evidence for age-specific rest patterns. *Trees* 19:66–72.
- 453 Peñuelas, J., and M. Boada. 2003. A global change-induced biome shift in the Montseny mountains (NE
454 Spain). *Global Change Biology* 9:131–140.
- 455 Peñuelas, J., I. Filella, and P. Comas. 2002. Changed plant and animal life cycles from 1952 to 2000 in the
456 Mediterranean region. *Global Change Biology* 8:531–544.
- 457 Petterle, A., A. Karlberg, and R. P. Bhalerao. 2013. Daylength mediated control of seasonal growth patterns
458 in perennial trees. *Current Opinion in Plant Biology* 16:301–306.
- 459 Polgar, C. A., R. B. Primack, E. H. Williams, S. Stichter, and C. Hitchcock. 2013. Climate effects on the
460 flight period of Lycaenid butterflies in Massachusetts. *Biological Conservation* 160:25–31.
- 461 Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D. S. Schoeman, P. J. Moore, K. Brander,
462 J. F. Bruno, L. B. Buckley, M. T. Burrows, et al. 2013. Global imprint of climate change on marine life.
463 *Nature Climate Change* 3:919.
- 464 Richardson, A. D., R. S. Anderson, M. A. Arain, A. G. Barr, G. Bohrer, G. Chen, J. M. Chen, P. Ciais,
465 K. J. Davis, A. R. Desai, et al. 2012. Terrestrial biosphere models need better representation of vegetation
466 phenology: results from the North American carbon program synthesis. *Global Change Biology*
467 18:566–584.
- 468 Richardson, A. D., T. F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag, and M. Toomey. 2013. Climate
469 change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural
470 and Forest Meteorology* 169:156–173.
- 471 Richardson, E. 1974. A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees.
472 *HortScience* 9:331–332.
- 473 Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints
474 of global warming on wild animals and plants. *Nature* 421:57–60.

- 475 Saikkonen, K., K. Taulavuori, T. Hyvönen, P. E. Gundel, C. E. Hamilton, I. Vännen, A. Nissinen, and
476 M. Helander. 2012. Climate change-driven species' range shifts filtered by photoperiodism. *Nature Climate
477 Change* 2:239.
- 478 Sakai, A. K., and W. Larcher. 1987. Frost Survival of Plants. *Ecological Studies*. Springer-Verlag.
- 479 Sanz-Perez, V., P. Castro-Diez, and F. Valladares. 2009. Differential and interactive effects of temperature
480 and photoperiod on budburst and carbon reserves in two co-occurring Mediterranean oaks. *Plant Biology
481* 11:142–51.
- 482 Sidaway-Lee, K., E.-M. Josse, A. Brown, Y. Gan, K. J. Halliday, I. A. Graham, and S. Penfield. 2010.
483 SPATULA links daytime temperature and plant growth rate. *Current Biology* 20:1493–1497.
- 484 Singh, R. K., T. Svystun, B. AlDahmash, A. M. Jönsson, and R. P. Bhalerao. 2017. Photoperiod-and
485 temperature-mediated control of phenology in trees—a molecular perspective. *New Phytologist* 213:511–
486 524.
- 487 Solbakken, V. A., T. Hansen, and S. O. Stefansson. 1994. Effects of photoperiod and temperature on growth
488 and parr-smolt transformation in Atlantic salmon (*Salmo salar* L.) and subsequent performance in seawater.
489 *Aquaculture* 121:13–27.
- 490 Spann, T. M., J. G. Williamson, and R. L. Darnell. 2004. Photoperiod and temperature effects on growth
491 and carbohydrate storage in southern highbush blueberry interspecific hybrid. *Journal of the American
492 Society for Horticultural Science* 129:294–298.
- 493 Suárez-López, P., K. Wheatley, F. Robson, H. Onouchi, F. Valverde, and G. Coupland. 2001. CONSTANS
494 mediates between the circadian clock and the control of flowering in *Arabidopsis*. *Nature* 410:1116.
- 495 Tanino, K. K., L. Kalcsits, S. Silim, E. Kendall, and G. R. Gray. 2010. Temperature-driven plasticity in
496 growth cessation and dormancy development in deciduous woody plants: a working hypothesis suggesting
497 how molecular and cellular function is affected by temperature during dormancy induction. *Plant Molecular
498 Biology* 73:49–65.
- 499 Taranger, G., E. Vikingstad, U. Klenke, I. Mayer, S. Stefansson, B. Norberg, T. Hansen, Y. Zohar, and

- 500 E. Andersson. 2003. Effects of photoperiod, temperature and GnRHa treatment on the reproductive
501 physiology of Atlantic salmon (*Salmo salar* L.) broodstock. Fish Physiology and Biochemistry 28:403–406.
- 502 Tobin, P. C., S. Nagarkatti, G. Loeb, and M. C. Saunders. 2008. Historical and projected interactions between
503 climate change and insect voltinism in a multivoltine species. Global Change Biology 14:951–957.
- 504 van der Schoot, C., L. K. Paul, and P. L. H. Rinne. 2014. The embryonic shoot: a lifeline through winter.
505 Journal of Experimental Botany 65:1699–1712.
- 506 Viherä-Aarnio, A., R. Häkkinen, and O. Junntila. 2006. Critical night length for bud set and its variation in
507 two photoperiodic ecotypes of *Betula pendula*. Tree Physiology 26:1013–1018.
- 508 Vitasse, Y., and D. Basler. 2013. What role for photoperiod in the bud burst phenology of European beech.
509 European Journal of Forest Research 132:1–8.
- 510 Wareing, P. 1956. Photoperiodism in woody plants. Annual Review of Plant Physiology 7:191–214.
- 511 Way, D. A., and R. A. Montgomery. 2015. Photoperiod constraints on tree phenology, performance and
512 migration in a warming world. Plant, Cell & Environment 38:1725–1736.
- 513 Weih, M. 2004. Intensive short rotation forestry in boreal climates: present and future perspectives. Canadian
514 Journal of Forest Research 34:1369–1378.
- 515 Willis, C. G., B. R. Ruhfel, R. B. Primack, A. J. Miller-Rushing, J. B. Losos, and C. C. Davis. 2010. Favorable
516 climate change response explains non-native species' success in Thoreau's woods. Plos One 5:e8878.
- 517 Wolkovich, E. M., B. I. Cook, J. M. Allen, T. M. Crimmins, J. L. Betancourt, S. E. Travers, S. Pau,
518 J. Regetz, T. J. Davies, N. J. B. Kraft, T. R. Ault, K. Bolmgren, S. J. Mazer, G. J. McCabe, B. J. McGill,
519 C. Parmesan, N. Salamin, M. D. Schwartz, and E. E. Cleland. 2012. Warming experiments underpredict
520 plant phenological responses to climate change. Nature 485:494–497.
- 521 Wolkovich, E. M., A. K. Ettinger, D. Flynn, T. Savas, C. Chamberlain, D. Buonaiuto, and
522 J. Samaha. 2019. Observed Spring Phenology Responses in Experimental Environments (OSPREE).
523 doi:10.5063/F1QV3JQR.

- 524 Yu, H. Y., E. Luedeling, and J. C. Xu. 2010. Winter and spring warming result in delayed spring phenology
525 on the Tibetan Plateau. Proceedings of the National Academy of Sciences of the United States of America
526 107:22151–22156.
- 527 Zhao, M., C. Peng, W. Xiang, X. Deng, D. Tian, X. Zhou, G. Yu, H. He, and Z. Zhao. 2013. Plant
528 phenological modeling and its application in global climate change research: overview and future challenges.
529 Environmental Reviews 21:1–14.
- 530 Zhu, K., C. W. Woodall, and J. S. Clark. 2012. Failure to migrate: lack of tree range expansion in response
531 to climate change. Global Change Biology 18:1042–1052.
- 532 Zohner, C. M., B. M. Benito, J. C. Svenning, and S. S. Renner. 2016. Day length unlikely to constrain
533 climate-driven shifts in leaf-out times of northern woody plants. Nature Climate Change 6:1120–1123.
- 534 Zydlowski, G. B., D. S. Stich, and S. D. McCormick. 2014. Photoperiod control of downstream movements
535 of Atlantic salmon *Salmo salar* smolts. Journal of Fish Biology 85:1023–1041.

⁵³⁶ **Figures**

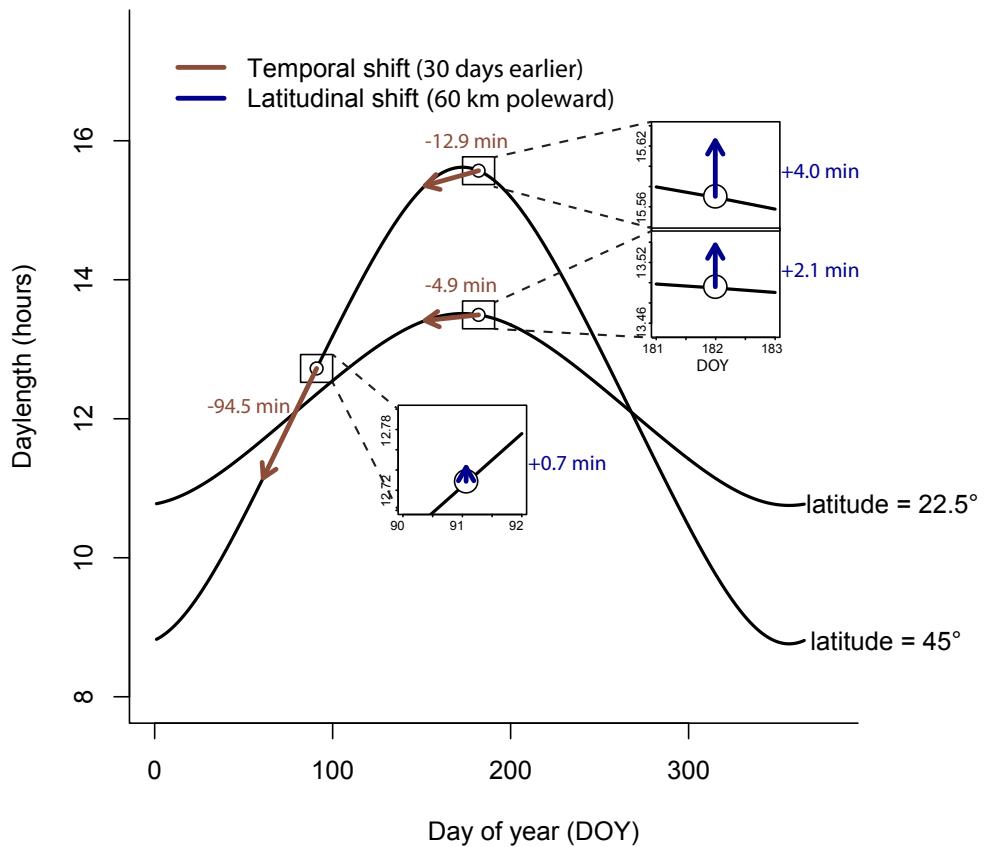


Figure 1: **Temporal (i.e., phenological) shifts in activity yield larger changes in experienced photoperiod compared to spatial (i.e., latitudinal) shifts** on the same day of year, due to patterns in photoperiod variation with latitude and by day of year. Here, we show this variation at two latitudes (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 from temporal shifts in the early spring, close to the vernal equinox (e.g., day of year 91), versus close to the summer solstice (e.g., day of year 182).

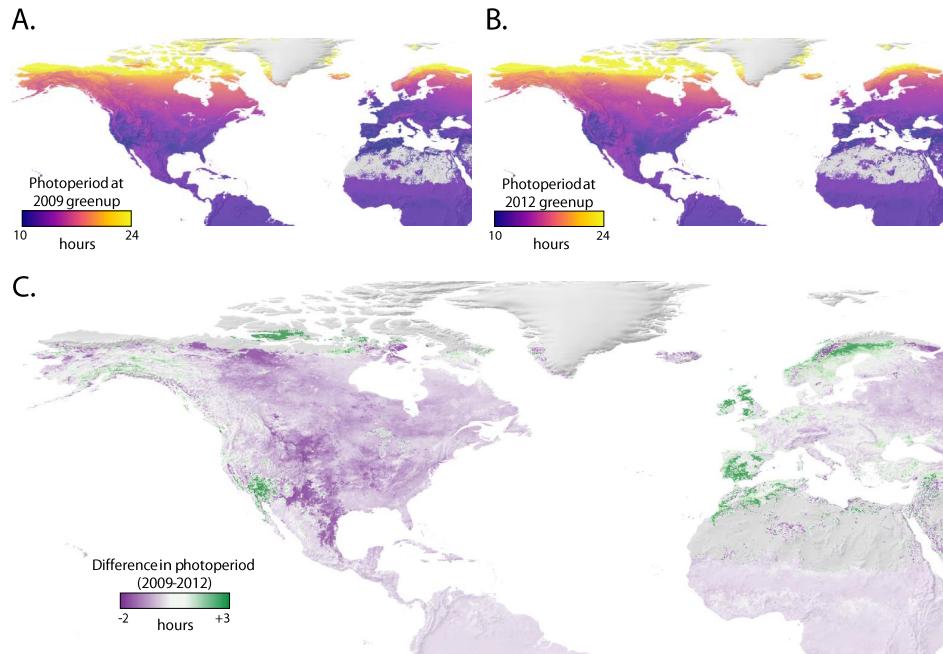


Figure 2: Photoperiod on ‘green-up’ date varies over space and between years ‘Green-up’ date is the beginning of seasonal greening, identified by satellite remote sensing measurements, taken regularly throughout the year, of concentrations of green leaf vegetation. Hours of daylight on the date of spring green-up (here from MODIS satellite data) across North America and Europe for an average (2009, A) and early (2012, B) North American start of spring. The differences between the years (in hours of daylength) are shown in (C). A negative difference signifies earlier green-up in 2012 versus 2009; a positive difference is the result of later green-up in 2012 compared with 2009. See ‘Quantifying and mapping differences in green-up across the United States and Europe’ in the Supplemental Materials for more details.

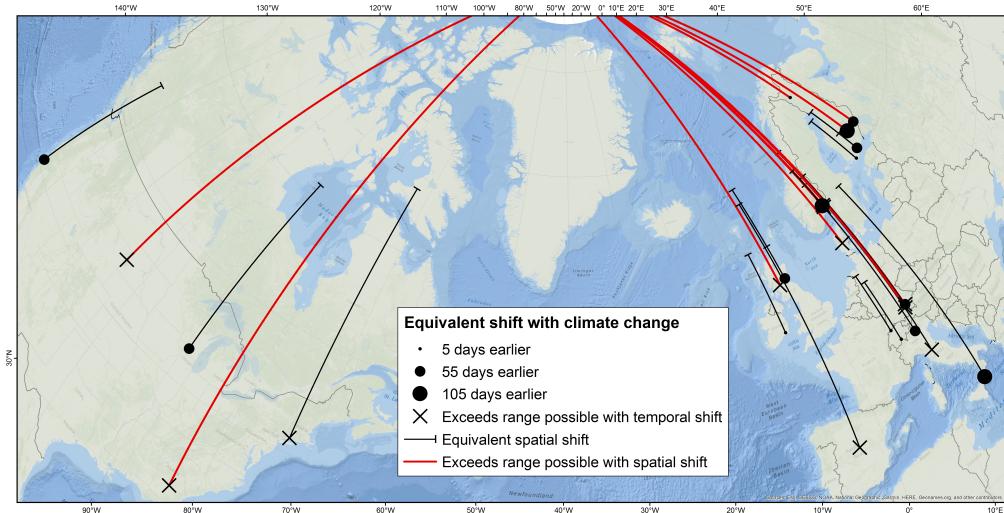


Figure 3: **Experimental photoperiod treatments and their equivalent spatial and temporal shifts** for experiments in the OSPREE database that manipulated photoperiod (see Box 1). See ‘Mapping temporal and spatial shifts in space and time’ in the Supplemental Materials for details on how we calculated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

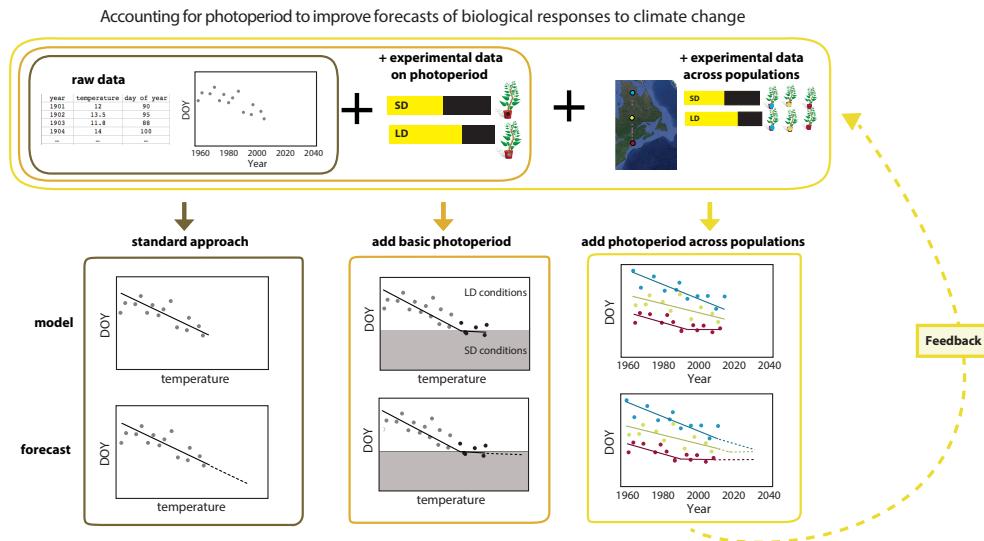


Figure 4: **Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change.** Current approaches for forecasting spring phenology with climate change frequently rely on linear relationships between historical temperature data and observed dates of spring phenology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

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

538 **plant spring phenology**

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

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

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

564 and Wolkovich et al. (2019) for details.

565 Growth chamber experiments in OSPREE suggest that the dominant photoperiod response in woody plant
566 species is earlier and more rapid budburst with longer days (e.g., Caffarra and Donnelly, 2011). Thirty-one
567 of the 85 studies in the OSPREE database included two or more different photoperiod treatments. Of these,
568 26 (84%) found significant photoperiod main effects or significant interactive effects with temperature (i.e.,
569 photoperiod x temperature effects), across 176 species (Table S1). Main effects included responses such as
570 growth (e.g., higher growth rates with longer days Ashby et al., 1962) and reproduction (e.g., increased
571 flowering with longer days Heide and Sønsteby, 2012).

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

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

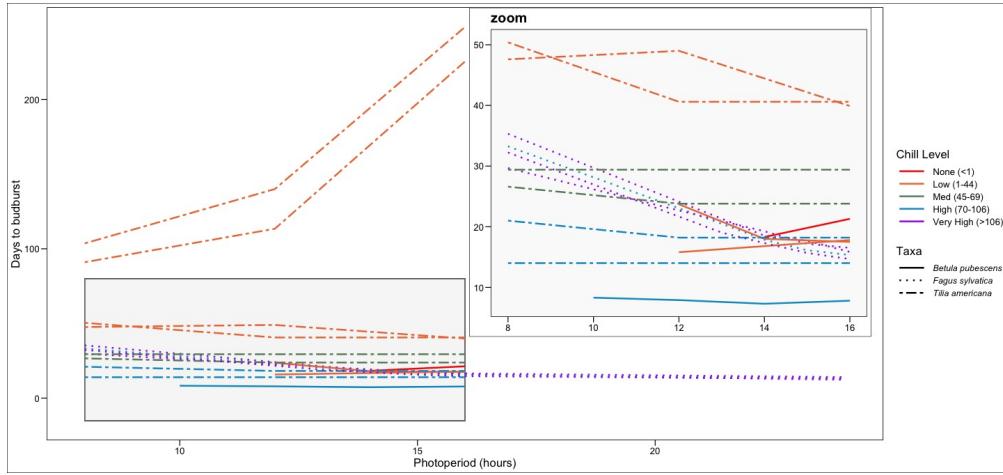


Figure: **Nonlinearities in phenological responses to daylength** are apparent in spring woody plant phenology experiments (from the OSPREE database) in which three or more photoperiod treatment levels were applied. The shape of the response curves for *Betula pubescens* (Caffarra et al., 2011b), *Fagus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

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

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

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

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

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

⁶³¹ few species will likely also be necessary for generating robust predictions with climate change.