European Journal of Forest Research
https://doi.org/10.1007/s10342-024-01750-5

RESEARCH

Carbon storage potentiality in successional and secondary old growth forests

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Received: 20 December 2023 / Revised: 7 October 2024 / Accepted: 21 November 2024

Abstract

As the capacity of old-growth forests to store carbon until very old ages has been proved, their conservation has become a mitigation strategy to reduce net CO_2 emissions and moderate climate warming. We investigated the effect of tree age, competition and climate on aboveground standing biomass and C stocks over a 50-years period in two Spanish forest stands (*successional Pinus pinea forests with old-growth attributes*, *OGFA* and *secondary Pinus nigra old-growth Forest, SOGF*), combining dendroecological methods with forest inventory data, using semiparametric modeling. *P. nigra* SOGF stored 69.9 t C ha^{-1} in standing volume, while *P. pinea* OGFA stored 58.2 t C ha^{-1}. Carbon stored during the last 50 years increased in both forests, with a steeper increase in *P. pinea* OGFA. The fraction of annual C stored by the oldest trees was 20–25% in *P. nigra* SOGF and 17–23% in *P. pinea OGFA*. The different patterns of biomass growth increment in the two forests were explained by different biophysical environments, climate and history effects. The response to contrasted climate events was forest-specific. Results for *P.nigra* showed a similar response to climate irrespective of tree age, while biomass growth in *P. pinea* increased in humid periods compared to dry periods in trees older than 100-years. The negative effect of drought is evidenced in *P. pinea* trees over 100-years old, while *P. nigra* showed a cumulative negative effect of drought for all ages. A lower effect of competition was recorded in the oldest trees in both forests. The interaction of competition with climate and tree age showed attenuated climate-mediated differences when competition was high.

Keywords Climate influence · Competition · *Pinus nigra* · *Pinus pinea* · Standing biomass · Tree age

Introduction

Forests play a main role in helping to mitigate the effects of anthropogenic climate change due to their ability to store substantial amounts of carbon (Gunn et al 2013). Currently, EU forests absorb around 10% of the total EU emissions (Korouso et al. 2023), thus being identified as “natural solutions" to climate change (González et al. 2020). Among their mitigation strategies, EU policies include the retention of mature trees to assure carbon sequestration in the long-term. Thus, the conservation of old-growth forests is one strategy aimed at reducing net carbon dioxide emissions and moderate the influence of future climate change (Fraser et al. 2023). The term “old-growth forest” is used differently in studies published about their effect in climate change mitigation (Kenina et al. 2023). What is common in all definitions is naturally regenerated forest stands of native tree species, the exclusion of significant human intervention for a long period, the presence of a dominant cohort of large, both

Communicated by Camilla Wellstein.

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live and dead, standing and fallen old trees, their complex structure (variety of tree sizes and tree ages, resulting in multilayered canopies), the accumulation of large deadwood material in different stages of decay, the provision of a wide range of ecosystem services and natural disturbance regimes (Wirth et al. 2009; Spracklen and Spracklen 2019; FAO 2020; O'Brien et al. 2021). According to Buchwald (2005) old-growth is not necessarily "virgin" or "primeval". Thus, old growth forests are able to develop following human disturbances. Very few undisturbed primary old-growth forests are found in Europe due to the long history of intense forest management and land-use (Sabatini et al. 2018). According to Keith et al. (2024), it is more appropriate in European forests to interpret the term "old-growth forests" as forests that have been unlogged for long (at least 60–80 years after the last harvesting event (O'Brien et al. 2021)) and have reached a level of maturity that includes many old-growth characteristics and a high degree of naturalness and ecological functioning, without implying that there was never human disturbance. Thus, the term "secondary old growth forests" is particularly useful in Europe (O'Brien et al. 2021).

Live carbon storage per unit leaf area is different depending on species composition, but it is also expected to be affected by tree age, site type and stand-growth dynamics (Kenina et al. 2023). Although young forests may yield greater rates of carbon accumulation on an annual basis when compared to old forests, they are usually subjected to more intense disturbances that reduce carbon stocks (Fraser et al. 2023). For decades, there was the perception that old-growth forests were carbon neutral, achieving a steady state with respect to net exchange with the atmosphere (Suchanek et al. 2004). However, there seems to be a more dynamic relationship with age, having demonstrated the capacity of old-growth forests to fix and store carbon until very old ages (Luyssaert et al. 2008). In fact, old-growth temperate forests may store the largest amounts of carbon per unit area among terrestrial ecosystems. Forests over 200 years-old continue to sequester over 1.6 ± 0.6 MgC ha^{-1} yr^{-1} (Gundersen et al. 2021), reaching up to 2.4 ± 0.8 MgC ha^{-1} yr^{-1} according to Luyssaert et al. (2008). The time that fixed carbon remains in the forest depends upon many factors, including productivity, structure, species composition and tree age (Sierra et al. 2017). Regardless species and forest biomes, or even competitive environments, large old trees continue to actively fix large amounts of carbon compared to smaller trees, thus not acting just as carbon reservoirs (Stephenson et al. 2014).

Under climate warming scenarios, tree growth rates, and subsequently biomass accumulation and carbon storage, will be affected. However, the assessment of climate change effects on tree biomass is far from straightforward due to the difficulty in disentangling the effects of temporal climate change drivers from temporal endogenous processes (Chen and Luo 2015). The climate effects on ecosystem structure and functioning may be modified by interactions of soil, vegetation and hydrologic patterns with spatially variability of land use histories and human activities over a range of time scales (Groffman et al. 2012). Simulation models to explore the effects of climate change on European forest carbon cycles suggest a reduced efficiency of forests to absorb carbon in the future because of drought, heat stress and wildfires (Hale et al. 2019). Age-modulated growth response to climate has been suggested as a widespread phenomenon for different tree species growing under variable environmental conditions (Carrer and Urbinati 2004). In fact, species-specific morphological and physiological shifts during ontogeny, jointly with limiting environmental conditions can lead to age-induced growth responses to climate (Rozas 2015). However, size-mediated extrinsic factors such as asymmetric inter-tree competition can modulate the individual sensitivity to climate more than tree age (Mencuccini et al. 2005). Most studies agree that the competition effects on individual tree growth are primarily negative (Aakala et al. 2013), predisposing trees to the damaging effects of a climatic stress (Linares and Tiscar 2010). On the other hand, the stress gradient hypothesis postulates that a tree can benefit from its neighbors when growing under a harsh environment (Bertness and Callaway 1994; Callaway and Walker 1997). However, the influence of tree age on growth and subsequent biomass and carbon storage, and its relationship with competition and drought remains poorly studied, especially in structurally heterogeneous old growth forests.

In the last three decades, the area of old-growth forest stands in Europe has been increasing due to a decrease in forest management intensity and an increase in forest protection (O'Brien et al. 2021). In Spain, given the current age distribution in mountain pine forests, a large forest area will be beyond its rotation period (100–120 years) in the next decades. Thus, understanding old-growth forest stands carbon dynamics and evaluating the influence of drought events and tree age becomes essential for assessing the full range of forest carbon mitigation as part of the life carbon cycle. In this respect, using tree-ring techniques offer a precise approach to estimate biomass accumulated and carbon fixed over time in forest aboveground biomass (Martín-Benito et al. 2021).

In this paper we analyze stand and tree aboveground biomass and carbon stocks over a 50-years period in two Spanish forest pine stands (*successional Pinus pinea forests with old-growth attributes*, *OGFA* and *secondary Pinus nigra old-growth Forest, SOGF*) to distinguish between age and competition effects and to explore climate influence as the explanatory driver behind the changes in carbon stores. We addressed the following questions: (1) will the two studied forest stands maintain their capacity for carbon fixation?;

(2) is there a significant and forest-specific trend in biomass growth with tree age?; (3) is this trend modulated by climate (ie, is it different in the humid vs dry periods)?; (4) is the capacity of the trees to fix carbon decreasing with the succession of intensive dry periods in the last fifty years?; (5) can the competitive environment modulate biomass growth rates?; (6) is this influence of competition modulated by climate (humid vs dry periods) and by tree age?

For this purpose, we combine dendroecological techniques with detailed forest inventory data.

Material and methods

Study sites

The study was performed using data from two representative Spanish forest pine stands: a *Pinus pinea forest stand* at Hoyo de Pinares (Ávila, 40°31′3,9″N, 4°23′52″W, at an elevation of 900 m) and a *Pinus nigra forest stand* at Sierra de Cazorla (Jaén, 37°48′49’’N, 2°57′30’’W, at an elevation of 1,800 m). Hoyo de Pinares and Sierra de Cazorla are home to some of the oldest pines dated for the species (Creus 1998; Natalini et al. 2016). The climate in Hoyo de Pinares is continental Mediterranean, the mean annual temperature is 12.2 ºC, the mean monthly temperatures range between 3 ºC in January and 23 ºC in July and the average annual precipitation is 511 mm. Lithology mainly consists of granitic and gneiss, and the main soil type is humic cambisol. The climate in Sierra de Cazorla is Mediterranean, the mean annual temperature is 11.7 ºC, the mean monthly temperatures range between 4 ºC in January and 21 ºC in August and the average annual precipitation is 1100 mm. The lithology consists of limestone and dolomites.

Data collection and dendrochronology analysis

One ha plot was installed in each of the two forest stands (*Pinus pinea* stand and *Pinus nigra* stand) in 2019 (Fig. 1). Plots were installed in areas with evidence of no recent silvicultural intervention. According to the reports from the Forest Service, and the aerial photographs made by the US Army Map service in 1956–57 that cover all Spain (https://fototeca.cnig.es/fototeca/), the *Pinus pinea* stand has not been logged since, at least, 1960. *Pinus nigra* stand has been unlogged for the last century (Linares and Tiscar 2010). Thus, following O’Brien et al. (2021), the *Pinus nigra* old-growth forest stand could be defined as ***secondary old-growth forest (SOGF)***, and *Pinus pinea* old-growth forest stand as ***successional forests with old-growth attributes (OGFA)***. For the sake of simplicity, both stands will be described by their acronyms throughout the text.

The *Pinus pinea* OGFA plot is dominated by *Pinus pinea*, with some scattered *Pinus pinaster* trees, while the *Pinus nigra* SOGF plot is pure. Every tree on each plot with diameter at breast height (DBH) over 7 cm was tagged

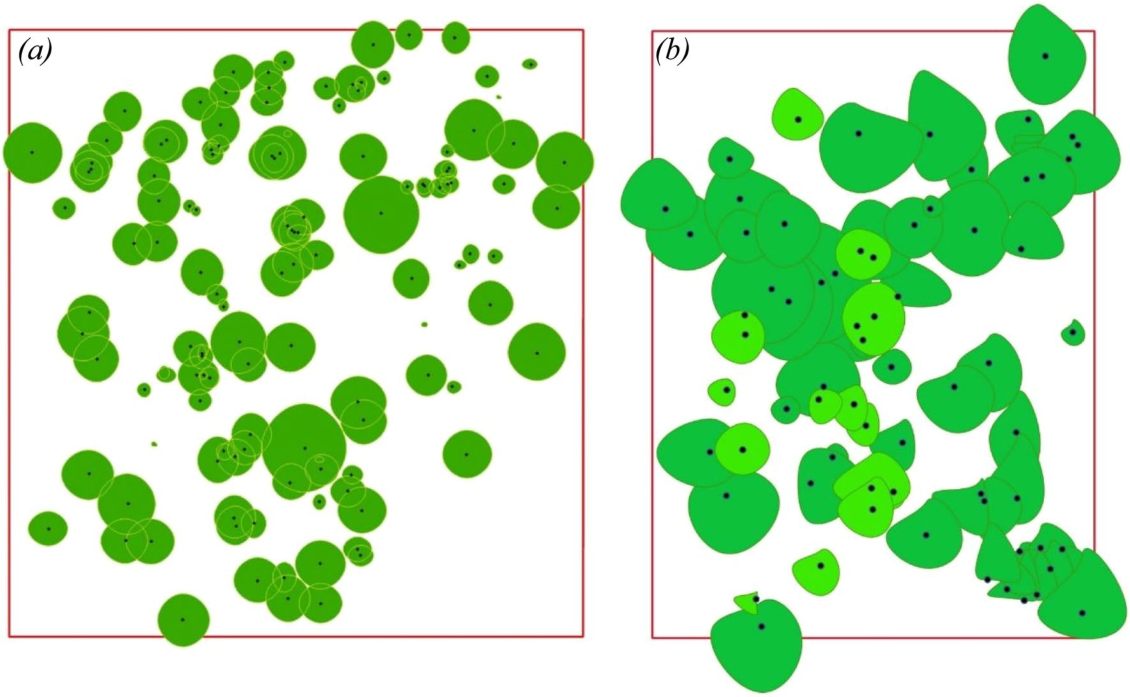


Fig. 1 Maps showing tree position within the (**a**) *Pinus nigra* SOGF and (**b**) *Pinus pinea* OGFA stands

Table 1 Dasometric characteristics of the two forest plots

Forest	Species	N (stems.ha^{-1})	G (m^2.ha^{-1})	DBH (cm)	H (m)	Trees DBHh > 50 cm	AGB (t DM.ha^{-1})	C stock (Mg. ha^{-1})
Hoyo de Pinares (*Pinus pinea* OGFA)	*P.pinea*	58	17.88	59.2 [17.5–96.6]	16.2 [4.5–22.2]	42	105.80	53.75
	P.pinaster	15	2.42	43.39 [17.5–71.00]	12.4 [4.7–16.3]	4	8.78	4.49
Hoyo de Pinares (*Pinus pinea* OGFA)	*P.nigra*	117	26.68	48.03 [9.9–127.7]	11.95 [3.1–21.1]	59	135.40	69.92

N number of stems, *G* basal area, *DBH* diameter above breast height, *H* total height, *AGB* aboveground biomass, *C stock* carbon stock

and positioned (X and Y coordinates), and DBH (in cm), total height (h, in m), height to crown base (hcb, in cm) and crown diameter (cw, in cm) were measured. Mean plot characteristics and histograms of the distribution of heights and DBH are shown in Table 1 and Figure S1 (Suppl. Material), respectively.

A sample of 34 trees in the *Pinus pinea* OGFA plot and 43 trees in the *Pinus nigra* SOGF plot were chosen, representing all age classes (between 24 and 220 years old in *Pinus pinea* and between 46 and 657 years old in *Pinus nigra*). Two perpendicular cores at breast height were taken per tree, from which annual ring widths were measured using standardized dendrochronological techniques (Speer 2010). Using mean annual ring width of both increment cores we calculated the tree basal area increment (BAI, cm^2):

$$BAI = \frac{\pi}{4}\left(d_t^2 - d_{t-1}^2\right) \quad (1)$$

where d_t is DBH at the end of a given annual ring increment corresponding to rings formed in year t; and d_{t-1} is DBH at the beginning of a given annual ring increment corresponding to rings formed in year t-1. To eliminate the biological growth trends and to produce stationary and residual tree ring width chronologies (Fritts et al. 1990) we used a detrending procedure and an autocorrelation removal with the Friedman supersmoother spline (Friedman 1984) and autocorrelation modeling. Through this procedure we obtained chronologies of dimensionless indices (CDI), preserving a common variance with interannual time scales. To measure the reliability of the chronogies we calculated RBAR (mean series intercorrelation) and EPS (expressed population signal of detrended BAI series) (Lindholm et al. 1999) for each of the species during the studied 1969–2018 period. We obtained a mean EPS of 0.954 and RBAR of 0.387 for *P. pinea*, and EPS of 0.968 and RBAR of 0.410 for *P. nigra.* These values confirm the reliability and replication of the chronologies, as they are above the EPS threshold of 0.85.

Plot backdating

Data of past DBH for all the trees (cored and non-cored) within each plot during the studied period (1969–2018) are required in order to calculate the current and past competitive status of each tree and to assess the stored biomass at stand scale. Past DBH of cored trees was reconstructed as explained in the above section. Diameter growth of non-cored trees was reconstructed using a backdating sequence (de Dios-García et al. 2015, Riofrío et al. 2019). First, we calculated BAI of each cored tree in 5-year intervals (1969–1973, 1974–1978, 1979–1983, 1984–1988, 1989–1993, 1994–1998, 1999–2003, 2004–2008, 2009–2013 and 2014–2018). Then, we fitted a linear regression between BAI at 5-year intervals and DBH in 2019 (when trees were cored) for each of the 10 analyzed periods:

$$log\left(BAI_{periodj}\right) = \alpha + \beta * log\left(DBH_{2019}\right) + \varepsilon_i \quad (2)$$

The fitted models were then used to predict the basal area increment of the non-cored trees for those 5-year intervals. Finally, we transformed BAI into DBH.

Climate data and selection of drought years

We used data on a monthly basis (mean, maximum and mínimum temperature and precipitation). Climate data were obtained from the E-OBS dataset from the EU-FP6 project UERRA (http://www.uerra.eu) and the data providers in the ECA&D project (https://www.ecad.eu) (Cornes et al. 2018). Monthly data were used to calculate mean annual temperature (T, ºC) and annual precipitation (P, mm) for the studied period (1969 to 2019).

We selected specific drought and humid periods for each forest. Drought and humid years were identified using climate data, by means of the Standardized Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al. 2010) that is based on a monthly balance of precipitation and potential evapotranspiration. An SPEI value below (-1) corresponded to a dry period and SPEI values above (+1) corresponded to humid periods. SPEI was obtained for months 1 and 12 from the E-OBS dataset. We considered drought years when at least 75% of the months showed an $SPEI_{12} \leq -1$ during the growing season (March to October, and mean minimum temperature above 8ºC). We considered humid years when at least 75% of the months showed an $SPEI_{12} \geq 1$ during the growing season. The effect of drought and humid periods on tree growth was assessed for the period 1969–2019. Drought and humid periods were specific to each forest stand, ranging from two to six (Table 2).

Distance dependent competition índices

We used the Hegyi Competition Index (HGCI) (Hegyi 1974) that was computed for each cored tree and year during the studied period (1969 to 2019). HGCI calculates the sum of the competition of each competing trees (k) over the subject tree (i):

$$HGCI_i = \sum_{k=1}^{n} \frac{DBH_k}{(DBH_i \times dist_{ik})} \tag{3}$$

where $dist_{ik}$ is the distance between the subject tree i and the neighbor tree k. We assume size-symmetric competition typical of mediterranean forests, and considered as competitors all the trees growing in a circle of fixed radius of 10 m, centered in the subject tree. Plot edge bias was corrected using Martin et al. (1977) method.

Aboveground biomass

Standing aboveground biomass was calculated for each tree and year (from 1969 to 2019). To this aim, first we calculated tree height at each age using a specific DBH-height model constructed for each species and plot (Dixon 2002). We assessed four bi-parametric DBH-height models, among those commonly used (Calama and Montero 2004). The DBH-height model finally selected for both species and plots was the model proposed by Wykoff et al. (1982):

$$h_i = 1.3 + exp\left[a + \frac{b}{(DBH_i + 1)}\right] \tag{4}$$

After fitting the model for each species (*Pinus pinea*: parameter a = 3.4003, parameter b = -39.046; *Pinus pinaster*: a = 3.0846, b = -27.1471; *Pinus nigra:* a = 3.0811, b = -27.0289) we computed the height increment for tree i during year t,δh_{it}, as the difference between height predicted for the tree i in years t and $t\text{-}1$, using the model in Eq. 4. These height increments were then subsequently subtracted from the observed height in 2019 in order to reconstruct the pattern in height growth of each tree and prevent inconsistencies. Then, we used the annual reconstructed values of tree height and diameter to calculate stem biomass, crown biomass and total biomass of each tree, by means of the species specific tree biomass model developed by Menéndez-Miguélez et al. (2021). Finally, annual biomass increment was calculated as the difference between standing tree aboveground biomass in two consecutive years. Previous studies show that aboveground biomass estimated from tree rings accurately represent stand biomass for several decades, particularly in the absence of large disturbances (Gea-Izquierdo and Sánchez-González 2022). Aboveground total biomass and annual increments in biomass were transformed into stocks of C stored by applying the rates of C content in dry biomass proposed by Montero et al. (2005): 0.508 for *Pinus pinea*, 0.509 for *Pinus nigra* and 0.511 for *Pinus pinaster.*

Exploratory analysis at stand scale

In order to answer question (1), we constructed general charts showing the evolution with time—on 5-year steps—of the total aboveground biomass (t D.M. ha^{-1}) or the C storage capacity (Mg C ha^{-1}) of each plot, as well as the annual rates of increment. To identify the contribution of the different age-classes to the total stock of biomass and C, trees in each plot were divided into three different classes: *Old trees*, including those trees with individual age over the 75th percentile of observed ages; *Intermediate*

Table 2 Selected drought and humid periods for each forest during the period 1969–2019

Forest	Drought periods	$SPEI_{12}$	Humid periods	$SPEI_{12}$
Hoyo de Pinares (*Pinus pinea* OGFA)	D1:1985–1986 D2:1991–1995 D3:2005 D4:2009–2012 D5:2014–2017	−1.181 −0.987 −1.243 −0.709 −0.830	H1:1977–1980 H2:1996–1998	1.471 0.998
Sierra de Cazorla (*Pinus nigra* SOGF)	D1:1981–1983 D2:1991–1994 D3:1999–2000 D4:2005–2006	−1.209 −0.979 −1.289 −1.110	H1:1970–1972 H2:1996–1998 H3:2009–2011	1.144 0.870 1.462

trees: trees with individual age between percentiles 25th and 75th; and *Young trees:* tree with age below the 25th percentile. Limits for age classes in the *Pinus nigra* plot were 160 and 300 years, and 70 and 150 years in the *Pinus pinea* plot.

Modelling approach at tree scale

Data structure and initial model structure

The dataset included annual biomass increments of the 77 cored trees of the two species (43 cores in *Pinus nigra* and 34 cores in *Pinus pinea*), corresponding to the periods identified as Humid (H) or Dry (D) [two humid (H1-H2) and five dry (D1-D5) subperiods in Hoyo de Pinares and three humid (H1-H3) and four dry (D1-D4) subperiods in Sierra de Cazorla (see Table 2)]. With this data structure we can expect some degree of correlation of the observations within a tree and between observations within the same subperiod for a certain tree. Moreover, an inspection of the scatterplot of the biomass growth and tree age suggests a trend that is highly non-linear and difficult to absorb by parametric functions (Figure S2, Suppl. Material). Similarly, we can observe some possible trend of biomass growth as a function of the competition index HGCI (Figure S3, Suppl. Material), which is also non-linear.

In order to answer the questions (2) to (6) arised in the introduction, we propose to fit the following model:

$$y_{ijkmn} = \mu + \alpha_j + \gamma_m + \delta_{n(m)} + t_{k(j)} + (\alpha\gamma)_{jm} + (\alpha\delta)_{j(nm)} + f(x_i) + g(s_i) + e_{ijkmn} \quad (5)$$

where y_{ijklmn}: biomass growth of tree k of species j with an age x_i and competition s_i in the climate subperiod n of climate period m; μ: general mean; α_j: fixed forest effect (j = 1,2).; $t_{k(j)}$: tree (inside site) random effect with initial hypothesis $t_{k(j)} \sim N(0, \sigma_t^2)$; γ_m: fixed period effect with $m = 1,2$; $(\alpha\gamma)_{jm}$: forest x period interaction fixed effect; $(\alpha\delta)_{jn(m)}$: forest x subperiod interaction fixed effect; f (x_i) is some non-parametric function to account for the trend of the biomass growth with tree age; $g(s_i)$ is some non-parametric function to account for the trend of biomass growth with competition and e_{ijkmn} is the error term. This is a semiparametric mixed model that incorporates fixed and random effects and non-parametric functions (*f* and *g*). The differences among the two forests should be read as a combination of site and species effects.

For the univariate trend functions *f* and *g* we chose low rank thin plate radial smoothers incorporated in the mixed model (Ruppert et al. 2003). The mixed model formulation of the radial smoother incorporates a fixed part, corresponding to the value of the covariates (tree age (x_i) in the case of *f* function and competition (s_i) in the case of *g* function) and a random part that is the solution of the spline coefficients. We followed Ruppert et al. (2003, chapter 13.4–13.5) to form the design matrices of the random effects corresponding to *f* and *g*. For selecting the number of knots K of *f* and *g* trend function we followed closely the rule (Ruppert et al. 2003): K = min(0.25 × number of unique x_i (or s_i for g), 35). We selected 33 knots for the *f* function and 9 for the *g* function. The advantage of the mixed model formulation is that the smoothing parameter is automatically determined through the estimation of the covariance parameters, once the knots have been selected, and the easy modularity with straightforward incorporation of other fixed and random effects and different covariance structures.

Selection of final model structure and parameter estimation

Different model alternatives were tested for selecting the best model structure. First alternatives concerned different approximations for the *f* and *g* non-parametric functions. As an example, for *f* function, if the biomass growth trend with age for both forests, periods and subperiods were very similar, then only one *f* trend function would absorb the trend efficiently. However, if trends were different by forests and/or periods and/or subperiods (or interactions), then it would be more appropriate to have specific *f* trend functions. In the case that specific trend functions were a better choice we should also test if it is better to consider different or the same degree of smoothness. Following this reasoning we have tested the following alternatives for *f* function: (1) no significant trend, (2) common general trend, (3) forest specific trend, (4) period specific trend, (5) forest x period specific trend, (6) subperiod specific trend, (6) forest x subperiod specific trend. For the *f* function we also considered the possibility of different degrees of smoothness for the specific trend functions. After selecting the best approach for the *f* function, we followed a similar approach for selecting the *g* trend function. For each alternative, the significance of the tree random effect and if the variance component at tree level was different in the two species were tested. We also considered and tested an autoregressive order one—AR(1)—correlation structure among observations within each subperiod of a tree. Variance components in the different model alternatives have been estimated with restricted maximum likelihood (REML). Comparison between alternative models have been done, in the case of nested models, comparing the values of –2 × log likelihood (-2LL) with a likelihood ratio test considering an α value of 0.05. For not nested models (i.e. one model is not the reduction of the other), Akaike's information criteria (AIC) has been taken into account for model selection. The significance of the fixed effects was tested with a F test.

Prediction of biomass growth at different ages and humid/dry periods

The final set up of the model will allow us to answer questions (2) to (5). In order to answer question (6) ("Is the influence of competition on biomass growth modulated by climate and tree age?") we need to predict the biomass growth at different tree ages and at different periods (humid/dry) for a series of increasing competition levels. We selected three different ages for each species (young/medium/old) corresponding to the percentiles 10, 50 and 95 of the age distribution respectively. These percentiles correspond to the values 60, 215 and 636 years old in the case of *Pinus nigra* and 24, 108 and 214 years old in the case of *Pinus pinea*. We then predicted the biomass growth at the three ages and two periods (humid/dry) for HGCI values ranging from 1 to 11 with steps of 1, and the simultaneous 95% confidence bands by simulation (Ruppert et al. (2003, pp. 142–143). The construction of the design matrices of fixed and random effects for prediction include the design of random effects for the trend functions *f* and *s*, which is detailed in Ruppert et al. (2003, Sect. 13.5). We used SAS 9.4 for statistical analysis.

Results

Exploratory analysis at stand level

At the moment of the inventory, the *Pinus nigra* SOGF stand at Cazorla stored 135.4 t D.M. ha^{-1} (equivalent to 69.9 Mg of stored C) in the standing biomass, a value that was higher to that stored in the *Pinus pinea* OGFA stand at Hoyo de Pinares (114.6 t D.M. ha^{-1}, 58.2 Mg of C). The evolution in C storage during the last 50 years showed a maintained increase in the total amount of C stored in both forests, being such increase much steeper in the *Pinus pinea* plot (Fig. 2). Annual rates of aboveground biomass increment, analyzed for different periods (Fig. 3), showed a positive trend in *Pinus pinea* plot in the initial phases, reaching maximum values over 1.30 t D.M ha^{-1} year^{-1} for the 1994–1998 period, coinciding with a humid period. In the last 20 years, biomass increment rates have remained constant (over 1.15 t D.M ha^{-1} year^{-1}), indicating the impact of recent droughts. In the case of the Pinus *nigra* SOGF stand, no clear trend was observed among periods, with values remaining quite constant (between 0.40—0.50 t D.M ha^{-1} year^{-1}).

Analyzing the contribution of each age group to the total C storage (Fig. 4), it is relevant to mention that in both stands the trees in the intermediate age class (70–160 years old in *Pinus pinea*; 150–300 years old in *Pinus nigra*) are those storing a large amount of C and biomass, also showing the largest rates of C increment. On the other hand, the oldest trees in both stands showed almost a constant amount of standing biomass and C stored, with mean annual increments over 0.054 Mg C ha^{-1} year$^{\mathbf{-1}}$ in the *Pinus nigra* SOGF

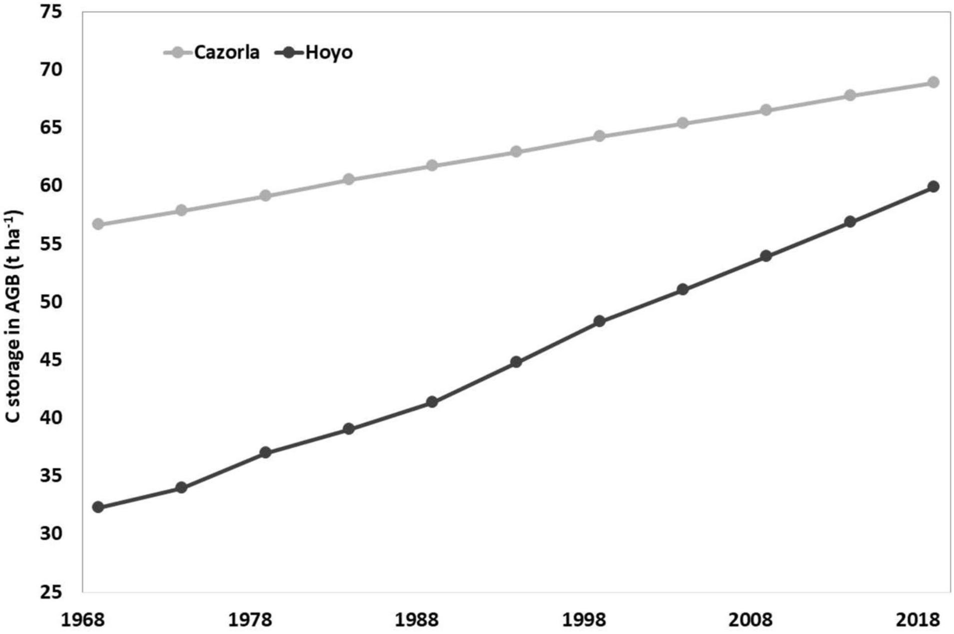


Fig. 2 Evolution of stock of C stored in aboveground biomass (AGB) during 1969–2018 in the *Pinus nigra* SOGF (Cazorla) and *Pinus pinea* OGFA (Hoyo de Pinares) stands

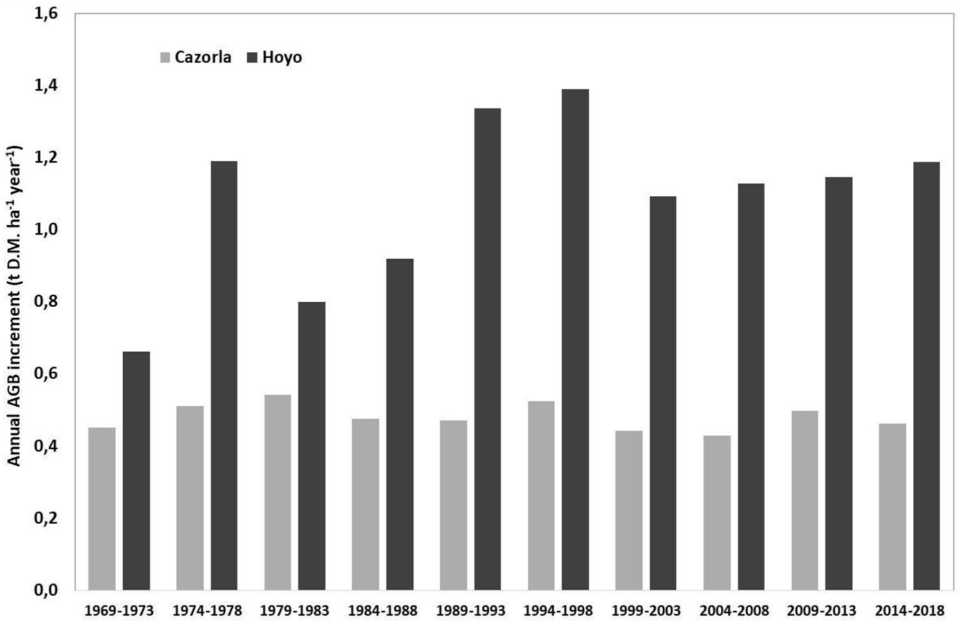


Fig. 3 Annual increment in aboveground biomass per 5-year period in the *Pinus nigra* SOGF (Cazorla) and *Pinus pinea* OGFA (Hoyo de Pinares) stands

stand and 0.105 Mg C ha^{-1} year^{-1} in the *Pinus pinea* OGFA stand. Despite these quite low values, the annual C stored by the oldest trees represents a significant contribution to the total amount of C annually stored in these stands (Figure S4, Suppl. Material), reaching 20–25% in the *Pinus nigra* SOGF stand and 17–23% in the *Pinus pinea* OGFA stand. However, we observed for both stands a reduction in this contribution in the last analyzed periods. Finally, the youngest trees in both stands, although still storing very low values of aboveground biomass and C, are currently contributing to total C storage almost the same as the oldest trees (0.059 Mg C ha^{-1} year^{-1} in the *Pinus nigra* SOGF stand and 0.056 Mg C ha^{-1} year^{-1} in the *Pinus pinea* OGFA stand), but showing a clear increasing trend.

Effect of age, climate and competition on individual biomass growth

Our semiparametric modeling approach reveals a significant trend on annual biomass increment with age (Table 3), which is forest-specific (Fig. 5). *Pinus pinea* showed significantly larger biomass growth in the medium and older classes (> 75 years old), but a trend to decrease in the oldest trees (> 200 years old). For *Pinus nigra* the trend is not so evident, though a decreasing pattern with age was also shown in the oldest trees (> 600 years old). Variability is much higher in *Pinus pinea* than in *Pinus nigra* (Fig. 2, Table 3, superiority of Model 3 over Model 2). For both forests it is remarkable to indicate that larger variability was shown in trees with intermediate ages.

This specific trend is mediated by the climate period (humid vs dry), which influences differently each forest, and by the subperiod within the period (Table 3, superiority of Models 6–9 over Model 5). A specific degree of smoothness for each species and period also resulted in better fit (Model 10 in Table 3). *Pinus pinea* (Fig. 6) showed a similar trend of maximum increment in intermediate ages in humid and dry periods, although reaching larger values of biomass increment in humid ones (especially in the especially humid period H2, 1996–1998). In the driest periods the decrease associated with increasing ages is more evident, while in humid ones there is a trend to constancy. In *Pinus nigra* (Fig. 7) the differences in the general trend of biomass increment with age between humid and dry was not so evident, with the main difference being that in humid periods there is much variability and larger values of increment for intermediate ages. For *Pinus nigra* it is relevant to remark that, for both humid and dry periods, there is a gradient of decreasing biomass increment between the oldest and the most recent subperiods, revealing a negative possible effect of cumulative recent droughts.

For both forests, competition exerted a significant and negative influence on biomass growth. This effect varied depending on the forest, being much sharper in *Pinus pinea* at Hoyo de Pinares than in *Pinus nigra at Sierra de Cazorla* (Fig. 8, Table 4, superiority of Model 12 over Model 10). Competition is also mediated by the climate period and the subperiod (Table 4, see superiority of Model 16 over Models 10–15), being the impact of competition attenuated in humid periods when compared with drier ones (Fig. 8). Nevertheless, in both forests the higher levels of competition resulted in the absence of differences between dry and humid periods in terms of growth.

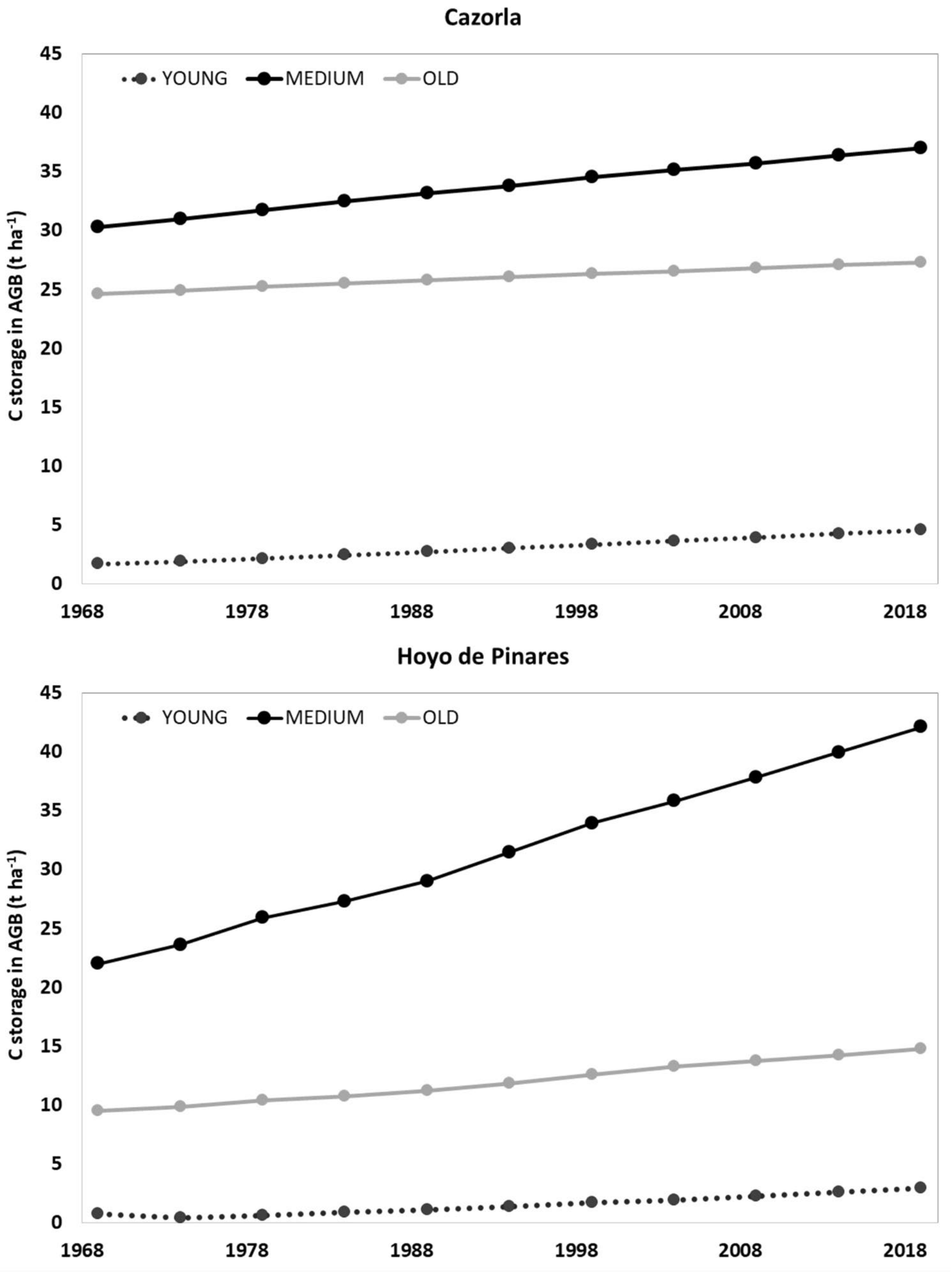


Fig. 4 Evolution of C stock stored in aboveground biomass (AGB) during 1969–2019, as a function of age-classes (young, medium and old), in the in the *Pinus nigra* SOGF (Sierra de Cazorla) and *Pinus pinea* OGFA (Hoyo de Pinares) stands

Given the strong relationship between age and competition (see Figure S5, Supplem. Material), with younger trees experiencing the higher rates of competition, we proposed a predictive approach to disentangle the joint effect of both factors (Figs. 9 and 10). The prediction process was done with the parameters obtained from the best model (Table 4, Model 18), which includes a significant autoregressive order one parameter between observations within a subperiod for a tree. When analyzing the interaction of competition with climate and tree age we observed, for both forests, that for the same level of competition, biomass growth decreased with tree age (especially in the oldest *Pinus nigra* trees (Fig. 10)). In *Pinus pinea* the differences in biomass increment due to age and climate were attenuated under extreme competition (Fig. 9). In *Pinus nigra,* when growing under higher competition rates, no differences were observed between dry and humid periods (Fig. 10).

Discussion

Our studied stands exhibited high structural diversity (DBH and height distribution) and wide spread of canopy classes across ages characteristics. The abundance of old trees, the multi-aged structure, and the wide range of ages, sizes and heights across canopy classes evidenced high vertical and spatial complexity, confirming the path

Table 3 Sequential procedure for model selection. Models 1 to 10

		Models									
		1	2	3	4	5	6	7	8	9	10
Effects		Fixed effect model	Tree effect	Tree effect (group = species)	f general trend	f forest specific	f period specific	f forest x period specific	f subperiod (period) specific	f forest x subperiod (period) specific	= 9 with different smooth for each forest and period
Fixed effects	Age	0.015***	0.012 (n.s)	0.002 (n.s)	0.001 (n.s)	0.008 (n.s)	0.004 (n.s)	0.006 (n.s)	0.002 (n.s)	0.005 (n.s)	0.003 (n.s)
	HGCI										
	Forest	***	***	***	***	**	***	***	***	***	***
	Period	***	***	***	***	***	**	***	***	***	*
	Forest x Period	**	***	***	***	***	***	*	***	*	*
	Subperiod (Period)	***	***	***	***	***	***	***	***	***	***
	Forest x Subperiod(Period)	***	***	***	***	***	***	***	***	***	***
Variance components	Tree		53.63								
	Tree (P. nigra)			3.81	3.74	3.72	3.72	3.76	3.8	3.8	3.88
	Tree (P. pinea)			118.86	109.85	95.38	117.54	117.53	117.02	113.41	108.28
	f trend				0.1749	0.4955	0.0244	0.0551	0.0789	0.1363	
	P. nigra. humid										0
	P.nigra. dry										0
	P. pinea. humid										1.3193
	P. pinea. dry										0.3745
	g trend										
	P. nigra										
	P-pinea										
	AR(1)										
Residual		79.33	25.8	25.8	25.7	25.7	25.6	25.55	25.04	24.6	24.3
-2LL		11,678	10,153	10,081	10,079	10,079	10,077	10,075	10,064	10,046	10,006
AIC		11,710	10,157	10,087	10,087	10,087	10,085	10,083	10,072	10,054	10,016

HGCI: Hegyi competition index. AR(1): order one autoregressive parameter. -2LL: -2 × log likelihood. AIC: Akaike's information criteria. n.s.: non-significant ($\alpha = 0.05$). ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$

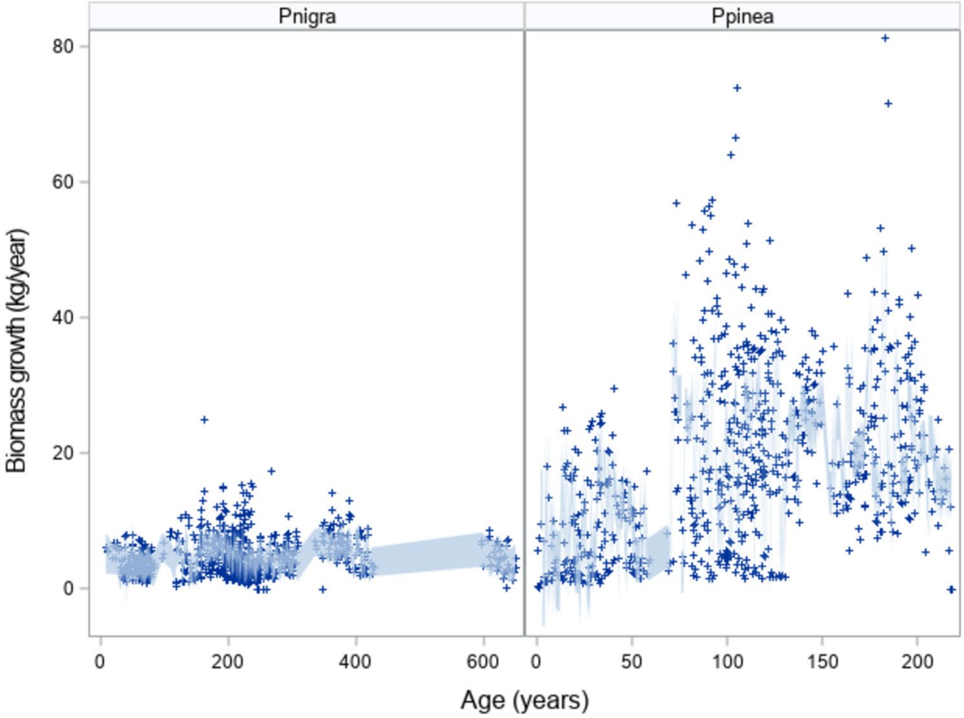


Fig. 5 Semiparametric models for annual biomass increment in the *Pinus nigra* SOGF stand (Sierra de Cazorla) and *Pinus pinea* OGFA stand (Hoyo de Pinares) as a function of age. Bands represent the 95% confidence interval for the fitted line

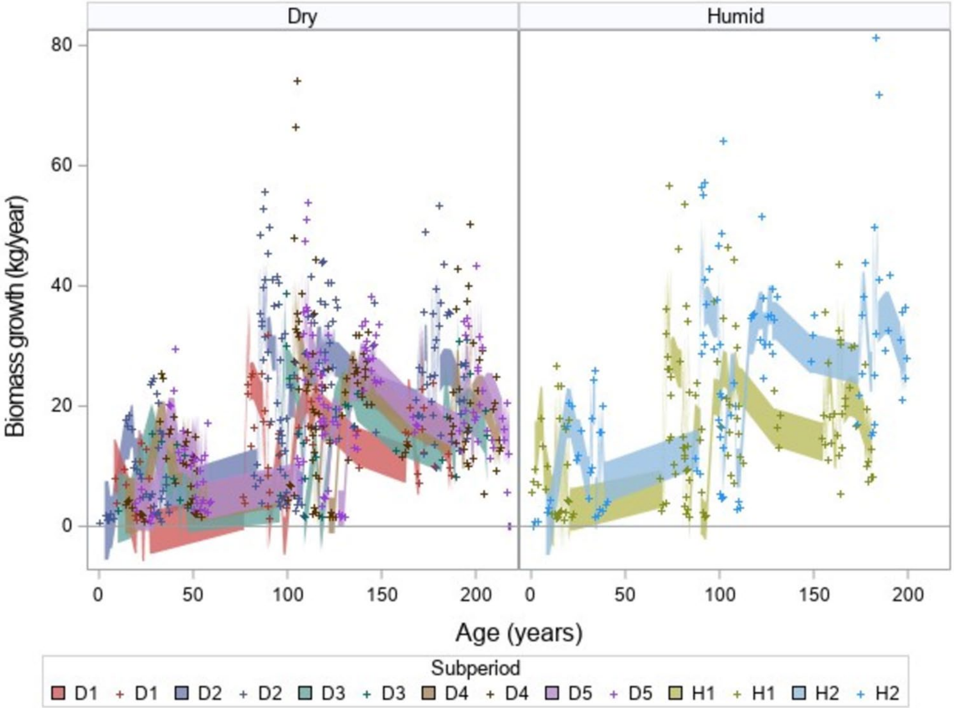


Fig. 6 Semiparametric models for annual biomass increment in *Pinus pinea* OGFA stand (Hoyo de Pinares) as a function of age, period (dry-humid) and specific subperiods. Bands represent the 95% confidence interval for the fitted line

towards old-growth forest state of the studied forests. The maximum ages observed (220 years in *Pinus pinea* and 657 years in *Pinus nigra*) are within the range of the oldest trees for both species (Creus 1998; Natalini et al. 2016). Stand structural characteristics (basal area, stand density and high presence of large living trees with DBH > 50 cm) in both stands were similar to those of other old-growth temperate forests in Europe and North America (Martín-Benito et al. 2020).

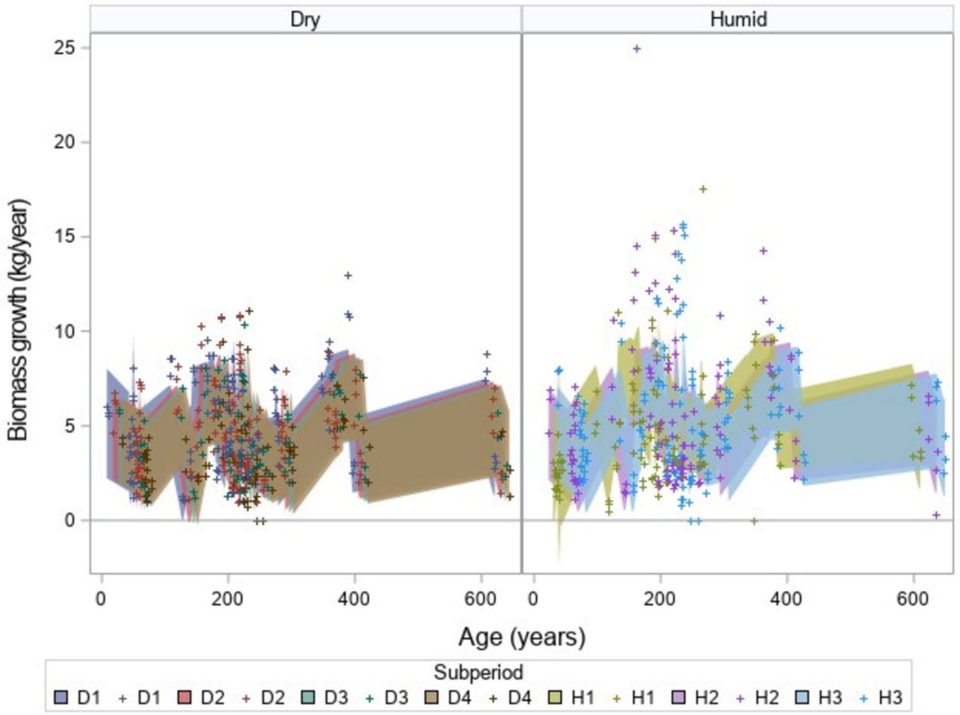


Fig. 7 Semiparametric models for annual biomass increment in the *Pinus nigra* SOGF stand (Sierra de Cazorla) as a function of age, period (dry-humid) and specific subperiods. Bands represent the 95% confidence interval for the fitted line

Stocks at stand level

The two studied forest stands maintain a C stock stored in the standing biomass of 58.2 t C ha^{-1} (equivalent to 114.5 t D.M. ha^{-1}) in *Pinus pinea* (Hoyo de Pinares stand) and 69.9 t C ha^{-1} (equivalent to 135 t D.M. ha^{-1}) in *Pinus nigra* (Cazorla stand). These values are below those observed for the mean standing stocking in an even-aged forest of the species through a typical rotation period of 100 years (127 t D.M. ha^{-1} in *Pinus pinea* forests and 200 t D.M. ha^{-1} in *Pinus nigra* forests according to Alejano (2008), Montero et al. (2008)). These results indicate that, in terms of biomass and C storage, the studied forest stands currently stock about 12–30% less biomass than the values expected for a typical cycle of managed even-aged forest of these two species. On the other hand, values in our forests are quite similar to the mean standing stocks proposed for managed uneven-aged stands in *Pinus pinea* (63 t C ha^{-1}, in del Río et al. 2017) and *Pinus nigra* (69.2 t C ha^{-1}, in Alejano et al. 2008). Despite this similarity, the annual increments observed in managed uneven-aged stands are largely over those observed in the studied stands (2.0 t D.M. ha^{-1} year^{-1} vs 1.2 t D.M. ha^{-1} year^{-1} for *Pinus pinea* OGFA), especially for *Pinus nigra* SOGF (3.5 t D.M. ha^{-1} year^{-1} vs 0.5 t D.M. ha^{-1} year^{-1}). This result evidence that our forests have not still reached the stability typical of old-growth forests, suggesting that they are secondary old-growth forests, or especially in the case of Hoyo de Pinares forest, successional forest in a transitional state between a managed uneven-aged forest and an old-growth one.

However, the oldest trees in the stands are still responsible for the 20–25% (in the *Pinus nigra* stand) or 15–20% (in the *Pinus pinea* stand) of the total annual increment in C and biomass stock, thus still playing an essential role in C fixation (Stephenson et al. 2014). These findings give response to question (1), showing that the studied forest stands maintain their C fixation capacity, but at lower rates than younger managed stands. This result is compatible with the well-known age-related decline in productivity at stand scale, associated with lower densities due to mortality, changes in growth efficiency and shifts in tree dominance hierarchies (Ryan et al. 1997; Piper and Fajardo 2011).

Individual capacity for biomass and C fixation

Despite the observed reduction in stand-level stocking biomass, the individual trees in the two studied forest stands are able to maintain their capacity for carbon fixation in tree biomass as tree age and size increase, with no signs of decline (Sillet et al. 2010, Stephenson et al. 2014), thus positively answering to question (2). The patterns of biomass growth increment are not fully consistent in *Pinus nigra* and *Pinus pinea*. *Pinus nigra* maintains a mean biomass growth increment of 4.9 kg D.M. tree^{-1} year^{-1} over the 600 years life-span, a result that is in agreement with recent studies on the growth patterns for the species (Linares and Tíscar

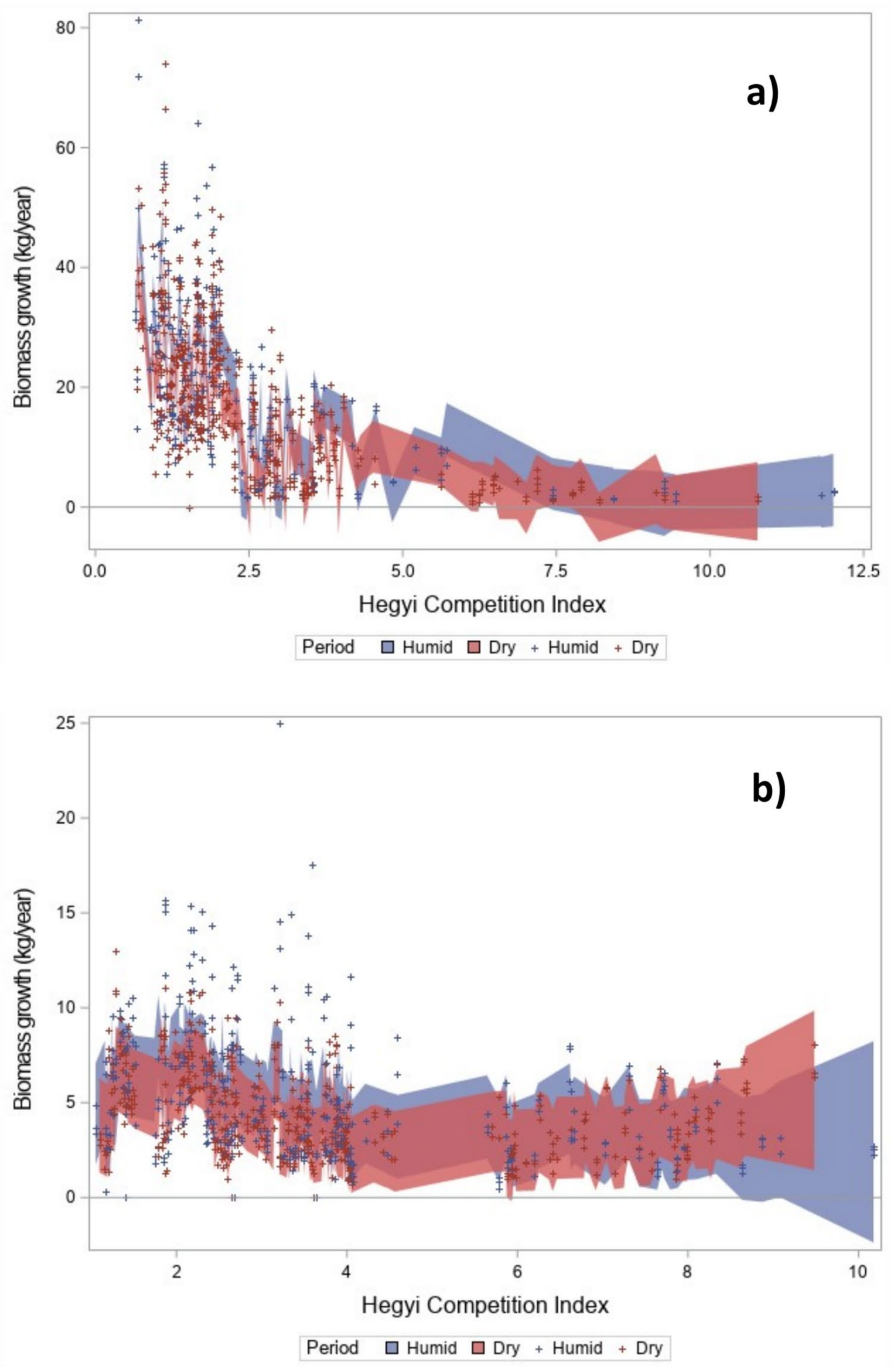


Fig. 8 Semiparametric models for annual biomass increment in *Pinus pinea* OGFA (**a**) and *Pinus nigra* SOGF (**b**) stands as a function of competition and period (dry-humid). Bands represent the 95% confidence interval for the fitted line

2010, 2012). However, it is relevant to mention that *Pinus nigra* trees in the intermediate age classes show large variability in biomass increment, reaching maximum values over 20 kg D.M. tree^{-1} year^{-1}. On the other hand, *Pinus pinea* showed an increase in the biomass growth from age 70, which is maintained up to 200 years (from 9,8 kg D.M. tree^{-1} year^{-1} to 21 kg D.M. tree^{-1} year^{-1}), when a slight decreasing pattern is observed in the oldest trees. Both findings might be behind the observed larger rates of biomass increment per hectare due to the presence of trees of intermediate age classes.

These specific patterns should be considered in the context of different biophysical environments (soil properties and soil moisture), climate and history effects between the

Table 4 Sequential procedure for model selection. Models 11 to 18

		Models							
		11	12	13	14	15	16	17	18
Effects		s common trend	s forest specific	s period specific	s forest x period specific	s sub-period (period) specific	s forest x subperiod(period) specific	= 16 with different smooth for species	= 17. AR(1) between observations within a subperiod of a tree
Fixed effects	Age	−0.013**	−0.009*	−0.011**	−0.009**	0.010**	−0.009**	−0.007*	−0.007*
	HGCI	−1.04 (n.s)	−2.19 (n.s)	−1.04*	−1.97**	1.02**	−1.58**	−0.79**	−0.83***
	Species	***	n.s	***	n.s	**	*	n.s	n.s
	Period	**	*	n.s	n.s	n.s	n.s	n.s	n.s
	Forest x Period	*	n.s	*	n.s	*	n.s	n.s	n.s
	Subperiod (Period)	***	*	***	*	n.s	n.s	n.s	n.s
	Forest x Subperiod(Period)	***	*	***	**	**	n.s	n.s	n.s
Variance components	Tree								
	Tree (P. nigra)	2.59	2.48	2.63	2.41	2.77	2.54	3.07	2.16
	Tree (P. pinea)	76.12	37.1	82.75	47.6	86.64	57.33	44.9	51.05
	f trend								
	P. nigra. humid	0	0	0	0	0.008	0	0	0
	P.nigra. dry	0	0	0	0	0	0	0	0
	P. pinea. humid	1.6325	2.0127	1.7039	2.67	1.134	0	2.7401	0
	P. pinea. dry	0.3982	2.2643	0.4107	0.7379	0.307	1.735	1.6006	0
	g trend	0.0352	0.1791	0.015	0.1004	0.0196	0.095		
	P. nigra							0	0
	P-pinea							0.4646	0.2034
	AR(1)								0.4075
Residual		24.1	23.83	24.09	23.89	23.78	22.91	22.47	24.02
-2LL		9939	9921	9945	9936	9943	9916	9881	9699
AIC		9951	9933	9957	9948	9959	9926	9893	9709

HGCI: Hegyi competition index. AR(1): order one autoregressive parameter. -2LL: -2 × log likelihood. AIC: Akaike's information criteria. n.s.: non-significant (α = 0.05). ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$

sites (Jandl et al. 2007; Gao et al. 2018). The *Pinus nigra* SOGF stand is located in an isolated mountainous area, which has remained inaccessible and unmanaged during centuries, having permitted the development of an unaltered forest (Linares and Tíscar, 2012). On the other hand, the *Pinus pinea* OGFA stand is located close to inhabited areas, and its current state is the result of the abandonment, during the decade of 1960s, of the traditional management focused on the conservation of old large cone producer trees spreaded on a pasture land maintained by the presence of goat grazing (Montero et al. 2003).

Some characteristics of the two studied tree species, such as light demand, regeneration and growth strategies, and longevity (Kenina et al. 2023), could also have a notable effect on the observed differences in carbon storage with age. *Pinus nigra* is a typical shade-tolerant, slow-growing species, and one of the longest-living trees in the Mediterranean basin, with dated trees over 1,000 years (Creus 1998) in the vicinity of the studied stand. Meanwhile, *Pinus pinea* is a light demanding species (except in initial phases, Calama et al. 2013), showing an initial high growth rate and low longevity. The oldest living trees of the species grow isolated in gardens, and are supposed to reach 400 years (see www.monumentaltrees.com/en/trees/pinuspinea/records/). However, the oldest dated dendrochronological series from natural forests (obtained in the Hoyo de Pinares stand) do not reach more than 250 years (Natalini et al. 2016, Baroni et al. 2020). The particularities of the historical legacies of each site, the differences in longevity of the species and the different patterns in biomass accumulation pattern may indicate that while the *Pinus nigra* stand constitutes a secondary old-growth forest, the *Pinus pinea* stand, even though

Fig. 9 Predicted annual biomass increment for a *Pinus pinea* tree of age classes “Young” (24 years old), “Medium” (108 years old) and “Old” (214 years) as a function of Hegyi competition index and climate (humid or dry). Bands represent the 95% confidence interval for the fitted line. Be aware that predicted negative values are predicted for higher rates of competition in old trees, a situation that is not observed in reality

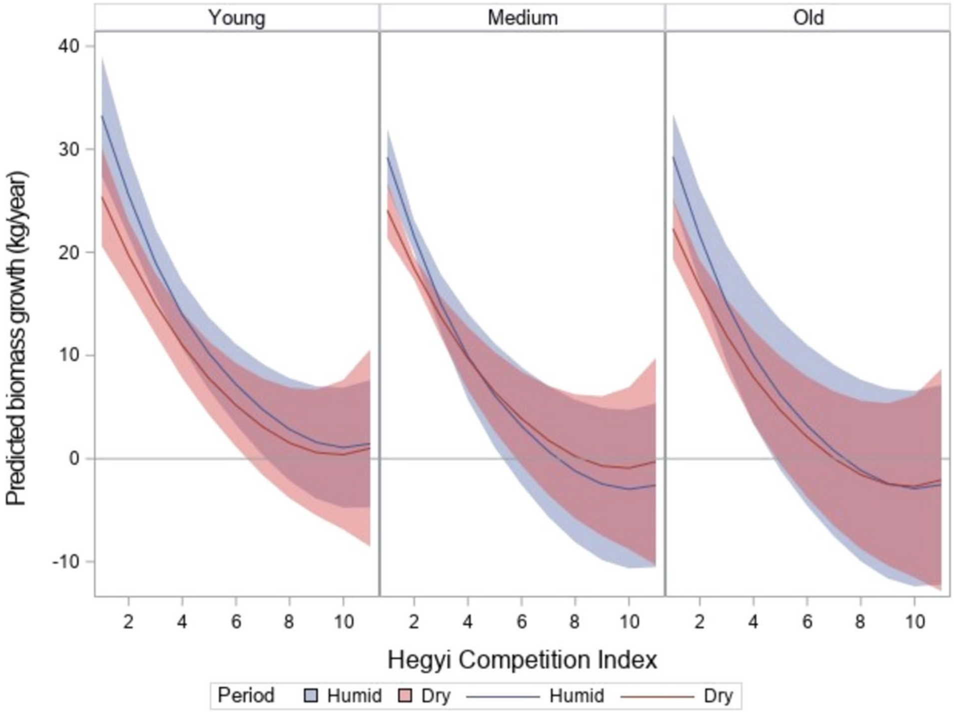
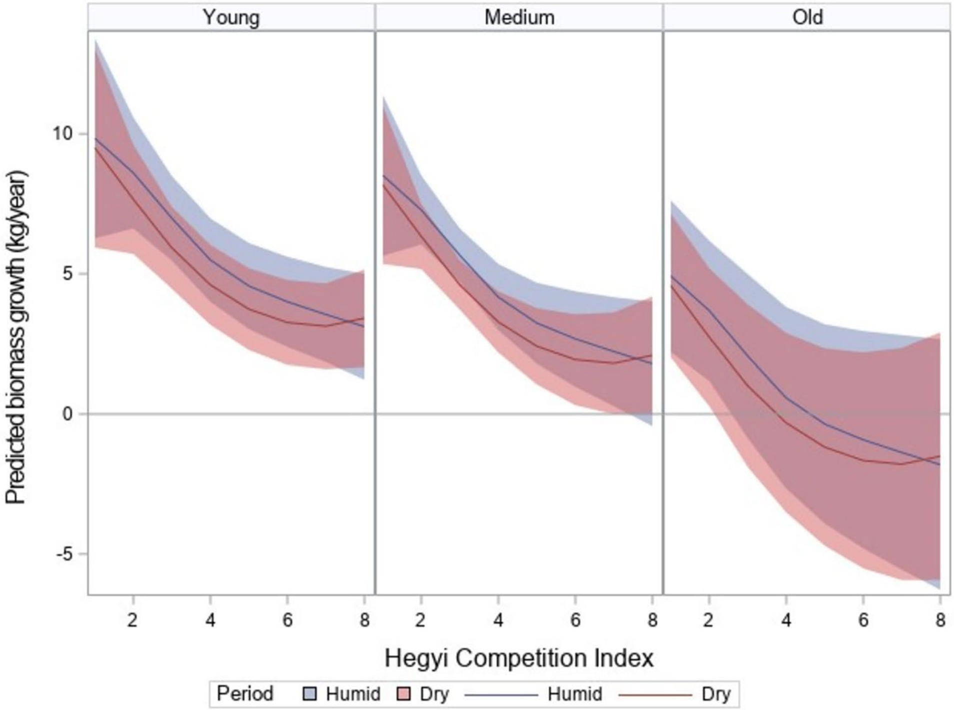


Fig. 10 Predicted annual biomass increment for a *Pinus nigra* tree of age classes “Young” (60 years), “Medium” (215 years) and “Old” (636 years) as a function of Hegyi competition index and climate (humid or dry). Bands represent the 95% confidence interval for the fitted line. Be aware that predicted negative values are predicted for higher rates of competition in old trees, a situation that is not observed in reality



including the oldest dated trees for the species, might have not reached this stage.

Among the disturbance agents potentially affecting biomass growth, the most likely agent in these forests is drought. Recent phenomena of growth reduction, associated with decay, have been described for *Pinus nigra* (Linares and Tiscar 2010; Navarro-Cerrillo et al. 2018) and *Pinus pinea* (Calama et al. 2019; Ferriz et al. 2021). In addition, both species have shown a great sensitivity to climate in terms of radial growth and carbon uptake (Natalini et al. 2016; Camarero et al. 2013; Navarro-Cerrillo et al. 2014).

Regarding other disturbance agents like pests, the potential effect of pine processionary moth in these forests seems to have been low for decades, as is suggested by the presence of *Pinus nigra* over 600 years old in the Sierra de Cazorla forest and *Pinus pinea* over 200 years old in the Hoyo de Pinares forest. However, the pine processionary moth is a severe pest of *Pinus* species in southern Spain, being *Pinus nigra* defined as a species especially sensitive and highly palatable to this moth in the studied region (Junta de Andalucía 2013; Ros-Candeira et al. 2019). The dynamics of the pine processionary moth strongly depends on temperature as a physiological driver for insect growth and development (Hódar et al. 2002), being highly sensitive to climate warming since the main feeding activity of larvae occurs in winter (Gazol et al. 2019). Predicted milder minimum temperatures during winter will promote the progression in altitude of the pest, as well as an increase in outbreak severity, resulting in heavier defoliation (Hódar et al. 2012). In addition, the interaction between drought and pine processionary moth defoliation could affect tree growth and, therefore, aboveground biomass, particularly in a palatable species such as *Pinus nigra*. For instance, a synergistic impact of both stressors could lead to more persistent and longer growth reductions and even contribute to growth decline (Camarero et al. 2022).

Effect of age, climate and competition on C fixation capacity

In the studied forest stands the response to contrasted climate events (dry *vs* humid periods) showed some differences in the pattern of biomass growth increment between the species. Weak differences were observed in *Pinus nigra* biomass growth pattern between humid and dry periods over the 600 years life-span analyzed, indicating similar response to climate irrespective of tree age (Esper et al. 2009). This result contrasts with Navarro-Cerrillo et al. (2014) that identified larger sensitivity to drought in young than in old trees of the species in a much more limiting environment, which might indicate that in our study other factors apart from drought are ruling interannual growth variability. On the other hand, *Pinus pinea* showed an increase in biomass growth in humid periods compared to dry periods for the medium-age and old trees (over 100 years old). Thus, the sensitivity of trees to climate as trees get older is not a constant, but site and species-specific, being more limiting for biomass growth in *Pinus pinea* oldest trees in our case study. This answers question (3), suggesting that there are different phases in the long-term dynamics of the climate-growth relationships that are site and species-dependent (Carrer and Urbinati. 2004). Among the different functional processes linked to tree growth, the hydraulic limitation hypothesis can play a major role in explaining how age may control the climate sensitivity of trees (Ryan and Yoder 1997; Mencuccini et al. 2005). As trees get older, hydraulic constraints are increasingly limiting, inducing stressful conditions in older trees. Such constraints can be intimately related to decreasing photosynthesis in old and tall trees, rather than to increasing respiratory demands (Kutsch et al. 2009).

The negative effect of drought is evidenced in *Pinus pinea* trees over 100-years old, through the decrease in biomass growth mainly during the two dry periods with lower SPEI (1985–1986 and 2005). *Pinus pinea* of this age (over 100 years old) also responded positively to humid periods, mainly during 1996–1998, while younger trees showed lower climatic sensitivity (Carrer and Urbaniti, 2004). Meanwhile, *Pinus nigra* showed a cumulative negative effect of drought, independently of tree age, reflecting the recent pattern of growth reduction due to drought observed for the species (Navarro-Cerrillo et al. 2014). These results answer question (4).

Under competition for water resources and light, differential space exploitation strategies may dictate how trees of different ages interact and establish dominance (Martín-Benito et al. 2020). Our results showed that competition decreased with age in both studied stands, thus a lower effect of competition was recorded in the oldest trees, and more significantly in 600 years-old *Pinus nigra* trees, which may be almost considered as open-growing trees. In addition, we found a general decrease in biomass growth increment as competition increased, positively responding to question (5). For both forests, older trees showed larger crowns compared to mature and young trees, which is indicative of their higher space exploitation efficiency (Vanninen 2004) and a lower effect of competition. When analyzing the interaction of competition with climate and tree age we observed that the climate-mediated differences in *Pinus pinea* and *Pinus nigra* biomass growth were attenuated when competition was high, responding to question (6). Following the stress gradient hypothesis (Bertness and Callaway 1994), this result suggests that when growing under a harsh environment, there is a positive interaction among conspecific individuals (Calama et al. 2019; Fajardo and McIntire 2011).

Conclusions

We assessed stands in their path to old-growth forest where *Pinus nigra* (46 to 657 years old) and *Pinus pinea* (24 to 220 years old) are still the dominant cohort, thus contributing to a better understanding of carbon storage in these Mediterranean forests in Europe. Although the two studied stands stocked around 35% less aboveground biomass than a typical *Pinus nigra* or *Pinus pinea* managed forest, our results confirmed the hypothesis that old-growth forests maintain a relatively high, rather than negligible, capacity for carbon fixation (Suchanek et al. 2004). Further investigation should focus on the contribution of other forest compartments (litter, woody debris, belowground and mineral soil) to total C uptake in old-growth forests.

The observed differences in carbon stocks in tree biomass between the two forests seemed related to their different growing environments and life-spans, with a main role of natural disturbances, mainly drought. In this sense, the explicit consideration of drought is essential for accounting potential carbon losses in old-growth forests (Gunn et al. 2013). For instance, the smaller mean annual biomass increment change in *Pinus nigra* SOGF stands, joined to its lower drought resistance and high palatability to the pine processionary moth, may render these forests less able to ensure the maintenance of climate neutrality; thus, they could serve as carbon reservoirs mainly in areas with limited natural disturbance influence.

The conservation and management of old-growth forests is at risk from different agents including climate change, which is exacerbated by the rarity and small size of old-growth forests on the landscape (Sabatini et al. 2018). As old-growth forests provide a diverse array of ecosystem services, including carbon fixation and storage among them, managing these forests to maintain their vertical complexity and spatial heterogeneity instead of just minimizing disturbances, will be an important component of a diverse forest carbon portfolio (Fraser et al. 2023).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10342-024-01750-5.

Acknowledgements We thank the Forest Service at Hoyo de Pinares y Sierra de Cazorla for providing the sampling permits required for the area and for their interest in the project. We acknowledge the E-OBS dataset from the EU-FP6 project UERRA (http://www.uerra.eu) and the data providers in the ECA&D project (https://www.ecad.eu). AH was supported by a II.4 fellowship from VII PPITUS 2022—Contratos de Acceso al Sistema Español de Ciencia, Tecnología e Innovación para el Desarrollo del Programa Propio de I+D+i de la US

Author's contribution Conceptualization, MP, JV-P, RA and RC; methodology, MP, JV-P and RC; formal analysis, MP, JV-P and RC; investigation, MP, JV-P, GM, RA, AH, AC, PAT and RC; resources, MP, JV-P, RA and RC; writing—original draft preparation, MP, JV-P, RC; writing—review and editing, MP, JV-P, RC; visualization, MP, JV-P and RC; supervision, MP, JV-P and RC; project administration, MP, JV-P, RA and RC; funding acquisition, MP, JV-P, RA and RC. All authors have read and agreed to the published version of the manuscript.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. This research was funded by Ministerio de Ciencia e Innovación, grant numbers AGL2017-83828-C2, PID2022-136906OB-C2 supported by MICIU/AEI /https://doi.org/10.13039/501100011033 and by FEDER-UE, and MITECO grant 2023-AF. 20234TE005. This research has also received financial support from the European Union´s Horizon Europe research and innovation funding programme under the grant agreement No. 101071300.

Availability of data and material (data transparency) The dataset generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

References

Aakala T, Fraver S, D'Amato DW, Palik BJ (2013) Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA. For Ecol Manag 308:128–135. https://doi.org/10.1016/j.foreco.2013.07.057

Alejano R (2008) Selvicultura de las masas béticas de P*inus nigra* Arn. In Montero G, Serrada R, Reque J (ed) Compendio de Selvicultura de Especies, INIA—Fundación Conde del Valle de Salazar, pp 329–346

Baroni C, Brunetti M, Cerrato R, Coppola A, Betti G, Salvatore MC (2020) A long-term chronology of Pinus pinea L. from Parco della Versiliana (Pietrasanta, Italy) derived from treefall induced by a windstorm on March 4th…5th, 2015. Dendrochronol 62:125710

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends Ecol Evol 9:191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Calama R, Montero G (2004) Interregional non-linear height-diameter model with random coefficients for stone pine in Spain. Can J For Res 34(1):150–163. https://doi.org/10.1139/X03-199

Calama R, Puértolas J, Madrigal G, Pardos M (2013) Modelling the environmental response of leaf net photosynthesis in Pinus pinea L. natural regeneration. Ecol Model 251:9–21. https://doi.org/10.1016/j.ecolmodel.2012.11.029

Calama R, Conde M, de-Dios-García J, Madrigal G, Vázquez-Piqué J, Gordo FJ, Pardos M (2019) Linking climate, annual growth and competition in a Mediterranean forest: *Pinus pinea* in the Spanish Plateau. Agric For Meteor 264: 309-321. https://doi.org/10.1016/j.agrformet.2018.10.017

Callaway RM, Walker LR (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78:1958–1965. https://doi.org/10.1890/0012-9658(1997)078

Camarero JJ, Manzanedo RD, Sánchez-Salguero R, Navarro-Cerrillo RM (2013) Growth response to climate and drought change along an aridity gradient in the southernmost *Pinus nigra* relict forests. Ann for Sci 70:769–780. https://doi.org/10.1007/s13595-013-0321-9

Camarero JJ, Tardif J, Gazol A, Conciatori F (2022) Pine processionary moth outbreaks cause longer growth legacies than drought and are linked to the North Atlantic Oscillation. Sci Tot Environ 819:153041. https://doi.org/10.1016/j.scitotenv.2022.153041

Carrer M, Urbinati C (2004) Age-dependent tree ring growth responses to climate in Larix decidua and Pinus cembra. Ecology 85:730–740. https://doi.org/10.1890/02-0478

Chen HYH, Luo Y (2015) Net aboveground biomass declines of four major forest types with forest ageing and climate change in western Canada's boreal forests. Glob Change Biol 21(10):3675–3684. https://doi.org/10.1111/gcb.12994

Cornes R, Van der Schrier G, van den Besselaar EJM, Jones PD (2018) An ensemble version of the E-OBS temperature and precipitation datasets. J Geophys Res Atmos 123(17):9391–9409. https://doi.org/10.1029/2017JD028200

Creus J (1998) A propósito de los árboles más viejos de la España peninsular: los *Pinus nigra* Arn. ssp. salzmanii (Dunal) Franco de Puertollano-Cabañas sierra de Cazorla. Jaén Montes 54:68–76

De Dios-García J, Pardos M, Calama R (2015) Interannual variability in competitive effects in mixed and monospecific forests of Mediterranean stone pine. For Ecol Manag 358: 230–239. https://doi.org/10.1016/j.foreco.2015.09.014

del Río M et al (2017) Mediterranean pine forests: management effects on carbon stocks. In: Managing forest ecosystems: the challenge of climate change, pp 301–327

Dixon GE (2002) Essential FVS: a user's guide to the forest vegetation simulator. Internal Rep. Fort Collins, CO: U. S. Department of Agriculture, Forest Service, Forest Management Service Center

Esper J, Niederer R, Belbi P, Frank D (2009) Climate signal age effects—evidence from young and old trees in the Swiss Engadin. For Ecol Manag 255(11):3783–3789. https://doi.org/10.1016/j.foreco.2008.03.015

Fajardo A, McIntire EJB (2011) Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. J Ecol 99:642–650. https://doi.org/10.1111/j.1365-2745.2010.01771.x

FAO Global Forest Resources Assessment (2020) Main Report. Rome. https://doi.org/10.4060/ca9825en

Ferriz M, Martín-Benito D, Cañellas I, Gea-Izquierdo G (2021) Sensitivity to water stress drives differential decline and mortality dynamics of three co-occurring conifers with different drought tolerance. For Ecol Manag 486:118964. https://doi.org/10.1016/j.foreco.2021.118964

Fraser JS, Pile Knapp LS, Graham B, Jenkins MA, Kabrik J, Saunders M, Spetich M, Shifley S (2023) Carbon dynamics in old-growth forests of the Central Hardwoods Region, USA. For Ecol Manag 537:120958. https://doi.org/10.1016/j.foreco.2023.120958

Friedman JH (1984) A variable span scatterplot smoother. Stanford University, Stanford

Fritts HC, Guiot J, Gordo GA, Schweingruber F (1990) Methods of calibration, verification, and reconstruction. Methods of dendrochronology. Springer, Netherlands, Dordrecht, pp 163–217

Gao B, Taylor AR, Searle EB, Kumar P, Ma Z, Hume AM, Chen HYH (2018) Carbon storage declines in old boreal forests irrespective of succession pathway. Ecosystems 21:1168–1182. https://doi.org/10.1007/s10021-017-0210-4

Gazol A, Hernández-Alonso R, Camarero JJ (2019) Patterns and drivers of pine processionary moth defoliation in Mediterranean mountain forests. Front Ecol Evol 7:458. https://doi.org/10.3389/fevo.2019.00458

Gea-Izquierdo G, Sánchez-González M (2022) Forest disturbances and climate constrain carbon allocation dynamics in trees. Glob Change Biol 28: 4342–4358. https://doi.org/10.1111/gcb.16172

González P, Ruiz-Benito P, Astigarraga J, Cruz V, Moreno D, Herrero A, Gosálbez J, Zavala MA (2020) Los bosques españoles como soluciones naturales frente al cambio climático: herramientas de análisis y modelización. Manual para la estimación del efecto sumidero de los bosques españoles y su aplicación a la planificación ambiental. MITECO

Groffman PM et al (2012) Long-term integrated studies show complex and surprising effects of climatechange in the northern hardwood forest. BioScience 62: 1056–1066. https://doi.org/10.1525/bio.2012.62.12.7

Gundersen P, Thybring EE, Nord-Larsen T, Vesterdal L, Nadelhoffer KJ, Johannsen VK (2021) Old-growth forest carbon sinks overestimated. Nature 591:E21–E25. https://doi.org/10.1038/s41586-021-03266-z

Gunn JS, Ducey MJ, Whitman AA (2013) Late-successional and old-growth forest carbon temporal dynamics in the Northern Forest (Northeastern USA). For Ecol Manag 312:40–46. https://doi.org/10.1016/j.foreco.2013.10.023

Hale K, Spencer M, Peterken GF, Mountford EP, Bradshaw RHW (2019) Rapid carbon accumulation within an unmanaged, mixed, temperate woodland. Scand J for Res 34(3):208–217. https://doi.org/10.1080/02827581.2019.1575975

Hegyi F (1974) A simulation model for managing jackpine stands. In: Growth models for tree and stand simulation: proceedings of meetings in 1973. Royal College of Forestry

Hódar JA, Zamora R, Castro J (2002) Host utilisation by moth and larval survival of pine processionary caterpillar *Thaumetopoea pityocampa* in relation to food quality in three *Pinus* species. Ecol Entomol 27:292–301. https://doi.org/10.1046/j.1365-2311.2002.00415.x

Hódar JA, Zamora R, Cayuela L (2012) Climate change and the incidence of a forest pest in Mediterranean ecosystems: can the North Atlantic Oscillation be used as a predictor? Clim Change 113:699–711. https://doi.org/10.1007/s10584-011-0371-7

Jandl R, Lindne M, Vesterdal L, Bauwens B, Baritz R, Hagedorn F, Johnson DW, Minkkinen K, Byrne KA (2007) How strongly can forest management influence soil carbon sequestration? Geoderma 137(3–4):253–268. https://doi.org/10.1016/j.geoderma.2006.09.003

Junta de Andalucía (2013) Plan de Lucha Integrada Contra la Procesionaria del Pino (Traumatocampa pityocampa Denis & Shiffermüller, 1775) en la comunidad autónoma de Andalucía. Consejería de Medio Ambiente y Ordenación del Territorio, Junta de Andalucía, Sevilla. https://www.juntadeandalucia.es/medioambiente/portal_web/web/temas_ambientales/ montes/sanidad_forestal/planes_lucha_integrada/pli_procesionaria.pdf

Keith H, Kun Z, Hugh S, Svoboda M, Mikoláš M, Adam D, [32 authors]. et al (2024) Carbon carrying capacity in primary forests shows potential for mitigation achieving the European Green Deal 2030 target. Commun Earth Environ 5(1):256. https://doi.org/10.1038/s43247-024-01416-5

Kēnina L, Elferts D, Jaunslaviete I, Bāders E, Jansons A (2023) Sustaining carbon storage: lessons from hemiboreal old-growth coniferous and deciduous forest stands. For Sci 69:158–166. https://doi.org/10.1093/forsci/fxac055

Korosuo A, Pilli R, Abad-Viñas R, Blujdea VNB, Colditz RR, Fiorese G, Rossi S, Vizzari M, Grassi G (2023) The role of forests in the EU climate policy: Are we on the right track? Carbon Balance Managem 18:15. https://doi.org/10.1186/s13021-023-00234-0

Kutsch WL, Wirth C, Kattge J, Nöllert S, Herbst M, Kappen L (2009) Ecophysiological characteristics of mature trees and stands—consequences for old-growth forest productivity. In: (eds C Wirth, G Gleixner, M Heimann) Old-growth forests, Function, fate and value. Ecological Studies, vol 207, Springer, pp 57–76

Linares JC, Tiscar PA (2010) Climate change impacts and vulnerability of the southern populations of *Pinus nigra* subsp. salzmannii. Tree Physiol 30(7):795–806. https://doi.org/10.1093/treephys/tpq052

Lindholm M, Eronen M, Timonen M, Jouko Meriläinen J (1999) A ring-width chronology of Scots pine from northern Lapland covering the last two millennia. Annales Botanici Fennici 36 (2):119–126. https://www.jstor.org/stable/23726620.

Luyssaert S, Schulze ED, Borner A, Knohl A, Hessenmoller D, Law BE, Ciais P, Grace J (2008) Old-growth forests as global carbon sinks. Nature Letters 455:11. https://doi.org/10.1038/nature07276

Martin GR, Ek AR, Monserud RA (1977) Control of plot edge bias in forest stand growth simulation models. Can J For Res 100–105. https://doi.org/10.1139/x77-014

Martín-Benito D, Pederson N, Lanter C, Köse N, Dohgan M, Bugmann H, Bigler C (2020) disturbances and climate drive structure, stability, and growth in mixed temperate old-growth rainforests in the Caucasus. Ecosystems 23:1170–1185. https://doi.org/10.1007/s10021-019-00462-x

Martín-Benito G, Pederson N, Ferriz M, Gea-Izquierdo G (2021) Old forests and old carbon: A case study on the stand dynamics and longevity of aboveground carbon. Sci Total Environ 765:142737. https://doi.org/10.1016/j.scitotenv.2020.142737

Mencuccini M, Martínez-Vilalta J, Vanderklein D, Hamid HA, Korakaki E, Lee S, Michiels B (2005) Size-mediated ageing reduces vigour in trees. Ecol Lett 8:1183–1190. https://doi.org/10.1111/j.1461-0248.2005.00819.x

Menéndez-Miguélez M, Ruíz-Peinado R, del Río M, Calama R (2021). Improving tree biomass models through crown ratio patterns and incomplete data sources. Eur J For Res 140(12). https://doi.org/10.1007/s10342-021-01354-3

Montero G, Cañadas N, Yagüe S, Bachiller A, Calama R, Garriga E, Cañellas I (2003) Aportaciones al conocimiento de las masas de *Pinus pinea* L. en los Montes de Hoyo de Pinares (Ávila – España). Revista Montes 73:30–40

Montero G, Ruiz-Painado R, Muñoz M (2005) Producción de biomasa y fijación de CO2 por los bosques españoles. Monografía Forestal 13. INIA. Madrid, 274 pp

Montero G, Calama R, Ruiz - Peinado R (2008) Selvicultura de Pinus pinea L. In Montero G., Serrada R, Reque J (Eds.) Compendio de Selvicultura de Especies, pp 431–470. INIA – Fundación Conde del Valle de Salazar

Natalini F, Alejano R, Vazquez-Pique J, Pardos M, Calama R, Büntgen U (2016) Spatiotemporal variability of stone pine (*Pinus pinea* L.) growth response to climate across the Iberian Peninsula. Dendrochronologia 40:72–84. https://doi.org/10.1016/j.dendro.2016.07.001

Navarro-Cerrillo RM, Sánchez-Salguero R, Manzanedo RD, Camarero JJ, Fernández-Cancio A (2014) Site and age condition the growth response to climate and drought of relict Pinus nigra subsp. Salzmannii populations in southern Spain. Tree Ring Res 70(2):145–155 https://doi.org/10.3959/1536-1098-70.2.145

Navarro-Cerrillo RM, Duque-Lazo J, Manzanedo RD, Sánchez-Salguero R, Palacios-Rodríguez G (2018) Climate change may threaten the southernmost *Pinus nigra* subsp. salzmannii (Dunal) Franco opulations: an ensemble niche-based approach. iForests 11:396–405. https://doi.org/10.3832/ifor2588-011

O'Brien L, Schuck A, Fraccaroli C, Pötzelsberger E, Winkel G, Lindner M (2021) Protecting old-growth forests in Europe—a review of scientific evidence to inform policy implementation. Final report. European Forest Institute, Bonn, Germany

Piper FI, Fajardo A (2011) No evidence of carbon limitation with tree age and height in *Nothofagus pumilio* under Mediterranean and temperate climate conditions. Ann Bot 108: 907–917. https://doi.org/10.1093/aob/mcr195

Riofrío J, del Río M, Maguire DA, Bravo F (2019) Species mixing effects on height-diameter and basal area increment models for scots pine and maritime pine. Forests 10(3):249. https://doi.org/10.3390/f10030249

Ros-Candeira A, Pérez-Luque AJ, Suárez-Muñoz M, Bonet-García FJ, Hódar JA, Giménez de Azcárate F, Ortega-Díaz O (2019) Dataset of occurrence and incidence of pine processionary moth in Andalusia, south Spain. ZooKeys 852:125–136. https://doi.org/10.3897/zookeys.852.28567

Rozas V (2015) Individual-based approach as a useful tool to disentangle the relative importance of tree age, size and inter-tree competition in dendroclimatic studies. iForests 8:187–194. https://doi.org/10.3832/ifor1249-007

Ruppert D, Wand MP, Carrol RJ (2003) Semiparametric regression. Cambridge University Press, New York, p 386

Ryan MG, Yoder BJ (1997) Hydraulic limits to tree height and tree growth. Bioscience 47:235–242. https://doi.org/10.2307/1313077

Ryan MG, Binkley D, Fownes JH (1997) Age-related decline in forest productivity: pattern and process. Adv Ecol Re 27:213–262. https://doi.org/10.1016/S0065-2504(08)60009-4

Sabatini FN: (35 authors), et al (2018) Where are Europe's last primary forests? Biodiv Rev 24:1426–1439. https://doi.org/10.1111/ddi.12778

Sierra CA, Muller M, Metzler H, Manzoni S, Trumbore SE (2017) The muddle of ages, turnover, transit, and residence times in the carbon cycle. Global Change Biol 23:1763–1773. https://doi.org/10.1111/gcb.13556

Sillett SC, Van Pelt R, Koch GW, Ambrose AR, Carroll AL, Antoine ME, Mifsud BM (2010) Increasing wood production through old age in tall trees. For Ecol Manag 259(5):976–994. https://doi.org/10.1016/j.foreco.2009.12.003

Speer JH (2010) Fundamentals of tree-ring research. University of Arizona Press

Spracklen BD, Spracklen DV (2019) Identifying European old-growth forests using remote sensing: a study in the Ukrainian Carpathians. Forests 10(2):127. https://doi.org/10.3390/f10020127

Stephenson NL, (37 authors), et al (2014) Rate of tree carbon accumulation increases continuously with tree size. Nature 507:90–93. https://doi.org/10.1038/nature12914

Suchanek TH, Mooney HA, Franklin JF, Gicinski H, Ustin SL (2004) Carbon dynamics of an old-growth for. Ecosystems 7:421–426. https://doi.org/10.1007/s10021-004-0134-7

Vanninen P (2004) Allocation of above-ground growth in Pinus sylvestris—impacts of tree size and competition. Silva Fennica 38(2):155–166

Vicente-Serrano SM, Beguería S, López-Moreno I (2010) A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J Clim 23:1696–1718. https://doi.org/10.1175/2009JCLI2909.1

Wirth C, Gleixner G, Heimann M (2009) Old-growth forests: function, fate and value—an overview. In: Wirth C, Gleixner G, Heimann M (eds) Old-growth forests, function, fate and value. Ecol Stud, vol 207, pp 3–9. Springer

Wykoff WR, Crookston NL, Stage AR (1982) User´s guide to the stand prognosis model. United States Department of Agriculture. Forest Service. Tech. Rep. INT-133