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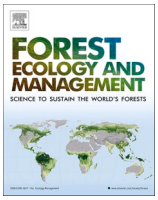

Forest structural diversity modulates tree growth synchrony in response to climate change

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ABSTRACT

Following centuries of deforestation, many industrialized countries have experienced an increase in forest area and biomass due to changes in land- and forest-use since the mid-20th century. At the same time, the impacts of climate change on forests are aggravating, but the interplay between past land- and forest-use (i.e. land- and forest-use legacies) and climate change in tree growth remains elusive. Tree growth synchrony, defined as the coincident increase in annual tree growth between different tree individuals over time, represents a comprehensive ecological measure of the level of environmental stress faced by forests, and consequently, can assess forest vulnerability to global change. Here using network theory and generalized linear mixed models, we tested whether tree size heterogeneity, resulting from different land- and forest-use legacies (i.e. recently-established, long-established, recently-pruned pollards and old-pruned pollards), modulated tree growth synchrony in response to heatwaves frequency synchrony between 1970 and 2020. We analyzed tree growth data from European beech (*Fagus sylvatica* L.) stands with different histories of forest management at the species' low-latitude margin. We found increased tree growth synchrony under more frequent heatwaves and late spring frosts, and reduced precipitation. Interestingly, tree growth synchrony in response to heatwave frequency was modulated by tree size heterogeneity, with the highest synchrony observed in stands with low tree size heterogeneity, mainly found in recently-established forests. Conversely, stands with high tree size heterogeneity did not show important changes in synchrony with increasing heatwaves frequency. Our results highlight the importance of maintaining structurally diverse forests to mitigate the negative effects of climate change on forest productivity, and thereby, increase forest resilience to future forest climate risks.

1. Introduction

Forests have undergone major human-induced changes, and today, 75 % of the world's forests are altered by humans (FAO, 2020). Anthropogenic impacts on forests can completely modify tree cover through land-use changes (e.g. deforestation, afforestation or natural regrowth; Song et al. 2018) or partially through changes in forest-use (e.g. increases in biomass after management abandonment; Jump et al. 2017). Furthermore, climate change is causing shifts in mean temperature, precipitation and extreme climatic events (IPCC, 2021), altering forest functioning (Hammond et al., 2022). Direct anthropogenic impacts on forests, through changes in land- and forest-use, and indirect impacts, through climate change, will largely determine future forest dynamics (McDowell et al., 2020). Thus, quantifying the interaction between these direct and indirect changes in forest functioning is both a scientific and management priority.

Since the mid-20th century, many industrialized countries have experienced a rise in forest area, density, and biomass due to changes in

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land- and forest-use, such as the abandonment of agriculture and traditional forest management (Garbarino et al., 2022; Infante-Amate et al., 2022; Song et al., 2018). Land-use changes determine forest age and structure, with an expected increase in vulnerability to climate change in recently-established forests compared to long-established forests (Alfaro-Sánchez et al., 2019; Correia et al., 2021; Mausolf et al., 2018). Changes in forest-use can alter forest structure, potentially influencing the way current forest ecosystems respond to climate (Marqués et al., 2022; Perring et al., 2018; Sangüesa-Barreda et al., 2015). For example, the abandonment of forest-use could lead to structural overshoot processes in which increased tree biomass in a mild climate can lead to forest decline (i.e. growth decrease, crown die-back and increased mortality) in response to more severe climatic conditions (Jump et al., 2017; Zhang et al., 2021). However, the underlying drivers by which trees may respond differently to climate as a function of past land- and forest-use (i.e. land- and forest-use legacies) have been largely unexplored.

In the current context of climate change, warming, increased aridity and heatwaves are impacting tree demography (Astigarraga et al., 2020; Peng et al., 2011; van Mantgem et al., 2009), shaping forest structure (McIntyre et al., 2015; Zhou et al., 2013), composition (Esquivel-Muelbert et al., 2019; Ruiz-Benito et al., 2017) and productivity (García-Valdés et al., 2021; Zhang et al., 2018). At the same time, variations in annual precipitation and late spring frosts are also affecting tree growth and leaf damage (Castagneri et al., 2015; Sangüesa-Barreda et al., 2021; Zohner et al., 2020). Although there is a broad scientific consensus on increased climate-induced tree mortality, the same is not true for tree growth since warming can have antagonistic effects (Allen et al., 2015; Díaz-Martínez et al., 2023). For example, anthropogenic climate change can increase tree growth, primarily through carbon dioxide (CO_2) and nitrogen (N) fertilization and the removal of low temperature limitations to photosynthesis, but excess warming may reduce tree growth due to reduced water availability and increased carbon respiration costs (Adams et al., 2009; D'Orangeville et al., 2018; Peñuelas, Ciais, et al., 2017). Tree growth is a demographic rate of paramount importance that integrates many environmental constraints of tree performance, being considered an indicator of tree vitality (Dobbertin, 2005) and it can be used as an early-warning signal of tree die-off (Cailleret et al., 2019).

In the last years, synchrony in tree growth (i.e. coincident increase in annual tree growth between different tree individuals over time) has received great attention by researchers worldwide (del Río et al., 2021; González de Andrés et al., 2022; Shestakova et al., 2016). Several studies have shown increased tree growth synchrony associated with pervasive climatic effects from local to regional scales (Gazol et al., 2020; Latte et al., 2015). Increased growth synchrony to climatic stressors exacerbates the risk of widespread negative impacts on tree vitality at population level by losing the benefits of individual-level variability in response to climate (Clark et al., 2012). Thus, tree growth synchrony is widely recognized as an indicator of forest vulnerability to climate change (Boden et al., 2014; Shestakova et al., 2016; Tejedor et al., 2020). Tree growth synchrony is generally calculated as shared variation within-population tree chronologies. However, since different tree sizes and tree growth forms usually respond differently to climatic stressors (Campbell et al., 2021; Mérian and Lebourgeois, 2011), growth synchrony analyses can benefit from an individual-level approach (i.e. focusing on pairs of individuals) to reveal synchrony patterns at population level. Therefore, assessing tree growth synchrony from an individual-based perspective in various forest structures resulting from different land- and forest-use legacies could provide new insights in the evaluation of forest vulnerability to climate change stressors.

In the Iberian Peninsula, the long-term interactions between humans and nature have created complex socioecological systems that shape forest structure, species distribution and forest composition (Blondel, 2006; Scarascia-Mugnozza et al., 2000). However, since the middle of the last century, the abandonment of agricultural activities is leading to an increase in forest extension and density (Poyatos et al., 2003; Vilà-Cabrera et al., 2017). Furthermore, the substitution of firewood for fossil fuels led to the abandonment of traditional forest-use, decreasing centuries-old management techniques such as coppicing and pollarding (Infante-Amate et al., 2022; Sjölund and Jump, 2013). All these anthropogenic impacts in land- and forest-use could interact with the increasing effects of climate change, leading to detrimental ecological effects in forests (Vilà-Cabrera et al., 2023).

Here, we tested whether tree size heterogeneity, resulting from different land- and forest-use legacies modulated tree growth synchrony in response to climate change. We hypothesized that (i) there will be an increase in tree growth synchrony regardless of land- and forest-use legacies as climatic conditions (such us precipitation, heatwaves and late spring frosts) are becoming an increasingly limiting factors for tree growth; and (ii) land- and forest-use legacies with greater forest structural diversity will show lower tree growth synchrony due to greater individual-level variability in response to climate change. To this end, we used the European beech (*Fagus sylvatica*, L.) as the target species, a widely-distributed species of great economic and ecological importance that is susceptible to droughts and late spring frosts (Archambeau et al., 2020; Packham et al., 2012; Sangüesa-Barreda et al., 2021). To test these hypotheses, we quantified tree growth synchrony in stands with contrasting land- and forest-use legacies in an area with similar biotic and abiotic conditions. We mixed 12 European beech stands with four different legacies (i.e. recently-established, long-established, recently-pruned pollards and old-pruned pollards) located in the north of the Iberian Peninsula analyzing *c.* 240 tree individuals. Our results provide evidence of the key role of anthropogenic legacies in modulating forest ecosystems responses to climate change by altering forest structural diversity.

2. Materials and methods

2.1. Study area

The study area is a natural forest dominated by *Fagus sylvatica*, located at the southern limit of the species global distribution (Packham et al., 2012). It is in the north of the Iberian Peninsula at the easternmost part of the Cantabrian Range (42°58'N - 2°24'W; altitude: 750–1000 m a.s.l.; Fig. 1). The studied forest is mainly composed of detrital sedimentary rocks and presents an oceanic climate (*Cfb*, Kottek et al., 2006), with average precipitation of 932 mm and average temperature of 13 °C (data from easyclimate R package (Cruz-Alonso et al., 2023; Pucher and Neumann, 2022)). Although *F. sylvatica* is the most abundant species, other tree species characteristic of European temperate forests can also be found (e.g. *Quercus robur* L., *Q. petraea* Matt., *Ilex aquifolium* L., *Sorbus aucuparia* L.).

During the last centuries, the forest was mainly used for charcoal and firewood, and its traces can be seen in the many pollards and coppiced trees that exist today in the area. Since the 1950s with the industrial transition, charcoal and firewood were replaced by fossil fuels, leading to an increase in tree density and biomass. Furthermore, agricultural and livestock activities in the region were also reduced or abandoned resulting in an increase in forest area.

2.2. Characterization of land- and forest-use legacies

We identified land- and forest-use legacies in the stands using aerial photographs, forest management plans and interviews with local inhabitants and forest managers. First, we distinguished recently-established from old-growth stands that were already occupied by trees in the mid-20th century using aerial photographs from 1945/46 (https://www.geo.euskadi.eus/comparador-de-ortofotos/webgeo00-content/es/). Then, among stands occupied by trees prior to 1945/46, we distinguished the pollarded from high-forest stands (i.e. trees originated from seeds resulting in forests with tall and mature trees with a closed

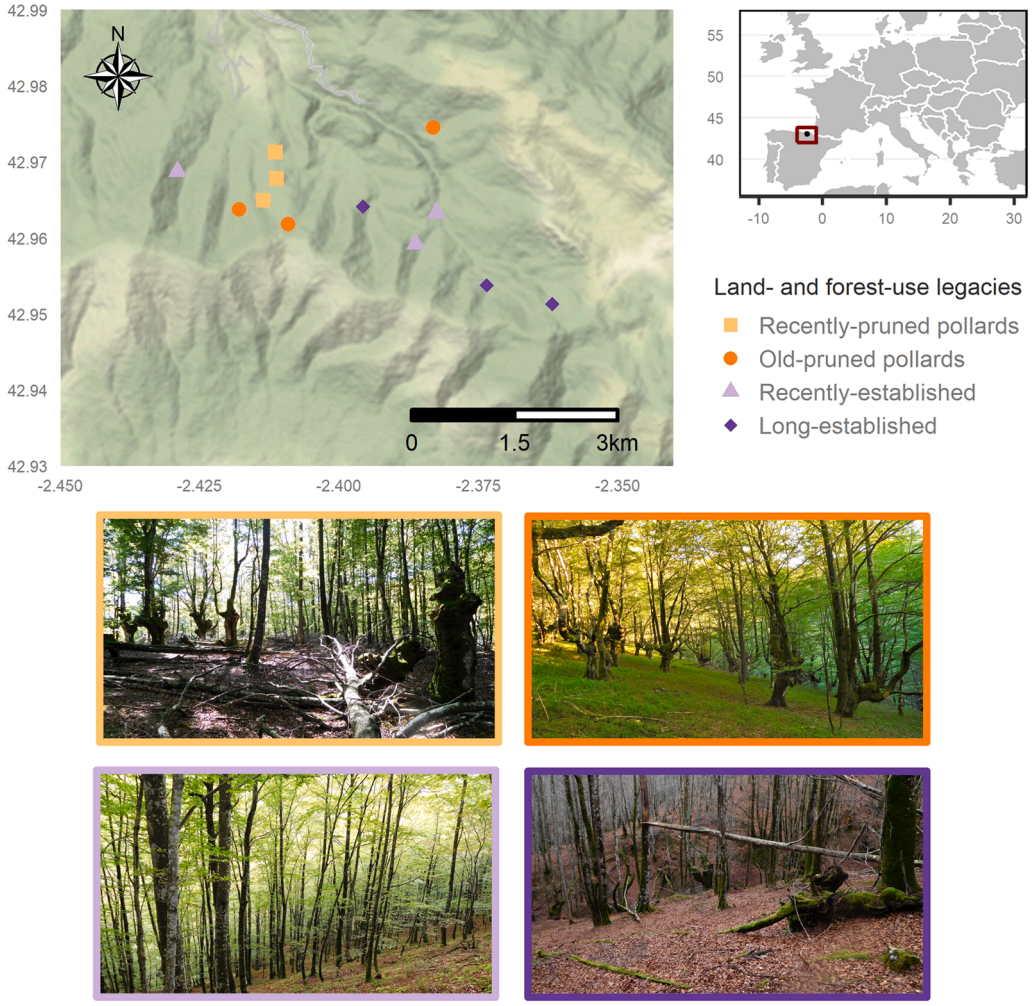

Fig. 1. Map of the study area showing the 12 sampled stands and photographs from each legacy type. The border colors of the photographs indicate the legacy type shown in the legend. See Appendix S1: Table S1.1 for information on the structure, composition, and demography of each legacy type. Photos by J. Astigarraga.

canopy). Pollarding is a traditional silvicultural technique that favors the production of a dense mass of branches above-ground level, beyond the reach of browsing mammals, often resulting in large trees with a longer lifespan than their naturally growing counterparts (Sjölund and Jump, 2013). Among pollard stands, we distinguished old-pruned pollard stands (pruned before 1970) and recently-pruned pollard stands (pruned before 1970 and in 2010 and 2014). Thus, we classified our 12 stands into (i) high-forest stands occupied by trees post to 1945/46 (hereafter, recently-established) and (ii) high-forest stands occupied by trees prior to 1945/46 (hereafter, long-established), (iii) old-pruned pollard stands, and (iv) recently-pruned pollard stands (Fig. 1 and Appendix S1: Table S1.1).

2.3. Field sampling

In 2020, we extracted two cores per tree in opposite directions using a Pressler increment borer and processed them using standard dendrochronology techniques (Fritts, 1976). Since each legacy type was replicated three times, we sampled 12 different stands (four legacies × three replicates = 12 stands, Fig. 1), collecting samples from 20 living individuals in each stand (four legacies × three replicates × 20 individuals per stand = 240 total individuals). Individuals were randomly selected, avoiding those in the immediate vicinity and excluding suppressed trees. All stands were located within *c.* 1300 ha and within the same hydrological valley, mixing stands with different land- and forest-use legacies across the entire spatial and altitudinal range–although recently-pruned pollards were concentrated in a specific area due to the localized pruning activities. We georeferenced each cored tree and measured the diameter at breast height (d.b.h.). Then, we measured ring widths using trini R package (Astigarraga et al., 2022) and averaged widths per year from both cores from each individual tree. All cores were visually cross-dated following the procedures described by Yamaguchi (1991). Finally, we transformed ring-width series into basal area increment (BAI), assuming stem growth to be approximately concentric, applying the following formula:

$$BAI = \pi(r_t^2 - r_{t-1}^2) \quad (1)$$

where r_t is the stem radius at the end and r_{t-1} at the beginning of a given annual ring (Appendix S1: Figure S1.1). BAI allows removing the geometrical constraint associated with adding volume of wood to a stem with increasing radius (Biondi and Qeadan, 2008). We also measured the number of individuals, their d.b.h., the species, and their status (alive or dead) in a 10 m radius around the cored trees (see d.b.h. differences of the cored trees in Fig. 2B and further details on differences between land- and forest-use legacies in Appendix S1: Table S1.1).

2.4. Climate data

We used daily data at ~1 km^2 resolution on precipitation and minimum and maximum temperatures from easyclimate R package (Cruz-Alonso et al., 2023; Pucher and Neumann, 2022). Given the spatial proximity of the stands, we determined that the primary focus of

our study would be on the climatic time series analyses rather than climatic differences between individual stands. As such, we consider any potential variability in climate data between stands to be negligible for the purposes of this study and helpful in maintaining consistency across the analyses. Using the centroid coordinates considering all sampled stands, we downloaded daily climate data spanning from 1950 to 2020. From this dataset, we calculated annual precipitation, late spring frosts frequency (i.e. number of days below 0 ºC in meteorological spring–from 1st of March to 31st of May) and heatwaves frequency (i.e. number of days above 32 ºC in meteorological summer–from 1st of June to 31st August) annually from 1950 to 2020. These three climatic variables largely determine beech growth, as supported by prior studies (Archambeau et al., 2020; Packham et al., 2012; Sangüesa-Barreda et al., 2021).

2.5. Statistical analyses

2.5.1. Tree growth synchrony

We used a network approach to evaluate time variations in tree growth synchrony. We built networks where nodes were trees and a link between a pair of trees was established if their growths were positively and significantly correlated over time ($P < 0.05$), based on Spearman rank correlations (Gauthier, 2001). If trees of a stand were growing synchronically, tree growth networks would be densely connected, indicating that several trees showed similar growth patterns over time. Thus, network density or connectance provides a direct measure of stand growth synchrony. We calculated network connectance (C) as the number of realized links relative to the number of potential links, applying the following formula:

$$C = \frac{N}{0.5 \times n \times (n - 1)} \quad (2)$$

where N denotes the number of observed links and n the number of nodes. Using a network approach, we synthesized information from tree pairs with statistical evidence of synchrony, avoiding the potential noise introduced by including all available pair correlations (Neuman et al., 2024). This novel method for estimating tree growth synchrony broadens the spectrum of analytical possibilities, including the ability to estimate individual-level tree growth synchrony (i.e. focusing on pairs of individuals).

To evaluate growth synchrony over time, we used a 20-year moving window starting in 1970, shifting year by year. This choice allowed us to maximize the number of tree samples while ensuring a sufficiently long period to test the effects of climate change on tree growth synchrony. This approach balances the need for statistical power to robustly calculate correlations between trees over time with the requirement for a sufficiently long temporal resolution to observe meaningful trends. Of the 240 tree cores, we discarded three cores that were younger than 1970 and two other cores due to ring detection problems. For each time window and stand, we built a network as described above and calculated its connectance. For each time window, we calculated the mean tree size (through mean d.b.h.), tree size heterogeneity (through the coefficient of variation of the d.b.h.) and the mean of the climatic variables used (i.e. annual precipitation, late spring frosts frequency and heatwaves frequency). Thus, using a 20-year moving time window from 1970 to 2020, we obtained 30 values of mean connectance, mean tree size, mean tree size heterogeneity, mean annual precipitation, mean late spring frosts frequency and mean heatwaves frequency for each of the 12 stands. This resulted in a total of 360 values of connectance, tree size, tree size heterogeneity, and climatic variables (n = 360).

2.5.2. The relationship between climate change and tree growth synchrony, considering forest structural diversity as an effect modifier

We expected that the effect of climate change on tree growth synchrony would be modulated by forest structural diversity. To test this hypothesis, we fitted a generalized linear mixed-effects model of tree growth synchrony (i.e. network connectance calculated as the number of realized links relative to the number of potential links (%)) including the main effects of heatwaves frequency, tree size heterogeneity, annual precipitation, late spring frosts frequency, mean tree size, and legacy type, as well as an interaction term between heatwaves frequency and tree size heterogeneity, assuming a beta distribution of errors and using stand identity as a random effect.

We included an interaction term between climate change and forest structural diversity to account for the effect modification that forest structural diversity might have on the effect of climate change on tree growth synchrony (Laubach et al., 2021). We considered three climate change-related variables and two forest structure-related variables. Including interaction terms between all of them would not only complicate the interpretation of the results but also leave us without degrees of freedom. Therefore, we included an interaction term between heatwaves frequency and tree size heterogeneity. We focused on this interaction for the following ecological reasons: (i) Heatwaves frequency represents a critical limiting factor for tree performance, pushing trees to their physiological limits (Gazol et al., 2020); (ii) Heatwaves may affect large and small trees differently. Large trees, for instance, might be more vulnerable to hydraulic stress or experience higher radiation and evaporative demand due to their exposed crowns (Bennett et al., 2015); (iii) We were interested in quantifying whether forests with greater tree size heterogeneity would exhibit lower tree growth synchrony due to the greater individual-level variability in response to heatwaves frequency; (iv) Legacy type is not a variable that can be easily quantified, while tree size heterogeneity is a variable that can be measured directly in the field, making tree size heterogeneity a practical and actionable variable for forest managers.

We included the main effects of heatwaves frequency, tree size heterogeneity, annual precipitation, late spring frosts frequency, mean tree size, and legacy type, as precision covariates that were only associated with tree growth synchrony to improve model efficiency (Laubach et al., 2021). Specifically, we included annual precipitation and late spring frosts frequency, as the European beech is highly susceptible to late spring frosts and water limitation (Packham et al., 2012; Sangüesa--Barreda et al., 2021). We included mean tree size to adjust for stand development, since mean tree size is usually correlated with stand development (Astigarraga et al., 2024), and legacy type to adjust for other variables that might be affecting tree growth synchrony but were not directly measured.

To test for non-independence between the time windows, we applied a Moran's I test to the residuals of the model, expecting a positive autocorrelation (Moran, 1950). For the weights, we used the fraction of overlap between consecutive time windows, using the spdep R package (Bivand and Wong, 2018). We analyzed 12 sites, each with 30 time windows of 20-year duration spanning from 1970 to 2020. In each site, the first time window overlaps with the second by 95 % (19/20), with the third by 90 % (18/20), with the fourth by 85 % (17/20), and so on, until there is no overlap starting from the 20th time window onwards.

The Moran's I test was significant, so we used an eigenvector filtering approach to remove the non-independence in the residuals (Dormann et al., 2007). Eigenvector filtering involves translating the overlapping arrangement of data points into explanatory variables that capture the effects of time window overlap. We selected those eigenvectors that best reduced these overlapping effects in the residuals as predictors. To achieve this, we computed eigenvectors from the matrix representing the temporal overlap of the time windows. For model selection, we chose the eigenvector that resulted in the lowest absolute Moran's I (i.e. no positive or negative temporal autocorrelation). We then fitted the model with all the explanatory variables of interest, as well as the eigenvector with the lowest absolute Moran's I. We applied the Moran's I test to the residuals of this model, using the fraction of overlap between consecutive time windows as weights. The test result was non-significant ($P = 0.11$).

The numerical main effects were standardized before being included

in the models and the models were fitted using glmmTMB R package (Brooks et al., 2022). We calculated the R^2 of the model using performance R package (Lüdecke et al., 2021), the model's fit was diagnosed using DHARMa R package (Hartig, 2022) and adjusted predictions were visualized using ggeffects R package (Lüdecke, 2018). All analyses and visualizations were conducted using the tidyverse R package (Wickham et al., 2019) within the R Statistical Software (v4.2.1; R Core Team, 2022).

3. Results

Quantifying tree growth synchrony using 20-year moving windows from 1970 to 2020 as a function of land- and forest-used legacies, we found more synchronous responses during dry years across all land- and forest-use legacies (Fig. 2A, C). Although the relationship between growth synchrony and frequencies of heatwaves and late spring frosts was less evident, we observed a general trend towards increased growth synchrony with higher frequencies of heatwaves and late spring frosts (Fig. 2A, D, E). However, the magnitude of tree growth synchrony varied depending on legacy type, with the highest synchrony in recently-established stands and the lowest synchrony in recently-pruned pollards (Fig. 2A and Appendix S1: Figure S1.2). In addition, tree growth synchrony remained higher over time in recently-established stands than in other legacy types when precipitation increased and the frequencies of heatwaves and late spring frosts decreased (see in Fig. 2A the decrease in tree growth synchrony *c.* 1990 for all legacy types except for recently-established stands).

The model testing whether the effect of climate change on tree growth synchrony was modulated by forest structural diversity had a marginal R^2 of 0.64, and a conditional R^2 of 0.89 (Appendix S2: Figure S2.1). The *p*-value for the interaction term between heatwaves frequency and tree size heterogeneity was significant, indicating that the effect of heatwaves frequency on tree growth synchrony was modified by tree size heterogeneity between 1970 and 2020. Specifically, we found that increasing heatwaves frequency led to increased tree growth synchrony in stands with low tree size heterogeneity (red regression line in Fig. 3), while stands with high tree size heterogeneity were not affected by increasing heatwaves frequency (yellow regression line in Fig. 3).

4. Discussion

Our results showed increased tree growth synchrony in response to climate change in a widely distributed temperate tree species with

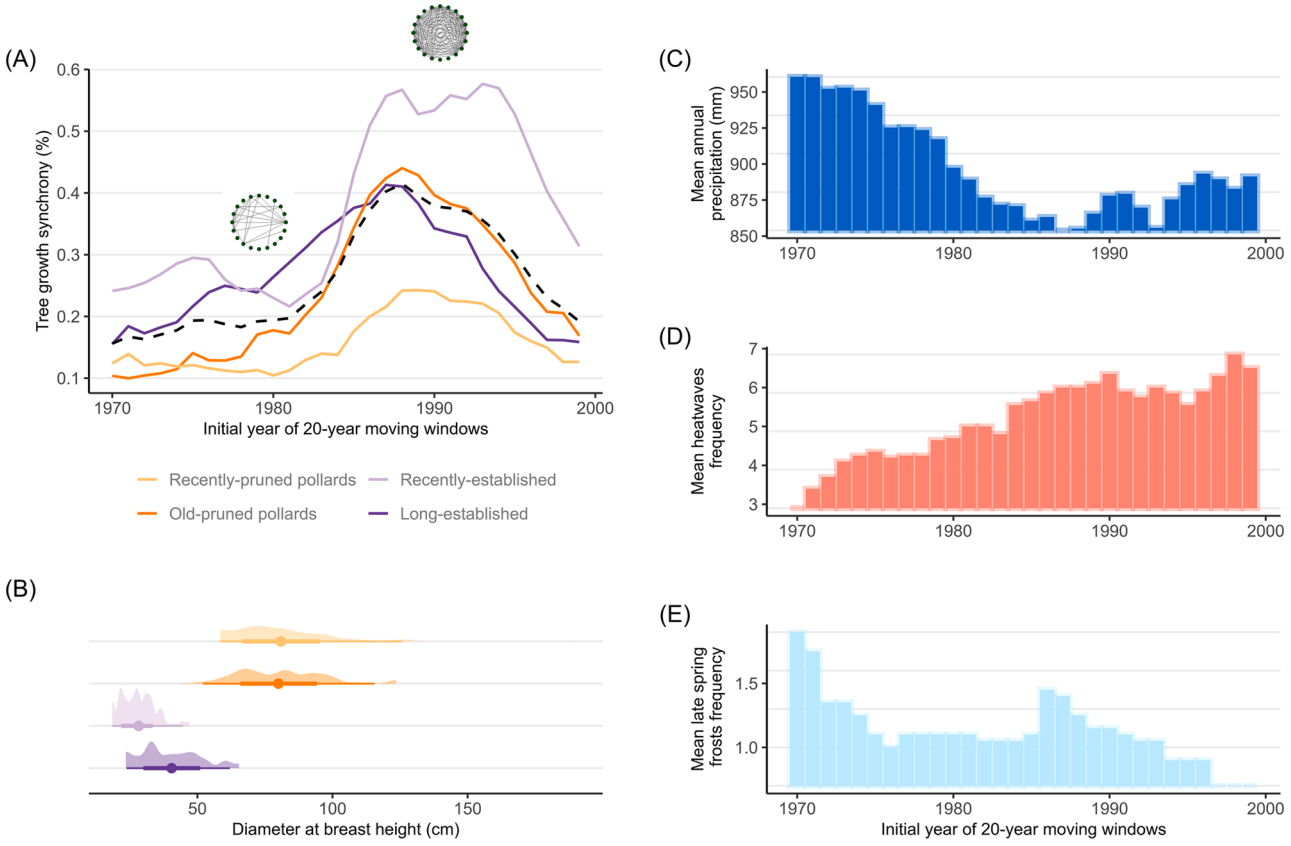

Fig. 2. Tree growth synchrony as a function of land- and forest- use legacies, structural diversity of each legacy type and climate trends in the last decades. (A) Tree growth synchrony using 20-year moving windows between 1970 and 2020 as a function of land- and forest-used legacies. The solid lines represent the mean tree growth synchrony of each legacy type, and the dashed line represents the overall mean of tree growth synchrony of all legacy types (see Appendix S1: Fig. S1.2 for stand-level tree growth synchronies). Two tree growth synchrony networks are shown, illustrating different levels of tree growth synchrony quantified as network connectance: one in a low synchrony period (few links) and one in a high synchrony period (many links). We built networks where nodes were trees and a link between a pair of trees was established if their growths were positively and significantly correlated over time ($P < 0.05$), based on Spearman rank correlations (Gauthier, 2001). We calculated network connectance as the number of realized links relative to the number of potential links. Note that the two networks shown correspond only to one recently-established stand in two time windows and are used as an example to show the calculation and shape of tree growth synchrony networks. (B) Density and interval plot of the diameter at breast height of cored trees where the points show the mean tree size, and the 95 % equi-tailed density intervals, the distribution of tree size of each legacy type. (C-E) Mean annual precipitation, mean heatwaves frequency and mean late spring frosts frequency using 20-year moving windows between 1970 and 2020. Climate data were normalized for visual comparison between climate variables, and the y-axis displays denormalized values in their original units for interpretability.

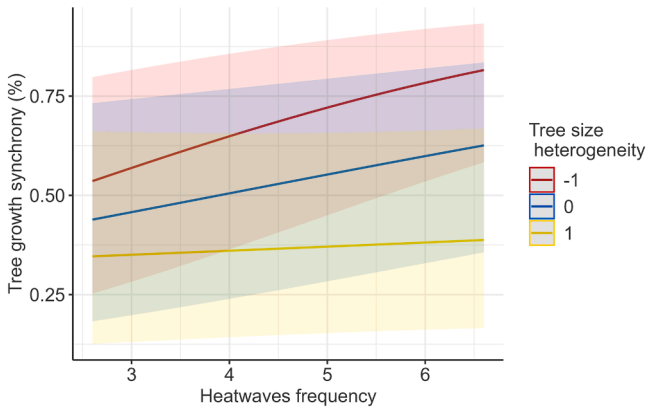

Fig. 3. Tree size heterogeneity modulates tree growth synchrony in response to heatwaves frequency. The regression lines of tree growth synchrony on heatwaves frequency are shown in different colours for low (red), mid (blue), and high (yellow) tree size heterogeneity. Tree size heterogeneity values are standardized. The shaded area represents the 95 % confidence intervals. Tree growth synchrony was quantified using network connectance, which was calculated as the number of realized links relative to the number of potential links. To generate adjusted predictions of tree growth synchrony for different combinations of heatwaves frequency and tree size heterogeneity, precision covariates of annual precipitation, late spring frosts frequency, and mean tree size were held at their mean values, while legacy type was held constant as long-established stands.

contrasting land- and forest-use legacies. Reduced annual precipitation and increased temperature-related extreme events underlay the observed increase in tree growth synchrony. However, land- and forest-use legacies modulated the magnitude of tree growth synchrony through changes in forest structural diversity (i.e. tree size heterogeneity). Recently-established forests exhibited the greatest tree growth synchrony, whereas the presence of heterogeneous tree sizes decreased growth synchrony. These findings have significant implications for forest management and adaptation, suggesting that heterogeneous structures could be functionally more resilient under the escalating impacts of climate change.

We observed increases in tree growth synchrony across all sampled stands, coinciding with reduced precipitation and increased heatwaves and late spring frosts frequencies. However, around 1990, there was a notable decline in tree growth synchrony despite heatwave frequency remaining high. This period coincided with increased precipitation and fewer late spring frosts, suggesting that the negative impact of rising heatwave frequency on tree growth synchrony may have been mitigated by the more favorable conditions in terms of precipitation and late spring frosts. This result confirms our first hypothesis and is consistent with previous studies that recorded increases in tree growth synchrony in response to increased climatic constraints for multiple species and forest types around the world (Boden et al., 2014; Gazol et al., 2020; Shestakova et al., 2016). Although climatic drivers of growth synchrony can vary depending on regional climate (Shestakova et al., 2016), the observed role of dry conditions and heatwaves agrees with the results obtained in populations of *F. sylvatica* in north-western Europe (Latte et al., 2015). Also, the effect of late frosts frequency in tree growth synchrony is in line with the detrimental influence of late frosts in the performance of *F. sylvatica* in southern populations (Sangüesa-Barreda et al., 2021). Increased growth synchrony is related to high population vulnerability to climate change (Boden et al., 2014), which in the case of dominant species such as *F. sylvatica*, could jeopardize the stability and persistence of the entire ecosystem. Thus, our results contribute to previous observations pointing to increased vulnerability to climate change of temperate forests, especially those located at the southern distribution limits (Lindner et al., 2010; Millar and Stephenson, 2015).

We found that the magnitude of tree growth synchrony varied depending on legacy type. Recently-established stands showed the highest tree growth synchrony and remained higher over time than in other legacy types when precipitation began to increase and heatwaves and late spring frosts frequencies started to decrease. These results suggest that, although recently-established forests are fundamental carbon sinks in the Iberian Peninsula (Vilà-Cabrera et al., 2017), they are vulnerable to climate change due to their homogeneous structure, which can lead to high tree growth synchrony. The high vulnerability of recently-established forests poses a risk to the carbon sink dynamics in Europe, which is mainly dominated by regrowing forests (Pugh et al., 2019) and where the first signs of carbon saturation are already visible (Nabuurs et al., 2013). Furthermore, both recently and old-pruned pollards exhibited lower synchrony compared to recently-established forests. The practice of pollarding is known to enhance tree stability and vigor (Camarero et al., 2022; Olano et al., 2023) and is likely responsible for the reduction in growth synchrony observed in pollarded trees.

The results obtained also support our second hypothesis, as land- and forest-use legacies with greater forest structural diversity are leading to reduced tree growth synchrony in response to climate change. Different drivers have been proposed to unravel why trees may respond differently to climate depending on past land- and forest-use, ranging from alterations in biomass (i.e. structural overshoot, Jump et al., 2017), in wood density (Alfaro-Sánchez et al., 2019) or in ectomycorrhizal communities (Correia et al., 2021; Mausolf et al., 2018). Our results suggest the key role of forest structural diversity in how anthropogenic legacies modulate forest vulnerability to climate change. Increasing tree growth synchrony with decreasing tree size heterogeneity could be due to intraspecific resource partitioning among different tree sizes, although this seems unlikely given the shallow root system and strong competition for light in beech forests (Packham et al., 2012). Thus, age- and size-specific responses to climate are more likely to be responsible for the observed lower synchrony (Day and Greenwood, 2011). This lower synchrony may increase forest resilience by increasing individual-level variability in response to climate (Clark et al., 2012).

The importance of tree size heterogeneity as a key driver of tree growth synchrony also has implications for community ecology, as increased synchrony can lead to greater intraspecific competition and affect species coexistence (Clark, 2010). Additionally, our study underscores the importance of conserving old-growth forests with diverse tree sizes, as they play a vital role in mitigating the adverse impacts of climate change on tree growth synchrony. This finding holds particular relevance for Europe, where old-growth forests are exceedingly rare (Sabatini et al., 2018). Although our results showed that forest structural diversity explained a large part of tree growth synchrony variance, other variables (e.g. ectomycorrhizal communities) may also affect growth synchrony, suggesting that legacy effects might affect to different forest properties that can act synergistically in modulating the impact of climate change on tree growth.

Future studies could build on our findings by incorporating the geographic or vertical position of trees into analyses of growth-climate sensitivity. For example, investigating whether growth synchrony differs between neighboring trees and those farther apart could provide valuable insights into the role of competition or facilitation in shaping growth responses to climate. Additionally, our approach combined with finer-scale climatic data might help clarify the influence of microhabitats or microclimates on growth-climate sensitivity. Expanding the geographic scope of the study to include other forest types and regions would also be useful in determining whether the relationships between tree growth synchrony, size heterogeneity, and climate change are consistent across various ecological and climatic contexts, thereby deepening our understanding of the mechanisms underlying the observed patterns.

Our results show key indications for management strategies to adapt forests to the increasing impacts of climate change. Specifically, recently-established forests could be handled by applying uneven-aged

management options to increase forest structural diversity and reduce tree growth synchrony (Lafond et al., 2014). Increasing forest structural diversity could also decrease tree mortality and enhance carbon sequestration by improving light use efficiency (Ma et al., 2023; Ray et al., 2023) and promote biodiversity by expanding the number of available niches (Heidrich et al., 2020). Furthermore, recovering tree pollarding—by reintroducing pruning to old pollards or by creating new ones—and associated wood pastures (i.e. open forests with a grazed understory (Bergmeier et al., 2010)) could bring additional benefits beyond reducing tree growth synchrony, such as decreased inter-individual tree competition, fostering the high biodiversity characteristic of these ecosystems and promoting the compatibility of livestock activities with forest-use (Sjölund and Jump, 2013).

CRediT authorship contribution statement

Asier Herrero: Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Enrique Andivia:** Writing – review & editing. **Julián Tijerín-Triviño:** Writing – review & editing, Data curation. **Miguel A. Zavala:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization. **Paloma Ruiz-Benito:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Jaime Madrigal-González:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Julen Astigarraga:** Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Joaquín Calatayud:** Writing – review & editing, Validation, Supervision, Software, Methodology, Investigation, Formal analysis, Conceptualization.

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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122505.

Data availability

Data and code used for this manuscript are openly available in Zenodo at https://doi.org/10.5281/zenodo.14576849

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