

Change of plant phenophases explained by survival modeling

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Abstract It is known from many studies that plant species show a delay in the timing of flowering events with an increase in latitude and altitude, and an advance with an increase in temperature. Furthermore, in many locations and for many species, flowering dates have advanced over the long-term. New insights using survival modeling are given based on data collected (1970–2010) along a 3000-km long transect from northern to eastern central Europe. We could clearly observe that in the case of dandelion (*Taraxacum officinale*) the risk of flowering time, in other words the probability that flowering occurs, is higher for an earlier day of year in later decades. Our approach assume that temperature has greater influence than precipitation on the timing of flowering. Evaluation of the predictive power of tested models suggests that Cox models may be used in plant phenological research. The applied Cox model provides improved predictions of flowering dates compared to traditional regression methods and gives further insights into drivers of phenological events.

Keywords Timing of flowering · Cox model with time dependent covariates · Biogeographical regions of Europe · *Taraxacum officinale*

Introduction

Phenology is the study of the seasonal timing of recurrent biological events (such as flowering, migration of birds, and emergence of insects), the causes of their timing with regard to biotic and abiotic forces, and the interrelations among phenophases (developmental stage) of the same or different species. Drivers of phenological responses range from macroclimatic circulation patterns (e.g., North Atlantic Oscillation) (Stenseth et al. 2003) to local environmental factors such as photoperiod (Körner and Basler 2010), edaphic factors (Wielgolaski 2001), precipitation (Fu et al. 2014), and temperature (IPCC 2007). Several studies have demonstrated significant changes in plant phenological events in the Northern and Southern Hemisphere (Menzel et al. 2006; Schwartz et al. 2006; Way 2011; Chambers et al. 2013). However, there are variations in the trends of phenological time series caused by phenophases, species, study periods, and geographical locations. Thus, differing responses to climate change can result in mismatches between the timing of plant and insect life cycles that impact other trophic levels and which may lead to population declines (Walther et al. 2002).

The phenology of most plant and insect species highly depends strongly on the thermal accumulation, determined by daily temperature. Each phenophase of an organism has its own total heat requirement and there have been many attempts to predict the onset of plant phenophases using heat sums. Most of these studies were conducted on agricultural species, e.g., budburst date in vineyards (Cortazar-Atauri

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et al. 2009), maturation in apricot cultivars (Ruml et al. 2011), or pollen prediction (Garcia-Mozo et al. 2009), where accurate forecasts are crucial.

Various methods have been tested previously to model the relevance of environmental conditions for plant phenophases. Current plant phenological studies either focus on temporal and spatial characterization of a stage in the annual life cycle of a plant based on observed or modeled data or attempt to predict the future timing of plant stages. Survival analysis is a branch of statistics (see, e.g., Rodriguez 2007) which deals with the analysis of the time duration until one or more events happen. Proportional hazard models—such as the one proposed by (Cox 1972)—were originally developed for the medical field. In our case, the event of interest is the flowering time of a plant species rather than patient survival time. Such models are nowadays applied to a broad range of “time to event” data sets in ecological studies as well (Kleinbaum and Klein 2012). Examples range from improved understanding of spring migration phenology (Bauer et al. 2004) and estimation of population growth predictions for an endangered species (DeCesare et al. 2013), as well as the development of a descriptive model for laying dates of birds (Gienapp et al. 2005, 2010).

We attempt to improve our understanding of flowering time by applying a non-traditional method, proportional hazard models to plant phenology. We used common dandelion as a model organism, because accurate long-term (1970–2010) data sets from biogeographical regions of Europe are available for this species. By calculating the hazard ratio of different climate variables, we showed their influence on flowering times and tested the predictive power of Cox models in phenological research.

Materials and methods

Phenological data

Plant phenological time series were collected for the period of 1970–2010 from northern to eastern central Europe. These data comprise phenological observations of common dandelion (*Taraxacum officinale* L., Asteraceae).

The studied beginning of flowering (BF) event was defined as “the appearance of the first flowers producing pollen on at least 10 percent of the observed plants visible.” This phenophase corresponds to event 61 according to the BBCH (Biologische Bundesanstalt, Bundessortenamt and Chemical Industry) code (Meier 2001). Data from nine European countries (Finland, Latvia, Lithuania, Poland, Hungary, Slovenia, Croatia, Bosnia and Herzegovina, Macedonia), between 40.9–67.9° in latitude and 13.6–32.1° in longitude, were collected (see Fig. 1). More

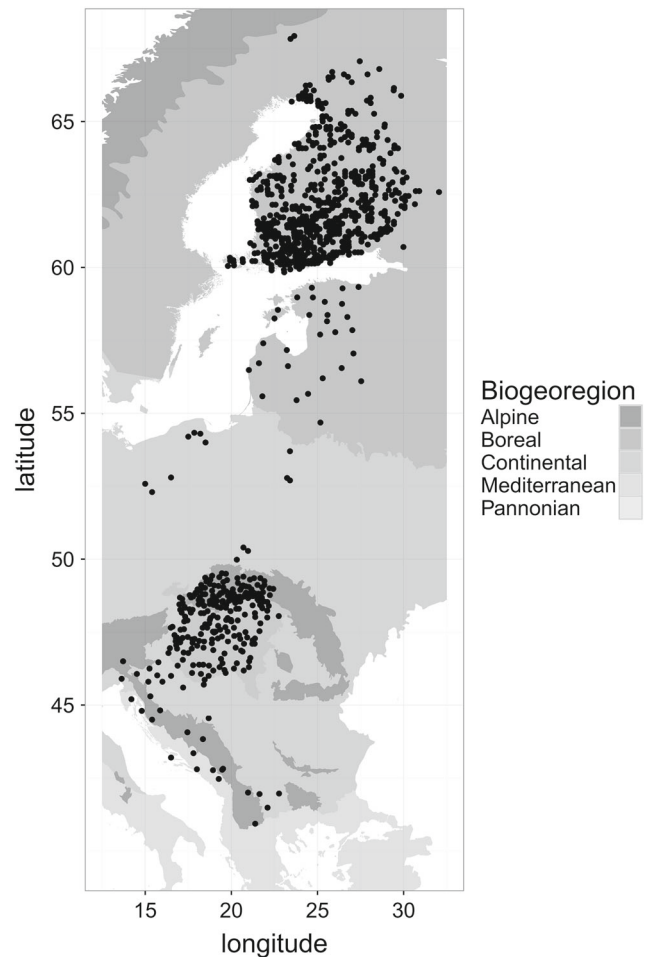


Fig. 1 Phenological observation sites and the studied north to south transect of biogeographical regions in Europe

precisely, data on common dandelion was taken from the NS-Pheno database (Templ et al. 2016, submitted). The NS-Pheno database includes phenological data collected from countries along the north-south transect across Europe, coordinated by the main author.

The database comprises records from the following national observation networks. Phenological data from Finland were recorded by the National Phenological Network (Kubin et al. 2007). Estonia has data over years compiled by the Estonian Naturalists Society and the Estonian Environment Agency (Ahas and Aasa 2006). Data from Lithuania originate from records collected by the Voke Branch of Lithuanian Research Centre for Agriculture and Forestry (Romanovskaja and Baksienė 2008). Observations from Latvia (Grisule and Baksienė 2008) originate from volunteer-collected sites of the humid continental climatic zones (Kalvane et al. 2009). The Institute of Meteorology and Water Management introduced and provided phenological observations from Poland (Niedzwiedz and Jatzczak 2008). The Slovak Hydrometeorological Institute collected

phenological observations from the territory of Slovakia (Remisová and Nejedlik 2008). The observational network of Hungary (Szalai et al. 2008; Szabò et al. 2016) (the main country of the Pannonian region) was maintained by the Hungarian Meteorological Service. Phenological data preserved by the Environmental Agency of the Republic Slovenia (Crepinsek et al. 2008) were also included in the database. The phenological network maintained by the Meteorological and Hydrological Service of Croatia (Vucetić et al. 2008) covers all of the main climatic zones (moderate continental, mountain, and Mediterranean) of the country. From historical reasons, Montenegro has similar phenological observations (Popovic and Drljevic 2008) to other former Yugoslavian states. Data were collected from Bosnia and Herzegovina too; however, the number of observational sites were affected by the wars in the 1990s (Hodzic and Voljevica 2008). The southernmost data provider for this study was Macedonia, which is a mostly unexplored region in terms of phenological research.

Environmental data

Temperature and precipitation data were obtained from the E-OBS regular gridded dataset developed by the ENSEMBLES EU-FP6 project¹ with a 0.25° spatial resolution (Haylock et al. 2008; Hofstra et al. 2009). Temperature data were available as daily minimum, maximum, and mean in degrees Celsius. Precipitation were available as millimeters per day. The temperature data contained some suspicious observations, where for instance the minimum temperature was greater than maximum temperature. To err on the side of caution, such observations were removed from the dataset before further data processing.

The relationship between growing degree days (GDD) and the onset of plant phenophases is well known (Cleland et al. 2007). A degree day is a measure of the amount of heat that accumulates above a specified base temperature during a 24-h period. Phenological models are usually based on accumulated temperature, termed growing degree days, which were calculated as:

$$GDD = \frac{T_{\max} + T_{\min}}{2} - T_{\text{base}}, \quad (1)$$

where T_{base} was chosen as 10°C for GDD calculations.

The data was collected in nine European countries representing five biogeographical regions, namely the Alpine, Boreal, Continental, Pannonian, and the Mediterranean (Fig. 1). We included the dataset of these regions from the European Environment Agency web page.² The biogeographical regions were first defined within the field of

conservation biology and are useful geographical reference units for describing habitat types and species which live under similar conditions (Roekaerts 2002; European Biological Diversity ETC 2006).

Instead of incorporating the geographical location of the station into the model (latitude, longitude, altitude), we stratified the model per station, i.e., we included the phenological stations in the Cox model as strata (see “Data analysis” section and Eq. 2). For the Cox model, this means that a separate baseline hazard function is fitted to each station. This way we lose the ability to make statements on the influence of geographic factors on a fine scale, but we minimize the influence of site-specific environmental conditions on our analysis by the influence of GDDs and precipitation on the beginning of flowering time. Because of the large numbers of climate and phenological stations that we have, we can nevertheless interpret the results by biogeoregion. This is also the strategy that yielded the best predictive power of all our attempts.

Data analysis

Dates of the phenological observations were converted to days of the year (doy) with 1st of January as the starting point. We found that the collected national phenological time series (see “Phenological data” section) were different in their length because of missing values. To handle this and to reach the best temporal and spatial coverage possible, the data were filtered based on the following selection criteria: (1) the station has at least 10 years of continuous records and (2) there are at least five stations within one biogeographical region. This way we created single homogenized phenological time series for each biogeographical region, using two-way crossed linear mixed models by using the pheno R package (Schaber 2012). This approach allows the aggregation of time series data in an optimal manner [details can be found in Schaber and Badeck (2002)].

We modeled the influence of climate variables on the timing of flowering onset as a survival analysis problem. We fitted the Cox proportional hazards model (Cox 1972) with time-dependent covariates (hereinafter Cox model), implemented in the R package survival (Therneau 2015). The Cox model can be used to calculate a hazard ratio for each time dependent covariate (climate variables). The hazard ratio can be regarded as the relative risk of an event occurring at time t . In other words, the relative risk is the ratio of the probability of an event occurring in the exposed group (influenced by environmental factors) versus a non-exposed group.

For the purpose of comparison, we also fitted a Cox proportional hazards model without time-dependent covariates and a classical linear regression model. We used five-fold cross-validation to compare the predictive power of

¹<http://www.ecad.eu/download/ensembles/ensembles.php>

²<http://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-1>

the models and reported the mean error (ME) and mean percentage error (MPE), to indicate whether the forecasts were biased.

In our case, GDD and precipitation were included in the Cox model as cumulative time-dependent covariates. To study whether the influence of these covariates varies between biogeographical regions, they were included as an interaction term. In addition, the model was stratified by station to account for geographical variations in flowering time. The hazard was thus defined as

$$h_s(t, X) = h_{0s}(t)e^{\beta_1 X_1(t)b + \beta_2 X_2(t)b} \quad (2)$$

where $h_s(t, X)$ is the hazard at time t for stratum (=station) s , $h_{0s}(t)$ is the time-dependent baseline hazard function for a given stratum, X contains the covariate vectors X_1 (growing degree days) and X_2 = (precipitation), and b is the vector of biogeoregions.

One of the principal results of this modeling approach is the hazard ratio—that is in our case the change in risk of flowering time associated with a unit increase of one of our covariates (GDD, precipitation). For example, a hazard ratio of 1.01 indicates a 1.01 times higher risk of flowering at a given day. Thus, the Cox model can further be used to predict a flowering risk for any given day of the year (daily hazard) based on climate data.

We made several attempts to include geographic parameters such as longitude, latitude, and altitude into the Cox model; however, we were not able to produce models that yielded satisfying predictions. This is likely due to the fact that those parameters are not sufficient to describe local climatic variations between stations well enough to account for variations in flowering. To get around this problem, we stratified the model by stations; thus, we removed all static, site-specific factors.

All analyses were performed using the statistical software and environment R (R Development Core Team 2016), the pheno package in version 1.6, the survival package in version 2.38.3., and, for visualization, we used the R package ggplot2 (Wickham 2009) in version 2.1.0.

Results

In order to calculate the risk of flowering time over Europe, we determined the long-term trends (1970–2010) of climate variables, which were included in the fitted models. We found that the monthly mean, minimum, and maximum temperatures (previous to the flowering onset dates) showed significant warming trends in the Alpine and continental regions. We did not find significant changes in temperature for the Boreal region from our dataset (but see Mikkonen et al. 2015). We present results from the Cox model, and we describe the shift of flowering dates using Kaplan-Meier

curves (Kaplan and Meier 1958). We also compare results on the prediction of survival dates with a traditional method (linear regression).

Shift of flowering date and the Kaplan-Meier Curves

An important part of survival analysis is to show the survival of each group of interest. In our case, various time periods were handled as groups (see Fig. 2). We visualized the shift in onset of flowering by generating the Kaplan-Meier survival curves from the phenological data. The Kaplan-Meier estimator is a stepwise estimator for survival probability, which in our case can be interpreted as the probability that common dandelion has already or has not yet flowered. Figure 2 shows the percentage of individuals that have not yet flowered at a given point in time. In general, we can see that the latter the decade the earlier the flowering date. More precisely, on a given day of year, the percentages of individuals that have not yet flowered is less in the following decade than in the preceding decade. Differences between the last two decades (1990–2000 and 2000–2010) are especially large. The survival curve relating to the time 1970–1980 period is the exception to this trend, since the temperatures in the 1970s (mean flowering time 110 and mean temperature (January till August) 9.36 °C) were higher than in the 1980s (mean flowering time 113 and mean temperature (January till August) 9.19 °C).

Cox model for time-dependent covariates

The hazard ratios and corresponding p values from the Cox model are reported for each covariate in Table 1. The main feature to note in such a table is whether the hazard ratio is greater or smaller than one. As mentioned earlier, a hazard ratio of 1.01 for instance means a 1.01 times higher risk that flowering will happen on any given day per additional growing degree day. A ratio of 1.01 % is thus not a

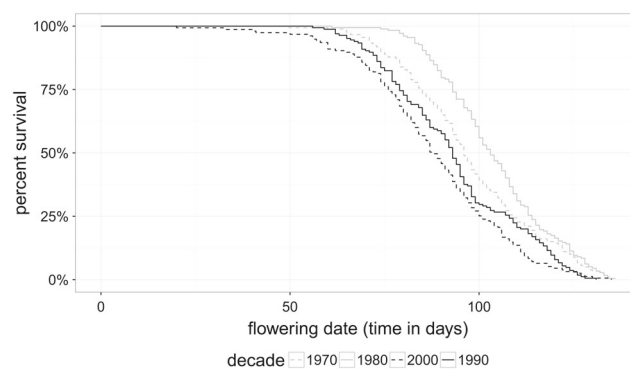


Fig. 2 Kaplan-Meier survival curves of *Taraxacum officinale* indicating shift in flowering dates over decades

Table 1 Hazard ratios, the change in risk of flowering time associated with a unit increase of one of the covariates

Covariates	Hazard ratio	<i>p</i> value
GDD × Alpine	<i>1.008</i>	0.001
GDD × Boreal	<i>1.016</i>	0.001
GDD × Continental	<i>1.012</i>	0.001
GDD × Mediterranean	<i>1.011</i>	0.001
GDD × Pannonian	<i>1.010</i>	0.001
Precipitation × Alpine	1.000	0.974
Precipitation × Boreal	<i>1.003</i>	0.035
Precipitation × Continental	0.999	0.327
Precipitation × Mediterranean	1.000	0.870
Precipitation × Pannonian	0.999	0.478

The higher hazard ratio value has the larger influence on the flowering risk, so that it triggers more the timing of flowering. Interaction terms between the covariates (growing days degree (GDD), precipitation) and biogeographical regions (see the “Environmental data” section) were also included in the Cox model. Relationships found to be significant ($p < 0.05$) are highlighted in italics. Three statistics were used to evaluate the model fit: concordance = 0.747 (se = 0.071), *R* square = 0.004 (max possible = 0.044), likelihood ratio test = 830.4 (on 10 df)

small number since it is—as mentioned before—a higher risk per day.

Our Cox model found a statistically highly significant link between GDD and onset of flowering time. This relationship varies slightly between different biogeographical regions (see Table 1). For precipitation, the calculated hazard ratios are ambiguous, because the Cox model found almost no statistically significant link between precipitation and onset of flowering. Only a slightly significant ($p \approx 0.035$) relationship can be shown for the Boreal region, which is likely an artifact because of the large amount of data, we have more statistical power, but the effect is not actually very strong. The likelihood ratio test confirmed that our model was significantly better than the null model (without predictors); the LR test statistics equals 830.4, $p \approx 0$.

We addressed two questions: (i) How do environmental covariates affect the relative risk of the onset of flowering? (ii) Is there a significant difference in this risk among the various regions and time periods? The shift of risk of flowering time among decades can be seen in Fig. 3. The relative risk is a measure relative to the mean covariate (GDD, precipitation, and their interaction with biogeographical region) value of each stratum (station). It can be observed that the risk of flowering time is higher for a given date in the year in later decades. Similarities can be seen between decades 1970–1980 and 1980–1990, because of similar temperature conditions. Notice also the similarities between the relative risk and the Kaplan-Meier curves in Fig. 2.

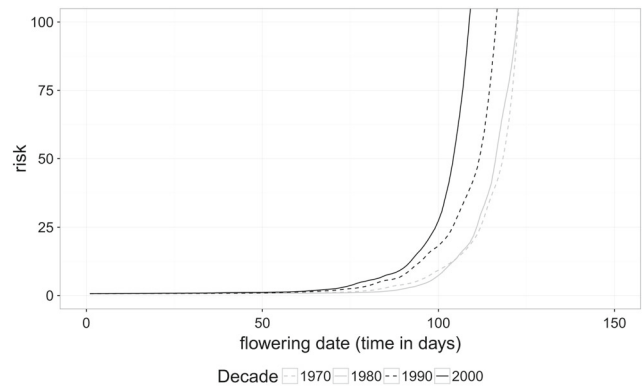


Fig. 3 Relative flowering time risk of *Taraxacum officinale* averaged by decades

Prediction of the flowering date

For comparison purposes, we predicted the mean flowering date from a classical linear regression model, as well as from a Cox model with and without time-dependent covariates. The Cox model itself does not directly predict a flowering date based upon given predictor variables (station, GDD,

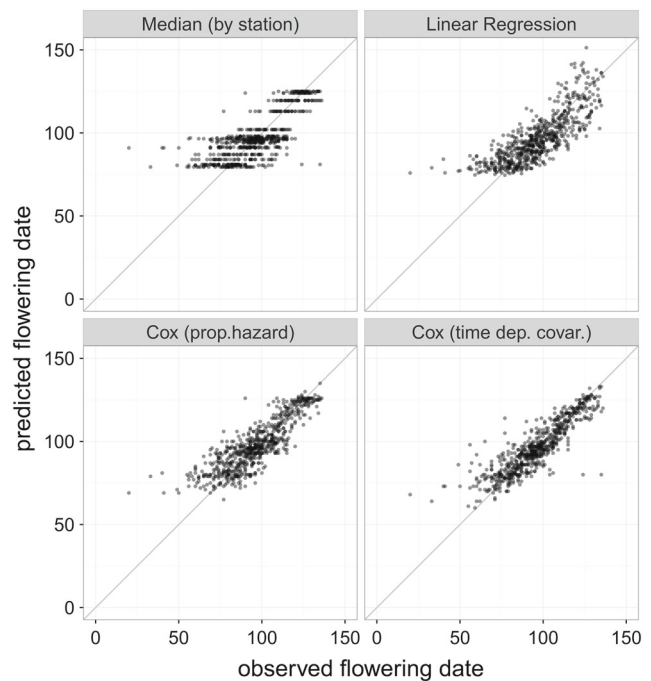


Fig. 4 Predicted against observed mean flowering dates (day of year) of *Taraxacum officinale*. For comparative purposes, the four cases indicate results from the median observed doys for each station against original observations (Median), the traditional regression model (Linear Regression), the Cox model without time-dependent covariates (Cox (prop.hazard)), and the Cox model with time-dependent covariates (Cox (time dep. covar.))

precipitation), but rather gives the probability that plants have not yet flowered by a given day. The mean predicted flowering date we use for our prediction is the date where there is a 50 % chance that the plant has flowered.

The results are visualized in Fig. 4. The predicted mean flowering of common dandelion correlated the best with the observed dates for the Cox model with time-dependent covariates (≈ 0.89 , see Fig. 4). Naturally, model deviations are highest for observations that depart from the bulk of the data. In our case, this mainly occurred with observed flowering dates earlier than day 45 and a few late flowering dates. According to Fig. 4, it becomes obvious that the Cox model, especially the one with time-dependent covariates (bottom right), gives better fit also to the extremes of the distribution as the traditional linear regression model (top right).

Table 2 shows several estimates of prediction accuracy based on stratified fivefold cross validation. We can see that the Cox model for time-dependent covariates outperforms the other models in terms of the root mean square error (RMSE), the mean absolute error (MAE), and the mean absolute percentage error (MAPE).

Discussion

Plant phenological responses are well documented across the Northern Hemisphere (Menzel et al. 2006; Schwartz et al. 2006) since such phenomena are sensitive to variations in climate, especially to temperature, as highlighted by recent studies on the ecological consequences of global climate change. Observed climate trends and future scenarios show regionally varying changes in temperature and precipitation in Europe (Kovats et al. 2014). Temperature increase in the Alpine region is expected to accelerate in the next century (Gobiet et al. 2014). We also detected warming trends (1970–2010) in two (Alpine and Continental) of the studied five biographical regions in Europe.

Table 2 Estimation of prediction accuracy using fivefold cross validation for the following models: (1) the median of the observed flowering date of each station (baseline model), (2) a simple linear regression model (classical modelling approach), (3) the Cox proportional hazard model (without time-dependent covariates), and (4) the Cox model with time-dependent covariates

	RMSE	MAE	MAPE
Median	12.84	9.72	10.51
Regression	11.01	8.52	9.10
Cox (prop.hazard)	11.71	8.92	9.53
Cox (time-dep. covar.)	10.46	7.44	8.07

RMSE root mean square error, MAE mean average error, MAPE mean average percentage error

Predictions of future warming necessitate further development of tools to better understand plant phenological responses, and this includes the testing of potentially useful non-traditional methods. Relative risk is a known terminology in epidemiology to describe the likelihood of developing a disease, as well as in environmental management to assess ecological risk. We present an application of this approach to the prediction of flowering time, by calculating the probability of flowering onset date by survival modeling. In general, survival models investigate follow-up time from a defined starting point to the occurrence of a given event (Bewick et al. 2004).

Compared to traditional linear regression, a major difference, and advantage of survival models is the possibility of including time-dependent (time-varying) covariates. These are predictor variables (in our case GDD and precipitation) whose values may change over the course of observation. Classical phenological models estimate plant developments by accumulating degree days between temperature thresholds throughout the season. The accumulation of degree days from a starting point can help to predict when a phenological stage will be reached. Similarly, survival models are able to integrate more environmental variables, but without the requirement to aggregate them. This is advantage, because of the usage of daily data (Pau et al. 2006) and the avoidance of the modifiable temporal unit problem (Jong and Bruin 2012). Based on the assumption that the probability of a phenological event happening can be interpreted as a survival event, we calculated the relative risk of flowering time for common dandelion across biogeographical regions in Europe. To our knowledge, this method has only been tested on bird phenological data (Gienapp et al. 2005; 2010; Visser et al. 2006; Williams et al. 2015) so far. Thus, the potential of this application is yet to be recognized by the plant phenological community.

Zeng et al. (2015) investigated recent changes in phenology over northern high latitudes from multi-satellite data. They found that the period 2000–2010 was associated with an advanced start of the growing season (SOS) of larger magnitude than the SOS trends of the 1980s and 1990s. Similar to these findings, based on the Kaplan-Meier estimation, we have found that within each decade since the 1980s, the timing of flowering of *T. officinale* has shifted towards earlier dates in Europe. By introducing survival curves to phenological research, it is possible to compare the timing of phenological phases by decades, locations, and species. There is potential in the development of the method to estimate the change in phenological phases under various climate scenarios (Gienapp et al. 2005).

There is evidence from a wide range of taxa and across a wide range of geographic locations that phenological events in spring have been happening earlier in recent decades (Sparks and Menzel 2002; IPCC 2007). As is the case for

most of the spring phenophases, flowering date of common dandelion exhibits a stronger phenological response to temperature in warmer than in colder countries (Menzel et al. 2006; Jatzcak and Walawender 2009). But what are the driving factors of such response? Phenology uses environmental cues to attune flowering to appropriate seasonal conditions (Tookey and Battey 2010). Several covariates (North-Atlantic Oscillation, precipitation, temperature, photoperiod, snowmelt) have been determined as appropriate predictors for flowering onset. In the case of common dandelion, we documented no significant influence of precipitation on the timing of flowering across biogeographical regions in Europe. Fu et al. (2014) showed that the GDD requirement for vegetation green-up onset plays an important role at higher latitudes along the geographical coordinates of 35°–70°. Our findings confirm the significant effect of GDD on plant phenology (Cox 1972).

We aimed, not only just to give a temporal-spatial description of climatic drivers of flowering onset dates across Europe but also to compare various models that can be used to predict phenological events. The forecasting of ecological responses to climate change represents a major challenge for many reasons (Cook et al. 2010), such as systematic errors in simulations (Migliavacca et al. 2012). Our work demonstrated that Cox models can compete with traditional regression models or even outperform them. We find that survival models can be a fruitful extension to well-established traditional approaches in phenology. However, the approach needs further testing, to assess whether it can be generalized for any other phenophase of living organisms.

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References

- Ahas R, Aasa A (2006) The effects of climate change on the phenology of selected Estonian plant, bird and fish populations. *Int J Biometeorol* 51:17–26
- Bauer S, Gienapp P, Madsen J (2004) The relevance of environmental conditions for departure decision changes en route in migrating geese. *Ecology* 89:1953–1960
- Bewick V, Cheek L, Ball J (2004) Statistics review 12: Survival analysis. *Crit Care* 8:389–394
- European Biological Diversity ETC (2006) The indicative map of european biogeographical regions: methodology and development. Technical report, National Museum of Natural History, France, <http://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-1>
- Chambers LE, Altwegg R, Barbraud C, Barnard P, Beaumont LJ, Crawford RJM, Durant JM, Hughes L, Keatley MR, Low M, Morellato PC, Poloczanska ES, Ruoppolo V, Vanstreels RET, Woehler EJ, Wolfaardt AC (2013) Phenological changes in the Southern Hemisphere. *PLoS ONE* 8:e0075514
- Cleland E, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. *Trends Ecol Evol* 22:357–365
- Cook BI, Terano A, Steiner A (2010) Ecological forecasting under climatic data uncertainty: a case study in phenological modeling. *Environ Res Lett* 5:044,014
- Cortazar-Atauri I, Brisson N, JP G (2009) Performance of several models for predicting budburst date of grapevine (*Vitis vinifera* L.) *Int J Biometeorol* 53:317–326
- Cox DR (1972) Regression models and life-tables. *J Royal Stat Soc Ser B* 34:187–220
- Crepinsek Z, Zrnc C, Susnik A, Zust A (2008) Slovenian phenological observations. In: Nekovar J, Koch E, Kubin E, Nejedlik P, Sparks T, Wielgolaski FE (eds) COST Action 725 - The history and current status of plant phenology in Europe. COST Office, Brussels
- DeCesare N, Hebblewhite M, Bradley M, Hervieux D, Neufeld L, Musiani M (2013) Linking habitat selection and predation risk to spatial variation in survival. *J Anim Ecol* 83:343–352
- Doi H (2008) Delayed phenological timing of dragonfly emergence in Japan over five decades. *Biol Lett* 4:388–391
- Fu Y, Piao S, Zhao H, Jeong SJ, Wang Z, Vitasse Y, Ciais P, Janssens I (2014) Unexpected role of winter precipitation in determining heat requirement for spring vegetation green-up at northern middle and high latitudes. *Glob Chang Biol* 20:3743–3755
- Garcia-Mozo H, Galan C, Belmonte J, Bermejo D, Candaud P, Diaz de la Guardia C, Elvira B, Gutierrez M, Jato V, Silva I, Trigo M, Valencia R, Chunie I (2009) Predicting the start and peak dates of the Poaceae pollen season in Spain using process-based models. *Agric Forest Meteorol* 149:256–262
- Gienapp P, Hemerik L, Visser M (2005) A new statistical tool to predict phenology under climate change scenarios. *Glob Chang Biol* 11:600–606
- Gienapp P, Hemerik L, Visser M (2010) Latitudinal variation in breeding time reaction norms in a passerine bird. *J Anim Ecol* 79:836–842
- Gobiet A, Kotlarski S, Beniston M, Heinrich G, Rajczak J, Stoffel M (2014) 21st century climate change in the European Alps—a review. *Sci Total Environ* 493:1138–1151
- Grisule G, Bakšienė E (2008) The history and current status of phenological recording in Latvia. In: Nekovar J, Koch E, Kubin E, Nejedlik P, Sparks T, Wielgolaski FE (eds) COST Action 725 - The history and current status of plant phenology in Europe. COST Office, Brussels

- Haylock MR, Hofstra N, Klein Tank AMG, Klok EJ, Jones PD, New M (2008) A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. *J Geophys Res: Atmos* 113. doi:10.1029/2008JD010201
- Hodzic S, Voljevic A (2008) Phenology in Bosnia and Hercegovina. In: Nekovar J, Koch E, Kubin E, Nejedlik P, Sparks T, Wielgolaski FE (eds) COST Action 725 - The history and current status of plant phenology in Europe. COST Office, Brussels
- Hofstra N, Haylock M, New M, Jones P (2009) Testing e-obs European high-resolution gridded data set of daily precipitation and surface temperature. *J Geophys Res* 114:D211011
- IPCC (2007) Technical summary. Cambridge University Press, Cambridge
- Kovats RS, Valentini LM, Bouwer E, Georgopoulou D, Jacob E, Rounsevell M, Soussana JF (2014) Europe. In: Barros VR, Field CB, Dokken DJ, Mastrandrea MD, Mach KJ, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL (eds) Climate change 2014: impacts, adaptation, and vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge
- Jatczak K, Walawender J (2009) Average rate of phenological changes in Poland according to climatic changes. *Adv Sci Res* 3:127–131
- Jong R, Bruin S (2012) Linear trends in seasonal vegetation time series and the modifiable temporal unit problem. *Biogeosciences* 9:71–77
- Kalvane G, Romanovskaja D, Briede A, Baksienė E (2009) Influence of climate change on phenological phases in Latvia and Lithuania. *Clim Res* 39:209
- Kaplan EL, Meier P (1958) Nonparametric estimation from incomplete observations. *J Amer Stat Assoc* 53:457–481
- Kleinbaum D, Klein M (2012) Survival analysis: a self-Learning text, 3rd edn. Statistics for Biology and Health, Springer
- Körner C, Basler D (2010) Phenology under global warming. *Science* 327:1461–1462
- Kubin E, Kotilainen E, Poikolainen J, Hokkanen T, Nevalainen S, Pouttu A, Karhu J, Pasanen J (2007) Monitoring instructions of the Finnish national phenological network. Technical report. Finnish Forest Research Institute (Metla), Muhos Research Unit
- Meier U (2001) BBCH-monograph: growth stages of mono- and dicotyledonous plants. Technical Report, 2nd edn. Federal Biological Research Centre for Agriculture and Forestry
- Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R, Alm-Kuebler K, Bissolli P, Braslavská O, Briede A, Chmielewski FM, Crepinsek Z, Cornuel Y, Dahl A, Defila C, Donnelly A, Filella Y, Jatczak K, Mage F, Mestre A, Nordli A, Penuelas J, Pirinen P, Remisova V, Scheffinger H, Striz M, Susnik A, Van Vliet AJH, Wielgolaski FE, Zach S, Züst A (2006) European phenological response to climate change matches the warming pattern. *Glob Chang Biol* 12:1969–1976
- Migliavacca M, Sonnentag O, Keenan TF, Cescatti A, O'Keefe J, Richardson AD (2012) On the uncertainty of phenological responses to climate change, and implications for a terrestrial biosphere model. *Biogeosciences* 9:2063–2083
- Mikkonen S, Laine M, Mäkelä H, Gregow H, Tuomenvirta H, Lahtinen M, Laaksonen A (2015) Trends in the average temperature in Finland, 1847–2013. *Stoch Environ Res Risk Assess* 29:1521–1529
- Niedźwiedz T, Jatczak K (2008) History of phenology phenology in Poland. In: Nekovar J, Koch E, Kubin E, Nejedlik P, Sparks T, Wielgolaski FE (eds) COST Action 725 - The history and current status of plant phenology in Europe. COST Office, Brussels
- Pau EM, Wolkovich EM, Cook BI, Davies TJ, Kraft NJB, Bolmgren K, Betancourt JL, Cleland EE (2006) Predicting phenology by integrating ecology, evolution and climate science. *Glob Chang Biol* 17:3633–364
- Popovic T, Drljevic M (2008) History and current status of phenology in Montenegro. In: Nekovar J, Koch E, Kubin E, Nejedlik P, Sparks T, Wielgolaski FE (eds) COST Action 725 - The history and current status of plant phenology in Europe. COST Office, Brussels
- Development Core Team R (2016) R: A language and environment for statistical computing r foundation for statistical computing, Vienna, Austria, <http://www.R-project.org>
- Remisová T, Nejedlik P (2008) History and present observations in slovak plant phenology. In: Nekovar J, Koch E, Kubin E, Nejedlik P, Sparks T, Wielgolaski FE (eds) COST Action 725 - The history and current status of plant phenology in Europe. COST Office, Brussels
- Rodriguez G (2007) Lecture notes on generalized linear models chapter 7: survival models. Technical report, Princeton University, <http://data.princeton.edu/wws509/notes/>
- Roekaerts M (2002) The biogeographical regions map of Europe: basic principles of its creation and overview of its development. Technical report, European Topic Centre Nature Protection and Biodiversity, European Environment Agency
- Romanovskaja D, Baksienė E (2008) Phenological investigations in Lithuania. In: Nekovar J, Koch E, Kubin E, Nejedlik P, Sparks T, Wielgolaski FE (eds) COST Action 725 - The history and current status of plant phenology in Europe. COST Office, Brussels
- Ruml M, Milatovic D, Vulic T, Vukovic A (2011) Predicting apricot phenology using meteorological data. *Int J Biometeorol* 55:723–732
- Schaber J (2012) Pheno: auxiliary functions for phenological data analysis. R Foundation for Statistical Computing; package version 1.6
- Schaber J, Badeck FW (2002) Evaluation of methods for the combination of phenological time series and outlier detection. *Tree Physiol* 22:973–982
- Schwartz MD, Ahas R, Aasa A (2006) Onset of spring starting earlier across the Northern Hemisphere. *Glob Chang Biol* 12:343–351
- Sparks T, Menzel A (2002) Observed changes in season: an overview. *Int J Climatol* 22:1715–1725
- Stenseth NC, Ottersen G, Hurrell J, Mysterud A, Lima M, Chan K, Yoccoz N, Adlandsvik B (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proc Royal Soc London Ser B: Biol Sci* 270:2087–2096
- Szabó B, Vincze E, Czúcz B (2016) Flowering phenological changes in relation to climate change in Hungary. *Int J Biometeorol* 60:1347–1356
- Szalai S, Bella S, Németh A, Dunay S (2008) History and present observations in slovak plant phenology. In: Nekovar J, Koch E, Kubin E, Nejedlik P, Sparks T, Wielgolaski F (eds) COST Action 725 - The history and current status of plant phenology in Europe. COST Office, Brussels
- Therneau T (2015) Package: survival—survival analysis. R Foundation for Statistical Computing; package version 2.38-3
- Tookey F, Battey N (2010) Temperate flowering phenology. *J Exp Bot* 61:2853–2862
- Visser ME, Holleman LJM, Gienapp P (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* 147:164–172
- Vucetić V, Vucetić M, Loncar Z (2008) History and present observations in Croatian plant phenology. In: Nekovar J, Koch E, Kubin E, Nejedlik P, Sparks T, Wielgolaski FE (eds) COST Action 725 - The history and current status of plant phenology in Europe. COST Office, Brussels
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416:389–399

- Way D (2011) Tree phenology responses to warming: spring forward, fall back? *Tree Physiol* 31:469–471
- Wickham H (2009) *ggplot2: Elegant graphics for data analysis*. Springer-Verlag, New York. <http://ggplot2.org>
- Wielgolaski F (2001) Phenological modifications in plants by various edaphic factors. *Int J Biometeorol* 45:196–202
- Williams T, Bourgeon S, Cornell A, Ferguson L, Fowler M, Fronstin R, Love O (2015) Mid-winter temperatures, not spring temperatures, predict breeding phenology in the European starling *Sturnus vulgaris*. *Royal Soc Open Sci* 2:140301
- Zeng H, Jia G, Epstein H (2015) Recent changes in phenology over the northern high latitudes detected from multi-satellite data. *Environ Res Lett* 6:045508