

# Spatial and temporal shifts in photoperiod with climate change

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## Introduction

Photoperiod is a critical cue 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). Variation in daylength affects many aspects of plant performance, from growth and reproduction to dormancy and senescence (e.g., Howe et al., 1996; Lagercrantz, 2009). Photoperiod represents a reliable cue 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 two 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 Despute et al), which generally focus on temperature (Figure 1). 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, ADD CITATIONS), and/or shifted their activity earlier in the year (i.e., phenological shifts, CITATIONS). These spatial and temporal shifts will alter the photoperiod regime experienced by organisms.

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 altered photoperiods for biological responses to climate change?
3. Can the large quantity 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. We find that temporal shifts are expected to have a major impact on experienced photoperiod, so testing for 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 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.

## 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 3a). Although this general pattern is consistent across years (Figure 3b), 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 3c).

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 species 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 2). 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 2). 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. 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 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 sensitivity to photoperiod varies across species (Sanz-Perez et al., 2009; Zohner et al., 2016), life stage (Partanen et al., 2005), and populations (

Photoperiod often interacts with temperature to affect phenology. The timing of 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 or exaggerated phenological shifts, compared to what would be expected based on temperature change alone (Wareing, 1956; Mimura and Aitken, 2007; Koerner and Basler, 2010).

(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)?

## Can existing experiments be applied to improve forecasting?

Current forecasts of biological responses to climate change 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, and across different species and populations. They also need to incorporate recent findings about the role of photoperiod in phenology.

In some cases, experiments manipulate photoperiod at relevant scales (e.g., XXX, Figure 4, Table 1). Many experiments, however, manipulate photoperiod much more dramatically than will occur with climate change (Figures 4, 5, 6, but see (Basler and Körner, 2012)), so it is difficult to extrapolate findings to forecasting. (This may not be true for all latitudes- for example high latitudes experience more dramatic changes in photoperiod across the year.)

## Outstanding questions

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 7) 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.

how much does model accuracy (process-based or correlational-statistical-SDMs) improve when we account for photoperiod? If models do not improve much or not at all, then I guess we could forget about it. However, it is likely that photoperiod be important for certain taxa, in certain regions and when using certain models, and answering that is really important, isn't it?

## 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. An altered photoperiod is likely to have implications for a variety of plant responses, given the diverse organisms that rely on daylength to cue their activities (e.g., Mcallan et al., 2006; Linn et al., 1996; ?; Solbakken et al., 1994).

## To do:

1. Update table/map with new column for significance (and perhaps direction of results). also, add 3 ER studies- if they are still there following treatment checks in october 2018.

## 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, Furnier 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)
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. (bradshaw1995)
  - (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.(keller2011)
  - (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.(weih2004)

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# Glossary

vernalization photoperiod endodormancy ectodormancy chilling forcing

## 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
falus190_exp1	europe	46.03	10.75	9-13	4.00	16	-82
falus196_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
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
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

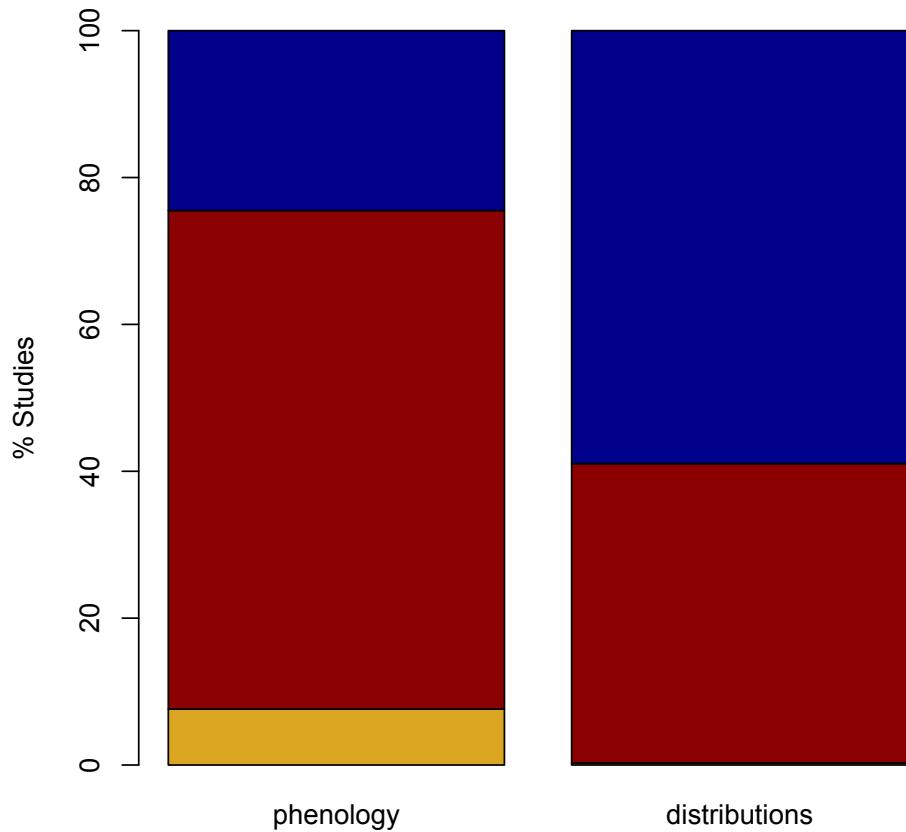


Figure 1: **Photoperiod is not a focus of many studies forecasting biological responses to climate change.** Temperature is more often included as a keyword than photoperiod.

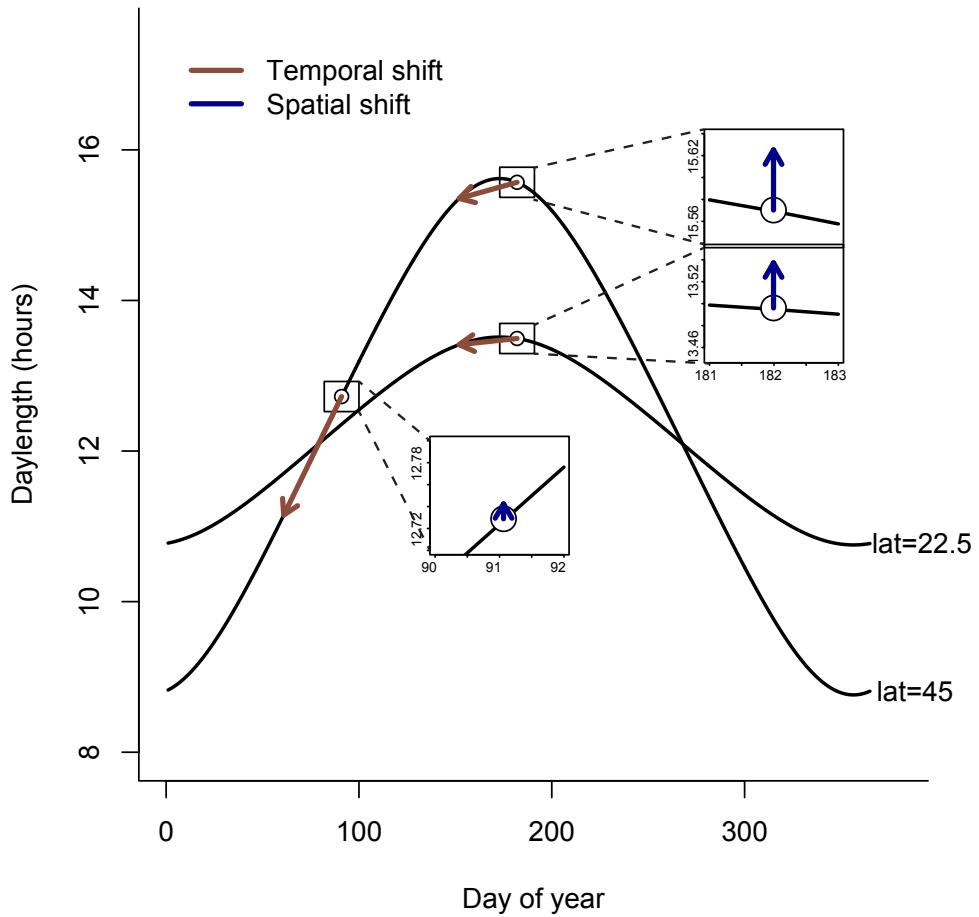
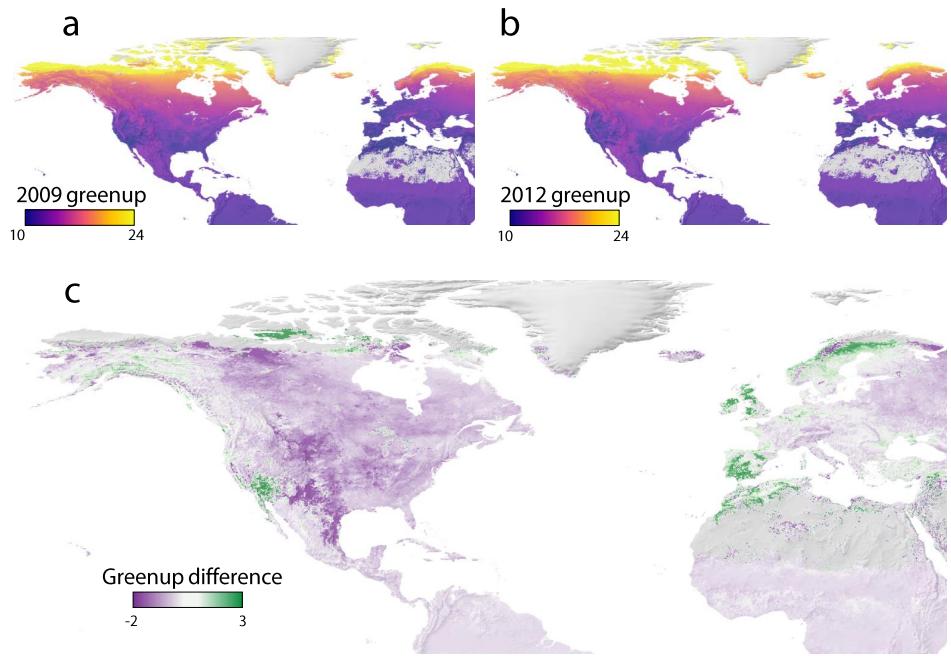


Figure 2: **Photoperiod varies with latitude and throughout the year**, such that temporal shifts in activity yield larger changes in experienced photoperiod compared with spatial shifts. Here, we show this variation at two latitudes, using hypothetical rates of spatial and temporal shifts: 30 days earlier for temporal shifts, and 0.5 degrees poleward for spatial shifts. These shifts, which are similar to observed average rates (Parmesan, 2006; Chen et al., 2011, e.g.), 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 3: 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).

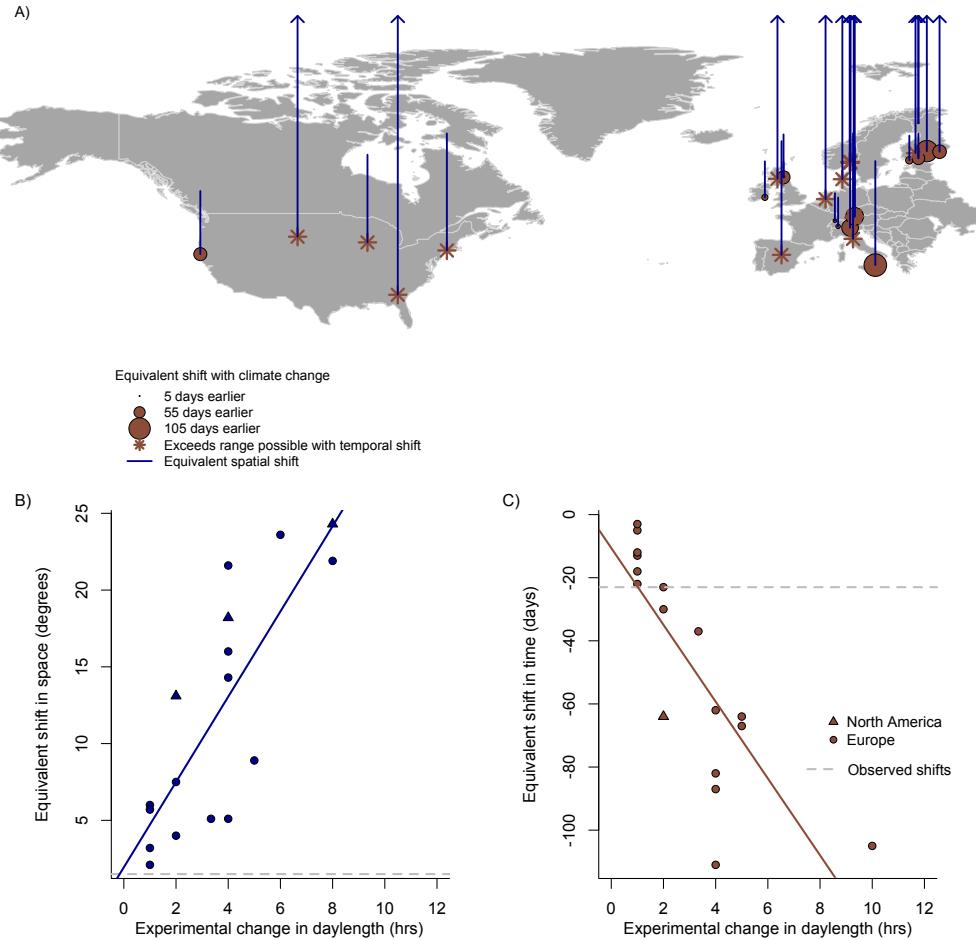


Figure 4: **OSPREE experiments that manipulate photoperiod**, and their equivalent spatial and temporal shifts, mapped (A), and graphed (B-C). Observed rates (dashed gray lines) 16.9 kilometers per decade (or approximately 1.5 degrees in 100 years) for spatial shifts (Chen et al. 2011) and 2.3 days per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

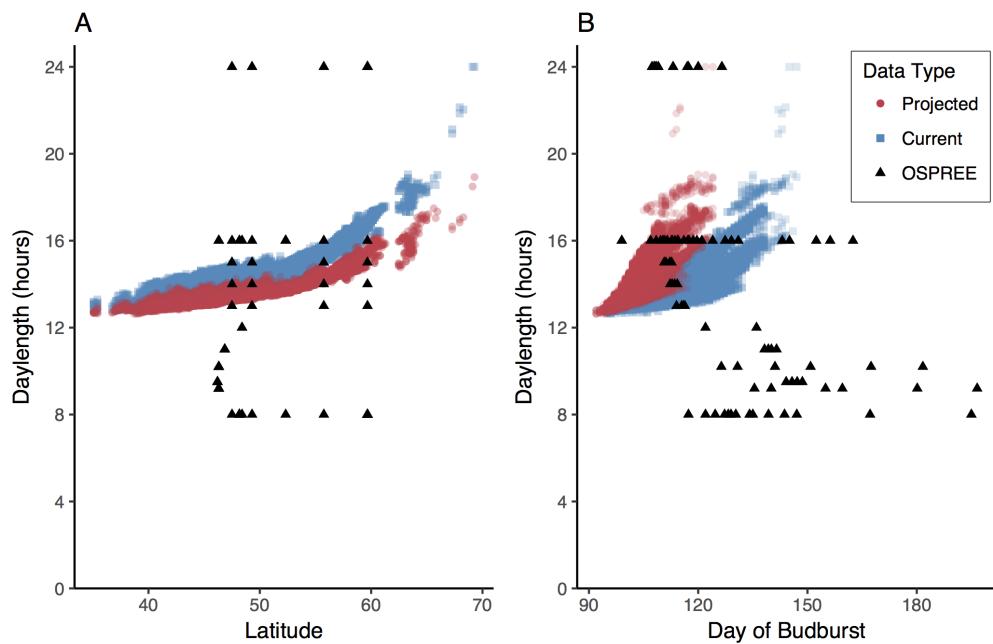
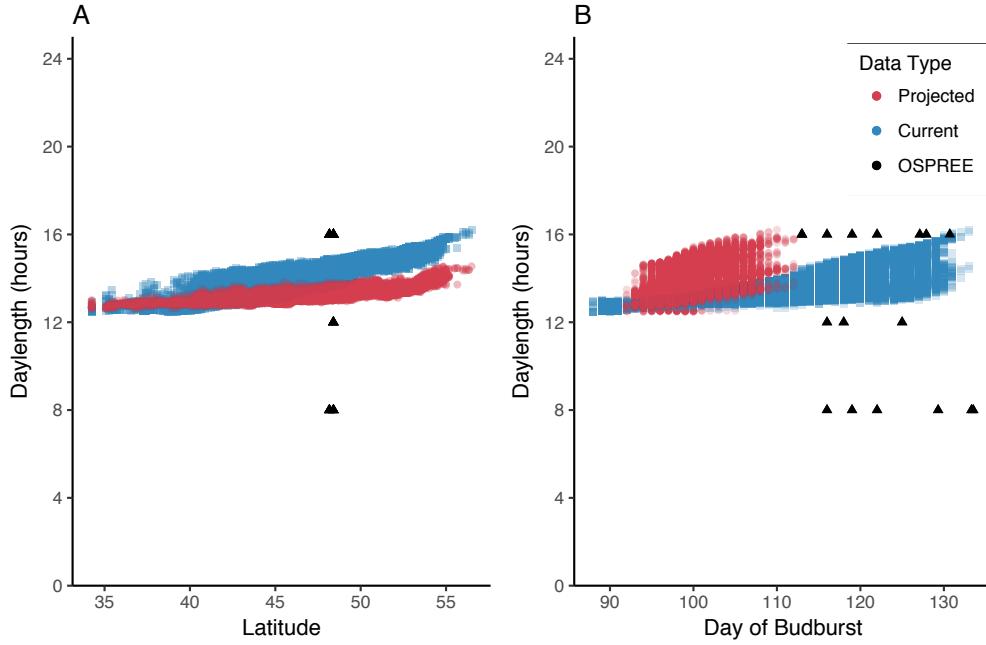
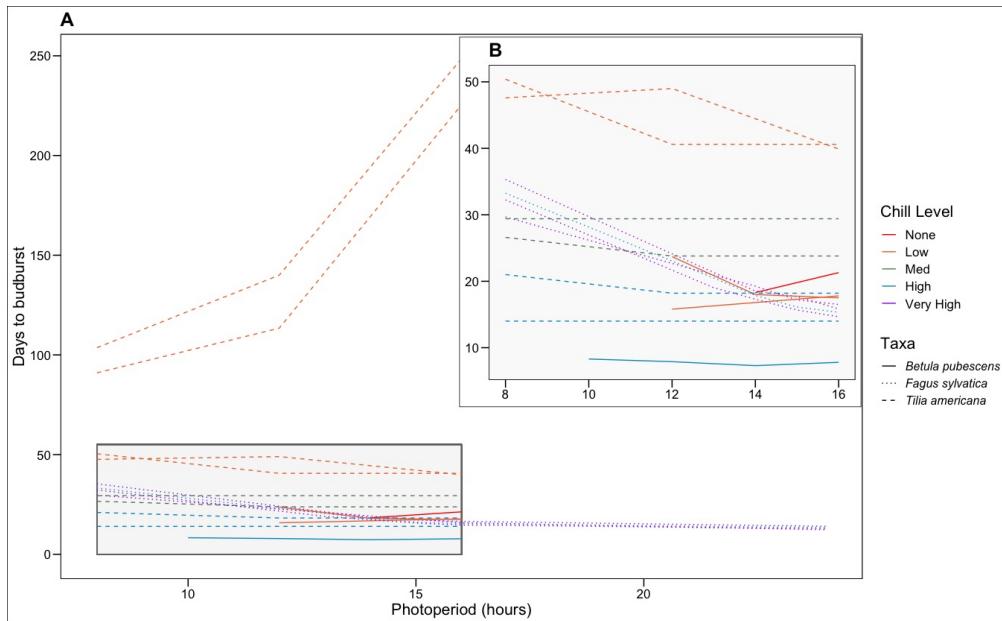


Figure 5: **Experimental treatments of daylength in the OSPREE database, shown by latitude (A) and by day of budburst (B)** for *Fagus sylvatica*. For comparison, we show the daylength when budburst occurs in its current and projected ranges (A) and in its current range only, with expected shifts in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



**Figure 7: Plant responses to changes in daylength vary across species and populations, and with the amount of chilling received.**