Spatial and temporal shifts in photoperiod with climate change

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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 precipition (Saikkonen et al., 2012).

Daylength may be stable and predictable over time, but the daylength that species *experience*, as they undergo climate change-induced shifts in space and time, will be altered. 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). It is unclear how these spatial and temporal shifts may 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 reaponses 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 it undergoes. Poleward shifts in species' ranges cause organisms to experience a wider range of daylength throughout the year (Figure 1). Elevational shifts, on the other hand, cause minimal changes in photoperiod throughout the year.

To date, most work 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 it's 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 organims may shift both their ranges and their phenology, simulataneously. Phenology typically varies with latitude (Figure 2a,b), and patterns can differ among years (i.e., a year that results in early green-up at 35°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 these altered photoperiods for forecasts of climate change impacts?

Daylength is known to control diverse 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 have alter these, and likely other, important responses.

It has been proposed that photoperiod may eventually become a limiting factor, constraining the ability of trees to shift their phenology with warming (Koerner and Basler, 2010; Vitasse and Basler, 2013; Morin et al., 2010). 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. 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 investifation. In some forecasting methods (e.g. species distirbution modelling), the role of photoperiod is largely ignored (i think this is true? add some citations). In other cases, photoperiod is incorporated into foreacasts, 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 temprature to break dormancy, as well as the type of response it ellicits (e.g., linear versus non-linear threshold) is unclear.

Conclusions

1. Organisms may experience large changes to the photoperiod they experience, under climate change, even if they do not shift their ranges spatially.
2. More studies needed with fine-scale changes in photoperiod.

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:

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, 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.
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.

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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
devries82_exp1	europe	51.98	5.66	8-24	16.00	ER	ER
falusi90_exp1	europe	46.03	10.75	9-13	4.00	16	-82
falusi96_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

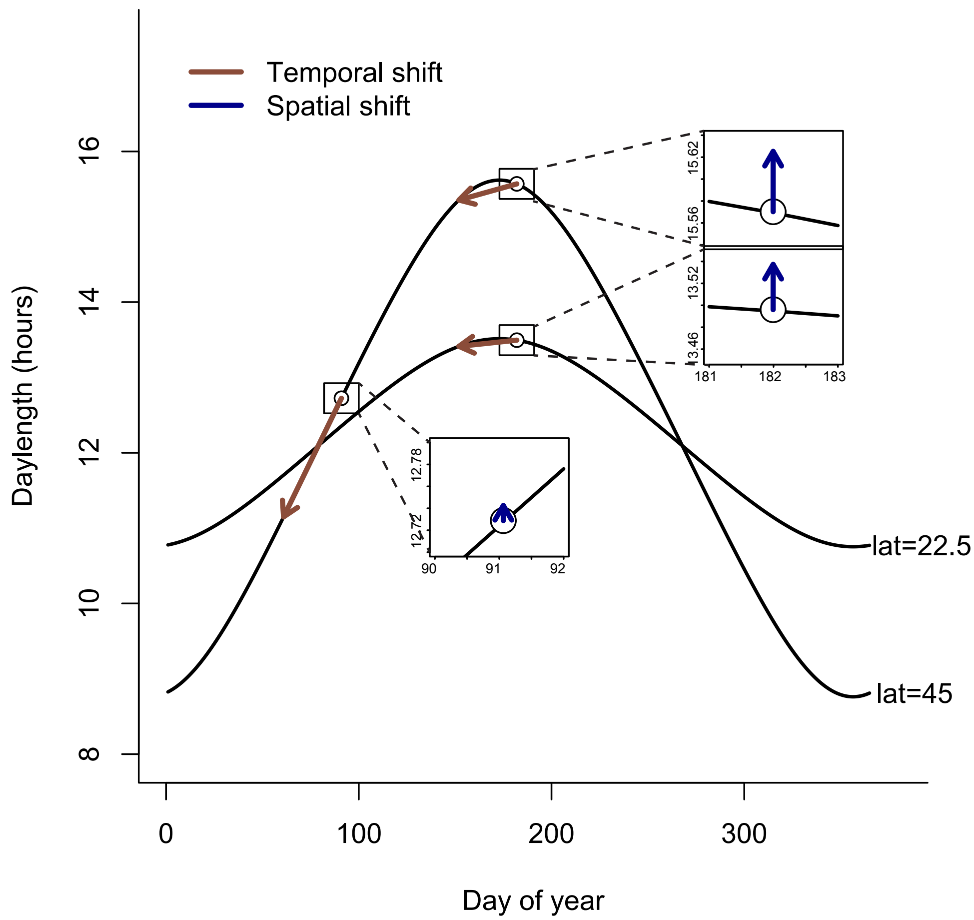

Figure 1: **Photoperiod varies with latitude and throughout the year**, such that temporal shifts in activity yield larger changes in experienced photoperiod compared with spatial shifts. Here, we show this variation at two latitudes, using hypothetical rates of spatial and temporal shifts: 30 days earlier 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 solcstice (e.g., DOY 182).

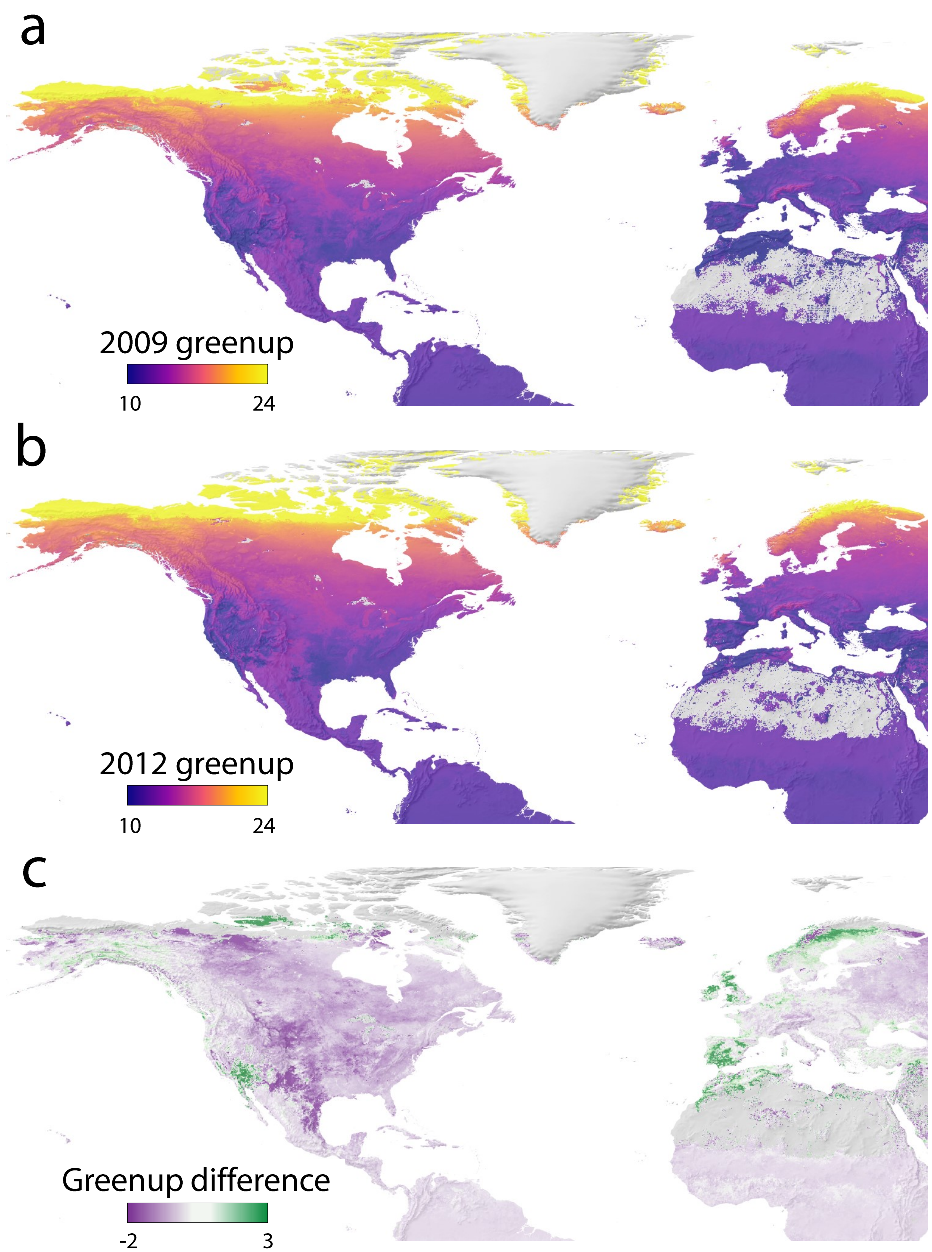

Figure 2: **The photoperiod on the green up date (start of spring) varies over space** and among years. Hours of daylight on the date of spring green up from MODIS satilite data across North America and Europe for an average (a) and early (b) North American start of spring. The differences between the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

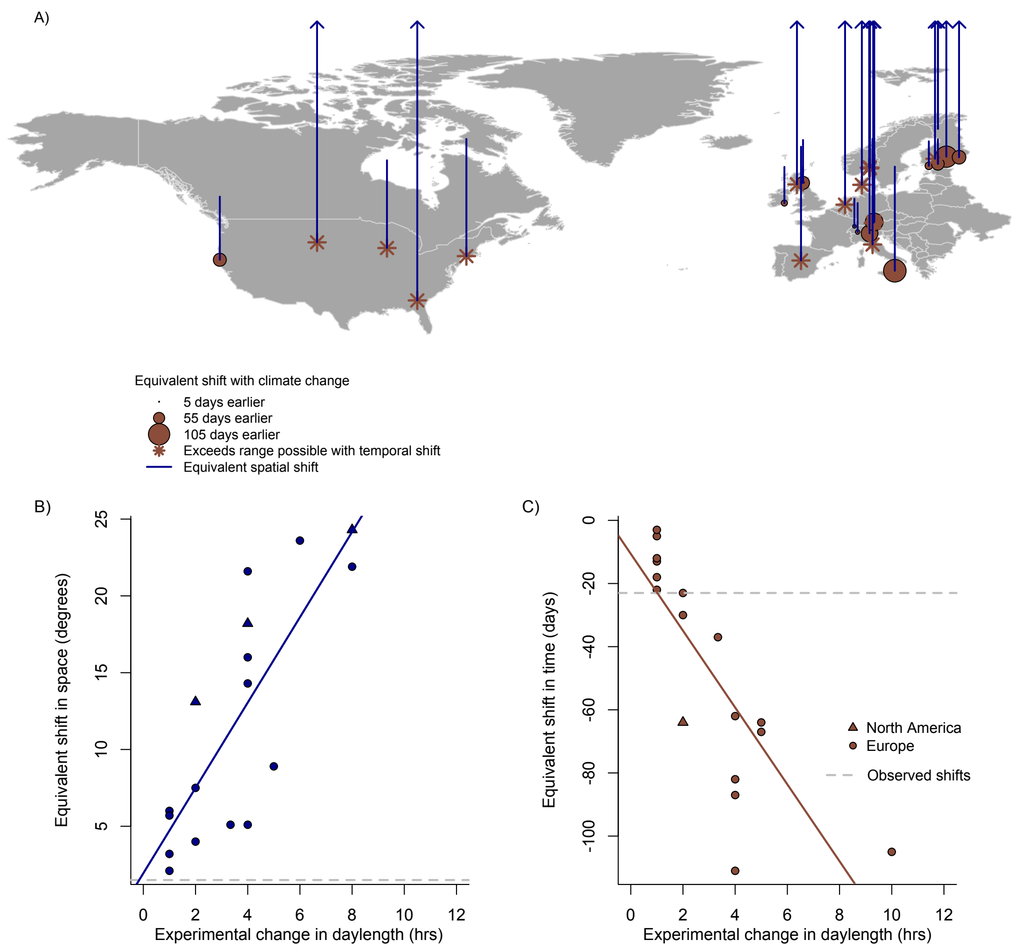

Figure 3: **OSPREE experiments that manipulate photoperiod**, and their equivalent spatial and temporal shifts, mapped (A), and graphed (B-C). Observed rates (dashed gray lines) 16.9 kilometers per decade (or approximately 1.5 degrees in 100 years) for spatial shifts (Chen et al. 2011) and 2.3 days per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

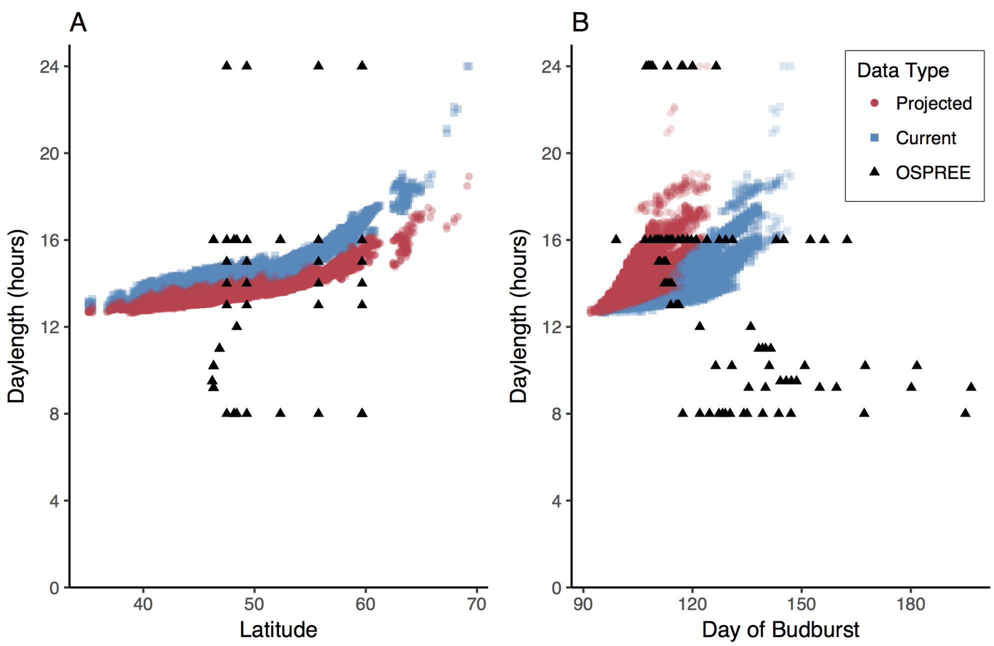

Figure 4: **Experimental treatments of daylength in the OSPREE database, shown by latitude (A) and by day of budburst (B)** for *Fagus sylvatica*. For comparison, we show the daylength when budburst occurs in its current and projected ranges (A) and in its current range only, with expected shifts in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

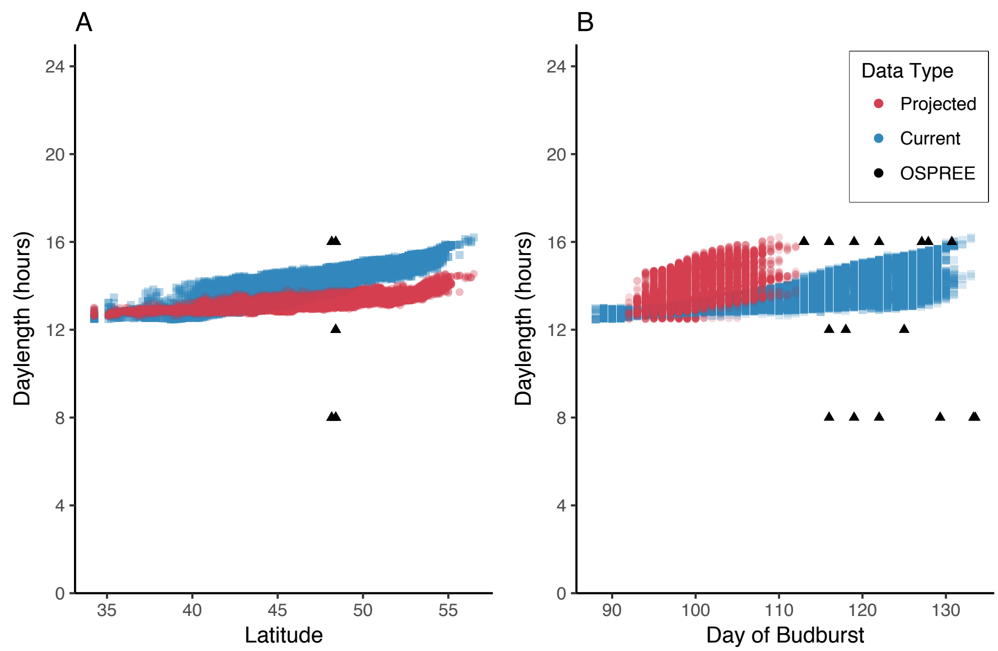

Figure 5: **Experimental treatments of daylength in the OSPREE database, shown by latitude (A) and by day of budburst (B)** for *Quercus robur*. For comparison, we show the daylength when budburst occurs in its current and projected ranges (A) and in its current range only, with expected shifts in phenology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

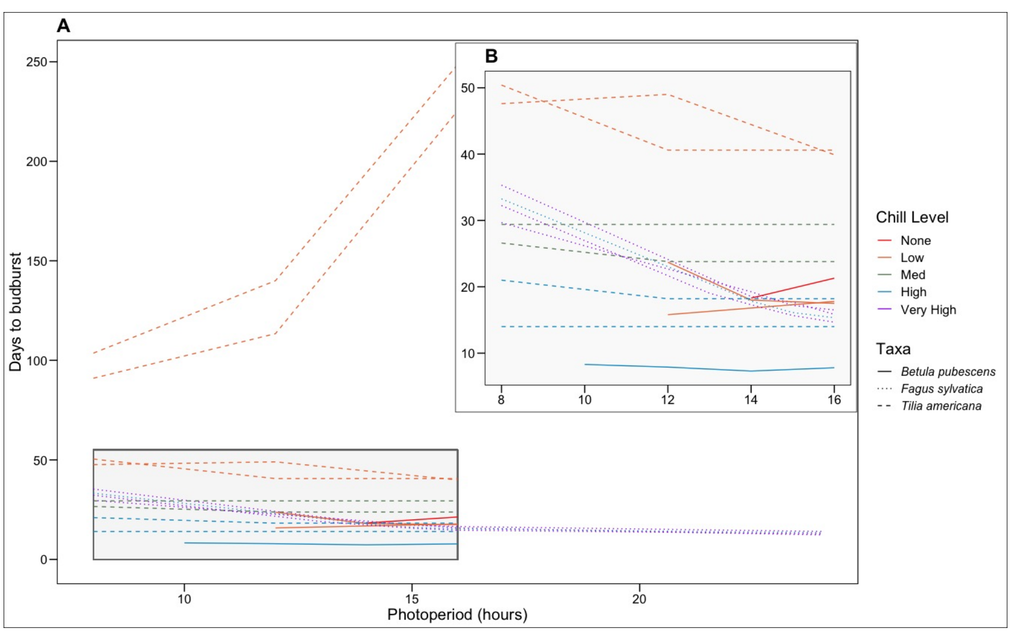

Figure 6: **Plant responses to changes in daylength vary across species and populations, and with the amount of chilling recieved**.