



Impacts of climate change on the phenology and distribution range of *Castanea sativa* (Mill.) varieties in the Cévennes mountainous region, Southern France

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Abstract

Climate change is expected to significantly impact agriculture by altering temperature and precipitation patterns, with notable effects on crop phenology and yields in Mediterranean regions. The European chestnut (*Castanea sativa* Mill., Fagaceae) is a culturally and economically important species in the Mediterranean area, particularly in mountainous regions of Cévennes in France where traditional chestnut-based agrosystems are under pressure. However, the potential impacts of climate change on chestnut phenology and varietal adaptation remain poorly investigated. This study used the process-based model PHENOFIT to assess the suitability of future climatic conditions (under scenarios RCP4.5 and RCP8.5) for three major chestnut varieties grown in Cévennes mountains. Originally developed for forest trees, this model estimates tree fitness based on survival and reproductive success under specific pedoclimatic conditions. A network of on-farm monitoring sites and a citizen-science approach provided phenological and climatic data to model the consequences of climate extremes and global warming on a shift of the cultivation area until 2100. Model projections suggest an upward and downward elevational expansion of potentially suitable chestnut growing areas, alongside a phenological advance from budburst to fruit maturation. Risks of spring and autumn frosts are projected to decline and winter warming is not projected to compromise exposure to chilling temperatures that break bud dormancy. Chestnut varieties showed different responses to climate change, indicating the need for further studies on their functional traits, especially drought tolerance, varietal plasticity and fruit quality, to enhance the model's projections' reliability and propose adaptive strategies for sustainable chestnut cultivation in the upcoming decades.

Keywords Process-based modelling · Chestnut (*Castanea sativa* Mill.) · Varieties · Phenology · Agroforestry · Citizen-science

Introduction

Climate change causes widespread adverse impacts to nature and people that are unequally distributed across ecosystems and regions, and is recognised to pose a significant threat to both agriculture and forests worldwide (IPCC 2023). Changes in temperature and precipitation are expected to reduce yields of most crops (Challinor et al. 2009; Dettori et al. 2017; IPCC 2023; Rezaei et al. 2023) due to shifts in phenology affecting crop development (Parker et al. 2020), exposure to late frost (Vitasse et al. 2018a, b; Zohner et al. 2020; Lamichhane 2021; Guo et al. 2024), early heat waves and summer drought (Fahad et al. 2017; Dietz et al. 2021), as well as reduction in chill accumulation causing developmental disorders (Leolini et al. 2018b, a; Rodríguez et al. 2021; Fernandez et al. 2022).

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The Mediterranean region, is a climate change hotspot (IPCC 2023), with a continued increase in temperature extremes, heatwaves and droughts (Lionello and Scarascia 2018; Seneviratne et al. 2021; IPCC 2023). Future projections predict similar trends (De Luis et al. 2010; Lorenzo and Alvarez 2022), with more frequent and intense droughts (Böhnisch et al. 2021, 2025; García-Valdecasas Ojeda et al. 2021; Soares et al. 2023) especially during summer months (Giorgi and Lionello 2008; Ozturk et al. 2015; IPCC 2023), thus significantly disrupting agriculture and forestry, two climate-sensitive sectors in this region (IPCC 2023).

Mediterranean forests show large events of tree mortality and diebacks consistently linked to warmer and drier average conditions (Sánchez-Salguero et al. 2020), exacerbated by biotic stresses such as pathogens (Homet et al. 2019). Projections suggest possible local extinction for many forest species that may not be able to migrate fast enough to keep up with changing climates (IPCC 2023).

Among tree crops sensitive to climate change, *Castanea sativa* (Mill.) known as the European sweet chestnut (Fagaceae), has a wide distribution range from Northern Europe to Asia Minor (Conedera et al. 2016; Freitas et al. 2021) and covers 2,715,050 ha in Europe (Gomes-Laranjo et al. 2024). It is mesophilic, thus displaying optimal growth in medium humidity and temperature (Gomes-Laranjo et al. 2009), but also grows in Mediterranean climates with warm summers and humid cold winters (Zhang et al. 2011). Climate change-induced shifts in precipitation regimes are expected to lead to more frequent and intense droughts (Böhnisch et al. 2021; García-Valdecasas Ojeda et al. 2021; Soares et al. 2023), further increasing the potential risks to chestnut cultivation in addition to other challenges encountered by this sector (Aumeeruddy-Thomas et al. 2012; Bellat et al. 2019).

Traditional chestnut agrosystems are complex agroforestry systems in the Mediterranean, that incorporate both orchard and forest components. People have been deeply linked to selected varieties of chestnut since the Middle Ages (Reyne 1984; Pitte 1986; Conedera et al. 2004). Between 400 and 500 varieties are known in France (Hennion et al. 2009; Bouffartigue 2020) and have been multiplied through vegetative propagation by grafting onto rootstock of chestnut (*Castanea sativa*) naturally growing from seedlings or on vegetative coppices grown from cut trees (Aumeeruddy-Thomas et al. 2012; Bouffartigue 2020). Most traditional farms are polyvarietal, representing a diversity of genetic resources originating from diverse regions that have been exchanged over time between farmers (Dupré 2002; Bouffartigue 2020), associated with a deep knowledge of farmers regarding their phenology, morphological traits, post-production treatment, conservation and sensitivity to pathogens (Aumeeruddy-Thomas et al. 2024).

Chestnut agrosystems are multifunctional, combining chestnut fruit production, livestock grazing (mostly sheep and goats), production of diverse fruits and vegetables, bee-keeping and management of forests for livestock and wood (Pitte 1986). Yet, the dominant species remains the chestnut, representing a significant part of farmers' revenue in France and across Europe (Castellana et al. 2021; Freitas et al. 2022; CTIFL 2023). Moreover, since agroforestry has been identified as an adaptive strategy for mitigating impacts of climate change, studying chestnut agrosystems are of particular interest for understanding their ability to thrive in the future and provide real solutions in the Mediterranean "climate change hotspot" (IPCC 2023).

There remains a significant knowledge gap regarding the ability of chestnut producers to endure the impacts of climate change, notably those associated with a production decrease (Freitas et al. 2021). Rising concerns were expressed by producers and stakeholders, encouraging them to take action notably by partnering with researchers (Aumeeruddy-Thomas et al. 2024). Studying chestnut trees' ability to cope with climate change and especially the large possibilities offered by selected varieties is important to implement appropriate adaptive solutions for chestnut growers (Freitas et al. 2021; Marques et al. 2025).

Projections for chestnut forests under climate change predict a decrease of the suitable growing area and of their productivity in Portugal and Turkey (Çobanoğlu et al. 2023; Erturk and Aricak 2024; Freitas et al. 2024; Álvarez-Álvarez et al. 2025). More precisely, phenological changes (Larue et al. 2021; Conedera et al. 2021) and drought-induced physiological stress (Alcaide et al. 2019; Pérez-Giron et al. 2020; Castellana et al. 2021) have been reported. These studies have described chestnut trees' behaviour at a species level and were mainly targeted towards forest. Little is known about variations at the varietal level within managed chestnut orchards (Gomes-Laranjo et al. 2012; Freitas et al. 2021). Yet, varieties are known to display substantial variation in their phenology, morphology (Furones-Pérez and Fernández-López 2009; Dinis et al. 2011) and functional traits (Gomes-Laranjo et al. 2006), but whether these differences translate into different capacities to adapt to future climatic conditions is largely unknown.

Crop yield modelling is a key aspect of agricultural research on climate change impacts on food security (Chaliner et al. 2009; Lobell et al. 2013; Zipper et al. 2016; Leng et al. 2019; Guo et al. 2019; Li et al. 2019). Several crop models describing key physiological mechanisms have been developed during the last decades, such as APSIM, DSSAT, STICS and ORYZA (Farooq et al. 2023; Gavasso-Rita et al. 2024). However, a clear modelling gap exists for perennial and underrepresented crops such as chestnut. Indeed, the vast majority of studies focuses on the main annual crops, i.e., maize, soybean, wheat and rice, highlighting the need to

extend research to other crops (Hu et al. 2024; Gavasso-Rita et al. 2024). Data scarcity on chestnut compared to other fruit trees (Fernandez et al. 2022) makes it challenging to use existing crop models. In this study, we propose to use a process-based model to study the impact of climate change on chestnut varieties in a major region of chestnut production in southern France, the Cévennes.

Originally developed for forest trees, the PHENOFIT model estimates a tree's fitness as a product of its survival and reproductive success across its lifetime, depending on the pedoclimatic conditions (Chuine and Beaubien 2001). The model is based on three main ecophysiological processes affecting survival and reproduction: phenology, resistance to drought and resistance to frost. Compared to other tree ecophysiology models such as FOREST-BGC, BIOMASS, 3-PG or TRIPLEX (Landsberg 2003; Lo et al. 2011), PHENOFIT uses a relatively small number of parameters, which makes it particularly suitable for use in data-poor environments, such as the rugged, mid-altitude regions where chestnuts are traditionally grown in southern Europe (Pérez-Girón et al. 2020). Nevertheless, its calibration requires phenological observations of leaf unfolding, flowering, fruit maturation and leaf senescence, and corresponding meteorological data that are not available in the literature. We thus established a participatory observation network in southern France to collect these data. This collaborative effort brings together chestnut growers, ecologists and regional agricultural institutions to co-construct phenological monitoring protocols (Aumeeruddy-Thomas et al. 2024). This group of people monitored fourteen varieties spanning a large range of precocity of fruit ripening, in order to evaluate intraspecific variability in climate sensitivity, a key component of adaptive capacity (Fernandez et al. 2022).

With this study we aimed to address the degree of suitability of future climatic conditions until 2100 for the main chestnut varieties cultivated in traditional orchards in Cévennes. More precisely, here we assess the extent to which climate change will shift chestnut phenology and how this will translate into changes in exposure to late frosts, developmental issues due to warmer winters, and changes in growing area distribution. Finally, given the great adaptability of *Castanea sativa* (Mill.) which occupies a wide range of habitats, and the existence of varieties historically selected to suit orchard systems with specific management regimes (Conedera et al. 2016), our aim is to assess their plasticity for cultivation in future climatic conditions.

Consistent with current predictions for other forest tree species, we expect a decrease of the growing area and a migration towards higher elevation for cultivated varieties notably because of a decreased frost risk. We also expect phenology changes, especially shifts towards earlier dates for all development stages as well as different responses to climate change of the chestnut varieties.

Materials and methods

Study area

Our study relied on phenological and meteorological observations from four sites located in the Cévennes, southern France, within a wider observation network (Aumeeruddy-Thomas et al. 2024). These sites lie in middle range mountainous regions characterised by a Mediterranean climate. Data were collected either by chestnut producers living on-site or by local non-governmental organizations (Fig. 1).

Chestnut varieties and orchards contexts

Varieties of *Castanea sativa* in France are clones as confirmed by genetic studies (Bouffartigue et al. 2020). They are preserved through vegetative propagation by grafting (Furones-Pérez and Fernández-López 2009; McKey et al. 2010). We observed 3 named and grown varieties in Cévennes, each observed at least in two sites within traditional orchards.

The orchards at the four study sites contain old trees (over 100-year-old) grafted onto rootstocks growing spontaneously and selected by farmers for their vigour and site-suitability. These trees grow in an irregular pattern, reflecting farmer's choices. Historically, soil conditions were improved through terracing, which is now largely abandoned, and by nutrient inputs linked to animal husbandry practices (Aumeeruddy-Thomas et al. 2012; Bouffartigue 2020). Although the rootstock may influence observed traits, it was not explicitly investigated and was controlled for in the experimental design (see below).

Varieties observed were selected with the producers in relation to our scientific questions, covering early and late varieties that are easily found in sites with distinct topoclimatic conditions, and in relation to producers' interest in terms of fruit quality, market relevance and cultural significance. The three chosen varieties were: Figarette, Gascaise and Pellegrine.

Phenology data

Phenological observation followed a simplified version of the Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie (BBCH) scale (Bleiholder et al. 1989), commonly used in agronomy (Larue 2021) and ecology (Badeau et al. 2017). To make it better fit with chestnut trees and field constraints, this scale was adapted during workshops with local stakeholders to ensure feasibility within farm settings (Badeau et al. 2017; Aumeeruddy-Thomas et al. 2024). Observers recorded five main phenological stages: budburst, leaf unfolding, flowering, fruit maturation

Table 1 Phenological data collected between 2021 and 2024 and used for modelling each phenology stage for each variety. For leaf senescence date, there were not enough data to reliably characterize each variety. Analyses were therefore conducted at the species level (*Castanea sativa*), using all available observations across all recorded varieties, including varieties other than Figarette, Gascaise and Pellegrine

Phenology stage	Variety	Number of sites	Number of observations	Mean date (day of year)
Budburst BBCH 06	Figarette	3	7	99 ± 7
	Gascaise	2	5	98 ± 4
	Pellegrine	4	11	107 ± 4
Budburst BBCH 07	Figarette	3	7	104 ± 6
	Gascaise	2	5	105 ± 3
	Pellegrine	4	11	112 ± 4
Leaf unfolding BBCH 11	Figarette	3	7	111 ± 5
	Gascaise	2	5	113 ± 5
	Pellegrine	4	11	119 ± 4
Leaf unfolding BBCH 15	Figarette	3	7	115 ± 6
	Gascaise	2	5	121 ± 1
	Pellegrine	4	11	125 ± 2
Flowering BBCH 61	Figarette	3	4	170 ± 4
	Gascaise	2	2	164 ± 5
	Pellegrine	4	7	170 ± 2
Flowering BBCH 65	Figarette	3	4	174 ± 5
	Gascaise	2	3	167 ± 4
	Pellegrine	4	7	172 ± 2
Fruit maturation BBCH 81	Figarette	4	6	270 ± 3
	Gascaise	2	4	276 ± 3
	Pellegrine	4	8	282 ± 3
Fruit maturation BBCH 85	Figarette	4	7	278 ± 3
	Gascaise	2	4	284 ± 5
	Pellegrine	4	8	290 ± 3
Leaf senescence BBCH 91	Castanea	16	17	303 ± 10
Leaf senescence BBCH 95	Castanea	16	17	312 ± 7

difference calculated between the nearest Météo France weather station Saint-Martin-de-Lansuscle (<https://donneespubliques.meteofrance.fr/>) and our own measurements.

Gridded climatic data

A topo-climatic interpolation at 100-m resolution was conducted for each meteorological variable (solar radiation, temperature and precipitation) over a 600 km² area corresponding to the growing chestnut area in a representative area of chestnut cultivation in Cévennes (Delrieu et al. 2025). This interpolation was realized for both historical and RCP4.5 & RCP8.5 scenarios daily climate data. Note that while the RCP4.5 scenario has a stabilisation trajectory expecting a 2 °C global surface temperature to increase by 2100, the

RCP8.5 scenario predicts at least a 4 °C increase by the end of the century if no action is undertaken (Calvin et al. 2023). The climate interpolation processing chain required elevation data from ASTER-GDEM, the daily meteorological data from the Météo France nearest weather station, the gridded SAFRAN and the meteorological data registered by iButtons as well as data from the DRIAS database for future projections. Due to the high spatial resolution required for the study over the area, and to avoid unnecessary energy consumption for the model simulations (Voosen 2024), we compared climate projections from several available models to identify whether we could use a single model's projections that lie at the median of the projections of all models. We chose the CNRM-CM5/ALADIN63, a regional climate model which projections of temperature and precipitation change are situated at the median of the projections of all models available.

Downscaling and predictive modelling of topo-climatic variables are detailed by Delrieu et al. (2025) (see Supplementary Material, Downscaling Methods section). The produced downscaled projections include daily (1) global solar radiations, (2) minimum, maximum and mean air temperatures, (3) potential evapotranspiration and (4) precipitation. Global solar radiation was calculated with the combination of direct and diffuse clearsky radiation (Druel et al. 2025) attenuated by a cloudiness proxy index (Hargreaves and Samani 1982). Daily temperatures were obtained using a refined data-driven topoclimatic interpolation of minimum and maximum temperatures with a Random Forest model, beyond the usual lapse-rate considering the effect of altitude on temperature decrease. Potential evapotranspiration was computed from solar radiation and mean air temperature with a simplified Priestley-Taylor equation (Allen et al. 1998; Anupoju et al. 2025). Precipitations were interpolated using the bilinear reprojection function `raster::projectRaster()` of the 8 km resolution SAFRAN gridded data.

Model calibration

To assess the climate suitability of the different varieties of chestnut tree, we used the process-based model PHENOFIT (Chuine and Beaubien 2001), that estimates tree survival and reproductive success under specified pedoclimatic conditions. This model has been used to predict the future geographic distribution of forest tree species (e.g. Morin et al. 2008; Saltré et al. 2015; Gauzere et al. 2020; Van der Meersch et al. 2025). The main ecophysiological processes represented in the model are the phenology (budburst, leaf unfolding, flowering, fruit maturation and leaf senescence) and resistance to abiotic stressors such as frost and drought. PHENOFIT estimates the suitability of pedoclimatic conditions for a particular species or variety using a fitness proxy defined as the product of (1) the probability of survival, (2)

the proportion of fruits not destroyed by frost and (3) the probability that fruits reach full maturation (Supplementary Fig. S1). The model runs on a daily time step using daily meteorological data and yearly yield outputs.

Model calibration requires first calibrating phenological sub-models of leaf unfolding, flowering, fruit maturation and leaf senescence using inverse modelling. This was done with the phenological data collected for each variety (except leaf senescence, which was calibrated with data for all varieties due to lack of data) and the associated daily temperature data from the data loggers. Second, other parameters related to frost and drought resistance were identified in the literature.

Calibration of phenology sub-models

To calibrate sub-models for each phenological stage we used the Phenology Modelling Platform 5 (PMP5), a software that allows building and calibrating phenology models (Chuine et al. 2013; Chuine and Régnière 2017). Among the models available, we selected the simplest models because of the relatively small amounts of data available for each phenological stage and each variety (see Supplementary Materials and Table S2 for the phenology models' description and calibration details).

For each phenological stage we calibrated several phenology models and selected the models providing the best efficiency ($EFF = \frac{SS_{tot} - SS_{res}}{SS_{tot}}$ with SS_{res} the residual sum of squares $\sum_1^n (y_i - \hat{y}_i)^2$ and SS_{tot} the total sum of squares $\sum_1^n (y_i - \bar{y})^2$ with y_i the observed dates, $\bar{y}$ the mean of the observed dates and $\hat{y}_i$ the predicted dates), the best Root Mean Squared Error ($RMSE = \sqrt{1/n \sum_1^n (y_i - \hat{y}_i)^2}$), the most realistic parameter values and the most realistic predictions at the scale of the whole growing area, especially regarding the hierarchy of precocity for all phenological stages between the varieties.

Calibration of frost and drought resistance

Sub-model parameter values for frost and drought resistance were extracted from the literature. *Castanea sativa* is a mesophilic species adapted to mean temperatures between 8 and 15 °C, tolerating maximum temperatures up to 31 °C and minimum temperatures down to −16 °C (Gomes-Laranjo et al. 2009; Zhang et al. 2011; Freitas et al. 2021). Tolerance of low temperatures could be even greater considering that *Castanea dentata* displays frost tolerance up to −28.9 °C (Schaberg et al. 2022). We set the lethal frost threshold at −30 °C (Schaberg et al. 2022) and temperature causing 50% damage of leaf tissues at −2 °C (Breisch 1995; Fernandez Lopez et al. 2005; Schaberg et al. 2022). Moreover, tolerance to humidity was set between 500- and 3500-mm annual precipitation (Nakhutsrishvili 2012; Conedera et al. 2016;

Metreveli et al. 2023). Parameters values for frost hardiness of flowers and fruits, as well as maximum frost hardiness during dormancy, data for chestnut were not available so we relied on values known for beech, *Fagus sylvatica* L., another Fagaceae species living in western Europe (Supplementary Table S2).

Model simulations

Using the climatic data produced at a 100-m resolution across the study area, the model PHENOFIT was run for the historical period (2001–2020) and future period (2076–2100) following RCP 4.5 and RCP 8.5. From pooling the model yearly output, we generated both maps and time series at four location points corresponding to the study sites.

Results

Phenology model calibration results

Two sets of parameters were selected per variety for the leaf unfolding-flowering stage and two sets of parameters for the fruit maturation stage. In each set, the first one had the highest model efficiency and the second one a slightly lower efficiency but was more consistent with parameter values obtained for the other studied varieties. Parameter values of the leaf senescence stage were identical for all varieties (see Material & methods). Thus, for each variety, we constructed four parameter sets (2 leaf unfolding-flowering × 2 fruit maturation sets) to describe their whole phenological cycle. These parameter sets showed intra-variety variability (Table 2). Using PHENOFIT, we then tested these parameter sets on past climatic data to assess their ability to replicate current observed phenology and varieties' precocity across the entire growing area. For future projections, we selected for each variety the set of parameters which provided the most consistent predictions of the entire phenological cycle across the growing area (Table 2).

The efficiency of the retained parameter sets for budburst was 0.93, 0.89 and 0.31 respectively for Figarette, Gascaise and Pellegrine (Table 2). Despite a weaker efficiency for the last variety, it achieved a RMSE value of 4.18 days which is acceptable compared to the data precision of 2–3 days. For fruit maturation of the three varieties, the efficiency ranged between 0.49 and 0.77 but these efficiencies were still accompanied by satisfactory RMSE values comprised between 2.96 and 2.07 days. The leaf senescence date was harder to predict accurately as data was combined for all varieties. It showed low efficiency ($EFF = 0.37$) and high RMSE ($RMSE = 8.36$ days). The calibrated models predict that the precocity of a variety is conserved from leaf unfolding to fruit maturation consistently with the local knowledge of chestnut farmers, e.g., Figarette is the earliest variety

Table 2 Parameter sets of the different phenological models used to obtain the projections with the model PHENOFIT for each variety

Process	Function	Parameter	Figarette	Gascaise	Pellegrine
Dormancy BBCH 00 to 07	Threshold inferior	t_0	−122	−122	−122
		V_b	16.41	17.29	19.24
		C_{crit}	27.86	92.10	34.62
	GDD	T_b	1.72	1.58	0.04
		F_{crit}^{bud}	1071.97	677.31	1516.21
		RMSE	1.89	1.32	4.18
	Efficiency		0.93	0.89	0.31
Leaf unfolding BBCH 07 to 15	GDD	$T_{b_{leaf}}$	1.72	1.58	0.04
		F_{crit}	109.68	176.59	165.81
		RMSE	4.46	1.76	3.14
	Efficiency		0.56	−0.55	−0.14
Flowering BBCH 07 to 65	GDD	T_b	1.72	1.58	0.04
		F_{crit}^{flower}	815.04	717.45	840.19
		RMSE	1.45	1.16	4.06
	Efficiency		−1.80	0.93	−2.42
Fruit maturation BBCH 65 to 85	Sigmoid	aa	−7.50	−16.01	−22.83
		bb	20.50	22.45	22.21
		F_{crit}^{fruit}	11.06	20.46	19.88
	Wang & Engel	T_{opt}	5.96	5.87	5.29
		Mat_{moy}	54.02	48.84	52.67
		RMSE	2.96	2.71	2.07
	Efficiency		0.49	0.77	0.65
Leaf senescence BBCH 95	Threshold inferior	t_0	244		
		V_b	20.64		
		F_{crit}	44.89		
	RMSE		8.36		

and Pellegrine the latest one from leaf unfolding to fruit maturation.

Shifts in phenology

Projections at the four sites revealed differences between varieties and between sites. Varieties especially differed for dates of leaf unfolding and fruit maturation (Fig. 2). In most cases, an early leaf unfolding date translated into an early fruit maturation date (Fig. 2). Figarette is always the earliest to achieve fruit maturation on a given site (except in La Jasse in 2001—2020), regardless of the climatic conditions, and Pellegrine is always the latest (Fig. 2). Climatic conditions of the RCP8.5 scenario generated a shift towards earlier dates of leaf unfolding (-11.8 ± 3.6 days), flowering (-17.5 ± 2.6 days) and fruit maturation (-22 ± 6.8 days), but later dates of leaf senescence of about a week (6.8 ± 0.3 days) compared to 2001—2020. Therefore, under future climatic conditions, the growing season enlarges and the time

between fruit maturation and leaf senescence is projected to be longer than in historical conditions.

Moreover, the differences between varieties in fruit maturation date is predicted to decrease (Supplementary Fig. S2). The range between the earliest and the latest varieties on each site decreased from 21.5 ± 4 days in historical conditions (2001—2020) to 14.8 ± 2.1 days under RCP8.5 conditions in 2076—2100.

At the scale of the growing area in Cévennes (hereafter Cévennes growing area), we observed that leaf unfolding (Fig. 3c) and flowering (Fig. S3e) currently occur earlier at valley bottoms and later on crests and summits. This pattern is projected to persist under future climatic scenarios. In contrast, fruit maturation (Fig. 3d) and leaf senescence (Fig. S3f) display non-linear elevational gradient under current and RCP4.5 conditions, with earlier dates at mid-elevations. Under RCP8.5, however, these events are projected to occur progressively earlier at lower elevations.

By 2100, projections under future climatic conditions indicate an overall advancement of all phenological stages

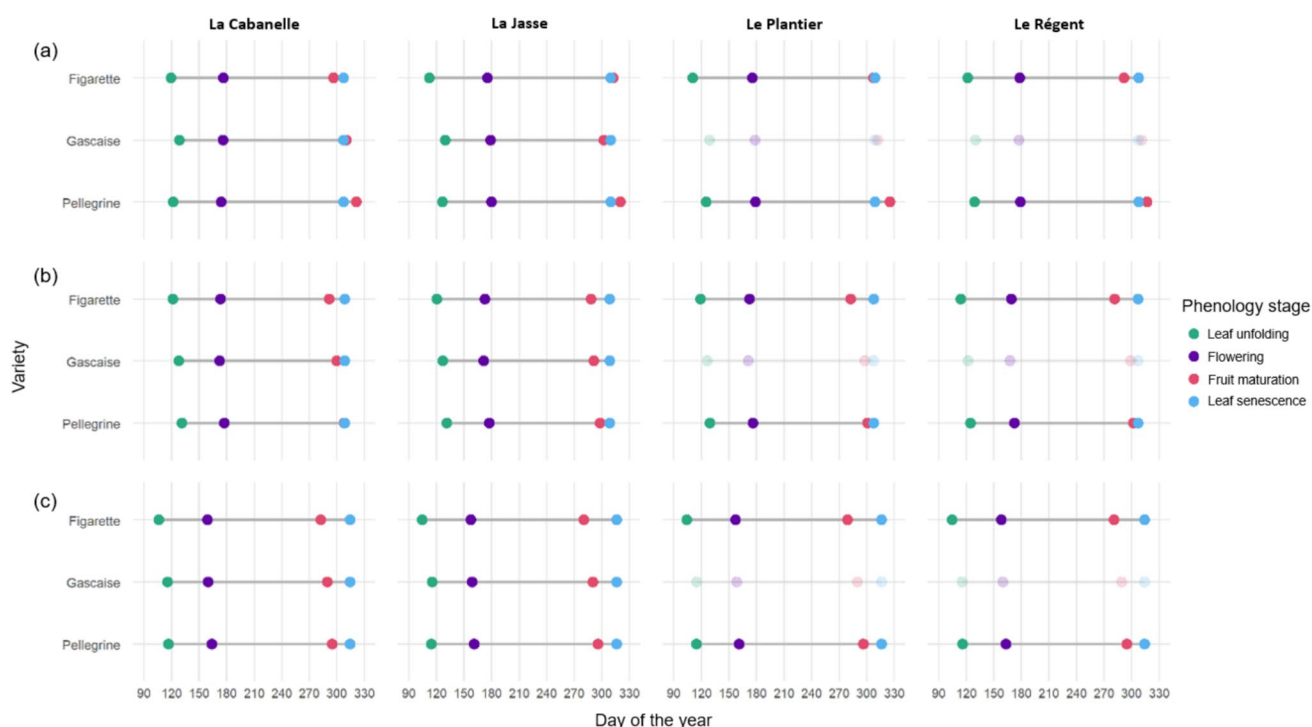


Fig. 2 Mean DOY of leaf unfolding (green), flowering (purple), fruit maturation (red) and leaf senescence (blue) for each variety, site and climatic conditions: **a** past (2001–2020), **b** RCP4.5 (2076–2100),

c RCP8.5 (2076–2100). Grey represents sites where the variety is actually absent

(except for leaf senescence) across the Cévennes growing area. This shift is particularly pronounced under the high-emission scenario RCP8.5 which predicts warmer temperatures on average. For fruit maturation (Fig. 3d) and leaf senescence (Fig. S3f), the non-linear gradient along elevation tends to vanish under RCP8.5, leading to a homogenization of the date of occurrence of these events regardless of elevation. In addition to these trends, interannual variations to the dates are observed (Fig. S4). The average variation of the dates across all varieties and climate scenarios is for leaf unfolding is 11 days (mean date 123 DOY), for flowering 9 days (mean date 172 DOY), for maturation 19 days (mean date 306 DOY), for leaf senescence 6 days (mean date 310 DOY). The interannual variation in the phenological dates is predicted to decrease under scenario RCP8.5 except for leaf senescence (Fig S4d).

Extension of the chestnut growing area

Projections for the three varieties under future climatic conditions in Cévennes reveal new potential growing areas, uphill and downhill from the current still viable cultivation zones, where chestnut could potentially be grown after 2050 (Fig. 3a). These extensions both uphill and downhill indicate an increasing ability of the varieties to meet their climatic requirements to achieve their entire annual development

undamaged by climatic hazards in future climatic conditions. More precisely, this extension results from three main effects. First, temperature warming increases the probability that fruit maturation will be completed before the end of the season because fruit maturation occurs earlier while leaf senescence occurs later (Fig. S3b). Second, projected temperature warming should progressively release leaves and flowers from exposure to frost, despite the advancing of leaf unfolding (Fig. 3c) and flowering dates (Fig. S3e). Third, projected climatic conditions used for this study do not result in an increase in summer drought that would impact survival and fruit development.

The wider spatial occurrence of successful leaf unfolding and flowering, suggests that rising temperature advances these developmental stages both uphill and downhill, while not exposing leaves and flowers to greater frost risk. Second, the extension downhill also reveals that temperature warming in this area does not prevent chilling requirements to be met in order to break bud dormancy. Fruit maturation is also reached earlier both uphill and downhill under both RCP4.5 and RCP8.5 conditions. This suggests a better ability of fruits to achieve maturity undamaged, i.e., a faster development and a lower risk of exposure of reproductive organs to frost in future climatic conditions. The expansion of the suitable growing area is particularly remarkable for the variety Pellegrine. This variety, occurring later than the

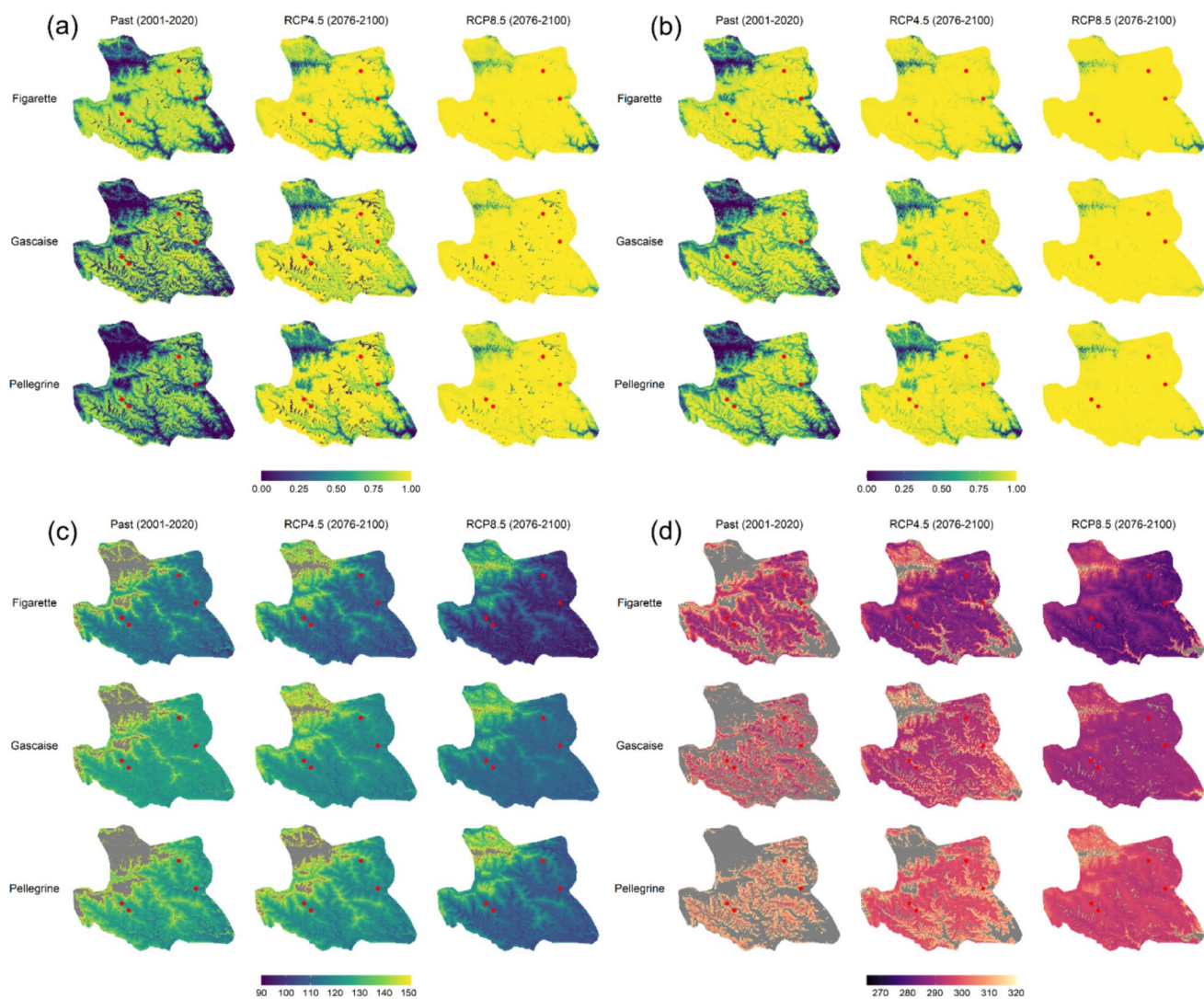


Fig. 3 Projections of PHENOFIT for each variety and climatic conditions. **a** Fitness index and **b** fruit index (proportion of undamaged fruits). Colour scale represents their probability between 0 and 1. **c** Leaf unfolding date and **d** fruit maturation date. Colour scale repre-

sents the mean values of each variable for all years of the time period. Areas in grey are outside a realistic range. Associated standard deviation is presented in Supplementary Fig. S4

others notably shows a much higher fruit index (proportion of flower-fruit undamaged by frost) under future climatic conditions (Fig. 3b) indicating a reduced exposure to frost events, while summer drought remains non-limiting.

Discussion

Chestnut varieties growing area extension and shifts in phenology

Our projections suggest a capacity of chestnut varieties to survive in their current growing area and to potentially extend beyond their current range. The considered chestnut

varieties are predicted to find adequate conditions to grow at higher but also lower elevations in the mountainous region of the Cévennes. Although phenology is influenced by environmental conditions and thus display regional variability, the relative order of precocity among varieties is maintained for budburst and fruit maturation. Our projections confirm that these precocity rankings remain stable under future climatic scenarios (Fig. 3).

Under RCP4.5, achievement of fruit maturation may restrict survival of chestnut varieties because of frost damage (Fig. 3d). In contrast, under RCP8.5, frost is no longer a restricting factor in the studied growing area (Fig. 3b–d). When frost still constrains the distribution of varieties either uphill or downhill, phenological events tend to occur later

than in the optimal range (Fig. 3d). The predicted increased distribution area is associated with a trend towards earlier leaf unfolding, flowering and fruit maturation in the current distribution area. This current shift towards earlier phenology has been identified in many other trees (Kramer et al. 2000; Vitasse et al. 2011; Asse et al. 2018) and Mediterranean crops (Moriondo and Bindi 2007). Projections under RCP8.5 also show a later occurrence of leaf senescence. Combined with an earlier budburst, this increases the growth period of chestnut trees. However, while spring displays optimal conditions for photosynthesis and growth, autumn is not optimal as photoperiod decreases. Moreover, despite being associated to accelerated leaf development and flowering for other Fagaceae species, these longer growth periods may increase water stress during summer and autumn through extended evapotranspiration (Puchalka et al. 2017, 2024) which could decrease chestnut growth and affect carbon balance (Flexas et al. 2006).

Under RCP8.5, where development of observed chestnut varieties is no longer limited downhill in valleys, we expect earlier achievement of phenological stages at lower elevation. Chilling requirements are predicted to be met, despite increased winter temperatures (Supplementary Fig. S5), which will allow for normal budburst (Lange et al. 2016; Chuine et al. 2016; Leolini et al. 2018b, a). Late-spring and autumn frost damages (Díaz et al. 2009; Freitas et al. 2022), of which frequency may increase with climate change and overlap because of earlier phenology (Zohner et al. 2020; Sangüesa-Barreda et al. 2021) are not predicted to affect the development of leaves, flowers and fruits for chestnut trees under the future climatic conditions used for this study in the Cévennes region. Similar observations have been made on beech suggesting that the decreasing frequency of late spring frost event due to climate change even confers a fitness advantage to trees with early budburst as it enables for a prolonged growing season and better fruiting probability (Duputié et al. 2015). However, our findings contrast with most previous studies which project a decrease in the extension of chestnut forests growing area based on a correlative modelling approach (Çobanoğlu et al. 2023; Erturk and Aricak 2024; Freitas et al. 2024; Álvarez-Álvarez et al. 2025). This difference can be due to the models used. Process-based models are notoriously less pessimistic than correlative models (Morin and Thuiller 2009; Keenan et al. 2011; Cheaib et al. 2012; Takolander et al. 2019) because less sensitive to climate change than correlative models, but they are also more robust (Van der Meersch et al. 2025). It can also reflect the difference between forest chestnut trees and the cultivated chestnut trees which have been selected for fruit production and are meant to survive in man-made agrosystems associated with management practices. The PHENOFIT model only predicts species potential distributions, i.e. the geographical realisation of their climatic niche,

while cultivated chestnut trees' occurrence also depends upon human management.

Chilling accumulation

Warmer winters due to climate change may compromise the ability of temperate trees to meet chilling requirements necessary for dormancy release and proper phenological development (Chuine et al. 2016; Funes et al. 2016; Rodríguez et al. 2019). Despite the fact that *Castanea sativa* requires only moderate chilling (Santos et al. 2017), winter chilling may become insufficient in regions like the Mediterranean. For chestnut tree, this could lead to developmental issues such as bud abscission, delayed flowering or decreased flower quality (Atkinson et al. 2013) that could dramatically impact fruit production (Luedeling et al. 2011; Iglesias et al. 2012; Fraga et al. 2021). However, our predictions show that the three varieties considered would still be able to meet their chilling requirement until 2100 under RCP8.5 scenario in the study area, despite a 6 °C temperature increase. This contrasts with previous studies which have forecasted dormancy break issues before the end of the twenty-first century for other fruit trees such as apricot and peach in low-elevation Mediterranean sites exhibiting warmer conditions than in Cévennes (Chuine et al. 2016; Rodríguez et al. 2019; Egea et al. 2021). However, our results align with studies on deciduous trees in mountainous areas, where chilling requirements are still expected to be fulfilled despite rising temperatures, leading to earlier budbreak due to more optimal chilling conditions (Güsewell et al. 2017; Asse et al. 2018). As chilling requirements are expected to be met until 2100 in the growing area, the warming of spring, particularly enhanced in this mountainous region (Bruley et al. 2022), accelerates cell growth and leads to earlier leaf unfolding and flowering, and as a consequence also of fruit maturation, as also observed by Santamaría et al. (2011).

Late spring and autumn frosts

Our results suggest that in the Cévennes growing area, frost is the main limiting factor to chestnut distribution downhill and uphill because of its effects on leaves and flowers. Late-spring frost is known for its adverse effects on plants' distribution and growth because of the tissue damage they cause (Kollas et al. 2014; Körner et al. 2016; Liu et al. 2018). Current exposure to spring frost can happen from March to mid-May and chestnut buds are increasingly sensitive as they unfurl (Osaer et al. 1998). Despite future predictions indicating a decrease in the total number of frost days per year (Supplementary Fig. S5), temperate trees, and especially fruit trees' exposure to these events has increased over the last decade and are predicted to increase in some areas due to earlier budbreak (Liu et al. 2018; Vitasse et al. 2018a, b;

Zohner et al. 2020). In future climatic conditions, we predict for the three chestnut varieties earlier leaf unfolding, flowering and fruit maturation, along with higher fruit and leaf indices, both of which indicate lower frost damage to flowers and leaves respectively, which is consistent with studies on European temperate trees (Vitasse et al. 2011). Moreover, despite earlier flowering, chestnut catkins of traditional varieties remain unaffected by frost under both RCP4.5 and RCP8.5 scenarios, as their flowering occurs mainly in June and thus falls outside the frost risk window. These results are consistent with studies on *Castanea sativa* highlighting correlation between flushing time and resistance to spring frost (Fernández-López et al. 2005).

If climate change seems to benefit Pellegrine, Gascaise and Figarette in the Cévennes, it might not benefit hybrid varieties which are known to be more sensitive to frost damage notably because of their earlier budburst (Gurney et al. 2011; CTIFL 2023). This is detrimental economically because these hybrids are known to have high yields and to fruit early, traits that are highly prized by chestnut farmers (Perulli et al. 2024). Moreover, fruit exposure to autumn frost is projected to decrease due to earlier fruit maturation, thus avoiding adverse consequences for chestnut production (Díaz et al. 2009). However, because of the lack of data on the frost hardiness of chestnut flowers and young fruits, we applied the parameter values used for beech (*Fagus sylvatica* L.), respectively -5.3°C and -6°C , which may be different from the three varieties frost hardiness.

Shortening of maturation period

We predicted a considerable shortening of the fruit maturation period. The difference between the earliest and the latest varieties decreased by almost a week to span on 14.8 ± 2.1 days in RCP8.5 (2076–2100) compared to historical conditions. This result is consistent with previous studies which showed a trend towards a weakening of the leaf unfolding date gradient along elevation in European mountainous regions with global warming (Vitasse et al. 2018a, b). Our results suggest a similar trend for fruit maturation. This shortening and uniformization of the maturation period across the growing area could have adverse effects on chestnut producers' ability to organise and complete harvesting before selling.

Varietal variation in behaviour

Our results highlight phenological variation among three varieties. On the four sites, leaf unfolding of Figarette and Pellegrine occurred on average at day 115 ± 6 and day 125 ± 2 , respectively in 2021–2024, and fruit maturation occurred at day 278 ± 3 and day 290 ± 3 on average

respectively. These phenological differences translate into different parameter values of the phenological models. For example, the threshold temperature value of the chilling function obtained for Figarette was 16.4 while it was 19.24 for Pellegrine. Genetic differences among chestnut varieties are well documented (Bouffartigue et al. 2020) and translate into distinct functional traits that may influence phenology or frost resistance (Lauteri et al. 2003; Furones-Pérez and Fernández-López 2009). Similar varietal differences in functional traits have also been demonstrated in other crops such as walnuts, grapevine and almonds (Díaz and Fernández-López 2005; Ortega-Farias and Riveros-Burgos 2019; Sakar et al. 2023). However, modelling studies rarely consider these variations in functional traits (Freitas et al. 2022; Álvarez-Álvarez et al. 2025). While frost is not predicted to be an issue for chestnut in the Cévennes under future climatic conditions, other functional traits could confer better survival ability to some varieties than others. These considerations highlight the importance of studying varietal responses to understand the resistance of a crop to climate change (Jacobsen 2014; Fraga et al. 2021), and highlight the importance of genetic variability for long term adaptation (Sheth and Angert 2016; Zettlemoyer and Peterson 2021). Regarding varietal selection based on phenology in the Cévennes region, our results do not suggest selecting varieties with lower chilling requirements by the end of the twenty-first century. However, this does not preclude that such selection might be necessary after 2100.

Role of the rootstock

In order to isolate varietal response to future climatic conditions, we deliberately chose not to include the rootstock effect in our analysis by pooling observations from five individuals per variety, despite its well-documented role in tree performance and resilience to environmental stress. This methodological choice allows a clearer interpretation of varietal behaviour, although grafting, and rootstocks in particular, can significantly influence multiple traits, from morpho-physiology and phenology to pest resistance and abiotic stress tolerance (Nimbolkar et al. 2016; Dogra et al. 2018; Schwarz et al. 2010; Baron et al. 2019). Rootstock can indeed modulate the plant's response to climatic challenges such as their ability to tolerate cold and drought (Marques et al. 2025). Therefore, while not directly addressed in this study, the genetic diversity and role of rootstocks remain crucial for the long-term adaptation and survival of chestnut crops, and should be the focus of dedicated complementary studies (Míguez-Soto et al. 2019; Zhang et al. 2011; Castellana et al. 2021; Freitas et al. 2021).

Drought tolerance

Drought is considered to be the most important limiting factors for chestnut along with frost (Díaz et al. 2009; Freitas et al. 2022; Álvarez-Álvarez et al. 2025). In the Mediterranean region, climate change is predicted to lead to shifts in precipitation patterns (De Luis et al. 2010; Lorenzo and Alvarez 2022), resulting in more frequent and intense droughts (García-Valdecasas Ojeda et al. 2021; Soares et al. 2023) including southern France and the Cevennes region (Ruffault et al. 2013). Chestnut tree has a wide range of tolerance for precipitation but its optimal range varies among places and studies, with minimum precipitations between 500 and 800 mm (Nakhutsrishvili 2013; Conedera et al. 2016; Metreveli et al. 2023) with exceptions as low as 200 mm in black sea region (Cedano Giraldo and Mumcu Küçük 2024) including areas with up to 3500 mm of precipitations (Nakhutsrishvili 2013; Metreveli et al. 2023). For this study, we selected an annual precipitation range of 500–3500 mm to predict survival to drought to account for full precipitation range besides exceptions which is not set to be limiting as the Cévennes record of mean annual precipitations is above 1000 mm since 1940 (meteoblue). According to CNRM-CM5/ALADIN63 projections, annual precipitation should not shift above 3500 mm or below 500 mm in the growing area under RCP8.5. Rainfall seasonality is recognised as critical for agriculture (Iglesias et al. 2012; Conedera et al. 2016). Long periods of drought, exceeding two months, constitute a major limiting factor for the growth of chestnut trees (Freitas et al. 2021) and may affect the quality of their fruits (Farooq et al. 2023). Moreover, chestnut trees require rainfall during the fruiting period at the end of summer or early September (Breisch 1995). This potential effect of drought on fruit development was properly taken into account in the model by using a daily water budget in the fruit development model. The shift towards earlier fruit maturation is likely to expose trees to higher temperatures and droughts during the fruiting period, resulting on detrimental consequences on chestnut fruits such as lower quality (Castellana et al. 2021), as already observed on grapevine (Ramos et al. 2018). Potential effects of very high temperatures were not taken into account in PHENOFIT. Yet, temperatures above 32 °C can induce thermo-inhibition in chestnut trees, with heatwaves during the growing season, expected to increase in the future (Ruffault et al. 2013), potentially reducing yield despite adequate precipitation conditions (Marques et al. 2025). In addition to its effects on yields, water stress could also lead to smaller leaves limiting photosynthesis as well as flower and fruit abscission (Fraga et al. 2021) which is not taken into account in the PHENOFIT model. Furthermore, in our study, chestnut trees occur in anthropized low tree density systems, comparable to Spanish oak-based Dehesa, known to enhance individual

water accessibility (Montero et al. 2008; Moreno and Cubera 2008). We concur with Conedera et al. (2016) that modelling chestnut and its growing area must account for long-standing human impacts that have shaped these habitats.

Limits to our study

The simulated topo-climatic data were obtained with CNRM-CM5/ALADIN63, which, in mountainous regions, tends to overestimate precipitations by 15%, especially during summer (+ 100%) and underestimate temperatures by more than 2 °C (Marson et al. 2024; Robin et al. 2024; Delrieu et al. 2025). These biases might explain why we see no drought in the projections until 2100 even under scenario RCP8.5. Therefore, our results might be overly optimistic regarding the potential effect of drought and must be taken with caution. To mitigate bias in climate projections, it is recommended to rely on several climatic models and bias correction techniques (Ruffault et al. 2013; Farooq et al. 2023). Unfortunately, our projections were very resource-intensive due to the high spatial resolution chosen which limited our ability to use multiple climate models. While future studies might consider using lower spatial resolution to better address this issue, this would likely reduce the usefulness of the projections for the farmers.

Another limitation to our study comes from the dataset and data available on chestnut tree ecophysiology. Phenological observations are challenging on chestnut tree. Observations of flowering are especially difficult since chestnut trees display a diversity of male catkins from astaminate to longistaminate (Solignat and Chapa 1975; Larue et al. 2021) and have shown behaviours such as premature catkin loss. Leaf senescence is also notoriously difficult to observe (Liu et al. 2018), especially because it is sensitive to external factors such as strong winds, storms or disease (Delpierre et al. 2009). The scarcity of data on leaf senescence obliged us to use a phenology model that was calibrated using all data available, regardless of variety. This model is therefore representative of the behaviour of *Castanea sativa* in the studied area rather than of each of the three varieties individually. Moreover, data scarcity on the other stages made it complicated to identify best parameter values for each stage because of compensations between some parameters leading to non-equifinality of parameter values (Van der Meersch and Chuine 2025). Because of this, we were not able to perform a cross validation of the phenological models (Chuine and Régnière 2017), which requires additional data not used during parameter adjustments (Stone 1977). We also found very few data and information on the ecophysiology of *Castanea sativa*, which is somehow puzzling given the socioeconomic importance of the species. Therefore, we had to rely on information on other Fagaceae species, especially for frost resistance which, thus, might be

under or overestimated. Yet, major differences in frost tolerance have been reported between species (Gomes-Laranjo et al. 2009; Zhang et al. 2011; Freitas et al. 2021; Schaberg et al. 2022). It is therefore important to assess frost hardiness of chestnut varieties through controlled freezing experiments (Díaz et al. 2009).

Data scarcity on chestnut tree also prevented us from using more complex ecophysiology model than PHENOFIT. In particular, it would have been interesting for farmers to get projections of the impact of climate change on fruit quantity and quality, as well as on chestnut tree diseases and pests (Bindi and Olsen 2011; Dorado et al. 2023), the influence of extreme climatic events and precipitation seasonality (Iglesias et al. 2012; Vitasse et al. 2019) or the effects of soils, highly heterogeneous, and associated management practices which affect water retention capacities (Aguilera et al. 2013). However, most models still struggle to integrate these effects (Clarke et al. 2021; Campillay-Llanos et al. 2024) and overcoming these barriers will require further research. For soil heterogeneity, testing extremes in depths could better inform on the extent to which it influences water stress. New versions of the model are being developed to better integrate trees' physiology and responses to their growth conditions. However, including more parameters could affect the quality of predictions, if not associated with very large datasets.

The increased complexity of process-based models, while improving realism, introduces a higher risk of overfitting and non-identifiability of parameters, especially when inverse calibration is used without adequate physiological constraints (Basler 2016; Higgins et al. 2020; Zhang et al. 2024). These issues are exacerbated by the scarcity of long-term series of ecophysiological data and the difficulty of directly measuring some biological processes such as carbon allocation, dormancy break or frost hardiness (Chuine et al. 2013; Franklin et al. 2020). Uncertainty is further compounded when simulations rely on a single deterministic parameter set, ignoring the range of plausible sets (Fu et al. 2020; Simmonds et al. 2024).

Conclusion

This study highlights that, under RCP 4.5 and RCP8.5 scenarios, in the mountainous Mediterranean region of the Cévennes, chestnut trees may display earlier phenology and increase of their potential growing area uphill and downhill from their current distribution range. This implies that chestnut trees are likely to continue meeting their chilling requirements for budburst despite a warming of fall and winter. While late-spring and autumn frosts remain key limiting factors for chestnut trees distribution and fruiting ability, climate change is expected to ease such constraints, potentially enabling cultivation at both higher and lower

altitudes. Warmer temperatures are projected to induce earlier budburst without significantly increasing the risk of frost damage on leaves and flowers. Fruit maturation is also expected to advance and shift towards a period less exposed to frost, while delayed leaf senescence could contribute to an extended growing season. However, the projected narrowing of the fruit maturation window under RCP8.5 may pose challenges for growers. Earlier fruit development could also coincide with periods of heightened drought risk, raising concerns about water availability. The different phenologies observed across the three studied varieties underscore the need for further investigation on varietal tolerance to both frost and drought. Exploring this genetic diversity may enable the identification and selection of varieties better suited to future climatic conditions.

While relying on a limited set of data obtained collaboratively with chestnut producers during four years, process-based modelling has proven effective for projecting the behaviour of distinct varieties. Nevertheless, improving our knowledge of chestnut ecophysiology is essential for improving models' projections, anticipating climate change impacts and informing adaptive strategies to help farmers make better-informed decisions and support the long-term sustainability of their agricultural systems. This study, initiated at the request of the chestnut fruit production sector to assess climate change impacts on orchards, deepens our understanding of varietal dynamics under real conditions and marks a first step towards exploring the resilience of exceptionally rich polyvarietal agrosystems.

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Data availability Data used will be available on InDores open access repository (DOI).

Declarations

Competing interests The authors declare no competing interests.

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