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The Many Phases of Phenology

Geographic and Inter-Specific Differences In
Phenological Between-Year Variation

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Abstract

As climate-driven changes in phenology are becoming more apparent, the need to quantify these changes is increasing. An important challenge in detecting phenological changes is that between-year variation in phenology is large. Between-year variation determines the statistical power of comparisons between contemporary and historical observations. For 44 plant species with different distributions across Sweden, geographic and inter-specific differences in between-year variation in different phenophases (bud burst, flowering, ripe fruits, and leaf fall) was studied. I also modeled and evaluated the response of bud burst, and flowering, to temperature using three different temperature sum models over a latitudinal gradient. The data used was a sub-sample from a dataset collected by a Swedish nation-wide phenology network between 1873-1917.

In agreement with previous studies, I show that early spring phases have a higher variability than phases occurring later in the season. However, the relation between onset and variation was not monotonically decreasing. In the geographical analyses, a unimodal relation between between-year variation and latitude was found, that is, the between-year variation decreased along the latitudinal gradient for early- and late-season events, while it increased over latitude for summer events. These patterns are, to a great extent, reflections of patterns in air temperatures which is discussed using meteorological data from adjacent climate stations.

Models were evaluated using Akaike's Information Criterion, and in 60% of all fits, the *Spring warming CF2* model (*SWCF2*; the model with the least number of parameters) was selected as the best model to describe the data. For *Sorbus aucuparia* bud burst, in the two parameter model *SWCF2*, both parameters (threshold temperature and temperature sum) correlated with latitude. However, future analysis using more locations and a wider span of species will be needed to understand the generality in these findings. In conclusion, future efforts to detect and quantify phenological changes need to consider differences in between-year phenological variability along geographical gradients and among species with different phenology.

1 Introduction

1.1 The context of phenology

For all living things, the timing of different life stages is crucial. Interaction and competition with other species and con-specifics, together with the constraints of the abiotic world, force the individual to optimize its use of resources, to keep up with the rest of the living world. By doing so, the organism not only ensures its own survival, but may also be allowed to complete its reproductive circle.

For a plant, the trade-off between successful exploitation of seasonally limited resources such as water, nutrients or light, and the risk of exposure to frost damage and heat-driven drought, are important in determining why an individual changes in accordance with the seasons. In the pursuit of maximum fitness, different species have developed various strategies to deal with these matters. This is the reason why we see inter-specific variability in the phenology of plants.

There is also a local property to the timing of phenological events since the optimum conditions, as perceived by a plant, occurs at different times depending on, for instance, day-length regime, the climate, and the water regime of the area. Not only does the timing of phenological events vary, but key life history traits, such as breeding systems and reproductive allocation are attuned to the environment as well (Sultan 2000). As an example, in Southern Europe accessions of Thale Cress (*Arabidopsis thaliana*) can be either winter or summer annual, whereas accessions from Northern Europe are typically winter annual (Shindo *et al.* 2007).

In all of ecosystems on earth, the system dynamics are maintained through the networks created by the bonds formed when the individuals of a community interact with one another (Campbell & Reece 2005). This is also true of many of the seasonal bonds that form during a specific part of the year and subsequently dissolve when its role is over, only to be re-formed again next year. The synchronization of bud burst and the emergence of larvae, or the coincident hatching of eggs in birds and insects, are examples of such bonds. Also the numerous mutualistic interactions between plants and their pollinators are illustrations of this connectivity existing in all ecosystems (Elzinga *et al.* 2007).

1.2 Phenology and the climate

Charles Françoise Antoine Morren (1807-1858), Belgian botanist and horticulturist, proposed the term *Phenology* in 1853 - described as “the art of observing life cycle phases or activities of plants and animals in their temporal occurrence throughout the year” (ref. Lieth 1974). Phenology, which was used in the country almanac as a way to forecast the weather long before computers and satellites were the common predictive tool, is based on the simple fact that distinct phases in the life of a species (so-called phenophases) are linked to local climate. This link between climate and phenology allows us, by studying natural phenomena such as leaf foliation, flowering, leaf fall, and their respective timing, to understand how ecosystem processes in a specific geographical area are affected by a changed climate.

1.2.1 Phenological change

As mentioned above, evolution has enabled organisms to evolve to initiate and undergo their different life stages when conditions are optimal to do so. The seasonality seen in life history is caused by the fact that these conditions, too, are seasonal. Current climate changes (IPCC 2007) are affecting the occurrence of optimal conditions, and thus the event, whether it is flowering, breaking of dormancy, hibernation waking or egg laying date, is also affected (Visser & Both 2005).

Parmesan (2007) estimated, in a meta-analysis spanning 203 species from the northern hemisphere, an overall spring advancement of 2.8 days decade⁻¹. Amphibians showed the highest advancement (with a mean of 7.6 days decade⁻¹). Trees showed a mean spring advancement of 3.3 days decade⁻¹, while herbs and shrubs had advanced 1.1 days decade⁻¹.

Another study by Fitter & Fitter (2002), showed an advancement of 4.5 days between the 1990s and the previous four decades for 385 British plant species. There is also evidence of a stronger advancement at higher latitudes, most likely due to a bigger increase in temperature in high versus low latitude regions (Parmesan 2007).

1.2.2 Effects of phenological change

As phenological changes are becoming increasingly pronounced, the ecological effects are getting more apparent. In a global meta-analysis by Parmesan & Yohe (2003), range shifts attributable to climate change were documented in over 30 percent of all covered species. In the northern hemisphere, the main limiting factor for frost-sensitive trees is low winter temperatures. A manifestation of this is seen in the common thermal thresholds for forest growth at high altitudes (Körner & Paulsen 2004).

As a result of increasing temperatures and a prolonged growing period, it is probable that boreal forests will increase their net primary production (the balance between gross primary production and autotrophic respiration), resulting in increased forest biomass and carbon dioxide exchange with the atmosphere (Saxe *et al.* 2001).

There can also be paradoxical consequences of a prolonged growing period that are detrimental to plant species. For instance, as an effect of an advanced spring arrival, the susceptibility to spring frost damage, which may lead to foliar necrosis, is increased (Gu *et al.* 2008).

The effect of a warmer climate can also have the opposite effect, depending on where on the globe we are looking. When looking at leafing out, Zhang *et al.* (2007) found that in response to warmer temperatures, species in colder regions showed earlier leafing out while species in warmer regions showed a delayed leafing out as a consequence of not overcoming winter chilling requirements. In addition to these direct effects of a changed climate, there is the possibility of indirect effects. For example, shifts in the cycling of nutrients as a consequence of climate change (Matear *et al.* 2010), might in turn affect the phenology of organisms.

Beyond these single-species effects there is also a risk of composite effects, resulting from differential responses between species to a climatic shift (Primack *et al.* 2009). Firstly, species from different taxa are likely to act on disparate cues. It is also true that there are other differences between species (e.g. physiological tolerances and life-history strategies) which will consequently lead to dissimilar responses even when the climatic trends are similar (Parmesan & Yohe 2003). The outcome of such differential responses may result in the mistiming of inter-specific interactions such as the poor synchrony between egg hatching in the winter moth (*Operophtera brumata*) and the bud

burst of oak (*Quercus robur*) as a consequence of warmer springs found by Visser & Holleman (2001). In regard to crop species, a reduction in food production, resulting from reduced pollination rates (FAO 2008), would have impacts on food availability which in turn could affect global economics.

Also, within the plant community itself there is a difference in response to climate factors between different plant species and within a species at different sites (e.g. Primack *et al.* 2009). This difference can either be attributable to the species plastic response or be a part of a more fundamental disparity between populations.

1.3. A renewed interest

At present, in the wake of global climate change, phenology is a growing area of research. A search using the terms *phenology* and *climate change* on the search service ISI Web of Knowledge produced over 1900 articles (March 2011).

1.3.1 Phenological networks - present and historical

Some of the oldest phenological records are the grape-harvest dates that have long been recorded in many European countries. In particular, the Burgundy region of France has continuous records dating back to the middle ages (Chuine *et al.* 2004). In Sweden, Carl von Linné recorded the bud burst of trees in Sweden between 1750 and 1752 which he subsequently included in his *Vernatio arborum*.

Today, there are several national phenology networks across Europe gathering phenological observations. There is also an ongoing attempt, The Pan European Phenology database (PEP725, <http://www.zamg.ac.at/pep725/>), to establish a European reference data set of phenological observations. The biggest contributors so far, are the central European countries (e.g. Germany, France and Austria) but there are also many observations from Eastern Europe (Romania), the Baltic states (Lithuania) and the Nordic countries (Finland). The Swedish National Phenology Network (SWE-NPN) was initiated in 2008 and is coordinated by researchers at The Swedish University of Agricultural Sciences (Sveriges Lantbruksuniversitet, SLU) and the Department of Plant and Environmental Sciences at The University of Gothenburg.

In 1873, the Uppsala Observatory instituted a national phenology network that provided willing observers with observation forms which were to be returned each year after observations had been completed. The network was entrusted to the Swedish National Meteorological-Hydrographical Institute (current SMHI) in 1882, which continued to collect and compile records nation-wide from a large number of observers at over 319 sites until 1926 (Arnell 1923, Arnell 1927, Arnell & Arnell 1930).

1.3.2 Discovering impacts of a changed climate

As implied above, comparison of contemporary and historical data enables detection and analysis of phenological changes. Not only is it possible to look at a single species at one specific location, one can also study trends over both species barriers and over different gradients such as latitude and altitude.

The County Administrative Board of Jönköping is collaborating with the SWE-NPN to develop a phenological tool that will function as an indicator of the national environmental quality objective 'Limited Climatic Influence' (Hassel *et al.* 2010). This tool will be based on standardized observations that will be compared with

corresponding observations from the older phenological data set from 1873 to 1926.

In order to quantify a phenological change, we need a high quality historical point of comparison. Also, if the observations are to be common over a wider geographical area, e.g. the better part of Sweden, we must choose species that are shared over the area. Another important challenge in making historical comparisons is that between-year variation (BYV) in phenology is large. In this study, BYV was analyzed and compared between different species and phenophases over the latitudinal gradient of Sweden. I also looked at what importance the different traits of pollination strategy, growth form, time of onset, and Ellenberg's Indicator values (Ellenberg *et al.* 1991), may have on BYV.

BYV determines the statistical power of comparisons between contemporary and historical observations. The statistical power of this comparison is the probability to reject a false null hypothesis (the ability to detect a difference when there is one) (Crawley 2005). The more BYV in an observational series there is, the lower the power will be.

1.4 Between-year variation in phenology

Published literature focusing on between-year variation (BYV) in phenology is currently scarce and the effect of BYV on the accuracy of comparisons has not been thoroughly addressed. Barr *et al.* (2004) showed a moderate BYV in the phenology of leaf area index (LAI) for a boreal aspen-hazelnut forest and related inter-annual differences in annual net ecosystem production to the seasonal cycle of LAI. In another study by Ellebjerg *et al.* (2008), the variation in onset of flowering for a high-arctic valley in Northeast Greenland with a short growing season (2-3 months), varied about one month between years for most included species.

As mentioned above, the power to detect differences between contemporary and historical data is determined by BYV, the magnitude of the difference to detect, the sample size, and the desired statistical significance. Thereby, if the BYV of a species is known, it is possible to determine the required duration of observations (number of years) that is needed to detect a change of a certain magnitude with a certain level of significance. Obviously, this is very useful information for a monitoring program.

There are different reasons to why some species are more variable in their timing of phenological events than others (Figure 1). One example is the observation that earlier events have a tendency to be more variable than events occurring later in the season as a consequence of the greater fluctuations (Menzel *et al.* 2006b) in the temperatures affecting earlier events (Sparks & Menzel 2002). There is also the possibility that BYV varies with geography. For instance, if temperatures vary more between years in a certain geographic region, we could presume that plants living there would show a higher phenological variability than those growing in places with more stable temperatures.

In line with the reasoning behind inter-specific differences in onset dates, we can also ask ourselves whether there are differences between different phenological phases

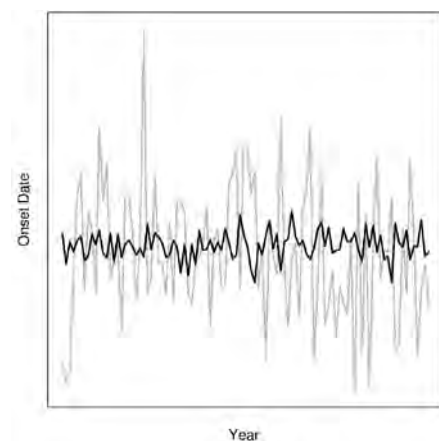


Figure 1. Example of species with low (black) versus high (gray) between-year variation. Data was generated using a random normal distribution number generator (*rnorm* in *R*).

and between different functional groups, such as pollination ecology or growth form, in BYV. If species have different ways to assess their surrounding world, then maybe this results in differences in BYV.

1.5 Phenological models

By modeling the response of e.g. bud burst to temperature, it is possible to identify important ecophysiological processes and gain insight into what causes the BYV that we observe in nature. Thus, the aim is to “identify a biologically meaningful model that explains the significant variability in the data, but excludes unnecessary parameters” (Lebreton *et al.* 1992). It is also possible to use the acquired model to predict how phenology will act given a certain future climate. However, if a model does not address the relevant ecophysiological aspects (i.e. a model with high realism), the accuracy of the model might suffer if conditions are extreme (Hänninen 1995).

Different models have been used to model the bud burst phenology of species in temperate regions (e.g., Hänninen 1995; Kramer 1996; Chuine 1998; Richardson & O’Keefe 2009). Some models use only temperature (Hänninen 1995; Chuine 1998; Richardson & O’Keefe 2009), while others may include additional input such as photoperiod (Kramer 1998). It is worth noting that in the tropics and in arid environments, phenology is more likely determined by precipitation than by temperature (Augsburger 1981; Forrest & Miller-Rushing 2010). Also, generalizations regarding a species at one location may not necessarily hold true for somewhere else (Richardson & O’Keefe 2009).

1.5.1 Temperature sums

There are several cues available to organisms for determining seasons and when there are favorable conditions to undergo certain stages. Good examples of this are the well-studied cues used by plants to decide when to initiate bud burst and flowering - temperature and photoperiod (Elzinga *et al.* 2007). The study by Diekmann (1996), for example, found that the cumulative sum of temperature over a certain period is a good proxy to determine the onset of bud burst and flowering.

The cumulative sum of temperature is often defined as the sum of daily temperatures (T_d) exceeding an established threshold value (T_b). If the daily temperature is below the threshold temperature, it has no effect on the sum.

$$TS = \sum_{d=1}^n (T_d - T_b), \text{ if } T_d \geq T_b$$

1.6 Summary and research objectives

To a large extent, this thesis is divided into two discrete parts. The first part is concerned with geographic and inter-specific differences in between-year variation, the quality of the historical data set and the consequences this has on the suitability of a species to act as an environmental quality objective indicator. Here, I analyzed 91 species-phase combinations.

The second part is an evaluation of temperature sum models to see how well they explain between-year variation in phenology. I also analyzed geographic variation in the

parameter values from the fitted temperature sum models. In this part, I used data from three species-phase combinations. The two parts are autonomous and will mainly be treated as separate studies. However, they are connected through the issue of geographic differences in phenology.

The research questions of this thesis were: (1) How does between-year variation vary over Sweden? (2) Is there a pattern in between-year variation that may be described through different factors such as pollination method, growth form, time of the year of flowering, or Ellenberg's species indicator values? (3) Which species are suitable to be included as an environmental quality objective indicator? (4) What temperature model is most successful in predicting onset time? (5) Is there a correlation between latitude and the optimal parameter values (start day of accumulation of temperature sum, threshold temperature and temperature sum) and/or model performance ?

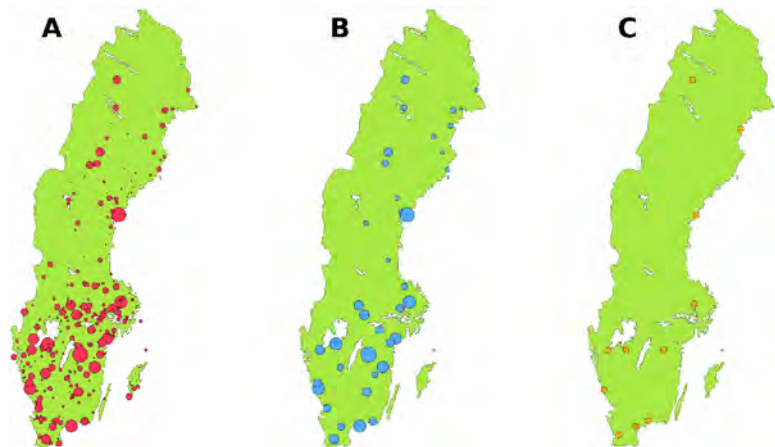
2 Method

2.1 Data

2.1.1 The phenological data

Between 1873-1930, a Swedish nation-wide phenology network documented plant phenology for about 50 species, and in total 91 species-phase combinations, at over 350 locations (Arnell 1923; Arnell 1927; Arnell & Arnell 1930). The observational practice behind the historical observations used in this study is described in detail in Arnell 1923. Bud burst (Bb) is decided to occur when trees or shrubs appear green from a distance. Onset of flowering (Fl) occurs when a larger proportion of flowers are developed and opened. Fruit ripening (Fr) occurs when fruits are commonly beginning to ripen, while leaf fall (Lf) occurs when the crowns of the trees of concern are one third yellow.

A subset of the locations in this historical data set, based on the observational period, was used in the subsequent analyses. For my purposes, I selected sites that had records of 20 years or more (Figure 2A and 2B). To compensate for the lack of longer series in the north of Sweden, sites having records of less than 20, but more than ten years, were added above *Limes Norrlandicus*. In total, the analysis is based on 37 locations.



2.1.2 The trait data

Pollination modes were either *insect* or *wind*, growth forms were divided into *herbs*,

Figure 2. A) All locations in the historical phenology data set. B) The subset of locations with data >20 years used for analysis. Above *Limes Norrlandicus* some shorter (>10 years) were added to create an even latitudinal distribution. The dot size increases with increasing length of each series. C) The ten SMHI climate stations used for temperature sum modeling.

dwarf shrubs, *shrubs*, and *trees*, and leaf phenologies (adopted from Ellenberg) into *evergreen*, *over-winter green* (often with green leaves in winter, which however are replaced in spring), *summer green* (green only in the warmest season), and *early summer green* (green from early spring until early summer, but thereafter mostly reducing).

Furthermore, I used least squares linear regression to test for relationships between BYV and Ellenberg's species indicator values (Ellenberg *et al.* 1991, Appendix A). These comprise hierarchic scales for *light* (*L*), *temperature* (*T*), *continentality* (*K*), *moisture* (*F*), *reaction* (*R*) (soil pH, or water pH), and *nitrogen* (*N*). These indicators are based on the realized ecological niche and can be regarded as continuous scales, where each value occupies a certain interval. For a definition of the Ellenberg indicator values in English, see Hill *et al.* 1999.

2.1.3 The meteorological data

In ten of the selected phenology locations I used meteorological data that overlapped in time with the phenological data to fit different models of bud burst and flowering phenology (Figure 2C). The meteorological data was from SMHI climate stations and contained temperature readings three times daily: at 6 am, 12 pm, and 6 pm. Each day has records of minimum and maximum temperatures, precipitation, and snow depth. However, I used only the temperature readings at noon since the readings made three times daily had a more thorough overlap than the minimum/maximum temperatures that were not available for the first years of some stations.

2.2 Analysis

A full list of the species and phenophases used in the subsequent analyses are given in Appendix A. For the purposes of this study, some species were excluded from the data set, either due to uncertainties in the quality of the data, or because they are regarded as naturalized or cultivated species. Black Alder (*Alnus glutinosa*) and Grey Alder (*A. incana*) were merged into *Alnus spp.* in the analysis since uncertainties regarding the forms have made it difficult to decide which of the two species an observation belongs to. The same is true for the now rejected species *Betula alba*, since this is regarded to be applied to both *B. pendula* and *B. pubescens*, it is referred to as *Betula spp.*. Omitted naturalized and cultivated species were the Poet's Daffodil (*Narcissus poëticus*), Garden Pea (*Pisum sativum*), Rye (*Secale cereale*), Common Lilac (*Syringa vulgaris*), Red Clover (*Trifolium pratense*), and Common Wheat (*Triticum aestivum*). The old data set includes a notation about the precision of each observation, which can be either certain or uncertain. For the analyses in this thesis, I used observations with the higher precision only.

All dates were converted to Julian days. All statistical calculations were conducted using the R language and environment for statistical computing. As some species-phase combinations (SPPHs) had fewer observations at some locations than the location's overall series length, if an SPPH had less than ten years of observations at a particular location, that particular SPPH/location combination was excluded from the analysis.

2.2.1 Analysis of between-year variation

Between-year variation (BYV) was quantified as the standard deviation of onset days (SD_{onset}). Inclinations along the latitudinal gradient were tested using least squares linear regression of SD_{onset} over latitude for each SPPH. Also, a scatter plot of SD_{onset} over mean onset date was used to compare the variability of a certain SPPH with the SPPHs relative occurrence during the season (*i.e.* early/late phases). The power analysis was configured to detect a seven-day change, using SD_{onset} for each SPPH at each location, yielding the relevant sample size for that particular SPPH at each site.

Using data from a location covering many years and SPPHs (Rasbo, Uppland (59° 90'), 79 SPPHs over 42 years), I used analysis of variance to test for differences in SD_{onset} between phenophase groups, types of pollination, growth forms and leaf phenologies.

2.2.2 Phenological models - model fitting and geographical analysis

I used the meteorological data to fit three different models of bud burst and flowering phenology of three SPPHs: The bud burst of European Rowan (*Sorbus aucuparia*) and Common Aspen (*Populus tremula*), and the flowering of the Lingonberry (*Vaccinium vitis-idaea*). Only observational series longer or equal to ten years were used.

The fitted models result in a number of parameter values (heat-sum, threshold temperature, and starting day of heat-sum accumulation. See below). The geographical variability in the different model parameters, was evaluated using linear regression between the parameter set of the best fitted model and latitude. I also compared the sum of squared errors of prediction (SSE) for each model between models and across Sweden to test whether model performance varied between models or with latitude.

The models used were the same as in Richardson & O'Keefe (2009) and Chuine (1999) and was based on Fortran code provided by Dr. Andrew D. Richardson at Harvard University, Massachusetts, USA. Thus, the following descriptions and nomenclature are largely covered by these two papers. The general design of the models was that onset was predicted to occur when a warming condition (also called forcing) was met. The state of forcing, S_f , is the time integral (from t_1) of the rate of forcing, R_f , which in turn, is a function of the daily temperature $x(t)$:

$$S_f(t) = \sum_{t_1} R_f(x(t))$$

I tested three different models: *Spring warming CF1* (SWCF1), *Spring warming CF2* (SWCF2) and *Alternating CF1* (ALTCF1). In the spring warming models, only forcing temperatures affect onset date. In the alternating model, there was, in addition to forcing, also a chilling condition. As time progresses from the start of accumulation (t_1), both the state of forcing, and the state of chilling (S_c , which is also a time integral similar to $S_f(t)$) accumulate parallel to each other. When the daily temperature is above the threshold temperature, forcing degrees are accumulated and when the temperature is below the threshold, chilling degrees are accumulated. As chilling accumulates, the required state of forcing (F^*) for onset is reduced according to the equation:

$$F^* = a \exp(bS_c(y))$$

Here, a and b are model constants. $CF1/CF2$ denote different forms of the equation for R_f . In the $CF1$ variant, R_f is calculated as $x(t) - T_{force}$ where $x(t) > T_{force}$ and $R_f = 0$ otherwise

(“forcing degree-days”). In the *CF2*, R_f is a sigmoid function of $x(t)$ where $x(t) > 0$:

$$R_f = \frac{28.4}{1 + \exp(-0.185(x(t) - 18.4))}$$

The numbers of parameters to fit differed between the three models. *SWCF1* has three (t_1 , T_{force} and F^*), *SWCF2* has two (t_1 and F^*) and *ALTCF1* has four (t_1 , T_{force} , a and b).

2.2.3 Parameter estimation and model evaluation

Models were fit using the simulated annealing method of Metropolis *et al.* (1953), which is an optimization algorithm based on iterative improvement. This algorithm is referring to a fundamental principle of statistical mechanics, called the Boltzmann probability distribution: a probability measure for the distribution of the states of a system. It is used when metals are heated and subsequently cooled to reduce crystallographic defects. According to the principle, $P(\Delta E) = \exp(-\Delta E/kBT)$, where $P(\Delta E)$ is the probability that the configuration is accepted given the energy difference ΔE between current and previous state. kB is Boltzmann’s constant, and T is temperature (Kirkpatrick *et al.* 1983).

In the Metropolis algorithm, ΔE is analogous to the *SSE* of a model given a set of parameter values. The sum of squares is defined through the function $f(x)$:

$$f(x) = \sum_i (d_i(x) - d_{iobs})^2$$

where d_{iobs} is the observed onset date of year i , while $d_i(x)$ is the predicted date given a certain set of parameter values. In each step of the algorithm, E is calculated with a given set of parameters. If $\Delta E \leq 0$ compared to the previous step, the new parameter set is accepted. If $\Delta E > 0$, the likelihood for the new parameter set to be accepted is $P(\Delta E)$. To include a randomization procedure, random numbers uniformly distributed in the interval (0,1) are compared with $P(\Delta E)$. If the number is smaller than $P(\Delta E)$, the new parameter set is accepted. If $P(\Delta E)$ is instead smaller, the original parameter set is used to start the next step. This step is repeated many times until a steady state (parameter set) has been reached.

To determine the relative goodness of fit of the models (explanatory power), while simultaneously considering the number of fitted parameters (complexity), I used the small-sample corrected Akaike Information Criterion (AIC_c). AIC_c is used in favor of AIC in cases where n is small relative to p and they are calculated as:

$$AIC = n \log(\sigma^2) + 2p$$

$$AIC_c = AIC + \frac{2p(p+1)}{n-p-1}$$

where n is the number of data points, p is the number of parameters estimated plus one and σ^2 is the residual sum of squares divided by n . The model with the lowest AIC_c is the model that has the best explanatory power while still keeping the complexity at a reasonable level.

It is worth noting that, due to the interval scale, an individual AIC value is not interpretable in isolation. Thus, only when compared to other AIC values in the same

model set, does an *AIC* value have a meaning.

3 Results

3.1 Patterns in phenology

The majority of all species-phase combinations (SPPHs) showed the expected pattern where bud burst and flowering began at earlier dates in lower latitudes and continued up through Sweden, while later autumn phases showed the reversed pattern where onset began earlier in northern Sweden and continued downwards (examples are shown in Figure 3).

Some SPPHs did not show such a pattern and had their mean onset dates at roughly the same time all over Sweden. These phases were all later phases, occurring in the middle of June or later, and comprised the flowering of the Common Heather (*Calluna vulgaris*), the ripe fruits of the European Rowan (*S. aucuparia*), the autumn leaves of the Bird Cherry (*Prunus padus*), and the Wych Elm (*Ulmus glabra*) (represented with smaller gray dots in Figure 4). Regressions of mean onset date on latitude are summarized in Figure 4. Species with a limited distribution in the data were omitted since the regression coefficient is affected by distribution. Spring phases showed the strongest coefficients and subsequent events showed a progressive decrease in magnitude towards summer SPPHs. In autumn phases, the coefficients were negative.

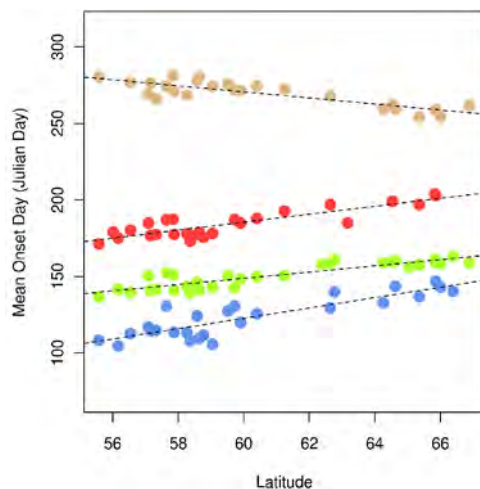


Figure 3. The general phenological pattern of phenophases in Sweden, exemplified here - for bud burst, flowering, and leaf fall - by Aspen (*Populus tremula*), and for ripe fruits by the Woodland Strawberry (*Fragaria vesca*). Bud burst and flowering onset begin in southern Sweden, while leaf fall begins in northern Sweden. Green = Bud Burst, Blue = Flowering, Red = Ripe Fruits, Brown = Leaf Fall.

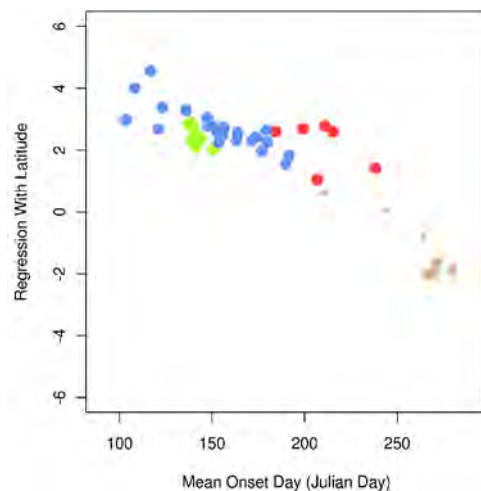


Figure 4. The regression coefficients for mean onset day over latitude for all species-phase combinations (SPPHs) plotted against mean onset day for each SPPH. Green = Bud Burst, Blue = Flowering, Red = Ripe Fruits, Brown = Leaf Fall, Gray = Non-significant regressions.

3.2 Between-year variation in phenology

Comparison between the mean standard deviations (over all locations for each SPPH), found earlier events having greater temporal variability than events occurring later in the season (Figure 5). The same is not true when looking at each location separately, where 15 locations showed this pattern while 21 locations did not show any correlation. One location (Mjällby, 56°01') showed the opposite pattern with an increasing SD_{onset} later in the season. Furthermore, the relation between onset and SD_{onset} did not seem to be monotonically decreasing, but curvilinear at best. To see whether a limited distribution automatically resulted in low SD_{onset} for an SPPH, SPPHs with a distribution over the whole latitudinal range of Sweden were annotated with “●”, while SPPHs with limited distributions were annotated with “x”.

The BYV ranged from 2.23 days in the autumn leaves of *S. aucuparia* (at 61°25' (Hanebo), n = 11) to 30.34 days in the flowering of the Common Hazel (*Corylus avellana* at 57°63' (Pelarne), n = 21). 16 of the 91 SPPHs (17%) had a linear correlation between SD_{onset} and latitude (Figure 6; Table 1).

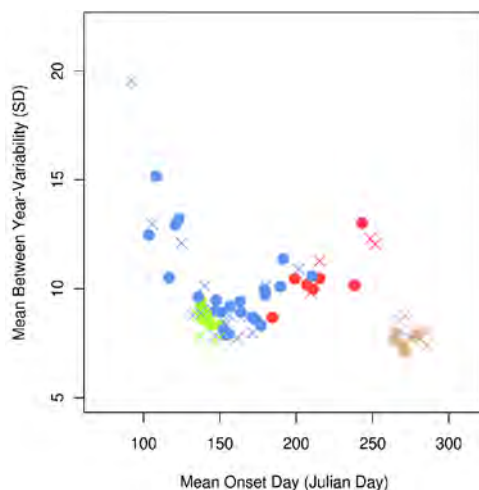


Figure 5. Mean SD_{onset} for all SPPHs plotted against mean onset day for each SPPH. Each data point represents the mean over all locations for one SPPH. $P < 0.005$. ●: full latitudinal distribution; x: limited distribution. Green = Bud Burst, Blue = Flowering, Red = Ripe Fruits, Brown = Leaf Fall.

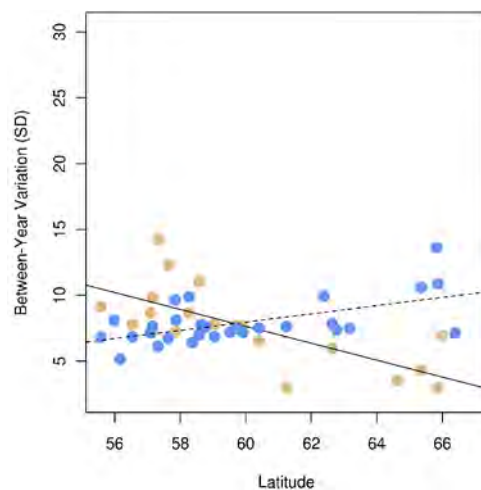


Figure 6. Examples of correlation between latitude and between-year variation (BYV). Flowering onset in the Lily of the Valley (*Convallaria majalis*; blue; positive correlation), and the leaf fall in Bird Cherry (*Prunus padus*; brown; negative correlation).

The sign of the correlation coefficient seemed to be influenced by when the phase was occurring in the season in a unimodal relationship. The early spring species had negative coefficients (which suggests that there was a bigger SD_{onset} at lower than in higher latitudes). Later in spring and early summer, the coefficients increased in magnitude; the pattern was reversed with a higher variability at higher latitudes in comparison to lower latitudes. In autumn, the coefficients were once again negative, indicating a higher variability at lower vis-à-vis higher latitudes (Figure 7).

Table 1. Species-phase combinations (SPPHs) with a correlation between between-year variation (BYV) in phenophase onset days and latitude ($P < 0.05$). +/- indicate the sign of the regression coefficient. Bb = Bud burst, Fl = Flowering, Fr = Ripe fruits, Lf = Autumn leaves.

species	phase
<i>Anemone nemorosa</i>	Fl-
<i>Betula sp.</i>	Bb+ Lf-
<i>Calluna vulgaris</i>	Fl+
<i>Convallaria majalis</i>	Fl+
<i>Filipendula ulmaria</i>	Fl+
<i>Hepatica nobilis</i>	Fl-
<i>Leucanthemum vulgare</i>	Fl+
<i>Menyanthes trifoliata</i>	Fl+
<i>Populus tremula</i>	Bb+
<i>Prunus padus</i>	Fl+ Lf-
<i>Ribes rubrum</i>	Fl+ Fr-
<i>Sorbus aucuparia</i>	Fl+
<i>Vaccinium vitis-idaea</i>	Fr-

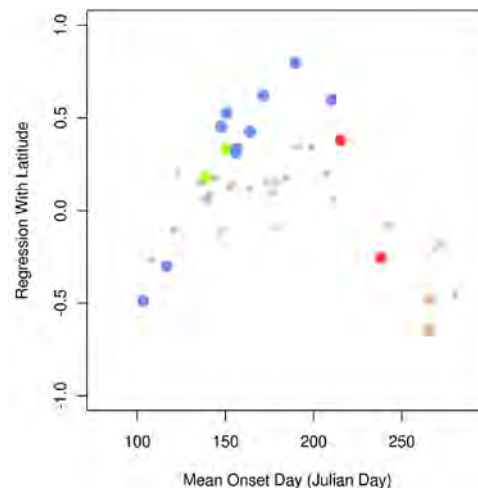


Figure 7. The regression coefficients of SD on latitude plotted against Julian day. Green = Bud Burst, Blue = Flowering, Red = Ripe Fruits, Brown = Leaf Fall, Gray = Non-significant regressions.

Among the SPPHs that did not show a geographical correlation, SD_{onset} varied. Some SPPHs had a high SD_{onset} (which also varied substantially between locations), while others were only present in lower latitudes, and some had a relatively rather low SD_{onset} . Table 2 shows the ten SPPHs with the highest mean SD_{onset} and the ten SPPHs with the lowest mean SD_{onset} .

Table 2. The ten SPPHs with the highest and lowest mean SD (cf. Figure 13).

	species	phase	mean SD
highest	<i>Corylus avellana</i>	Fl	19.54
	<i>Alnus sp.</i>	Fl	15.15
	<i>Populus tremula</i>	Fl	13.20
	<i>Sorbus aucuparia</i>	Fr	13.02
	<i>Tussilago farfara</i>	Fl	12.95
	<i>Salix caprea</i>	Fl	12.92
	<i>Hepatica nobilis</i>	Fl	12.47
	<i>Malus sylvestris</i>	Fr	12.30
	<i>Ulmus glabra</i>	Fl	12.10
	<i>Corylus avellana</i>	Fr	12.04
lowest	<i>Sorbus aucuparia</i>	Lf	7.11
	<i>Prunus cerasus</i>	Lf	7.38
	<i>Populus tremula</i>	Lf	7.42
	<i>Quercus robur</i>	Lf	7.42
	<i>Quercus robur</i>	Bb	7.58
	<i>Prunus padus</i>	Lf	7.66
	<i>Aesculus hippocastanum</i>	Lf	7.68
	<i>Tilia cordata</i>	Lf	7.71
	<i>Fraxinus excelsior</i>	Lf	7.73
	<i>Viscaria vulgaris</i>	Fl	7.73

3.2.1 Power analysis

Figure 10 summarizes the results from the power analysis. Here, the SPPHs were ranked after increasing national mean value of SD_{onset} . For the result of the power analysis, the number of required observation years to detect a 7-day change within a 95% CI is written over the x-axis for each SPPH and ranged from 8 years up to 41 years (median values). Leaf fall (Lf) events had a mean SD_{onset} below average while those of ripe fruits (Fr) were above average. However, the phases with the highest SD_{onset} were flowering phases and the flowering of *C. avellana* had a considerably higher SD_{onset} than any other SPPH. Also, looking at all bud burst phases, they showed a less variability in SD_{onset} than the other phases.

3.2.2 Functional group analysis

In the analysis of differences between different functional groups, neither pollination mode, growth form, or leaf phenology differed in SD_{onset} , and among the different Ellenberg indicators, only the Reaction Indicator showed a correlation with SD_{onset} ($P < 0.05$, $R^2 = 0.06$). However, only about 6% is accounted for by the model.

Using analysis of variance, I found differences ($P = 3.1e-06$) between the different phase groups in mean SD. *Post hoc* comparisons using Tukey's HSD showed differences between all groups except for bud burst and flowering (Figure 10).

3.3 Phenological models

Three different phenological models (*SWCF1*, *SWCF2*, and *ALTCF1*) were analyzed for three species-phase combinations (*Sorbus aucuparia* bud burst, *Vaccinium vitis-idaea* flowering, and *Populus tremula* bud burst) at ten different locations (latitudinal range: $55^{\circ}58' - 66^{\circ}88'$). The temperature difference between high and low latitudes was greater in the winter months with a gradual increase from the summer months (Figure 8). The temperature was also clearly more variable between years in the early and late months of the year with lowest variability during summer months (Figure 9).

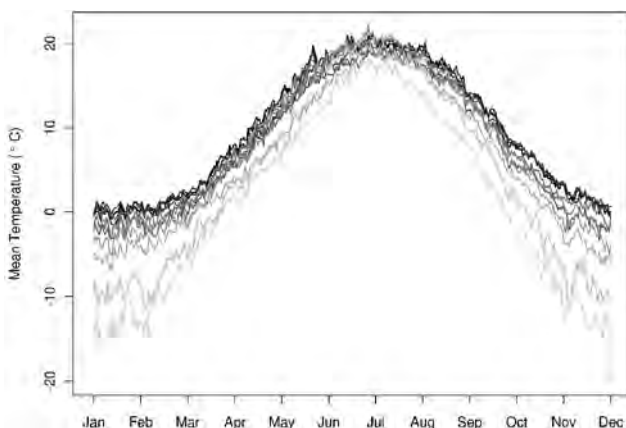


Figure 8. Mean temperatures over the year for different latitudes. Blackness decreases with increasing latitude.

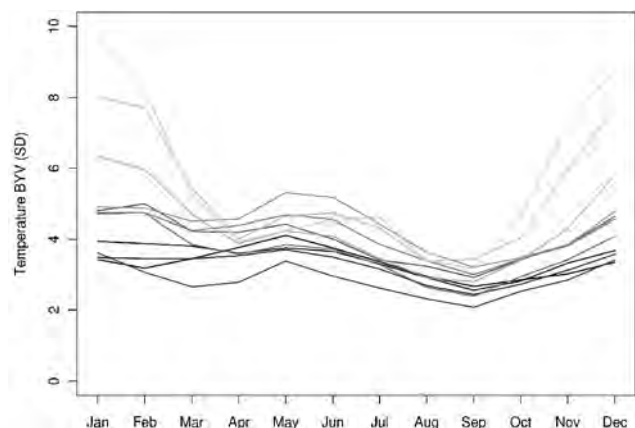


Figure 9. Monthly means of between-year variation in temperature. Blackness decreases with increasing latitude.

Looking at latitudinal differences in temperature variability, the difference was lowest in the summer months, where higher latitudes showed only a slightly bigger variability. From October on, the latitudinal heterogeneity increased and reached its peak in mid-winter where higher latitudes had a significantly bigger between-year temperature variability than lower latitudes. From January on, the difference decreased once again up until the summer.

3.3.1 AIC model selection

For parameter values of all fitted models, see Appendix B. From the fits of the three different models (*SWCF1*, *SWCF2* and *ALTCF1*) for the bud burst of *S. aucuparia* and *P. tremula*, and the flowering of *V. vitis-idaea* at the ten different locations, in 18 out of all 30 fits (60%), *SWCF2* was selected by the AIC_c test as the best model to describe the data, while *ALTCF1* was the best model in 8 fits (29%) (Table 3). *SWCF1* was considered the best model in only one case (bud burst of *S. aucuparia* at 66° 88').

If $\Delta AIC_c \leq 2$ for a model, it can still be considered to be well-supported by the data (Burnham & Anderson 2002). For the different models, this was true in 3 (10%) (*SWCF1*), 20 (67%) (*SWCF2*) and 9 (30%) (*ALTCF1*) fits respectively. The limit where models can be regarded to have any support at all is estimated to when $\Delta AIC_c \leq 6$ which occurred in 15 (50%) (*SWCF1*), 23 (77%) (*SWCF2*) and 13 (43%) (*ALTCF1*) fits respectively. I did not find any difference between models in the sum of squared errors of prediction. Neither did I find any correlation with latitude in model performance which means that each model performed equally good or bad over the whole latitudinal gradient.

Table 3. ΔAIC_c (the difference between a model's AIC_c and the lowest AIC_c of all the models tested for a species. The best model has $\Delta AIC_c = 0$ and is marked with bold type and dark shading. Models with $\Delta AIC_c \leq 2$ have only dark shading. Models with $\Delta AIC_c \leq 6$ have light shading.

SPPH	latitude	SWCF1	SWCF2	ALTCF1
<i>S. aucuparia</i> Bb	55° 58'	5.7	0.0	15.6
	55° 97'	10.4	0.0	55.3
	57° 15'	5.3	0.0	8.1
	58° 26'	13.4	0.0	8.1
	58° 36'	3.8	0.0	6.7
	58° 58'	18.7	0.0	9.0
	59° 90'	17.9	0.0	14.4
	62° 64'	8.0	4.8	0.0
	65° 35'	3.1	7.8	0.0
	66° 88'	0.0	1.7	5.3
<i>V. vitis-idaea</i> Fl	55° 58'	9.4	0.0	8.3
	55° 97'	NO DATA	NO DATA	NO DATA
	57° 15'	8.0	0.0	7.1
	58° 26'	2.0	8.7	0.0
	58° 36'	2.6	0.0	6.0
	58° 58'	4.9	2.2	0.0
	59° 90'	7.4	0.0	8.6
	62° 64'	16.7	0.0	23.6
	65° 35'	2.8	0.0	1.7
	66° 88'	NO DATA	NO DATA	NO DATA
<i>P. tremula</i> Bb	55° 58'	4.9	0.0	7.1
	55° 97'	NO DATA	NO DATA	NO DATA
	57° 15'	12.1	0.0	9.2
	58° 26'	22.6	17.9	0.0
	58° 36'	3.1	2.8	0.0
	58° 58'	11.3	0.0	5.3
	59° 90'	2.6	0.9	0.0
	62° 64'	5.3	6.9	0.0
	65° 35'	4.8	0.0	9.8
	66° 88'	1.5	0.0	2.7
	<i>best model</i>	1	18	8
	$\Delta AIC_c \leq 2$	3	20	9
	$\Delta AIC_c \leq 6$	15	23	13

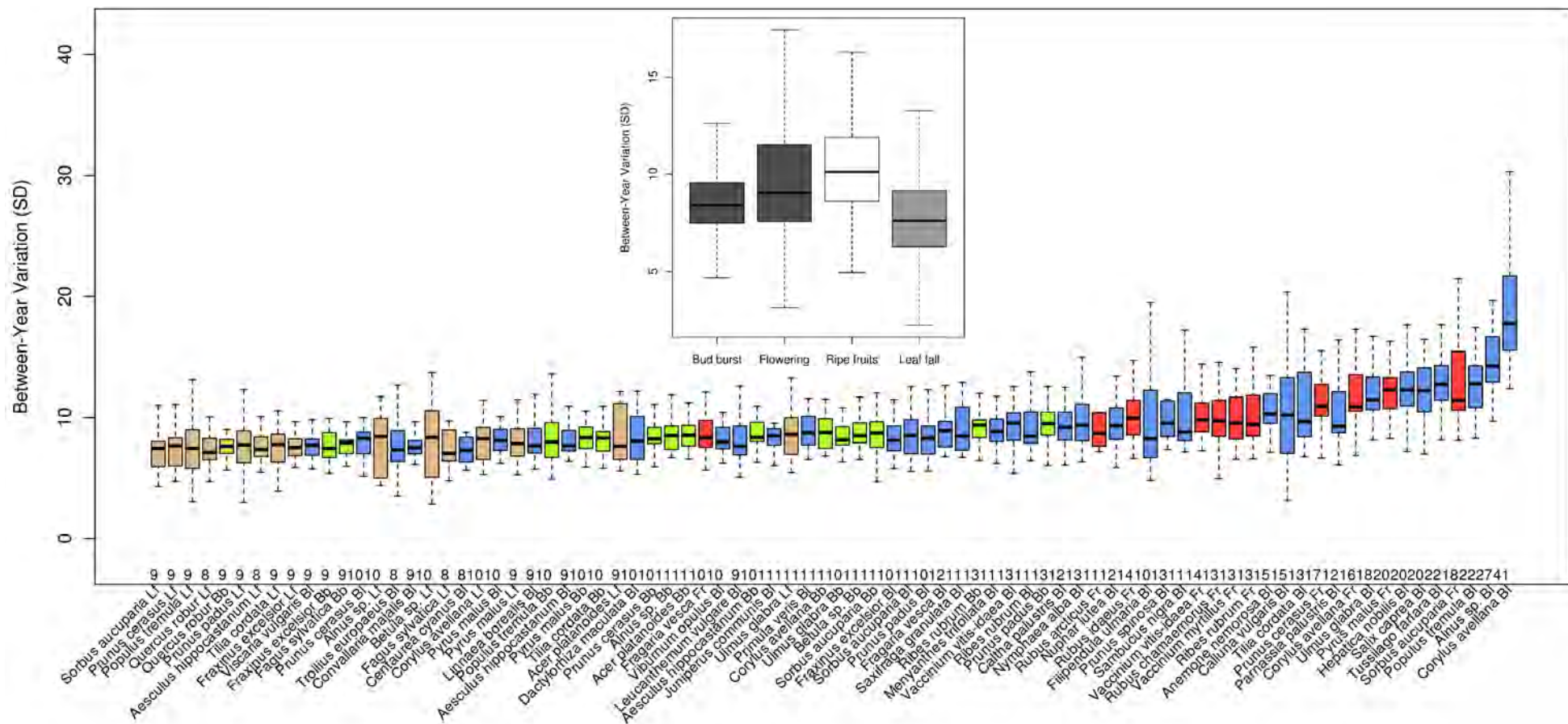


Figure 10. Between-year variation in phenophase onset days for the analyzed species-phenophase combinations (SPPHs) ranked after increasing mean *SD*. The number of required observation years to detect a 7-day change is stated above the x-axis for each SPPH. Green = Bud burst, Blue = Flowering, Red = Ripe fruits, Brown = Autumn leaves. Box plots show the median, 1st and 3rd quartiles, and the full range of the sample. In the group boxplot, shading indicate groups from Tukey's HSD.

3.3.2 Geographical variability in parameter values

While I did not find any correlation between geography and best fit model as selected by AIC, I did observe a latitudinal correlation for both fit parameters (t_1 and F^*) of SWCF2 for *S. aucuparia* Bb, where t_1 increased, while F^* decreased with latitude (Figure 11). It is important to emphasize the fact that, for the models, days are counted from the 1st of September instead of the 1st of January (which is day 123 here).

For *S. aucuparia* bud burst, I also found a positive correlation with latitude for t_1 in SWCF1, and a negative for T_{force} in ALTCF1, and for *P. tremula* bud burst I found a positive correlation for F^* in SWCF1 (Table 4). For *V. vitis-idaea* Fl, I did not find correlation with latitude in any of the parameters.

Table 4. Summary of correlations between parameter values and latitude.

SPPH	parameter/model	m (slope)	P
<i>S. aucuparia</i>	t_1 SWCF1	5.1	0.01
	t_1 SWCF2	6.4	0.004
	F^* SWCF2	-13.5	0.008
	T_{force} ALTCF1	-0.8	0.02
<i>P. tremula</i>	F^* SWCF1	100.1	0.03

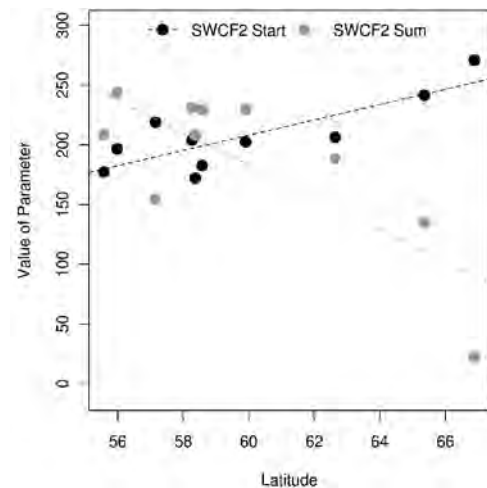


Figure 11. Regressions of parameter values against latitude. Start is the fitted starting day for heat sum accumulation, and Sum is the fitted heat sum in the model SWCF2 for *Sorbus aucuparia* bud burst.

4 Discussion

4.1 Phenological between-year variation

In compliance with previous studies (Menzel *et al.* 2006b; Sparks & Menzel 2002), I show that earlier events have a bigger BYV than later events (Figure 5). This is likely to be a reflection of the higher inter-annual variability in temperature of winter months compared to summer months (Figure 9). However, although we see an increase in variability of temperature in later months as well, this is not reflected in the autumn phases that do show a low BYV. This could be explained by an initiation of senescence triggered by a shortening photoperiod (Fracheboud *et al.* 2009).

When looking at a particular phenophase and its onset, the duration of the time frame to occur across Sweden is greater for early and late phases (Figure 4). For early phases, this could be explained by the greater temperature difference between high and low latitudes during winter (Figure 8). For the autumn phases, it is possibly the gradual increase in photoperiod span over Sweden during autumn that is causing the increase in onset span. Mid-summer phases do not show the same spatial heterogeneity in

occurrence as early and late phases, which is also a reflection of the fact that summer temperatures are not as varying across Sweden as the winter temperatures are.

A previous study by Menzel *et al.* (2006a) showed an ambiguous response in leaf coloring phases to warming temperatures (some were advancing while others were delayed). Moreover, the Pearson's product moment correlation coefficients between annual mean onset dates and temperature for these phases were lower than for spring and summer phases, which indicates a weaker response to temperature. Instead, the ambiguities in responses of leaf coloring found by Menzel *et al.*, could in part be explained by the vast geographic spread of the dataset used for the analyses. As previously mentioned, the response of leafing out to warmer temperatures was found to move forward in colder regions while the effect is reversed in warmer regions (Zhang *et al.* 2007). This may in turn influence studies covering areas encompassing environmental gradients without accounting for them.

The differences in variability in temperature in spring between latitudes, is gradually declining and is more or less gone come April. However, the latitudinal differences in BYV reach the lowest point in May (Figure 5). Also, there is a hump in the seasonality of BYV peaking in late summer. In fact, this hump seems to be present also in Figure 9, but occurring in May-June. Both of these findings suggest that there is a time-lag between temperatures experienced by a plant and occurrence of phases, giving further support to the temperature sum-hypothesis as a mechanistic model of plant phenological onset.

The suggestion of a unimodal relation found here between SD_{onset} and latitude (Figure 7) is, to the best of our knowledge, previously unpublished. More specifically, it is the fact that some SPPHs show a correlation between BYV and latitude, and that the size and sign of the regression coefficient seem related to which time of the year the phase is occurring in a unimodal fashion. The earliest and latest SPPHs show less variability at higher latitudes while summer phases show an opposite pattern with more variability at higher, compared to lower, latitudes. This finding, at a first glance, might seem counter-intuitive since I previously explained a higher variability in mean onset dates with a higher variability in temperature for winter months. However, we must take into account that the growing season is considerably shorter at higher latitudes (Perttu & Morén 1995).

For spring phases, timing is under evolutionary pressure from two opposing directions: an earlier onset increases the available growing season while a delayed onset decreases the risk of frost damage. Thus, there is an optimal trade-off between adaptation to capacity on the one hand, and to survival on the other (Lockheart 1983), creating a stabilizing selection (Bennie *et al.* 2010). The experiences gathered in this thesis, do suggest that the relative strengths of these pressures may have an effect on the amount of between-year variation.

In northern latitudes, there is an increased pressure for later onset (i.e. survival adaptation) since, frost nights last longer in the spring here. Also, the force to maximize the growing season (i.e. capacity adaptation) is stronger because of the shorter growth season. The increased pressure for earlier onset from capacity adaptation, together with the increased survival pressure for later onset, is reducing the time frame for onset to occur. Hence, the onset peak will be higher and the standard deviation reduced.

In autumn, phases also show less BYV in higher vis-à-vis lower latitudes. With an increased risk of frost exposure (resulting in foliar necrosis or undeveloped seeds), due to a steeper temperature decrease, the adaptive pressure is reversed and is forcing onset to occur earlier. Also in autumn, there is the strong capacity maximizing pressure preventing plants from leafing out too early, resulting again, in a stronger onset peak

with a lower standard deviation.

To a large extent, differences in BYV between phenophase groups (analysis of variance, Figure 10), reflect the seasonal timing of phases already discussed, and the fact that bud burst and flowering do not show any differences could thus be a result of their overlap in time.

The start and duration of the growing season, is dependent not only on latitude, but also on altitude (Perttu & Morén 1995). Thus, to further increase the understanding of variability in phenology, it would be interesting to include altitude as a variable in future analyses of this kind. Also, taking the influence of the warm waters of the Atlantic Ocean on the phenology of species on the west coast of Sweden (Arnell 1930) into account, could help explain variability even further.

4.1.1 A phenological climate indicator

The topic of phenological variability over time often refers to the way species change over time, i.e. the potential *trends* in phenological change, as reflections of changes in long term climatic circumstances. However, there is also a variability occurring on the scale of only a few years that has an effect on the statistical power when looking at larger scale changes.

In Figure 10, since the ranking and the power analysis is performed on national mean values, it is legitimate to suspect that species with a limited distribution (such as phases of southern species) perform better in the ranking, compared to species with a full distribution since a limited number of samples might reduce the mean. Indeed, among the phases that require short observation periods to detect a phenological change of one week, we do see many southern species. However, if we look at Figure 5, there is no apparent tendency towards lower mean SD_{onset} for phases with limited distributions. Also, when looking at plots of individual phases, southern species seem to have a lower SD_{onset} than most species occurring at the same location.

Furthermore, early spring phases will have lower power. This includes the flowering of *Hepatica nobilis*, *Anemone nemorosa*, *Tussilago farfara*, *Salix caprea* and *Corylus avellana* - phases commonly used by the SWE-NPN. However, even if these early phases do show a higher BYV, they also tend to show a stronger phenological response to temperature (Menzel *et al.* 2006a), which might outweigh the lower power.

In an ecological sense, this short-scale variability reflects a difference between species in sensitivity to weather variability. A part of this variability may however stem from sampling error. In this case it is inaccuracies in the determination of onset due to incorrect observation. As with all data series that are quite old, there is no way to validate the quality of the observations. However, with the analysis performed here, any greater inaccuracies or peculiarities would most likely have appeared. However, any bias related to differences in the practice of individual observers is difficult to either rule out or account for (for example differences in sampling frequency or differences in the sheer ability to determine onset).

Another methodological issue is the conformity of observational practice. It is impossible to be certain whether observations stem from the same individuals each year, and not the earliest individuals in an area, which could erase the effects of micro-climate (such as ground cover and slope angle) and reduce BYV. Another related concern is that in populations of temperate-zone perennials, large plants frequently flower earlier than smaller individuals (Forrest & Miller-Rushing 2010).

Apart from the effect of BYV on the power to detect phenological changes, we must consider several other factors that are affecting the suitability of species to act as

climate indicators on a national scale. First and foremost, the sheer distribution of some species will avert some species from even being considered, no matter how suitable they might be in other aspects. Even so, in some cases it could still be desirable to observe a species with a limited distribution in a region where, for instance, previous data records of good quality and length are available. Also, the need for species to have easily determinable phases is crucial if the use of phenological data, in the monitoring of ecological responses to climate change, is to follow the path envisioned by its proponents. This stems from the fact that with an increasing body of sampling data, it is probable that an increasing proportion will originate from amateur observers. If these observations come from phases that are easily recognizable, there will be less hesitation regarding inclusion of this data in analyses.

Presumably, different fields of application (for example allergenic flora, climate change, or commercial forestry) have different requirements for what constitutes good indicator species, relating to different factors such as distribution, precision, et cetera. Also, with the advancement of remote sensing techniques, the science of phenology as a whole is changing radically.

4.2 Phenological models

I evaluated three phenological models differing in the way that onset is predicted. *CF1/CF2* refer to different functions for the rate of forcing (R_f), while *Spring warming* and *Alternating* are different ways to calculate the state of forcing (F^*) which is the temperature sum where onset occurs. Although not consistent, the overall best choice of model to explain the data seemed to be the *SWCF2* model, a similar result to that of Richardson and O'Keefe (2009), which is explained by the fact that *SWCF2* has lowest amount of fit parameters among the models since all models performed equally well according to the sum of squared errors of prediction.

I did find correlation with latitude in a few of the fitted parameters. However, the results were inconsistent across models and across species which makes it difficult to discern the ecological interpretability of the results. Even so, the correlation of both parameters in *SWCF2* for *Sorbus aucuparia* bud burst show a decrease in required temperature sum with increasing latitude, and a latitudinal increase in the start day of accumulation of temperature sum which seem to concur with evidence of a decrease in temperature sum requirement for provenances from sites with shorter growing season (such as sites from higher latitudes) (Sarvas 1967).

As far as I know, phenological modeling has to date been used mainly for prediction rather than ecophysiological interpretations of model variables (Hänninen 1995). Most studies so far, have aimed at determining best-fit models and parameters for novel geographical ranges and species, and do not attempt to establish ecological relationships (however see Schaber & Badeck 2003). Also, even if provenance studies suggest varying temperature sum requirements according to environmental gradients (Chmura & Rozkowski 2002), the temperature sum concept is based on conceptual theory (Hänninen 2006) while the ecophysiological mechanisms behind bud burst and flowering is not fully understood. However, the prevailing opinion is that these phases are regulated by hormones interacting to promote or inhibit growth (Powell 1987).

In a few cases, very low threshold temperatures (T_{force}) were fit (-15°C), which seem difficult to translate into an ecophysiological explanation. It is of course possible to set pre-defined limits to parameter values (to get more reasonable values), but the potential (if it *does* exist) to compare results between locations is then lost.

Suggested by the trade-off between capacity and survival, another problem arises

when applying a model across regions, or across species. If there is geographic variability in bud burst strategies, models might be valid only for the species and locations they were fitted for (Bennie *et al.* 2010). Thus, in future analyses it would be interesting to study the effect of latitude on the external validity of phenological models by looking at the ability of models fitted for medium latitudes to maintain predictive accuracy when applied to lower versus higher latitudes. It would also be interesting to test whether the precision of predictions is affected by the between-year variation of the fitted phenophases. To improve future predictions, we could also include additional explanatory data. For instance, photoperiod (Schaber & Badeck 2003) and rainfall (Spano *et al.* 1998) have been found to increase precision and are both examples of data that is easily acquired from meteorological, or similar, services.

4.3 Synopsis

The changing climate has had an effect on the phenology of many species. Even if empirical evidence confirming this is abundant, there are still problems with the prediction of future responses of populations due to the effects of landscape heterogeneity on ecophysiological mechanisms.

However, concerns have been raised to whether observed phenological shifts really describe the behavior of entire populations since many studies rely on first flowering dates instead of mean or peak flowering dates. According to Miller-Rushing *et al.* (2008), this could result in incorrect conclusions about phenological shifts since first flowering dates represent only one extreme of the flowering distribution. Whether a population is increasing or declining, this could result in opposite conclusions about phenological shifts.

Previously, there have been attempts to put a globally coherent fingerprint of climate change on animals and plants (Parmesan & Yohe 2003; Parmesan 2007; Root *et al.* 2003; Root *et al.* 2005), by putting a number on the magnitude of phenological change as, for instance, overall spring advancement per decade or the percentage of species showing a response to warming temperatures. However, since the response of species to climate change vary considerably in both direction and magnitude, it is reasonable to question the benefits and possible uses of such a fingerprint.

Future efforts should aim at quantifying the effects of phenological changes at an individual and community level respectively, with regard to both temporal and geographic variability. For instance, for interacting species, geographical differences in phenological variability of the interacting species could possibly have effects on interaction strength and susceptibility to change. Thus, by quantifying the effect of phenological change on the interactions of species, we would increase the insight to what the ecological impacts of phenological change is. As a final note, while phenological climate change assessment is centered on detecting, interpreting and discussing change, let us not forget that danger lies also with species that do not respond to a changing climate (Hulme 2011).

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6 References

- Amano, T., Smithers, R. J., Sparks, T. H., and Sutherland, W. J. 2010. A 250-year index of first flowering dates and its response to temperature changes. *Proceedings of The Royal Society B* 277: 2451-2457.
- Arnell, H. W. 1923. Vegetationens årliga utvecklingsgång i Svealand. *Meddelanden från Statens meteorologisk-hydrografiska anstalt* 2: 1-79.
- Arnell, K. 1927. Vegetationens utvecklingsgång i Norrland. *Meddelanden från Statens meteorologisk-hydrografiska anstalt* 4: 1-28.
- Arnell, K., and Arnell, S. 1930. Vegetationens utveckling i Götaland. *Meddelanden från Statens meteorologisk-hydrografiska anstalt* 6: 1-70.
- Augsburger, C.K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* 62: 775-788.
- Barr, A. G., Black, T. A., Hogg, E. H., Kljun, N., Morgenstern, K., and Nesic, Z. 2004. Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. *Agricultural and Forest Meteorology* 126: 237-255.
- Bennie, J., Kubin, E., Wiltshire, A., Huntley, B., and Baxter, R. 2010. Predicting spatial and temporal patterns of bud-burst and spring frost risk in north-west Europe: the implications of local adaptation to climate. *Global Change Biology* 16(5): 1503-1514.
- Burnham, K. P., and Anderson, D. R. 2002. Model selection and multi model inference: A practical information-theoretic approach. 2nd ed. Springer, New York.
- Campbell, N. A., and Reece, J. B. 2005. *Biology*. 7th ed. Pearson Benjamin Cummings.
- Chmura, D. J., and Rozkowski, R. 2002. Variability of beech provenances in spring and autumn phenology. *Silvae genetica* 51(2-3): 123-127.
- Chuine, I., Cour, P., and Rousseau, D. D. 1998. Fitting models predicting dates of flowering of temperate-zone trees using simulated annealing. *Plant, Cell and Environment* 21: 455-466.
- Chuine, I., Cour, P., and Rousseau, D. D. 1999. Selecting models to predict the timing of flowering of temperate trees: implications for tree phenology modelling. *Plant, Cell and Environment* 22: 1-13.
- Chuine, I., Yiou, P., Viovy, N., Seguin, B., Daux, V., and Le Roy Ladurie, E. 2004. Grape ripening as a past climate indicator. *Nature* 432: 289.
- Crawley, M. J. 2005. *Statistics: an introduction using R*. John Wiley & Sons Ltd, West Sussex.
- Diekmann, M. 1996. Relationship between flowering phenology of perennial herbs and meteorological data in deciduous forests of Sweden. *Canadian Journal of Botany* 74: 528-537.
- Ellebjerg, S. M., Tamstorf, M. P., Illeris, L., Michelsen, A., and Hansen, B. U. 2008. Inter-annual variability and controls of plant phenology and productivity at Zackenberg. *Advances In Ecological Research* 40: 249-273.
- Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., & Paulißen, D. 1991. *Zeigerwerte von Pflanzen in Mitteleuropa*. 1st ed. Scripta Geobotanica XVIII. Göttingen: Verlag E. Goltze. Gimingham, C. H.
- Elzinga, J. A., Atlan, A., Biere, A., Gigord, L., Weis, A. E., and Bernasconi, G. 2007. Time after time: flowering phenology and biotic interactions. *Trends in Ecology and Evolution* 22(8): 432-439.

- Fitter, A. H., and Fitter, R. S. R. 2002. Rapid changes in flowering time in British plants. *Science* 296: 1689-1691.
- FOA, 2008. Climate change and food security: a framework document. WWW document: <http://www.fao.org/docrep/010/k2595e/k2595e00.htm>. Date visited 6 May.
- Forrest, J., and Miller-Rushing, A. J. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of The Royal Society B* 365: 3101-3112.
- Fracheboud, Y., Luquez, V., Björkén, L., Sjödin, A., Tuominen, H., and Jansson, S. 2009. The control of autumn senescence in European Aspen. *Plant Physiology* 149(4): 1982-1991.
- Gu, L., Hanson, P. J., Post, W. M., Kaiser, D. P., Yang, B., Nemani, R., Pallardy, S. G., and Meyers, T. 2008. The 2007 Eastern-US spring freeze: increased cold damage in a warming world. *BioScience* 58(3): 253-262.
- Hassel, L., Bolmgren, K., and Langvall, O. 2010. Upptäck effekterna av klimatpåverkan. Länsstyrelsen i Jönköping, Meddelande: nr 2010:07.
- Hill, M. O., Mountford, J. O., Roy, D. B., and Bunce, R. G. H. 1999. *Ellenberg's indicator values for British plants*. Institute of Terrestrial Ecology, Huntingdon, UK.
- Hulme, P. E. 2011. Contrasting impacts of climate-driven flowering phenology on changes in alien and native plant species distributions. *New Phytologist* 189: 272-281.
- Hänninen, H. 1995. Effects of climatic change on trees from cool and temperate regions: an ecophysiological approach to modeling of bud burst phenology. *Canadian Journal of Botany* 73: 183-199.
- Hänninen, H. 2006. Climate warming and the risk of frost damage to boreal forest trees: identification of critical ecophysiological traits. *Tree Physiology* 26: 889-898.
- IPCC, 2007: *Climate Change 2007: The Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 996 pp.
- Kirkpatrick, S., Gelatt, C. D. Jr., and Vecchi, M. P. 1983. Optimization by simulated annealing. *Science* 220(4598): 671-680.
- Kramer, K., Friend, A., and Leinonen, I. 1996. Modelling comparison to evaluate the importance of phenology and spring frost damage for the effects of climate change on growth of mixed temperate-zone deciduous forest. *Climate Research* 7: 31-41.
- Körner, C., and Paulsen, J. 2004. A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* 31: 713-732.
- Lieth, H. 1974. *Phenology and seasonality modeling*. Berlin - Heidelberg - New York, Springer-Verlag.
- Lockheart, J. A. 1983. Optimum growth initiation time for shoot buds of deciduous plants in a temperate climate. *Oecologia* 60: 34-37.
- Matear, R. J., Wang, Y., and Lenton, A. 2010. Land and ocean nutrient and carbon cycle interactions. *Current Opinion in Environmental Sustainability* 2: 258-263.
- Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F. M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A. J. H., Wielgolaski, F-E., Zach, S., and Zust, A. 2006a. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12: 1969-1976.

- Menzel, A., Sparks, T. H., Estrella, N., and Roy, D. B. 2006b. Altered geographic and temporal variability in phenology in response to climate change. *Global Ecology and Biogeography* 15: 498-504.
- Metropolis, N., Rosenbluth, A. W., Rosenbluth, M. N., and Teller, A. H. 1953. Equation of state calculations by fast computing machines. *The Journal of Chemical Physics* 21(6): 1087-1092.
- Miller-Rushing, A. J., Inouye, D. W., and Primack, R. B. 2008. How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. *Journal of Ecology* 96: 1289-1296.
- Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology* 13: 1860-1872.
- Parmesan, C., and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37-42.
- Perttu, K., and Morén, A-S. 1995. Regionala klimatindex - verktyg vid bestämning av skogsproduktion. *Fakta Skog* 13. SLU Info/Skog, Umeå.
- Powell, L. E. 1987. Hormonal aspects of bud and seed dormancy in temperate-zone woody plants. *Hortscience* 22: 845-850.
- Primack, R. B., Ibáñez, I., Higuchi, H., Lee, S. D., Miller-Rushing, A. J., Wilson, A. M., and Silander, J. A. Jr. 2009. Spatial and interspecific variability in phenological responses to warming temperatures. *Biological Conservation* 142: 2569-2577.
- Richardson, A. D., and O'Keefe, J. 2009. Phenological differences between understory and overstory: a case study using the long-term Harvard forest records. In: Noormets, A. (ed.), *Phenology of Ecosystem Processes: Applications in Global Change Research*, pp. 87-117. Springer Science+Business Media, LLC.
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., and Pounds, J. A. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57-60.
- Root, T. L., and Hughes, L. 2005. Present and future phenological changes in wild plants and animals. In: Lovejoy, T. E., and Hannah, L. (ed.), *Climate change and biodiversity*. Yale University Press, New Haven, Connecticut, USA.
- Sarvas, R. 1967. The annual period of development of forest trees. *Proceedings of the Finnish Academy of Science and Letters* 1965: 211-231.
- Saxe, H., Cannell, M. G. R., Johnsen, Ø., Ryan, M. G., and Vourlitis, G. 2001. Tree and forest functioning in response to global warming. *New Phytologist* 149(3): 369-399.
- Schaber, J., and Badeck, F-W. 2003. Physiology-based phenology models for forest tree species in Germany. *International Journal of Biometeorology* 47: 193-201.
- Shindo, C., Bernasconi, B., and Hardtke, C. S. 2007. Natural genetic variation in *Arabidopsis*: Tools, traits and prospects for evolutionary ecology. *Annals of Botany* 99: 1043-1054.
- Spano, D., Cesaraccio, C., Duce, P., and Snyder, R. L. 1999. Phenological stages of natural species and their use as climate indicators. *International Journal of Biometeorology* 42: 124-133.
- Sparks, T. H., and Menzel, A. 2002. Observed changes in seasons: An overview. *International Journal of Climatology* 22: 1715-1725.
- Sultan, S. E. 2000. Phenotypic plasticity for plant development, function and life history. *Trends In Plant Science* 5(12): 537-542.
- Visser, M. E., and Both, C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of The Royal Society B* 272: 2561-2569.
- Visser, M. E., and Holleman, L. J. M. 2001. Warmer springs disrupt the synchrony of oak

and winter moth phenology. *Proceeding of The Royal Society of London B* 268: 289-294.

Zhang, X., Tarpley, D., and Sullivan, J. T. 2007. Diverse responses of vegetation phenology to a warming climate. *Geophysical Research Letters* 34, L19405, doi:10.1029/2007GL031447.

Appendix A: Species and trait data

Species	Observed Phases				Poll.	L	T	K	F	R	N	Leaf Phen.
<i>Acer platanoides</i>	Bb	Fl		Lf	I	4	x	4	6	x	7	S
<i>Aesculus hippocastanum</i>	Bb	Fl		Lf	I	x	x	x	x	x	x	x
<i>Anemone nemorosa</i>		Fl			I	x	x	3	5	x	x	V
<i>Calluna vulgaris</i>		Fl			I	8	x	3	x	1	1	I
<i>Caltha palustris</i>		Fl			I	7	x	x	9	x	x	S
<i>Centaurea cyanus</i>		Fl			I	7	6	5	x	x	x	W
<i>Convallaria majalis</i>		Fl			I	5	x	3	4	x	4	S
<i>Corylus avellana</i>	Bb	Fl	Fr	Lf	W	6	5	3	x	x	5	S
<i>Dactylorhiza maculata</i>		Fl			I	7	x	2	8	x	2	S
<i>Fagus sylvatica</i>	Bb			Lf	W	3	5	2	5	x	x	S
<i>Filipendula ulmaria</i>		Fl			I	7	5	x	8	x	4	S
<i>Fragaria vesca</i>		Fl	Fr		I	7	x	5	5	x	6	W
<i>Fraxinus excelsior</i>	Bb	Fl		Lf	W	4	5	3	x	7	7	H
<i>Hepatica nobilis</i>		Fl			I	4	6	4	4	7	5	I
<i>Juniperus communis</i>		Fl	Fr		W	8	x	x	4	x	x	I
<i>Leucanthemum vulgare</i>		Fl			I	7	x	3	4	x	3	W
<i>Linnea borealis</i>		Fl			I	5	x	5	5	2	2	I
<i>Menyanthes trifoliata</i>		Fl			I	8	x	x	9	x	3	W
<i>Nuphar lutea</i>		Fl			I	8	6	4	11	7	6	S
<i>Nymphaea alba</i>		Fl			I	8	6	3	11	7	5	S
<i>Parnassia palustris</i>		Fl			I	8	x	x	8	7	2	S
<i>Populus tremula</i>	Bb	Fl		Lf	W	6	5	5	5	x	x	S
<i>Primula veris</i>		Fl			I	7	x	3	4	8	3	W
<i>Prunus cerasus</i>	Bb	Fl	Fr	Lf	I	4	5	4	5	7	5	S
<i>Prunus padus</i>	Bb	Fl	Fr	Lf	I	5	5	3	8	7	6	S
<i>Prunus spinosa</i>		Fl			I	7	5	5	4	7	x	S
<i>Pyrus malus</i>	Bb	Fl	Fr	Lf	I	6	6	5	5	8	x	S
<i>Quercus robur</i>	Bb			Lf	W	7	6	6	x	x	x	S
<i>Ribes rubrum</i>	Bb	Fl	Fr		I	4	6	7	8	6	6	S
<i>Rubus arcticus</i>		Fl	Fr		I	x	x	x	x	x	x	x
<i>Rubus chamaemorus</i>		Fl	Fr		I	9	3	7	8	2	1	S
<i>Rubus idaeus</i>		Fl	Fr		I	7	x	x	x	x	6	S
<i>Salix caprea</i>		Fl			I	7	x	3	6	7	7	S
<i>Sambucus nigra</i>	Bb	Fl			I	7	5	3	5	x	9	S
<i>Saxifraga granulata</i>		Fl			I	x	6	2	4	5	3	V
<i>Sorbus aucuparia</i>	Bb	Fl	Fr	Lf	I	6	x	x	x	4	x	S
<i>Tilia cordata</i>	Bb	Fl		Lf	I	5	5	4	5	x	5	S
<i>Trifolium pratense</i>		Fl			I	7	x	3	x	x	x	S
<i>Trollius europaeus</i>		Fl			I	9	3	5	7	6	5	S
<i>Tussilago farfara</i>		Fl			I	8	x	3	6	8	x	S
<i>Ulmus glabra</i>	Bb	Fl		Lf	W	4	5	3	6	7	7	S
<i>Vaccinium myrtillus</i>		Fl	Fr		I	5	x	5	x	2	3	S
<i>Vaccinium vitis-idaea</i>		Fl	Fr		I	5	x	5	4	2	1	I
<i>Viburnum opulus</i>	Bb	Fl			I	6	5	3	x	7	6	S
<i>Viscaria vulgaris</i>		Fl			I	7	6	4	3	4	2	W

Phases
Bb = Bud burst, **Fl** = Flowering, **Fr** = Ripe Fruits, **Lf** = Leaf Fall

Pollination
I = Insect, **W** = Wind

Elleberg Indicator Values

L = Light, **T** = Temperature, **K** = Continentality, **F** = Moisture, **R** = Reaction (soil pH, or water pH), **N** = Nitrogen; x = no data available

Leaf Phenology

S = Summer green, **V** = early summer green, **I** = evergreen, **W** = over-winter green

Appendix B: Summary of model parameter values

SPPH	Latitude	SWCF1			SWCF2		ALTCF1			
		t_1	T_{force}	F^*	t_1	F^*	t_1	T_{force}	a	b
<i>S. aucuparia</i> Bud burst	55.58°	186.5	4.4	164.7	177.3	208.6	191.4	6.0	123.4	-0.01
	55.97°	197.7	-0.03	435.8	196.6	243.6	199.9	-0.7	460.2	-0.02
	57.15°	219.7	3.3	172.9	218.9	154.3	96.4	5.0	502.4	-0.01
	58.26°	205.7	2.27	200.3	204.1	231.2	168.9	5.3	327.7	-0.01
	58.36°	171.9	-13.1	1394.5	172.1	208.4	140.6	-2.0	741.8	-0.01
	58.58°	205.5	4.1	188.4	182.6	229.3	66.9	5.0	454.1	-0.01
	59.90°	200.7	-1.32	476.8	202.5	229.8	153.2	-2.7	776.6	-0.01
	62.64°	210.7	-3.92	541.5	206.3	188.5	205.6	-1.6	461.9	-0.02
	65.35°	225.6	0.36	304.8	241.52	135.2	218.1	-1.8	379.1	0.11
	66.88°	266.9	-5.2	123.7	270.9	22.3	206.7	-7.0	895.2	-0.13
<i>V. vitis-idaea</i> Flowering	55.58°	202.7	5.5	417.9	198.1	490.0	202.0	7.4	266.3	0.01
	55.97°	N. D.	N. D.	N. D.	N. D.	N. D.	N. D.	N. D.	N. D.	N. D.
	57.15°	245.2	-3.0	547.2	246.8	284.3	36.8	-0.21	1625.1	-0.01
	58.26°	187.6	-10.21	1745.5	183.3	524.6	204.4	0.3	824.8	-0.03
	58.36°	201.2	1.2	611.4	156.2	458.2	155.9	-8.04	1756.2	-0.02
	58.58°	198.2	-10.4	1852.6	75.2	720.0	197.9	-10.0	1737.1	0.17
	59.90°	216.3	2.0	609.2	206.3	510.9	66.3	5.2	1205.8	-0.01
	62.64°	235.7	1.8	539.2	184.1	488.2	207.8	-3.05	1021.1	-0.02
	65.35°	232.3	2.2	561.1	232.7	445.9	257.1	9.1	155.9	0.02
	66.88°	N. D.	N. D.	N. D.	N. D.	N. D.	N. D.	N. D.	N. D.	N. D.
<i>P. trememula</i> Bud Burst	55.58°	222.1	6.4	172.2	197.1	310.3	225.6	3.96	249.8	-0.05
	55.97°	N. D.	N. D.	N. D.	N. D.	N. D.	N. D.	N. D.	N. D.	N. D.
	57.15°	202.2	4.0	230.7	201.5	242.8	203.3	2.0	350.6	-0.01
	58.26°	232.2	6.48	193.3	207.1	333.7	161.3	7.2	378.2	-0.01
	58.36°	201.0	-3.5	656.4	233.8	164.9	139.5	-4.94	1190.8	-0.01
	58.58°	222.7	9.7	106.5	222.2	284.4	225.4	-1.1	482.5	0.3
	59.90°	242.7	12.4	63.0	220.7	316.4	36.5	10.0	1098.8	-0.01
	62.64°	201.5	-8.07	1187.7	252.7	192.7	201.8	-1.8	749.2	-0.02
	65.35°	219.9	2.0	374.2	82.0	363.9	218.7	-1.04	491.2	0.12
	66.88°	201.3	-15.6	1599.0	260.8	107.0	202.8	-7.6	890.1	0.1

Models

SWCF1 = Spring Warming CF1, SWCF2 = Spring Warming CF2, ALTCF1 = Alternating CF1

Parameters

t_1 = Start date of accumulation, T_{force} = Threshold temperature, F^* = Temperature sum, a and b = ALTCF1 model constants