

Spatial and temporal shifts in photoperiod with climate change

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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 (advancing spring phenology) and geographic shifts (range expansion
3 poleward) in species; these shifts affect the daylength (photoperiod) experienced. As photoperiod is a common
4 trigger of seasonal biological responses (affecting plant phenology in 84% of reviewed studies that manipulated
5 photoperiod), shifts in experienced photoperiod may have important implications for future distributions and
6 fitness. However, photoperiod has not been a focus of climate change forecasting to date, especially for early-
7 season ('spring') events often assumed to be driven by temperature. We synthesize published studies to
8 show that impacts on experienced photoperiod from temporal shifts could be orders of magnitude larger
9 than from spatial shifts (1.6 hours of change for expected temporal versus one minute for latitudinal shifts).
10 For woody plant phenology, for example, shifts in experienced photoperiod may increasingly constrain their
11 ability to respond to additional warming. Incorporating these effects into forecasts is possible by leveraging
12 existing experimental data; for example, growth chamber experiments on woody plant spring phenology
13 often have data relevant for climate change impacts. We highlight how combining modeling approaches and
14 empirical work on when, where, and how much photoperiod affects spring phenology could rapidly advance
15 our understanding 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 informative for migratory species, because it reflects annual
²¹ cycles across Earth, filtering out noise in local conditions that do not correlate with remote conditions
²² of the destination (Winkler et al., 2014). It is also a useful cue for nonmigratory species to synchronize
²³ activities with seasonal climatic changes (e.g., Singh et al., 2017; Basler and Körner, 2012; Hsu et al., 2011)
²⁴ because it is consistent across years, especially compared to other seasonal cues such as temperature and
²⁵ precipitation (Saikkonen et al., 2012). For example, relying on a threshold photoperiod (see *Glossary*),
²⁶ rather than temperature alone, may prevent woody plants from leafing out during “false spring” events and
²⁷ experiencing frost damage (unusually warm periods during winter that are followed by a return of cold
²⁸ temperatures, Gu et al., 2008).

²⁹ For many organisms, the timing of spring events—i.e., phenology, including flowering, bird arrival, egg hatch-
³⁰ ing and myriad other biological activities—is thought to be determined by photoperiod interactively with
³¹ temperature (Fu et al., 2019; Winkler et al., 2014, see also Box 1). The strong role of temperature is appar-
³² ent in recent advances in spring phenology, some of the most widely documented signals of climate change.
³³ At a given location on Earth, annual patterns in photoperiod have not changed as climates have warmed.
³⁴ Yet, across taxa, from plants and insects to mollusks and mammals, spring phenology is occurring earlier as
³⁵ temperatures warm, with average shifts of 1.2 to 5.1 days earlier per decade (Bradley et al., 1999; Parmesan
³⁶ and Yohe, 2003; Poloczanska et al., 2013; Root et al., 2003) or 1.3 to 5.6 days earlier per °C of warming
³⁷ (Polgar et al., 2013; Wolkovich et al., 2012). These changes are some of the largest climate change-induced
³⁸ shifts observed, with early spring phenology shifting more rapidly than later season phenology in most cases
³⁹ (Bradley et al., 1999; Menzel et al., 2006). If photoperiod interacts with temperature to determine spring
⁴⁰ phenology, we might expect that, as current rapid warming continues, photoperiod should begin to curb
⁴¹ trends in advancing spring phenology.

⁴² Recent studies offer inconsistent views about whether photoperiod may eventually restrict advances in spring

43 phenology in a warmer world. Some suggest that, with additional climate change, photoperiod will limit
44 phenological shifts of certain species such that they will not track rising temperatures (Fu et al., 2015; Way
45 and Montgomery, 2015; Basler and Körner, 2012; Körner and Basler, 2010a). Instead, these species' responses
46 will increasingly become constrained by daylength and the trend of ever-earlier springs with warming may
47 halt. Other studies, however, suggest that photoperiod will not constrain responses to warming for most
48 species (Chuine et al., 2010; Zohner et al., 2016). The extent to which daylength constrains phenology will
49 depend in part on how rapidly photoperiod responses can acclimate or adapt to new environmental conditions,
50 which remains poorly understood (Grevstad and Coop, 2015; Bradshaw and Holzapfel, 2007).

51 Perhaps because of these variable and uncertain responses, photoperiod is often not included in forecasts of
52 biological responses to climate change, especially in the spring, even though it is known to be an important
53 cue for biological activity (but see Caffarra et al., 2011a; Duputié et al., 2015; Grevstad and Coop, 2015).
54 The exclusion of photoperiod may be problematic: although photoperiod itself is stable over time, the
55 photoperiod that species *experience*, as they undergo climate change-induced shifts in space and time, is
56 likely to be much less stable. In addition to shifting activity earlier with recent warming, many species have
57 shifted their distributions poleward and upward in elevation (i.e., range shifts, Chen et al., 2011; Harsch et al.,
58 2009; Parmesan, 2006; Peñuelas and Boada, 2003). These spatial and temporal shifts alter the photoperiod
59 experienced by organisms (Fig. 1); altered photoperiods may have cascading effects on species' performance,
60 since daylength can affect the timing of development (Grevstad and Coop, 2015; Muir et al., 1994; Tauber
61 and Tauber, 1975), migration (Dawbin, 1966), reproduction (Dunn, 2019; Dardente, 2012; Ben-David, 1997),
62 and other important responses.

63 The implications of potential climate change-induced shifts in experienced photoperiod are unclear, as the
64 magnitude of potential shifts has not been described. Effects of photoperiod shifts may be relatively mi-
65 nor, especially because there can be substantial year-to-year variation in experienced photoperiod (Fig. 2).
66 Alternatively, photoperiod may begin to constrain species' responses to climate change (Körner and Basler,
67 2010b).

68 Using published plant growth chamber studies, we ask:

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

- 70 2. What are the implications of altered photoperiods for biological responses to climate change?
- 71 3. Can researchers apply data from experiments that alter photoperiod to aid in forecasting biological
- 72 implications of climate change?

73 Focal examples from spring woody plant phenology

74 These questions are broadly relevant for diverse species. Here, we use a case study of spring woody plant
75 phenology to illustrate our points (Box 1). We focus on spring events, as phenology during this time is one
76 of the most widely observed and rapidly changing biological responses to climate change (Parmesan, 2006).

77 In addition, the role of photoperiod is less well-understood in spring phenology compared with autumn
78 phenophases, but recent studies showing declines in responses of spring budburst to warming (e.g. Fu et al.,
79 2019; Güsewell et al., 2017; Yu et al., 2010) suggest that photoperiod constraints may be imminent. Woody
80 species are a useful focal group because they have been the subject of decades of growth chamber experiments,
81 are at the center of an important and controversial debate on the relative effects of photoperiod versus
82 temperature on their phenology, and because their phenology (i.e., the length of the growing season) has
83 critical implications for global carbon cycling and feedbacks to the climate system (Richardson et al., 2013).

84 We use studies included in Observed Spring Phenology Responses in Experimental Environments (OSPREE),
85 a new database of plant growth chamber studies that manipulate photoperiod and temperature to measure
86 plant phenological responses, including budburst and flowering (Wolkovich et al., 2019). The database in-
87 cludes studies that manipulate photoperiod (by applying treatments with different daylength durations, ap-
88 plying long-day versus short-day conditions for different lengths of time, and/or applying varying vs constant
89 photoperiods) and temperature (by imposing different chilling and/or forcing treatments). The OSPREE
90 database spans 201 woody plant species; all experiments in the database use dormant plant tissue (grown
91 in greenhouses or taken directly from the field) exposed to experimental conditions (Wolkovich et al., 2019)
92 for which we could identify forcing, photoperiod, and chilling treatments quantitatively. See Supplemental
93 Methods and Wolkovich et al. (2019) for details.

94 How will climate change alter the photoperiod experienced by or-
95 ganisms?

96 Species experience different photoperiod regimes depending on their location on Earth (Fig. 1, 2), the
97 seasonal timing of their activity, and inter-annual variation in climate. The daylength experienced by plants
98 on the date that spring “green-up” occurs, for example, varies with latitude (Fig. 2a). This is in part because
99 latitudinal variation in green-up date, which occurs earlier toward the equator and later toward the north pole,
100 is strongly driven by climatic differences that affect phenology, and in part because of latitudinal variation
101 in photoperiod (e.g., at the north pole, the daylength at the summer solstice is 24 hours; see also Fig. 1).

102 Some general latitudinal patterns in experienced photoperiod are apparent. For example, the pattern of longer
103 photoperiod at green-up toward the poles is consistent across years (i.e., on the day of year when green-up
104 occurs close to the north pole, daylength approaches 24 hours in both an average year, Fig. 2A, and in an
105 early year, Fig. 2B). Note that green-up does not appear to occur at daylengths less than 10 hours, across
106 North America and Europe.

107 Despite these consistent patterns at a broad scale, there is also strong spatiotemporal variation in experienced
108 photoperiod across years. Compare the photoperiod at green-up in an “early” versus an “average” year (Fig.
109 2): experienced photoperiod at green-up can vary by two to three hours from one year to the next in the same
110 location (Fig. 2c). Though green-up date corresponds to plant phenology, we expect that spatiotemporal
111 patterns would be similarly heterogeneous in spring phenology of other organisms (Ovaskainen et al., 2013;
112 Peñuelas et al., 2002).

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

¹²⁰ To date, where the scientific literature has addressed shifts in photoperiod with climate change, the focus has
¹²¹ been on how spatial range shifts will affect photoperiod (e.g., Saikkonen et al., 2012; Way and Montgomery,
¹²² 2015). However, shifting phenology—especially the large changes seen in spring phenology—will also alter
¹²³ experienced photoperiod, because of the seasonal patterns of daylength (Fig. 1).

¹²⁴ Despite a focus on range shifts, current data suggest that temporal shifts will yield much larger changes in
¹²⁵ experienced photoperiod than latitudinal shifts (Fig. 1). For example, consider an insect that emerges from
¹²⁶ diapause or a tree that bursts its buds at latitude 45°, on average, around day of year 91 (April 2, when
¹²⁷ daylength is 12.8 hours). If the organism’s phenology shifts 30 days earlier over the next century (i.e., a rate
¹²⁸ of 3 days per decade, as has been observed, Parmesan and Yohe, 2003), it will experience a daylength that
¹²⁹ is 1.6 hours shorter. This 1.6 hour decrease in daylength is equivalent to moving up 28.5° in latitude on this
¹³⁰ day of year. However, if the same species shifts its range up in latitude 0.5°(i.e., 60 km over the next century,
¹³¹ comparable to observed rates, Chen et al., 2011; Parmesan and Yohe, 2003), it will experience a daylength
¹³² that differs by less than a minute on the same day of year.

¹³³ In many cases organisms may shift both their ranges and their phenology simultaneously (i.e., due to new
¹³⁴ climatic conditions, Duputié et al., 2015; Grevstad and Coop, 2015). In addition, photoperiod sensitivity
¹³⁵ (see *Glossary*) can vary with latitude, likely due to population-level differences in sensitivity (Gauzere et al.,
¹³⁶ 2017; Saikkonen et al., 2012; Caffarra et al., 2011b; Bradshaw and Holzapfel, 2007; Viherä-Aarnio et al., 2006;
¹³⁷ Partanen et al., 2005; Howe et al., 1996). With future climate change, it is unclear how these complexities
¹³⁸ will affect the photoperiod experienced by organisms and whether these shifts in photoperiod will have im-
¹³⁹ portant implications for biological responses. This lack of clarity stems, in part, from the fact that phenology
¹⁴⁰ both affects and is affected by experienced photoperiod: climate change-induced shifts in phenology alter
¹⁴¹ experienced photoperiod, which in turn affects phenology.

¹⁴² **What are the implications of altered photoperiods for biological
143 responses to climate change?**

¹⁴⁴ Daylength, often in combination with temperature, can play a role in controlling critical biological functions,
¹⁴⁵ including vegetative growth, cell elongation, budburst, and flowering in plants (Fu et al., 2019; Heide and
¹⁴⁶ Sønsteby, 2012; Heide, 2011; Hsu et al., 2011; Sidaway-Lee et al., 2010; Mimura and Aitken, 2007; Linkosalo
¹⁴⁷ and Lechowicz, 2006; Erwin, 1998; Ashby et al., 1962) and growth rate, maturation, reproduction, migration,
¹⁴⁸ and diapause in animals (Dunn, 2019; Winkler et al., 2014; Zydlewski et al., 2014; Dardente, 2012; Tobin
¹⁴⁹ et al., 2008; Bradshaw and Holzapfel, 2006; Ben-David, 1997; Muir et al., 1994; Saunders and Henderson, 1970;
¹⁵⁰ Dawbin, 1966). Climate change-induced shifts in photoperiod are therefore likely to alter these functions.
¹⁵¹ Indeed, growth chamber studies demonstrate that the magnitude of daylength shifts we can expect with
¹⁵² climate change (i.e., 1-2 hours of difference in daylength with temporal shifts over the next century) are
¹⁵³ substantial enough to affect spring phenology in trees (Table S1). The direction and magnitude of responses
¹⁵⁴ will vary, however, because of variation in photoperiod sensitivity, and because photoperiod often interacts
¹⁵⁵ with other environmental drivers, such as temperature, to affect phenology (Box 1).

¹⁵⁶ The climate change-induced trend toward ever earlier springs means that experienced photoperiod may in-
¹⁵⁷ creasingly approach threshold photoperiod for many species, constraining their ability to respond to additional
¹⁵⁸ warming (Fu et al., 2019; Vitasse and Basler, 2013; Körner and Basler, 2010b; Morin et al., 2010; Nienstaedt,
¹⁵⁹ 1966). Interactions between photoperiod and temperature may therefore result in muted phenological shifts,
¹⁶⁰ compared to what would be expected based on temperature change alone (Körner and Basler, 2010b; Mimura
¹⁶¹ and Aitken, 2007; Wareing, 1956). If photoperiod does become limiting, the average trend of earlier phe-
¹⁶² nology with warming (Ovaskainen et al., 2013; Polgar et al., 2013; Peñuelas et al., 2002; Menzel, 2000) may
¹⁶³ stop.

¹⁶⁴ A challenge in understanding the implications of altered photoperiods under climate change, and for force-
¹⁶⁵ casting whether and when the trend of earlier phenology with warming may slow or stop abruptly, is the wide
¹⁶⁶ range of observed photoperiod sensitivity across species (Flynn and Wolkovich, 2018; Sanz-Perez et al., 2009;
¹⁶⁷ Zohner et al., 2016), populations (Tanino et al., 2010), and ecotypes (Howe et al., 1995). How much genotype
¹⁶⁸ versus environment explain this variation is an active area of research (e.g., Franks et al., 2014; Gould et al.,

169 2010; Mimura and Aitken, 2010; Fréjaville et al., 2019). Environmental conditions clearly play a role, since
170 different combinations of ambient temperature and photoperiod may explain some of this variation, because
171 temperature cues can override photoperiod requirements under certain conditions (e.g., Tanino et al., 2010).
172 In such cases, climate change-induced phenological shifts may occur at different rates than past shifts with
173 warming. On the other hand, some of this variation may be due to underlying genetic differences, because
174 photoperiod responses can be under strong genetic control (Bradshaw and Stettler, 1995; Keller et al., 2011;
175 Weih, 2004, , see also Box 1). Teasing out the relative roles of genetics versus environmental conditions will
176 be critical to accurate forecasts of future phenology under climate change.

177 Species- and population-level variation in photoperiod sensitivity may result in altered communities as climate
178 change progresses. For example, a species or population that is relatively insensitive to photoperiod can take
179 advantage of warmer springs by having an earlier start to its growing season. Indeed, phenological tracking of
180 temperature (e.g., earlier flowering, leafout, migration with warming) has been linked with higher performance
181 in plants and animals (Cleland et al., 2012; Muir et al., 1994; Willis et al., 2010). Species or populations
182 that are sensitive to temperature but relatively insensitive to photoperiod may therefore outcompete slower-
183 growing or later-emerging ones that are limited by photoperiod and thus cannot take advantage of longer
184 growing season conditions. To identify where, when, and how communities may be altered, quantifying
185 species-specific photoperiod sensitivity and developing methods for incorporating photoperiod into forecasting
186 future phenology are critical.

187 Future directions: outstanding questions and incorporating pho- 188 toperiod into forecasting

189 Incorporating photoperiod into forecasting is complex for a few major reasons. Future rates of phenological
190 shifts are unlikely to be straightforward extrapolations from past and current rates. In addition, an organism's
191 experienced photoperiod is both a driver and an effect of phenological shifts.
192 Approaches for forecasting can be grouped into two broad categories: statistical models and process-based
193 models. These two modelling paradigms differ in at least two ways, in terms of relating phenology to

194 climate change. First, statistical models generally assume linear relationships between species' responses and
195 environmental variables (e.g., Flynn and Wolkovich, 2018; Van Belle et al., 2007; Ibáñez et al., 2010); instead
196 process-based models often incorporate nonlinear threshold relationships as well (e.g. Chuine and Beaubien,
197 2001; Morin and Thuiller, 2009; Xie and Hsieh, 1989). Second, statistical models of phenology under climate
198 change have typically ignored photoperiod, focusing instead on seasonal or annual temperature (e.g. Diez
199 et al., 2012; Ibáñez et al., 2010; Van Belle et al., 2007, but see Richardson et al. (2013)). whereas process-
200 based models of phenology more frequently incorporate photoperiod, along with temperature (Lundell et al.,
201 2020; Duputié et al., 2015; Morin and Thuiller, 2009; Xie and Hsieh, 1989; Zhao et al., 2013; ?). A challenge
202 of process-based models is that they require detailed data that are often not readily available (e.g., daily
203 climate data, nonlinear biological responses to fine-scale changes in temperature). Perhaps because of this
204 challenge, statistical models remain more commonly used in climate change forecasts of biological responses
205 (e.g., Basler and Körner, 2012; Diez et al., 2012; García-Valdés and Morales-Castilla, 2016; Ibáñez et al.,
206 2010; Van Belle et al., 2007; Zhu et al., 2012).

207 Future modelling can incorporate photoperiod by leveraging the large amount of experimental data on pho-
208 toperiod responses (Fig. 3, Table S1), especially when process-based approaches are used. Researchers can
209 use these data to first learn whether the study species (or a phylogenetically closely related species) shows a
210 photoperiod effect and, ideally, identify its threshold photoperiod and how it varies by population, ecotype,
211 or other factors (Bradshaw and Holzapfel, 2006; Gwinner, 1996; Tobin et al., 2008). If there is evidence of
212 a photoperiod response (e.g., *Fagus grandifolia*, or *Tilia americana* with low chilling in Fig. 4), daylength
213 should be added to forecasting models, using the threshold photoperiod to define short-day and long-day
214 conditions (Fig. 6). Given the large change in experienced photoperiod with temporal shifts (Fig. 1), this
215 may be particularly important for phenological forecasting. Since spatial shifts are associated with smaller
216 changes in experienced photoperiod, it may be less important for distribution forecasts. Many species, how-
217 ever, may shift in *both* space and time simultaneously. Thus, even though experienced photoperiod changes
218 little as species distributions shift in space, phenology may be altered significantly.

219 For some species, experimental data can be immediately used in forecasting because experiments manipulate
220 photoperiod at relevant scales (e.g., Basler and Körner, 2014; Heide and Sonsteby, 2015, Figs. 3, 5 A, Table
221 S1). For example, photoperiod treatments from growth chamber experiments with *Fagus sylvatica* span

the variation in both current and expected future ranges (Fig. 5A, Duputié et al., 2015), and may allow identification of threshold photoperiods (Fig. 6). In other cases, attempting to incorporate photoperiod into forecasts of future phenology will reveal gaps in our understanding of many aspects of photoperiod responses. For example, photoperiod treatments from existing experiments of *Quercus robur* do not accurately represent experienced photoperiods from current or future estimates (Fig. 5B), making fine-scale projections difficult, even for this relatively well-studied species. This gap extends to many species, as most experiments manipulate photoperiod much more dramatically than will occur with climate change (Figs. 3, 5). Although these studies can be useful for understanding mechanistically how photoperiod responses work, extrapolating them to climate change models may not be reasonable.

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

As researchers more fully integrate photoperiod into forecasting, a critical area of further study is understanding *how* photoperiod acts as a cue. Photoperiod seems to interact with temperature to affect phenology (e.g., Zydlewski et al., 2014); this would explain the divergent effects of photoperiod observed across studies in woody plants (e.g., Fig. 4). However, exactly how it interacts with temperature is not well-defined for most species or populations (Boxes 1, S1). For many species, additional experimental and physiological research is necessary, since the dormancy-breaking processes that photoperiod affects often require microscopy and detailed physiological approaches to observe (Hänninen et al., 2019; Chuine et al., 2016). Understanding the drivers, as well as the consequences, of variations in photoperiod responses across species and populations will be particularly beneficial for forecasting. For example, what traits are associated with photoperiod sensitivity and does variation in photoperiod sensitivity or related traits have a strong genetic component? If so, are species or populations from some locations or lineages more likely than others to be constrained by

250 photoperiod in their responses to climate change?

251 Conclusions

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

263 Glossary

- 264 • budburst: when one or more leaf buds have visible green tips.
- 265 • chilling: the intensity and duration of winter temperature, often a certain sum of chilling that is required
266 (e.g., some amount of hours or days of cold temperatures, defined by a specific critical temperature or
267 range of temperatures, such as between 0 and 7.2 °C, Richardson, 1974), that must be experienced for
268 budburst to occur.
- 269 • daylength: the period of time during a 24-hour period during which an organism receives light.
- 270 • diapause: period of suspended development or growth, usually used to describe invertebrates during
271 unfavorable environmental conditions such as winter.
- 272 • dormancy: halted or reduced growth or activity, usually used to describe plants.

- 273 • forcing: warm spring temperatures, often a certain sum of forcing that is required (e.g., some amount
274 of hours or days above a specific temperature) for budburst or flowering can occur.
- 275 • green-up: The beginning of a new cycle of plant growth, usually evaluated at the landscape scale.
- 276 • phenology: the timing of life cycle events in organisms
- 277 • photoperiod: the daily duration of light (daylength) and dark to which an organism is exposed; often
278 used synonymously with daylength.
- 279 • photoperiod sensitivity: the degree to which phenology is controlled by daylength; may be a nonlinear,
280 or “threshold”, response in plants (Box S1) and animals (Tobin et al., 2008; Grevstad and Coop, 2015).
- 281 • photoperiodism: the ability to assess the length of day or night to regulate behavior, physiology, growth,
282 development or reproduction.
- 283 • threshold photoperiod: length of day that causes an organism to switch from a short– to a long–day
284 response (or vice versa). For example, in European larch (*Larix decidua*), budburst development may
285 be constrained under short-day conditions, when daylengths are less than a threshold photoperiod of
286 10-11 hours (Migliavacca et al., 2008). Above this threshold photoperiod, the long-day response of
287 unconstrained budburst development can occur.

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

290 Photoperiod responses are particularly well-studied in woody plant phenology. Decades of experimental
291 growth chamber studies have shown that photoperiod is an important cue for spring budburst phenology
292 in woody plants (e.g., Flynn and Wolkovich, 2018; Basler and Körner, 2014; Heide, 1993b). These experi-
293 ments often manipulate photoperiod in combination with temperature to address basic questions about how
294 these two environmental conditions act as biological cues. Temperature has a dual role in regulating woody
295 plant phenology: chilling—the prolonged exposure to cold temperatures after growth cessation in the fall—is
296 required to initiate budburst; and forcing—prolonged exposure to warm temperatures—is required for bud-

297 burst to occur. Thus, chilling and forcing treatments are often altered in addition to photoperiod in growth
298 chamber experiments (e.g., Campbell and Sugano, 1975; Falusi and Calamassi, 1990; Heide, 1977; Laube
299 et al., 2014; Spann et al., 2004).

300 Woody plant growth chamber studies have been conducted for decades, but have only recently been syn-
301 thesized (Wolkovich et al., 2019), revealing that photoperiod sensitivity is widespread, though with wide
302 variation across studies and species. Growth chamber experiments in OSPREE suggest that the dominant
303 photoperiod response in woody plant species is earlier and more rapid budburst with longer days (e.g., Caf-
304 farra and Donnelly, 2011). Thirty-one of the 85 studies in the OSPREE database included two or more
305 different photoperiod treatments. Of these, 26 (84%) found significant photoperiod main effects or significant
306 interactive effects with temperature (i.e., photoperiod x temperature effects), across 176 species (Table S1).
307 Main effects included responses such as growth (e.g., higher growth rates with longer days Ashby et al., 1962)
308 and reproduction (e.g., increased flowering with longer days Heide and Sønsteby, 2012).

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

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

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₅₉₃ **Figures**

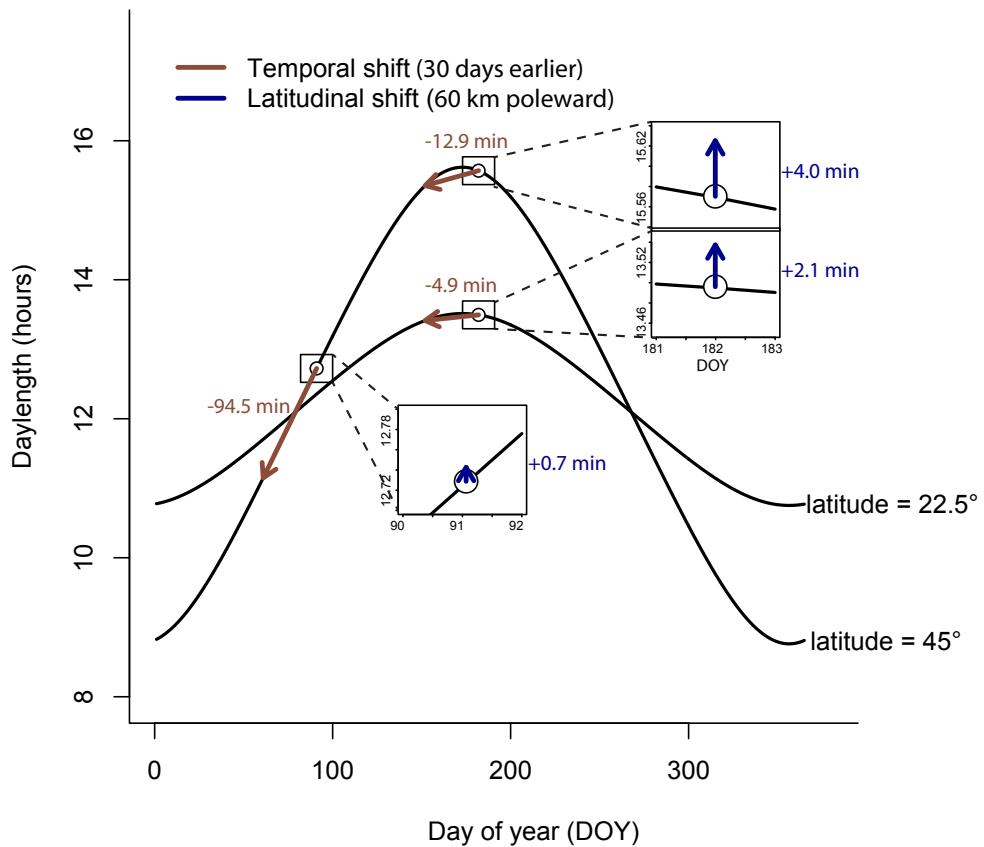


Figure 1: **Temporal (i.e., phenological) shifts in activity yield larger changes in experienced photoperiod compared to spatial (i.e., latitudinal) shifts** on the same day of year, due to patterns in photoperiod variation with latitude and by day of year. Here, we show this variation at two latitudes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

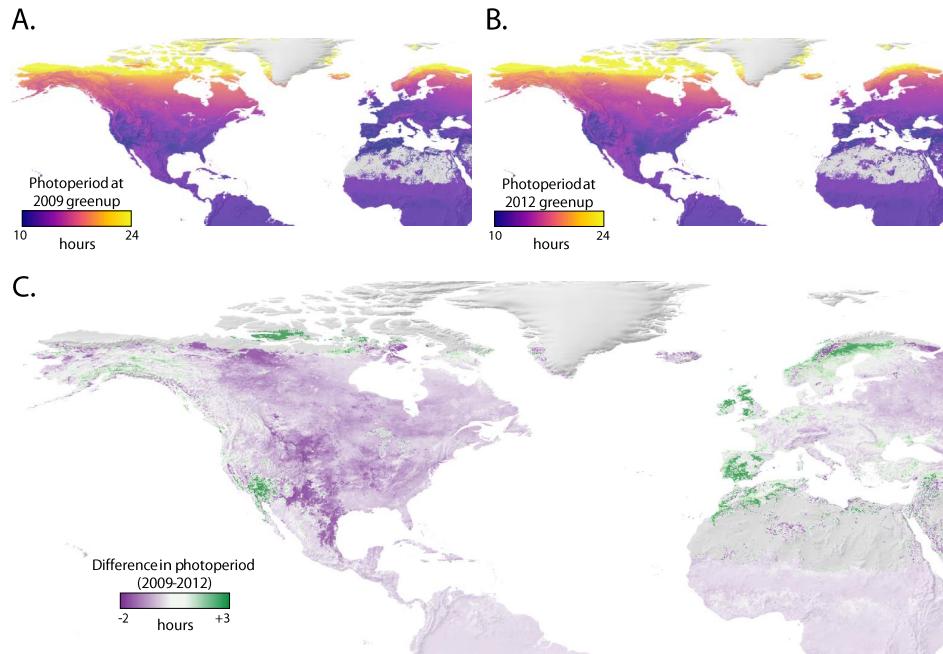


Figure 2: Photoperiod on the “green-up” date varies over space and between years “Green-up” date is the beginning of seasonal greening, identified by satellite remote sensing measurements taken regularly throughout the year of the concentrations of green leaf vegetation. Hours of daylight on the date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

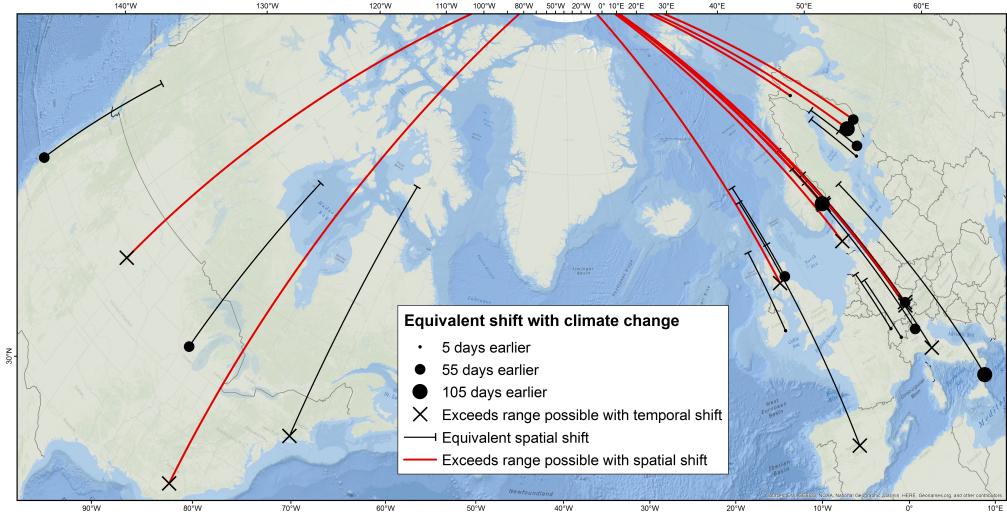


Figure 3: Experimental photoperiod treatments and their equivalent spatial and temporal shifts for experiments in the OSPREE database that manipulated photoperiod. See ‘Mapping temporal and spatial shifts in space and time’ in the Supplemental Materials for details on how we calculated the required spatial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

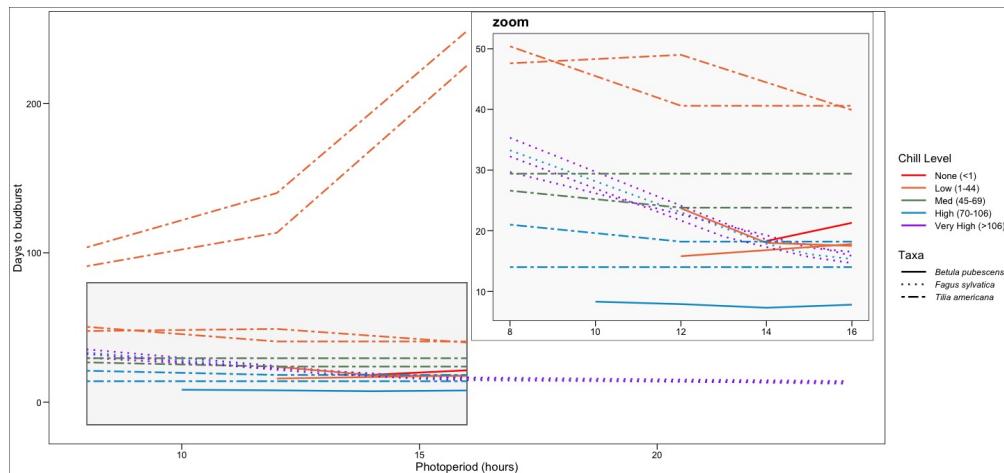


Figure 4: Nonlinearities in phenological responses to daylength are apparent in spring woody plant phenology experiments (from the OSPREE database) in which three or more photoperiod treatment levels were applied. The shape of the response curves for *Betula pubescens* (Caffarra et al., 2011b), *Fagus sylvatica* (Heide, 1993b) and *Tilia americana* (Ashby et al., 1962) differ depending on the amount of winter chilling received (measured in Chill portions). Species and chilling levels with multiple lines represent plant material from different populations.

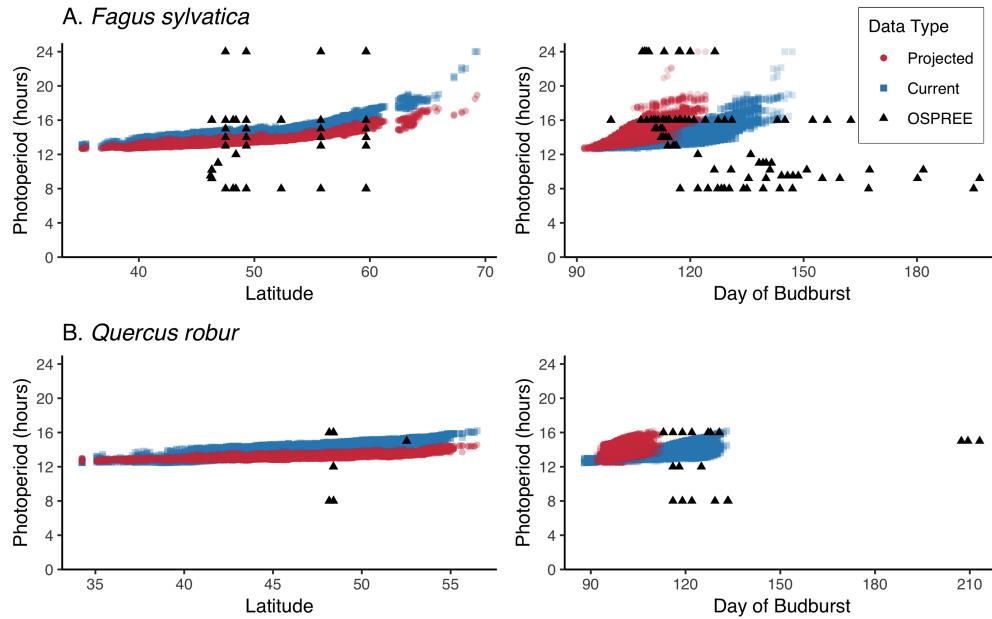


Figure 5: Experienced photoperiods in experiments differ from those in the natural world, shown here by latitude (left panels) and by day of budburst (right panels) for *Fagus sylvatica* (A, upper panels) and *Quercus robur* (B, lower panels). Triangles show experimental treatments of photoperiod in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

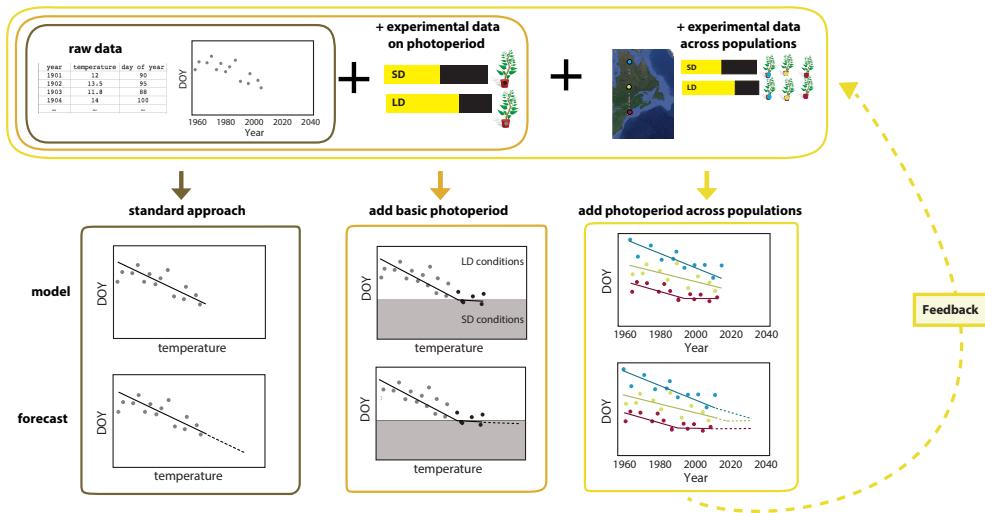


Figure 6: **Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change.** Current approaches for forecasting spring phenology with climate change frequently rely on linear relationships between historical temperature data and observed dates of spring phenology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