



Climate change adaptation of Iberian dehesa: a simulation approach using the Hi-sAFe model

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Abstract

Agroforestry is a promising solution to enhance the resilience of agricultural systems against climate change. However, evidence on the long-term response of semi-natural agroforestry systems, such as extensive silvopastures, remains limited. To address this knowledge gap, this study assessed the production and temporal stability of a Mediterranean silvopastoral system, the Iberian dehesa, under climate change. The process-based Hi-sAFe model was used to simulate tree growth, pasture production, and their temporal stability from 1990 to 2100 under the very high emissions Representative Concentration Pathway 8.5 scenario in open grasslands and silvopastures with 25 and 50 trees ha⁻¹. Simulations were validated with long-term data on tree growth (2011–2023) and pasture production (2014–2024). We explored the optimal farm composition to maximize production and its temporal stability. The model accurately simulated tree growth (stem diameter; RMSE=1.63 cm, R² = 0.98) and pasture production (RMSE=0.4 t ha⁻¹, R²=0.95). Results indicated higher tree development and pasture biomass temporal stability at 25 than at 50 trees ha⁻¹, with 40% and 111% higher diameter increase and temporal stability, respectively. Open pastures had higher productivity than agroforestry and declined at all tree land covers over the 1990–2100 period. The agroforestry scenario at 25 trees ha⁻¹ showed the smallest decrease in pasture production (-1.4 kg ha⁻¹ yr⁻¹), compared to open pastures (-2.1 kg ha⁻¹ yr⁻¹) and 50 trees ha⁻¹ (-4.1 kg ha⁻¹ yr⁻¹), indicating a buffering effect against increased aridity. The optimal farm composition showed an increasing share of agroforestry at 25 trees ha⁻¹ density as climate change effects intensify. At the farm/landscape scale, a combination of open pastures and dehesas with different tree densities is recommended. This is the first study to apply the Hi-sAFe model to complex silvopastoral systems, indicating its usefulness and limitations in exploring trends and outcomes associated with different tree density scenarios under climate change.

Keywords Agroforestry · Land cover optimization · Tree density · Pasture production · Silvopastoral system · Process-based model · Temporal stability

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1 Introduction

Climate change will pose several challenges to agricultural systems in the coming decades (Vermeulen et al. 2012; IPCC 2023). The expected increase in extreme events, such as droughts and heatwaves, will increase temporal and spatial variability, reducing plant and livestock production (Ghahramani and Moore 2016; Sloat et al. 2018). Agroforestry systems (AF) are argued to be a feasible land use option for increasing the resilience against climate change (Hernández-Morcillo et al. 2018; Mosquera-Losada et al. 2018; Quandt et al. 2023). Trees can buffer climate extremes, ameliorate microclimatic conditions, and improve the soil water holding capacity, soil carbon content, and overall soil functioning (Moreno and Obrador 2007; Rolo et al. 2023). These beneficial effects have the potential to improve the response of agricultural systems to disturbances and provide long-term temporal stability of production (Raseduzzaman and Jensen 2017). Previous works have shown a higher temporal stability of crop production in silvoarable systems compared to open crops (e.g., Arenas-Corraliza et al. 2018; Dobhal et al. 2024). However, there is little evidence on the response of other types of AF, such as silvopasture, and more importantly, on the combined effect of AF on the productivity and temporal stability of agricultural systems.

A major barrier to assessing the climatic advantages of AF is the lack of long-term data, due to the difficulties in establishing and maintaining this type of study. AF studies are often short, involving only a few years. As a result, most research is based on young AF plots, which may limit the generalization of the results, as they may depend on the duration of the experiment and the age of the trees (Li et al. 2022; Roberti et al. 2025). Process-based models can

overcome these limitations, in part, by allowing the integration of different sources of observational data, providing mechanistic insights into ecological processes and allowing long-term temporal and/or spatial generality (Caldararu et al. 2023). For instance, process-based models may help to better design the spatial arrangement of vegetation components to optimize facilitative and limit competitive interactions between vegetation layers. There are several process-based models available for simulating (see Kraft et al. 2021; Rahman et al. 2023 for a review), such as the Yield-SAFE model (Graves et al. 2007; van der Werf et al. 2007; Burgess et al. 2023), WaNuLCAS (Van Noordwijk and Lusiana 1998), APSIM (Holzworth et al. 2018), and Hi-sAFe (Dupraz et al. 2019). The Hi-sAFe model is a three-dimensional (3D), process-based model that has been designed to account for interactive relationships between vegetation layers for light, soil available water, and soil nitrogen, while considering heterogeneous microclimatic effects (Dupraz et al. 2019). The three-dimensional and spatially explicit approach of Hi-sAFe may provide a more realistic representation of tree-pasture interactions than simpler models such as Yield-SAFE or WaNuLCAS that was developed for tropical regions, and may pose generalization issues in Mediterranean environments. The agroforestry module of APSIM Next Generation is still listed as under review and may require improvements for the reliable simulation of tree-crop interactions (Rahman et al. 2023; APSIM 2026). The characteristics of Hi-sAFe allow for the modelling of AF in a changing environment and to explore the behavior of complex ecological processes, such as long-term temporal stability and resilience, to anticipate their response to climate change. Hi-sAFe has been recently used to assess the climate change mitigating effect of wheat alley cropping in a Mediterranean environment (Reyes et al. 2021; Soulard

Fig. 1 Photo of the dehesa landscape at the “Majadas de Tiétar” Research Station (Photocredit: Gerardo Moreno Marcos)



et al. 2024) and to investigate interspecific water relationships under a dryland apple-Brassica intercropping system (Huo et al. 2021).

However, the use of biophysical models in heterogeneous silvopastoral systems is still limited (Luedeling et al. 2016). One of the most iconic silvopastoral systems worldwide is the oak open woodland of the Iberian Peninsula, known as dehesas in Spain and montados in Portugal (Fig. 1) (Tieskens et al. 2017; Pinto-Correia et al. 2018). They are considered an outstanding example of high nature value (HNV) farming systems and constitute the largest silvopastoral system in Europe, covering 3.1 million hectares (Plieninger et al. 2015, 2021). As a cultural landscape, their open woodland structure has been shaped by centuries of human management through forest clearing, cropping, and livestock grazing (Bugalho et al. 2011). Dehesas are renowned for being an example of integration of land-use and biodiversity conservation in a highly multifunctional system with a unique potential to provide multiple ecosystem services (Moreno et al. 2018). Along with other uses and products such as game, firewood, and cork, the main activity in these systems is livestock rearing. Livestock production in dehesas, although complemented by browse, acorns, and crops, depends primarily on pasture production. The production and dynamics of dehesas are strongly influenced by a Mediterranean climate with hot, dry summers and strong seasonality. Driven by these climatic constraints, pasture production shows high inter- (year-to-year) and intra- (month-to-month) annual variability (Olea and San Miguel 2006; Vázquez-De-Aldana et al. 2008), which is projected to increase in the coming decades (Godde et al. 2020).

Previous studies have highlighted the beneficial effects of trees in this system (Moreno 2008), but also the outstanding role of competition for water among trees and the pasture understory in drier years/conditions (Maestre et al. 2005; Cubera and Moreno 2007; Gea-Izquierdo et al. 2009). Bearing this in mind, it remains unclear to what extent trees could buffer the foreseen negative impact of climate change on Mediterranean and other semiarid pastures (Rolo and Moreno 2019; Hidalgo-Galvez et al. 2022), which may depend on competitive-facilitative interactions between pasture and trees (Dupraz et al. 1999; Gea-Izquierdo et al. 2009). In addition, previous research analyzing tree effects has focused on the effect of trees in isolation by comparing the position beneath and beyond tree canopies (e.g., Moreno 2008). There is also a lack of research on the effect of tree density, which is particularly variable in these systems (Olea and San Miguel 2006; Moreno and Pulido 2009; Herguido et al. 2017). Understanding the role of trees in pasture production and temporal stability can provide valuable insights to inform management practices that can facilitate the adaptation of silvopastoral systems to climate change. Additionally, density-dependent resource competition can affect tree

productivity and its stability. This is especially relevant in water-limited systems such as Iberian dehesas, where competition for water strongly determines tree performance, its interaction with pasture, and likely the response to future climatic conditions under climate change (Moreno and Cubera 2008; Morán-López et al. 2016; Moreno-de-las-Heras et al. 2023). Dehesas are experiencing a severe decline process over the last decades due to extreme heat waves and drought associated with climate change, tree ageing, and diseases such as root rot (Fernández-Habas et al. 2019; Marques et al. 2025). In this context, conservation and reforestation efforts demand information on the temporal stability of trees and pasture at varying tree densities under future climate change scenarios. Such information is also crucial for landscape planning, as it can help understand the trade-offs in functions and services of different land covers at the landscape level (Rolo et al. 2021). The use of bio-physical models offers the opportunity to provide insights into the effect of varying tree densities under a future, drier, and more variable climate, on pasture production, tree development, and their temporal stability.

This study aimed to assess tree growth, pasture production, and their temporal stability in the Mediterranean silvopastoral dehesa system (Fig. 1) in the context of climate change. To do so, we performed a virtual experiment by calibrating the bio-physical model Hi-sAFé (Dupraz et al. 2019) to the specific case of dehesas, comparing three different land covers: Open (no trees), 25 trees ha⁻¹ (typical dehesa stands), and 50 trees ha⁻¹ (dense dehesa stands) (Fig. 2). Based on the results, we explore the tree density that optimizes tree growth, pasture production, and their temporal stability under a future climate change scenario. This is the first study to apply the Hi-sAFé model to complex silvopastoral systems such as dehesas.

2 Material and methods

The workflow to implement Hi-sAFé followed four steps schematized in Fig. 2:

1. Data gathering on pasture production and tree growth from the validation site (2.1 Validation site).
2. Preparation of unbiased and homogenized weather data from 1900-1990 and according to the RCP8.5 climate change scenario for 1990-2100 (2.2. Weather data).
3. Calibration and validation of the Hi-sAFé model (2.3. The Hi-sAFé model and simulated scene, and 2.4. Model calibration and validation)
4. Running virtual experiments for the three tree densities (2.5. Virtual Experiments)

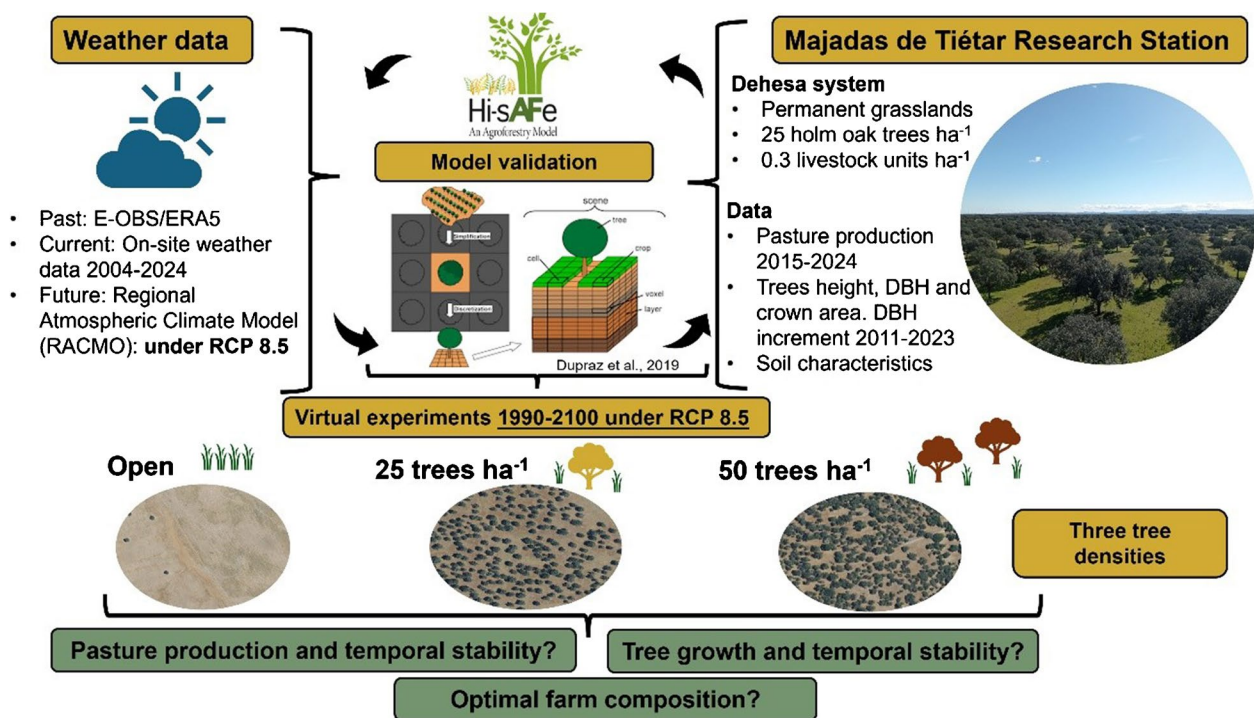


Fig. 2 Study workflow and research questions. Central illustration showing a schematic representation of a simulated Hi-sAFe scene and its corresponding 3D voxel grid (modified from Dupraz et al. 2019). Upper right photo taken at the “Majadas de Tiétar” Research Station

showing the typical dehesa landscape (Photo taken by Jesús Fernández Habas). Bottom images are aerial images (summer 2019) of areas representing examples of the three modeled tree densities (Source: PNOA 2019).

2.1 Validation site

The application of the Hi-sAFe model to the dehesa system was validated based on the “Majadas de Tiétar Research” Station of the Integrated Carbon Observation System network (ICOS site ES-LMa: https://meta.icos-cp.eu/resources/stations/ES_ES-LMa). Equipped with two Eddy covariance towers, the station has been operating since 2003, measuring CO₂ fluxes, meteorological variables, vegetation indices, soil respiration, sap flow, water dynamics, and ecosystem productivity (Max Planck Institute 2025). The measurements and data generated provide the opportunity to validate a process-based model with large parameter needs such as Hi-sAFe.

This station is located in the Extremadura region (Spain) 39° 56' N; 5° 46' W at about 260 m above sea level with an average slope of 3.6%. The climate is typical Mediterranean, characterized by strong seasonality with a dry summer and wet and mild winters. Mean annual precipitation is about 670 mm, and mean monthly temperature about 17.2 °C. The soil is classified as a Dystric Cambisol

over Pliocene-Miocene alluvial deposits. The structure of the vegetation is typical of a dehesa landscape, characterized by a permanent grassland layer interspersed with scattered trees at an average density of 25 trees ha⁻¹. The main tree species is Holm-oak (*Quercus ilex*), being mainly mature individuals over 100 years old (Camarero et al. 2025). The herbaceous layer is dominated by annual species such as *Tolpis barbata* (L.) Gaertn, *Gaudinia fragilis* (L.) P. Beauv, *Anthoxanthum aristatum* Boiss, *Avena barbata* Pott ex Link, *Lotus parviflorus* Desf and *Ornithopus compressus* L (Köbel et al. 2024). The dynamics of these annual grasslands are determined mainly by the seasonality of the Mediterranean climate, showing a senescence period during the summer season that lasts 4–5 months (San Miguel et al. 2017). The main purpose of the site is livestock rearing, mainly cattle and sheep, in an extensive system at a stocking rate of 0.3 livestock units (LU) ha⁻¹.

Table 1 Data sources used for calibration, validation, and simulation of Hi-sAFé for a dehesa system located at “Majadas de Tiétar” Research Station

Data	Years	Sample size	Used for	Source
Soil data	2014	-	Soil simulation and scene design	Direct measurement of soil layers in a profile
On-site weather data	2004-2024	-	Model calibration and validation	On-site weather station
E-OBS gridded observational weather data	1950-2024	-	Bias correction of RACMO output data	(Cornes et al. 2018)
ERA5 reanalysis weather data	1950-2024	-	Bias correction of RACMO output	(Hersbach et al. 2020)
RACMO RCP8.5 weather data	1990-2100	-	Simulation period 1990-2100	Source: (van Meijgaard et al. 2008; 2012) Access: (Palma 2017)
Allometric holm oak measurements	-	-	Fitting allometric equations to characterize holm oak trees	(Bogdanovich et al. 2021; MITECO 2020; Montero et al. 2005, 2008)
On-site tree height, DBH, and crown area	2015	105	Validation of tree growth simulations/ Independent data	On-site measurements (Bogdanovich et al. 2021)
On-site tree DBH increment	2011-2023	10	Validation of tree growth simulations/ Independent data	On-site measurements
Phenological data of pasture from MODIS Land Cover Dynamics (MCD12Q2)	2003-2022	-	Model parameterization: Pasture phenology	(Friedl et al. 2019)
Pasture production open areas	2015-2021	12/year	Model calibration: pasture production	0.5×0.5 m grazing exclusion cages
Pasture production open areas	2022-2024	12/year	Model validation: pasture production/ Independent data	0.5×0.5 m grazing exclusion cages
Pasture production below canopy	2015-2024	12/year	Model validation: pasture production/ Independent data	0.5×0.5 m grazing exclusion cages

2.2 Weather data

Daily weather variables, namely maximum and minimum temperature, maximum and minimum relative humidity, wind speed, solar radiation, and precipitation, are required to run Hi-sAFé. We used several sources to build a weather dataset covering the spin-up (1900-1990, see below 2.4. Model calibration and validation) and simulated period from 1990 to 2100 (Table 1). First, we obtained field data from a weather station installed on-site covering the period from 2004-2024. We supplemented this dataset with data from E-OBS, the Europe-wide gridded observational dataset, which are available on a 0.1° resolution (approx. 9 km) and provide data from 1950 to the present (Cornes et al. 2018). Further supplementary dataset is taken from the ERA5 reanalysis, available on a 0.25° resolution. For the period to initialize tree growth, from 1900 to 1949, we created an artificial dataset by sampling complete years from 1950-1970. Recycling weather data is commonly used to characterize and reach equilibrium in process-based models (e.g., Nemo Klumpp et al. 2017).

For future climate, data were collated from the Regional Atmospheric Climate Model (RACMO) (van Meijgaard et al. 2008; 2012). RACMO is a contributing model to the European Coordinated Regional Downscaling Experiment (EURO-CORDEX; Jacob et al. 2014) and has been

shown to perform well relative to other regional climate models (Vautard et al. 2021). The realization used here is driven by the EC-Earth global climate model (Hazeleger et al. 2010). While using projections from multiple models generally increases robustness, the use of a single, internally consistent global-regional model chain avoids mixing structural uncertainties across models. This is advantageous for our principal purpose to interpret climate signals, rather than quantify the full spread of model uncertainty. CliPick, a web tool to access climate data for forestry and agriculture (Palma 2017), was used to access RACMO data for the study site. Typically, climate change projections are generated by climate model simulations under one or more Representative Concentration Pathways (RCPs), which describe future scenarios of greenhouse gas emissions as defined by the Intergovernmental Panel on Climate Change (IPCC). The RCPs map directly to the Shared Socioeconomic Pathways included in the 6th and most recent IPCC Assessment Report (IPCC 2023). In this study, we used RCP8.5, which represents a “very high” emissions scenario. While RCP8.5 is considered low-probability under current socioeconomic and energy trends (e.g., Hausfather and Peters 2020a; 2020b; Pielke and Ritchie 2021; Scafetta 2024), its selection here provides a high-end exploratory scenario to stress-test agroforestry responses under severe climatic pressure. Rather

than investigate AF futures under alternative emissions pathways, we instead aim to evaluate outcomes at specific temperature thresholds associated with a warming world that are foreseen under RCP8.5 at different time horizons. Using warming levels has two key advantages. First, it decouples impact assessment from the choice of emissions scenario, allowing results to be interpreted independently of whether warming arises under a high-emissions or mitigation pathway. Second, it offers a scenario-agnostic measure of climate stress, ensuring that differences in impacts reflect the level of warming itself rather than scenario-specific socio-economic or forcing assumptions.

Climate models may suffer from systematic errors and biases, which limit their direct application to assess actual climate impacts on local ecosystems (Ruffault et al. 2014). Using the complete observational dataset (i.e., field station observations supplemented by E-OBS and ERA5) as a reference, a multivariate bias correction method based on quantile mapping was applied to all RACMO output data (Cannon 2018). The multivariate correction ensures that the inter-variable relationships are maintained as much as possible and is therefore preferable to correcting individual variables separately.

2.3 The Hi-sAFe model and simulated scene

Hi-sAFe is a 3D model that simulates tree and crop growth, management interventions, soil water and nitrogen fluxes, and soil organic matter processes (Dupraz et al. 2019). The model combines in a single platform the crop model STICS (Brisson et al. 2003; Beaudoin et al. 2023) and the tree model sAFe-Tree (Dupraz et al. 2019). Hi-sAFe simulates a rectangular scene divided into cells. Each cell is then divided into various soil layers, which are further divided into voxels (see Fig. 2 in Dupraz et al. 2019). In each cell, one crop or tree can be planted depending on the agroforestry design (see 2.5 Virtual Experiments below). Tree and crop above- and below-ground biomass is estimated daily. Tree biomass is calculated based on allometric equations. The light, water, and nutrients are used interactively by the two vegetation layers.

In this study, the simulated scene size was 20 x 20 m, and it was divided into cells of 2 x 2 m. In each cell, five soil layers were defined as follows: 0–20 cm, 20–40 cm, 40–60 cm, 60–100 cm, and 100–300 cm. The thickness of the soil layers was set according to direct measurement of a soil profile in the study site (Table S1).

2.4 Model calibration and validation

In this study, we adapted the Hi-sAFe model to the specific case of dehesa systems. To do so, we used (i) the core Hi-sAFe default parameters, (ii) soil and weather site-specific

data referred to before, and (iii) specific parameterizations for tree and pasture components using data from the literature as well as from the validation site (but in different years and/or conditions than the validation data) (Table 1).

2.4.1 Tree component

Hi-sAFe includes default parameterizations for several tree and crop species (Lecomte 2017, 2023; Dupraz et al. 2019). Originally, Hi-sAFe was designed for deciduous trees typical of temperate climates: poplar, wild cherry, and walnut hybrid (Dupraz et al. 2019). The current version allows modelling evergreen species, with olive trees (*Olea europaea* L.) as the default species (Lecomte 2017, 2023). However, holm oak is not included. To parameterize this species, we gathered tree structural values (i.e., diameter at breast height (DBH), age, and height) from multiple sources, such as on-site field measurements, the 4th Spanish National Forest Inventory (MITECO 2020), and specific on-site databases for the dehesas ecosystem (Montero et al. 2005, 2008; Bogdanovich et al. 2021). These sources allowed us to generate a dataset of structural characteristics of trees ranging from young to mature individuals (Table S2). The data were used to fit allometric equations (Table S2) needed to characterize tree architecture (Dupraz et al. 2019). This parameterization was performed using as base the default parameters of olive trees and settings for evergreen species (Lecomte 2017, 2023). Current efforts on agroforestry modelling are based on the simulation of recently established (e.g., <10–15 years) systems. However, the system simulated here represents a cultural ecosystem that has existed in the southwestern part of the Iberian Peninsula for a long time (Plieninger et al. 2015, 2021). The estimated age of the standing trees in the studied site is more than 100 years old (see Camarero et al. 2025). As a result, we did a spin-up run from 1900 to simulate the current tree structural characteristics of the studied site.

Simulations were validated using the 25 trees ha⁻¹ simulated scene (see below 2.5 Virtual Experiments). We validated the modelled tree parameters (height, DBH, and crown area) with independent data gathered on-site in an area with a tree density of 25 trees ha⁻¹. This includes data on the size of 105 trees measured in 2015 (Bogdanovich et al. 2021), and data on the annual DBH increment of 10 trees monitored from 2011 to 2023 with dendrometer bands (Table 1). The annual DBH increment was used as a proxy for tree vitality because it provides higher temporal reliability than other structural parameters, such as tree height or canopy width, in long-term periodical measurements. Since trees are not harvested and perform key ecosystem functions in dehesa systems as “ecosystem engineers” (Moreno and Pulido 2009), we were interested in tree vitality and multiple ecosystem service delivery, rather than in their wood production.

2.4.2 Pasture

As for trees, Hi-sAFé includes a series of default parameterizations for the herbaceous layer, considering crops mainly (Lecomte 2017; Dupraz et al. 2019). Natural pastures in the studied site are composed of a diverse herbaceous community (Köbel et al. 2024); however, Hi-sAFé and the underlying STICS model on which it relies for soil and crop modelling do not allow complex species mixtures (Beaudoin et al. 2023). To simulate the pasture community typical of dehesa systems, we followed a similar approach to Graux et al. (2020) and simulated temporary grasslands composed of pure grass using the grass crop option of Hi-sAFé. This crop option simulates a pasture composed of tall fescue (*Festuca arundinacea* Schreb.) and cocksfoot (*Dactylis glomerata* L.) perennial grasses (Beaudoin et al. 2023).

We modified grass parameters based on the principle that grass phenological stages in Hi-sAFé are determined by the sum of a daily thermal index expressed in degree days. Therefore, we gathered phenological stages from the MODIS Land Cover Dynamics (MCD12Q2) product covering the period from 2003 to 2022. Previous works have shown good correspondence between phenological data obtained from MODIS and on-site phenocams measurements (Melendo-Vega et al. 2018; Luo et al. 2020). For each year, we used the MCD12Q2 first cycle, which covers the main biomass peak, to extract the green-up (date when the EVI2 vegetation index crosses 15% of the amplitude) and maturity (date when the EVI2 vegetation index crosses 90% of the amplitude) stages. Then, we calculated growing degree days (GDD) for each phenological stage to obtain a first estimate of parameters related to leaf area index (LAI) dynamics in Hi-sAFé (*stlevamf* and *stamflax*), similar to Jégo et al. (2013). *Stlevamf* indicates the growing degree days from emergence to maximum acceleration of leaf growth (end of juvenile phase), while *stamflax* measures the growing degree days from maximum acceleration of leaf growth to maximum leaf area index (end of leaf growth) (Lecomte 2017; Beaudoin et al. 2023). We used these starting values in an optimization procedure to assess the best estimates of the growing degree days to reach maturity and maximum LAI. We also included in the optimization the parameter controlling maximum growth efficiency (g MJ^{-1}) during the vegetative phase (*efcroiveg*) (Lecomte 2017; Beaudoin et al. 2023). The optimization procedure was carried out in R using the DEoptim package (Mullen et al. 2009), which performs evolutionary global optimization via the Differential Evolution algorithm (Ardia et al. 2011). The optimization seeks for values of *stlevamf*, *stamflax*, and *efcroiveg* that minimized the RMSE and maximized R^2 calculated for the relationship between measured and simulated pasture production from 2015 to 2021 (Table 1). Parameters values used in the simulations of pasture dynamics were 375, 483

GDD, and 5.6 g MJ^{-1} for *stlevamf*, *stamflax*, and *efcroiveg*, respectively.

We performed the optimization of the pasture simulation using the Open (no trees) simulated scene (see below 2.5 Virtual Experiments). Pasture production, on a dry matter yield (DMY) basis, was measured at the validation site in open areas, without tree influence, at peak growth using 12 grazing exclusion plots, each measuring 0.5×0.5 meters (Table 1). Production over the seven years (2015–2021) ranged from very low ($0.85 \text{ DMY t ha}^{-1}$ in 2017) to high ($2.38 \text{ DMY t ha}^{-1}$ in 2016) for the studied grasslands, which shows an average production of 1.5 t ha^{-1} (Olea et al. 1989; Olea and San Miguel 2006).

The calibration of the pasture production was validated with independent data, both in open areas and below the tree canopy to check the ability of the Hi-sAFé. We validated the pasture production in open areas using the three years (2022–2024) not used for the calibration as previously explained (Table 1). The validation dataset included years with very low ($0.55 \text{ DMY t ha}^{-1}$ in 2023), average ($1.63 \text{ DMY t ha}^{-1}$ in 2022), and highly productive years ($2.59 \text{ DMY t ha}^{-1}$ in 2024). For the validation of the pasture production below tree canopy, we used independent data of pasture production measured at the validation site from 2015 to 2024 in 12 $0.5 \times 0.5 \text{ m}$ grazing exclusion plots located below tree canopy (Table 1). Each variable for both trees and pasture was validated against the longest available independent record. The modelled pasture production below the canopy was extracted by averaging the DMY of cells of the 25 tree ha^{-1} simulated scene whose relative PAR incident (% of above-tree-canopy direct PAR that is incident on the pasture) was less than 75%.

2.4.3 Management and nitrogen inputs

Grazing can have a profound impact on the nutrient dynamics of silvopastoral systems, directly by the return of nutrients in faeces and urine, or indirectly by the amount of biomass left in the field unconsumed. To adapt the Hi-sAFé model to silvopastoral systems, we included these two mechanisms through adaptations of the crop management input file.

The return of N in agrosilvopastoral systems by grazing livestock was considered using the residue incorporation options of Hi-sAFé, which include animal waste and crop residues (Lecomte 2017; Dupraz et al. 2019). The return of N in faeces and urine was accounted for by incorporating animal waste, while the return from the decomposition of pasture aerial biomass was included by considering the addition of crop residues. Based on data with and without grazing exclusion cages that were used to assess pasture production on the validation site (Table 1), we estimated an average removal by grazing of annual pasture production of 80% (1.56 t ha^{-1}) of grass biomass produced annually. We

assumed that the N corresponding to this consumed pasture production was returned to the system via the manure and urine of cattle. This was simulated by the addition of 1.02 t ha^{-1} of animal waste with a 3.2 % of N (Iglesias 1994; Iguácel et al. 2018) in eight applications of $\sim 0.13 \text{ t ha}^{-1}$ one month apart (October–May), to minimize unrealistic losses by leaching. The N of the remaining 20% of the average annual aboveground pasture production was considered to be returned to the system in the form of crop residues at a rate of 0.31 t ha^{-1} with 2.28 N% (Carrascosa et al. 2024; Fernández-Habas et al. 2025) in July at the soil surface without tilling. In total, the N added by animal waste and crop residues was approximately $40.2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. These additions were calculated to include the estimated N fixed by legumes in a dehesa pasture. The latter was calculated based on an N fixation of 2.33% of the legume's biomass (based on Carranca et al. 2015) and an average proportion of legumes of 12.5% in Mediterranean pastures (Olea et al. 1989; López-Carrasco et al. 2015; Carrascosa et al. 2024; Fernández-Habas et al. 2025). The atmospheric N deposition was calculated using data from one of the monitoring plots of the pan-European forest monitoring and research network (ICP Forests) to monitor air quality, nutrient deposition, soil water chemistry, and tree growth among other variables (ICP Forests 2025). This plot (code 07 Qi) is located in a holm oak dehesa 2 km away from the experimental site ($X=261.000$; $Y=4.424.000$, UTM) (MITECO 2025). The N deposition rate measured on average in this plot is $3.05 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (MITECO 2025).

2.5 Virtual experiments

Unlike temperate planted agroforestry systems, in Iberian dehesas and other traditional silvopastures, tree density can vary in space within a single farm because it has been shaped throughout time by ecological and anthropogenic drivers (Plieninger et al. 2015; Hartel et al. 2018). In the studied site, tree density ranges between 6 (i.e., mainly grasslands almost devoid of trees) and 30 trees ha^{-1} . Given the key role of trees in these types of systems, the virtual experiments considered three contrasting tree density classes: open grasslands (i.e., devoid of trees) and agroforestry (AF) with 25 and 50 trees ha^{-1} , respectively (Fig. 2). For each land cover type, we ran a separate Hi-sAF simulation keeping the same structure of the plots, pasture and tree parameters and management with the only modification of tree density.

2.6 Data analysis

To assess temporal trends of pasture production, tree growth, and their temporal stability under the RCP8.5 scenario at varying tree densities, we used the Theil–Sen method. This estimator is commonly used in temporal trend analysis, as it

is robust to outliers and provides accurate confidence intervals (CI) even with non-normal data and heteroscedasticity (Carslaw and Ropkins 2012).

Temporal stability is commonly measured using the variability in a time series of species abundances, production of biomass, or growth (Tilman 1999; Lehman and Tilman 2000). This has been done traditionally using the coefficient of variation (CV) (Tilman 1996). However, the coefficient of variation has several drawbacks: i) sensitive to rare events, ii) estimation of variability with CV increases with increasing length of the time series, iii) is insensitive to the chronological order of time series (Fernández-Martínez et al. 2018). To overcome these limitations, we used the disparity index as a measure of temporal stability (Fernández-Martínez et al. 2018) using the package “CValternatives” (Engel 2019). This index avoids the common limitations of the CV and provides, simultaneously, information about the variability and the autocorrelation of the time series as it considers the order of the events in the time series (see Fernández-Martínez et al. 2018). Lower values indicate higher temporal stability. To ease the interpretation, we calculated its inverse, so it relates directly to temporal stability.

We computed bootstrapped mean values and 95% confidence intervals for pasture production, tree growth, and their temporal stability during the period from 1990 to 2100 under the RCP8.5 scenario for each land cover. The significant differences in production/growth and temporal stability between land covers were interpreted based on the confidence intervals of the difference between groups. Following this approach, if the confidence interval of the difference (not shown) does not include zero, the difference is statistically significant.

Finally, we calculated the theoretical land cover composition that optimizes tree development, pasture production, and their temporal stability using the package “optimLanduse” (Husmann et al. 2022). This package implements the innovative, robust land-cover optimization approach developed by Knoke et al. (2016) that allows for the consideration of uncertainty in a multicriteria land cover optimization (see Knoke et al. 2016; Husmann et al. 2022 for a detailed description of the method and package). The optimization function requires first identifying the indicators for the land cover optimization, in our case: i) pasture production, ii) tree DBH increment, iii) Temporal stability of pasture production, and iv) temporal stability of tree DBH increment. The values used for these indicators were the bootstrapped mean values of pasture production and tree DBH increment. Then, uncertainty is taken into consideration by providing a value for the parameter *indicatorUncertainty*. This value was calculated as the standard errors of the bootstrapped means of the previous indicators. These values must be provided for each land cover. In this case, we considered that, *a priori*, the proxies for productivity and temporal stability of the

system had the same importance in optimizing land-cover composition, assuming that it is equally important to ensure pasture production and tree growth, as well as their temporal stability. Therefore, equal weights were assigned to all the parameters included in the optimization. The decision to give equal weight to production and stability was motivated by the crucial role that the variability of pasture production plays in Mediterranean silvopastoral systems, as it directly affects ecosystem dynamics, poses important income risk, and greater uncertainty for farmers (see Baumgärtner and Quaas 2009; Iglesias et al. 2016; Sloat et al. 2018 for a discussion on that topic).

We split the analysis and results into three different periods that represent an increase in temperature up to 1.5 °C, 2.5 °C, and more than 2.5 °C (Fig. S1) to explore the effect of increasing arid conditions on the optimal land cover composition. To calculate temperature anomalies, we used the period from 1961 to 1990 as a baseline, following the convention of the World Meteorological Organization (WMO 2022) and the bias-corrected output from RACMO. The thresholds were surpassed in 2017 and 2055 for 1.5 °C and 2.5 °C, respectively (Fig. S1). All data analyses were carried out with R version 4.4.0 (R Core Team 2024).

3 Results

3.1 Model validation

The results showed that the model adequately simulated the current structure of the tree layer, based on stem DBH, tree height, and crown area (Fig. 3). The large spread of tree structural values highlights the high heterogeneity of tree sizes in the studied site (Fig. 3), especially for tree height, ranging from 5 to 11 m. The average measured tree at the validation site in 2015 was 7.8 m height (95% CI 7.6–8.0 m), 44.9 cm DBH (95% CI 43.4–46.3 cm), and 89 m² of crown area (95% CI 84.2–95.7 m²). Simulated values fell within the 95% confidence intervals of the measured values for DBH (46.0 cm), and were slightly higher than the upper limit for height (8.1 m) and crown area (101.0 m²).

We found similar results for tree DBH growth from 2011 to 2023, observing a close relationship between modelled and observed values (RMSE = 1.63 cm and $R^2 = 0.98$) (Fig. S2). The model tended to overestimate tree growth, as the values fell above the 1:1 line, although the confidence interval showed a wide range of variation (Fig. S2).

Regarding pasture production, the model simulations adequately tracked the field measurements in the validation site (Fig. 4). The parameterization reached an excellent fit with RMSE = 0.19 t ha⁻¹ and $R^2 = 0.91$ (Fig. 4B). In addition, the modelled values fell within the 95% confidence intervals of the observed values for all seven years of measurements,

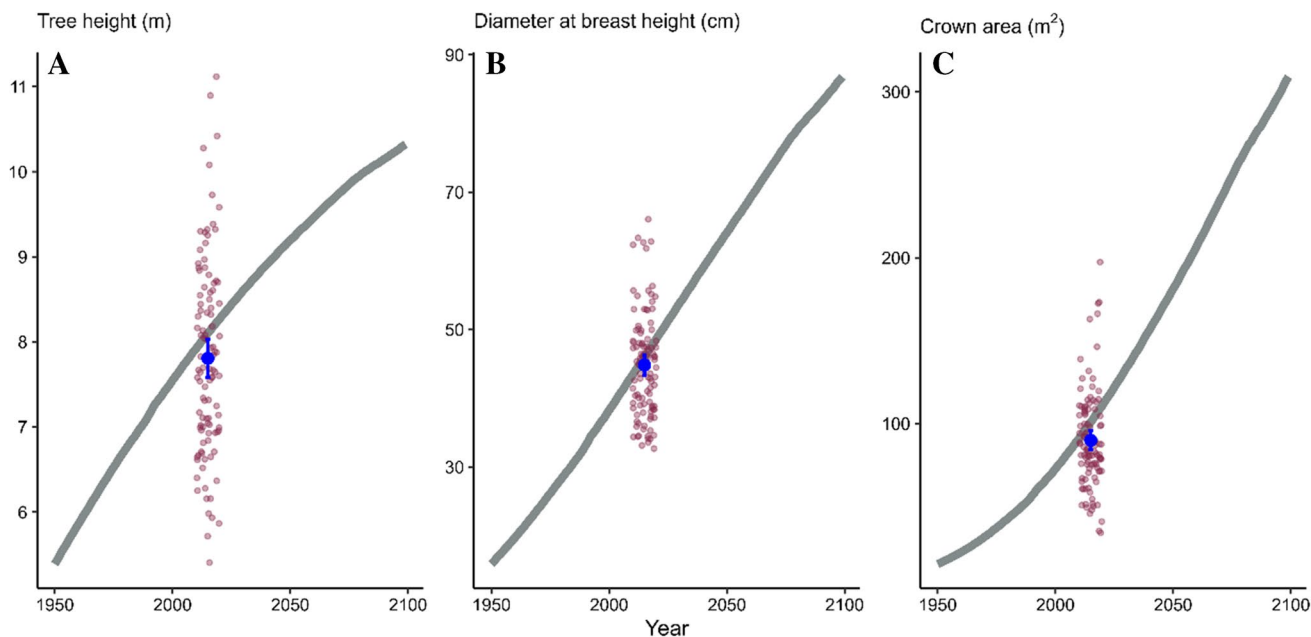
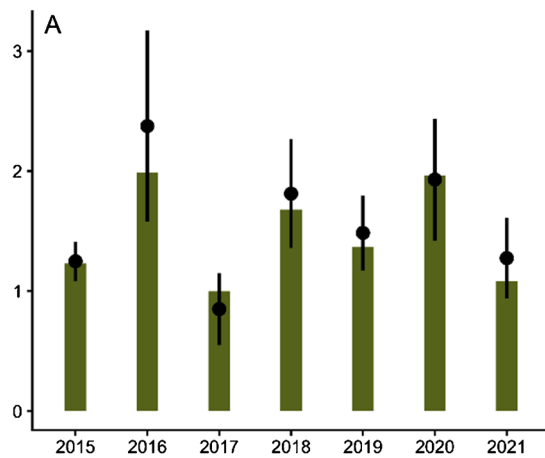


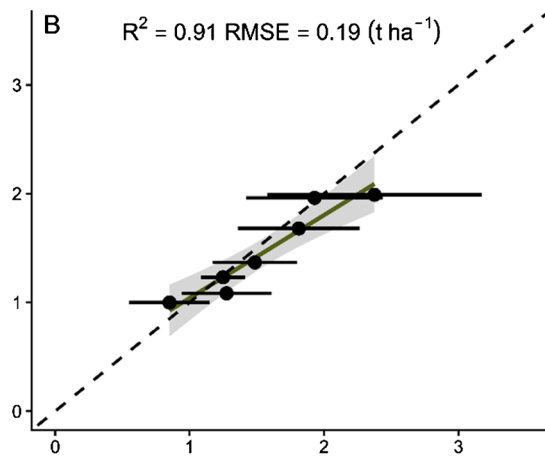
Fig. 3 Simulated (grayline) and mean $\pm$ 95% confidence intervals (blue dots) of measured (2015) tree height (A), diameter at breast height (B), and crown area (C). The spread of the 105 trees measured (purple points) on the x-axis was added to ease the visualization. $N=105$

Parameterization of pasture production in open areas

DMY (t ha^{-1})

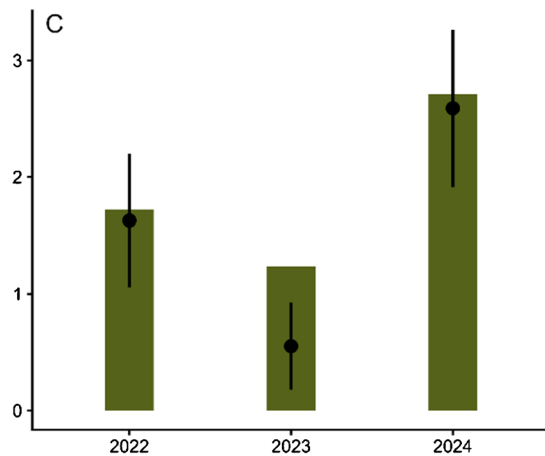


Modelled DMY (t ha^{-1})

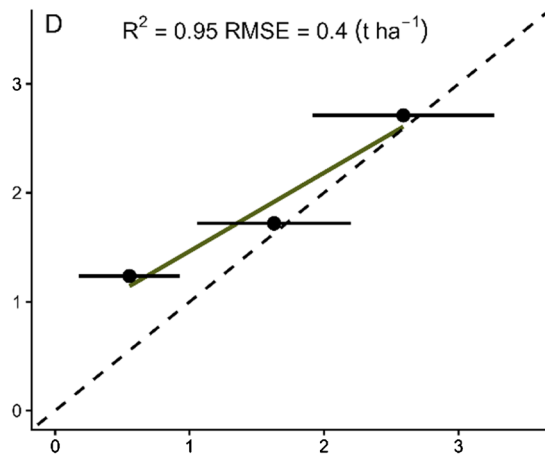


External validation of pasture production in open areas

DMY (t ha^{-1})

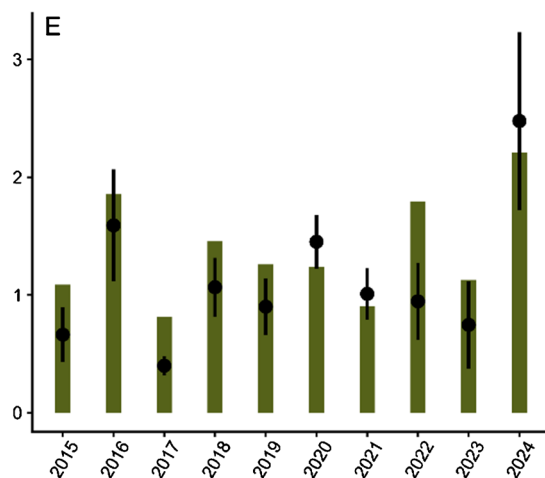


Modelled DMY (t ha^{-1})



External validation of pasture production below canopy

DMY (t ha^{-1})



Modelled DMY (t ha^{-1})

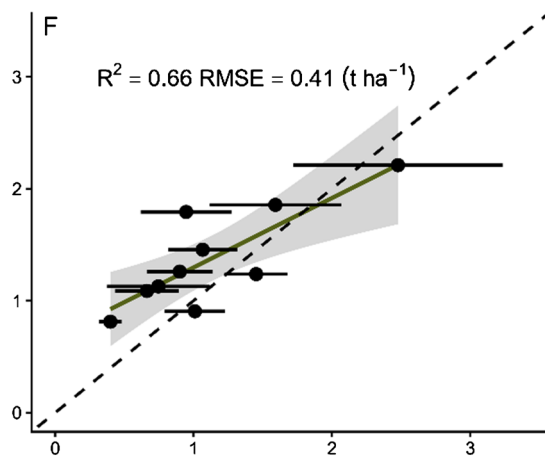


Fig. 4 Results of the model parameterization (A and B) and external validation (C and D) of pasture production (dry matter yield; DMY) in open areas. E) and F) represent the external validation of the modeled pasture production below the tree canopy. Left: Dots indicate mean $\pm$ 95% confidence intervals of observed pasture DMY (tons ha^{-1}), bars represent modeled DMY. Right: Modeled versus observed DMY and accuracy statistics. $N=12 \text{ year}^{-1}$. The shaded area represents the 95% confidence interval for the fitted regression (omitted in panel D due to insufficient data to calculate a stable 95% confidence interval)

which showed high variability in productivity. The external validation showed that the model closely simulated field measurements of open pasture in the validation years (RMSE = 0.40 t ha^{-1} and $R^2 = 0.95$) (Fig. 4D). The model was rather conservative in estimating pasture productivity decrease in dry years such as 2023 and highly accurate in average and highly productive years (Fig. 4C). The results of the model external validation of pasture production below canopy (Fig. 4F) also reported a suitable estimate of pasture production with a lower model fit ($R^2=0.66$) but same accuracy (RMSE= 0.40 t ha^{-1}) than for the production in open areas. In any case, the model successfully captured the typical inter-annual variability of pasture production of the studied system. Our field measurement data set includes multiple years with varying levels of production, from low productive levels in 2017 to high productive years as 2016. This led to a close relationship between modelled and observed values as most of them fell around the 1:1 line (Fig. 4).

3.2 Trends of tree growth, pasture production, and temporal stability under RCP8.5

According to climate projections simulated by RACMO and following local-scale correction of systematic model bias, the site is projected to be associated with significant increases in maximum and minimum temperature between 1990 and 2100 (Fig. S3). Daily maximum temperatures lie in the 23–24 °C range during the period for which observational is available, rising to greater than 26 °C by the end of the century (Fig. S3). Change in minimum daily temperature over the same period is from approximately 8 °C to 12 °C (Fig. S3). There are no long-term trends in annual precipitation (Fig. S3).

A significant reduction in DBH increment was observed at both tree densities (25 and 50 trees ha^{-1} ; $p < 0.001$; Fig. 5A). However, the slope of this decrease changed substantially with tree density, being 3.1 folds higher for 50 trees ha^{-1} ($28 \times 10^{-4} \text{ cm yr}^{-1}$) than for 25 trees ha^{-1} ($9 \times 10^{-4} \text{ cm yr}^{-1}$).

The mean tree DBH increment for the whole period was 0.49 cm yr^{-1} for 25 trees ha^{-1} and 0.35 cm yr^{-1} for 50 trees ha^{-1} , a 28.6% lower value (Fig. 5B). Similarly, the temporal stability was 2.1 times higher at the lower density than

at 50 trees ha^{-1} (Fig. 5C). The simulations of the structural parameters (height, DBH and crown area) started to diverge between densities from 2025 onwards, showing a clear decrease in growth rate of trees under 50 trees ha^{-1} density (Fig. S4). By the end of the century, trees at this density would have considerably lower size than those at 25 trees ha^{-1} (Fig. S4). As expected, the 50 trees ha^{-1} density resulted in a higher canopy cover during the whole period, reaching full canopy cover by 2080, while at the lower tree density, the canopy cover was 80% at the end of the century (Fig. S5). The current (2025) modelled canopy cover for 25 trees ha^{-1} is 30% (Fig. S5), slightly higher than the measured one (23%) at the validation site.

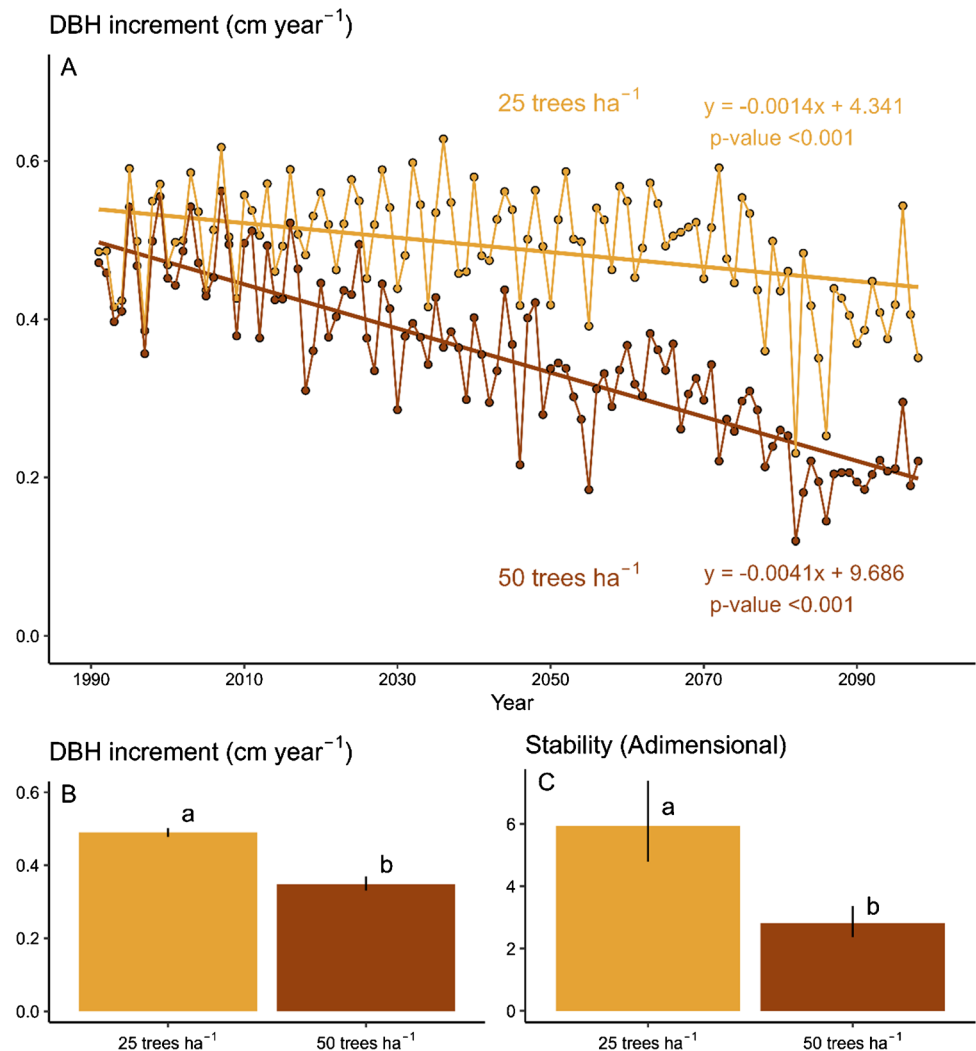
The model simulated a significant ($p < 0.001$) decrease in pasture production for all three land covers under the RCP8.5 scenario (Fig. 6A, B, C). However, this decrease varied considerably among them. The highest decrease was for the 50 trees ha^{-1} density, with a slope of $-4.1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of pasture production (Fig. 6C), double that for Open with $-2.1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Fig. 6A). The 25 trees ha^{-1} density showed the lowest decrease in pasture production with only $-1.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Fig. 6B). By the end of the century, the Open scenario showed an 8.4% decrease in pasture production as compared to current conditions (2025) (Fig. 6A), slightly higher than at the lower tree density (25 trees ha^{-1}) with 7.0% decrease. However, the pasture production at 50 trees ha^{-1} was estimated to decrease about 22% by 2100 (Fig. 6C).

Overall, during the whole period from 1990 to 2100, the Open land cover had a higher mean pasture production (1.9 t ha^{-1}) than the scenarios with trees (Fig. 6D). Specifically, compared to Open, the presence of trees reduced the mean pasture production by 23.2% and 27.8% for 25 trees ha^{-1} and 50 trees ha^{-1} , respectively. The difference in mean pasture production during this period between the two tree densities was rather small, with only 88 kg more at the 25 trees ha^{-1} density. Pasture temporal stability tended to be higher in silvopastoral scenarios, and with increasing tree density (Fig. 6E). Tree densities of 25 trees ha^{-1} and 50 trees ha^{-1} showed a 13.8 and 22.7 % higher pasture temporal stability, respectively, than in Open, although these differences were not statistically significant (Fig. 6E).

3.3 Optimization of theoretical land cover composition

For a hypothetical farm with varying tree density across locations, the optimal land composition (tree density vs. open) changed over time (Fig. 7). The different scenarios were modelled by maximizing tree growth (as a proxy of tree vitality and ecosystem services delivery), pasture production, and the temporal stability of these factors. The clearest trend was a shift towards a higher share of locations with 25 trees ha^{-1} at the expense of the area at 50 trees ha^{-1}

Fig. 5 **A** Simulated temporal dynamics of tree growth increment rate (cm year^{-1}) at both tree densities. Panels **B** and **C** show simulated mean tree growth and temporal stability, respectively, for the period between 1990 and 2100. Bars depict bootstrapped mean values and 95% confidence intervals. Means not sharing any letter are significantly different



density and of open areas. Specifically, the optimum share with 25 trees ha^{-1} was 18.9% in the period 1990–2016 and increased up to 30% for the 2055–2100 period, while the optimum share with 50 trees ha^{-1} shifted from 34.4% to 29.7% (Fig. 7). The share of Open decreased slightly from 46.6% during 1990–2016 to 41.4% during 2017–2054 and remained at the same value for the last period.

4 Discussion

In this study, we calibrated and validated the process-based model Hi-sAFe for a silvopastoral system for the first time. The use of long-term data on pasture production and tree development enabled a robust calibration and provided a suitable representation of system productivity and temporal stability. The results of the virtual experiments contributed to shedding light on the climate-change adaptation of Mediterranean silvopastoral systems under varying tree densities.

4.1 Better tree growth and temporal stability at 25 trees ha^{-1} compared to 50 trees ha^{-1}

The results clearly show that, under the studied conditions, a tree density of 50 trees ha^{-1} severely reduces tree growth and temporal stability, indicating greater vulnerability to climate change under RCP8.5 compared to a density of 25 trees ha^{-1} . This is explained by the higher tree water uptake (transpiration) at the plot level and PAR interception at 50 trees ha^{-1} , which imposes a strong competition for resources. Specifically, the mean yearly water uptake (1990–2100) by trees at the plot level at the 50 trees ha^{-1} density was 233.8 mm (or L m^{-2}), 37.8% higher than for a density of 25 trees ha^{-1} (169.6 mm). Over that period, water uptake by trees continues to increase for both densities, albeit the increase is smaller at 50 trees ha^{-1} (Fig. S6). In very dry years, this water uptake is strongly reduced for 50 trees ha^{-1} from 2050 onwards. At 25 trees ha^{-1} , this is less frequent, and it begins only around 2080 (Fig. S6). This indicates severe competition for soil

Fig. 6 Simulated temporal dynamics of pasture dry matter yield from 1990 to 2100 for Open (A), 25 trees ha⁻¹ (B), and 50 trees ha⁻¹ (C). Panels D and E show mean pasture dry matter yield and temporal stability, respectively, for the period between 1990 and 2100. Bars depict bootstrapped mean values and 95% confidence intervals. Means not sharing any letter are significantly different

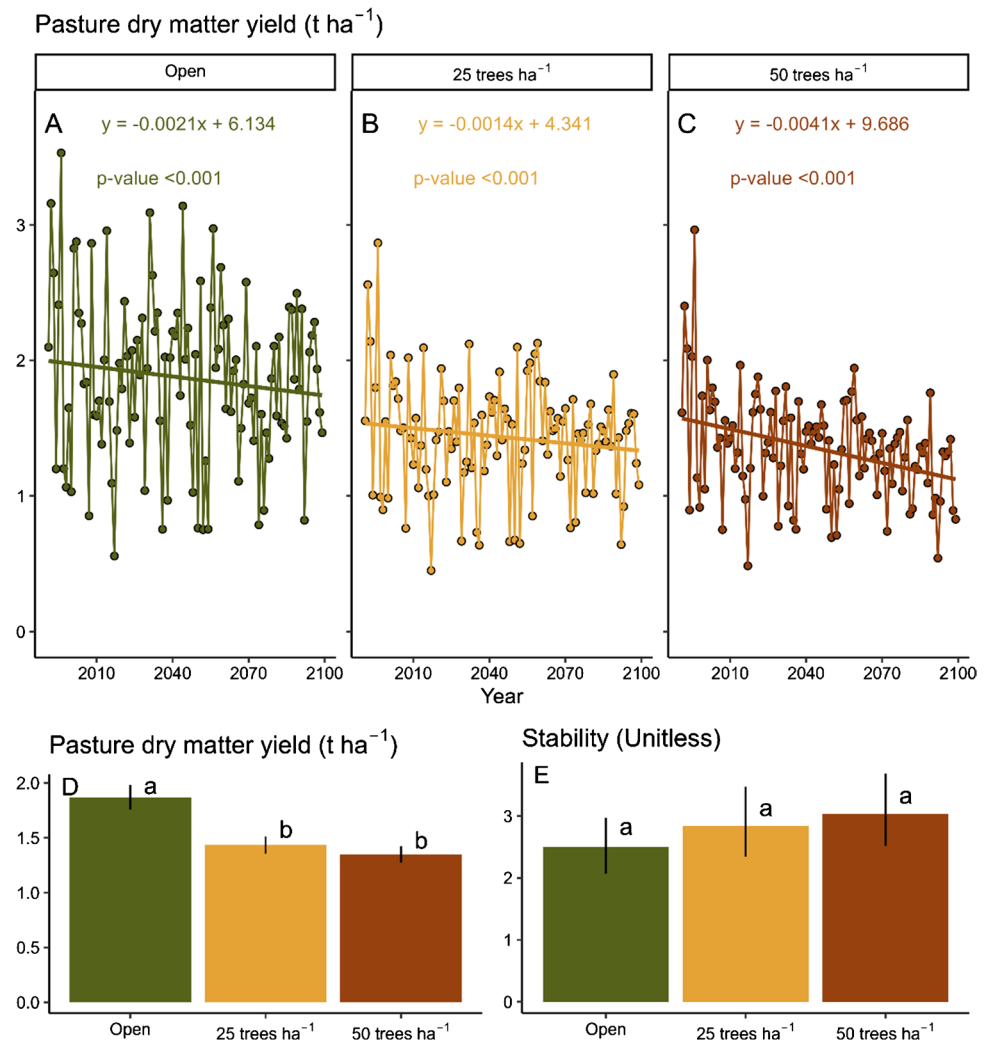
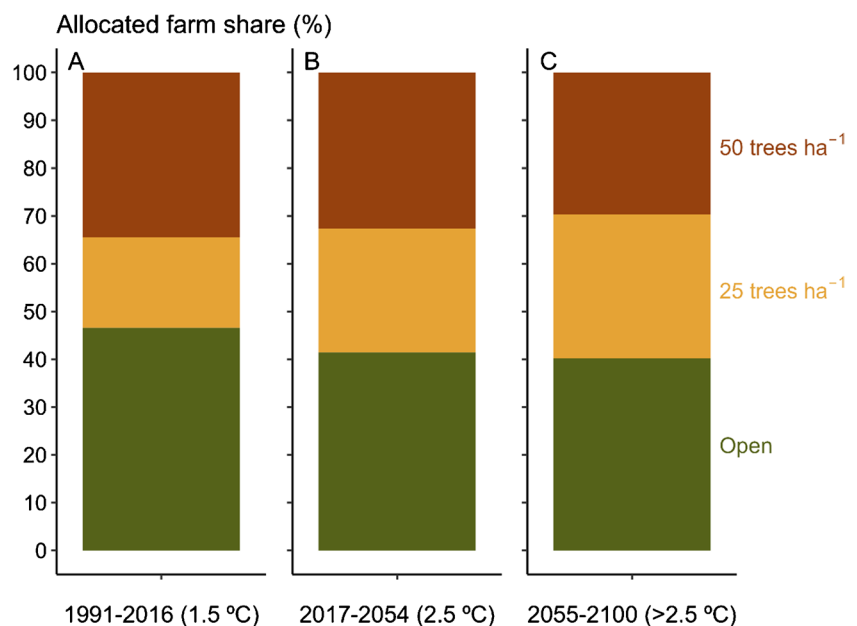


Fig. 7 Optimal farm tree density composition based on tree and pasture production and temporal stability for three different periods that represent an increase in temperature up to 1.5 °C (A), 2.5 °C (B), and more than 2.5 °C (C) as compared to the baseline



water in the second half of the century in dry years under RCP8.5 at 50 trees ha⁻¹.

At the tree level, the estimated mean annual tree water uptake (1990–2100) at 25 trees ha⁻¹ was 67,840 L tree⁻¹ yr⁻¹ (results not shown). Increasing tree density to 50 trees ha⁻¹ led to a 31.1% reduction in mean annual tree water uptake (46,760 L tree⁻¹ yr⁻¹). These values are of the same order of magnitude as previous measurements of tree water uptake in dehesas (Moreno and Cubera 2008; Morales et al. 2021). The strong competition at the 50 trees ha⁻¹ density resulted in trees of considerably lower size, from 2050 onwards (Fig. S4). The beneficial effect of lower tree densities on water status and development has also been reported at the tree level in the studied system by Moreno and Cubera (2008), who compared densities of 20 versus 200 trees ha⁻¹. They found that at the higher density, more soil water was consumed than at lower densities, leading to intense competition due to the likely presence of lateral roots of neighbouring trees (Cubera and Moreno 2007). Joffre et al. (1999) argued that, at the landscape level in the Iberian Peninsula, dehesas tend to reach an ecohydrological equilibrium that optimizes tree density following a water availability gradient. According to our results, the 50 trees ha⁻¹ density seems to be above this ecohydrological equilibrium for the studied environmental conditions, while 25 trees ha⁻¹ seems to be optimal also in a future scenario of increasing aridity (Cubera and Moreno 2007). Given the prominent root system of holm oaks (Dinis 2014; Moreno et al. 2005; Rolo and Moreno 2012), tree spacing in dehesa systems is key to preventing competition for water between individual trees (Cubera and Moreno 2007; Morán-López et al. 2016). Episodes of severe drought may induce severe tree mortality in water-limited ecosystems such as dehesas (see Peñuelas et al. 2001; Carnicer et al. 2011; Moreno-de-las-Heras et al. 2023). Therefore, lower tree densities could be more resistant and resilient to these expected more frequent drought events (Cubera and Moreno 2007; Moreno-de-las-Heras et al. 2023). In addition, pressures on the human population due to water scarcity are expected to increase in the future, particularly where dehesas are located (see Roper Szymańska et al. 2025). Therefore, water yield and groundwater recharge will become key ecosystem services in a drier future. Our results show that drainage tends to decrease as tree density increases; it was highest in the Open, but the 25 trees ha⁻¹ density was higher than the 50 trees ha⁻¹ density, probably due to a higher transpiration rate (Fig. S6). This result suggests that a lower tree density could reduce the trade-off between ecosystem water yield and tree presence while keeping the ecosystem services provided by trees (Sohn et al. 2016; Del Campo et al. 2022; Sun et al. 2024).

Acorn production is one of the main functions of dehesas and a key motivation for their transformation from closed forests to open woodlands (Olea and San Miguel 2006). Previous research has suggested that tree density is a crucial factor involved in acorn production (Vicente et al. 1998; Gea-Izquierdo et al. 2006; Camarero et al. 2010), due to the interspecific competition in dense stands, which can cause severe water stress and lead to massive fruit abortion in summer (Alejano et al. 2008; Carevic et al. 2010; Morán-López et al. 2016). The improved hydric conditions of trees at the tree level at a density of 25 trees ha⁻¹ due to lower soil water competition may allow for higher acorn production, especially in the second half of the century.

Nevertheless, at the lower tree density, the improved acorn yield per tree may not compensate for the lower canopy cover as compared to higher tree densities. Indeed, up to a certain threshold, there is a trade-off between production per tree and per hectare (Vicente et al. 1998; Gea-Izquierdo et al. 2006; Carbonero 2011). For instance, in cork oak dehesas, it has been suggested that a canopy cover of 60% could be optimal for canopy occupancy and illumination (Vieira 1991 in Carbonero 2014). However, the 80% canopy cover reached by 2050 at 50 trees ha⁻¹ may be related to excessive tree-to-tree competition (Moreno and Cubera 2008) for a suitable acorn production (Vicente et al. 1998; Gea-Izquierdo et al. 2006). The incorporation of acorn production in future versions of Hi-sAFe is essential for a comprehensive modelling of the production of dehesas and to identify critical thresholds of tree density for acorn production.

These results underline the importance of adjusting tree density to local environmental conditions in the adaptation to a future climate change scenario. In this regard, during the period 1993–2006, 468,000 ha of agricultural land were afforested with holm and cork oaks in Spain (Jiménez and Navarro 2014; Vadell et al. 2016) under the initiative of the European Economic Community's (EEC) directive 2080/92 to transform agricultural lands into forested areas. These afforestations were made at densities above 300 trees ha⁻¹ in areas of similar environmental conditions to our simulations. According to our results, these densities put at risk the persistence and temporal stability of these newly established forests (see Duque-Lazo et al. 2018) and reduce groundwater recharge in the context of climate change. Transitioning to lower tree density silvopastoral systems may be advisable, depending on the expected role of these afforestations. It also highlights the threat that land abandonment, and subsequent shrub encroachment may pose on dehesa adaptation to climate change (Lecomte et al. 2022). The traditional management that creates and sustains silvopastoral systems should be valued not only for preserving these multifunctional systems and their ecosystem services, but also for its role in climate change adaptation.

4.2 Trees reduce pasture production but may alleviate impact of climate change and increase temporal stability

Concerning the effects on pasture, the presence of trees reduced the pasture production compared to Open. Crous-Duran et al. (2019), using the model Yield-SAFE, also reported higher production of treeless pasture compared to silvopastures. Previous experimental studies have reported both positive (Escuder et al. 1985; Joffre and Rambal 1988; Gallardo et al. 2000; Cubera and Moreno 2007) and negative net effects (López-Díaz et al. 2015; Hidalgo-Gálvez et al. 2022; Martins-Noguerol et al. 2023) of tree canopy in the pasture production of Mediterranean dehesas. Positive effects are attributed to increased soil fertility and favorable microclimatic conditions induced by tree shade (Moreno et al. 2007b; Moreno 2008), whereas negative effects are mainly due to competition for light and water (Hidalgo-Gálvez et al. 2022; Martins-Noguerol et al. 2023). These facilitative-competitive interactions in tree-grass ecosystems are context-dependent and highly reliant on water availability (Moreno 2008; Gea-Izquierdo et al. 2009; Hidalgo-Gálvez et al. 2022), showing strong intra- and inter-annual variations (Olea et al. 1989; Olea and San Miguel 2006; Vázquez-De-Aldana et al. 2008; San Miguel et al. 2017). According to our results, in the long term and in the context of climate change, the presence of trees seems to reduce pasture production, with tree density being the main factor. The reduction in pasture production over time in Open and at a tree density of 50 trees ha^{-1} was 50% and 193% higher, respectively, than at the 25 trees ha^{-1} . This suggests that, despite an overall reduction in production at 25 trees ha^{-1} , low tree density has a buffering effect against climatic variability and increased aridity compared to the two alternative land covers. This result highlights the key role of maintaining optimal tree density in enhancing the positive effects of trees on the resilience of agroforestry livestock systems to climate change (Ripamonti et al. 2025; Teodoro et al. 2025). Although not statistically significant, we observed a trend toward increased temporal stability of pasture production with increasing tree cover, which aligns with previous long-term observations comparing silvopastoral and open pasture systems (Munaro et al. 2023). This effect may result from the role of the trees in alleviating extreme weather conditions (Munaro et al. 2023; Rolo et al. 2023), although the strong interannual variability may prevent observing statistically significant differences.

Our results suggest that the lower production in wooded than treeless land covers could be mainly driven by the competition for light. The available mean daily water stock was 29% higher for wooded than treeless land covers (data not shown). Similarly, available mean N stock (NH_4^+ and NO_3^-) from 1990 to 2100 was similar for Open (266.8 kg N ha^{-1})

and 25 trees ha^{-1} (264.2 kg N ha^{-1}), and slightly higher at the 50 trees ha^{-1} density (288.1 kg N ha^{-1}), suggesting that trees were not competing with pasture for water, nor N. However, the mean intercepted PAR by pasture from 1990 to 2100 was 39.8% and 55.1% lower at 25 trees ha^{-1} and 50 trees ha^{-1} , respectively, compared to the Open (Fig. S7). This agrees with previous studies finding reduced pasture production below canopy in dehesas due to tree shade among other factors (Hidalgo-Gálvez et al. 2022; Martins-Noguerol et al. 2023). However, Moreno et al. (2007a, b, c) and Moreno (2008) reported higher production below tree canopy due to increased soil fertility in the uppermost soil layer and improved microclimatic conditions, although they also cautioned that these results may vary depending on rainfall and pasture composition at specific sites. Gea-Izquierdo et al. (2009) indicated that the balance of facilitation-competition for pasture production in dehesas tends to be positive, and the pasture benefits from higher soil fertility below canopy only if there is no water limitation during growth (Maestre et al. 2005). This aligns with an overall reduction in pasture production in AF systems compared to Open in a drier future. It also supports the smaller decrease in pasture production at 25 trees ha^{-1} over the studied period (1990–2100), as climate change effects intensify, due to a better facilitative-competitive equilibrium. This density may reduce thermal stress on pasture compared to open areas and impose less water and light competition than the higher tree density. However, it must be noted that multiple factors are involved in these facilitative-competitive interactions between trees and pasture (Moreno et al. 2007b; Gea-Izquierdo et al. 2009), not all of which are considered in Hi-sAFE (Dupraz et al. 2019), namely nutrients other than nitrogen (e.g., phosphorus) and, especially, differences in species or functional group composition. The latter has been shown to play a critical role in explaining differences in pasture production beneath and beyond the tree canopy, as well as its interannual variation, since different species and functional groups in Mediterranean grasslands adapt differently to tree shade and competition (Gea-Izquierdo et al. 2009; López-Carrasco et al. 2015; Hernández-Esteban et al. 2018, 2019). Also, other beneficial effects of trees not studied here must be considered when evaluating the role of trees in silvopastoral systems. For example, trees affect the phenology of pasture by advancing emergence and delaying senescence, which has important implications for pasture quality and thus animal production (Gómez-Gutiérrez and Pérez-Fernández 1996; Moreno et al. 2007c; Ludwig et al. 2008; Sousa et al. 2010; Hidalgo-Gálvez et al. 2022; Martins-Noguerol et al. 2023). Other effects include enhanced carbon storage (Reyna-Bowen et al. 2020), acorn, wood, and browse production (Gea-Izquierdo et al. 2006; Olea and San Miguel 2006), and shade for livestock (Moreno and Pulido 2009).

4.3 Optimizing landscape composition of silvopastoral systems in the face of climate change

Although ecological processes are usually studied for a specific ecosystem structure (e.g., tree density), at landscape/farm level, the processes and services provision are governed by the trade-offs between different land covers, especially in heterogeneous landscapes (Rolo et al. 2021). Typical dehesa landscape composition consists of a mixture of silvopastoral systems at varying tree density and open grasslands (Olea and San Miguel 2006; Moreno and Pulido 2009). Our results suggest that the optimal composition in terms of tree development, pasture production, and their temporal stability will vary in a future climate change scenario. Overall, the simulations show that a transition to landscapes with a higher share of dehesas at lower densities (20–25 trees ha⁻¹) may be beneficial to optimize temporal stability and production. This is mainly driven by the low temporal stability of tree development at higher tree densities as competition for resources increases in a more arid scenario (Rolo et al. 2021; Moreno-de-las-Heras et al. 2023). Nevertheless, the results reported here should be understood as an approximation of a theoretical optimal composition, while the actual composition depends on additional ecological and socioeconomic drivers. Also, the three land covers represent a simplification of intermediate situations and overlook within-land cover heterogeneity, which may play an important role in production and ecosystem dynamics.

The share of Open remained fairly constant (around 40%) due to its higher pasture production despite a trend to lower temporal stability than in agroforestry land covers. These results also underscore the key role of landscape composition of silvopastoral systems in balancing trade-offs of the different land covers (Rolo et al. 2021; Lecegui et al. 2022). However, management is essential to adapt this composition to climate change scenarios (Moreno de las Heras et al. 2023).

In our case, tree growth, pasture production, and their temporal stability have been used as proxies of the productivity of dehesa systems. Nonetheless, acorn production is a central product in the configuration, economy, and management of dehesas, which has not been included in the analysis of landscape composition. As discussed earlier, trade-offs between acorn production per tree and per hectare may affect the optimal balance at varying tree densities. For example, using Forage-SAFE to assess the impact of tree cover on dehesas profitability, García de Jalón et al. (2018) found that considering pasture, browse, and acorns together, the production of metabolizable energy was maximized at a tree cover of around 40%. However, the maximum net margin was obtained at a tree cover of around 32% (García de Jalón et al. 2018), close to the current (2025) 30% canopy cover

of 25 trees ha⁻¹ in our modelling approach. Similarly, the provision of important ecosystem services such as carbon storage, nutrient cycling, or biodiversity is highly responsive to landscape composition and shows important trade-offs among land covers (Rolo et al. 2021). Therefore, the results here reported must be interpreted as contingent on the Hi-sAFé parameterization and selected proxies, a wider analysis, including other ecosystem services and acorn production, although challenging, may provide a closer view of the optimal tree density in dehesa systems.

4.4 Using Hi-sAFé to model silvopastoral systems: limitations and future improvements

Simulation models are constrained by their intrinsic trade-offs between model complexity, the errors incurred by uncertainties regarding input data and processes, and representativity of the target system (Palma et al. 2007; Luedeling et al. 2016). Often, too simplistic models are easier to use but fail in representing complex agroecosystem interactions. In contrast, more realistic models are complex in their application, difficult to calibrate, and the required input data can be a source of variability. As with any other process-based model, the assumptions and simplifications required to make Hi-sAFé practical involve a certain degree of deviation from the system reality. One of these deviations, especially important in the case of dehesas, is the heterogeneity of the system, which is quite distinct from other agroforestry systems previously modelled with Hi-sAFé or Yield-SAFE, such as alley cropping (Crous-Duran et al. 2019; Huo et al. 2021; Reyes et al. 2021; Giannitsopoulos et al. 2025). This heterogeneity can be compositional at the landscape level, which we have mitigated by the modelling of three different tree densities usually intertwined, but it also involves differences in tree size within particular land covers. The latter is clearly illustrated by the large spread of tree structural values in the studied site (Fig. 3). Numerical models, as in this study, will simulate an “average” tree, while the structure of the real system will include a range of tree sizes which can determine in a great extent the provision of ecosystem services (Bagella et al. 2020). Considering this, Hi-sAFé indicated a good ability to match the current “average” tree at the study site. However, simulations tended to overestimate tree growth and structure, suggesting potential cascading effects on resource usage in the second half of the century. Also, as outlined earlier, modelling acorn production in Hi-sAFé, although challenging, could enable a more comprehensive simulation of productivity and optimal land cover composition. Though the strong spatial, temporal, and intraspecific variability in acorn production (Vicente et al. 1998; Gea-Izquierdo et al. 2006; Carbonero 2011) pose important challenges for reliable modelling. Similarly, in this study, it was only considered one cohort of trees without accounting for

key processes such as tree regeneration or mortality, both of major concern for the persistence of the dehesa (Plieninger et al. 2021). Lack of effective tree regeneration, both natural or artificial, remains a major challenge to dehesa systems due to permanent grazing or socioeconomic drivers (Plieninger et al. 2004; 2007; 2021). Also, severe tree mortality events due to abiotic and biotic factors, such as pathogens and pests like *Phytophthora cinnamomi* Rands. and *Cerambyx spp.*, are common in dehesas (Duque-Lazo and Navarro-Cerrillo 2017; Fernández-Habas et al. 2019). In this study, the low tree densities tested together with the possibility of uptaking water by trees from deeper voxels with limited soil evaporation and pasture root competition, prevented the decay of trees. In any case, despite both processes are crucial for the management of tree density, that must account for tree demographics, still remain underrepresented in AF process-based models.

Regarding the modelling of the pasture layer, Hi-sAFe successfully captured the interannual variation in pasture production, which is one of the main features of this system (Olea et al. 1989; Vázquez-De-Aldana et al. 2008; Olea and San Miguel 2006). The most important simplification of our modelling approach was the pasture composition and dynamics. Dehesas are known to harbor a high plant diversity in the herbaceous layer (Marañón 1985; Olea and San Miguel 2006). This diversity plays a crucial role in determining production, quality, and phenology and their response to aridity and tree competition-facilitation (Gea-Izquierdo et al. 2009; Hidalgo-Gálvez et al. 2022). Thus, the simplification of its composition, despite the consideration of a base N_2 incorporation by legumes (see 2.3.3 Management and nitrogen inputs), may affect pasture production, N cycling, water use, and therefore tree-grass interactions. Modelling a pasture layer of 12–20 species m^2 may be unfeasible. A suitable approach could be simulating the dynamics of the dominant species of the different functional groups (grasses, legumes, and non-leguminous forbs) and their proportions with and without tree influence to advance towards a more realistic representation of the dehesa pasture dynamics under climate change. In that sense, models such as GrasslandTraitSim.jl v1.0.0 (Nöblier et al. 2025) and ModVege (Pisceddu et al. 2022) that incorporate grasslands' functional diversity and grazing effects may provide useful insights. Lastly, grazing is a major driver in silvopastoral systems affecting pasture biomass, dynamics, and the N cycle. Although we simulated grazing by pasture removal through cutting and manure incorporation (following Dupraz et al. 2019), their effects may vary considerably from direct grazing. Unmodelled grazing effects include soil compaction, addition of other important nutrients such as P and K, and modification of pasture composition and structure through grazing selection (Carrascosa et al. 2024). Therefore, incorporating these grazing effects and carrying capacity calculations for

different livestock species into Hi-sAFe may be desirable to fully simulate silvopastoral systems. Finally, the closer representation of tree-grass interactions by Hi-sAFe compared to other models comes at the cost of high data requirements and computational demands. This must be taken into account when considering its transference to practitioners and farm advisors (DigitAF 2026).

Hi-sAFe model does not take into account the effect of temperature on all biological processes. This characteristic could limit its capacity for modelling the adaptation of AF to climate change. For example, root turn-over is not affected by temperature, while studies have shown that increased temperature reduces root life-span in trees, thus impacting carbon fluxes and nutrient cycling (Primka et al. 2021). Regarding climate change mitigation, and in particular carbon storage, Hi-sAFe is also limited by the simplifying hypothesis of STICS (which was developed mainly for arable crops) that mineralization happens uniformly above a certain depth (typically chosen as the ploughing depth), and not below. This leads to overestimating carbon storage, as carbon injected in deep soil layers as root litter is never mineralized.

In summary, this is the first time that the Hi-sAFe model is used to simulate a Mediterranean silvopastoral system. Future improvements of Hi-sAFe for an enhanced modelling of these complex systems should incorporate: i) acorn production, ii) diverse pasture composition, iii) and iii) grazing and associated effects. These processes, especially acorn production and pasture composition, show strong interannual and spatial variability in Mediterranean silvopastoral systems (Gea-Izquierdo et al. 2006; Vázquez-De-Aldana et al. 2008; Carbonero 2011), which may be difficult to capture with process-based models within reasonably practical and realistic boundaries. In that sense, it is worth mentioning the ongoing improvements in the modelling of Mediterranean AF system driven by projects such as AGFORWARD (<https://www.agforward.eu>), AGROMIX (<https://cordis.europa.eu/project/id/862993/reporting/es>), and DigitAF (<https://cordis.europa.eu/project/id/101059794/es>). In parallel with these model developments, future analysis would benefit from (i) explicit diagnostics of extreme events (e.g., multi-year drought sequences, compound heat-drought conditions), and (ii) exploring multiple global-regional climate model chains and a wider set of emissions scenarios or warming levels to assess the robustness of the projected responses across structural model differences and scenario assumptions.

5 Conclusions

Process-based models are useful tools to simulate long-term complex ecological processes. This is the first study that calibrates and validates Hi-sAFe for modelling heterogeneous Mediterranean silvopastoral systems, providing further evidence that AF can be a feasible option to adapt agricultural systems to the risk associated with severe climate change stress. Yet careful attention should be paid to tree density. Overall, the simulations show that, under the studied conditions (600–700 mm rainfall Mediterranean silvopastoral system), a tree density of 25 trees ha⁻¹ may improve tree development and temporal stability under the RCP8.5 scenario (defined by very high levels of future greenhouse gas emissions) compared to 50 trees ha⁻¹. Although the AF scenarios did not lead to pasture overyielding, the 25 trees ha⁻¹ tree density showed potential to minimize the reduction in pasture production caused by climate change compared to a tree density of 50 trees ha⁻¹ or open pasture. The findings indicate that traditional dehesas with relatively low tree densities of 20–30 trees per hectare are adapted not only to the past and present but also to the future climatic conditions. At the farm/landscape scale, a mixture of land-cover is recommended, with open pastures and dehesa plots of different tree densities. These results highlight the potential threat of land abandonment, and subsequent encroachment, or high-density plantations, to maintain the productive potential of one of the best examples of high nature value farming systems, and to improve the adaptation of Mediterranean landscapes to climate change. However, the results on optimal landscape composition are constrained by the unmodelled acorn production by oak trees in Hi-sAFe. Also, the results reported here are scenario-dependent, thus; climatic patterns different from those modelled affecting recurrent droughts, rainfall regimes, or extreme-event frequencies could alter the responses observed under each land cover.

The study demonstrates that Hi-sAFe can successfully model the current average tree structure and the interannual variability of pasture production, a key feature in Mediterranean silvopastoral systems in the face of severe climate change. We identified three key aspects of the Hi-sAFe model that future research should address for improving the modelling of silvopastoral systems: unmodelled acorn production, oversimplified pasture diversity, and inflexible grazing modelling. Overall, the results illustrate the potential and limitations of using process-based models to optimize Mediterranean silvopastoral systems for future conditions and pave the way for future improvements of this type of model, alongside their application to the forthcoming generation of climate models and climate change projections.

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Authors' contributions J. Fernández-Habas: data curation, formal analysis, investigation, software, visualization, writing—original draft. G. Moreno: conceptualization, funding acquisition, project administration, supervision, writing—review and editing. A. Carrascosa: data curation, writing—review and editing. M. L. López-Díaz, data curation, writing—review and editing. A. Carrara, data curation, writing—review and editing. C. Dupraz, software, writing—review and editing. J. Eden, data curation, writing—review and editing. M. Gosme, software, writing—review and editing. F. Herzog, project administration, writing—review and editing. K. A. Jarosch, project administration, writing—review and editing. M. Pilar Martín, data curation, writing—review and editing. V. Rolo conceptualization, data curation, formal analysis, investigation, software, visualization, supervision, writing—original draft.

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Data availability The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Code availability The code generated during and/or analysed during the current study is available from the corresponding author on reasonable request

Declarations

Ethics approval Not applicable

Consent to participate Not applicable

Consent for publication Not applicable

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