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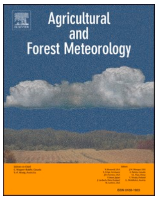

Contrasting responses to climate change – predicting bloom of major temperate fruit tree species in the Mediterranean region and Central Europe

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ABSTRACT

Climate change is shifting the timing of leaf emergence and bloom in temperate-zone trees. While warming typically advances spring phenology, insufficient winter chill can delay or prevent bloom. Understanding species- and cultivar-specific responses is vital for adaptation planning. We calibrated the PhenoFlex phenology model using long-term bloom data for 110 cultivars of seven temperate fruit and nut tree species (apple, pear, apricot, sweet cherry, plum, almond, pistachio) across Spain, Tunisia, Morocco and Germany. The models projected bloom dates and potential bloom failure – when agroclimatic requirements are not met – under current (2015) and future scenarios for two time periods (2035–2065, 2070–2100) and four warming scenarios (SSP1–2.6, SSP2–4.5, SSP3–7.0, SSP5–8.5), using 14–18 General Circulation Models. Three key trends emerged: advancing bloom dates in Germany, delayed bloom for most species in southern Spain, Tunisia, and Morocco, and largely unchanged bloom dates in northern Spain and for almonds in Morocco. The contrasting shifts in bloom result from differences in the primary driver of bloom timing: heat where bloom advances, chill where bloom is delayed and chill and heat substitution where bloom is stationary. In the short term (2035–2065), agroclimatic requirements for most species are expected to be met, except for apricots in southern Spain and pistachios in central Tunisia. Predicted bloom failure rates spiked for most species in Tunisia, Morocco, and southern Spain under pessimistic warming scenarios in the long term (2070–2100) and, to a lesser extent, in northern Spain. Our results reveal cultivar-specific differences in bloom date shifts and failure rates, indicating variation among cultivars in their adaptability to winter warming. This information may guide the design of climate-resilient orchards based on cultivars' alignments with projected agroclimatic conditions.

1. Introduction

Climate change affects natural and agricultural ecosystems worldwide through changes in rainfall patterns, increased frequency of extreme weather events, rising temperatures or shifting pest and disease dynamics. One of the most widely observable manifestations of climate change impacts on the biosphere are shifts in plant phenology (Piao et al., 2019). Changes in the timings of bud-break, bloom and fruit set can have far-reaching consequences, including direct implications for agricultural production. Many studies have documented earlier flowering of forest trees (Menzel et al., 2020, 2006) and fruit trees (Chmielewski et al., 2004; Kunz and Blanke, 2022) in response to higher temperatures in central Europe. For example, the apple (*Malus domestica* Borkh.) cultivars 'Golden Delicious', 'Cox Orange' and 'Boskoop'

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advanced their bloom by roughly two days per decade over the past 60 years in Bonn, Germany (Kunz and Blanke, 2022). In Spain, flowering advanced by six days per decade since the mid-1970s for several perennial species (Gordo and Sanz, 2009). The often-observed bloom advances are caused by rising air temperatures in spring, when bloom is limited by low spring temperatures (heat-limited), as heat requirements are met earlier in the year. Whether these trends will continue in a warming future, however, is far from clear (Guo et al., 2015; Picornell et al., 2024). In some regions, higher temperatures in winter can have an opposite effect, leading to delayed bloom in spring (Bartolini et al., 2019; Martínez-Lüscher et al., 2017). Delayed bloom appears to be linked to situations when bloom is chill-limited, i.e. flowering time is mostly determined by the rate of chill accumulation in winter rather than by the dynamics of the subsequent heat accumulation. In consequence, forecasts of how bloom will develop under warming conditions need to consider chill accumulation during winter, heat accumulation during spring and the interaction of the two processes.

Many species of temperate fruit trees use temperature as an environmental cue to enable them to flower during a favorable period of the year and avoid frost damage to the sensitive flower tissue. Declining temperatures and daylength in fall induce trees to enter a state of dormancy. Dormancy is a period during which active development is suspended and trees are unresponsive to favorable conditions (Faust et al., 1997). In general, the winter dormancy period can be split into three distinct periods: paradormancy, endodormancy, and ecodormancy (Lang et al., 1987). Only the latter two dormancy phases are usually relevant for predicting bloom in spring, as paradormancy describes conditions in which the growth of buds is inhibited by physiological factors outside the bud, such as apical dominance. During endodormancy, buds need to spend time under cool conditions to fulfill their chill requirement. As the chill requirement is met, buds enter the ecodormancy stage. During ecodormancy, buds become increasingly responsive to favorable conditions as they accumulate heat, enabling them to eventually continue their development into leaves or flowers. In consequence, bloom date forecasts are usually based on how much chill and heat is accumulated during the winter endodormancy and ecodormancy phases, respectively. While the framework of endo- and ecodormancy is a simplification, and pathways of overcoming dormancy involve a complex array of physiological processes (Ding et al., 2024; Fadón et al., 2020), this framework offers valuable insights into the process of rest-breaking in trees.

Temperate fruit and nut tree species and even cultivars differ in their chill and heat requirements during dormancy and thus respond differently when temperature conditions change. In general, bloom dates can advance, remain unchanged, or be delayed in response to warming winters, depending on local chill and heat availability and the demands of the tree (Fadón et al., 2021). Mismatches between local agroclimatic conditions and crop requirements can cause a range of production problems for tree fruit growers. If chill and heat requirements are met too early, buds may resume growth at a time when the risk of damaging frost events poses a threat. On the other hand, when agroclimatic requirements are not fully met, flowering may be delayed or irregular. Warmer conditions during winter leading to low chill accumulation have been linked to several undesirable physiological symptoms. Physiological disorders in response to insufficient chill include abnormal development of flowers, erratic budbreak, bud fall, delayed bloom, low yield, poor fruit set and low fruit quality for peach (*Prunus persica* Batsch), apricot (*Prunus armeniaca* L.), plum (*Prunus domestica* L.), almond (*Prunus dulcis* D.A.Webb) and pistachio (*Pistacia vera* L.) (Benmoussa et al., 2017b, 2017a; Borgini et al., 2024; Elloumi et al., 2024; Ghrab et al., 2014). Varying responses in the flowering time of cultivars to changing conditions may become critical in systems that rely on cross-pollination between different cultivars, as is the case for pistachios (Benmoussa et al., 2017b; Elloumi et al., 2024), apples (Ramírez and Davenport, 2013) and pears (*Pyrus communis* L.) (Sanzol and Herrero, 2002). As planted orchards usually remain productive for 15 to 20 years (or even longer), depending on the species, anticipating future agroclimatic conditions and matching them with appropriate cultivars is essential for successful production.

The Mediterranean region is one of the most important growing regions of fruits and nuts in the Northern Hemisphere, featuring extensive orchards of apples, almonds, apricots, cherries, peaches, pistachios, plums, olives and other species. Many orchards in this region are highly productive, even though most of the fruit crops grown in them evolved under continental conditions with much colder winters. For instance, most *Prunus* species are believed to originate from East Asia (Chin et al., 2014) and apple from Central Asia (Brite, 2021). Recent evidence has indicated that the high productivity of Mediterranean orchards may be threatened by climate change (Osorio-Marín et al., 2024). The Mediterranean region is expected to be more strongly affected by climate change than other temperate regions (Bravo et al., 2008; Giorgi and Lionello, 2008). In Spain and northern Africa, warming winters are expected to reduce available winter chill (Benmoussa et al., 2020; Fernandez et al., 2023). Even under current conditions, winters with particularly low chill accumulation have already led to asynchronous bloom and reduced pollination for pistachios in Tunisia (Elloumi et al., 2024) and reduced the number of viable flower buds and fruit set in several *Prunus* species in southern Spain (Delgado et al., 2025). Therefore, forecasting future chill and matching it with agroclimatic requirements of tree cultivars is critical for ensuring sustainable production of temperate fruits and nuts in the Mediterranean region.

When forecasting flowering dates of temperate fruit trees, the accumulation of both chill and heat, as well as possible interactions between them, need to be represented adequately. Among several existing approaches to modeling chill accumulation, the so-called *Dynamic Model* (Fishman et al., 1987b, 1987a) is widely considered as the most appropriate framework, especially in warmer climates such as those prevailing in northern Africa (Fernandez et al., 2020; Luedeling, 2012). For heat accumulation, modelers commonly use the *Growing Degree Hours Model* (Anderson et al., 1986). Many process-oriented phenology models have combined models for chill and heat accumulation (Chmielewski and Götz, 2023; Chuine, 2000; Pope et al., 2014), but they have usually relied on strong assumptions about the interaction between both processes. Some models assume strictly sequential accumulation of chilling and forcing (Chmielewski and Götz, 2023), while others assume an almost completely parallel process (Chuine, 2000). Some researchers have attempted to find a middle ground between parallel and sequential implementation, postulating a certain degree of overlap (Pope et al., 2014). The recently proposed *PhenoFlex* framework (Luedeling et al., 2021), in contrast, does not make assumptions on the nature of this interaction, allowing for the entire spectrum between fully sequential and fully parallel accumulation of chill and heat. Another unique feature of *PhenoFlex* is that it does not rely on the common parameterization of the *Dynamic Model*, which was originally developed for peaches and may not be appropriate for other species. Selecting cultivar-specific parameters for the *Dynamic Model* has been shown to allow capturing the endodormancy period more consistently (Egea et al., 2021). *PhenoFlex* thus facilitates the development of cultivar-specific chill models that are flexible in their representation of the interaction between chill and heat accumulation.

In this study, we calibrate the *PhenoFlex* framework with data for seven temperate tree species, with a total of 110 cultivars, collected in several locations within the Mediterranean region (northern Spain, southern Spain, northern Morocco, and central Tunisia) and in one location with a temperate climate (western Germany). We make bloom projections for a dataset with unprecedented extent, both in terms of covered cultivars and in terms of climate scenarios. We predict bloom dates under current and future climatic conditions to estimate potential climate change impacts. Furthermore, we estimate potential rates of bloom failure based on the percentage of years in which thermal requirements (chill and heat) are not met. We hope that such information can support orchard managers in selecting tree cultivars that remain productive in a warming climate.

2. Materials and methods

2.1. Phenological data

We evaluated phenological data for three stone fruit species: apricot (*Prunus armeniaca* L.), European plum (*Prunus domestica* L.) and sweet cherry (*Prunus avium* L.), two pome fruit species: apple (*Malus domestica* Borkh.) and pear (*Pyrus communis* L.), and two nut tree species: almond (*Prunus dulcis* D.A.Webb) and pistachio (*Pistacia vera* L.). Data were collected at six locations in four countries: Spain (Cieza, Santomera and Zaragoza), Morocco (Meknes), Tunisia (Sfax) and Germany (Klein-Altendorf) (Fig. 1). The data are a subset of a long-term phenology dataset (Luedeling et al., 2024a) from which we selected all cultivars with a minimum of 20 years of phenological data across all locations (Fig. 2). After filtering for cultivars with sufficiently long phenological records, our study covered 110 cultivars across all seven species, with the majority represented by almond (39 cultivars) and sweet cherry (34 cultivars), followed by pear (15 cultivars), apricot (13 cultivars), apple (5 cultivars), pistachio (2 cultivars) and European plum (2 cultivars) (Supplementary Table S1).

In our analysis, we focused on first bloom (10 % flower buds open, BBCH stage 61) and full bloom (50 % flower buds open, BBCH stage 65). Other phenological stages that may interact with bloom, such as the timing of leaf unfolding (in *Prunus* species and pistachio after bloom, in apple and pear overlapping with bloom), were not included in our analysis. Depending on data availability, we considered either the dates of first bloom (apple, European plum) or full bloom (almond, apricot, pear, sweet cherry) for our analysis. The phenological observations of almonds and pistachios made in Tunisia only included first bloom (5 % flowers open) and end of bloom (95 % flowers open). We calculated the mean of the two observations to derive full bloom (50 % of flower buds open), to make observations comparable to data collected in Spain and Morocco, which only included observations of full bloom. Preliminary analysis showed no differences in model accuracy (root mean square error of predicted compared with observed dates) when using the original first flowering observations or the calculated full flowering in the case of almonds in Tunisia. The period covered by phenological observations varied among species and locations (Supplementary Table S1). In total, we used 548 distinct phenological observations made in Klein-Altendorf, 1312 observations from Zaragoza, 67 observations from Cieza, 87 observations from Santomera, 148 observations from Meknes, and 862 observations from Sfax, resulting in a total of 3024 phenological observations.

2.2. Temperature data

We obtained daily minimum and maximum temperature data either from weather stations located within the orchards (Cieza, Zaragoza, Meknes and Klein-Altendorf) or from nearby weather stations covered by the Global Summary of the Day (GSOD) data set (Santomera and Sfax). We filled gaps in temperature data with bias-corrected observations from nearby weather stations (Luedeling, 2018) or, where such data were also unavailable (affecting a total of 104 days in Meknes), through simple linear interpolation using the ‘fix_weather’ function of the chillR package (Luedeling et al., 2024b). We adjusted auxiliary observations by accounting for the long-term difference between the original and auxiliary station for the shared period of observations based on fifteen-day windows centered on the day of the year of the missing observation. The weather data covered the earliest available phenological records for each location and extended until 2021 for all locations.

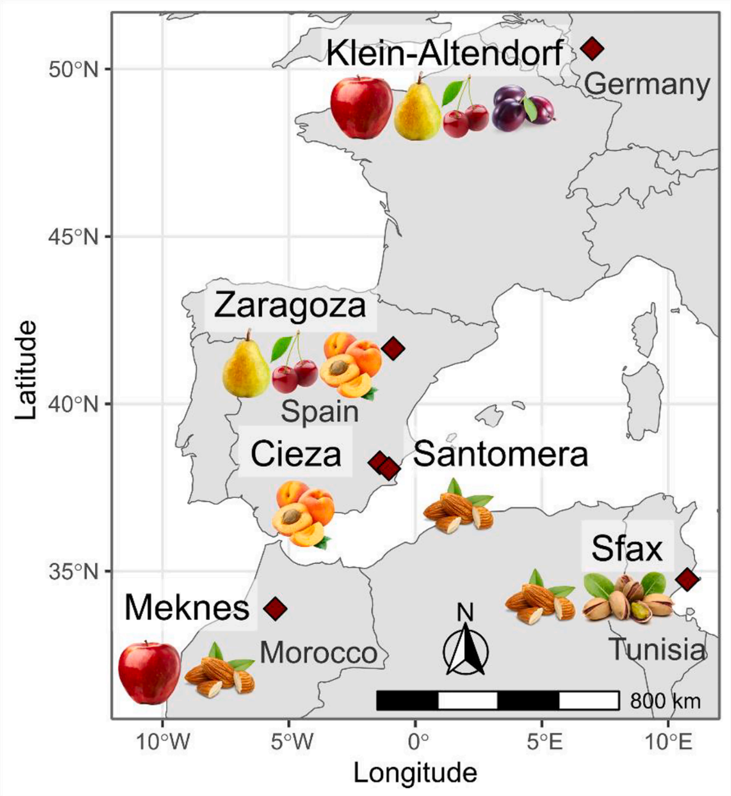

Fig. 1. Map showing the locations where phenological data were collected and indicating the species for which the locations provided data. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

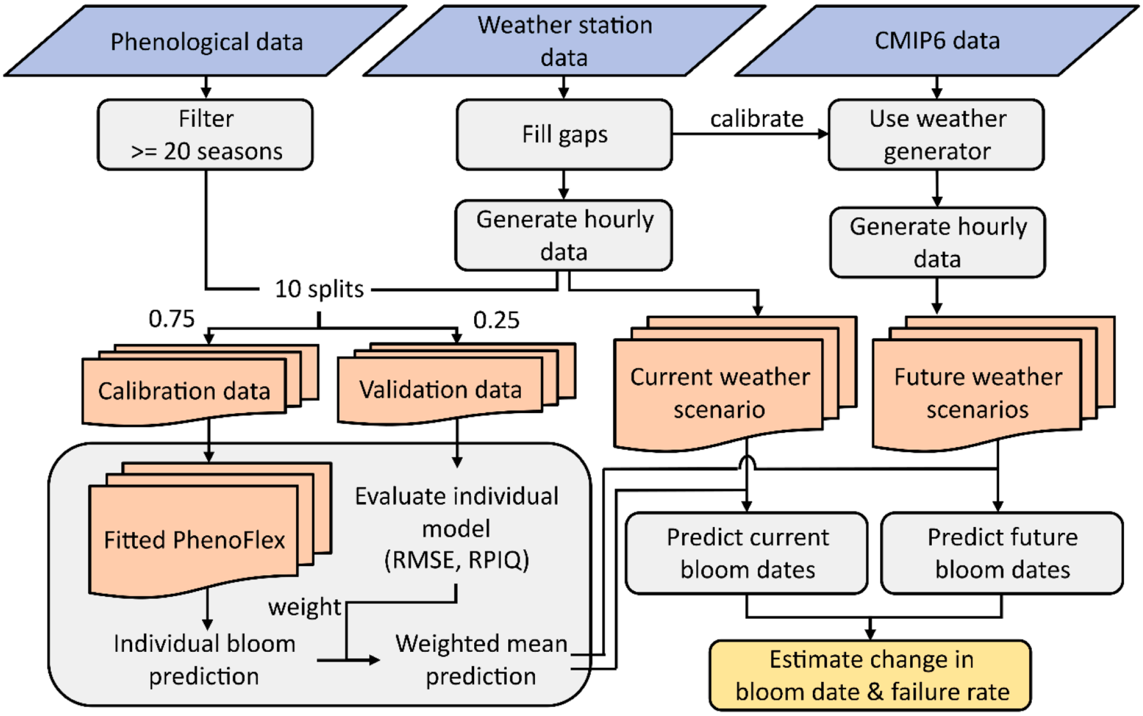

Fig. 2. General workflow showing all major steps to convert input data (blue shapes) to intermediate outputs (red shapes) to the result of the analysis (yellow box). Processes are indicated by grey boxes. RMSE: root mean square error, RPIQ: ratio of performance to interquartile distance.

2.3. *The PhenoFlex phenology model*

We used the *PhenoFlex* modeling framework (Luedeling et al., 2021) to predict bloom dates of all tree cultivars. *PhenoFlex* combines the commonly used *Dynamic Model* (Fishman et al., 1987b, 1987a) for winter chill accumulation and the *Growing Degree Hours Model* (Anderson et al., 1986) for the accumulation of heat. The model is controlled by 12 parameters, with six belonging to the chill sub-model and three to the heat sub-model. The chill sub-model, based on the *Dynamic Model*, models the accumulation of chill in a two-step process: under cold conditions, a precursor of the dormancy-breaking factor (PDBF) accumulates. This PDBF quickly degrades at high temperatures. In a second step, the PDBF gets converted to a temperature-stable substance called dormancy-breaking factor (DBF). The remaining three parameters specify the critical chill accumulation (y_c), the heat requirement (z_c) and the nature of the transition between endodormancy and ecodormancy (between gradual and sudden; s_1). With accumulated chill progressively getting closer to the chill requirement y_c, more heat accumulates. The fraction of accumulated heat, based on the potential heat calculated in the heat sub-model, is described by a sigmoidal curve, with the inflection point centered on the chill requirement y_c, and with a slope s_1 (see also in the Supplementary Materials, Figure S1). An exemplary season illustrating the dynamics of chill and heat accumulation can be found in the Supplementary Materials (Figure S2). The model determines the flowering date by registering when accumulated heat matches the heat requirement. A total failure of flowering is possible when thermal conditions prevent the accumulation of sufficient chill or heat. We calculate the failure rate as the share of seasons with unfulfilled agroclimatic requirements. For more details on the model parameters, refer to Supplementary Materials part A, Caspersen et al. (2024) and Luedeling et al. (2021).

2.4. *Model calibration and validation*

We calibrated *PhenoFlex* with the phenological data of each individual cultivar along with corresponding temperature data. We combined all available observations of a particular cultivar when we had data from multiple locations. For each phenological observation, we provided to the model the corresponding temperature time series, starting in August of the year preceding the observation and ending in June of the observation year. The optimization algorithm and model parameters remained consistent with those used by Caspersen et al. (2024), who adapted an optimization approach proposed by Egea et al. (2021) for use with the *PhenoFlex* framework. We opted to fix two of the 12 model parameters, as preliminary sensitivity analysis based on the fitted almond models presented by Caspersen et al. (2024) indicated that the parameters θ^* (optimal constant temperature for chill accumulation) of the chill sub-model and T_c (critical temperature for heat accumulation) of the heat sub-model in *PhenoFlex* did not greatly influence model performance. These parameters were therefore kept at default values ($T_c = 36$ °C, $\theta^* = 5.85$ °C). The remaining ten parameters (y_c, z_c, s_1, T_b, T_u, θ_c, τ, π_c, T_f, *slope*) were estimated using the Enhanced Scatter Search optimization algorithm combined with the Dynamic Hill Climbing algorithm provided by the MEIGOR package version 1.28.0 (Egea et al., 2014). For detailed descriptions of each parameter, see Supplementary Material Part A, Table S2 and the original publication of the model by Luedeling et al. (2021). We split the data into calibration (75 %) and validation (25 %) subsets (Fig. 2). To minimize the potential model bias resulting from the data split, we repeated the splitting and model-fitting process 10 times, using 30,000 iterations in the individual global optimization runs for each cultivar and repetition. The calibrated models were evaluated based on Root Mean Square Errors (RMSE) and the Ratio of Performance to InterQuartile distance (RPIQ) for both calibration and validation datasets and the ten repetitions individually. Estimated model parameters and the performance metrics for the individual models are accessible in a publicly available repository: https://doi.org/10.60507/FK2/NJVZNP (Caspersen, 2024).

For historical and future bloom projections, we used an ensemble modeling approach. We combined the predictions of the 10 calibrated models per cultivar (Fig. 2), weighting predicted bloom dates according to the validation RPIQ value achieved for the respective parameter set. If at least half of the members of the ensemble indicated flowering failure because thermal requirements were not met, the overall ensemble prediction was interpreted as indicating bloom failure.

2.5. Historical and future bloom projections

We used the RMAWGEN weather generator version 1.3.7 (Cordano and Eccel, 2017) to create plausible synthetic weather time series based on locally observed weather data. Aside from generating temperature data that are representative of the observation period, the weather generator allows producing time series for deviating climatic conditions, which are defined by scenarios that consist of mean daily temperature extremes for each month of the year. Using a weather generator with the output of General Circulation Models (GCM) offers several key advantages over directly applying raw GCM weather projections: First, the spatial resolution of GCM output is very coarse, typically ranging from 50 to 100 km depending on latitude, so that projections are often not representative of local climate conditions. Second, weather generators can simulate a range of plausible weather time series that are consistent with the large-scale climatic patterns projected by GCMs. In contrast, raw GCM outputs present only a single possible realization of future weather under a given climate scenario, limiting the exploration of variability and extremes. Third, weather generators can be used to generate weather data that reflect climatic conditions over a 30-year period, a time frame commonly used in meteorology to define local climate. This approach provides a more robust basis for long-term projections than relying on the single year-to-year variation in the GCM outputs. Weather generators have been successfully applied in climate change impact studies related to tree dormancy (Benmoussa et al., 2020, 2018; Caspersen et al., 2024; Fernandez et al., 2022; Shinwari et al., 2025).

We created such temperature scenarios reflecting current conditions. The scenario information for future climate conditions was derived from the General Circulation Models participating in the Coupled Model Intercomparison Project Phase 6 (CMIP6) (Eyring et al., 2016). We downloaded monthly means of daily minimum and maximum temperatures for 2015–2100 for between 14 and 18 GCMs, depending on availability, from the Climate Data Store (Copernicus Climate Change Service, 2021). A complete list of the GCMs that we included in our analysis can be found in the Supplementary Materials (Table S4). These climate change data encompassed projections for four canonical Shared Socioeconomic Pathways, SSP1–2.6, SSP2–4.5, SSP3–7.0, and SSP5–8.5, which we refer to as SSP1, SSP2, SSP3 and SSP5 throughout the remaining text. The dataset did not contain projections for all combinations of GCMs and SSPs, resulting in slight variation in the number of projections across the SSP scenarios. Using the weather generator, we computed 100 weather time series for two periods (2035 – 2065 and 2070 – 2100), which we refer to by their central years 2050 and 2085, for each location, scenario and GCM, resulting in 8000 to 10,000 temperature series for each time and location. We focused our projections on two forecast horizons, centered around 2050 and 2085, to represent conditions during the middle and end of the 21st century. To be able to generate weather conditions that are representative of the climate during the projection years, we characterized the climatic settings during these years based on periods that included the 15 years before and after the reference years. Accordingly, data for 2035–2065 were used to calibrate the weather generator for the 2050 scenario, whereas data for 2070–2100 informed the 2085 scenario. For the baseline temperature conditions, we created a temperature scenario for the 2008–2022 period (denoted by the central year 2015). The historical weather scenarios were used to generate 100 time series per location and served as the baseline for calculating future shifts in bloom dates. Similar to the model calibration step, we supplied the generated temperature time series for each season starting in August and ending in June of the following year. We used the estimated model parameters (including chill and heat requirements) from the calibration step to project bloom dates for historical and future conditions.

2.6. Technical information

All analyses presented in this study were implemented using the R programming language (R Core Team, 2022) and RStudio (Posit team, 2024) version 2024.4.0.735. Weather data handling and phenological predictions using *PhenoFlex* were executed with the *chillR* package version 0.75 (Luedeling et al., 2024b). Model calibration was done with the *MEIGOR* package version 1.28.0 (Egea et al., 2014). For basic data manipulation and visualization, we relied on packages within the *tidyverse* version 1.3.2 (Wickham et al., 2019). Climate change data was queried using *epwshiftr* version 0.1.3 (Jia and Hong, 2021) and further processed with the help of the *raster* (version 3.6–11, Hijmans et al., 2023) and *ncdf4* (version 1.19, Pierce, 2023) packages. All procedures developed to collect data, conduct analyses and generate figures are available in a public GitHub repository (https://github.com/larscaspersen/AdaMedOr_climate-change-projections). Estimated model parameters and model evaluation scores (RMSE, RPIQ) per cultivar, as well as generated baseline and future weather data can be accessed via https://doi.org/10.60507/FK2/NJVZNP (Caspersen, 2024).

3. Results

3.1. Evaluation of fitted bloom time models

When evaluating the performance of the phenology models, we observed species-specific and location-specific differences. On a species level, we noted lower RMSE values for pome fruits (apple, pear) and stone fruits (apricot, European plum, sweet cherry) than for the nut species (almond, pistachio). The median RMSE ranged from 3.1 days (90 % confidence interval (90 % CI): 1.4 – 6.5 days) for pear to 10.5 days (90 % CI: 6.4 – 17.7 days) for pistachio (Fig. 3A). Similarly, we observed the greatest median RPIQ in European plums (3.5, 90 % CI: 2.3 – 6.3) and the smallest median RPIQ in almonds (1.1, 90 % CI: 0.7 – 2.6; Fig. 3C). Models fitted for almond, pistachio and apricot cultivars showed a poor validation RPIQ <1.0 more often than models for apple, pear, sweet cherry, or European plum. Besides the species-specific trends, we observed notable differences among the cultivars of the same species. For instance, the apple cultivar ‘Golden Delicious’ had a median validation RMSE of 6.7 days, which is greater than the median across the other four apple cultivars (4.0 days, 90 % CI: 2.7 – 5.8 days, Figures S3 and S4). While the model for the cultivar ‘Golden Delicious’ was calibrated and validated with observations from Klein-Altendorf (Germany) and Meknes (Morocco), we only had observations from Klein-Altendorf for the other cultivars. We observed lower validation RMSEs for most apricot cultivars when observations came exclusively from Zaragoza than for cultivars with observations only coming from Cieza or cultivars with observations from both locations. In general, we observed that cultivars fitted and calibrated for locations with cooler climate (mean daily minimum temperature for 1990 – 2020 of 5.8 °C in Klein-Altendorf and 10.1 °C in Zaragoza) tended to have lower validation RMSEs and higher RPIQs than those fitted for warmer locations like Cieza (10.8 °C), Santomera (13.1 °C), Meknes (11.6 °C), and Sfax (14.7 °C) (Figs. 3B and 3D).

Within the same species and cultivar, the validation error varied among the different calibration–validation splits. Across all species and cultivars, the median difference between the split with the lowest validation RMSE and the split with the highest validation RMSE was 6.4 days (90 % CI: 2.9 – 11.8 days). Moreover, we noted that the variation among calibration–validation splits was greater for almond, pistachio and apricot than for the other pome and stone fruit species. Despite the large variation among the repetitions, using the ensemble model led to a high agreement between observed and predicted bloom dates (Fig. 4 and Figures S5 – S11). We observed that, overall, the weighted-mean approach decreased the RMSE for most species compared to the median performance of individual models (Fig. 3), with the greatest reductions for the nut trees. Weighted-mean predictions showed low mean

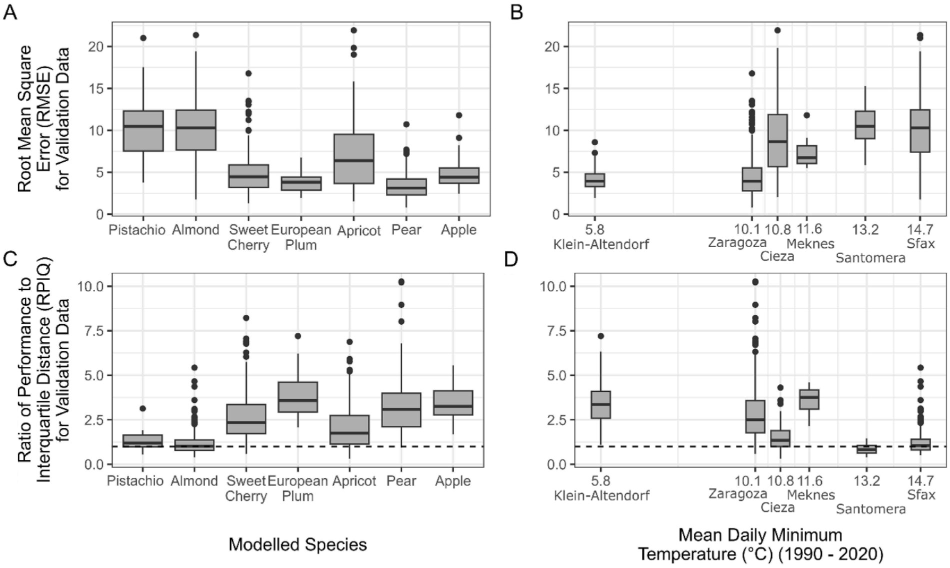

Fig. 3. Root Mean Square Error (RMSE) and Ratio of Performance to Interquartile Distance (RPIQ) of the predicted bloom dates of the validation data splits of the 10 repeated splits per cultivar, summarized at species level (A and C, respectively) and models summarized by the average minimum temperature (1990 – 2020) of the location the model was calibrated for (B and D, respectively; minimum temperatures are shown on the x-axes). Models calibrated with observations from multiple locations were assigned to the mean temperature of the warmest location.

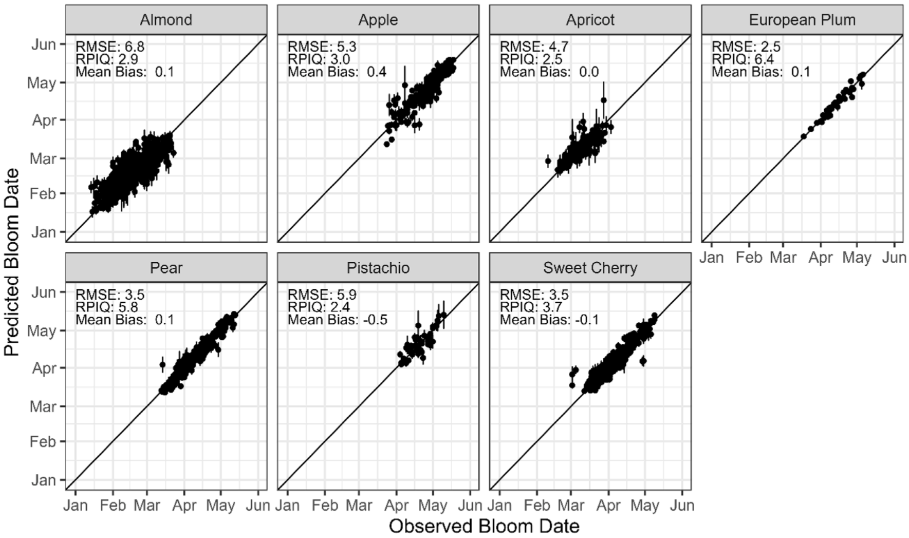

Fig. 4. Correlations between observed bloom dates and validation-RPIQ-weighted predictions of the 10 repetitions of fitted models within a cultivar (ensemble model) for almond, apple, apricot, European plum, pear, pistachio and sweet cherry. Performance is summarized at species level, predictions are made at cultivar level. Error bars show the standard deviation of the ensemble member predictions.

biases in prediction ranging from −0.5 days for pistachio to 0.4 days for apple. Using the weighted mean of the models obtained from different calibration–validation splits of the same cultivar led to high agreement of predicted and observed bloom dates.

3.2. Projected shifts in bloom dates

We predicted shifts in bloom dates by comparing the predictions under 2015 conditions with those for future conditions representing the periods 2035 – 2065 and 2070 – 2100 (denoted by their central years 2050 and 2085, Fig. 5). We noticed three patterns among future bloom dates. First, bloom dates are expected to advance in the coldest location (Klein-Altendorf). Second, bloom dates are delayed compared to current conditions in warm, chill-limited locations like Sfax, Santomera and Cieza. We projected delayed bloom dates for apricots in Cieza, almonds in Sfax and Santomera, pistachios in Sfax and apples in Meknes, independently of the modeled period, SSP or GCM. Finally, we noted stagnating bloom dates for 2050 but delayed bloom dates under 2085 conditions for pome and stone fruits in Zaragoza and apples in Meknes. In these cases, bloom dates under 2015 conditions are close to the median bloom date under 2050 conditions irrespective of SSP and GCM, but bloom dates tend to be delayed under 2085 conditions for the more pessimistic scenarios SSP3 and SSP5.

Within the three identified patterns, we observed differences in the magnitude of bloom date shifts, depending on the modeled species, cultivar, location and period (Fig. 6). We predicted mainly advancing

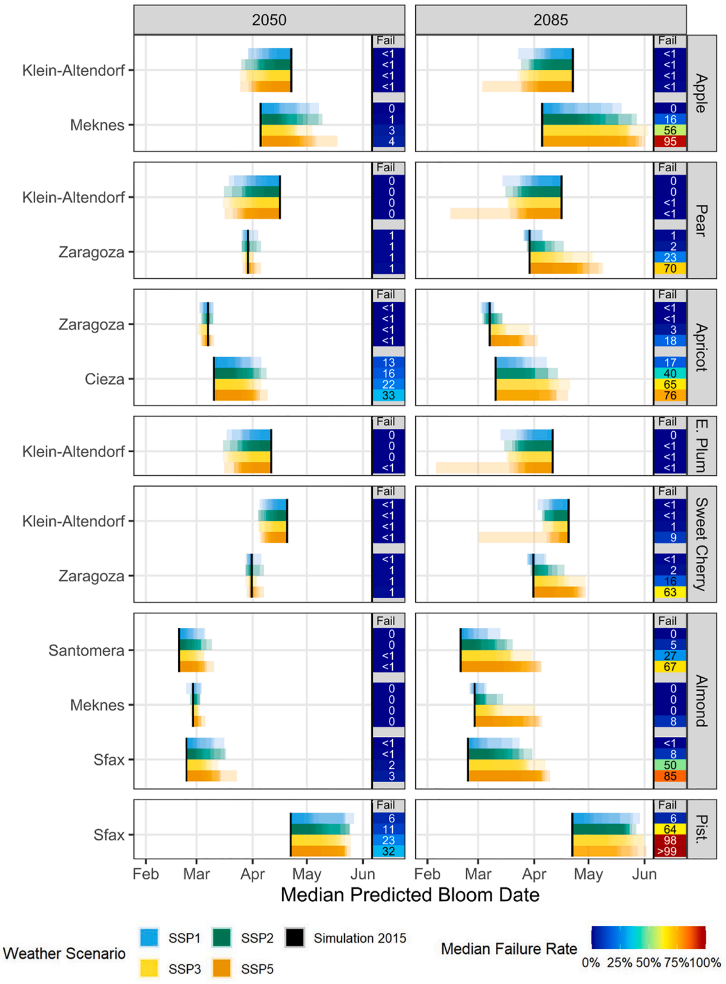

Fig. 5. Changes in median bloom dates, relative to simulated 2015 conditions (black vertical lines), under projected future conditions for the four shared socio-economic pathways SSP1 (blue horizontal strip), SSP2 (green), SSP3 (yellow) and SSP5 (orange), in 2050 (left) and 2085 (right), accompanied by the median rates of unfulfilled thermal requirements (heatmap). Bloom shifts were calculated for each of the 14 to 18 General Circulation Models (GCM) individually. The degree of saturation of the strip colors indicates agreement among GCMs, with strong saturation indicating strong agreement.

bloom dates in Zaragoza (northern Spain) and Klein-Altendorf (Germany), with stronger advances for European plum, apple and pear compared to sweet cherry. Under 2050 conditions, the median bloom date shift of apples, pears and European plum ranged between −12 days (SSP1) to −19 days (SSP5), while for sweet cherry it ranged from −8 days (SSP1) to −10 days (SSP5). Under 2085 conditions, bloom dates advanced more strongly than under 2050 conditions for apples, pears and European plums (between −14 days for SSP1 and −23 days for SSP3), while in sweet cherries the bloom date shifts were less pronounced under more pessimistic scenarios than for optimistic ones (between −11 days for SSP2 and −1 day for SSP5). We observed differences in projected bloom date advances among the apple and sweet cherry cultivars. The projected advances were less pronounced for sweet cherry cultivars ‘Regina’ (between −7.0 for SSP1 to −7.3 days for SSP5 in 2050) and ‘Schneiders’ (between −7.3 for SSP1 to −7.8 days for SSP5 in 2050) as well as for apple cultivar ‘Berlepsch’ (between −9.0 for SSP1 and −9.6 days for SSP5 in 2050) than for the other cultivars (between −10.2 for SSP1 and −20.5 for SSP5 in 2050) (Fig. 7). The rate of unfulfilled thermal requirements was low for almost all species, cultivars, and climate scenarios for both modeled periods (Figs. 5 and 7).

In cases of overall projected delays in bloom dates, we observed strong differences among the modeled species and cultivars. Modeled bloom dates of apricots in Cieza, pistachios in Sfax and apples in Meknes shifted more strongly than those of almonds in Sfax and Santomera. Under 2050 conditions, the bloom date shifts for apples, apricots and pistachios ranged between +10 days (SSP1) and +27 days (SSP5), while bloom dates advanced for almonds between 5 days for SSP1 and 12 days for SSP5. Similarly, we observed that the rate of unfulfilled thermal requirements increased for apricots in Cieza earlier and more strongly than for almonds in Santomera and Sfax. We observed differences in the intensity of delayed bloom dates and failure rates among apricot cultivars in Cieza and almond cultivars in Sfax and Santomera (Figs. 6 and 7). For 2050, projected shifts in bloom dates were less pronounced for apricot cultivars ‘Búlida’, ‘Canino’, and ‘Dorada’ (between 5 days for SSP1 and 19 days for SSP5) than for cultivars ‘Goldrich’, ‘Pepito del Rubio’, ‘Stark E. Orange’, and ‘Sunglo’ (between 18 days for SSP1 and 34 days for SSP5). Several almond cultivars showed less pronounced shifts in bloom dates and lower failure rates even under pessimistic conditions, including ‘Desmayo’, ‘Marcona’ and ‘Ferragnes’ in Santomera and ‘Garnghzel’, ‘Ferragnes’ or ‘Tarragona’ in Sfax. While the delay in bloom dates for apricot in Cieza and almond is generally large, we identified cultivars that are less affected in terms of delayed bloom dates and failure to fulfill thermal requirements.

For the group of species and locations with stagnating bloom dates in 2050, we observed that bloom dates and failure rates are only affected under the assumptions of the most pessimistic scenarios in 2085. Under 2050 conditions, median bloom dates are expected to remain close to those under current conditions. Median shifts under 2050 conditions

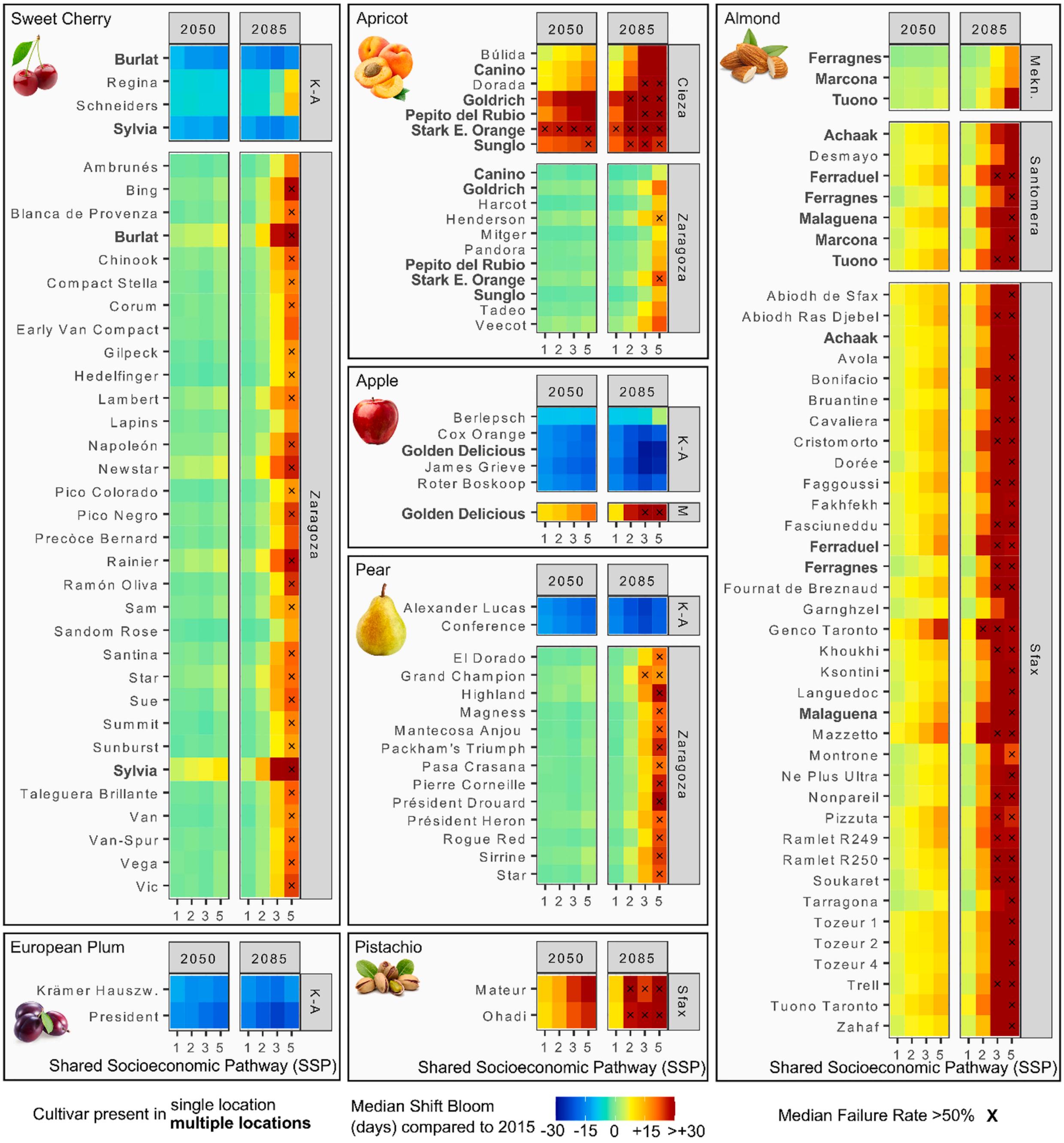

Fig. 6. Heatmap showing changes in median bloom date (days), relative to simulated 2015 conditions, for projected future conditions for four shared socioeconomic pathways (SSP1, SSP2, SSP3, SSP5) summarized at cultivar level. Cultivars with observations from several locations are marked in bold font. Cases with rates of >50 % unfulfilled thermal requirements are marked with an ‘x’. The modeled location Klein-Altendorf is abbreviated as ‘K-A’ and Meknes as ‘Mekn.’ and ‘M’.

ranged from −1 day for SSP1 to +1 day for SSP5 for pear, apricot and sweet cherry in Zaragoza, and from +3 days for SSP1 to +4 days for SSP5 for almond cultivars in Meknes (Fig. 5). Similarly, the failure rates for 2050 conditions remained lower than 1 % for apricot, sweet cherry and pear cultivars in Zaragoza and for almond cultivars in Meknes. We observed similar shifts in bloom dates and failure rates for 2085 for the optimistic scenarios SSP1 and SSP2. For scenarios SSP3 and SSP5 under 2085 conditions, we projected delays with stronger trends for pear and sweet cherry in Zaragoza and almond cultivars in Meknes (SSP3: −8 to −12 days, SSP5: −20 to −25 days) compared to apricot in Zaragoza (SSP3: −4 days, SSP5: −13 days). We observed cultivar-specific differences in the projected failure rates for the pessimistic climate scenario SSP5. For example, sweet cherry cultivars ‘Ambrunés’, ‘Lapins’ or ‘Sandom Rose’, apricot cultivars ‘Canino’, ‘Harcot’ or ‘Mitger’, and almond cultivars ‘Ferragnes’ and ‘Marcona’ showed lower failure rates and smaller delays in bloom dates than the species average (Figs. 6 and 7).

4. Discussion

4.1. *Model performance is influenced by marginal climate in northern Africa*

We calibrated the *PhenoFlex* model for seven temperate fruit and nut

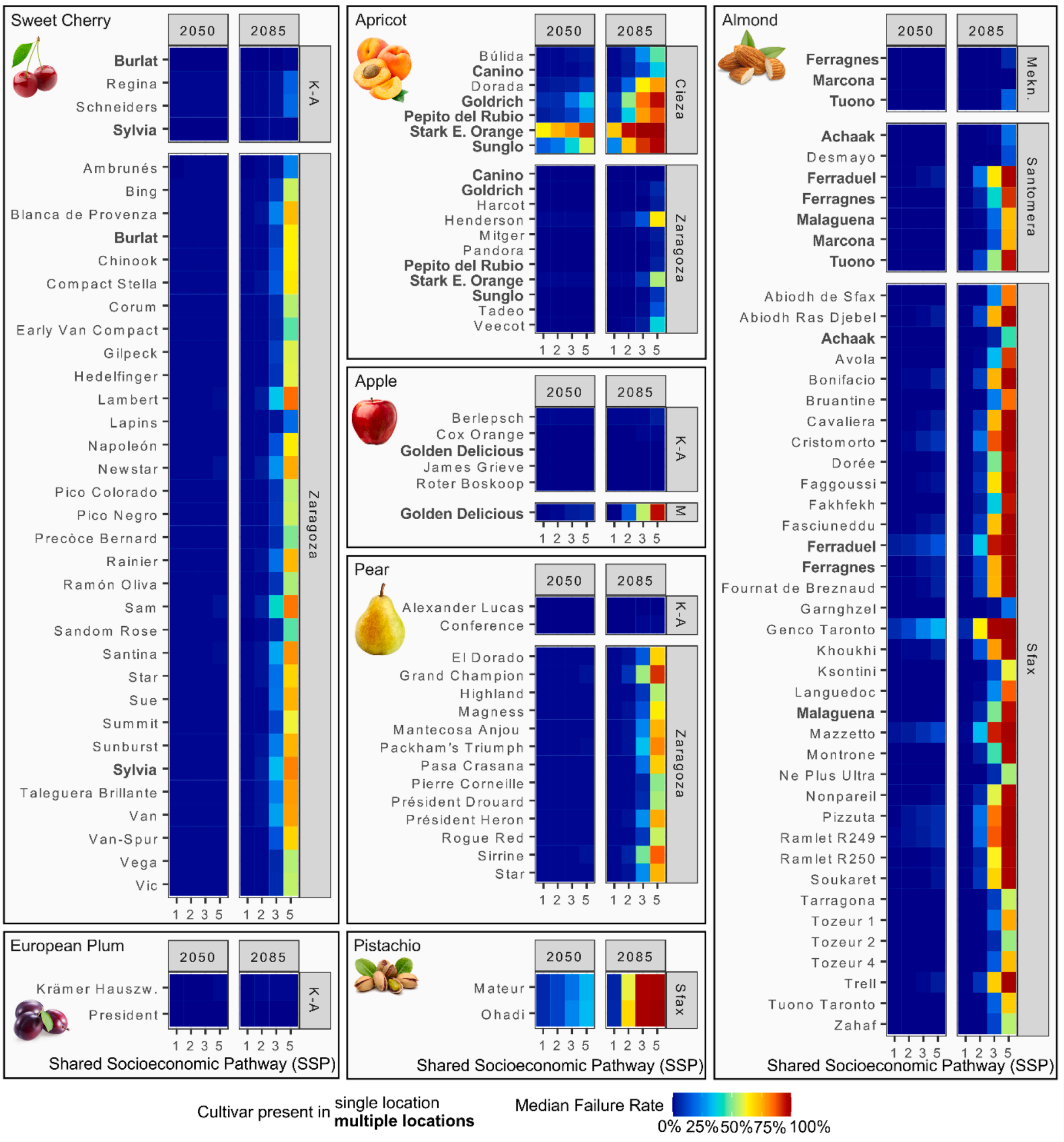

Fig. 7. Heatmap showing the rates of unfulfilled thermal requirements (%) for four shared socioeconomic pathways (SSP1, SSP2, SSP3, SSP5) summarized at cultivar level. Cultivars with observations from several locations are marked in bold font. The modeled location Klein-Altendorf is abbreviated as ‘K-A’ and Meknes as ‘Mekn.’ and ‘M’.

tree species of relevance in the Mediterranean region and Germany, covering 110 cultivars in total. The climate change impact projections revealed contrasting responses of bloom dates to warming winters, ranging from advancing bloom in Germany to largely unchanged bloom dates in northern Spain and delayed bloom in southern Spain, Morocco and Tunisia. Climate change scenarios entailing strong warming (SSP3 and SSP5) also indicate an increased risk of bloom failure for apricots, pistachios and almonds in southern Spain and northern Africa.

The fitted models appeared to adequately capture the bloom dates of the modeled species and locations, even though the accuracy differed among the species. For apple cultivars, we obtained a median validation RMSE of 4.4 days, and for pear cultivars a median validation RMSE of 3.1 days. Similarly precise results were reported by Luedeling et al. (2021), who used the *PhenoFlex* framework to model the apple cultivar ‘Boskoop’ (RMSE 3.8 days) and the pear cultivar ‘Alexander Lucas’ (RMSE 4.0 days) in western Germany. Modeling apple bloom date with a sequential model, El Yaacoubi et al. (2019a) reported similar accuracy (RMSE 4.4 days) for several locations in Morocco, Italy and France. Applying a different variant of a sequential model consisting of the *Dynamic Model* and the *GDH* model for apple and pear cultivars in Belgium, Drepper et al. (2020) reported validation RMSE values ranging from 4.2 to 8.4 days, while a lower validation error (RMSE 2.3 days) was reported for predictions with a continuous model for the apple cultivar ‘Fuji’ in Japan (Asakura, 2011). In contrast, our almond models had a median validation RMSE of 9.1 days, which is much higher than the 4.0 - 5.3 days reported by Caspersen et al. (2024), who used *PhenoFlex* for three almond cultivars in California. Similarly, Pope et al. (2014) obtained a validation RMSE of 2.7 - 4.5 for almond cultivars in California, and Lorite et al. (2020) reported a validation RMSE of 2.5 – 5.6 days for almond cultivars in southern Spain, with both studies using a fixed-overlap model. The higher RMSE of nut tree models is likely due to the warm climates from which our data originated. Climate conditions in Sfax (Tunisia) and Meknes (Morocco) – where most records of almond and pistachio phenology were collected – offer only marginally sufficient chill. Irregular bloom for almonds and pistachios due to insufficient chilling has been commonly observed in warm locations (Benmoussa et al., 2017a, 2017b; Elloumi et al., 2024, 2013). This may have reduced the consistency of recorded bloom dates, hampering the suitability of the observed data for model calibration.

We observed large variation in performance across the 10 bloom prediction models for each cultivar, indicating that the random split into calibration and validation data can greatly affect the quality of the resulting models (Fig. 3, Supplementary materials Figure S3). This observation was the main motivation for using a weighted-mean approach across all models. We sampled different calibration and validation datasets from the pool of observations, obtaining an ensemble of models for each cultivar. As a result, each observation was used in the calibration of at least one of the models. Due to the limited sizes of the datasets, we were unable to set aside a meaningful number of observations for validating the weighted-mean model. We recommend validating the weighted-mean approach with unseen data (i.e. data that were not used at all during calibration), yet this will require larger datasets than were available to us. Another aspect of the model we have not yet been able to validate is the endodormancy release date, since observational data on this is not widely available. Incorporating endodormancy release dates estimated from forcing experiments on cut branches collected from orchards might improve the calibration of the s_1 parameter of the model, which controls the transition from chill accumulation to heat accumulation. To harness this potential, however, forcing experiment protocols may need to be adjusted to accommodate the possibility of gradual endodormancy release that is contained in the *PhenoFlex* model. While we estimated chill and heat requirements for each cultivar, these estimates cannot be directly used by growers because they are tied to the parameters of the chill and heat submodels. Both the estimated requirements and the submodel parameters vary across cross-validation folds, so reporting mean requirements would be misleading. This aspect could be improved in future work, as accurate estimates of chill and heat requirements are of high value for fruit growers.

4.2. Projected shifts in bloom depend on species and local climate

The phenology models indicated shifts in median bloom dates for most species and locations (Fig. 5, 6). For cool locations (Klein Altendorf, Germany), we observed a trend of advancing bloom dates. For moderately warm locations (Zaragoza, Spain), the models indicated no major changes by 2050, but delays by 2085. For warm conditions (Sfax in Tunisia, Meknes in Morocco and Santomera and Cieza in Spain), models predicted delayed median bloom dates. The shifts in bloom phenology match findings reported in other studies, which described bloom patterns in warm locations such as Sfax (Tunisia) or Meknes (Morocco) as chill-limited (Benmoussa et al., 2017a; El Yaacoubi et al., 2019a). Bloom dates in moderately warm locations like Zaragoza have also been described as mainly chill-limited (Fadón et al., 2023a). However, we predicted delays in response to warming winters only for the long run (2085) rather than for the near future (2050). The bloom patterns in cool locations like France or Germany have been described as mostly heat-limited (El Yaacoubi et al., 2014; Fadón et al., 2023a), which aligns with the predictions of advancing bloom dates in Klein-Altendorf. Our results indicate that, in the case of Klein-Altendorf, the average advances in bloom date are proportional to faster heat accumulation, with no clear association with changes in chill accumulation (Supplementary Materials Figures S12–14). Our results emphasize that shifts in phenology are cultivar- and location-specific. Leaf unfolding and flowering have been reported to differ in their sensitivity to temperature (Buonaiuto and Wolkovich, 2021; Guo et al., 2023; Picornell et al., 2023). This implies that climate change can affect the synchronization of leaf unfolding and flowering, leading to mismatches between the vegetative and reproductive cycles of the plants. These potential mismatches between the availability of photosynthetic gains and energy requirements for flowering can compromise tree survival as well as fruit production (Fu et al., 2015; Geng et al., 2020; Stuble et al., 2021). However, this factor was not included in our calculations due to lack of data for the leaf unfolding phenophase. It would be interesting for future studies to integrate the flowering risks calculated in this study with other factors related to fruit production such as desynchronization among phenophases. According to our findings, the overall direction of the bloom shift depends on whether chill or heat limitations are currently preventing earlier bloom and on how well increases in forcing can substitute for decreases in the accumulated chill.

4.3. Identifying species and cultivars that are adapted to projected climate change

According to our results, apricot production in Cieza (southern Spain) and almond production in Sfax (central Tunisia) are especially threatened by the prospect of warming winters (Fig. 7). The risk of failure to fulfill thermal requirements is already elevated by 2050 for the SSP2, SSP3 and SSP5 scenarios. Egea et al. (2022) showed that apricot-producing regions in inland areas in the southeast of Spain, close to the Mediterranean Sea, are projected to experience decreasing chill availability during the winter months. Projections of chill availability for the whole Mediterranean region by Fernandez et al. (2023) point in a similar direction. Fernandez et al. (2023) linked prospects of decreasing chill accumulation in the Mediterranean region with risks of delayed flowering, physiological disorders of the flower and reduced fruit quality. The flowering timing of pistachios in Tunisia is already chill-limited under current conditions, and there have already been several instances of delayed flowering in response to particularly warm winters (Elloumi et al., 2024). The average shift in almond bloom date in Meknes, Sfax and Santomera is proportional to changes in the chill accumulation period, but not to changes in the heat accumulation period (Supplementary Materials Figures S12-S14). Our projections for non-optimistic scenarios under 2050 conditions and for almost all scenarios under 2085 conditions indicate an elevated risk of failure to fulfill thermal requirements of pistachios in Tunisia, suggesting that the suitability of this region for pistachio is threatened by climate change.

Our study points out potentially climate change-resilient cultivars that are already present in the study locations. We documented strong cultivar differences in terms of shift in bloom dates and rate of unfulfilled thermal requirements for apricots in Cieza and Zaragoza, as well as sweet cherry in Zaragoza and almonds in Sfax and Santomera. Several recent studies have used PLS regression to cast light on chill requirements, e.g. for sweet cherry (Fadón et al., 2023c) and pear in Zaragoza, Spain (Fadón et al., 2023b), or for almond (Benmoussa et al., 2017a; El Yaacoubi et al., 2019b) and pistachio in Sfax, Tunisia (Benmoussa et al., 2017b; Elloumi et al., 2024). In contrast to the PLS-regression-based studies, our approach also considered the possibility that some chill deficiencies may be compensated by additional heat. In PLS-based studies, chilling and forcing requirements are calculated independently, whereas the *PhenoFlex* model also considers their interaction, enabling more explicit predictions on the fulfillment of thermal requirements. A disadvantage of both approaches (PLS regression and *PhenoFlex*) for climate change impact analysis is that long phenology time series ($\geq$20 observations per cultivar) are needed for the analysis, limiting the number of covered species and cultivars. On the other hand, predicting the adaptability of the cultivars based only on the percentage of years in which chill availability exceeds the cultivar-specific chilling requirements (Delgado et al., 2021; Fadón et al., 2023c) is highly dependent on the methodology used to quantify the chill requirement (Delgado et al., 2024). The approach presented in this study does not require prior characterization of the agroclimatic requirements to forecast the adaptability of the cultivars to future climatic conditions.

It is worth pointing out that we only differentiated between thermal requirements being fulfilled or remaining unfulfilled. It is quite possible, however, that in our analysis trees are projected to flower successfully, but at a time that is either too early or too late for commercial production. For example, while agroclimatic requirements of almonds in northern Spain are easily met, only the introduction of late-blooming cultivars allowed commercially viable almond production (Alonso Segura et al., 2017), because most traditional cultivars flowered too early – during frost-prone periods. Shifts in phenology may have ramifications that can only be fully appreciated by viewing projected changes in bloom dates in the wider context of specific production locations. For instance, a warming climate may reduce the overall likeliness of spring frost events. Advancing bloom dates, however, such as those predicted for Klein-Altendorf, may counteract this trend, possibly resulting in an overall increase in frost risk (Bosdijk et al., 2024; Pfleiderer et al., 2019). Accurate information on how these opposing trends will play out would support growers in taking appropriate adaptation measures, such as the adoption of new cultivars, which may help them avert frost-related fruit yield and quality losses and the resulting shortfalls in revenue (Dalhaus et al., 2020). Advancing bloom dates due to increased forcing temperatures may accelerate fruit ripening and thus reduce fruit quality, as reported for peach cultivars (Lopez et al., 2007; Wert et al., 2009). On the other hand, delays in bloom caused by insufficient chill accumulation are linked to other adverse agronomic effects such as reduced fruit set or increased bud abscission (Elloumi et al., 2024; Ghrab et al., 2014). Future modeling efforts should link location-specific risks with shifting bloom dates to make climate change impacts more tangible for practitioners and advisors. Selecting low-chill cultivars for growing regions where chill is a limiting factor is also crucial. Shifts in flowering can become problematic for self-incompatible species such as pistachio, but also for some cultivars of apple, plum, apricot, cherry and almond. It is possible that the bloom periods of pollen donors and acceptors are no longer synchronized, threatening pollination success.

4.4. Next steps in phenology modeling

Understanding the spatial or, to be more precise, thermal limits of the phenology models would be an important step when projecting climate change impacts for locations without observations. Ideally, predictions based on locally calibrated models should be accompanied by an estimate of the thermal validity range of such models. Even models that represent phenology under current conditions well may lose their accuracy with progressive warming. Indications of such validity limitations have been derived from comparisons of chill models (Fernandez et al., 2020; Luedeling and Brown, 2011) or by confronting different types of phenology models with climate change experiments (Chmielewski and Götz, 2016).

We identified several opportunities for future research that may expand on our findings. We only predicted bloom dates and bloom failure rates, yet tree performance will also depend on additional factors, such as the thermal conditions during bloom. Trees may flower during frost-prone periods as a result of advancing bloom dates. In cases of delayed flowering, bloom may occur during heat-prone periods, and strong delays may shorten the period of fruit development. While some studies have suggested that delayed flowering could be compensated by faster fruit ripening (Vanalli et al., 2021), others have indicated that faster ripening may reduce fruit size and thus lower fruit quality (Lopez et al., 2007). In essence, to fully assess impacts of climate change on fruit production, the entire fruit development cycle from dormancy, through flowering to ripening needs to be considered. Increasing temperatures during all phenological stages may have negative implications for fruit yield and quality, which consideration of thermal conditions around bloom may help clarify. We also encourage the compilation of larger multi-location observation datasets on specific tree cultivars to help clarify the impacts of cultivar and location on model parameters and performance. Our models were calibrated on observed temperature conditions, but controlled experiments would be needed to judge the range of conditions for which the models can be expected to make sound predictions. Finally, to comprehensively support farmers in their decision-making on cultivar selection, thermal considerations should be linked to non-climatic aspects, such as yield or fruit quality, that growers must consider when choosing cultivars for their orchards.

5. Conclusion

We detected contrasting responses of bloom dates to climate change, including delayed bloom under chill-limited conditions, stagnant bloom in situations where declining chill can be compensated by additional heat, and advancing bloom under heat-limited conditions. The calibrated *PhenoFlex* models reveal non-linear bloom date responses to warming and suggest that the patterns observed today may transition into a different change regime in the future, with the nature of this transition depending on the location and cultivar. For instance, stagnant bloom dates of sweet cherries in northern Spain are projected to pivot to delays under pessimistic warming scenarios. Such non-linear dynamics in bloom timing are easily overlooked when datasets cover only a few species, cultivars or climatic conditions.

Our cultivar-specific climate change impact projections offer insights into potential adaptation strategies. For several species and locations, we have identified cultivars with less pronounced bloom shifts that may be better adapted to changing climatic conditions. Shifts in spring phenology signal further changes in production risk factors, including changes in frost risk, evolving disease occurrence patterns, heat stress during the growing period and other impacts on fruit yield and quality. Integrating phenology projections with models that can predict such risks can support the decision-making process for stakeholders involved in fruit tree cultivation, ensuring more resilient production systems in a changing climate.

Developing robust climate change impact projections requires comprehensive datasets, which are often unavailable, rare or inaccessible. The fragmented and short datasets that exist for many cultivars are typically inadequate for making reliable projections. This study demonstrates that combining existing datasets allows us to improve our ability to anticipate climate change impacts and to expand the applicability of our tools to a wider range of species and cultivars.

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CRediT authorship contribution statement

Lars Caspersen: Conceptualization, Data curation, Formal analysis, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. **Katja Schiffers:** Methodology, Supervision, Writing – review & editing. **Antonio Picornell:** Methodology, Software, Writing – review & editing. **Jose A. Egea:** Software, Writing – review & editing. **Alvaro Delgado:** Data curation, Writing – review & editing. **Adnane El Yaacoubi:** Writing – review & editing. **Haïfa Benmoussa:** Writing – review & editing. **Javier Rodrigo:** Writing – review & editing. **Erica Fadón:** Writing – review & editing. **Mehdi Ben Mimoun:** Writing – review & editing. **Mohamed Ghrab:** Writing – review & editing. **Ossama Kodad:** Writing – review & editing. **David Ruiz:** Writing – review & editing. **Eike Luedeling:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2025.110859.

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