

Spatial and temporal shifts in photoperiod with climate change

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Data Accessibility Should the manuscript be accepted in *Nature Plants*, the data supporting our results will be archived in an appropriate public repository. The OSPREE database will be publicly archived at KNB, doi:10.5063/F1QV3JQR (?).

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1 Abstract

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

¹⁶ Introduction

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

²³ Spring phenology is not controlled solely by temperature, however. Photoperiod is also a critical cue, signalling
²⁴ changes in growth and reproduction across diverse species (e.g., ?????), and spring phenology is thought to
²⁵ be determined interactively by photoperiod and temperature (?; see also Box 1). Photoperiod is a useful
²⁶ cue to synchronize activities with seasonal climatic changes (e.g., ???) because it is consistent across years,
²⁷ especially compared to other cues such as temperature and precipitation (?). For example, relying on a
²⁸ threshold photoperiod (see *Glossary*), rather than temperature alone, may prevent woody plants from leading
²⁹ out during “false spring” events (unusually warm periods during winter that are followed by a return to cold
³⁰ temperatures ?).

³¹ Recent studies suggest that photoperiod cues may eventually restrict advances in spring phenology in a
³² warmer world. With additional climate change, photoperiod will limit phenological shifts of certain species
³³ such that they will not track rising temperatures (????). Instead, these species’ responses will increasingly
³⁴ become constrained by daylength and the trend of ever-earlier springs with warming may halt. The idea of
³⁵ photoperiod constraints is controversial, however, as other studies suggest that photoperiod will not constrain
³⁶ responses to warming for most species (??). The extent to which daylength constrains phenology will depend
³⁷ in part on how rapidly photoperiod responses can acclimate or adapt to new environmental conditions, which
³⁸ remains poorly understood (?).

³⁹ Perhaps because of these variable and uncertain responses, photoperiod is often not included in forecasts of
⁴⁰ biological responses to climate change, especially in the spring, even though it is known to be an important cue
⁴¹ for biological activity (but see ???). The exclusion of photoperiod may be problematic: although photoperiod
⁴² itself is stable over time, the photoperiod that species *experience*, as they undergo climate change-induced

⁴³ shifts in space and time, is likely to be much less stable. In addition to shifting activity earlier with recent
⁴⁴ warming, many species have shifted their distributions poleward and upward in elevation (i.e., range shifts,
⁴⁵ ????). These spatial and temporal shifts alter the photoperiod experienced by organisms (Fig. 1).

⁴⁶ The implications of potential climate change-induced shifts in experienced photoperiod are unclear, as the
⁴⁷ magnitudes of potential shifts have not been described. Effects of photoperiod shifts may be relatively
⁴⁸ minor, especially because there can be substantial year-to-year variation in experienced photoperiod (Fig.
⁴⁹ 2). Alternatively, photoperiod may begin to constrain species' responses to climate change (????).

⁵⁰ Here, we ask:

- ⁵¹ 1. How will climate change alter the photoperiod experienced by organisms?
- ⁵² 2. What are the implications of altered photoperiods for biological responses to climate change?
- ⁵³ 3. Can researchers apply data from experiments that alter photoperiod to aid in forecasting biological
⁵⁴ implications of climate change?

⁵⁵ We focus on spring events, as phenology during this time is one of the most widely observed and rapidly
⁵⁶ changing biological responses to climate change (?). In addition, the role of photoperiod is less understood in
⁵⁷ spring phenology compared with autumn phenophases (reviewed in, e.g., ????), but recent studies showing
⁵⁸ declines in responses of spring budburst to warming (e.g., ???) suggest that photoperiod constraints may be
⁵⁹ imminent. While our questions are broadly relevant for diverse species, we use a case study of spring woody
⁶⁰ plant phenology to illustrate some of our points (Boxes 1, 2).

⁶¹ **How will climate change alter the photoperiod experienced by or- ganisms?**

⁶³ Species experience different photoperiod regimes depending on their location on Earth, the seasonal timing
⁶⁴ of their activity, and inter-annual variation in climate (Fig. 1, 2). Consider, as an example, the daylength
⁶⁵ experienced by plants on the date that spring “green-up” occurs. Spring green-up varies with latitude (Fig.
⁶⁶ 2a), in part because latitudinal variation in green-up date, which occurs earlier toward the equator and later

⁶⁷ toward the poles, is strongly driven by climatic differences that affect phenology, and in part because of
⁶⁸ latitudinal variation in photoperiod (e.g., at the poles, the daylength at the summer solstice is 24 hours; see
⁶⁹ also Fig. 1).

⁷⁰ Some consistent patterns in experienced photoperiod are apparent at a broad scale. Across years, photoperiod
⁷¹ at green-up is longer toward the poles (i.e., on the day of year when green-up occurs close to the north pole,
⁷² daylength approaches 24 hours in both an average year, Fig. 2A, and in an early year, Fig. 2B). In addition,
⁷³ green-up does not appear to occur at daylengths less than 10 hours, across North America and Europe.

⁷⁴ Despite these consistent broad-scale patterns, there is also strong spatiotemporal variation in experienced
⁷⁵ photoperiod across years. Comparing the photoperiod at green-up in an “early” versus an “average” year (Fig.
⁷⁶ 2) shows that experienced photoperiod at green-up can vary by two to three hours from one year to the next
⁷⁷ in the same location (Fig. 2C). We use green-up date as an example here because it is an available dataset
⁷⁸ and represents an important biological event, signalling the start of the growing season.

⁷⁹ Against this existing background variation, climate change will cause shifts in experienced photoperiod as
⁸⁰ species respond to warming temperatures. Spatial shifts in species’ ranges and temporal shifts in phenology
⁸¹ will alter the photoperiods experienced by organisms with future climate change. The magnitude of these
⁸² alterations will vary depending on the organism’s location and the type of shift(s) it undergoes. For example,
⁸³ poleward shifts in species’ ranges cause organisms to experience a wider range of daylength throughout the
⁸⁴ year (Fig. 1). Elevational shifts, in contrast, cause minimal change to the range of daylength throughout the
⁸⁵ year.

⁸⁶ To date, most focus on shifts in photoperiod with climate change has been centered on how spatial range
⁸⁷ shifts will affect photoperiod (e.g., ??). However, shifting phenology—especially the large changes seen in
⁸⁸ spring phenology—will also alter experienced photoperiod, because of the seasonal patterns of daylength (Fig.
⁸⁹ 1).

⁹⁰ Despite a focus on range shifts, current data suggest that temporal shifts will yield much larger changes
⁹¹ in experienced photoperiod than latitudinal shifts (Fig. 1). Consider a tree species that bursts its buds
⁹² at latitude 45°, on average around day of year 91 (April 2), when daylength is 12.8 hours. If the species’
⁹³ phenology shifts 30 days earlier over the next century (i.e., a rate of 3 days per decade, as has been observed,

94 ?), it will experience a daylength that is 1.6 hours shorter. This 1.6 hour decrease in daylength is equivalent
95 to moving up 28.5° in latitude on this day of year. However, if the same species shifts its range up in latitude
96 0.5° (i.e., 60 km over the next century, comparable to observed rates, ??), it will experience a daylength that
97 differs by less than a minute on the same day of year.

98 In many cases organisms may shift both their ranges and their phenology simultaneously (i.e., due to new
99 climatic conditions, ?). In addition, photoperiod sensitivity (see *Glossary*) can vary with latitude, likely due
100 to population-level differences in sensitivity (????????). With future climate change, it is unclear how these
101 complexities will affect the photoperiod experienced by organisms and whether these shifts in photoperiod
102 will have important implications for biological responses. This lack of clarity stems, in part, from the fact
103 that phenology both affects and is affected by experienced photoperiod: climate change-induced shifts in
104 phenology alter experienced photoperiod, which in turn affects phenology.

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

107 Daylength, often in combination with temperature, can play a role in controlling critical biological functions,
108 including vegetative growth, cell elongation, budburst, and flowering in plants (??????????) Climate change-
109 induced shifts in photoperiod are therefore likely to alter these functions. Indeed, growth chamber studies
110 demonstrate that the magnitude of daylength shifts we can expect with climate change (i.e., 1-2 hours of
111 difference in daylength with temporal shifts over the next century) are substantial enough to affect spring
112 phenology in trees (Table S1). The direction and magnitude of responses will vary, however, because of
113 variation in photoperiod sensitivity, and because photoperiod often interacts with other environmental drivers,
114 such as temperature, to affect phenology (Box 1).

115 The climate change-induced trend toward ever-earlier springs means that experienced photoperiod may in-
116 creasingly approach threshold photoperiods (see *Glossary*) for many species, constraining their ability to
117 respond to additional warming (?????). Interactions between photoperiod and temperature may therefore
118 result in muted phenological shifts, compared to what would be expected based on temperature change alone

¹¹⁹ (???). If photoperiod does become limiting, the average trend of earlier phenology with warming (???) may
¹²⁰ stop.

¹²¹ A challenge in understanding the implications of altered photoperiods under climate change, and for forecast-
¹²² ing whether and when the trend of earlier phenology with warming may slow or stop abruptly, is the wide
¹²³ range of observed photoperiod sensitivity across species (???), populations (?), and ecotypes (?). How much
¹²⁴ genotype versus environment explain this variation is an active area of research (e.g., ???). Environmental
¹²⁵ conditions clearly play a role, since different combinations of ambient temperature and photoperiod may
¹²⁶ explain some of this variation and because temperature cues can override photoperiod requirements under
¹²⁷ certain conditions (e.g., ?). In such cases, climate change-induced phenological shifts may occur at different
¹²⁸ rates than past shifts with warming. On the other hand, some of this variation may be due to underlying
¹²⁹ genetic differences, because photoperiod responses can be under strong genetic control (???, see also Boxes
¹³⁰ 1, 2). Teasing out the relative roles of genetics versus environmental conditions will be critical to accurate
¹³¹ forecasts of future phenology under climate change.

¹³² Species- and population-level variation in photoperiod sensitivity may result in altered communities as climate
¹³³ change progresses. For example, a species or population that is relatively insensitive to photoperiod can
¹³⁴ take advantage of warmer springs by having an earlier start to its growing season. Indeed, phenological
¹³⁵ tracking of temperature (e.g., earlier flowering, leafout, migration with warming) has been linked with higher
¹³⁶ performance in plants and animals (???). Species or populations that are sensitive to temperature but
¹³⁷ relatively insensitive to photoperiod may therefore outcompete slower-growing or later-emerging ones that
¹³⁸ are limited by photoperiod and thus cannot take advantage of longer growing season conditions. Not all
¹³⁹ studies, however, find links between performance and high sensitivity to temperature (e.g., ?), and early-
¹⁴⁰ season species in most temperature zones risk losing to tissue to frost (?). Thus, the advantages of tracking
¹⁴¹ warming may depend on how quickly mean temperatures versus last frost dates shift (e.g., ?), such that
¹⁴² in some systems photoperiod cues could prevent species from starting growth or reproduction too early
¹⁴³ (when they risk losing their investments in new tissue). To identify where, when, and how communities
¹⁴⁴ may be altered therefore requires quantifying species-specific temperature and photoperiod sensitivities, and
¹⁴⁵ developing methods that incorporate both photoperiod and environmental events that impact fitness (such
¹⁴⁶ as frosts).

¹⁴⁷ Future directions: outstanding questions and incorporating photoperiod into forecasting

¹⁴⁹ Incorporating photoperiod into forecasting is complex for a few major reasons. Future rates of phenological
¹⁵⁰ shifts are unlikely to be straightforward extrapolations from past and current rates. In addition, an organism's
¹⁵¹ experienced photoperiod is both a driver and an effect of phenological shifts.

¹⁵² Approaches for forecasting can be grouped into two broad categories: statistical models and process-based
¹⁵³ models. These two modelling paradigms differ in how they relate phenology to climate change. Statistical
¹⁵⁴ models relating phenology to climate change often assume linear relationships between species' responses
¹⁵⁵ and environmental variables (e.g., ??), whereas process-based models often incorporate nonlinear threshold
¹⁵⁶ relationships (e.g. ??). Further, statistical models of phenology under climate change frequently ignore
¹⁵⁷ photoperiod, focusing instead on seasonal or annual temperature (e.g. ??, but see ?), whereas process-based
¹⁵⁸ models of phenology more frequently incorporate photoperiod, along with temperature (????). Process-based
¹⁵⁹ models may thus seem superior for integrating photoperiod, but they can be challenging to develop, requiring
¹⁶⁰ detailed data that are often not readily available (e.g., daily climate data, nonlinear biological responses to
¹⁶¹ fine-scale changes in temperature). Perhaps because of this, statistical models remain more commonly used
¹⁶² in climate change forecasts of biological responses (e.g., ?????).

¹⁶³ Future modelling of spring woody plant phenology can incorporate photoperiod by leveraging the large
¹⁶⁴ amount of experimental data on photoperiod responses (e.g., Fig. 3, Table S1, Box 2), especially when
¹⁶⁵ process-based approaches are used. Researchers can use these data to first learn whether the study species
¹⁶⁶ (or a phylogenetically closely related species) shows a photoperiod effect and, ideally, identify its threshold
¹⁶⁷ photoperiod and how it varies by population, ecotype, or other factors (??). If there is evidence of a photoperiod
¹⁶⁸ response (e.g., *Fagus grandifolia*, or *Tilia americana* with low chilling shown in Box 1), daylength should
¹⁶⁹ be added to forecasting models, using the threshold photoperiod to define short-day and long-day conditions
¹⁷⁰ (Fig. 4). Given the large change in experienced photoperiod with temporal shifts (Fig. 1), this may be
¹⁷¹ particularly important for phenological forecasting. Since spatial shifts are associated with smaller changes
¹⁷² in experienced photoperiod, it may be less important for distribution forecasts. Many species, however, may
¹⁷³ shift in *both* space and time simultaneously. Even though experienced photoperiod changes little as species

174 distributions shift in space, phenology may be altered significantly.

175 For some species, experimental data can be immediately used in forecasting because experiments manipulate
176 photoperiod at relevant scales (e.g., ??, Figs. 3, S1A, Table S1). For example, photoperiod treatments
177 from growth chamber experiments with *Fagus sylvatica* span the variation in both current and expected
178 future ranges (Fig. S1A, ?), and may allow identification of threshold photoperiods (Fig. 4). In other cases,
179 attempting to incorporate photoperiod into forecasts of future phenology will reveal gaps in our understanding
180 of many aspects of photoperiod responses. For example, photoperiod treatments from existing experiments
181 of *Quercus robur* do not accurately represent experienced photoperiods from current or future estimates (Fig.
182 S1B), making fine-scale projections difficult, even for this relatively well-studied species. This gap extends
183 to many species, as most experiments manipulate photoperiod much more dramatically than will occur with
184 climate change (Figs. 3, S1). Although these studies can be useful for understanding mechanistically how
185 photoperiod responses work, extrapolating them to climate change models may not be reasonable.

186 Photoperiod is not fully integrated into most current forecasts of biological responses to climate change (but
187 see ?, for an example in insects); this omission could affect forecast accuracy. Forecasts from ecosystem models
188 often incorporate photoperiod, along with other variables such as evaporative demand and temperature (e.g.,
189 the Ecosystem Demography model ??), but photoperiod is rarely included in species distribution models (e.g.,
190 ??). The sensitivity of model outcomes to assumptions made about experienced photoperiod and threshold
191 responses to photoperiod needs further study, including understanding how variation in photoperiod responses
192 across ecosystems, species, populations, and life stages impacts forecasts.

193 As researchers more fully integrate photoperiod into forecasting, a critical area of further study is under-
194 standing *how* photoperiod acts as a cue. Photoperiod seems to interact with temperature to affect phenology
195 (e.g., Box 1, ?); this would explain the divergent effects of photoperiod observed across studies in woody
196 plants (Box 1). However, exactly how it interacts with temperature is not well-defined for most species
197 or populations. For many species, additional experimental and physiological research is necessary, since
198 the dormancy-breaking processes that photoperiod affects often require detailed physiological approaches to
199 observe (Box 2, ??). Understanding the drivers, as well as the consequences, of variations in photoperiod
200 responses across species and populations will be particularly beneficial for forecasting. For example, what
201 traits are associated with photoperiod sensitivity and does variation in photoperiod sensitivity or related

202 traits have a strong genetic component? If so, are species or populations from some locations or lineages
203 more likely than others to be constrained by photoperiod in their responses to climate change?

204 Conclusions

205 Organisms may undergo large changes to the photoperiod they experience with climate change, even if they
206 do not shift their ranges spatially. Here we have shown that these altered photoperiods may result in stalled
207 future advances of spring phenology with warming (e.g., Table S1, Fig. S1, ???), with cascading effects on
208 growth, fitness, and community composition due to the large variation in photoperiod responses across species
209 and populations (Box 1). We have focused on woody plant spring phenology, but shifts in photoperiod with
210 climate change have implications for a variety of plant and animal responses, given that daylength affects
211 critical activities for diverse species from insects (?) and salmon (?) to birds (?) and marsupials (?).
212 Given what we know, incorporating photoperiod into forecasting of climate change responses should improve
213 model accuracy (Fig. 6), and will illuminate additional experiments that could improve our mechanistic
214 understanding of photoperiod as a critical cue for diverse biological responses.

215 Glossary

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

- 225 • forcing: warm spring temperatures, often a certain sum of forcing that is required (e.g., some amount
226 of hours or days above a specific temperature) for budburst or flowering can occur.
- 227 • green-up: The beginning of a new cycle of plant growth, usually evaluated at the landscape scale.
- 228 • phenology: the timing of life cycle events in organisms
- 229 • photoperiod: the daily duration of light (daylength) and dark to which an organism is exposed; often
230 used synonymously with daylength.
- 231 • photoperiod sensitivity: the degree to which phenology is controlled by daylength; may be a nonlinear,
232 or “threshold”, response in plants (Box 2) and animals (??).
- 233 • photoperiodism: the ability to assess the length of day or night to regulate behavior, physiology, growth,
234 development or reproduction.
- 235 • threshold photoperiod: length of day that causes an organism to switch from a short- to a long-day
236 response (or vice versa). For example, in European larch (*Larix decidua*), budburst development may
237 be constrained under short-day conditions, when daylengths are less than a threshold photoperiod of
238 10-11 hours (?). Above this threshold photoperiod, the long-day response of unconstrained budburst
239 development can occur.

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248 **References**

²⁴⁹ **Figures**

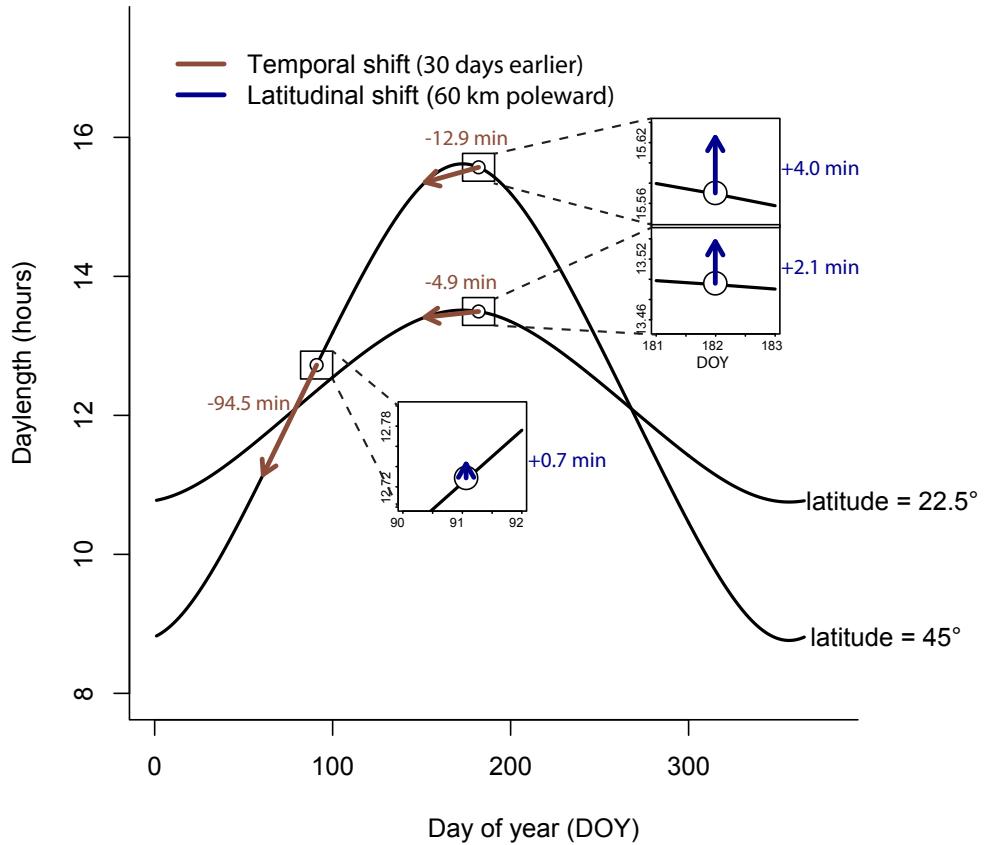


Figure 1: **Temporal (i.e., phenological) shifts in activity yield larger changes in experienced photoperiod compared to spatial (i.e., latitudinal) shifts on the same day of year, due to patterns in photoperiod variation with latitude and by day of year.** Here, we show this variation at two latitudes (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 (??), and 2-3 days per decade, or 30 days in 100 years, for temporal shifts (??). They highlight the greater magnitude in daylength changes in the early spring, close to the vernal equinox (e.g., day of year 91), versus close to the summer solstice (e.g., day of year 182).

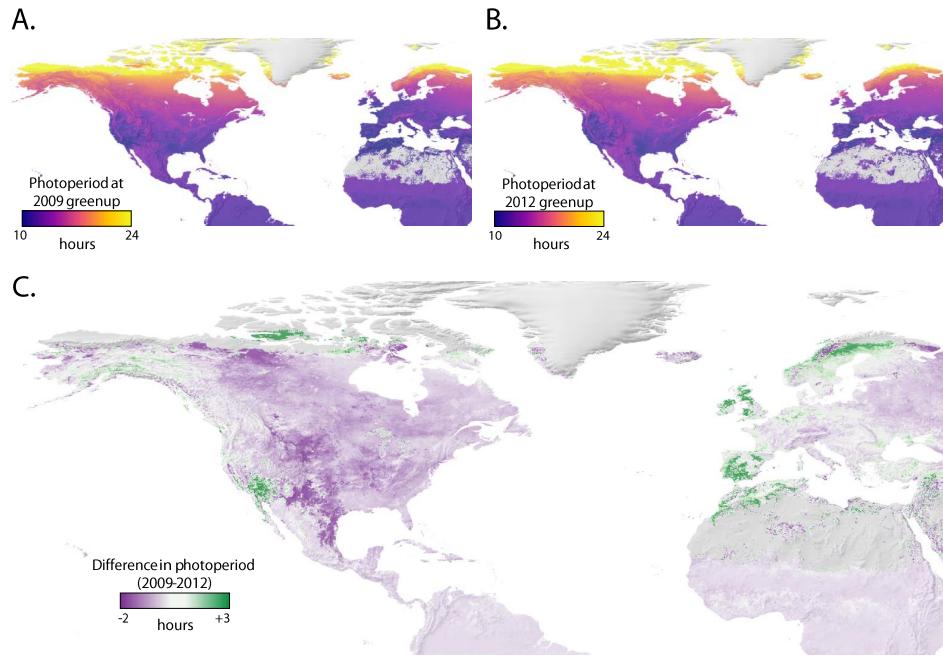


Figure 2: Photoperiod on “green-up” date varies over space and between years “Green-up” date is the beginning of seasonal greening, identified by satellite remote sensing measurements taken regularly throughout the year of the concentrations of green leaf vegetation. Hours of daylight on the date of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

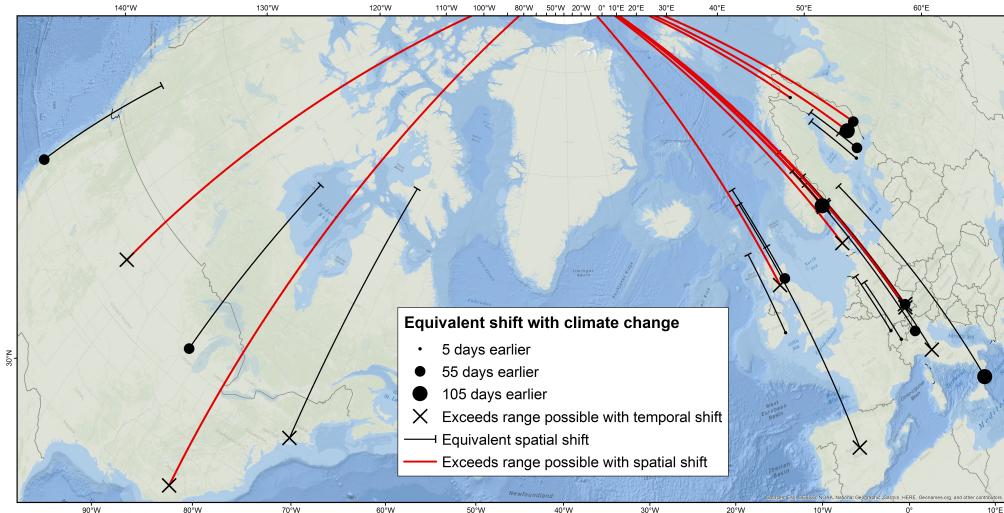


Figure 3: Experimental photoperiod treatments and their equivalent spatial and temporal shifts for experiments in the OSPREE database that manipulated photoperiod (see Box 1). See ‘Mapping temporal and spatial shifts in space and time’ in the Supplemental Materials for details on how we calculated the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

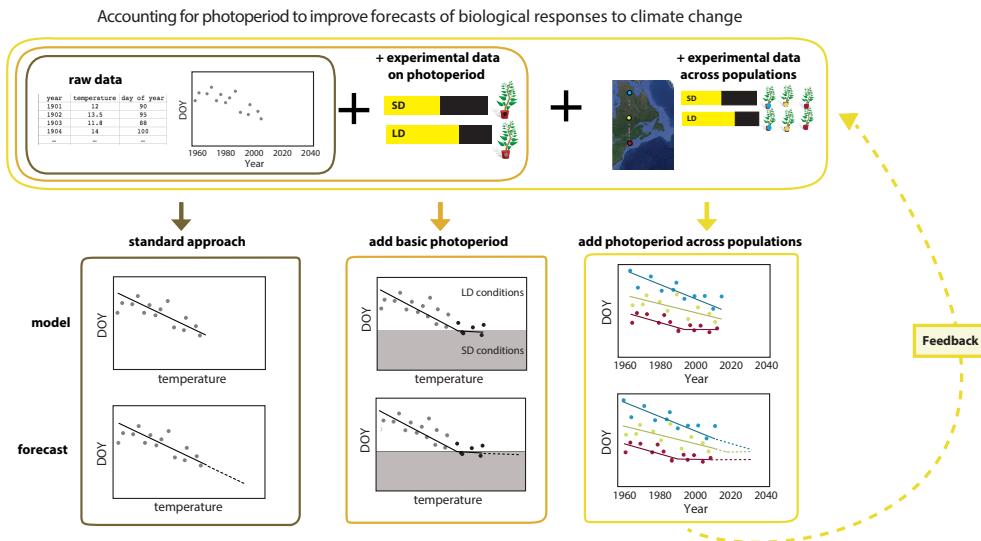


Figure 4: Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change. Current approaches for forecasting spring phenology with climate change frequently rely on linear relationships between historical temperature data and observed dates of spring phenology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

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

251 **plant spring phenology**

252 Photoperiod responses are particularly well-studied in woody plant phenology, making this a useful case study
253 to consider climate change-induced shifts in photoperiod. Spring woody plant phenology in particular has
254 critical implications for global carbon cycling and feedbacks to the climate system (?), and has been at the
255 center of an important and controversial debate on the relative effects of photoperiod versus temperature on
256 phenology (e.g., ???).

257 Experimental growth chamber studies have shown that photoperiod is an important cue for spring budburst
258 phenology in woody plants (e.g., ???). These experiments often manipulate photoperiod in combination
259 with temperature to address basic questions about how these two environmental conditions act as biological
260 cues. Temperature has a dual role in regulating woody plant phenology: chilling—the prolonged exposure to
261 cold temperatures after growth cessation in the fall—is required to initiate budburst; and forcing—prolonged
262 exposure to warm temperatures—is required for budburst to occur. Different photoperiod treatments are
263 typically applied during the forcing treatment phase in growth chamber experiments (e.g., ?????).

264 Woody plant growth chamber studies have been conducted for decades, but have only recently been syn-
265 thesized to show that photoperiod sensitivity is widespread, with large variation across studies and species.
266 These studies have been synthesized in Observed Spring Phenology Responses in Experimental Environments
267 (OSPREE), a new database of plant growth chamber studies that manipulate photoperiod and temperature
268 to measure plant phenological responses, including budburst and flowering (?). The database includes studies
269 that manipulate photoperiod (by applying treatments with different daylength durations, applying long-day
270 versus short-day conditions for different lengths of time, and/or applying varying versus constant photope-
271 riods) and temperature (by imposing different chilling and/or forcing treatments). The OSPREE database
272 spans 201 woody plant species; all experiments in the database use dormant plant tissue (grown in green-
273 houses or taken directly from the field) exposed to experimental conditions (?) for which we could identify
274 forcing, photoperiod, and chilling treatments quantitatively. See Supplemental Methods and ? for details.

275 Growth chamber experiments in OSPREE suggest that the dominant photoperiod response in woody plant
276 species is earlier and more rapid budburst with longer days (e.g., ?). Thirty-one of the 85 studies in

277 the OSPREE database included two or more different photoperiod treatments. Of these, 26 (84%) found
278 significant photoperiod main effects or significant interactive effects with temperature (i.e., photoperiod x
279 temperature effects), across 176 species (Table S1). Main effects included responses such as growth (e.g.,
280 higher growth rates with longer days ?) and reproduction (e.g., increased flowering with longer days ?).

281 Growth chamber experiments highlight that responses to photoperiod vary depending on temperature con-
282 ditions. For example, more rapid advancement of budburst was observed under long versus short days with
283 low chilling, than with high chilling in *Betula payrifera* (? see figure). Similarly, across species, as chilling
284 accumulates from winter to spring, sensitivity to both forcing and photoperiod sensitivity can decrease (?).
285 Frequently, long photoperiods can compensate for low amounts of chilling (???).

286 Woody plant growth chamber experiments also demonstrate that, though photoperiod responses are common,
287 they are variable, as shown in the figure. Responses to photoperiod differ by species (e.g., ??????). For
288 example, with longer chilling treatments some species seem insensitive to daylength (e.g., *Hammamelis* spp.,
289 *Prunus* spp., ?), whereas others seem to be highly sensitive to daylength (e.g. *Fagus* spp., Fig. S1A, even
290 with long chilling treatments (?). In addition, some species demonstrate a response to photoperiod opposite
291 to that typically observed: *Tilia*, for example, showed delayed budburst with longer daylengths (see figure,
292 ?). Photoperiod sensitivity also varies by population and ecotype (e.g., see figure). For example, photoperiod
293 effects on budburst were more significant for lower latitude populations of *Betula pendula* and *B. pubescens*
294 (?).

295 **Box 2. Dominant models of how photoperiod affects spring woody 296 plant phenology**

297 The cues and molecular pathways underlying photoperiod sensitivity are poorly understood for most or-
298 ganisms, even in relatively well-studied phenophases and taxa, such as spring budburst in woody plants (?).
299 Decades of growth chamber experiments suggest three main cues—chilling, forcing, and photoperiod—control
300 spring budburst for woody species (???), with many models suggesting a dominant role of forcing in most
301 natural conditions. Forcing requirements, however, appear to increase given shorter photoperiods or lower

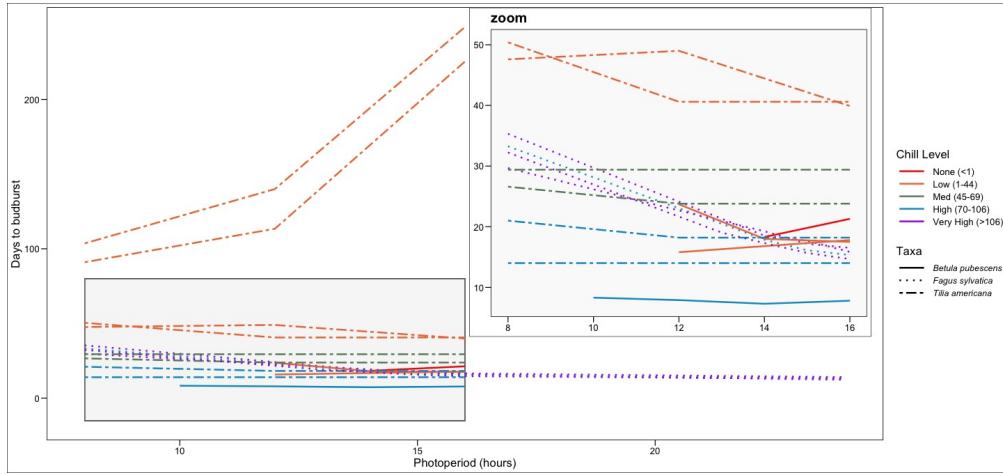


Figure: **Nonlinearities in phenological responses to daylength** are apparent in spring woody plant phenology experiments (from the OSPREE database) in which three or more photoperiod treatment levels were applied. The shape of the response curves for *Betula pubescens* (?), *Fagus sylvatica* (?) and *Tilia americana* (?) 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.

chilling (??). 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, then, there is currently little agreement on the underlying model for how photoperiod affects spring phenology for most species (??). 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 models (??).

Additional cellular and molecular studies may quickly advance understanding and scale up to improved photoperiod models. While our understanding of how plants interpret photoperiod at the molecular-level comes from fewer species, largely from studies of flowering in the model plant *Arabidopsis thaliana* (e.g., ?) and fall budset in woody plant species (e.g., ?), these studies have proved useful across other species. For example, the “external coincidence model” (where plants sense light via blue light receptors and phytochromes, then interpret photoperiod through a coordinated response to light in relation to the time of day, see ?) has been most widely studied in *Arabidopsis*, but appears to be a relevant mechanism for photoperiod responses in diverse perennial and woody plant species (????????). The model proposes the existence of a circadian rhythm of light sensitivity, in which the night-phase is sensitive to light and the day-phase is insensitive to light. As days get longer in the spring, daylight illuminates the light sensitive phase, triggering a response.

318 This provides a clear mechanistic pathway to build into models (?).

319 We expect progress on spring phenology will benefit from similar physiological research that spans the molec-
320 ular to whole-plant levels. To date, little is known about the genetic pathways responsible for the light-sensing
321 apparatuses involved in spring budburst, and how they may vary across species or populations. Some genes
322 have been identified that play a role in coordinating budburst in poplar (*Populus* spp.), and may occur in
323 other woody species as well. Many similarities exist between the proposed regulatory networks of vegetative
324 growth in *Populus* and those controlling floral initiation in *Arabidopsis*, (?). For example, vegetative growth
325 and inhibition of budset are promoted by the FLOWERING LOCUS T2 (FT2) gene, a homolog of *Arabidop-*
326 *sis thaliana* gene FLOWERING LOCUS (FT). FT2 expression appears to be controlled by a pathway that
327 is effective in long days and warm temperatures, marking the onset of the growing season (?). Its loss of
328 expression in autumn, when the days are getting shorter, is associated with the onset of dormancy (?).

329 Efforts to better map the genetic and cellular pathways of spring phenology combined with common garden
330 studies can provide a powerful method to test mechanistic understanding and improve models (e.g., ??). Here
331 we have mainly outlined how to combine growth chamber studies with long-term data to improve models
332 and forecasting; a greater physiological understanding of at least a few species will likely also be necessary
333 for generating robust predictions with climate change.