

Investigating climate-phenology relationships among the most common Italian forest species using Sentinel-2-derived vegetation phenology and productivity products

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ABSTRACT

Climate change is profoundly altering forest phenology and productivity across Europe, particularly in Mediterranean regions characterized by high climatic heterogeneity. Understanding how climatic and site-specific drivers regulate the start, end, and length of the growing season, and how these phenological shifts translate into productivity responses, remains a key challenge for predicting forest carbon dynamics. In this study, we investigate phenological timing and total seasonal productivity across multiple Italian forest species spanning Mediterranean, temperate, and mountain environments, leveraging the new High-Resolution Vegetation Productivity and Phenology product from the Copernicus Land Monitoring Service, machine learning (random forests) modeling, and explainable artificial intelligence analysis (SHAP). Our results indicate a general tendency toward lengthening of the growing season driven mainly by chilling accumulation and spring temperatures. Warmer conditions advance the start of the season by 1–10 days across species, while the combined effects of temperature, radiation, and moisture can extend the growing season by up to 20–30 days. End-of-season dynamics and season length are more strongly controlled by light and water availability than by temperature alone. In several Mediterranean species, the end of the season can advance by up to 40 days due to summer drought, high vapor pressure deficit, and site exposure. Mediterranean species often show compensatory shifts between season onset and senescence, maintaining a relatively stable length of the season, whereas mountain species exhibit a tighter coupling between delayed onset and shortened season length. Because of phenological shifts, overall season length is often decoupled from productivity, which is mainly regulated by energy and water availability, highlighting species- and site-specific responses to climate change. The findings of this study highlight the substantial advantage of combining remote sensing data with machine learning to advance understanding of forest phenology and productivity across broad spatial and climatic gradients.

1. Introduction

Climate change is the primary driver of global temperature rise, having already caused an increase of 0.8 to 1.3 °C since 1850, with

projections reaching 1.5 °C by mid-century (IPCC, 2022). In Europe, where climate impacts are occurring faster than the global average—particularly in Mediterranean and boreal regions (Santini et al., 2014; Noce et al., 2016)—the European Green Deal and Climate

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Law mandate climate neutrality by 2050. Among the multitude of key biotic and abiotic climate change indicators, plant phenology is extremely sensitive and reactive to changes in temperature and precipitation patterns (Keenan et al., 2014; Leblans et al., 2017; Kim et al., 2021), making it a perfect fingerprint of climate change impacts (Parmesan and Yohe, 2003; Peano et al., 2019; Morichetti et al., 2024). Vegetation phenology refers to the timing of recurrent biological events, their causes, and the relationships among them, whether within or across species (Lieth, 2013). These events, or phases, include observable periodic changes, such as budburst, flowering, fruiting (including masting), and leaf yellowing and abscission (in deciduous species), as well as changes that are not directly observable, including the respiration cycle and dormancy in temperate and boreal biomes.

Nearly 30 years ago, these phases, which we had long known to be linked to seasonal variability (Piao et al., 2019), were first linked to long-term changes in weather patterns (e.g., Schwartz, 1998; Menzel and Fabian, 1999). Since then, an increasing number of studies in different biomes and species have acknowledged the effect of climate drift on plant phenology, with significant consequences in the carbon and water cycles and energy flows (e.g., Cleland et al., 2007; García-Mozo et al., 2010; Keenan et al., 2014; Caparros-Santiago et al., 2021; Ren et al., 2024; Morichetti et al., 2024). Different studies in central and northern Europe have reported positive effects on forest growth and carbon uptake associated with a prolonged growing season driven by increasing temperatures and atmospheric CO₂ concentrations, suggesting a tight coupling of season length and overall productivity (Pretzsch et al., 2014; He et al., 2023; Vangi et al., 2024b). However, tree growth responses to environmental variability arise from the complex interplay and co-variation of multiple abiotic and endogenous species-specific biotic factors (Decarsin et al., 2024). This complexity is particularly evident in Italy, where, in over >14 degrees of latitude, there is a wide transition from temperature-limited alpine forests to water-limited Mediterranean ecosystems. Despite the drought-induced adaptation of different Mediterranean tree species, projected higher temperatures and reduced precipitation under climate change are expected to increase drought-induced dieback and impair tree growth (Gazol and Camarero, 2022). Dalmonech et al. (2026) have already found a strong signal of decoupling between carbon assimilation capacity and basal area increment in southern Italy. However, how limiting factors, such as water and nutrient availability, will interact with other climatic and environmental variables and how these interactions will affect the phenology-productivity link, remains an ongoing debate.

Traditionally, monitoring vegetation phenology has relied on field-based, species-specific observations (Templ et al., 2018), often labor-intensive, spatially limited, and time-consuming (Aono and Kazui, 2008). Also, field observations can be subject to sample and human bias (Liu et al., 2021). Advancements in remote sensing (RS) technologies have significantly enhanced land surface phenology (LSP) monitoring, bringing it to a more mature and efficient stage, thanks to their high spatial and temporal resolutions (Delpierre et al., 2016; Piao et al., 2019; Caparros-Santiago et al., 2021). A structured approach has been established to derive phenological metrics (hereafter referred to as 'phenometrics') from RS products. This process involves creating a vegetation index time series (usually NDVI or EVI indices), fitting a function over time (e.g., smoothing functions such as double logistic, Gaussian, or polynomial functions, or Fourier transforms), and extracting relevant phenometrics (Piao et al., 2019; Caparros-Santiago et al., 2021). Common phenometrics include the day of the year (DoY), which marks the start and end of the growing season (SOSD and EOSD, respectively). These days mark the start of the green-up phase (i.e., budburst), when greenness begins, cambial activity starts, and the greening-up period ends, corresponding to dormancy (Rodríguez-Galiano et al., 2015). The start and the end of the growing season also define the length of the season (LOS = EOSD-SOSD). Among the multispectral missions, one of the most used for retrieving dense and long-term time series of Earth

Observation data is the MODIS mission (Zhang et al., 2003; Ahl et al., 2006; Li et al., 2010; see the review by Shin et al., 2023), which offers a temporal resolution of 1–2 days. However, the MODIS sensor has low spatial resolution (ranging from 250 m to 1 km, depending on the bands), making it less suitable for canopy- and species-level applications. In particular, coarse-resolution sensors inevitably aggregate multiple land-cover types, elevations, and species mixtures within a single pixel, especially in complex and heterogeneous environments such as the Mediterranean, where sharp climatic and topographic gradients occur over very short distances. Other often-used satellites for monitoring LSP include the Landsat (Melaas et al., 2016) and Sentinel-2 constellations (see the review by Misra et al., 2020), which mitigate the aggregation effect at the pixel level, offering a better trade-off between spatial and temporal resolution across a wide range of applications and spatial scales.

Recently, the Sentinel-2A and 2B time series have been leveraged to produce high-resolution (10 m x 10 m) and high-frequency (5-day) time series of the plant productivity index (PPI) at the European level. The PPI is a physically based vegetation index, derived from the radiative transfer equations, and is linearly correlated with Leaf Area Index (LAI, m² m⁻²), having the same measurement unit. It has been shown that LAI is linked to canopy reflectance via the modified Beer's law, which also holds for the difference vegetation index (DVI = red-NIR) (Jin and Eklundh, 2014). The PPI can be derived from the DVI version of the modified Beer's law:

$$PPI = -K * \ln \left(M - \frac{DVI}{M} - DVI_s \right) \quad (1)$$

Where DVI is the difference between red and NIR, M is the maximum DVI for a site-specific canopy, DVI_s is the DVI of the soil, and K is a gain factor. For a detailed explanation of the PPI formulation and validation, refer to Jin & Eklundh (2014), particularly Eqs. (2)–6. The authors also show that PPI performs better than NDVI and EVI, particularly in boreal biomes, because it is insensitive to snow cover and noise during transition phases.

Because of its strong linear correlation with LAI, whose changes are among the easiest to observe in the canopy during the growing season, PPI is particularly well suited to characterizing and monitoring phenological phases. When combined with the spatial scale and frequency of Sentinel-2 observations, it enables the derivation of essential phenometrics highly correlated with physical vegetation variables (such as Leaf Area Index and Gross Primary Productivity). Since 2023, the Copernicus Land Monitoring Service (CLMS) has produced a suite of High-Resolution Vegetation Productivity and Phenology (HRVPP) products. These products, at unprecedented spatial and temporal scales, will enable harmonized large-scale monitoring of the status and changes of ecosystems and land cover (Smets et al., 2024), as well as contribute to reporting on land use and land use change (LULUCF) duties.

However, the interactions among phenology, climate, and environmental factors are extremely complex due to the inherent multicollinearity in the data. Despite meaningful causal relations between phenology and climate variables having been established, the forest-climate system remains highly complex and non-linear, with climate change increasingly weakening the coupling between forest state and climate. For example, while spring warming generally advances green-up (Jibran et al., 2013), recent findings suggest that changing environmental conditions can alter these relationships, increasing discrepancies between phenological markers and functional activity in both spring and autumn (Marqués et al., 2023; Yu et al., 2026). In particular, earlier or delayed senescence may occur independently of photosynthetic cessation, challenging the assumption that growing-season length directly represents changes in ecosystem productivity (Zani et al., 2020, 2021; Zohner et al., 2023). Understanding this phenology-productivity decoupling is therefore critical for accurately assessing how climate change alters the seasonal dynamics of forest carbon uptake. To

disentangle the climate-phenology relation, recent studies have used machine learning (ML) algorithms that can capture complex, non-linear relationships, including random forests (RF), extreme gradient boosting (XGBoost), support vector machines (SVMs), and various neural network architectures. In particular, inferring causal relationships is increasingly important for understanding and mitigating the impacts of climate change on forest and agricultural ecosystems, while leveraging the enormous amounts of data and processing capabilities available today. Recently, explainable artificial intelligence (XAI) methods have been developed and used to access the ML black-box decision-making process and support the interpretability of model results. SHapley Additive exPlanations (SHAP) analysis is particularly suited to such aims and is increasingly used in this field thanks to its model-agnostic framework and its ability to compute variable contributions in the same units as the dependent variable (Štrumbelj and Kononenko, 2014; Lundberg and Lee, 2017; Yu et al., 2026). By making ML predictions more physiologically interpretable, SHAP helps in reducing the gap between mechanistic understanding of physiological processes and data-driven ML approaches. Previous studies have successfully used HRVPP phenometrics to characterize urban vegetation phenology (Borgogno-Mondino and Fissore, 2022; Ojasalo et al., 2025), monitoring crop phenology (Prikaziuk et al., 2025), and assessing the impact of topography on forest species (Sang et al., 2024).

Traditional phenological studies often focus on a limited set of variables or a single species to isolate specific physiological mechanisms. However, the increasing availability of high-resolution RS missions, derived products, and dense time series of climate datasets requires a parallel shift in analytical frameworks. Robust, scalable pipelines are now required to translate complex, high-dimensional RS information into interpretable ecological signals. Therefore, the primary aim of this study is to provide a proof of concept for a data-driven ML framework capable of processing large-scale, high-dimensional climate and phenology datasets for monitoring purposes. To the best of our knowledge, this study is the first to combine the CLMS HRVPP phenometrics, ML, and XAI to investigate forest phenology and productivity at the country level, across *Multiple species* and a wide range of environmental and climatic conditions. Rather than testing a single physiological pathway a priori, our objective is to demonstrate that coupling high-resolution VPP data with an automated ML pipeline can simultaneously:

1. Replicate established macro-ecological patterns across 10 species, thereby validating the robustness of the ML approach.
2. Uncover complex, fine-scale interactions among a large set of climate metrics, specifically testing the hypothesis that warming-induced season lengthening is decoupled from changes in productivity in Mediterranean ecosystems due to compounding abiotic stressors.

2. Materials and methods

2.1. Study area

The study focused on the Italian peninsula, covering >300,000 km² and spanning over 11° of latitude, making the area extremely variable and heterogeneous from both environmental and climatic perspectives. Two main mountain ranges cross the peninsula: from north to south, the Apennine range, and from east to west, the Alps, with peaks reaching up to 4000 m a.s.l. Temperate and Mediterranean climates are the primary climate regimes in Italy, followed by an Alpine climate in the mountainous northern regions. >35% of the entire territory is covered by forest, according to the 2015 Italian NFI (INFC, 2021), totaling 11,054,458 hectares. Broad-leaved species represent the dominant forest category (68% of forest area), composed primarily of oak species (*Quercus petraea* (Matt.) Liebl., *Q. pubescens* Willd., *Q. robur* L., *Q. cerris* L.) and European beech (*Fagus sylvatica* L.). Needle-leaved species dominate the seacoast (*Pinus pinae* L., *P. pinaster* Aiton) and northern regions (*P. sylvestris* L., *P. nigra* J.F. Arnold, *Picea abies* (L.) H. Karst, *Larix decidua*

L.) and form most of the plantation areas. Italian forests are primarily broadleaved, with pure conifers and mixed forests accounting for just over 10% of the total, except in the Alpine regions, where pure conifer forests predominate. The main silvicultural systems are coppice and high forest, which account for 87% of the total area. The result of these silvicultural systems is the prevalence of even-aged, single-layered forests.

2.2. Data

2.2.1. Overview of HRVPP phenometrics

The HRVPP suite comprises three different datasets, consisting of (Camacho et al., 2021):

1. Vegetation index time series: generated in near-real time at the pixel level, including LAI, NDVI, Fraction of Absorbed Photosynthetically Active Radiation (FAPAR), and PPI.
2. Seasonal trajectory (ST): generated yearly from the 10-day PPI time series by fitting a smoothing and gap-filling function.
3. Vegetation Phenology Parameters (VPP): generated yearly from the ST product, consisting of 13 different phenometrics describing vegetation dynamics during the growing season. Depending on vegetation type, up to two growing seasons can be identified.

Fig. 1 reports a schematic representation of the VPP phenometrics, and Table 1 reports the description of each product.

All 13 phenometrics are available from 2017 to 2023 (accessed May 27, 2025), and each new year's product will be provided at the start of the subsequent year (e.g., VPP for 2024 will be available at the beginning of 2025). Below, we provide a brief description of the algorithm and the theoretical basis for these products. For a detailed description of the products, refer to the theoretical basis (European Union, 2026).

The HRVPP phenometrics process comprises three serial modules. The first module, named BIOPAR-IV, generates VIs (NDVI, FPAR, LAI, and PPI) from time series of Sentinel-2A and -2B images at a 10 m x 10 m spatial resolution. The PPI time series is passed to the next module, TIMESAT-4, to generate annual seasonal trajectories and VPP phenometrics. TIMESAT-4 is a software package for high-resolution time-series analysis (Jönsson & Eklundh, 2004; Eklundh & Jönsson, 2016) that first removes the influence of clouds and shadows from the PPI time series using the QFLAG2 method. After removing clouds and shadows, outliers are identified by fitting a smoothing spline to the raw PPI series and computing the global and local median differences between the smoothed and raw series at each point. An observation is considered an outlier if it exceeds six times the global and/or local median difference. The lower 5th percentile of each pixel in the PPI time series is used as the baseline for the entire series. These values represent the snow-free reflectance of bare ground or stable vegetation. They are used for gap filling and to assist the next step, which involves fitting a double logistic function to identify potential seasons that will form the ST products. The double logistic does not assume that the right and left parts of the season are symmetric and ensures that it captures most of the PPI peak, which corresponds to the center of each season. Potential neighboring seasons identified from the smoothed PPI trajectory were merged when the difference between adjacent local minima was smaller than 20% of the corresponding seasonal amplitude.

The iterative merging procedure was constrained to combined season lengths shorter than 365 days. Finally, phenometrics are derived for each season from the ST. SOSD and ESOD are computed from ST as the DoY in which the PPI reaches 25% and 15% of the ST amplitude, respectively. From SOSD and EOSD, additional parameters are derived, including LOS, SOSV, and EOSV. All final products have a spatial resolution of 10 m, consistent with the original Sentinel-2 bands from which they are derived. The high resolution of this new suite of products significantly reduces the aggregation of different elevation gradients, land cover, and ultimately forest types within a single pixel, especially in

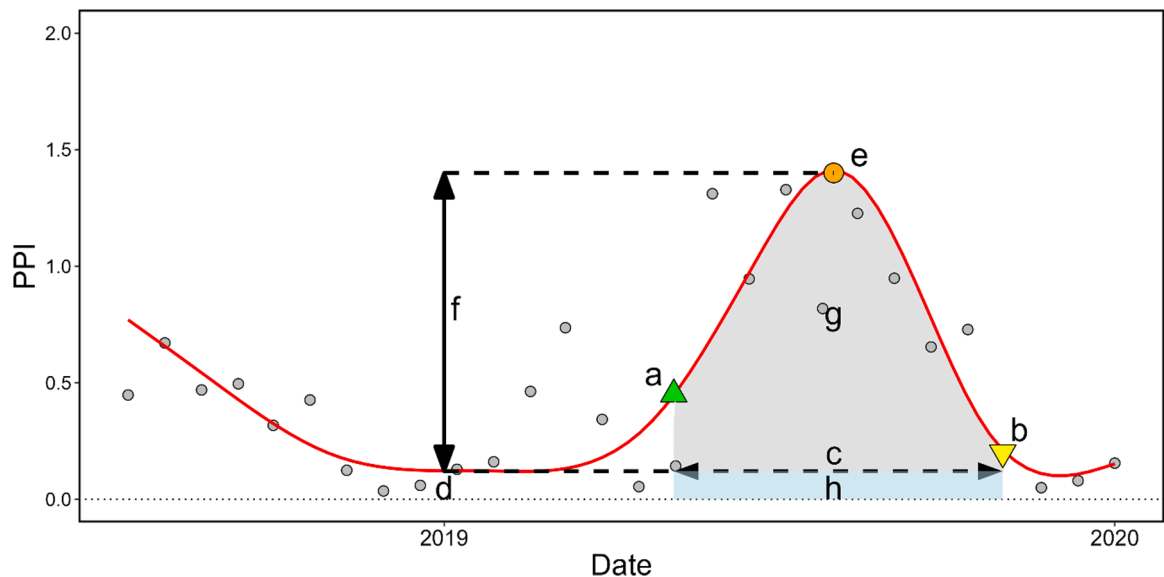


Fig. 1. Schematic representation of VPP phenometrics. Gray points represent raw observations; the red line is the fitted double-logistic curve. VPPs are: (a) start of season (date, PPI value and slope), (b) end of season (date, PPI value and slope), (c) length of season, (d) minimum of season, (e) peak of the season (date and PPI value), (f) amplitude, (g) seasonal productivity without base level, (h) base-level productivity, (g+h) total productivity.

Table 1
List of VPP phenometrics and their significance with respect to PPI time series. In light grey, the phenometrics used in the present study are highlighted.

VPP		
Variable name	Letter	Description
SOSD	a	Start of the growing season on a specific date
SOSV	a	PPI value at SOSD
EOSD	b	End of the growing season on a specific date
EOSV	b	PPI value at EOSD
LOS	c	Length of the season
MAXD	e	Day of maximum productivity
MAXV	e	PPI value at MAXD
MINV	d	Minimum PPI value between two seasons
AMPL	f	Amplitude of the season (MAXV-MINV)
LSLOPE	a	Slope of the green-up period
RSLOPE	b	Slope of the green-down period
SPROD	g	Seasonal productivity between SOSD and EOSD minus their base level value
TPROD	g+h	Total seasonal productivity between SOSD and EOSD

mountain and heterogeneous environments, such as the Mediterranean one, allowing a more consistent representation of forest-specific phenology.

Four of 13 products were analyzed in this study, specifically those related to phenological phases and productivity: SOSD, EOSD, LOS, and TPROD.

2.2.2. NFI data

Field data for this study were collected as part of the third Italian NFI, which was formally reported in 2015. The NFI design followed a systematic, unaligned 1 km x 1 km grid sampling with three phases (Fattorini et al., 2006). In the first phase, each sampling point is photointerpreted to assign a land use category. In the second phase, qualitative field data are collected from a subset of points in the forest category. That information includes the silvicultural system, management system, forest category, property, constraints, and accessibility. Finally, in the third phase, a subgroup of the second-phase points, totaling 6174, is surveyed to acquire quantitative information in 13-m-radius circular plots, including tree species. In this study, we selected all plots in which the dominant species accounted for at least

80% of the basal area to minimize noise in the phenological response due to mixed forests in the phenometrics, thereby ensuring a more accurate representation of each species' phenology. After this initial selection, a total of 91 species were identified across 3678 plots. Among these species, we selected those present in at least 100 plots, resulting in 10 species distributed in 2453 plots (Fig. 2). The selected species are: *Castanea sativa*, *Fagus sylvatica*, *Larix decidua*, *Picea abies*, *Pinus halepensis*, *P. nigra*, *Quercus cerris*, *Q. ilex*, *Q. pubescens*, and *Q. suber*.

2.2.3. Climate variables

To capture the physiological constraints of Italian forest species, we calculated specific climate metrics representing thermal forcing (spring temperatures), phenotypic triggers (winter chilling accumulation), and drivers of energetic/water stress (shortwave radiation, vapor pressure deficit, and precipitation) (Guralnick et al., 2024). We retrieved climate data from the downscaled ERA5 reanalysis for Italy (Raffa et al., 2021). This reanalysis comprises hourly time series at a higher spatial resolution of 2.2 km for the main climate variables, including air temperature (T), solar radiation (solar rad), precipitation (Pr), vapour pressure deficit (VPD), and dew point temperature (TD), obtained through the Regional Climate Model COSMO5.0_CLM9 and INT2LM 2.06 (Rockel and Geyer, 2008). We downloaded the aforementioned variables for the period 2017–2023 for the entire country. For each year, hourly data were aggregated daily to calculate the minimum, maximum, and mean T (°C), the mean solar rad (MJ m⁻² d⁻¹), the mean VPD (kPa), and the total Pr (mm d⁻¹). From the daily climate input, we extracted monthly and seasonal metrics. In particular, the mean, maximum, minimum, range, and sum of T were calculated for each month and season (1 variable x 5 metrics x 16 time frames = 80). Additionally, we computed the monthly and seasonal mean of VPD, solar rad, and Pr (3 variables x 1 metric x 16 time frames = 48) and finally, from the daily average T, solar rad, and Pr, we computed the rate of change as the slope of the linear regression of the variable against time for each month and season (3 variables x 1 metrics x 16 time frames = 48). All climate metrics were calculated independently for each year, yielding a total of 80 + 48 + 48 = 176 metrics that capture the full spectrum of physiological constraints.

2.2.4. Auxiliary variables

Elevation, slope, and aspect were taken from the 10 m resolution digital elevation model (DEM) TINITALY (Tarquini et al., 2007, <http://ti>

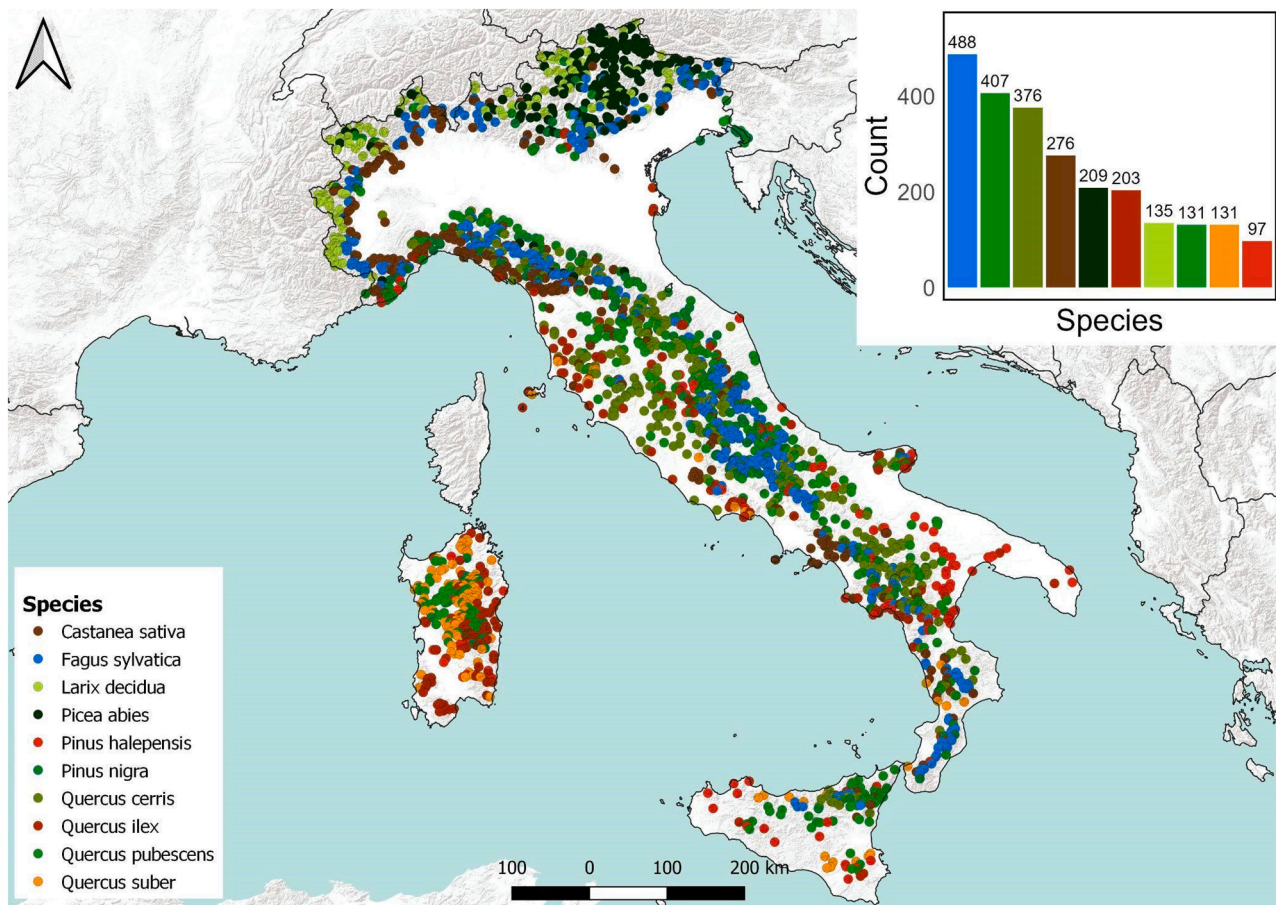


Fig. 2. Distribution of the NFI plots analyzed in this study. In the top-right bar plot, the number of plots per species is shown. The bar plot colors correspond to the species indicated in the map legend.

nitaly.pi.ingv.it/). Additionally, latitude and sea distance were used as auxiliary variables, serving as proxies for precipitation and temperature gradients, which play a crucial role in defining the different phenological phases (Vogel, 2022). These variables represent the local growth conditions for the forest species and remain unchanged throughout their life cycle, unlike climatic metrics. Lastly, we also include stand age as an auxiliary variable, as it is known to affect various physiological processes linked to phenology (Drake et al., 2011; Goulden et al., 2011), including leaf emergence timing, biomass accumulation, and tree species composition. The distribution of these auxiliary variables for each species is shown in Figure S1 (Supplementary Materials).

2.3. Methods

2.3.1. Metrics extraction

The four aforementioned phenometrics (namely SOSD, EOSD, LOS, and TPROD) were downloaded from the WEKEO data catalog (<https://wekeo.copernicus.eu/data?view=catalogue>, accessed on May 28, 2025) via the Harmonized Data Access (HDA) API using the R software (version 4.2.1). For each phenometrics, we downloaded the full available time series from 2017 to 2023, covering the entire national territory, resulting in 128 tiles per parameter per year. The final database comprises 128 tiles $\times$ 4 parameters $\times$ 7 years, totaling 3584 tiles and 400 GB of data. We selected only the first season for each year and phenometrics, since seasons are stored chronologically, and we assume that the growing season begins at the start of the year for all Italian forest species. We selected only the seasons that start and end in the same year. The restriction to the first growing season and to seasons fully contained within a calendar year was applied to ensure consistent alignment

between phenometrics and annual climate predictors. In Mediterranean systems, secondary growth pulses and cross-year senescence, despite not yet being well documented (Pavón-Núñez et al., 2025; Campelo et al., 2021; La Mantia et al., 2003; De Micco et al., 2020), can introduce ambiguity in season attribution and increase noise in automated detection. Furthermore, because the HR-VPP season-merging procedure is based solely on the amplitude and shape of remotely sensed canopy greenness trajectories, it may fail to discriminate short-term physiological stasis or dormancy periods that do not produce a pronounced decline in vegetation index values. Consequently, interruptions in cambial activity or phloem conductance, detectable through radial growth or ecophysiological measurements, may remain unresolved within a single merged growing season. By focusing on the primary season, we prioritize robustness and comparability across species, while acknowledging that secondary cycles are not explicitly captured in this framework. Each tile was cropped and masked with the Italian national boundary, then reprojected to the common reference system WGS 84 UTM 32 N (EPSG: 32,632). Within a 13 m buffer around each plot center, the mean values of all variables were extracted, including all phenometrics, climate metrics, and auxiliary variables for each year. For the phenometrics measured in days of the year (DoY), the mode was extracted instead of the mean. The resulting database consisted of 2453 plots $\times$ 7 years = 17,171 observations, including 4 phenometrics, 176 climate variables, and five auxiliary variables, for a total of 185 variables. Fig. 3 shows the distribution of SOSD and TPROD values across all selected plots, while Figure S2 (Appendix) shows the distribution of all studied phenometrics across all species and years.

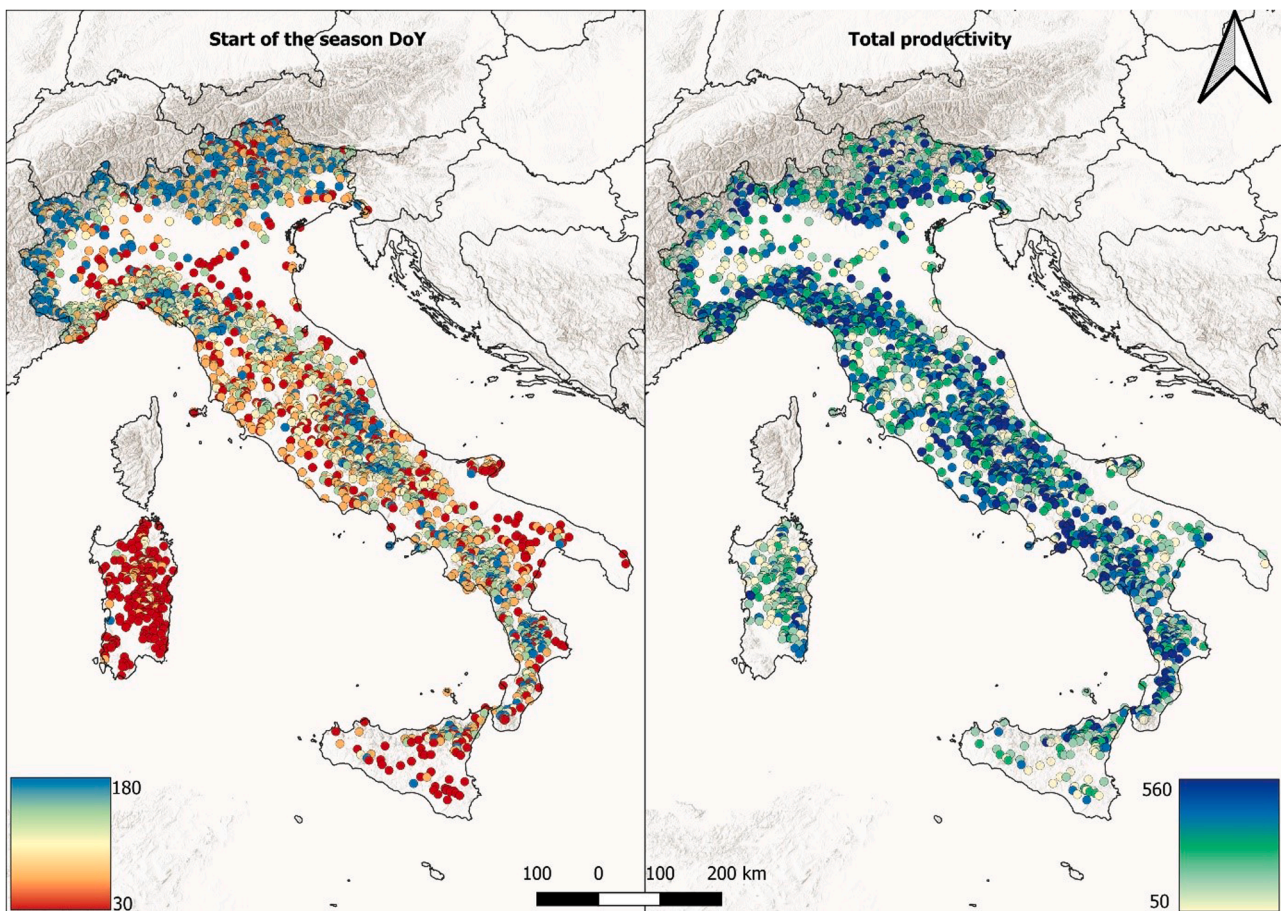


Fig. 3. Spatial distribution of SOSD and TPROD across the NFI plots network.

2.3.2. Environmental and climate variable contribution

2.3.2.1. Overview of the methodology. The analytical workflow implemented in this study follows a multi-stage, data-driven pipeline to model, explain, and evaluate macroecological patterns and climate interactions across 10 key Italian forest species, in a space-for-time substitution approach. An overview of the methods is described below:

1. **Data preparation:** We intersected the geographic coordinates of NFI plots with the HRVPP dataset. Concurrently, a comprehensive matrix of 176 climatic and topographic variables was compiled per plot, capturing localized gradients in temperature, precipitation, photo-period, radiation, and terrain characteristics.
2. **Feature Selection:** To address multicollinearity among environmental predictors and prevent model overfitting, we independently selected variables for each species-metric combination to isolate the most parsimonious, ecologically meaningful subset of climate drivers, using the VSURF algorithm.
3. **Predictive Modeling:** Using the optimized feature subsets, we trained a conditional Random Forest (RF) regression model and used it to predict each species and phenometric trait.
4. **Explainable AI:** To translate predictive models into interpretable ecological signals, we conducted post-modeling tree-based SHAP analysis. SHAP values were computed on each model's prediction to estimate additive feature contribution. Finally, to test and confirm coupling versus decoupling between structural leaf phenology and seasonal productivity, we performed an anomalies analysis based on z-score values

2.3.2.2. Variable selection using random forests. To determine the

significance and contribution of each metric to the phenological phases of the 10 selected species, we used the variable importance (VarImp) from the random forests (RF) algorithm. The original RF algorithm, developed by Breiman (2001), has been shown to be robust to variable autocorrelation and variable scales. It does not assume a linear relationship between the outcome and the predictors, and, thanks to its structure, it can be used to compute a measure of each predictor's importance. In regression problems, the most common and robust index for importance is the permutation importance, calculated for each predictor as the variation in performance (assessed with an error metric, such as the mean absolute error or mean squared error) after permuting the chosen predictor and keeping all the other variables unpermuted (Breiman, 2001) in the out-of-bag sample (i.e., the sample of data not selected in the tree building). With this method, the relationship between the outcome and each predictor is broken in turn, reducing performance when the outcome is associated with the permuted predictor (Strobl et al., 2007). When selecting variables, the RF permutation-based VarImp offers an advantage over univariate screening methods because it accounts not only for the individual effects of each predictor but also for their interactions with other predictors. However, Strobl et al. (2007) demonstrated that its reliability decreases when predictor variables differ in measurement scales or number of categories.

Furthermore, importance scores tend to be biased toward variables that are correlated with one another. This limitation becomes especially apparent when combining different predictors, including their interactions, or when predictors of the same type exhibit different category counts within a sample.

Different studies have shown how the original RF algorithm may be biased in variable selection during the split of each tree (Breiman et al.,

1984; Kim and Loh, 2001; Hothorn et al., 2006; Strobl et al., 2007), e.g., by selecting categorical variables with many levels, variables with many possible splits, and/or variables with missing values, seriously affecting the interpretation of the variable's importance. To address this issue, Genuer et al. (2015) developed a third-step, fully data-driven variable selection procedure based on RF algorithms, called "variable selection using random forest" (VSURF). The rationale for the approach is to identify, among all important variables highly related to the response variable, the minimal subset that ensures acceptable predictive power when included in a RF model.

Below is a brief description of the VSURF algorithm:

First step

- n RF models with 2000 trees each are fit on the data, and the out-of-bag VarImp is calculated.
- For each variable, VarImp is averaged over the n models, and its standard deviation is computed.
- The averaged VarImp are then ranked in decreasing order; a classification and regression tree model is fit with the VarImp standard deviation as the dependent variable and the ranks as the independent variable.
- Then, only the variables with an averaged VarImp exceeding the classification and regression tree model's minimum prediction are retained. Let's call this number of variables m .

Second step: interpretation of variables

- Construct n' RF models involving the k first variables, for $k = 1$ to m , and select the variables involved in the model leading to the smallest out-of-bag error. This leads to considering m' variables.

Third step: prediction variables

- Starting with the ordered variables retained for interpretation, construct an ascending sequence of n' RF models by sequentially adding variables and testing them. A variable is added only if the decrease in error exceeds a threshold. The variables of the last model are selected.

The above-mentioned procedure is implemented in the R package 'VSURF'.

To compute the VarImp of the environmental and climatic predictors for predicting phenometrics, we first averaged annual VPP values at the plot level and for all predictors. We did this for two main reasons: first, the current VPP time series is insufficient to estimate the effect of climate variability on phenological responses, so we used a space-for-time substitution approach, exploiting the wide range of environmental conditions in which the species under study grows. Second, we wanted to minimize the effect of year-to-year climate fluctuations on the species' phenological signature. We conducted an exploratory analysis of VPP statistical differences across years using Dunnett and Post hoc tests, as described in the Supplementary Materials (figures S2 and S3). Then, for each species, we applied the VSURF approach using, in turn, the phenometrics as the outcome and all climate and auxiliary variables as predictors. We used $n = 50$ in the first step of VSURF, corresponding to fitting 50 different RF models with 2000 trees each, for a total of 50 RF $\times$ 4 VPP $\times$ 10 species = 2000 models used to compute VarImp. The VarImp for each variable was calculated as the average VarImp resulting from the first step of VSURF. We also report the out-of-bag root-mean-squared

error (RMSE) of the model fitted with the selected variables. The advantage of this method is that the cutoff for determining whether a variable is essential is derived directly from the data itself, without requiring any assumptions.

Furthermore, VSURF was designed to be efficient and robust, particularly for high-dimensional ($n \ll p$) data with many redundant variables, as in this study. Given the highly non-linear and interactive nature of climate metrics, pre-selecting variables based solely on traditional linear assumptions or on expert knowledge risks missing compounding effects. Therefore, VSURF was employed not as a data-mining tool, but to reduce dimensionality and identify the most predictive features while preserving non-linear interactions and predictive power.

The variables selected in the VSURF prediction step were used to calculate Shapley values for each observation using the SHAP approach.

2.3.2.3. Model fitting. A Conditional RF model was fitted for each species-phenometrics combination using the key predictors identified by the VSURF algorithm for that combination. The conditional RF framework is implemented in the `ctree()` function of the `party` R package (Hothorn et al., 2006). Model performance was assessed via the out-of-bag RMSE. Each model was used to predict the corresponding phenometrics for all NFI pure plots. The predictions of each model were then explained using SHAP analysis.

2.3.2.4. Variable contribution with SHapley additive explanation (SHAP). Shapley values, originating in cooperative game theory (Shapley, 1953), have become a prominent method for explaining black-box machine learning predictions and quantifying each feature's marginal contribution. This method is particularly valued for its theoretical properties and model-agnostic nature, making it applicable to a wide range of machine learning models (Štrumbelj and Kononenko, 2014). The Shapley value is a method for distributing the value of individual predictions into feature contributions. That is, the Shapley values explain the difference between the individual prediction and the global average prediction of a particular model:

$$\phi_i = \sum_{S \subseteq N \setminus \{i\}} \frac{|S|!(M - |S| - 1)!}{M!} [f_x(S \cup \{i\}) - f_x(S)] \quad (2)$$

where ϕ_j is the contribution of the j^{th} feature, M is the number of features in the model, S is a subset of features, and $v(S)$ is a contribution function.

In this form, the Shapley value is a weighted average of the differences in the contribution functions across all feature subsets S that exclude feature j (Aas, Jullum, and Løland, 2021).

Lundberg and Lee (2017) have developed the Kernel SHAP method, a practical approach to computing Shapley values in real-world scenarios, since the calculation of Eq. (2) may be computationally unfeasible for large datasets due to the exponential increase in the number of S . Furthermore, the original method was limited to independent features, which is often not the case for remote sensing and climate - derived predictors. Various methods have been proposed to address this assumption (Aas, Jullum, and Løland, 2021; Redelmeier, Jullum, and Aas, 2020; Olsen et al., 2022). In this study, we employed the conditional inference tree approach from Redelmeier, Jullum, and Aas (2020), which uses `ctree` to model each S 's conditional distribution and is implemented in the 'shapr' R package (Jullum et al., 2025). SHAP values are expressed in the same physical unit as the response variable (e.g., days for SOSD, EOSD, and LOS; PPI value for TPROD), and their sign and magnitude reveal both the direction and strength of the predictor's impact on predictions. The sign of a SHAP value denotes whether a variable pushes the prediction above or below the prediction mean: a positive value (>0) represents a calendar delay for timing metrics (SOSD and EOSD), an extension of growing season duration (LOS), or an increase in annual productivity (TPROD), whereas a negative value (<0) represents a calendar advancement (earlier green-up or senescence), a shorter season duration, or suppressed

productivity. The absolute magnitude ($|\text{SHAP}|$) quantifies the effect size in original physical units, where larger values indicate primary drivers dominating plot-level predictions and values approaching zero denote negligible variable influence.

For visualization purposes, we grouped climate metrics into five groups: winter/chilling temperature, spring temperature, water availability, photoperiod, and topography (see supplementary materials for the grouping table). For each group, we computed the total SHAP value, exploiting SHAP's additive nature (i.e., within a given group, the total SHAP value is the sum of the SHAP values for all variables in that group). We chose this framework to minimize collinearity-driven bias when selecting ecologically important variables, using VSURF for variable reduction and ctree SHAP for interpretation.

Furthermore, to address possible decoupling between season length and total productivity, we examine whether interannual variability in LOS predicts interannual variability in TPROD. We quantified the interannual relationship between phenological timing (LOS) and seasonal productivity (TPROD) at the pixel level using standardized anomalies (z-scores), and then fit an OLS model between the paired anomalies ($z_{\text{TPROD}} = \beta_0 + \beta_1 z_{\text{LOS}}$) to calculate the coefficient of determination (R^2). An $R^2 \sim 0$ indicates a weak or absent relationship between LOS and TPROD, suggesting a decoupling effect.

3. Results

3.1. Environmental and climate variable ranking

The VSURF underscores that phenology is a multivariate process, modulated by a complex interplay between topography, water availability, and thermal conditions. Generally, climate variables emerged as

primary predictors, with temperature and precipitation-related metrics dominating the selection across almost all VPPs. Topographical factors, particularly slope and elevation, were also highly important, being selected by *M. species* (e.g., *Castanea sativa*, *Fagus sylvatica*, and *Larix decidua*) for key periods such as EOSD, LOS, and TPROD, reflecting the strong influence of local microclimate and drainage on vegetation dynamics Fig. 4. This pattern highlights the critical role of early-season growing conditions, in which low temperatures are often the limiting factor for budburst, and accumulated winter/spring moisture reserves influence the duration and productivity of the growing season.

3.1.1. Start, end, and length of the growing season

The number of selected variables for SOSD ranged from three (*Picea abies*) to nine (*Quercus cerris* and *Q. suber*), with a mean of six across all species. A total of 33 unique variables were selected, with elevation selected in half of the species. Elevation was the variable most strongly affecting phenology in *Fagus sylvatica*, *Castanea sativa*, *Picea abies*, *Quercus cerris*, and *Larix decidua*. For other species, the most influential variables were related to winter/spring temperature and radiation (Tmin in January for *Quercus ilex* and *Q. pubescens*, Tmax in April for *Pinus nigra*, the mean spring radiation for *P. halepensis*, and the total spring precipitation for *Quercus suber*).

In particular, 1 metrics were selected 25 times, followed by VPD and Pr metrics (9 times), and finally solar rad metrics (7 times). The importance magnitude ranged from 1 to 12 days in RMSE. However, it is essential to note that a low magnitude for a single variable does not imply that the variable is unrelated to the outcome; instead, it suggests that its unique contribution to performance is minimal or that it is highly correlated with other variables. This occurs for *Picea abies*, *Larix decidua*, and *Fagus sylvatica*, for which elevation may explain most of the model's

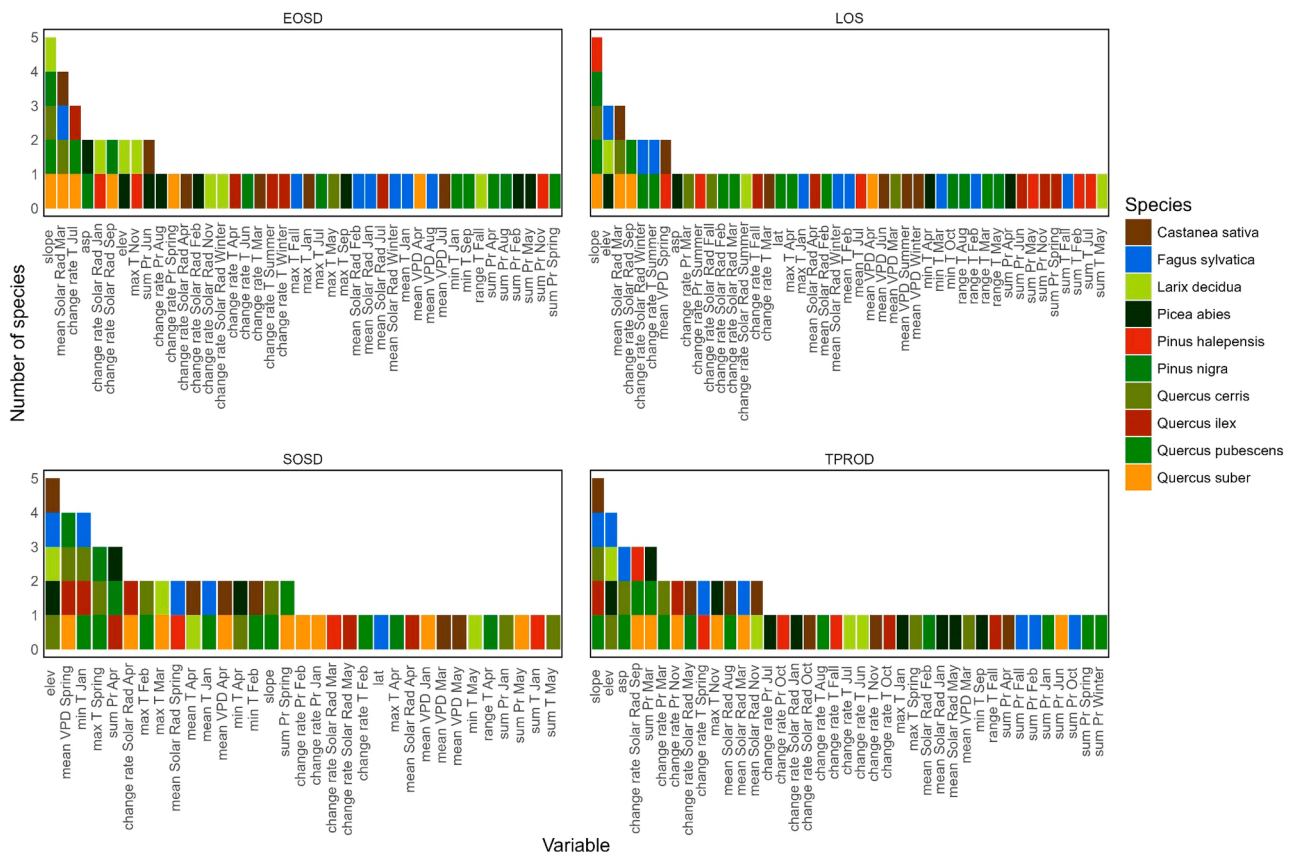


Fig. 4. Selected variables in the VSURF procedure for each VPP. Colours map the species for which each variable was selected. EOSD is the DoY of the end of the growing season, LENGTH is the length of the season, SOSD is the DoY of the start of the growing season, TPROD is the total seasonal productivity between SOSD and EOSD.

variance. At the same time, different variables are generally highly correlated. In the conditional framework, there is no importance leakage from correlated predictors, so the algorithm will downrank variables that don't provide unique information beyond what's already captured. By contrast, most *Quercus* species exhibited a more uniform decrease in importance across the selected variables, indicating a complex pattern in SOSD that a simple model cannot readily explain. Model's performance ranges from 8 to 15 days (for *Fagus sylvatica* and *Pinus halepensis*, respectively), with a mean RMSE of 11.5 across species (Table 1).

In summary, spring onset appears to be governed by a parsimonious set of climate drivers, where spring temperatures and elevation emerge as the dominant predictors in both Mediterranean and mountain ecosystems.

Different results were obtained in predicting the EOSD. The number of selected variables ranged from three (*Pinus halepensis*) to nine (*Picea abies*), with a mean of six across all species, similar to SOSD. A total of 42 variables were selected. The variables affecting EOSD the most were related to environmental characteristics (the slope for *Quercus cerris* and *Q. pubescens*, and the elevation for *Larix decidua*), the spring/autumn Pr (*Picea abies*, *Pinus halepensis*, *Quercus suber*), and the autumn/winter solar rad (for *Fagus sylvatica* and *Pinus nigra*). T metrics were selected 19 times, followed by solar rad (16), Pr and VPD metrics (10 and 3 times, respectively), and finally environmental metrics (9 times). The importance magnitude ranged from 1.5 to 14.6 days in RMSE. The model's performance ranges from 13 to 56 days (for *Fagus sylvatica* and *Pinus halepensis*, respectively), with a mean RMSE of 28 days across species (Table 1).

In general, autumn senescence requires a much higher dimensionality than spring, reflecting a complex, non-linear dependence on late-summer moisture constraints, photoperiod, and minimum autumn temperatures.

The most important variables for estimating LOS ranged from three (*Larix decidua*) to 10 (*Quercus pubescens*), with a mean of six variables. Slope and elevation were the most important variables for six species, followed by autumn/winter T metrics (*Quercus ilex* and *Pinus halepensis*) and the rate of change of solar rad in September (for *Quercus suber*). In many Mediterranean species, variables related to VPD and total Pr in autumn were frequently selected. The magnitude of VarImp ranged between 1.5 and 12 days in RMSE. The model performance ranged from 16 (*Fagus sylvatica*, *Castanea sativa*) to 50 (*Pinus halepensis*) days in RMSE (Table 1).

The length of the season appears to be controlled mostly by late-season temperature, photoperiod, and their proxies, such as elevation. In contrast, in Mediterranean species, variables related to water availability (VPD, Pr, slope) are more important than in a mountain environment.

3.1.2. Productivity

In the TPROD forecast, the number of selected variables ranges from 2 (*Pinus nigra*) to 9 (*Quercus pubescens* and *Picea abies*), with an average of 5.9 across all species. A total of 38 different variables were used, with the slope chosen by half of the species. The most important variables were related to environmental characteristics (the slope for *Quercus cerris*, *Q. pubescens*, and *Castanea sativa*, and the elevation for *Larix decidua*, *Picea abies*, and *Fagus sylvatica*), seasonal thermal dynamics, and the spring/autumn Pr (*Picea abies*, *Pinus halepensis*, and *Quercus suber*). The model's performance varies from 46 to 72 in RMSE (for *Quercus suber* and *Fagus sylvatica*, respectively), with an average of 58 among species (Table 2).

In summary, environmental characteristics such as slope, elevation and aspect, act as different proxies in different climate: in mountain and Alpine biomes, productivity is more influenced by environmental proxies that capture fine-scale changes in climatic gradients (i.e., elevation), whereas in the Mediterranean environment, water availability tend to be represented by environmental proxies such as slope and aspect.

Table 2

Out-of-bag RMSE for each species-phenometrics combination.

	SOSD days	EOSD PPI	LOS	TPROD
<i>Castanea sativa</i>	9	15	16	60
<i>Fagus sylvatica</i>	8	13	16	72
<i>Larix decidua</i>	10	15	19	51
<i>Picea abies</i>	14	14	22	57
<i>Pinus halepensis</i>	15	56	50	52
<i>Pinus nigra</i>	13	25	28	71
<i>Quercus cerris</i>	11	28	26	63
<i>Quercus ilex</i>	11	20	23	49
<i>Quercus pubescens</i>	12	42	33	57
<i>Quercus suber</i>	10	39	34	46

3.2. SHAP analysis

3.2.1. Start, end, and length of the growing season

The SHAP results for SOSD indicate that winter and spring temperature variables (minimum and maximum temperatures in January, February, and April) are the primary drivers for most species, particularly in mountain environment where SOSD can advance by up to 0.75 days per degree. In contrast, Mediterranean species are more sensitive to winter chilling, with SOSD advancing by ~0.5 days per additional degree, compared with ~0.3 days for mountain species (see figures in Data and Code Availability Repository: SOSD_SHAP.rar). Solar radiation indicators (average intensity and rate of change in April and May) and spring and summer VPD show significant contributions, particularly for Mediterranean species (*Quercus ilex*, *Q. suber*, *Pinus halepensis*). For mountain species (*Larix decidua*, *Picea abies*, and *Fagus sylvatica*), elevation has a positive effect (higher elevation favors an earlier start to the season). Warmer conditions advance the start of the season by 1–10 days across species, while the combined effects of temperature, radiation, and moisture can extend the growing season by up to 20–30 days. At the same time, topographic variables such as slope emerge as secondary but sometimes significant factors for some oak species (*Quercus cerris* and *Q. pubescens*). In Fig. 5, the total SHAP values for each variable's group are reported. It is important to note that group-level SHAP values represent the net contribution of all variables within a group and should therefore not be interpreted as indicating that all variables in the group act in the same direction, with the same strength. Individual variables may contribute positively or negatively, with the group-level SHAP value reflecting their aggregated effect (see the figures in the Data and Code Availability Repository: SOSD_SHAP.rar for single-variable contribution plots).

In the EOSD analysis (Fig. 6), winter and spring thermal variables (minimum and maximum temperatures in January, February, and April) confirm their role as determinants for most species (see the figures in the Data and Code Availability Repository: EOSD_SHAP.rar for single-variable contribution plots). Solar radiation indicators, such as spring radiation rate of change and average, spring and summer vapor pressure deficit (VPD), and precipitation, are particularly influential for Mediterranean species (*Quercus ilex*, *Q. suber*, *Pinus halepensis*), advancing the end of the season by up to 40 days. Elevation has a primary impact on mountain species (*Larix decidua* and *Picea abies*), with solar radiation indicators of relative importance.

The SHAP analysis reveals that for LOS (Fig. 7), the most contributing variables are temperature, water availability, and vapor pressure deficit (VPD), which are determining factors for most Mediterranean species (*Quercus ilex*, *Q. suber*, and *Pinus halepensis*). Summer precipitation and spring VPD significantly affect the duration of the season in *Castanea sativa*. Mountain species (*Larix decidua* and *Picea abies*) exhibit strong elevational and summer solar radiation dependencies, confirming their preference for cool, bright environments. Slope is a limiting factor for *Pinus nigra*, *Quercus cerris*, and *Q. pubescens*, reducing seasonal length. Overall, LOS can vary by up to 20 days, with Mediterranean species

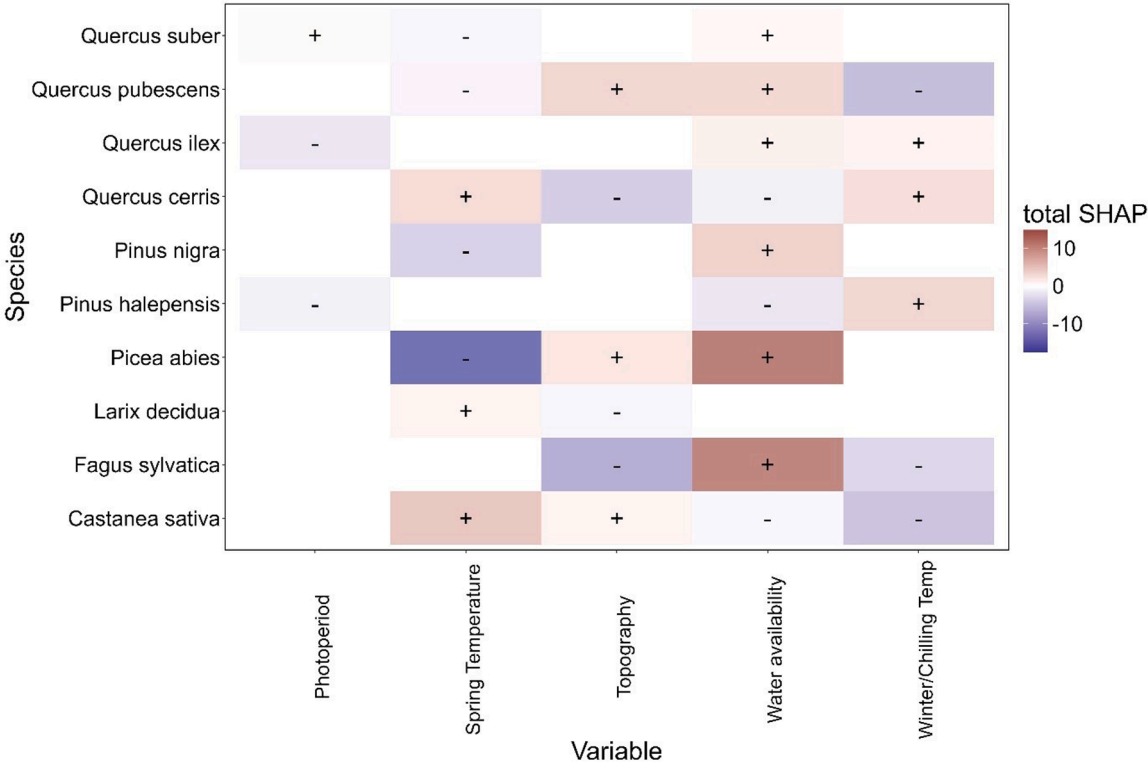


Fig. 5. Total SHAP value (color gradient) of SOSD per group of variables (x-axis) for each species (y-axis). The SHAP unit of measurement is the same as that of the independent variable and represents the difference in days relative to the mean prediction. The "+" and "-" sign indicate whether the total SHAP value is positive or negative, respectively.

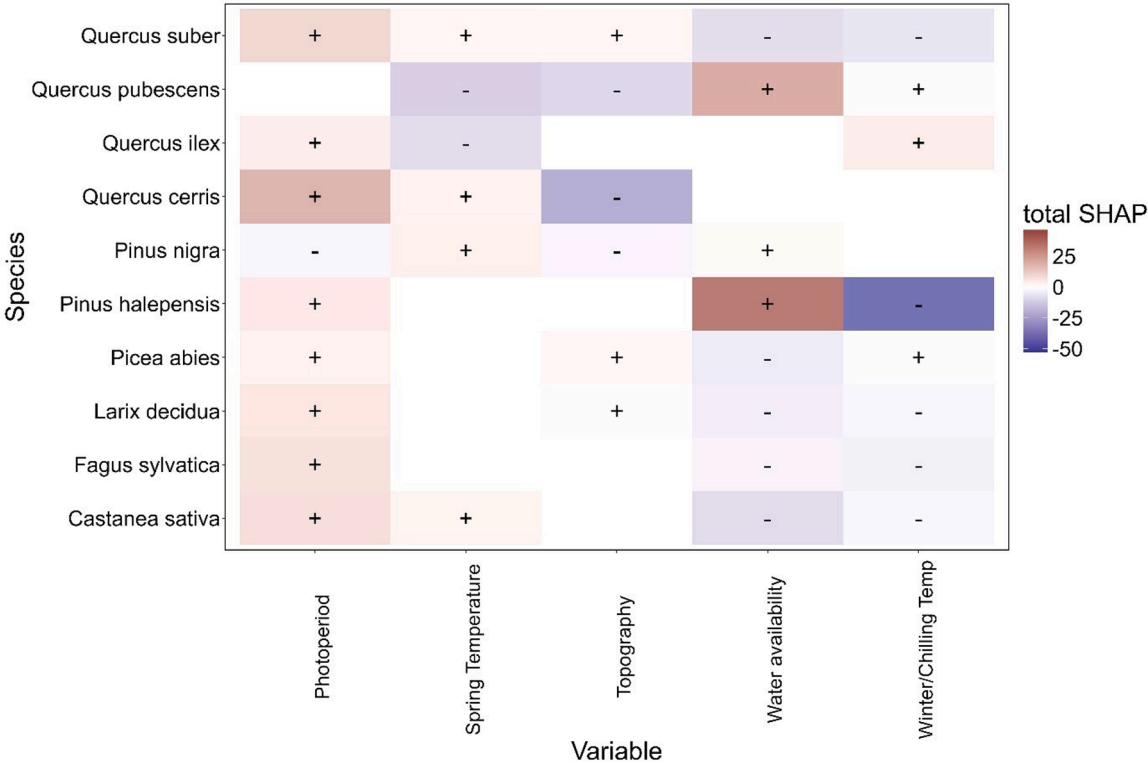


Fig. 6. Total SHAP value (color gradient) of EOSD per group of variables (x-axis) for each species (y-axis). See Fig. 5 for visual details.

tending to shorten the total season length and mountain species showing the opposite. See the figures in the Data and Code Availability Repository: LOS_SHAP.rar for single-variable contribution plots (beeswarm plots).

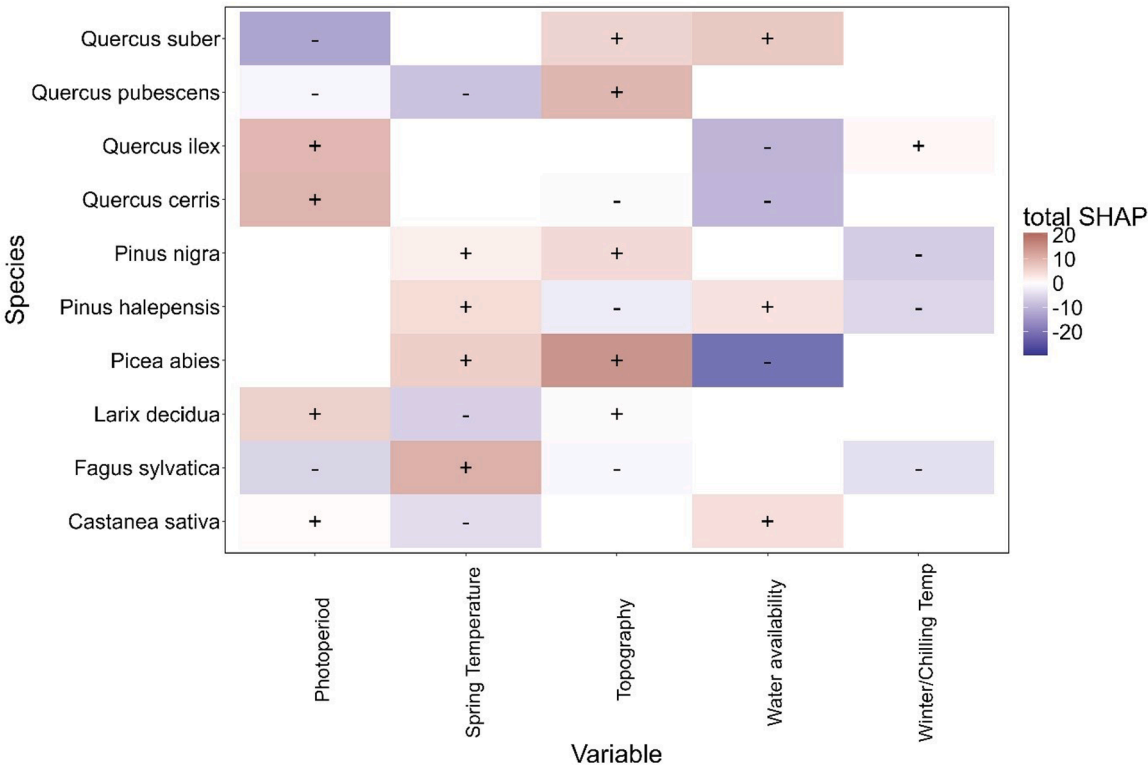


Fig. 7. Total SHAP value (color gradient) of LOS per group of variables (x-axis) for each species (y-axis). See Fig. 5 for visual details.

3.2.2. Productivity

The SHAP-based models for TPROD (Fig. 8) show that solar radiation, particularly the average and rate of change in spring and autumn, is a major driver for the productivity of species such as *Pinus nigra* and *Castanea sativa*, indicating a strong dependence on energy availability.

For Mediterranean species (*Pinus halepensis*, *Quercus ilex*, *Q. suber*), productivity demonstrated marked non-linear relationships and threshold effects with respect to autumn climate predictors. For instance, the autumn solar radiation rate of change yielded positive SHAP values only when seasonal reductions remained moderate (i.e.,

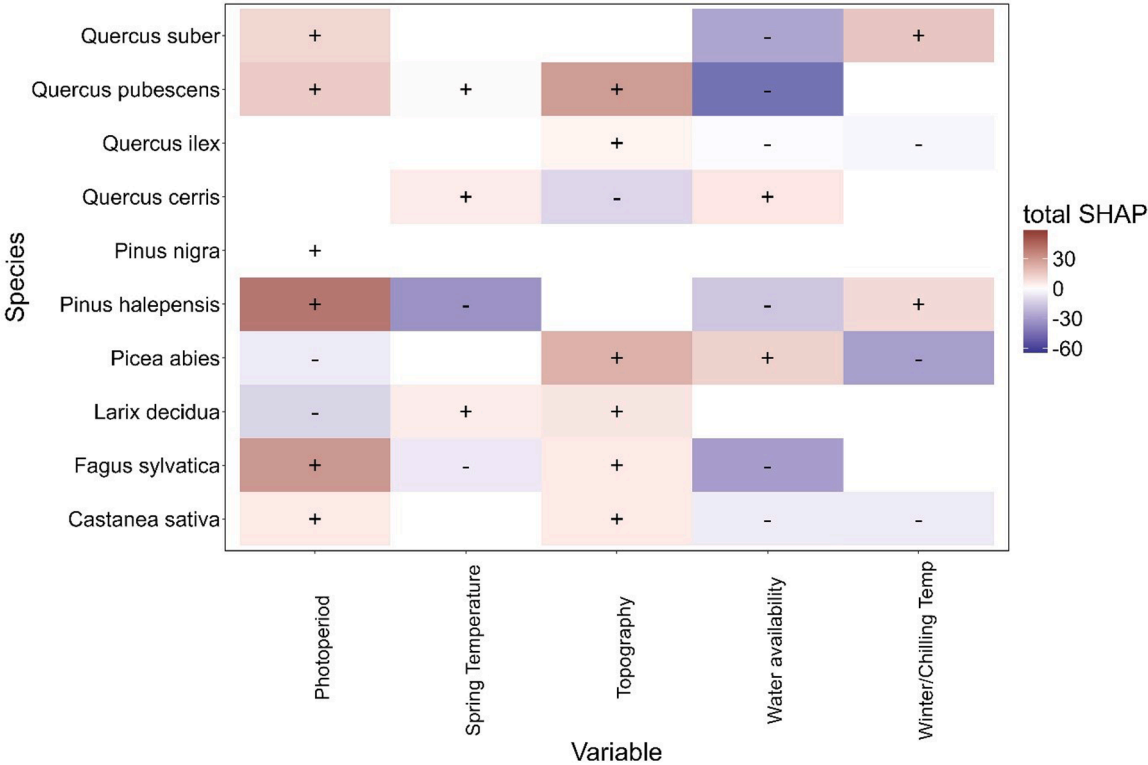


Fig. 8. Total SHAP value (color gradient) of TPROD per group of variables (x-axis) for each species (y-axis). See Fig. 5 for visual details.

linear regression slope > -2); an equivalent threshold response characterized the autumn temperature rate of change (see individual SHAP response figures in the Data Availability Repository). For mountain species (*Picea abies*, *Larix decidua*, and *Fagus sylvatica*), elevation remains a critical factor. Slope remains a limiting factor for several species, particularly *Quercus cerris* and *Q. pubescens*. Moreover, for species such as *Fagus sylvatica*, *Quercus cerris*, and *Q. pubescens*, aspect is a key factor that can influence sunlight and microclimate conditions, with positive SHAP contributions between 0° and 90° and 250° – 360° . See the figures in the Data and Code Availability Repository: TPROD_SHAP.rar for single-variable contribution plots (beeswarm plots).

Finally, the z-score analysis (Supplementary Materials, Figure S5) reveals a weak correlation between season length and overall productivity for each investigated species. In particular, the strength of the correlations, measured via R^2 , was well below 0.2 for all species, with a maximum of 0.14 in *Larix decidua* and a minimum < 0.01 for all the *Quercus* species (see fig. S5 in Supplementary Materials).

4. Discussion

4.1. Start, end, and length of the season

Climate change is markedly altering weather conditions, especially in Mediterranean areas. Increases in mean air temperatures, more frequent severe heat waves, longer droughts, and altered precipitation patterns are lengthening the growing season and reshaping the regional climate regime, as well as carbon and water cycles. These climatic shifts have influenced the phenology not only of Mediterranean species but also of other mountain species, such as European beech (Nezval et al., 2025), Norway spruce (*Picea abies*, K. 1881), and Scots pine (*Pinus sylvestris* L., 1753) in central and northern Europe (Vangi et al., 2024a; 2024b). In Italy, due to extreme variation in climatic and environmental variables, individuals of the same species face very different conditions, enabling the assessment of phenological responses to environmental variability.

In this study, climate sensitivity was assessed through spatiotemporal variability analysis (space-for-time substitution) rather than long-term temporal trend detection, given the still-limited time coverage of the phenology data. Nevertheless, our results confirm this common behavior across many Italian species: individuals exposed to higher winter and spring temperatures (winter chilling) anticipate the start of the season by 1 to 10 days, thereby lengthening the growing season by up to 10 days solely due to temperature. We found that the trend in minimum temperature was more influential in shifting the season than the average and maximum temperatures, confirming the role of chilling temperatures in quiescence and budburst (Hänninen, 2016). The frequent selection of minimum temperatures in winter months (January–February) and maximum temperatures in April suggests that both chilling accumulation and spring forcing are relevant. However, we found that in Mediterranean species, winter chilling has a greater effect on advancing the start of the season than in mountain species (advancing by ~ 0.5 days per additional degree, compared with ~ 0.3 days). In contrast, the latter are more sensitive to higher spring temperature, advancing the start of the season by 0.75 days per degree (see figures in Data and Code Availability Repository: SODS_SHAP.rar). When other climatic drivers are taken into account, the growing season can be extended by 20–30 days in many considered species (e.g., *Quercus ilex*, *Q. pubescens*, *Q. cerris*, *Pinus halepensis*, *Larix decidua*, *Picea abies*), reinforcing the findings of Nezval et al. (2020, 2025) in the Czech Republic.

Other sites' characteristics act as proxies for climatic drivers and their interactions, such as elevation and latitude, thereby shifting the start of the season along climatic gradients, especially in Alpine species, where temperature and snow persistence determine the length of the growing season. Collinearity among temperature, radiation, and moisture variables along elevational gradients may have led the model to favor

topographic factors, and the higher spatial resolution may also have played a role. In fact, topography was derived from a high-resolution dataset, consistent with the phenometrics resolution, thereby capturing microclimatic variations that are blurred in the ERA5 dataset, particularly in complex mountain environments characterized by ridges, valleys, and varied slopes. This may explain the relatively few individual climatic variables selected for these mountain species in the VSURF framework. In such cases, elevation effectively captures most of the variance relevant to SODS and LOS, downweighting other correlated predictors despite their known physiological relevance and widespread species (i.e., *Quercus cerris* and *Castanea sativa*, which vegetated along some of the widest altitudinal gradients in Italy). In contrast, *Quercus* species exhibit a more complex and plastic phenological response, with greater interannual variability, suggesting that more factors jointly regulate the onset of seasons.

The end of the season and its length appear to be regulated predominantly by light and water availability, including air and soil humidity, precipitation, and terrain proxies like slope and aspect. Notably, these environmental factors tend to exert a stronger regulatory effect on autumn dynamics than on spring onset. In mountain species such as *Larix decidua* and *Picea abies* (and even *Fagus sylvatica* at higher latitudes and elevations), a strong coupling between delayed season onset and reduced season length was observed, reflecting the dominant role of temperature and energy limitations in this environment, as also reported by Keenan et al. (2014). On the contrary, Mediterranean species display a more complex response to water and light availability. *Quercus pubescens* and *Q. cerris* often display compensatory shifts between the start and end of the growing season, resulting in relatively stable season lengths. However, water availability (soil and air moisture and precipitation) can trigger stomatal closure and shorten the overall growing season, as observed in *Pinus halepensis*, *Quercus suber*, and *Q. ilex* (isohydric Mediterranean species). The divergent responses to summer drought observed across Mediterranean species suggest different isohydric-anisohydric responses. In strict isohydric species, prolonged summer drought induces rapid stomatal closure and subsequent leaf shedding to prevent cavitation, thereby advancing the end of the season (McDowell et al., 2008). Conversely, in more anisohydric or drought-tolerant species (*Quercus pubescens*, *Q. cerris*), severe moisture deficits can induce physiological stasis, halting growth during the summer peak (Tognetti et al., 2007). Upon the arrival of transitional autumn precipitation, these species resume metabolic activity, effectively delaying the final senescence date. These results are consistent with previous studies indicating that phenological plasticity in Mediterranean ecosystems is constrained by summer drought and atmospheric water demand (Delpierre et al., 2016; Caparros-Santiago et al., 2021). However, it is worth noting that there is no consensus on the factors driving the end of the season (Campioli et al., 2025; Nezval et al., 2025), as evidenced by the model's generally poor performance in predicting it. From our data, it appears that summer conditions (in particular, precipitation amounts and the rate of summer heating) play an important role in determining leaf senescence (i.e., for *Castanea sativa*, *Picea abies*, and *Quercus ilex*), usually by retarding the season end (but the shift is site- and species-dependent), as found by other studies (Dox et al., 2022; Xie et al., 2018).

Furthermore, our results suggest that spring temperature can also influence leaf senescence, as hypothesized by Zani et al. (2020) and Zohner et al. (2023). The observed influence of spring temperature on autumn senescence points to two possible intra-seasonal legacy effects. First, higher spring temperatures may accelerate early-season evapotranspiration, depleting soil water reserves prematurely and intensifying late-summer hydraulic stress, thereby forcing an earlier season end. Second, a carbon sink-limitation mechanism may contribute to earlier senescence. Enhanced spring radiation and temperature can stimulate early-season carbon assimilation and structural growth, potentially saturating sink capacity earlier. Under reduced sink demand, non-structural carbohydrates may accumulate in leaves, leading to

photosynthetic down-regulation and to sugar-signaling pathways associated with chloroplast degradation and senescence (Asad et al., 2024). A third possible effect of higher spring temperature on leaf senescence may involve age-dependent senescence-associated genes (Jibran et al., 2013) rather than stress alone: leaf senescence is co-regulated by intrinsic physiological age and extrinsic stress; consequently, earlier spring leaf unfolding advances physiological maturation, driving earlier autumn senescence as leaves reach their functional longevity limits sooner (Meier et al., 2025). In our study, solar radiation was selected across all species except one (*Quercus pubescens*), consistent with a productivity- and carbon-sink-limited mechanism rather than with temperature-driven passive decay alone. Interestingly, in mountain and Alpine species, radiation was selected as the rate of change (a proxy for the photoperiod), which has been hypothesized to be a more important factor at high latitudes and altitudes (Jiang et al., 2022) than radiation intensity, which instead regulates senescence in many European deciduous species (Liu et al., 2021).

4.2. Productivity

A common assumption in climate change studies is that phenological shifts, particularly earlier spring onset and longer growing seasons, lead to increased ecosystem productivity and carbon uptake (Keenan et al., 2014; Piao et al., 2019). However, the results of this study reveal a more complex relationship, with phenological timing and productivity often decoupled. Several species show significant intra-annual differences in the timing of the season's start or end without corresponding changes in total seasonal productivity. In contrast, others exhibit productivity variations in the absence of marked phenological shifts, as suggested by the z-score analysis of anomalies (see supplementary materials, Figure S5). Mediterranean species, in particular, show a very weak relationship between season length and total productivity anomalies, with R^2 values of 0.01 or lower and no evident trends, which can be explained by a compensatory shift in season timing to avoid drought stress. The low R^2 , coupled with the SHAP analysis, also suggests that the duration of the growing season is only partially driven by the same environmental variables that determine seasonal productivity, further strengthening the conclusion that calendar time is decoupled from growth. In the Mediterranean context, a lengthening of the season may signal a prolonged drought period, with consequent stress on many species, especially strict anisohydric.

Similar non-linear and context-dependent relationships have been reported in recent studies (Ren et al., 2024; Morichetti et al., 2024; Andreatta et al., 2025), highlighting the role of limiting factors such as VPD, precipitation seasonality, and light availability. However, productivity depends not only on phenological phases but also on physiological traits, disturbance history, and site conditions, which explain the generally lower predictive performance of the models for TPROD (Saponaro et al., 2024).

As for phenological phases, productivity seems to be regulated primarily by water and energy availability in Mediterranean species, particularly spring-autumn precipitation and autumn solar radiation intensity, as Liu et al. (2024) have found for about 40% of European broadleaved species. We observed non-linear relationships between productivity and these variables, with many exhibiting threshold effects (see supplementary figures). For instance, the rating of the change in solar radiation in autumn has a positive effect only when it is slightly negative (i.e., the slope of the linear regression > -2), and the same applies to the heating rate of autumn (see figures in Data and Code Availability Repository: TPROD_SHAP.rar). Aspect exhibits a similar behavior, being positively influential from 0° to 90° and from 250° to 0° . On the contrary, on the most exposed slopes, temperatures and solar radiation can become limiting factors, reducing water availability and potentially leading to stomatal closure. Aspect can play a key role in shaping local microclimatic conditions, particularly beneath the forest canopy, by reducing the variability of air and soil temperatures and

buffering the impacts of climate change (Rita et al., 2021). On the contrary, precipitation and temperature, regardless of the metric and period, are always positively correlated with total productivity (see the figures in the Data and Code Availability Repository: TPROD_SHAP.rar). Several studies on xylem and phloem phenology agreed that a warming climate would result in a lengthening of the growing season; however, when accounting for drought effects, this extension may be offset by a reduction in the period available for wood formation, cell enlargement, and secondary cell wall thickening (Pérez-de-Lis et al., 2017; Dox et al., 2020; Redemacher et al., 2021; Campioli et al., 2025).

Alpine and mountain species once again show a dominant elevational signal, reinforcing the idea that productivity in these ecosystems is constrained by temperature regimes and growing season length rather than by water availability.

It is worth noting that climatic conditions are not the only factors in determining phenological processes and their coupling with physiological responses, such as radial growth and biomass accumulation. As a matter of fact, different species in the same or similar environments show very different behavior, as found, for example, by Camarero et al. (2010) and Cuny et al. (2012). Different strategies among species, and even annual weather patterns, affect tree carbon allocation, favoring or hindering the early development of leaves, productivity, and, therefore, growth, as well as delaying leaf abscission and dormancy (Vicente-Serrano et al., 2016).

5. Limitations

Despite the advantages of remote sensing monitoring at large spatial scales and a machine-learning-based approach, coupled with a recently developed XAI technique, several limitations should be acknowledged. A primary limitation concerns the indirect nature of remotely sensed phenology. Vegetation indices do not directly observe phenological events (e.g., budburst, leaf senescence, or cambial reactivation) but rather capture changes in canopy optical properties that integrate multiple biological and structural processes, including understory phenology. As a result, the detected start or end of the season may lag behind or precede true physiological transitions, particularly for processes occurring below the canopy, such as xylem and phloem activity (Cuny et al., 2012; Delpierre et al., 2016; Piao et al., 2019). To limit this discrepancy, we have selected field plots dominated by a single species (basal area $> 80\%$). However, spectral mixing due to spatial resolution, differences in species or age cohorts, snow cover, clouds, and shadows is extremely difficult to control. In future studies, spectral unmixing techniques could be tested to disentangle the effects of different species on phenological responses.

Another limitation is the inherently complex, multi-causal nature of autumn phenology (senescence, leaf abscission, lignification), which is influenced by factors not explicitly captured here, such as interannual legacy effects, soil properties, biotic interactions, and disturbance history. This is reflected in the generally higher RMSE of the EOSD models compared with the SOSD models. Furthermore, the presence of unmeasured factors forces the distribution of their possible role into the predictors actually used, potentially biasing the statistical influence of SHAP importance estimates.

Finally, aggregating VPP over 2017–2023 reduced interannual variability in phenophases at the cost of losing information about specific short-term yearly extreme events, which are increasingly relevant to forest functioning. Extending the analysis to longer time series and explicitly incorporating climate extremes would improve the robustness of predictions under future scenarios.

6. Future directions

Future research should integrate mechanistic variables, including soil moisture dynamics, snow-cover duration, and physiological indicators of stress, to better understand end-of-season processes and their

drivers. Furthermore, coupled with current-year conditions, previous-year climatic factors and phenophases also affect current-year phenology (Dox et al., 2022; Gu et al., 2022). Moreover, the HR-VPP suite comprises 13 phenological products, of which only four were analyzed in this study. Demonstrating that a highly automated, data-driven approach can confirm established results and observe new ones opens up enormous possibilities for fully exploiting this new suite. Furthermore, each year the HRVPP time series grows longer, allowing a shift from a space-for-time substitution approach to a direct analysis of temporal changes.

More broadly, integrating phenology-based remote sensing products with the emerging framework of satellite biodiversity represents a promising future direction. Long-term, high-resolution phenological metrics, combined with information on vegetation productivity and structural complexity, can serve as spatially explicit proxies for habitat heterogeneity and biodiversity patterns across taxa, especially at this unprecedented spatial resolution. Coupling phenological indicators with biodiversity-relevant earth observation products (such as phenological variables) could support integrated assessments of climate impacts on ecosystem functioning, carbon cycling, and biodiversity.

Finally, coupling data-driven approaches with process-based models could help resolve discrepancies between observed canopy-level signals and underlying physiological processes, improving predictions of end-of-season dynamics and linking phenological shifts to productivity and carbon cycling, especially in the context of climate change.

7. Conclusion

This study is among the first to apply the Copernicus High Resolution Vegetation Phenology and Productivity (HRVPP) products to investigate forest phenology and productivity across *M. species* and bioclimatic contexts. We integrated ML-based variable importance with SHAP analyses to jointly preserve predictive performance and ecological interpretability across *M. species* on a wide environmental gradient. This dual framework allows the identification of both dominant drivers and non-linear responses, while accounting for the collinearity among climate data. Moreover, the inclusion of diverse bioclimatic contexts, from Mediterranean to montane species, enables a comparative assessment of species-specific sensitivities to climatic and topographic constraints. Phenological models and RS monitoring bridge gaps in observations with limited spatial or temporal coverage by effectively scaling field information, such as transect surveys or phenocams. Since the recognition of climate-driven shifts in phenology, there has been increasing interest in collecting long-term time series, which has enabled modeling of phenological patterns and trends, thereby enhancing our understanding of tree physiology, carbon assimilation, species distributions, and disturbance dynamics (Silvestro et al., 2025). By demonstrating the applicability of HRVPP phenometrics to species-level phenological analyses, this work provides an important bridge between process understanding and operational-scale monitoring, particularly in regions known as climate-change hotspots, where coarse-resolution analyses may introduce systematic biases in inferred ecosystem responses.

Given the expected increase in temperatures, the decrease in precipitation and relative humidity driven by climate change and already observable between the period 2017–2023 and 1981–2005 (see Supplementary Materials), and the results of this study, it can be inferred that Italian forest species are undergoing important physiological changes (changes in phenological phases and productive cycles), trying to adapt to a fast-changing environment. Ecologically, the findings suggest that future warming may continue to advance the start of the season across species. However, its effects on autumn phenology, the total length of the season, and productivity will be far more species- and site-specific, particularly in water-limited environments. This complexity has important implications for forecasting forest responses to climate change and for the parameterization of dynamic vegetation and ecosystem models.

CRedit authorship contribution statement

Elia Vangi: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Giovanni D’Amico:** Writing – review & editing, Methodology. **Vincenzo Saponaro:** Writing – review & editing, Methodology. **Mattia Niccoli:** Methodology. **Gioele Tiberi:** Writing – original draft, Data curation. **Saverio Francini:** Writing – review & editing. **Costanza Borghi:** Writing – review & editing. **Alessio Collalti:** Writing – review & editing, Writing – original draft. **Francesco Parisi:** Writing – original draft. **Gherardo Chirici:** Project administration.

Declaration of competing interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.agrformet.2026.111496](https://doi.org/10.1016/j.agrformet.2026.111496).

Data availability

<https://doi.org/10.5281/zenodo.20344611> (The HRVPP and climate data are freely available from their original sources. All other data and codes will be made available upon request to the corresponding author. All figures and plots not presented in the main text nor in the supplementary materials are uploaded to the following Data and Code Availability Repository in Zenodo:)

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