Impact of environmental variables on tundra vegetation onset of flowering explained by survival modelling

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Miljövariablers påverkan på tidpunkt för blomning hos tundravegetation förklarat med riskmodellering
Impact of environmental variables on tundra vegetation onset of flowering explained by survival modelling

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Master thesis, 30 credits, in physical geography and ecosystem science

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Preface

This thesis was conducted with data from Gothenburg university collected within the International tundra project. First, I would like to give a special thanks to Mats Björkman and Robert Björk who introduced me to the topic and taking the time to give comments and valuable inputs on my project. Thanks also to Ulf Molau who started up the data collection, as well as to all the field assistants who have been collecting the data in field and making this project possible. Finally, I would like to thank Veiko Lehsten for introducing me to the potential of hazard models and for valuable input to the project.

Hanna Jonsson

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Abstract

Timing of phenological events are highly related to climate and is one of the first signs of ecosystem responses to the climate change. Timing of flowering phenology is an important trait influencing the distribution and fitness of plants species. Tundra ecosystems are particularly important to study these effects due to short growing seasons, poor pollinator community and a particularly pronounced expected climate change. In this study proportional hazard models are used to explain the impact of environmental variables and experimental warming tundra plant species' onset of flowering. The results show that global radiation and precipitation are negatively linked to onset of flowering, whereas thawing degree days only showed some weak relationship to flowering. The negative impact of both radiation and precipitation are addressed to cooling the soil surface temperature and indicate further that local air temperature is not sufficient for explaining changes in onset of flowering.

In concordance with earlier research higher TDD sum previous year show a negative effect on the timing following year. The effect was particularly large on the early flowering species. Responses to OTCs were stronger among late flowering dwarf shrubs, although the effect on early flowering species may have been out competed by snow melt dates. The study further suggests that survival modelling can be successfully used in phenology research providing accurate predictions of onset of flowering. Further studies of how the model application perform beyond the study area still needs to be tested.

Keywords: Flowering, Phenology, Cox proportional hazard model, Tundra, International tundra experiment, Climate change, Physical Geography and Ecosystem analysis

Sammanfattning

Tidpunkten för växters fenologiska skeenden är starkt kopplat till klimatet och ett av de första tecknen på ekosystemens gensvar på klimatförändringar. Tidpunkten för blomning är viktig för växtens kapacitet och fördelning av arter. Dessa effekter är särskilt viktiga att studera i tundraekosystem där växtsäsongen är kort, där det finns relativt få pollinerare, samtidigt som klimatförändringarna förväntas bli särskilt påtagliga. I den här studien används proportionella riskmodeller för att förklara effekterna av miljövariabler och experimentell uppvärmning på tundraväxters första blomning. Resultaten visar att global instrålning och nederbörd är negativt kopplade till första blomningen. Temperatur i form av ackumulerade grader över 0 visar bara svag effekt. Den negativa påverkan från både instrålning och nederbörd kan förklaras med förändrad marktemperatur och indikerar vidare att lokal lufttemperatur inte är tillräcklig för att förklara förändringar i första blomning.

Liksom tidigare forskning visat, har tidigares år ackumulerade temperatursumma en försenande effekt på efterföljande års blomningstider. Effekten är särskilt stor på tidigt blommande arter. Responsen på experimentell uppvärmning var kraftigast hos sent blommande ris. Effekten kan dock ha reducerats av tidpunkten för snösmältning. Studien fastslår vidare att proportionella riskmodeller kan framgångsrikt användas inom fenologi studier för att ge noggranna förutsägelser om blomningsstart. Vidare studier i hur modellerna presterar utanför studieområdet behöver fortfarande undersökas.

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1. Introduction

Plant phenology is the study of the seasonal timing of reoccurring plant events such as flowering, leaf bud burst and senescence and how it is affected by biotic and abiotic factors. Timing of phenological events are highly related to climate and is one of the first signs of ecosystem responses to the climate change (Parmesan, 2007). Global warming is occurring more rapidly in high latitude areas than elsewhere and therefore phenological changes in this region may be more pronounced (IPCC, 2014). Flowering phenology is an important trait influencing the distribution and fitness of plants species both due to the probability of meeting harsh climatic conditions (e.g. spring frost events damaging buds) and competition with other plants (Chuine, 2010, Wheeler et al., 2015). Changes in flowering timing may also influence the seed-set success because of the potential temporal mismatches with pollinators. This is particularly relevant for tundra ecosystems where the pollinator community is poor and the growing seasons is short (Gillespie et al., 2016). In order to understand how the tundra ecosystem plant communities are affected by climate change and further will be, it is important to estimate the effect of environmental variables.

The temperature is increasing and precipitation patterns are changing but even though there are some general trends in how the climate is changing in the Arctic and sub-Arctic (IPCC, 2013), there is no global consistent direction of spring phenology trends. Previous studies have revealed both preponed and postponed spring flowering dates the last 30 years and the responses of environmental variables have shown to be both species specific and location specific (CaraDonna et al., 2014).

We need a better understanding of drivers of variation in phenological responses to climate change to be able to predict future responses in tundra communities. A common method to study the effect of climate and environment on plant phenology is mixed linear regressions and threshold models. Flowering events are described by threshold of e.g. temperature sums such as thawing degree days and growing degree days or regressed against fixed periods of temperature (e.g. mean June temperature) and snowmelt (Molau et al., 2005, Oberbauer et al., 2013, Prevéy et al., 2019, Mulder et al., 2017, Gillespie et al., 2016). This is an efficient and user-friendly approach, but it is also a simplification of phenology and require a causal connection between the climatic variable and the timing. Using fixed periods of observation also require the causal connection to be constant with time which for many ecosystems is not the case, especially when the climate is changing. Further, these methods do not give within year variation because it is a regression made by annual averages instead of individual events. Annual variations are however important to examine in this context because even if the average individual of a plant species is advancing towards mistiming, there may still be so that the earlier or later individuals may be still synchronized with pollinators (Gienapp et al., 2005).

Survival analysis is a division of statistics dealing with time until event analyses. Proportional hazard models, such as the one proposed by Cox (1972), was initially used for medicinal analyses of patients survival. By taking all values measured until the onset of flowering for all individual observations instead of annual means based on fixed time periods, it allows us to predict also within year variation.

Survival analyses can be used for any *time to event* data (Kleinbaum, 1996) and in later years survival modelling has also been used in ecological studies. Examples range from improved understanding of first occurrence of potato late blight (Lehsten et al., 2017) to developing a descriptive model for timing of laying of birds (Gienapp et al., 2005). Templ et al. (2016) found that survival modelling could be used as an adequate tool to analyse what influences flowering phenology, using data from first flowering events of dandelions (*Taraxacum officinale*). The study further suggests that the survival model (proportional hazard model) could outcompete traditional regression models (Templ et al., 2016). Similar results was found for survival modelling on cherry tree flowering (*Cerasus spp.*) (Terres et al., 2013). This method has however, to the knowledge of the author, not been used to analyse the impact of environmental variables on tundra plant species.

Due to the time consuming and expensive nature of day by day phenological measurements and the often remote location of tundra ecosystems, there is still few continuous long term records of plant phenology available. An attempt to capture the phenological changes in a more efficient way is snapshot phenology (Molau and Molgaard, 1996, ITEX, 2014). Snapshot phenology is a method of counting buds/flowers of plant species on a plots level every 10th day as a substitute for day by day measurements.

1.2 Aim

The objective of this study is to improve our understanding of environmental controls on first flowering timing on sub-arctic tundra vegetation by applying proportional hazard models to flower phenology. I have used 10 years of snapshot phenology data for 8 species in 4 alpine tundra plant communities, from the Latnjajaure catchment in northern Lapland, Sweden, to answer three research questions:

Q1. How do environmental covariates affect the onset of flowering?

Q2. Does experimental warming lead to earlier onset of flowering?

Q3. Can proportional hazard models be used for onset of flowering and if yes what is the predictive power?

2. Theoretical background

2.1 Spatial and temporal differences in flower phenology

The effects of climate change on successional phenology vary among species and plant communities. There is a species-specific response to climatic variables and the effect differs also with different phenophase stages in the annual reproductive cycle. Different phenological stages of flowering such as first day of flowering, peak flowering and flower senescence, have shown to not shift uniformly but respond differently to climate changes (Molau, 1997, CaraDonna et al., 2014). The effect of warming climate seem to have a greater impact on late flowering species than early-flowering tundra species, resulting in a shortened flowering season on a community level as the late bloomers tend to flower earlier in the season (Prevéy et al., 2019). There may also be variation in responses to climate within the same species depending on local conditions. A study of the dwarf shrub *Cassiope tetragona* showed, for example, a greater shift towards earlier flowering dates in colder high arctic sites than same species in warmer sites (Prevéy et al., 2017).

2.2. Environmental drivers on onset of flowering

2.2.1 Temperature

The environmental variable which is most commonly used to explain onset of flowering in tundra ecosystems is temperature. Both predefined period averages of temperature (Prevéy et al., 2017) as well as cumulative temperatures until the onset of a phenological event have been able to explain flowering phenology (Molau et al., 2005, Oberbauer et al., 2013, Wheeler et al., 2015). Temperature is a main limiting factor for tundra plant species. With temperatures $> 0°C$ the soil melts and can provide plant roots with water and nutrients again. Thawing degree days (TDD)(the accumulated sum of temperature above $0°C$) can therefore be a sufficient tool for modelling the effect of temperature on phenology (Molau et al., 2005). The responses to temperature differ between species and ecosystems. Dry communities are generally located on ridges exposed to wind which gives thin snow cover in winter. This gives both colder winter soil temperature due to less snow insulation and makes the ground snow free earlier in the season than in the protected depressions. Plants in dryer communities are therefore generally more limited by temperature than more moist snow patch communities (Walker et al., 1993).

2.2.2 Global radiation

Global radiation is a measure of the solar radiation reaching the earth surface and it is necessary for photosynthesis to occur. For the plants to start grow in spring a certain amount of global radiation is needed to trigger the development. However, not all studies show the same pattern. Molau (1997) found accumulated global radiation (AGR) to be positively corelated to the pre-floration time, which is the number of days from snow melt to first flowering, for the tundra forb *Ranunculus nivalis*. Another study from the same area did not

find the same correlation between AGR and the onset of flowering for the studied tundra species (Molau et al., 2005).

2.2.3 Precipitation

Alpine sub-arctic ecosystems are generally not limited by growing season precipitation for growth (Keuper et al., 2012). The relatively low temperatures make the total evapotranspiration stay low so that even poorer precipitation regimes keep a lot of the moisture in the ground. Previous studies have shown that precipitation can even have a negative effect on flowering timing due to a cooling effect on the surface temperature. Precipitation has shown to be negatively liked to the timing of flowering (Molau, 1997).

2.2.4 Preformation

Most early flowering arctic/alpine plant species produce flower buds already in the year prior to flowering e.g. *Eriophorum vaginatum* (Shaver et al., 1986) and *C. tetragona* (Hollister et al., 2005). This makes growing season length and temperature sums important for the following year. Mulder et al. (2017) found that both the total accumulated thawing degree day from previous growing season has impact on the flower phenology. Years with summer temperatures above average caused delayed onset of flowering whereas lower than average summer temperatures preponed the onset. The effect of colder summer temperatures was however stronger than for the warmer years which had a mitigating effect on the overall trend towards earlier flowering dates (Mulder et al., 2017). The effect of previous seasons total degree days does not, however, always relate to the coming years flowering. Thórhallsdóttir (1998) found in her study of flowering phenology on the central highland of Iceland, no such relationship.

2.3 Open top chambers and onset of flowering

Open top chambers (OTC) have been used successfully for in situ experimental warming on several locations within the international tundra experiment (ITEX). The effects of OTCs on the microclimate vary between sites but Bokhorst et al. (2013) estimated from 20 OTC warming experiments a mean increase in annual temperature (both air, soil and soil surface) by 0.8°C, with a range of 0.5-1.3°C. Although the effect of temperature is not always apparent as increased mean soil temperatures the chamber has shown to increase the number of high temperature extremes during summer and decrease freeze thawing events in spring (Bokhorst et al., 2013). The OTCs only have insignificant influence on incoming radiation and precipitation (Marion et al., 1997).

The chambers act as snow traps by increasing snow depth, which act as winter soil warming as well as giving later snowmelt. The warming has shown to increase vegetation biomass growth, canopy height and change species composition. Tundra ecosystems with already high ambient temperatures show an increase in deciduous shrubs. In areas with colder temperatures (e.g. high arctic) the response has been strongest among graminoids. Evergreen

shrubs have shown to be rather moisture dependent than actual effects of warming itself. Long term warming experiments also show trends of vascular plant diversity decline (Elmendorf et al., 2012).

3. Method

3.1 Site description and set up

Plant phenological data were collected for the time period 2009-2018 from in total 40 plots around the Latnjajaure Field Station (LFS) (68°22'N, 18°13'E, ~1000 m above sea level). The LFS is situated in the Latnjajaure valley in northern Lapland, Sweden (Figure 1) and has a mean annual temperature of -1,31 C° (± 7.71 C°) although there are large between year variations (Molau, 2001). Mean summer temperature (JJA) is 6,8 C° (± 4,5 C°) (LFS meteorological station 1992-2018) and mean annual precipitation is 846.5 mm (Katterjokk meteorological station 1992-2015) (SMHI, 2019). The valley is covered by a vegetation representative of the low Arctic with *Dryas octopetala*, *Cassiope tetragona* and *Carex spp.* as dominant species. The plots were established in four plant communities; dry heath, dry meadow, wet meadow and tussock tundra (Table 1) distributed on the eastern hillside of the Latnjajaure valley (Molau, 2001) (Figure 1).
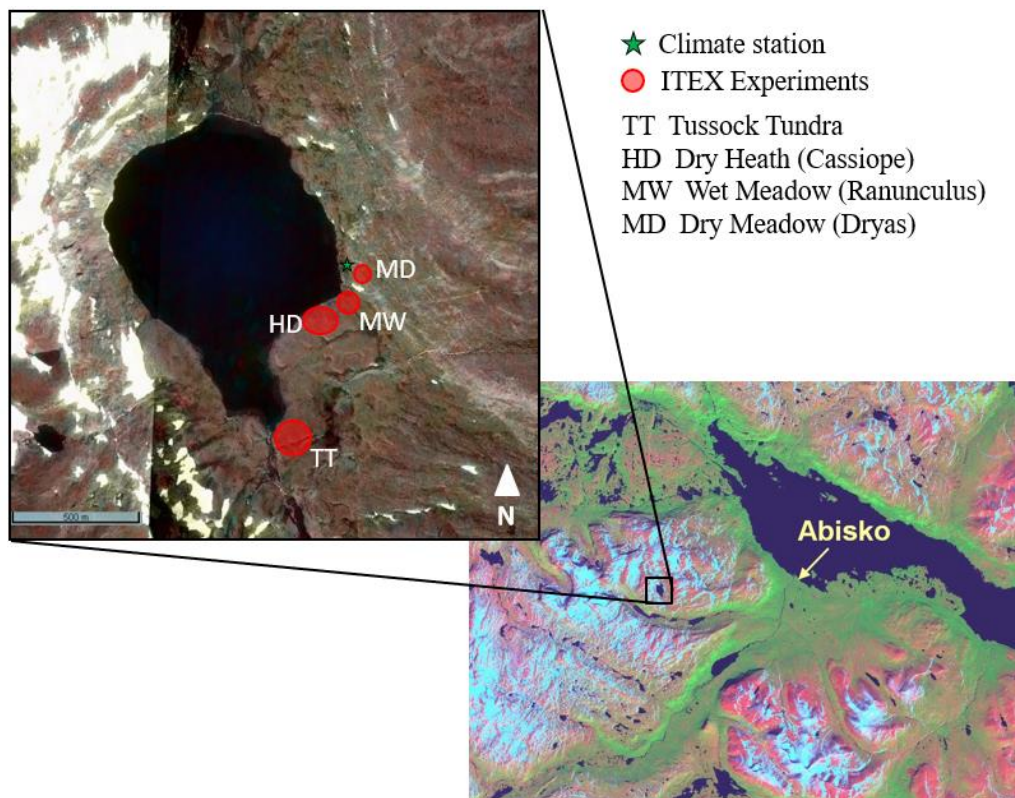
Figure 1. Location of Latnjajaure relative to Abisko and experiment setup in Latnjajaure valley.

Table 1. Species measured within each plant community.

Species	Plant Functioning Type	Common name	Community
Ranunculus nivalis	Forb	Snow buttercup	Wet meadow
Carex stans	Sedge	Water sedge	
Cassiope tetragona	Evergreen dwarf shrub	Arctic white heather	Dry heath
Vaccinium vitis-idea	Evergreen dwarf shrub	Lingonberry	
Eriophorum vaginatum	Sedge	Tussock cottongrass	
Phyllodoce caerulea	Evergreen dwarf shrub	Purple mountain heather	Tussock tundra
Vaccinium vitis-idea	Evergreen dwarf shrub	Lingonberry	
Dryas octopetala	Evergreen dwarf shrub	Mountain Avens	
Bistorta vivipara	Forb	Alpine bistort	Dry meadow
Vaccinium vitis-idea	Evergreen dwarf shrub	Lingonberry	

For each plant community there were 10 plots, of which 5 was exposed to experimental warming using hexagonal OTC (Molau and Molgaard, 1996) and 5 control plots. During 2017 and 2018 soil temperature and soil water content (SWC) was measured during 6 opportunities throughout the growing season. To analyse the difference between OTCs and control plot, paired t-tests were used.

3.2 Data collections

3.2.1 Snapshot phenology

Throughout the growing season the plots were visited every 10th day starting approximately 15 June until 20 August for the years 2009–2018. The field work was done by field assistants through Gothenburg University. In the field, six phenological stages were recorded; bud, flowers just open, full flower, late flower, flower shed/wilted/fruit, unripe fruit and ripe fruits. Whether or not a species was present but without flowers was also recorded as yes/no but not used for analysis in this study. The numbers of flowers for each species and phenophase was counted and noted in a standardized protocol together with date and Julian day; day of year (DOY) starting from January 1. The species recorded are specified in Table 1.

During 2009, 2010 and 2014 the plots were visited 2, 4 and 5 times respectively. Thus, for early flowering species such as *E. vaginatum* and *R. nivalis* only data starting 2011 was used for modelling. The selection of what years to use for what species was done manually with the other year's data as proxy for whether first flowering events would be captured or not with the few data points available.

To minimize the bias of having different field assistants counting the flowers throughout the growing season and between the years, a phenophase score was calculated for each plot and measurement occasion. Following the example of Mulder (et al., 2014), buds (score = 1), flowers just open (score = 2), full flower (score = 3), late flower (score = 4), flower shed/wilted/unripe fruit (score = 5), ripe fruits (score = 6) was given a score from which an

average score for each plot and measurement occasion was calculated (e.g. a plot with in total 2 buds and 2 fully open flowers of *V. vitis-idea* would receive a score of 2). In this study first flowering event is set to when a plot reaches a phenophase score > 2.

3.2.2 Climate data

Climatic data was gathered mainly from the LFS meteorological station, where mean daily temperature and global radiation are measured hourly. Precipitation data is obtained at the nearby meteorological station in Katterjokk, providing daily mean values. The last 11 days in august 2018 there is missing data for temperature and global radiation. Data was instead taken from Katterjokk metrological station and calibrated using a formula derived from the relationship between the temperature and radiation data from LFS and data from Katterjokk meteorological station.

From the temperature, global radiation and precipitation, accumulated thawing degree days (TDD), accumulated global radiation (AGR) and accumulated summer precipitation (ASP) were calculated using the start date of May 15. TDD was calculated as the accumulated sum of mean daily temperatures above 0 C°(Molau and Molgaard, 1996). AGR was calculated as accumulated sum of mean daily global radiation. ASP was calculated as the accumulated sum of mean daily precipitation. Total growing season TDD sum of previous seasons (TDD_{sum}^{1yr}) was also calculated from the temperature data.

2.3 Data analysis

2.3.1 Cox proportional hazard model with time dependent covariates

To study how the environmental covariates affect the timing of flowering onset, Cox proportional hazard model with time dependent variables (from now on referred to as Cox model) was used to calculate their relative hazard ratios. The Cox model estimates the times to event as a baseline hazard multiplied by the effects of a set of covariates (Cox, 1972). The Cox model formula used in this study is defined in Equation 1.

$$h(t,X) = h0(t)_s e^{(\beta_1 X_1(t) + \cdots + \beta_n X_n(t))}$$ **Equation 1.**

Where *h (t, X)* is the hazard ratio at time *t*. *h0 (t)* is the time-dependent baseline hazard, with OTC specific responses stratified as *s*. β_n is the covariate coefficients from the fitted model and X_n contains the covariate vector. In this case the hazard is the probability of flowering at each time, given the subject is still a closed bud. The cox model assumes that the hazard is proportional for all subjects and the ratios do not change over time. A covariate can act to multiply the hazard by a certain amount, for example having an increase in AGR would increase the chance of flowering earlier by the power of the covariate specific hazard ratio.

Thus, the Cox model can further be used to predict a flowering probability for any given day of the year (daily hazard) based on input covariate data.

Different covariates were used for the different species due to species specific responses. Altogether, TDD, AGR, ASP and TDD_{sum}^{1yr} were the covariates used in different combinations. Several attempts were made to include other covariates into the Cox model such as previous year total nr of flowers, normalized difference vegetation index from satellite images as well as growing degree days (above 5 °C). Since none of these gave any statistically significant responses they were discarded in the final models.

The accumulated climate covariates (TDD, AGR and ASP) all correlated to each other ($r^2 >$ 0.65, p < 0.005) indicating that only one should be used at the time as input to the model. Therefore, the climate covariates with the best fit (lowest p-value, most reasonable residuals and highest coefficient) was used in the final model. Further, other covariates were added one at the time and then compared to the previous model (forward selection procedure). The model with the lowest Akaike information criterion (AIC) was finally used for coefficient estimation. This was done separately for all species and the covariates used in the final screening differed between species. In order to separate each event, a cluster function (in the survival package) was used to cluster the data by year. This is important since the covariates of each DOY changes between years.

2.3.2. Modelling OTC impact and community differences
Half of the plots were treated with OTC warming which consequently influence the microclimate of the plots. Hence, OTC presence was added as a stratum to the model. The strata function fits the model with two different baseline hazards, one for each stratum (OTC/control in this case). The difference in baseline hazard of OTC and control plots was then computed by running the model with all input covariates as 0 with the survfit function from the Survival package (Therneau and Grambsch, 2015).

To further analyse if there is a significant difference between OTC plots and control, a randomization test (Permutation test) was performed on the sample. Randomization test (Figure 2) tells the user if there is a pattern in the data that did not arise by chance. It is not possible to extrapolate beyond the sample since the sample in this test becomes the population, however, it gives a robust answer to whether there is a significant difference between the OTC and control plots (Manly, 2007). The procedure was to resample the entire sample 1000 times (events of both OTC and control plots) into groups with same OTC /control-ratio as the actual sample. Each resampling gave a new difference between the groups in the sum of the for the species-specific used climate variable (e.g. AGR) at the time of flowering. If the difference between OTC plots and control plots is greater than the 95% confidence interval, it is accepted as a significant difference.
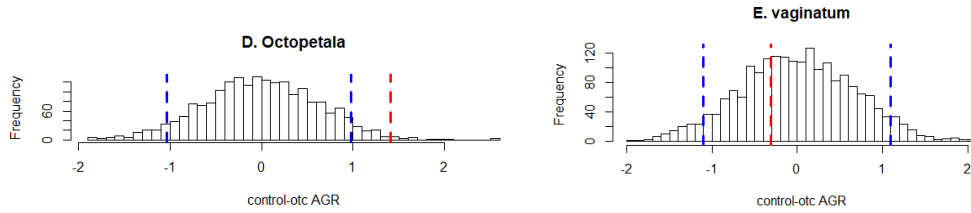
Figure 2. Examples of randomization test where the null hypothesis a) rejected and the response to climate variable is difference between OTC and control plots are flower with less b) accepted, no difference between. Blue lines representing 95% confidence interval of resampling, red line the measured difference between OTC and control plots.

3.3.4 Model prediction and validation

For model validation 70% of the data from all species was selected for bootstrap resampling 1000 times in order to get the 95 % confidence interval (CI 95%) for the model coefficients and p-value. To test the predictive power of the models, the function Survfit from the Survival package (Therneau and Grambsch, 2015) was used on the fitted models together with the 30% of the data left for model testing. The function produces survival curves with 95% confidence intervals within which there is a 95% chance that the interval contains the true percentage survival.

Following the example of Templ et al. (2016), the DOY when there was a predicted > 50 % chance of having a flowering event was extracted from the survival curves produced by the test data. The model predictions were then compared to the observed DOY for the same data points. The differences between modelled and observed DOY could then be used to calculate a root mean square error (RMSE) using Equation 2:

$$RMSE = \sqrt{\frac{\sum_n (M-O)^2}{n}}$$
   **Equation 2.**

The whole procedure of model training and validation was repeated 100 times to get a robust result, minimizing the effect of getting unrepresentable sub samples for either training or testing.

All data analysis and plotting was computed in R studio version 1.1.463 (with R version 3.5.2 (2018-12-20)) (RStudioTeam, 2016). For most graphics ggplot2 package was used (Wickham, 2016).

4. Results

4.1. Flowering dates and environmental covariates

The timing of first flowering event varies between species but also between years (Figure 3). Early flowering species, such as *E. vaginatum*, *R. nivalis* and *C. tetragona*, have for most years reached first flowering phase around DOY 180 with some exceptions. Whereas the later flowering species such as *V. vitis-idea* almost exclusively reaches first flowering stage after DOY 200. During the 10-year period there were no advancing or delaying trends for either of the species. The variance in timing could rather be liked to annual differences in environmental variables plotted in Table 2.
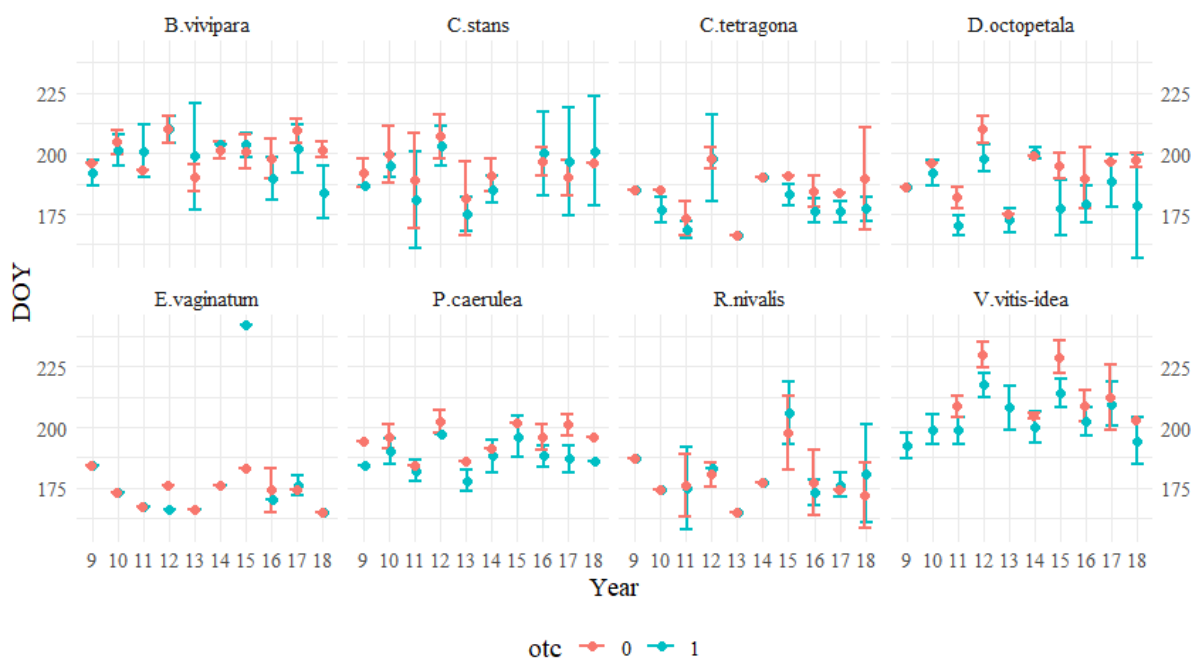
Figure 3. Mean day of year (DOY) for reaching first flowering stage (2) for the studied species. Error bars show standard deviation of replicates. Red points are control (slightly to the left) blue points (slightly right) are plots with experimental warming.

The two years that stand out with latest onset of flowering for most species are 2012 and 2015, which can be linked to 2012 having the coldest mean May temperature of all years and among the coldest June and July and with relatively high precipitation. 2015 is the year with the coolest June temperatures, highest June precipitation and overall lowest TDD for all three months. Protocol notes of spring frost events in all communities and flooding of the wet meadow plots could further be linked to the strong delayed flowering times in 2015 of the early flowering species *E. vaginatum* and *R. nivalis* respectively, as well as no flowering event at all for *C. stans*.

The years of earlier onset of flowering such as 2011, 2013 and for some species 2018 (*B. vivipara, V. vitis-idea* and *E. vaginatum*), also follow the climate data. For 2013 this is particularly apparent with both highest June temperatures, generally high temperatures all

months and relatively low precipitation. For 2011, June temperatures are particularly high and all three months' AGR is below the overall mean. 2018 had among the warmest May and July temperatures, although colder and more precipitation in June. The species responding same year are however mainly early flowering species (*E. vaginatum* and *R. nivalis* and the OTC plots) or the latest flowering species (*V. vitis-idea*).

Table 2. Climate data for May, June and July 2009-2018 from Latnjajaure Field station. Precipitation data from SMHI's meteorological station Katterjokk. Mean temperature, TDD, AGR and ASP separated year and month.

	Year	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
May	Mean Temperature °C	2,2	4,7	0,5	-1,5	3,3	-1,0	-0,5	1,7	-3,1	3,0
	TDD	33,2	74,3	15,2	15,7	53,2	25,2	3,5	14,7	6,6	29,1
	AGR (kWh/m2)	23,7	4,6	16,9	22,0	22,2	22,1	22,7	22,5	24,1	19,0
	Mean precipitation (mm)	2,3	1,3	1,7	2,4	0,7	0,9	1,8	0,8	1,7	1,6
June	Mean Temperature °C	3,8	2,1	6,8	2,8	7,2	4,0	1,8	3,7	4,3	2,3
	TDD	92,9	146,6	130,7	63,6	227,7	134,0	39,2	101,9	79,5	97,5
	AGR (kWh/m2)	77,2	32,0	68,6	77,7	75,9	80,0	82,3	80,5	91,5	66,2
	Mean precipitation (mm)	1,3	3,4	2,1	1,4	2,4	2,0	3,4	2,9	0,9	5,6
July	Mean Temperature °C	8,1	8,2	9,4	6,6	8,3	13,1	6,7	9,3	7,3	12,7
	TDD	286,5	319,4	378,9	216,6	458,8	386,0	172,8	311,8	245,3	322,7
	AGR (kWh/m2)	145,8	88,1	131,2	140,5	124,3	156,1	152,3	137,6	155,5	123,9
	Mean precipitation (mm)	2,0	3,6	2,4	4,5	3,9	1,0	2,5	3,2	2,6	1,4

Abbreviations: AGR = accumulated global radiation; TDD = thawing degree days (temperature sum above 0°C).

Incoming global radiation as AGR, is not fluctuating particularly much during the time period measured except for a dip in 2010. The highest and lowest AGR values do not seem to alone influence timing of flowering. 2017 for example, a year with particularly high AGR, only has some delayed flowering (e.g. *V. vitis-idea* and *B. vivipara*) and no apparent advanced flowering. The between year fluctuation which can be seen in global radiation do not correlate to temperature. (Figure 4 A). When AGR and TDD are plotted against each other, naturally they are correlated (both being cumulative) but exponentially (Figure 4B).
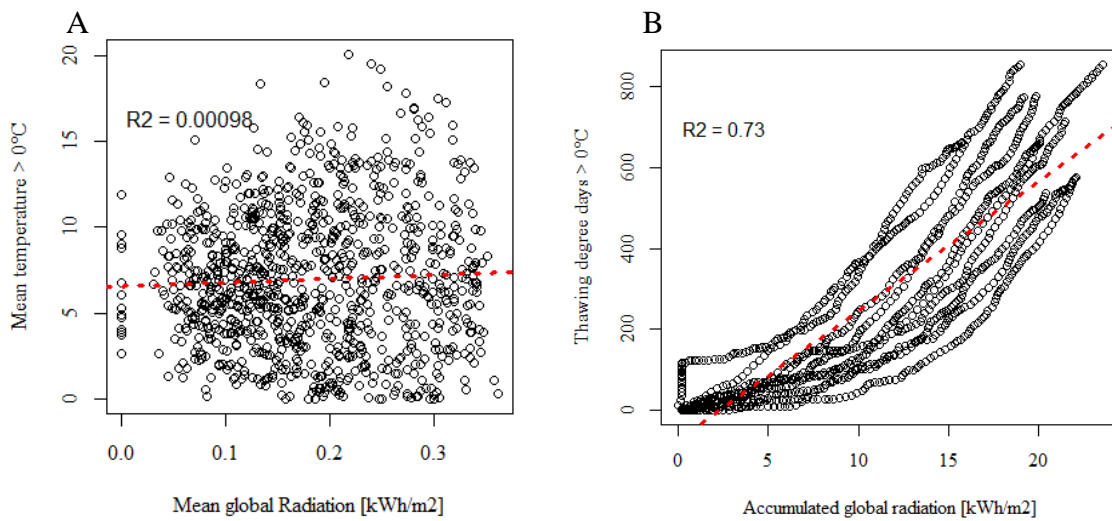
Figure 4. Temperatures > 0°Cc and global radiation plotted against each other as A) daily growing season means B) accumulated form as TDD and AGR. Dashed line representing linear fit and corresponding R^2 printed.

4.2. Cox model hazard ratios

Figure 5 show the probability of non-flowering, or survival which in this study is the chance of a plot reaching flowering stage, for one of the studied species (*D. octopetala*). The probability is a measure relative to the model specific covariate mean and the interactions with the experimental warming/control plots. This example tells us that the probability of flowering is higher for each given day of the year in the OTC plots. It does also show us that the confidence interval of the survival probability changes throughout the season. The dashed line for median flowering date corresponds to a 50 % chance of flowering.
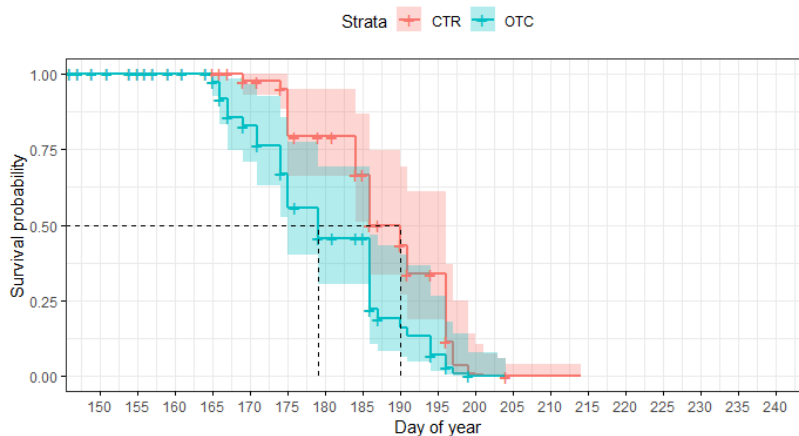
Figure 5. Survival curve of *Dryas octopetala* averaged over 2009-2018, divided by stratum where blue curve (first to flower) is from plots treated with experimental warming (OTC) and red curve control plots. Shadow areas show 95% confidence interval. Median flowering timing for both strata is marked out with dashed lines.

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In Table 3. hazard ratios, p values and model performances of the Cox model are reported. The hazard is calculated by multiplying the baseline hazard ($h0_{(t)s}$) with the exponential covariate ($X_{(t)}$) times their coefficients (β) (Equation 4);

$$h0(t)_s e^{(\beta X(t))}$$ **Equation 4**

A covariate coefficient (hereafter hazard ratios) larger than 1 consequently means that a variable has a positive effect on the hazard, i.e., it increases the probability of flowering. Hazard ratios below 1, indicate a decreased chance of flowering with every unit of the covariate.

The Cox models found statistically significant links between AGR and first flowering for half of the investigated species, *D. octopetala, E. vaginatum, C. tetragona* and *V. vitis-idea* (Table 3). All AGR hazard ratios are negative which imply that an increase in AGR has a delaying effect on onset of flowering.

The species who had a stronger link to precipitation (ASP) was *B. vivipara, R. nivalis* and *C. stans.* All were negatively liked to ASP (hazard ratios < 1). The hazard ratio was however not significant for *B. vivipara,* although <0.1 indicate a trend. Both *R. nivalis* and *C. stans* are wet meadow species, the community with the highest soil moisture levels (Figure 6).

P. caerulea was the only species responding strongest to TDD, although with non-significant hazard ratio. This was also the only positive hazard ratio.

The model of *V. vitis-idea* fitted with community as an interaction of AGR showed slightly different hazard ratios between the communities. The dry heath generated the lowest ratios suggesting these plots to be more delayed by increasing AGR than the Tussock tundra and the Dry meadow.

The end of growing season TDD sums from previous year (TDD_{sum}^{yr1}) does all have negative hazard ratios but are statistically significant only for *E. vaginatum, P. caerulea*, *R.nivalis* and *C. tetragona*.

4.3 Baseline hazards of open top chambers

SWC was significantly lower in the OTC plots than the control plots for both the dry meadow (34 % compared to 18 %, $p<0.05$, paired t test) and wet meadow (54% compared to 61%, $p<0.05$, paired t test) (Figure 6). No significant difference was found for tussock tundra or the dry heath plots. Highest mean SWC of both OTC and control was found in the wet meadow community. The lowers SWC was found in the dry heath. For soil temperature there was no significant differences between the communities ($p>0.05$). The was also no significant differences in summer soil temperature between the OTCs and the control plots for either of the plant communities (Figure 6).

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Table 3. Coefficients and significance of covariates of the best models for each species. The covariates give the change in risk of flowering time associated with a unit increase of the covariates. Bold symbols indicate significance.

Community	Species	Covariate	Covariates Coefficient [CI 95%]	p value	Model Likelihood ratio test	df	p value	RMSE
Dry meadow	Dryas octopetala n=92	**AGR**	**0.8158 [0.80-0.83]**	<0.01	15.59	2	**0.004**	7.66 [7.1-8.2]
		TDDsum yr - 1	0.997 [0.99-1.00]	<0.1				
	Bistortia vivipara n=82	ASP	0.9924 [0.99-1.00]	<0.1	9.97	2	**0.049**	8.02 [6.7-9.9]
		TDDsum yr - 1	0.995 [0.99-1.00]	<0.1				
Tussock tundra	Eriophorum vaginatum n=69**	**AGR**	**0.6183 [0.60-0.64]**	<0.001	24.18	2	**<0.001**	7.95 [6.8-9.2]
		TDDsum yr - 1	**0.9948 [0.99-1.00]**	<0.05				
	Phyllodoce caerulea n=80*	TDD	1.0049 [1.00-1.01]	0.15	13.82	2	**0.008**	5.74 [4.3-6.8]
		TDDsum yr - 1	**0.9953 [0.99-1.00]**	<0.05				
	Ranunculus nivalis n=64*	**ASP**	**0.9640 [0.96-0.97]**	<0.001	31.16	2	**<0.001**	5.26 [4.4-6.1]
		TDDsum yr - 1	**0.994 [0.99-1.00]**	<0.01				
Wet meadow	Carex stans n=67	**ASP**	**0.9767 [0.97-0.98]**	<0.05	11.12	2	**0.02**	8.41 [7.3-9.3]
		TDDsum yr - 1	0.996 [0.99-1.00]	<0.1				
Dry heath	Cassiope tretagona n=84*	**AGR**	**0.7948 [0.77-0.81]**	<0.05	21.9	2	**<0.001**	7.172 [5.4-8.7]
		TDDsum yr - 1	**0.9942 [0.99-1.00]**	<0.05				
Multiple	Vaccinium vitis-idea n=162	**AGR x Dry Heath**	**0.6757 [0.66-0.71]**	<0.01	33.9	4	**<0.001**	6.54 [6.1-7.8]
		AGR x Dry Meadow	0.6971 [0.68-0.74]	<0.01				
		AGR x Tussock Tundra	**0.6948 [0.67-0.73]**	<0.01				
		TDDsum yr - 1	0.9975 [0.99-1.00]	0.2				

Abbreviations: AGR – accumulated global radiation, TDD – thawing degree days, ASP-accumulated summer precipitation, OTC – open top chamber (experimental warming), TDDsumyr1 – accumulated end of season TDD previous year. RMSE – root mean square error.

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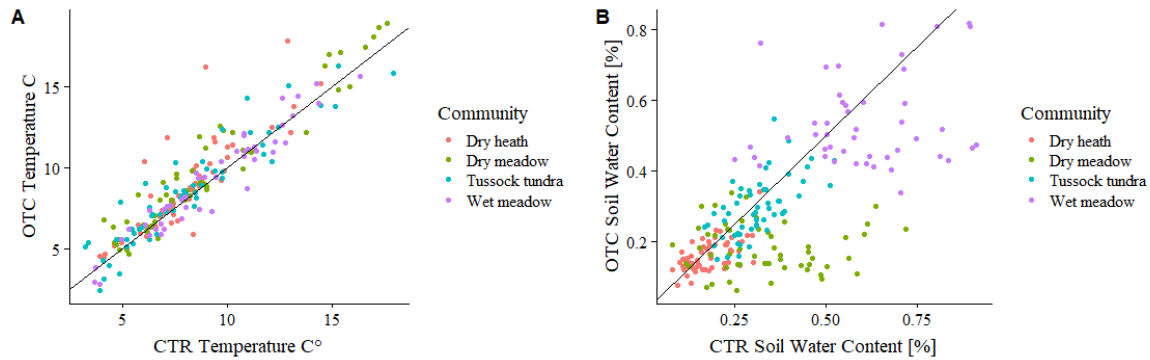
Figure 6. Comparison of plots with experimental warming (OTC) and control plots A) Soil temperature and B) Soil water content. Black line shows 1:1

The effect of OTCs investigated by randomization test was significant for three species, *D. octopetala*, *P. caerulea* and *V. vitis idea* (Table 4). This indicates that the difference in accumulated climate covariate reached at time of flowering was not increased by chance but could be addressed to the presence of OTCs. This was not confirmed for the other species, indicating that the OTCs did not have any significant effect. A similar pattern was found in the stratified baseline hazard (the risk of flowering at time t in case of no covariate interactions). For all three species suggested to be influenced by the OTCs the mean probability of having a flowering event for the OTC plots reaches 0.5 before the control plots (Figure 7A-C). The difference between treatments is significant (no overlap of confidence intervals) especially early in the growing season. The difference between treatments is not apparent for the species not responding to OTC warming (e.g. Figure 7D).

Table .4. Results from a two-way randomization tests on if there is an effect of OTC on onset of flowering.

| Community	Species	Covariate	OTC effect
Dry meadow	Dryas octopetala n=92	AGR	Positive
	Bistortia vivipara n=88	AGR	n.s
Tussock tundra	Eriophorum vaginatum n=69	AGR	n.s
	Phyllodoce caerulea n=80	TDD	Positive
Wet meadow	Ranunculus nivalis n=64	ASP	n.s
	Carex stans n=67	ASP	n.s
Dry heath	Cassiope tretagona n=84	AGR	n.s
Multiple	Vaccinium vitis-idea n=162	AGR	Positive
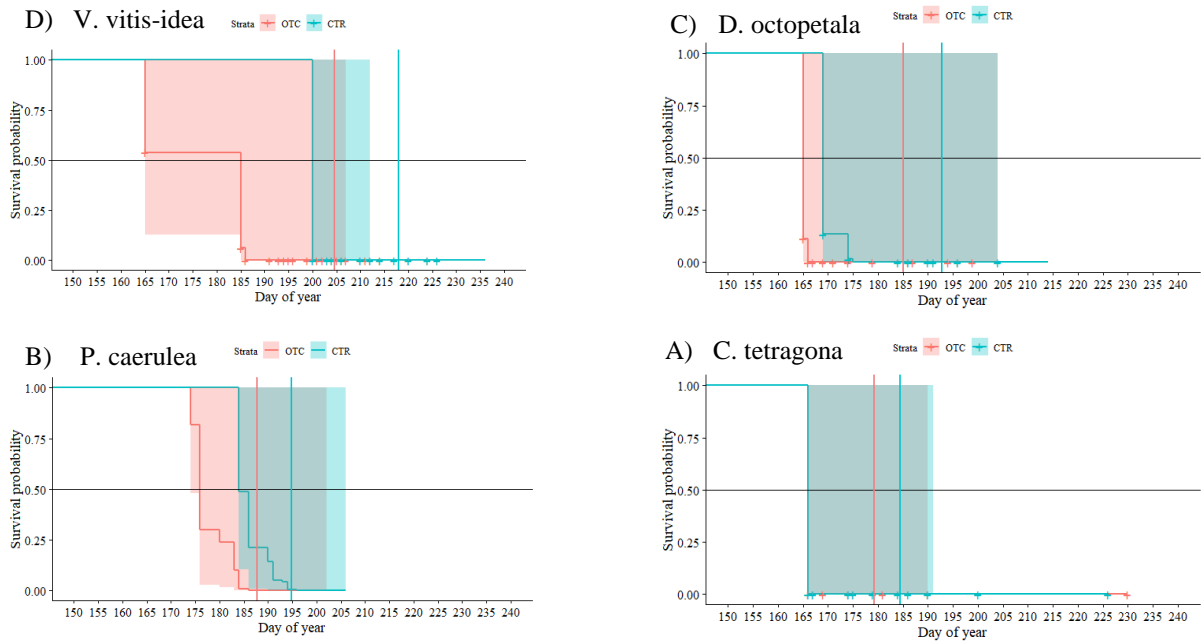
Figure 7. Baseline hazard of first flowering stage for species responding to OTC treatment (A-C) and one of the species not responding to OTC treatment (D). Shaded area corresponds to 95 % confidence intervals. Vertical lines show mean flowering timing with covariate interactions included for OTC (red, to the left) and control (blue to the right).

4.4 Predicting onset of flowering

The predicted DOY where there is a 50% chance of reaching first flowering fit to the observed with a RMSE range of 5.2-8.4 (Table 3). The two lowest RMSE values was gained by the *R. nivalis* model and the *P. caerulea* model although the later had a nonsignificant hazard ratio and the likelihood ratio test shows the model to be only slightly better than the null model (without predictors).

For all models the deviations were highest for observations which were earlier or later than the *bulk*. For *E. vaginatum* where most of the observed flowering dates were between DOY 170-175 and only a few residuals (Figure 3), this was particularly apparent for the few late flowering events observed (Figure 8). The magnitude of the deviations differed between the species.
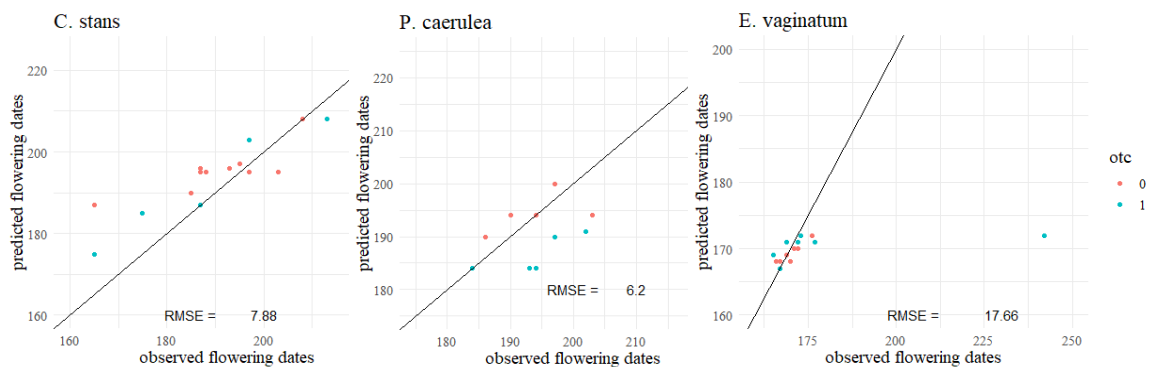
Figure 8. Examples of modelled day of year against observed for onset of flowering with the sample specific root mean square error (RMSE) calculated for three of the studied species.

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5. Discussion

5.1 Hazard ratios

Global radiation as AGR was the climate covariate which most species responded strongest to. The effect was negative for all four species *(D. octopetala, E. vaginatum, C. tetragona and V. vitis-idea)*, meaning that an increase in radiation would delay onset of flowering. Although this contradicts the theory of the plants requiring radiation for photosynthetic activity and heat, radiation is also linked to cloudiness. Clouds can have an insolating effect on air temperatures, especially during night, depending on the cloud properties. If the isolating warming effect of clouds overrise the effects of radiation heating the surface, the negative hazard ratios of radiation acts as a proxy for this cooling effect of having clear skies. This is further supported by the fact that the mean temperatures and global radiation for the study period are not positively correlated. Similar effects have been found in an earlier study where radiation had a positive effect on pre-floration times for *R. nivalis* (Molau, 1997). This could be the explanation for the species here too.

The community interaction with AGR for *V. vitis-idea* showed little difference in hazard ratio although the dry heath showed the lowers hazard ratio, hence greater response to AGR. This could be explained by both tussock tundra and the dry meadow plots having higher mean soil water content than the dry heath plots. The higher soil moisture could have a mitigating effect on the potential night cooling effect of AGR by storing daytime heat.

Tundra ecosystems in the subarctic are generally not limited by precipitation and this seems to be the case for the species responding strongest to ASP*, R. nivalis, C. stans* and *B. vivipara* (not significantly). These hazard ratios are all negative (~ 0.97), having delayed onset of flowering with increase in accumulated precipitation.

Molau (1997) found from a three-year study of *R. nivalis* at the Latnjajaure site, that precipitation was most significantly correlated with pre-floration time, the number of days from snow melt until flowering event. The study showed that increased precipitation, by cooling the surface, prolonged the pre-floration time (r^2 =0.363, p=0.0103; r^2 = 0.311, p= 0.0008 if OTC plots was included in the analysis). The r^2 was not as great for TDD or global radiation (Molau, 1997). Similar cooling effects of precipitation could explain why we see negative ASP hazard ratios for *R. nivalis* and *C. stans.*

Only one species*, P. caerulea,* responded strongest to TDD although the coefficient was not significant. This is, however, the only one with similar hazard ratios for flowering events found in the literature (Templ et al., 2016). *P. caerulea* is a relatively late flowering species and is suggested to respond to increasing temperatures rather than radiation or snowmelt (Molau et al., 2005).

The hazard ratio of TDD$_{sum}^{yr1}$ were negative for *E. vaginatum, P. caerulea, R. nivalis* and *C. tetragona*. This goes in line with the study of Mulder et al. (2017) where the previous seasons with higher total growing season TDD generated lag effects delayed the flowering timing following year for early flowering species. The authors find two potential explanations to this. Either that the warmer temperatures might cause an early bud set and then induce a dormancy which has been found for e.g. birches (*Betula spp*.). The dormancy could, in the following spring delay the maturing of the bud and further the onset of flowering. Another explanation could be that the warm temperatures may induce bud maturation already in autumn, making it look as if there is a delay due to the remaining buds being less advanced and flowering late (Mulder et al., 2017). Both explanations could apply for this study, although further studies on bud preformation in these ecosystems would be required to determine which one is more likely.

5.2 Responses to OTCs

The OTC had a significant effect on *D. octopetala, P. caerulea* and *V. vitis idea*. All three species are dwarf shrubs and none of them early flowering species. This goes in line with earlier studies showing late flowering species responding stronger to increased temperatures (Oberbauer et al., 2013). *V. vitis idea*, which is a boreal species preferring drained, sand and gravel rich soils is limited in its tundra distribution by the short dry snow free period (Molau, 2010). *P. caerulea* is also favoured by dryer conditions. Earlier studies from the Latnjajaure tussock tundra plots show that *P. caerulea* increased in biomass between the years 1996-2005 both in OTC plots and control plots as the permafrost degradation dries out the soils (Molau, 2010). The observed negative impact on soil water content by OTCs could therefore be an explanation to the responses.

D. octopetala is an arctic species but generally grow on ridges and are therefore topographically more exposed to early low temperatures. Molau (2001) found *D. octopetala* to flower significantly earlier in control plots than OTCs and the difference was particularly large for years with lower air temperature. The responses of first flowering and pre-floration times on OTCs does however show various results for the same species even at the same site. Molau (1997) found in a 2-year study, similarly to the results of this study, that *C. tetragona* in Latnjajaure was not significantly impacted by OTC warming. On the contrary, a later 5-year study of *C. tetragona* in the same valley showed significant responses in reduced perforation days due to OTC warming although the difference between years was greater (Molau, 2001). Given the lack of response in this study for *C. tetragona,* this further suggests that variations in environmental factors might have a larger impact than the OTCs.

R. nivalis, which in the present study did not respond significantly to OTCs, did similarly not respond in a two year study of the same site (Molau, 1997). There was however a significant difference in the later study, Molau (2001) although relatively small. Bjorkman et al. (2015)

found that early flowering species responded more to timing of snowmelt than to experimental warming. Snow melt timing depends on several variables (topography, precipitation patterns etc.) other than just spring temperatures. Therefore, the two can be partially decoupled, hence correlate differently to timing of flowering onset (Assmann et al., 2019). This could also be an explanation for the other earlier flowering species, not having any significant impact from OTC.

5.3. Model performance

The models with the highest likelihood ratio test (LRT) results were the models of the species with the highest model significance level, such as *E. vaginatum*, *R. nivalis*, *C. tetragona* and *V. vitis-idea*. The other models are all significant but with low LRT indicating that there is little difference between the model and a null model (with no predictors). The higher LRT scores of the earlier mentioned species tells us that these models are robust and suitable to use.

The RMSE tells us the deviation between the observed and modelled values, a measure of by how much the residuals are spread out. The RMSE values of the modelled and observed DOY for onset of flowering in this study range from 5.3 to 8.4 which suggests that all models on average simulate DOYs that are within the 10 days intervals of the input data resolution. The predictive power of all the models are further better fitted than the one found for dandelion by Templ et al. (2016) who in their predictions got RMSE values of 10.46 from a fivefold cross validation. However, this do not necessarily suggest that any of the models in this study to have a higher predictive power since the sampling is from one location only. Whereas the study by Templ et al. (2016) were data from different biomes. The models developed in this study does however capture the local conditions in a sufficient way. How well the cox model with hazard ratios from Latnjajaure works on same species on other locations still needs to be tested. As mentioned, previous studies have shown that same species can respond differently to e.g. warming depending on ambient temperatures (Prevéy et al., 2017).

5.4. Method discussion

The model results indicate that it would be possible to predict future flowering events using climate model simulations of AGR, ASP and TDD. However, the model is not dynamic and assumes that the ecosystem is constant in terms of neighbour plant interactions and plant-pollinator activity etc. Using the model alone for future predictions would therefore give a prediction limited to function within the boundaries of the ecological state of the input data. The subarctic tundra of this region has shown to respond to the already apparent climate change (Callaghan et al., 2013) which suggests that future climate change will keep on changing the functioning and interactions of plant communities and ecosystem.

Both AGR and ASP showed impacts on the timing of flowering. The explanations of why the hazard rates are negative does however imply that in the end it's a matter of local temperature. In this study, information of whether the precipitation fell as rain or as snow is missing which would influence the impact it would have on the plant phenology. With future changes in precipitation patterns, expecting more precipitation in the subarctic (IPCC, 2013), both AGR (more clouds) and ASP (increased precipitation) covariates may change.

The effects of having OTCs alone is not enough to explain the changes in phenology with climate change. Bjorkman et al. (2015) found a significant impact of OTC on tundra vegetation during a long term study (21-year). The control plot vegetation, however, did not change through the study period although the ambient temperature had increased by more than 1 °C. The lack of change with higher temperatures was instead addressed to delays in snowmelt due to increased winter precipitation (Bjorkman et al., 2015). Since the model capture the differences in baseline hazard between OTCs and control plots, it could also be argued that the hazard ratios would stay constant also under warmer conditions, assuming the OTCs simulate realistic warming. The impact of snow melt dates should be examined before assuming that there is no impact of warming on the species not responding to OTCs. Snow data was not available for either of the communities during the study period and could therefore not be included as covariates. This would be interesting to include in the model for future studies.

CaraDonna et al. (2014) found that by only analysing one measure of flower phenology (e.g. first flowering or peak flowering), not all species will respond since the climatic variable may only impact one part of the phenological cycle. Therefore, it would be necessary to investigate also other measures of the reproductive phenology with survival modelling, especially end of flowering and fruit formation, to get the full picture on environmental covariates impact on reproductive success.

6 Conclusion

The hazard ratios from the species specific models imply that AGR and ASP are important for timing of onset of flowering, whereas TDD only showed some weak relationship to flowering. The negative impact of both AGR and ASP on timing of flowering onset are addressed to cooling the surface temperature and indicate further that local air temperature is not sufficient for explaining changes in onset of flowering. The relationship between AGR and ASP to plant phenology needs to be further assessed, both to understand the impact of these environmental variables and to make sure the impact is valid also for future predictions.

In concordance with earlier research higher TDD sum previous year show a negative effect on the timing following year. The effect was particularly large on the early flowering species. Responses to OTCs were stronger among late flowering dwarf shrubs, although the effect on early flowering species may have been out competed by snow melt dates. The effect of snow melt should therefore be included in future models.

Cox proportional hazard model was an adequate tool to analyse snapshot phenology with and the fitted models was able to accurately predict onset of flowering. Further studies of how the model application perform beyond the study area still needs to be tested.

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