

# 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 and geographic shifts in species; these shifts affect the daylength  
3 (photoperiod) experienced. As photoperiod is a common trigger of seasonal biological responses (e.g., affecting  
4 plant phenology in 84% of reviewed studies that manipulated photoperiod), shifts in experienced photoperiod  
5 may have important implications for future distributions and fitness. However, photoperiod has not been a  
6 focus of climate change forecasting to date, especially for early-season ('spring') events often assumed to be  
7 driven by temperature. We synthesize published studies to show that impacts on experienced photoperiod  
8 from temporal shifts could be orders of magnitude larger than from spatial shifts (e.g., 1.6 hours of change  
9 for expected temporal versus only one minute for latitudinal shifts). For woody plant phenology, for example,  
10 shifts in experienced photoperiod may increasingly constrain their ability to respond to additional warming.  
11 Incorporating these effects into forecasts is possible by leveraging existing experimental data; for example,  
12 growth chamber experiments on woody plant spring phenology often have data relevant for climate change  
13 impacts. We highlight how combining novel 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.

## <sup>16</sup> Introduction

<sup>17</sup> Photoperiod is a critical cue for the onset of spring in plants and animals, signaling changes in growth,  
<sup>18</sup> migration, and reproduction across diverse species (e.g., Flynn and Wolkovich, 2018; Howe et al., 1996;  
<sup>19</sup> Lagercrantz, 2009; Bradshaw and Holzapfel, 2007; Mcallan et al., 2006; Solbakken et al., 1994; Barker and  
<sup>20</sup> Herman, 1976; FARNER, 1964). Photoperiod is informative for migratory species, because it reflects annual  
<sup>21</sup> cycles across Earth, filtering out noise in local conditions that do not correlate with remote conditions  
<sup>22</sup> of the destination (Winkler et al., 2014). It is also a useful cue for nonmigratory species to synchronize  
<sup>23</sup> activities with seasonal climatic changes (e.g., Singh et al., 2017; Basler and Körner, 2012; Hsu et al., 2011)  
<sup>24</sup> because it is consistent across years, especially compared to other seasonal cues such as temperature and  
<sup>25</sup> precipitation (Saikkonen et al., 2012). For example, relying on a threshold photoperiod (see *Glossary*),  
<sup>26</sup> rather than temperature alone, may prevent woody plants from leafing out during “false spring” events and  
<sup>27</sup> experiencing frost damage (unusually warm periods during winter that are followed by a return of cold  
<sup>28</sup> temperatures, Gu et al., 2008).

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

<sup>42</sup> 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 Here, 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  
99 because latitudinal variation in green-up date, which occurs earlier toward the equator and later toward the  
100 north pole, is strongly driven by climatic differences that affect phenology, and in part because of latitudinal  
101 variation in photoperiod (e.g., at the north pole, the daylength at the summer solstice is 24 hours; see also  
102 Fig. 1). A general pattern of longer photoperiod at green-up toward the poles is consistent across years (Fig.  
103 2b) and green-up does not appear to occur at daylengths less than 10 hours. There is strong spatiotemporal  
104 variation in experienced photoperiod across years (compare the photoperiod at green-up in “early” versus  
105 “late” years, Fig. 2): experienced photoperiod at green-up can vary by two to three hours from one year to  
106 the next in the same location (Fig. 2c). Though green-up date corresponds to plant phenology, we expect that  
107 spatiotemporal patterns of variation in spring phenology would be similar for other organisms (Ovaskainen  
108 et al., 2013; Peñuelas et al., 2002).

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

116 To date, where the scientific literature has addressed shifts in photoperiod with climate change, the focus has  
117 been on how spatial range shifts will affect photoperiod (e.g., Saikkonen et al., 2012; Way and Montgomery,  
118 2015). However, shifting phenology—especially the large changes seen in spring phenology—will also alter  
119 experienced photoperiod, because of the seasonal patterns of daylength (Fig. 1).

120 Despite a focus on range shifts, current data suggest that temporal shifts will yield much larger changes in

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

129 In many cases organisms may shift both their ranges and their phenology simultaneously (i.e., due to new  
130 climatic conditions, Duputié et al., 2015; Grevstad and Coop, 2015). In addition, photoperiod sensitivity  
131 (see *Glossary*) can vary with latitude, likely due to population-level differences in sensitivity (Gauzere et al.,  
132 2017; Saikkonen et al., 2012; Caffarra et al., 2011b; Bradshaw and Holzapfel, 2007; Viherä-Aarnio et al., 2006;  
133 Partanen et al., 2005; Howe et al., 1996). With future climate change, it is unclear how these complexities  
134 will affect the photoperiod experienced by organisms and whether these shifts in photoperiod will have im-  
135 portant implications for biological responses. This lack of clarity stems, in part, from the fact that phenology  
136 both affects and is affected by experienced photoperiod: climate change-induced shifts in phenology alter  
137 experienced photoperiod, which in turn affects phenology.

## 138 **What are the implications of altered photoperiods for biological 139 responses to climate change?**

140 Daylength, often in combination with temperature, can play a role in controlling critical biological functions,  
141 including vegetative growth, cell elongation, budburst, and flowering in plants (Fu et al., 2019; Heide and  
142 Sønsteby, 2012; Heide, 2011; Hsu et al., 2011; Sidaway-Lee et al., 2010; Mimura and Aitken, 2007; Linkosalo  
143 and Lechowicz, 2006; Erwin, 1998; Ashby et al., 1962) and growth rate, maturation, reproduction, migration,  
144 and diapause in animals (Dunn, 2019; Winkler et al., 2014; Zydlewski et al., 2014; Dardente, 2012; Tobin  
145 et al., 2008; Bradshaw and Holzapfel, 2006; Ben-David, 1997; Muir et al., 1994; Saunders and Henderson, 1970;  
146 Dawbin, 1966). Climate change-induced shifts in photoperiod are therefore likely to alter these functions.

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

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

A challenge in understanding the implications of altered photoperiods under climate change, and for forecasting whether and when the trend of earlier phenology with warming may slow or stop abruptly, is the wide range of observed photoperiod sensitivity across species (Flynn and Wolkovich, 2018; Sanz-Perez et al., 2009; Zohner et al., 2016), populations (Tanino et al., 2010), and ecotypes (Howe et al., 1995). How much genotype versus environment explain this variation is an active area of research (e.g., Franks et al., 2014; Gould et al., 2010; Mimura and Aitken, 2010; Fréjaville et al., 2019). Environmental conditions clearly play a role, since different combinations of ambient temperature and photoperiod may explain some of this variation, because temperature cues can override photoperiod requirements under certain conditions (e.g., Tanino et al., 2010).

In such cases, climate change-induced phenological shifts may occur at different rates than past shifts with warming. On the other hand, some of this variation may be due to underlying genetic differences, because photoperiod responses can be under strong genetic control (Bradshaw and Stettler, 1995; Keller et al., 2011; Weih, 2004, , see also Box 1). Teasing out the relative roles of genetics versus environmental conditions will be critical to accurate forecasts of future phenology under climate change.

Species- and population-level variation in photoperiod sensitivity may result in altered communities as climate change progresses. For example, a species or population that is relatively insensitive to photoperiod can take

advantage of warmer springs by having an earlier start to its growing season. Indeed, phenological tracking of temperature (e.g., earlier flowering, leafout, migration with warming) has been linked with higher performance in plants and animals (Cleland et al., 2012; Muir et al., 1994; Willis et al., 2010). Species or populations that are sensitive to temperature but relatively insensitive to photoperiod may therefore outcompete slower-growing or later-emerging ones that are limited by photoperiod and thus cannot take advantage of longer growing season conditions. To identify where, when, and how communities may be altered, quantifying species-specific photoperiod sensitivity and developing methods for incorporating photoperiod into forecasting future phenology are critical.

## **Future directions: outstanding questions and incorporating photoperiod into forecasting**

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

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

201 Körner, 2012; Diez et al., 2012; García-Valdés and Morales-Castilla, 2016; Ibáñez et al., 2010; Van Belle  
202 et al., 2007; Zhu et al., 2012).

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

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

227 Photoperiod is not fully integrated into most current forecasts of biological responses to climate change (but  
228 see Tobin et al., 2008), an omission that could affect the accuracy of forecasts. Forecasts from ecosystem mod-

229   els often incorporate photoperiod, along with other variables such as evaporative demand and temperature  
230   (e.g., the Ecosystem Demography model Jolly et al., 2005; Medvigy et al., 2013), but photoperiod is rarely  
231   included in species distribution models (e.g., Morin and Thuiller, 2009; Zhu et al., 2012). The sensitivity of  
232   model outcomes to assumptions made about experienced photoperiod and threshold responses to photope-  
233   riod needs further study, including understanding how variation in photoperiod responses across ecosystems,  
234   species, populations, and life stages impacts forecasts. We have focused here on spring phenology, but future  
235   work could also address the sensitivity of model outcomes to shifts experienced photoperiod at the end of the  
236   growing season (i.e., autumn phenology).

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

## 249   **Conclusions**

250   Organisms may undergo large changes to the photoperiod they experience with climate change, even if they  
251   do not shift their ranges spatially. Here we have shown that these altered photoperiods may result in stalled  
252   future advances of woody plant phenology with warming (Table S1, Fig. 5), with cascading effects on growth,  
253   fitness, and community composition due to the large variation in photoperiod responses across species and  
254   populations (Fig. 4). Shifts in photoperiod with climate change have implications for a variety of plant and

255 animal responses, given that daylength affects critical activities for diverse species from insects (Bradshaw  
256 and Holzapfel, 2006; Linn et al., 1996) and salmon (Solbakken et al., 1994; Taranger et al., 2003) to birds  
257 (Dawson et al., 2001) and marsupials (McCallan et al., 2006; Solbakken et al., 1994). Given what we know,  
258 incorporating photoperiod into forecasting of climate change responses should improve model accuracy, and  
259 will illuminate additional experiments that could improve our mechanistic understanding of photoperiod as  
260 a critical cue for diverse biological responses.

## 261 **Glossary**

- 262 • budburst: when one or more leaf buds have visible green tips.
- 263 • chilling: the intensity and duration of winter temperature, often a certain sum of chilling that is required  
264 (e.g., some amount of hours or days of cold temperatures, defined by a specific critical temperature or  
265 range of temperatures, such as between 0 and 7.2 °C, Richardson, 1974), that must be experienced for  
266 budburst to occur.
- 267 • daylength: the period of time during a 24-hour period during which an organism receives light.
- 268 • diapause: period of suspended development or growth, usually used to describe invertebrates during  
269 unfavorable environmental conditions such as winter.
- 270 • dormancy: halted or reduced growth or activity, usually used to describe plants.
- 271 • forcing: warm spring temperatures, often a certain sum of forcing that is required (e.g., some amount  
272 of hours or days above a specific temperature) for budburst or flowering can occur.
- 273 • green-up: The beginning of a new cycle of plant growth, usually evaluated at the landscape scale.
- 274 • phenology: the timing of life cycle events in organisms
- 275 • photoperiod: the daily duration of light (daylength) and dark to which an organism is exposed; often  
276 used synonymously with daylength.
- 277 • photoperiod sensitivity: the degree to which phenology is controlled by daylength; may be a nonlinear,  
278 or “threshold”, response in plants (Box S1) and animals (Tobin et al., 2008; Grevstad and Coop, 2015).

- 279 • photoperiodism: the ability to assess the length of day or night to regulate behavior, physiology, growth,  
280 development or reproduction.
- 281 • threshold photoperiod: length of day that causes an organism to switch from a short- to a long-day  
282 response (or vice versa). For example, in European larch (*Larix decidua*), budburst development may  
283 be constrained under short-day conditions, when daylengths are less than a threshold photoperiod of  
284 10-11 hours (Migliavacca et al., 2008). Above this threshold photoperiod, the long-day response of  
285 unconstrained budburst development can occur.

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

288 Photoperiod responses are particularly well-studied in woody plant phenology. Decades of experimental  
289 growth chamber studies have shown that photoperiod is an important cue for spring budburst phenology  
290 in woody plants (e.g., Flynn and Wolkovich, 2018; Basler and Körner, 2014; Heide, 1993b). These experi-  
291 ments often manipulate photoperiod in combination with temperature to address basic questions about how  
292 these two environmental conditions act as biological cues. Temperature has a dual role in regulating woody  
293 plant phenology: chilling—the prolonged exposure to cold temperatures after growth cessation in the fall—is  
294 required to initiate budburst; and forcing—prolonged exposure to warm temperatures—is required for bud-  
295 burst to occur. Thus, chilling and forcing treatments are often altered in addition to photoperiod in growth  
296 chamber experiments (e.g., Campbell and Sugano, 1975; Falusi and Calamassi, 1990; Heide, 1977; Laube  
297 et al., 2014; Spann et al., 2004).

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

<sup>305</sup> Main effects included responses such as growth (e.g., higher growth rates with longer days Ashby et al., 1962)  
<sup>306</sup> and reproduction (e.g., increased flowering with longer days Heide and Sønsteby, 2012).

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

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

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584 **Figures**

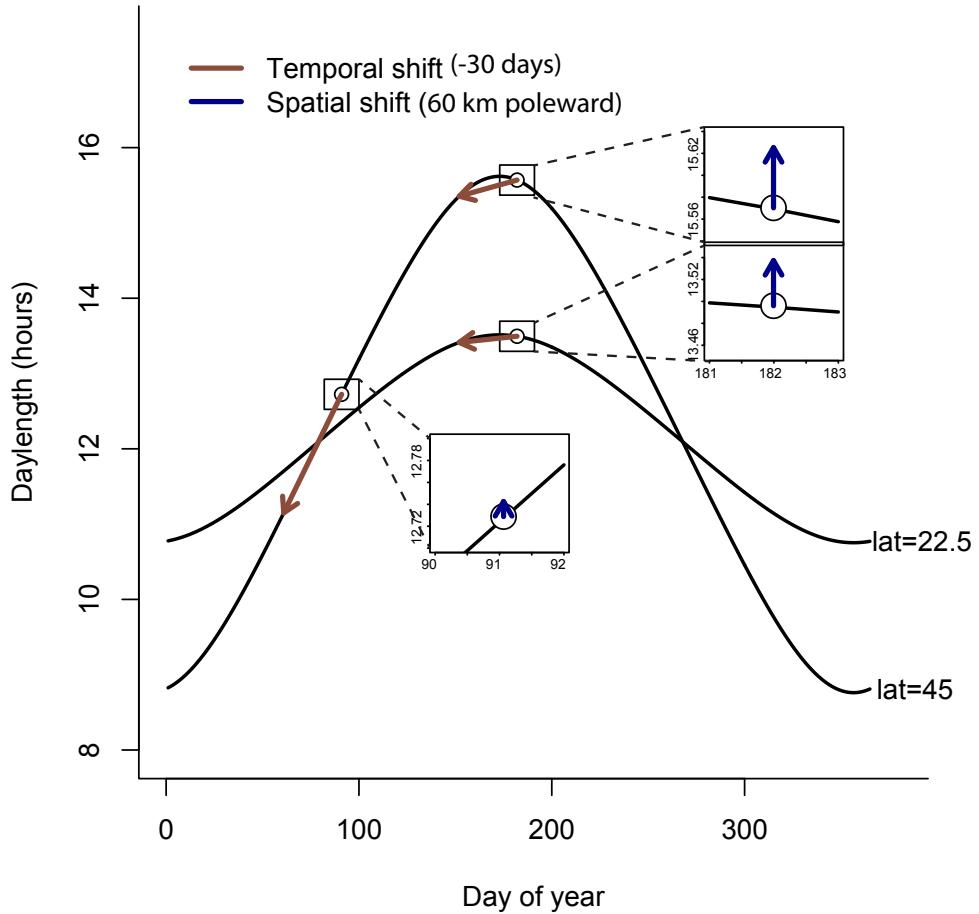
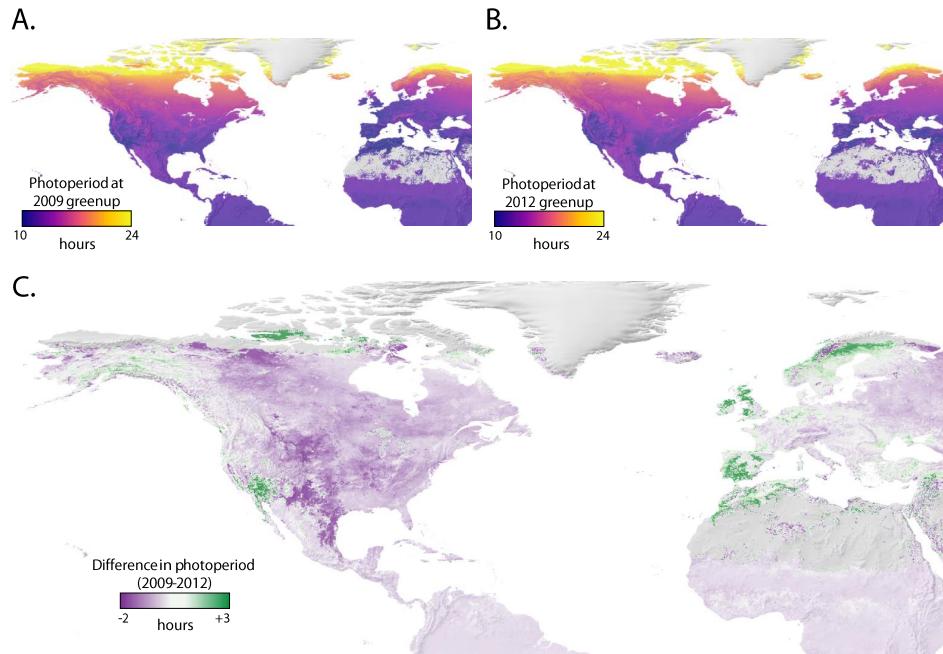
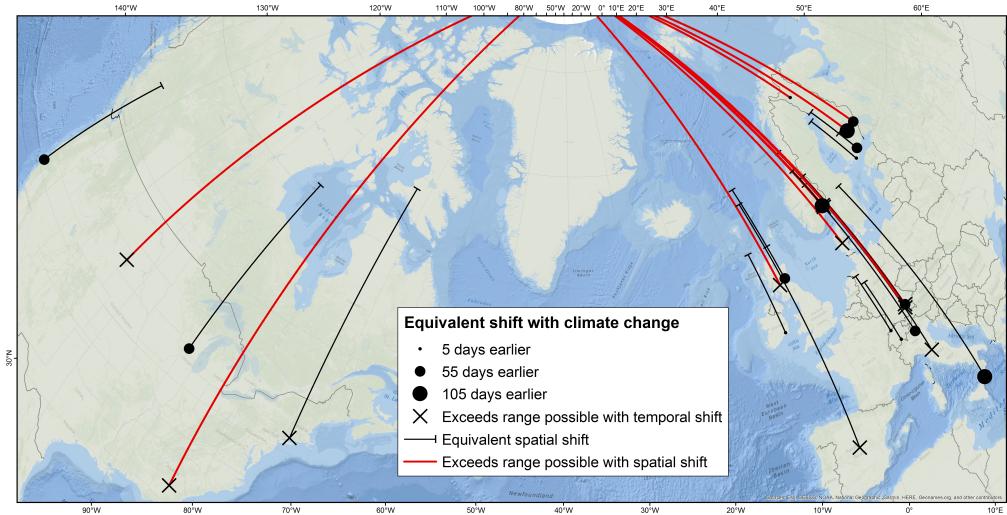


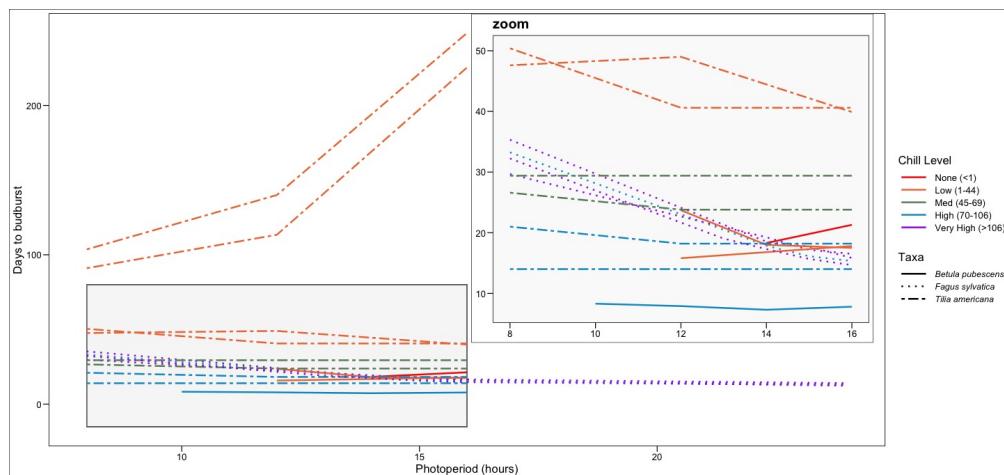
Figure 1: **Temporal shifts in activity yield larger changes in experienced photoperiod compared to spatial (latitudinal) shifts** on the same day of year, due to patterns in photoperiod variation with latitude and by day of year. Here, we show this variation at two latitudes ( $22.5^\circ$ ,  $45^\circ$ ), 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).



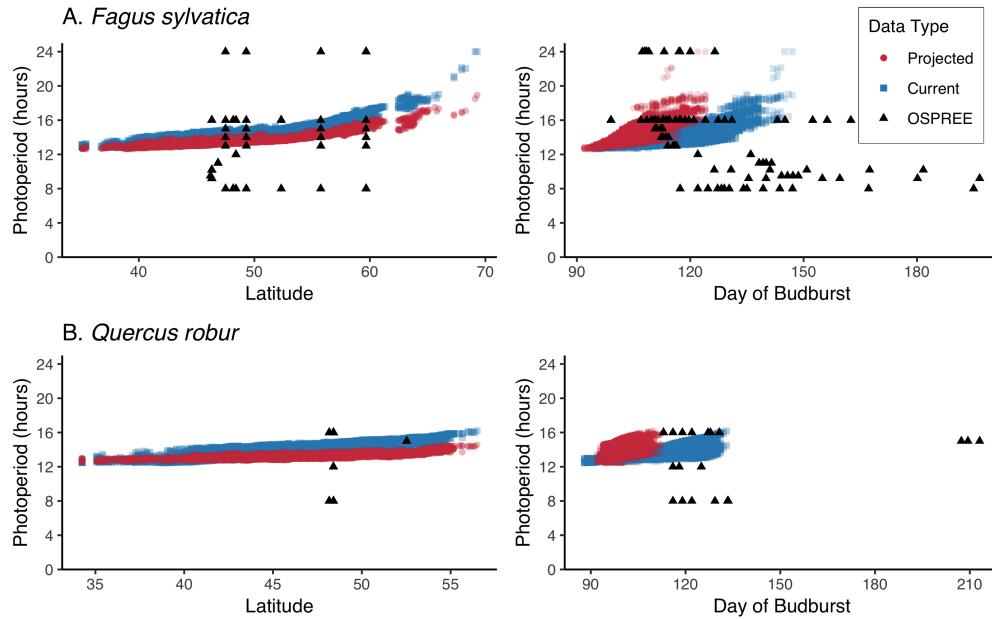
**Figure 2: Photoperiod on the “green-up” date varies over space and between years** “Green-up” date is the beginning of seasonal greening, identified by satellite remote sensing measurements taken regularly throughout the year of the concentrations of green leaf vegetation. Hours of daylight on the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

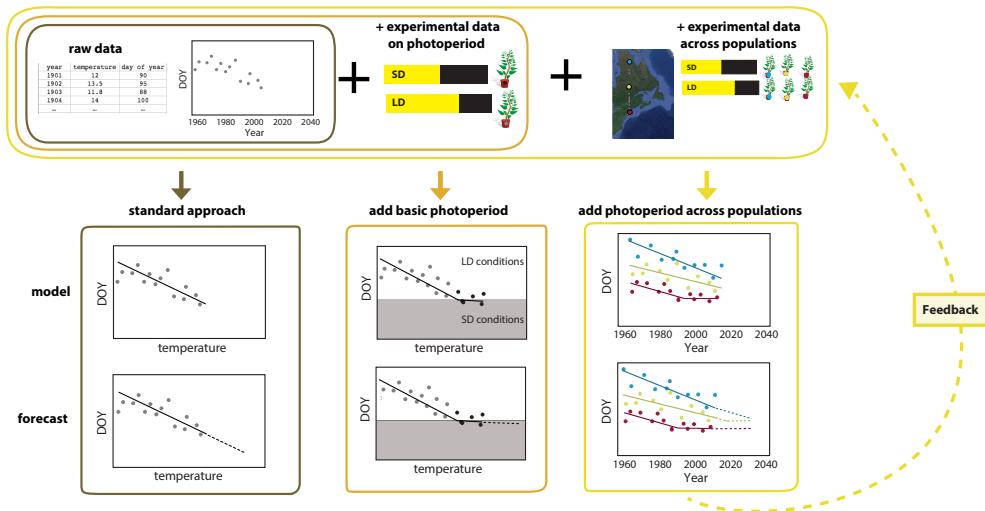


Figure 6: **Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change.** Current approaches for forecasting spring phenology with climate change frequently rely on linear relationships between historical temperature data and observed dates of spring phenology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