

Spatial and temporal shifts in photoperiod with climate change

A.K. Ettinger, D. Buonaiuto, C. Chamberlain, I. Morales-Castilla, E. Wolkovich

October 22, 2018

Introduction

Photoperiod is a critical cue used by organisms to synchronize their activities with seasonal climatic changes (e.g., Hsu et al., 2011; Singh et al., 2017; Basler and Körner, 2012). Diverse important responses, from the timing of mating in marsupials (McAllan et al., 2006) and pheromone production in moths (Linn et al., 1996), to growth rates in salmon and the timing of budburst in woody plants (Flynn and Wolkovich, In Review.; Solbakken et al., 1994), are affected by photoperiod. Photoperiod provides a stable signal by which organisms can align events with the season, because it is consistent across years, especially compared to other seasonal cues such as temperature and precipitation (Saikkonen et al., 2012).

Daylength is predictable over time, but the daylength 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), and/or shifted their activity earlier in the year (i.e., phenological shifts). These spatial and temporal shifts will affect the photoperiod regime experienced by organisms. An altered photoperiod is likely to have implications for a variety of biological responses, given the diverse organisms that rely on daylength to cue their activities (e.g., McAllan et al., 2006; Linn et al., 1996; Flynn and Wolkovich, In Review.; Solbakken et al., 1994). However, this aspect of climate change has not generally been a focus of attempts to forecast biological responses.

Although daylength is rarely incorporated into forecasts of biological responses to climate change, growth chamber experiments that alter photoperiod have been conducted for decades to address basic questions about how photoperiod may act as a biological cue. These experiments often manipulate temperature, in addition to photoperiod (e.g., Campbell and Sugano, 1975; HEIDE, 1977; Falusi and Calamassi, 1990; Spann et al., 2004; Laube et al., 2014). Thus, although photoperiod treatments in these experiments are not typically designed for climate change forecasting, it is possible that their results may be used to inform these forecasts. Here, we ask:

1. How will climate change alter the photoperiod experienced by organisms, given observed climate change-induced biological shifts, both spatially and temporally?
2. What are the implications of these altered photoperiods for forecasts of climate change impacts?
3. Can the large quantity of experiments altering photoperiod be applied to forecasting biological implications of climate change (i.e., do they occur at the appropriate scale)?

How will climate change alter the photoperiod experienced by organisms?

Spatial shifts in species ranges and temporal shifts in species phenology and activity 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 1). E elevational shifts, on the other hand, would cause minimal changes in photoperiod 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?), but temporal shifts are actually likely to yield bigger changes in experienced photoperiod than spatial shifts (Figure 1). For example, consider an insect at latitude 45° that normally becomes active in the spring, around DOY 91 (April 2), on average. If its phenology shifts 30 days earlier (i.e., a rate of XX days per degree of warming, as has been observed) it will experience a daylength that is XX hours shorter. However, if the same insect shifts its range up in latitude 0.5 degrees (i.e., a rate of XX km per degree of warming, as has been observed), it will experience a daylength that is only XX minutes shorter on the same DOY.

Of course, in many cases organisms may shift both their geographic ranges and their phenology simultaneously. Adding further complication is the observation that phenology typically varies with latitude (Figure 2a,b), and that patterns can differ among years. A year that results in early green-up at 35°, for instance, may not be an early year at 50° latitude (Figure 2c). Furthermore, photoperiod sensitivity, or the degree to which phenology is controlled by daylength, can also 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). It is unclear how all of these complications will interact to affect the photoperiod experienced by organisms, with future climate change.

What are the implications of altered photoperiods for forecasts of climate change impacts?

Daylength is known to control critical functions, from vegetative growth, cell elongation, and budburst (Linkosalo and Lechowicz, 2006; Erwin, 1998; Sidaway-Lee et al., 2010; Hsu et al., 2011) in plants, to XXXX in animals. Climate change-induced shifts in photoperiod are therefore likely to alter important responses across diverse species.

Photoperiod may eventually become a limiting factor, constraining the ability of species to respond to additional warming. To date, many biological responses to recent climate change can be explained by shifts in temperature (e.g. EXAMPLES). If daylength cues become limiting, however, species may not respond to additional warming. For example, the timing of budburst in woody plants is controlled by interactions between chilling (a critical amount of cold temperatures that must be experienced to break dormancy), forcing (a critical amount of warm temperatures), and daylength. Warming over the past century has caused budburst to shift earlier in diverse woody species (CITES). However, in the future, interactions between photoperiod, forcing, and chilling could result in muted or exaggerated phenological shifts, compared to what would be expected based on temperature change alone. Phenology may be prevented from shifting earlier with additional warming because daylength cues will become limiting (Koerner and Basler, 2010; Vitasse and Basler, 2013; Morin et al., 2010). "photoperiod cues can dampen phenological advance (Wareing 1956; Ashby et al. 1992; Mimura Aitken 2007; Aldrete, Mexal Burr 2008; Lopez et al. 2008; KáČnorner Basler 2010; Cooke, Eriksson Juntila 2012)." (Say something about crossing thresholds of daylength and the "external coincidence model" for photoperiod control (Bastow and Dean, 2002; Kobayashi and Weigel, 2007; Andrés and Coupland, 2012; Singh et al., 2017)?

Effects of photoperiod on forecasting of biological impacts of climate change needs additional investigation. In some forecasting methods (e.g. species distribution modelling), the role of photoperiod is largely ignored (I think this is true? add some citations). In other cases, photoperiod is incorporated into forecasts, along with other variables such as evaporative demand, and temperature (e.g. ED Jolly et al., 2005; Medvigy et al., 2013). These models need to be more widely tested, e.g. in different ecosystems/species, and need to incorporate recent findings about the role of photoperiod in phenology.

Can existing experiments be applied to forecasting?

In some cases, experiments manipulate photoperiod at relevant scales (e.g., XXX, Figure 3, Table 1). However, most experiments manipulate photoperiod much more dramatically than will occur with climate change (Figures 3, 4,5, but see (Basler and Körner, 2012)), so it is difficult to extrapolate findings. (This may not be true for all latitudes- for example high latitudes experience more dramatic changes in photoperiod across the year.) There is a great need to better understand exactly how photoperiod acts as a cue. The divergent effects of photoperiod observed across studies (e.g., Figure 6) 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 unclear.

Conclusions

Organisms may experience large changes to the photoperiod they experience, under climate change, even if they do not shift their ranges spatially. To incorporate photoperiod into forecasting of climate change responses, more studies are needed with fine-scale changes in photoperiod. What else??!

To do:

1. Make Table of studies testing if photoperiod varies by latitudinal origin- cat started on this (Table 2)?
2. Update table/map to use 3 ER studies.

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.
 - (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.
3. Response to photoperiod is under strong genetic control

- (a) Bradshaw HD, Stettler RF: 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*. 1995; 139: 963-973.
- (b) Keller SR, Soolanayakanahally RY, Guy RD, Silim SN, Olson MS, Tiffin P: Climate-driven local adaptation of ecophysiology and phenology in balsam poplar, *Populus balsamifera* L. (Salicaceae). *Am J Bot.* 2011; 98: 99-108. 10.3732/ajb.1000317.
- (c) Weih M: Intensive short rotation forestry in boreal climates: present and future perspectives. *Can J Forest Res.* 2004; 34: 1369-1378. 10.1139/x04-090.

References

- Andrés, F., and G. Coupland. 2012. The genetic basis of flowering responses to seasonal cues. *Nature reviews. Genetics* 13:627.
- Basler, D., and C. Körner. 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology* 165:73–81.
- Bastow, R., and C. Dean. 2002. The molecular basis of photoperiodism. *Developmental cell* 3:461–462.
- 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.
- 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.
- Falusi, 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. In Review. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. .
- 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.
- HEIDE, O. M. 1977. Photoperiod and temperature interactions in growth and flowering of strawberry. *Physiologia Plantarum* 40:21–26.
- 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.
- 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.

- 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.
- 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.
- McCallan, 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.
- 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.
- 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.
- 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.
- 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.
- 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.

Tables

Table 1: **Growth chamber experiments and their photoperiod treatments**, compared 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	day_range	delta	space	time
ashby62_exp1	north america	42.99	-89.41	8-16	4.00	18.2	min NA (9)
basler14_exp1	europe	46.31	8.27	9.2-16	1.00	6	-22
caffarra11b_exp2	europe	52.32	-6.93	10-16	2.00	7.5	-30
falus90_exp1	europe	46.03	10.75	9-13	4.00	16	-82
falus96_exp3	europe	38.27	15.99	9-13	4.00	21.6	-111
ghelardini10_exp1	europe	43.72	11.37	8-16	8.00	21.9	ER
heide05_exp1	europe	56.18	-4.32	10-24	14.00	ER	ER
heide08_exp1	europe	48.40	11.72	10-24	14.00	ER	ER
heide11_exp1	europe	59.67	10.67	10-20	10.00	ER	max NA (18.7)
heide12_exp1	europe	56.50	-3.06	10-24	5.00	8.9	-64
heide15_exp2	europe	56.50	-3.06	10-15	1.00	3.2	-13
heide93_exp1	europe	59.50	10.77	8-24	16.00	ER	ER
heide93a_exp1	europe	59.67	10.83	8-24	16.00	ER	ER
heide93a_exp3	europe	47.50	7.60	13-16	1.00	5.7	-18
howe95_exp1	north america	40.55	-124.10	9-24	2.00	13.1	-64
laube14a_exp1	europe	48.40	11.71	8-16	4.00	14.3	-87
myking95_exp1	europe	56.10	9.15	8-24	16.00	ER	ER
myking97_exp1	europe	59.67	10.77	12-24	12.00	ER	max NA (18.7)
nienstaedt66_exp1	north america	44.17	-103.92	8-20	12.00	ER	ER
okie11_exp1	north america	32.12	-83.12	0-12	12.00	ER	ER
partanen01_exp1	europe	61.93	26.68	6-16	10.00	ER	-105
partanen05_exp1	europe	61.82	29.32	5-20	5.00	ER	-67
partanen98_exp1	europe	60.03	23.05	8.66-12	3.34	5.1	-37
pettersen71_exp1	europe	59.66	10.77	10-24	2.00	4	-23
Sanz-Perez09_exp1	europe	40.40	-3.48	10-16	6.00	23.6	ER
skuterud94_exp1	europe	61.50	24.33	8-24	16.00	ER	ER
viheraaarnio06_exp1	europe	60.45	24.93	16-17	1.00	2.1	-12
viheraaarnio06_exp1	europe	67.73	24.93	20-21	1.00	ER	-5
viheraaarnio06_exp2	europe	60.45	24.93	15-19	4.00	5.1	-62
viheraaarnio06_exp2	europe	67.73	24.93	22-23	1.00	ER	-3
worrall67_exp 3	north america	41.31	-72.93	8-16	8.00	24.3	ER
zohner16_Exp1	europe	48.16	11.50	8-16	8.00	ER	ER

Figures

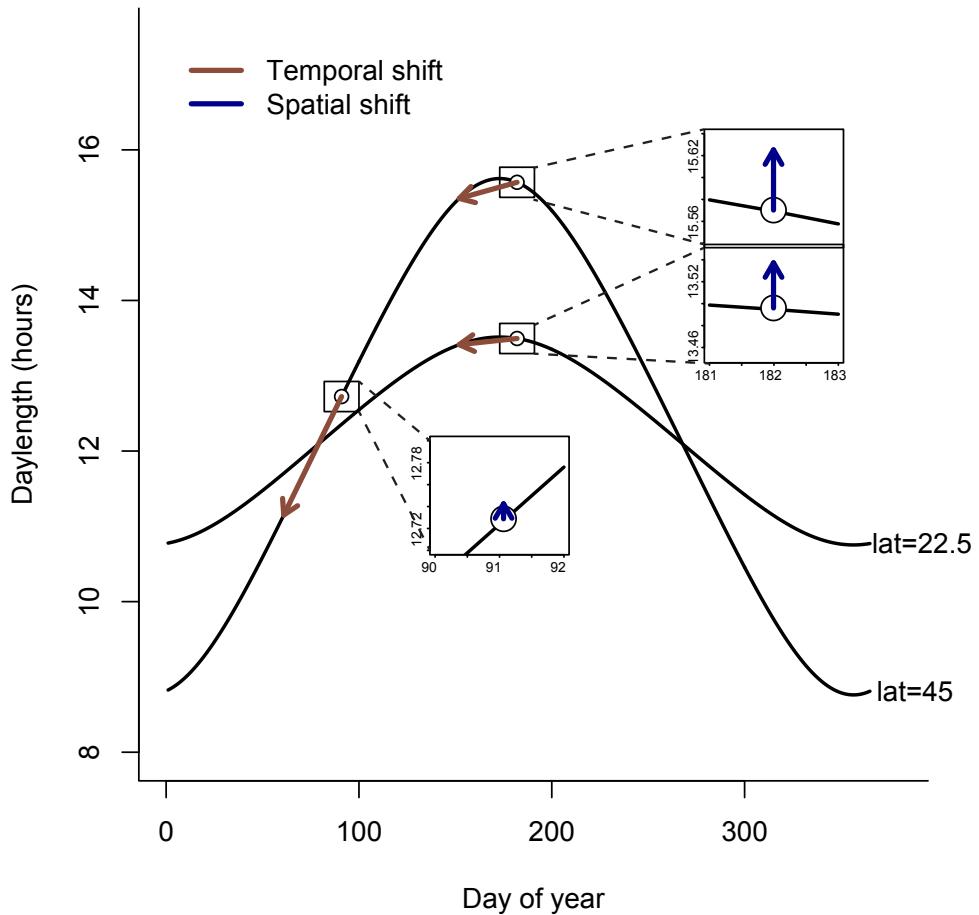


Figure 1: **Photoperiod varies with latitude and throughout the year**, such that temporal shifts in activity yield larger changes in experienced photoperiod compared with spatial shifts. Here, we show this variation at two latitudes, using hypothetical rates of spatial and temporal shifts: 30 days earlier for temporal shifts, and 0.5 degrees poleward for spatial shifts. These shifts, which are similar to observed average rates (e.g., Parmesan et. al 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).

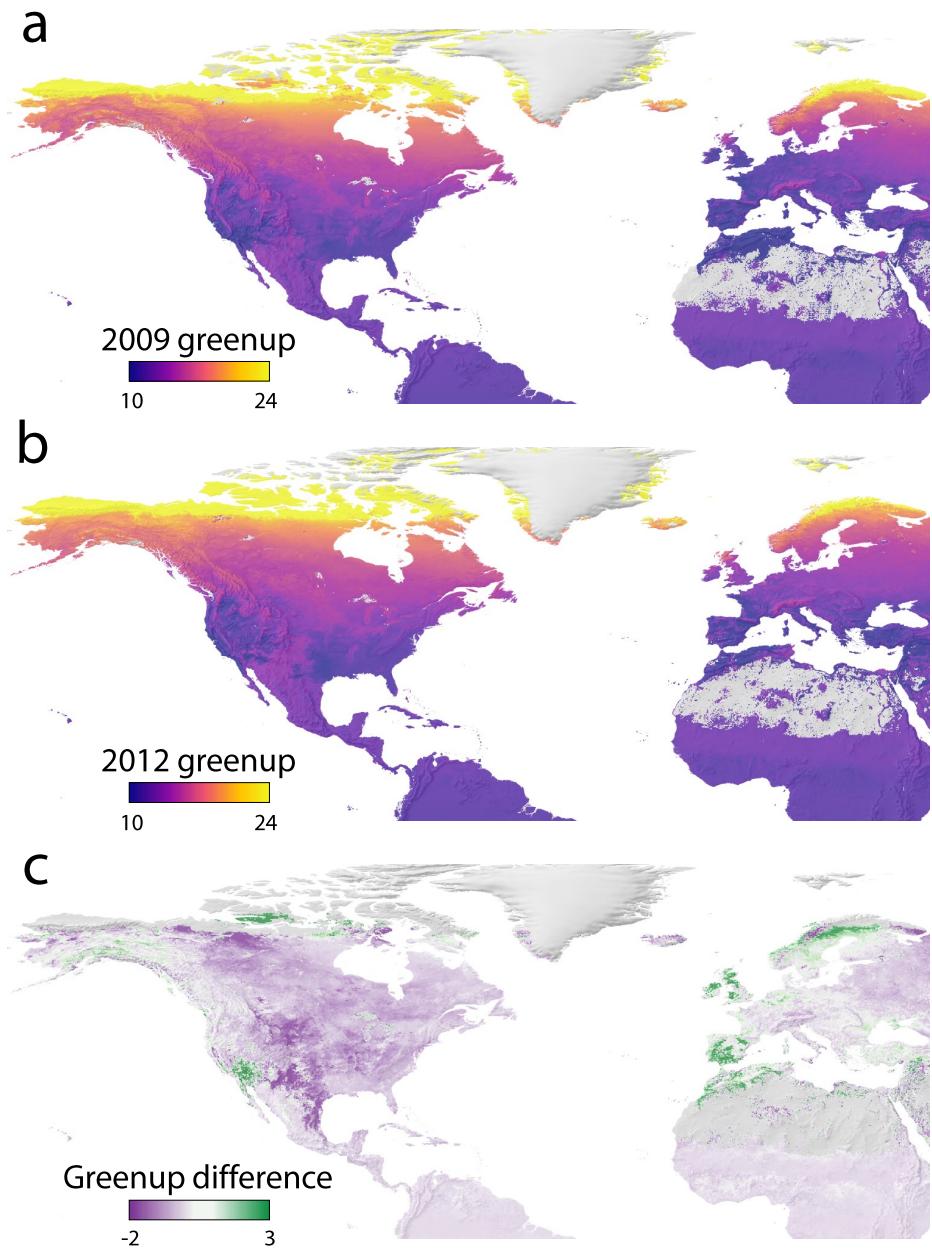


Figure 2: **The photoperiod on the green up date (start of spring) varies over space and among years.** Hours of daylight on the date of spring green up from MODIS satellite data across North America and Europe for an average (a) and early (b) North American start of spring. The differences between the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

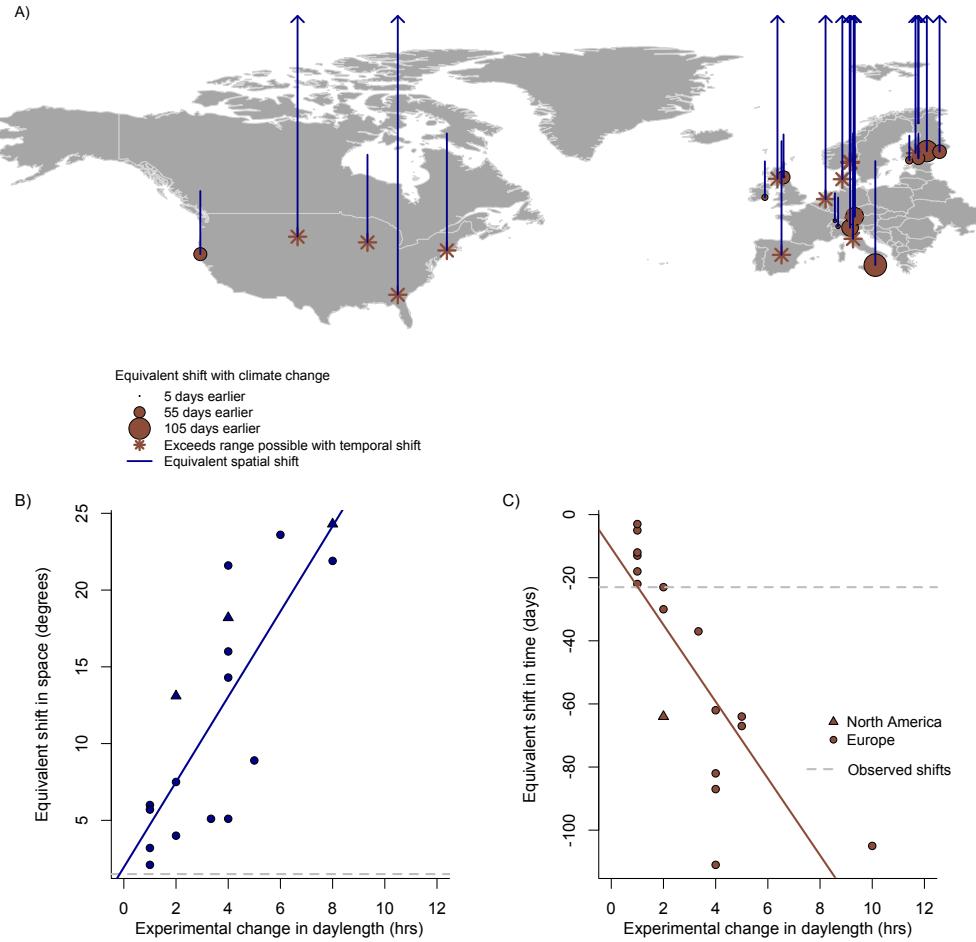


Figure 3: **OSPREE experiments that manipulate photoperiod**, and their equivalent spatial and temporal shifts, mapped (A), and graphed (B-C). Observed rates (dashed gray lines) 16.9 kilometers per decade (or approximately 1.5 degrees in 100 years) for spatial shifts (Chen et al. 2011) and 2.3 days per decade (or 23 days in 100 years) for temporal shifts (Parmesan and Yohe 2003).

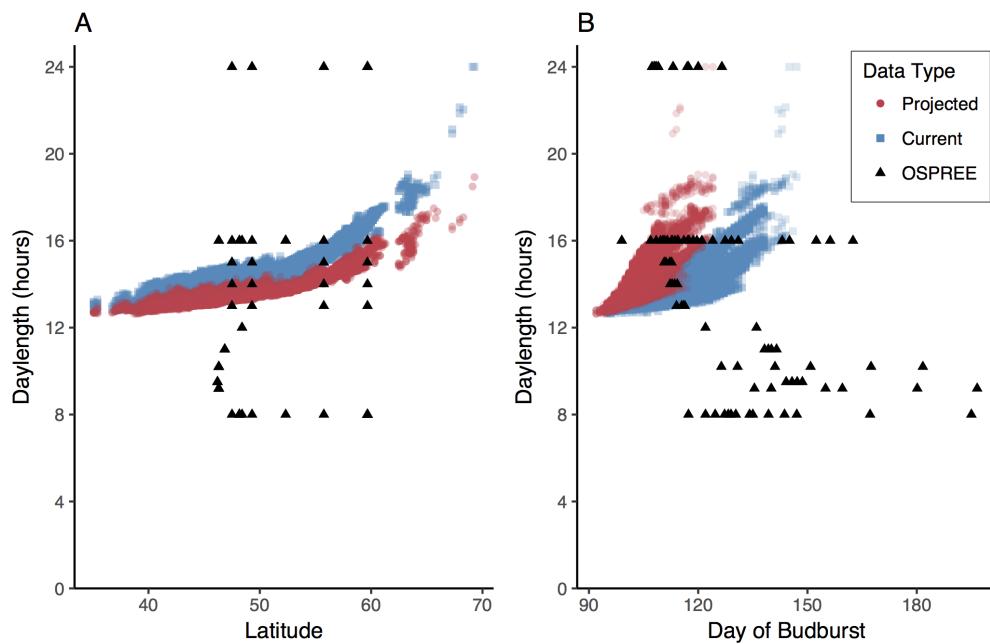


Figure 4: **Experimental treatments of daylength in the OSPREE database, shown by latitude (A) and by day of budburst (B)** for *Fagus sylvatica*. For comparison, we show the daylength when budburst occurs in its current and projected ranges (A) and in its current range only, with expected shifts in phenology (B). Estimates and projections are from Phenofit (Duputié et al., 2015)

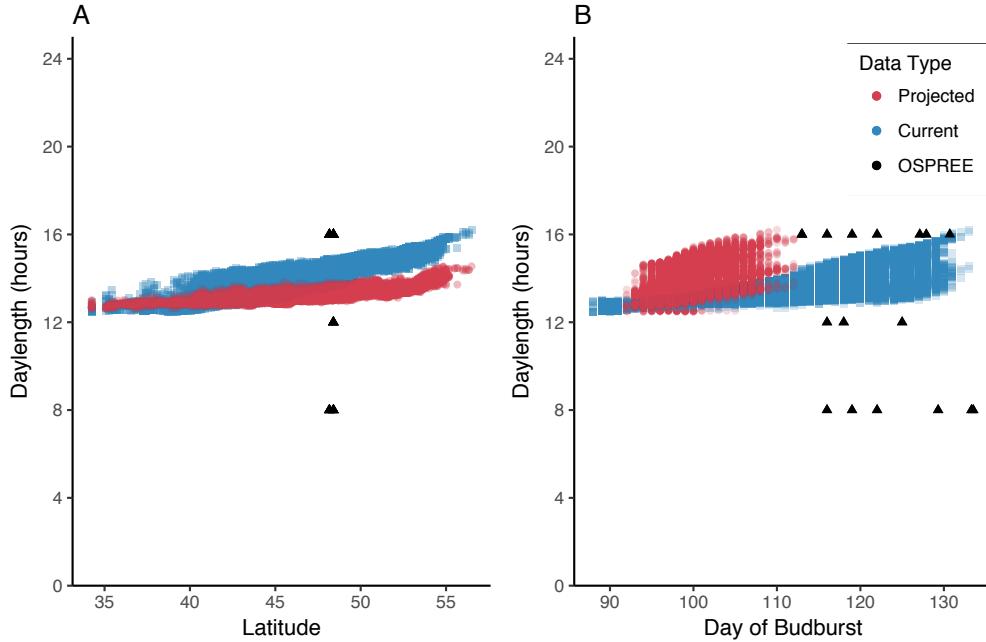


Figure 5: Experimental treatments of daylength in the OSPREE database, shown by latitude (A) and by day of budburst (B) for *Quercus robur*. For comparison, we show the daylength when budburst occurs in its current and projected ranges (A) and in its current range only, with expected shifts in phenology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

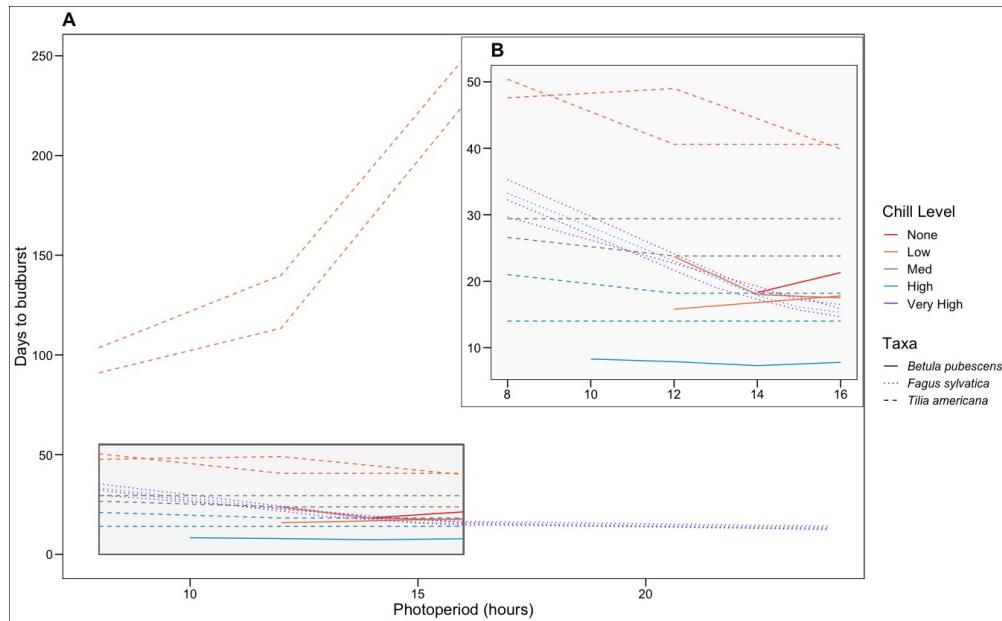


Figure 6: Plant responses to changes in daylength vary across species and populations, and with the amount of chilling received.