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Impact of climate change on plant phenology in Mediterranean ecosystems

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Abstract

Plant phenology is strongly controlled by climate and has consequently become one of the most reliable bioindicators of ongoing climate change. We used a dataset of more than 200 000 records for six phenological events of 29 perennial plant species monitored from 1943 to 2003 for a comprehensive assessment of plant phenological responses to climate change in the Mediterranean region. Temperature, precipitation and North Atlantic Oscillation (NAO) were studied together during a complete annual cycle before phenological events to determine their relative importance and potential seasonal carry-over effects. Warm and dry springs under a positive phase of NAO advance flowering, leaf unfolding and fruiting dates and lengthen the growing season. Spatial variability of dates (range among sites) was also reduced during warm and dry years, especially for spring events. Climate during previous weeks to phenophases occurrence had the greatest impact on plants, although all events were also affected by climate conditions several months before. Immediate along with delayed climate effects suggest dual triggers in plant phenology. Climatic models accounted for more than 80% of variability in flowering and leaf unfolding dates, and in length of the growing season, but for lower proportions in fruiting and leaf falling. Most part of year-to-year changes in dates was accounted for temperature, while precipitation and NAO accounted for $<10\%$ of dates' variability. In the case of flowering, insect-pollinated species were better modelled by climate than wind-pollinated species. Differences in temporal responses of plant phenology to recent climate change are due to differences in the sensitivity to climate among events and species. Spring events are changing more than autumn events as they are more sensitive to climate and are also undergoing the greatest alterations of climate relative to other seasons. In conclusion, climate change has shifted plant phenology in the Mediterranean region.

Keywords: flowering, fruiting, global warming, growing season, leaf falling, leaf unfolding, North Atlantic Oscillation, precipitation, Spain, temperature

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Introduction

Phenology has received much attention during the last decade because many organisms are changing their life cycles in response to ongoing climate change (Parmesan & Yohe, 2003; Menzel *et al*., 2006a; Rosenzweig *et al*., 2008). The timing of biological events (especially in regions with a marked seasonality) is strongly controlled by climate and consequently, this response was expected (Margary, 1926; Kington, 1974; Leith, 1974). Plants are especially appropriate organisms to study climate effects in phenology because they are sessile and thus must endure all weather conditions occurring where they are located. Such sessile life-style has led plants to show an especially high plasticity in their phenotypes, such as phenology, to deal with environmental variability (Schlichting, 1986). For instance, Fitter *et al*. (1995) found that flowering timing in 90% of 243 studied plant species in England was significantly related to temperatures, i.e. the overwhelming majority of plants were able to tune their flowering dates according to particular temperature conditions of each year. This strong dependence on climate explains why, of all taxonomic groups, plants have the highest portion of species shifting their phenology in the predicted direction under current climate change (Parmesan & Yohe, 2003).

Temperature has been demonstrated as one of the most important factors for plant phenology (Margary, 1926; Fitter *et al*., 1995; Sparks *et al*., 2000; Peñuelas *et al*.,

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2002; Matsumoto *et al*., 2003; Menzel, 2003; Gordo & Sanz, 2005; Ahas & Aasa, 2006; Estrella & Menzel, 2006; Lu *et al*., 2006; Menzel *et al*., 2006a). However, its true relevance for plants could be overestimated, since few studies have assessed the effect of other environmental factors such as precipitation, photoperiod, availability of soil nutrients or soil physical properties and consequently, evidence for their impact on phenology remains scarce (Badeck *et al*., 2004). Photoperiod is an important trigger of plant phenology, but regrettably the relative importance of this environmental cue with respect to temperature has been established in only a few wild species (Hunter & Lechowicz, 1992; Kramer, 1994). The balance between rainfall and evaporation plays a key role in ecosystem functioning in many regions of the planet (e.g. in Mediterranean biomes). However, precipitation has received little attention in studies of historical records of plant phenology (Sparks *et al*., 1997; Peñuelas *et al*., 2002, 2004; Williams & Abberton, 2004; Gordo & Sanz, 2005; Estrella & Menzel, 2006), despite of precipitation patterns will change in the future (Solomon *et al*., 2007) and thus, they could promote alterations in plant phenological patterns as well. Furthermore, precipitation effect in plant phenology is complex and difficult to forecast due to its close relationship with soil moisture. For instance, rainy autumns are related to earlier springs in the following year in some ecosystems (Sparks *et al*., 1997; Peñuelas *et al*., 2004; but see Cayan *et al*., 2001). This fact suggests that precipitation may affect individuals even much time later than the last rainy day. Similarly, temperature may reveal its effect with some delay, e.g. through chilling requirements during the winter to break bud dormancy. Such temporal gap between plant phenotype expression (i.e. a certain phenological date) and the potential effect of some of its climatic triggers requires a view beyond the present to assess such potential carry-over effects of climate.

Plant phenology responds to the stimuli imposed by local weather, but many studies have also demonstrated a connection to large-scale atmospheric circulation patterns. In Europe, when the North Atlantic Oscillation (NAO) index is positive, spring advances (Post & Stenseth, 1999; Chmielewski & Rötzer, 2001; Post *et al*., 2001; Scheifinger *et al*., 2002; Menzel, 2003; Stöckli & Vidale, 2004; Menzel *et al*., 2005b; Ahas & Aasa, 2006; Nordli *et al*., 2008). This relationship is likely mediated by NAO effect in local weather, e.g. through temperature and rainfall. For instance, positive values of NAO from December to March are related to warm and wet springs in central and northern Europe, but cold and dry springs in the Mediterranean Basin (Ottersen *et al*., 2001). While NAO influence on plant phenology is well-established for central and northern Europe, no study has evaluated the effect of NAO on long-term phenological responses of plants from the Mediterranean (Söckli & Vidale, 2004; Menzel *et al*., 2005b). This fact becomes especially relevant taking into account that NAO effects differ between the Mediterranean Basin and the rest of the European continent (Ottersen *et al*., 2001). NAO has a strong influence on precipitation patterns in this region (Hurrell & van Loon, 1997), especially in the westernmost areas, such as the Iberian Peninsula (Rodó *et al*., 1997; Goodess & Jones, 2002; Trigo *et al*., 2004). Water availability is a key factor for plant functioning in Mediterranean ecosystems and consequently, NAO may exert an important influence on plant ecology as a driver of precipitation patterns (Rodó & Comín, 2000; Vicente-Serrano & Heredia-Laclaustra, 2004).

The aim of this study is to carry out a comprehensive assessment of climate impacts on plant phenology in the Mediterranean region to provide a mechanistic explication for the observed changes in plant phenology during the last decades (Gordo & Sanz, 2009). In fact, understanding the effect of climate in plant phenology is an essential step to establish a plausible link between recent climate change and plant phenological responses, and to make reliable predictions about future plant responses. We have attained our objective by dividing our study into four steps or analytical stages. First, we have searched for potential carry-over effects of climate by studying climate influence on plant phenology during the complete annual cycle before each phenological event and identifying the time within the annual cycle with the greatest influence. There is evidence that the effects of climate are delayed (Fitter *et al*., 1995; Sparks *et al*., 1997, 2000; Heide, 2003; Estrella & Menzel, 2006; Miller-Rushing & Primack, 2008c) and hence, the complete annual cycle before any phenological event should be explored. Second, we determined the best predictor of plant phenology among three climate variables, including temperature, rainfall and NAO. These variables have been demonstrated as relevant to plant phenology, but no study has assessed their effect together in an effort to disentangle the actual relevance of each (but see Stöckli & Vidale, 2004). In Mediterranean ecosystems, water availability is a limiting factor for plant function and hence, we expect an important effect of rainfall on phenology as well (Ogaya & Peñuelas, 2004; Llorens & Peñuelas, 2005; Prieto *et al*., 2008; Matesanz *et al*., 2009). Furthermore, by comparing NAO effects with temperature and precipitation we will ascertain the impact of macroscale atmospheric circulatory patterns in relation to local weather conditions (i.e. are NAO effects simply a matter of collinearity with local weather?). If NAO effect remains after controlling for local temperature and precipitation, this implies that

NAO index has other climate information (e.g. radiation, atmospheric pressure, wind, etc.) relevant for plant phenology. However, if NAO effect is overridden by local weather variables, NAO effect on plant phenology is in fact mediated by weather at local scale. Therefore, there would be no scientific reason to employ such climate index instead of climatic variables, such as temperature or rainfall, which have a well-established functional link with plant phenology. Third, we investigated why some phenological events and species are more sensitive to climate than others. Patterns of variability among species are poorly understood (Miller-Rushing *et al.*, 2007, 2008b, c), but a number of biological characteristics, such as pollination mechanism, life form or water content, are related to differential responses among taxa (Fitter *et al.*, 1995; Fitter & Fitter, 2002; Peñuelas *et al.*, 2002; Miller-Rushing & Primack, 2008b, c). Differential responses to climate among plant species may alter community composition by disrupting interactions and survival under a climate change scenario (Fitter & Fitter, 2002; Lloret *et al.*, 2004; Sherry *et al.*, 2007; Willis *et al.*, 2008). Finally, in the fourth step, we related climate effects found in previous steps to long-term temporal plant responses observed in a previous study (Gordo & Sanz, 2009). This analysis is the keystone to determine the role of recent climate change in the observed phenological shifts and to understand why plants are changing their phenology in Mediterranean ecosystems and how responses vary among species and events.

Materials and methods

Phenological data

Since the 1940s, the phenological network of the Spanish Meteorological Agency (AEMET) has been recording several plant and animal phenological events according to standardized methods (Anonymous, 1943; Gordo & Sanz, 2006a, 2009). About 204 000 records of flowering, leaf unfolding, fruit ripening, fruit harvesting and leaf falling, and duration of the growing season for 29 species of trees and bushes were gathered and digitized from the AEMET archives for the period 1943–2003. The six studied phenological events were defined as (number of species shown in brackets):

- Flowering (27): Appearance of first flowers in some individuals.
- Leaf unfolding (24): Appearance of first leaves in some individuals, which confers certain greenness. This event was available only since 1969.
- Fruit ripening (15): Several ripe fruits are present in several individuals. For fleshy fruits, ripening implies that fruits show their final colour and must be easily detached. For dry fruits, ripening implies that capsules burst.
- Fruit harvesting (9): Date when fruits are harvested.
- Leaf falling (22): Half of the leaves have fallen.
- Growing season (22): It was calculated as the number of days elapsed between leaf unfolding and leaf falling for the same species during the same year at the same locality.

Therefore, reported dates by observers were estimates of the beginning of each phenological event in the populations of each species occurring at each study site of the phenological network. Such phenological measurement is really robust and accurate because by carrying out monitoring at population level, phenological records are protected against unrepresentative individuals (e.g. sick, isolated or too young/old trees). Furthermore, misidentifications were very improbable, since selected species were common, widespread in Spain and quite popular for any potential observer. The AEMET provided also a field guide to each volunteer observer to ensure a perfect identification of all plants species (Anonymous, 1943, 1989). Summarizing, there were available dates at population level for 118 phenophases in more than 1500 Spanish sites (Gordo & Sanz, 2009). A phenophase was defined as a certain phenological event of a certain species. Data quality was checked by searching for potential biases in the sampling day of the week and for outliers. There was a negligible bias towards oversampling in Mondays. Outliers whenever possible were amended, otherwise they were removed (see details in Gordo & Sanz, 2009).

The average date and the standard deviation of all records belonging to the same phenophase were calculated for each year. Therefore, we had 118 time-series for average dates and 118 time-series for their corresponding standard deviation values from 1943 to 2003. Time-series for averaged dates provided us the interannual changes in the occurrence dates of each phenophase. By averaging values annually, we avoided pseudoreplication (i.e. records from the same year are not fully independent) and reduced any influence of undetected incorrect records. The annual standard deviation values quantified the range of dates during each year. This range is due to phenological differences among sites (i.e. spatial variability). Thus, time-series for standard deviation values estimated year-to-year changes in the range of onset dates of each phenophase. In all cases, our time-series were representative of a group of populations spread over the broad geographical area of Spain.

We also calculated two parameters for each phenophase: the average date (μ) and standard deviation (σ)

of all records. These parameters defined the position within the annual calendar and the plasticity, respectively, of each phenophase (see details in Gordo & Sanz, 2009). Plasticity refers to the ability of each phenophase to show a range of different phenotypes (i.e. phenological dates) in response to the environmental gradients of the Iberian Peninsula. Our study species were distributed across most part of Spain and we had a sample of sites representative of the entire distribution range. Therefore, all studied species were subjected to a similar range of environmental conditions and consequently differences in ranges of onset dates (σ) among phenophases were due to differences in plasticity among species.

For flowering time-series, species were classified according to their pollination system as wind or insect pollinated. Pollination mechanism may act as an important evolutionary pressure imposing differential responsiveness to climate. We expect a stronger relationship to climate in insect-pollinated species to better adapt their phenological responses to climatic fluctuations and ensure an exact match with their pollinators (Fitter & Fitter, 2002).

Climatic data

Temperature and precipitation were simultaneously recorded by volunteers at most sites of the phenological network. This resulted in a highly representative climate dataset for our phenological dataset. Climatic data were averaged to obtain single time-series of monthly values of temperature and precipitation during the period 1942–2003 for all of Spain. Mean, maximum and minimum average monthly temperatures were available. These three temperature types are strongly collinear but they stress different aspects of daily temperature patterns. They were compared to determine the most important type of temperature for plant phenology. Finally, NAO index was obtained as monthly values from http://www.cru.uea.ac.uk/cru/data/nao.htm.

The standard deviation (σ) for the 118 studied phenophases was on average 19.9 days. Therefore, an interval of $\pm 2\sigma$ (79.6 days $\sim$ 3 months) included approximately 95% of data in all phenophases. For this reason, temperatures and NAO index were averaged and precipitation was summed in quarters. Twelve different quarters were defined within the annual cycle, i.e. January to March, February to April, March to May, and so on. Hence, we worked with response (phenological) and explanatory (climatic) variables coming from the same temporal interval within the calendar (i.e. 3 months).

Assessment of climate effects during a complete annual cycle

We explored the influence of climate during a complete annual cycle in each phenological event to answer the following questions: (1) What is the most important period for each phenophase? and (2) Are there lagged effects of climate? Pearson's correlation coefficients were calculated between each phenological time-series (both for average dates and standard deviations) and the climatic time-series (temperature, precipitation and NAO) belonging to the 12 quarters of a complete annual cycle moving backward month to month from the onset date of each phenophase. For instance, the first quarter (Q_0) for a species with an average flowering date (μ) in April is February–April, while the last quarter (Q_{-12}) is March–May of the previous year. Correlation values for each quarter were averaged within each phenological event and fluctuations during a complete annual cycle were explored.

Q_0 could not be defined for the length of the growing season. For this event, we assessed changes of correlation coefficients during a period of 20 quarters (12 from the current year and eight from the previous year). Since the length of the growing season depends on its beginning and end dates, we decided to include all variables that potentially influence leaf unfolding (beginning) and leaf falling (end). By including eight quarters of the previous year in models, we aimed to account for possible delayed effects on leaf unfolding. We included eight quarters because the average onset of leaf unfolding in all studied species is April and hence a complete backward annual cycle finishes in May of the previous year (i.e. Q_{-8}).

Explanatory capacity of climate variables

Multiple regression models between phenological time-series as response variables and 12 quarters (from Q_0 to Q_{-12}) of mean temperature, precipitation or NAO as predictor variables were carried out for each phenophase. For growing season models, all quarters of the same year along with the last eight quarters of the previous year (i.e. a total of 20 predictors) were included. Forward stepwise selection was applied to obtain reduced models including only significant quarters. We retained from each model the value of adjusted R^2 as a measure of the explanatory capacity of temperature, precipitation or NAO in each phenophase. We carried out one ANOVA of repeated-measures with adjusted R^2 values from temperature, precipitation and NAO models as dependent variables and the phenological event as factor to determine the climatic variable most closely related to phenology.

Models obtained for mean temperature were repeated including the same quarters with maximum or minimum temperatures. Another ANOVA of repeated-measures was carried out with the explanatory capacity (adjusted R^2) of the regression models for mean, maximum and minimum temperature as dependent variables and the phenological event as factor to determine what type of temperature is the best fitted to plant phenology. In all repeated-measures ANOVAs, the assumption of circularity in the variance–covariance matrix was assessed by the Greenhouse–Geisser and Huynh–Feldt epsilons (ε_{GG} and ε_{HF}) for compound symmetry (von Ende, 1993).

Phenology modelling by climate

We constructed complete climatic models by including those significant variables included in the temperature, precipitation and NAO best models previously found. Forward stepwise was applied for model selection. Complete models determined the highest explanatory capacity of phenology by climate. The adjusted R^2 values of these models were used as response variables in several analyses of variance. Firstly, we built models with the event as a categorical factor and the effect of the average date (μ) or standard deviation (σ) of each phenophase nested within the events. We aimed to investigate whether patterns of variability in R^2 values were related to the date of occurrence or to the plasticity of phenophases. The growing season was not included in the ANOVA of average date because this parameter cannot be defined for this event. Secondly, we performed a one-way ANOVA to look for differences between wind- and insect-pollinated species in the ability of climate to model their flowering dates.

Complete models were also used to determine the extent to which the variance explained by temperature, precipitation and NAO in their respective models is a true estimate of their influence on plant phenology. Climatic variables show strong collinearity because they result from common weather conditions. Consequently, a high correlation between plant phenology and several climatic variables reflects a strong influence of weather rather than a strong and independent effect of each of the climatic variables analysed. For instance, high temperature is related to scarce precipitation and positive values of NAO in Spain (see Supporting Information, Appendix S1). A hierarchical variance partitioning was carried out to ascertain the true explanatory power of each type of variable. For this purpose, we constructed four new saturated models in each phenophase corresponding to the three possible pairs among temperature, precipitation and NAO along with a full model. The pure effect of each type of variable (pure adjusted R^2) was calculated as the average of the variability explained by each type of climate variable in the models in which it appears. Finally, another repeated-measures ANOVA was carried out with pure adjusted R^2 values for each type of climate variable as response variables and phenological event as factor to reexamine differences among variables and events.

Relationship between climate effects and temporal trends of phenology

The key question is whether or not plant phenological changes observed in recent decades in Spain are in response to ongoing climate change. It is expected that those phenophases more responsive to climate (i.e. with larger phenological responses per unit of any climate variable) have the greatest potential to change over time as a result of a certain shift in climate conditions with all else being equal. Therefore, in a changing climate, more sensitive phenophases should show steeper temporal responses. To check this hypothesis we related the rate of change (i.e. slope from regression with year) during the period 1973–2003 of all phenophases to the sensitivity to climate in Q_0 (i.e. slope from regression with temperature, precipitation or NAO during the quarter when the phenophase occurs). Since the sensitivity to climate variables differed among phenological events (i.e. there was no parallelism, see Fig. 1), we built models with the relationship between temporal and climatic slopes nested within each phenological event. In the case of the growing season, we used the quarter with the highest value of correlation (Q_{best}) among the 20 quarters used for this event.

All statistical analyses were performed with STATISTICA software [StatSoft, 2001, (data analysis software system), version 6. (http://www.statsoft.com)].

Results

Climatic effects on average dates during a complete annual cycle

Leaf unfolding and flowering showed quite similar patterns of correlation during a complete annual cycle for all climate variables (Fig. 1). Both events showed the greatest influence of climate during Q_0. Leaf unfolding and flowering advanced in warmer and drier springs under positive values of NAO (Fig. 2). Nevertheless, a remarkable delayed effect of the previous autumn was found. Both events advanced after cool and wet autumns under negative values of NAO (Fig. 1). Only in the case of precipitation did correlation values in Q_0 (i.e. immediate effect) and Q_{-5} (i.e. delayed effect) have similar magnitude ($|r| \sim 0.4$).

Leaf falling showed small correlations in most cases (Fig. 1). This event was delayed when the period from the end of summer to the beginning of autumn (August–October) was warm and dry (Fig. 2). It is interesting to note that the effect of precipitation reached its maximum at Q_{-2}, which is at the height of summer (June-August). Leaf falling also delayed after cool springs, but only in some species (the large error

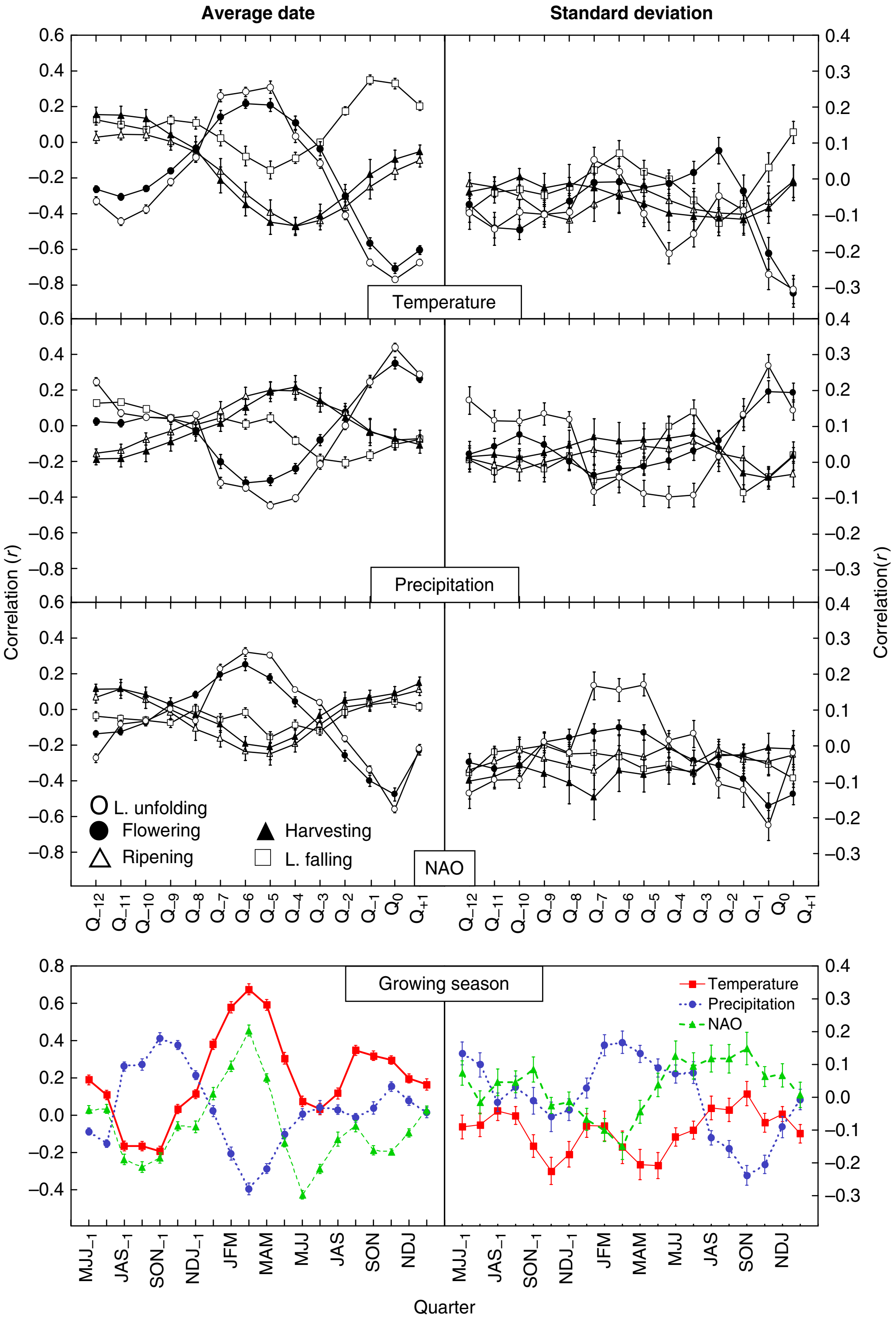


Fig. 1 Evolution of Pearson's correlation coefficients between phenological time-series and all climatic variables along a complete annual cycle. Mean value of correlations for all species available in each event is shown for each quarter from the moment when the phenophase occurs (Q_0) to one year before (Q_{-12}). An extra quarter (Q_{+1}) has been added to improve visualization. In the left part of the figure, there are graphs for average dates time-series, while in the right for standard deviation time-series. Error bars are standard errors. Correlations between growing season length and 20 quarters (see 'Materials and methods') are shown as independent graphs in the bottom of the figure. See embedded colour legend for correspondence with climate variables.

bar in Fig. 1 denotes high variability among species). The effect of NAO on this phenophase was negligible.

Fruit ripening and harvesting showed the same pattern. Greatest correlations were found with a certain delay (in Q_{-4} and Q_{-5}), but only reached significance with temperature. Fruiting advances when the period between the end of spring and the beginning of summer (around May and June) is warmer and drier and has negative values of NAO. Nevertheless, it is important to note that there was much variability among phenophases, as the large error bars denote (Fig. 1).

The growing season was maximally correlated with climate during the February–April quarter (Fig. 1). Leaves live longer in those years with a warm and dry February–April quarter with positive values of NAO. Some effect of autumn, both of the current and previous year, was also found. Interestingly, each autumn had an opposite effect. The growing season is longer in those years preceded by a cool and wet autumn and with a warm and dry autumn in the current year. Interestingly, autumn rainfall from the preceding year showed some effect, which suggests indirect effects through soil moisture. The effect of NAO shifts radically from February–April to May–July, since positive values of NAO at the beginning of the summer shorten the growing season. In summary, growing season showed the same climate effects as leaf unfolding and falling.

Climatic effects during a complete annual cycle on standard deviation

Standard deviation did not show clear patterns of correlation with climate during a previous annual cycle in most events (Fig. 1). Although average correlation values for each quarter were significantly different from 0 (i.e. there is some effect), such average r had low values (range between -0.2 and 0.2). Phenophases compressed in most cases their range of onset dates in response to warm and dry quarters under positive values of NAO index. The greatest effects were found during Q_0, although such effects were only noticeable for flowering and leaf unfolding (Fig. 2). In the particular case of temperatures, fitting with Q_{+1} was better than with Q_0 (Fig. 1). This fact could stress a more immediate impact of temperature for standard deviation than for average date.

Climate effects showed greatest fluctuations during the annual cycle in the case of the growing season (Fig. 1). Warmer temperatures were related to decreased variability in the length of the growing season (Fig. 2). Main effects were found in spring (March–June) and in autumn of the preceding year (October–December). However, large amounts of precipitation decreased intersite variability, but only when rained during the autumn of the current year. Precipitation during the preceding spring had the opposite effect. NAO effects were in general weaker than those of temperature or precipitation. The most important period was February–April. High values of NAO index during this quarter reduced the variability of the growing season.

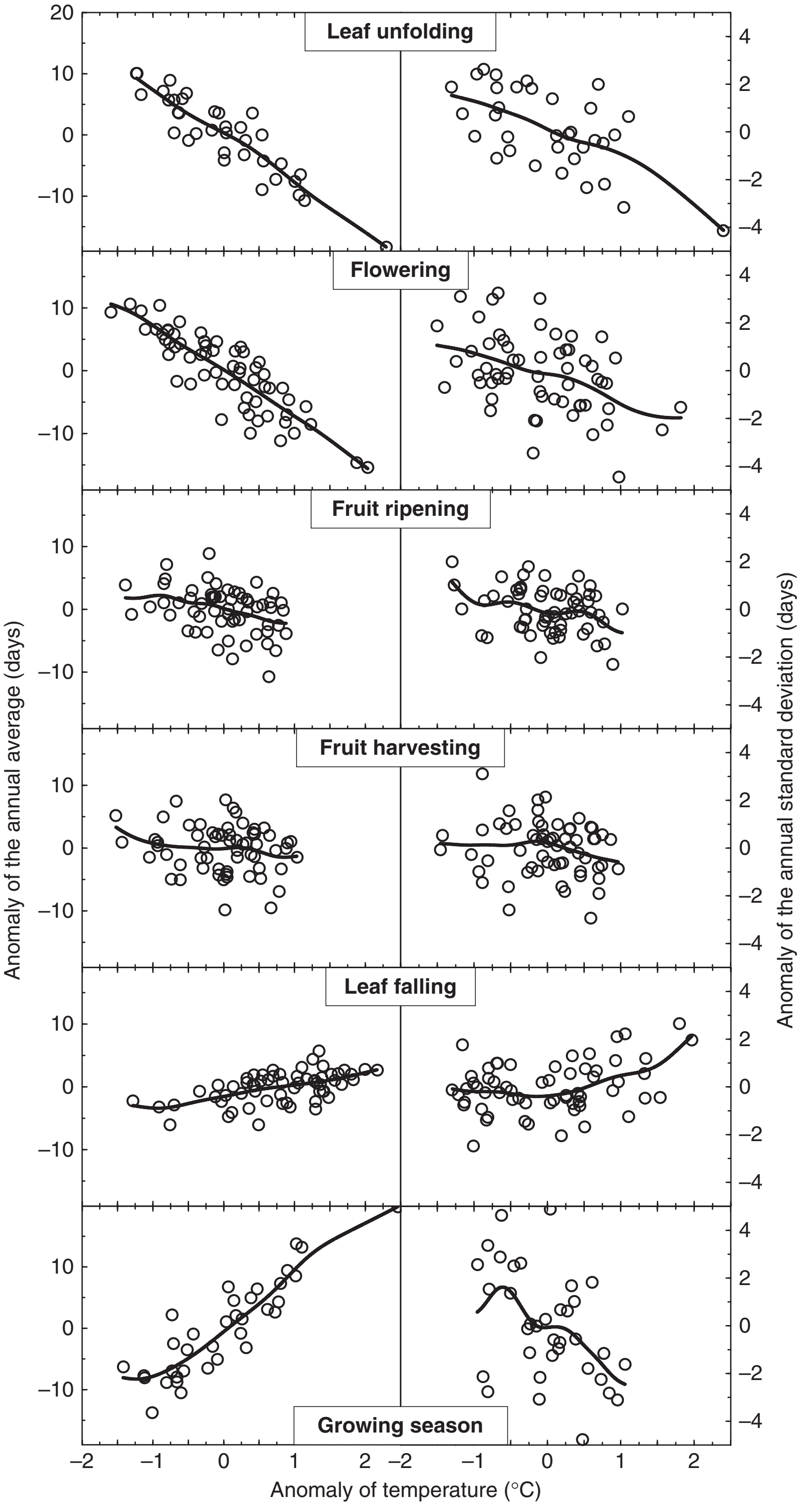
Differences in the explanatory capacity of temperature, precipitation and NAO

The explanatory capacity both in average date and standard deviation models differed among climate variables and phenological events (Fig. 3; see Appendix S3, Table S1). Temperature showed the highest explanatory capacity in all cases. NAO and precipitation had similar R^2 values, with the exception of the time-series of growing season average dates. Flowering, leaf unfolding and growing season stood out as the best modelled phenological events. The interaction between the phenological event and the type of climatic variable was only significant for average dates (Table S1). In fact, differences between temperature, precipitation and NAO were larger in flowering and leaf unfolding than in the rest of the events. It is important to note that the explanatory capacity of standard deviation models was remarkably smaller than the explanatory capacity of average date models (Fig. 3).

Differences in the explanatory capacity of models were partially due to the number of variables included. In models for average date, temperature models included on average 1.9 predictors, while precipitation included 1.4 and NAO 1.6. The mode for the three types

Fig. 2 Effects of temperatures on plant phenology. Each point is the annual average anomaly of phenology and temperatures for all available species in each event. We have represented anomalies instead real values to avoid scale effects when merging data from all species. Phenological anomalies were calculated as departures of the annual phenological values (average dates or standard deviations) from the average of each phenological time-series during the period 1943–2003. For annual average dates, positive values denote late years, while negative values early years. For the standard deviation, positive values denote years with a broader range of dates (i.e. more spatial variability), while negative values denote years with a narrower range (i.e. more synchronization in the onset of phenophases among sites). Temperature anomalies were also calculated as departures of annual temperatures from the average temperature during the period 1943–2003. Error bars in the x- and y-axes are not represented to improve visualization. A smoothed line has been added to show relationship between phenology and temperature. Negative trends imply advancement of dates or compression of dates' distributions in response to warmer temperatures.

of climate variables was two predictors because most species included both immediate and delayed climatic effects. Only three out of 118 phenophases were not related to any temperature variables, while we found up to 15 and 12 phenophases for precipitation and NAO, respectively. Nevertheless, the degree of parameterization of models could not fully explain differences in the explanatory capacity of models among phenological events. Flowering and growing season included the highest number of variables (2.0 and 1.9



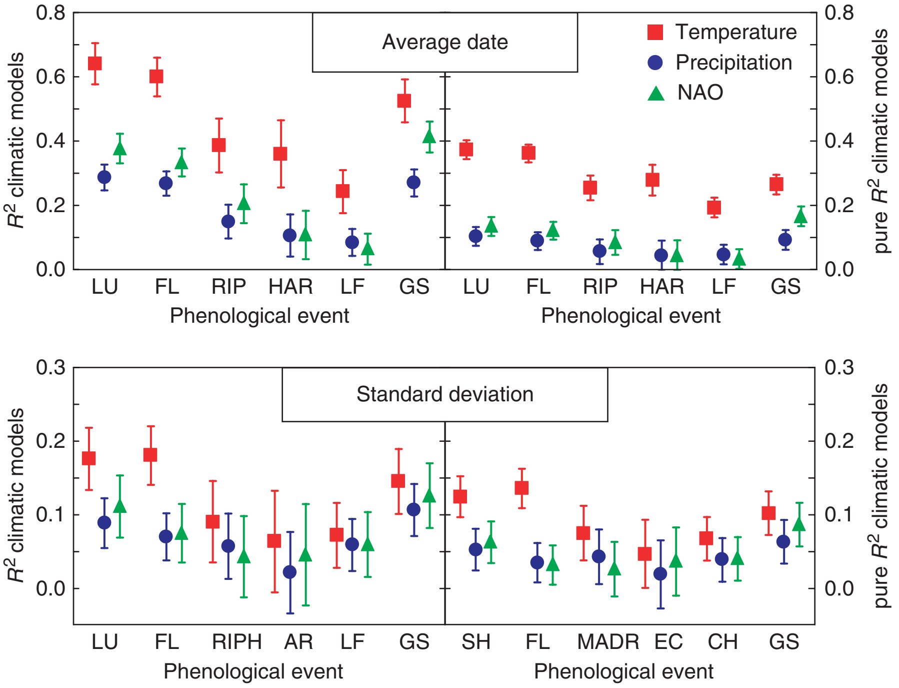


Fig. 3 Explanatory capacity of climatic models for average date and standard deviation time-series. Mean values for adjusted R^2 (in the left) and for pure adjusted R^2 (in the right) are shown for all events and types of variables. Error bars denote the 95% confidence interval. LU, leaf unfolding; FL, flowering; RIP, fruit ripening; HAR, fruit harvesting; LF, leaf falling; GS, growing season.

on average, respectively). However, best explanatory models were found for leaf unfolding (Table 1; Fig. 3), which included 1.6 variables on average. The same number of variables was found for fruit ripening, but models for this event showed a patently lower explanatory capacity than leaf unfolding (Table 1; Fig. 3). In standard deviation models, precipitation and NAO models showed a poor modelling ability because many phenophases were not related to any quarter (56 and 55 out of 118 phenophases, respectively). For those species with a significant model, an overwhelming majority included just one predictor (67 for temperature, 46 for precipitation and 50 for NAO), which in most cases corresponded to Q_0.

Differences in the effect of mean, maximum and minimum temperatures

Mean and maximum temperature models showed similar and large explanatory capacities, while minimum temperature showed the lowest explanatory capacity (Appendix S3, Fig. S1). Mean temperatures showed the best modelling ability in all events. The inability of minimum temperatures to model time-series was especially evident in average dates of flowering and leaf unfolding. In the case of standard deviation, differences among temperature types were more subtle than in the case of average dates, but differences were still strongly significant (Appendix S3, Table S2).

Complete climatic models for average dates: explanatory capacity and composition of variables

Modelling abilities shown by complete models decreased markedly from early to late phenophases during the year ($r = -0.681$, $t_{96} = 9.027$, $P < 0.0001$). However, date effect disappeared when the relationship was nested within phenological events (Fig. 4a; Appendix S3, Table S3). Leaf unfolding and flowering (the earliest events of the year) showed the highest explanatory capacity of complete models (Table 1). However, leaf falling, the latest event of the year, was the worst modelled (Table 1). Fruit ripening and fruit harvesting showed intermediate models (Table 1). This ordination pattern is the same found for single climatic models (Fig. 3). Therefore, there is a decrease of climate modelling abilities from early to late events, but not from early to late phenophases within each event. In the case of the growing season, explanatory capacity of complete models was not related to the length of this period ($r = -0.085$, $t_{22} = -0.381$, $P = 0.707$).

Explanatory capacity of complete climatic models was not related to the standard deviation (σ) of each

Table 1 Climate models for plant phenology

			Average date models						Standard deviation models					
			Temperature						Temperature					
Species	Date	SD	Mean	Maximum	Minimum	Precipitation	NAO	Complete	Mean	Maximum	Minimum	Precipitation	NAO	Complete
Leaf unfolding														
Prunus dulcis	9–3	21.3	0.615	0.518	0.347	0.420	0.226	0.654	0.331	0.321	0.201	0.195	0.353	0.468
Cydonia oblonga	26–3	18.9	0.724	0.736	0.357	0.199	0.378	0.724	0.181	0.192	0.084	–	0.180	0.181
Prunus armeniaca	28–3	18.6	0.620	0.602	0.372	0.306	0.251	0.620	0.211	0.142	0.239	0.196	0.124	0.308
Salís alba	29–3	24.8	0.642	0.570	0.322	0.234	0.303	0.642	0.182	0.215	0.058	0.137	–	0.182
Sambucus nigra	29–3	28.4	0.639	0.607	0.399	0.434	0.424	0.727	0.459	0.299	0.325	0.224	0.212	0.224
Prunus persica	31–3	17.1	0.738	0.728	0.310	0.302	0.507	0.784	0.149	0.186	0.038	–	0.121	0.149
Alnus glutinosa	6–4	20.8	0.638	0.537	0.489	0.396	0.345	0.671	0.133	0.100	0.102	–	0.159	0.254
Rosa canina	7–4	26.9	0.441	0.386	0.311	0.102	0.404	0.498	0.120	0.122	0.055	0.139	0.138	0.139
Pyrus communis	7–4	19.7	0.798	0.788	0.434	0.371	0.517	0.820	0.228	0.181	0.210	0.136	0.142	0.228
Crataegus monogyna	8–4	24.1	0.693	0.594	0.519	0.372	0.384	0.693	–	–	–	–	0.116	0.116
Ficus carica	8–4	19.8	0.500	0.523	0.212	0.360	0.287	0.500	–	–	–	0.133	0.140	0.140
Aesculum hippocastanum	9–4	17.5	0.634	0.530	0.493	0.188	0.300	0.634	0.141	0.168	0.051	–	0.198	0.198
Hacer pseudoplatanus	11–4	18.1	0.315	0.199	0.306	–	–	0.315	0.251	0.155	0.280	–	–	0.251
Corylus avellana	11–4	23.1	0.534	0.554	0.281	0.221	0.362	0.534	0.173	0.138	0.155	0.200	–	0.200
Fraxinus excelsior	15–4	26.6	0.743	0.649	0.528	0.259	0.524	0.744	0.104	0.075	0.079	0.129	–	0.261
Populus nigra	16–4	20.3	0.852	0.758	0.672	0.255	0.561	0.852	0.151	0.156	0.070	–	0.144	0.151
Vitis vinifera	17–4	20.2	0.770	0.703	0.425	0.315	0.532	0.770	0.299	0.246	0.224	–	–	0.299
Malus domestica	17–4	19.3	0.618	0.711	0.203	0.349	0.382	0.653	0.121	0.171	0.012	0.104	0.138	0.233
Betula pendula	17–4	20.4	0.711	0.641	0.473	0.419	0.336	0.750	0.147	0.075	0.148	–	–	0.147
Ulmus minor	19–4	18.4	0.713	0.625	0.572	0.285	0.521	0.766	0.161	0.127	0.144	–	–	0.161
Prunus spinosa	19–4	21.2	0.737	0.717	0.397	0.248	0.394	0.737	0.373	0.318	0.265	0.125	0.211	0.373
Juglans regia	23–4	17.5	0.790	0.793	0.355	0.248	0.401	0.790	0.187	0.122	0.184	–	–	0.187
Castanea sativa	2–5	17.0	0.369	0.321	0.284	0.314	0.235	0.369	–	–	–	0.086	–	0.086
Fagus sylvatica	4–5	14.5	0.541	0.565	0.277	0.280	0.466	0.541	0.122	0.245	−0.022	0.327	0.296	0.327
Average			**0.641**	**0.598**	**0.389**	**0.299**	**0.393**	**0.658**	**0.201**	**0.179**	**0.138**	**0.164**	**0.178**	**0.219**
Flowering														
Prunus dulcis[e]	19–2	22.7	0.810	0.697	0.505	0.352	0.100	0.832	0.531	0.540	0.312	0.221	0.319	0.655
Corylus avellana[a]	3–3	38.1	0.356	0.373	0.121	0.199	0.133	0.356	0.105	0.162	0.011	0.172	0.171	0.225
Salís alba[a]	12–3	27.6	0.397	0.459	0.118	0.223	0.255	0.438	0.200	0.217	0.109	–	0.070	0.200
Prunus armeniaca[e]	15–3	15.9	0.797	0.770	0.460	0.411	0.455	0.838	0.307	0.201	0.305	0.118	0.080	0.307
Prunus persica[e]	20–3	14.7	0.834	0.838	0.460	0.386	0.554	0.869	0.167	0.172	0.089	0.072	0.137	0.167
Fraxinus excelsior[a]	31–3	31.8	0.323	0.345	0.143	0.202	0.291	0.418	0.166	0.223	0.060	–	–	0.166
Pyrus communis[e]	1–4	17.0	0.811	0.787	0.501	0.377	0.515	0.830	0.248	0.186	0.233	0.109	0.142	0.248
Ulmus minor[a]	1–4	24.8	0.413	0.445	0.198	0.198	0.374	0.413	0.075	0.056	0.048	–	–	0.075
Ulex europaeus[e]	5–4	28.3	0.657	0.637	0.379	0.262	0.378	0.657	0.303	0.209	0.275	0.068	0.064	0.303
Prunus spinosa[e]	7–4	22.4	0.706	0.745	0.372	0.362	0.499	0.724	0.058	0.054	0.036	–	–	0.058
Cydonia oblonga[e]	7–4	18.6	0.821	0.875	0.401	0.383	0.575	0.862	0.254	0.271	0.150	0.124	0.122	0.307

Continued

Table 1. (*Contd.*)

			Average date models						Standard deviation models					
			Temperature						Temperature					
Species	Date	SD	Mean	Maximum	Minimum	Precipitation	NAO	Complete	Mean	Maximum	Minimum	Precipitation	NAO	Complete
Populus nigra[a]	8–4	25.0	0.621	0.619	0.401	0.333	0.522	0.657	0.163	0.131	0.132	–	–	0.163
Ficus carica	12–4	25.8	0.353	0.334	0.216	0.080	0.237	0.353	0.226	0.245	0.086	–	0.171	0.226
Malus domestica[e]	13–4	18.8	0.802	0.785	0.516	0.378	0.488	0.809	0.247	0.234	0.160	0.105	–	0.247
Betula pendula[a]	13–4	24.5	0.455	0.522	0.173	0.340	0.343	0.497	–	–	–	0.090	0.082	0.090
Acer pseudoplatanus[a]	14–4	23.7	0.307	0.283	0.145	0.158	0.133	0.307	–	–	–	–	0.048	0.048
Citrus sinensis[e]	15–4	19.0	0.681	0.566	0.540	0.249	0.352	0.681	0.074	0.088	0.022	0.051	0.060	0.074
Juglans regia[a]	20–4	17.9	0.712	0.649	0.514	0.240	0.436	0.732	0.300	0.330	0.131	–	–	0.300
Crataegus monogyna[e]	24–4	26.8	0.796	0.700	0.608	0.268	0.438	0.803	0.291	0.258	0.175	0.100	0.067	0.343
Aesculum hippocastanum[e]	25–4	16.1	0.740	0.712	0.490	0.321	0.383	0.740	0.118	0.121	0.067	0.059	–	0.118
Iris pseudacorus[a]	10–5	23.1	0.386	0.318	0.330	0.191	0.226	0.386	0.161	0.103	0.125	–	0.080	0.223
Sambucus nigra[e]	18–5	24.5	0.837	0.767	0.575	0.249	0.337	0.837	0.220	0.237	0.146	0.168	0.094	0.220
Rosa canina[e]	20–5	24.3	0.664	0.590	0.516	0.218	0.353	0.673	0.191	0.210	0.112	0.143	0.067	0.191
Olea europaea[a]	22–5	21.2	0.670	0.585	0.540	0.329	0.219	0.670	0.058	0.082	0.015	0.147	0.099	0.147
Vitis vinifera	22–5	25.9	0.470	0.500	0.242	0.177	0.147	0.470	0.249	0.210	0.250	0.146	0.150	0.293
Castanea sativa[a]	24–6	18.1	0.649	0.635	0.494	0.344	0.200	0.649	–	–	–	–	–	–
Hedera helix[e]	7–10	22.0	0.112	0.077	0.142	–	0.060	0.112	0.163	0.140	0.133	–	–	0.163
Average			**0.599**	**0.578**	**0.374**	**0.278**	**0.333**	**0.615**	**0.203**	**0.195**	**0.133**	**0.118**	**0.112**	**0.214**
Fruti Ripening														
Prunus armeniaca	22–6	20.4	0.416	0.339	0.329	0.189	0.137	0.416	0.077	0.053	0.085	–	0.099	0.099
Ficus carica 'breval'	28–6	13.1	0.351	0.300	0.289	0.074	0.220	0.353	–	–	–	–	0.108	0.108
Malus domestica 'early'	6–7	17.4	0.457	0.412	0.332	0.139	0.100	0.457	0.167	0.095	0.205	–	–	0.167
Prunus persica 'early'	12–7	22.2	–	–	–	–	–	–	–	–	–	–	–	–
Ficus carica	2–9	20.5	0.484	0.485	0.416	0.132	0.180	0.484	0.098	0.044	0.151	0.052	–	0.206
Prunus dulcis	6–9	20.8	0.107	0.156	0.018	0.241	0.131	0.241	0.050	0.053	0.029	0.127	0.075	0.127
Prunus persica 'late'	8–9	15.7	0.476	0.460	0.348	0.153	0.343	0.476	0.180	0.197	0.086	0.266	0.185	0.291
Vitis vinifera	23–9	16.0	0.503	0.488	0.430	0.131	0.234	0.503	0.343	0.268	0.326	0.064	0.079	0.343
Juglans regia	2–10	14.4	0.502	0.396	0.509	0.069	0.229	0.527	–	–	–	–	–	–
Malus domestica 'delicious'	3–10	14.8	0.358	0.410	0.160	0.260	0.288	0.405	–	–	–	0.131	–	0.131
Cydonia oblonga	6–10	17.3	0.552	0.472	0.464	0.180	0.254	0.552	–	–	–	0.066	0.060	0.113
Castanea sativa	18–10	11.6	0.601	0.548	0.521	0.165	0.325	0.624	0.105	0.094	0.058	–	–	0.105
Olea europaea	5–12	24.2	0.487	0.409	0.440	0.178	0.228	0.487	0.100	0.065	0.114	0.097	–	0.168
Citrus sinensis	8–12	21.0	0.113	0.133	0.043	0.183	0.200	0.200	0.150	0.103	0.150	–	–	0.150
Average			**0.416**	**0.444**	**0.364**	**0.200**	**0.233**	**0.495**	**0.155**	**0.134**	**0.128**	**0.122**	**0.101**	**0.179**
Fruti harvesting														
Prunus armeniaca	22–6	18.9	0.164	0.139	0.124	–	–	0.164	0.116	0.108	0.091	–	–	0.116
Ficus carica	7–9	20.6	0.193	0.184	0.158	0.058	0.119	0.193	0.126	0.078	0.155	–	0.121	0.126
Prunus dulcis	9–9	20.4	0.328	0.357	0.199	0.141	–	0.328	–	–	–	–	0.085	0.085
Prunus persica 'late'	12–9	14.9	0.300	0.291	0.227	–	0.119	0.300	–	–	–	0.096	0.072	0.072

Vitis vinifera	30–9	14.0	0.493	0.492	0.403	0.267	0.283	0.569	0.087	0.094	0.060	0.097	–	0.097
Juglans regia	4–10	14.0	0.526	0.430	0.446	0.177	0.073	0.526	0.126	0.096	0.087	–	–	0.126
Cydonia oblonga	12–10	17.6	0.403	0.353	0.339	–	–	0.403	0.118	0.082	0.084	–	–	0.118
Castanea sativa	23–10	11.0	0.453	0.408	0.342	0.171	0.196	0.480	–	–	–	–	0.062	0.062
Olea europaea	18–12	24.4	0.382	0.318	0.317	0.142	0.178	0.415	–	–	–	–	0.072	0.072
Average			**0.360**	**0.330**	**0.284**	**0.159**	**0.162**	**0.375**	**0.115**	**0.092**	**0.095**	**0.097**	**0.083**	**0.097**
Leaf falling														
Populus nigra	8–11	15.4	0.368	0.300	0.289	0.198	–	0.431	0.136	0.141	0.097	–	–	0.136
Fagus sylvatica	10–11	15.6	0.219	0.239	0.086	0.084	0.117	0.219	0.070	0.053	0.049	0.096	0.171	0.252
Fraxinus excelsior	10–11	15.1	0.339	0.322	0.193	0.138	–	0.339	0.130	0.116	0.091	–	0.080	0.130
Juglans regia	10–11	15.1	0.384	0.372	0.215	0.183	0.078	0.384	–	–	–	0.067	–	0.067
Pyrus communis	11–11	15.2	0.390	0.381	0.225	0.220	–	0.433	0.065	0.061	0.030	0.053	0.062	0.195
Aesculum hippocastanum	11–11	13.7	0.219	0.133	0.234	0.076	0.052	0.219	0.147	0.079	0.182	0.219	0.147	0.288
Prunus dulcis	12–11	20.9	0.260	0.206	0.258	–	0.066	0.260	0.276	0.174	0.333	0.106	–	0.327
Crataegus monogyna	13–11	16.2	0.213	0.049	0.417	–	0.100	0.260	0.145	0.140	0.084	–	–	0.145
Acer pseudoplatanus	13–11	15.6	0.221	0.169	0.220	0.069	–	0.271	–	–	–	0.204	0.627	0.216
Prunus persica	13–11	15.4	0.221	0.180	0.197	0.053	0.058	0.221	0.079	0.117	0.017	0.177	–	0.228
Prunus armeniaca	14–11	15.8	0.235	0.222	0.160	0.111	0.106	0.235	–	–	–	0.062	–	0.062
Vitis vinifera	14–11	16.0	0.429	0.429	0.336	0.159	0.106	0.429	–	–	–	–	–	–
Ficus carica	14–11	14.4	0.358	0.288	0.323	0.085	0.132	0.358	–	–	–	0.140	–	0.140
Sambucus nigra	16–11	17.0	0.261	0.125	0.344	–	0.133	0.261	0.124	0.088	0.100	–	0.227	0.178
Ulmus minor	16–11	15.3	0.275	0.133	0.320	0.072	–	0.322	0.124	0.138	0.058	–	–	0.124
Corylus avellana	16–11	17.4	0.163	0.083	0.164	0.062	0.167	0.372	0.145	0.107	0.133	–	–	0.145
Betula pendula	16–11	17.1	–	–	–	0.172	0.073	0.201	–	–	–	–	–	–
Malus domestica	17–11	16.3	0.293	0.217	0.296	–	0.081	0.293	0.051	0.063	0.010	–	–	0.051
Cydonia oblonga	22–11	14.7	0.114	0.108	0.063	–	0.059	0.114	–	–	–	0.175	–	0.175
Salix alba	22–11	18.0	–	–	–	–	–	–	–	–	–	–	–	–
Castanea sativa	23–11	14.6	0.321	0.337	0.177	0.180	0.072	0.321	0.094	0.091	0.049	–	–	0.094
Alnus glutinosa	26–11	15.7	0.058	0.090	0.009	–	–	0.058	–	–	–	–	–	–
Average			**0.267**	**0.219**	**0.226**	**0.124**	**0.093**	**0.286**	**0.122**	**0.105**	**0.095**	**0.130**	**0.219**	**0.164**
Growing season														
Fagus sylvatica	5–7	22.0	0.603	0.552	0.469	0.230	0.508	0.603	0.331	0.267	0.245	0.155	0.251	0.331
Juglans regia	18–7	24.5	0.481	0.524	0.212	0.185	0.436	0.481	0.244	0.204	0.179	0.120	0.151	0.455
Populus nigra	21–7	26.8	0.651	0.532	0.528	0.264	0.479	0.692	–	–	–	0.144	–	0.144
Castanea sativa	23–7	20.8	0.134	0.127	0.077	–	0.099	0.134	–	–	–	–	0.208	0.208
Fraxinus excelsior	25–7	31.5	0.558	0.517	0.385	0.213	0.509	0.558	0.346	0.148	0.395	0.107	–	0.346
Ulmus minor	27–7	26.1	0.667	0.550	0.576	0.380	0.495	0.667	0.278	0.221	0.211	–	–	0.278
Vitis vinifera	30–7	28.2	0.660	0.601	0.460	0.352	0.506	0.660	0.117	0.019	0.180	0.150	–	0.150
Betula pendula	30–7	28.0	0.559	0.527	0.354	0.549	0.513	0.559	0.244	0.136	0.281	–	–	0.244
Malus domestica	31–7	25.8	0.639	0.654	0.425	0.393	0.458	0.678	0.231	0.142	0.288	0.190	0.156	0.231
Acer pseudoplatanus	3–8	23.8	0.248	0.216	0.215	0.314	0.268	0.366	0.270	0.172	0.327	0.099	0.088	0.270
Pyrus communis	3–8	25.9	0.689	0.690	0.412	0.222	0.548	0.735	0.207	0.192	0.141	0.373	0.289	0.373
Crataegus monogyna	3–8	34.4	0.512	0.447	0.404	0.111	0.405	0.528	–	–	–	–	0.219	0.219
Corylus avellana	4–8	33.0	0.495	0.458	0.343	0.294	0.470	0.495	–	–	–	0.113	0.235	0.235

Continued

Table 1. (*Contd.*)

Species	Date	SD	Average date models						Standard deviation models					
			Temperature						Temperature					
			Mean	Maximum	Minimum	Precipitation	NAO	Complete	Mean	Maximum	Minimum	Precipitation	NAO	Complete
Aesculum hippocastanum	5–8	22.3	0.562	0.461	0.451	0.232	0.359	0.562	0.138	0.054	0.237	–	0.338	0.425
Ficus carica	7–8	25.2	0.528	0.442	0.368	0.253	0.282	0.528	–	–	–	0.184	0.113	0.221
Prunus persica	14–8	23.0	0.572	0.529	0.446	0.329	0.437	0.622	0.144	0.074	0.209	0.110	0.189	0.189
Sambucus nigra	17–8	41.1	0.656	0.599	0.491	0.436	0.537	0.685	0.107	−0.022	0.207	0.329	0.144	0.329
Prunus armeniaca	18–8	25.7	0.591	0.509	0.476	0.357	0.285	0.642	0.245	0.203	0.263	–	0.391	0.391
Alnus glutinosa	21–8	27.4	0.528	0.450	0.394	–	0.360	0.528	0.195	0.168	0.132	–	–	0.195
Salix alba	23–8	36.0	0.426	0.217	0.431	0.339	0.306	0.407	0.100	0.003	0.174	0.121	–	0.121
Cydonia oblonga	30–8	27.0	0.370	0.428	0.141	0.288	0.371	0.437	–	–	–	0.149	–	0.149
Prunus dulcis	3–9	28.8	0.426	0.436	0.215	0.195	0.446	0.493	–	–	–	–	–	–
Average			**0.525**	**0.476**	**0.376**	**0.297**	**0.413**	**0.548**	**0.213**	**0.132**	**0.231**	**0.167**	**0.213**	**0.262**

For the 118 studied phenophases, it is shown: the occurrence date in the calendar (date), the standard deviation (SD), the values of the adjusted R^2 obtained for each climate variable [mean, maximum and minimum temperature, precipitation, and North Atlantic Oscillation (NAO)], and the maximum modelling ability of climate (adjusted R^2 of complete model). In the last row of each event, there is the average value for all phenophases.
–, phenophases that included no significant variable in their model.

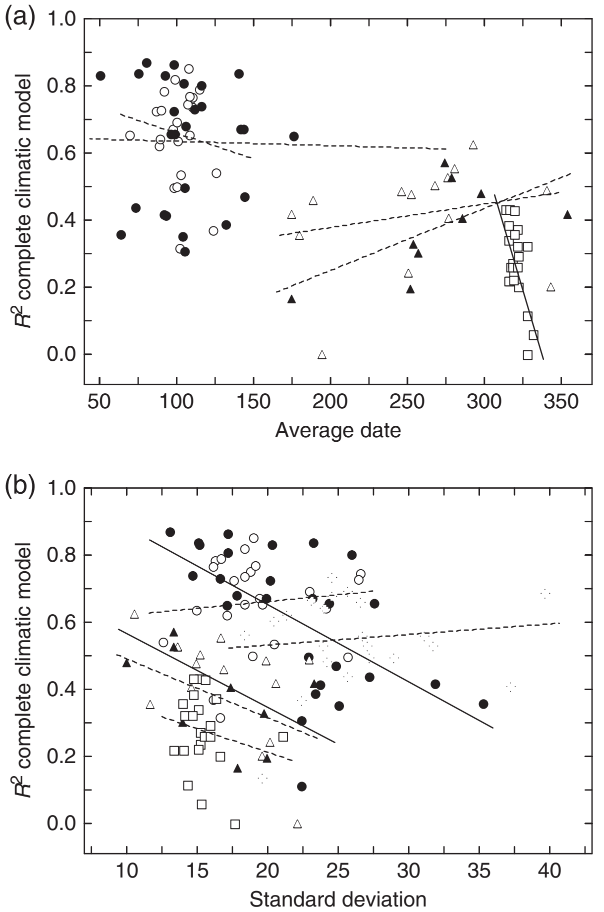


Fig. 4 Scatterplots of explanatory capacity (adjusted R^2) of complete climatic models for average date time-series with absolute average date (a) and standard deviation (b). Fitted lines represent nested relationship within each event. Dotted lines are nonsignificant and solid lines are significant at $P = 0.05$. Leaf unfolding, ○ ; flowering, ● ; fruit ripening, △; fruit harvesting, ▲; leaf falling, □; growing season, + .

phenophase overall ($r = 0.130$, $t_{118} = 1.414$, $P = 0.160$; Fig. 4b). Interestingly, a significant effect of standard deviation arose when this relationship was nested within the phenological events (Fig. 4b; Table S3). In all events, with the exception of leaf unfolding and growing season, species with greater variability among sites were related to poor modelling abilities of climate. This effect was especially strong for flowering.

Insect-pollinated species showed significantly better models than wind-pollinated species (average adjusted $R^2 = 0.781 \pm 0.032$ and 0.502 ± 0.034, respectively). The pollination mechanism accounted for up to 60% of variability among explanatory capacity of species climatic models (One-way ANOVA: $F_{1,22} = 35.49$, $P < 0.0001$).

Differences in the explanatory capacity of complete climatic models among phenological events mimicked almost exactly differences among events found with temperature models (Fig. 3; Fig. S1). Such resemblance was due to the overwhelming majority of temperature variables in complete models (199 out of 263 climate variables included). This ratio was strongly biased in relation to the initial pool of climatic variables used to build complete models (239 temperatures, 175 precipitations and 196 NAOs). Temperature explained the greater part of variance as a consequence of this overrepresentation of temperature variables in complete models (Fig. 3; Table S4). However, the pure effect of climatic variables was markedly reduced in relation to their particular models (Fig. 3). This fact highlights the strong concomitance of the three types of climatic variables (see also Appendix S1).

Complete climatic models for standard deviation: explanatory capacity and composition of variables

Models for standard deviation had higher explanatory capacity in phenophases early in the year than in later ones ($r = -0.402$, $t_{96} = -4.253$, $P < 0.0001$; Fig. 5a). Leaf unfolding and flowering showed slightly better models than the rest of the events (Table 1). The calendar effect was just marginally significant, when the average date (μ) effect was nested within each event (Table S3). Date effect was only significant for flowering and leaf falling. In the case of the growing season, explanatory capacity of complete models was negatively related to the length of this event ($r = -0.471$, $t_{22} = -2.391$, $P = 0.027$). Hence, the longer the growing season, the lesser the climate control in the spatial variability of this event.

The explanatory capacity of complete climatic models was not related to the standard deviation (σ) of each event both overall ($r = 0.175$, $t_{96} = 1.725$, $P = 0.088$; Fig. 5b) and within each event (Table S3). Only in the case of leaf falling, did species with higher spatial variability show the worst climatic models for this variable.

Insect-pollinated species tended to show better models than wind-pollinated species (One-way ANOVA: $F_{1,22} = 3.70$, $P < 0.067$).

The majority of variables included in complete models were temperatures (89 out of 166, with only 44 for precipitation and 33 for NAO). This ratio was biased towards temperature variables in relation to the initial pool of predictor climatic variables used to build models (109 temperatures, 78 precipitations and 78 NAOs). This composition of climatic variables caused significant differences in the pure effect of each type of climate variable (Table S4). However, R^2 values did not diminished so much in relation to those values obtained for single models (Fig. 3). Therefore, each type of climate variable is indeed acting on different aspects of the temporal trends of standard deviation values. Nevertheless, it is important to stress that explanatory capacity of complete climate models was overall around 20% (Table 1) and hence the real contribution of each type of climate variables was indeed small (<7%).

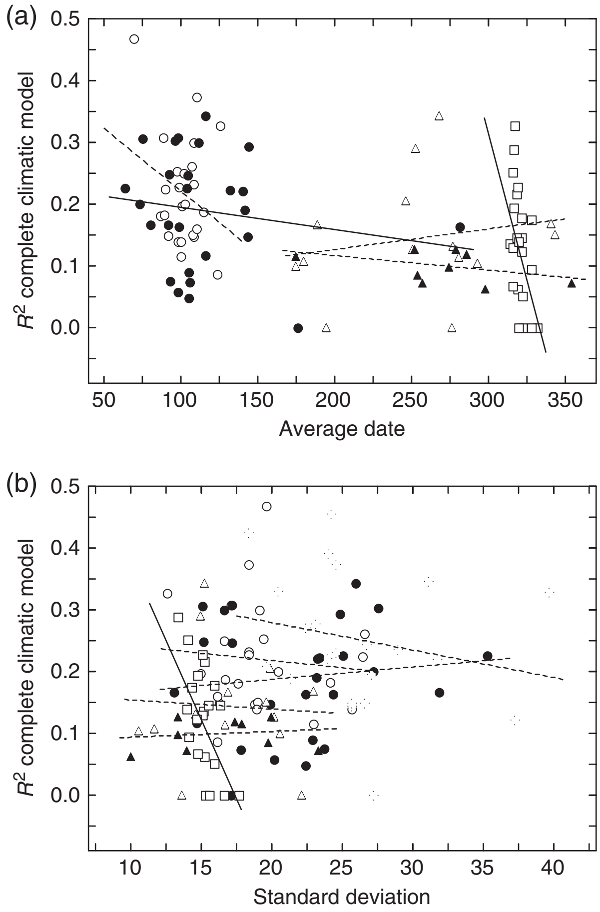


Fig. 5 Scatterplots of explanatory capacity (adjusted R^2) of complete climatic models for standard deviation time-series with absolute average date (a) and standard deviation (b). Fitted lines represent nested relationship within each event. Dotted lines are nonsignificant and solid lines are significant at $P = 0.05$. Leaf unfolding, ○ ; flowering, ● ; fruit ripening, △; fruit harvesting, ▲; leaf falling, □; growing season, +.

Relationship between temporal trends of phenology and climate sensitivity

Those phenophases with the greatest sensitivity (both positive and negative) showed the greatest temporal phenological changes in their average dates (Fig. 6). However, when the relationship between these variables was nested within each event, marked and significant differences arose among events (Table 2). Leaf unfolding and flowering trends were dependent on the degree of sensitivity, while fruit ripening and harvesting was never dependent on the degree of sensitivity. Leaf falling also showed significant relationships

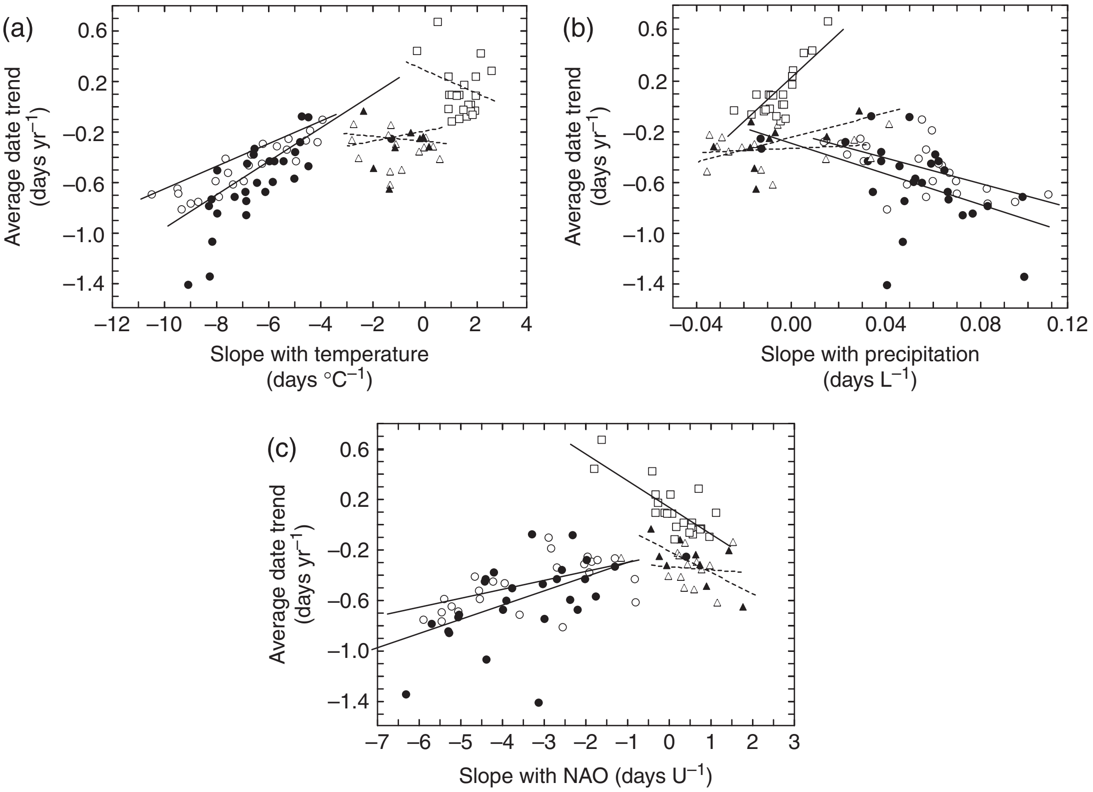


Fig. 6 Scatterplots of temporal trend of average date time-series with the relationship (slope) of this variable with temperature (a), precipitation (b) and North Atlantic Oscillation (NAO) (c) at the moment when each phenophase occurs (Q_0). Fitted lines represent nested relationships within each event. Dotted lines are nonsignificant and solid lines are significant at $P = 0.05$. Leaf unfolding, ○ ; flowering, ● ; fruit ripening, △; fruit harvesting, ▲; leaf falling, □; growing season, + .

between temporal trends and sensitivity to precipitation and NAO. The slope had a sign opposite to that for leaf unfolding or flowering, but its biological meaning was the same: a greater temporal shift is related to higher sensitivity. Such a difference arose from the fact that leaf falling is affected in a different way by climate (Fig. 1 and 2). In the particular case of growing season, simple correlations between temporal trends and slopes with temperature and NAO at Q_{best} yielded strong positive associations (temperature: $r = 0.966$, $t_{22} = 16.67$, $P < 0.0001$; NAO: $r = 0.678$, $t_{22} = 4.12$, $P = 0.0005$). In both cases, higher sensitivity was related to greater lengthening of this phase from 1973 to 2003. In the case of precipitation, the relationship was only marginally significant ($r = -0.389$, $t_{22} = -1.89$, $P < 0.073$). This fact was a result of the identity of the quarter selected for Q_{best}. Nine species selected a quarter from spring (i.e. negative slope with rainfall; see Fig. 1), while 12 species selected a quarter from autumn of the previous year (i.e. positive slope). Greater lengthening of the growing season from 1973 to 2003 was related to greater sensitivity (slope), but such sensitivity had positive values (slopes) in species that selected an autumn quarter as Q_{best} and negative values in species that selected a spring quarter as Q_{best}. Such a difference in signs blurred the relationship between sensitivity and temporal trends. If we remove the sign of the slopes with Q_{best}, we obtain a strongly significant relationship ($r = 0.780$, $t_{22} = 5.58$, $P < 0.0001$) for precipitation sensitivity as well. Overall, climate sensitivity accounted for between 68% and 75% of temporal trends variability (Table 2). Thus, differences among events and species in temporal trends were mainly due to their particular sensitivity to climate.

Those phenophases with the greatest sensitivity to climate also showed the greatest temporal changes in the last decades in their ranges of onset dates (Fig. 7). Nested design was especially suitable due to the marked differences in slopes among events (Table 2). Leaf unfolding and flowering showed opposite relationships in relation to leaf falling, while fruiting events did not show any relationship. Such differences among leaf unfolding, flowering and leaf falling are due to the different effects of climate on the standard deviation of each event (see Fig. 1). In the particular case of the growing season, temporal trends of standard deviation were significantly related only to temperature

Table 2 Results of the six ANOVA for the temporal trends of phenology (slope for the period 1973–2003) as a dependent variable and the relationship with each climatic variable at the moment when the phenophase occurs (slope with Q_0) as a predictor nested within the phenological event

		Temperature				Precipitation				NAO			
	df	SS	MS	F	P	SS	MS	F	P	SS	MS	F	P
Average dates													
Event	4	1.519	0.380	12.32	<0.001	2.636	0.659	16.46	<0.001	1.790	0.448	11.79	<0.001
Slope Q_0(Event)	5	2.412	0.482	15.66	<0.001	1.618	0.324	8.081	<0.001	1.797	0.359	9.466	<0.001
Error	86	2.650	0.031			3.444	0.040			3.265	0.038		
Adjusted R^2		0.753			<0.001	0.679			<0.001	0.696			<0.001
Standard deviation													
Event	4	0.039	0.010	0.667	0.617	0.040	0.010	0.528	0.716	0.017	0.004	0.249	0.910
Slope Q_0(Event)	5	0.697	0.139	9.622	<0.001	0.326	0.065	3.474	0.007	0.451	0.090	5.203	<0.001
Error	86	1.246	0.014			1.616	0.019			1.492	0.017		
Adjusted R^2		0.374			<0.001	0.188			0.001	0.251			<0.001

Tests for average dates are in the upper portion and for standard deviation in the inner portion. Degrees of freedom (df), sum of squares (SS), mean squares (MS), F-statistic (F) and p-value (p) for each predictor variable are shown. In the last row of each model, the explanatory capacity (Adjusted R^2) and its significance is also shown.

sensitivity ($r = 0.714$, $t_{22} = 4.55$, $P = 0.0001$). Sensitivity to precipitation ($r = 0.116$, $t_{22} = 0.51$, $P = 0.611$) or NAO ($r = -0.365$, $t_{22} = -1.75$, $P = 0.094$) was not related to the temporal trends, and this fact was not due to differences in signs. Overall, models accounted for less variability in the temporal trends of standard deviations than in the case of average dates, although temperature model was able to explain a noteworthy 37% of variability among phenophases (Table 2).

Discussion

Climate: a key factor to understand fluctuations in plant phenology

The main conclusion of the present study is that plant phenology is strongly controlled by climate and as consequence phenological temporal changes observed during last decades can be attributed to the recent climate change. Therefore, plants are a reliable bioindicator of climate change. This conclusion is not a novel finding, since many studies have demonstrated this fact yet (Sparks *et al.*, 2000; Chmielewski & Rötzer, 2001; Menzel *et al.*, 2001, 2006a; Fitter & Fitter, 2002; Ahas & Aasa, 2006; Doi, 2007; Estrella *et al.*, 2007; Miller-Rushing *et al.*, 2007, 2008c; Doi & Katano, 2008). However, the value of our study is its broad spatial and long-term temporal scales, which are the largest and the longest, respectively, available for the Mediterranean region (Peñuelas *et al.*, 2002; Gordo & Sanz, 2005). Moreover, this large spatial scale nature of our dataset offered a unique opportunity to study another poorly explored facet of plant phenology: the intersite variability. In a previous study, we demonstrated that not only the position in the calendar but also the shape of distributions of onset dates changed during the last decades (Gordo & Sanz, 2009). Here, we have shown that time-series for annual standard deviation values are significantly related to climate and this could be the cause for the observed temporal trends. Warm and dry years reduced spatial variability in plant phenology, while cold and wet years increased it (see Fig. 1). These results fully agree with recent findings in artic ecosystems, which have demonstrated that changes in spatial variability of plant phenology in response to climate fluctuations have serious consequences for the reproductive success of higher trophic levels, such as herbivores (Post *et al.*, 2008a, b). Unfortunately, we do not know whether observed changes in the spatial variability of plant phenology are having or not an impact in other trophic levels of Mediterranean ecosystems. However, if spatial variability plays an important role in phenological matching processes between trophic levels, we suggest that climate change may have additional impacts in Mediterranean ecosystems through alterations in the spatial variability of phenology. Future climate scenarios predict warmer and drier conditions for the Mediterranean region (de Castro *et al.*, 2005; Solomon *et al.*, 2007) and hence, there will be further compression in the range of onset dates of plant phenology.

We used a simple approach based on multiple regressions and monthly climate variables to study the effect of climate on plant phenology, similarly to other previous studies (Sparks *et al.*, 1997, 2000; Menzel, 2003; Tryjanowski *et al.*, 2006; Miller-Rushing *et al.*, 2007; Doi & Katano, 2008). However, plant phenology studies

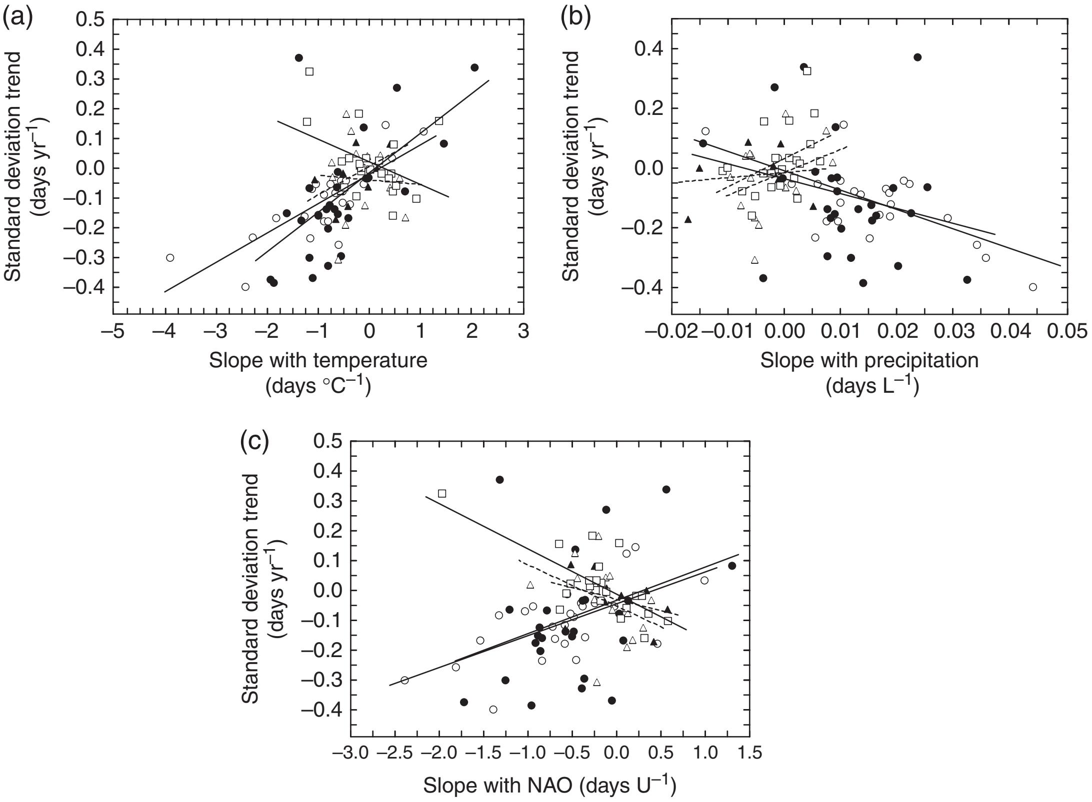


Fig. 7 Scatterplots of temporal trend of standard deviation time-series with the relationship (slope) of this variable with temperature (a), precipitation (b), and NAO (c) at the moment when each phenophase occurs (Q_0). Fitted lines represent nested relationships within each event. Dotted lines are nonsignificant and solid lines are significant at $P = 0.05$. Leaf unfolding, ○ ; flowering, ● ; fruit ripening, △; fruit harvesting, ▲; leaf falling, □; growing season, + .

have traditionally used models based on variables, such as cumulative degree days, chilling requirements, sensitivity thresholds or photoperiod (Leith, 1974; Hunter & Lechowicz, 1992; Kramer, 1994; Chuine *et al.*, 1999). Such phenology modelling techniques are complex, but provide accurate tools for plant phenology prediction. Probably, the studied time-series here could be better modelled using this kind of variables with a daily basis and defined according to plant physiology. Nevertheless, our aim was not to find the most accurate and predictive model for each one of the 118 studied phenophases. Our approach based on simple regressions and easily available climatic variables was perfectly suited to answer key questions such: Is there a significant effect of climate on plant phenology? How is the influence of different types of variables? What are the interspecific patterns of variability? Is climate change the origin for phenological responses? Moreover, our models were really good for some species, especially in leaf unfolding and flowering events (see Table 1). This fact supports the idea that even simple modelling techniques can be useful to discover the most important climate effects on plant phenology and hence, are suited methods to explore causal links between climate change and phenological alterations.

Dual climate triggers on plant phenology?

The effect of climate at the moment of phenophase occurrence (Q_0) showed the greatest impact on phenology, but many phenophases were also affected simultaneously by climate of previous seasons. For instance, 78% and 52% of complete climatic models for average date and standard deviation time-series, respectively, included 'delayed' quarters, i.e. quarters ending several months before phenophase occurrence. Therefore, it is necessary to consider the whole annual cycle because plant phenological responses are also triggered by past weather. Interestingly, present and past climate showed opposite effects on plant phenology (see Fig. 1). For instance, warmer temperatures advance spring phenology but only when such positive anomalies occur during the spring. During late summer (August–September), increased temperatures delay spring events of the following year (Fitter *et al*., 1995; Sparks *et al*., 2000; Heide, 2003; Chmielewski *et al*., 2005; but see Williams & Abberton, 2004). Therefore, climate conditions during the initiation of bud dormancy are important to understand phenological responses of buds in the next spring. According to our results, a marked warming of autumn temperatures in relation to spring temperatures could lead plants to delay their spring phenology, which seems a counterintuitive phenological response in a warming world (Heide, 2003). Such dual effect of climate on all phenological events (excepting fruiting) offers a complex regulation of phenology by climatic counterweights, which may constrain plant phenological responses. Therefore, if we aim to make reliable predictions about plant phenological responses to future climatic conditions, it is necessary to know climatic influences over a complete annual cycle and the climate change experienced during each season.

Rainfall is concentrated at two peaks, one during spring and another during autumn, in Mediterranean climates (McKnight & Hess, 1999). Interestingly, plant phenology was maximally influenced by climate during these seasons (see Fig. 1). This fact suggests that plants in Mediterranean climates have evolved to become especially sensitive to climate during these two key times of the year. One could argue that such dual triggering of phenology by spring and autumn climate is a result of some temporal autocorrelation between successive seasons. However, this hypothesis is not supported by our findings. First, most of the climatic models (both for each type of variable and for complete models) included spring and autumn quarters together. Second, there are indeed weak or null relationships between climate during a certain season and the rest of the seasons of the year (see Appendix S1).

Temperature: the most important climatic variable

Temperature effect over plant phenology remarkably surpassed effects of precipitation and NAO. This is in agreement with most previous studies (Fitter *et al*., 1995; Sparks *et al*., 2000; Cayan *et al*., 2001; Stöckli & Vidale, 2004; Gordo & Sanz, 2005; Ahas & Aasa, 2006; Menzel *et al*., 2006a, b; Zheng *et al*., 2006; Doi, 2007; Estrella *et al*., 2007; Doi & Katano, 2008), although these three climatic variables have never been simultaneously examined. A simultaneous approach is important due to the strong collinearity among climatic variables (see Appendix S1). Such collinearity causes an overestimation of the true magnitude of their effects, when they are individually modeled. For instance, single models for average dates overestimated the explanatory capacity of all climate variables by 20–30% (see Fig. 3). In the case of rainfall and NAO, such a reduction implied that both variables have a really low relevance for plant phenology. Therefore, most of their effects in single models are because of collinearity with temperature. In the case of rainfall, this result went against our prediction. Water availability is a key element for plant function in Mediterranean ecosystems and has demonstrated effects on plant phenology (Ogaya & Peñuelas, 2004; Peñuelas *et al*., 2004; Llorens & Peñuelas, 2005; Prieto *et al*., 2008; Matesanz *et al*., 2009; but see Gordo & Sanz, 2005). This result becomes especially striking when considering that rainy seasons (spring and autumn) were in fact the most influential seasons for plant phenology. In the case of NAO, its lack of true relevance means that plant phenology is better modelled by local weather than by macroscale climatic indices. Thus, there is no reason to use this index despite its predictive power. Plant phenology should be related to and modelled by climate variables recorded in weather stations close to the studied populations because local weather has the true effect on plant phenology (Schwartz & Chen, 2002; Schwartz *et al*., 2006). Interestingly, NAO had the same effect on spring events as in northern latitudes (Post & Stenseth, 1999; Chmielewski & Rötzer, 2001; Post *et al*., 2001; Scheifinger *et al*., 2002; Menzel, 2003; Menzel *et al*., 2005b; Ahas & Aasa, 2006; Nordli *et al*., 2008). This was unexpected as NAO typically results in opposite climatic consequences in the Mediterranean Basin (Ottersen *et al*., 2001).

Minimum temperature was noticeably less relevant for plant phenology than maximum or mean temperature. Interestingly, minimum temperatures are changing at the fastest rate (see Appendix S2) and hence, it is of paramount importance to determine if an inability to tune precisely phenology to nocturnal temperatures imposes some level of constraint in plant responses to climate change (Alward *et al*., 1999).

Delayed effects of climate on fruiting phenology: potential causes and consequences

Fruit ripening and harvesting phenology were poorly correlated to climate during Q_0. For this reason, temporal trends during 1973–2003 and climate sensitivity were not related in these events (see Figs 6 and 7). Nevertheless, fruiting phenology is affected by climate, at least its onset date, as the high R^2 values for complete climatic models of average date demonstrated (see Table 1). Interestingly, climate affected fruiting with some delay. The most influential quarter for fruit ripening and harvesting phenology was March–May in the majority of studied species (see Fig. S2). This result fully agrees with correlations reported by Estrella *et al*. (2007) for fruit trees in Germany. These authors found highest correlation coefficients between fruit ripening/picking phenology and climate from April to June. This period

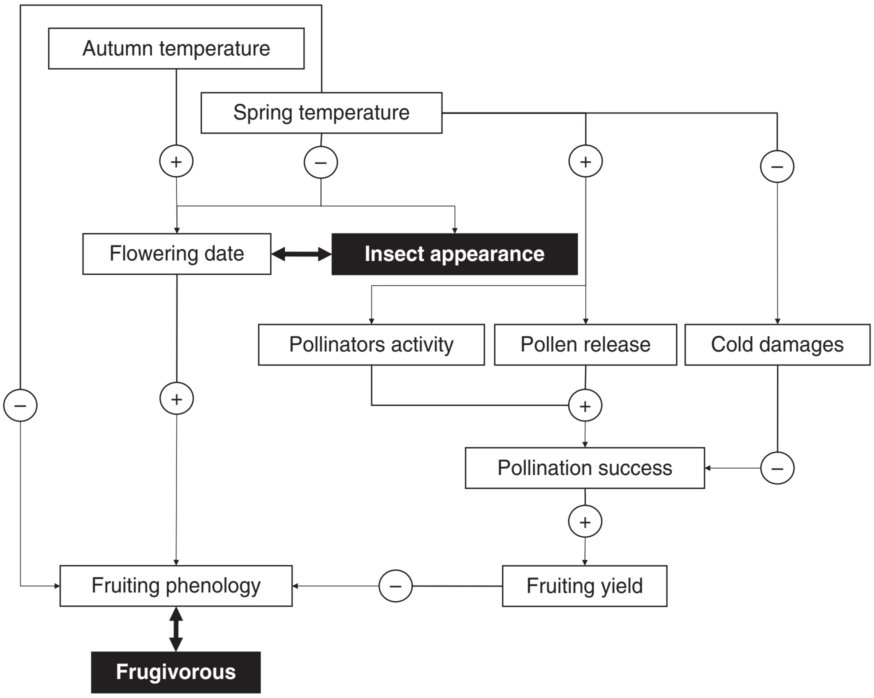


Fig. 8 Diagram flow for plant phenology responses to climate. Some of the potential indirect effects through other mechanisms and the expected correlation sign between processes are shown. Black boxes indicate other trophic levels and thick arrows potential interactions. See 'Discussion' for more details.

in Germany is equivalent to March–May in Spain, since phenology in Germany is delayed ca. 1 month due to its northernmost location [Rötzer *et al*., 2001; compare data of Table 1 with flowering dates reported by Estrella *et al*., 2007: *Prunus armeniaca* 11 April, *P. persica* 19 April, *P. communis* 2 May, *Malus domestica* (early varieties) 9 May]. March–May period is the main flowering period for most of the studied species in Spain (average flowering date of our studied species, 14 April; see Table 1). We suggest three hypotheses to understand such delayed climate effect on fruiting phenology (see Fig. 8).

Fruit yield effect. Weather conditions, such as temperatures, number of rainy days, humidity, wind or sun radiation hours, affect fruit crop. In wind-pollinated species, such as the olive *Olea europaea*, warmer and drier conditions enhance pollen production and release and as a consequence pollination success is increased (Galán *et al*., 2004; García-Mozo *et al*., 2008). In insect-pollinated trees, warm and dry weather during flowering season favour activity and abundance of pollinator insects (Vicens & Bosch, 2000; Willmer & Stone, 2004) along with a decrease of cold-induced damages in flowers' buds, fertile flowers or even incipient fruits in those earliest species (Inouye, 2000; Chmielewski *et al*., 2004). More abundance of fruits may favour an earlier presence of some ripe fruits just by an effect of population size (Miller-Rushing *et al*., 2008a). Unfortunately, we do not have information about fruit yield in the studied species during our study period to check this hypothesis.

Cascade effect. Flowering and ripening/harvesting are the beginning and the end, respectively, of one reproductive cycle in spermatophytes. If flowering date advances in response to warmer and drier conditions during the spring, fruiting will advance being fruit development length equal. The average correlation coefficient between flowering and fruit ripening time-series in the studied species was $r = 0.459$ (SD 0.143). This value is relatively low and become even lower if correlations are calculated with detrended (i.e. without year effect) time-series for both events ($r = 0.383$, SD 0.172). Such correlation values are smaller than those observed between fruiting phenology and spring climate (see Fig. S2). Thus, empirical evidence gives little support to this hypothesis. Moreover, if spring weather is affecting fruiting phenology through flowering onset, why are maximum correlations reached during March–May instead of February–April, the truly most important period for flowering phenology?

Real effect. Our results could be showing a real effect of climate during spring on fruiting phenology. For instance, experimental manipulation of temperatures during the postblooming period in apple trees

Malus domestica have demonstrated that many biochemical and physiological features of fruits are different under low or high temperature treatments (Tromp, 1997; Warrington *et al.*, 1999). Among these features, ripening rate in the final stage of fruit development was dependent on the temperature experienced by fruits during their earlier development stages. Such modulation of fruit development by climate helps to understand better the relatively low dependence of fruiting dates on flowering dates.

Our results do not allow disentangling the real cause for the effect of spring climate on fruiting phenology. Moreover, the proposed hypotheses are not mutually excluding (Fig. 8). Whichever the cause is, spring climate predicts accurately the onset of the fruiting season. This fact may be useful for agricultural planning and managing (fertilization, application of biocides or temporary manpower contracting), since the timing of the fruiting season can be predicted in advance several months before. Under an ecological perspective, this temporal gap between plant phenotype expression (i.e. onset of fruit ripening) and its best predictive trigger (i.e. spring temperatures) gives rise to interesting questions. We realize most of our studied species are fruit trees and thus, a general discussion about ecological consequences of their fruiting phenology would be purely speculative. However, a few species of our dataset, the olive, the chestnut *Castanea sativa* and the walnut *Juglans regia*, play an important ecological role, at least in some areas of the Mediterranean region. Olive groves have replaced original Mediterranean shrublands in large areas of the Mediterranean basin. As a consequence, olive groves have become the main habitat for large numbers of passage and wintering birds (especially genus *Sylvia*, *Turdus*, *Sturnus* and *Erithacus*; Rey, 1993). All of these bird species are frugivorous and exploit the abundance of olives during the autumn to obtain essential fat reserves to continue their migration or to survive during the winter (Soler *et al.*, 1988; González-Solís & Ruiz, 1990; Blanco *et al.*, 1994). As any trophic interaction, the interaction between birds and olives should rely on a good spatio-temporal matching of both participants. If the best environmental cue to predict olive fruiting season is climate during the spring (e.g. the correlation between March–May temperature and olive ripening date is $r = 0.684$), how can birds predict the optimal passage and/or arrival date to the Spanish olive groves? This is a key question due to the observed changes in olive phenology. The onset of ripening and harvesting dates has advanced 19 days and the spatial variability has reduced 9 days during the last three decades in response to climate change (Gordo & Sanz, 2009). We predict further advance and compression of fruiting dates as a consequence of expected warming in Spain during the current century (de Castro *et al.*, 2005). If frugivorous birds arrive at the same date than three decades ago, they will find no olives yet in many areas. Furthermore, the increased synchronicity would reduce chances to use spatial heterogeneity of olives harvesting to find other suitable places. Gordo & Sanz (2005) showed that two wintering species advanced their arrival date in a locality from northeastern Spain, but other studies have demonstrated no changes (e.g. Mezquida *et al.*, 2007) or even delays (e.g. Jenni & Kéry, 2003) in passage dates of short-distance migrants. Therefore, there is a potential for a serious mismatching between birds and one of the most important trophic resources for migrating and wintering bird populations, if birds are unable to use a reliable cue of fruiting phenology, such as spring climate, to adjust properly their arrival schedule to Spain.

The chestnut and the walnut are an important part of the diet of many forest mammals. During autumn and winter, hard mast constitute a 87% of the diet in wild boars *Sus scrofa* from northern Spain (Irizar *et al.*, 2004) and a 55% in the brown bear *Ursus arctos* (Clevenger *et al.*, 1992). These species are sedentary and thus, the spatio-temporal matching between both trophic levels is ensured. However, the onset of the chestnuts and walnuts season may vary more than 20 days in response to cold or warm springs. In fact, fruiting dates have advanced more than 1 week in both species during the last decades (Gordo & Sanz, 2009). Therefore, it would be important to know the ecological consequences of these interannual variations in the timing of availability of trophic resources for forest animals. Does fruiting phenology have an effect on winter survival, health condition or future fitness of mast-eater animals? If so, wildlife managers could use spring weather to predict the onset of chestnuts and walnuts availability and apply the necessary measures, for instance, to improve conservation of critically endangered species, such as the Iberian brown bear.

Climate sensitivity and temporal trends

Leaf unfolding, flowering and growing season were the phenological events most strongly influenced by climate, while leaf falling was the least influenced (see Table 1 and Fig. 3). Fruiting was intermediate. This mirrors the observed order in magnitude of temporal responses of plant phenology (Gordo & Sanz, 2009), which is also the chronological order of phenological events within the year (excluding the growing season). Therefore, phenological events at the beginning of the annual plant cycle (spring) are more affected by weather than events at the end of the cycle (autumn) and hence, events early in the year undergo greater temporal responses given a similar change in climate. Moreover, differences in the sensitivity among events are enhanced by differences in climate trends among seasons (see Appendix S2). Spring is becoming markedly warmer, while autumn is not. Thus, spring events are prone to advance and reduce their ranges of onset dates, while autumn events show little change due to their lesser sensitivity and the smaller changes of autumnal climate.

Gordo & Sanz (2009) found that event identity was important *per se* to account for differences in the temporal trends of plant phenology in Spain. However, they failed to find a convincing origin for intraevent variability, because the date of occurrence (μ) or the plasticity (σ) of each species explained only partially the observed variability in temporal trends within a few events. Here, we have solved this question because we have demonstrated that differences in climate sensitivity are the main origin for differences in temporal responses among species in each event (see Figs 6 and 7). Therefore, events and species respond differently to climate and this is the primary origin for the observable variability in their temporal trends in recent decades. This result leads us necessarily to the next question: why do events/species differ in their sensitivity to climate? Miller-Rushing *et al.* (2007) found that responses to temperature were closely related to the flowering date in cherry trees (genus *Cerasus*). However, we found that phenophase date (μ) and variability (σ) were not related in most cases to the explanatory capacity of climate (see Figs 4 and 5). Biological characteristics of species may explain the variety of responsiveness to climate (Fitter *et al.*, 1995; Fitter & Fitter, 2002; Peñuelas *et al.*, 2002; Miller-Rushing *et al.*, 2008b). Pollination mechanism explained up to 60% of variability in climate modelling ability of flowering dates in the studied species. Phenology of insect-pollinated species was better fitted to climate than that for wind-pollinated species, but interestingly sensitivity to climate (i.e. slope) did not differ significantly between both groups. The average slope with temperature during Q_0 in insect-pollinated species was -6.87 days °C^{-1}, while in wind-pollinated species was -6.73 days °C^{-1} (t-test: $t_{22} = 0.295$, $P = 0.771$). Therefore, climate has the same effect in both groups, but insect-pollinated species respond more accurately to climatic fluctuations. This suggests that insect-dependent species have evolved to respond strongly to climate fluctuations, as insects do (Roy & Sparks, 2000; Stefanescu *et al.*, 2003; Gordo & Sanz, 2006b), and to maintain a perfect match with their insect pollinators. Nevertheless, insect-pollinated species are advancing their flowering dates more dramatically than some insects, such as the honey bee *Apis mellifera* (Gordo & Sanz, 2006b, 2009). The honey bee advances its appearance by only -6.06 days °C^{-1} during the February–April quarter (Q_0 for most plant species). This small but significant difference (t-test: $t_{13} = -2.849$, $P = 0.015$) could lead to a growing mismatching between both trophic levels under future climate scenarios. Furthermore, plant responses to temperature were perfectly linear through all observed temperatures range (see Fig. 2). Therefore, if plant phenotypic plasticity does not diminish under extreme values of temperature (Sparks *et al.*, 2000; Menzel *et al.*, 2005a), there will potentially be a further increase in mismatching between insects and plants (Hegland *et al.*, 2009). In addition, spatial variability of flowering dates diminishes on average by -1.39 days °C^{-1} in insect-pollinated species. A reduction in the range of flowering dates may further impair mismatching processes (Post *et al.*, 2008b; Gordo & Sanz, 2009).

In our previous study (Gordo & Sanz, 2009), we found that wind-pollinated species advanced more their flowering dates than insect-pollinated ones. This temporal response cannot be due to a greater sensitivity to climate. Furthermore, flowering dates were quite similar in both groups (insect-pollinated April 10, wind-pollinated April 17, see Table 1) and thus, they were subjected to the same rate of climate change during the last decades. This result is probably reflecting that other factors acting also in a long-term temporal scale are affecting plant phenology. Miller-Rushing *et al.* (2008a) demonstrated that an increase of population size may advance detected first flowering dates. However, our phenological measures were done at population level (see 'Materials and methods') in common species and thus, this artefact does not seem probable in our data. Similarly, sampling methodology has been kept without changes during 60 years and there is no reason to expect an excess of monitoring effort in flowering dates of wind-pollinated species in relation to insect-pollinated ones (Miller-Rushing *et al.*, 2008a). The latter hypothesis is supported by the absence of significant differences in temporal trends for leaf unfolding dates between both groups of species (wind-pollinated -0.517 days yr^{-1}; insect-pollinated -0.476 days yr^{-1}; t-test: $t_{20} = 0.480$, $P = 0.636$). Leaf unfolding occurs at similar dates than flowering and consequently leaf unfolding monitoring could suffer also from this hypothesized sampling artefact. Therefore, differences in flowering phenology trends are real and not an artefact, although there is no climatic origin for them. An important feature of the studied insect-pollinated species is that half of them are fruit trees. Interestingly, their temporal trends and temperature sensitivity in Q_0 were significantly smaller than for the rest of insect-pollinated species (fruit trees:

-0.386 days yr^{-1}, -6.14 days °C^{-1}; nonfruit trees: -0.709 days yr^{-1}, -7.72 days °C^{-1}; *t*-tests for both variables $P < 0.001$). In conclusion, insect-pollinated species advance their flowering dates less than wind-pollinated species due to fruit trees, which have smaller sensitivity to temperature and phenological trends than the rest of studied species. This result agrees with the hypothesis that plant species or phenophases under human influence ('false' phases) are less responsive to climate change (Menzel *et al.*, 2006b). In spite of the fact that fruit trees are less plastic than wild species, fruit trees have also altered their phenology in response to climate change and thus they can be used as reliable bioindicators (Chmielewski *et al.*, 2004; Estrella *et al.*, 2007). Moreover, information for species with an agricultural interest may be valuable for crop managing in the future.

Why are some phenological responses disproportionate in the Mediterranean?

The comprehensive analysis of climate effects carried out in the present study provides us the essential tool to understand why flowering and leaf unfolding (spring phenophases) in Spain are showing some of the largest phenological responses to climate change reported in plants (Menzel *et al.*, 2006a; Gordo & Sanz, 2009). Gordo & Sanz (2009) suggested that a higher sensitivity to temperature in southern populations could be the origin for these observed disproportionate advances. Now, we can check this hypothesis by comparing our results to some others reported previously. For instance, flowering dates advanced overall by -6.47 days °C^{-1} in the 27 study species (see Fig. 2). In the case of leaf unfolding, the rate is even greater at -6.99 days °C^{-1}. The latter value is similar to the estimates for the beginning of the growing season in Europe using data from the International Phenological Gardens (-6 days °C^{-1}, Menzel & Fabian, 1999; -6.7 days °C^{-1}, Chmielewski & Rötzer, 2001), which did not include any station in southwestern Europe (Menzel *et al.*, 2005b). However, leaf unfolding sensitivity is notably greater than the estimated value for Germany (-4.7 days °C^{-1}; Chmielewski *et al.*, 2004; see also Estrella *et al.*, 2007). Differences with a country-wide assessment of Germany can be statistically tested for by paired *t*-tests using the published results by Menzel (2003) in seven phenophases that were also studied in the current work. The explanatory capacity of temperature was slightly larger in Germany ($R^2 = 0.66$) than in Spain ($R^2 = 0.62$), but the difference was not significant (paired *t*-test: $t_7 = 1.323$, $P = 0.234$). However, sensitivity estimates were markedly larger in Spanish populations (8.80 days °C^{-1}) than in German populations (3.68 days °C^{-1}; paired *t*-test: $t_7 = 6.358$, $P < 0.001$). In summary, a comparison of sensitivity coefficients to temperature reported in literature for the same species in other parts of Europe suggests a higher sensitivity of populations in the Mediterranean. This fact would agree with the higher sensitivity found in plant populations from warmer regions (Menzel *et al.*, 2005a; Lu *et al.*, 2006; Tryjanowski *et al.*, 2006; Doi & Takahashi, 2008), which could be a result of the lower probability of late frost damage (Askeyev *et al.*, 2005).

A combination of high sensitivity and sharp increases in temperature during a key quarter, as in February–April (see Appendix S2), promoted very strong responses in plant phenology in the Mediterranean (Gordo & Sanz, 2009). Nevertheless, the advance of flowering and leaf unfolding dates since the 1970s is greater than expected. Spring temperature showed similar rates of shift in prior decades. For instance, temperatures in the February–April quarter decreased during the period 1943–1972 at a similar rate to its increase during 1973–2003 (-0.048 vs. $+0.053$ °C yr^{-1}). Moreover, the average temperature did not differ between periods (1943–1972: 9.31 °C; 1973–2003: 9.26 °C; $t_{59} = 0.240$, $P = 0.811$). However, flowering phenology delayed between 1943 and 1972 at a rate of $+0.292$ days yr^{-1}, while during recent decades it advanced at a rate of -0.592 days yr^{-1}. Therefore, while temperatures had a similar magnitude and changed at a similar rate during both periods, plants are responding at almost double this rate during recent decades. Plant phenology may respond more to warming than to cooling because below a certain threshold of low temperatures plant phenology becomes unresponsive (Sparks *et al.*, 2000; Menzel *et al.*, 2005a; Tryjanowski *et al.*, 2006). However, this hypothesis is not supported by our data. Plant responses coped perfectly with the entire range of temperatures experienced during the 60 years of study without a decrease in their plastic response both in spring and autumn events (see Fig. 2).

The previous autumn is another influential period for spring phenology (see Fig. 1). Interestingly, since the mid-1970s spring and autumn temperatures have shown opposite temporal trends (see Fig. 9; Appendix S2). During the first decades of our study period, spring events delayed their dates due to the cooling of spring temperatures. However, cooling of autumn temperatures partially counterbalanced the effect of spring temperatures and consequently spring phenology delayed less than expected. Since the mid-1970s, increasing spring temperature is accompanied by a marked decrease in autumn temperatures (see Fig. 9). Currently, spring phenology is doubly triggered towards early dates. In the rest of the phenological events, there were no disproportionate temporal shifts, as in flowering or

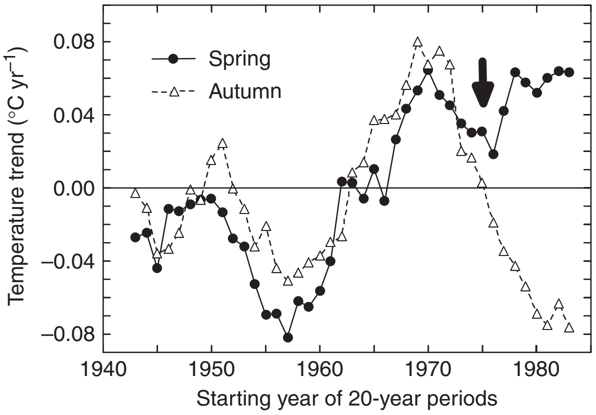


Fig. 9 Evolution of temporal trends of spring and autumn temperatures. Spring temperature is represented by the February–April quarter, while autumn temperature by September–November. The slope of temperatures during each quarter has been calculated in a moving window of 20 years between 1943 and 1983. The arrow shows the moment when trends in temperatures of both seasons became decoupled.

leaf unfolding, because there is no such synergy between climate trends of influential seasons.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Explanatory capacity of models for the three types of temperature.
Figure S2. Delayed effect of climate on fruiting phenology.
Table S1. Results of the repeated-measures ANOVA to test for differences in the explanatory capacity of temperature, precipitation and NAO models.
Table S2. Results of the repeated-measures ANOVA to test for differences in the explanatory capacity of mean, maximum and minimum temperature models.
Table S3. Results of the relationship between explanatory capacity of complete climatic models and date nested within events.
Table S4. Results of the repeated-measures ANOVA to test for differences in the pure explanatory capacity of climatic variables.
Appendix S1. Exploration of collinearity between climatic variables.
Appendix S2. Temporal trends of climate in Spain 1943–2003.
Appendix S3. Supplementary figures (S1–S2) and tables (S1–S4).

APPENDIX S1

In this electronic appendix, we explored the degree of collinearity between the employed predictor climatic variables. We have estimated the collinearity by Pearson's correlation coefficients between quarters for the period 1943-2003 (n = 61). Collinearity was assessed both between and within types of climatic variables. In the case of collinearity between climatic variables, we aimed to know to what extent the three types of climatic variables employed in our study (temperature, precipitation and NAO) are related among them. As we have shown in the results section, the explanatory capacity of all variables (especially precipitation and NAO) is overestimated, since pure values of adjusted R^2 are notably lower than adjusted R^2 values obtained in each climatic model both for average dates and standard deviation time-series. Phenology was better related to temperature than to any other climatic variable. Therefore, precipitation and NAO showed also good fitted models to phenology because they are indeed related to temperature through weather conditions. Diagonal of correlation matrices is highlighted in grey to improve visualization of results. Significant correlations at $P = 0.05$ are in bold. Acronyms for quarters: J=January, F=February, M=March, etc. Value -1 indicates previous year.

CORRELATIONS BETWEEN TEMPERATURE AND PRECIPITATION

	Temperature																					
Precipitation	JFM-1	FMA-1	MAM-1	AMJ-1	MJJ-1	JJA-1	JAS-1	ASO-1	SON-1	OND-1	NDJ	DJF	JFM	FMA	MAM	AMJ	MJJ	JJA	JAS	ASO	SON	OND
JFM-1	-0.079	**-0.275**	-0.233	-0.066	0.026	-0.087	-0.042	0.020	0.113	**0.254**	0.112	-0.016	-0.098	-0.014	0.105	-0.069	-0.209	**-0.256**	0.154	0.113	0.184	0.171
FMA-1	-0.229	**-0.424**	**-0.301**	-0.087	0.132	0.084	0.022	0.007	0.110	**0.316**	0.184	0.031	-0.084	0.034	0.206	0.038	-0.194	**-0.383**	-0.023	0.002	0.009	-0.008
MAM-1	-0.170	**-0.348**	**-0.464**	**-0.392**	-0.179	0.148	**0.267**	**0.263**	0.209	**0.303**	0.104	-0.056	-0.235	-0.160	0.060	0.062	-0.160	**-0.254**	-0.118	-0.002	0.063	0.021
AMJ-1	-0.051	-0.247	**-0.458**	**-0.574**	**-0.376**	0.000	**0.300**	**0.281**	0.218	**0.261**	0.119	-0.021	-0.184	-0.150	0.070	0.089	-0.072	-0.108	0.000	0.030	0.110	-0.007
MJJ-1	-0.071	-0.104	**-0.407**	**-0.599**	**-0.591**	-0.246	0.221	0.234	0.176	0.161	0.095	0.002	-0.087	-0.130	-0.034	-0.092	-0.140	-0.034	0.097	0.196	**0.266**	0.109
JJA-1	-0.091	-0.051	-0.219	**-0.475**	**-0.536**	**-0.447**	0.123	0.096	0.083	-0.028	-0.015	-0.079	-0.093	-0.126	-0.094	-0.126	-0.135	0.045	0.127	0.157	0.152	0.014
JAS-1	-0.122	-0.058	-0.184	-0.138	-0.246	**-0.266**	**-0.296**	**-0.260**	-0.204	-0.197	-0.133	-0.101	0.053	0.189	0.164	-0.032	-0.168	-0.097	0.061	0.109	0.090	-0.091
ASO-1	-0.109	-0.088	-0.088	-0.032	-0.137	-0.204	**-0.331**	**-0.456**	**-0.318**	-0.161	0.015	0.096	0.195	**0.359**	0.198	-0.025	-0.243	-0.196	0.101	0.079	0.092	-0.064
SON-1	-0.103	-0.157	-0.200	-0.063	-0.084	-0.037	**-0.342**	**-0.579**	**-0.389**	-0.075	0.195	0.208	0.235	**0.355**	**0.308**	0.078	-0.087	-0.211	0.046	-0.025	0.081	-0.030
OND-1	-0.191	-0.213	-0.240	-0.077	-0.067	0.053	-0.049	**-0.327**	-0.131	0.239	**0.462**	**0.400**	0.213	0.166	0.127	0.021	-0.062	-0.203	-0.056	-0.017	0.081	0.021
NDJ	-0.166	-0.189	**-0.331**	-0.157	-0.134	0.051	-0.042	-0.132	-0.032	**0.331**	**0.476**	**0.418**	0.202	0.026	0.060	0.003	0.015	-0.125	-0.058	0.021	0.084	-0.021
DJF	-0.068	-0.078	-0.129	-0.050	-0.074	-0.041	0.082	0.112	0.212	**0.449**	**0.464**	**0.377**	0.074	-0.139	-0.100	0.032	0.062	-0.123	-0.170	-0.008	0.079	0.112
JFM	0.059	0.057	0.065	-0.003	-0.029	-0.117	0.147	**0.252**	**0.289**	**0.350**	**0.269**	0.181	-0.086	**-0.256**	-0.212	-0.046	0.010	-0.079	-0.026	0.033	0.107	0.240
FMA	0.035	0.081	0.151	-0.005	-0.064	-0.123	**0.272**	**0.330**	**0.288**	0.240	0.122	0.002	-0.230	**-0.418**	**-0.296**	-0.081	0.120	0.085	0.029	0.019	0.112	**0.312**
MAM	0.038	0.188	0.191	-0.014	-0.130	-0.160	**0.306**	**0.309**	**0.267**	0.185	0.085	0.017	-0.158	**-0.358**	**-0.490**	**-0.414**	-0.189	0.129	**0.255**	**0.276**	0.232	**0.328**
AMJ	-0.057	0.154	0.213	0.014	-0.167	-0.227	0.199	0.144	0.142	0.060	0.086	0.052	-0.035	-0.247	**-0.478**	**-0.591**	**-0.394**	-0.025	**0.282**	**0.308**	**0.253**	**0.297**
MJJ	-0.096	0.131	0.244	0.192	-0.016	-0.239	-0.019	-0.025	0.101	0.004	-0.001	-0.028	-0.054	-0.099	**-0.420**	**-0.609**	**-0.606**	**-0.263**	0.207	**0.267**	0.215	0.199
JJA	-0.129	0.064	0.237	0.241	-0.009	**-0.263**	-0.145	-0.061	0.080	-0.013	-0.059	-0.103	-0.065	-0.033	-0.226	**-0.474**	**-0.558**	**-0.450**	0.109	0.160	0.146	0.037
JAS	0.082	0.055	0.027	0.049	-0.089	-0.239	-0.089	0.044	0.231	0.129	0.003	-0.088	-0.110	-0.040	-0.184	-0.143	**-0.280**	**-0.276**	**-0.290**	-0.209	-0.160	-0.162
ASO	0.153	0.031	-0.084	-0.066	-0.173	**-0.297**	-0.149	0.034	**0.273**	0.197	0.096	-0.077	-0.102	-0.089	-0.099	-0.044	-0.149	-0.213	**-0.336**	**-0.430**	**-0.291**	-0.139
SON	0.133	0.054	-0.056	-0.063	-0.075	-0.225	-0.100	-0.008	0.177	0.059	0.022	-0.089	-0.107	-0.164	-0.198	-0.057	-0.066	-0.029	**-0.342**	**-0.587**	**-0.398**	-0.089
OND	-0.018	-0.046	-0.054	0.005	0.093	-0.085	-0.214	-0.138	-0.107	-0.202	-0.195	-0.197	-0.194	-0.222	-0.243	-0.075	-0.050	0.058	-0.051	**-0.339**	-0.142	0.224

Temperature and precipitation values for the same quarter were significantly correlated in almost all cases (see diagonal). Warm years were related to dry conditions, excepting in winter months. For winter season, moist years are related to milder temperatures. The relationship between temperature and precipitation was especially strong during the spring (March-June). There was also a connection between spring and autumn conditions. Warmer autumns (August-November) were related to moister winter-springs (January-May) in the next year and vice versa. Nevertheless, *r* values for these cases are low (about 0.3) and thus these associations are significant but weak.

CORRELATIONS BETWEEN TEMPERATURE AND NAO

		Temperature																					
		JFM-1	FMA-1	MAM-1	AMJ-1	MJJ-1	JJA-1	JAS-1	ASO-1	SON-1	OND-1	NDJ	DJF	JFM	FMA	MAM	AMJ	MJJ	JJA	JAS	ASO	SON	OND
NAO	JFM-1	**0.407**	**0.529**	0.204	0.015	-0.132	0.055	-0.052	-0.076	-0.202	-0.198	-0.042	0.116	0.163	0.073	-0.076	-0.040	-0.089	-0.012	-0.131	0.015	-0.056	-0.050
	FMA-1	**0.397**	**0.685**	0.237	0.027	**-0.318**	-0.019	0.007	0.023	-0.220	**-0.362**	-0.159	0.018	0.118	0.046	-0.066	-0.004	-0.034	0.154	0.041	0.108	0.018	0.046
	MAM-1	0.183	**0.487**	**0.522**	**0.281**	-0.100	-0.203	-0.106	-0.072	-0.128	-0.247	-0.044	0.123	0.212	0.170	0.013	0.053	-0.076	0.058	0.041	0.158	0.023	0.023
	AMJ-1	0.006	**0.327**	**0.450**	**0.454**	0.004	-0.210	-0.209	-0.122	-0.166	**-0.298**	-0.161	-0.013	0.094	0.086	0.001	0.055	-0.042	0.001	0.028	0.148	0.039	0.031
	MJJ-1	0.126	**0.286**	**0.503**	**0.491**	0.241	-0.042	-0.196	-0.101	-0.088	-0.143	-0.093	-0.004	0.046	0.069	-0.014	0.082	-0.099	-0.088	-0.050	0.082	-0.018	-0.021
	JJA-1	0.177	**0.271**	**0.282**	**0.386**	0.115	0.141	-0.106	-0.020	-0.169	-0.177	-0.109	0.037	0.080	0.085	0.017	0.029	-0.088	-0.127	-0.030	0.055	0.044	0.043
	JAS-1	0.158	0.223	0.171	0.119	-0.030	0.101	**0.282**	**0.380**	0.180	-0.026	-0.024	-0.040	-0.063	-0.101	-0.010	0.051	0.078	0.041	0.081	0.134	0.127	0.227
	ASO-1	0.072	0.141	0.047	-0.075	-0.231	-0.094	0.213	**0.464**	0.173	-0.151	**-0.252**	-0.196	-0.175	-0.163	0.060	0.102	0.173	0.020	0.049	0.106	0.155	0.245
	SON-1	0.102	0.176	0.064	-0.165	-0.244	-0.134	**0.255**	**0.481**	**0.296**	-0.100	-0.241	-0.196	-0.201	-0.207	-0.142	-0.042	0.069	0.105	0.184	0.176	0.086	0.151
	OND-1	0.200	0.194	0.031	**-0.258**	**-0.281**	-0.122	0.084	**0.252**	0.110	-0.133	**-0.261**	-0.159	-0.105	-0.060	-0.108	-0.084	0.027	0.067	0.133	0.036	0.011	0.060
	NDJ	0.205	0.177	0.068	-0.207	-0.182	0.010	0.150	0.155	0.079	-0.116	-0.105	-0.082	-0.042	-0.042	-0.143	-0.089	-0.017	0.063	0.101	-0.034	-0.059	0.058
	DJF	0.133	0.096	0.038	-0.177	-0.076	-0.020	-0.024	-0.043	-0.010	-0.074	-0.086	0.077	0.194	**0.305**	0.021	-0.045	-0.092	0.071	0.043	-0.034	-0.130	-0.079
	JFM	-0.002	0.050	0.043	-0.068	-0.037	-0.068	-0.123	-0.214	-0.114	-0.109	-0.007	0.211	**0.391**	**0.512**	0.196	0.001	-0.140	0.040	-0.052	-0.075	-0.219	-0.201
	FMA	-0.034	0.006	0.082	0.069	0.026	-0.136	-0.247	**-0.282**	-0.045	0.076	0.043	**0.285**	**0.393**	**0.690**	0.233	0.019	**-0.320**	-0.028	0.007	0.017	-0.230	**-0.364**
	MAM	-0.152	-0.074	0.070	0.107	-0.031	-0.162	-0.234	**-0.254**	-0.115	0.010	-0.010	0.114	0.202	**0.516**	**0.527**	**0.281**	-0.090	-0.207	-0.109	-0.096	-0.135	**-0.264**
	AMJ	-0.024	-0.055	0.015	0.015	-0.021	-0.080	-0.085	-0.062	0.001	0.077	-0.027	0.057	0.024	**0.340**	**0.447**	**0.438**	0.017	-0.220	-0.209	-0.159	-0.182	**-0.325**
	MJJ	0.094	0.020	-0.045	-0.142	-0.103	-0.015	0.059	0.013	-0.056	0.025	0.059	0.143	0.137	**0.287**	**0.494**	**0.468**	0.247	-0.060	-0.195	-0.142	-0.111	-0.180
	JJA	**0.282**	0.169	0.024	-0.122	0.025	0.129	0.162	0.014	-0.054	0.087	0.203	**0.286**	0.176	0.246	**0.266**	**0.339**	0.123	0.096	-0.106	-0.088	-0.203	-0.230
	JAS	0.052	0.148	**0.275**	0.109	0.210	0.138	0.160	0.070	0.061	0.139	0.140	0.233	0.152	0.204	0.166	0.100	-0.023	0.074	**0.274**	**0.329**	0.147	-0.064
	ASO	-0.109	0.066	0.204	0.148	0.212	0.073	0.063	0.024	0.054	0.081	-0.002	0.105	0.080	0.147	0.050	-0.078	-0.225	-0.100	0.210	**0.435**	0.162	-0.165
	SON	-0.177	0.003	0.085	0.041	0.014	-0.010	0.056	0.056	0.091	0.099	-0.008	0.072	0.103	0.187	0.064	-0.159	-0.247	-0.123	**0.256**	**0.488**	**0.307**	-0.080
	OND	-0.062	-0.034	-0.093	-0.132	-0.231	-0.106	-0.051	-0.101	0.002	0.082	0.086	0.115	0.205	0.209	0.032	-0.251	**-0.282**	-0.112	0.085	**0.262**	0.122	-0.115

Collinearity between temperature and NAO in the same quarter was especially strong during spring. Temperatures during a key quarter for plant phenology (FMA) were driven by NAO index during a long period (from January to May). In all cases, higher values of NAO are related to warm temperatures during the same quarter. Temperatures patterns during the autumn (OND) were also related to NAO index during the previous spring (MAM), which stresses again a weak but existent connection between spring and autumn weather conditions. In this case, higher values of NAO during the spring are related to cooler autumns.

CORRELATIONS BETWEEN PRECIPITATION AND NAO

		NAO																					
		JFM-1	FMA-1	MAM-1	AMJ-1	MJJ-1	JJA-1	JAS-1	ASO-1	SON-1	OND-1	NDJ	DJF	JFM	FMA	MAM	AMJ	MJJ	JJA	JAS	ASO	SON	OND
Precipitation	JFM-1	**-0.752**	**-0.457**	0.034	**0.274**	**0.274**	-0.089	-0.032	-0.198	0.063	0.018	-0.041	-0.104	-0.042	-0.003	0.150	-0.005	0.126	-0.027	0.088	0.056	0.102	-0.025
	FMA-1	**-0.577**	**-0.614**	-0.114	0.128	**0.296**	-0.027	0.018	-0.103	0.111	0.126	0.000	-0.120	-0.111	0.127	**0.425**	**0.297**	0.231	0.037	0.106	0.061	0.149	-0.007
	MAM-1	-0.236	**-0.415**	**-0.474**	-0.112	0.151	**0.263**	0.135	0.065	-0.022	0.082	-0.013	-0.010	-0.061	0.182	**0.404**	**0.317**	0.094	0.042	-0.045	-0.079	-0.054	-0.029
	AMJ-1	0.112	-0.174	**-0.480**	**-0.483**	-0.112	0.195	**0.280**	0.160	-0.007	0.003	0.048	0.054	0.019	0.125	**0.257**	0.223	0.181	0.148	-0.011	-0.059	-0.054	0.055
	MJJ-1	0.061	0.049	**-0.362**	**-0.384**	**-0.269**	0.073	0.207	0.066	-0.066	-0.109	0.037	0.052	0.106	-0.012	-0.012	-0.082	0.062	0.205	0.063	-0.004	-0.034	0.096
	JJA-1	0.017	0.065	-0.010	-0.216	-0.232	-0.189	0.106	-0.001	-0.037	-0.172	0.017	0.037	0.134	-0.021	-0.113	-0.112	0.096	**0.261**	0.171	0.080	0.086	0.169
	JAS-1	-0.030	0.161	**0.273**	0.249	0.055	-0.095	**-0.289**	**-0.275**	-0.209	0.000	0.020	0.150	0.191	0.243	0.122	0.045	-0.180	-0.210	-0.166	-0.122	0.005	-0.033
	ASO-1	-0.049	0.146	**0.346**	**0.386**	0.173	0.014	**-0.265**	**-0.478**	**-0.306**	0.060	0.247	**0.284**	0.249	**0.303**	0.176	0.094	-0.131	-0.107	-0.113	-0.050	-0.059	-0.154
	SON-1	0.029	0.206	0.207	0.245	0.112	0.086	-0.181	**-0.281**	**-0.385**	-0.097	0.023	0.161	0.116	0.156	0.124	0.091	-0.061	-0.031	-0.077	-0.017	-0.173	**-0.287**
	OND-1	0.114	**0.254**	0.117	0.076	-0.012	0.008	-0.116	-0.092	**-0.278**	**-0.414**	**-0.359**	-0.182	0.018	0.079	0.024	-0.049	0.022	0.164	0.114	0.050	-0.122	-0.099
	NDJ	0.013	0.014	-0.137	-0.122	-0.120	-0.080	-0.089	0.116	-0.114	**-0.460**	**-0.715**	**-0.546**	**-0.318**	-0.090	-0.007	0.013	0.128	0.095	0.080	-0.067	-0.106	-0.085
	DJF	-0.050	-0.084	-0.123	-0.088	-0.061	-0.047	-0.050	0.149	0.079	**-0.320**	**-0.657**	**-0.745**	**-0.509**	-0.216	0.108	0.088	0.177	-0.070	0.031	-0.177	0.047	0.044
	JFM	-0.040	-0.162	-0.230	-0.107	-0.017	0.099	0.096	**0.293**	0.144	-0.134	**-0.482**	**-0.710**	**-0.763**	**-0.480**	0.032	**0.268**	**0.275**	-0.098	-0.033	-0.206	0.052	0.005
	FMA	0.063	0.048	-0.100	-0.033	-0.023	0.142	0.221	**0.407**	0.188	-0.102	-0.201	**-0.458**	**-0.565**	**-0.601**	-0.104	0.142	**0.307**	-0.015	0.017	-0.108	0.124	0.125
	MAM	0.070	0.151	-0.057	0.019	-0.054	0.027	0.159	0.231	0.062	-0.194	-0.107	-0.093	-0.217	**-0.389**	**-0.470**	-0.095	0.156	**0.289**	0.137	0.078	0.003	0.100
	AMJ	-0.134	0.096	0.093	0.198	-0.008	-0.131	-0.081	-0.103	-0.051	-0.191	-0.026	0.082	0.132	-0.146	**-0.475**	**-0.470**	-0.112	0.218	**0.283**	0.175	0.016	0.024
	MJJ	-0.189	-0.073	-0.028	0.142	0.090	-0.042	-0.135	-0.162	0.003	-0.057	-0.072	0.000	0.038	0.027	**-0.370**	**-0.384**	**-0.279**	0.077	0.209	0.095	-0.057	-0.080
	JJA	-0.245	**-0.255**	-0.140	0.080	0.075	-0.001	-0.087	-0.014	0.112	0.054	-0.036	-0.056	0.022	0.082	-0.007	-0.205	-0.233	-0.174	0.108	0.018	-0.020	-0.148
	JAS	-0.025	-0.165	**-0.307**	-0.192	-0.080	0.084	0.113	0.108	0.037	-0.047	-0.087	-0.085	-0.015	0.193	**0.282**	**0.262**	0.058	-0.082	**-0.290**	**-0.265**	-0.196	0.008
	ASO	0.094	0.004	-0.023	0.015	0.057	0.127	0.000	0.010	0.004	0.038	-0.003	-0.090	-0.027	0.166	**0.350**	**0.379**	0.183	0.005	**-0.265**	**-0.499**	**-0.315**	0.025
	SON	0.105	-0.046	-0.058	-0.001	0.079	0.047	-0.096	-0.077	-0.036	-0.020	-0.079	-0.052	0.033	0.199	0.204	0.228	0.119	0.064	-0.181	**-0.309**	**-0.401**	-0.131
	OND	0.052	-0.090	-0.096	-0.026	-0.002	-0.141	**-0.278**	-0.192	-0.033	0.048	-0.109	0.011	0.108	0.234	0.112	0.058	-0.007	-0.016	-0.118	-0.124	**-0.303**	**-0.438**

Excepting the period JJA, precipitation and NAO patterns were negatively and significantly related in all quarters. The higher is the NAO the scarcer the rainfall. In contrast to the two previous correlation matrices, strongest relationships were found during winter season. Some other weak and positive correlations were found again between spring and autumn. For instance, high NAO values at the end of the spring (April-May) were associated with moister ends of summers (August-September).

In the case of collinearity within climatic variables, we aimed to know to what extent climatic patterns of a season are related to climatic patters in another season for the same variable (i.e., is there temporal autocorrelation in climate?). We have shown that climate has delayed effects on plant phenology (see Fig. 1 and S1). Such delayed effects were real, since many delayed climatic variables (i.e., quarters) were included in climatic models together with quarters at the onset date of phenophases (Q_0). Nevertheless, it is important to explore the relationship between climate at Q_0 and climate in previous quarters. Correlation matrices are symmetric and for this reason only a half is shown. Significant correlations at $P = 0.05$ are in bold. Acronyms for quarters: J=January, F=February, M=March, etc. Value -1 indicates previous year.

CORRELATIONS WITHIN TEMPERATURES

	JFM-1	FMA-1	MAM-1	AMJ-1	MJJ-1	JJA-1	JAS-1	ASO-1	SON-1	OND-1	NDJ	DJF	JFM	FMA	MAM	AMJ	MJJ	JJA	JAS	ASO	SON
FMA-1	**0.771**																				
MAM-1	**0.444**	**0.702**																			
AMJ-1	0.219	**0.444**	**0.825**																		
MJJ-1	0.201	0.187	**0.570**	**0.808**																	
JJA-1	0.235	0.152	**0.270**	**0.524**	**0.805**																
JAS-1	0.197	0.180	0.089	0.138	**0.329**	**0.584**															
ASO-1	0.245	**0.309**	0.156	0.097	0.112	**0.298**	**0.784**														
SON-1	0.166	**0.304**	0.149	0.047	0.035	0.089	**0.485**	**0.779**													
OND-1	0.132	**0.275**	0.228	0.086	0.054	-0.012	-0.015	**0.303**	**0.694**												
NDJ	0.209	**0.255**	**0.277**	0.126	0.126	0.032	-0.049	0.072	**0.418**	**0.814**											
DJF	0.200	0.218	0.246	0.063	0.031	-0.062	-0.202	-0.085	0.068	**0.502**	**0.731**										
JFM	**0.265**	0.219	0.250	0.094	0.051	0.000	-0.199	-0.102	-0.095	0.106	**0.309**	**0.759**									
FMA	0.079	0.087	0.223	0.153	0.064	-0.025	**-0.304**	**-0.271**	-0.190	-0.039	0.004	**0.447**	**0.772**								
MAM	0.040	0.068	**0.304**	**0.270**	0.196	0.086	-0.211	-0.177	-0.176	-0.045	-0.011	0.142	**0.460**	**0.709**							
AMJ	0.012	0.051	0.225	0.206	0.196	0.144	-0.128	-0.088	-0.027	0.058	0.071	0.069	0.225	**0.445**	**0.826**						
MJJ	0.108	0.097	0.093	0.008	0.033	0.092	0.018	0.076	0.060	0.089	0.063	0.068	0.200	0.191	**0.581**	**0.818**					
JJA	**0.266**	0.186	0.031	-0.104	-0.093	-0.035	-0.011	0.097	0.159	0.162	0.145	0.130	0.215	0.150	**0.301**	**0.559**	**0.816**				
JAS	0.175	0.118	0.049	-0.075	-0.089	-0.102	-0.040	0.059	0.154	0.124	0.075	0.196	0.183	0.178	0.119	0.179	**0.362**	**0.604**			
ASO	0.170	0.185	0.143	0.069	-0.003	-0.086	-0.068	0.010	0.114	0.100	0.053	0.231	0.250	**0.312**	0.166	0.114	0.131	**0.313**	**0.788**		
SON	0.040	0.098	0.060	0.030	-0.042	0.010	0.034	0.067	0.094	0.030	-0.075	0.064	0.171	**0.302**	0.134	0.025	0.012	0.050	**0.459**	**0.763**	
OND	0.053	0.079	0.003	-0.071	-0.122	-0.036	-0.013	0.019	0.061	0.007	-0.073	-0.050	0.140	**0.275**	0.213	0.066	0.034	-0.037	-0.026	**0.293**	**0.696**

Correlations between Q_0 and Q_{+1} and Q_{+2} were in all cases significant as a result of the shared months between consecutive quarters. This fact is also valid for precipitation and NAO matrices (see below). Temperatures during FMA were related significantly to autumn (September-October) temperatures of the same year. The correlation was weak ($r \sim 0.28$) and positive. Therefore, warmer springs are followed by warmer autumns. This fact is fully in agreement with the close temporal trends showed by spring and autumn temperatures until mid-1970s (see appendix S2). However, temperatures in August-September were negatively related to temperatures in FMA in the next spring. Thus, warmer autumns are followed by cooler springs. Only in a couple of quarters (JFM and MAM), temperatures of consecutive years were related. Nevertheless, we should be cautious with regard to some of these weakly significant correlation values, since some of them could be due by chance as a result of the large number of correlations performed.

CORRELATIONS WITHIN PRECIPITATIONS

	JFM-1	FMA-1	MAM-1	AMJ-1	MJJ-1	JJA-1	JAS-1	ASO-1	SON-1	OND-1	NDJ	DJF	JFM	FMA	MAM	AMJ	MJJ	JJA	JAS	ASO	SON
FMA-1	**0.692**																				
MAM-1	0.227	**0.617**																			
AMJ-1	-0.220	0.142	**0.646**																		
MJJ-1	-0.095	-0.129	**0.354**	**0.743**																	
JJA-1	-0.108	-0.153	-0.083	**0.322**	**0.636**																
JAS-1	-0.011	-0.005	-0.006	-0.165	0.028	**0.360**															
ASO-1	0.088	0.088	-0.068	-0.206	-0.118	0.112	**0.666**														
SON-1	0.088	0.030	-0.074	-0.170	-0.090	0.001	**0.518**	**0.779**													
OND-1	-0.003	-0.120	-0.179	-0.111	0.010	0.130	**0.290**	**0.418**	**0.703**												
NDJ	0.007	-0.039	-0.048	-0.038	-0.003	0.029	0.124	-0.070	**0.275**	**0.730**											
DJF	0.022	0.086	0.074	0.069	0.022	-0.031	-0.015	-0.150	-0.026	**0.453**	**0.813**										
JFM	0.025	0.201	0.222	0.217	0.035	-0.111	-0.249	**-0.260**	-0.109	0.116	**0.505**	**0.774**									
FMA	-0.045	-0.008	0.070	0.165	0.091	0.003	**-0.331**	**-0.312**	-0.132	0.032	0.127	**0.375**	**0.706**								
MAM	-0.017	-0.224	-0.170	-0.027	0.078	0.218	-0.217	-0.212	-0.132	0.067	0.057	-0.009	0.231	**0.603**							
AMJ	0.151	-0.246	**-0.298**	**-0.277**	0.041	**0.306**	0.079	0.048	0.017	0.097	-0.018	-0.142	-0.222	0.121	**0.641**						
MJJ	0.190	-0.072	-0.102	-0.150	0.033	**0.272**	0.226	0.123	-0.007	0.076	0.084	0.008	-0.107	-0.118	**0.385**	**0.770**					
JJA	0.192	0.068	0.033	-0.162	-0.098	0.048	0.241	0.067	-0.053	-0.062	-0.008	0.005	-0.112	-0.165	-0.086	**0.324**	**0.651**				
JAS	0.037	0.066	0.228	0.104	-0.038	-0.148	-0.091	-0.228	**-0.329**	-0.155	-0.027	0.056	-0.010	-0.023	-0.022	-0.178	0.044	**0.358**			
ASO	-0.065	0.135	**0.271**	0.082	-0.077	-0.123	0.087	-0.010	-0.160	-0.036	0.019	0.183	0.100	0.080	-0.096	-0.232	-0.137	0.086	**0.645**		
SON	-0.070	0.069	0.133	0.042	-0.112	-0.137	-0.040	0.033	-0.047	0.116	0.111	0.212	0.097	0.039	-0.083	-0.182	-0.122	-0.018	**0.507**	**0.793**	
OND	-0.043	0.008	0.059	-0.002	-0.002	-0.054	0.070	0.095	0.030	0.077	0.104	0.154	0.006	-0.101	-0.178	-0.116	-0.029	0.114	**0.291**	**0.448**	**0.715**

The only correlations out of the diagonal that merit further attention are some negative values between spring (FMA) and previous end of summer (ASO-1). Moist ends of summer are related to drier springs in the next year. This is full in agreement with the previous findings with temperatures.

CORRELATIONS WITHIN NAO

	JFM-1	FMA-1	MAM-1	AMJ-1	MJJ-1	JJA-1	JAS-1	ASO-1	SON-1	OND-1	NDJ	DJF	JFM	FMA	MAM	AMJ	MJJ	JJA	JAS	ASO	SON
FMA-1	**0.712**																				
MAM-1	0.163	**0.530**																			
AMJ-1	-0.164	0.240	**0.679**																		
MJJ-1	-0.076	-0.043	**0.385**	**0.597**																	
JJA-1	**0.283**	0.222	-0.089	0.114	**0.449**																
JAS-1	0.098	0.051	-0.191	**-0.302**	0.070	**0.607**															
ASO-1	0.154	0.057	-0.188	**-0.321**	-0.203	**0.272**	**0.691**														
SON-1	-0.066	-0.083	0.102	-0.105	0.095	-0.103	**0.362**	**0.594**													
OND-1	0.015	-0.085	0.150	-0.029	0.165	-0.059	0.006	0.123	**0.609**												
NDJ	0.147	0.137	**0.298**	0.090	0.230	0.150	0.147	-0.101	0.233	**0.685**											
DJF	0.188	0.157	0.196	0.037	0.062	0.056	-0.016	-0.210	-0.130	**0.342**	**0.758**										
JFM	0.109	0.152	0.215	0.064	-0.034	-0.025	-0.088	**-0.266**	-0.227	-0.027	**0.446**	**0.790**									
FMA	0.036	-0.022	0.077	-0.043	-0.071	-0.027	-0.053	-0.213	-0.169	0.010	0.140	**0.487**	**0.702**								
MAM	-0.252	**-0.261**	-0.041	-0.036	-0.073	0.028	0.084	-0.027	-0.168	-0.079	-0.046	-0.033	0.154	**0.530**							
AMJ	-0.043	-0.165	-0.062	-0.126	-0.046	0.054	0.196	0.180	-0.024	0.028	-0.030	-0.056	-0.183	0.227	**0.675**						
MJJ	-0.227	**-0.293**	-0.190	-0.240	**-0.310**	-0.238	0.042	0.082	-0.136	**-0.293**	-0.207	-0.148	-0.082	-0.055	**0.383**	**0.592**					
JJA	0.161	0.052	-0.112	-0.204	-0.165	-0.066	0.179	0.076	-0.076	**-0.282**	-0.039	0.183	**0.268**	0.206	-0.097	0.110	**0.441**				
JAS	-0.016	0.029	0.005	0.019	0.013	0.002	0.162	0.071	0.081	-0.210	-0.112	-0.010	0.099	0.055	-0.191	**-0.301**	0.069	**0.610**			
ASO	-0.031	-0.014	0.041	0.105	0.111	-0.027	0.108	0.087	0.120	-0.035	-0.012	0.114	0.145	0.060	-0.187	**-0.306**	-0.209	**0.284**	**0.682**		
SON	-0.212	-0.108	0.035	0.053	-0.111	-0.083	0.045	0.105	0.105	-0.012	-0.097	-0.181	-0.086	-0.107	0.094	-0.107	0.086	-0.101	**0.364**	**0.604**	
OND	-0.143	-0.052	0.003	-0.085	-0.206	0.018	0.179	0.202	0.037	-0.056	-0.006	-0.115	0.002	-0.090	0.144	-0.022	0.152	-0.044	0.010	0.154	**0.616**

As in previous variables, the number of significant correlations out of the diagonal is low, which means the absence of strong connections between climatic patterns between seasons. NAO values at the end of the spring (AMJ) were negatively related to values at the end of the summer (August-September), as did autumn values (OND) with values in the next beginning of summer (June-July). Both connections do not have relevance with regard to delayed effects on phenology, since involved pairs of quarters do not occur in any phenological event. The weak but significant correlation between ASO-1 and JFM could be pointing toward a certain effect of autumn conditions over the early spring.

APPENDIX S2

In this appendix, temporal trends of the employed climatic variables during the period 1943-2003 are shown. These results may help to understand better long-term phenological responses of plant phenology.

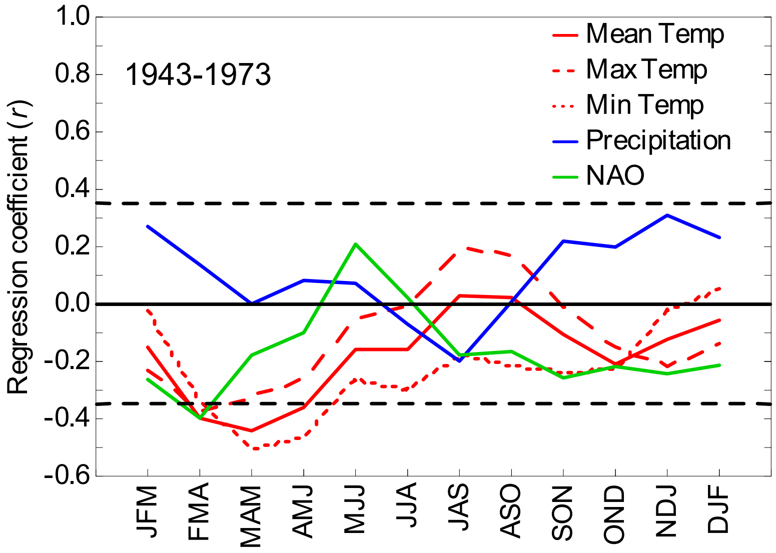
Firstly, we carried out multiple regression models with climate time-series for the period 1943-2003 as dependent and year as explanatory variables. We included the quadratic term of the year, when it was significant, to account for non-linear trends. Results for each quarter and climatic variable are shown in the next table:

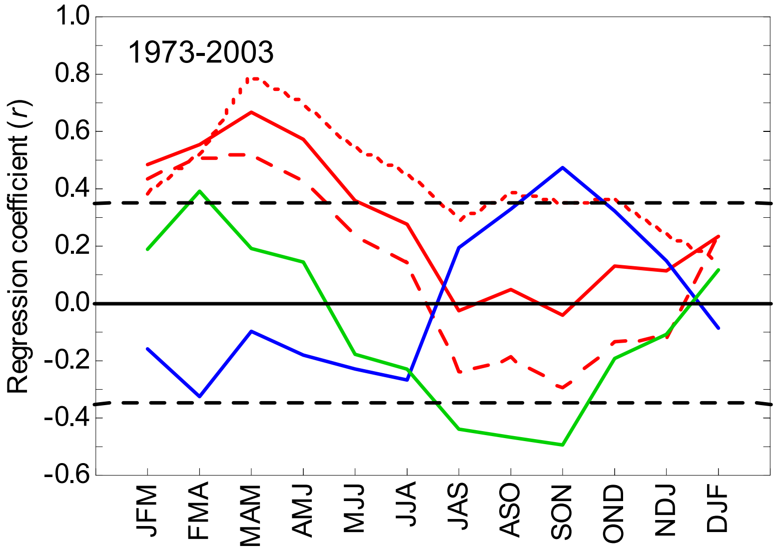
Climatic variables	JFM	FMA	MAM	AMJ	MJJ	JJA	JAS	ASO	SON	OND	NDJ	DJF
Mean Temperature												
year	**0.012**	**-0.073**	**-0.096**	**-0.093**	-0.003	0.002	-0.001	-0.002	-0.007	0.001	0.007	**0.006**
year^2		**0.0012**	**0.0014**	**0.0013**								
Max Temperature												
year	**0.016**	**-0.090**	**-0.097**	**-0.095**	0.000	0.007	0.004	-0.001	-0.010	-0.003	0.004	**0.013**
year^2		**0.0015**	**0.0015**	**0.0014**								
Min Temperature												
year	0.010	**-0.056**	**-0.094**	**-0.091**	**-0.056**	**-0.049**	-0.006	-0.005	-0.004	0.005	0.010	0.013
year^2		**0.0009**	**0.0013**	**0.0013**	**0.0008**	**0.0008**						
Precipitation												
year	-0.170	-0.176	-0.098	0.028	-0.026	-0.062	-0.030	0.082	0.227	0.272	0.645	0.038
NAO												
year	0.015	**-0.062**	-0.007	**-0.016**	-0.004	0.000	-0.009	**-0.015**	**-0.017**	-0.007	0.000	0.008
year^2		**0.0011**										

In bold significant parameters at $P<0.05$. Acronyms for quarter are initial letters for each month (e.g., JFM=January, February, March).

Only 19 out of 60 climatic models showed significant temporal trends during the period 1943-2003. Most of them (12) included also the quadratic term of the year. Therefore, some variables showed curvilinear temporal patterns. All of these quadratic models had a negative sign in the linear term and a positive in the quadratic one. Therefore, climate variables decreased up to mid-1970s and increased since then. In the case of mean and maximum temperatures, winter quarters (DFJ and JFM) showed a warming trend during all the period. Precipitation did not show any significant temporal trend. Quarterly NAO values showed a quadratic model only for FMA, while for the intervals of AMJ, ASO and SON showed a significant negative linear trend.

Non-lineal patterns were comprehensively explored by splitting the study period into two periods. Regression coefficients for all climatic time-series during the period 1943-1973 and the period 1973-2003 are plotted in the next figures (dotted lines indicate thresholds of significance at $P<0.05$):





During the period 1943-1973, both temperature and NAO tended to diminish. Nevertheless, this trend was only significant in a few spring quarters. Patterns were completely opposed during the period 1973-2003. This fact is especially obvious for temperatures. There were positive trends (warming) in most quarters of the year. In almost all cases, minimum temperatures showed steeper increases than mean or maximum temperatures. Such differences reached their greatest range in some summer and autumn quarters. Interestingly, minimum temperatures increased between JAS and NDJ, while maximum temperatures decreased.

It is also important to note that summer and autumn showed a remarkable stability in temperatures trends during both periods. However, winter and especially spring showed a noteworthy cooling during 1943-1973, while a manifest warming during 1973-2003. During the period 1973-2003, the first half of the year (January to June) tended to be drier, while the second half (July to December) moister. However, only temporal trend of rainfall during SON quarter was significant. NAO showed a quite similar pattern to temperature with the highest increase in FMA quarter and the highest decrease around September.

Another important difference between both sub-periods is the strong agreement in quarterly trends among three types of climatic variables since 1973. Pearson's correlation coefficients between quarterly temporal trends of climatic variables are shown in the next table:

	Mean temperature	Maximum temperature	Minimum temperature	Precipitation	NAO
Mean temperature		**0.850**	**0.700**	-0.100	0.130
Maximum temperature	**0.970**		0.230	-0.530	0.330
Minimum temperature	**0.760**	**0.620**		0.490	-0.210
Precipitation	**-0.810**	**-0.870**	-0.450		-0.400
NAO	**0.870**	**0.910**	0.390	**-0.750**	
Annual slope 43-73	-0.017	-0.015	-0.019	3.144	**-0.021**
Annual slope 73-03	**0.025**	0.014	**0.038**	0.973	-0.008

In bold significant values at $P<0.05$

In the upper half of the correlation matrix, there are correlation values for the period 1943-1973. In the inner part, there are values for the period 1973-2003. The slope for the annual values of all variables is also shown for both periods. Temperature, precipitation and NAO are co-fluctuating closely during the last three decades ($|r| > 0.81$), while they did not do in the period 1943-1973 ($|r| < 0.13$).

APPENDIX S3

Table S1: Results of the two repeated-measures ANOVA (one for average dates and another for standard deviation) to test for differences in the explanatory capacity of temperature, precipitation and NAO models. The phenological event was included also as factor. Degrees of freedom (d.f.), sum of squares (SS), mean squares (MS), F-statistic (F), unadjusted p-value (p), adjusted p-value according to Greenhouse-Geisser epsilon (p_{GG}) and according to Huynh-Feldt epsilon (p_{HF}) for each factor are shown.

		Average date						Standard deviation					
	d.f.	SS	MS	F	p	p_{GG}	p_{HF}	SS	MS	F	p	p_{GG}	p_{HF}
between species													
Event	5	4.959	0.992	30.77	<0.001	<0.001	<0.001	0.321	0.064	4.643	<0.001	<0.001	<0.001
Error	112	3.610	0.032					1.546	0.014				
whithin species													
Variable	2	3.989	1.995	254.68	<0.001	<0.001	<0.001	0.171	0.085	11.42	<0.001	<0.001	<0.001
Event x Variable	10	0.443	0.044	5.651	<0.001	<0.001	<0.001	0.109	0.011	1.452	0.159	0.164	0.159
Error	224	1.754	0.008					1.673	0.007				

Average date ANOVA:
Greenhouse-Geisser epsilon $\varepsilon_{\mathrm{GG}} = 0.959$
Huynh-Feldt epsilon $\varepsilon_{\mathrm{HF}} = 1.000$

Standard deviation ANOVA:
Greenhouse-Geisser epsilon $\varepsilon_{\mathrm{GG}} = 0.941$
Huynh-Feldt epsilon $\varepsilon_{\mathrm{HF}} = 0.999$

Fig. S1: Explanatory capacity (adjusted R^2) of complete climatic models for the three types of temperature in all phenological events for average date and standard deviation. Mean values and error bars (95% confidence interval) are shown. Acronyms: LU Leaf Unfolding, FL Flowering, RIP Fruit Ripening, HAR Fruit Harvesting, LF Leaf Falling, GS Growing Season. Legend: mean ○, maximum □, minimum △.

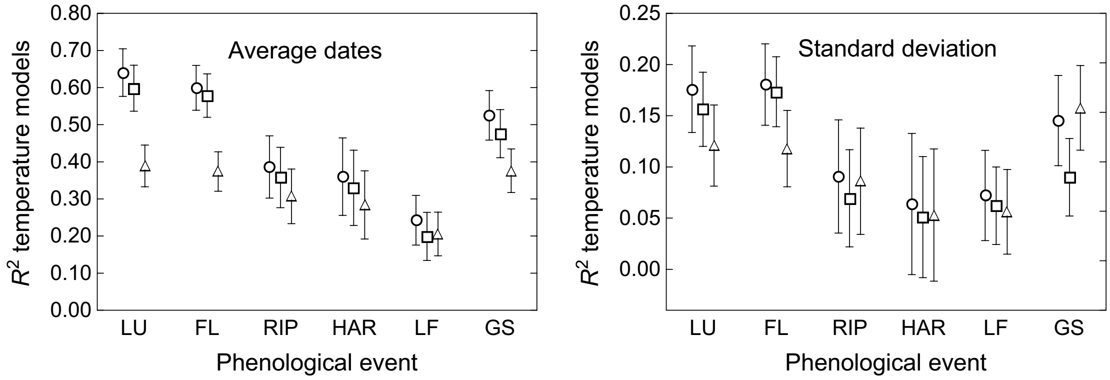


Table S2: Results of the two repeated-measures ANOVA (one for average dates and another for standard deviation) to test for differences in the explanatory capacity of mean, maximum and minimum temperature models and including the phenological events as factor. Degrees of freedom (d.f.), sum of squares (SS), mean squares (MS), *F*-statistic (*F*), unadjusted *p*-value (*p*), adjusted *p*-value according to Greenhouse-Geisser epsilon (p_{GG}) and according to Huynh-Feldt epsilon (p_{HF}) for each factor are shown.

		Average date						Standard deviation					
	d.f.	SS	MS	*F*	*p*	p_{GG}	p_{HF}	SS	MS	*F*	*p*	p_{GG}	p_{HF}
between species													
Event	5	5.145	1.029	17.40	<0.001	<0.001	<0.001	0.569	0.114	4.54	<0.001	<0.001	<0.001
Error	112	6.624	0.059					2.808	0.025				
whithin species													
Variable	2	1.023	0.511	116.17	<0.001	<0.001	<0.001	0.033	0.016	9.58	<0.001	<0.001	<0.001
Event x Variable	10	0.558	0.056	12.67	<0.001	<0.001	<0.001	0.116	0.012	6.76	<0.001	<0.001	<0.001
Error	224	0.986	0.004					0.384	0.002				

Average date ANOVA:
Greenhouse-Geisser epsilon $\varepsilon_{GG} = 0.569$
Huynh-Feldt epsilon $\varepsilon_{HF} = 0.596$

Standard deviation ANOVA:
Greenhouse-Geisser epsilon $\varepsilon_{GG} = 0.611$
Huynh-Feldt epsilon $\varepsilon_{HF} = 0.642$

Table S3: Results of the ANOVA for the explanatory capacity (adjusted R^2) of complete climatic models of average dates and standard deviation as dependent variables and the absolute average date (upper part) and standard deviation (inner part) as predictors nested within the phenological event. Degrees of freedom (d.f.), sum of squares (SS), mean squares (MS), *F*-statistic (*F*) and *p*-value (*p*) for each predictor variable are shown. In the last row of each model, the explanatory capacity (adjusted R^2) and its significance is also shown.

		R^2 climatic models average date				R^2 climatic models standard deviation			
	d.f.	SS	MS	*F*	*p*	SS	MS	*F*	*p*
Event	4	0.308	0.077	3.476	0.011	0.082	0.021	2.192	0.077
Date(Event)	5	0.204	0.041	1.841	0.113	0.107	0.021	2.291	0.053
Error	86	1.885	0.022			0.806	0.009		
Adjusted R^2		0.542			<0.001	0.184			0.001
Event	5	0.316	0.063	3.079	0.012	0.072	0.014	1.426	0.221
SD(Event)	6	0.561	0.093	4.553	<0.001	0.068	0.011	1.116	0.358
Error	106	2.175	0.021			1.060	0.010		
Adjusted R^2		0.532			<0.001	0.181			<0.001

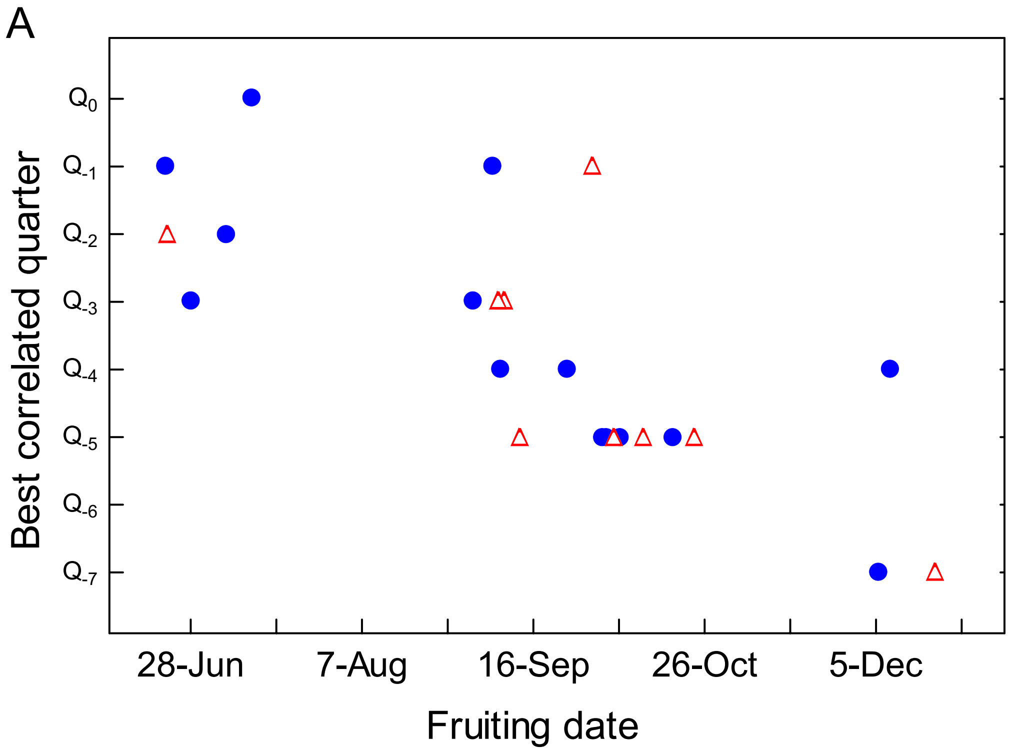
Table S4: Results of the two repeated-measures ANOVA (one for average dates and another for standard deviation) to test for differences in the pure explanatory capacity of each type of climatic variable. Models included phenological event as factor. Degrees of freedom (d.f.), sum of squares (SS), mean squares (MS), *F*-statistic (*F*), unadjusted *p*-value (*p*), adjusted *p*-value according to Greenhouse-Geisser epsilon (p_{GG}) and according to Huynh-Feldt epsilon (p_{HF}) for each factor are shown.

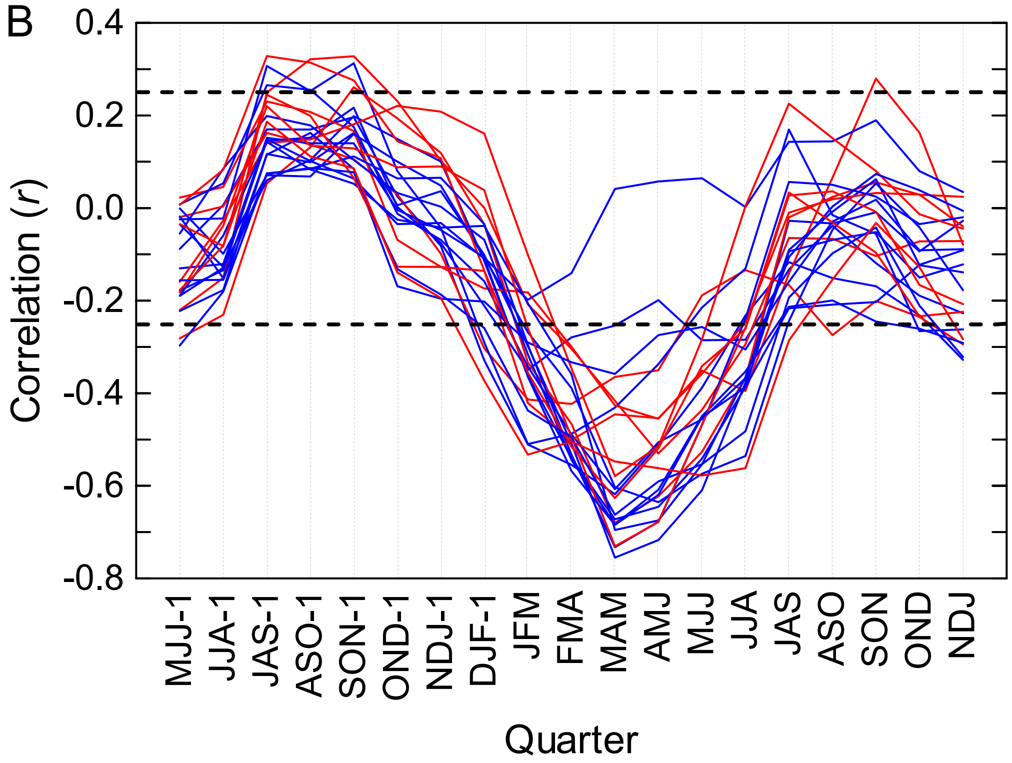
		Average date						Standard deviation					
	d.f.	SS	MS	*F*	*p*	p_{GG}	p_{HF}	SS	MS	*F*	*p*	p_{GG}	p_{HF}
between species													
Event	5	0.613	0.123	18.58	<0.001	<0.001	<0.001	0.096	0.019	5.048	<0.001	<0.001	<0.001
Error	112	3.610	0.032					0.426	0.004				
whithin species													
Variable	2	2.846	1.423	303.22	<0.001	<0.001	<0.001	0.155	0.077	13.83	<0.001	<0.001	<0.001
Event x Variable	10	0.252	0.025	5.364	<0.001	<0.001	<0.001	0.083	0.008	1.492	0.143	0.148	0.143
Error	224	1.051	0.005					1.251	0.006				

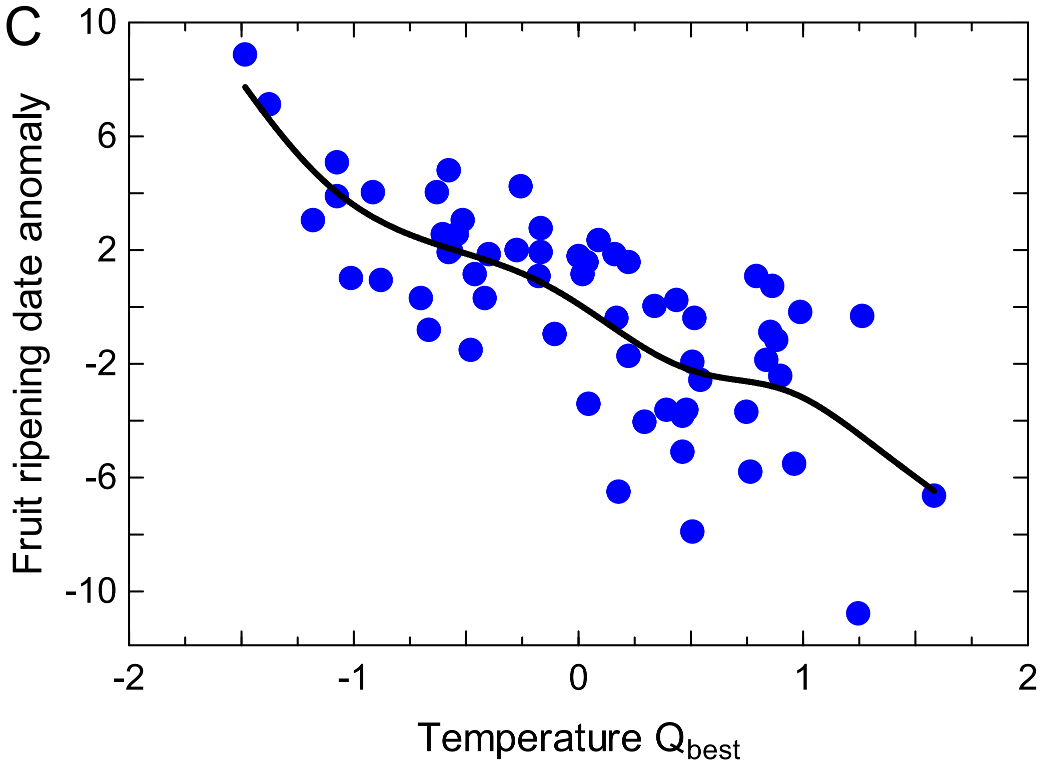
Average date ANOVA:
Greenhouse-Geisser epsilon $\varepsilon_{GG} = 0.796$
Huynh-Feldt epsilon $\varepsilon_{HF} = 0.842$

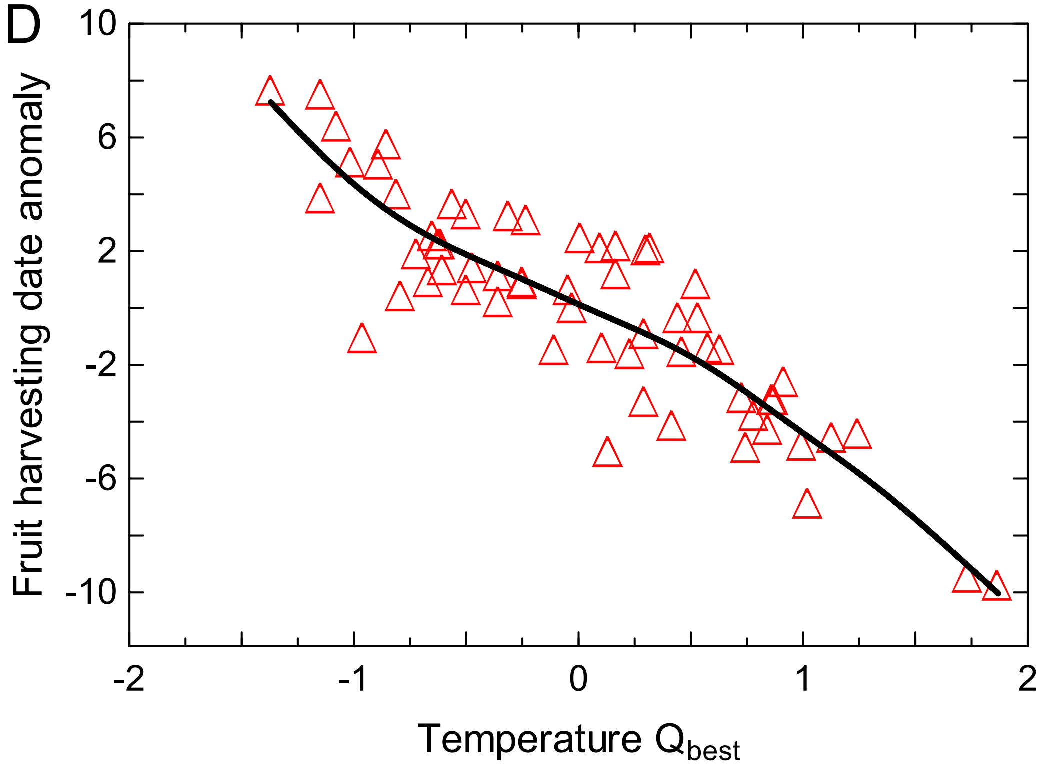
Standard deviation ANOVA:
Greenhouse-Geisser epsilon $\varepsilon_{GG} = 0.946$
Huynh-Feldt epsilon $\varepsilon_{HF} = 1.000$

Fig. S2: Delayed effect of climate on fruiting phenology. **A**) In this graph, the average date (μ) of fruit ripening (●) or harvesting (△) is plotted against the identity of Q_{best} (i.e., the quarter with the highest correlation value) with mean temperature. Q_{best} is further in the calendar as fruiting phenology is later in the year because in almost all species highest climate influence on fruiting was reached during the end of the spring (March-May). **B**) Evolution of correlation values between fruiting dates and mean temperature during each quarter for all the studied species (each line represents one species; — ripening; — harvesting). Pattern is almost the same in all species despite fruiting range between June and December. Highest correlations are reached with March-May or April-June quarters. Dashed horizontal lines denote significance threshold at $P < 0.05$. Quarters followed by -1 belong to the previous year. **C** y **D**) Relationship between fruit ripening and harvesting dates and temperatures during Q_{best}. Each point is the annual averaged value for all species. Compare with the analogous graphs of Fig. 2. See legend of Fig. 2 for details.




B
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
Correlation (r)
MJJ-1
JJA-1
JAS-1
ASO-1
SON-1
OND-1
NDJ-1
DJF-1
JFM
FMA
MAM
AMJ
MJJ
JJA
JAS
ASO
SON
OND
NDJ
Quarter


C
10
6
2
-2
-6
-10
Fruit ripening date anomaly
-2
-1
0
1
2
Temperature Q_best


D
Fruit harvesting date anomaly
10
6
2
-2
-6
-10
-2
-1
0
1
2
Temperature Q_{best}