



The ecological scale mediates whether trees experience drought legacies in radial growth



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ABSTRACT

The impact of lag effects produced by disturbances on primary production has been a major concern among ecologists during the last decade. Sudden and extreme climatic events are imposing drastic reductions in radial growth of trees as evidenced in tree-rings series. Dendrochronological samples are obtained at tree level but analyzed at an aggregated scale (i.e., mean chronologies), although aggregating tree-ring chronology on a regional scale may reduce the possibility of studying the variability of individual tree response to drought, by amplifying the average population response. Here, we conducted experimental research in which 370 trees of 5 species were analyzed to assess the potential statistical and scaling issues that may occur when using regression-based methods to analyze ecosystem responses to disturbances. Drought legacy effects were quantified using individual and aggregated scales. Then, lag effects were validated using confidence and prediction intervals to identify values falling outside the certainty of the climate-growth model. Individual scale legacy effects contrasted with confidence intervals were commonly distributed across species but were scarce when compared with prediction intervals. The analysis of aggregated scale legacies detected significant growth reductions when validated using prediction intervals; however, individual scale legacy lag effects were not detected. This finding directly contrasts the results obtained when using an aggregated scale. Our results provide empirical evidence on how aggregating ecological data to infer processes that emerge from an individual scale can lead to distorted conclusions. We therefore encourage the use of individual based statistical and ecological procedures to analyze tree rings as a means of further understanding the ecosystem responses to disturbances.

1. Introduction

Impacts of droughts on forests are affecting the carbon cycle beyond the disturbance itself (Schwalm et al., 2017) and will continue to increase in the coming decades (Spinoni et al., 2018). In light of this climatic scenario, some researchers are using dendrochronology to study the negative impact of climatic disturbances on tree growth as it is easy to obtain long time-series using tree cores (Lloret et al., 2011; Anderegg et al., 2015; Peltier et al., 2016). This technique is usually based on the aggregation of tree-ring width series to quantify mean growth as a measure of forest stand performance; thus, neglecting the role of individual trees as the actual response units. However, while there are indications that correlations between climate and growth may appear different when tested on an individual scale (Carrer, 2011), the examination of drought disturbances remains unexplored from the perspective of individual trees (Peltier and Ogle, 2020). This ecological,

individual-based approach could open new venues to address the lagged effects of tree growth on the terrestrial carbon cycle (Lee et al., 2021).

The impact of extreme climatic events on productivity is frequently studied under the assumption that such disturbances are so intense that they lead to a sustained and anomalous low growth episode during the immediate post-disturbance period (Sala et al., 2012). The ecological memory, i.e., the intrinsic capability of biological systems to be conditioned by past states, is the main proposed effect by which post-disturbance tree performance can appear undermined (Klesse et al., 2022). Various physiological and mechanistic processes supporting biological memory have been proposed. Sudden loss of plant water potential in the root-to-leaf could lead to drought-induced cavitation (Feng et al., 2021), affecting the recovery of the hydraulic transport after severe stress episodes. Additionally, the role of nonstructural carbohydrates (NSC) could similarly be claimed to mediate biological memory. Stem growth appears reduced when NSCs are reallocated to sustain leaf

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photosynthetic activity under stressful conditions (Huang et al., 2021). Furthermore, leaf area losses produced by droughts could derive to reduced stem xylogenesis and NSCs decline (Schönbeck et al., 2018). Pervasive decline in forest growth also leads to lagged impacts on carbon cycle because of decoupling between biological and climatic processes (Sippel et al., 2018). Soil moisture stress mediates canopy carbon assimilation, being able to inhibit photosynthesis not only during droughts and heatwaves, but days after (Desai, 2014).

In the face of such environmental stress, there is still a lack of consensus on how lag effects should be addressed although many methodologies have been proposed (Lemoine, 2021). Focusing on dendrochronology, the standard practice is to examine these disturbances using an aggregated scale. Conventional methods often require a somehow arbitrary reference period to compare the growth experienced before, during and/or after a disturbance (Lloret et al., 2011). Others rely on the comparison of pre- and post-disturbance attributes using long-term means or linear models during a given period to avoid such complications (Griffin-Nolan et al., 2018). Among the latter, legacy effects were defined as the long-lasting reduced growth that severe droughts cause in trees (Anderegg et al., 2015). This process comprises the fit of a climate-growth model, avoiding the handicap of determining a reference period, and the quantification of residuals between predicted values obtained using prewhitened growth series (series free of autocorrelation) and the observed values encompassing temporal autocorrelation. Thus, this approach allows to examine the impact of a drought based on two elements: the magnitude or intensity of growth reduction and the temporal span during which legacies are present. These attributes of legacy effects may vary depending on factors such as the wood anatomy and the climatic conditions. Stronger effects have been found in species with non-porous wood anatomy rather than in porous anatomy (Anderegg et al., 2015; Huang et al., 2018; Gazol et al., 2020) probably due to the cheapest and comparatively less dense xylem of gymnosperms that may confer less cavitation resistance (Brodrribb et al., 2012); but also, the opposite pattern has been described (Kannenberg et al., 2019a). The use of alternative proxies dependent of wood architecture known to correlate differently with climate (e.g., wood density, water use efficiency, vessel area) would help to disentangle how drought legacies operate from an anatomical and physiological based approach (McCarroll and Loader, 2004; Björklund et al., 2019; Olano et al., 2022). Furthermore, legacies have been proposed to be contingent on environmental humidity since drought-prone forests suffer more profound impacts (Anderegg et al., 2015; Gazol et al., 2020; Klesse et al., 2022). Legacies in larger ecological scales, e.g., NDVI index, are less frequent and shorter than those found in secondary growth under the hypothesis that trees allocate carbohydrates to restore leaf and canopy damages caused by droughts instead of stimulating woody tissue production (Kannenberg et al., 2019b; Gazol et al., 2020). This decoupled response of tree traits to abrupt disturbances suggests that woody plants can minimize drought legacies by compensatory mechanisms (Huang et al., 2021); thus, the presence of legacies can be contingent on the compartment and/or scale examined.

The aggregation of biological data to infer processes known to arise from a different scale has been a standard in many ecological disciplines (Schneider, 2001; Chave, 2013), and dendroecology is not an exception. The usual practice for assessing tree growth is to use mean chronologies (Fritts, 1976; Speer, 2010). To do this, individual-scale growth series are detrended and averaged into mean values representative of a geographical area. The purpose of this technique is varied and can be used, for example, to remove long-term trends associated to growth variability and forest dynamics. In addition, it is carried out to maximize the influence of climatic elements on secondary growth (Cook and Kairiukstis, 1990). Accordingly, climatic correlations observed at tree scale may differ from those found on an aggregated scale (Carrer, 2011; Trouillier et al., 2018). Bearing in mind such evidence, it is worth considering whether the statistical artifact produced in averaging measurements may interfere in our

understanding of ecosystem functioning.

The study of ecological disturbances using regression-based methods, such as legacy effects, is not absent from statistical issues (Lemoine, 2021; Klesse et al., 2022). For example, the usual procedure to check the “significance” of legacy effects is carried out by testing if the values observed fall outside of the 95% Confidence Interval (CI) of the fitted model. This raises the problem that the number of significant legacy effects increases according to the sample size, and with it, the probability of committing type I errors. This concern can be avoided by using prediction intervals (PI), which are independent of sample size (Lemoine, 2021). This trouble was previously raised (Kannenberg et al., 2020), but it remains unexplored in the literature in relation to legacy effects until now. In this experimental work, we aim to test a possible scaling effect of drought legacy effects from the perspective of two ecological scales: individual and aggregated. Moreover, our fieldwork favored the selection of each tree within sampling plots instead of sampling only the dominant trees to avoid magnifying growth responses to climate (Mérian et al., 2013) since these trees suffer the most during droughts (Bennett et al., 2015). With this in mind, we assessed the impacts derived from extreme droughts on individual tree growth series and the mean chronologies of five species with contrasting biogeographical character co-habiting in a drought-prone Mediterranean mountainous environment and subject to turning into a drought hot-spot (Spinoni et al., 2020). The validation of legacy effects was conducted using confidence intervals as well as prediction intervals. We hypothesize that (i) the magnitude of drought legacies computed on an individual-level is overall less pronounced than that of an aggregated-scale. This should be true due to a possible overmagnification of the role of climate on models using mean-chronologies and by the loss of growth variability that results from averaging processes. If a mismatch between individual- and aggregated-scale legacies is found, selection of the methodology protocol will be critical to assess lagged effects on forests and hence improve the estimation of carbon fluxes after severe droughts. In addition, we hypothesize that (ii) the number of significant legacies will be smaller if validated using prediction intervals instead of confidence intervals.

2. Materials and methods

2.1. Study area

The study area was located in the central region of the Sistema Central Mountain range (Sierra de Gredos regional park, Castile and León, Spain) (Fig. 1a). The Sistema Central divides the main Iberian Peninsula plateau into two parts in a west-east direction, providing cold and humid conditions on the northern slopes. Such conditions allow the presence of tree species of contrasting biogeographical character: Eurasian and temperate species (*Pinus sylvestris* and *Castanea sativa*) and Mediterranean species (*Pinus nigra*, *P. pinaster* and *Quercus pyrenaica*) (Fig. 1a, Table 1). The study area comprises the gentle slopes of the Sierra de Gredos which is configured by multiple bedrock rivers originated in glacial, upland lakes. Other woody species representative in the area are *Betula alba* in the mountain tops, and the riverine *Salix* spp., and *Alnus glutinosa*. Most common understory species are *Frangula alnus*, *Daphne gnidium*, *Sambucus nigra*, *Sorbus aucuparia* and *Cytisus* spp. (more information about the vegetation and habitats of the study area can be consulted in the archives of the European Habitats Directive (EU, 1992)). The local climate presents mean annual rainfall values of 474 mm and an average annual temperature of 11.4 °C during the 1950–2020 period as shown by the gridded observational dataset for precipitation, temperature, and sea level pressure in Europe (E-OBS v23.1e; Cornes et al., 2018; Supplementary Material Fig. S1) and is characterized by dry-warm summer conditions emblematic of Mediterranean climates that are expected to increase in severity and frequency in the upcoming decades (Spinoni et al., 2020). The substrates are primarily comprised of granite whereas the soil is represented predominately by cambisols.

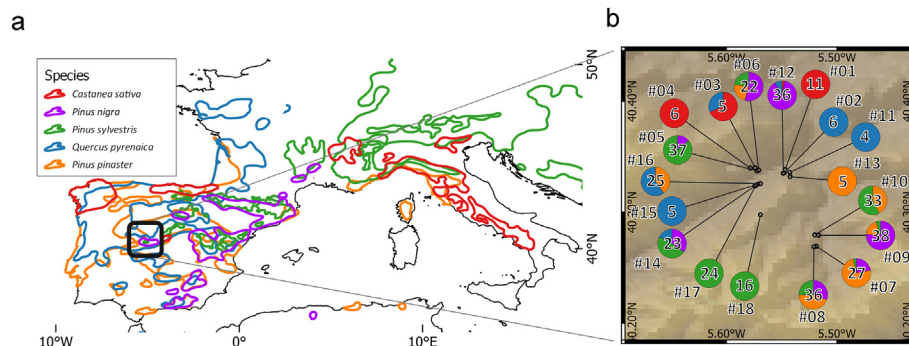


Fig. 1. (a) Map showing the distribution range (Caudullo et al., 2017) of the five tree species of interest and the study area. (b) Detail map with the location of sampling plots (points), plot identification (# number) the number of cores used for analysis (numbers inside pie charts) and its relative specific composition (pie charts).

Table 1

Descriptive information about geographic conditions of the sampling plots and the adult tree (DBH ≥ 5.00 cm) population. Elevation (meters above sea level), aspect (cardinal direction), estimated average age using a common approximation (Duncan, 1989) (years), mean Diameter at Breast Height (DBH) \pm standard deviation, mean Ring Width (RW) \pm standard deviation of the cores employed in the legacies analysis, and growth series intercorrelation (R^2) of sampled trees as indicated in COFECHA output (Holmes, 1983). EPS (expressed population signal) of mean chronologies was derived from dplR R library (Bunn, 2010).

Plot level descriptives							Mean chronology descriptives	
Plot	Elevation (m a.s.l.)	Aspect	Mean age (years)	Mean DBH (cm) \pm SD	Mean RW (mm) \pm SD (1980–2015 period)	Series intercorrelation (R^2)	Species	Expressed Population Signal (EPS)
#01	1040	–	67	33.67 \pm 17.35	1.45 \pm 0.60	0.626	<i>P. nigra</i>	0.989
#02	1080	NW	34	13.20 \pm 8.75	1.32 \pm 0.96	0.612	<i>P. pinaster</i>	0.989
#03	1115	NE	45	28.57 \pm 11.70	3.25 \pm 1.76	0.547	<i>P. sylvestris</i>	0.988
#04	1145	SE	45	24.59 \pm 13.23	2.11 \pm 1.51	0.786	<i>C. sativa</i>	0.984
#05	1090	SE	60	30.23 \pm 7.15	1.67 \pm 1.00	0.727	<i>Q. pyrenaica</i>	0.967
#06	1095	SE	52	32.43 \pm 14.81	3.58 \pm 1.40	0.668		
#07	1185	S	60	33.83 \pm 12.04	2.57 \pm 1.50	0.669		
#08	1310	S	61	30.41 \pm 8.62	1.46 \pm 0.92	0.682		
#09	1190	E	63	32.52 \pm 6.59	1.60 \pm 0.99	0.712		
#10	1270	E	62	23.93 \pm 7.31	1.17 \pm 0.70	0.670		
#11	1075	N	33	15.10 \pm 10.59	2.68 \pm 1.27	0.537		
#12	1080	NW	48	22.27 \pm 8.08	2.68 \pm 1.73	0.722		
#13	1200	W	33	20.31 \pm 11.06	3.89 \pm 2.63	0.673		
#14	1090	W	47	19.69 \pm 8.79	2.91 \pm 1.60	0.525		
#15	1085	–	39	14.84 \pm 9.59	3.05 \pm 1.79	0.505		
#16	1075	W	53	20.73 \pm 14.84	2.20 \pm 1.57	0.525		
#17	1090	NW	58	21.31 \pm 4.93	1.44 \pm 0.97	0.691		
#18	1440	–	44	17.28 \pm 4.81	2.59 \pm 1.72	0.647		

2.2. Sampling design and data collection

In total, 18 sampling plots of 900 m² size were established, ranging from 1075 to 1440 m a.s.l. and encompassing diverse terrain slope exposures, in forest stands where silvicultural practices were not detected (Fig. 1b). Living trees were identified according to the species and categorized as adults when the Diameter at Breast Height (DBH) was ≥ 5.0 cm. Up to 45 adult trees per plot were sampled by extracting one core per tree perpendicular to the maximum slope using Pressler increment borers (Häglof, Sweden) at a height of 0.3–0.4 m above the ground to record as many rings as possible (Veblen, 1992). During this process, we first selected less abundant species to give preference to diversity rather than abundance. Samples presenting signs of compression/reaction wood were discarded from further analysis. Increment cores were mounted and sanded following the procedure established by Stokes and Smiley (1996) and scanned at 2,400 dpi resolution (Perfection V550, Epson, Japan). We carried a first visual crossdating using skeleton plots (Speer, 2010) on stereo microscope (LanOptics® model 250LED). Then we measured tree-ring widths with a 0.01-mm resolution on the scanned JPG images using the software Coorecorder 7.6 (Cybis, Sweden). After a statistical cross-dating (Table 1) using Cofecha (Holmes, 1983), a total of 370 trees of age ≥ 35 years were selected and analyzed (Table 1): 103

P. nigra, 77 *P. pinaster*, 119 *P. sylvestris*, 29 *C. sativa* and 42 *Q. pyrenaica*. EPS values showed an appropriate common signal among samples of a mean chronology (Table 1). All cores were collected between March 2017 and November 2019.

Tree-ring series were detrended and converted to tree-ring indices (RWI) using consecutively a negative exponential model and a cubic smoothing spline ($f = 0.5$, wavelength = 2/3 of series length) using the dplR R library (Bunn, 2010; R Core Team, 2019). Double standardization is necessary to ensemble mean chronologies composed by trees of different cohorts since negative exponential models can remove noise associated to ontogeny growth patterns characteristic of young trees and cubic splines remove the noise recorded in old trees subject to forest dynamic processes and tree competence (Helama et al., 2004; Sangüesa-Barreda et al., 2019). Avoiding the negative exponential detrend using only a cubic smoothing spline of wavelength fixed to 24 years resulted in similar legacies results (Supplementary Material S2). In addition, the application of autoregressive models to the RWI series allowed us to obtain pre-whitened residual series (Residual-RWI). This step was implemented using the “Ar” option in *detrend.series* function of dplR R library. This process was applied to individual growth series and served to assemble mean-chronology series for each species (Fig. 2b).

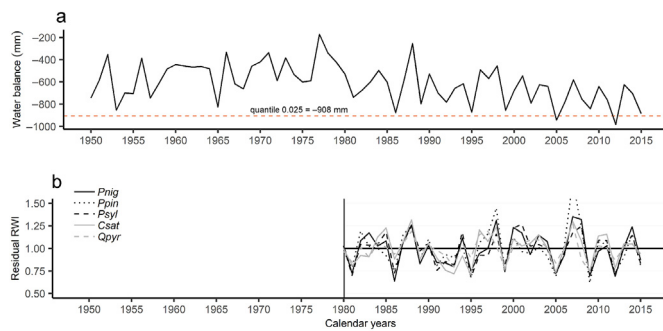


Fig. 2. Time series of (a) Water Balance showing the drought threshold (dashed line); and (b) mean Residual-RWI individual series. *Pnig*: *Pinus nigra*, *Ppin*: *Pinus pinaster*, *Psyl*: *Pinus sylvestris*, *Csat*: *Castanea sativa* and *Qpyr*: *Quercus pyrenaica*.

2.3. Climatic data

We assessed water balance as a climatic aridity proxy during the hydrological year:

$$\text{Water Balance} = P - PET \quad (1)$$

where P and PET represent the sum of monthly precipitation and potential evapotranspiration respectively from September of the previous year to August. PET was computed as the modified Hargreaves equation (Droogers and Allen, 2002) using the *hargreaves* function of the R SPEI package (Beguería et al., 2014) and monthly averages of minimum and maximum temperatures, precipitation and external radiation estimated from the latitude.

All climatic variables were downloaded from E-OBS v23.1e (<https://surfobs.climate.copernicus.eu/>, Cornes et al., 2018) and averaged from daily to a monthly scale. This gridded data provides interpolated climatic values derived from observations of meteorological stations at a 0.1-degree resolution. Local climate is highly correlated with the 3 closest long-term meteorological stations (located about 100 km away) from which E-OBS computes the interpolation and therefore supports its use here (Hernández-Alonso et al., 2021). We selected the nearest grid of each sampling plot to compute water balance.

2.4. Data analysis

To identify extreme dry years, we defined drought events as those years in which Water Balance was inferior to the 0.025 quantile. The region below this threshold corresponds with the lowest 2.5% part of a distribution and depicts anomalously dry years. After examining the entire climatic dataset available from 1950 to 2015, the drought threshold resulted in -908 mm and, therefore, the selected years were 2005 and 2012 (Fig. 2a).

We fitted linear mixed-effects models for each tree species differently using the function *lme* of the nlme R library (R Core Team, 2019; Pinheiro et al., 2021) in the case of individual-level tree ring measurements. The model can be written as follows:

$$Y_{ij} = \alpha + \alpha_j + \beta (\text{Water Balance}_{ij}) + \varepsilon_{ij} \quad (2)$$

where Y_{ij} is residual-RWI of the tree i and year j , α is the intercept, α_j is the random intercept of tree individual/sampling plot nested effect, β is the vector of general slopes, $\text{Water Balance}_{ij}$ is the vector containing fixed effects, and ε_{ij} is the error.

Linear models were fitted with *lm* R core function at the aggregated (mean-chronology) level. This model can be written as follows:

$$Y_j = \alpha + \beta (\text{Water Balance}_j) + \varepsilon \quad (3)$$

where Y_j is residual-RWI of year j , α is the intercept, β is the vector of general slopes; Water Balance_j is the vector containing fixed effects, and ε is the error.

Specifically, we modelled Residual-RWI using Water Balance as a covariate during the period covering 1980 to 2015. We assumed a stationary response of growth as this period is < 60 years (Wilking et al., 2020). Residual-RWI was transformed into a logarithmic scale to achieve the normal assumptions of linear models when necessary. The suitability of the drought variable was tested by comparing Akaike's Information Criterion corrected for small sample sizes (AICc) of the fitted models with their equivalent null models (ΔAICc , Burnham and Anderson, 2004). A null model was assembled by removing the drought variable but keeping the random structure intact.

Inspired by Anderegg et al. (2015), drought legacy effects were calculated at the individual scale and at the mean-chronology scale as the departure of the observed RWI from the expected Residual-RWI predicted in linear models. Legacy effects were examined for 1–3 years after events. To distinguish legacy values from random, we performed two contrasting methods. First, we computed Superposed Epoch Analysis (SEA) in a time-window encompassing 3 years before and after the drought events and considered a significant drought legacy when values were lower than the bootstrapped 95% Confidence Interval (CI) level threshold. Second, we computed Prediction Intervals (PI) of the models, where legacies were considered significant when inferior to 95% PI.

3. Results

Mixed models fitted with the drought variable presented lower AICc values than null models (Table 2). Regarding individual-scale models, pine species growth was more dependent on water balance than that exhibited by the broadleaved species, as shown by the ΔAICc scores. Consequently, goodness of fit varied from $R^2 > 0.3$ in the case of *P. nigra*, *P. pinaster* and *P. sylvestris*, to $R^2 < 0.3$ in *C. sativa* and *Q. pyrenaica*. Concerning aggregated-scale, the species more influenced by the drought variable was *C. sativa* followed by *P. nigra* and *P. pinaster*. Additionally, these models showed an enhancement of the explanatory power ($R^2 > 0.4$ for all species) when compared with the individual scale.

Legacy effects at the tree level resulted above and below zero at the same frequency for all species during 1–3 years after drought events (Fig. 3). About 10%–20% of the individuals suffered significant negative legacies using bootstrapped 95% CI after disturbances, except for *P. pinaster* and the second drought episode of *Q. pyrenaica*, where lower than 10% of individuals showed significant negative legacies. None of the individual legacies were outside 95% PI, except for 2 cases identified in *P. sylvestris*. Similarly, in most of the cases the averaged individual-level legacies were placed in the region of positive values. On the contrary, when negative, the CI around the individual-level averaged legacies overlapped the non-negative region of legacies (Fig. 3) as seen in *P. nigra* (2005 drought), *P. sylvestris* (2012 drought) and *Q. pyrenaica* (2012 drought). In all species and drought events, the averaged individual legacies were situated entirely within the 95% PI derived from the mixed models, indicating a total absence of drought lagged effects on secondary growth.

The legacies examined using the aggregated-scale proxy, that is mean chronologies, differed from those shown at the individual-level. All legacies were inferior to the lower 95% PI limit due to prediction intervals were totally placed in the positive region (Fig. 4). Significant negative legacies were common during the next year following the first drought (*P. nigra* and *P. sylvestris*) and widespread in all species in the first year after the second dry drought. In addition, negative legacies were more profound after the second drought, as determined by the smaller legacy values. However, attending to the 95% CI, none of the legacies could be considered significant since they were not placed outside the inferior bootstrapped 95% CI.

Table 2

AIC comparisons between models fitted with the drought variable (WB: Water Balance) and their corresponding null models on the individual (tree) and aggregated (mean-chronology) scales. Goodness of fit is represented by the marginal and conditional coefficient of determination (R^2) that characterizes the variance explained by the entire best model.

Scale	Species	<i>P. nigra</i>	<i>P. pinaster</i>	<i>P. sylvestris</i>	<i>C. sativa</i>	<i>Q. pyrenaica</i>
Individual	AICc _{WB model}	−4850.80	−3443.39	−4773.23	−1762.17	−2592.80
	AICc _{null model}	−3973.91	−2843.06	−4079.99	−1559.09	−2394.46
	ΔAICc	876.90	600.30	693.20	203.10	198.30
	conditional R^2 _{WB model}	0.41	0.35	0.31	0.20	0.14
Aggregated (Mean-chronology)	AICc _{WB model}	−33.323	−39.146	−38.070	−36.622	−66.158
	AICc _{null model}	−12.657	−18.549	−20.494	−13.403	−48.109
	ΔAICc	20.666	20.597	17.576	23.219	18.049
	marginal R^2 _{WB model}	0.466	0.465	0.419	0.5017	0.426

4. Discussion

This study demonstrates that the legacy effects of drought in tree-ring widths are likely to depend on the ecological scale used to assess their response and on the statistical test used to assess their response significance. At the tree scale, droughts did not have a clear impact on the individual growth of trees since legacy effects were found to be positive as often as they were negative. When negative, legacies were inside 95% PI, but they were found to be significant according to the bootstrapped 95% CI. Furthermore, in one of the five tree species analyzed (*P. sylvestris*), long-lasting growth reductions were observed during the first and second drought events that were outside both PI and bootstrapped CI (Fig. 3). This result may be specific to just one case as it is difficult to justify how a tree could suffer a legacy the third year after the disturbance and not during the previous time-lapse. At the mean-chronology scale, legacies occurred essentially in all species during the first year after the second drought; however, legacies that were outside the PI did not exceed the bootstrapped CI (Fig. 4). The scaling up of individual-level legacies to the population level showed results that were different to those found at the aggregated level. Averaged individual-scale legacy effects were only detected in *P. nigra* and *P. pinaster* during the first year after the second drought spell, but again they were inside the PI boundaries of mixed-effects models. This ambiguous result highlights the importance of choosing the statistical method to test the effects of legacies. Moreover, it symbolizes the importance and necessity of considering the scale at which dendrochronological data should be used to examine ecological processes (Peltier and Ogle, 2020).

Climatic site conditions seem to play an important role in modulating the recovery patterns of plant communities after disturbances at many levels, including the recovery speed in terms of tree radial growth (Gazol et al., 2017; Ibáñez et al., 2019). In addition, trees whose growth is more intensively controlled by climate are also less able to buffer the negative effects of severe droughts (Anderegg et al., 2015; Klesse et al., 2022). Recovery after a stress is dependent on how xylem is prepared to deal with droughts as well, what points to the ability of conduits to operate under some degree of negative pressure and hence to the drought induced cavitation resistance dependent of wood functional groups (Brodrribb et al., 2012). Our analyses show moderate correlations between climate and growth depending on tree species as indicated in previous results (Hernández-Alonso et al., 2021), where authors also concluded the use of E-OBS grid is satisfactory to correlate with local climate. However, correlations were contingent on the ecological scale at which they were computed since climate signal appeared magnified using mean chronologies in contrast with the results of individual-level models (Table 2). This effect is derived from the assembling of mean tree-ring growth chronologies that eliminate growth variability and maximize climate signals (Carrer, 2011). In consequence, the magnification of climate signals would lead to concomitant magnification of the impact of climatic lagged effects in methods that derive from residuals of climate-growth models. This artifact may explain why legacies are more common when computed with mean chronologies than in the scaled-up

individual legacies (Figs. 3 and 4). A climatic bias can be introduced even during the core sampling step, as standard dendroclimatological procedures intend to maximize climate-growth relationships by carrying out a deliberate sampling of trees and sites of preferred characteristics (Fritts, 1976; Cook and Kairiukstis, 1990; Mérian et al., 2013). Random sampling of trees in forest stands provides more accurate growth-climate predictions than relying solely on sampling dominant trees, which can lead to overestimations (Klesse et al., 2018). *Ad hoc* sampling designs may favor an artificial understanding of ecosystem processes since it may mask the real functioning of tree assemblages based on a biased portion of it (Carrer, 2011; Nehrbass-Ahles et al., 2014).

Local adaptation of species to stress seems to be a key factor to cope with the ongoing extreme climatic events (Valladares et al., 2014). Our models showed an impact-recover pattern in all species, more patent in pines, since observed growth during 1–3 years after drought events were higher than expected (Figs. 3 and 4). This supports the idea that gymnosperms' radial growth after drought disturbances is undermined probably because the resources derived to xylem reconstruction (Brodrribb et al., 2012; Huang et al., 2018). The buffering of post-drought growth reductions to cope with drought stress is a pattern characteristic of Mediterranean woodlands (Raúl Sánchez-Salguero et al., 2013; Sánchez-Salguero et al., 2018), but less evident in drought-sensitive species (Bose et al., 2020). The underlying causes for such differences in recovery are likely driven by physiological aspects, e.g., the flexibility to adjust their growth to the water availability during the start and/or end of the growing season (spring/autumn) (Gazol et al., 2020). Bimodal growth patterns in the wood formation during the year have been suggested to serve as a regulation mechanism to adjust growth in environments with intra-annual climatic constraints (Castagneri et al., 2018; Pacheco et al., 2018).

Individual-level and scaled-up individual legacies were placed inside the 95% confidence boundaries (Fig. 3). Drought legacy effects computed in regression-based methods rely primarily on the divergence of the predicted growth that a biological system should present according to a climate-growth model (Sala et al., 2012; Anderegg et al., 2015). To validate that growth reductions after discrete events are different from what is expected by chance, some authors have used bootstrapped CIs obtained by quantifying legacies during random years (Anderegg et al., 2015), and similarly, Superposed Epoch Analysis are also utilized (Haurwitz and Brier, 1981; Rao et al., 2019; Gazol et al., 2020; Klesse et al., 2022). However, the use of these methods produces an increasing number of significant legacies dependent on the sample size (Lemoine, 2021). This may be one of the reasons in support to the idea that the number of significant legacy effects validated with confidence intervals is less than those found in the work by Anderegg et al. (2015), who used the International Tree-Ring Data Bank (ITRDB; Grissino-Mayer and Fritts, 1997), to the work by Gazol et al. (2020) located on the Iberian Peninsula, and our work using a local approach. Moreover, legacies are absent at the individual-scale if contrasted with 95% PIs. Regarding mean chronology legacies, we could confirm its significance, however, it could be possible that the PIs may appear wider if more chronologies were

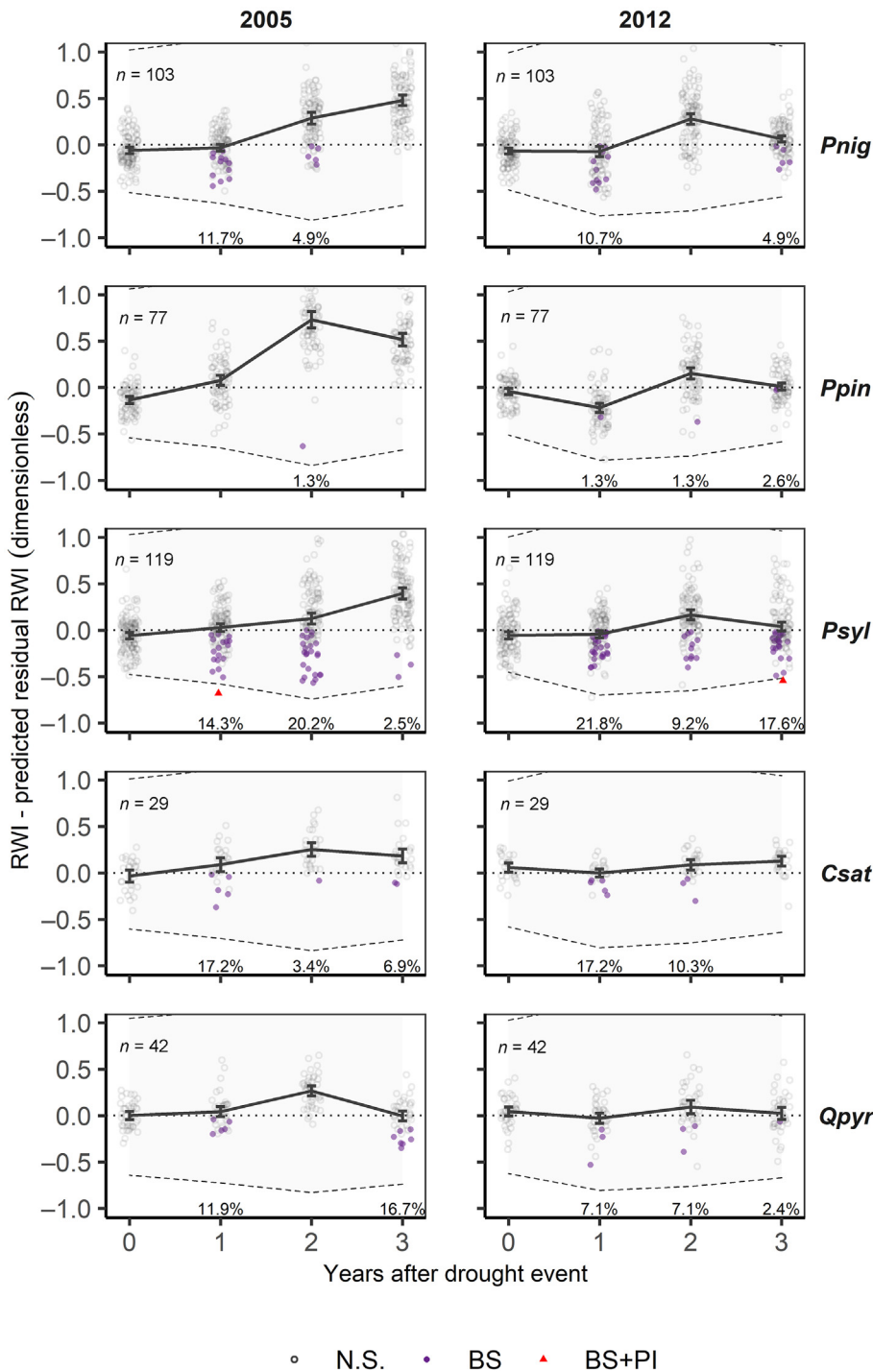


Fig. 3. Graphical representation of the individual-scale and averaged individual-scale tree growth legacies during the drought spells of 2005 and 2012. Points depict individual-scale legacies and their color shows bootstrapped non-significance (N.S.), bootstrapped CI significance (BS) and both bootstrapped CI and PI (BS + PI). The proportion of bootstrapped significant legacies is shown as percentages (%) based on sample size (n). Solid lines and error bars show average individual-scale legacies and the associated 95% confidence interval around the mean. *Pnig*: *Pinus nigra*, *Ppin*: *Pinus pinaster*, *Psyl*: *Pinus sylvestris*, *Csat*: *Castanea sativa* and *Qpyr*: *Quercus pyrenaica*. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

added to the model. The current use of PIs associated with model predictions is scarce or inexistent. For this reason, [Kannenberg et al. \(2020\)](#) pointed out that studies using regression-based methods seldom consider reporting such intervals. Nonetheless, prediction intervals should always be reported and used instead of confidence intervals when addressing individual responses, since it is the accepted measure of uncertainty in predictive inference ([Altman et al., 2000](#)). This detail is critical because a legacy effect is not a statistical parameter that can be estimated within a confidence interval, but rather a measure of how exceptionally an observation deviates from an expected value ([Lemoine, 2021](#)).

5. Conclusions

Aggregating biological data to analyze a process that operates at a different scale may draw distorted conclusions ([Clark et al., 2011](#)). In dendrochronology, cores are obtained at the tree level and thus represent individual measurements ([Galván et al., 2014](#)). However, they are traditionally analyzed at an aggregated scale: mean-chronologies ([Fritts, 1976](#)). Our results show a discrepancy between the individual-scale legacies, which are mostly non-significant, and mean chronology legacies, which are negative and significant. Averaging growth series

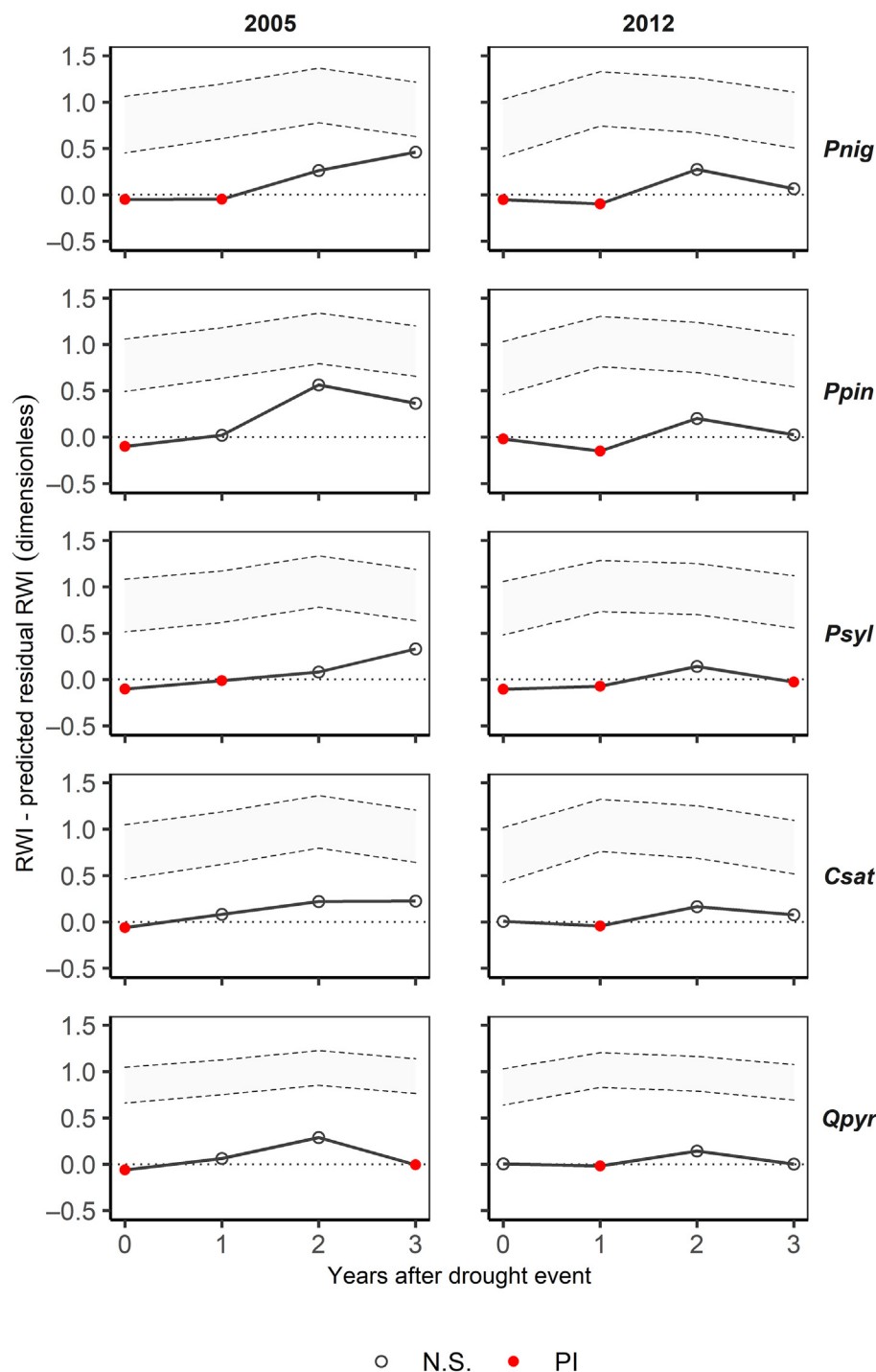


Fig. 4. Graphical representation of aggregated-scale (mean-chronology) tree growth legacies during the drought spells of 2005 and 2012. Points depict legacies and their color shows bootstrapped non-significance (N.S.) and negative legacies outside the lower 95% PI boundary). Note that legacies as computed here are the result of the difference between RWI and the predicted residual RWI. As RWI series are much smaller than the predicted residual RWI, legacies are displaced outside boundaries of 95% PI of the climatic-growth regression. *Pnig*: *Pinus nigra*, *Ppin*: *Pinus pinaster*, *Psyl*: *Pinus sylvestris*, *Csat*: *Castanea sativa* and *Qpyr*: *Quercus pyrenaica*. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

removes growth variability, which narrow the model's confidence and prediction intervals and amplify climate signals, what ultimately determines the magnitude and significance of lagged effects measured with regression-based methods. In addition, good practices in sampling collection should also involve the selection of trees of all tree cohorts to ensure the representativeness of the forest ecosystem. Furthermore, these results warn about the negative consequences of neglecting scale issues, as it can modify drastically the inference of our understanding of ecosystems. Given that mean chronologies represent statistical abstractions of reality and do not capture the biological variability (Mayr, 1989), an alternative for conceptualizing and describing processes at larger

ecological scales should be done by scaling up the individual responses of trees to disturbances. Hence, it is crucial to account for the whole variability of ecosystem processes to sustain a fruitful debate able to cope with the challenges imposed by global change on forest functioning.

Author contributions

Héctor Hernández Alonso: Conceptualization; Héctor Hernández Alonso: Formal analysis; Héctor Hernández Alonso: Resources; Héctor Hernández Alonso: Writing – original draft; Héctor Hernández Alonso, Jaime Madrigal González, Fernando Silla: Writing – review & editing.

Availability of data and materials

The original contributions presented in the study are included in the article, further inquiries can be directed to the corresponding author.

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. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2023.100112>.

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