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Models to predict the start of the airborne pollen season

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Abstract

Aerobiological data can be used as indirect but reliable measures of flowering phenology to analyze the response of plant species to ongoing climate changes. The aims of this study are to evaluate the performance of several phenological models for predicting the pollen start of season (PSS) in seven spring-flowering trees (*Alnus glutinosa*, *Acer negundo*, *Carpinus betulus*, *Platanus occidentalis*, *Juglans nigra*, *Alnus viridis*, and *Castanea sativa*) and in two summer-flowering herbaceous species (*Artemisia vulgaris* and *Ambrosia artemisiifolia*) by using a 26-year aerobiological data set collected in Turin (Northern Italy). Data showed a reduced interannual variability of the PSS in the summer-flowering species compared to the spring-flowering ones. Spring warming models with photoperiod limitation performed best for the greater majority of the studied species, while chilling class models were selected only for the early spring flowering species. For *Ambrosia* and *Artemisia*, spring warming models were also selected as the best models, indicating that temperature sums are positively related to flowering. However, the poor variance explained by the models suggests that further analyses have to be carried out in order to develop better models for predicting the PSS in these two species. Modeling the pollen season start on a very wide data set provided a new opportunity to highlight the limits of models in elucidating the environmental factors driving the pollen season start when some factors are always fulfilled, as chilling or photoperiod or when the variance is very poor and is not explained by the models.

Keywords

Airborne pollen *Ambrosia artemisiifolia* *Artemisia vulgaris* Chilling units Forcing units Phenology models Winter dormancy Turin

Introduction

Aerobiological data have been increasingly used as indirect but reliable measures of flowering phenology because their trend is similar to the flowering pattern derived from field observations (García-Mozo et al. [2010](#); Estrella et al. [2006](#)) and because these data have been widely collected in many European cities as a support for allergologists (Mandrioli et al. [1998](#)). For example, aerobiological data have been used to analyze the flowering response of different species to the rising temperatures, and several modeling approaches have been used to make predictions regarding temporal shifts in pollen dispersal (Prank et al. [2013](#)).

A variety of different models have been developed and applied to analyze spring flowering phenology of temperate deciduous and boreal tree species in Europe (Chuine et al. [1999](#); Defila and Clot [2001](#); Linkosalo et al. [2006](#); Menzel et al. [2006](#); Cleland et al. [2007](#); Estrella et al. [2009](#)).

Model results showed that flowering response is sensitive to increasing winter/spring temperature, and overall, there has been a trend toward advancement of flowering dates. For instance, Menzel et al. (2006) reported an advance of flowering around 2.5 days per decade from 1970 to 2000. The correlation between earlier pollen dispersal and increasing spring temperature has been widely demonstrated, e.g., in species belonging to the order Fagales in temperate climates (Bortenschlager and Bortenschlager 2005), and in *Betula* (Emberlin et al. 2002; Frei and Gassner 2008; Yli-Panula et al. 2009; Veriankaitė et al. 2010 and references therein), *Alnus* (Emberlin et al. 2007; González-Parrado et al. 2006; Rodríguez-Rajo et al. 2006, 2009), and *Castanea* (Rodríguez-Rajo et al. 2005). A similar advance with increasing winter/spring temperature has been observed also in *Platanus* (Norris-Hill 1998; Sabariego Ruiz et al. 2008). These spring-flowering trees share a similar response to environmental conditions establishing winter dormancy, which is related not only to decreasing temperatures but also to shortened photoperiod, giving rise to autumn bud set (Kozłowski and Pallardy 2002; Allona et al. 2008; Caffarra et al. 2011).

The relative importance of temperatures (chilling and forcing) and photoperiod has been tested in a climate chamber experiment with a large number of woody species (Laube et al. 2014a) showing that in *Acer negundo* and *Carpinus betulus* chilling outweighs photoperiod in influencing the spring development. For the majority of the species considered in that research, lack of chilling leads to a considerable delay in budburst and the response to photoperiod was found to be significant only when chilling was not fulfilled.

In contrast to what observed for species living in temperate climates, a clear correlation between increasing temperature and an early pollen dispersal has not been documented in tropical or Mediterranean tree species, probably because precipitation is more important as a driving factor (Prieto et al. 2008). Moreover, the late flowering herbaceous taxa (such as some Poaceae and species of the genus *Artemisia*) usually show a reduced interannual variability, with lower or no clear correlations between spring temperatures and pollen release (Menzel et al. 2006; Estrella et al. 2009). For these taxa, flowering seems to be mainly controlled by precipitation and photoperiod rather than by temperature alone (Galán et al. 2005; García-Mozo et al. 2009, 2010; Clark and Thompson 2010).

Phenological research on summer-flowering species has focused on species of agronomic (García-Mozo et al. 2009) or of allergenic interest like *Ambrosia artemisiifolia* (ragweed) (Prank et al. 2013). This alien North American species is continuously increasing its distribution range in Europe with relevant impacts on public health (Burbach et al. 2009). Therefore, forecasting summer flowering of ragweed is useful to improve the effectiveness of therapies. Simple temperature sum models considering the period April–July generated substantial errors in forecasting the start of the pollen season, whereas a multiple regression model incorporating temperature, relative humidity, and insolation performed better—suggesting that these are the main factors controlling pollen dispersion of ragweed (Laaidi et al. 2003). Recently, nonparametric time-varying regression methods were developed for sites in Northern Italy, France, and Hungary (Makra et al. 2011) and showed that the most important predictor for the start of the pollen season in this species is the cumulated mean temperature of the last days before flowering.

The different responses obtained for different species suggest that collecting more data is needed to test whether models accurately predict the interannual variability of pollen release, considering the variety of environmental factors influencing the flowering process in groups of species with different strategies and flowering periods.

Moreover, although several modeling approaches have been developed and proposed in literature to make predictions regarding flowering, which might be applied to model the pollen dispersal shifts,

there is no consensus about the mechanisms controlling phenological events either in trees or herbaceous species since models showed contrasting results when applied on data sets collected in different geographical areas, even for the same species. For instance, more complex models, considered physiologically realistic, have been found to perform worse than simpler empirical models, based solely on temperature sums (Hunter and Lechowicz [1992](#); Linkosalo et al. [2006](#); Richardson and O’Keefe [2009](#); Migliavacca et al. [2012](#)).

In this context, we aim to evaluate the performance of several temperature-based phenological models for predicting the pollen start of season (PSS) in a highly populated urban area (Turin, Italy). Models were evaluated by using 26 years of airborne pollen records collected over the period 1983–2009. The models used in this study were largely based on those presented by Chuine et al. ([1999](#)) and recently updated by Richardson and O’Keefe ([2009](#)) and by Migliavacca et al. ([2012](#)) and were applied to model the PSS of the following temperate-zone tree species: *Acer negundo*, *Alnus glutinosa*, *Alnus viridis*, *Carpinus betulus*, *Platanus occidentalis*, *Juglans nigra*, *Castanea sativa* and of two late-flowering herbaceous species, *Ambrosia artemisiifolia* and *Artemisia vulgaris*, both of particular interest in pollination studies due to their strong allergenic power.

The specific aims of the study were (i) to identify models suitable to describe with the higher accuracy the pollen season start of each species, (ii) to evaluate the environmental factors and mechanism governing the onset of the season in the early- and late-spring-flowering trees and in the two summer-flowering herbaceous species.

Data and methods

Study area and climatic conditions

Turin (45° 4' 41" N, 7° 40' 33" E) is a city with over one million inhabitants. There are more than 70,000 ornamental trees planted along the city’s avenues and in urban green spaces.

The species studied here are among the most commonly cultivated along the city’s avenues: *Platanus occidentalis* (16,500 plants), *Carpinus betulus* (2,800), *Acer negundo* (1,500), and *Juglans nigra* (1,300). Woods of *Carpinus betulus* and *Castanea sativa* are dominant on the hills flanking the Po river, near the city center, while *Alnus glutinosa* is common in moist areas. *Alnus viridis* is widely spread through the alpine valleys located west of the city, from about 1,000-m elevation upward. *Ambrosia artemisiifolia* and *Artemisia vulgaris* are widespread along the roads and especially in disturbed areas of the city suburbs. While *Ambrosia artemisiifolia* is the only species of its genus occurring in Turin, other *Artemisia* species are present beyond *Artemisia vulgaris*, namely, *Artemisia verlotorum* and *Artemisia annua*. A previous aerobiological, morphometric, and phenological study carried on in Turin (Caramiello et al. [1989](#)) highlighted however that *Artemisia vulgaris* is the main source of airborne *Artemisia* pollen in the city.

Pollen dataset description

Airborne pollen data were recorded continuously in Turin in the period 1983–2009 using a 7-day Hirst spore trap placed in the center of the city at 12 m above the ground level and absorbing 10 l air/min (Hirst [1952](#); Caramiello et al. [1994](#)). The location of the spore trap was not changed in the monitoring period. The standard method of collection described by Mandrioli et al. ([1998](#)) was used, and average daily pollen concentration was expressed as grains/m³ of air.

Direct phenological observation of the species, repeated in several years, highlighted that *Alnus glutinosa*, *Acer negundo*, and *Carpinus betulus* are early-flowering species (February and March), while *Juglans nigra* and *Platanus occidentalis* are mid-flowering (April and beginning of May), and *Alnus viridis* and *Castanea sativa* are late-flowering species (end of May and June). Regarding the two *Alnus* species, it should be noted that although their pollen grains cannot be easily discerned from one another, their pollen seasons in the study area do not overlap. The pollen season of *Alnus glutinosa* typically starts around the end of February and ends around the end of March, while for *Alnus viridis*, the pollen season starts around the second half of May. In this study, *Alnus* pollen grains collected before April 15 were therefore considered to belong to *Alnus glutinosa*, while grains collected after this date were considered as belonging to *Alnus viridis*.

Ambrosia artemisiifolia and *Artemisia vulgaris* are summer-flowering herbaceous species (July and August).

Time series filtering and PSS computation

The yearly pollen concentration time series of the different taxa were first of all visually inspected in order to ascertain possible problems in the data. This preliminary analysis showed that in some of the years, the pollen record of some taxa showed long “no data” periods within the typical pollen season, or showed a very small cumulated concentration due to high precipitations or to incorrect sporetrap functioning. These years were therefore removed from the data set. The number of removed years varied between the different species, from a minimum of 2 for *Alnus viridis* and *Alnus glutinosa*, to a maximum of 7 for *Carpinus betulus*.

The PSS of each taxon in the retained years was determined as the day at which the cumulative daily pollen concentration reached 5 % of the total for the year, according to methods already described in the literature (Nilsson and Persson 1981; Jato et al. 2000; Rodríguez-Rajo et al. 2003) (Fig. 1).

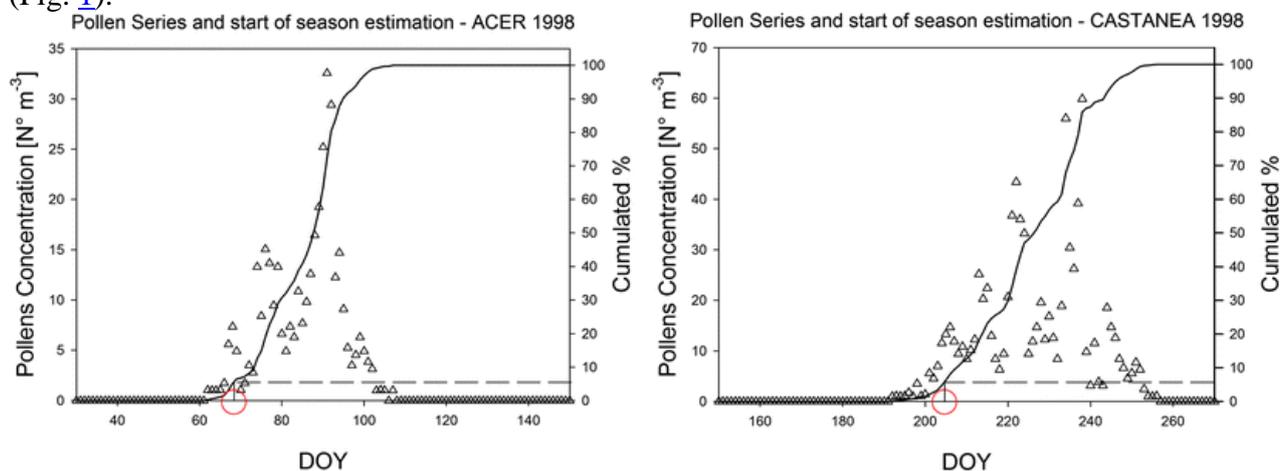


Fig. 1

Daily pollen concentration values (grains/m³) and cumulated curve (%) for *Acer* (a) and *Castanea* (b) in 1998. Circles indicate the estimated PSS dates

Modeling strategy: type of models and estimation of model parameters

The PSS of the different tree species and of *Ambrosia artemisiifolia* and *Artemisia vulgaris* was simulated using a variety of phenological models widely used in literature for modeling tree spring phenology (budburst, flowering, and leaf unfolding).

All the applied models are based on the assumption that PSS occurs only when some combination of chilling and warming requirements are reached, but they differ in their assumptions on how cold and warm temperatures control developmental processes. The models applied in this study can be first of all divided in two big categories: “spring warming” (SW) and “chilling” (CH) models, as specified in Table 1. In the SW models, PSS is assumed to occur when accumulated forcing units $S_f(t)$ reach a threshold value (F^*), regardless of any chilling requirements. Accumulation of forcing units starts at a specified date t_2 . In the CH models, the effect of warm temperatures on plant development is instead assumed to vary as a function of the amount of “cold temperatures” to which plants has been subjected. The models used in this study differ structurally (1) for the way in which chilling units are accumulated and (2) for the way in which chilling and forcing units are computed: Table 1

Characteristics of the phenological models used in this study

Model	Model class	Model parameters							Assumptions	b
		t_1	t_2	T_f	T_c	F^*	C^*	a		
SW-CF1	Spring warming	X	X		X					
SW-CF2	Spring warming	X			X					
SW-CF1 t_0	Spring warming		X		X			$t_2 = \text{January 1}$		
SW-CF2 t_0	Spring warming				X			$t_2 = \text{January 1}$		
Alt-CF1	Alternating	X	X			X	X	$t_2 = t_1; T_c = T_f$		
Alt CF1 t_0	Alternating		X			X	X	$t_2 = t_1 = \text{January 1}; T_c = T_f$		
Seq-CF1	Sequential	X	X	X	X	X		$t_2 = \text{Date at which } C^* \text{ is reached}$		
Seq-CF2	Sequential	X		X	X	X		$t_2 = \text{Date at which } C^* \text{ is reached}$		
Par1-CF1	Parallel	X	X	X	X	X	X	$t_2 = \text{Date at which } C^* \text{ is reached}$		
Par1-CF2	Parallel	X		X	X	X	X	$t_2 = \text{Date at which } C^* \text{ is reached}$		
Par2-CF1	Parallel	X	X	X		X	X	$t_2 = t_1$		
Par2-CF2	Parallel	X		X		X	X	$t_2 = t_1$		

Spring warming, alternating, sequential, and parallel model structures are described in text. CF1 and CF2 refer to different ways to compute daily chilling and forcing rates, as described in text. X corresponds to the model parameters used by each model

t_1 time step at which accumulation of chilling units begins, t_2 time step at which accumulation of forcing units begins, C^* chilling state after which accumulation of forcing units begins, F^* forcing state at which budburst occurs, T_c critical temperature for chilling function $R_c(t)$, T_f critical temperature for forcing function $R_f(t)$, a, b model constants ($a > 0, b < 0$) relating F^* to $S_c(t)$ (i.e., $F^* = a \exp(b S_c(t))$)

1. In chilling models, the PSS occurs therefore only when a particular combination (depending on model structure) of chilling and forcing units have been reached;
2. CH models are further divided in *sequential* (*Seq*), *alternating* (*Alt*), and *parallel* (*Par*) according to the way in which chilling and forcing units are computed.

Seq models assume that plants accumulate chilling units first and then accumulate forcing units. The accumulation of chilling units starts from a date t_1 , estimated as model parameter. The accumulation of forcing units starts at the date t_2 at which the accumulated chilling units $S_c(t)$ reach a threshold value C^* .

Alt models assume that starting from t_1 , plants accumulate chilling units whenever daily mean air temperature is below a threshold T_c and accumulate forcing units whenever temperature is above that threshold. The forcing units threshold F^* above which PSS occurs is assumed to decrease as $S_c(t)$ increases according to a logistic function, so that the warming needed for the plant to start the pollination is reduced on cold winters.

Par models assume that plants can accumulate both chilling and forcing units at the same time. Differently from *Alt* models, however, chilling and forcing are not reciprocal, so that forcing may not occur even if the plant is not accumulating chilling units. We distinguish two subcategories of parallel chilling. In the first one (*Par1*), similarly to *Seq* models, accumulation of forcing units starts when $S_c(t)$ reaches a threshold value C^* . In the second one (*Par2*), chilling and forcing both accumulate from the same date t_1 . For both subcategories, F^* is assumed to decrease as $S_c(t)$ increases, as described for *Alt* models.

The models used also differ on the basis of the functions used to compute the accumulated forcing units. In the models denoted with *CF1*, the daily rate of forcing ($R_f(t)$) is computed as a degree-day sum above a threshold T_f . However, the daily rate of chilling ($R_c(t)$) equals 1 if the mean air temperature is below a base threshold T_c , and zero otherwise (Chuine et al. 1999; Richardson and O’Keefe 2009) (Eq. 1):

$$\{R_f(t)=x(t)-T_f \text{ if } x(t)>T_f; R_f(t)=0 \text{ otherwise } R_c(t)=1 \text{ if } x(t)<T_c; R_c(t)=0 \text{ otherwise}$$

(1) where $x(t)$ is the daily mean temperature at date t .

In *CF2* models, $R_f(t)$ is instead computed as a sigmoid function of $x(t)$, while $R_c(t)$ is computed as a triangular function of $x(t)$ (Eq. 2):

$$R_f(t)=\frac{28.41+e^{-0.185(x(t)-18.4)}}{1+e^{-0.185(x(t)-18.4)}} \quad R_c(t)=\begin{cases} 0 & \text{if } x(t) < -3.4 \text{ or } x(t) \geq 10.4 \\ x(t)+3.4 & \text{if } -3.4 < x(t) \leq T_c \\ T_c-10.4 & \text{if } T_c < x(t) \leq 10.4 \end{cases}$$

(2) In both cases, the rates of chilling and forcing reached at time t are computed as the sums of $R_f(t)$ or $R_c(t)$ starting from t_1 or t_2 , respectively.

$$S_c(t)=\sum_{t_1}^t R_c(t) \quad S_f(t)=\sum_{t_2}^t R_f(t)$$

(3) In all the models considered, photoperiod can be assumed to control the point at which chilling or forcing units start to have an effect. In this study we made use of models that include photoperiod limitation as well as models that do not include photoperiod limitation. The photoperiod limitation was described by including an additional free parameter, corresponding to the day-length threshold at which the chilling and forcing start to have an effect. This parameter was kept fixed at January 1 in models without photoperiod limitation (hereafter denoted by the suffix “ t_0 ”).

Models were driven by daily air temperature data and by daylength data, computed from sunrise and sunset data derived from the local time and standard sun-geometrical routines.

Model parameters were estimated separately for each species and model using the long-term PSS time series ([Pollen dataset description](#) section). Parameter estimation was based on the use of simulated annealing-type routines based on Monte Carlo techniques (Metropolis et al. 1953), as described in detail by Richardson et al. (2010) and Migliavacca et al. (2012). The cost function selected was the sum of squared errors (SSE) between observed and modeled data. Although slower than other model optimization methods, the simulating annealing approach has been already demonstrated to perform well in the context of estimation of free parameters of phenological models (e.g., Chuine et al. 1999), that are characterized by cost functions with multiple local minima.

The fitting performances of the different models were evaluated by computing the Pearson's correlation coefficient (r) and the root mean squared error (RMSE) between observed and estimated PSS, for each combination of model and species.

The identification of the models better suited for modeling the PSS of the different species was instead based on the approach of an information criterion developed by Akaike (1973), which is considered a useful metric for model selection (e.g., Anderson et al. 2000). Unlike other measures of model performance, the Akaike information criterion (AIC) accounts for the trade-off between the goodness of fit (model explanatory power) and model complexity (number of parameters) and is therefore particularly well suited for quantifying how well the data at hand support candidate models characterized by a different number of free parameters.

In this study we used a formulation of the AIC metric that includes a correction factor for small datasets, thus reducing the tendency of the original AIC to select the more complex models when the number of available observations is small (Shono 2005). The corrected AIC (AICc) is formulated as follows (Eq. 4):

$$AICc = n \log \sigma^2 + 2p + \frac{2p(p+1)}{n-p-1}$$

The model with the lowest AICc was then selected as to be the best suited for predicting the PSS of the considered species. Models with small absolute differences in AICc with respect to the best model ($dAICc < 2.0$) can however be thought to perform essentially equally to be the best model and were therefore identified.

Results

Climate

Turin has one among the longest climate time series in Europe, with continuous numerical observations starting from 1753 (Di Napoli and Mercalli 2008). Concerning the last decades (Fig. 2), the yearly mean temperature of the period 1983–2009 was 13.9 °C, with maximum of 14.9 in 2007 and minimum of 12.9 °C in 1984. During this period, winter temperatures showed a high interannual variability, but their variation in time did not show any statistically significant trend. Spring temperatures showed instead a lower interannual variability, but a statistically significant increase of about 0.5 °C per decade ($p < 0.01$) was observed from 1989 onwards, with reference to the period 1961–1990 which has been considered as a reference period in several research studies (Di Napoli and Mercalli 2008). Exceptionally warm conditions characterized winter and spring in 1990 (with temperatures up to 24 °C in mid-February due to föhn events) and in 2007 (the November 2006–April 2007 period was the warmest ever recorded in Turin, at that time of year, since 1753). Furthermore, summer 2003 was extremely hot (the hottest since 1753) with maximum temperatures of 39–41 °C in the urban area.

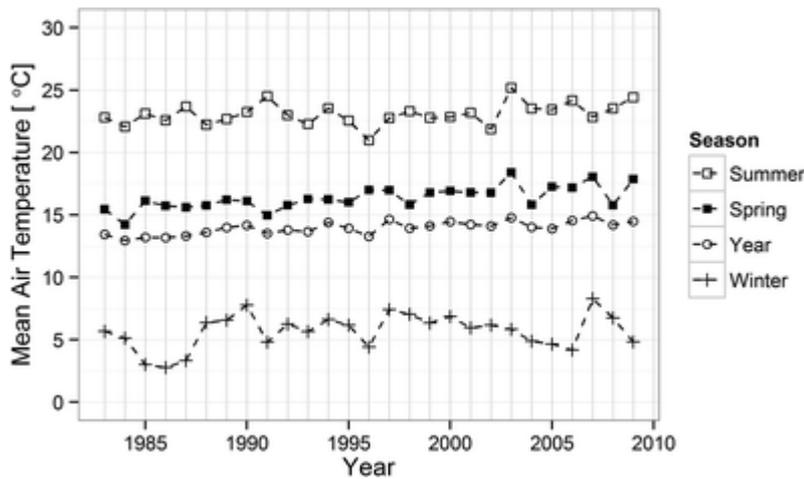


Fig. 2

Mean annual, winter, spring, and summer air temperature in the period 1983–2009

The mean annual precipitation between 1983 and 2009 was 817 mm but ranged from the wet 2008 (1,251 mm) to the semiarid 2001 (438 mm).

The prevailing winds are generally from the Alps to the city, with a dominant west-east direction and are generally characterized by low speeds in all seasons. The mean annual wind speed was 5.2 km/h, with very few days showing speeds higher than 8–10 km/h registered in any year.

Time series of estimated PSS dates

The PSS dates determined for the different taxa are shown in Fig. 3. The figure shows that early-spring-flowering species present a quite strong interannual variation of the estimated PSS (standard deviation (s.d.) ± 30.4 day in *Alnus glutinosa*, ± 10.5 in *Acer*). The interannual variation in PSS is lower for the mid- and late-spring-flowering tree species (s.d. ± 11.3 in *Carpinus*, ± 10.3 in *Alnus viridis*, ± 11.4 in *Juglans*, ± 9.6 in *Platanus*, and ± 6.3 in *Castanea*). Moreover, for the summer-flowering herbaceous species the interannual variations is also low (s.d. ± 6.8 for *Ambrosia*, and ± 5.4 in *Artemisia*). The reduced interannual variability of the late-flowering species with regard to the spring-flowering ones has been already documented on other large European data sets (Menzel et al. 2006; Estrella et al. 2009).

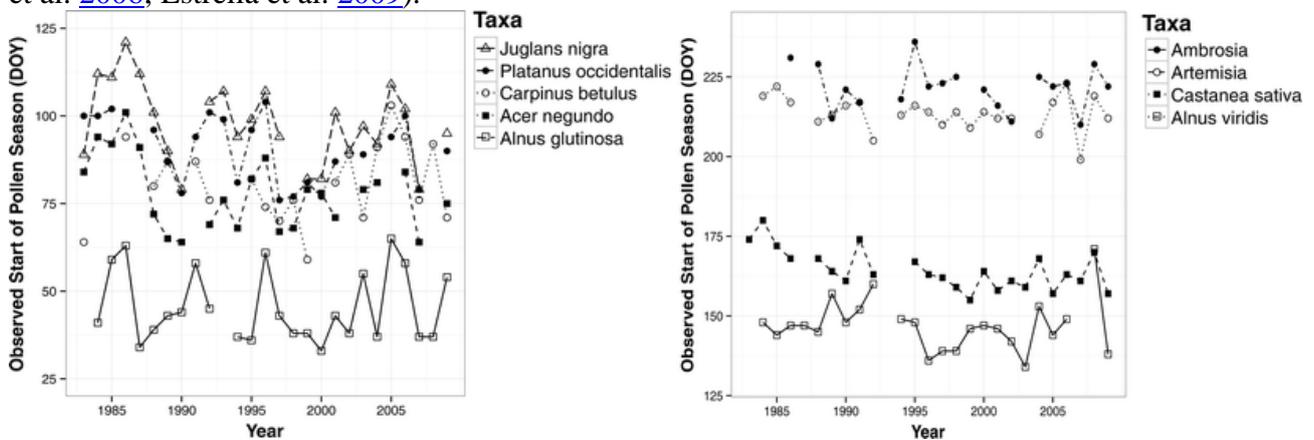


Fig. 3

Determined PSS of the studied species from 1983 to 2009: **a** the early-spring-flowering *Alnus glutinosa* and *Acer negundo* and the mid-flowering *Carpinus betulus*, *Platanus occidentalis*, and *Juglans nigra*; **b** the late-flowering *Alnus viridis* and *Castanea sativa* and the summer-flowering

Artemisia vulgaris and *Ambrosia artemisiifolia*. Data have not been represented if the yearly pollen record of some taxa showed a very small cumulated concentration, due to high precipitations or to uncorrect sporetrap functioning

The estimated PSS dates generally do not show any statistically significant trend in time over the period we analyzed, in accordance to the lack of a significant trend in temperature. The only exception comes from *Castanea sativa*, which shows a significant trend toward earlier flowering (slope = -0.47 days per year; $R^2 = 0.39$; $p < 0.01$).

The time series of PSS dates estimated for the different taxa show various degrees of correlation to each other (Table 2). In general, the PSS of early-flowering species such as *Alnus glutinosa*, *Acer*, *Platanus*, and *Juglans* are fairly positively correlated among each other. This fact suggests that they likely respond to temperature, although the relatively low correlation coefficients between some species indicate that some species may respond differently to the interannual climatic variability. Correlations with the late-flowering species *Alnus viridis* and *Castanea* are instead generally lower. For *Ambrosia*, low correlation coefficients with several other species are observed. Lower correlations for this latter species might be related to the fact that the periods of variation in environmental and meteorological variables to which it is sensitive does not overlap with the earlier species. This emphasizes the need for model selection and parameterization for each species separately.

Table 2

Pearson's correlation coefficients between PSS dates observed for the analyzed taxa in the 1983–2009 period with each other and with winter, spring, and summer temperatures, and corresponding significance levels

	<i>Alnus glutinosa</i>	<i>Acer negundo</i>	<i>Carpinus betulus</i>	<i>Platanus occidentalis</i>	<i>Juglans nigra</i>	<i>Alnus viridis</i>	<i>Castanea sativa</i>	<i>Artemisia vulgaris</i>	<i>Ambrosia artemisiifolia</i>	T Winter	T Spring
<i>Acer negundo</i>	0.45**										
<i>Carpinus betulus</i>	0.30 ^{n.s.}	0.26									
<i>Platanus occidentalis</i>	0.59** *	0.69** *	0.28								
<i>Juglans nigra</i>	0.55** *	0.70** *	0.52**	0.79***							
<i>Alnus viridis</i>	-0.30 ^{n.s.}	-0.13 ^{n.s.}	0.42*	0.15 ^{n.s.}	-0.06 ^{n.s.}						
<i>Castanea sativa</i>	0.00 ^{n.s.}	0.58** *	0.21 ^{n.s.}	0.53**	0.37*	0.40*					
<i>Artemisia vulgaris</i>	0.46**	0.57**	0.53**	0.42*	0.52**	0.04 ^{n.s.}	0.41*				
<i>Ambrosia artemisiifolia</i>	0.07 ^{n.s.}	0.60**	0.09 ^{n.s.}	0.33 ^{n.s.}	0.53**	0.09 ^{n.s.}	0.36 ^{n.s.}	0.43*			

	<i>Alnus glutinosa</i>	<i>Acer negundo</i>	<i>Carpinus betulus</i>	<i>Platanus occidentalis</i>	<i>Juglans nigra</i>	<i>Alnus viridis</i>	<i>Castanea sativa</i>	<i>Artemisia vulgaris</i>	<i>Ambrosia artemisiifolia</i>	T Winter	T Spring	T Summer
T Winter	-0.61**	-0.87**	-0.41*	-0.77**	-0.80**	0.14 ^{n.s.}	-0.32 ^{n.s.}	-0.55**	-0.31 ^{n.s.}			
T Spring	0.21 ^{n.s.}	-0.34 ^{n.s.}	-0.19 ^{n.s.}	-0.31 ^{n.s.}	-0.36*	-0.52**	-0.78**	-0.34 ^{n.s.}	-0.39*	0.20 ^{n.s.}		
T Summer	0.19 ^{n.s.}	-0.15 ^{n.s.}	0.08 ^{n.s.}	-0.21 ^{n.s.}	-0.10 ^{n.s.}	0.05 ^{n.s.}	-0.17 ^{n.s.}	0.16 ^{n.s.}	-0.01 ^{n.s.}	-0.10 ^{n.s.}	0.25 ^{n.s.}	

*** $p < 0.01$; ** $p < 0.05$; * $p < 0.1$; n.s. = not significant

We found that winter temperatures show the highest (negative) correlation coefficients with the early- and mid-spring-flowering tree species, while spring temperatures with the late-flowering species *Alnus viridis* and *Castanea*.

Model selection

The differences in the values of AICc obtained with the different models, with respect to the best-performing one are shown in Table 3. The fitting performances (r and RMSE) of the best model selected according to AICc, as well as the estimated date at which the different species start accumulating forcing units, and the modeled average PSS and its standard deviation, are shown instead in Table 4.

Table 3

Matrix of the corrected differences between the corrected Akaike information criterion for each model and the AICc for the best model

	<i>Alnus glutinosa</i>	<i>Acer negundo</i>	<i>Carpinus betulus</i>	<i>Platanus occidentalis</i>	<i>Juglans nigra</i>	<i>Alnus viridis</i>	<i>Castanea sativa</i>	<i>Artemisia</i>	<i>Ambrosia</i>
SW-CF1	5.1	7.6	0.0	0.9	0.0	2.4	0.3	2.2	0.0
SW-CF2	14.1	6.1	1.4	0.0	1.3	1.5	0.0	0.0	2.2
SW-CF1t0	24.9	10.7	1.2	3.7	0.1	14.5	5.3	5.7	3.8
SW-CF2t0	23.1	7.9	2.6	0.3	2.0	14.0	5.1	10.7	10.8
Alt-CF1	9.3	10.4	3.3	3.2	1.5	0.0	2.8	22.8	7.6
Alt-CF1t0	26.9	12.6	4.6	4.2	2.2	4.9	4.3	28.0	6.8
Seq-CF1	0.9	7.9	5.2	4.8	2.0	17.7	4.5	149.9	130.7
Seq-CF2	102.9	0.0	5.0	3.9	0.5	95.9	129.0	95.4	68.5
Par1-CF1	0.0	15.8	14.5	8.2	5.8	11.9	10.0	18.2	9.2
Par1-CF2	22.0	1.2	6.2	3.4	2.3	1.0	7.5	15.4	12.2
Par2-CF1	40.1	18.2	13.5	21.6	18.0	9.9	16.2	25.9	13.9
Par2-CF2	23.7	13.2	6.8	8.1	13.4	3.7	4.5	14.4	14.2

Dark gray cells with value zero correspond to the best model selected for each tree species. Other gray areas with numbers different from zero represent, for each species, the model formulations performing “as good as” the best model

Table 4

Performances of the best selected models for the different species

	Best model (second best in parenthesis)	t_2 date	r	RMSE	Average PSS (s.d.)
<i>Alnus glutinosa</i>	Par-CF1 (Seq-CF1)	4 December	0.94***	3.20	45.4 (10.2)
<i>Acer negundo</i>	Seq-CF2 (Par-CF1)	26 October	0.96***	3.10	77.9 (10.5)
<i>Carpinus betulus</i>	SW-CF1 (SW-CF2; SW-CF1 t_0)	10 February	0.54**	9.70	80.8 (11.2)
<i>Platanus occidentalis</i>	SW-CF2 (SW-CF1; SW-CF1 t_0)	14 December	0.85***	4.20	90.4 (9.6)
<i>Juglans nigra</i>	SW-CF1 (SW-CF2; Alt-CF1; SW-CF1 t_0 ; SW-CF2 t_0)	15 January	0.85***	6.30	97.9 (11.3)
<i>Alnus viridis</i>	Alt-CF1 (SW-CF2; Par-CF2)	4 February	0.60***	6.40	147.0 (8.00)
<i>Castanea sativa</i>	SW-CF2 (SW-CF1)	27 April	0.84***	4.20	164.5 (6.3)
<i>Artemisia</i>	SW-CF2	17 July	0.40 ^{n.s.}	4.10	215.0 (4.3)
<i>Ambrosia</i>	SW-CF1	24 December	0.57*	4.10	224.6 (4.6)

Best and second best performing models model according to data (Best Model), estimated date at which the different species start accumulating forcing units in the best model, Pearson's correlation coefficient of fitting (r) and corresponding significance levels (*** $p < 0.01$; ** $p < 0.05$; * $p < 0.1$; n.s. = not significant), root mean square error (RMSE, days), average estimated PSS and corresponding standard deviation are reported

Analysis of these tables highlights that the models belonging to the SW class are well suited for six species and equally performing as the best model for all nine species. SW models with photoperiod control are overall better supported by data. CH class models (Alt-CF1, Par-CF1, Par-CF2, Seq-CF1, Seq-CF2) were selected as best only for three species and as equally performing as the best model for six species. Among CH class models, Alternating models were selected as best for one species, as well as parallel and sequential models. In particular, note that CH models provide the best simulation of PSS dates for early-flowering species. The use of the Seq-CF2 model leads, for example, to a r of 0.96 and a RMSE of about 3 days for *Acer negundo* (PSS 77.9 and s.d. 10.5), while a r of 0.94 and a RMSE of 3.2 (PSS 45.4 and s.d. 10.2) are obtained for *Alnus glutinosa* using the Par-CF1 model.

The SW models are instead better suited to model PSS dates of mid- and late-flowering species (i.e., *Carpinus betulus*, *Platanus occidentalis*, *Castanea sativa*, *Alnus viridis*). For these tree species, r varied between 0.54 (PSS 80.8 and s.d. 11.2) for *Carpinus* and 0.85 for *Platanus* (PSS 90.4 and s.d. 9.6), with RMSE varying between 9.7 and 4.2 days, respectively (Table 4). SW models were identified as the best models for the summer-flowering species *Ambrosia* and *Artemisia* although the overall performances for herbaceous species are poor both in terms of r and RMSE (PSS of *Ambrosia* 224.6 and s.d. 4.6 while r 0.57 and RMSE 4.1; PSS of *Artemisia* 215 and s.d. 4.3 while r 0.40 and RMSE 4.10).

Among the SW models, the AICc analysis shows that SW-CF1 and SW-CF2 models perform similarly and generally better than the corresponding t_0 models.

The only species for which SW and CH (both *Alt* and *Seq*) models showed similar performances in terms of AICc was *Juglans nigra*. The best results were however once again obtained using the SW-CF1 model ($r = 0.85$; RMSE = 6.2 with PSS 97.9 and s.d. 11.3).

In Fig. 4, we show scatterplots between observed and modeled PSS (obtained with the best-performing model) for each species. The scatterplots highlight the generally good performances in fitting of the models when used for predicting the PSS of the seven tree species, while the performances are poorer when the models are applied to the two herbaceous species.

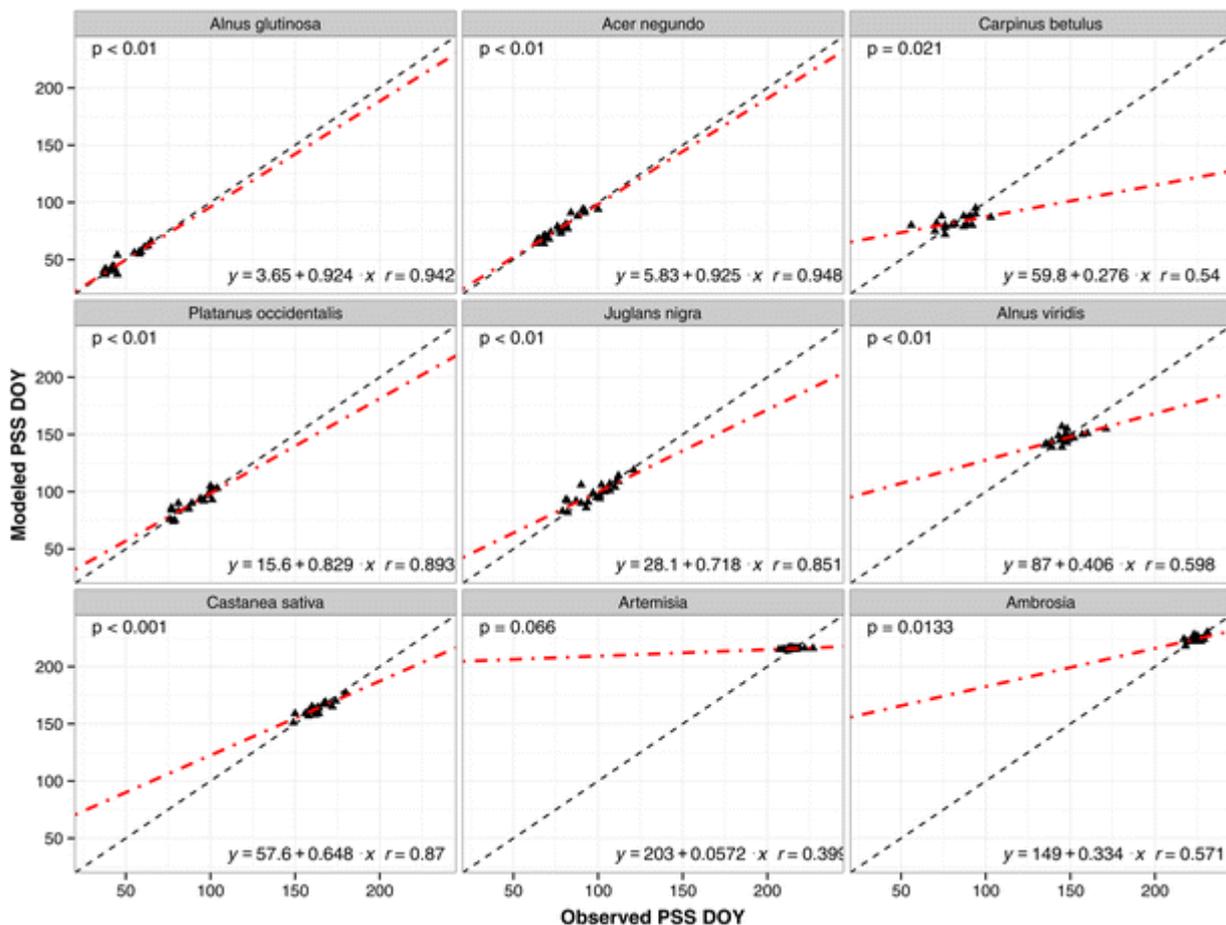


Fig. 4

Comparisons between the observed PSS and the estimated PSS obtained from the best-performing model for the nine studied species

Discussion

In this study, we evaluate several phenological models described by Migliavacca et al. (2012), for predicting the PSS in seven spring-flowering trees (*Alnus glutinosa*, *Acer negundo*, *Carpinus betulus*, *Platanus occidentalis*, *Juglans nigra*, *Alnus viridis*, and *Castanea sativa*) and in the two summer-flowering herbaceous species (*Artemisia vulgaris* and *Ambrosia artemisiifolia*) by using a 26-year aerobiological data collected in Turin (Northern Italy).

We evaluate the applicability of this modeling framework, developed in the literature to predict budburst dates, for the prediction of PSS, obtaining insights on the strength and limits of models in elucidating the environmental factors driving the pollen season start.

Different models were selected as “best model” in predicting PSS of different species. SW models were more often selected in trees (except for *Alnus glutinosa*, *Acer negundo* and *Alnus viridis*), and in *Ambrosia* and *Artemisia*, confirming that simple models performed better than more complex ones in predicting the flowering processes and that forcing temperatures appear to be the most important driving factor. However, it should be kept in mind that the general selection of SW models could be related to our specific conditions, i.e., to the fact that the temperatures experienced during the winter by the majority of tree species in the region were not warm enough to produce a clear signal of the chilling control. For all the studied species, both the best and the second best models were limited by photoperiod, indicating that the dates from which chilling and forcing units starts to be accumulated are related to this parameter.

For the very early-flowering *Alnus glutinosa* and *Acer negundo*, CH class models limited by photoperiod were selected as best models, as warm winters resulted in a flowering delay when cold spells were lacking (Polgar and Primack 2011 and references therein). The preferential selection of CH models for these species indicates their higher sensitivity to chilling requirements as opposed to mid- and late-flowering species. This is very likely related to the fact that the time at their disposal for accumulating chilling units is shorter, so that even short periods of particularly warm temperatures in winter could hamper the reaching of chilling requirements. This is confirmed by studies conducted in Poland on *Alnus glutinosa* by Rodriguez-Rajo et al. (2009), who calculated chilling accumulation as starting at beginning of November and ending during January, with an average chilling requirement of 985 CH hours and temperature lower than -0.25 °C necessary to release bud dormancy. However, interannual differences for chilling and forcing requirements were observed, highlighting that the physiological basis of rest break and budburst are not fully understood.

For mid- and late-spring flowering tree species, SW models with photoperiod limitations could describe all of the studied species, consistent with previous studies (Linkosalo et al. 2008, 2006; Vitasse et al. 2011 and references therein). The fact that models considering only temperatures from a fixed date (i.e., January 1) are never selected as “the best” suggests the existence of a significant control of photoperiod on the date at which the accumulation of forcing units starts and that this control should be considered when modeling PSS dates using climate-driven models (e.g., Migliavacca et al. 2012). The values estimated for the t_2 parameter (i.e., day at which chilling and forcing temperatures begin to be accumulated) show that *Alnus glutinosa*, *Acer negundo* and *Platanus* start accumulating degree days from December or even October. Thus, temperatures during the previous year may influence bud dormancy release, as suggested by Chuine et al. (1999). *Alnus viridis* and *Castanea* instead accumulated degree days beginning in February and April, respectively.

All these species clearly respond to high winter-spring temperatures by flowering earlier, as observed in the warm 2006–2007 winter: for example, *Platanus* advanced flowering of 41 days and *Castanea* 21 days, compared to the much colder winter that was experienced in 1986. This indicates that for these species, warm temperatures in winter/spring are by far the most important driver, whereas chilling requirement are either less important or, more likely, always easily fulfilled. Even with the quite long (26 years) data set we used here, there was no evidence for a relation between chilling units and flowering time for these species. The role of spring temperature is also clarified by the low correlation between late-flowering species and winter temperatures ($r = 0.13$, -0.33 for *Alnus viridis* and *Castanea sativa*, respectively) and by the highest correlation with spring temperatures ($r = -0.52$ and -0.78 for *Alnus viridis* and *Castanea sativa*, respectively).

The relatively poor correlations observed for *Carpinus* both between observed PSS and air temperature (i.e., r with winter temperature of -0.41) and between observed and modeled PSS (i.e.,

r in fitting of 0.54) could be due to genetic differences, e.g., cultivars in the city versus wild plants in the hills. The differences could also be due to temperature differences in the city and the hills. Moreover, we acknowledge that the time series of pollen concentration for *Carpinus* were found to be characterized by anomalous spikes that hampered a robust extraction of PSS dates and increased the associated uncertainty of observed PSS. Therefore, the estimation of models' parameters for these taxa was difficult as the models were poorly constrained.

It is however worth considering that in a scenario of increasing winter and spring temperatures (IPCC 2007 and Fig. 1), the chilling requirement might become an important limiting factor also for mid- and late-spring-flowering species, as observed for *Castanea* seedlings in experiments carried out in the Mediterranean climate of Montpellier (Chuine et al. 1999). This suggests that milder winters can be sometimes insufficient to release bud dormancy and that consequently a higher number of forcing units are required to obtain the pollen season start.

Although substantial uncertainty still exists about the best model structure to be used in a context of rising temperatures, recent work generally recommends the use of models including chilling and forcing units when generating projections under future conditions (Vitasse et al. 2011).

Finally, for *Ambrosia* and *Artemisia* the SW models limited by photoperiod were selected as best models. The models are optimized in order to reduce the mean errors between observations and model, and the procedure leads to very low RMSE values. However, we found very low correlations between modeled and observed data for these species, whereas for the great majority of tree species, the correlation between model and observations was very good. This could be partly due to the low interannual variations of PSS of these herbaceous species, which causes even small errors in the estimated PSS dates to strongly reduce the correlation with observed dates. This small interannual variability is consistent with experiments carried out in controlled conditions, which established that *Ambrosia artemisiifolia* is a quantitative short-day flowering species, whose flowering is highly sensitive to photoperiod (Deen et al. 1998) and potentially to water availability. Like many weeds and ruderal species, *Ambrosia* is adapted to develop in a wide temperature range.

Moreover, model calibration led temperature sums to be calculated from end of December for *Ambrosia* and from mid-July for *Artemisia*. This is in contrast with the biological development of both species: the first is in fact an annual species and has seeds germinating in spring, while the second is a perennial which present only underground organs during winter. This suggests that SW models, although selected as best models, are inconstinent with the biological development of the two species. It seems clear that other environmental parameters, besides temperature sums, determine the processes leading to flowering and anther dehiscence. The low interannual variability and the poor variance explained by the models suggest that caution has to be applied in these as in other similar cases of overfitting models.

Conclusions

With our analysis, we demonstrated the applicability of the selected model structures to model PSS for temperate trees. The results of model selection and the optimized models can be considered robust enough to forecast the beginning of the pollen season start. The model RMSE ranged from 3–4 (*Alnus glutinosa*, *Acer negundo*, *Platanus occidentalis*, *Castanea sativa*) to 6 days (*Juglans nigra* and *Alnus viridis*) in all species, except for *Carpinus betulus* (9 days).

We identified three groups of functional types with regard to flowering: the early-flowering trees, the mid- and late-spring-flowering trees, and the summer-flowering herbaceous species (*Ambrosia* and *Artemisia*). We showed that for early- and late-flowering tree species, CH and SW models are

identified, respectively, as the best models. The selected models show the importance of chilling units for the very early flowering species, of forcing units, and also of photoperiod for the other species, highlighting the importance of this parameter which is rarely considered in modeling the PSS. However, the effects of chilling have been recently demonstrated to greatly exceed the importance of photoperiod (Laube et al. [2014a](#)) in regulating precocious spring development. Moreover, the responses to photoperiod was restricted to individuals that had not been fully chilled, suggesting that the mechanism related to chilling requirements and also to photoperiod limitation evolved in temperate trees to avoid flowering during the winter period, when the development of fruits could be damaged by low cold spells.

On the basis of the correlation observed between PSS dates and temperatures, we suggest, as future research directions, the analysis of how model selection (CH vs SW) changes in late-flowering species by including years with extremely high winter temperatures. This might help to disentangle the role of SW and CH in these species. In the meantime, an approach based on the use of ensemble runs with models with different structures should be considered as a conservative strategy (Migliavacca et al. [2012](#)).

This analysis clarifies the driving role of temperature for flower development and pollen release in trees but also suggests that there can be hidden environmental factors, such as chilling for the late-spring-flowering species, which has been always fulfilled in the 26-year data set, or humidity (Laube et al. [2014b](#)) that may contribute to determining the pollen season start. For *Ambrosia* and *Artemisia*, further research should be focused on the analysis of the factors affecting the interannual variability of the PSS. In fact, the results of our modeling exercise for these two species showed a good agreement in terms of RMSE but a poor variance explained by the models. Further analysis on other summer flowering herbaceous species are needed to understand if the lower PSS variability, found in this work and in some others (as in Menzel et al. [2006](#)), is confirmed and to elucidate the potential role of other environmental factors driving flowering.

The comparison of aerobiological data of nine species, representing different functional types and flowering periods, over a long time series, showed that the pollen season start variability decreased from the early- and mid-flowering tree species to the summer-flowering herbaceous weeds. Modeling the pollen season start on a very wide data set provided a new opportunity to highlight the role of chilling and forcing for the early-flowering and the late-flowering tree species. Moreover, the results give insights on the strength and limits of models in elucidating the environmental factors driving the pollen season start when some factors (i.e., chilling or photoperiod) are always fulfilled or when the variance is very low and is not explained by the models.

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