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Tree growth response to drought partially explains regional-scale growth and mortality patterns in Iberian forests

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Abstract

Tree-ring data has been widely used to inform about tree growth responses to drought at the individual scale, but less is known about how tree growth sensitivity to drought scales up driving changes in forest dynamics. Here, we related tree-ring growth chronologies and stand-level forest changes in basal area from two independent datasets to test if tree-ring responses to drought match stand forest dynamics (stand basal area growth, ingrowth and mortality). We assessed if tree growth and changes in forest basal area covary as a function of spatial scale and tree taxa (gymnosperm or angiosperm). To this end, we compared a tree-ring network with stand data from the Spanish National Forest Inventory. We focused on the cumulative impact of drought on tree growth and demography in the period 1981–2005. Drought years were identified by the Standardized Precipitation Evapotranspiration Index (SPEI), and their impacts on tree growth by quantifying tree-ring width reductions. We hypothesized that forests with greater drought impacts on tree growth will also show reduced stand basal area growth and ingrowth and enhanced mortality. This is expected to occur in forests dominated by gymnosperms on drought-prone regions. Cumulative growth reductions during dry years were higher in forests dominated by gymnosperms and presented a greater magnitude and spatial autocorrelation than for angiosperms. Cumulative drought-induced tree growth reductions and changes in forest basal area were related, but initial stand density and basal area were the main factors driving changes in basal area. In drought-prone gymnosperm forests we observed that sites with greater growth reductions had lower stand basal area growth and greater mortality. Consequently, stand basal area, forest growth and ingrowth in regions with large drought impacts was significantly lower than in regions less impacted by drought. Tree growth sensitivity to drought can be used as a predictor of gymnosperm demographic rates in terms of stand basal area growth and ingrowth at regional scales, but further studies may try to disentangle how initial stand density modulates such relationships. Drought-induced growth reductions and their cumulative impacts have strong potential to be used as early-warning indicators of regional forest vulnerability.

Key words: basal area increment, drought vulnerability, national forest inventory, mortality, Spain, stand structure, tree growth.

Introduction

The recent increase in land surface temperatures and the occurrence of climate change-related extreme events, such as heat waves and droughts, have triggered forest growth reductions and mortality events in many temperate and Mediterranean regions (Allen et al. 2010, 2015). Notably, recent hotter droughts are characterized by increased air temperatures, which raise the atmospheric demand for water, exacerbating water storage and disrupting the functioning of trees by reducing their growth rates and limiting forest carbon uptake (Anderegg et al. 2015, Babst et al. 2019). Extreme droughts or their accumulated effect over time (Peltier et al. 2016) stress trees and deteriorate their vigour, ultimately triggering their mortality (Cailleret et al. 2017, Jump et al. 2017, Cailleret et al. 2019, DeSoto et al. 2020). Nevertheless, how all these processes scale-up from trees to forest dynamics and their influence on carbon and water fluxes at the ecosystem level, remains unresolved (Anderegg et al. 2016, Babst et al. 2018).

Radial growth is a reliable proxy of tree vigour and so it can be used to study the effects of climate change on trees (Marchand et al. 2019). Drought events can lead to abrupt growth reductions that can last for several years (Schweingruber 1986). However, how tree growth reacts to drought may depend on multiple factors (Anderegg et al. 2013), with longer and more severe droughts most likely resulting in greater growth reductions (Gao et al. 2018). In the worst case, intense droughts can induce to irreversible growth reductions preceding tree death (Sánchez-Salguero et al. 2012, Camarero et al. 2015, Cailleret et al. 2017, DeSoto et al. 2020). Even when trees survive drought, there might be lagged effects of water deficit (i.e. “drought legacy effects”), that tend to be stronger in regions where tree performance is strongly constrained by drought (Anderegg et al. 2015) as it is the case of the Mediterranean region (IPCC 2018). However, a recent study found that Mediterranean Spanish forests are resilient to recent droughts in terms of canopy greenness derived from satellite imagery (Khoury and Coomes 2020), pointing that different sources of information need to be combined in order to get more complete, long-term pictures of how forests respond to drought.

Tree growth sensitivity to drought also varies across tree populations, tree species, functional groups (i.e., gymnosperms, angiosperms), and forest biomes (Anderegg et al. 2015, Peltier et al. 2016, Gazol et al. 2017a, 2017b, D'Orangeville et al. 2018, Serra-Maluquer et al. 2019, Vilà-Cabrera and Jump 2019). Lagged effects on tree growth seem to be higher and last longer in gymnosperms than in angiosperms (Anderegg et al. 2015), probably because angiosperms have a more efficient hydraulic and leaf transpiration systems compared to gymnosperms (Brodribb and McAdams 2013). Furthermore, angiosperms and gymnosperms have different xylem traits in terms of wood anatomy and density, which results in different strategies to avoid drought-induced cavitation (Brodribb et al. 2010, Carnicer et al. 2013, Rosas et al. 2019). For instance, Gazol et al. (2018) found that gymnosperms from drought-prone Spanish regions presented more conspicuous drought-induced growth reductions and lower growth resistance; *sensu* Lloret et al. 2011 than angiosperms from wet, temperate areas. The sensitivity of tree growth to drought has important implications to understand the resilience capacity of forests (Lloret et al. 2011). However, reconstructions of forest growth using tree-ring records are affected by sampling biases related to the selection of representative and dominant individuals (Brienen et al. 2017, Alexander et al. 2018), and it remains unclear how tree-ring based responses to drought scale up to understand forest dynamics processes such as forest growth, ingrowth and mortality (Kannenberg et al. 2019).

Shifting dynamics in forest growth, productivity and mortality relies on the interaction between climate conditions, structure, and composition (Vayreda et al. 2016, Ruiz-Benito et al. 2017a). Most large-scale studies on forest dynamics take advantage of forest inventory data which provide tree-level information, gathered systematically and periodically at large spatial extents (Kunstler et al. 2016, Liang et al. 2016). It has been found that forest growth and aboveground carbon storage are strongly determined by variations in mean tree size, stand basal area and tree density (e.g. Gómez-Aparicio et al. 2011, Vayreda et al. 2012, Ruiz-Benito et al. 2014). Further, variations in tree size and stand density underlay competition from neighbours which in turn influence growth (Gómez-Aparicio et al. 2011, Lechuga et al. 2017; Condés et al. 2017) and modulate drought-induced mortality events (Jump et al. 2017). In this respect, drought can also impact forest growth and mortality rates by delineating demography and species distribution ranges (e.g. Benito-Garzón et al. 2013, Vilà-Cabrera et al. 2011, Changenet et al. 2021) and by controlling the carrying capacity of the stands (Bravo-Oviedo et al. 2018). However, forest inventories do not always provide long-term annual measures of individual tree growth, hindering the assessment of drought impacts on tree growth (e.g. Sánchez-Salguero et al. 2013, Serra-Maluquer et al. 2018). Therefore, the combination of tree-ring databases with forest inventory data allow distance-dependent comparisons (Dye et al. 2016), and provide complementary and valuable information of forest dynamics in response to drought (Biondi 1999, Sánchez-Salguero et al. 2013, Klesse et al. 2016, Evans et al. 2017, Etzold et al. 2019, Ruiz-Benito et al. 2020).

To quantify responses to drought from different data sources we take advantage of an extensive network of cross-dated tree-ring data (hereafter abbreviated as RWI-net; see Gazol et al. 2020) with increment cores from 16 tree species (**Appendix S1: Table S1**) sampled across the Spanish Iberian Peninsula, and of the Spanish National Forest Inventory (hereafter abbreviated as NFI) sampling tree and plot level data each km in forested areas. We aim to understand how the cumulative impact of droughts during the period 1981–2005 affected Spanish forests. We hypothesize that tree-ring vulnerability underlies forest responses to drought (i.e. growth, ingrowth and mortality). We expect the cumulative impacts of drought to be stronger in drought-prone regions and particularly in gymnosperm forests affecting radial growth as well as the growth, ingrowth, and mortality of NFI plots. In particular, we expect that: (i) RWI-net growth responses to severe droughts will display a stronger sensitivity in drought-prone regions, thus the cumulative impact of severe droughts will be stronger in arid than in milder sites, resulting in an spatially aggregated pattern of radial growth as well as in forest growth, ingrowth, and mortality; (ii) NFI growth changes will be strongly dependent on initial structure, particularly stand density and basal area, but concurrently NFI plots will display lower growth and potentially greater mortality in sites more severely impacted by drought, thus resulting in a spatial covariation between RWI-net and NFI growth responses; and (iii) RWI-net sensitivity to drought informs about forest vulnerability to drought, particularly in gymnosperms.

Material and Methods

Study area

The study covers the Spanish Iberian Peninsula and Balearic Islands (492,175 km^2; **Fig. 1**) which represents a transitional area between temperate and Mediterranean climates. In general, humidity decreases from the north to south and from the west to east due to the contrasting influences of the Atlantic Ocean and the Mediterranean Sea, which also affect seasonal precipitation regimes (Martín-Vide and Olcina 2001). Total annual precipitation in northern regions can reach up to 2000 mm, with maxima in winter and spring, whereas in the south eastern regions the total annual precipitation ranges between 250 and 300 mm, often with maxima in autumn. Air temperature decreases towards the northern regions and with elevation. Several Eurosiberian tree species find their southern distribution limit (rear edge) in mountain areas of the Spanish Iberian Peninsula (e.g., *Abies alba* Mill., *Fagus sylvatica* L., *Pinus sylvestris* L.*, Pinus uncinata* Ram.*, Quercus robur* L., *Q. petraea* (Matt.) Liebl.). Natural regenerated forests coexist with pine plantations which represent around 20% of the total forest area in Spain (FAO 2013).

Spanish National Forest Inventory (NFI)

To quantify changes in forest growth, ingrowth and mortality we used data from the second (NFI2; carried out in 1986–1996) and the third (NFI3; carried out in 1997–2007) Spanish National Forest Inventories (NFI), both of them established in the 80’s and continuously monitoring ever since the Spanish forests. The NFI consist of georeferenced, permanently established circular plots of 25-m radius systematically distributed on a 1-km^2 cell grid over forested areas (cf. Villaescusa and Díaz 1998). Inside each plot, each tree with a dbh > 75 mm and height > 1.3 m was mapped. The 25-

m radius plots are divided in sub-plots of 5, 10, 15 and 25 m long radii within which all trees with diameters at breast height (dbh) of 7.5-12.4, 12.5-22.4, 22.5-42.5 and ≥ 42.5 cm were measured, respectively. Each individual tree was also classified as dead or alive. Repeated measures over the same individuals are taken periodically (i.e., every ca. 10 years), which allows quantifying demographic changes such as forest growth, ingrowth, and mortality between the NFI2 and the NFI3. In this study, we excluded NFI plots that were completely logged or have been burnt by wildfires between consecutive inventories. Plots that were sampled in the third (NFI3) but not in the second (NFI2) inventory were also excluded. Forest growth was quantified as the increment in basal area (ΔBA, in m^2 ha^{-1} $year^{-1}$) of living trees between the two consecutive inventories (i.e., NFI2 and NFI3) divided by the number of years between inventories (**Appendix S1: Fig. S1a**). Forest ingrowth (R; in m^2 ha^{-1} $year^{-1}$) was quantified as the basal area of trees sampled in NFI3 but not in NFI2 divided by the number of years between inventories. Forest mortality (in m^2 ha^{-1} $year^{-1}$) was quantified as the sum of the basal area (-ΔBA) of the trees sampled as alive in NFI2 and dead in NFI3 divided by the number of years between inventories. All basal area calculations were done at the individual tree level (m^2 ha^{-1}) to account for the variable sampling radius plot (i.e. each NFI plot has four concentric sub-plots and the minimum tree size is different in each concentric sub-plot). The basal area at the plot level was calculated summing the basal area of each tree relative to hectare and, therefore, considering the concentric circle in which each tree was measured. With this method, we avoided biases in basal area calculations plots dominated by large of small tress, as it has been proved as an efficient and unbiased method for volume and basal estimation (Henttonen and Kangas 2015).

Drought data

The Standardized Precipitation-Evapotranspiration Index (SPEI; Vicente-Serrano et al. 2010, Beguería et al. 2014) was used to assess drought severity. We calculated 12-month long June SPEI values for the period 1981–2005 in each plot since this SPEI scale has been shown to be tightly related to tree growth in Spanish tree species (Pasho et al. 2011). To calculate SPEI, we used 1.1 km^2-gridded climatic data assembled at a weekly timescale (Vicente-Serrano et al. 2017). This high-resolution gridded dataset was based on values of daily mean temperature, sunshine duration, wind speed, relative humidity, and precipitation, all available from the Spanish Meteorological Agency (AEMET). All available datasets were homogenized and quality-checked prior to the estimation of gridded values (see Vicente-Serrano et al. 2017).

Bioclimatic variables were downloaded from the WorldClim data base (https://www.worldclim.org/data/bioclim.html) at a spatial resolution of 0.5 minutes. We focused on four bioclimatic variables that influence cumulative drought impacts on forests: mean annual temperature and precipitation (bio1 and bio12, respectively), and temperature and precipitation seasonality (bio4 and bio15, respectively).

Tree-ring data (RWI-net)

We used an extensive network of cross-dated tree-ring chronologies (RWI-net, see Gazol et al. 2018, Vicente-Serrano et al. 2020) of annually resolved tree-ring width series from 29 tree species sampled across Spain to quantify tree growth and responses to climate. For this study, we selected 16 (9 gymnosperms and 7 angiosperms, **Appendix S1: Table S1**) out of these 29 tree species. All 16 species were sampled in at least 2 populations across their distribution ranges (**Appendix S1: Table S1**). We only included chronologies spanning at least the period 1981–2005.

Each of the populations included in this study was represented by 10 or 12 dominant or codominant trees (Gazol et al. 2018). Trees were cored at 1.3 m using Pressler increment borers to obtain from 1 to 4 wood cores per tree. These cores were air dried, mounted on wooden grooves, and sanded until tree-rings were clearly visible, which allowed the visual cross-dating of the samples (Fritts 2001). The width of all tree-rings was measured to 0.01 mm resolution using a binocular microscope and measuring stands (Velmex, Lintab-TSAP). The COFECHA software was used to assess the accuracy of the visual cross-dating (Holmes 1983).

To construct robust mean site chronologies, tree-ring width measurements were processed following dendrochronological protocols (Fritts 2001). Individual tree-ring width measurements were detrended with a cubic smoothing spline with a 50% frequency response cutoff at 30 years. The observed tree-ring width measures were divided by the fitted values to obtain standardized ring-width indices. Finally, bi-weight robust means were used to average individual standardized ring-width series into mean site chronologies. Residual chronologies were obtained by pre-whitening each series (i.e., removing autocorrelation) prior to averaging. These site, standard and residual chronologies were scaled to have an exact mean of one for the period 1981–2005 in each population. These analyses were performed using the "*dplR*" library (Bunn *et al.* 2018).

Calculating drought impacts on tree growth and forest dynamics

To quantify the sensitivity of tree growth to drought, we selected the five most severe droughts that have affected each selected RWI-net population in the period 1981–2005 (**Fig. 1b** and **Appendix S1: Fig. S2)**. The 12-month long June SPEI values for the period 1981–2005 in each site were used for selecting droughts. Thus, drought years were selected for each site by considering the five years with the lowest SPEI values in that period.

Severe droughts were frequent across sites in 1986, 1994, 1995, 1999 and 2005 although other years such as 1992 were also considered dry in some populations (**Fig. 1b**, **c**). In general, these droughts corresponded to growth reductions (**Fig. 1c** and **Appendix S1: Fig. S2**) and have triggered extensive forest dieback in many sites across the Spanish Iberian Peninsula (Génova et al. 2012, Camarero et al. 2015, Gazol et al. 2018, Sánchez-Salguero et al. 2018).

To test how the cumulative impacts of drought affected the growth of the sampled RWI-net populations, we calculated drought-induced cumulative growth reductions (CDI, cumulative drought impact) as the summed impact of the selected droughts on growth of each population (**Appendix S1: Fig. S1b**). Drought impact was calculated as the difference between the mean growth during the period 1981–2005 and the observed growth during the drought year. Note that since the mean growth equals 1 this is equivalent to a z-score. Values greater than one indicate that growth during drought was greater than average and so they were truncated to zero (427 drought events: 26% of the situations). The cumulative impact of drought on growth was calculated as the summed values over the different droughts (**Appendix S1: Fig. S1b**). We used standard chronologies to quantify drought impacts and their cumulative effect because standard chronologies account for potential autocorrelative effects when two droughts occur consecutively (or in a relatively short period of time). Further, preliminary analyses showed that similar results were obtained when using either standard or residual chronologies (**Appendix S1: Fig. S3**).

To assess the relationship between plot level NFI-estimated growth, ingrowth and mortality, and the cumulative impact of drought on RWI-net growth estimations, we used a distance approach. For each NFI plot, we selected those RWI-net populations of the same species dominating the NFI plot (i.e. the species accounting for 60% of the basal area of the plot) that were located at a distance lower than 10 km (**Appendix S1: Fig. S1a**). Thus, for each NFI plot we considered the cumulative impact of drought of the RWI-net site located less than 10 km away to the NFI plot. Second, we quantified the number of severe droughts to which each NFI plot was exposed to by counting the number of droughts with stand growth reductions higher than 50% between NFI2 and NFI3. Severe droughts were defined as those having a SPEI lower than the selected threshold and growth reductions higher than 50% for the nearby RWI-net population (i.e. drought impact for the selected drought > 0.5; for further details see **Appendix S1: Fig. S1**). A total of 334 RWI-net sites with chronologies that covered the period 1981-2005 for the 16 species, were finally used. For 192 of these RWI-net sites, 1883 NFI plots were found at distances < 10 km (**Appendix S1: Table S1**).

Statistical analyses

We used spatial autocorrelation techniques to describe the patterns of the cumulative drought impacts observed in the RWI-net population and the growth, ingrowth, and mortality of the selected NFI plots. For this purpose, we used spline correlograms, which is a generalization of spatial correlograms (Bjørnstad and Falck 2001). For each variable, correlograms were calculated up to 200 km and the significance was estimated by generating a bootstrapped distribution (999 resamples). Finally, cross-correlograms were applied to estimate the spatial dependency between the cumulative drought impacts (RWI-net) and the observed growth, ingrowth, and mortality (NFI).

Autocovariate regression was used to study the effect of bioclimatic variation on cumulative drought impacts in the RWI-net populations (Dormann et al. 2007). This procedure relies on the inclusion of a spatial autocovariate as an additional explanatory variable into a linear model to account for spatial autocorrelation. Thus, we studied the effect of different bioclimatic variables while accounting for spatial autocorrelation in cumulative drought impacts. We fitted the full models using ordinary least square regression and evaluated them through the increase in the Akaike Information Criterion (ΔAIC) with respect to the model showing the lowest AIC, using model comparison and averaging to select the model and to assess the relative importance (Akaike relative weight) of each variable (Burnham and Anderson 2002).

To evaluate whether the occurrence of abrupt growth reductions in the corresponding RWI-net population correlates with forest growth reductions or enhanced forest mortality in NFI plots, we compared the forest growth (ΔBA), ingrowth (R) and mortality (-ΔBA) between plots that were exposed to different numbers of severe droughts. The Dunnett's modified Tukey-Kramer pairwise multiple comparison test (Dunnett 1980) was used to compare NFI plots in the neighborhood of the RWI-net populations displaying growth reductions in response to none, one or two droughts. Furthermore, we also compared if the occurrence of two severe droughts showed different impact depending on whether such droughts occurred in consecutive or separated years.

Autocovariate spatial regressions were also used to evaluate how cumulative drought impacts was related to changes in forest growth (ΔBA), ingrowth (R) and forest mortality (-ΔBA). We created models including RWI-net based cumulative drought impacts and other covariates that may influence changes in forest growth and structure and can be related with tree to tree competition. We tested the influence of the bioclimatic variables listed above, the mean dbh (mDBH, mm) of the trees from the second inventory (NFI2), as well as the basal area of the plot (BA, m^2 ha^{-1}) and the tree density (Dens, No. trees ha^{-1}) recorded in the second inventory (NFI2) and the minimum 12-month long SPEI to account for a metric of drought independent on growth. ΔBA, R and – ΔBA were log-transformed (log(x+1)) prior to the analyses. Furthermore, the explanatory variables were standardized prior to the analyses to facilitate the interpretation of their effect (Schielzeth 2010).

Separate models were created for gymnosperms and angiosperms. In the case of mortality, NFI plots in which mortality equaled zero were not included in the autocovariate regression analysis (around 60% were removed). However, these plots were considered for the spatial correlation and cross-correlation, and the Dunnett analyses.

All statistical analyses were performed in R 3.5.2 (R Core Team 2018). The “dplR” package (Bunn 2018) was used to calculate ring-width index (RWI) and mean site chronologies, the “raster” package to manage spatial data (Hijmans 2019), the “ncf” package (Bjørnstad, 2020) was used to calculate spline-correlograms, the “spdep” package (Bivand et al. 2013) was used for the autorregresive modelling. Finally, the “MuMIn” (Barton 2012) package was used to perform the multi-model selection.

Results

Cumulative drought impacts on growth prevail in dry regions, particularly for gymnosperms

We found a significant positive autocorrelation in the cumulative drought impacts on tree growth for gymnosperms (**Fig. 2**). For angiosperms, the spatial autocorrelation was not significant (**Fig. 2**), suggesting that the positive significant autocorrelation found when all sites are analyzed together is caused by the higher weight of gymnosperm forests. Along this, the cumulative impact of drought on tree growth was higher for gymnosperms than for angiosperms (**Appendix S1: Fig. S4**). The total annual precipitation was the main factor driving the biogeographical variation of cumulative drought impacts both for angiosperms and gymnosperms (**Fig. 2b** and **Table 1**). Cumulative drought impacts were more pervasive in dry regions, particularly in forests dominated by gymnosperms (mostly pine species) from the semi-arid southeastern Spain (**Fig. 2b**).

Drought decreased stand growth and increased mortality, especially for gymnosperms

We found a negative spatial cross-correlation between cumulative drought impacts on tree growth and stand growth (see magnitude of negative values in **Appendix S1: Fig. S5**). In other words, large radial-tree growth reductions in response to droughts in RWI-net populations converged with reduced stand growth in nearby NFI forests at distances up to 50 km (angiosperms) or 150 km (gymnosperms). This pattern was particularly evident in gymnosperm forests (**Appendix S1: Fig. S5**). Similar results were obtained when cumulative drought impacts on growth were cross-correlated with forest ingrowth, but no significant spatial cross-correlation was found between cumulative drought impacts on growth and nearby forest mortality either in angiosperms or gymnosperms (**Appendix S1: Fig. S5**). In agreement with this, the spatial correlation of forest growth and ingrowth was significant at distances up to 20-30 km, whereas the pattern in mortality showed less spatial autocorrelation and up to distances of 10-20 km (**Appendix S1: Fig. S6**).

Drought-induced severe growth reductions (i.e. higher than 50%) were more common in gymnosperms than angiosperms (*c.* 33% vs. 15% of the studied sites respectively). For angiosperms, two drought-induced severe growth reductions between NFI2 and NFI3 were not observed, whereas for gymnosperms they were observed in

17% of the sites studied (i.e. 297 forests). For angiosperms, forest growth and ingrowth were significantly greater near RWI-net populations not impacted by drought (**Fig. 3a,b**), while higher mortality rates in stands not impacted by drought were observed (**Fig. 3c**). For gymnosperms, the occurrence of one or two severe droughts caused strong reductions in forest growth and ingrowth (**Fig. 3a,b**), which were even stronger when the two droughts occurred consecutively (**Table 2**). A significant increase in mortality of gymnosperms was observed in forests impacted by two droughts (**Fig. 3c**) with no differences between the droughts occurring separated or consecutively.

Tree growth sensitivity to drought as a critical driver of forest dynamics, particularly for gymnosperms

Forest growth was significantly influenced by tree growth sensitivity to drought when covariates were not included in the model (**Appendix S1: Fig. S7**). In the case of mortality, this effect was significant for gymnosperms only. As expected, the effect of drought sensitivity was not the most important driver of forest changes in stand basal area when the climatic and structural covariates were included in the models (**Fig. 4** and **Appendix S1: Table S2**). Forest growth and ingrowth increased with in initial stand density and basal area (**Fig. 5a,b**), whereas these variables had disparate impacts on mortality (**Fig. 5c**). In general, forest growth decreased, and forest mortality increased with tree sensitivity to drought (i.e. accumulated growth decreases in response to drought; **Fig. 4** and **Appendix S1: Table S2**). The relationships between tree growth and forest changes in stand basal area were more important (i.e. significant in the case of growth and mortality) for gymnosperms than for angiosperms (**Fig. 4**, **Appendix S1: Table S2** and **Appendix S1: Fig. S7**).

Discussion

We found a spatial imprint in the cumulative impact of drought on tree growth and changes in forest stand basal area during the transition from the 20th to the 21st century in Spain. Severe droughts particularly impacted the gymnosperms from dry sites, highlighting the great sensitivity to drought of these species. Our results were obtained by using two independent datasets: an extensive tree-ring network (RWI-net) and permanent plot (NFI) data re-surveys covering from Atlantic to Mediterranean climates of the Spanish Iberian Peninsula. According to our main hypothesis, we found common signals of drought-induced tree growth on stand forest dynamics particularly for gymnosperms and dry regions. We also found greater forest growth reductions and mortality increases in the case of gymnosperms when tree growth reductions were strongly impacted by drought, as stated by our second hypothesis. Notably, these drought impacts were more evident in gymnosperms than angiosperms probably due to the more frequent distribution of gymnosperms in drought-prone regions, but also because of their higher representativeness in our dataset. Nonetheless, our third hypothesis was partially supported, stating that tree growth reductions determine forest growth and mortality patterns because initial stand conditions were the main factors determining changes in growth. Hence, we obtained a weak effect of tree sensitivity to drought on changes in stand basal area when the structural covariates were accounted for (see **Fig. 4**). Our study indicates that combining different sources of information (i.e., plot resurveys, NFI; and tree-ring widths, RWI-net), despite challenging, may provide valuable and complementary information on forests responses to drought across multiple spatial and temporal scales (see also Sánchez-Salguero et al. 2013, Zhang et al. 2017, Babst et al. 2018, Gazol et al. 2018, Kannenberg et al. 2019, Khoury and Coomes 2020, Ruiz-Benito et al. 2020). However, our results also evidence that site differences make difficult to obtain solid conclusions and, therefore, a complete picture on forest responses to climate change can be obtained from the Spanish National Forest Inventory and the quantification of "in situ" tree-ring widths samplings. This will also allow to determine how initial stand conditions such as density interacts with tree sensitivity to drought on modulating forest growth.

Convergence between tree growth sensitivity to drought and changes in forest stand basal area patterns

We found a positive tree-forest growth cross-correlation that could be related to a common climatic signal, which determines secondary growth both in tree ring (RWI-net) and forest inventory datasets (NFI). The cumulative impact of drought on tree and forest stand basal area growth were positively cross-correlated (**Appendix S1: Fig. S5**). However, the moderate magnitude of the correlation coefficients suggests a strong impact of local factors that can modulate tree sensitivity to climate and growth production (Monserud and Sterba 1996, Sánchez-Salguero et al. 2015) such as stand structure (Gómez-Aparicio et al. 2011), soil water holding capacity and nutrient availability (e.g. Manrique-Alba et al. 2017, Marchand et al. 2019). The moderate impact of drought-induced tree responses on forest dynamics was even clearer in the case of mortality, probably because local factors play a key role (e.g. tree-to-tree competition and soil moisture availability; Hartmann et al. 2018). This is particularly evident in the case of angiosperms, where we found lower mortality in forests impacted by drought. Given that many Iberian angiosperm forests are still in an early successional stage, self-thinning because of competition for space and light might be more important than drought on driving mortality patterns (cf. Astigarraga et al. 2020). However, we found no significant impacts of stand density on forest mortality in the case of angiosperms, suggesting that our capacity to explain changes in angiosperms mortality is more reduced.

We found greater drought-induced growth sensitivity in gymnosperms than angiosperms, which also resulted in a stronger spatial autocorrelation of drought impacts (**Fig. 2**). Our results agree with recent temporal trends in the Iberian forests suggesting increased mortality and reduced growth in gymnosperms when compared to angiosperms (Astigarraga et al. 2020), and it could be related to contrasting drought-avoidant and drought-resistant strategies that confers them contrasting vulnerability to drought (Greenwood et al. 2017, Ruiz-Benito et al. 2017b, Khoury and Coomes 2020). Furthermore, the increased sensitivity of forests dominated by gymnosperms could be strongly influenced by marked differences in their distributional patterns across Spain (**Fig. 1**). On the one hand, conifer forests studied cover the entire climatic range in the Spanish Iberian Peninsula (Costa et al. 2005), but a high proportion of gymnosperm-dominated forests are in the most arid regions of the Iberian Peninsula (Ruiz-Benito et al. 2012). On the other hand, angiosperms are more abundant in regions with mild, wet climatic conditions (see **Fig. 1**). Overall, the distribution of species along the water availability gradients of the Iberian Peninsula markedly influences both stand characteristics and forest productivity (Alberdi et al. 2010, Gómez-Aparicio et al. 2011, Vayreda et al 2012, Benito-Garzón et al. 2013). For example, this is reflected in the amplitude of the gradients in stand density covered in our study, which is longer in the case of angiosperms (Fig. 5).

Gradients in water availability may determine changes in angiosperms and gymnosperms productivity (Vayreda et al. 2012, Khoury and Coomes 2020) due to their impacts on stand density (Condés et al. 2017). However, the covariation between cumulative drought impact on tree and stand growth and ingrowth suggests that stand-level changes in stand basal area are partially modulated by drought-induced tree-level responses. Our results are in line with the greater sensitivity to drought of gymnosperms, also in terms of lasting drought legacies (Anderegg et al. 2015, Greenwood et al. 2017), which is also supported by their greater drought vulnerability (**Appendix S1: Fig. S4**). However, the spatial gradient in water availability can induce strong changes in growth responses to climate (Lebourgeois et al. 2012) and drought (Gazol et al. 2017a, 2017b, Sánchez-Salguero et al. 2015, 2018). The relatively frequent presence of drought-tolerant gymnosperms in the driest south-eastern Spanish Iberian regions (where droughts are more common and intense as e.g., *Pinus halepensis*) and the prevalence of productive angiosperms in the wettest regions (less impacted by drought, Gazol et al. 2018 and see **Fig. 1** and **Fig. 2**) might be determining the greater drought vulnerability in gymnosperms than angiosperms.

Drought-induced tree-level effects on stand growth, ingrowth, and mortality depend on drought frequency and functional groups

The frequency of severe droughts caused abrupt tree growth reductions (**Fig. 1b, c**) and, accordingly, nearby forests had lower growth rates than forests where no drought occurred (**Fig. 3**). Interestingly, drought-induced effects on forest growth and mortality were in general significant pointing to the convergence between RWI-net and NFI responses to drought. The impact of tree responses on changes in forest stand basal area might be due to the spatial characteristics of droughts, which can impact across broad regions (Vicente-Serrano et al. 2017). At smaller scales, local factors influencing tree growth might play a more relevant role masking the regional drought signal (Tardif et al. 2003, Caminero et al. 2018). Thus, part of the relationship between tree and forest growth might be due to local variations in key drivers of tree responses to drought such as microsite, topography or soil conditions that can differ across species (Camarero et al. 2017, Sánchez-Salguero et al. 2015, 2018, Gazol et al. 2017a, b, 2018), and between populations within the same species (Linares and Tiscar 2011, Gazol et al. 2017a, Sánchez-Salguero et al. 2018, Sangüesa-Barreda et al. 2019, Serra-Maluquer et al. 2019).

We did not find evidence for greater growth reductions with the increase in drought frequency (i.e. from one to two droughts, **Fig. 3**). However, when such droughts occurred consecutively the growth of nearby forests was more impacted in line with previous studies (Anderegg et al. 2020). This suggests that drought legacies can be easier to detect in forests dominated by gymnosperms, where ecological memory plays a relevant role (e.g. Anderegg et al. 2015, Peltier et al. 2016). Previous results reported abrupt growth reductions in mortality responses to droughts lasting more than one year as being common in gymnosperms (Cailleret et al. 2017). Notably, the occurrence of two droughts, either separately or consecutively, resulted in a marked increase in gymnosperm mortality (**Fig. 3**). However, two severe droughts were not detected in sites dominated by angiosperms, which might lead to underrepresented sampling. This might be because most angiosperm populations come from less drought-prone regions and angiosperms are less represented in our study sites as the number of tree-ring width series was half the number of gymnosperm series (see also Gazol et al. 2018). Caution is thus required when interpreting the results of multiple droughts.

Scaling up tree sensitivity to drought to stand dynamics

After illustrating the existence of a positive link between tree and stand growth by studying tree-ring and inventory datasets, we could expect a significant influence of drought sensitivity, as a surrogate of forest vulnerability to drought, on forest basal area changes, which might be partially attributable to the direct impact of drought but also to the existence of drought legacy effects (Anderegg et al. 2015). We found lower growth and ingrowth, and higher mortality rates in forests located near more RWI-net populations accumulating larger drought impacts, being again this association more marked in gymnosperms. Stronger and more pervasive legacy effects of drought on growth can be expected in major families of gymnosperms (e.g. Pinaceae) than in angiosperms (e.g. Fagaceae) according to Anderegg et al. (2015). Such legacies also influence their post-drought resilience and mortality rates (DeSoto et al. 2020). We did not test for the impact of legacies of drought on growth, because their occurrence is strongly variable between sites and species (Gazol et al. 2020) and it would require the data to be gathered in the same stands. The only exception to this is when two droughts occur consecutively, or almost, and so the impact of the first year can affect growth reductions in the next year. In such cases, we have seen that growth reductions, in nearby stands are more marked that when droughts occur separately (**Fig. 3**), pointing again to the possible impact of legacies. Thus, the convergent patterns found between our two independent datasets suggest that drought and related legacy effects can affect stand dynamics. Drought reduces photosynthetic activity and increases the risk of xylem embolism thus reducing hydraulic conductivity, growth and increasing the risk of tree death (Brodribb et al. 2010, Cailleret et al. 2019). Higher wood density and the ability to enable partial dieback to avoid drought might make angiosperms (e.g., Fagaceae species) less susceptible to drought than coexisting Pinaceae species (Greenwood et al. 2017). A trend towards greater dominance of angiosperms over gymnosperms has been observed in temperate forests (Alfaro-Reyna et al. 2018), which might be partially explained by trait variations between these two functional groups driving their post-drought successional dynamics (Ruiz-Benito et al. 2017b). However, longer time studies are required to evaluate how forest composition will evolve in the future in response to hotter droughts and consider the potential influence of other land use legacies and demographic processes such as recruitment (Lines et al. 2020).

We found an effect of drought vulnerability on forest growth and mortality, even when structural and climatic variables were included as covariates in the models. However, caution is required due to the existence of multiple sources of variation in the forest growth rates estimated from NFI plots with climate accounting for a relatively lower percentage of explained variability than structural factors (e.g. Ruiz-Benito et al. 2014). We found that stand density has a strong positive impact on forest growth and ingrowth suggesting the importance of carrying capacity on determining growth along regional climate gradients. How initial stand density modulates forest growth can vary along climate gradients and depending on species-specific traits (Condés et al. 2017; Bravo-Oviedo et al. 2018), thus partially accounting for the impacts of drought vulnerability. Furthermore, forests responses to drought were quantified relying solely on basal area changes without accounting for changes in forest productivity, primary growth (leaf, shoot, and root production; e.g. Khoury and Coomes 2020), fruiting or regeneration (e.g. Camarero et al. 2018, Kannenberg et al. 2019). Secondly, tree-ring data comes from living, dominant or codominant individuals, which are preferentially sampled in extreme populations to strengthen the climatic signal (Fritts 2001), and the response of either dead (often fast-growing individuals) or suppressed individuals is often missing (Brienen et al. 2017, Alexander et al. 2018, Babst et al. 2018, Klesse et al. 2018). This contrast with the data coming from plot resurveys where all the individuals surpassing a size threshold are measured. Consequently, we based our estimations of drought impacts on growth in dominant, and mostly healthy, trees and compared it with the dynamic of dominant and suppressed trees in a stand. However, the fact that we found a signal of tree vulnerability on forest level responses is relevant because tree vulnerability had generally a lower effect compared to other local factors and, therefore, further studies considering more refined datasets, e.g. evaluating tree and growth relationships with data derived from complete samplings of tree populations along altitudinal gradients (e.g. Sánchez-Salguero et al. 2015), are required to further understand the scalability from individual trees to forest stands. The dendrochronological sampling of trees in NFI plots along environmental gradients may provide complementary information on forest dynamics and tree growth and allow testing if tree-ring records are related to other stand characteristics such as changes in density or regeneration. For example, the positive effect of initial stand density on forest growth and ingrowth turned negative for mortality in the case of gymnosperms (**Fig. 5**). It has been found that the impact of density on growth varies along humidity gradients (Condés et al. 2017) as does the role of drought tolerance on determining maximum density (Bravo-Oviedo et al. 2018). Thus, we can expect a covariation between tree response to drought and stand density on determining changes in stand growth, which might also vary from angiosperm to gymnosperm dominated forests. (see e.g. Jump et al. 2017, Zhang et al. 2021). In this respect, we found that the relationship between initial stand density and forest growth and ingrowth was stronger in the case of gymnosperms than for angiosperms. How stand density modulates growth and mortality depends on climate, but it also varies depending on stand age and across species (Condés et al. 2017) making difficult to drive strong conclusions with the studied data. Thus, testing such hypothesis will require a more refined within site determination of both, density, and tree growth response to drought, and this aim is outside the scope of this study.

Conclusions

We compared tree growth assessments based on individual tree-ring width data (RWI-net) with forest dynamics based on inventory plot structural (NFI) data demonstrating the existence of a common regional climate signal suggesting scalability of responses from trees to forests. The coherent signal in the two datasets allowed us to detect how tree vulnerability to drought can determine regional stand and forest structural responses depending on the forest type. We showed that high mortality rates at regional scales can be expected in forests dominated by gymnosperms and severely impacted by drought (i.e. those located in dry regions), in terms of tree growth reduction and increased vulnerability. Overall, our results show that changes in tree ring-width index in response to drought (i.e. sensitivity measures) may be used as an early warning signal to pinpoint forests particularly vulnerable to drought at regional scales (i.e. those stands showing low growth and high mortality rates).

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References

Alberdi, I., S. Condés, J. Martínez Millán, S. Saura Martínez de Toda, G. Sánchez Peña, F. Pérez Martín, J. A. Villanueva Aranguren, and R. Vallejo Bombin. 2010. National Forest Inventories Report, Spain. Pages 529-540 *in* E. Tomppo, T. Gschwantner, M. Lawrence and R. E- McRoberts, editors. National Forest Inventories. Pathways for Common Reporting. Springer, Dordrecht.

Alexander, M.R., C. R. Rollinson, F. Babst, V. Trouet, and D. J. P. Moore. 2018. Relative influences of multiple sources of uncertainty on cumulative and incremental tree-ring-derived aboveground biomass estimates. Trees 32:265–276.

Alfaro-Reyna, T., J. Retana, and J. Martínez-Vilalta. 2018. Is there a substitution of Pinaceae by Fagaceae in temperate forests at the global scale? Global and Planetary Change 166:41–47.

Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:129.

Anderegg, L. D. L., W. R. L. Anderegg, and J. A. Berry. 2013. Not all droughts are created equal: translating meteorological drought into woody plant mortality. Tree Physiology 33:672–683.

Anderegg, W. R. L., et al. 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349:528–532.

Anderegg, W. R. L., et al. 2016. When a Tree Dies in the Forest: Scaling Climate-Driven Tree Mortality to Ecosystem Water and Carbon Fluxes. Ecosystems 19:1133–1147.

Anderegg, W. R. L., A. T. Trugman, G. Badgley, A. G. Konings, and J. Shaw. 2020. Divergent forest sensitivity to repeated extreme droughts. Nature Climate Change 10:1091–1095.

Astigarraga, J, E. Andivia, M. A. Zavala, A. Gazol, V. Cruz-Alonso, S. M. Vicente-Serrano, and P. Ruiz-Benito. 2020. Evidence of non-stationary relationships between climate and forest responses: Increased sensitivity to climate change in Iberian forests. Global Change Biology 26:5063– 5076.

Babst, F., et al. 2018. When tree rings go global: Challenges and opportunities for retro- and prospective insight. Quaternary Science Reviews 197:1–20.

Babst, F., O. Bouriaud, B. Poulter, V. Trouet, M. P. Girardin, and D. C. Frank. 2019. Twentieth century redistribution in climatic drivers of global tree growth. Science Advances 5:eaat4313.

Barton, K. 2012. MuMIn: Multi-model inference. R package version 1.7.7. Retrieved from http://CRAN.R-project.org/package=MuMIn.

Beguería, S., S. M. Vicente-Serrano, F. Reig, and B. Latorre. 2014. Standardized precipitation evapotranspiration index (SPEI) revisited: parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. International Journal of Climatology 34:3001–3023.

Benito-Garzón, M., P. Ruiz-Benito, and M. A. Zavala. 2013. Interspecific differences in tree growth and mortality responses to environmental drivers determine potential species distributional limits in Iberian forests. Global Ecology and Biogeography 22:1141-1151.

Bivand, R. S., E. Pebesma, and V. Gomez-Rubio. 2013. Applied spatial data analysis with R, Second edition. Springer, NY. http://www.asdar-book.org/

Biondi, F. 1999. Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. Ecological Applications 9:216–227.

Bjørnstad, O.N. and W. Falck. 2001. Nonparametric spatial covariance functions: Estimation and testing. Environmental and Ecological Statistics 8:53–70.

Bjørnstad, O. N. 2020. ncf: Spatial Covariance Functions. R package version 1.2-9. https://CRAN.R-project.org/package=ncf

Bravo-Oviedo, A., S. Condés, M. del Río, H. Pretzsch, and M. J. Ducey. 2018. Maximum stand density strongly depends on species-specific wood stability, shade and drought tolerance, Forestry: An International Journal of Forest Research, 91:459–469.

Brienen, R. J., M. Gloor, and G. Ziv. 2017. Tree demography dominates long-term growth trends inferred from tree rings. Global Change Biology 23:474-484.

Brodribb, T.J., and S. A. M. McAdam. 2013. Unique responsiveness of angiosperm stomata to elevated CO2 explained by calcium signalling. PLoS One 8:e82057.

Brodribb, T. J., D. J. Bowman, S. Nichols, S. Delzon, and R. Burlett. 2010. Xylem function and growth rate interact to determine recovery rates after exposure to extreme water deficit. New Phytologist 188:533–542.

Bunn, A., et al. 2018. dplR: Dendrochronology Program Library in R. R package version 1.6.9. https://CRAN.R-project.org/package=dplR

Burnham, K.P. and D. R. Anderson. 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. Springer, New York, NY.

Cailleret, M., et al. 2017. A synthesis of radial growth patterns preceding tree mortality. Global Change Biology 23:1675-1690.

Cailleret, M., et al. 2019. Early-warning signals of individual tree mortality based on annual radial growth. Frontiers in Plant Science 9:1964.

Camarero, J.J., A. Gazol, G. Sangüesa-Barreda, J. Oliva, and S. M. Vicente-Serrano. 2015. To die or not to die: early-warning signals of dieback in response to a severe drought. Journal of Ecology 103:44–57.

Camarero, J.J., et al. 2018. Forest growth responses to drought at short- and long-term scales in Spain: squeezing the stress memory from tree rings. Frontiers in Ecology Evolution 6:9.

Camarero, J.J., J. C. Linares, G. Sangüesa-Barreda, R. Sánchez-Salguero, A. Gazol, R. M. Navarro-Cerrillo, and J. A. Carreira. 2017. The Multiple Causes of Forest Decline in Spain: Drought, Historical Logging, Competition and Biotic Stressors. Pages 307–324 *in* Amoroso, M. M., L. D. Daniels, J. P. Baker, and J. J. Camarero. Dendroecology. Tree-ring analyses applied to ecological studies, Ecological Studies 231. Springer International Publishing, Cham.

Caminero, L., M. Génova, J. J. Camarero, and R. Sánchez-Salguero. 2018. Growth responses to climate and drought at the southernmost European limit of Mediterranean Pinus pinaster forests. Dendrochronologia 48:20–29.

Carnicer, J., A. Barbeta, D. Sperlich, M. Coll, and J. Peñuelas. 2013. Contrasting trait syndromes in angiosperms and conifers are associated with different responses of tree growth to temperature on a large scale. Frontiers in Plant Science 4:409.

Changenet, A., Ruiz-Benito, P., Ratcliffe, S., Fréjaville, T., Archambeau, J., Porte, A.J., Zavala, M.A., Dahlgren, J., Lehtonen, A., Benito Garzón, M. 2021. Occurrence but not intensity of mortality rises towards the climatic trailing edge of tree species ranges in European forests. Global Ecology and Biogeography 30:1356-1374.

Condés, S., Vallet, P.; Bielak, K.; Bravo-Oviedo, A., Coll, Ll., Ducey, M.J., Pach, M., Pretzsch, H., Sterba, H., Vayreda, V.; del Río, M.. 2017. Climate influences on the maximum size-density relationship in Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) stands. Forest Ecology and Management 385:295–307.

Costa, M., C. Morla, and H. Sainz. 2005. Los Bosques Ibéricos: una interpretación Geobotánica. 2nd edition, Editorial Planeta, Barcelona.

DeSoto, L., et al. 2020. Low growth resilience to drought is related to future mortality risk in trees. Nature Communications 11:545.

D'Orangeville, L., et al. 2018. Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. Global Change Biology 24:2339–2351.

Dormann, F.C., et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609–628.

Dunnett, C.W. 1980. Pairwise multiple comparisons in the unequal variance case. Journal of the American Statistical Association 75:796–800.

Dye, A., A. Barker-Plotkin, D. Bishop, N. Pederson, B. Poulter, and A. Hessl. 2016. Comparing tree-ring and permanent plot estimates of aboveground net primary production in three eastern U.S. forests. Ecosphere 7:e01454.

Etzold, S., K. Ziemińska, B. Rohner, A. Bottero, A. K. Bose, N. K. Ruehr, A. Zingg, and A. Rigling. 2019. One century of forest monitoring data in Switzerland reveals species- and site-specific trends of climate-induced tree mortality. Frontiers in Plant Science 10:307.

Evans, M. E. K., D. A. Falk, A. Arizpe, T. L. Swetnam, F. Babst, and K. E. Holsinger. 2017. Fusing tree-ring and forest inventory data to infer influences on tree growth. Ecosphere 8:e01889.

FAO 2013. State of Mediterranean Forests 2013. FAO, Rome.

Fritts, H.C. 2001. Tree Rings and Climate. Balckburn Press, Caldwell, New Jersey, NJ.

Gao, S., R. Liu, T. Zhou, W. Fang, C. Yi, R. Lu, X. Zhao, and H. Luo. 2018. Dynamic responses of tree-ring growth to multiple dimensions of drought. Global Change Biology 24:5380–5390.

Gazol, A., J. J. Camarero, W. R. L. Anderegg, and S. M. Vicente-Serrano. 2017a. Impacts of droughts on the growth resilience of Northern Hemisphere forests. Global Ecology and Biogeography 26:166–176.

Gazol, A., M. Ribas, E. Gutiérrez, and J. J. Camarero. 2017b. Aleppo pine forests from across Spain show drought-induced growth decline and partial recovery. Agricultural and Forest Meteorology 232:186–194.

Gazol, A., et al. 2018. Forest resilience to drought varies across biomes. Global Change Biology 24:2143–2158.

Gazol, A., et al. 2022. Tree growth response to drought partially explains regional-scale growth and mortality patterns in Iberian forests. Dryad, data set. https://doi.org/10.5061/dryad.sj3tx965x

Gazol, A., et al. 2020. Drought legacies are short, prevail in dry conifer forests and depend on growth variability. Journal of Ecology 108:2473– 2484.

Génova, M. 2012. Extreme pointer years in tree-ring records of Central Spain as evidence of climatic events and the eruption of the Huaynaputina Volcano (Peru, 1600 AD). Climate of the Past 8:751–764.

Gómez-Aparicio, L., R. García-Valdés, P. Ruiz-Benito, and M. A. Zavala. 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. Global Change Biology 17:2400–2414.

Greenwood, S., et al. 2017. Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. Ecology Letters 20:539–553.

Hartmann, H., et al. 2018. Research frontiers for improving our understanding of drought-induced tree and forest mortality. New Phytologist 218:15–28.

Henttonen, H.M., and A. Kangas. 2015. Optimal plot design in a multipurpose forest inventory. Forest Ecosystems 2:31.

Hijmans, R. J. 2019. raster: Geographic data analysis and modeling. R package version 3.0-2. https://CRAN.R-project.org/ package=raster

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bulletin 44:69–75.

IPCC 2018. Summary for Policymakers. Pages 1–32 *in* Masson-Delmotte, V., P. et al. Global warming of 1.5°C. an IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change. World Meteorological Organization, Geneva.

Jump, A.S., P. Ruiz-Benito, S. Greenwood, C. D. Allen, T. Kitzberger, R. Fensham, J. Martínez-Vilalta, and F. Lloret. 2017. Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. Global Change Biology 23:3742–3757.

Kannenberg, S. A., K. A. Novick, M. R. Alexander, J. T. Maxwell, D. J. Moore, R. P. Phillips, and W. R. L. Anderegg. 2019. Linking drought legacy effects across scales: From leaves to tree rings to ecosystems. Global Change Biology 25:2978–2992.

Khoury, S., and D. A. Coomes. 2020. Resilience of Spanish forests to recent droughts and climate change. Global Change Biology 26:7079–7098.

Klesse, S., S. Etzold, and D. Frank. 2016. Integrating tree-ring and inventory-based measurements of aboveground biomass growth: research opportunities and carbon cycle consequences from a large snow breakage event in the Swiss Alps. European Journal of Forest Research 135:297–311.

Klesse, S., R. J. DeRose, C. H. Guiterman, A. M. Lynch, C. D. O'Connor, J. D. Shaw, and M. E. K. Evans. 2018. Sampling bias overestimates climate change impacts on forest growth in the southwestern United States. Nature communications 9:5336.

Kunstler, G., et al. 2016. Plant functional traits have globally consistent effects on competition. Nature 529:204–207.

Lebourgeois, F., P. Mérian, F. Courdier, J. Ladier, and P. Dreyfus. 2012. Instability of climate signal in tree-ring width in Mediterranean mountains: a multi-species analysis. Trees 26:715–729.

Lechuga, V., V. Carraro, B. Viñegla, J. A. Carreira, and J. C. Linares. 2017. Managing drought-sensitive forests under global change. Low competition enhances long-term growth and water uptake in *Abies pinsapo*. Forest Ecology and Management 406:72–82.

Liang, J., et al. 2016. Positive biodiversity-productivity relationship predominant in global forests. Science 354:aaf8957.

Linares, J.C., and P. Tíscar. 2011. Buffered climate change effects in a Mediterranean pine species: range limit implications from a tree-ring study. Oecologia 167:847-859.

Lines, E.R., M. A. Zavala, P. Ruiz-Benito, and D. A. Coomes. 2020. Capturing juvenile tree dynamics from count data using Approximate Bayesian Computation. Ecography 43:406-418.

Lloret, F., E. G. Keeling, and A. Sala. 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120:1909–1920.

Marchand, W., M. P. Girardin, H. Hartmann, S. Gauthier, and. Y. Bergeron. 2019. Taxonomy, together with ontogeny and growing conditions, drives needleleaf species' sensitivity to climate in boreal North America. Global Change Biology 25:2793– 2809.

Manrique-Alba, À., S. Ruiz-Yanetti, H. Moutahir, K. Novak, M. De Luis, and J. Bellot. 2017. Soil moisture and its role in growth-climate relationships across an aridity gradient in semiarid *Pinus halepensis* forests. Science of the Total Environment 574:982–990.

Martín-Vide, J., and J. Olcina. 2001. *Climas y Tiempos de España*. Alianza, Madrid.

Monserud, R.A., and H. Sterba. 1996. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. Forest Ecology and Management 80:57–80.

Pasho, E., J. J. Camarero, M. de Luis, and S. M. Vicente-Serrano. 2011. Impacts of drought at different time scales on forest growth across a wide climatic gradient in north-eastern Spain. Agricultural and Forest Meteorology 151:1800–1811.

Peltier, D. M. P., M. Fell, and K. Ogle. 2016. Legacy effects of drought in the southwestern United States: A multi-species synthesis. Ecological Monographs 86:312–326.

R Core Team 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosas, T., M. Mencuccini, J. Barba, H. Cochard, S. Saura-Mas, and J. Martínez-Vilalta. 2019. Adjustments and coordination of hydraulic, leaf and stem traits along a water availability gradient. New Phytologist 223:632–646.

Ruiz-Benito, P., L. Gómez-Aparicio, and M. A. Zavala. 2012. Large-scale assessment of regeneration and diversity in Mediterranean planted pine forests along ecological gradients. Diversity and Distributions 18:1092-1106.

Ruiz-Benito, P., L. Gómez-Aparicio, A. Paquette, C. Messier, J. Kattge, and M. A. Zavala. 2014. Diversity effects on forest carbon storage and productivity. Global Ecology and Biogeography 23:311–322.

Ruiz-Benito, P., et al. 2017a. Functional diversity underlies demographic responses to environmental variation in European forests. Global Ecology and Biogeography 26:128–141.

Ruiz-Benito, P., et al. 2017b. Climate- and successional-related changes in functional composition of European forests are strongly driven by tree mortality. Global Change Biology 23:4162–4176.

Ruiz-Benito, P., et al. 2020. Available and missing data to model impact of climate change on European forests. Ecological Modelling 416:108870.

Sánchez-Salguero, R., R. M. Navarro-Cerillo, J. J. Camarero, and A. Fernández-Cancio. 2012. Selective drought-induced decline of pine species in southeastern Spain. Climatic Change 113:767-785.

Sánchez-Salguero, R., J. J. Camarero, M. Dobbertin, A. Fernández-Cancio, A. Vilà-Cabrera, R. D. Manzanedo, M. A. Zavala, and R. M. Navarro-Cerillo. 2013. Contrasting vulnerability and resilience to drought-induced decline of densely planted vs. natural rear-edge *Pinus nigra* forests. Forest Ecology and Management 310:956–967.

Sánchez-Salguero, R., et al. 2015. Disentangling the effects of competition and climate on individual tree growth: A retrospective and dynamic approach in Scots pine. Forest Ecology and Management 358:12–25.

Sánchez-Salguero, R., et al. 2018. Resist, recover or both? Growth plasticity in response to drought is geographically structured and linked to intra-specific variability in *Pinus pinaster*. Journal of Biogeography 45:1126–1139.

Sangüesa-Barreda, G., J. J. Camarero, R. Sánchez-Salguero, E. Gutiérrez, J. C. Linares, M. Génova, M. Ribas, P. A. Tíscar, and J. A. López-Sáez. 2019. Droughts and climate warming desynchronize Black pine growth across the Mediterranean Basin. Science of the Total Environment 697:133989.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103–113.

Schweingruber, F.H. 1986. Abrupt growth changes in conifers. IAWA Bulletin 7:277–283.

Serra-Maluquer, X., M. Mencuccini, and J. Martínez-Vilalta. 2018. Changes in tree resistance, recovery and resilience across three successive extreme droughts in the northeast Iberian Peninsula. Oecologia 187:343–354.

Serra-Maluquer, X., A. Gazol, G. Sangüesa-Barreda, R. Sánchez-Salguero, V. Rozas, M. Colangelo, E. Gutiérrez, and J. J. Camarero. 2019. Geographically structured growth decline of rear-edge Iberian *Fagus sylvatica* forests after the 1980s shift toward a warmer climate. Ecosystems 22:1325–1337.

Tardif, J., J. J. Camarero, M. Ribas, and E. Gutiérrez. 2003. Spatiotemporal variability in tree growth in the central Pyrenees: climatic and site influences. Ecological Monographs 73:241–257.

Vayreda, J., J. Martinez-Vilalta, M. Gracia, J. G. Canadell, and J. Retana. 2016. Anthropogenic-driven rapid shifts in tree distribution lead to increased dominance of broadleaf species. Global Change Biology 22:3984–3995.

Vayreda, J., J. Martínez-Vilalta, M. Gracia, and J. Retana. 2012. Recent climate changes interact with stand structure and management to determine changes in tree carbon stocks in Spanish forests. Global Change Biology 18:1028–1041.

Vicente-Serrano, S.M., S. Beguería, and J. I. López-Moreno. 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. Journal of Climate 23:1696–1718.

Vicente-Serrano, S.M., et al. 2020. Linking tree-ring growth and satellite-derived gross primary growth in multiple forest biomes. Temporal-scale matters. Ecological Indicators 108:105753.

Vicente-Serrano, S.M., et al. 2017. A high resolution dataset of drought indices for Spain. Data 2:22.

Vilà-Cabrera, A., J. Martínez-Vilalta, J. Vayreda, and J. Retana. 2011. Structural and climatic determinants of demographic rates of Scots pine forests across the Iberian Peninsula. Ecological Applications 21:1162-1172.

Vilà-Cabrera, A., and A. S. Jump. 2019. Greater growth stability of trees in marginal habitats suggests a patchy pattern of population loss and retention in response to increased drought at the rear edge. Ecology Letters 22:1439–1448.

Villaescusa, R., and R. Díaz. 1998. Segundo Inventario Forestal Nacional (1986-1996). ICONA, Ministerio de Medio Ambiente, Madrid.

Zhang, Z., F. Babst, V. Bellassen, D. Frank, T. Launois, K. Tan, P. Ciais, and B. Poulter. 2017. Converging climate sensitivities of European forests between observed radial tree growth and vegetation models. Ecosystems 20:1–16.

Tables

Table 1. Autocovariate regression models relating cumulative drought impacts on the growth of forest dominated by gymnosperms and angiosperms with the bioclimatic variables. For each variable, the coefficient (± standard error, SE) according to a conditional model averaging and the variable relative importance are shown. Significant effects are indicated with * (P < 0.05) and ** (P < 0.01).

Variables	Gymnosperms		Angiosperms	
	Coefficient ± SE	Importance	Coefficient ± SE	Importance
Annual mean precipitation	-0.34 ± 0.14*	0.99	-0.37 ± 0.15*	0.93
Annual Mean Temperature	0.39 ± 0.13**	0.92	0.09± 0.19	0.30
Precipitation seasonality	0.12 ± 0.09	0.48	-0.18 ± 0.16	0.42
Temperature seasonality	-0.10 ± 0.07	0.51	-0.12 ± 0.21	0.36

Table 2. Differences in gymnosperm's stand growth, ingrowth, and mortality between NFI plots situated near RWI-net sites which were affected either by two separate or two consecutive droughts. Note that angiosperms forests could not be tested because sites suffering two droughts between NFI2 and NFI3 were absent. The mean value of forest growth, ingrowth, and mortality together with the standard errors are shown. Significant differences (P < 0.05) are based on the Dunnett's modified Tukey-Kramer pairwise multiple comparison test (the confidence interval for the test statistic does not include 0).

	Two separate droughts	Two consecutive droughts	Dunnett test
Growth	0.266 ± 0.017	0.133 ± 0.020	-0.133 (-0.185 – -0.081)
Ingrowth	0.203 ± 0.016	0.108 ± 0.018	-0.094 (-0.142 – -0.047)
Mortality	0.184 ± 0.026	0.210 ± 0.047	0.026 (-0.080 – 0.132)

Figure legends

Figure 1. Relationships between the selected tree-ring sites (RWI-net) and the Spanish National Forest Inventory database (NFI). (a) Permanent NFI forest plots (grey areas) measured in Spanish forests with tree-ring width (RWI-net) sites overlapped: brown dots, gymnosperms; green dots, angiosperms. (b) Density of sampled NFI plots per year in (grey areas) and the 12-month long June SPEI for the 1981–2005 period that informs about drought occurrence (continuous red line mean). (c) Growth reductions ($\mathrm{RWI}_{\mathrm{mean}}$ – $\mathrm{RWI}_{\mathrm{obs}}$ in percentage) during the period 1981–2005 in the selected RWI-net populations separating angiosperms (green area) and gymnosperms (brown area). The black line (secondary y-axis) shows the number of sites for which the year was classified as drought (20% lowest SPEI values). Note that tree growth reductions were more common in dry years.

Figure 2. Spatial autocorrelation and biogeographical patterns of cumulative drought impacts on tree growth. (a) The spatial autocorrelation of cumulative drought impact in angiosperms (dashed line and green area represent the mean correlation and 95% confidence intervals, respectively) and gymnosperms (solid line and brown area represent the mean correlation and 95% confidence intervals, respectively) (b) The biogeographical distribution of cumulative drought impacts on tree growth (size of the dots) in angiosperm- (green symbols) and gymnosperm-dominated (brown symbols) forests. The background colour represents the total annual precipitation (TAP).

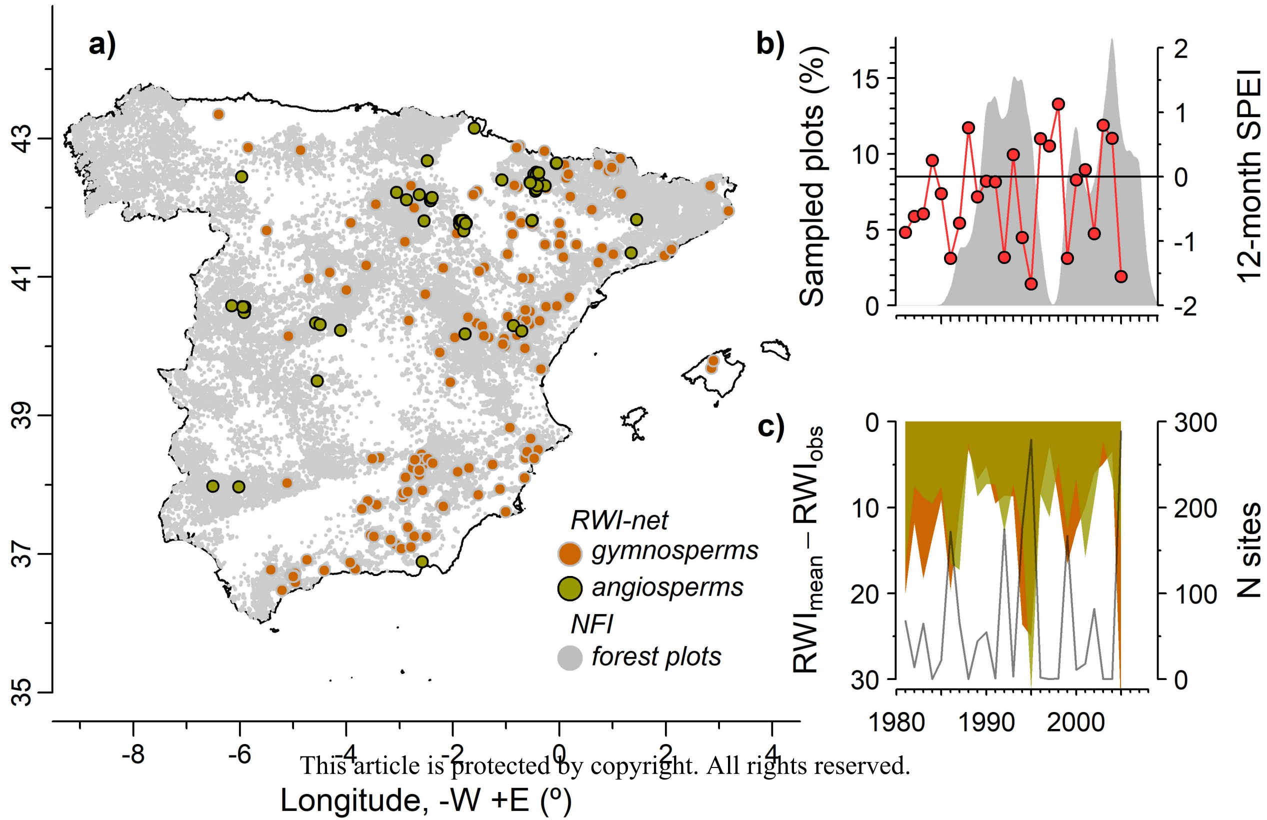
Figure 3. Forest demographic rates including growth increment in stand basal area (ΔBA); ingrowth or increment in stand basal area due to recruited individuals (R); and

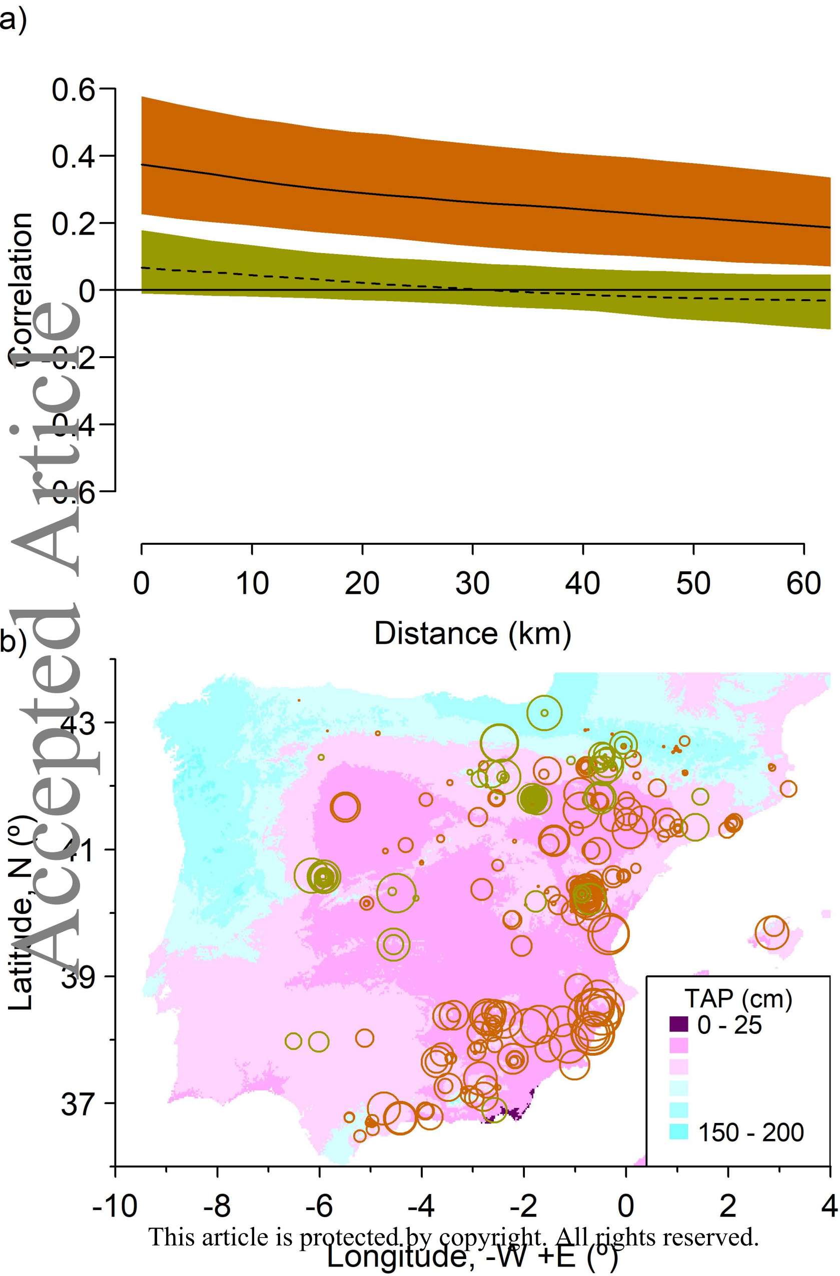
mortality or basal area loss (-ΔBA), measured in NFI plots as a function of drought frequency and severity. Different colours are used for angiosperms (green bars) and gymnosperms (brown bars) across drought frequency classes: no drought, one and two droughts. The bars represent the mean values and the lines the standard error for the mean. The letters above the bars represent the existence of significant differences ($p. < 0.05$) in growth, ingrowth, or mortality between sites experiencing different drought frequencies.

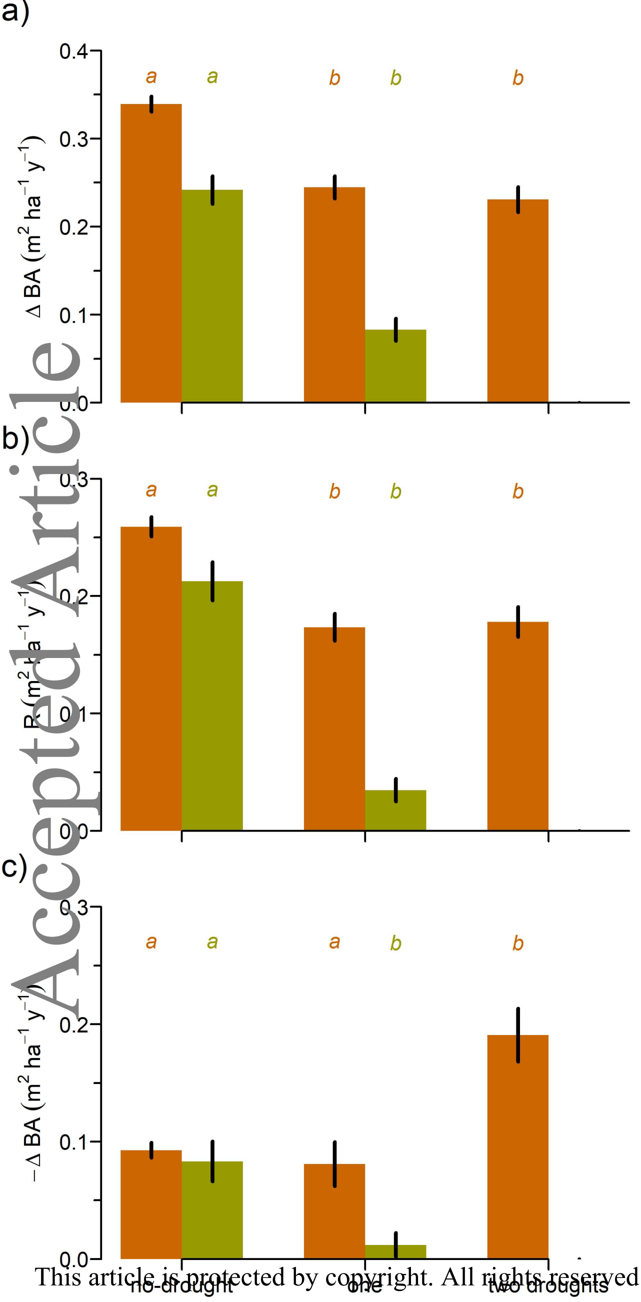
Figure 4. Importance of cumulative drought impact on growth in autocovariate models of (a) forest growth (rate of increase in basal area, ΔBA), (b) forest ingrowth (new individuals, R), and (c) forest mortality (rate of decrease in basal area, –ΔBA) in angiosperms (green bars) and gymnosperms (brown bars). Bar length is proportional to the Akaike relative weight (importance) of each variable in the models, the larger the value the greater the importance. Variables are: CDI, cumulative drought impact; BA, stand basal area in NFI2; Dens, stand density in NFI2; d.b.h., stand mean d.b.h. in NFI2; TAP, total annual precipitation; MAT, mean annual temperature; PCV, precipitation variability (coefficient of variation); TCV, Temperature variability (coefficient of variation) and SPEI, the minimum 12-month long SPEI between NFI2 and NFI3

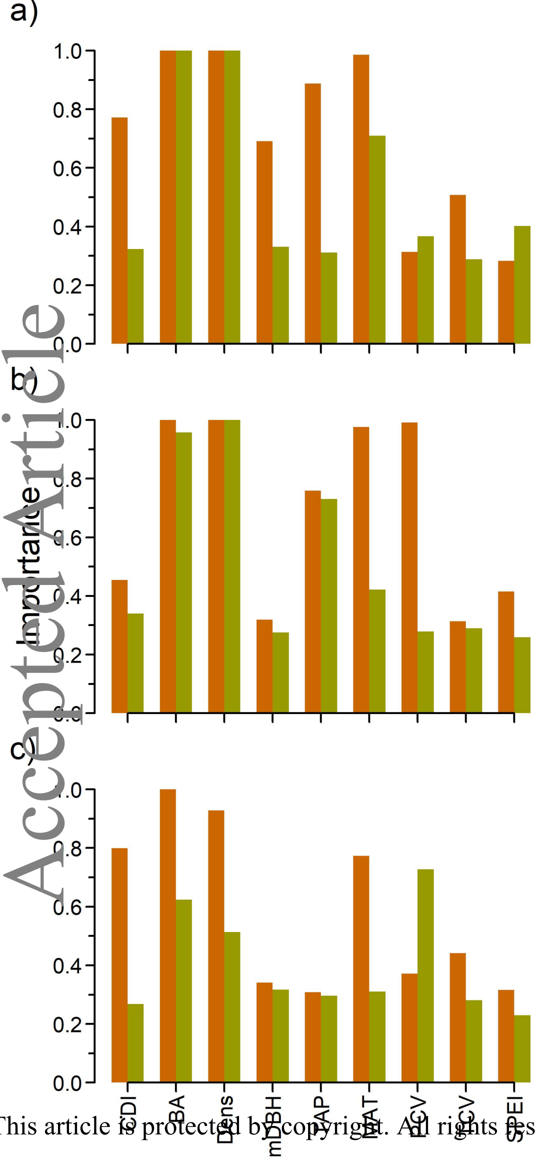
Figure 5. Relationships observed between initial stand density (No. ind. ha^{-1}, stand density in NFI2) and forest demographic rates including: (a) growth increment in stand basal area (ΔBA); (b) ingrowth or increment in stand basal area due to recruited individuals (R); and (c) mortality or basal area loss (-ΔBA), measured in NFI plots as a function of drought frequency and severity. . The continuous and dashed lines show the

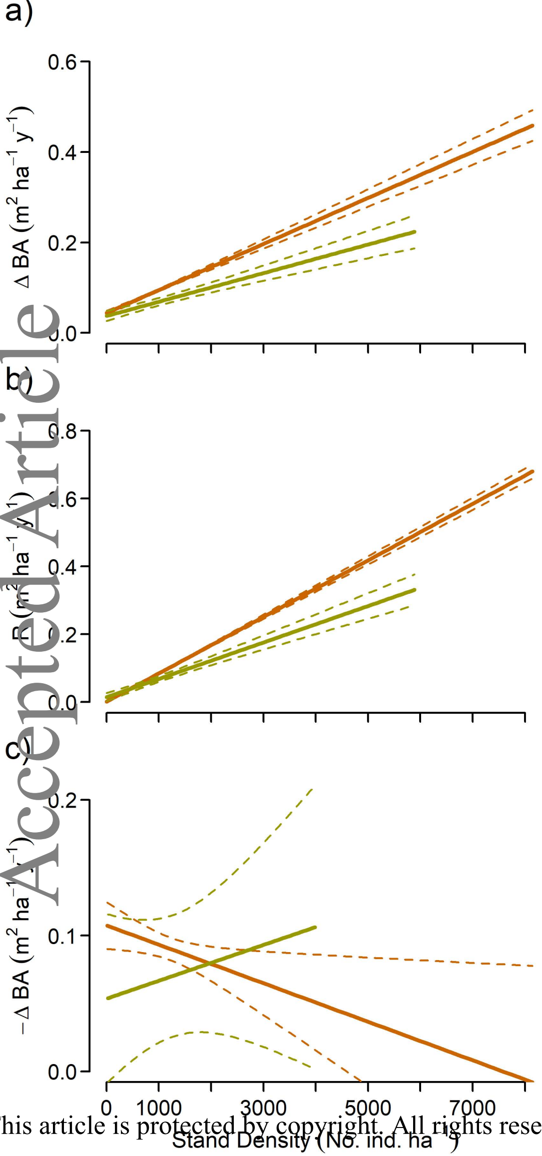
fitted regression and its 95 % confidence intervals for gymnosperms (brown lines) and angiosperms (green lines).


a)
Latitude (º)
43
41
39
37
35
Longitude, -W +E (º)
-8
-6
-4
-2
0
2
4
RWI-net
● gymnosperms
● angiosperms
NFI
● forest plots
b)
Sampled plots (%)
0
5
10
15
12-month SPEI
-2
-1
0
1
2
c)
$RWI_{mean} - RWI_{obs}$
0
10
20
30
N sites
0
100
200
300
1980
1990
2000


a)
Correlation
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
0
10
20
30
40
50
60
Distance (km)
b)
Latitude, N (°)
43
41
39
37
TAP (cm)
0 - 25
150 - 200
-10
-8
-6
-4
-2
0
2
4
Longitude, -W +E (°)


a)
Δ BA (m^2 ha^{-1} y^{-1})
0.0
0.1
0.2
0.3
0.4
a
a
b
b
b
b)
R (m^2 ha^{-1} y^{-1})
0.0
0.1
0.2
0.3
a
a
b
b
b
c)
−Δ BA (m^2 ha^{-1} y^{-1})
0.0
0.1
0.2
0.3
a
a
a
b
b
no-drought
one
two droughts


a)
b)
c)
1.0
0.8
0.6
0.4
0.2
0.0
Importance
CDI
BA
Dens
mDBH
AP
MAT
PCV
TCV
SPEI


a)
Δ BA (m² ha⁻¹ y⁻¹)
0.6
0.4
0.2
0.0
b)
B (m² ha⁻¹ y⁻¹)
0.8
0.6
0.4
0.2
0.0
c)
−Δ BA (m² ha⁻¹ y⁻¹)
0.2
0.1
0.0
0
1000
3000
5000
7000
Stand Density (No. ind. ha⁻¹)