

# Spatial and temporal shifts in photoperiod with climate change

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## Summary

Recent warming temperatures have brought about temporal shifts in biological activity, such as spring budburst and fall senescence, as well as spatial shifts in species' distributions. These temporal and spatial shifts are expected to continue with future warming, and will alter the photoperiod experienced by diverse species. To date, photoperiod has not been a focus of climate change forecasting, despite the fact that photoperiod responses are common (observed in 26/31 or 84% of studies that manipulated photoperiod in woody plant species). We argue that temporal shifts are expected to have a major impact on experienced photoperiod, so additional testing of the importance of photoperiod to phenology and adding it to forecasts of biological shifts should be a major goal. We also find that current experiments often go well beyond the expected spatial and temporal shifts of climate change. However, there are studies with treatments that seem to overlap with potential shifts and therefore appear relevant for forecasting biological impacts of climate change. We highlight outstanding questions that are in need of study and possible modelling approaches to improve predictions of when, where, and how much photoperiod is likely to affect future phenology.

## Introduction

Photoperiod is a critical cue for woody plants, signalling changes to their activities, such as photosynthesis, growth, reproduction, dormancy, and senescence (e.g., Howe et al., 1996; Lagercrantz, 2009). Photoperiod is used by plants to synchronize their activities with seasonal climatic changes (e.g., Hsu et al., 2011; Singh et al., 2017; Basler and Körner, 2012) because it is consistent across years, especially compared to other seasonal cues such as temperature and precipitation (Saikkonen et al., 2012). For example, relying on photoperiod, rather than temperature alone, may prevent plants from leafing out during "false spring" events (unusually warm periods during winter that are followed by a return of cold temperatures).

We know that photoperiod is an important cue for woody plant phenology, largely through growth chamber experiments. These experiments often manipulate photoperiod in combination with temperature to address basic questions about how these environmental drivers act as biological cues. Air temperature has a dual role in regulating phenology: chilling, the prolonged exposure to cold temperatures, after growth cessation in the fall, that is required to break dormancy within the bud; and forcing, prolonged exposure to warm temperatures that are required for bud burst or flowering to occur. Chilling and forcing temperatures are therefore often altered in addition to photoperiod in growth chamber experiments (e.g., Campbell and Sugano, 1975; HEIDE, 1977; Falusi and Calamassi, 1990; Spann et al., 2004; Laube et al., 2014). Growth chamber studies have been conducted for decades, revealing wide variation sensitivity to photoperiod, chilling, and forcing across populations and species, but have only recently been synthesized (cite our paper).

Despite the fact that photoperiod is known to be an important cue for plant activity, it is often not included in forecasts of biological responses to climate change (but see Despujols et al.), which generally focus on

temperature. The exclusion of photoperiod may be problematic because, although photoperiod itself is stable over time, the photoperiod that species *experience*, as they undergo climate change-induced shifts in space and time, is likely to be much less stable. With recent warming, many species have shifted their distributions poleward and upward in elevation (i.e., range shifts Parmesan, 2006; Chen et al., 2011; Harsch et al., 2009))), and/or shifted their activity earlier in the year (i.e., phenological shifts Parmesan, 2006; Wolkovich et al., 2012). These spatial and temporal shifts will alter the photoperiod regime experienced by organisms.

Here, we ask:

1. Do results from growth chamber experiments suggest that photoperiod responses are common in woody plants?
2. How will climate change alter the photoperiod experienced by organisms, given observed climate change-induced biological shifts, both spatially and temporally?
3. What are the implications of altered photoperiods for biological responses to climate change?
4. Can data from growth chamber experiments altering photoperiod be applied to forecasting biological implications of climate change (i.e., do they occur at the appropriate scale)?

We address these questions using a new database of plant growth chamber studies that manipulate photoperiod and temperature and measure plant responses, including budburst, flowering, and growth.

## Are photoperiod responses common in woody plants?

Growth chamber experiments suggest that photoperiod responses are common in woody plant species. Thirty-one of the 85 studies in the OSPREE database included two or more different photoperiod treatments. Of these, 26 (84%) found significant photoperiod main effects or significant interactive effects with temperature (Table 1). Main effects included responses such as growth (e.g., higher growth rates with longer days Ashby et al., 1962), onset of dormancy (e.g., more rapid induction of budset with shorter days Howe et al., 1995), and reproduction (e.g., increased flowering with longer days Heide and Sønsteby, 2012).

Growth chamber experiments highlight that responses to photoperiod are nonlinear in many cases (Figure 1). In addition, photosensitivity frequently involves interactions with temperature. For example, more rapid advancement of budburst was observed under long versus short days with low chilling, than with high chilling (Hawkins and Dhar, 2012).

Growth chamber experiments demonstrate that, though photoperiod responses are common, they are variable (Figure 1). Responses to photoperiod, either alone or interactively with temperature, commonly differ by species and population or ecotype (e.g., Howe et al., 1996; Basler and Körner, 2012, 2014; Zohner et al., 2016; Flynn and Wolkovich, 2018). Should we go into more detail- call out some specific examples here?

## How will climate change alter the photoperiod experienced by organisms?

Species experience different photoperiod regimes depending on their location in space and the seasonal timing of their activity. Spring green-up date, for example, varies with latitude, occurring earlier toward the equator and later toward the poles (Figure 2a). Although this general pattern is consistent across years (Figure 2b), there is spatiotemporal variation. A year that results in early green-up at 35°, for instance, may not be an early year at 50°latitude (Figure 2c).

Against this existing background variation, climate change is likely to cause average shifts in experienced photoperiod, as species respond to warming temperatures. Spatial shifts in species' ranges and temporal shifts in phenology will alter the photoperiods experienced by organisms with future climate change. The magnitude of these alterations will vary depending on the organism's location and the type of shift(s) it undergoes. For example, poleward shifts in species' ranges cause organisms to experience a wider range of daylength throughout the year (Figure 3). Elevational shifts, on the other hand, would cause minimal changes in daylength throughout the year.

To date, most of the scientific literature has focused on how spatial range shifts with climate change will affect photoperiod (Saikkonen et al., 2012) (other citations?). Shifting phenology will also alter experienced photoperiod, because of the seasonal patterns of daylength (Figure 3). We wanted to understand the magnitude of change in experienced photoperiod with spatial versus temporal shifts in organisms activity. To do this, we compared photoperiods across latitudes and days that differed at relevant scales, given observed shifts in species' ranges and phenology (Parmesan and Yohe, 2003; Chen et al., 2011). We found that temporal shifts are actually likely to yield bigger changes in experienced photoperiod than spatial shifts (Figure 3). For example, consider a tree at latitude 45° that completes spring budbursts, on average, around DOY 91 (April 2, when daylength is 12.78 hours). If its phenology shifts 30 days earlier over the next century (Parmesan and Yohe, 2003, i.e., a rate of 3 days per decade, as has been observed), it will experience a daylength that is 1.57 hours shorter. However, if the same tree species shifts its range up in latitude 0.5 degrees (i.e., 60 km over the next century, comparable to observed rates(Parmesan and Yohe, 2003; Chen et al., 2011)), it will experience a daylength that differs by less than a minute on the same DOY.

In many cases organisms may shift both their geographic ranges and their phenology simultaneously. In addition, photoperiod sensitivity, or the degree to which phenology is controlled by daylength, can vary with latitude (Howe et al., 1996; Saikkonen et al., 2012; Partanen et al., 2005; Viherä-Aarnio et al., 2006; Caffarra et al., 2011; Gauzere et al., 2017), perhaps because of population-level differences in sensitivity. It is unclear how all of these complications will interact to affect the photoperiod experienced by organisms, with future climate change, and potential shifts in photoperiod may have important implications for biological responses to climate change.

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

Daylength plays a role in controlling critical plant functions, including vegetative growth, cell elongation, budburst, and flowering (Linkosalo and Lechowicz, 2006; Erwin, 1998; Sidaway-Lee et al., 2010; Hsu et al., 2011; Heide, 2011; Ashby et al., 1962; Heide and Sønsteby, 2012; Mimura and Aitken, 2007). Climate change-induced shifts in photoperiod are therefore likely to alter these functions. The direction and magnitude of such alterations will vary, however, because of variation in photoperiod sensitivity, and because photoperiod often interacts with other environmental drivers, such as temperature, to affect phenology.

Plants interpret photoperiod through a coordinated response to light in relation to the time of day. The "external coincidence model," which has been widely studied in *Arabidopsis*, is thought to be a relevant mechanism for photoperiod responses in diverse perennial and woody plant species as well (Davis, 2002; Petterle et al., 2013; Bastow and Dean, 2002; Kobayashi and Weigel, 2007; Andrés and Coupland, 2012; Singh et al., 2017). (add Bunning 1936). 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 spring, daylight illuminates the photosensitive phase, triggering a response.

Phenology is generally controlled by photoperiod and temperature. For example, the timing of spring budburst in woody plants is controlled by interactions between chilling, forcing, and daylength (Flynn and Wolkovich, 2018; Heide, 2008; Zohner et al., 2016). Over the past century, budburst has shifted earlier in

diverse woody species (CITES), a pattern that, to date, can be largely explained by warming temperatures. Photoperiod may eventually become a limiting factor, however, constraining the ability of species to respond to additional warming (Koerner and Basler, 2010; Vitasse and Basler, 2013; Morin et al., 2010; Nienstaedt, 1966). Interactions between photoperiod and temperature could therefore result in muted phenological shifts, compared to what would be expected based on temperature change alone (Wareing, 1956; Mimura and Aitken, 2007; Koerner and Basler, 2010).

A challenge in understanding biological responses to shifts in photoperiod is the wide range of sensitivity, observed across species (Sanz-Perez et al., 2009; Zohner et al., 2016; Flynn and Wolkovich, 2018), ecotypes (Howe et al., 1995), and populations (Tanino et al., 2010). Some of this variation is likely due to underlying genetic differences, because photoperiod responses are thought to be under strong genetic control Bradshaw and Stettler (1995); Weih (2004); Keller et al. (2011). This variation may also be explained by different combinations of ambient temperature and photoperiod, because temperature cues can override photoperiod requirements under certain conditions (e.g., during growth cessation Tanino et al., 2010). In such cases, climate change induced phenological shifts may still occur at different rates than past shifts with warming.

## Can existing experiments be applied to improve forecasting?

Approaches to forecasting biological responses to climate change can be grouped into broad categories: statistical models and process-based models. These two modelling extremes differ in at least two ways, in terms of relating plant phenology to climate change. First, statistical models generally assume linear relationships between species' responses and environmental variables (e.g., ), whereas process-based models incorporate nonlinear/threshold relationships as well (e.g., PhenoFit). Second, statistical models of phenology under climate change have typically ignored photoperiod and focus instead on seasonal or annual temperature, whereas process-based models are more likely to incorporate photoperiod, along with forcing and chilling. The challenge of process-based models is that they often require detailed data (e.g., daily climate data, nonlinear biological responses). Perhaps because of this challenge, statistical models remain more commonly used in climate change forecasts of biological responses (I think this is true, but need data/citation to back this up!).

We suggest that, whether statistical or process-based approaches are used, future modelling should incorporate photoperiod. This can be done by leveraging the large amount of experimental data on photoperiod responses (Figure 4, Table 1). Researchers can use these data to first learn if their species (or a closely related species) shows a photoperiod effect, and, ideally, how it varies by population, ecotype, or other factors. If there is evidence of a photoperiod response, as for many species, daylength should be added to forecasting models (Figure 7).

In many cases, experimental data can be immediately used in forecasting because experiments manipulate photoperiod at relevant scales (e.g., Basler and Körner (2014); Heide and Sonstebø (2015), Figures 4, 5, Table 1). The available data can inform critical non-linearities and variations across species, and/or populations (Figure 7. Adding photoperiod and variable responses to forecasts could fundamentally alter the future species and communities we expect.

Models ideally will then guide additional experiments to test some of the critical predictions and assumptions that they make. Through the process of incorporating experimental data into more process-like models, it is likely that knowledge gaps will be identified. For example, many experiments manipulate photoperiod much more dramatically than will occur with climate change (Figures 4, 5, 6. Extrapolating these findings with models may lead to less accurate forecasts.

## Outstanding questions

There is a great need to better understand many aspects of photoperiod and photoperiod responses. For example,

1. How does photoperiod act as a cue? The divergent effects of photoperiod observed across studies (e.g., Figure 1) suggests that photoperiod interacts with other environmental drivers, such as chilling and forcing, to affect phenology and other activities. However, exactly how it interacts with temperature to break dormancy, as well as the type of response it elicits (e.g., linear versus non-linear threshold) is not well-defined for many species.
2. How much does model accuracy (process-based or statistical) improve when we include for photoperiod responses and changes in photoperiod?
3. Does incorporating photoperiod responses alter forecasting outcomes, at population, community, and ecosystem scales? Photoperiod is incorporated into forecasts, along with other variables such as evaporative demand, and temperature, in many ecosystem models (e.g. ED Jolly et al., 2005; Medvigy et al., 2013). The sensitivity of model outcomes to assumptions made about photoperiod and photoperiod responses should be more widely tested, e.g. in different ecosystems, and across different species and populations.

## Conclusions

Organisms may undergo large changes to the photoperiod they experience, with climate change, even if they do not shift their ranges spatially. An altered photoperiod is likely to have implications for a variety of plant responses, as well as responses in animals and other organisms, given the diverse species for which daylength affects activities (e.g., Taranger et al., 2003; Bradshaw and Holzapfel, 2006; McCallan et al., 2006; Linn et al., 1996; ?; Solbakken et al., 1994). Incorporating photoperiod into forecasting of climate change responses may improve model accuracy, and is likely to highlight additional experiments needed to improve our mechanistic understanding of photoperiod as a cue to diverse biological responses.

## To do:

1. Move/reword Question 1 around?
2. Update table/map to fix 2 studies have a max NA and a min NA- these look reasonable so add them with an \*
3. Make lines thicker/darker in Figure 2 (looks a bit washed out)
4. Combine Figures 5 and 6 into one figure with 4 panels.
5. Work Figures 5 and 6 more explicitly into the paper
6. Add a glossary? could include vernalization, endodormancy, ectodormancy, chilling, forcing

## Random notes that may be useful to work in somewhere:

1. Bradshaw and Holzapfel (2001) showed that the pitcher plant mosquito, *Wyeomyia smithii*, has evolved a shorter critical photoperiod in association with a longer growing season. Northern populations of this

mosquito now use a shorter day-length cue to enter winter diapause, doing so later in the fall than they did 24 years ago.

2. Decreasing day-length is the main environmental cue inducing growth cessation and bud set in many perennial plants, including poplar
  - (a) Lagercrantz U: At the end of the day: a common molecular mechanism for photoperiod responses in plants?. *J Exp Bot.* 2009, 60: 2501-2515. 10.1093/jxb/erp139. (lagercrantz2009)
  - (b) Howe GT, Gardner G, Hackett WP, Fournier GR: Phytochrome control of short-day-induced bud set in black cottonwood. *Physiol Plant.* 1996, 97: 95-103. 10.1111/j.1399-3054.1996.tb00484.x. (Howe: 1996)

## References

- Andrés, F., and G. Coupland. 2012. The genetic basis of flowering responses to seasonal cues. *Nature reviews. Genetics* 13:627.
- Ashby, W., et al. 1962. Germination capacity in american basswood [*tilia americana*]. *Transactions of the Illinois State Academy of Science* 55:120–3.
- Basler, D., and C. Körner. 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology* 165:73–81.
- . 2014. Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. *Tree physiology* 34:377–388.
- Bastow, R., and C. Dean. 2002. The molecular basis of photoperiodism. *Developmental cell* 3:461–462.
- Bradshaw, H., and R. F. Stettler. 1995. Molecular genetics of growth and development in *populus*. iv. mapping qtls with large effects on growth, form, and phenology traits in a forest tree. *Genetics* 139:963–973.
- Bradshaw, W. E., and C. M. Holzapfel. 2006. Evolutionary response to rapid climate change. *Science(Washington)* 312:1477–1478.
- Caffarra, A., A. Donnelly, I. Chuine, and M. B. Jones. 2011. Modelling the timing of *betula pubescens* bud-burst. i. temperature and photoperiod: A conceptual model. *Climate Research* 46:147.
- Campbell, R. K., and A. I. Sugano. 1975. Phenology of bud burst in douglas-fir related to provenance, photoperiod, chilling, and flushing temperature. *Botanical Gazette* pages 290–298.
- Chen, I.-C., J. K. Hill, R. Ohlemueller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026. PT: J; TC: 22.
- Davis, S. J. 2002. Photoperiodism: the coincidental perception of the season. *Current Biology* 12:R841–R843.
- Duputié, A., A. Rutschmann, O. Ronce, and I. Chuine. 2015. Phenological plasticity will not help all species adapt to climate change. *Global change biology* 21:3062–3073.
- Erwin, J. E. 1998. Temperature and light effects on stem elongation (plant growth regulation by physical and mechanical stimuli, for further development of horticulture in east asia). *Journal of the Japanese Society for Horticultural Science* 67:1113–1120.
- Falus, M., and R. Calamassi. 1990. Bud dormancy in beech (*fagus sylvatica* l.). effect of chilling and photoperiod on dormancy release of beech seedlings. *Tree physiology* 6:429–438.

- Flynn, D. F. B., and E. M. Wolkovich. 2018. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist* 0.
- Gauzere, J., S. Delzon, H. Davi, M. Bonhomme, I. G. de Cortazar-Atauri, and I. Chuine. 2017. Integrating interactive effects of chilling and photoperiod in phenological process-based models. a case study with two european tree species: *Fagus sylvatica* and *quercus petraea*. *Agricultural and Forest Meteorology* 244:9–20.
- Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? a global meta-analysis of treeline response to climate warming. *Ecology Letters* 12:1040–1049. PT: J.
- Hawkins, C. D., and A. Dhar. 2012. Spring bud phenology of 18 *betula papyrifera* populations in british columbia. *Scandinavian Journal of Forest Research* 27:507–519.
- HEIDE, O. M. 1977. Photoperiod and temperature interactions in growth and flowering of strawberry. *Physiologia Plantarum* 40:21–26.
- Heide, O. M. 2008. Interaction of photoperiod and temperature in the control of growth and dormancy of *prunus* species. *Scientia Horticulturae* 115:309–314.
- . 2011. Temperature rather than photoperiod controls growth cessation and dormancy in *sorbus* species. *Journal of experimental botany* page err213.
- Heide, O. M., and A. Sønsteby. 2012. Floral initiation in black currant cultivars (*ribes nigrum* l.): Effects of plant size, photoperiod, temperature, and duration of short day exposure. *Scientia Horticulturae* 138:64–72.
- Heide, O. M., and A. Sonsteby. 2015. Simultaneous dormancy induction interferes with short day floral induction in black currant (*ribes nigrum* l.). *Scientia Horticulturae* 185:228–232. Times Cited: 0 Heide, Ola M. Sonsteby, Anita O.
- Howe, G. T., G. Gardner, W. P. Hackett, and G. R. Furnier. 1996. Phytochrome control of short-day-induced bud set in black cottonwood. *Physiologia Plantarum* 97:95–103.
- Howe, G. T., W. P. Hackett, G. R. Furnier, and R. E. Klevorn. 1995. Photoperiodic responses of a northern and southern ecotype of black cottonwood. *Physiologia Plantarum* 93:695–708.
- Hsu, C.-Y., J. P. Adams, H. Kim, K. No, C. Ma, S. H. Strauss, J. Drnevich, L. Vandervelde, J. D. Ellis, B. M. Rice, et al. 2011. Flowering locus t duplication coordinates reproductive and vegetative growth in perennial poplar. *Proceedings of the National Academy of Sciences* 108:10756–10761.
- Jolly, W. M., R. Nemani, and S. W. Running. 2005. A generalized, bioclimatic index to predict foliar phenology in response to climate. *Global Change Biology* 11:619–632.
- Keller, S. R., R. Y. Soolanayakanahally, R. D. Guy, S. N. Silim, M. S. Olson, and P. Tiffin. 2011. Climate-driven local adaptation of ecophysiology and phenology in balsam poplar, *populus balsamifera* l.(salicaceae). *American Journal of Botany* 98:99–108.
- Kobayashi, Y., and D. Weigel. 2007. Move on up, it's time for change—mobile signals controlling photoperiod-dependent flowering. *Genes & development* 21:2371–2384.
- Koerner, C., and D. Basler. 2010. Warming, photoperiods, and tree phenology response. *Science* 329:278–278.
- Lagercrantz, U. 2009. At the end of the day: a common molecular mechanism for photoperiod responses in plants? *Journal of experimental botany* 60:2501–2515.
- Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* 20:170–182.
- Linkosalo, T., and M. J. Lechowicz. 2006. Twilight far-red treatment advances leaf bud burst of silver birch (*betula pendula*). *Tree physiology* 26:1249–1256.

- Linn, C. E., M. G. Campbell, K. R. Poole, W.-Q. Wu, and W. L. Roelofs. 1996. Effects of photoperiod on the circadian timing of pheromone response in male *trichoplusia ni*: relationship to the modulatory action of octopamine. *Journal of Insect Physiology* 42:881–891.
- Mcallan, B. M., C. R. Dickman, and M. S. Crowther. 2006. Photoperiod as a reproductive cue in the marsupial genus *antechinus*: ecological and evolutionary consequences. *Biological Journal of the Linnean Society* 87:365–379.
- Medvigy, D., S.-J. Jeong, K. L. Clark, N. S. Skowronski, and K. V. Schäfer. 2013. Effects of seasonal variation of photosynthetic capacity on the carbon fluxes of a temperate deciduous forest. *Journal of Geophysical Research: Biogeosciences* 118:1703–1714.
- Mimura, M., and S. Aitken. 2007. Adaptive gradients and isolation-by-distance with postglacial migration in *picea sitchensis*. *Heredity* 99:224.
- Morin, X., J. Roy, L. Sonié, and I. Chuine. 2010. Changes in leaf phenology of three european oak species in response to experimental climate change. *New Phytologist* 186:900–910.
- Nienstaedt, H. 1966. Dormancy and dormancy release in white spruce. *Forest Science* 12:374–384.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37:637–669.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37.
- Partanen, J., H. Hänninen, and R. Häkkinen. 2005. Bud burst in norway spruce (*picea abies*): preliminary evidence for age-specific rest patterns. *Trees* 19:66–72.
- Petterle, A., A. Karlberg, and R. P. Bhalerao. 2013. Daylength mediated control of seasonal growth patterns in perennial trees. *Current Opinion in Plant Biology* 16:301–306.
- Saikkonen, K., K. Taulavuori, T. Hyvönen, P. E. Gundel, C. E. Hamilton, I. Vänninen, A. Nissinen, and M. Helander. 2012. Climate change-driven species' range shifts filtered by photoperiodism. *Nature Climate Change* 2:239.
- Sanz-Perez, V., P. Castro-Diez, and F. Valladares. 2009. Differential and interactive effects of temperature and photoperiod on budburst and carbon reserves in two co-occurring mediterranean oaks. *Plant Biol (Stuttg)* 11:142–51.
- Sidaway-Lee, K., E.-M. Josse, A. Brown, Y. Gan, K. J. Halliday, I. A. Graham, and S. Penfield. 2010. Spatula links daytime temperature and plant growth rate. *Current biology* 20:1493–1497.
- Singh, R. K., T. Svystun, B. AlDahmash, A. M. Jönsson, and R. P. Bhalerao. 2017. Photoperiod-and temperature-mediated control of phenology in trees—a molecular perspective. *New Phytologist* 213:511–524.
- Solbakken, V. A., T. Hansen, and S. O. Stefansson. 1994. Effects of photoperiod and temperature on growth and parr-smolt transformation in atlantic salmon (*salmo salar l.*) and subsequent performance in seawater. *Aquaculture* 121:13–27.
- Spann, T. M., J. G. Williamson, and R. L. Darnell. 2004. Photoperiod and temperature effects on growth and carbohydrate storage in southern highbush blueberry interspecific hybrid. *Journal of the American Society for Horticultural Science* 129:294–298.
- Tanino, K. K., L. Kalcsits, S. Silim, E. Kendall, and G. R. Gray. 2010. Temperature-driven plasticity in growth cessation and dormancy development in deciduous woody plants: a working hypothesis suggesting how molecular and cellular function is affected by temperature during dormancy induction. *Plant molecular biology* 73:49–65.

- Taranger, G., E. Vikingstad, U. Klenke, I. Mayer, S. Stefansson, B. Norberg, T. Hansen, Y. Zohar, and E. Andersson. 2003. Effects of photoperiod, temperature and gnrha treatment on the reproductive physiology of atlantic salmon (*salmo salar l.*) broodstock. *Fish Physiology and Biochemistry* 28:403–406.
- Viherä-Aarnio, A., R. Häkkinen, and O. Junntila. 2006. Critical night length for bud set and its variation in two photoperiodic ecotypes of *betula pendula*. *Tree physiology* 26:1013–1018.
- Vitasse, Y., and D. Basler. 2013. What role for photoperiod in the bud burst phenology of european beech. *European Journal of Forest Research* 132:1–8.
- Wareing, P. 1956. Photoperiodism in woody plants. *Annual Review of Plant Physiology* 7:191–214.
- Weih, M. 2004. Intensive short rotation forestry in boreal climates: present and future perspectives. *Canadian Journal of Forest Research* 34:1369–1378.
- Wolkovich, E. M., B. I. Cook, J. M. Allen, T. M. Crimmins, J. L. Betancourt, S. E. Travers, S. Pau, et al. 2012. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485:494–497.
- Zohner, C. M., B. M. Benito, J. C. Svensson, and S. S. Renner. 2016. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* .

## Tables

Table 1: **Growth chamber experiments and their photoperiod treatments.** We note whether or not photoperiod had a significant effect ('effect' column) and compared treatments to the spatial and temporal shifts required for organisms to experiments photoperiod changes equivalent to those treatments. For shifts in space, 'ER' indicates that the photoperiod treatments exceeds the change of photoperiod from moving up to 40 degrees latitudinally on June 21. For shifts in time, 'ER' indicates that the range of photoperiod treatments exceeds the change in daylengths at that latitude during the entire year. 'max NA' indicates that the maximum daylength treatment does not exist at that latitude; 'min NA' indicates that the minimum daylength treatment does not exist at that latitude.

idstudy	continent	lat	long	effect	day_range	delta	space	time
ashby62_exp1	north america	42.99	-89.41	Y	8-16	4.00	18.2	min NA (9)
basler14_exp1	europe	46.31	8.27	Y	9.2-16	1.00	6	-22
caffarra11b_exp2	europe	52.32	-6.93	Y	10-16	2.00	7.5	-30
falus190_exp1	europe	46.03	10.75	N	9-13	4.00	16	-82
falus196_exp3	europe	38.27	15.99	Y	9-13	4.00	21.6	-111
ghelardini10_exp1	europe	43.72	11.37	N	8-16	8.00	21.9	ER
heide05_exp1	europe	56.18	-4.32	Y/N	10-24	14.00	ER	ER
heide08_exp1	europe	48.40	11.72	Y	10-24	14.00	ER	ER
heide11_exp1	europe	59.67	10.67	N	10-20	10.00	ER	max NA (18.7)
heide12_exp1	europe	56.50	-3.06	Y	10-24	5.00	8.9	-64
heide15_exp2	europe	56.50	-3.06	Y	10-15	1.00	3.2	-13
heide93_exp1	europe	59.50	10.77	Y	8-24	16.00	ER	ER
heide93a_exp1	europe	59.67	10.83	Y	8-24	16.00	ER	ER
heide93a_exp3	europe	47.50	7.60	Y	13-16	1.00	5.7	-18
howe95_exp1	north america	40.55	-124.10	Y	9-24	2.00	13.1	-64
laube14a_exp1	europe	48.40	11.71	N	8-16	4.00	14.3	-87
myking95_exp1	europe	56.10	9.15	Y	8-24	16.00	ER	ER
nienstaedt66_exp1	north america	44.17	-103.92	Y	8-20	12.00	ER	ER
okie11_exp1	north america	32.12	-83.12	Y	0-12	12.00	ER	ER
partanen01_exp1	europe	61.93	26.68	Y	6-16	10.00	ER	-105
partanen05_exp1	europe	61.82	29.32	Y	5-20	5.00	ER	-67
partanen98_exp1	europe	60.03	23.05	Y	8.66-12	3.34	5.1	-37
pettersen71_exp1	europe	59.66	10.77	N	10-24	2.00	4	-23
Sanz-Perez09_exp1	europe	40.40	-3.48	Y	10-16	6.00	23.6	ER
viheraaarnio06_exp1	europe	60.45	24.93	Y	16-17	1.00	2.1	-12
viheraaarnio06_exp1	europe	67.73	24.93	Y	20-21	1.00	ER	-5
viheraaarnio06_exp2	europe	60.45	24.93	Y	15-19	4.00	5.1	-62
viheraaarnio06_exp2	europe	67.73	24.93	Y	22-23	1.00	ER	-3
worrall67_exp 3	north america	41.31	-72.93	Y	8-16	8.00	24.3	ER
zohner16_Exp1	europe	48.16	11.50	Y	8-16	8.00	ER	ER
hawkins12_				Y				

## Figures

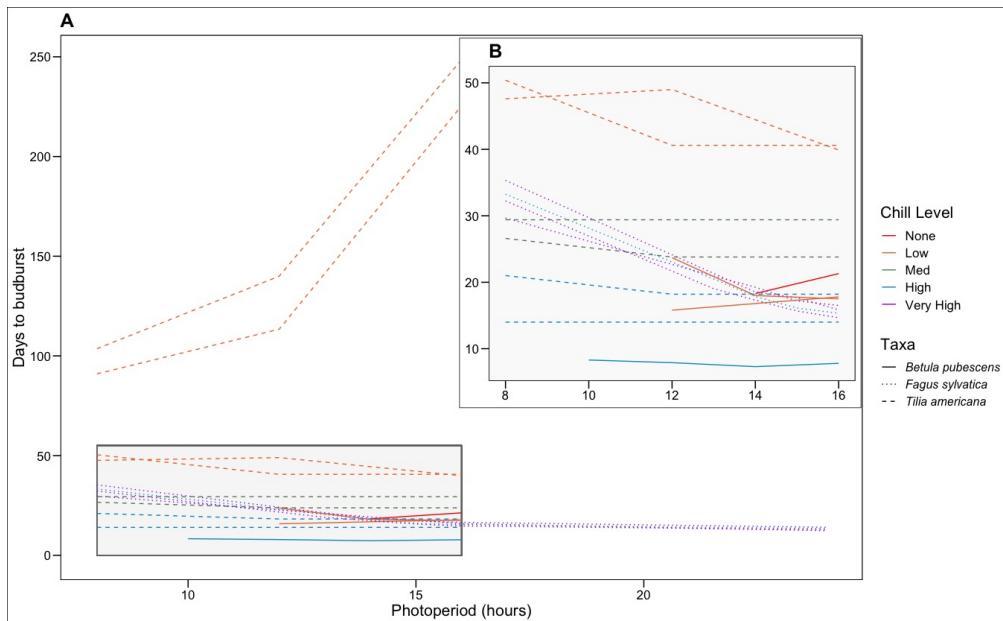


Figure 1: **Plant responses to changes in daylength vary across species and populations, and with the amount of chilling received.**

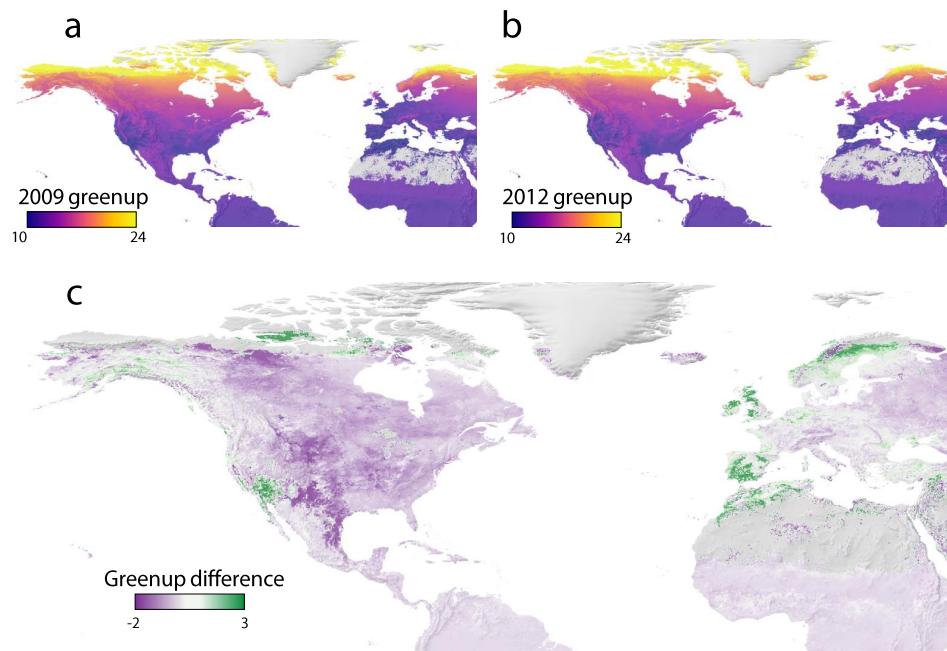


Figure 2: **The photoperiod on the green up date (start of spring) varies over space and among years.** Hours of daylight on the date of spring green up from MODIS satellite data across North America and Europe for an average (2009, a) and early (2012,b) North American start of spring. The differences between the years are shown in (c).

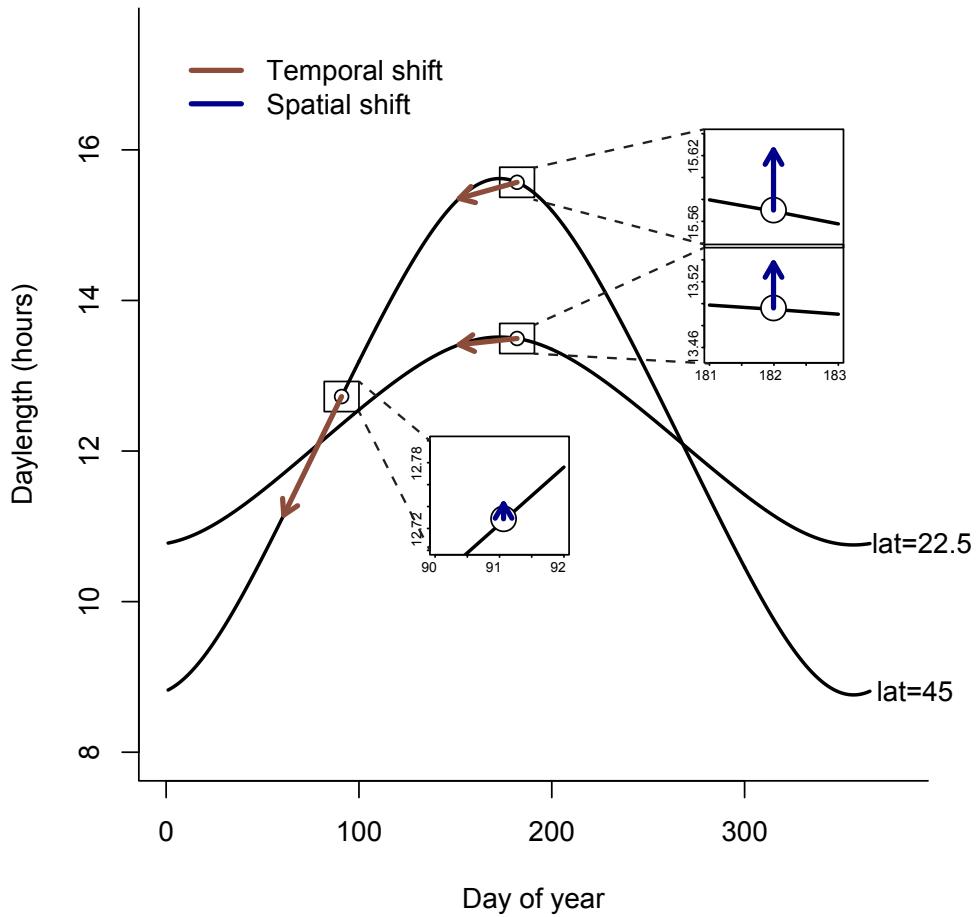


Figure 3: **Photoperiod varies with latitude and throughout the year**, such that temporal shifts in activity yield larger changes in experienced photoperiod compared with spatial shifts. Here, we show this variation at two latitudes, using hypothetical rates of spatial and temporal shifts: 30 days earlier for temporal shifts, and 0.5 degrees poleward for spatial shifts. These shifts, which are similar to observed average rates (e.g., Parmesan, 2006; Chen et al., 2011), highlight the greater magnitude in daylength changes close to the equinox (e.g., DOY 91), versus close to the summer solstice (e.g., DOY 182).

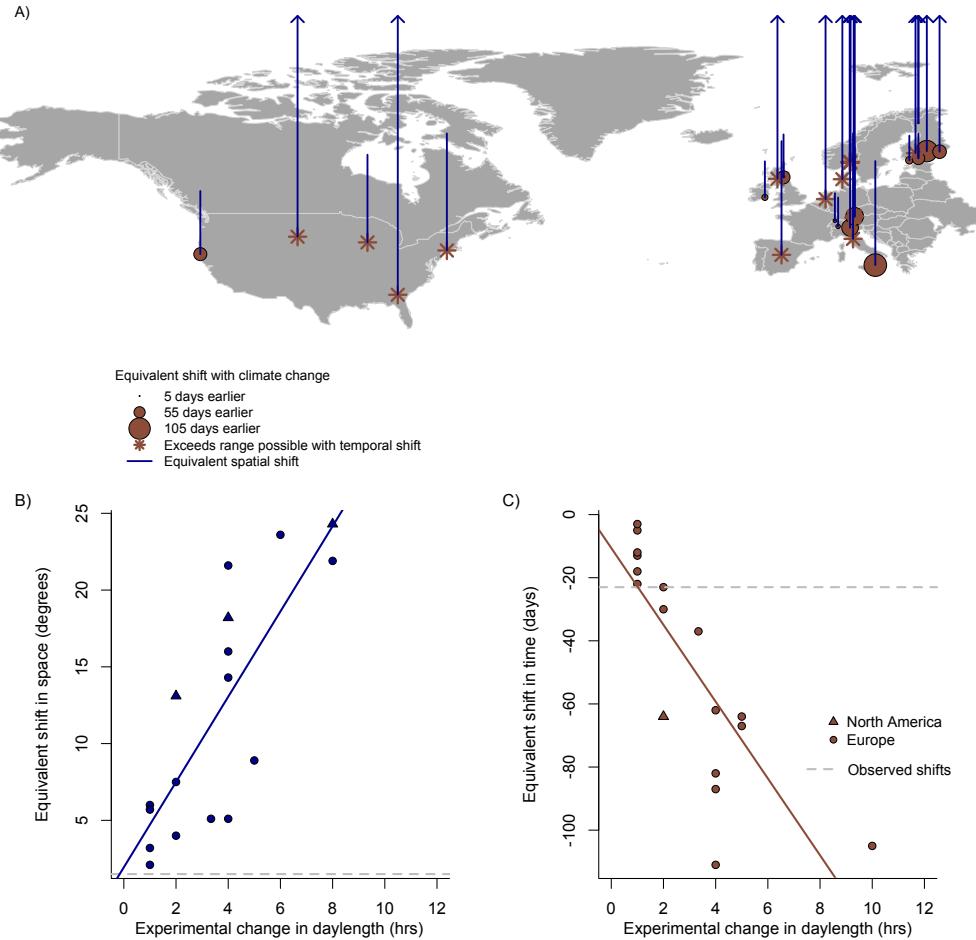


Figure 4: **OSPREE experiments that manipulate photoperiod**, and their equivalent spatial and temporal shifts, mapped (A), and graphed (B-C). Observed rates (dashed gray lines) 16.9 kilometers per decade (or approximately 1.5 degrees in 100 years) for spatial shifts (Chen et al. 2011) and 2.3 days per decade (or 23 days in 100 years) for temporal shifts (Parmesan and Yohe 2003).

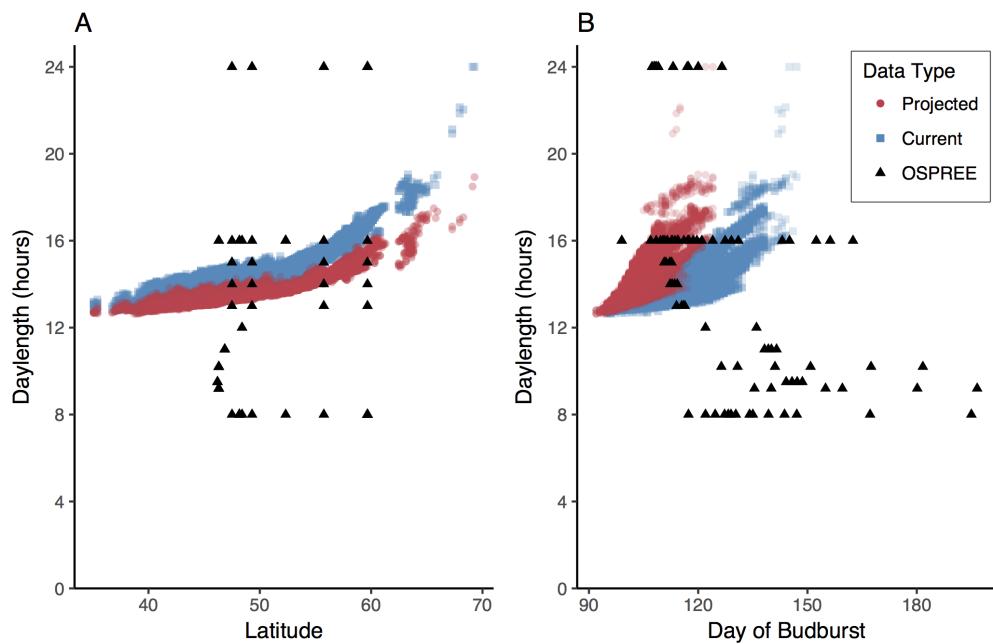


Figure 5: **Experimental treatments of daylength in the OSPREE database, shown by latitude (A) and by day of budburst (B)** for *Fagus sylvatica*. For comparison, we show the daylength when budburst occurs in its current and projected ranges (A) and in its current range only, with expected shifts in phenology (B). Estimates and projections are from Phenofit (Duputié et al., 2015)

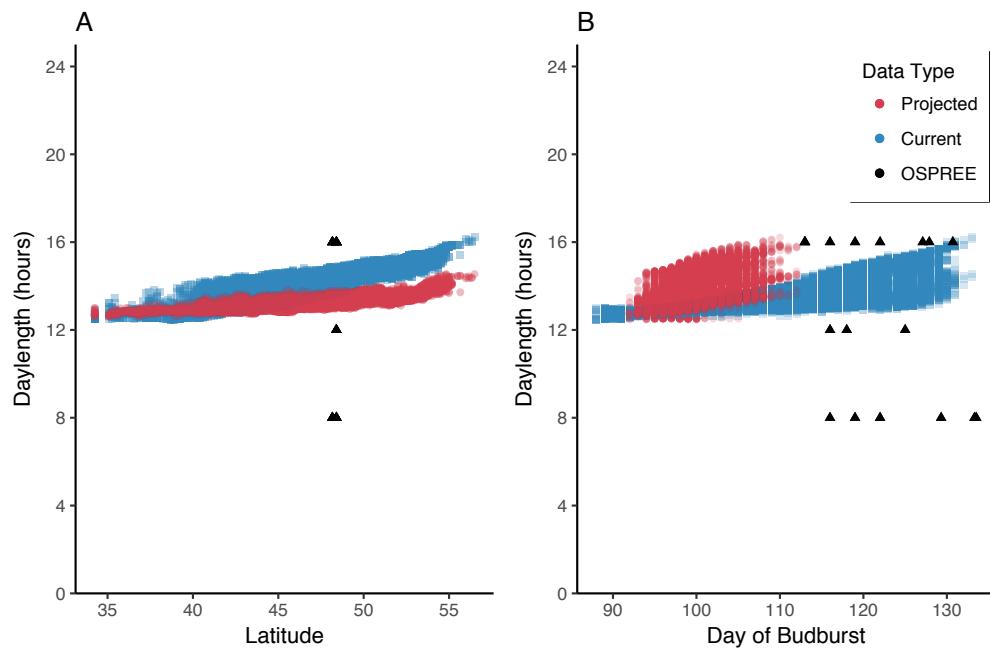


Figure 6: **Experimental treatments of daylength in the OSPREE database, shown by latitude (A) and by day of budburst (B)** for *Quercus robur*. For comparison, we show the daylength when budburst occurs in its current and projected ranges (A) and in its current range only, with expected shifts in phenology (B). Estimates and projections are from Phenofit (Duputié et al., 2015).

Accounting for photoperiod to improve forecasts of biological responses to climate change

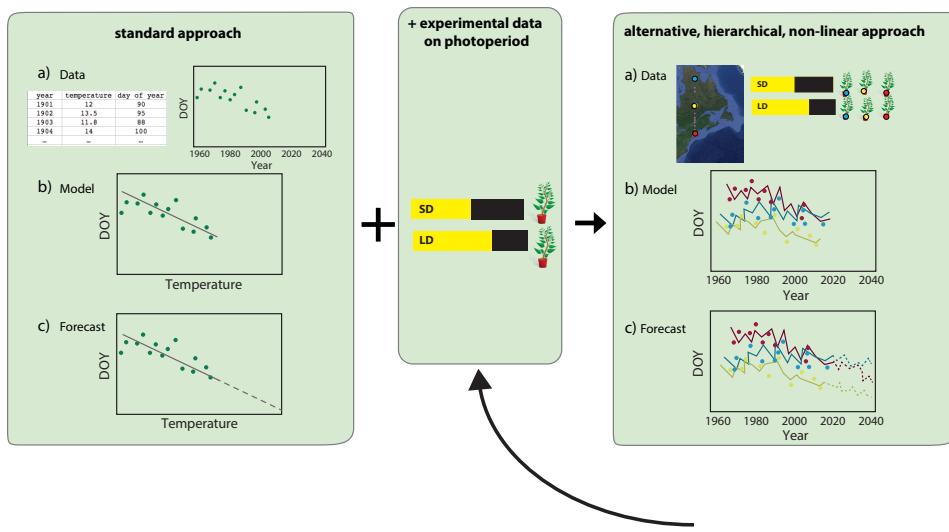


Figure 7: Conceptual diagram of how to include photoperiod in forecasting biological responses to climate change.