

# Spatial and temporal shifts in photoperiod with climate change

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## **1 Abstract**

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

## <sup>16</sup> Introduction

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

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

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

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

43 2015).

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

47 The exclusion of photoperiod may be problematic: although photoperiod itself is stable over time, the  
48 photoperiod that species *experience* at critical developmental stages (henceforth, ‘experienced photoperiod’),  
49 as they undergo climate change-induced shifts in space and time, is likely to be much less stable (Fig. 1).  
50 This shift in experienced photoperiod extends to distributional shifts due to climate change, as many species’  
51 distributions have moved poleward and upward in elevation (i.e., range shifts, Chen et al., 2011; Harsch et al.,  
52 2009; Parmesan, 2006; Peñuelas and Boada, 2003).

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

58 Here, we ask:

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

64 We focus on spring events, as phenology during this time is one of the most widely observed and rapidly  
65 changing biological responses to climate change (Parmesan, 2006). In addition, the role of photoperiod is  
66 less understood in spring phenology compared with autumn phenophases (reviewed in, e.g., Azeez and Sane,  
67 2015; Gallinat et al., 2015; Lagercrantz, 2009; Allona et al., 2008), but recent studies showing declines in  
68 responses of spring budburst to warming (e.g., Fu et al., 2019; Güsewell et al., 2017; Yu et al., 2010) suggest

69 that photoperiod constraints may be imminent. While our questions are broadly relevant for diverse species,  
70 we use a case study of spring woody plant phenology to illustrate several of our points (Boxes 1-2).

## 71 **How will climate change alter the photoperiod experienced by or- 72 ganisms?**

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

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

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

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

<sup>94</sup> (Fig. 1). Elevational shifts, in contrast, cause minimal change to the range of daylength throughout the year.

<sup>95</sup> To date, most focus on shifts in photoperiod with climate change has been centered on how spatial range  
<sup>96</sup> shifts will affect photoperiod (e.g., Saikkonen et al., 2012; Way and Montgomery, 2015). However, shifting  
<sup>97</sup> phenology—especially the large changes seen in spring phenology—will also alter experienced photoperiod,  
<sup>98</sup> because of the seasonal patterns of daylength (Fig. 1).

<sup>99</sup> Current data suggest that temporal shifts will yield much larger changes in experienced photoperiod than  
<sup>100</sup> latitudinal shifts (Fig. 1). Consider a tree species that bursts its buds at latitude 45°, on average around  
<sup>101</sup> day of year 91 (April 2), when daylength is 12.8 hours. If the species' phenology shifts 30 days earlier over  
<sup>102</sup> the next century (i.e., a rate of 3 days per decade, as has been observed, Parmesan and Yohe, 2003), it will  
<sup>103</sup> experience a daylength that is 1.6 hours shorter. This 1.6 hour decrease in daylength is equivalent to moving  
<sup>104</sup> up 28.5° in latitude on this day of year. However, if the same species shifts its range up in latitude 0.5° (i.e.,  
<sup>105</sup> 60 km over the next century, comparable to observed rates, Chen et al., 2011; Parmesan and Yohe, 2003), it  
<sup>106</sup> will experience a daylength that differs by less than a minute on the same day of year.

## <sup>107</sup> **What are the implications of altered photoperiods for biological <sup>108</sup> responses to climate change?**

<sup>109</sup> Climate change alters the experienced photoperiod, but the implications of this change for plants is currently  
<sup>110</sup> unclear, in part, because phenology both affects and is affected by experienced photoperiod: climate change-  
<sup>111</sup> induced shifts in phenology alter experienced photoperiod, which in turn affects phenology. Daylength,  
<sup>112</sup> often in combination with temperature, can play a role in controlling critical biological functions, including  
<sup>113</sup> vegetative growth, cell elongation, budburst, and flowering in plants (Fu et al., 2019; Heide and Sønsteby,  
<sup>114</sup> 2012; Heide, 2011; Hsu et al., 2011; Sidaway-Lee et al., 2010; Mimura and Aitken, 2007; Linkosalo and  
<sup>115</sup> Lechowicz, 2006; Erwin, 1998; Ashby et al., 1962) Climate change-induced shifts in photoperiod are therefore  
<sup>116</sup> likely to alter these functions.

<sup>117</sup> Growth chamber studies show that the magnitude of daylength shifts expected with climate change (i.e., 1-2  
<sup>118</sup> hours of difference in daylength with temporal shifts over the next century) are substantial enough to affect

<sup>119</sup> spring phenology in trees (Table S1). The direction and magnitude of responses will vary, however, because  
<sup>120</sup> of variation in photoperiod sensitivity, and because photoperiod often interacts with other environmental  
<sup>121</sup> drivers, such as temperature, to affect phenology (Box 1).

<sup>122</sup> The climate change-induced trend toward ever-earlier springs means that experienced photoperiod may in-  
<sup>123</sup> creasingly approach threshold photoperiods (see *Glossary*) for many species, constraining their ability to  
<sup>124</sup> respond to additional warming (Fu et al., 2019; Vitasse and Basler, 2013; Körner and Basler, 2010a; Morin  
<sup>125</sup> et al., 2010; Nienstaedt, 1966). Interactions between photoperiod and temperature may therefore result in  
<sup>126</sup> muted phenological shifts, compared to what would be expected based on temperature change alone (Körner  
<sup>127</sup> and Basler, 2010a; Mimura and Aitken, 2007; Wareing, 1956). This has been a topic of much interest in  
<sup>128</sup> the climate change literature because it predicts that as photoperiod becomes limiting, the average trend of  
<sup>129</sup> earlier phenology with warming (Polgar et al., 2013; Peñuelas et al., 2002; Menzel, 2000) may stop.

<sup>130</sup> A challenge in predicting if or when the trend of earlier phenology with warming may slow or stop abruptly  
<sup>131</sup> is the wide range of observed photoperiod sensitivity (see *Glossary*) across species (Flynn and Wolkovich,  
<sup>132</sup> 2018; Zohner et al., 2016; Sanz-Perez et al., 2009), populations (Gauzere et al., 2017; Saikkonen et al., 2012;  
<sup>133</sup> Caffarra et al., 2011b; Bradshaw and Holzapfel, 2007; Viherä-Aarnio et al., 2006; Partanen et al., 2005), and  
<sup>134</sup> ecotypes (Howe et al., 1995). How much genotype versus environment explain this variation is an active  
<sup>135</sup> area of research (e.g., Fréjaville et al., 2019; Franks et al., 2014; Gould et al., 2010; Mimura and Aitken,  
<sup>136</sup> 2010). Environmental conditions clearly play a role, since different combinations of ambient temperature  
<sup>137</sup> and photoperiod may explain some of this variation and because temperature cues can override photoperiod  
<sup>138</sup> requirements under certain conditions (e.g., Tanino et al., 2010). In such cases, climate change-induced  
<sup>139</sup> phenological shifts may occur at different rates than past shifts with warming. On the other hand, some of  
<sup>140</sup> this variation may be due to underlying genetic differences driven by local adaptation, because photoperiod  
<sup>141</sup> responses can be under strong genetic control (Bradshaw and Stettler, 1995; Keller et al., 2011; Weih, 2004,  
<sup>142</sup> see also Boxes 1, 2). Teasing out the relative roles of genetics versus environmental conditions will be critical  
<sup>143</sup> to accurate forecasts of future phenology under climate change.

<sup>144</sup> Species- and population-level variation in photoperiod sensitivity may scale up to altered communities as  
<sup>145</sup> climate change progresses. For example, a species or population that is relatively insensitive to photoperiod  
<sup>146</sup> can take advantage of warmer springs by having an earlier start to its growing season. Indeed, phenological

<sup>147</sup> tracking of temperature (e.g., earlier flowering, leafout, migration with warming) has been linked with higher  
<sup>148</sup> performance in plants and animals (Cleland et al., 2012; Muir et al., 1994; Willis et al., 2010). Species  
<sup>149</sup> or populations that are sensitive to temperature but relatively insensitive to photoperiod may therefore  
<sup>150</sup> outcompete slower-growing or later-emerging ones that are limited by photoperiod and thus cannot take  
<sup>151</sup> advantage of longer growing season conditions. Not all studies, however, find links between performance  
<sup>152</sup> and high sensitivity to temperature (e.g., Block et al., 2020), and early-season species in most temperature  
<sup>153</sup> zones risk losing tissue to frost (Sakai and Larcher, 1987). Thus, the advantages of tracking warming  
<sup>154</sup> may depend on how quickly mean temperatures versus last frost dates shift (e.g., Inouye et al., 2002), such  
<sup>155</sup> that in some systems photoperiod cues could prevent species from starting growth or reproduction too early  
<sup>156</sup> (when they risk losing their investments in new tissue). To identify where, when, and how communities  
<sup>157</sup> may be altered therefore requires quantifying species-specific temperature and photoperiod sensitivities, and  
<sup>158</sup> developing methods that incorporate both photoperiod and environmental events that impact fitness (such  
<sup>159</sup> as frosts).

## <sup>160</sup> Future directions: outstanding questions and incorporating pho- <sup>161</sup> toperiod into forecasting

<sup>162</sup> The complexity of photoperiod effects on phenology and how warming alters experienced photoperiod high-  
<sup>163</sup> light that future rates of phenological shifts are unlikely to be straightforward extrapolations from past  
<sup>164</sup> and current rates. Statistical models and process-based models—the two broad categories of forecasting  
<sup>165</sup> approaches—both acknowledge this difficulty, but differ importantly in how they relate phenology to climate  
<sup>166</sup> change. Statistical models relating phenology to climate change often assume linear relationships between  
<sup>167</sup> species' responses and environmental variables (e.g., Flynn and Wolkovich, 2018; Ibáñez et al., 2010), whereas  
<sup>168</sup> process-based models often incorporate nonlinear threshold relationships (e.g. Chuine and Beaubien, 2001;  
<sup>169</sup> Morin and Thuiller, 2009). Further, statistical models of phenology under climate change frequently ignore  
<sup>170</sup> photoperiod, focusing instead on seasonal or annual temperature (e.g. Diez et al., 2012; Ibáñez et al., 2010,  
<sup>171</sup> but see Richardson et al. (2013)), whereas process-based models of phenology more frequently incorporate  
<sup>172</sup> photoperiod, along with temperature (Lundell et al., 2020; Duputié et al., 2015; Zhao et al., 2013; Morin

173 and Thuiller, 2009). Process-based models may thus seem superior for integrating photoperiod, but they  
174 can be challenging to develop, requiring detailed data that are often not readily available (e.g., daily climate  
175 data, nonlinear biological responses to fine-scale changes in temperature). Perhaps because of this, statistical  
176 models remain more commonly used in climate change forecasts of biological responses (e.g., García-Valdés  
177 and Morales-Castilla, 2016; Basler and Körner, 2012; Diez et al., 2012; Zhu et al., 2012; Ibáñez et al., 2010).

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

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

201 these studies can be useful for understanding mechanistically how photoperiod responses work, extrapolating  
202 them to climate change models may not be reasonable.

203 Photoperiod is not fully integrated into most current forecasts of biological responses to climate change (but  
204 see Tobin et al., 2008, for an example in insects); this omission could affect forecast accuracy. Photoperiod  
205 is incorporated into some ecosystem models (e.g., the Ecosystem Demography model Jolly et al., 2005;  
206 Medvigy et al., 2013) used for forecasting, but not other (e.g., Richardson et al., 2012), and photoperiod  
207 is rarely included in species distribution models (e.g., Morin and Thuiller, 2009; Zhu et al., 2012). The  
208 sensitivity of model outcomes to assumptions made about experienced photoperiod and threshold responses  
209 to photoperiod needs further study, including understanding how variation in photoperiod responses across  
210 ecosystems, species, populations, and life stages impacts forecasts.

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

## 223 Conclusions

224 Organisms may undergo large changes to the photoperiod they experience with climate change, even if they  
225 do not shift their ranges spatially. Here we have shown that these altered photoperiods may result in stalled  
226 future advances of spring phenology with warming (e.g., Table S1, Fig. S1, Fu et al., 2019; Güsewell et al.,

<sup>227</sup> 2017; Yu et al., 2010), with cascading effects on growth, fitness, and community composition due to the large  
<sup>228</sup> variation in photoperiod responses across species and populations (Box 1). We have focused on woody plant  
<sup>229</sup> spring phenology, but shifts in photoperiod with climate change have implications for a variety of plant and  
<sup>230</sup> animal responses, given that daylength affects critical activities for diverse species from insects (Bradshaw and  
<sup>231</sup> Holzapfel, 2006) and salmon (Taranger et al., 2003) to birds (Dawson et al., 2001) and marsupials (McAllan  
<sup>232</sup> et al., 2006). Given what we know, incorporating photoperiod into forecasting of climate change responses  
<sup>233</sup> should improve model accuracy (Fig. 6), and will illuminate additional experiments that could improve our  
<sup>234</sup> mechanistic understanding of photoperiod as a critical cue for diverse biological responses.

## <sup>235</sup> Glossary

- <sup>236</sup> • budburst: when one or more leaf buds have visible green tips.
- <sup>237</sup> • chilling: the intensity and duration of winter temperature, often a certain sum of chilling that is required  
<sup>238</sup> (e.g., some amount of hours or days of cold temperatures, defined by a specific critical temperature or  
<sup>239</sup> range of temperatures, such as between 0 and 7.2 °C, Richardson, 1974), that must be experienced for  
<sup>240</sup> budburst to occur.
- <sup>241</sup> • daylength: the period of time during a 24-hour period during which an organism receives light.
- <sup>242</sup> • dormancy: halted or reduced growth or activity.
- <sup>243</sup> • forcing: warm spring temperatures, often a certain sum of forcing that is required (e.g., some amount  
<sup>244</sup> of hours or days above a specific temperature) for budburst or flowering can occur.
- <sup>245</sup> • green-up: The beginning of a new cycle of plant growth, usually evaluated at the landscape scale.
- <sup>246</sup> • phenology: the timing of life cycle events in organisms
- <sup>247</sup> • photoperiod: the daily duration of light (daylength) and dark to which an organism is exposed; often  
<sup>248</sup> used synonymously with daylength.
- <sup>249</sup> • photoperiod sensitivity: the degree to which phenology is controlled by daylength; may be a nonlinear,  
<sup>250</sup> or “threshold”, response in plants (Box 2).

- 251 • photoperiodism: the ability to assess the length of day or night to regulate behavior, physiology, growth,  
252 development or reproduction.
- 253 • threshold photoperiod: length of day that causes an organism to switch from a short- to a long-day  
254 response (or vice versa). For example, in European larch (*Larix decidua*), budburst development may  
255 be constrained under short-day conditions, when daylengths are less than a threshold photoperiod of  
256 10-11 hours (Migliavacca et al., 2008). Above this threshold photoperiod, the long-day response of  
257 unconstrained budburst development can occur.

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<sup>539</sup> **Figures**

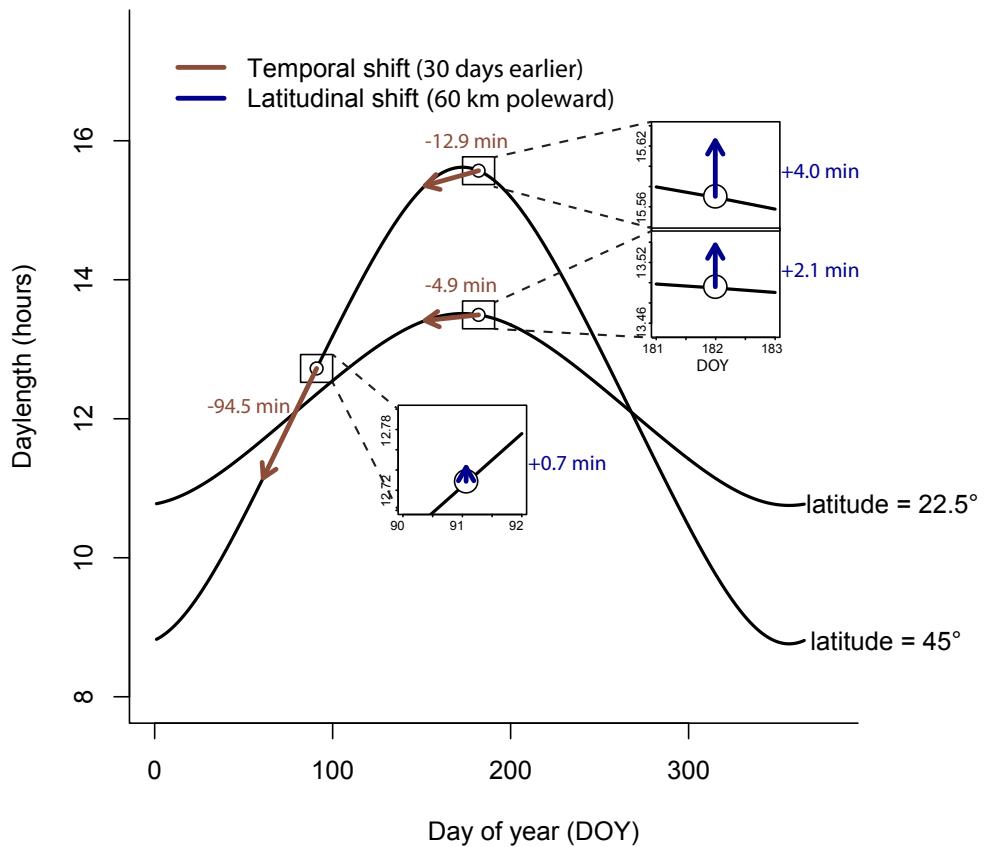
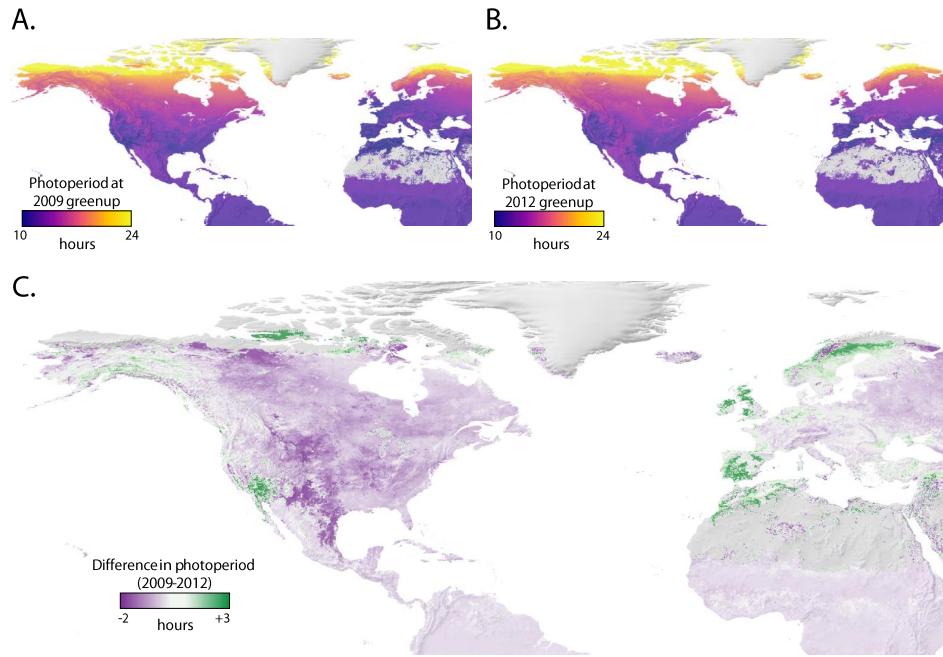


Figure 1: **Temporal (i.e., phenological) shifts in activity yield larger changes in experienced photoperiod compared to spatial (i.e., latitudinal) shifts** on the same day of year, due to patterns in photoperiod variation with latitude and by day of year. Here, we show this variation at two latitudes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

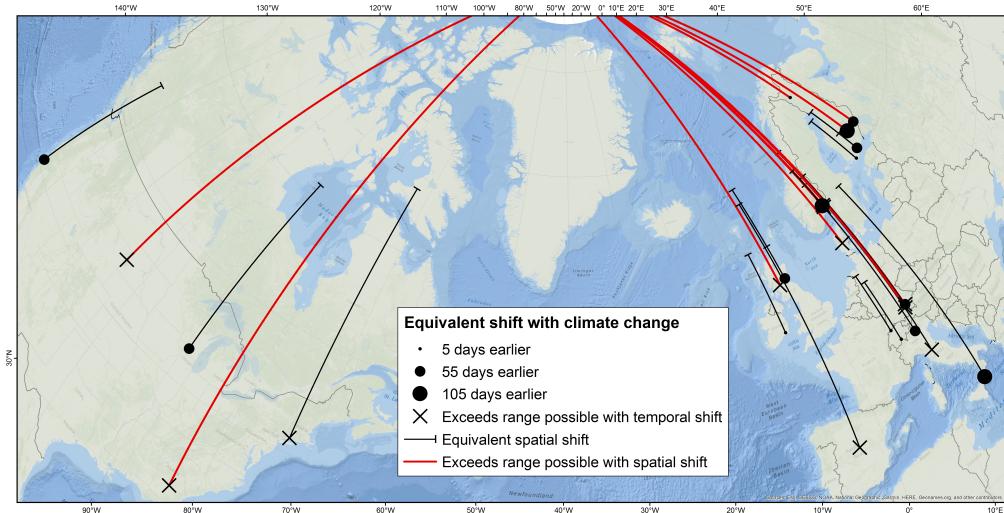


Figure 3: **Experimental photoperiod treatments and their equivalent spatial and temporal shifts** for experiments in the OSPREE database that manipulated photoperiod (see Box 1). See ‘Mapping temporal and spatial shifts in space and time’ in the Supplemental Materials for details on how we calculated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

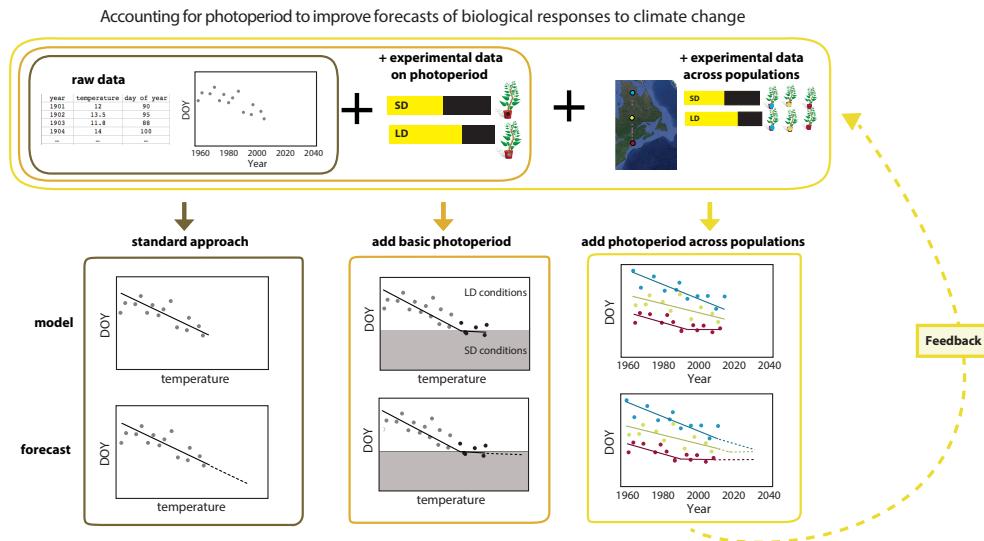


Figure 4: **Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change.** Current approaches for forecasting spring phenology with climate change frequently rely on linear relationships between historical temperature data and observed dates of spring phenology (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).

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

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

547 Experimental growth chamber studies have shown that photoperiod is an important cue for spring budburst  
548 phenology in woody plants (e.g., Flynn and Wolkovich, 2018; Basler and Körner, 2014; Heide, 1993*b*). These  
549 experiments often manipulate photoperiod in combination with temperature to address basic questions about  
550 how these two environmental conditions act as biological cues. Temperature has a dual role in regulating  
551 woody plant phenology: chilling—the prolonged exposure to cold temperatures after growth cessation in the  
552 fall—is required to initiate budburst; and forcing—prolonged exposure to warm temperatures—is required  
553 for budburst to occur. Different photoperiod treatments are typically applied during the forcing treatment  
554 phase in growth chamber experiments (e.g., Laube et al., 2014; Spann et al., 2004; Falusi and Calamassi,  
555 1990; Heide, 1977; Campbell and Sugano, 1975).

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

567 Supplemental Methods and Wolkovich et al. (2019) for details.

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

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

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

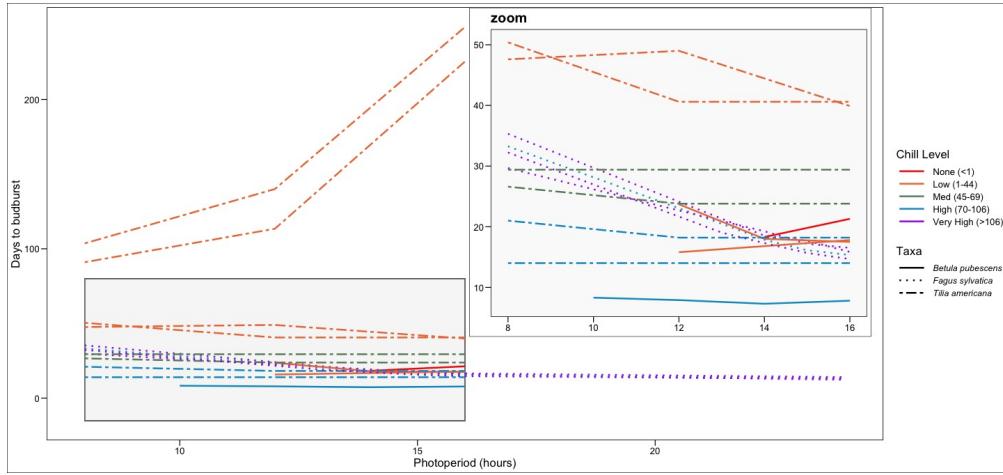


Figure: **Nonlinearities in phenological responses to daylength** are apparent in spring woody plant phenology experiments (from the OSPREE database) in which three or more photoperiod treatment levels were applied. The shape of the response curves for *Betula pubescens* (Caffarra et al., 2011b), *Fagus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

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

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

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

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

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

<sup>634</sup> few species will likely also be necessary for generating robust predictions with climate change.