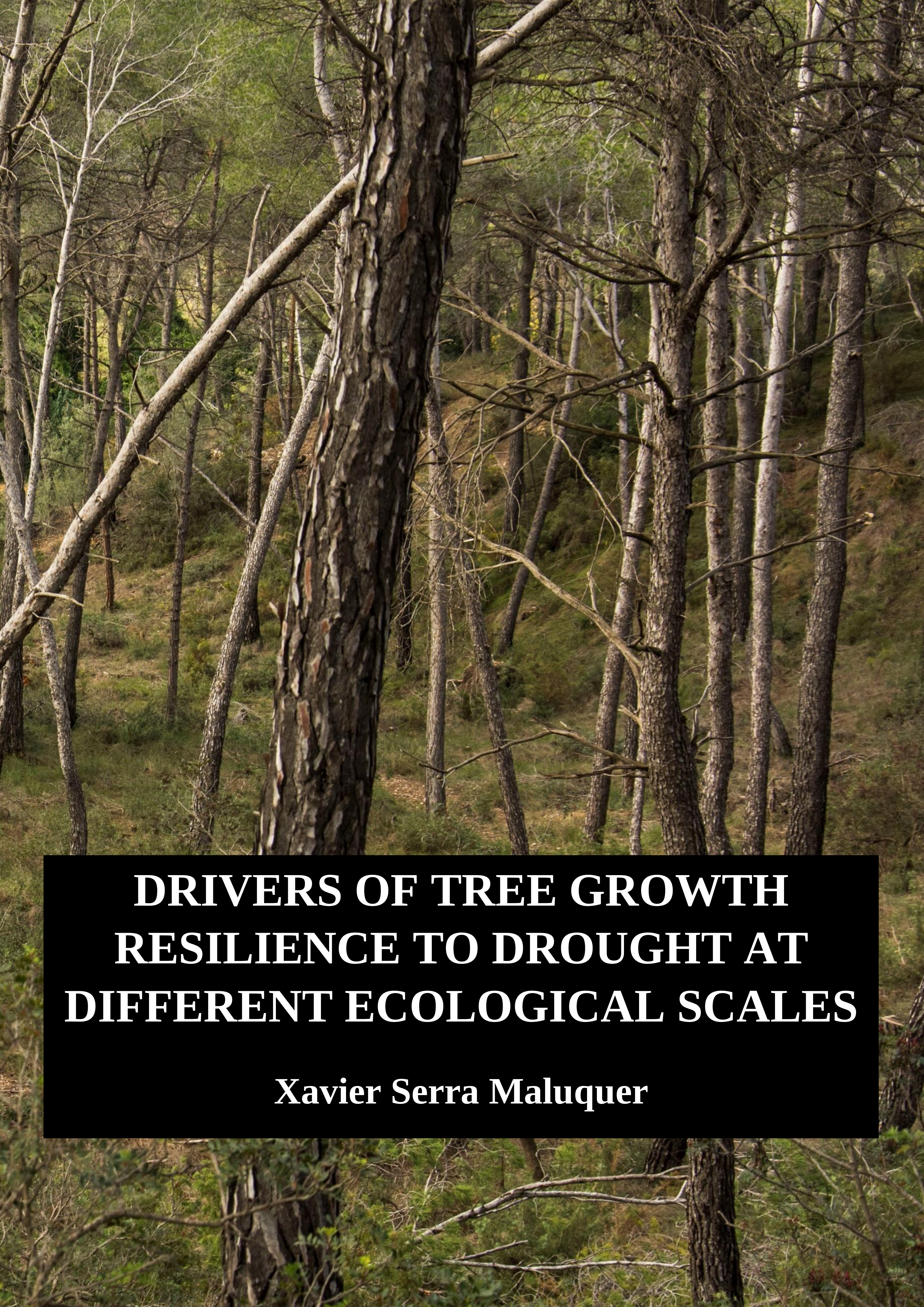
Drivers of tree growth resilience to drought at different ecological scales

Xavier Serra Maluquer



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Dissertation presented by

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to obtain the degree of Doctor

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Summary

Global change exerts a lot of pressure in forests worldwide, which results in a threat to the ecosystem services they provide to humanity. Within the several threats forests suffer, the increasing trend of drought frequency and intensity is receiving many attentions from the scientific community. Drought induced dieback is occurring worldwide. However, not all trees, populations and species respond equally to drought, some survive while others die, which means that there is some characteristics that confer resilience to certain trees, populations or species. Nevertheless, we are far from understanding which are the characteristics that confer resilience to extreme drought events, at which scale they act and which mechanisms drive them. The heterogeneity of forest responses to drought makes it difficult to have a global picture of the characters conferring resilience to drought, which makes predictions of forest demography and ecosystem fluxes under future climate scenarios enormously challenging.

In the present thesis I try to put some light on which variables, biotic and abiotic, are associated with resilience during extreme drought events at different ecological scales. To do that, I study the responses of tree growth to drought from individuals to species. The thesis focuses on secondary growth responses to drought, which is, in the drought influences in tree-ring growth variability. We use tree rings as a retrospective method to evaluate how responses to past extreme drought events correlate to individual, stand and species level characteristics. We show the complexity of tree and forest growth resilience to extreme events across different trees from the same forest (Chapter 3 & 4), populations and across biogeographic gradients (Chapter 2 & 4) and across species worldwide (Chapter 5). Overall, the results presented here show the high complexity of tree ring growth resilience to drought. We observe that some biotic and abiotic variables were good predictors at one scale (i.e., between species) but not others (i.e., within species), showing a scale dependence of the variables associated to growth resilience to drought. Challenges related to prediction on future forest demography, ecosystem fluxes and ecosystem services under future climate predictions are related to the described variability in the following thesis. Research aiming to integrate forest resilience to drought from individual trees to species level will help to predict the future of forests in a changing world. Evaluating patterns of forest responses to drought in the field is a first step towards understanding the capacity of present forest to

withstand drought. The present thesis goes in this direction, and tries to provide useful information on the biotic and abiotic characteristics associated with patterns of growth response to drought at different ecological scales.

Resum

El canvi global exerceix una gran pressió sobre els boscos a escala mundial, que resulta en una amenaça per als serveis ecosistèmics que proveeixen a la humanitat. Entre les diferents amenaces que pateixen els boscos, l'increment en la intensitat i la freqüència de les sequeres està rebent molta atenció per part de la comunitat científica. Episodis de mortalitat forestal associada a la sequera han estat descrits en diferents poblacions d'arbres, espècies i biomes. Tot i això, no tots els arbres, poblacions, boscos i espècies responen igual davant un episodi de sequera, alguns sobreviuen mentre d'altres no. Això significa que hi ha característiques que confereixen resiliència a la sequera en alguns individus, poblacions o espècies. Però encara estem lluny d'entendre quines són aquestes característiques i a quines escales actuen. La resiliència a la sequera pot ser estudiada a diferents escales ecològiques, des del nivell individual fins al d'espècies concretes. En cada cas, la resiliència a la sequera pot estar associada a diferents característiques. Aquesta heterogeneïtat entre diferents escales ecològiques complica la mirada global i holística necessària per entendre la capacitat dels boscos de respondre enfront sequeres extremes, complicant futures prediccions en la demografia forestal i fluxos ecosistèmics en un món canviant.

En aquesta tesi intento entendre quines són les variables, biòtiques i abiòtiques, que estan associades a la resiliència a sequeres extremes en diferents escales ecològiques. Per a fer això utilitzem una combinació d'estudis avaluant la resiliència a la sequera a escala individual, poblacional i d'espècie. La tesi se centra en la resposta del creixement secundari o radial a la sequera, el que significa, en la variabilitat del gruix dels anells de creixement. Utilitzo els anells de creixement amb una visió retrospectiva que permet avaluar com les respostes a episodis de sequera passats estan relacionades amb característiques a escala individual (Capítols 3 & 4), poblacional (Capítols 2 & 4) i d'espècies (Capítol 5). Mostro una alta complexitat en la resiliència a la sequera entre els diferents nivells d'estudi. També, com aquesta variabilitat està relacionada amb diferents característiques abiòtiques i biòtiques i que, aquestes relacions varien en l'escala d'estudi, per exemple una variable pot ser un bon predictor a escala intraespecífica, però no a escala interespecífica. La predicció de la demografia forestal, dels fluxos ecosistèmics i dels serveis ecosistèmics presenta molts reptes, alguns dels quals relacionats a la gran variabilitat de resposta a la sequera presentada en aquesta tesi. L'avaluació de patrons de resiliència a la sequera en estudis de camp és un

primer pas per a poder predir la futura resposta dels boscos a un increment de sequeres extremes. La tesi presentada va en aquesta direcció, i prova de donar informació útil respecte quines característiques estan associades a la resposta dels boscos a la sequera a diferents escales ecològiques.

Resumen

El cambio global ejerce una gran presión sobre la masa forestal a escala mundial, que resulta en una amenaza para los servicios ecosistémicos que los bosques proveen a la humanidad. Entre las diferentes amenazas que sufren los bosques, el incremento de intensidad y frecuencia en episodios de sequía extrema está recibiendo mucha atención por parte de la comunidad científica. Episodios de mortalidad forestal asociada a la sequía se han descrito en diferentes poblaciones, bosques, especies y biomas. Sin embargo, no todos los árboles, poblaciones y especies sucumben delante de una misma sequía, mientras unos sobreviven los otros mueren. Esto significa que existen diferentes características que confieren resiliencia a la sequía en los individuos, poblaciones y especies. Sin embargo, aún estamos muy lejos de comprender cuáles son estas características y a que escalas actúan. La resiliencia a la sequía puede ser estudiada a diferentes escalas ecológicas, des del nivel individual hasta el propio de la especie. En cada caso la resiliencia a la sequía puede estar asociada a diferentes características. Esta heterogeneidad entre diferentes niveles ecológicos complica la mirada global y holística necesaria para poder hacer predicciones de la futura capacidad de los bosques de responder a la sequía.

En esta tesis trato de entender que variables, bióticas y abióticas, están asociadas a la resiliencia en frente de la sequía extrema en diferentes niveles ecológicos. Para realizarlo, utilizo una combinación de estudios evaluando la resiliencia a la sequía a nivel individual, poblacional y de especie. La tesis se centra en la respuesta del crecimiento secundario a la sequía, lo que significa, en la variabilidad de los anillos de crecimiento. Utilizo los anillos de crecimiento con una visión retrospectiva que permite evaluar las respuestas a episodios de sequía pasados y como están relacionadas con características individuales (Capítulos 3 & 4), poblacionales (Capítulos 2 & 4) y de especie (Capítulo 5). En conjunto, los resultados obtenidos nos muestran una gran complejidad de respuesta del crecimiento a la sequía. Se muestra como esta variabilidad está relacionada con diferentes características bióticas y abióticas, y que, dichas relaciones son dependientes de la escala, es decir, una relación que se presenta a nivel interespecífico no tiene por qué aparecer a nivel intraespecífico. La predicción de la demografía forestal, los flujos ecosistémicos y los servicios asociados a estos presenta muchos retos, algunos de ellos relacionados con la gran variabilidad presentada en esta tesis. Esfuerzos para integrar la investigación en diferentes escalas

relativas a la resiliencia forestal a la sequía ayudarán a una mejor predicción del futuro de nuestros bosques en un mundo cambiante. La evaluación de los patrones de resiliencia a la sequía en estudios de campo es un primer paso para poder predecir la respuesta futura de los bosques en frente de un incremento en la intensidad y la frecuencia de las sequías. La presente tesis va en esta dirección e intenta proporcionar información útil respecto a cuáles son las características que están asociadas a la resiliencia de los bosques frente a la sequía a diferentes escalas ecológicas.

Chapter 1

Introduction

1.1. The global context: forests in a changing world

Forest’s cover ~30% of the land surface and their influence on climate and biological processes provide many goods to humankind. Exchange of energy, water and chemical components between the atmosphere and forests has the potential to buffer anthropogenic climate change (Bonan, 2009). For instance, through CO_2 uptake and storage, forests take off carbon from the atmosphere acting as a carbon sink and buffering negative effects of anthropogenic emissions such as climate warming (Pan et al. 2011). Furthermore, forest conservation ameliorates the biodiversity crisis, as forests act as life reservoirs, being the habitat of animal and plant species across the world (Gibson et al. 2011; Gamfeldt et al. 2013). Other benefits as the provision of raw materials such as timber, food or medicines play crucial roles for local communities. Last but not least, forests have an important aesthetic value and provide a recreational area. There is an increasing acknowledgment of the benefits that forests provide to people’s health, both physically and emotionally. In summary, humans benefit from forest through a wide range of ecosystem services at different spatiotemporal scales, therefore forest preservation has become of crucial importance for human societies.

However, anthropogenic global change can put at risk forests and the ecosystem services they provide. Global change impacts on forests can be directly exerted by humans through logging/clearing or indirectly, related to associated shifts in land uses, climate, biodiversity, and disturbances worsening forest health (Dale et al. 2001; Trumbore, Brando & Hartmann, 2015). Although forests have always dealt with threats such as biotic invasions, droughts and heat waves or fires, the non-stationary condition of these processes and their increasing trend under global change can have serious consequences for forests and their associated services (Anderegg et al. 2020a). That is, there is a risk that novel conditions could surpass an ecological threshold, triggering tree performance and thus forest maintenance (McDowell et al. 2020).

Disturbances associated to climate change, such as heat waves, droughts, fires and biological pests result in widespread forest dieback and tree mortality (Michaletz & Johonson, 2007; Kurz et al. 2008; Allen, Breshears & McDowell, 2015). Furthermore, such disturbance act synchronously and feedbacks between them increase their severity (Sangüesa-Barreda et al. 2015; Littell et al. 2016; Netherer et al. 2019) altering pre-disturbance forest dynamics. For instance, growth and mortality patterns may change after disturbance (Camarero et al. 2015; Furniss et al. 2020), which has consequences for different ecological processes such as carbon stocks (Hicke et al. 2013), forest composition (Batllori et al. 2020) and species range shifts (Mueller et al. 2005). The projected increase in frequency and intensity of drought and heat waves (IPCC, 2014) will generate water shortage across many regions. This situation is already causing struggle to many forests around the world (Allen et al. 2010) and has generated an increasing interest among scientists to investigate the patterns and mechanisms of drought related effects on forests (Allen, Breshears & McDowell, 2015).

1.2. Forest resilience to drought

Within the several effects of global change on forests health, the likely increase in drought frequency and intensity has received increasing attention from the scientific community (Allen, Breshears & McDowell, 2015). Such interest increased after acknowledging that drought related tree mortality was a phenomenon occurring on different forest types across the globe (Allen et al. 2010). Episodes of drought triggered tree mortality have been described in Mediterranean, temperate, boreal and tropical forests (Galiano, Martínez-Vilalta & Lloret, 2010; Peng et al. 2011; Camarero et al. 2015; McDowell et al. 2017), indicating that vulnerability to drought is present across different species and biomes (Choat et al. 2012).

Evaluation of forests response to drought is done by many scientific disciplines. Ecophysiological studies of drought induced tree mortality propose different mechanisms causing tree death during drought episodes (McDowell et al. 2008). These mechanisms are related to water transport (hydraulic failure) and carbon storage (carbon starvation) and are non-exclusive; however, recent studies seem to give more importance to hydraulic failure (Adams et al. 2017). Nevertheless, the vast majority of these studies were conducted under experimental conditions, and predicting tree mortality events at large spatial scales remains challenging (Trugman et al. 2021). The fact is, that in the field, not all trees of the same population respond equally to similar drought conditions (Camarero et al. 2015). Similarly, across populations different patterns of forest response to drought are observed (Vilà-Cabrera & Jump, 2019). Different response of trees and populations to the same drought event leads us to the concept of resilience, and why some trees, populations and species maintain their performance during and after the drought, while others do not, and sometimes, die. Or in other words, why some trees are more resilient to drought than others?

If the goal is to preserve forests resilience under an increasing trend of drought frequency and intensity, the first step is to understand the characteristics that make trees more resilient to drought. Questions such as: Which trees/forests are more resilient to drought events? which trees, populations and species will be more vulnerable to the increase in frequency and intensity of drought episodes? And others are yet far to be resolved. There is no simple answer to such questions; the complexity of the dynamics of natural tree populations requires different approaches to decipher characteristics related to resilience at different scales, from individual to populations, and at different life stages. However, knowledge advances are made in relatively little and closed topic compartments. The large life span of trees compared to humans makes it difficult to seek for holistic approaches on tree resilience to drought. To attempt such task, collective efforts coming from different disciplines and teams are needed (Hartmann et al. 2015; Ruiz-Benito et al. 2020). Yet tree growth has become a paramount component of questions related to tree resilience to drought. Growth is a useful indicator of forest performance and thanks to natural archives such as tree rings, reconstructions of tree resilience during past events at different spatiotemporal scales are possible (Camarero et al. 2018).

1.3. Tree-ring growth to evaluate resilience to drought

At the time to evaluate tree resilience to drought several challenges appear. In field studies it is difficult to evaluate resilience to drought if there is not a long-term monitoring or an experimental manipulation. However, when such conditions are met, spatial resolution is limited to local areas due to infrastructure limitations, which reduce the evaluation of drought resilience across broader spatial scales. One way to solve the spatial and temporal challenges required to evaluate patterns of forests resilience to drought in field studies is the use of natural archives such as tree-rings. Information stored in tree rings goes back to many centuries, and it is spatially distributed across the species distribution area resulting on a record of the growth performance across tree life history. Historically, the study of tree rings or dendrochronology has been used for many different purposes, from climate reconstruction, hydrological studies, evaluation of archaeological samples and ecological studies of forest demography. Tree rings reflect past climate effects on tree growth (Fritts, 2001) which make them a valuable tool to reconstruct and study how tree individuals and populations responded to past extreme drought events and to forecast how they will respond in the future.

Reconstruction of tree growth allows determining the resilience of individual trees to past drought events reducing temporal limitations of drought resilience studies. Drought effects on tree growth can be evaluated in different ways, showing a wide range of possibilities to assess forests resilience to drought at different time scales albeit comparing studies is often difficult (Nikinmaa et al. 2020). Dendrochronology, has generally evaluated drought effects on growth by correlating the interannual ring width variability with monthly environmental variables such as precipitation or different drought indices (Palmer Drought Severity Index, Standardized Precipitation Evapotranspiration Index) (Pasho et al. 2011). Such approach identifies how strong a certain environmental variable (e.g., drought) limits growth. Albeit the great potential of growth-climate correlations to evaluate drought effect on growth, other methods that allow to focus on the effects of single extreme drought events are more commonly used. The evaluation of pointer years (i.e., years with extreme growth decreases compared to preceding growth) has been classically used to determine which extreme climatic events result in abnormal growth decreases (Schweingruber et al. 1990). If the pointer years coincide with extreme droughts, one can infer that under such circumstances, drought constantly exerts damages on growth. However, pointer years does not allow to evaluate how different trees or forests respond to a single extreme drought event, as some trees may not present an abnormally growth decrease during the drought. The use of resilience components (Lloret, Keeling & Sala, 2011) has been widely used to this purpose. These components are the following ones: Resistance, which is the growth decrease during drought year respect to pre-drought growth, Recovery, which is the post-drought growth increase respect to the growth during the drought year, and Resilience, which is the capacity of post-drought growth to come back to pre-drought growth conditions. Such indices have been used in many studies across different sites and species (Gazol et al. 2017a; Gazol et al. 2018b; Serra-Maluquer, Mencuccini & Martínez-Vilalta, 2018; Vitasse et al. 2019), and they have the advantage of being easily measurable and having an intuitive interpretation. However, caution about their uncritically use due to different limitations has been made (Schwarz et al. 2020). Another way to quantify the drought impacts on growth is calculating the so called “legacy effects” (Anderegg et al. 2015a), which is the differences of the expected modelled growth (based on different climatic and biotic variables) and the observed growth during the years after drought (Anderegg at el. 2015a, Peltier, Fell & Ogle, 2016, Kannenberg, Schwalm & Anderegg, 2020; Gazol et al. 2020). Furthermore, another common evaluation method is to look for divergent growth trends after an extreme drought, for instance decaying growth trends after extreme events can be present in some trees for decades, and are interpreted as a sign or early-warning signal of mortality risk (Camarero et al. 2015; Cailleret et al. 2017). Overall, several measures can be used to study effects of extreme drought events on tree radial growth. Each method has its advantages and disadvantages and explicitly accounting for the study aims should lead to the selection of the appropriate metric, and acknowledging its limitations is needed to fully interpret the results (Zheng et al. 2021). Finally, forest may have different temporal responses to drought (i.e., the impact during the drought year and the possible legacies several years after it), so that, using a combination of different indices to evaluate such temporal characteristics must help to have a better picture of how tree growth responds to extreme drought events at different temporal scales (Camarero et al. 2018).

Combining dendrochronological metrics describing growth resilience to drought with biotic and abiotic information regarding the status of the trees must help to understand which characteristics confer growth resilience to drought. This is a key aspect, as understanding which abiotic and biotic characteristics are associated to higher resilience to extreme drought will help to better predict future forests response to drought across species and populations. However, multiple variables are involved in forest responses to drought and act at different scales, temporally, spatially and ecologically. So, it becomes crucial to critically decide which metric and which variables to study depending on the question to be answered.

1.4. Factors influencing tree resilience to drought

As stated in the previous section, many variables could determine tree and forest response to drought. Growth resilience has many drivers acting at different ecological, temporal and spatial scales. Listing all them exhaustively is not the aim of this introduction but it is worthy to mention the most important ones.

Among the abiotic factors, the most relevant one is the drought itself, the intensity, duration and seasonality. The more intense the drought, the worst the consequence for forests (Greenwood et al. 2017). Furthermore, other aspects such as when the drought occurs and how long it is may differently affect vegetation (Vicente-Serrano et al 2013; Gao et al. 2018; Huang et al. 2018). Defining drought is not always easy, while at small spatial scales (i.e., within a forest) the use of raw data or standardized indices might be irrelevant (Slette et al. 2019a), across larger scales (i.e., across forests and biomes) discussions on whether using raw or standardized data has arisen (Slette et al. 2019b; Zang et al. 2019) and usually, drought definitions are linked to impacts on the study system. Therefore, not all droughts are equal, and different types of vegetation might present divergent responds depending on timing, seasonality and duration of droughts. Local climate conditions may also influence forest responses to drought. Drier sites more exposed to chronic drought stress might suffer higher drought induced dieback (Anderegg et al 2019; Camarero et al. 2021); however, populations located at milder regions may be more affected than expected (Cavin & Jump, 2017; Vilà-Cabrera, Premoli & Jump, 2019). Such contrasting results difficult predictions of drought resilience solely based on macroclimatic conditions of the site. Other important factors, which could alter broad biogeographic expectations, may be related to terrain topography, soil conditions, and bedrock water resources. Such conditions can ameliorate or worsen forest response to drought to the point to override expectations expected by macroclimatic conditions. For example, equatorward populations growing near the drier species distribution edge, may buffer drought effects thanks to microclimatic conditions. Such populations may be on the latitudinal edge of the species, but not on the climatic edge (Camarero et al. 2021). Therefore, it is important to know the stand level conditions reflecting the microenvironmental situation of each population.

Biotic and abiotic factors related to stand structure can influence forest resilience to drought. One of the most important is competition, which is expected to cause negative effect on growth resilience to drought (Bottero et al. 2017). However, recent studies show a more complex issue, where competition effects may vary depending on the metric, species and site (Castagnieri et al. 2021). Biodiversity is another driver that could play a crucial role; however, it is little understood and controversy is present on the literature.

Higher species richness reduces competition effects (Kunstler et al. 2016), which may benefit forests under drought (Gazol & Camarero 2016). It is postulated that positive effects of biodiversity may be more prevalent under harsh conditions than under resources surplus (Messier & Paquette, 2011). However, studies reporting, positive, negative or absent effects of biodiversity on growth responses to drought are present (Gazol & Camarero 2016, Merlin et al. 2015; Gillerot et al. 2021). That is probably because at stand level biodiversity may promote resilience to drought (one species being less affected than other), but at tree level, tree to tree interactions may be contingent on functional characteristics being redundant or complementary, so that biodiversity effects may be detrimental, positive or absent based on the species composition. Furthermore, the use of different biodiversity indices may complicate comparability among studies. Interestingly, the potential influence of biodiversity on tree growth has its roots in niche theory which states that species may differ to coexist. Thus, functional diversity metrices appear to be more informative that simple measures of species richness (Gazol & Camarero 2016).

Interactions with other organisms from different trophic levels may also drive forest response to drought. For instance, biotic communities on the soil adjacent to the trees can alter tree access to nutrients. However, little is known on possible relationships between soil biota and tree responses to drought (but see Gazol et al. 2018a). Other biotic agents such as pests or pathogens may negatively predispose trees to drought, reducing their resilience (Anderegg et al. 2015b). The effect of herbivores is not well known, but must also play a role on the tree responses to drought. Finally, we cannot forget that human influence through management modulates drought resilience; generally, it is thought that thinning and reducing competition improve forest resilience to drought (Bottero et al. 2016); however, it might not always be the case (Castagnieri et al. 2021).

Then, there are individual characteristics of trees which could be associated to higher or lower resilience to drought. Basic metrics such as tree age or size are expected to play a crucial role on the growth resilience to drought. Bigger trees suffer more under drought due to longer hydraulic pathways (Mencuccini et al. 2005; Olson et al. 2018). Therefore, under projected climatic conditions, small trees may be benefited (Fajardo, McIntere & Olson, 2019). However, in some situations bigger trees are more efficient under drought, as a bigger root system may allow them to access deeper water resources (Nepstad et al. 2007). Structural and functional traits of the tree also play a role, fast-growing trees developing great aerial parts in contrast to root systems may struggle to maintain them under drought conditions (Jump et al. 2017).

The fast-slow growth continuum of across species variability is related to different capacities of plants to acquire and process resources at different turnover rates (Reich, 2014). Many attributes or functional traits have been used to describe interspecific spectra of plant form and function based on different organs or plant tissues (Wright et al. 2004, Chave et al. 2009; Gleason et al. 2016). To summarize, in one side of the spectra there are plants with high resource uptake and turnover, which are considered fast-growing species with acquisitive strategy, while in the opposite there are slow-growing plants with low rates of resource uptake and turnover, a more conservative strategy. Theoretically, the acquisitive strategy will be advantageous under resource abundant environments, but may be detrimental under harsh conditions, where a conservative strategy may allow plants to maintain their performance. So that, one would expect that trees presenting traits related to conservative strategies would be more resilient to drought. However, there is little empirical support relating different functional traits with tree drought resilience. It is important to acknowledge that all the conceptual framework of functional plant ecology has grown over comparisons of different plant species. Little is known on how such interspecific spectra accommodate within species. Functional trait intraspecific variability is huge (Fajardo & Piper, 2011) and in some cases broad interspecific gradients of trait variability could not be found at the within species level (Anderegg et al. 2018; Rosas et al. 2019).

Overall, tree resilience to drought events can be influenced by many factors of biotic and abiotic nature. Given the methodological difficulties to provide a wide holistic picture, it is important to understand when and why a certain condition and characteristic may modulate tree growth resilience to drought. The scale dependence of many variables makes so hard to generate a picture of the characteristics associated to forest resilience to drought, highlighting the importance of studies at different levels to generate knowledge allowing filling research gaps.

1.5. The tree, the population and the species

As partially stated before, the scale at which drought resilience is evaluated is a key factor to understand how different drivers determine resilience to drought. Each driver will act at one or multiple ecological, temporal and spatial scales influencing drought resilience through different mechanisms. So that, the relative weight of a driver which may be relevant at the tree level could be dismissed at stand or species levels, and the opposite could occur for another variable. Thus, when assessing resilience to drought is key to acknowledge the scale at which the study is performed and to discern whether a certain variable is useful to understand resilience to drought at such scale.

Some variables may act at different scales; however, the measure at which they are done should vary (Figure 1.1). For instance, competition is expected to be detrimental at any scale. However, proxies such as stand density or basal area may give us an idea of population characteristics, while not being relevant to understand how an individual tree will respond to drought. In such case neighbouring competition indexes, based on direct distance and size of competitors must be more adequate. Dendrochronological studies have a great potential to test tree growth resilience at different scales. Resolution of the data can be obtained for single individuals and then could be aggregated into populations or species. Such potential allows performing observational studies at different scales testing for correlations between growth resilience and different biotic and abiotic factors.

Individual based approaches have gained popularity in recent years, and many studies evaluated tree growth resilience to drought at this scale. Ultimately, the individual level scale is where mechanisms conferring resilience to drought will act. Individuals are the subject who will suffer drought stress and their characteristics altogether with their environment will determine if a tree survive a drought or otherwise die. However, as spatial resolution increases, difficulties to obtain dependent variables at individual level decrease. In these cases, stand level chronologies are useful and correlations with environmental and stand level variables give information about how different stands respond to drought (Gazol et al. 2017a; 2018b)

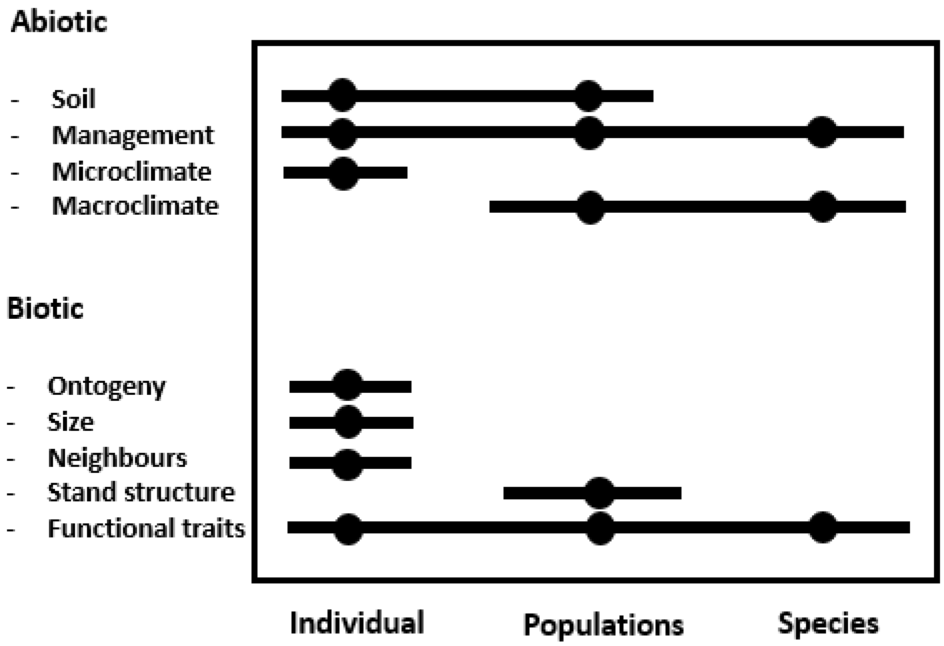

Figure 1. Abiotic and biotic drivers of growth resilience to drought are scale dependent, ecologically they act at different levels, i.e., from individual trees to species. Therefore, acknowledging the study scale is crucial to understand the output of the results.

Furthermore, different responses may appear at higher scales such as species. Whether two coexisting species present different resilience to a drought event may be explained by their traits. Hydraulic architecture, allocation patterns and functional traits greatly differ across species and potentially could result in different interspecific responses to drought via coexistence mechanisms. As explained in the above section, functional ecology has broadly been done in across species studies. Does such functional trait interspecific variation relate to interspecific differences in resilience to drought? If so, how does this covariation varies across scales? It is possible that broad interspecific functional trait spectra do not hold at small scales and that other compensatory mechanism, such as allocation patterns to restructure hydraulic architecture are more relevant (Martínez-Vilalta et al. 2009).

Therefore, it is important to acknowledge that variation in resilience to drought will vary across scales. Any approximation to decipher drivers of the resilience capacity of trees or forests to drought will fail to understand huge parts of the variability not associated to the studied scale. This complexity must not take us back, on the contrary a clear though on the potential of each variable to decipher resilience patters should help us, little by little, to understand the great amount of variation of growth responses to drought.

1.6. Aims of the thesis and contributions

In the present thesis I aim to test how tree growth resilience to drought varies across individuals, populations and species and the drivers associated at each scale. To do that, I will combine different studies including individual level, stand level and species level evaluation of how drought resilience is related to different biotic and abiotic factors. A combination of local, regional and global studies is present (Figure 1.2).

1. *"Geographically structured growth decline of rear-edge Iberian Fagus sylvatica forests after the 1980 shift toward a northern climate"*. In this chapter, an evaluation of the growth constrains of the north eastern Iberian *Fagus sylvatica* forests after 1980 temperature increase has been made. Growth trends and pointer years were compared to evaluate biogeographical differences across forests growing in contrasting climate conditions. This chapter was published in Ecosystems, DOI: 10.1007/s10021.019-0339-z

2. *"Silver fir growth responses to drought depend on interactions between tree characteristics, soil and neighbourhood features*". Here three Pyrenean mixed forests dominated by *Abies alba* were studied. An individual level approach was used to test the influence of tree characteristics (size, growth rate), neighbourhood composition (competition, competitor specie) and soil biotic and abiotic characteristics as drivers of growth resistance, recovery and resilience of individual *A. alba* trees to drought. This chapter was published in Forest Ecology and Management, DOI: 10.1016/j.foreco.2020.118625

3. *"Impacts of recurrent dry and wet years alter long-term tree growth trajectories"*. In this chapter an individual, population and species comparison of growth response to repeated extreme events was done. Three populations of six different species (*Pinus halepensis*, *Pinus nigra*, *Pinus sylvestris*, *Abies alba*, *Quercus faginea* and *Quercus ilex*) were sampled across

a broad biogeographical gradient. Individual level functional traits (size, wood density and specific leaf area) were measured and related to repeated growth increases and decreases. Then, the effects of such growth decrease on long term growth trajectories were compared across populations and across species. This chapter was published on Journal of Ecology: DOI: 10.111/1365-2745-13579.

4. *"Wood density and hydraulic traits influence species' growth response to drought across biomes"*. In the final chapter, a global dataset of tree ring chronologies was combined with interspecific functional trait data on leaf, wood and hydraulic traits. Interspecific covariation between growth-drought relationship and resistance, recovery and resilience to extreme drought episodes with functional traits was tested while controlling for climate factors. This Manuscript is under review on Global Change Biology, ms ID: *GCB-21-1783*

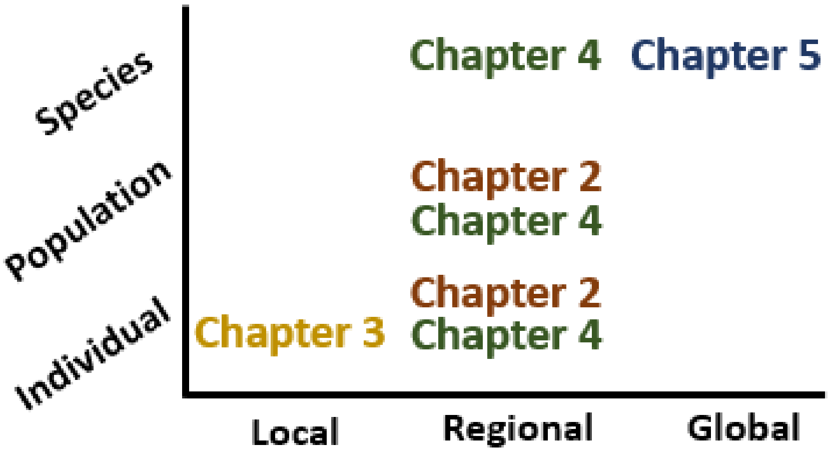

Figure 2. Distribution of chapters across different ecological (y axis) and spatial scales (x axis).

Chapter 2

Geographically structured growth decline of rear-edge Iberian *Fagus sylvatica* forests after the 1980s shift toward a warmer climate

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2.1 Abstract

Warming-related growth decrease on southern *Fagus sylvatica* forests has been observed in different regions, however whether it is a generalized fact or not remains unclear. Here we investigate the geographical pattern on growth response of the southwestern European beech forests to the warming climate shift which started in the 1980's. We sampled 15 beech forests (215 trees) across four climatically contrasting regions (Mediterranean, Pyrenean, low- and high-elevation Atlantic areas) near the southern distribution limit of the species in the Iberian Peninsula. Dendrochronological analyses were carried out to evaluate the growth of European beech since the 1950s. Growth responses quantified as pointer years, abrupt growth changes and long-term growth trends were compared between periods (before and after the 1980's climate shift), geographical regions and tree sizes. Analyses of the studied variables indicated a growth decrease in basal area increment after the climate shift in three of the four studied regions. Pyrenean stands were not negatively influenced by the climate shift, although an increase in the frequency of negative abrupt growth changes was also found there. Growth after the climate shift presented divergent patterns depending on the geographical region. While Mediterranean and Atlantic stands presented different indicators of constrained growth, Pyrenean stands showed rising long-term growth trends. Such results suggest that regional characteristics differentially determine the growth response of the southern European beech forests to recent warming periods. Iberian beech forests located at the Pyrenees would benefit from forecasted warming conditions, whereas Atlantic and Mediterranean forests would be more prone to suffer warming related growth decline.

2.2 Introduction

Tree populations growing in the southernmost distribution limits of the species range (xeric rear edges) face harsh climate conditions, which can compromise their performance and growth (Gazol et al. 2015; Sánchez-Salguero et al. 2017a). Future climate projections forecast warmer climate and an increase of extreme weather events such as droughts and/or heat waves (IPCC, 2014), which could trigger local extinctions and/or range shifts of the most vulnerable rear-edge tree populations (Chen et al. 2011). Warming-related growth decline and forest dieback triggered by dry spells is a major concern for scientists and managers (Allen et al. 2010; Allen, Breshears & McDowell, 2015), and its influence on forest dynamics and possible retractions of rear-edge tree populations is still under debate (Sánchez-Salguero et al. 2017b).

European beech (*Fagus sylvatica* L.) is a drought-sensitive tree species widely distributed across Europe (Köcher et al. 2009; Zimmermann et al. 2015) which displays productivity and growth reduction (Lendzion & Leuschner, 2008; Thiel et al. 2014), and leaf and root trait alteration as a consequence of drought (Knutzen, Meier & Leuschner, 2015). Increasing temperature and water shortage affects beech radial growth across the entire continent, indicating a widespread vulnerability to future warming climate (Hacket-Pain et al. 2016). Special attention must be paid at drought-prone rear edge forests in continental areas such as the Iberian Peninsula, where warm and dry summers constrain beech performance (Gutiérrez, 1988; Rozas et al. 2015; Dorado-Liñán, Akhmetzanov & Menzel, 2017). In the last four decades a warming trend has been observed in the Iberian Peninsula, particularly a rapid rise in temperatures has occurred since the 1980s followed by successive severe droughts in the 1990s, 2000s and 2010s (González-Hidalgo et al. 2010). Such abrupt warming occurred in the transition from the 1970s to the 1980s and it was partly linked to changes in the winter atmospheric circulation over the northern Atlantic Ocean (Hurrell, 1996) and impacted ecosystems worldwide by accelerating climate warming (Reid et al. 2016). This climate shift has led to warmer and more arid conditions on several European regions, generating harsher climatic conditions for beech forests. For instance, Jump, Hunt & Peñuelas (2006) found a warming-related growth decline in low-elevation beech stands in the Montseny Mountains (NE Spain) due to warming conditions after the 1980s. In a previous study in the same forest water shortage was suggested as the main constrain of tree growth, indicating that an increase in evapotranspiration could seriously compromise future forest productivity (Gutiérrez, 1988). Comparable episodes of warming-induced growth decline have been found at rear-edge stands from Italy (Piovesan et al. 2008) and Hungary (Garamszegi & Kern, 2014). In the core of its distribution range, beech populations growing at lower altitudes in dry areas have also experienced marked growth declines (Zimmermann et al. 2015; Dulamsuren et al. 2016; Knutzen et al. 2017). Nevertheless, increased climate sensitivity has been also found in mesic stands whilst stands from dry sites were not so responsive, suggesting local adaptation to water shortage and extreme conditions in populations from dry sites (Weber et al. 2013, Cavin & Jump, 2017). Similarly, rising growth trends or absence of a warming-triggered growth decline have been reported for recent decades in other European beech rear-edges forests (Tegel et al. 2014; Cavin & Jump, 2017; Hacket-Pain & Friend, 2017).

The occurrence of warming- and drought-related growth decreases could be modulated by different intrinsic factors (McDowell et al. 2008; Galván et al. 2012). For instance, tree size has been suggested as a key factor of the resistance to extreme drought events, with larger trees more susceptible to such events than small ones (Bennett et al. 2015). In addition, trees of the same species but different size can respond differently to climate (Rozas, 2015). Warming- and drought-related growth decline could thus be a consequence of the combined effect of extrinsic (climatic) and intrinsic (size) factors influencing tree growth (Colangelo et al. 2017). Therefore, considering individual characteristics as tree size might help to better depict the causes of warming and drought effects on beech radial growth.

Here we study the stem secondary growth of fifteen Iberian beech forests during the period 1950-2008. Our study region covers a large area and includes a wide climatic gradient, from dry Mediterranean to wet Atlantic sites, encompassing the major climatic conditions where beech grows at southwestern Europe. Our aim is to quantify the effect of the 1980s climate shift on radial growth of the studied beech forests. We use a dendrochronological approach, considering tree-ring width as a reliable proxy of tree growth rate and vitality. We evaluate growth variability at different time scales, from short (year to year) to long-term growth changes (30-year periods), to investigate the possible warming- and drought-related effects on tree growth. Furthermore, we also evaluate the effect of tree size (stem diameter at breast height) on the response of trees to a climate shift towards warmer and more arid conditions. Our specific aims are to determine: (1) If there has been a negative effect on growth of Iberian beech populations caused by the 1980s climate shift; (2) if there is any biogeographical pattern in the response of these beech populations to climate warming; (3) If tree size partially modulates the growth response of beech to the 1980s climate shift. We hypothesize that, after the 1980s climate shift, forests from xeric sites will present more growth constraints than those in mesic sites. We expect that Iberian beech forests growth responses to warming climate would vary among regions and would depend on tree size.

2.3 Material and methods

2.3.1. Study sites and data sampling

Our study was conducted in the northeast Iberian Peninsula, which represents the southwestern distribution limit of European beech (Figure 2.1). We sampled 15 forests across a marked climatic gradient, with mean annual temperatures ranging from 6.7 ºC to 15.7 ºC, and mean annual precipitation ranging from 579 mm to 1208 mm (CRU TS 4.01 climate data from 1950 to 2008) (Harris & Jones, 2017) (Figure 2.2, Supplementary Materials, Figure S1). During the growing season (May to September) the mean temperature and precipitation vary considerably depending on the sampled region (Rozas et al. 2015). For instance, stands in the Mediterranean and Atlantic areas have higher temperatures (16 ºC) than stands found in the Pyrenees (12 ºC). In terms of growing season precipitation, Atlantic and Pyrenean stands present higher values than Mediterranean stands, with mean values of 446, 497 and 378 mm respectively. A different range of altitudes was also present on the sampled stands, going from 300 m to 1530 m a. s. l. More detailed characteristics of each plot are described in Table 2.1.

2.3.2. Climate variables and climatic areas

Monthly temperature and precipitation series from 1901 to 2010 at 0.5º resolution were downloaded from CRU TS 4.01 dataset (Harris & Jones, 2017). Next, mean annual temperature (MAT) and mean annual precipitation (MAP) series for the period 1950-2008 were calculated (Figure 2.2). To assess the aridity of each site, we calculated De Martonne's aridity index (hereafter, AI), which is calculated as the ratio of mean annual precipitation and mean annual temperature plus 10 (Tuhkanen, 1980). High values of AI indicate wet conditions and low values indicate arid conditions. To estimate drought severity at each site, time series from 1950 to 2008 of the Standardized Precipitation and

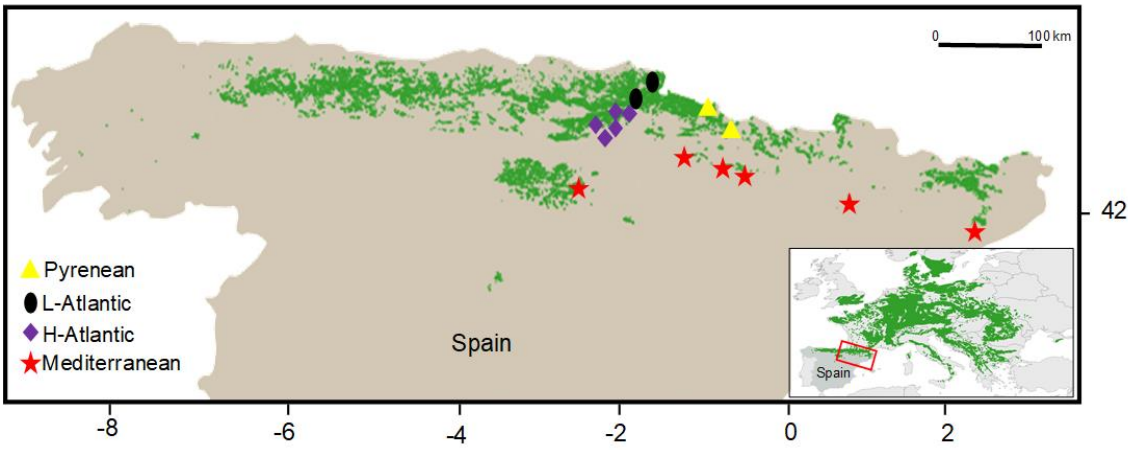

Figure 2.1. Beech (*Fagus sylvatica*) distribution in Europe (right down inset) and northern Spain showing the four biogeographical forest groups: Pyrenean (yellow triangles), low-elevation Atlantic (black circles), high-elevation Atlantic (purple rhombus) and Mediterranean (red stars).

Site name	Biogeographical region	No. trees / No. cores	Mean BAI ($mm^2\ yr^{-1}$)		First-order autocorrelation	Mean sensitivity	Mean inter-series correlation	EPS
			1950-1979	1980-2008				
Aisa	PYR	7/14	402	442	0.72	0.22	0.59	0.93
Bertiz	L-ATL	17/32	1241	1018	0.58	0.29	0.62	0.95
Diustes	MED	7/14	1063	786	0.79	0.23	0.78	0.96
Eraso	L-ATL	14/14	801	1231	0.64	0.31	0.39	0.82
Gamueta	PYR	13/23	514	1498	0.47	0.36	0.61	0.95
Izki	H-ATL	20/39	2979	2387	0.73	0.27	0.76	0.97
Lokiz	H-ATL	22/22	841	956	0.63	0.28	0.57	0.92
Luesia	MED	9/18	900	982	0.82	0.22	0.83	0.98
Monrepos	MED	11/22	748	1688	0.75	0.22	0.63	0.97
Montsec	MED	15/18	723	643	0.65	0.22	0.64	0.95
Montseny	MED	13/31	1406	1542	0.70	0.23	0.53	0.87
Opakua	H-ATL	26/32	1101	1223	0.53	0.31	0.63	0.95
Peiró	MED	6/12	1590	1398	0.67	0.24	0.66	0.92
Urbasa	H-ATL	19/38	2969	2436	0.57	0.31	0.73	0.97
Arutz	H-ATL	16/16	884	1324	0.63	0.24	0.48	0.84

Table 2.1. Characteristics of the study beech forests . Forests were grouped into four biogeographical regions based on climate data (mean annual temperature –MAT– and mean annual precipitation –MAP–, De Martonne Aridity Index –AI) and elevation: Low-elevation Atlantic (L-ATL), high-elevation Atlantic (H-ATL), Pyrenean (PYR) and Mediterranean (MED) forests. DBH is the diameter measured at breast height (1.3 m).

Evapotranspiration Index (hereafter, SPEI) at 0.5º resolution (Vicente-Serrano, Beguería & López-Moreno, 2010) were downloaded (Figure 2.2). We used March to August SPEI in order to cover the main growth season of beech. We evaluated mean annual precipitation, mean annual temperature and SPEI along the studied period in order to detect possible climate shifts. We looked for shifts in climate variables using the function *breakpoints* from the *strucchange* (Zeileis et al. 2003) package in R (R core team, 2018). This function detects breakpoints that mark separation between segments of time series. Series are divided in segments of constant mean values, thus years between segments, which we call breakpoint, are years where an increase or decrease of mean values occurs. Furthermore, we calculated trends of spring-summer mean values of temperature and precipitation to evaluate changes on the climate variables during the growing season (Supplementary Materials, Figure S2).

In order to find groups of stands with similar climatic conditions, we performed a hierarchical cluster analysis based on the Euclidean distance of the climate variables (MAT, MAP and AI for the 1950-2008 period) including the site elevation. These analyses resulted in four different groups that would be used in all the analyses (Supplementary Materials, Table S1, Figure S3). Two stands with low temperatures, high precipitation and situated at high elevation, the Pyrenean stands; six stands situated at high elevations, with warm temperature and low precipitation, the Mediterranean stands; finally, two groups characterized by high precipitation and temperatures, one with two stands located at low elevation, and one formed by four stands located at high elevation, the low- and high- Atlantic stands respectively.

2.3.3. Tree radial-growth data

At each stand from 6 to 26 trees (20 in Pyrenean bioregion, 77 in Mediterranean bioregion, and 31 and 103 in Low- and High-Atlantic bioregions respectively) were cored at 1.3 m height using Pressler increment borers (Table 2.2). These cores were air dried in the laboratory and mounted on wooden supports for further processing. The samples were sanded with progressively finer sandpaper until tree rings were clearly visible. Ring widths were measured at 0.01 mm resolution using measuring device systems (Lintab, F. RinnTech, Germany; Velmex Inc., USA). Visual cross-dating was performed and checked with the program COFECHA (Holmes, 1983). Tree-ring widths were transformed to basal area increments (BAI_t) (Figure 2.3), which allows removing the geometrical constraint of adding a volume of wood to a stem of increasing radius (Biondi & Qeadan, 2008), using the following formula:

$$BAI_t = \pi * (R_t^2 - R_{t-1}^2)$$

Where R_t is the radius of the ring formation year and R_{t-1} is the radius of the year preceding the ring formation. BAI_t was used to compute different analyses of tree growth variability and determine the 1980s climate shift effects on the studied beech stands. We calculated standardized BAI values by dividing the raw BAI values by the mean BAI value.

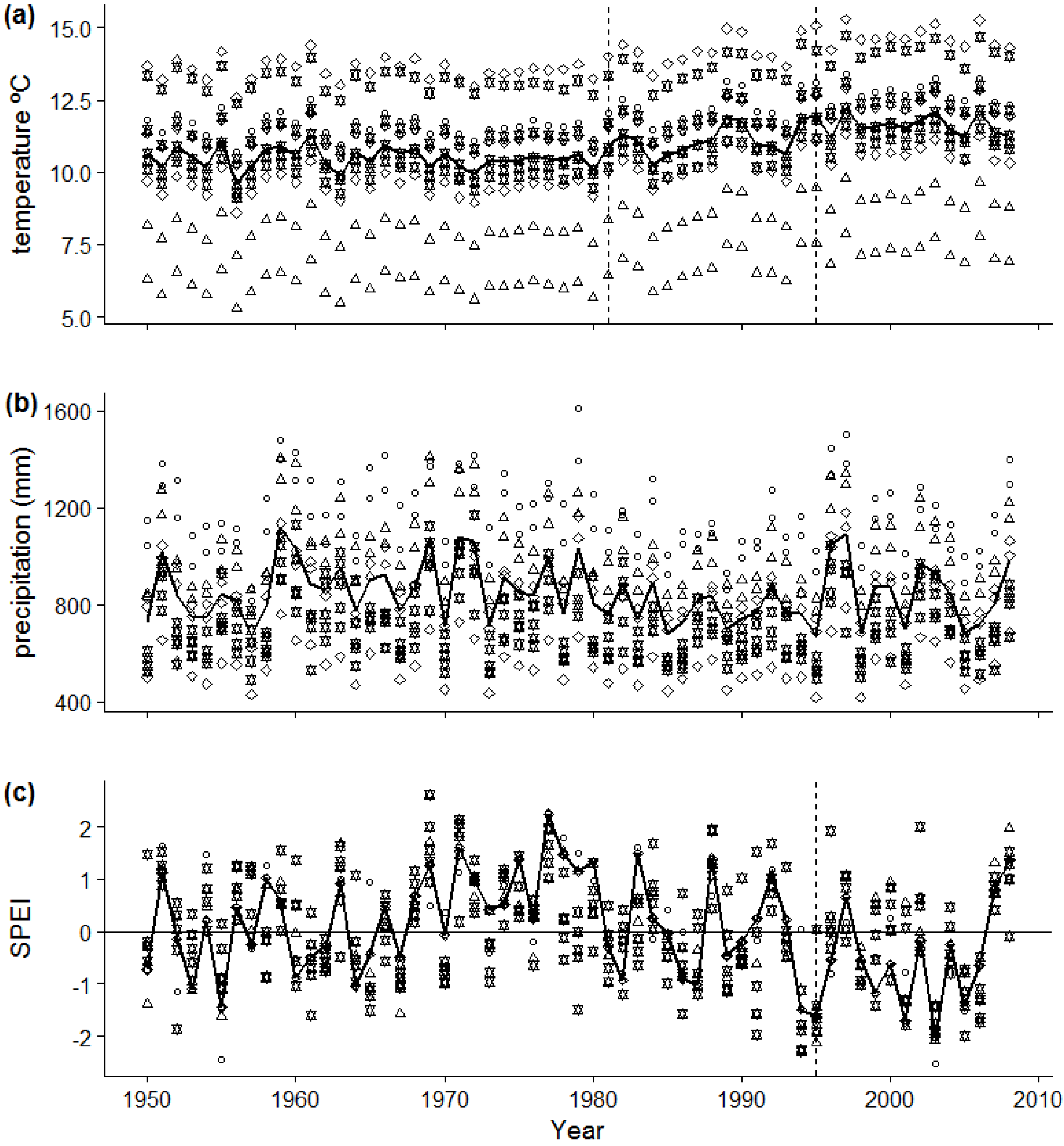

Figure 2.2. (a) Temperature, (b) precipitation and (c) Standardized Precipitation and Evapotranspiration Index (SPEI) on the area during 1950-2008 period. Bold lines represent mean values. Points represent single site values. Vertical dashed lines represent the detected shifts on the mean temperature and SPEI series. Symbols indicate the biogeographical area: Mediterranean (stars), Pyrenean (triangles), low-(circles) and high-elevation Atlantic (rhombus).

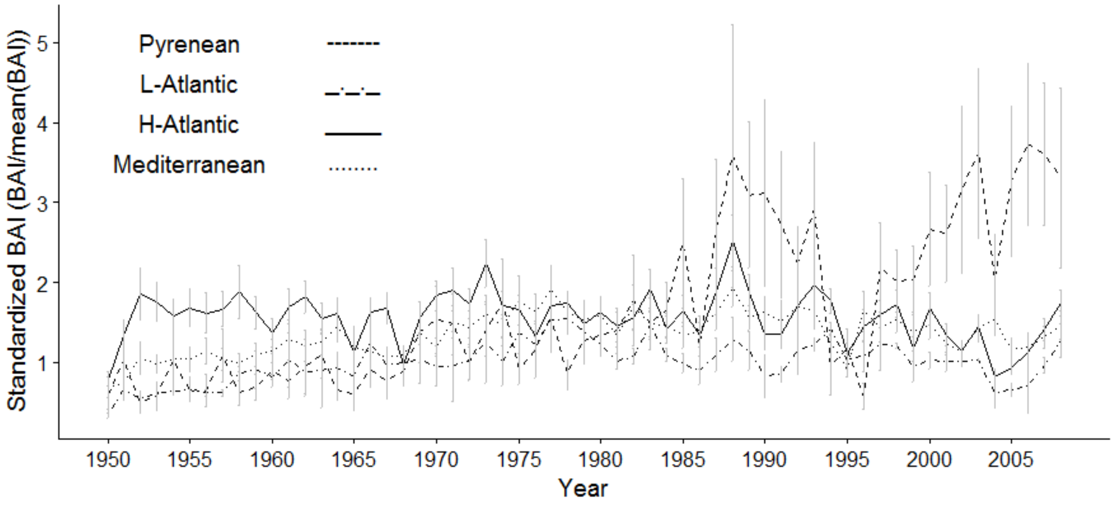

Figure 2.3. Mean series of standardized basal area increment (basal area increment / mean basal area increment) of the Pyrenean, high- (H-) and low-elevation (L-) Atlantic and Mediterranean forests. Values are means ± SE.

Tree-ring width data were detrended to calculate mean series of ring-width indices for each site so as to assess the quality of each site chronology. In short, individual horizontal series were fitted using the mean of the series to obtain dimensionless ring-width indices. We calculated several dendrochronological statistics based on these chronologies (Table 2.2). Specifically, we calculated the first-order autocorrelation of ring-width data; and the mean sensitivity, mean inter-series correlation, and Expressed Population Signal (EPS) of ring-width indices. Such statistics were calculated on data from 1950 until present. These analyses were carried out using the *dplR* package (Bunn et al. 2018).

To quantify short-term tree growth response to drought, we calculated the number of years with extreme low growth at individual level (hereafter, individual pointer years), from 1950 to 2008. Individual pointer year analyses reflect growth variability at inter-annual scales and may be associated to extreme climate events, such as droughts, frosts, etc. (cf. Schweingruber et al. 1990). To detect individual pointer years we used the function *pointer.norm* of the package *pointRes* (van der Maaten-Theunissen et al. 2015). Individual pointer years were calculated using normalized growth deviations in a five years length window, with a >0.5 threshold on the so-called Cropper values (Cropper, 1979). As we were interested in warming- and drought-related growth decline, we analyzed the individual negative pointer years only. Furthermore, we also defined regional pointer years as those years in which more than 50% of the trees per biogeographical region presented an individual pointer year. With these metrics we expect to see if climate shift has changed the pattern of extreme short-term low growth episodes.

To quantify mid-term tree growth response to drought, we analyzed abrupt growth changes resulting in longer periods of low growth. This was accomplished using the function *breakpoints* from the package *strucchange* (Zeileis et al. 2003). We set that minimum distance between breakpoints cannot be shorter than 10% length of the tree-ring series, in order to avoid changes in shorter BAI trends. Therefore, a year with an abrupt growth change indicates a growth deviation that last at least for more than 6, giving an intermediate time-scale effect compared with the one offered by pointer years. As in the case of pointer years, we only analyzed negative abrupt growth changes. Finally, we also evaluated long-term growth trends, calculated as the slope of the linear regression between BAI raw data series and calendar years in two different periods (1950-1979 and 1980-2008). These long-term growth trends indicate whether, in overall, growth is increasing or decreasing before and after the 1980s climate shift (Camarero et al. 2018).

Site name (code)	MAT (ºC)	MAP (mm)	Elevation (m a.s.l.)	Biogeographical region	AI	Mean DBH ± SE (cm)	Mean Age at 1.3 m ± SE (years)
Aisa (AIS)	6.5	1054	1105	PYR	173	19 ± 2	78 ± 5
Bertiz (BER)	11.6	1111	300	L-ATL	106	20 ± 1	126 ± 3
Diustes (DIU)	10.7	658	1320	MED	71	15 ± 1	90 ± 2
Eraso (ERA)	12.0	1208	600	L-ATL	110	16 ± 1	103 ± 4
Gamueta (GAM)	8.4	972	1400	PYR	126	25 ± 2	179 ± 24
Izki (IZK)	10	889	800	H-ATL	99	15 ± 1	94 ± 4
Lokiz (LOK)	11.6	845	984	H-ATL	83	14 ± 1	120 ± 7
Luesia (LUE)	11.7	691	1250	MED	69	16 ± 1	77 ± 3
Monrepos (MRE)	10.9	744	1290	MED	78	14 ± 1	95 ± 5
Montsec (MSC)	10.3	802	1340	MED	88	16 ± 1	90 ± 5
Montseny (MNY)	13.5	702	1530	MED	62	12 ± 2	111 ± 6
Opakua (OPK)	10.0	889	975	H-ATL	99	19 ± 1	133 ± 9
Peiró (PEI)	10.89	744	1350	MED	78	19 ± 2	96 ± 10
Urbasa (URB)	11.58	845	920	H-ATL	83	30 ± 1	148 ± 5
Arutz (ART)	13.9	556	1000	H-ATL	50	16 ± 1	94 ± 5

Table 2.2. Main statistics of the tree-ring width data considered from 1950 to the present.

2.3.4. Statistical analyses

To evaluate differences between tree growth before and after the climate shift we used the following linear mixed model:

$$Y_{ij} = \alpha_{ij} + \beta_1 * period_i + \beta_2 * DBH_{ij} + \beta_3 * biogeography_j + \beta_4 * (period_i * DBH_{ij} + \beta_5 * (period_i * biogeography_j) + \beta_6 * (DBH_{ij} * biogeography_j) + \epsilon_{ij}$$

where Y_{ij} represents the growth variable, either negative individual pointer years, negative abrupt growth changes or long-term growth trends. The sub index *i* represents the stand level and the sub index *j* represents the tree level; α_{ij} represents the random effect for each tree *j* nested in each stand *i*; β_1 to β_6 are the coefficients for every fixed effect and their interactions; ε_{ij} is the error term for each tree *j* nested in each stand *i*. The fixed effects are: period, a factor with two levels, i.e., before (1950-1979) or after (1980-2008) the climate shift; biogeography, a factor with four levels determined by the aforementioned cluster analyses (Mediterranean, low- and high-elevation Atlantic, and Pyrenean) and diameter at breast height (DBH). Three different models were considered, one per each of the different tree growth variables (negative individual pointer years, negative abrupt growth changes and long-term growth trends). First, we evaluated the individual pointer years, using the total number of individual negative pointer years per tree as a response variable. Second, we analyzed the individual tree growth trends along each period. Finally, to evaluate the abrupt growth changes, we reduced the variability to stand level by calculating the percentage of trees in each stand that suffered an abrupt growth change, thus in this latter model DBH was also calculated at stand level and not at individual level, as well as the random effect that represented only the variability at stand level. The percentage of abrupt growth changes was log-transformed to achieve normality.

The models were fitted using the *nlme* package (Pinheiro et al. 2017). When significant influence of factors and interactions were found, post-hoc comparisons between levels of factors and interactions were done using the package *emmeans* (Lenth, 2018). All statistical analyses were performed in the R environment (R Core Team, 2018).

2.4. Results

2.4.1. Climate shift

We detected a significant climate shift on the mean annual temperature series of the studied stands (Figure 2.2a, Supplementary Materials, Figure S2). Specifically, two changes were observed on the temperature data, one in 1981 and another one in 1994 (Figure 2.2a), indicating the 1980s temperature increase and the 1990s warming hiatus. However, no changes were detected in the precipitation series along the studied period (Figure 2.2b), but a negative shift in August SPEI was detected in 1994 for most of the studied regions (Figure 2.2c).

2.4.2. Pointer-year analyses

Fewer individual pointer years were found after the 1980s climate shift than before (Table 2.3), a pattern independent of the biogeographical region (Table 2.4). A change in the effect of DBH on the number of pointer years was found after the climate shift (marginally significant interaction period*dbh, Table 2.4), changing from negative in 1950-1979 (mean ± SE = -0.03 ± 0.02) to positive in 1980-2008 (0.01 ± 0.02).

Considering regional pointer years (years were >50% of trees in a region showed an individual pointer year) we found that at Mediterranean and Atlantic forests, the number of regional pointer years increased after the 1980s climate shift (Figure 2.4). Contrarily, the number of regional pointer years decreased at Pyrenean stands (Figure 2.4). When analyzing the four regions altogether, no differences were found between regional pointer years before and after the 1980s ($p = 0.15$).

2.4.3. Abrupt growth changes

Abrupt growth changes varied among the two analyzed periods (Table 2.3), with a higher percentage of trees experiencing abrupt growth changes after the 1980s climate shift (Table 2.3, Figure 2.4). Such effect was independent of the biogeographical region or tree size (Table 2.4, Figure 2.4).

Variables	Period	
	1950-1979	1980-2008
Individual pointer years (No. pointer year tree/period)	8.73 ± 0.18	8.15 ± 0.18
Abrupt growth changes (% trees showing abrupt growth changes / site)	0.15± 0.04	0.37 ± 0.04
Long-term growth trends (regression coefficient BAI ~ calendar year, mm^2 $year^{-1}$)	18.2 ± 4.18	-3.56 ± 4.18

Table 2.3. Comparisons between values (means ± SE) of the studied tree growth variables (individual pointer years, abrupt growth changes, negative long term growth trends) for the periods 1950-1979 and 1980-2008, i.e., before and after the 1980s climate shift. All values showed highly significant (*p* = 0.001) differences between the two compared periods. BAI stands out for basal area increment.

	Pointer Years	Abrupt growth changes	Long-term growth trends
Period (Pre- or post-1980 shift)	**0.01**	**0.0005**	**<.0001**
Biogeographical región	0.37	0.23	0.33
DBH	0.33	0.33	0.37
Period * Biogeography	0.24	0.27	**0.0003**
Period * DBH	**0.05**	0.09	0.08
Biogeography * DBH	0.88	0.39	0.32

Table 2.4. Results of the linear mixed-effects models (ANOVA table) testing the different growth variables (individual pointer years, abrupt growth changes, long-term growth trends) as a function of period, biogeographical region (Pyrenees, Atlantic Low-elevation, Atlantic High-elevation and Mediterranean), tree size (DBH, diameter measured at breast height) and their interactions. Bold characters highlight significant (*p* < 0.05) variables.

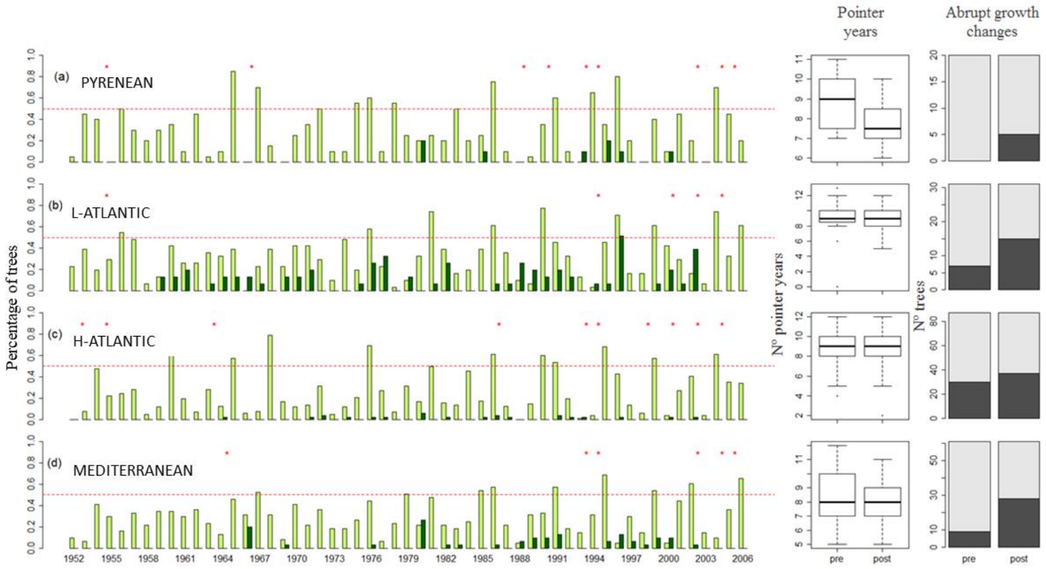

Figure 2.4. Percentage of individual pointer years per region (olive-green bars) and percentage of abrupt growth changes (dark-green bars), boxplots of number of individual pointer years detected before and after the 1980s climate shift and percentage of abrupt growth changes before and after the shift for (a) Pyrenean (PYR), (b) low elevation Atlantic (L-ATL), (c) high elevation Atlantic (H-ATL), and (d) Mediterranean (MED) stands. Red stars mark the dry years with Standardized Precipitation and Evapotranspiration Index values lower than -1.

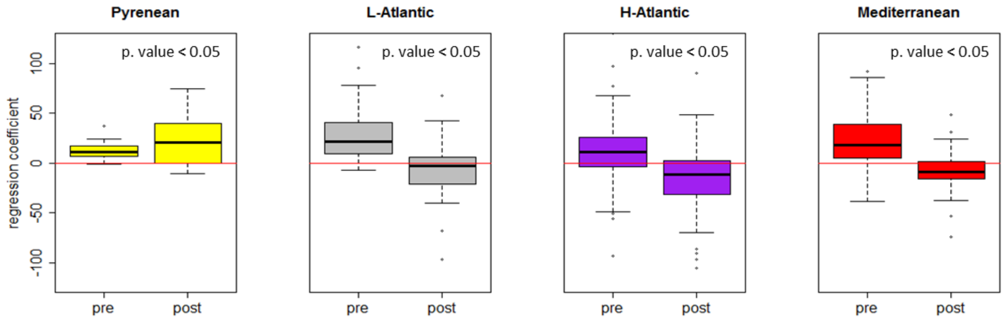

Figure 2.5. Boxplots of long-term growth trends of standardized basal area increment (BAI/ mean BAI) for the periods before (pre, 1950-1979) and after (post, 1980-2008) the 1980s climate shift. Values represent the coefficients of linear regressions among basal area increment and calendar year calculated for the four biogeographical groups: Pyrenean (yellow), low-elevation Atlantic (L-Atlantic, grey), high-elevation Atlantic (H-Atlantic, purple) and Mediterranean (red) and forests.

2.4.4. Long-term growth trends

We found overall positive growth trends before the climate shift that turned negative after the 1980s (Table 2.3, Figure 2.5). Such change was related to the biogeographical region (Table 2.4). Negative post-shift trends were found in forests from Mediterranean and Atlantic areas (Figure 2.5). Contrarily, positive growth trends were observed in Pyrenean forests (Figure 2.5). There was no effect of tree size on the long-term growth trends at any of the studied periods (Table 2.4).

2.5. Discussion

Understanding the temporal and spatial growth variability among contrasting biogeographical regions in response to recent climate shifts is fundamental to assess long-term changes in forest productivity, growth and adaptability of tree species to forecasted climate warming (Sánchez-Salguero et al. 2017b). Our results present a marked growth reduction after the 1980s climate shift in most beech stands investigated within southwest Europe, near the species' rear-edge. We also found a marked increase in the occurrence of negative abrupt growth changes across all biogeographical regions and a generalized decrease in long-term growth trends in many regions. Thus, while the number of individual pointer years per tree did not increase during the second studied period, all the other parameters pointed out a growth decline after the 1980s climate shift. Notably, the Pyrenean stands, which are located at higher elevation and present the low temperature and high precipitation values, were the only forests showing a long-term growth enhancement. These results agree with previous studies observing warming related growth decreases in southern and xeric edges of beech distribution (Gutiérrez, 1988; Jump, Hunt & Peñuelas, 2006; Piovesan et al. 2008; Zimmerman et al. 2015; Dulamsuren et al. 2016; Knutzen et al. 2017; but see Tegel et al. 2014; Hacket-Pain & Friend, 2016; Cavin & Jump, 2017). However, the comparison between regions allowed us to disentangle that regional climate variability modulates warming-induced growth reductions.

Although there was no increase in individual pointer years after the climate shift, a different effect of tree size (DBH) between periods was observed (Table 2.4). Before the 1980s, larger trees presented a lower number of pointer years, which changed after the climate shift. This change suggests that under warming periods, larger trees experience harsher conditions making them more vulnerable to drought-related growth decline and potential damage (Benett et al. 2015). This size-related effect could be explained by physiological constraints related to the higher xylem tension that suffer the hydraulic systems of larger trees (Ryan et al. 2006). However, the reverse pattern has also been observed and attributed to a higher hydraulic capacitance due to more sapwood volume in larger trees (Colangelo et al. 2017). Moreover, the frequency of individual pointer years differed among periods in some of the biogeographical regions. Regional pointer years (>50% of trees in a region) increased in three out of the four regions, as they did in temperate beech populations of central Europe (Zimmerman et al. 2015; Knutzen et al. 2017). Such increase on the number of regional pointer years indicates that, even if the number of individual pointer years is similar between periods, their distribution along the periods is different. Individual pointer years before the 1980s shift were more homogeneously distributed (i.e., more years with equal number of trees showing pointer years) and more heterogeneously distributed after the shift (i.e., some years with many trees having a pointer year and other years with almost no tree having pointer years, i.e., extreme growth responses) (Supplementary Materials, Figure S4). That could be explained by an increase of growth sensitivity to drought caused by an increase of dry spells as climate warms, thus reducing radial growth rates (van der Werf et al. 2007). The fact that the hottest and most extreme droughts of the study period occurred after 1980s supports this hypothesis (Figure 2.4). Pyrenean forests were the only ones where the number of regional pointer years did not increase. The Pyrenean region is relatively cooler than the other regions, moreover it also registers high precipitation, thus, droughts there are expected to be less intense, with lower impacts on those forests (Greenwood et al. 2017; Gazol et al. 2018b). Therefore, the climatic conditions of the Pyrenees may benefit beech stands growth and provide them topographic refuges against the climate warming. Other climate extremes (e.g., frosts) could explain this biogeographical differentiation. Since Pyrenean forests are located in the coldest conditions, they might be also more prone to suffer early-spring or late-autumn frost damage resulting in narrow rings (Príncipe et al. 2017). As Pyrenean stands has equal number of regional pointer years before and after 1980s shift, but extreme droughts occurred mostly after 1980s, our results suggest that contrary to the other regions, frost could be limiting growth more than drought on these stands.

The percentage of abrupt growth changes per forest (i.e., percentage of trees displaying abrupt growth reductions lasting for more than 6 years) increased after the 1980s probably as a consequence of the higher number of extreme droughts observed after the 1980s climate shift (Camarero et al. 2015). For instance, Vanoni et al. (2016) found that higher drought intensity increased the probability to suffer an abrupt growth change. In this case, a similar pattern is shown for the four biogeographical regions, including the Pyrenean stands. Here frost events may not play a relevant role as it was the case in pointer years, as beech can recover quickly from late frosts (Príncipe et al. 2017).

The long-term growth trends indicate that tree growth had an increasing tendency before 1980s climate shift, but this changed in the subsequent decades. Consequently, during the 1980-2008 period a decreasing growth trend was observed in all regions with the exception, again, of Pyrenean forests (Figure 2.4). These results seem to indicate a growth constraint after the climate shift and match with previous studies reporting a growth decline after 1980s for beech in the southern distribution limit of the species (Jump, Hunt & Peñuelas, 2006; Piovesan et al. 2008; but see Tegel et al. 2014; Cavin & Jump 2017) and also in central Europe (Zimmerman et al. 2015; Dulamsuren et al. 2017). However, Pyrenean forests did not show any growth decrease, in terms of long-term growth-trends, after the climate shift. These mountain forests present a climate that can buffer the stressing conditions of the warming observed after the climate shift. As summer temperatures strongly limit beech growth at high elevation (Dittmar , Zech & Elling, 2003), the warming trend could be positively influencing beech growth in the Pyrenean stands, as observed in high elevation beech forests in central Europe (Dulamsuren et al. 2017). Moreover, the abrupt topography of the Pyrenees generates a wide range of microclimatic conditions, which can alter climate-growth relationships (Adams, Bernard & Loomis, 2014), resulting in a possible range of environments where beech can find more appropriate conditions (e.g., lower atmospheric water vapor demand and evapotranspiration, higher soil moisture). Such effects of topography and elevation would be also expected in Mediterranean sites with similar elevation as Pyrenean forest. Nevertheless, precipitation is usually lower in the Mediterranean area, mainly summer, and even if these forests are located at high elevation, negative long-term growth trends were observed. Our results suggest a divergent response in the studied beech forests near the southern distribution limit of the specie. Such divergence is in accordance with the idea that vegetation chronic stress caused by increased drought frequency is higher in drier sites at the Iberian Peninsula (Carnicer et al. 2011). Alternatively, legacies of historical forest management, such as removing big and fast-growing individuals though selective logging or former coppicing in some stands (Camarero et al. 2011) could have caused reduced growth rates. This explanation does not seem plausible on our results since most sampled forests had similar ages (Table 2.1).

The decreases of tree growth after the climate shift could be caused by multiple reasons. Drought stress suffered by consecutive drought episodes can promote higher defoliation rates (Carnicer et al. 2011), and as a consequence lower photosynthetic carbon gain and a reduction in radial growth and forest productivity (Gazol et al. 2018b). Increasing temperatures and drought stress may also limit water consumption and enhance water-use efficiency, as seen in declining silver fir populations of the Pyrenees, promoting a long-term growth reduction (Linares & Camarero, 2012). Moreover, warming temperatures and drought stress may promote carbon starvation and hydraulic failure, which can compromise tree performance and cause die-off episodes (Adams et al. 2009; McDowell et al. 2008; Camarero et al. 2015; Adams et al. 2017). As explained above, the most severe droughts in the study area (e.g., 1986, 1994, 2005) occurred after the climate shift, and it is well known that trees can have legacy effects after droughts lasting several years (Anderegg et al. 2015a; Peltier, Fell & Ogle, 2016; Gazol et al. 2017a; Gazol et al. 2018b) that, together with an increase in the time of recovery (Schwalm et al. 2017), could compromise the long-term growth of some beech forests in a nearby future. Even if we did not study tree mortality, we focused on how tree growth can be constrained under a period of high temperatures. Low growth or productivity can be a signal of impending tree death, even several years before the mortality episode occurs (Camarero et al. 2015; Rogers et al. 2018), thus our results anticipate the vulnerability of the studied forests if the temperature increase persists. Lastly, our findings are relevant to better understand how warmer and drier climate conditions will impact similar temperate mesic forests dominated by deciduous tree species. These impacts will vary as a function of climatic conditions acting at different spatial scales, and the negative effects of droughts on trees could be buffered in topographic refuges with favorable conditions.

In conclusion, we show that after the 1980s climate shift a divergent response was observed on the studied beech forests near the species’ rear edges. Mediterranean and Atlantic beech stands showed negative growth trends and growth limitations after the 1980s shift, but Pyrenean stands presented a long-term growth enhancement. These biogeographical differences indicate that regional climate characteristics can buffer, at some extent, the negative effects of warmer and drier conditions on beech forests near their southern distribution limits in Europe. Our results suggest a high vulnerability of beech forests in the northeast Iberian Peninsula out of the Pyrenean stands, which agrees with the forecasted beech retraction in the area (Benito-Garzón et al. 2008). Therefore, under the projected warming scenario, the future distribution range of beech in the northeast Iberian Peninsula would be likely restricted to cold and wet mountainous areas acting as climatic refuges.

Chapter 3

Silver fir growth responses to drought depend on interactions between tree characteristics, soil and neighbourhood features

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3.1 Abstract

Mixed forests are expected to be more productive and resilient against disturbances than pure forests. However, tree to tree interactions are complex and vary depending on tree characteristics and multiple site features including soil properties. Such complexity is not normally accounted for in studies of mixing effects on tree response to drought. Here, we evaluate if neighbourhood tree identity influence soil biotic and abiotic characteristics in three mature, mixed Silver fir (*Abies alba*) forests. Further, we investigate the relationships between radial growth response to drought, tree characteristics (growth rate, size and competition pressure), tree neighbourhood, and soil physico-chemical and biological properties. Patterns of covariation between tree size, competition pressure, soil microbial composition, and growth recovery after drought were observed among different neighbourhood types. Slow-growing, small Silver fir trees experiencing high competitive pressure were associated with higher proportions of Scots pine (*Pinus sylvestris*) in the neighbourhood, high soil C:N ratios, and showed a faster growth recovery after drought. A neighbourhood dominated by broadleaf species (mainly European beech, *Fagus sylvatica*) was associated with high biomass of arbuscular mycorrhizal fungi, and low biomass of Gram-positive bacteria and Eukaryote, together with lower tree growth recovery. Therefore, coexistence with other Silver fir, Scots pine or European beech trees is associated to different covariation patterns of tree, soil and drought performance variables of the target Silver fir trees. Finally, our study remarks that combining tree, soil and neighbour variables at individual level helps to understand patterns of tree growth and growth response to drought under different stand mixtures.

3.2. Introduction

Recent research suggests that tree diversity increases forest productivity (Vilà et al. 2007; Paquette & Messier, 2011; Ruiz-Benito et al. 2014; Liang et al. 2016; but see Dormann, Schneider & Georges, 2019) and potentially enhances the resistance of ecosystems to climate extremes (Isbell et al. 2015: Gazol & Camarero, 2016, but see Grossiord et al. 2014a). However, tree diversity relationships with productivity and resilience to extreme events are very complex and depend on many factors such as climate conditions, soil characteristics, stand density, and species composition (Ammer, 2019). All these variables may be related to each other resulting in a complex network of interactions influencing individual tree performance and its resilience to drought.

Some studies report greater resilience to drought in mixtures (Lebourgeois et al. 2013; Metz et al. 2015; Vitali, Forrester & Bauhus, 2018) while others do not (Merlin et al. 2015; Goisser et al. 2016). The disparate results concerning tree diversity effects on forest growth resilience during drought in mixed stands may be reconciled by considering additional factors. For example, complementary effects may depend on size distributions in the stand (i.e., structural diversity), independently of the tree species present. Thus, changes from complementary to competition depending on size class combinations might occur (Madrigal-González et al. 2016). Moreover, positive diversity effects on growth may not be equally strong in different environments (González de Andrés et al. 2017; Ratcliffe et al. 2017) because resource availability can determine whether complementarity or competition is the dominant relationship between neighbouring trees (Paquette & Messier, 2011). Mixture effects may also depend on species-specific relationships, which do not need to be bidirectional, causing different mixtures responses depending on neighbourhood identity (Vitali, Forrester & Bauhus, 2018). The functional niche occupancy of all neighbourhood species (i.e., functional diversity) can also determine responses to drought through a more efficient use of the limited resources (Gazol & Camarero, 2016; Granda, Gazol & Camarero, 2018).

Species identity can influence soil chemical, physical and biological properties (hereafter soil conditions). Such influence could affect tree radial growth and performance in response to drought. High specificity in microbial communities under different tree species has been observed (Urbanová, Šnajdr & Baldrian, 2015), which may be exacerbated when comparing communities under deciduous angiosperms against evergreen gymnosperms, since the former are usually linked to a more rapid decomposition of litter than the latter (Augusto et al. 2015). Thus, neighbourhood identity may influence microbial communities around a single tree. However, to what extent a given microbial community may be related to individual tree growth performance or resistance to drought is unknown. Overall, neighbour effects on tree performance might depend on a complex network of interactions. In this regard, Mina et al. (2018) showed the high complexity of the effects of several variables (age and stand development, topography, soil, etc.) on productivity across different mixtures. All this variability is rarely taken into account when evaluating tree performance under drought conditions, and when so, it is assessed at stand level. Thus, covariation between tree characteristics, soil biotic and abiotic characteristics and tree neighbourhood is expected to be related to different growth performance during drought.

Here we explore the relationships and covariation between aboveground (trees) and belowground (soil microbiota) diversity, soil conditions, tree characteristics (size, growth rate and competition pressure), and growth resistance to drought at the individual scale. We study three mixed Pyrenean forests dominated by Silver fir (*Abies alba* Mill.), where Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) co-occur. These forests represent the southern distribution limit of the species, which make them of particular interest to understand how Silver fir could respond to future warming in climate. We aim to address the following questions: (i) Are neighbour species related to the microbial composition and soil physic-chemical characteristics under focal *Abies alba* trees? And (ii) Which are the covariation patterns of growth response to drought, tree characteristics (size, growth rate and competition pressure), soil biotic and abiotic characteristics, and neighbourhood composition in focal *Abies alba* trees?

3.3. Material and methods

3.3.1 Study sites

Three different montane, mixed conifer-broadleaf forests were selected in the Spanish Pyrenees (Paco Ezpela, Jasa and Orús; see more detailed information in Table 3.1, Figure 3.1). All three forests grow in humid, north-facing slopes and are dominated by Silver fir (*Abies alba* Mill.). In all three forests, European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.) grow as secondary species (Table 3.1). Paco Ezpela has higher percentages of *F. sylvatica* and *P. sylvestris* basal area (40%) than Jasa and

Orús, (20 and 30%, respectively). The Pyrenees represent the southernmost distribution limit of *A. alba* in Europe, and cases of drought-induced dieback have been reported in some sites (Camarero et al. 2011). Silver fir forests where managed in the Pyrenees during the past century (Cabrera, 2001), such practices were abandoned in the last decades of the past century.

Site	Latitude (N)	Longitude (W, E)	Elevation (m a.s.l.)	Aspect	Mean anual temperature[1] (ºC)	Total anual precipitation[1] (mm)	*Abies alba* (%)	*Fagus sylvatica* (%)	*Pinus sylvestris* (%)
Paco Ezpela	42º 45’	0º 52’ W	1078	N-NE	10.8	1153	60	20	20
Jasa	42º 42’	0º 38’ W	1378	N-NE	9.5	1210	80	10	10
Orús	42º 34’	0º 06’ E	1306	N-NW	10.0	1195	70	15	15

[1] Climate data were obtained from the following nearby climate stations: Ansó (42º 45’ N, 0º 49’ W, 858 m) for Paco Ezpela; Jasa (42º 41’ N, 0º 40’ W, 936 m) for Jasa; and Broto (42º 36’ N, 0º 07’ W, 903 m) for Orús.

Table 3.1. Site characteristics for each one of the three Pyrenean *Abies alba* forests studied. The last three columns indicate relative basal area for each tree species.

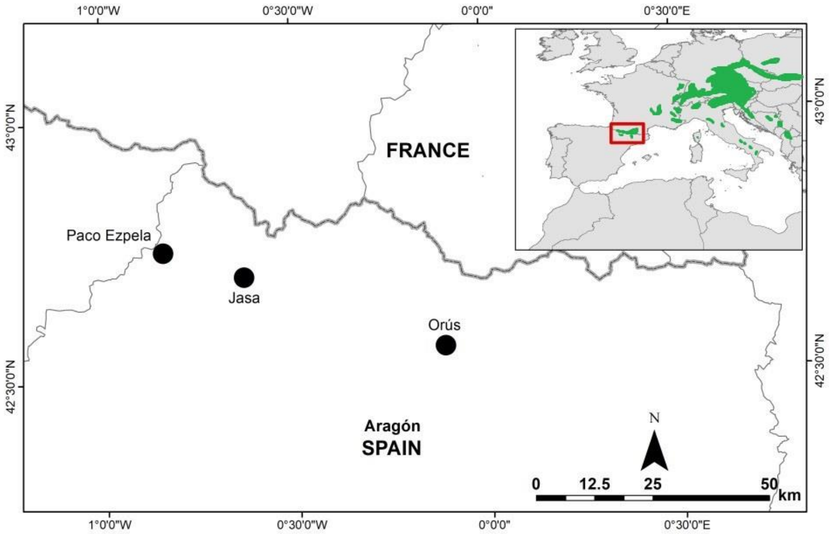

Figure 3.1. Map showing the north of Aragon region (Spanish Pyrenees) and its borders with France (dark line) and other Spanish and French regions (grey lines). Black points represent each one of the studied forests (Paco Ezpela, Jasa and Orús). On the top right of the image, there is a European map with a red square on the Pyrenees and the distribution of Silver fir in Europe.

3.3.2. Drought selection

To characterize drought severity, 1.1-km^2 resolution series of the Standardized Precipitation-Evapotranspiration Index (SPEI) from 1961 to 2015 were used (Vicente-Serrano et al. 2017). This is a multi-scalar drought index with negative values indicating a negative cumulative water balance calculated at different time scales and as a function of precipitation and temperature (Vicente-Serrano, Beguería & López-Moreno, 2010). The August SPEI calculated at 12-month scale was used to select 2005 and 2012 as drought years because they were the most severe and recent dry spells affecting the three study forests (Supplementary Materials, Figure S1).

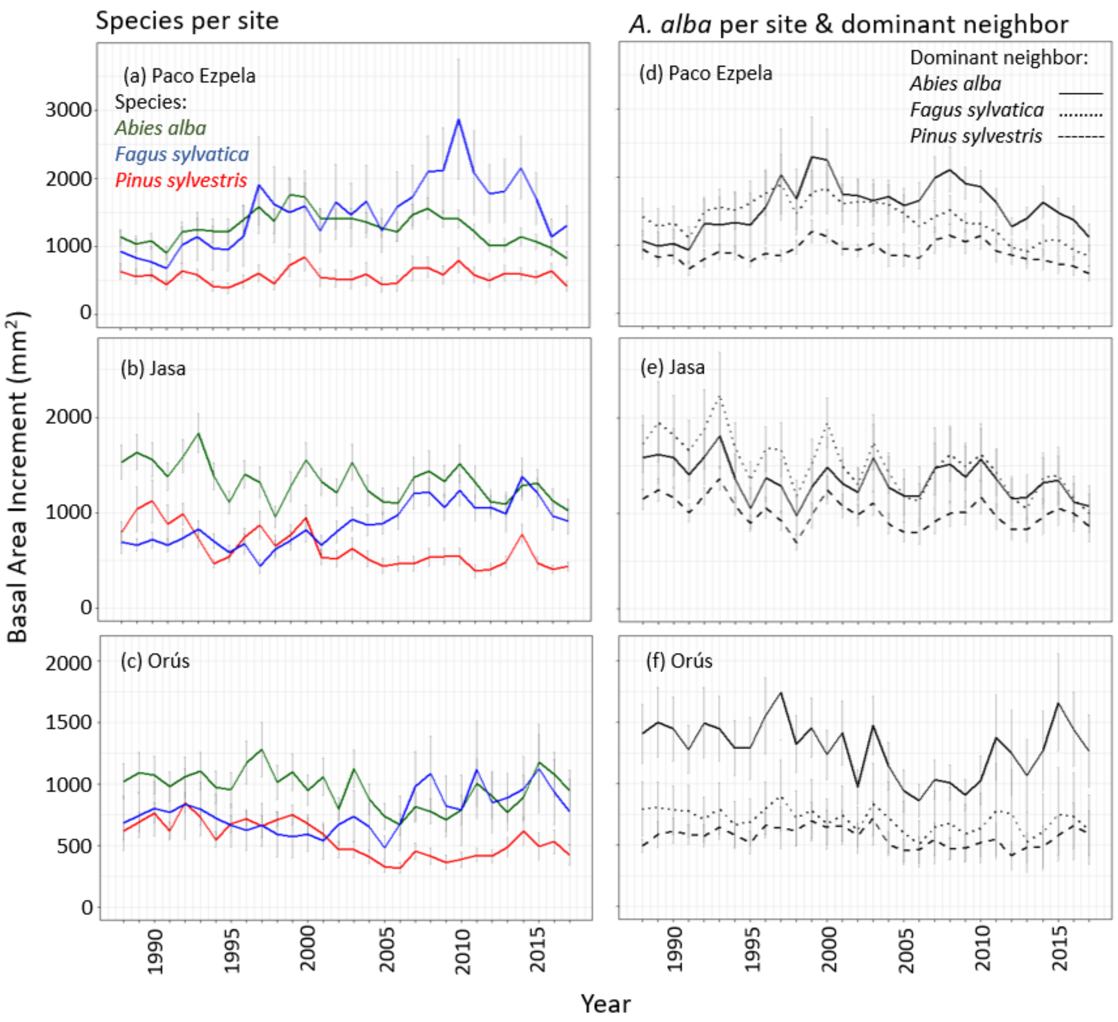

Figure 3.2. Mean basal area increment (BAI) ± standard error (SE) of *Abies alba* (green lines), *Fagus sylvatica* (blue lines, broadleaf species) and *Pinus sylvestris* (red lines) at (a) Paco Ezpela, (b) Jasa and (c) Orús study sites. Mean BAI of *A. alba* growing with: conspecific neighbours (solid lines), broadleaf species (dotted lines) and *P. sylvestris* (dashed lines) at (d) Paco Ezpela, (e) Jasa and (f) Orús sites. Note that the *y* axes are common between figures from the same site, but not between different sites.

3.3.3. Tree growth and drought performance

At each forest 30 adult and apparently healthy *A. alba* individuals were selected as focal trees. Trees were randomly selected within three categories based on dominant neighbours. The categories were: *A. alba*, *P. sylvestris* and broadleaf species (mainly *F. sylvatica*) as main neighbours (Neighbour distance ranged from 0.5 to 11 meters). Radial growth of all focal *A. alba* and a selection of *F. sylvatica* and *P. sylvestris* individuals was evaluated using dendrochronology (Figure 3.2). In total 150 trees (90 *A. alba*, 25 *F. sylvatica* and 35 *P. sylvestris* trees) were cored (for detailed information on neighbour identity and characteristics see Supplementary Materials, Tables S1, S2, S3 and S4). We randomly selected healthy, non-supressed *F. sylvatica* and *P. sylvestris* neighbours to core.

Each tree was cored at breast height (1.3 m) using Pressler increment borers. Afterwards, cores were taken to the laboratory, mounted and air dried. Then the cores were sanded until tree rings were easily recognizable. Visual cross-dating was carried out. Ring width measurement at 0.01 mm resolution was done using a measuring device system (LINTAB-TSAP, F. Rinn, Germany). Cross-dating was checked with the COFECHA program (Holmes, 1983). To assess the quality of tree-ring width chronologies basic dendrochronological statistics were calculated (Supplementary Materials, Table S2). To remove geometrical growth constraints, we transformed ring widths to basal area increment (BAI) following Biondi and Qaedan (2008). BAI series for each of the three species and site were reconstructed from 1988 to 2017 for the three tree species (Figure 3.2a, b, c) and for *A. alba* individuals surrounded by other *A. alba*, broadleaf species or *P. sylvestris* (distances between 0.5 and 11 meters from the focal tree) (Figure 3.2d, e, f). Mean BAI values from the last 30 years (hereafter BAI30) were used as a measure of tree growth rate. Mean BAI values give an idea of absolute growth, indicating which individuals perform better under normal conditions. We selected a 30-year time span because in the 1986 there was an extreme drought that triggered a dieback process in some Pyrenean *A. alba* populations (Camarero et al. 2011).

Growth response to extreme drought was measured as resistance (*Rt*), recovery (*Rc*) and resilience (*Rs*) indices (Lloret, Keeling & Sala,. 2011) based on the ratios of pre-drought, drought and post-drought growth BAI values. The indices were calculated as follows:

$$Rt = \frac{BAI_D}{BAI_{preD}} \quad (1)$$

$$Rc = \frac{BAI_{postD}}{BAI_D} \quad (2)$$

$$Rs = \frac{BAI_{postD}}{BAI_{preD}} \quad (3)$$

Where BAI_{preD} is the mean BAI of the three years preceding the drought (2002-2004 and 2009-2011), BAI_D is the BAI of the 2005 and 2012 drought years, and BAI_{postD} is the mean BAI of the three years following the drought (2006-2008 and 2013-2015). We averaged *Rt, Rc* and *Rs* values for the 2005 and 2012 droughts to have a single value per tree, which reflected the tree performance across the two droughts (Supplementary Materials, Figure S2).

3.3.4. Competition and neighbourhood identity

For every focal *A. alba* tree, we measured its nearest neighbour in each cardinal point and annotated its species identity, diameter at breast height (DBH) and distance from the target tree. Mean distance (± SE) of neighbours were 3.4 ± 0.2 m in Paco Ezpela and Jasa, and 3.5 ± 0.3 m in Orús. *F. sylvatica* was the dominant broadleaf species, nevertheless the presence of other broadleaf species was also noted (Supplementary Materials, Table S4).

The competitive pressure of a focal tree due to its direct neighbours was calculated following Hegyi (1974) distance-dependent competition index (hereafter DCI). The index was calculated as follows:

$$DCI = \sum_{n=i} \frac{DBHj}{DBHi} * \left(\frac{1}{DISTij}\right) \quad (4)$$

Where DBH_i is the DBH of the focal tree, DBH_j is the DBH of the neighbour tree, and $dist_{ij}$ is the distance between both trees. This index measures the competition relative to the size (DBH) of the focal tree. High values of DCI represent focal trees that are smaller than their neighbours and low values of DCI reflect the opposite.

We calculated the % of each neighbour type using basal area increment (*A. alba*, broadleaf species, *P. sylvestris*). This approach reflected the importance of the neighbourhood depending on if it was dominated by conspecific trees, another conifer or a broadleaf species. Neighbour type was used as a single categorical variable (three types representing the specie which had higher % of basal area; *A. alba*, broadleaf species, *P. sylvestris*) or as three numerical variables (% of each category) depending on the analyses (See Statistical analyses section). BAI series of *A. alba* trees surrounded by each dominant neighbour class and site were computed from 1988 to 2017 (Figure 3.2d, e, f).

3.3.5. Soil sampling and analyses

Under each focal *A. alba* tree three soil subsamples were collected below the projection of the canopy (up to 2-3 m from the tree stem), one at each 120^o respect to each other. To collect the subsamples a soil borer of 20 cm was used. Litter was removed before soil sample collection. The three subsamples were mixed in a plastic bag and taken to the laboratory. Once in the laboratory each sample was divided in two equal parts. One was saved on the freeze. The other was air dried on a greenhouse and sieved with a 2-mm mesh size. The unfrozen sample was used to measure: concentrations of C, N, and P; percent organic matter; pH, electric conductivity, and the C:N ratio. Soil C, N and P were determined with an elemental analyser (Element Analyzer VarioMAX N CM, Hanau, Germany). Soil texture was analysed and classified following the USDA criteria (Supplementary Materials, Figure S3). Soil texture analyses were carried out to evaluate differences in water retention capacity.

The frozen soil samples were used for phospholipid fatty acid (PLFAs) analyses to quantify the biomass of major groups composing soil microbiota. The samples were lyophilized and aliquots of 2 g used for lipid extraction. Lipids were extracted with a one-phase chloroform-methanol-phosphate buffer solvent. Phospholipids were separated from nonpolar lipids and converted to fatty acid methyl esters before analysis following the methodology described by Buyer & Sasser (2012). The resulting fatty acids methyl esters (FAMEs) were separated by gas chromatography using an Agilent 7890A GC System (Agilent Technologies, Wilmington, DE) equipped with a 25-m Ultra 2, 5%-phenyl-methylpolysiloxane column (J&W Scientific, Folsom, CA) and with a flame ionization detector (FID). FAMEs identification and quantification were carried out using the PLFAD1 method of Sherlock® software version 6.3 from MIDI, Inc (Newark, DE, USA). The internal standard 19:0 phosphatidylcholine (Avanti Polar Lipids, Alabaster, AL, USA) was used for quantification of FAMEs. Specific PLFAs were used as biomarkers to quantify biomasses of eukaryotes, Gram-positive and Gram-negative bacteria, actinobacteria, fungi, arbuscular mycorrhizal (AM) fungi and anaerobic bacteria (Frostegård & Bååth, 1996; Zelles, 1997, 1999).

3.3.6. Statistical analyses

To perform the following analyses all variables were centred within the site level. This was done to reduce the variability between sites of some of the studied variables (Supplementary Materials, Figures S4, S5). Centring the variables allowed us focusing on the variability between trees and the covariation of the studied variables at the tree level while removing confounding effects due to the variation between sites. DCI was logarithmically transformed prior to be centred to obtain a normal distribution.

To find common patterns between aboveground diversity (neighbourhood type) and soil biotic and abiotic characteristics we performed different analyses. First, multivariate analyses of variance (MANOVA) were performed on soil biotic and abiotic variables. We fitted two models, one with abiotic soil characteristics (soil C, N, P, percent of organic matter, pH, electric conductivity and the C:N ratio) and one with PLFA groups (eukaryotes, Gram-positive and Gram-negative bacteria, actinobacteria, fungi, arbuscular mycorrhizal (AM) fungi, anaerobic bacteria and total fungi and bacteria) as dependent variables. Dominant neighbor type (categorical variable, three levels: *A. alba, P. sylvestris* and broadleaved) was used as independent variable. Then, two Principal Component Analyses (PCA), one for soil abiotic variables and the other for the soil biotic variables (PLFA groups), were done. We selected the PCA axes with eigenvalues > 1 and correlated them (Pearson correlation) to evaluate the relationships between soil biotic and abiotic variables. Finally, we correlated soil biotic and abiotic axes to know the influence they exert to each other (Pearson correlation).

To evaluate the covariations between different variables and their effect on Silver fir performance during drought we used a network analysis. First all variables were classified in four groups: growth performance to drought (*Rt*, *Rc*, *Rs*), tree characteristics (BAI30, DBH, DCI), neighbours' type (numerical variable; % *A. alba*, % *P. sylvestris,* % broadleaf species) and soil characteristics (selected axes of PCA analyses). All these variables were represented as nodes in the network and significant relationships between them as edges (links between nodes). Pearson correlations and Kendall tau were used to test significance of the correlation coefficients. To do the analyses the *igraph* package (Csardi & Nepusz, 2006) was used. A value of centrality for each node was calculated using the *degree* function, which counts the number of connections of each node, in our case, significant correlations. Thus, variables showing a high number of significant correlations will present high centrality values, and variables that present few numbers of significant correlations will have low centrality values. Network analyses allow us to show the full complexity of the relationships in our study system and to enlighten patterns of covariation between apparently different data sources (e.g., tree rings and PLFAs) (Ramirez et al. 2018). All statistical analyses were performed in R (R Core Team, 2018).

3.4. Results

3.4.1. Tree growth and response to drought between sites and neighbour types

Tree growth showed variation between species but a common growth reduction in response to drought in *A. alba* between sites (Figure 3.2). In Paco Ezpela, *F. sylvatica* presented higher BAI than the other two species after the 2005 drought (Figure 3.2a). This is accompanied by decreases in growth of *A. alba* surrounded by *F. sylvatica* in this site (Figure 3.2d). *P. sylvestris* trees presented low growth values, as well as *A. alba* surrounded by them (Figure 3.2a, d; Supplementary Materials, Tables S5 and S6). In all sites, *A. alba* surrounded by conspecifics grew more than *A. alba* surrounded by *P. sylvestris* (Figure 3.2f). The same is true for *A. alba* surrounded by broadleaf species neighbours, with the exception of Jasa site, where they present similar BAI values as other *A. alba* surrounded by conspecific trees (Figure 3.2e; Supplementary Materials, Tables S5 and S6).

3.4.2. Relationship between soil characteristics and neighbourhood

Multivariate analyses of variance (MANOVA) showed no significant differences in soil abiotic characteristics between neighbour types (Figure 3.3). The only variable that presented differences between neighbour type was the C:N ratio, being higher under *P. sylvestris* than in *A. alba* or broadleaf neighbour type (Figure 3.4, Supplementary Materials, Table S7). Principal component analyses of soil chemical characteristics resulted in two main axes which together explained 75 % of the variance in the dataset (Figure 3.3). The first axis (46 % of variance) represented a gradient going from high to low values of organic matter, carbon (both total and organic) and nitrogen. The second axis (29.1 % of variance) was more influenced by low pH, electric conductivity, assimilable phosphorus and high C:N ratio.

Multivariate analyses of variance (MANOVA) showed significant differences in soil PLFA groups between neighbour type (Figure 3.3). Higher biomass of AM Fungi and lower biomass of Eukaryotes were found on soils below *A. alba* surrounded by broadleaf species compared to *A. alba* surrounded by *P. sylvestris* (Figure 3.5, Table S7). Lower biomass of Gram-positive bacteria was found on soils under *A. alba* surrounded by broadleaf species compared to soils of *A .alba* surrounded by conspecific trees (Figure 3.5, Table S7). Principal component analyses of the soil PLFA groups resulted in three significant axes explaining 82.0 % of the variance (Figure 3.3, Supplementary Materials, Figure S6). The first axis (52.5 % of the variance) represented soils w1ith abundant fungi in one side and soils with abundant Gram-negative bacteria in the other (Figure 3.3). The second axis (16.9 % of the variance) represents a gradient of Gram-positive bacteria in one side and AM fungi, actinomycetes and anaerobes in the other side (Figure 3.3). Finally, the third axis (14.1 % of the variance) represented a gradient between Gram-positive and Gram-negative bacteria.

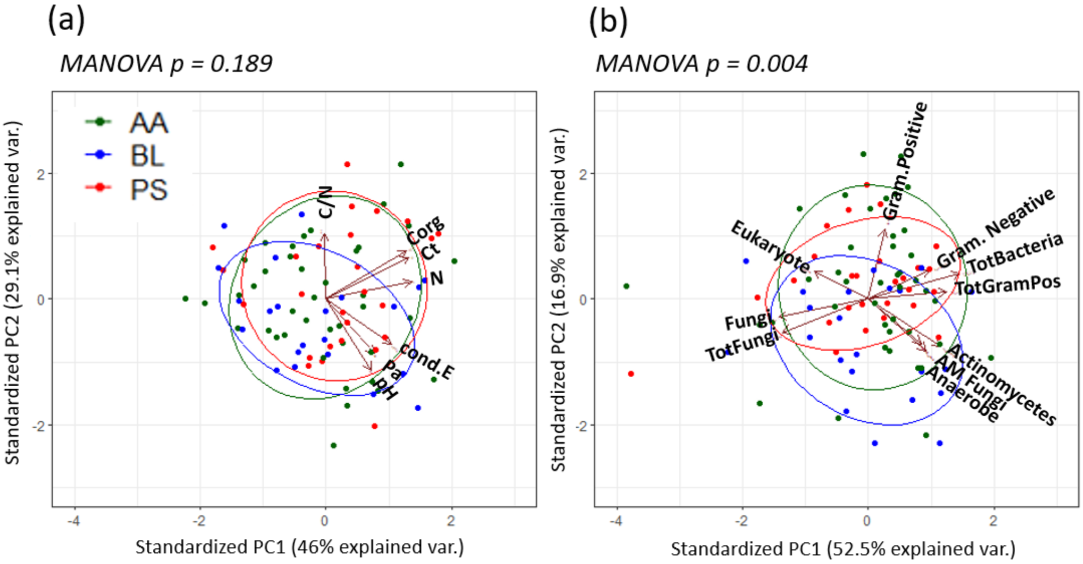

Figure 3.3. Biplots representing the two first standardized axis of the Principal Component Analysis (PCA) explaining variability in (a) soil chemical characteristics and (b) PLFA microbial groups. Each point refers to a single tree. Point colour refers to the dominant neighbour type (green symbols, AA = *Abies alba*; red symbols, PS = *Pinus sylvestris*; blue symbols, BL = broadleaf species). Red arrows indicate the direction of microbial group in the ordination. Soil abiotic characteristics abbreviations: Ct = total Carbon, Corg = organic carbon, N = nitrogen, Pa = assimilable phosphorus, Cond. E = electric conductivity. Significance level of MANOVA tests between all the included variables as a function of neighbour type is given. A triplot representing the third axis of the PCA analysis can be found on the Supplementary Materials, Figure S6.

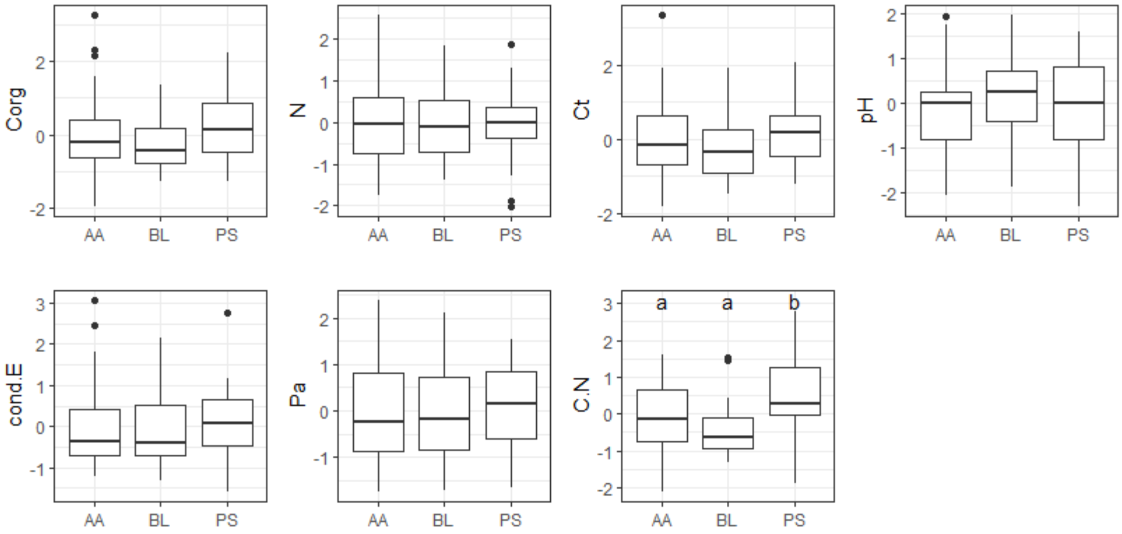

Figure 3.4. Boxplots representing differences among the studied soil variables and neighbour type (AA = *Abies alba*, BL = Broadleaf species, PS = *Pinus sylvestris*). Different letters represent significant ($p < 0.05$) differences across neighbour type. N.S. represents nonsignificant differences. Values are centred at site level.

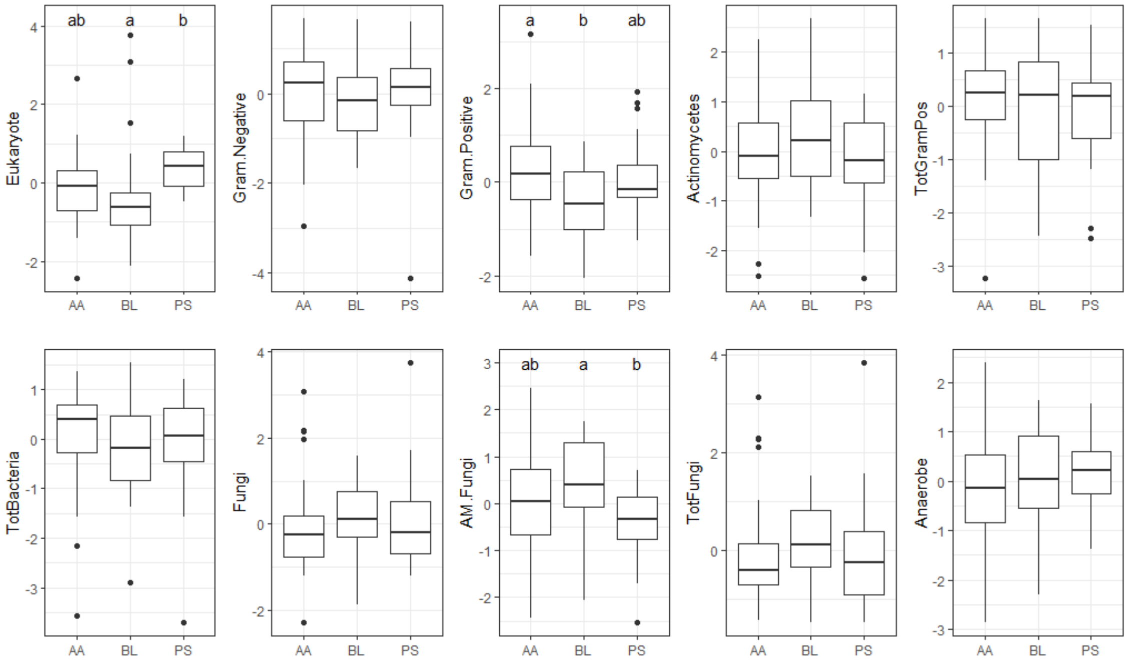

Figure 3.5. Boxplots representing differences among the studied PLFA biotic groups and neighbour type (AA = *Abies alba*, BL = Broadleaf species, PS = *Pinus sylvestris*). Different letters represent differences across neighbour types. N.S. represents non-significant differences. Values are centred at site level.

3.4.3. Network analyses

Network analyses showed that DBH and BAI30, *Rc*, the relative basal area of *P. sylvestris* and soil biotic PCA axis 2 were the variables with higher centrality within their groups, i.e., with more significant correlations (Table 3.2). Significant correlations of variables within groups were found (Figure 3.6). As expected, *Rt* and *Rc* were positively related to *Rs* (Figure 3.6). Tree characteristics presented a positive relationship between BAI30 and DBH, and, as expected, these two variables were negatively related with DCI (Figure 3.6, Supplementary Materials, Figure S7). The axis 2 of the soil physic-chemical variables was negatively related to axis 1 of PLFA groups PCA and positively with axis 2 and while axis 1 of soil physic-chemical variables was positively related to axis 1 of PLFA groups (Figure 3.6).

Variable	**Group**	**Centrality**
Diameter at Breast Height (DBH)	Tree	5
Distance Competition Index (DCI)	Tree	4
Basal Area Increment 30 year (BAI30)	Tree	5
Resistance (Rt)	Drought performance	4
Recovery (Rc)	Drought performance	5
Resilience (Rs)	Drought performance	4
Proportion of *Abies alba* (% *Aa*)	Neighbourhood	2
Proportion of broadleaf species (% Bl)	Neighbourhood	4
Proportion of *Pinus sylvestris* (% *Ps*)	Neighbourhood	6
Soil Abiotic PCA axis 1 (SA1)	Soil	1
Soil Abiotic PCA axis 2 (SA2)	Soil	2
Soil Biotic PCA axis 1 (SB1)	Soil	1
Soil Biotic PCA axis 2 (SB2)	Soil	4
Soil Biotic PCA axis 3 (SB3)	Soil	0

Table 3.2. Studied variables, their abbreviations and values for degree centrality (number of edges per node) in the established network.

Furthermore, several variables of different groups were related showing covariation between drought performance, tree and soil characteristics and neighbour’s type. For instance, all tree characteristics related with proportion of *P. sylvestris* indicated that *A. alba* trees surrounded by *P. sylvestris* were smaller, experienced more competitive pressure and grew less (Figures 3.6 and S8). *Rt* covaried with all tree characteristics, while *Rc* did it with the proportion of *P. sylvestris* and broadleaf species as well as with soil microbial PCA axis 2 and tree size (Figure 3.6). *Rs* covaried with BAI30 and soil microbial PCA axis 2 (Figure 3.6). Finally, from all soil variables only axis 2 of microbial PCA was related to variables of other groups (*Rc*, *Rs* and proportion of broadleaf species; Figure 3.6).

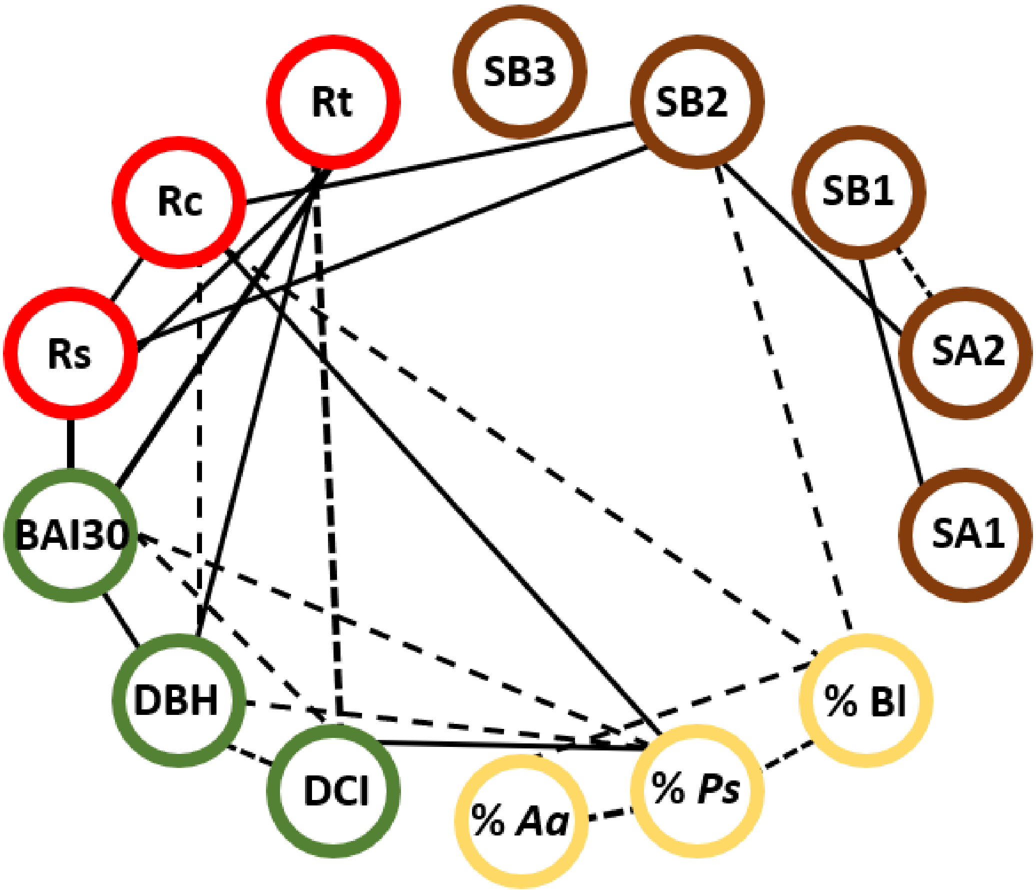

Figure 3.6. Network representing Pearson correlations (edges) between tree level characteristics (green symbols, Diameter at Breast Height = DBH, 30 years mean Basal Area Increment = BAI30, and distance dependent competition index = DCI), drought stability indices (red symbols, Resistance = Rt, Recovery = Rc, Resilience = Rs), neighbour types (yellow symbols, percentage of *A.alba* = % *Aa*, percentage of *P. sylvestris* = % *Ps*, and percentage of broadleaf species = % Bl) and soil variables (brown symbols, soil biotic PCA axis 1 = SB1, soil biotic PCA axis 2 = SB2, soil biotic PCA axis 3 = SB3, soil abiotic PCA axis 1 = SA1 and soil abiotic PCA axis 2 = SA2). These variables are represented as nodes. Solid edges represent positive correlations, and dashed edges negative correlations. Only significant correlations are plotted ($p < 0.05$).

3.5. Discussion

We observed how growth response to drought of Silver fir present common patterns of variation with tree and soil characteristics, which at the same time varied with neighbour type. Our results suggest that neighbourhood effects on growth response to drought can be interpreted within a network of relationships from different variables (tree, soil, neighbours). We show that the composition of a tree neighbourhood is related with the belowground microbial composition. Moreover, *A. alba* growing under different neighbours type present different sizes, competition pressures, soil characteristics and responses to drought. Covariation between these variables makes difficult to infer direct neighbour effects and suggests that approaches integrating information from different sources (soil biotic and abiotic, neighbourhood composition, tree ring growth) should help us to better understand tree growth responses to drought.

Host tree identity strongly influences the structure and composition of soil microbial communities (Šnajdr et al. 2013; Urbanová, Šnajdr & Baldrian, 2015). Here we found that neighbour composition is also important as microbial communities below *A. alba* trees differ between neighbour type (Gram-positive bacteria, Eukaryotes and AM. Fungi; Figure 3.5). Changes on microbial composition under broadleaf neighbours type, rather than *P. sylvestris*, reflects the importance of the neighbour leaf habit on the microbial communities (Ishida, Nara & Hogetsu, 2007; Zechmeister-Boltenstern, Michel & Pfeffer, 2011). Differences on microclimate conditions (through shading, canopy water interception, etc.), tree specific fungal symbionts, litter quality, fine root turnover and production of exudates may explain these results (Prescott & Gaystone, 2013). However, neighbours type is only related soil biotic PCA axis2 which represents a small portion of the soil biotic variability (Figure 3.3). On the contrary, soil chemical variables as pH and C:N ratio (Figure 3.6) show a high covariation with microbial community variability, where basic soils with low C:N values present more bacteria and less fungi, whilst the opposite is found on more acid soils (Pennanen et al. 1999; Fierer & Jackson, 2005; Wan et al. 2015). Surprisingly, among the physic-chemical variables only C:N was related to neighbours type (Figure 3.4). Neither tree size (DBH) nor the competition index (DCI) are related with any soil PCA axis (Figure 3.6), indicating that soil biotic and abiotic variability below the canopy of *A. alba* is not explained by tree size and competition pressure. Gazol et al. (2018b) showed how declining and non-declining *A. alba* trees presented different microbial communities, with higher biomass of bacteria, this results are similar to ours where soil microbial communities and growth resilience and recovery to drought show a relationship (Figure 3.6), however the causality of these relationships is not clear and can be due to third factors (i.e., neighbour type). Feedbacks between drought performance and microbial composition can be related to reduction of carbohydrate supply and alteration of soil nutrient composition during drought (Brunner et al. 2015; Dannenmann et al. 2009). On the other hand, drought alters soil chemical and physical properties affecting bacterial communities which lead to alteration on mineralization rates, nutrient availability and tree growth (Kreuzwieser & Gessler, 2010; Szukics et al. 2010). Diversity of the forest soil microbial communities affects ecosystem processes such as productivity and decomposition (van der Heijden et al. 2008; Maron et al. 2018). Here we observed that different neighbourhoods can change the soil microbial community under *A. alba* trees.

Growth response to drought depends on multiple factors, from tree characteristic such as size, complementarity and competition (tree to tree relationships) to climate and site conditions (Bennett et al. 2015; Bottero et al. 2017; Rita et al. 2019). Furthermore, all these variables may interact, which makes difficult to separate the effect of a single variable in field studies. The covariation shown by our results (Figure 3.6) indicates the interdependence of tree characteristics, neighbourhood, soil variation and growth performance during drought. Tree size is strongly correlated with growth (Coomes et al. 2007), and negatively related with tree performance during drought (Bennett et al. 2018; Serra-Maluquer, Mencuccini & Martínez-Vilalta, 2018). In our sites, tree size (i.e., DBH) correlates with multiple variables showing high centrality (Table 3.2, Figure 3.6). Tree DBH correlates with BAI30, DCI and drought vulnerability variables, but also with neighbour’s type. The interaction between tree characteristics can be summarized as a gradient between big, fast-growing *A. alba* trees with low competition pressure and small, slow-growing *A. alba* trees with high competition pressure (Supplementary Materials, Figure S8).

Mixture effects on forest growth performance and responses to drought are not consistent across forests but rather vary as a function of variables such as soil, forest structure, environment and species identity (Mina et al. 2018; Ammer, 2019). Here, proportions of broadleaf species and *P. sylvestris* neighbours’ types covaried with several tree characteristics, soil and drought performance variables, while proportion of *A. alba* did not (Figure 3.6). Thus, the neighbour type influence on performance and response to drought of the studied *A. alba* trees may be related to changes in tree size, competition and soil variables. The interaction between these variables does not necessarily enhanced growth and post-drought recovery of *A. alba*. Actually, the proportion of *P. sylvestris* in the studied forests is negatively related to BAI30 and DBH and positively to DCI. Thus, *A. alba* trees surrounded by *P. sylvestris* grow less are smaller and have lower competition ability (Figure 3.6; Supplementary Materials, Figure S8). Drier and less shady microclimate conditions in *P. sylvestris* neighbour type due to soil or canopy differences could derive in this combination of factors all leading to low growth of *A. alba*. For instance, higher C:N ratios are found under *P. sylvestris* neighbour type (Figure 3.4). Overall, these results agree with the notion that other factors such as site, climate or density can surpass benefits of mixing (Forrester et al. 2013). The lack of positive effects of mixture on growth does not necessarily contradict studies that found overyielding on mixtures of *A. alba* with other species found (Vallet & Perot, 2011; Toïgo et al. 2015) as we evaluated tree level growth rather than overall stand productivity.

Mixture effects on drought responses may vary depending on the coexisting species which makes neighbour identity an important factor to consider when evaluating growth responses to drought (Vitali, Forrester & Bauhus, 2018, Grossiord, 2019). We found how the proportion of broadleaf species and *P. sylvestris*, two functionally contrasting neighbour types, were related in opposite ways to the growth recovery after drought of *A. alba* (Figure 3.6). The covariation of proportion of *P. sylvestris* with tree size, which also affected growth recovery, suggests that heterogeneity of tree sizes under different mixture combinations may end up in the observed contrasting responses to drought, making difficult to establish causal relationships between neighbour type and growth responses to drought. Possible mechanisms such as root stratification or canopy packing between different tree species, causing spatial separation for resources such as water or light (Bolte & Villanueva, 2005; Grossiord et al. 2014b; Forrester et al. 2018), may be responsible for such differences. Our results suggest another possibility, which is that different microbial composition related to different neighbour type may be associated with changes in tree response to drought. Even though, this remains speculative as we cannot prove that association since our analyses are correlative. However, the covariation between soil biotic PCA axis 2, which is related to proportion of broadleaf species, with growth recovery and resilience to drought supports this explanation and the need for further research on this direction (i.e., effects of neighbourhood on tree responses to drought through changes in soil microbial communities).

Our results were obtained by studying *A. alba* populations in the western Pyrenees, near the species' southernmost distribution limit (Figure 3.1); therefore, caution must be taken when extrapolating them to other areas. However, the observed complexity in our study system may be present elsewhere suggesting species and site dependency of mixture effects on *A. alba* forests. This complexity agrees with the notion that forest management to preserve ecosystem services under climate change must be site and species specific (Mina et al. 2017). For instance, we did not detect benefits in terms of growth enhancement or better growth recovery after drought of *A. alba* under the studied neighbour types. Different neighbour types were associated with different stand structures and degrees of soil microbial diversity. However, a higher structural diversity did not necessarily lead to higher growth or better growth performance after drought.

The soil microbial diversity of *A. alba* mixed forests can be promoted through management tools such as selective thinning; however, its direct and indirect (throughout influence on ecosystem properties) effects over individual tree performance deserve further investigation. Management techniques promoting higher percentages of broadleaf species and *P. sylvestris* in these mixed forests will not necessarily result in a higher growth or a better recovery of *A. alba* after drought. We recommend promoting and managing pure *A. alba* stands in the target region (western Pyrenees) if the objective is improving Silver fir growth performance whereas mixed Silver fir-European beech forests should be managed and preserved to improve soil microbial diversity.

In conclusion, the growth performance of Pyrenean Silver fir trees during drought events covaries with multiple variables from tree characteristics, soil conditions and percentages of dominant specie in the neighbourhood. To some degree, variables of all groups (performance during drought, tree, soil and neighbourhood) are interconnected in a network of relationships showing common patterns between neighbour types. Thus, complexity affecting tree growth biodiversity relationships with stand level variables (Mina et al. 2018) are also present at individual level when evaluating responses to drought. Therefore, evaluation of temporal and spatial differences on covariation patterns of features related to growth responses to drought across different tree species and neighbourhoods should help us to better understand mixing effects on growth responses to drought at individual level.

Chapter 4

Impacts of recurrent dry and wet years alter long-term tree growth trajectories

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4.1. Abstract

1. Climate extremes, such as abnormally dry and wet conditions, generate abrupt shifts in tree growth, a situation which is expected to increase under predicted climate conditions. Thus, it is crucial to understand factors determining short- and long-term tree performance in response to higher frequency and intensity of climate extremes.

2. We evaluated how three successive droughts and wet years influenced short- and long -term growth of six dominant Iberian tree species. Within species variation in growth response to repeated dry and wet years was evaluated as a function of individual traits related to resource and water use (diameter at breast height (DBH), wood density (WD) and specific leaf area (SLA)) and tree-to-tree competition across climatically contrasted populations. Furthermore, we assessed how short-term accumulated impacts of the repeated dry and wet years influenced long-term growth performance.

3. All species showed strong short-term growth decreases and enhancements due to repeated dry and wet years. However, patterns of accumulated growth decreases (AcGD) and enhancements (AcGE) across climatically contrasting populations were species-specific. Furthermore, individual trait data were weakly associated to either AcGD or AcGE and the few relevant associations were found for conifers. Intraspecific variations in tree growth responses to repeated climates extremes were large, and not explained by intraspecific variability in SLA and WD. Accumulated impacts of repeated dry and wet years were related to long-term growth trends, showing how the recurrence of climate extremes can determine growth trajectories. The relationships of AcGD and AcGE with long-term growth trends were more common in conifers species.

4. "Synthesis". Repeated climate extremes do not only cause short-term growth reductions and enhancements, but also determine long-term tree growth trajectories. This result shows how repeated droughts can lead to growth decline. Conifers were more susceptible to the accumulated effects of extreme weather events indicating that in the future, more intense and frequent climate extremes will alter growth performance in forests dominated by these species.

4.2. Introduction

Climate models forecast an increase in the frequency and intensity of climate extremes such as abnormally dry and wet years (IPCC, 2014). Forest vulnerability to drought has been highlighted worldwide (Allen et al. 2010), but the consequences of increasing drought frequency for forest long-term growth dynamics are poorly understood. Most forest responses to drought are studied at short-time interannual scales (Lloret, Keeling & Sala, 2011; Gazol et al. 2017a), and miss the long-term perspective (e.g. decades) needed to understand how forest will respond to climate change (Camarero et al. 2015; Camarero et al. 2018; Peltier & Ogle, 2019). Extreme wet years also influence growth, and their occurrence between dry years could mitigate the damage caused by droughts (Jiang et al. 2019). However, the importance of wet years has received relatively little attention and our ability to quantify their lasting impact is still limited. Thus, a better understanding of the long-term impact on tree growth caused by repeated dry and wet years should improve our capacity to predict forest vulnerability to climate projections.

Tree rings archive past climate influence on tree performance (Fritts, 2001) which makes radial growth a good proxy to study tree responses to climate change (Marchand et al. 2019). For instance, evaluation of tree-ring growth during and after extreme weather events allows us to examine the stability of forest productivity and tree growth across different spatial and temporal scales (Lloret, Keeling & Sala, 2011; Gazol et al. 2017a; Cavin & Jump, 2017; Sánchez-Salguero et al. 2017a, 2018; Gazol et al. 2018b). Furthermore, impacts of drought on tree growth can last for years, resulting in the so called “legacy effects” (Cavin et al. 2013; Anderegg et al. 2015a, Peltier, Fell & Ogle, 2016; Kannenberg et al. 2019; Gazol et al. 2020). These legacy effects increase as drought episodes become longer and occur closer in time (Peltier & Ogle, 2019). Moreover, high drought impacts on growth might lead to lower growth resilience to the next drought period (Vilà-Cabrera & Jump, 2019). However, Jiang et al. (2019) suggested that growth responses to extreme wet years might compensate for drought legacy effects. Therefore, repeated wet periods between droughts might buffer trees from pervasive growth reductions caused by drought (Matías, González-Díaz & Jump, 2014). Nevertheless, enhanced growth on mesic sites or during periods of resource surplus (i.e., extreme wetness, competition release) might result in a structural overshoot leading to a higher predisposition to damage during periods of water scarcity (Jump et al. 2017). These potentially conflicting responses raise the question of how the recurrence of dry and wet periods determines growth performance across long time scales, i.e., to what extent repeated dry and wet years impact growth.

Tree growth response to drought varies across a species geographic range (Cavin & Jump, 2017; Sánchez-Salguero et al. 2018; Vilà-Cabrera & Jump, 2019; Sánchez-Salguero et al. 2017b; Gazol et al. 2017b). However, patterns of growth resistance to drought across species biogeographical gradients are not yet clear. While some studies point to higher vulnerability to drought of rear-edge (equatorward) tree populations, particularly in xeric sites (Sánchez-Salguero et al. 2017b; Anderegg et al. 2019), others found that core populations are more affected than expected (Cavin & Jump, 2017; Lloret & Kitzberger, 2018). One explanation to these disparate results may be that in some rear edges, microclimatic refugia allow some populations to avoid droughts, promoting patchy effects across the distribution range limit rather than a widespread growth decline (Vilà-Cabrera, Premoli & Jump, 2019; Oldfather et al. 2019).

Intraspecific responses to extreme climate events may vary based on individual characteristics such as tree size, competition pressure and functional trait variability. For instance, big and/or low competitive trees are prone to drought damage (Nepstad et al. 2007). Functional traits such as wood density (WD) and specific leaf area (SLA) have been used to describe plant strategies related to resource acquisition gradients (Wright et al. 2004; Chave et al. 2009; Reich, 2014). These traits have been linked, although weakly, to demography (mortality and growth rates) across species (Martínez-Vilalta et al. 2010; Greenwood et al. 2017). However, intraspecific trait variation of functional traits such as SLA and WD is high for some species (Fajardo & Piper, 2011). Whether this intraspecific trait variability is related tree radial growth performance during dry and wet years is unclear.

Here we evaluate the impact of repeated dry and wet years on tree growth and their relationship with individual functional traits and competitive tree-to-tree interactions. Subsequently, we explore whether such impacts determine long-term growth trends. To this end, we studied growth dynamics in six tree species dominant in Iberian forests across a 26-year period. We selected species growing in contrasting climatic regions, including Eurosiberian (*Pinus sylvestris* L., *Abies alba* Mill.) and Mediterranean species (*Pinus halepensis* Mill., *Pinus nigra* Arn., *Quercus faginea* Lam., and *Quercus ilex* L.). Specifically, we aim to answer the following questions: (i)- Is there a geographical variation in the growth response to repeated dry and wet years? (ii)- do individual functional traits and competitive interactions between neighbour trees influence growth responses to repeated dry and wet years? and (iii)- do short-term growth responses to repeated dry and wet years influence individual growth trends in the long-term? We hypothesize that the impacts of repeated dry and wet years on growth are more prevalent on tree populations located in dry sites (xeric rear edges; cf. Anderegg et al. 2019). Furthermore, we expect that drought year impacts will be more prevalent in trees with strong competitive pressure (Bottero et al. 2017). We also expect relationships of WD and SLA with drought resistance at intraspecific level to follow patterns observed at interspecific level (Greenwood et al. 2017). Finally, we expect that the short-term growth impacts of repeated dry and wet years will strongly determine growth trajectories across the studied period (see Figure 4.1).

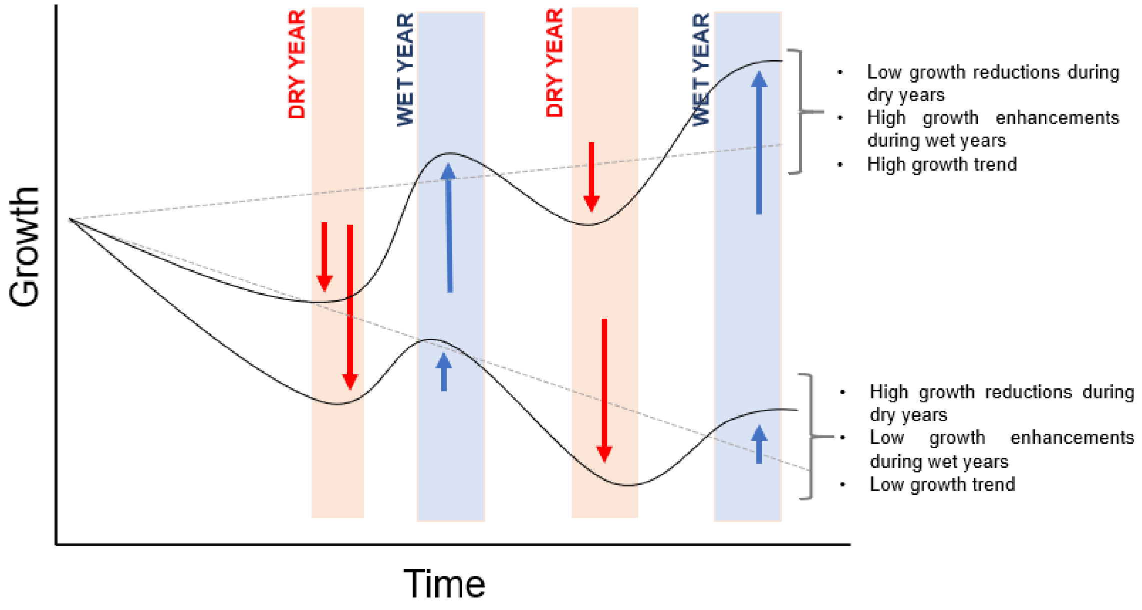


Figure 4.1. Theoretical effects of consecutive dry and wet years on radial growth trends. Two successive dry and wet years (vertical red and blue rectangles, respectively) cause low and high growth (red and blue arrows respectively). The magnitude of these low and high growth years (AcGD, accumulated growth decreases; AcGE, and accumulated growth enhancements) could end up determining the overall tree performance within a specific period (i. e. different growth trends, represented by grey dashed lines).

4.3. Material and methods

4.3.1. Species and study sites

We studied six tree species, four gymnosperms of the *Pinaceae* family (*Abies alba* Mill., *Pinus sylvestris* L., *Pinus nigra* Arn., *Pinus halepensis* Mill.) and two angiosperms of the *Fagaceae* family (*Quercus faginea* Lam. and *Quercus ilex* L.). *A. alba* is a montane or subalpine fir widely distributed across Europe, and it reaches its southwestern distribution limit in the Iberian Peninsula, forming abundant populations in the Pyrenees and isolated stands in the Pre-Pyrenees (Supplementary Materials, Figure S1a). *P. sylvestris*, has a Eurosiberian distribution that reaches its southern distribution at the Iberian Peninsula (Supplementary Materials, Figure S1b). *P. nigra* is a pine present across the Mediterranean Basin and Central Europe (Supplementary Materials, Figure S1c). *P. halepensis* is a drought-tolerant species distributed across the Mediterranean Basin with its biggest populations located in the Iberian Peninsula (Supplementary Materials, Figure S2d). *Q. ilex* is an evergreen oak mainly distributed across the Western Mediterranean Basin (Supplementary Materials, Figure S2f). *Q. faginea* is a deciduous Mediterranean oak present in the north of Africa and the Iberian Peninsula (Supplementary Materials, Figure S2e). In Spain, this species forms abundant hybrid populations with *Quercus humilis* Mill., resulting in *Quercus x cerrioides,* which does not have clear morphological differentiation from the parental species (See Supplementary Materials). In recognition of the complex taxonomy of these oaks, we take a conservative approach to sampled *Q. faginea* and refer to it here as *Q. faginea/Q. humilis*.

We sampled three populations across the distribution area of each species in the Iberian Peninsula (Supplementary Materials, Figure S1). We selected populations subjected to contrasting climatic conditions for each species and classified them as dry, intermediate and wet sites. A precipitation gradient between the dry and wet site was present for all species, albeit the range of precipitation between dry and wet sites varied across species (Supplementary Materials, Figure S2). For *Q. ilex* and *Q. faginea /Q. humilis* wet and intermediate sites precipitation difference was only 35 mm; however, the wet Collserola coastal site presented mild temperatures conditions (Table 4.1). Detailed information of each sampled population can be found in Table 4.1. In the case of *Q. ilex* and *Q. faginea/Q. humilis,* we sampled three sites were both taxa coexisted. For conifers, species composition of the sampled stands ranged from coexistence with several species (both conifers and deciduous) to pure stands (Supplementary Materials, Table S1).

At each site, we randomly selected between 21 and 31 adult, healthy and non supressed individuals and obtained increment cores, functional traits and neighbourhood measures at the individual level as described below.

4.3.2. Individual tree level measures

To characterize each individual tree, we measured structural and functional variables. For each tree, we measured the four closest neighbours at each cardinal point. Diameter at Breast Height (DBH), distance and species identity of each neighbour were recorded (Table 4.1). Then, the following competition index (CI) was calculated to assess potential effects of each neighbour depending on its size and distance to focal tree (Forrester et al. 2013):

$$CI = \sum_{i}^{n} \frac{DBH\ i}{Distance\ i-j} \qquad (1)$$

Where *i* is the neighbour tree and *Distance i-j* is the distance between the neighbour (*i*) and focal tree (*j*).

Furthermore, we measured wood density (WD) and specific leaf area (SLA) for each focal individual (Cornelissen et al. 2003; Supplementary Materials, Figure S3). To quantify WD, we extracted one wood sample (5 cm long) at 1.3 m using 12- and 5-mm increment borers for pine and oak species, respectively. We measured wood samples fresh volume following the volume replacement method. We oven dried the samples at 100 ºC for 48 hours before weighting them at 0.01g precision. We divided the fresh volume by the dry weight what gave us WD. To quantify SLA, we collected two sun-exposed branches per individual. Once in the laboratory, we separated between 5 and 10 leaves per branch. We measured leaf area in a scanner (Epson Expression 10000XL) using the ImageJ software (Schneider, Rasband & Elicieri, 2012). Then, we oven dried leaves at 100 ºC for 48 hours and weighted them at 0.01g precision. Finally, we calculated SLA as the fresh leaf area divided by the dry leaf weight.

Species	Site	Site type	Coordinates	Altitude (m a.s.l.)	MAT (Cº)´ (MATmin-MATmax)	MAP (mm)	Mean ± SE DBH (cm)	Mean ± SE neighbour DBH (cm)	Mean ± SE neighbour distance (m)
Quercus ilex									
	Alcubierre	DRY	41º 48’ 17’’N 0º 30’ 37’’ W	635	13 (6-19)	405	15.4 ± 1	15.5 ± 0.5	5.3 ± 0.2
	Sansoain	INT	42º 33’ 15’’N 1º 35’ 22’’W	742	11 (6-17)	657	14.3 ± 0.8	13.5 ± 0.6	3.1 ± 0.2
	Collserola	WET	41º 25’ 34’’N 2º 4’ 17’’E	300	15 (10-19)	692	18 ± 0.9	18.9 ± 0.8	4.8 ± 0.2
Quercus faginea/humilis									
	Alcubierre	DRY	41º 48’ 17’’N 0º 30’ 37’’ W	635	13.0 (6-19)	405	18.5 ± 1.2	15.4 ± 0.5	4.6 ± 0.2
	Sansoain	INT	42º 33’ 15’’N 1º 35’ 22’’W	742	11 (6-17)	657	16.5 ± 0.9	13.2 ± 0.5	3.9 ± 0.2
	Collserola	WET	41º 25’ 34’’N 2º 4’ 17’’E	300	15 (10-19)	692	18.5 ± 1.2	19.3 ± 0.8	4.7 ± 0.1
Pinus halepensis									
	Peñaflor	DRY	41º 47’ 11’’ N 0º 43’ 21’’ W	284	14 (8-21)	403	33.9 ± 1.5	13.3 ± 0.9	5.4 ± 0.2
	Carcastillo	INT	42º 21’ 26’’ N 1º 26’ 51’’ W	374	13 (7-19)	480	35.7 ± 1.1	32 ± 1.2	6.4 ± 0.2
	Collserola	WET	41º 25’ 34’’N 2º 4’ 17’’E	300	15 (10-19)	692	34.8 ± 1.5	18.6 ± 0.9	4.2 ± 0.2
Pinus nigra									
	Sierra María	DRY	37º 40’ 52’’ N 2º 13’ 19’’ W	1421	12 (5-18)	446	25.3 ± 1.1	15 ± 0.7	5.2 ± 0.3
	Corbalán	INT	40º 25’ 06’’ N 0º 59’ 13’’ W	1400	11 (5-17)	483	22.15 ± 1.1	16 ± 0.7	3.1 ± 0.1
	Villalangua	WET	42º 25’ 06’’ N 0º 48’ 18’’ W	700	12 (6-18)	806	28.4 ± 1.9	20.3 ± 0.8	5.2 ± 0.2
Pinus sylvestris									
	Corbalán	DRY	40º 25’ 06’’N 0º 59’ 13’’ W	1202	11 (5-17)	483	26.2 ± 1.5	22 ± 0.9	3 ± 0.1
	Pico del Águila	INT	42º 18’ 19’’N 0º 24’ 18’’W	1434	9 (3-15)	811	34.2 ± 2.8	33.7 ± 1.6	6.8 ± 0.3
	Las Eras	WET	42º 52’ 42’’ N 0º 48’ 17’’ W	1299	8 (2-14)	1527	39.7 ± 3.6	33.4 ± 1.6	5.5 ± 0.3
Abies alba									
	La Betosa	DRY	42º 18’ 02’’ N 0º 11’ 56’’ W	1399	8 (1-14)	1022	32.9 ± 3.1	23.9 ± 1.1	5.3 ± 0.2
	Paco Ezpela	INT	42º 45’ 05’’ N 0º 50’ 33’’ W	1152	9 (3-15)	1240	30.8 ± 2.1	23.9 ± 1	3.3 ± 0.1
	Las Eras	WET	42º 52’ 42’’ N 0º 48’ 17’’ W	1299	8 (2-14)	1527	32.7 ± 2.8	28.6 ± 0.9	3.9 ± 0.1

Table 4.1. Description of the sampled sites. Coordinates, altitude, mean annual temperature (MAT), mean maximum (MATmax) and minimum (MATmin) temperatures, and mean annual precipitation (MAP) are given. Temperature and precipitation data were extracted from the Climatic Atlas of the Iberian Peninsula (Ninyerola, Pons & Roure, 2005). Position in the sampled climatic gradient is indicated by the site type variable as WET, INT (intermediate) and DRY. Name of the sampled localities are given as sites. Tree data variables are presented as means ± SE (standard error).

4.3.3. Tree-ring width data

We cored each focal tree at 1.3 m height using 5-mm borers. Once in the laboratory, we air dried and mounted the cores on wood supports and sanded them with progressively finer grits until tree rings were clearly recognisable. We performed visual cross dating and measured tree-ring width at 0.01 mm resolution using a LINTAB-TSAP^{TM} measuring device (Rinntech, Heidelberg, Germany). We checked the visual cross-dating reliability using the COFECHA software (Holmes, 1983). Due to non-reliable cross-dating, we excluded 16 *Q. ilex* and 4 *Q. faginea/Q. humilis* trees from the following analyses. Common dendrochronological statistics were calculated (Supplementary Materials, Table S2). We transformed tree-ring widths to basal area increment (BAI) to account for geometrical effects of stem enlargement on growth (Biondi & Qeadan, 2008). We calculated BAI using the *bai.out* function of the *dplR* package (Bunn et al. 2018). Furthermore, we standardized BAI as follows: BAI/mean(BAI_{site}), where mean(BAI_{site}) is the mean BAI in each site. This standardization allowed us to eliminate differences in BAI level between sites.

We calculated relative growth decreases (RGD) for drought episodes as the inverse of the ratio of BAI during the drought year ($BAI_{drought}$) by the mean BAI of the four preceding years ($BAI_{pre\text{-}drought}$):

$$RGD = 1/(BAI_{drought}/BAI_{pre-drought}) \quad (2)$$

Note, that this is the inverse of the resistance index defined by Lloret, Keeling & Sala (2011). Then, we computed the accumulated growth decrease (AcGD) of all the studied droughts as the sum of the RGD of each drought period:

$$AcGD = RGD_1 + \ldots + RGD_n \quad (3)$$

AcGD quantifies the drought impact on tree growth across longer periods of time by reflecting cumulative RGD effects. Furthermore, we also calculated the relative growth enhancement (RGE) for the wet years as the ratio of BAI during the wet (BAI_{wet}) and the mean BAI values of the four years preceding the wet year ($BAI_{pre\text{-}wet}$):

$$RGE = BAI_{wet}/BAI_{pre-wet} \quad (4)$$

The accumulated growth enhancement (AcGE) of the recurrent wet years was then calculated as the sum of the RGE of each wet period:

$$AcGE = RGE_1 + \ldots + RGE_n \tag{5}$$

RGE can be interpreted as a measure of tree capacity to grow when resources are available (in this case high water availability). Both, AcGD and AcGE were calculated at individual tree level. In cases when RGD or RGE for a single event were lower than 1 (i.e., no decrease/increase of growth), we set the value to 0 to account for the lack of response of the tree to that event (Supplementary Materials, Figure S4). We also calculated AcGD and AcGE using different reference periods (from 1 to 7 years). This was done to evaluate the influence of the reference period in the calculation of RGD and RGE and thus on further results.

4.3.4. Selection of dry and wet years

To evaluate the effect of recurrent droughts on tree growth performance we focused on the period from 1990 to 2016. We downloaded series of the Standardized Precipitation Evapotranspiration Index (hereafter SPEI) at 1.1-km^2 resolution (Vicente-Serrano et al. 2017) for each studied site. The SPEI reflects the cumulative drought stress experienced by vegetation as it is calculated as a function of temperature and precipitation data (Vicente-Serrano, Begueria & Lopéz-Moreno, 2010). We selected three common droughts (1994-1995, 2005 and 2012) for all sites. To select these common years, we used the following criterion: in all sites, SPEI had to be below the lower 30% values of the 1990-2016 period for at least one of both, September 6-month scale or September 12-month scale. To select wet years, we used the following criterion: in all sites SPEI had to be above the higher 30% values of 1990-2016 period for at least one of both, September 6 or September 12-month resolution. The years 1997, 2008 and 2013 were selected as wet years. More detailed information on methods for selection of dry and wet years can be found in Supplementary Materials.

4.3.5. Statistical analyses

To evaluate the effects of recurrent dry and wet years on tree growth performance during the 1990-2016 period we used the following analyses. First, to evaluate tree structural and functional characteristics and site effects on growth response to repeated dry and wet years we fitted a set of species-specific generalized linear models. For each species, AcGD and AcGE were modelled as function of site, DBH, CI, SLA and WD (all variables were log transformed prior to the analyses) using the following formulae:

$$AcGD = \beta_0 + \beta_1 * site + \beta_2 * \log(DBH) + \beta_3 * \log(CI) + \beta_4 * \log(SLA) + \beta_5 * \log(WD) + \varepsilon \tag{6}$$

$$AcGE = \beta_0 + \beta_1 * \ site + \beta_2 * \log(DBH) + \beta_3 * \log(CI) + \beta_4 * \log(SLA) + \beta_5 * \log(WD) + \varepsilon \tag{7}$$

Where β_0 represents the overall intercept and β_1 to β_5 the parameters adjusting each predictor variable and ε the error term.

Then, to evaluate the effect of recurrent dry and wet years on growth performance across longer period we used linear mixed-effect models. Log-transformed BAI for the 1990-2016 was modelled as a function of calendar year, AcGD, AcGE (as proxies of cumulative dry and wet year impact) and the interaction of calendar year with AcGD and AcGE.

$$\log(BAI_i) = \beta_0 + \alpha_{0i} + \beta_1 * Year_i + \beta_2 * AcGD_i + \beta_3 * AcGE_i + \beta_4 * (Year_i * AcGD_i) + \beta_5 * (Year_i * AcGE_i) + \varepsilon_i \tag{8}$$

Where *i* represents individual tree identity, β_0 the overall intercept and β_1 to β_5 the parameters adjusting fixed effects, α_0 the random effects on the intercept associated with tree. An error term ε_i with a first-order temporal autocorrelation [AR(1)] was also included in the model. Log transformation was applied to standardized BAI to achieve a normal distribution. The inclusion of the factor "Year" allows to determine growth trajectories across the studied period. The inclusion of AcGD and AcGE was used to detect the cumulative effects of recurrent dry and wet years on tree growth trajectories (interaction Year * AcGD/AcGE). We applied this model to each species (6 species) and at population level (18 models, one per species and site). Mixed models were fitted using the package *nlme* (Pinheiro et al. 2019). Finally, the marginal R^2 (R^2m, variance explained by fixed effects) and conditional R^2 (R^2c, variance explained by fixed and random effects) were calculated following Nakagawa et al. (2017). Furthermore, we evaluated the fit of the models by graphical inspection of the residuals and the fitted values. We performed all analyses in R environment (R Project Team, 2018).

All models presented here use a reference period of 4 years to calculate AcGD and AcGE, results using other reference period (from 1 to 7 years) are presented in the Supplementary Materials, Figures S5 and S6. To perform the abovementioned analyses some trees had to be discarded due to their young age (5 *Q. ilex*; 7 *Q. faginea/Q. humilis*;

13 *P.halpensis*; 3 *P. nigra*;13 *P. sylvestris* and 9 *A. alba*) which left us with a total sample of 468 trees (71 *Q. ilex*, 79 *Q. faginea/Q. humilis*, 77 *P. halpensis*, 87 *P. nigra*, 77 *P. sylvestris* and 77 *A. alba*).

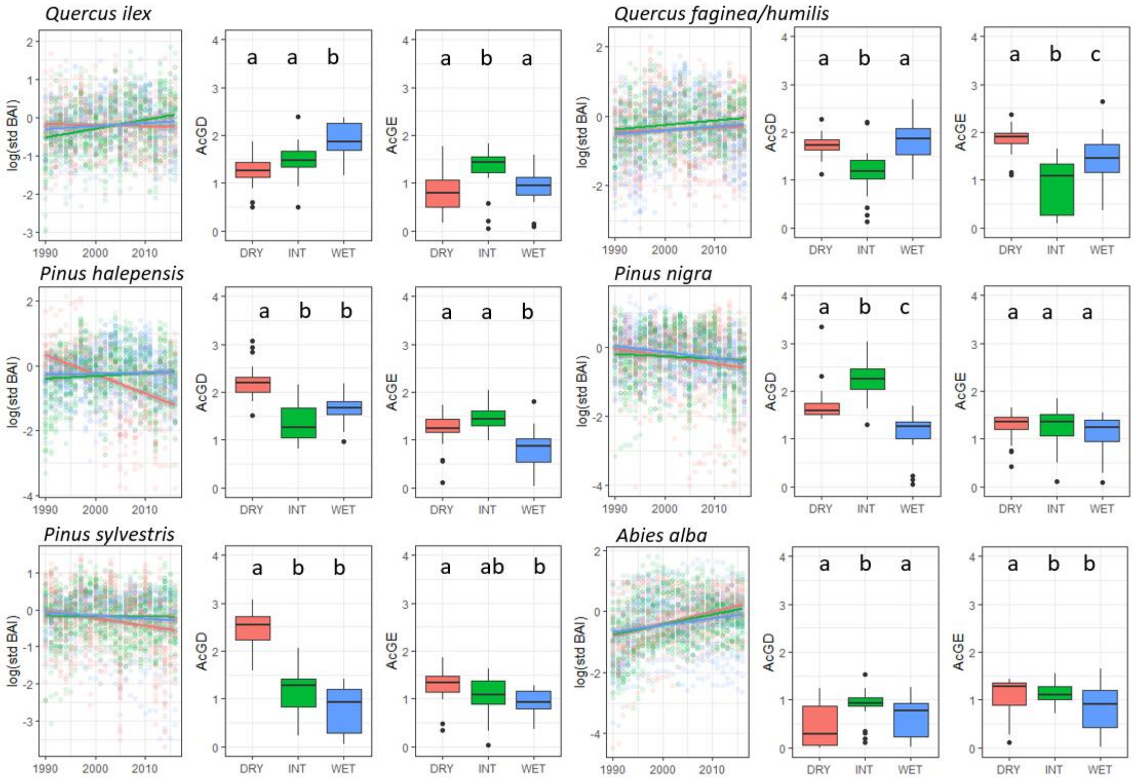


Figure 4.2. Growth trajectories represented as linear regressions of log-transformed Standardized Basal Area Increment (BAI) against calendar year (from 1990 to 2016) for each studied tree population. Boxplots of accumulated growth decreases (AcGD) and accumulated growth enhancements (AcGE) are shown for each population. Colour defines population classification being red, dry populations (DRY), green, intermediate populations (INT), and blue, wet populations (WET). In the boxplots, different letters indicate significant ($p < 0.05$) differences in AcGD or AcGE between populations following post hoc tests of the generalized linear models (Table 4.2.)

4.4. Results

4.4.1. Growth impacts

Accumulated growth decreases (AcGD) and enhancements (AcGE) due to recurrent dry and wet years, occurred for all tree species (Figure 4.2). Site differences in AcGD and AcGE were evident in all species except AcGE in *P. nigra* (Table 4.2, Figure 4.2). However, AcGD/AcGE differences across populations with contrasting climate conditions were species-specific (Figure 4.2). The impact of recurrent dry years on growth was higher in dry populations of *P. sylvestris* and *P. halepensis*, the intermediate population of *P. nigra*, the wet population of *Q. ilex*, both dry and wet populations of *Q. faginea/Q. humilis,* and intermediate population of *A. alba* (Figure 4.2). The impact of recurrent wet years on growth was also species specific. For example, *Q. ilex* presented the higher growth enhancement in intermediate sites (Figure 4.2) whilst this was observed for *P. sylvestris, Q. faginea/Q. humilis* and *A. alba* on the dry site and *P. halepensis* at both dry and intermediate sites (Figure 4.2).

The influence of functional traits and competition on AcGD and AcGE was weak and species-specific (Table 4.2). Conifer species were affected by structural and functional variables (Table 4.2). AcGD of *P. nigra* was higher in big trees suffering high competition (Table 4.2). AcGE of *A. alba* was negatively related to CI and DBH (Table 4.2). AcGE of *P. sylvestris* and *A. alba* was higher in trees with low SLA. AcGD of *A. alba* was higher in trees with high SLA.

Species	Variable	Site	DBH	CI	SLA	WD
Quercus ilex	AcGD	+	ns	ns	ns	ns
	AcGE	+	ns	ns	ns	ns
Quercus faginea/humilis	AcGD	+	ns	ns	ns	ns
	AcGE	+	ns	ns	ns	ns
Pinus halepensis	AcGD	+	ns	ns	ns	ns
	AcGE	+	ns	ns	ns	ns
Pinus nigra	AcGD	+	0.27*	0.22**	ns	ns
	AcGE	Ns	ns	ns	ns	ns
Pinus sylvestris	AcGD	+	ns	ns	ns	ns
	AcGE	+	ns	ns	-1.56*	ns
Abies alba	AcGD	+	ns	ns	1.52*	ns
	AcGE	+	-0.56*	-0.46*	-2.57***	ns

Table 2. Results of the generalized linear models evaluating intraspecific effects of site, diameter at breast height (DBH), competition Index (CI), Specific leaf area (SLA) and wood density (WD) on accumulated growth decreases (AcGD) and accumulated growth enhancements (AcGE) caused by recurrent dry and wet years, respectively. One model per species is presented. For site, results of post-hoc analyses between the different sites are reported, + means that at least two sampled sites differ in values of AcGE or AcGD. For continuous variables, variable estimates are reported once effects are significant ($p < 0.05$). ns indicates non-significant effect. Significance levels: *, $p < 0.05$; **, $p < 0.01$, ***, $p < 0.001$. + indicate differences among site levels.

4.4.2. AcGD, AcGE and growth trends

Successive dry and wet years determined growth trends across the study period (Figure 4.3a, b). In all species but *Q. ilex*, trees suffering higher cumulative drought impact (i.e., higher AcGD) showed more negative growth trends (negative significant interaction year * AcGD, Table 4.3, Figure 4.3a). In all species, trees that grew more during wet years presented the most positive growth trends (positive significant interaction year * AcGE, Table 4.3, Figure 4.3b). For *P. halepensis* and *P. sylvestris*, the AcGD-growth trend relationship was influenced by the dry population showing extreme growth reductions (Figure 4.2) while, for the other species, populations with higher AcGD did not present the more negative growth trends (Figure 4.2).

Differences in AcGD and AcGE also resulted in different growth trends at the within-population (Table 4.3, Figure 4.4). Recurrent dry years resulted in negative growth trends (significant negative year * AcGD interaction; Table 4.3, Figure 4.4) in all conifer populations except at the dry site of *P. sylvestris* (Table 4.3, Figure 4.4). The effect of successive wet years on growth trends was present (significant year * AcGE interaction; Table 4.3) in two or more populations of all species (Table 4.3, Figure 4.4).

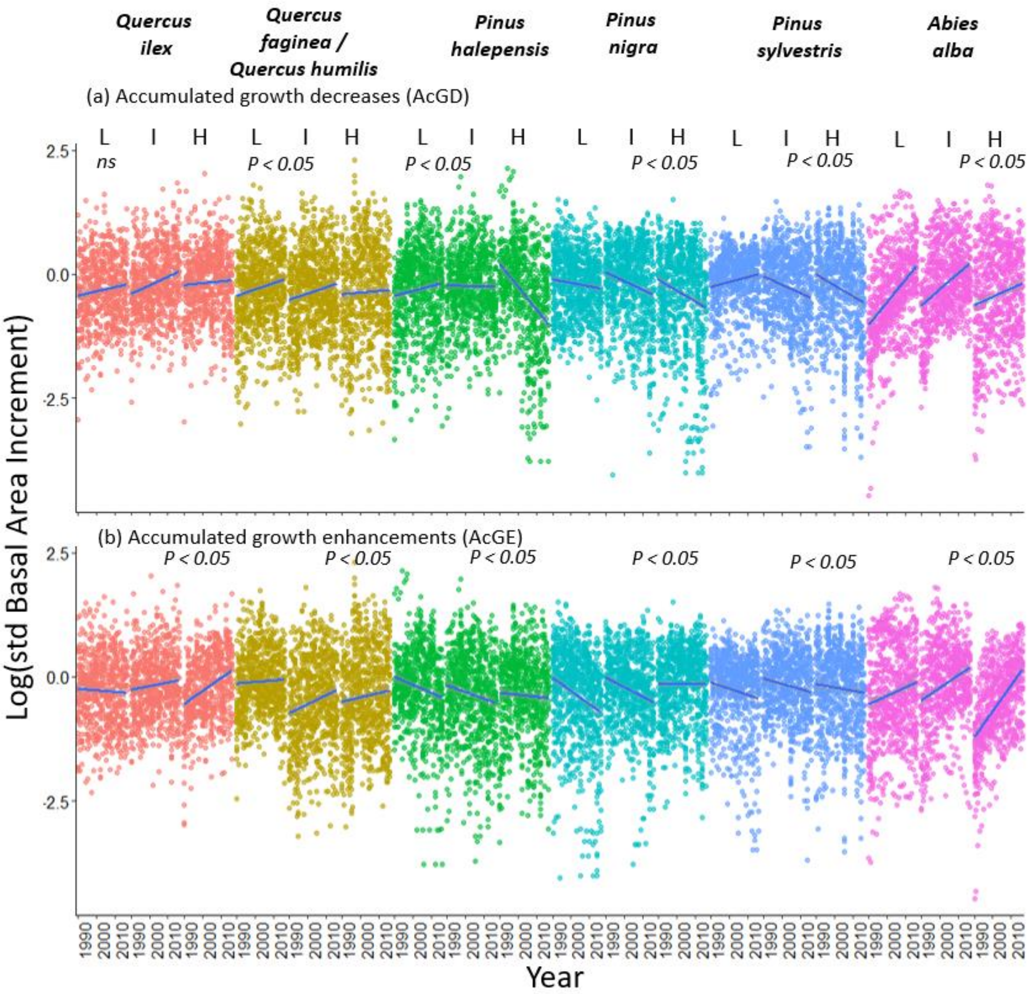


Figure 4.3. Changes in growth trends during 1990-2016 period depending on (a) accumulated growth decrease (AcGD) and (b) accumulated growth enhancement (AcGE) at intraspecific level. Individual trees irrespective of their population are classified in three categories depending on the intensity of AcGD or AcGE: L, low AcGD and AcGE = 1 – 32%, I, intermediate AcGD and AcGE = 33 - 65%; H, high AcGD and AcGE = 66-100%. Significance levels (*p*) from the interaction term of Year * AcGD/AcGE in the intraspecific models are given (Table 3). ns = non-significant.

Species	**Site**	**Year**	**AcGD**	**AcGE**	**Year*AcGD**	**Year * AcGE**	**R^2m**	**R^2c**
Quercus ilex	All	-0.010*		-16.06***		0.008***	0.03	0.41
	Dry	-					0.009	0.48
	Int			-18.833***		0.009***	0.10	0.47
	Wet		7.655*	-14.003**	-0.003**	0.006 **	0.06	0.38
Quercus faginea/humilis	All	0.010**	3.086*	-3.151*	-0.002*	0.002*	0.03	0.64
	Dry		9.839*	-8.364*	-0.005*	0.004**	0.05	0.74
	Int	-0.013+		-18.284**	-	0.009**	0.05	0.70
	Wet	-					0.16	0.54
Pinus halepensis	All	0.028***	17.500***	-9.050***	-0.009***	0.005***	0.09	0.52
	Dry	-0.064***	11.397***	-35.537***	-0.006***	0.018***	0.25	0.59
	Int		14.060***	-16.830***	-0.007***	0.008***	0.04	0.48
	Wet	0.026**	12.179**	-9.363*	-0.006***	0.005**	0.02	0.58
Pinus nigra	All	-0.040***	6.612***	-25.558***	-0.003***	0.013***	0.11	0.57
	Dry	-0.039**	16.635***	-36.768***	-0.008***	0.019***	0.38	0.65
	Int		5.046**	-11.849*	-0.003**	0.006*	0.07	0.47
	Wet		23.692***	-15.310***	-0.012***	0.008***	0.14	0.77
Pinus sylvestris	All	-0.026***	5.274***	-21.040***	-0.003***	0.011***	0.08	0.60
	Dry	-0.025*					0.12	0.54
	Int		14.633***	-15.337***	-0.007***	0.008***	0.03	0.66
	Wet	-0.073***	16.226***	-70.961***	-0.008***	0.036***	0.41	0.81
Abies alba	All		21.045***	-33.614***	-0.011***	0.017***	0.12	0.79
	Dry	0.009*	30.595***	-31.928***	-0.015***	0.016***	0.24	0.92
	Int		10.197+	-34.479***	-0.005+	0.017***	0.13	0.69
	Wet	0.016*	31.043**	-24.798***	-0.016***	0.012***	0.16	0.82

Table 4.3. Mixed models of intraspecific (All) and intra-population (Dry, Int, Wet) effects of accumulated growth decreases (AcGD) and enhancements (AcGE), year and year*AcGD/AcGE interaction on log-transformed basal area increment (BAI). Estimates are given for significant or marginally significant variables. Marginal (R^2m) and conditional R^2 (R^2c) values for each model are also given. Significant levels: +, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

4.5. Discussion

Our results show how successive extreme dry and wet conditions strongly influence tree growth. Widespread accumulated growth decreases (AcGD) and enhancements (AcGE) after three successive dry and wet years were present for all species. These AcGD and AcGE were related to long term growth trajectories (Figure 4.1). As a consequence, the three drought and wet years studied determined the trajectory of tree performance throughout the 1990-2016 period. This pattern was more prevalent for conifers, although with variation between and within populations (Figure 4.2, 4.3 and 4.4).

4.5.1. Geographical variation of AcGD and AcGE

Geographical variation in growth responses to extreme weather events depends on several factors, which result in species-specific responses across the studied climatic and biogeographic gradients. First, topographical complexity generates microclimatic conditions that can decouple tree response and macroclimatic weather events (Adams, Barnard & Loomis, 2014). Non-climatic environmental conditions (i.e., soil texture and nutrients) may exacerbate this disparity between macroclimatic conditions and growth response to dry and wet years (Lévesque, Walthert & Weber, 2016). For instance, here we only found two species, *P. sylvestris* and *P. halepensis* that presented higher AcGD on the dry sites (Figure 4.2). Besides, differences in biotic conditions and species-specific traits can result in different performance across species growing under the same regional climate conditions (Battipaglia et al. 2009; Friedrichs et al. 2009). For example, different growth phenology may result in contrasted responses during dry and wet years. In this sense, *Q. ilex* and *Q. faginea/Q. humilis* coexist in the same sites but showed different responses to repeated dry years in the dry site and to repeated wet years in all sites (Figure 4.2). *Q. ilex* is able to grow in early-summer and fall, whereas most of the *Q. faginea/Q.humilis* radial growth occurs in spring and summer (Montserrat-Martí et al. 2009) suggesting higher drought vulnerability to summer water shortage in the latter. Furthermore, different strategies related to water use result in different responses to drought under the same conditions (Anderegg & HilleRisLambers, 2016). In this study, *P. halepensis* populations which were sampled in the same or nearby *Q. ilex* and *Q. faginea/Q. humilis* sites presented different responses to repeated dry and wet years which could be explained by differences in water use (Figure 4.2). Therefore, site, population and even tree specific characteristics (i.e., population density, age, community compositions…) can be related to different response to dry and wet years, exacerbating or mitigating predictions solely made by macroclimatic conditions. Furthermore, precipitation variability between dry and wet sites differed across tree species, which may contribute to the lack of common geographical pattern of AcGD/AcGE across species. This suggests that wider gradients across the species distribution range should be used.

4.5.2. Effects of structural and functional characteristics on AcGD and AcGE

Empirical evidence indicates that the occurrence of drought years strongly reduces radial growth (Zang et al. 2014; Martínez-Vilalta, et al. 2012; Gazol et al. 2017a; Cavin & Jump, 2017; Serra-Maluquer, Mencuccini & Martínez-Vilalta, 2018; Kannenberg et al.

2019). However, which individual traits and stand-level abiotic and biotic factors are related to these growth reductions is less clear (Kannenberg, Schwalm & Anderegg, 2020). We found weak, species-specific relationships between functional traits (SLA) and competition intensity and/or tree dominance (competition index and tree size) with AcGD and AcGE of successive dry and wet years. Our expectations based on tree size and competition (higher response to water scarcity in bigger trees and higher growth reductions but lower enhancements under highly competitive pressure) were only found on AcGD for *P. nigra* and AcGE for *A. alba* (Table 4.2). High resource acquisitive strategies (high SLA, low WD) were only related to AcGD and AcGE in two species (*P. sylvestris* and *A. alba*). However, only the patterns observed for *A. alba* supported the idea that more resource acquisitive strategy (high SLA) would lead to higher drought damage (Table 4.2, Greenwood et al. 2017). Recent studies suggest that functional traits have low potential to predict variability in resource use strategy at the within-species scale (Anderegg et al. 2018; Rosas et al. 2019). For instance, Fajardo (2016, 2019) found no relationship between WD and growth rates or competition ability in *Nothofagus pumilio*. Our results agree with these studies, and indicate that variability of WD and SLA are poorly related to growth responses to extreme events at the intraspecific level, although they can determine to some degree growth seasonality (Camarero, 2019). It is also possible that the absence of relationships between CI, tree size and the measured functional traits with AcGD and AcGE are due to differences in the temporal resolution of the data. We evaluate present information (CI and traits) and changes in this data through the study period (i.e., differences in stand structure) may influence lack of patterns in our results. Furthermore, hydraulic traits may be more informative than WD or SLA, however, such data is difficult to obtain in a sample size as ours, but further research is needed in this direction (Hartmann et al. 2018).

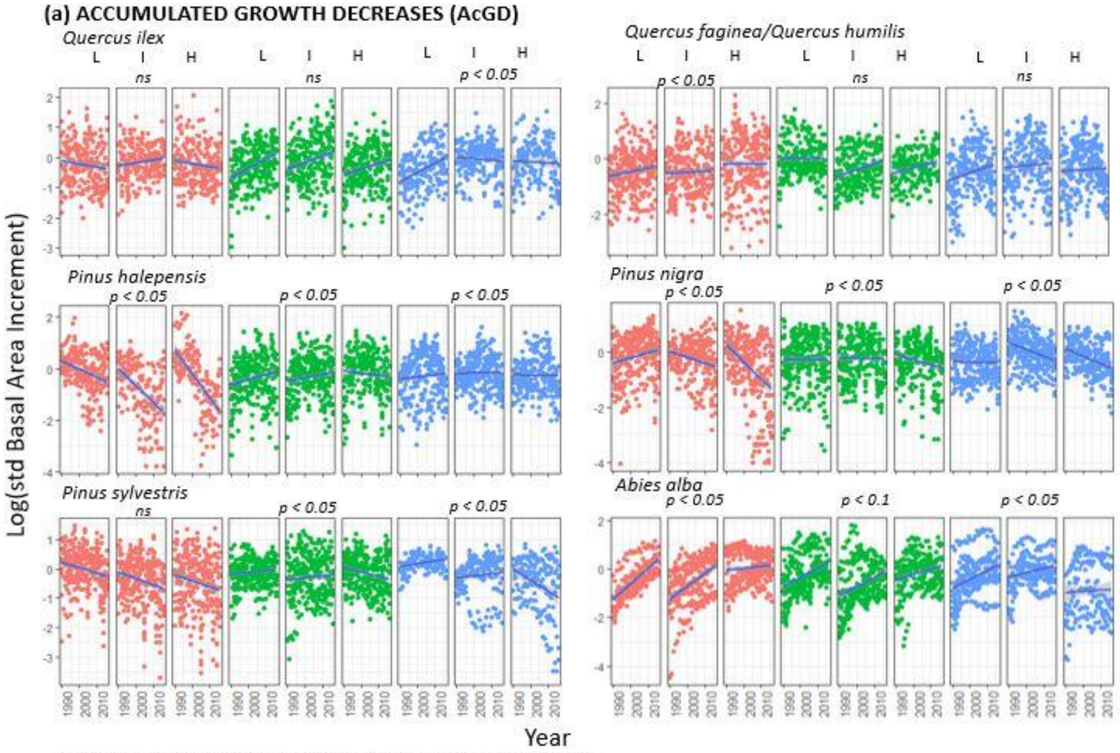
When within-species results are compared across species, the relationships of AcGD and AcGE with structural and functional variables are only present in gymnosperms (Table 4.2). Hence, our expectations of the relationships between growth responses to extreme events and structural and functional characteristics were only present in conifers. In the Iberian Peninsula variability in tree growth response to drought (Gazol et al. 2018b), growth responses to climate and competition (Gómez-Aparicio et al. 2011) and functional traits (Poorter et al. 2012; Carnicer et al. 2013; Vilà-Cabrera, Martínez-Vilalta & Retana, 2015) reflect differences between *Pinaceae* and *Fagaceae* species, mainly pine and oaks. As a result, differences in the incidence of structural and functional variables on growth response to extreme events between these groups was expectable.

4.5.3. Relationships between AcGD, AcGE and growth trends

Extreme weather impacts on tree growth can last for several years causing legacies (Anderegg et al. 2015a, Jiang et al. 2019), and if they occur several times, their effects might accumulate affecting long-term tree performance. For instance, Peltier & Ogle (2019) showed how successive droughts resulted in larger legacy effects on tree-ring growth of *Pinus ponderosa* than a single drought. Our results agree with this previous evidence, i.e., accumulated growth reductions of successive droughts resulted in negative long-term growth trends (Figures 4.3 & 4.4). The fact that successive droughts ended up reducing the growth trends of populations with overall positive, negative, and neutral growth (Figures 4.2 & 4.4) indicates that recurrent drought impacts affect tree performance independently of the mean population growth trends. This finding suggests widespread vulnerability to growth decline, which has been identified as an indicator of reduced health and increased probability of tree death (Camarero et al. 2015; Cailleret et al. 2017). Furthermore, the accumulated effects of repeated droughts could also generate a decrease in growth resistance across time, a pattern already seen in some pine species in the studied area (Serra-Maluquer, Mencuccini & Martínez-Vilalta, 2018, Gazol et al. 2018b). Moreover, repeated wet years may result in positive or stable growth trends (Figures 4.2 & 4.3), which in fact could potentially reverse negative trends caused by repeated dry years (Jiang et al. 2019). However, caution must be taken as growth enhancement due to water surplus may be overestimated due to competition releases after drought-induced tree death, a process observed in the study area (Galiano, Martínez-Vilalta & Lloret, 2010; Camarero et al. 2015). Finally, the effects of repeated dry and wet years on growth trends were predominant in conifers, which is in accordance with studies reporting higher legacy effects in these species compared to angiosperms (i.e., oaks) after both dry and wet years (Anderegg et al. 2015a; Jiang et al. 2019).

Low growth rates and declining growth trends are observed in dead individuals when comparing them to living conspecifics in the same populations (Hereş, Martínez-Vilalta & Camarero, 2012, Camarero et al. 2015, Cailleret et al. 2017). Recently, De Soto et al. (2020) reported that dead trees presented lower resilience (short-term impact) to past drought events than their surviving neighbours. Here we show that these two growth

(a) ACCUMULATED GROWTH DECREASES (AcGD)



(b) ACCUMULATED GROWTH ENHANCEMENTS (AcGE)

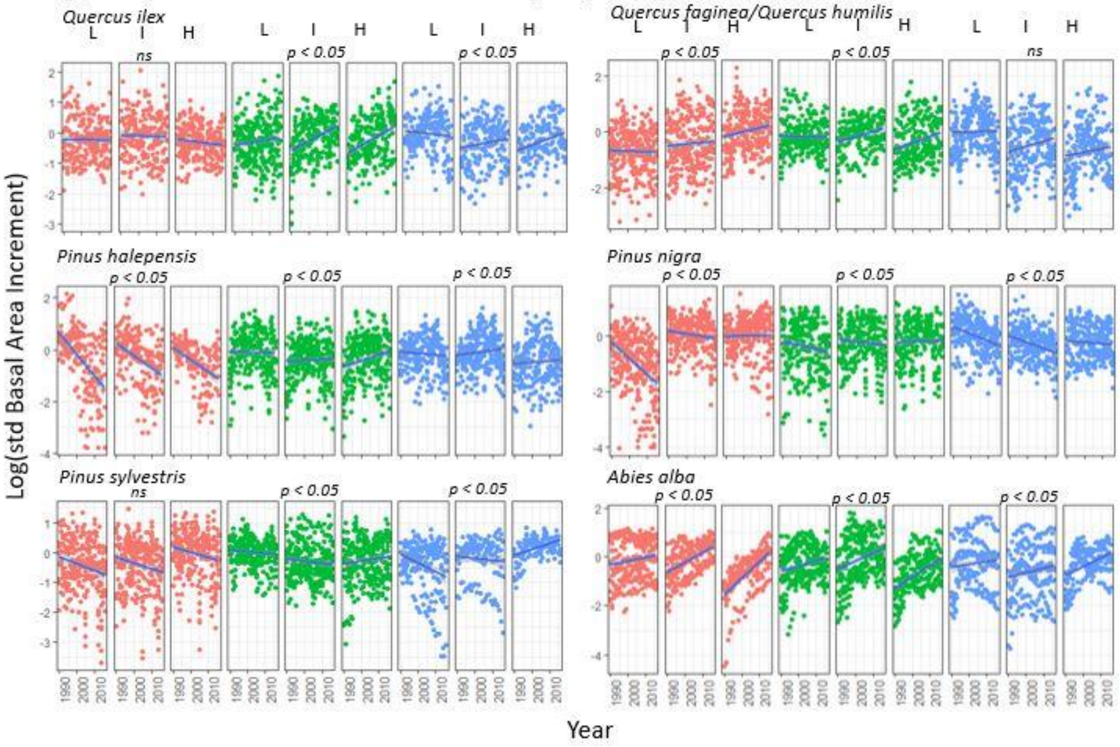


Figure 4.4. Changes in growth trends during 1990-2016 period depending on (a) accumulatedgrowth decrease (AcGD) (b) accumulated growth enhancement (AcGE) at intra-population level. Individual trees within populations are classified in three categories depending on the intensity of AcGD or AcGE: L, low AcGD and AcGE = 1 – 32%, I, intermediate AcGD and AcGE = 33 - 65%; H, high AcGD and AcGE = 66-100%. Significance (*p)* levels from the interaction term of Year * AcGD/AcGE in the intra-population models are given (Table 3). ns = non-significant. Colour defines population classification being red, dry populations (DRY), green, intermediate populations (INT), and blue, wet populations (WET).

responses potentially leading to tree death, i.e., short-term growth reductions and long-term negative growth trends, are related and that the accumulation of successive droughts impacts may increase the declining growth trends.

Climate projections indicate that the frequency and intensity of extreme climate events will increase. These will cause higher impacts on tree growth and as a consequence determine their future growth trajectories. If the frequency and severity of extreme drought events increase, their accumulated impacts will be higher, which will lead to increasingly widespread growth decline, dieback and, potentially, tree death. The intraspecific growth and trait variability presented here suggests that, to accurately predict when and where the effects of successive extremes climate events will be more pervasive, better knowledge on which site and individual characteristics prevent drought vulnerability is needed.

Chapter 5

Wood density and hydraulic traits influence species' growth responses to drought across biomes

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5.1. Abstract

Tree species display a wide variety of water use strategies, growth rates and capacity to tolerate drought. However, if we want to forecast species capacity to cope with increasing aridity and drought, we need to identify which measurable traits confer resilience to drought across species. Here, we use a global tree ring network (65 species; 1931 site series of ring-width indices - RWI) to evaluate the relationship of long-term growth-drought sensitivity (RWI-SPEI drought index relationship) and short-term growth response to extreme drought episodes (resistance, recovery and resilience indexes) with functional traits related to leaf, wood and hydraulic properties. Furthermore, we assess the influence of climate (temperature, precipitation and climatic water deficit) on these trait-growth relationships. We found that assessing the relationship between RWI and SPEI is fundamental to understand the resistance and recovery of tree growth to drought episodes. Species displaying a stronger RWI-SPEI relationship to drought and low resistance and high recovery to extreme drought episodes tended to have higher wood density (WD) and more negative leaf minimum water potential (Ψmin). Such associations were largely maintained when accounting for direct climate effects. Our results indicate that, at the global scale, wood and hydraulic functional traits explain species' growth responses to drought at short- and long-term scales. These trait-growth relationships drought can improve our understanding of species capacity to withstand climate change and better predict its effects on forest demography and ecosystem services.

5.2. Introduction

Drought stress limits the radial growth of trees across their lifespan and extreme drought episodes result in growth reductions that can last several years (Anderegg et al. 2015a; Peltier & Ogle, 2016; Gazol et al. 2018b; Gazol et al. 2020; Serra-Maluquer et al. 2021). Drought has become a greater growth constraint during the past century (Babst et al. 2019) and more frequent and intense droughts expected from human-caused climate change are likely to exacerbate these impacts and lead to additional growth decreases. Increased drought impacts on tree growth can influence forests dynamics, as a result of growth decline, canopy dieback and tree mortality (Camarero et al. 2015; Cailleret et al. 2017; De Soto et al. 2020), reducing the climate change mitigation capacity of forests (Anderegg et al. 2020a). However, future projected drought increases are likely to differentially threaten tree species based on their morphological, structural and physiological characteristics and their capacity to tolerate water limitation (Greenwood et al. 2017). Thus, unravelling how morphological and physiological traits influence species' growth responses to drought is an important research need.

Species traits may help predict forest response to drought (Greenwood et al. 2017). Morphological, structural and chemical characteristics of different plant organs and tissues result in coordinated sets of traits relating to plant form and function (Reich,2014). The leaf (LES) and the wood economic spectra (WES) (Wright et al. 2004; Chave et al. 2009) are among the most studied. However, specific leaf area (SLA) and wood density (WD), two key traits of LES and WES, are only weakly correlated with cross-species patterns of drought-induced tree mortality (Greenwood et al. 2017). Although such "soft" traits have the advantage of being easily measurable for a large number of individuals, their weak links to plant physiology and water use limit their capacity to predict growth responses to drought. By contrast, "hard", process-based traits mechanistically related to water use and transport, such as hydraulic traits, may be better descriptors of growth relationships and responses to drought (Brodribb, 2017; Rowland et al. 2021). Hydraulic traits summarise cross-species differences in water transport, with important implications for species physiology and ecology (Venturas, Hacke & Sperry, 2017; Oliveira et al. 2021). Hydraulic traits such as the water potential at 50% loss of conductivity (P50), the minimum leaf and xylem water potentials (Ψmin), and the hydraulic safety margin (HSM = Ψmin – P50) correlate with cross-species vulnerability to drought and drought-induced mortality (Choat et al. 2012; Anderegg et al. 2016), as well as ecosystem fluxes in response to drought (Anderegg et al. 2018; Garcia-Valdés et al. 2021).

Tree rings store information of climate effects on tree growth (Fritts, 2001) and are a useful tool to study drought impacts on multi-year tree performance (Babst et al. 2019). Previous studies observed lower resistance and higher recovery in species located in arid sites compared to species growing in humid sites (Gazol et al. 2017a; Gazol et al. 2018b). Higher drought "legacy effects" (lower than expected growth after a drought event, Kannenberg, Schwalm & Anderegg, 2020) have also been found in conifer species from arid sites compared to humid sites (Anderegg et al. 2015a; Gazol et al. 2020). Interannual growth variability is also expected to be more limited by year-to-year drought changes in more arid places where water scarcity is the main limiting factor on growth (Fritts, 2001). For instance, in the long term, growth is more limited by drought in lowland arid sites, while temperature limits growth in northern latitudes and higher elevation forests (Babst et al. 2013; Pompa-García et al. 2021), albeit increasing growth-drought relationships may already be occurring under climate change (Babst et al. 2019). Although tree ring variability in response to drought is strongly driven by the climatic conditions (D'Orangeville et al. 2018; Gazol et al. 2017a), the role of species traits on both tree ring growth-drought relationships and responses to extreme drought is not yet clear.

To predict species-specific responses to drought using functional traits, an evaluation of the variability of growth responses to drought at different scales (across species, within species, within sites) is needed. This partitioning of variance allows contextualizing the role of cross-species variability in functional traits and should help understand future forest dynamics under climate change. Recently, Li et al. (2020) evaluated how much of the spatial variability of tree ring growth responses to drought was explained by several functional traits and found that some traits were related to spatial differences in growth response to drought, although methodological issues may preclude broad conclusions (Zheng et al. 2021). Functional traits and growth-drought relationship and response to extreme events vary across environmental gradients (Wright et al. 2004; Babst et al. 2013; Gazol et al. 2017a), and it is unclear how long-term growth climate relationships affect short-term growth responses to drought at global scales (but see Huang et al. 2018; Serra-Maluquer et al. 2021). Increasing our knowledge about the direction of these relationships, and the possible effects of climatic variables on these relationships is important for disentangling geographic covariations from possible causal relationships.

Here we aim to evaluate bivariate relationships between cross-species responses to drought (resistance, recovery and resilience, *sensu* Lloret, Keeling & Sala, 2011) and interannual growth-drought relationship (Ring Width Index ~ Standardized Precipitation and Evapotranspiration Index; Pearson correlation) and different functional traits related to leaf and wood spectra and hydraulic function. We aimed to answer the following questions: (i) Do we see consistent differences across species in their response to single year extreme drought and interannual growth-drought relationship?, (ii) do hydraulic traits, which are physiologically relevant to plant water use, explain variations in cross-species response to single year extreme drought and interannual growth-drought relationships better than "soft" leaf and wood traits?, (iii) if covariation between traits and growth responses to single year extreme drought and interannual growth-drought relationships are present, to what extent is this covariation driven by climate effects on both traits and growth?

5.3. Material and methods

5.3.1. Tree Ring Data

We analysed tree ring data available from the International Tree Ring Data Bank (ITRDB; Grissino-Mayer & Fritts, 1997). We used a cleaned version of the database compiled at the end of 2017 (Zhao et al. 2018). The ITRDB presents tree ring data for all forested continents. It has more than 4000 chronologies including tree-ring information such as ring widths, density and anatomical features. However, the ITRDB is strongly spatially biased to Europe and North America, and taxonomically biased towards high representation of Pinaceae and Fagaceae species (Zhao et al. 2018).

We selected ring width chronologies that fulfilled the following requirements. First, we selected chronologies with a minimum of 40 years of data after 1950 and that were created with more than 5 trees (2541 chronologies). Then, chronologies without years containing an extreme drought event (160 chronologies, see below the criteria to define them) and chronologies of species with no trait information, or from species with less than 5 chronologies presenting extreme drought events were also discarded (450 chronologies). Our final dataset resulted in 1931 chronologies from 65 different species (Figure 5.1; Supplementary Materials, Table S1). Chronologies were detrended using a spline of two third of the growth series length and a 0.5 response cut off. A bi-weight robust mean was used to calculate mean site standardized chronologies of ring width indices (RWI). Detrending and mean site chronologies calculation were conducted using the *dplR* package (Bunn et al. 2021).

5.3.2. Climate data and drought indices

Temperature and precipitation data were downloaded from CRU TS v. 4.04 (Harris et al. 2020. https://crudata.uea.ac.uk/cru/data/hrg/) at 0.5° resolution. To characterize site climate conditions, means of mean annual temperature (MAT) and accumulated annual precipitation (MAP) across the study period were calculated. We also download the 1950 – 2018 series of the Standardized Precipitation and Evapotranspiration Index (SPEI) (Vicente-Serrano, Beguería & López-Moreno, 2010; https://spei.csic.es/index.html). September and March 12-month SPEI (northern and southern Hemisphere respectively) were download at 0.5° resolution. Climatic Water Deficit (CWD, difference between precipitation and potential evapotranspiration) was downloaded from http://www.climatologylab.org/terraclimate.html. Due to limited data availability mean site CWD was calculated using data from 1958 to 2018.

5.3.3. Functional trait data

We downloaded species level functional trait data from published literature. To represent the LES, we used Specific Leaf Area (SLA), Nitrogen mass (Nmass) and Phosphorus mass (Pmass). We used wood density (WD) to represent the WES. For hydraulic traits, we used stem specific conductivity (Ks), leaf minimum midday water potential (Ψmin), the water potential at the 50% loss of conductivity (P50), and the hydraulic safety margin (HSM). The TRY database (Kattge et al. 2020) was used to obtain leaf traits. For SLA we downloaded data considering the petiole excluded, included or undefined, and species mean values were calculated. For WD we used the Global Wood Density database (Zanne et el., 2009) and data for four species was completed using TRY. Finally, for hydraulic traits data we used an updated version of the Xylem Functional Trait database (XFT; Choat et al. 2012) (Sánchez-Martinez et al. 2020). Information about number of species per trait can be found in Supplementary Materials, Table S2.

5.3.4. Drought selection and metrics

First, we calculated the RWI–SPEI relationship. This was done using Pearson correlations between the standardized RWI chronologies and September (northern hemisphere) or March (southern hemisphere) 12-month SPEI. Thus, for each site we had a value based on the linear relationship between tree ring growth and drought across the length of each chronology (starting in 1950, Supplementary Materials, Figure S1).

Then, we defined extreme drought years as those with 12-month SPEI values lower than -1.5 (7806 drought episodes). We removed 2176 drought episodes, 1278 because of excluded chronologies and chronologies without extreme droughts, 898 because post- and pre- drought periods overlapped. Finally, we analysed 5630 drought episodes affecting 1931 chronologies from 65 different species (Supplementary Materials, Table S1). The *pointRes* R package (van der Mateen-Theunissen et al. 2015) was used to calculate resistance (Rt), recovery (Rc) and resilience (Rs) indices (Lloret, Keeling & Sala, 2011), using windows of 4 years before and after drought occurrence. These indices were calculated using the standardized chronologies without pre-whitening. In the case of the RWI-SPEI relationship, the RWI indexes obtained from standardized and from the residual, pre-whitened chronologies were also compared (Supplementary Materials, Figure S2); since the two series were strongly correlated, we decided to use standardized chronologies for further analyses.

5.3.5. Statistical analyses

Path analysis was used to inspect the relationships and potential covariations between RWI-SPEI relationships, Rt, Rc, Rs and climate (MAT and MAP). The analyses were conducted using the *lavaan* package (Rosseel, 2012). This analysis was carried out using chronology-level RWI-SPEI relationship, Rt, Rc and Rs. We started with a first model where climate variables influenced the strength of the RWI-SPEI relationships (quantified by the correlation coefficient; hereafter RWI-SPEI relationship), Rt, Rc and Rs. At the same time the RWI-SPEI relationships influenced Rt and Rc, with all these variables influencing Rs. Covariation between Rt and Rc was also included in the model. We deleted non-significant paths until the model significantly differed (based on chi-squared test) from the described theoretical one.

To test how the variability in RWI-SPEI relationships, Rt, Rc and Rs was structured across different scales, and specifically to assess the importance of variation across species, we fitted a general linear model to the variance with the following random structures: species for RWI-SPEI relationship (one value per chronology) and species plus site nested within species for Rt, Rc and Rs (multiple values per chronology). We used the *lme* and *varcomp* functions in R (Messier, McGill & Lechowicz, 2010). Residual variances were attributed to sites plus random error in the case of RWI-SPEI relationship and to year plus random error in the case of Rt, Rc and Rs.

Once the proportion of variation attributed to species level was evaluated, species-specific mean RWI-SPEI relationships, Rt, Rc and Rs were calculated for the following analyses. Covariation between species mean RWI-SPEI relationships, Rt, Rc and Rs with species mean functional traits (SLA, Nmass, Pmass, WD, Ks, P50, Ψmin, HSM) was tested using linear models. Separate models were fitted for RWI-SPEI relationships, Rt, Rc and Rs with each trait. We compared models with trait, trait plus clade (angiosperm vs gymnosperm), and trait interacting with clade as fixed factors. We compared models using the Akaike Information Criterion (AIC) values (*AIC* function in R), and when AIC differences were lower than 2, the simpler model was selected (i.e., the one containing less fixed factors). Leaf traits, Ks, and Rc were log transformed prior to analyses to achieve normality. In the case of RWI-SPEI relationships, all models were weighted by the number of chronologies present for each species (Supplementary Materials, Table S1). For Rt, Rc and Rs, all models were weighted by the number of droughts each species was exposed to (Supplementary Materials, Table S1, Figure S3).

To evaluate the influence of climate on the significant correlations between RWI-SPEI relationships, Rt, Rc and Rs with traits we used a partial correlation analysis approach. First, we fitted linear models with each trait as dependent variable and temperature (MAT, mean annual temperature across all sites per species), precipitation (MAP, mean annual precipitation across all sites per species) and climatic water deficit (MACWD, mean annual CWD across all sites per species) as predictors. Only models for traits that showed a significant covariation between them and RWI-SPEI relationships, Rt, Rc or Rs were fitted. Then, the same models but using RWI-SPEI relationships, Rt and Rc as dependent variables were fitted. As above, in the case of RWI-SPEI relationships, all models were weighted by the number of chronologies for each species. For Rt, Rc and Rs, all models were weighted by the number of droughts each species was exposed to (Supplementary Materials, Tables S1, Figure S3). To estimate partial correlations between traits and growth indices, the residuals of growth index relationships with climate were regressed against the residuals of the trait's climate relationships using linear models. Significance of explanatory variables and model adjusted R2 were compared to those of the previous linear models using the original growth indices and trait variables. All analyses were conducted using R software (R Core team 2020).

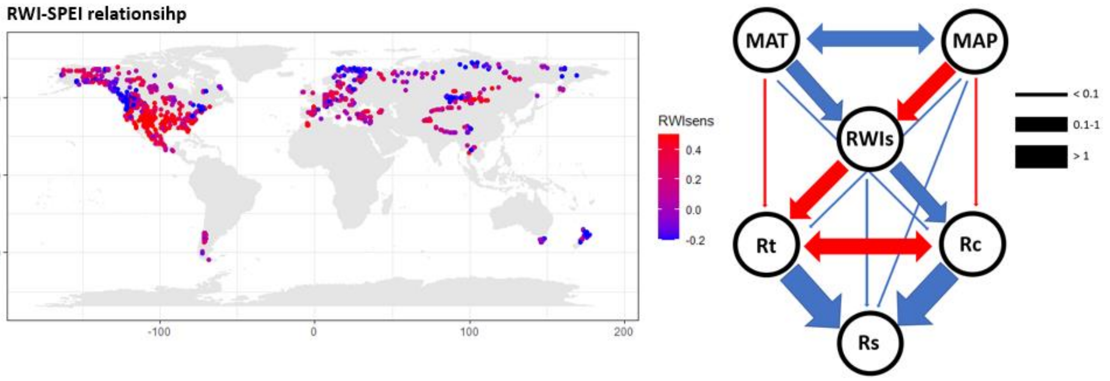


Figure 1. Left panel. Distribution of the analyzed tree ring width chronologies (1931 sites) across the globe. Each point represents one site mean series of ring-width indices (RWI) or chronology. Colors represent RWI-SPEI relationships, which is defined as the Pearson correlation between the RWI indices (1950- end of chronlogy) and the 12-month SPEI, for September or March in northern or southern hemispheres, respectively. Blue colors represent sites with negative RWI - SPEI correlations, and red colors sites with positive RWI - SPEI correlations while colour intesity represent the strengh of the relationship. Right panel. Path diagram resulting from the path analysis, only significant paths are plotted. Blue arrows represent positive relationships, red arrows represent negative relationships. Arrow size is proportional to the value of the standardized coefficients. MAT = mean annual temperature across the study perido (1950-present), MAP = mean year accumulated precipitation across the study period. RWIs = strength of the RWI-SPEI relationship, quantified as correlation coefficient, Rt = Resistance, Rc = Recovery, Rs = Resilience. Complete output of the model can be found in Supplementary Materials, Table S3.

5.4. Results

RWI-SPEI relationship, resistance and recovery were spatially structured across the globe, (Figure 5.1; Supplementary Materials, Figure S4). Path analysis (chi-square test = 1.594, p. value = 0.207, Supplementary Materials, Table S3) indicated that climate effects on Rt and Rc were mostly driven by RWI-SPEI relationship (Figure 5.1). A pattern of high correlations coefficients in the RWI-SPEI relationship, low Rt and high Rc on sites with high MAT and low MAP was observed, while the opposite was present for sites with low MAT and high MAP (Figure 5.1).

The Lloret indices are mathematically related to each other; for instance, Rt and Rc inherently have a negative relationship, which is expected by the use of extreme drought year growth in the numerator in the former and in the denominator in the latter

(Figure 5.1; Supplementary Materials, Figure S5). Rt and Rc had a positive linear relationship with Rs (Figure 5.1; Supplementary Materials, Figure S5). Furthermore, species aggregated Rt and Rc were linearly related to RWI-SPEI relationship (Figure 5.1; Supplementary Materials, Figure S6).

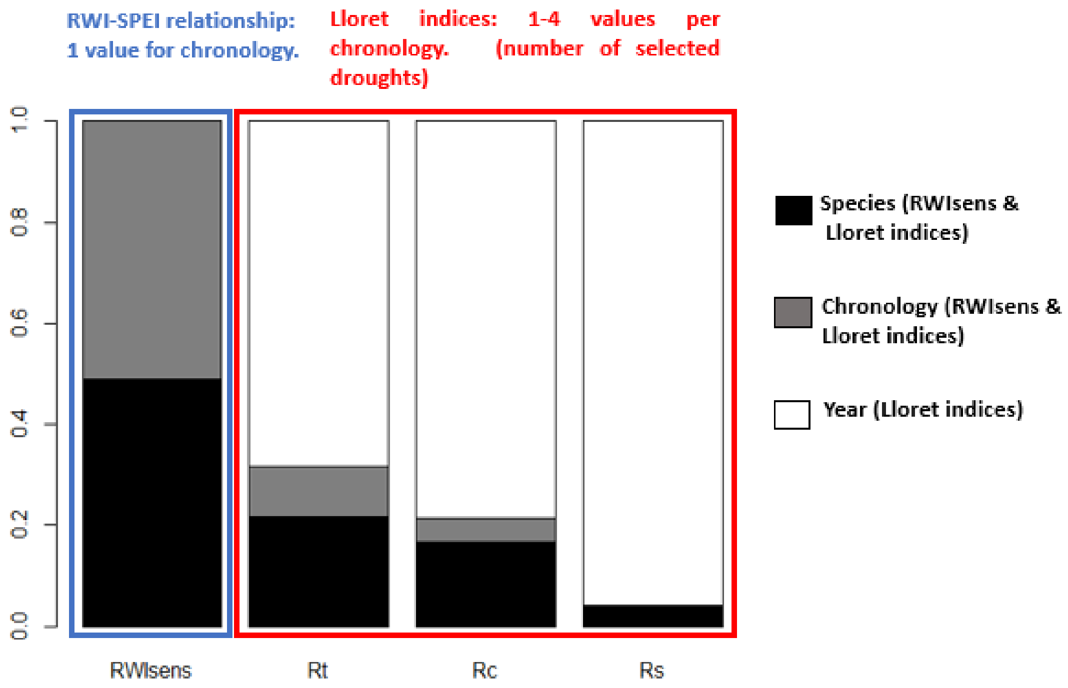


Figure 2. Percentage of variance across different scales for the strength of RWI-SPEI relationship, resistance (Rt), recovery (Rc) and resilience (Rs). Fitted general linear models to the variance were used to calculate the proportion of variance at each scale (Messier et al. 2010). As RWI-SPEI relationship was calculated at chronology level, and Lloret's resilience indices at year level, two different models were used. For RWI-SPEI relationship, the random structure was species, where residual was interpreted as site + error. For Lloret indices, site was nested in species and residual variance was interpreted as year + error. Blue and red boxes are plotted to differentiate the scales used in each model.

The variance partitioning analyses showed that species represented a relatively high proportion of the variation in RWI-SPEI relationship, Rt and Rc. For Lloret indices, species variance was always higher than site level variance (Figure 5.2). For RWI-SPEI relationship, a metric calculated at chronology level, almost half of the variance was associated with species, while the residual variance (here interpreted as site effects plus error) was 51%. In the case of Lloret indices, where the metrics were calculated at year scale, and thus more than one value per chronology could be obtained, variance associated with species was 22% for Rt, 17% for Rc and 4% for Rs. Variance associated with site was 10 % for Rt, 5% for Rc and around 0% for Rs. Finally, residual variance (interpreted as year effects plus error) represented the vast majority of variance for the three Lloret indices (Figure 5.2).

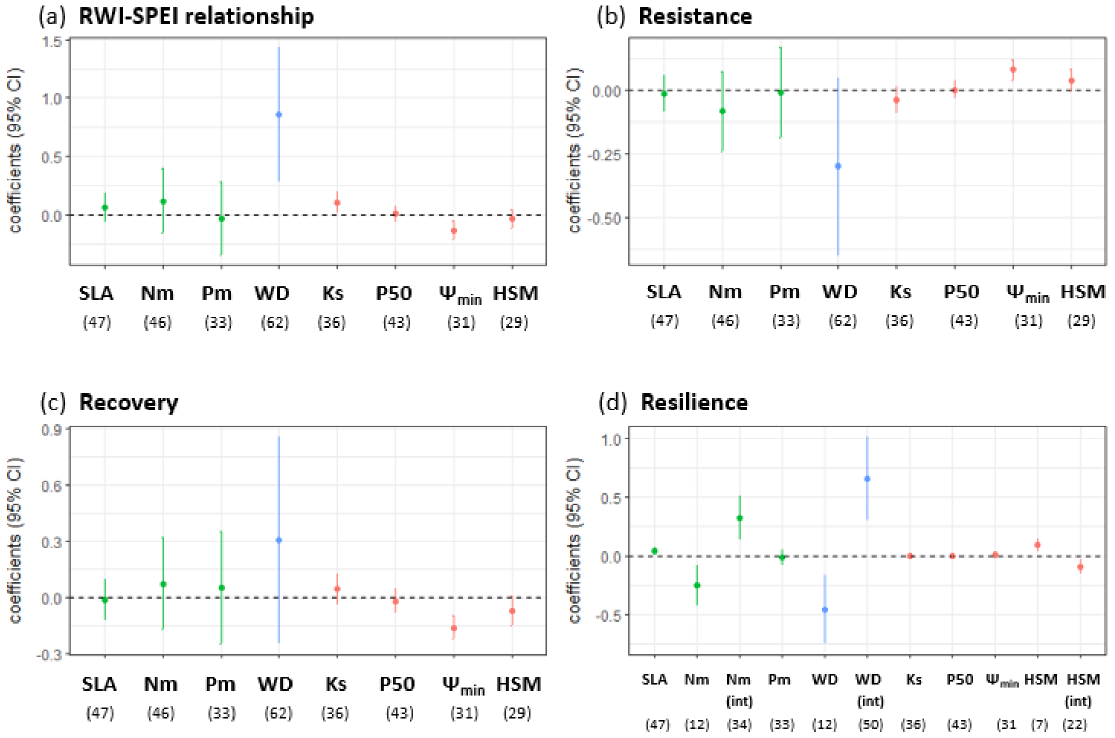


Figure 3. Results of the best models evaluating relationships between growth metrics, (a) strength of RWI-SPEI relationship, (b) Rt, (c) Rc and (d) Rs and functional traits. Points represent the estimates of means and 95 % confidence intervals are plotted as vertical lines. Horizontal dashed line at estimate = 0 is depicted (i.e., no significant effect). Significant interaction (int) shows the estimate difference of gymnosperms respect to angiosperm (reference level). Point colors indicate the trait spectrum, green = leaf traits, blue = wood traits and red = hydraulic traits. SLA = Specific Leaf Area, Nm = Nitrogen per unit of mass, Pm = Phosphorous per unit of mass, WD = wood density, Ks = stem specific conductivity, P50 = water potential at 50% percentage loss of conductivity, Ψmin = minimum leaf water potential and HSM = Hydraulic Safety Margin. Numbers in brackets below trait names in the x axis indicate the number of species for which data were available.

Models using traits as single predictors had AIC lower or equal to models using trait + Clade or trait * Clade as predictors, for RWI-SPEI relationship, Rt and Rc (Supplementary Materials, Table S4). In the case of Rs, models using Pmass, Ks and P50, Ψmin and SLA as single predictors presented the lower AIC. Models with Clade in interaction with Nmass, WD and HSM were selected as best-fitting models (Supplementary Materials, Table S4). However, it must be noted that for resilience, little variance is associated with species or site (Figure 5.2). RWI-SPEI relationship to SPEI was higher in species with high WD, high Ks, and low Ψmin (Figure 5.3 & 5.4). Resistance was higher in species with less negative Ψmin and high HSM, and the opposite pattern was found for recovery (Figures 5.3 & 5.4). Resilience was high in species with high SLA (Figure 5.3). For the same Nmass and WD values angiosperms were less resilient than Gymnosperms, on the contrary for the same HSM values angiosperms were more resilient than gymnosperms. (Figure 5.3). Effects of HSM on resistance and recovery depended on the weighting variable (e.g., relationships became non-significant if models were weighted by number of chronologies instead of number of droughts), although the direction of the trend remained the same (Supplementary Materials, Table S4, S5 & Figure S7).

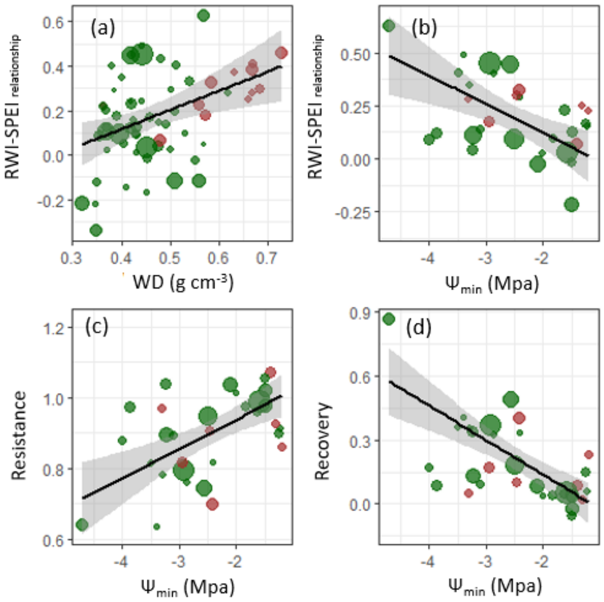


Figure 4. Linear relationships between (a) RWI-SPEI relationship and wood density, (b) RWI-SPEI relationship and Ψmin, (c) Resistance and and Ψmin and (d) Recovery and Ψmin. WD = wood density, Ψmin = minimum leaf water potential. Green points represent gymnosperm species, brown points represent angiosperm species. Point size is proportional to the weight in the models (number of chronologies per species for RWI-SPEI relationship, number of droughts per species for resistance and recovery).

After partially sorting out the effects of climate on both growth indices and traits, the relationships between residuals of RWI-SPEI relationship, Rt or Rc and residuals of traits had generally lower adjusted R^2 but remained significant, although the decrease in R^2 as well as the significance level varied for each case (Figure 5.5). Only in two cases, corresponding to the relationships of resistance and recovery with HSM, the significant relationships disappeared when accounting for mean annual temperature (MAT) effects (Figure 5.5). Accounting for MAT reduced R^2 the most in all cases, with the exception of the relationships between RWI-SPEI relationship and Ks, where mean total annual precipitation across the study period was the most important climatic variable affecting the relationship (Figure 5.5). In 9 of the 21 models adjusted R^2 actually increased when accounting for the corresponding climatic variable (Figure 5.5).

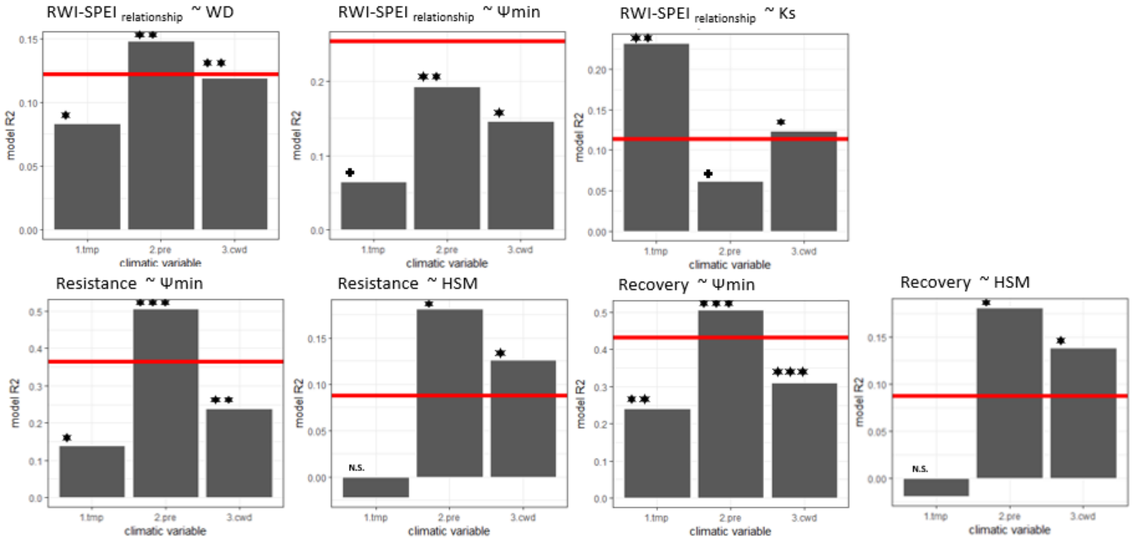


Figure 5. Squared partial correlations of the significant or marginally significant bivariate relationships between RWI-SPEI relationship, resistance and recovery with functional traits accounting for climatic variables (MAT, MAP, CWD, precipitation and climatic water deficit). WD = wood density, Ψmin = minimum leaf water potential and HSM = Hydraulic Safety Margin. Horizontal red line represents de R2 of the original models representing bivariate relationships without accounting for climate effects on growth indices or traits. Black signs represent the level of significance of the partial correlations: +; $p < 0.1$, *; $p < 0.05$, **; $p < 0.01$, ***; $p < 0.001$.

5.5. Discussion

Using a global tree ring database, our results indicate that the strength of RWI-SPEI relationships, resistance and recovery to extreme drought variation are associated to cross-species variation in functional traits such as WD and hydraulic traits and that these relationships are largely robust across broad climate gradients (MAT, MAP or CWD). We showed that species-level variability accounts for a substantial amount of the variation in RWI-SPEI relationships (49%), resistance (22 %) and recovery (17 %). All together, these results point to a possible physiological relationship between WD, hydraulic traits and species RWI-SPEI relationships, resistance and recovery to drought. RWI-SPEI relationships play a central role in our analyses, integrating short-term growth response to extreme drought years and their covariation with traits (Figures 5.1, 5.3 & 5.4). A common axis of variation where species with higher Pearson correlation coefficient of RWI-SPEI relationships, resist less and recover more from single extreme drought years arises from our analyses (Figure 5.1). In arid sites growth is more limited by drought (Babst et al. 2013) and presents lower resistance and higher recovery from extreme droughts (Gazol et al. 2017a; Gazol et al. 2018b), a pattern we link with species-level functional traits.

Disentangling site- from species-specific effects on growth response to drought is difficult as species are not randomly distributed across the globe. Overall, a wide array of climate effects over species-specific effects on growth responses to drought is expected (Figure 5.1). Some studies have found relatively limited differences among species' growth responses to climate (D'Orangeville et al. 2018, Martin-Benito & Pederson, 2015). However, these studies were limited to certain forest types (NE North America). By contrast, others found species to be an important factor explaining growth responses to climate (Drobyshev et al. 2013; Marchand et al. 2019; Li et al. 2021). Across the European continent, species-specific growth responses to climate have been reported (Babst et al. 2013) and in the case of short-term response to single extreme events, variation is related to climate (Gazol et al. 2017a), but species-level functional traits also play a role, globally and locally (Li et al. 2020; McGregor et al. 2020). The reported 49 % variance in RWI-SPEI relationships associated to species level and the higher species-level proportion of variance with respect to site in Rt and Rc suggest an important role of species-specific growth strategies to cope with drought.

Climate controls of growth vary geographically, temperature being the main limiting factor at poleward latitudes and high elevation, and drought on lowland and dry areas (Babst et al. 2013). Arid sites show lower resistance and higher recovery (*sensu* Lloret) compared to wetter sites (Gazol et al. 2017a; Gazol et al. 2018b). Here we observe stronger RWI-SPEI relationships, lower resistance and higher recovery in arid sites (Figure 5.1, Supplementary Materials, Figure S8). One could expect that during extreme drought years, growth would be decoupled from their general relationship with macroclimate and suffer a strong decrease at both, humid and arid sites. However, we do not observe that pattern here and, at the species level, RWI-SPEI relationships are strongly related to resistance and recovery. It is possible that the drought index used here is not equally relevant for all species and sites (i.e., variation in drought timing, drought length, winter versus summer droughts, etc., Huang et al. 2018), resulting in geographical variation in RWI-SPEI relationships, resistance and recovery. Across the globe vegetation responds to different drought dimensions regarding timing, time scale and intensity (Vicente-Serrano et al. 2013; Gao et al. 2018: D'Orangeville et al. 2018). Although standardized drought indices are a powerful tool, they have their own limitations, and additional indices may need to be considered in some applications (Slette et al. 2019a; Zang et al. 2019; Slette et al. 2019b). Hydrological year drought metrics, such as 12-month time-scale SPEI may be more relevant in dry sites (Vicente-Serrano et al. 2013) dependent on deep bedrock water resources. On the contrary, for species inhabiting wet and cold regions, very negative SPEI values may correspond to conditions where these is no water deficit in absolute terms (i.e., rainfall > potential evapotranspiration), and hence no ‘drought’ response is expected. This is consistent with increasing growth rates with declining SPEI (negative RWI-SPEI relationships) and no or even positive growth responses to individual droughts (determined by SPEI) at these sites (Figure 5.1).

Species level variation on growth response to drought is likely to be influenced by functional traits related to morphological, physiological and life history species characteristics. Still, studies of common traits related to plant functional resource strategies as predictors of climate-growth relationships and single-year drought response are relatively rare. In a study on 24 tree species across eastern north America, D’Orangeville et al. (2018) found no effect of P50 and rooting depth on tree growth sensitivity to SPEI, which agrees with the absence of a P50 relationship with all the indices used here (Figure 5.3). McGregor et el., (2020), explored the effect of functional traits on *sensu*-Lloret response to drought of 12 species from a deciduous forest in Virginia (USA), and found results similar to ours, i.e., hydraulic traits were more relevant than leaf traits for growth response to drought variation. In our case, the most relevant traits were WD and Ψmin and, to a lower extent, Ks and HSM.

The importance of WD and Ψmin over leaf traits suggest that tree ring growth responses to drought are associated to wood and hydraulic spectra (Chave et al. 2009; Gleason et al. 2016). WD is related to water transport, mechanical stability and growth rates (Chave et al. 2009). In gymnosperms, which compose the majority of our dataset, WD reflects the relationship between lumen area and tracheid wall thickness. At the same time, tracheid’s formation is strongly influenced by Ψmin, as low pressures result in reduced cell expansion and thus lower lumen areas, increasing wood density. These relationships could explain the strength of the RWI-SPEI relationship covariation with WD and Ψmin, although species-level Ψmin values should be interpreted with caution (Martínez-Vilalta et al. 2021). Ψmin depends on atmospheric vapor pressure deficit, soil water potential, water use regulation and tree architecture (i.e., rooting depth) (Bhaskar

& Ackerley, 2006; Martínez-Vilalta & García-Forner, 2017), conditions that also affect cambial activity (Cabon et al. 2020). Species growing on more arid sites, where water is a limiting factor, with high VPD and low soil water potential, tend to experience lower Ψmin and, therefore, low rates of cell expansion. On the contrary in more humid sites, species may present less negative Ψmin and other factors may be more important on woody cell development (e.g., low temperatures). In the case of coexisting species under similar VPD, tree architecture adjustments such as increased rooting depth or microsite soil conditions should alter species Ψmin values, modifying the degree of drought exposure and the strength of RWI-SPEI relationships. In our case, there is a range of ~ 0.5 mean Pearson correlation coefficient across species growing under similar CWD (Supplementary Materials, Figure S8) supporting that microsite and species adjustments must be strong drivers of RWI-SPEI relationship.

Causal relationship between RWI-SPEI relationship, resistance and recovery with functional traits are difficult to establish, however, covariation between them did not disappear when accounting for mean site climate conditions (Figure 5.4). Narrower wood cell with thicker walls should prevent drought induced cavitation (Hacke et al. 2001), thus, higher wood density may be beneficious in terms of avoiding xylem damage due to water shortage, however this should be interpreted with caution, as P50 was not related to any metric used here. In sites where wood cell development is limited by long-term drought stress, species with high WD may have an advantage, through lower drought-induced mortality and lower Ψ_{lethal} across species (Greenwood et al. 2017; Liang et al. 2020). Relationship between Ψmin (drought exposure) with the strength of the RWI-SPEI relationship (negative), resistance (positive) and recovery (negative) must arise from the same pattern (Figure 5.1), which is that in species more exposed to drought, where growth is limited by water shortage (high strength of RWI-SPEI relationship), under extreme droughts years suffer higher growth reductions (low resistance) and rapidly recover pre-drought growth rates when conditions are ameliorated (high recovery). The degree to which these drought responses ~ trait covariations are influenced by covariation of both drought responses and traits with climate is difficult to cleanly parse out. However, the fact that partial correlations support our main results suggests a mechanistic link between drought response and traits.

Hydraulic Safety Margins have been proposed as a key trait to determine species vulnerability to drought (Choat et al. 2012; Oliveira et al. 2021), including species drought induced mortality (Anderegg et al. 2016) and effects on ecosystem fluxes (Anderegg et al. 2018, García-Valdés et al. 2021). In our case, HSM was positively related to growth resistance and negatively to recovery, which indicates that species operating with narrower safety margins are more sensitive to extreme drought events. These results should be interpreted with caution for two reasons, however. First, by contrast to the WD or Ψmin effects on the RWI-SPEI relationship, resistance and recovery, the significance of HSM effects depended on the weighting method in linear models, making this result less robust (Supplementary Materials, Table S2). Second, such relationships were no longer significant when accounting for climate (temperature) variation (partial correlations). In addition, the fact that HSM is calculated as the difference between Ψmin and P50, suggests that this result may come from the observed relationship between Ψmin, Rt and Rc.

Tree growth responses to drought can be evaluated at different ecological scales, thus affecting the interpretation of causes and consequences of growth responses. The high percentage of variation associated to year in the Lloret indices (resistance, recovery and resilience, Figure 5.2), describing short-term responses to extreme drought years, must be caused by temporal heterogeneity in forest characteristics and drought intensity. Changes in land uses, active or passive management and succession followed by alteration of stand age and structure over time should lead to different growth responses to drought, as observed spatially (Bottero et al. 2019; Bennett et al. 2015). Similar to mortality due to drought, fire and pests also result in forest structural changes, and thus in different growth responses to drought across time. Furthermore, drought effects can persist several years (Anderegg et al. 2015a; Peltier, Fell & Ogle, 2016), a pattern increasing under more frequent droughts (Peltier & Ogle. 2019), which may result in temporal differences if damages accumulate over time (Anderegg et al. 2020b). Although we avoid the use of drought events overlapping in pre- and post-drought recover periods (i.e., 4 years) the impacts of drought on growth can last for longer periods and affect long-term growth trends (Serra-Maluquer et al. 2021). Overall, this result indicates that all these circumstances, relating to different conditions across drought episodes, contribute to the complexity of observed forest response to drought, making future projections of forest response to climate change at fine scales an enormous challenge.

Climate change will pose higher pressure on forests through increasing temperatures and higher frequency and intensity of droughts, exerting higher drought limitations on growth while reducing low temperature limitations (Babst et al. 2020; Pompa-García et al. 2021). Such changes may influence species distributions, promoting retractions and drought induced mortality at dry edges (Anderegg et al. 2019) and growth – temperature decoupling and expansion at cold treelines (Camarero et al. 2021) with potential influences on carbon stocks and ecosystem fluxes (Martin, Doraisami & Thomas, 2018; Sabot et al. 2019; Eller et al. 2020; Flo et al. 2021). Our results indicating that cross-species interannual growth variability associated to drought is related to WD and hydraulic traits support the importance of such traits on regulating carbon fluxes, which is particularly relevant under the expected increase of drought pressures on forests.

Chapter 6

Discussion

In the present thesis I evaluated how tree ring growth resilience to drought varied across individuals, populations and species and the drivers associated at each ecological scale. To disentangle possible patterns of growth resilience to drought different approaches were combined, from local individual based studies to global assessments of interspecific patterns. The main results of each chapter are discussed below.

6.1. Geographical variation on within species response to drought

Biogeographical theory predicts that under extreme weather conditions the drier and most equatorward populations would suffer more drought induced damage than core or central populations (Brown, 1984). Increase in drought frequency and intensity should promote growth decline in equatorward tree populations, followed by drought induced dieback and retractions of the species distribution range margins. However, while some empirical studies and meta-analyses support such predictions (Sánchez-Salguero et al. 2017b, Anderegg et al. 2019; Camarero et al. 2021), other studies showed how central populations may be more vulnerable than expected to climate change (Cavin & Jump, 2017). In chapter 2, the intraspecific variability of secondary growth across climatically contrasted *Fagus sylvatica* populations in its southern distribution edge was evaluated. Overall, growth constrain during the last decades was found, with more negative growth trends caused by an increase in pointer years associated to extreme droughts. In other words, the higher frequency of drought occurrence has limited radial growth capacity in some *F. sylvatica* populations. Such results supported that in the southern limit of its distribution, *F. sylvatica* growth is constrained by drought.

However, the intraspecific variation on drought constrains of growth was found across the study area. While previous studies focusing on drought limitations on growth of Iberian *F. sylvatica* forest were located on restricted areas (Gutiérrez, 1988; Jump et al. 2006), our broader sampled area allowed to discern between different responses across populations. While stands located in Atlantic and Mediterranean areas suffered from temperature increases, Pyrenean populations did not. These results show that in the same region different responses to warming and drought increases can be found due to climatic and topographic heterogeneity. Such results emphasize the heterogeneous responses of forests to drought at their equatorward edges. We must consider that latitudinal distribution limits might not coincide with climatic and ecological limits of the species (Vilà-Cabrera, Premoli & Jump, 2019). Such discordance between the latitudinal and the climatic distribution limits of the species may cause result disparities. It is possible that in southern or rear edges some populations persist in climatic refugia which buffer them from the macroclimatic conditions (Camarero et al. 2021). All this complexity should result in a mosaic type of species retraction or shift, rather than simply growing better, showing an improved performance migrating to northern, wetter areas.

Within species differences on growth constraints to drought across their distribution range are well known (Cavin & Jump, 2017). In this chapter such divergences are also found at regional scales and must be taken into account when evaluating species dynamics at their distribution ranges.

6.2. How much does biodiversity affect growth resilience to drought?

One central topic in ecology is the relationship between stability and biodiversity, which implies that more diverse ecosystems will be more resilient to perturbations (Isbell et al. 2015). In forests, biodiversity has been seen to benefit productivity (Vilà et al. 2007; Liang et al. 2016; but see Dormann, Schneider & Georges, 2019) and to reduce competition (Kunstler et al. 2016), while disparate results have been found on its effects on resilience to climate extreme events (Isbell et al. 2015; Gazol & Camarero, 2016; Grossiord et al. 2014). If biodiversity increases resilience to climate extremes, it does so through complementarity, which means that characteristics of different species help to buffer climate extreme effects. At landscape scale, biodiversity effects might be caused by the bigger species pool, as it is more likely that in more diverse systems some species will be more resilient. However, at individual level, having a diverse neighbour may not have positive effects, and competition may override complementarity making structural diversity more important than taxonomic and functional diversity.

In chapter 3, how drought resilience of *Abies alba* trees varied when growing surrounded by: i) conspecific trees, ii) another evergreen gymnosperm, *Pinus sylvestris*, and iii) a deciduous angiosperm *Fagus sylvatica* was evaluated. Furthermore, it was assessed how soil biotic and abiotic characteristics were related to neighbour identity and the possible patterns across soil, neighbours and *A. alba* response to drought at individual level. It was shown how having neighbour of different species is related to different soil conditions (microbial community structure and soil nutrient content). However, support for higher drought resilience on individuals growing with non-conspecific neighbours was not found. Biodiversity-resilience relationships may depend on several factors and at individual level may rely on species specific relationships (Vitali, Forrester & Bauhus, 2018) and environment conditions (Messier & Paquette, 2011). So that, general ecosystem-stability relationships may still be present, even though some species are not benefited. Evaluating the response of *F. sylvatica* and *P. sylvestris* should give some light to see which species and trees take advantage on the studied forests.

In this chapter I tried to evaluate patterns across different variables focusing at the individual level. As far as we know, this is one of the first studies combining tree level growth data, with individual level neighbourhood and soil biotic and abiotic conditions (but see Gazol et al. 2018a). The used correlational approach did not allow us to test for causal relationships but helped to highlight some patterns which will be worth exploring in the future. Although variable sources come from different temporal scales (growth; many years, soil: on sample at a given time) some patterns arise suggesting some potential for future research lines. For instance, giving that soil microbial composition under *A. alba* trees seem to be dependent on neighbour species, understanding if vulnerable trees lack some specific microbial groups might be of interest.

6.3. Repeated climate extreme events

Although much has been done on the evaluation on drought effects on tree growth, the highest risks coming from future climate predictions is the increase in frequency and intensity of droughts. So that, it is not only how single droughts affect tree resilience, but how multiple repeated events are faced by trees. It has been seen that recovery after drought can last at least 4 years in some species (Anderegg et al. 2015a), furthermore, such “legacies” increase in time when droughts are recurrent (Peltier & Ogle, 2019). However, precipitation extremes are expected to occur in both directions, increasing dry and wet years, and very few is known on the potential of wet years potential to mitigate or worsen the effects of dry years on growth. Recently, Jiang et al. (2019) suggested that growth during wet years may compensate drought legacy effects on growth. However, caution must be taken as it has also been postulated that an increase in aboveground biomass during periods of resource surplus may be detrimental under following drought episodes (Jump et al. 2017).

In chapter 4, how short-term responses of tree growth to three dry and wet years influenced long-term growth trends across 26 years was studied. It was observed that the individual response to these events was linked to long-term growth trends. Showing that the effects of consecutive droughts leaded to long term growth decline. Repeated extreme dry and wet years influenced growth trends independently of growth trajectory, which is that trees in populations with positive, neutral or negative growth trends were affected. It was also tested if individual level functional traits were related to growth impacts of both, dry and wet years. Specific Leaf Area (SLA) and wood density (WD), traits reflecting the fast-slow growth continuum at interspecific level (Wright et al 2004; Chave et al. 2009; Reich, 2014), were used. We hypothesised that trees with higher SLA and lower WD will be more impacted by dry years and grow more during wet years, and the opposite for trees showing low SLA and high WD. However, support for these hypotheses was not found, which suggest a poor link between “soft” functional traits and tree growth responses to drought at intraspecific level. SLA and WD reflect strategies related to resource acquisition at interspecific scale; however, although the high variation at intraspecific level (Fajardo & Piper, 2011), such patterns might not appear when evaluating within species variation (Anderegg et al. 2018; Rosas et al. 2019) indicating scale dependence. The poor links of these traits with physiological processes, compared with “hard” hydraulic traits, related to water use, may be the reason for the absent relationships at intraspecific level.

If frequency and intensity of extreme drought events increase, as predicted for many regions, our results indicate that the accumulation of drought impacts will result in widespread growth decline, especially for gymnosperm species. These may be added to the legacy effects on growth after extreme droughts (Anderegg et al. 2015a; Peltier & Ogle, 2016; Kannenberg et al. 2019; Gazol et al. 2020), which are longer under consecutive droughts (Peltier & Ogle, 2019). So that, if repeated extreme growth decreases occur at the same time as those legacies, and drought events become closer, growth rates will be reduced, which may have consequence for the carbon stocks and fluxes. An extreme drought could change drought sensitivity of trees through damaging its tissues or altering its environment (reducing competition) (Peltier & Ogle, 2020). Therefore, drivers of growth resilience to drought may change across time and features conferring resilience to a single drought may not be enough to support several repeated periods of water stress. Evaluating when resilience is lost after repeated extremes will help to better understand episodes of drought induced mortality.

6.4. Functional traits and interspecific growth responses to drought

Interspecific variability in tree growth responses to drought is not well quantified, while some studies found taxonomic differences on growth responses to drought others did not (D’Oragenveille et al. 2019; Babst et al. 2013), being local conditions the only drivers of them. While acknowledging that climate and soil conditions may be the most important drivers of tree growth responses to drought, species specific responses driven different strategies are expected. Such strategies should be reflected by cross-species functional traits, for instance, species with higher SLA and lower WD are more prone to suffer drought induced tree mortality (Greenwood et al. 2017). Furthermore, traits relating to water use, which more direct physiological links to plant performance, should be better predictors of cross-species growth response to drought variability. However, a broad evaluation of relationships between growth response to drought and functional traits is lacking.

In Chapter 5, it was characterized how tree growth-drought relationship, resistance, recovery and resilience to extreme droughts variation was structured across different ecological scales (species, sites and years). Then, covariation between species-specific variation in these growth response and functional traits related to leaf, wood and hydraulic function was evaluated. It was found that species level variation of growth-drought relationship, resistance and recovery to extreme droughts was non-negligible, suggesting geographically-constrained and species-specific responses to drought. At global scale and across species, growth-drought relationship was linearly related to resistance and recovery, which indicated that the three resilience indices represented the same response axis. More sensitive species present lower resistance and higher recovery, this variation was associated to functional traits, as such species were located at drier sites and presented higher wood density and their xylem experience lower leaf water potentials. Leaf traits were not related to interspecific variation of tree growth responses to drought. Covariation between growth responses to drought and functional traits was maintained even when accounting for large climate gradients.

These results indicate, that although growth response to drought is strongly driven by drought characteristics and climatic conditions, species specific responses are present. Such species-specific responses to drought are associated to functional traits relating to wood and hydraulic function and show different strategies of species to cope with drought. The fact that wood density and hydraulic traits are associated to species specific responses to drought indicates the potential of these traits to predict future forest responses to increasing drought frequency and intensity, and how different species will be influenced by it. Such species-specific responses may have consequences for ecosystem fluxes and carbon stocks (Anderegg et al. 2020a).

6.5. Concluding remarks

Across the different chapters of this thesis, it is shown that tree growth resilience to drought is highly variable within and across tree species. It was evidenced that different drivers determine drought resilience to drought and that such drivers are scale-dependent. For instance, patterns not observed at intraspecific level with wood density and drought resilience (Chapter 4) emerge at interspecific level at global scales (Chapter 5). The contrasting results indicate that drivers which may be useful to understand growth resilience to drought at one level (species) may not be relevant at other level (individual trees).

Individual based approaches allowed digging into patterns of covariation between soil microbiota, neighbour identity and growth resilience (Chapter 3). However, the little portion of variance explained reveals the high complexity of processes driving tree level resilience to drought. In the same line of these results there is null predictive capacity of functional traits to explain individual level accumulated growth decreases (Chapter 4). Although individual level approaches should reveal the most precise drivers of tree resilience to drought, it is still a challenge to find general patterns of tree level characteristics conferring resilience in adult trees during field studies. As shown here, contingencies depending on species specific neighbour identity and microclimate alteration (Chapter 3) may alter growth responses to drought which complicates any generalization. Furthermore, broad interspecific patterns do not need to hold at intraspecific level when evaluating tree level data (Chapter 4) as other mechanism (e.g., allocation patterns) could be more relevant at this level. At population level, regional variability can be present across the southern distribution range of a species, pointing to the importance of microsite conditions on driving growth resilience (Chapter 2). However, we did not find universal patterns in differences on response to repeated dry and wet years across six Iberian tree species, on the contrary the effect of these extreme episodes was visible in almost all populations, independently of the macroclimatic condition (Chapter 4).

Conclusions

1. Intraspecific variability of growth response to drought in *Fagus sylvatica* populations at its southern distribution limit is structured across populations. This implies that growth decline might occur in the geographic peripheral populations, but that local conditions can buffer it. Thus, rather than widespread declines a patchy retraction across species distribution areas is expected under more frequent drought conditions.
2. Individual level resilience to drought is affected by many features, including tree characteristics, soil biotic and abiotic conditions and neighbourhood species. *Abies alba* populations from three different mixed forests showed correlational patterns between soil, neighbour type (conspecific, broadleaf angiosperm or evergreen gymnosperm) and resilience components to drought. These results show that mixtures do not always benefit growth resilience after drought and are dependent on neighbour type. Furthermore, soil conditions, which are related to drought recovery, vary depending on neighbour type.
3. Increasing frequency and intensity of extreme drought events will result on more growth decreases, influencing individual and stand level growth trends. If recovery times are not long enough and such accumulated growth impacts in trees become closer in time, the probability of growth declines will increase. Therefore, is important to find which characteristics will confer individual level resilience to such increase. Our results indicated that specific leaf area and wood density were not good predictors of accumulated growth decreases/enhancements. Therefore, shifting to more mechanistically relevant traits for water use such as hydraulic traits is needed.
4. Species level variation in drought resilience components and growth sensitivity to drought is non-negligible. Such variation is associated to across species variation in functional traits (wood density and hydraulic traits). Such covariation indicates the potential of functional ecology and specially plant hydraulics to predict future interspecific variation in growth responses to increasing frequency and intensity of droughts. Thus, including these variables on global vegetation models will help to better predicts ecosystem fluxes under future climate projections.
5. Overall, growth resilience to drought is a complex process. Drivers determining growth resilience to drought are scale dependent and vary temporally and spatially. This thesis has tried to put some light on how tree growth resilience to

drought varied within and across species, and which drivers were more correlated to this variation. Evaluation of patterns of variation and covariation is important in science, as will lead future research to disentangle possible mechanisms. In the case of this thesis, I hope that observed patterns will help to develop future ideas and research directions of who might read it.

Appendices

Supplementary Materials
Chapter 2

Table S1. Mean annual temperature, mean annual precipitation and mean elevation values for the four regions obtained from the cluster analyses (Pyrenean, Mediterranean, low- and high-elevation Atlantic).

	Mean annual temperature (Cº)	Mean annual precipitation (mm)	Mean elevation (m a.s.l.)
Pyrenean	7.5	1013	1252
Mediterranean	11.3	723	1346
Low-Atlantic	11.8	1159	450
High-Atlantic	10.7	867	919

Figure S1. Mean annual temperature and total annual precipitation time series from each studied biogeographical region.

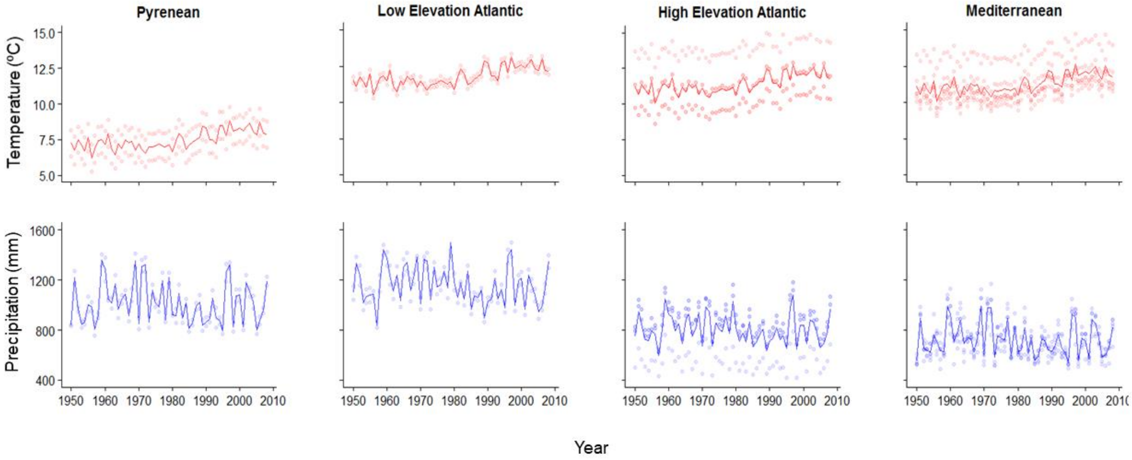


Figure S2. Spring-to-summer (April to September) mean values of temperature and precipitation for Mediterranean, Pyrenean, Low-Atlantic and High-Atlantic regions from 1950 to 2008. Trends for the studied period are reported. R^2 and significance (*p*) values from linear regressions between temperature and precipitation against calendar year are also reported.

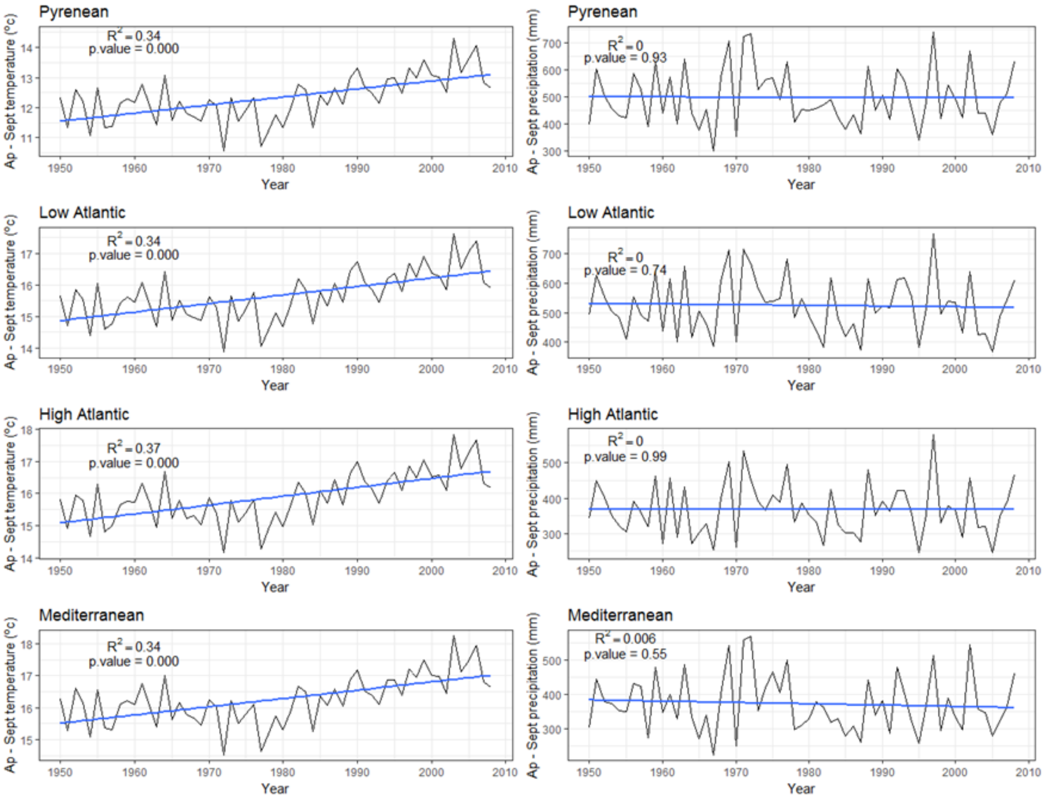


Figure S3. Cluster dendrogram obtained from hierarchical cluster analyses of the climate and geographical data (mean annual temperature, annual precipitation, De Martonne aridity Index and elevation) of the studied beech stands. The biogeographic regions considered were: low-elevation Atlantic (L-Atlantic), high-elevation Atlantic (H-Atlantic), Mediterranean and Pyrenean. See sites' codes in Table 1.

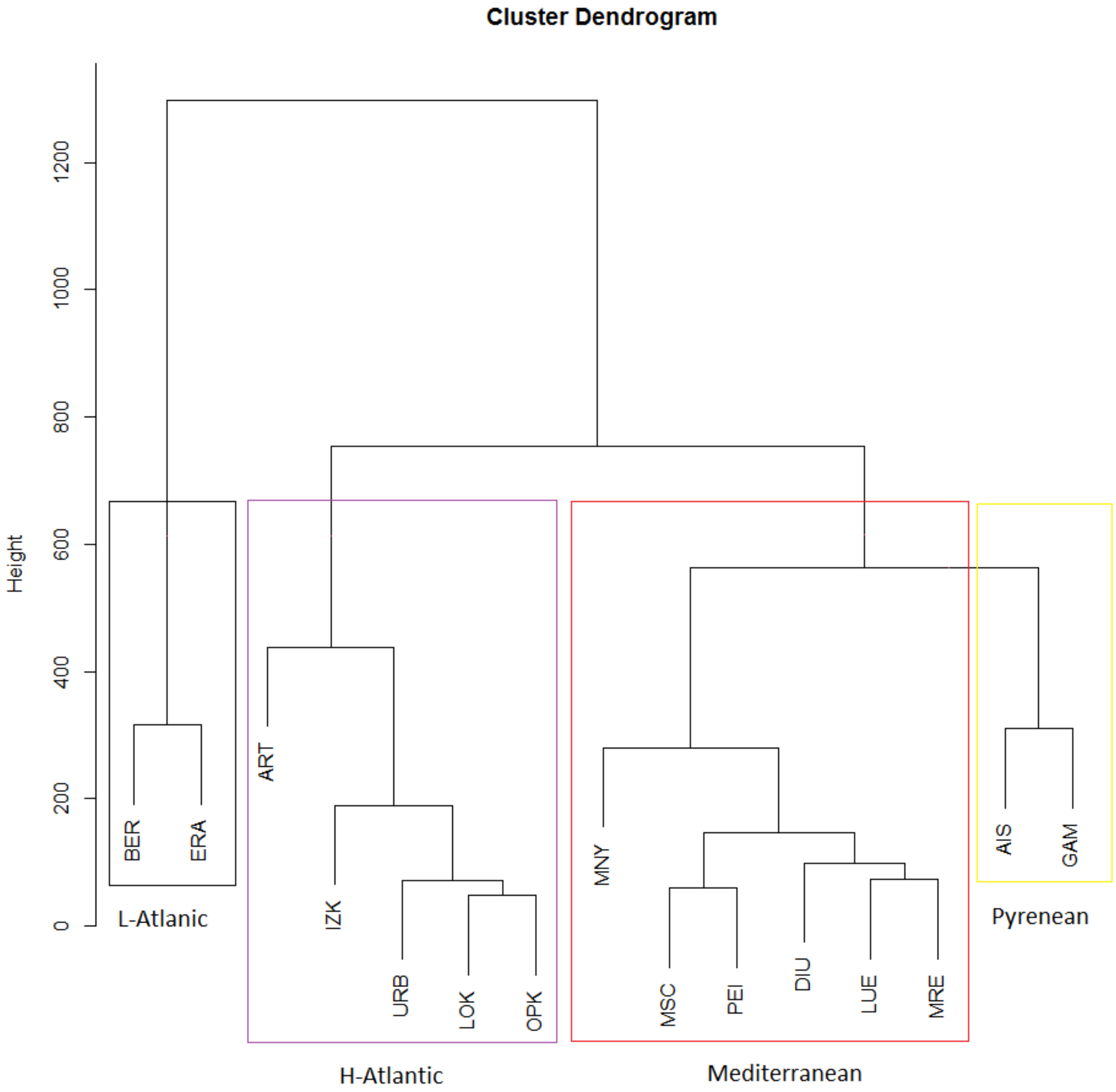
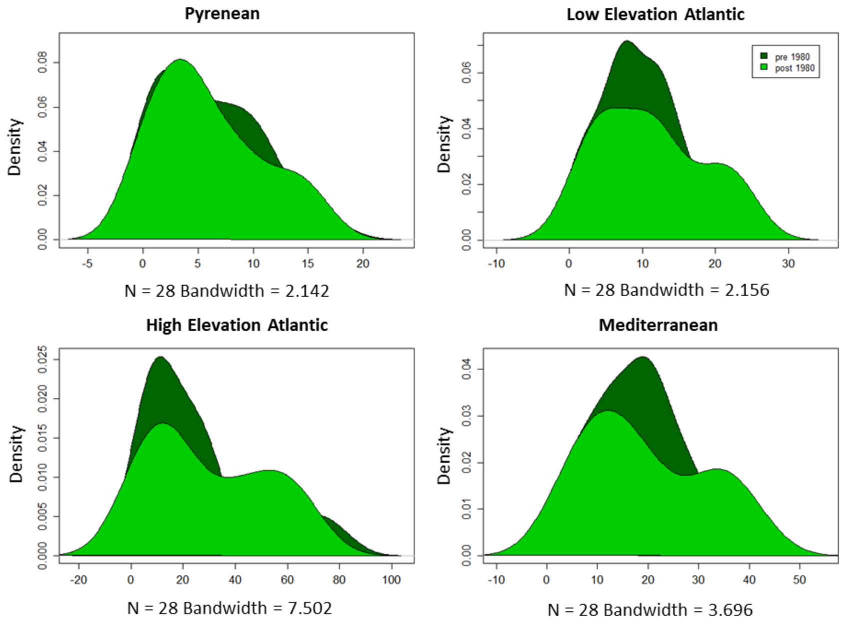


Figure S4. Kernel density distribution plots showing the individual pointer year distribution. The x axis represents the number of trees showing a pointer year per year. Dark green represents the pre-1980s period and light green represents the post-1980s period.



Appendices

Supplementary Materials
Chapter 3

Table S1. Diameter at breast height (DBH) and age estimated at 1.3 m for focal *Abies alba* trees, neighbour *A. alba* trees, neighbour broadleaved trees (mainly *Fagus sylvatica* see table S4 for a detailed description of each neighbourhood) and neighbour *Pinus sylvestris* trees. Note that for neighbour *A. alba* trees there is not information about age, this is because these trees were not cored as growth information of *A. alba* was obtained from focal trees.

Site	**Trees**	**DBH (cm)**	**Age (years)**
Paco Ezpela			
	Focal *Abies alba*	31 ± 1	96 ± 12
	Neighbour *Abies alba*	23 ± 1	—
	Broadleavef neighbour	21 ± 1	53 ± 2
	Pinus sylvesris neighbour	35 ± 2	97 ± 11
Jasa			
	Focal *Abies alba*	33 ± 1	96 ± 6
	Neighbour *Abies alba*	29 ± 2	—
	Broadleavef neighbour	30 ± 2	79 ± 4
	Pinus sylvesris neighbour	33 ± 5	99 ± 6
Orús			
	Focal *Abies alba*	33 ± 2	127 ± 15
	Neighbour *Abies alba*	29 ± 1	—
	Broadleavef neighbour	20 ± 1	116 ± 9
	Pinus sylvesris neighbour	27 ± 2	121 ± 8

Table S2. Tree-ring width statistics for each site and tree species. The following dendrochronological statistics are presented: Mean Sensitivity; measure of relative year to year variability in width, rbar; the average correlation between series, EPS (Expressed Population Signal), a measure of common variability and replication of the mean tree-ring series or chronology.

Site	**Species**	**Nº trees**	**Mean sensitivity**	**Rbar**	**EPS**
Paco Ezpela	*Abies alba*	30	0.22	0.20	0.81
	Fagus sylvatica	7	0.27	0.29	0.70
	Pinus sylvestris	14	0.30	0.27	0.76
Jasa	*Abies alba*	30	0.19	0.46	0.94
	Fagus sylvatica	9	0.27	0.53	0.89
	Pinus sylvestris	9	0.30	0.52	0.89
Orús	*Abies alba*	30	0.21	0.31	0.86
	Fagus sylvatica	8	0.28	0.24	0.67
	Pinus sylvestris	12	0.26	0.43	0.84

Table S3. Neighbourhood information for each one of the three sampled forests (Paco Ezpela, Jasa and Orús). Mean values plus standard errors (SE) are given. Minimum, maximum, mean (± SE) values of distance and sizes (DBH) and mean % of neighbour type are reported.

Measure	**Paco Ezpela**	**Jasa**	**Orús**
Minimum DBH (cm)	10.0	2.2	10.0
Maximum DBH (cm)	53.3	55	53.3
Mean DBH (cm)	25.0 ± 0.9	27.0 ± 1.0	25.0 ± 0.9
Minimum distance (m)	0.5	0.4	0.5
Maximum distance (m)	11.0	9.0	11.0
Mean distance between trees (m)	3.4 ± 0.2	3.4 ± 0.2	3.5 ± 0.3
% *Abies alba*	42 ± 1.18	57 ± 1.27	39 ± 1.26
% Broadleaf	30 ± 1.23	20 ± 1.11	33 ± 1.14
% *Pinus sylvestris*	26 ± 1.09	22 ± 1.12	26 ± 1.3

Table S4. Species identity of each neighbour sampled for every focal *Abies alba* tree (target tree) in each site. Dominant neighbour in terms of basal area is also given.

Site	Target tree	N1	N2	N3	N4	Dominant neighbor
Paco Ezplea	Aa 1	*Pinus sylvestris*	*Abies alba*	*Pinus sylvestris*	*Pinus sylvestris*	*Pinus sylvestris*
	Aa 2	*Abies alba*	*Pinus sylvestris*	*Fagus sylvatica*	*Abies alba*	*Abies alba*
	Aa 3	*Pinus sylvestris*	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	*Pinus sylvestris*
	Aa 4	*Pinus sylvestris*	*Pinus sylvestris*	*Abies alba*	*Abies alba*	*Pinus sylvestris*
	Aa 5	*Pinus sylvestris*	*Pinus sylvestris*	*Abies alba*	*Abies alba*	*Pinus sylvestris*
	Aa 6	*Pinus sylvestris*	*Pinus sylvestris*	*Abies alba*	*Abies alba*	*Pinus sylvestris*
	Aa 7	*Pinus sylvestris*	*Abies alba*	*Abies alba*	*Pinus sylvestris*	*Pinus sylvestris*
	Aa 8	*Abies alba*	*Fagus sylvatica*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 9	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 10	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 11	*Abies alba*	*Abies alba*	*Abies alba*	*Fagus sylvatica*	*Abies alba*
	Aa 12	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 13	*Abies alba*	*Pinus sylvestris*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 14	*Abies alba*	*Fagus sylvatica*	*Pinus sylvestris*	*Crataegus monogyna*	Broadleaf
	Aa 15	*Abies alba*	*Crataegus monogyna*	*Fagus sylvatica*	*Pinus sylvestris*	*Pinus sylvestris*
	Aa 16	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 17	*Fagus sylvatica*	*Fagus sylvatica*	*Acer sp.*	*Fagus sylvatica*	Broadleaf
	Aa 18	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	*Abies alba*	Broadleaf
	Aa 19	*Fagus sylvatica*	*Fagus sylvatica*	*Abies alba*	*Fagus sylvatica*	Broadleaf
	Aa 20	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	Broadleaf
	Aa 21	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	Broadleaf
	Aa 22	*Fagus sylvatica*	*Abies alba*	*Fagus sylvatica*	*Abies alba*	Broadleaf
	Aa 23	*Fagus sylvatica*	*Abies alba*	*Fagus sylvatica*	*Acer sp.*	Broadleaf
	Aa 24	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	Broadleaf
	Aa 25	*Fagus sylvatica*	*Fagus sylvatica*	*Abies alba*	*Fagus sylvatica*	Broadleaf
	Aa 26	*Pinus sylvestris*	*Pinus sylvestris*	*Abies alba*	*Abies alba*	*Pinus sylvestris*
	Aa 27	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 28	*Abies alba*	*Abies alba*	*Abies alba a*	*Abies alba*	*Abies alba*
	Aa 29	*Pinus sylvestris*	*Pinus sylvestris*	*Fagus sylvatica*	*Fagus sylvatica*	*Pinus sylvestris*
	Aa 30	*Pinus sylvestris*	*Fagus sylvatica*	*Pinus sylvestris*	*Abies alba*	*Pinus sylvestris*
Jasa	Aa 1	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	*Abies alba*	Broadleaf
	Aa 2	*Abies alba*	*Abies alba*	*Fagus sylvatica*	*Abies alba*	*Abies alba*
	Aa 3	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 4	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	*Abies alba*	*Abies alba*

	Aa 5	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	Broadleaf
	Aa 6	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	Broadleaf
	Aa 7	*Fagus sylvatica*	*Fagus sylvatica*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 8	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	*Abies alba*	Broadleaf
	Aa 9	*Fagus sylvatica*	*Fagus sylvatica*	*Fagus sylvatica*	*Abies alba*	Broadleaf
	Aa 10	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 11	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 12	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 13	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 14	*Abies alba*	*Abies alba*	*Abies alba*	*Pinus sylvestris*	*Abies alba*
	Aa 15	*Fagus sylvatica*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 16	*Abies alba*	*Abies alba*	*Fagus sylvatica*	*Abies alba*	*Abies alba*
	Aa 17	*Fagus sylvatica*	*Abies alba*	*Abies alba*	*Fagus sylvatica*	*Abies alba*
	Aa 18	*Fagus sylvatica*	*Abies alba*	*Fagus sylvatica*	*Abies alba*	*Abies alba*
	Aa 19	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 20	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 21	*Pinus sylvestris*	*Pinus sylvestris*	*Abies alba*	*Fagus sylvatica*	*Pinus sylvestris*
	Aa 22	*Pinus sylvestris*	*Abies alba*	*Pinus sylvestris*	*Abies alba*	*Pinus sylvestris*
	Aa 23	*Pinus sylvestris*	*Abies alba*	*Abies alba*	*Fagus sylvatica*	*Abies alba*
	Aa 24	*Pinus sylvestris*	*Abies alba*	*Pinus sylvestris*	*Pinus sylvestris*	*Pinus sylvestris*
	Aa 25	*Pinus sylvestris*	*Pinus sylvestris*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 26	*Pinus sylvestris*	*Pinus sylvestris*	*Pinus sylvestris*	*Abies alba*	*Pinus sylvestris*
	Aa 27	*Pinus sylvestris*	*Pinus sylvestris*	*Abies alba*	*Abies alba*	*Pinus sylvestris*
	Aa 28	*Pinus sylvestris*	*Pinus sylvestris*	*Abies alba*	*Abies alba*	*Pinus sylvestris*
	Aa 29	*Abies alba*	*Pinus sylvestris*	*Pinus sylvestris*	*Abies alba*	*Pinus sylvestris*
	Aa 30	*Pinus sylvestris*	*Pinus sylvestris*	*Abies alba*	*Abies alba*	*Pinus sylvestris*
Orús	Aa 1	*Fagus sylvatica*	*Abies alba*	*Fagus sylvatica*	*Abies alba*	*Abies alba*
	Aa 2	*Abies alba*	*Fagus sylvatica*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 3	*Fagus sylvatica*	*Fagus sylvatica*	*Abies alba*	*Fagus sylvatica*	*Abies alba*
	Aa 4	*Fagus sylvatica*	*Abies alba*	*Abies alba*	*Fagus sylvatica*	*Abies alba*
	Aa 5	*Fagus sylvatica*	*Acer sp.*	*Abies alba*	*Fagus sylvatica*	Broadleaf
	Aa 6	*Fagus sylvatica*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 7	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 8	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
	Aa 9	*Abies alba*	*Abies alba*	*Fagus sylvatica*	*Abies alba*	*Abies alba*
	Aa 10	*Fagus sylvatica*	*Fagus sylvatica*	*Abies alba*	*Fagus sylvatica*	Broadleaf
	Aa 11	*Fagus sylvatica*	*Fagus sylvatica*	*Acer sp.*	*Fagus sylvatica*	Broadleaf
	Aa 12	*Fagus sylvatica*	*Fagus sylvatica*	*Populus tremula*	*Acer sp.*	Broadleaf
	Aa 13	*Fagus sylvatica*	*Abies alba*	*Acer sp.*	*Fagus sylvatica*	*Abies alba*
	Aa 14	*Fagus sylvatica*	*Ilex aquifolium*	*Abies alba*	*Fagus sylvatica*	Broadleaf

Aa 15	*Abies alba*	*Fagus sylvatica*	*Acer sp.*	*Fagus sylvatica*	Broadleaf
Aa 16	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*	*Abies alba*
Aa 17	*Abies alba*	*Pinus sylvestris*	*Pinus sylvestris*	*Pinus sylvestris*	*Pinus sylvestris*
Aa 18	*Pinus sylvestris*	*Pinus sylvestris*	*Fagus sylvatica*	*Pinus sylvestris*	*Pinus sylvestris*
Aa 19	*Pinus sylvestris*	*Pinus sylvestris*	*Abies alba*	*Abies alba*	*Pinus sylvestris*
Aa 20	*Abies alba*	*Pinus sylvestris*	*Pinus sylvestris*	*Abies alba*	*Pinus sylvestris*
Aa 21	*Abies alba*	*Abies alba*	*Abies alba*	*Fagus sylvatica*	*Abies alba*
Aa 22	*Abies alba*	*Abies alba*	*Fagus sylvatica*	*Fagus sylvatica*	*Abies alba*
Aa 23	*Abies alba*	*Abies alba*	*Abies alba*	*Fagus sylvatica*	*Abies alba*
Aa 24	*Abies alba*	*Abies alba*	*Abies alba*	*Acer sp.*	Broadleaf
Aa 25	*Pinus sylvestris*	*Pinus sylvestris*	*Fagus sylvatica*	*Acer sp.*	*Pinus sylvestris*
Aa 26	*Pinus sylvestris*	*Pinus sylvestris*	*Abies alba*	*Populus tremula*	*Pinus sylvestris*
Aa 27	*Pinus sylvestris*	*Pinus sylvestris*	*Fagus sylvatica*	*Abies alba*	*Abies alba*
Aa 28	*Pinus sylvestris*	*Pinus sylvestris*	*Fagus sylvatica*	*Pinus sylvestris*	*Pinus sylvestris*
Aa 29	*Fagus sylvatica*	*Pinus sylvestris*	*Pinus sylvestris*	*Fagus sylvatica*	*Pinus sylvestris*
Aa 30	*Pinus sylvestris*	*Pinus sylvestris*	*Pinus sylvestris*	*Fagus sylvatica*	*Pinus sylvestris*

Table S5. Post-hoc Tukey tests of Basal Area Increment (BAI) of the 1988-2017 period comparing *Abies alba* trees growing under different neighbour type (*Abies alba*, *Pinus sylvestris* and broadleaved, mainly *Fagus sylvatica*) at each of the three forests studied.

Site	Neighbour type comparation	P adj
PACO EZPELA		
	Abies alba - Broadleaved	0.02
	Abies alba - *Pinus sylvestris*	0
	Broadleaved - *Pinus sylvestris*	0
JASA		
	Abies alba - Broadleaved	0.07
	Abies alba - *Pinus sylvestris*	0
	Broadleaved - *Pinus sylvestris*	0
ORUS		
	Abies alba - Broadleaved	0
	Abies alba - *Pinus sylvestris*	0
	Broadleaved - *Pinus sylvestris*	0.09

Table S6. Post-hoc Tukey tests of Basal Area Increment (BAI) of the 1988-2017 period comparing *Abies alba, Pinus sylvestris* and broadleaved (mainly *Fagus sylvatica*) trees at each of the three forests studied.

Site	**Specie comparations**	**P adj**
Paco Ezpela		
	Abies alba - Broadleaved	0.001
	Abies alba - *Pinus sylvestris*	0
	Broadleaved - *Pinus sylvestris*	0
Jasa		
	Abies alba - Broadleaved	0
	Abies alba - *Pinus sylvestris*	0
	Broadleaved - *Pinus sylvestris*	0.0006
Orús		
	Abies alba - Broadleaved	0.0004
	Abies alba - *Pinus sylvestris*	0
	Broadleaved - *Pinus sylvestris*	0.0004

Table S7. Results of the ANOVA analyses of soil abiotic characteristics and PLFA microbial groups as a function of dominant neighbour type (*Abies alba*, *Pinus sylvestris* and broadleaved species –mainly *Fagus sylvatica*). The significant p-values are given.

	Variables	*P* (>*F*)
Soil abiotic characteristics		
	Organic Matter	-
	Carbon	-
	Nitrogen	-
	Phosphorus	-
	Electric conductivity	-
	pH	-
	C: N	0.003
Soil Microbial groups		
	Eukaryote	0.04
	Gram. Negative	-
	Gram. Positive	0.02
	Actinomycetes	-
	Total Gram. Positive	-
	Total Bacteria	-
	Fungi	-
	AM. Fungi	0.01
	Total Fungi	-
	Anaerobes	-

FIGURES

Figure S1. August Standardized Precipitation and Evapotranspiration Index (SPEI) calculated for a 12-month scale (period 1960-2015). Red stars indicate 2005 and 2012 drought events, which are the driest of the period 1987-2017.

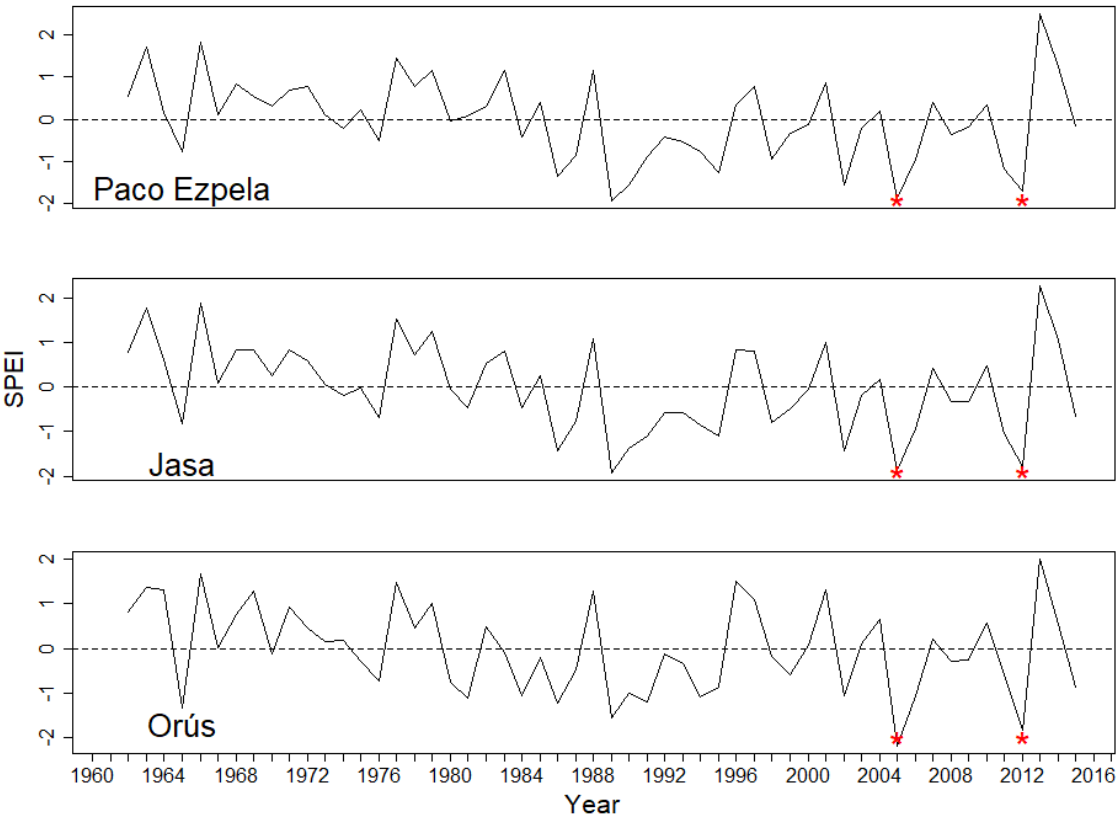


Figure S2. Relationship between mean resistance, recovery and resilience from 2005 and 2012 droughts with the single values of resistance, resilience and recovery for each one of these two years.

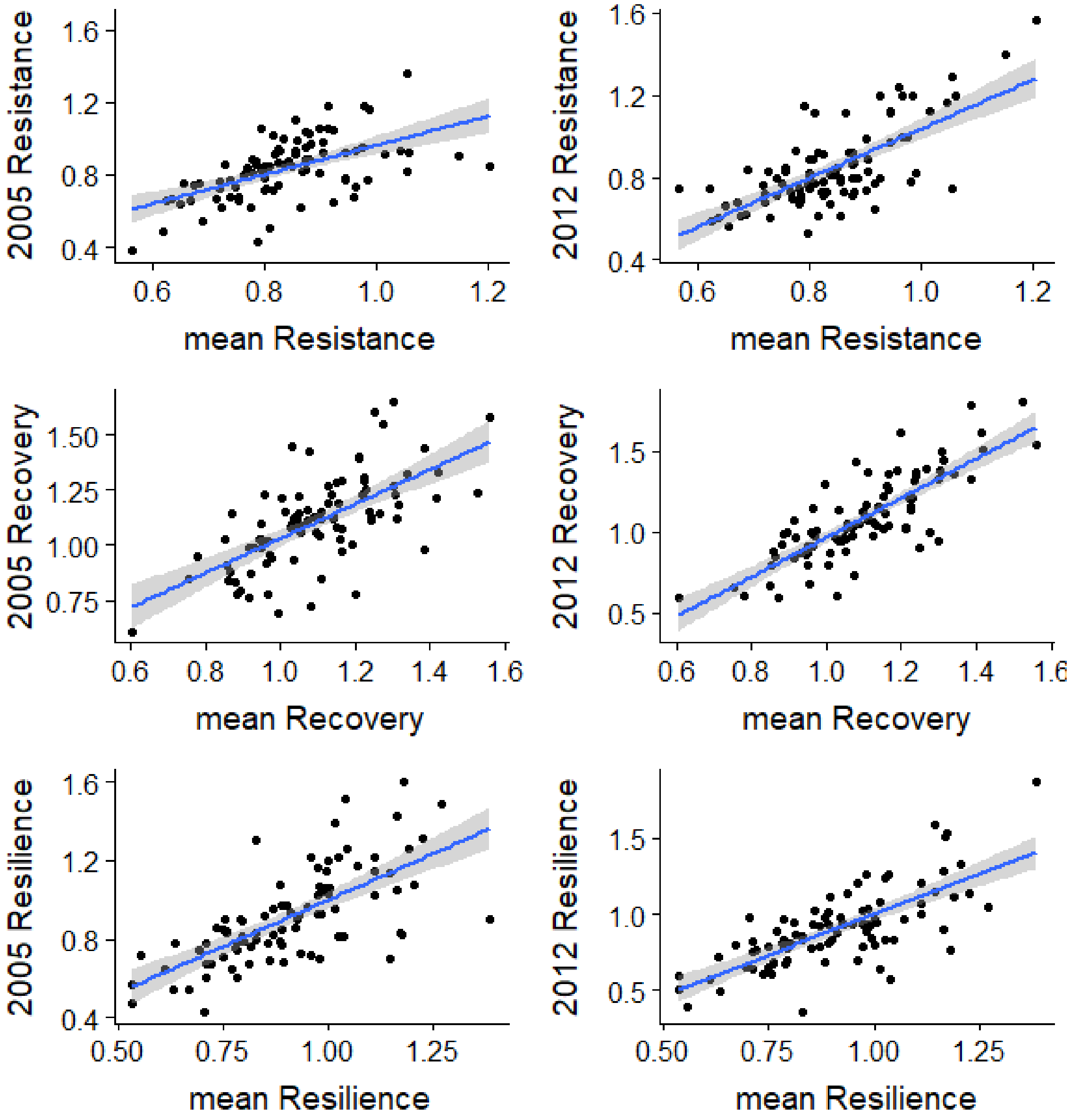


Figure S3. Soil texture triangles for: all sites together, and for the Paco Ezpela, Jasa and Orús sites, respectively. Point colour varies depending on dominant neighbour: *Abies alba* (black dots), *Pinus sylvestris* (green dots) and *Fagus sylvatica* (red dots).

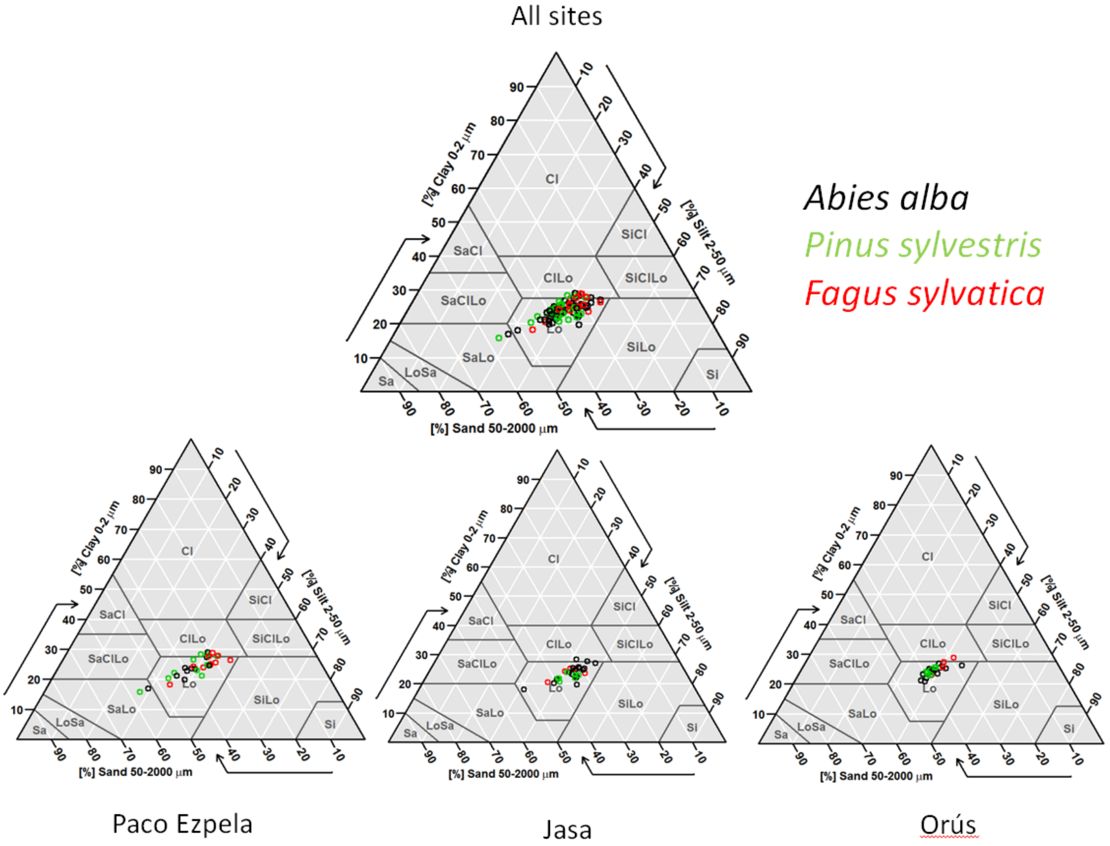


Figure S4. Boxplots representing differences across the studied soil variables and different sites (JA = Jasa, OR = Orús, and PE = Paco Ezpela). Different letters represent differences across sites.

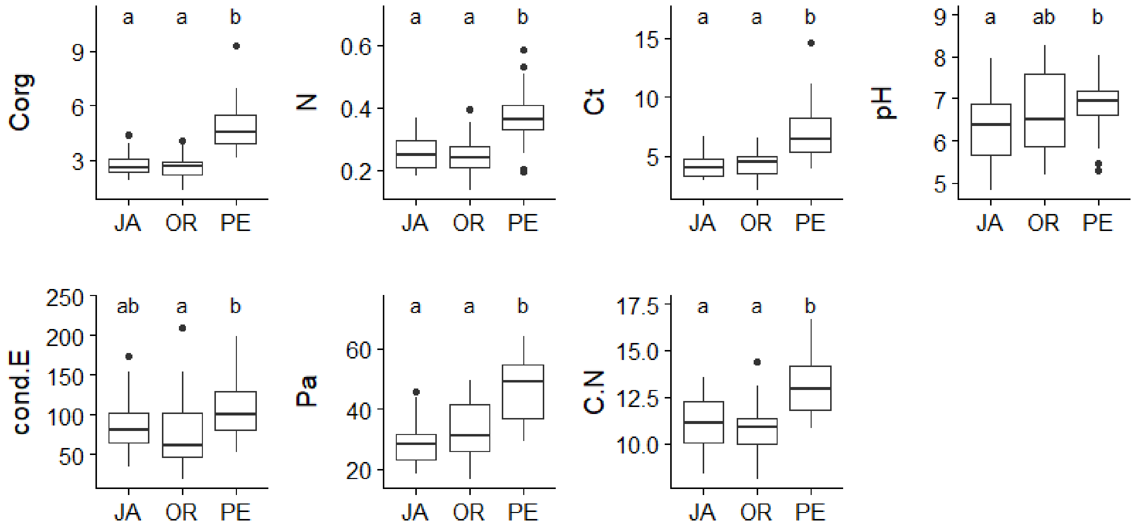


Figure S5. Boxplots representing differences across the studied PLFA biotic groups and different sites (JA = Jasa, OR = Orús and PE = Paco Ezpela). Different letters represent differences across sites.

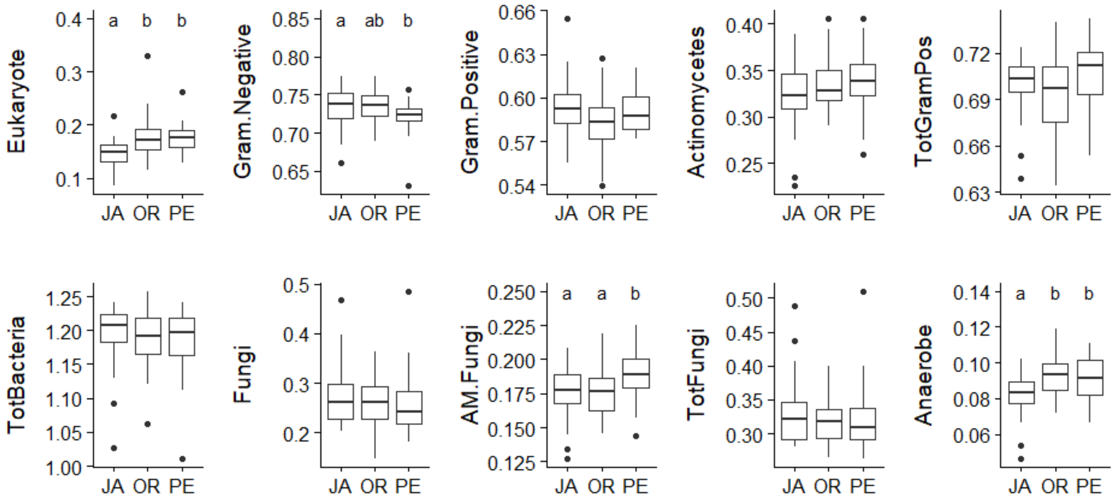


Figure S6. Triplot representing the three significant principal component analyses (PCA) axes of the PLFA groups ordination. Each point represents an individual tree. Colour represents dominant species in the neighbourhood (green symbols = *Abies alba*, blue symbols = Broadleaf species, red symbols = *Pinus sylvestris*).

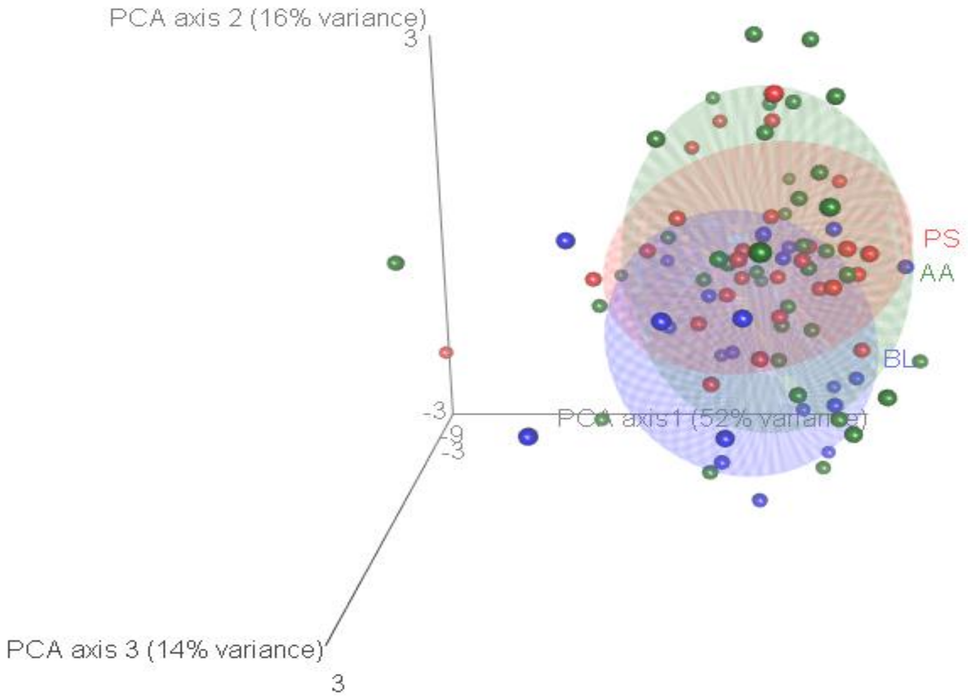


Figure S7. Relationships between tree characteristics (DCI = Distance competition index, DBH = Diameter at breast height, and BAI30 = mean basal area increment for the period 1987–2017). The p and R^2 values are given. All values are centred.

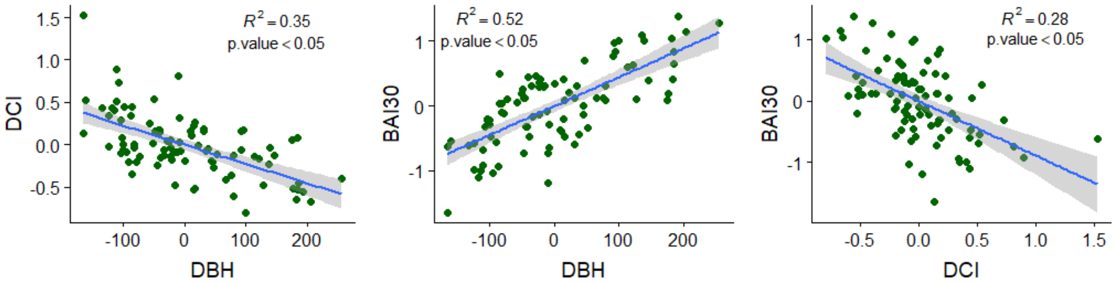
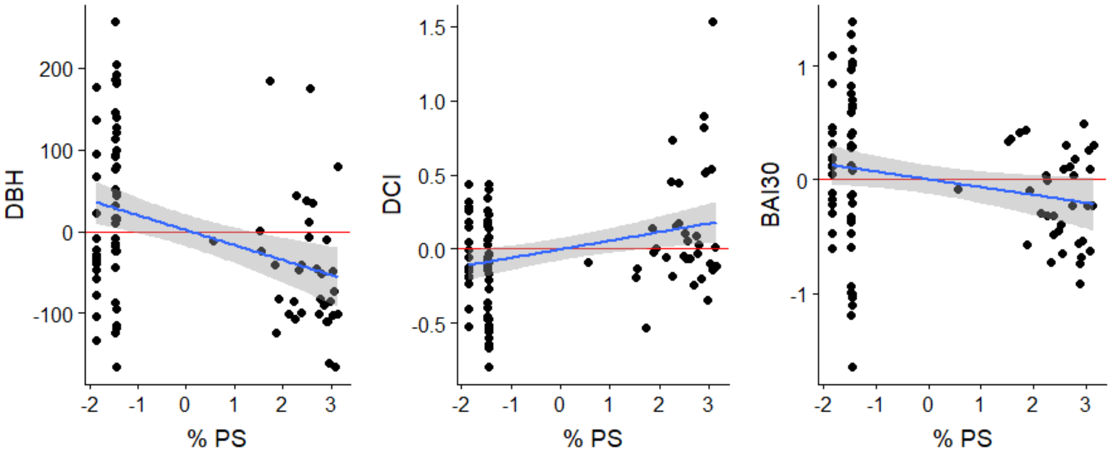


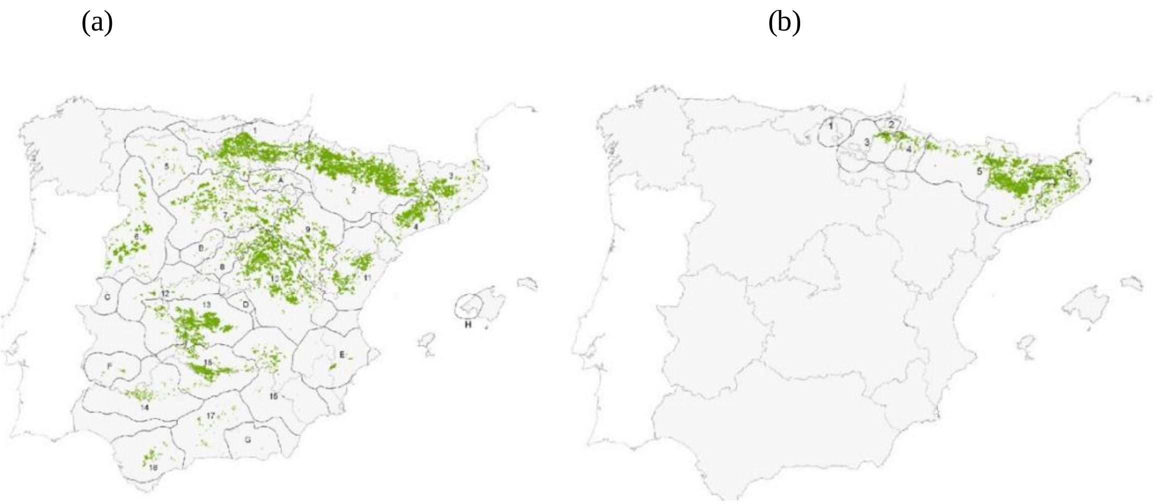
Figure S8. Relationships (blue lines) between the percentage of *Pinus sylvestris* on the neighbourhood (% PS) and focal *Abies alba* diameter at breast height (DBH), distance competition index (DCI), and mean basal area increment for the 1987–2017 period of the focal species, *Abies alba* (BAI30). All values are centred.



Appendices

Supplementary Materials
Chapter 4

Quercus faginea / Quercus humilis in the Iberian Peninsula



F1. Distribution of (a) *Quercus faginea* Lam. and (b) *Quercus humilis* Mill. in Spain.

The *Quercus* genus is highly diverse due the environmental heterogeneity of its habitats and the high levels of hybridization (Kleinschmit & Kleinschmit, 2000). In the Iberian Peninsula there are six species of white oaks which are all highly hybridized (Olalde et al. 2002). *Q. faginea* and *Q. humilis* are winter-deciduous Mediterranean oaks forming ring-porous wood. They present similar ecophysiological characteristics and morphological traits (Himrane et al. 2004). The two species grow on seasonally dry sites, with indifference to substrate type, and are more drought tolerant than the other white oaks in the Iberian Peninsula and central Europe, but less than the evergreen oak *Q. ilex*. *Q. faginea* is only present in the Iberian Peninsula and Northwest Africa while *Q. humilis* present a wider distribution in wetter sites through southern Europe, the Caucasus and Asia Minor. In Spain *Q. humilis* is only present in the northeast, whereas *Q. faginea* is more abundant in drier sites on basic soils (Fig. F1). In this region both species present high levels of hybridization and pure populations of *Q. humilis* are rare (Olalde et al. 2002). The high hybridization and polymorphism makes it difficult to determine morphologic limits between the two species (Castroviejo, 1986-2012). The hybrid between the two species is called *Quercus x subpyrenaica* or *Quercus x cerrioides* which are considered synonyms (Bolòs & Vigo, 1990). Such hybrids present a huge variance in morphological and physiological traits spanning the variation presented by parental taxa. (Himrane et al. 2004)

In our case, we sampled three populations of *Q. faginea/Q. humilis*. Two of these populations, Sansoain and Alcubierre, are *Quercus faginea* according to their leaf and acorn morphological features. The other population (Collserola) presents morphological characteristics closer to *Q.*

humilis. So as both species present the same ecophysiological characteristics and the high level of hybridization makes it difficult to draw a species barrier based in morphological traits, our sampling strategy does not affect the purpose of our study. Furthermore, the coastal Collserola site presented the same mixing (*Q. ilex* and *Q. faginea/Q. humilis*) with contrasting climate (Mediterranean influence) respect to the other two sampled sites.

7

Selection of dry and wet years

To select dry and wet years we used the Standardized Precipitation and Evapotranspiration Index (hereafter SPEI) (Vicente-Serrano, Beguería & López-Moreno, 2010). The SPEI is a multi-scalar drought index which takes into account the potential evapotranspiration suffered by vegetation, making it a better descriptor of vegetation drought stress than other indices such as SPI or PDSI (Vicente-Serrano, Beguería & López-Moreno, 2010). As our sampling sites were situated across a relatively large area, from south to north Iberia, and encompassing different climate conditions (Mediterranean, continental and mountain with oceanic influence), dry and wet years varied in timing and intensity across them. Furthermore, difference in drought timing has different effects on growth depending on the species (Pasho et al. 2011). So that to evaluate common dry and wet years for all sites we used the following approach.

First we calculated the mean, quartiles and deciles of the 6- (SPEI6) and 12-month (SPEI12) September SPEI values in the period 1990-2016 for all sites. Then, the selected years had to be on the lowest 30% (dry years) or the highest 30% (wet years) for at least one of the two SPEIs calculated. Finally, they had to be common for all sites.

(a)

Mean	-0.26										
	0%	25%	50%	75%	100%						
Quartiles	-1.99	-1.1	-0.24	0.55	2.06						
	0%	10%	20%	30%	40%	50%	60%	70%	80%	90%	100%
Deciles	-1.99	-1.45	-1.19	-0.93	-0.63	-0.24	0.04	0.39	0.67	0.91	2.06

(b)

Mean	-0.28										
	0%	25%	50%	75%	100%						
Quartiles	-2.3	-1.05	-0.24	0.37	2.54						
	0%	10%	20%	30%	40%	50%	60%	70%	80%	90%	100%
Deciles	-2.3	-1.52	-1.22	-0.88	-0.48	-0.24	0.01	0.22	0.54	0.91	2.54

(c)

SPEI6	1994	1995	1997	2005	2008	2012	2013
AA.D	-1.24	-1.33	1.46	-1.47	1.61	-0.001	0.89
AA.I	-1.18	-1.92	1	-1.25	1.05	-0.24	0.89
AA.W	-0.94	-1.92	0.82	-0.45	0.92	-0.23	0.94
PS.D	-1.92	-0.36	0.92	-1.03	1.85	-1.38	0.73
PS.I	-1.26	-1.79	1.32	-1.49	1.28	0.13	0.76
PS.W	-0.94	-1.92	0.82	-0.45	0.92	-0.23	0.94
PN.D	-1.54	-1.07	2.06	-1.94	0.59	-0.74	0.89
PN.I	-1.42	-0.36	0.92	-1.03	1.85	-1.38	0.73
PN.W	-1.12	-1.85	1.44	-1.51	1.11	-0.7	0.78
PH.D	-1.54	-1.07	2.06	-1.94	0.59	-0.74	0.89
PH.I	-1.42	-0.36	0.92	-1.03	1.85	-1.38	0.73
PH.W	-1.55	-0.05	-0.53	-1.14	0.54	-1.17	-0.04
Qsp.D	-1.74	-1.44	1.38	-1.80	0.74	-0.69	0.5
Qsp.I	-1.60	-1.81	1.02	-1.07	0.89	-0.67	0.86
Qsp.W	-1.55	-0.05	-0.53	-1.14	0.54	-1.17	-0.04

(d)

SPEI12	1994	1995	1997	2005	2008	2012	2013
AA.D	-1.17	-1.02	1.1	-2.07	0.84	-0.97	1.74
AA.I	-0.9	-1.41	0.44	-1.66	-0.22	-1.55	2.37
AA.W	-0.62	-1.23	0.27	-1.25	-0.29	-1.48	2.19
PS.D	-2.28	-1.26	0.66	-1.55	0.9	-1.58	0.90
PS.I	-1.61	-1.33	0.97	-2.30	0.25	-1.09	1.54
PS.W	-0.62	-1.23	0.27	-1.25	-0.29	-1.48	2.19
PN.D	-1.74	-1.28	1.13	-1.87	-0.66	-1	1.22
PN.I	-2.28	-1.26	0.66	-1.55	0.9	-1.58	0.90
PN.W	-0.48	-1.36	0.92	-2.1	-0.31	-1.85	1.91
PH.D	-1.95	-1.66	1.73	-2.03	0.19	-2.26	1.23
PH.I	-1.49	-1.41	1.19	-1.64	-0.24	-1.67	2.31
PH.W	-2.09	-0.76	0.86	-1.75	-0.38	-0.55	0.61
Qsp.D	-1.89	-1.80	1.19	-2.31	-0.43	-1.54	1.09
Qsp.I	-1.40	-1.52	0.56	-1.28	-0.22	-1.52	2.54
Qsp.W	-2.09	-0.76	0.86	-1.72	-0.38	-0.55	0.61

F2. Tables of mean, quartiles and deciles of (a) 6- month September SPEI and (b) 12-month September SPEI values. Tables of selected years (dry years: 1994-1995, 2005 and 2012; wet years: 1997, 2008 and 2013). (c) Six-month September SPEI and (d) 12-month September SPEI. Light red signifies values on the three first deciles, dark red values on the first decile, light blue values on the three last deciles and dark blue values on the last decile. W, D and I indicate wet, dry and intermediate populations. Species' abbreviations: AA, *A. alba*; PS, *P. sylvestris*; PN, *P. nigra*; PH, *P. halepensis*; Qsp, *Quercus* species.

Selected years

As dry years we selected 1994-1995, 2005 and 2012. All of them have caused growth reductions and even in some areas resulted in drought-related dieback and elevated tree mortality (Camarero et al. 2015; Gazol et al. 2018b). The 1994-1995 drought was characterized by extreme negative SPEI values both at 6- and 12-month SPEI scales. The drought started in 1994 and it was followed by a very dry 1995, especially in Pre-Pyrenean sites. The 2005 year was an extreme drought mainly characterized by low values of 12-month SPEI. Similarly, the 2012 drought was characterized by extreme negative values of the 12-month SPEI.

The selected wet years were 1997, 2008 and 2013. The 1997 presented extreme positive SPEI values for both time scales, with several sites being on the last decile (Fig. F2). The 2008 was an extreme wet year only when evaluating 6-month SPEI values. Finally, the 2013 presented extreme positive SPEI values for both time scales but the intensity was higher for the 12-month scale.

TABLES

Table S1. Percentage of species present in the neighborhood by site. Percentages are calculated from the sum of all measured neighbors (4 individuals per tree).

Species	Site type	Neighbours	Neighbours %
Quercus ilex			
	DRY		
		Quercus ilex	57
		Quercus faginea	27
		Pinus halepensis	20
		Juniperus oxycedrus	5
	INT		
		Quercus ilex	65
		Quercus faginea	29
		Juniperus oxycedrus	3
		Acer campestre	2
	WET		
		Quercus ilex	58
		Quercus faginea/humilis	25
		Pinus halepensis	15
		Arbutus unedo	<1
Quercus faginea/humilis			
	DRY		
		Quercus ilex	48
		Quercus faginea	35
		Pinus halepensis	15
		Juniperus communis	<1
		Juniperus phoenicea	1
	INT		
		Quercus ilex	52
		Quercus faginea	42
		Juniperus oxycedrus	1
		Acer campestre	3
	WET		
		Quercus ilex	47
		Quercus faginea/humilis	36
		Pinus halepensis	12
		Arbutus unedo	3
Pinus halepensis			
	DRY		
		Pinus halepensis	79
		Juniperus phoenicea	21
	INT		
		Pinus halepensis	100
	WET		
		Quercus ilex	47
		Quercus faginea/humilis	17
		Pinus halepensis	30
		Erica arborea	2
		Arbutus unedo	1

Pinus nigra			
	DRY		
		Quercus ilex	49
		Pinus nigra	35
		Pinus halepensis	11
		Juniperus oxycedrus	2
		Pinus pinea	1
	INT		
		Pinus nigra	31
		Juniperus thurifera	37
		Quercus ilex	15
		Pinus sylvestris	13
		Juniperus oxycedrus	2
	WET		
		Pinus nigra	74
		Pinus sylvestris	23
		Quercus faginea	7
		Juniperus communis	1
Pinus sylvestris			
	DRY		
		Pinus sylvestris	50
		Pinus nigra	25
		Juniperus thurifera	16
		Quercus ilex	5
		Quercus faginea	>1
		Juniperus communis	>1
	INT		
		Pinus sylvestris	92
		Quercus faginea	8
	WET		
		Pinus sylvestrus	63
		Fafus sylvatica	35
		Crataegus monogyna	2
Abies alba			
	DRY		
		Abies alba	72.5
		Pinus sylvestris	22.5
		Taxus baccata	5
	INT		
		Abies alba	43.3
		Fagus sylvatica	22.3
		Pinus sylvestris	20.8
		Populus tremula	1
		Acer opalus	>1
	WET		
		Abies alba	96.6
		Fagus sylvatica	2.5
		Salix caprea	>1

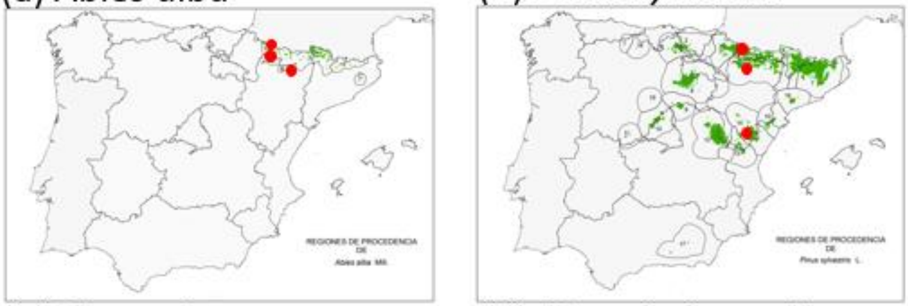
Table S2. Tree-ring width statistics for each site and tree species (period 1950-present). The following dendrochronological statistics are presented: number of sampled trees, number of cores, time -span, mean inter series correlation. rbar; the average correlation between series, EPS (Expressed Population Signal), a measure of common variability and replication of the mean tree-ring series or chronology, mean ± SE Basal Area Increment (BAI) of the 1990-2016 period, mean ± SE difference between dry years BAI (BAI DY) and wet years BAI (BAI WY) respect to mean BAI 1990-2016 period.

Species	Site	No. trees	No. Cores	Time-span	Mean inter-series correlation	Rbar	EPS	Mean ± SE BAI (mm^2)	Mean ± SE BAI DY – BAI (mm^2)	Mean ± SE BAI WY – BAI (mm^2)
Quercus ilex										
	DRY	26	30	1963-2017	0.4	0.212	0.839	373 ± 373	-61 ± 17	29 ± 17
	INT	29	44	1938-2017	0.5	0.315	0.892	361 ± 32	-130 ± 15	150 ± 22
	WET	21	27	1956-2017	0.37	0.21	0.795	600 ± 44	-205 ± 22	74 ± 28
Quercus faginea/humilis										
	DRY	29	37	1954-2017	0.76	0.608	0.97	566 ± 76	-280 ± 46	453 ± 78
	INT	29	30	1939-2017	0.58	0.295	0.903	382 ± 45	-63 ± 12	63 ± 17
	WET	29	29	1931-2017	0.64	0.56	0.964	592 ± 72	-27 0 ± 36	136 ± 43
Pinus halepensis										
	DRY	31	61	1849-2017	0.6	0.573	0.975	541 ± 70	-83 ± 44	133 ± 34
	INT	29	53	1912-2017	0.72	0.535	0.969	1210 ± 117	-315 ± 45	544 ± 78
	WET	30	54	1915-2017	0.65	0.417	0.951	1766 ± 152	-544 ± 75	84 ± 73
Pinus nigra										
	DRY	30	58	1884-2016	0.66	0.403	0.949	506 ± 43	-155 ± 15	138 ± 23
	INT	30	60	1814-2016	0.75	0.723	0.987	358 ± 28	-148 ± 11	99 ± 12
	WET	30	50	1947-2016	0.64	0.411	0.937	1032 ± 87	-107 ± 24	236 ± 34
Pinus sylvestris										
	DRY	30	61	1870-2016	0.8	0.668	0.983	529 ± 49	-235 ± 20	165 ± 26
	INT	30	56	1837-2016	0.45	0.28	0.903	1000 ± 87	-210 ± 33	83 ± 29
	WET	30	44	1825-2016	0.45	0.235	0.857	3964 ± 374	-361 ± 95	423 ± 111
Abies alba										
	DRY	30	60	1919-2016	0.63	0.405	0.928	3070 ± 393	-313 ± 41	322 ± 74
	INT	30	52	1826-2016	0.59	0.319	0.93	1356 ± 165	-180 ± 37	192 ± 36
	WET	30	41	1944-2016	0.59	0.605	0.975	3394 ± 593	-73 ± 61	521 ± 69

FIGURES

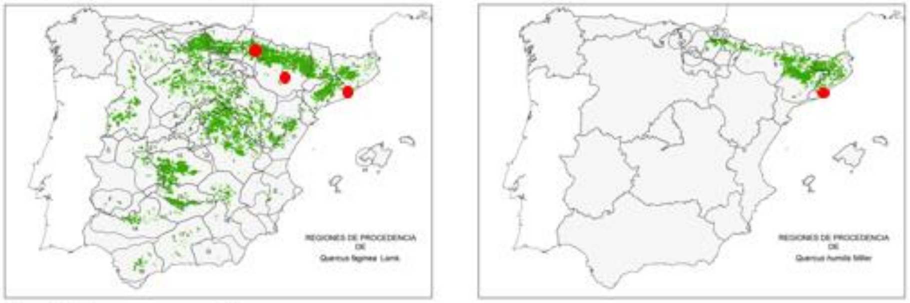
Figure S1. Distribution maps of the studied tree species in the Iberian Peninsula. Green areas represent the distribution area of each species in Spain. Red points represent the localities were populations where sampled (Note that for *Q. humilis* only Collserola site is marked, see the "*Q. faginea* / *Q. humilis* in the Iberian Peninsula" section above). Green and blue patches indicate natural and planted stands, respectively. The species provenances are also indicated (Martín et al. 1998).

(a) *Abies alba*
(b) *Pinus sylvestris*



(c) *Pinus nigra*
(d) *Pinus halepensis*

(e) *Quercus faginea*
(f) *Quercus humilis*



(g) *Quercus ilex*

Figure S2. Climo-graphs of all sampled sites. Monthly precipitation (blue bars), minimum temperatures (orange line), mean temperatures (yellow line) and maximum temperatures (grey lines) are displayed. For references on which species were sampled at each site, see Table 1. Climate information was obtained from the Atlas Climático Digital de la Península Ibérica (Ninyerola, Pons & Roure 2005).

Figure S3. Boxplots showing (A) log transformed Wood Density (WD) and (B) Specific Leaf Area (SLA) variability between sites for all six species. AA = *Abies alba*, PH = *Pinus halepensis*, PN = *Pinus nigra*, PS = *Pinus sylvestris*, QF = *Quercus faginea/Quercus humilis* and QI = *Quercus ilex*.

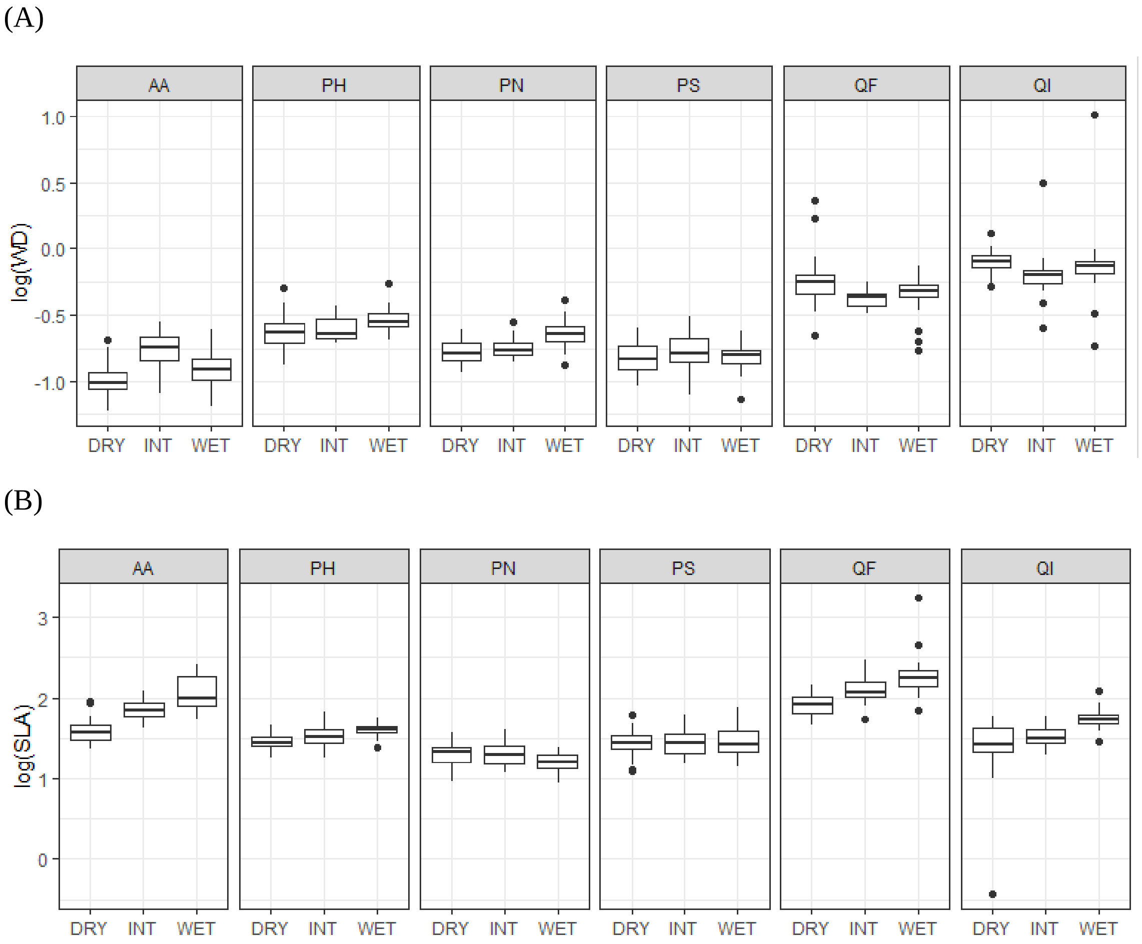


Figure S4. Boxplots of (A) growth decreases and (B) enhancements for the selected dry and wet years. Note that growth decreases are presented as Resistance index (Lloret, Keeling & Sala, 2011), but to compute AcGD are transformed to 1/Rt. Response values above 1 (for decreases) or below 1 (enhancements) where considered as no response to the events, thus to calculate the AcGD or AcGE where set to 0 (i.e., no presence of growth decrease during a dry year is considered an absence of tree response to this year, therefore, no negative accumulated effect from it).

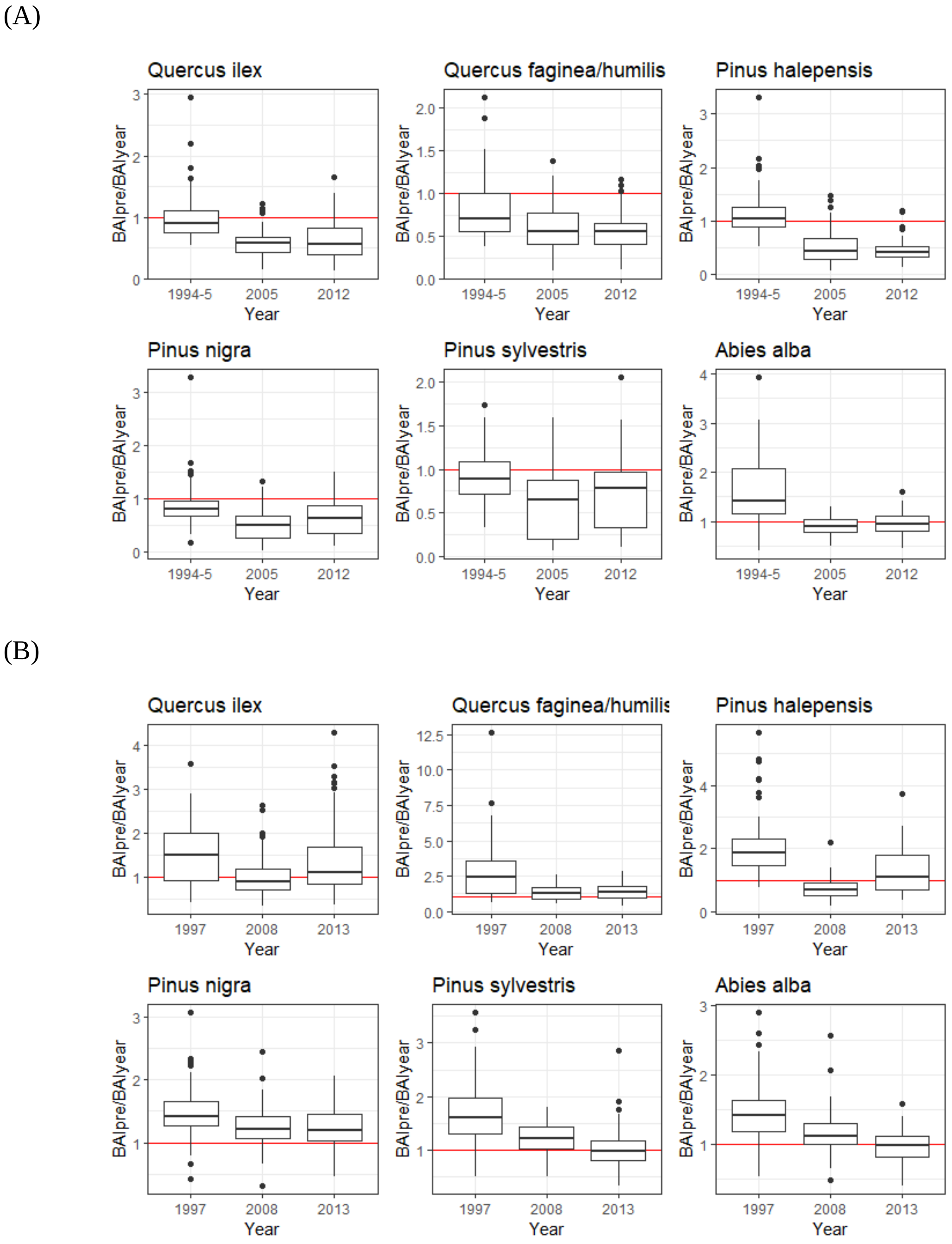


Figure S5. Dot whisker plots showing the results of models evaluating AcGD & AcGE as a function of site, DBH, competition index (CI), Specific Leaf Area (SLA) and wood density (WD). Seven different models per species and response variable (AcGD & AcGE) are presented, each one using a different reference period (from 1 to 7 years) to calculate AcGE & AcGD.

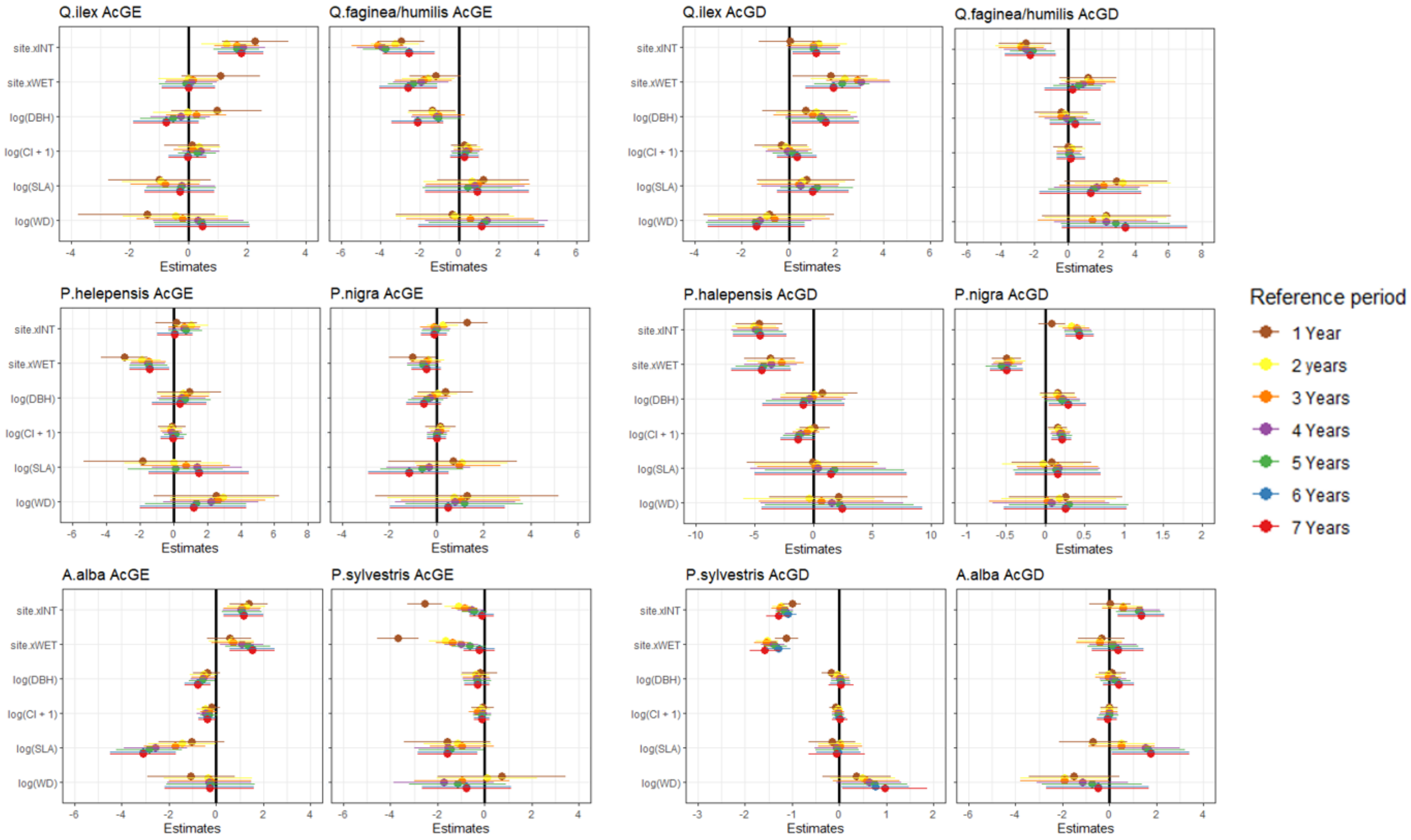
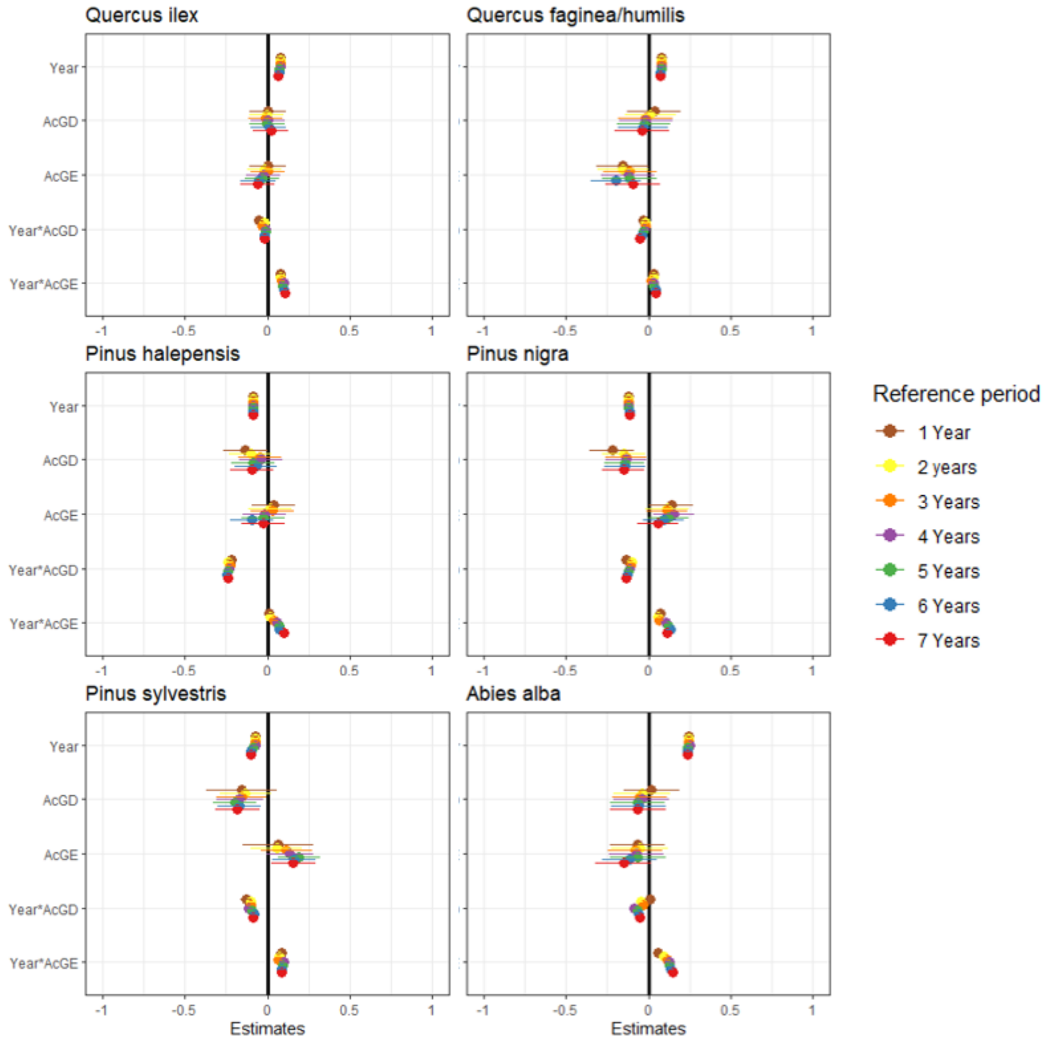


Figure S6. Dot whisker plots showing the results of models evaluating log transformed standardized Basal Area Increment (BAI) as a function of Year, AcGD, AcGE, Year*AcGE and Year * AcGD. Tree was used as random variable. Seven different models are presented per specie, each one using a different reference period (from 1 to 7 years) to calculate AcGE & AcGD.



Appendices

Supplementary Materials
Chapter 5

Table S1. Tree species used in the analyses, number of chronologies per species (No. Chronologies), number of droughts per species (No. Droughts), mean time span of all chronologies from the same species (Time Span) and mean number of trees (No. trees; i.e., sample depth) of all chronologies from the same species. Species selection criteria was based on trait data availability and a minimum number of chronologies (5) with more than 40 years of data after 1950.

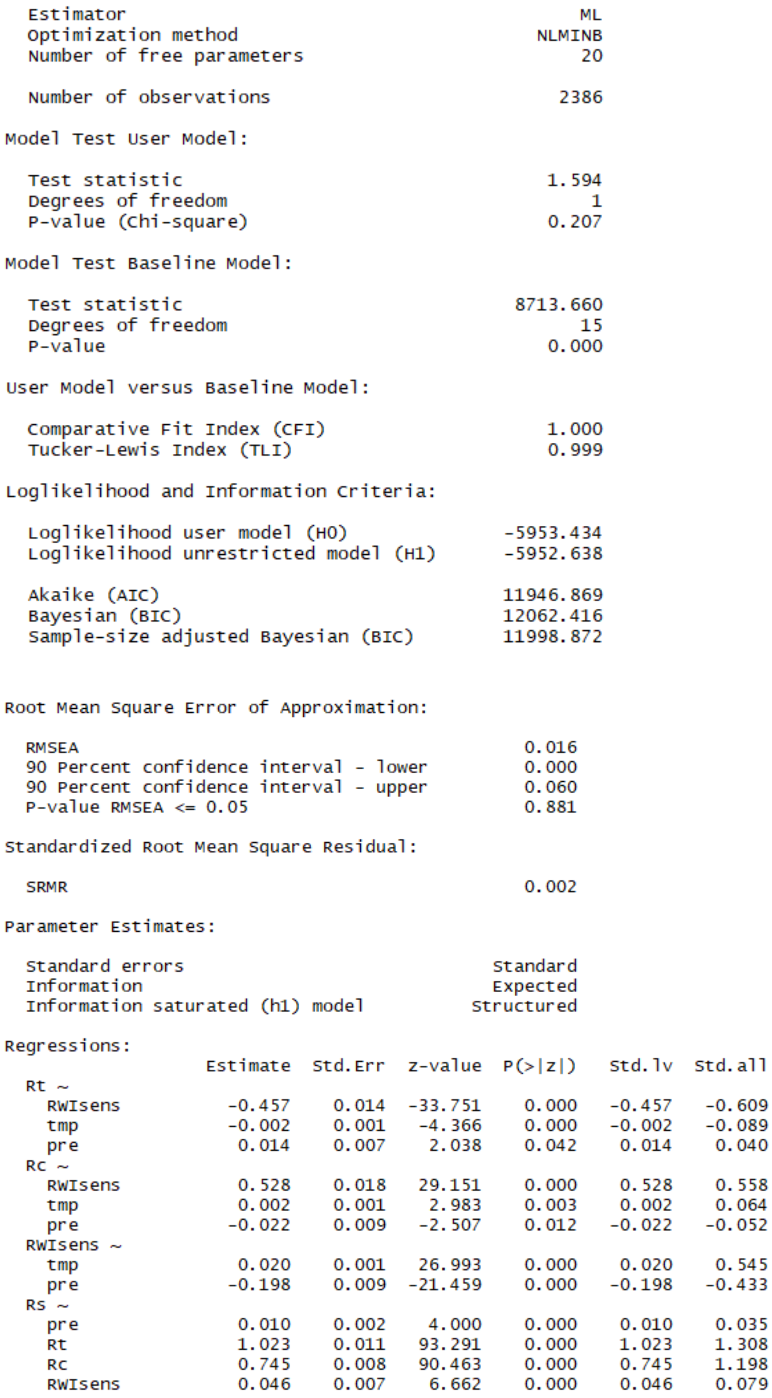
Species	**No. Chronologies**	**No. Droughts**	**Time Span (years)**	**No. trees**
Abies alba	25	38	49.00	25.61
Abies concolor	9	17	48.12	48.47
Abies lasiocarpa	64	181	49.14	39.61
Abies magnifica	5	7	40.00	35.14
Agathis australis	6	27	49.52	33.15
Araucaria araucana	10	21	55.57	35.43
Athrotaxis selaginoides	6	15	59.93	34.07
Austrocedrus chilensis	10	17	41.24	18.12
Cedrus atlantica	7	13	52.23	41.54
Cedrus deodara	6	10	56.30	31.70
Cedrus libani	10	40	50.85	25.38
Fagus sylvatica	40	121	54.65	25.93
Fitzroya cupressoides	7	13	43.00	19.77
Juniperus occidentalis	13	25	53.88	28.92
Juniperus virginiana	17	37	47.81	25.59
Larix decidua	32	85	55.82	26.65
Larix gmelinii	49	134	48.11	32.03
Larix laricina	5	25	53.00	36.76
Larix sibirica	84	214	51.82	28.77
Libocedrus bidwillii	16	42	41.40	29.17
Liriodendron tulipifera	11	40	52.45	27.45
Nothofagus pumilio	37	103	51.95	32.91
Picea abies	102	232	49.35	37.85
Picea engelmannii	40	107	46.69	30.85
Picea glauca	158	654	52.36	51.81
Picea likiangensis	6	33	49.18	31.58
Picea mariana	31	179	56.56	46.54
Picea schrenkiana	17	41	52.46	42.27
Picea sitchensis	15	50	47.30	18.44
Picea smithiana	7	17	55.53	32.12
Phyllocladus aspleniifolius	12	18	48.44	34.94
Pinus albicaulis	22	56	48.59	28.52
Pinus banksiana	23	72	54.81	37.58

Pinus cembra	9	14	53.79	19.07
Pinus contorta	16	51	55.00	26.29
Pinus echinata	19	43	53.12	31.84
Pinus edulis	42	126	51.03	30.94
Pinus flexilis	26	67	51.76	28.07
Pinus jeffreyi	13	29	48.62	40.14
Pinus lambertiana	9	18	47.67	38.56
Pinus merkusii	7	26	51.15	39.69
Pinus nigra	32	110	53.86	31.76
Pinus palustris	11	31	50.06	49.77
Pinus pinea	6	12	53.33	20.92
Pinus ponderosa	107	260	52.42	34.03
Pinus resinosa	14	33	55.27	33.79
Pinus strobus	21	41	51.00	35.76
Pinus sylvestris	148	437	49.92	35.06
Pinus uncinata	6	9	53.89	40.33
Pinus wallichiana	5	19	52.89	23.11
Pseudotsuga menziesii	185	588	54.30	47.04
Quercus alba	22	65	50.80	27.11
Quercus coccinea	9	20	52.00	54.20
Quercus macrocarpa	38	148	51.64	18.18
Quercus michauxii	32	95	54.37	14.26
Quercus petraea	10	33	50.27	32.06
Quercus robur	30	88	51.16	28.05
Quercus rubra	8	32	52.34	28.09
Quercus stellata	35	66	47.52	49.06
Quercus velutina	15	43	51.74	51.33
Taxodium distichum	14	33	51.33	38.00
Taxodium huegelii	18	64	55.83	30.36
Tsuga canadensis	22	80	54.71	33.99
Tsuga dumosa	15	61	52.25	26.75
Tsuga mertensiana	85	204	48.07	41.72

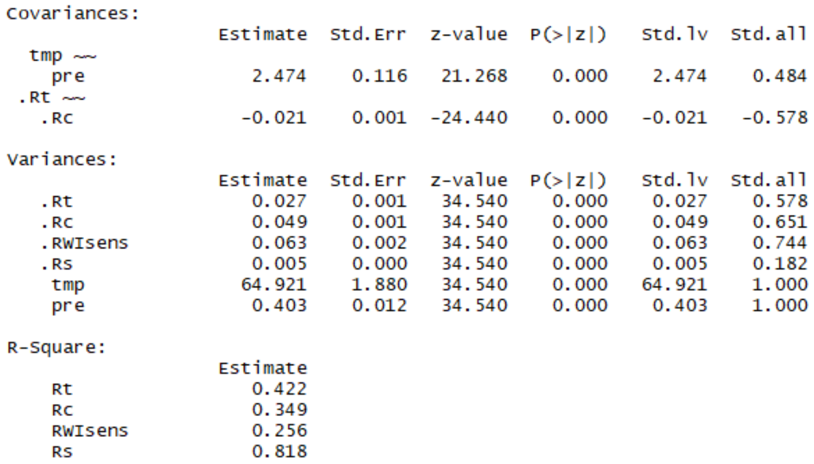
Table S2. Number of tree species for which we have data in each functional trait.

Traits	Angiosperms	Gymnosperms	Units
SLA	12	35	$mm^2\ mg^{-1}$
Nmass	12	34	mg/g
Pmass	11	22	mg/g
Wood density	12	50	g/cm^3
Ks	6	30	$Kg\ m^{-1}\ MPa^1\ s^{-1}$
P50	9	34	MPa
Ψ min	7	24	MPa
HSM	7	22	Ψ min – P50

Table S3. Output of the final path analyses (R screenshoot), which is the last one remaining equal (based on chi-square test) to the theoretical model after removing non-significant variables.



```
  Estimator                                         ML
  Optimization method                           NLMINB
  Number of free parameters                         20

  Number of observations                          2386

Model Test User Model:

  Test statistic                                 1.594
  Degrees of freedom                                 1
  P-value (Chi-square)                           0.207

Model Test Baseline Model:

  Test statistic                              8713.660
  Degrees of freedom                                15
  P-value                                        0.000

User Model versus Baseline Model:

  Comparative Fit Index (CFI)                    1.000
  Tucker-Lewis Index (TLI)                       0.999

Loglikelihood and Information Criteria:

  Loglikelihood user model (H0)              -5953.434
  Loglikelihood unrestricted model (H1)      -5952.638

  Akaike (AIC)                               11946.869
  Bayesian (BIC)                             12062.416
  Sample-size adjusted Bayesian (BIC)        11998.872


Root Mean Square Error of Approximation:

  RMSEA                                        0.016
  90 Percent confidence interval - lower       0.000
  90 Percent confidence interval - upper       0.060
  P-value RMSEA <= 0.05                        0.881

Standardized Root Mean Square Residual:

  SRMR                                         0.002

Parameter Estimates:

  Standard errors                           Standard
  Information                               Expected
  Information saturated (h1) model        Structured

Regressions:
                   Estimate  Std.Err  z-value  P(>|z|)   Std.lv  Std.all
  Rt ~
    RWIsens          -0.457    0.014  -33.751    0.000   -0.457   -0.609
    tmp              -0.002    0.001   -4.366    0.000   -0.002   -0.089
    pre               0.014    0.007    2.038    0.042    0.014    0.040
  Rc ~
    RWIsens           0.528    0.018   29.151    0.000    0.528    0.558
    tmp               0.002    0.001    2.983    0.003    0.002    0.064
    pre              -0.022    0.009   -2.507    0.012   -0.022   -0.052
  RWIsens ~
    tmp               0.020    0.001   26.993    0.000    0.020    0.545
    pre              -0.198    0.009  -21.459    0.000   -0.198   -0.433
  Rs ~
    pre               0.010    0.002    4.000    0.000    0.010    0.035
    Rt                1.023    0.011   93.291    0.000    1.023    1.308
    Rc                0.745    0.008   90.463    0.000    0.745    1.198
    RWIsens           0.046    0.007    6.662    0.000    0.046    0.079
```



```
Covariances:
                   Estimate  Std.Err  z-value  P(>|z|)   Std.lv  Std.all
  tmp ~~
    pre               2.474    0.116   21.268    0.000    2.474    0.484
 .Rt ~~
   .Rc               -0.021    0.001  -24.440    0.000   -0.021   -0.578

Variances:
                   Estimate  Std.Err  z-value  P(>|z|)   Std.lv  Std.all
   .Rt                0.027    0.001   34.540    0.000    0.027    0.578
   .Rc                0.049    0.001   34.540    0.000    0.049    0.651
   .RWIsens           0.063    0.002   34.540    0.000    0.063    0.744
   .Rs                0.005    0.000   34.540    0.000    0.005    0.182
    tmp              64.921    1.880   34.540    0.000   64.921    1.000
    pre               0.403    0.012   34.540    0.000    0.403    1.000

R-Square:
                   Estimate
    Rt                0.422
    Rc                0.349
    RWIsens           0.256
    Rs                0.818
```

Table S4. Akaike Information Criteria (AIC) values for the models evaluating correlation between drought indices and functional traits. RWI-SPEI = Ring Width Indices – Standardized Precipitation and Evapotranspiration Index relationship; Rt = Resistance; Rc = Recovery; Rs = Resilience. Mod 1 = growth index ~ trait; Mod 2 = growth index ~ trait +; Mod 3 = growth index ~ trait * Clade. Traits' abbreviations: SLA, Specific Leaf Area, Nmass, Nitrogen mass, Pmass, Phosphorus Mass, WD, Wood density, Ks, stem conductivity, minWP, leaf minimum midday water potential, HSM, Hydraulic Safety Margin. Bold values indicate the selected models.

Model 1: growth index ~ trait

Model 2: growth index ~ trait + Clade

Model 3: growth index ~ trait * Clade

Drought index	Model	SLA	Nmass	Pmass	WD	Ks	P50	Pmin	HSM
RWI-SPEI	Model 1	**16.44**	**16.19**	**9.79**	**13.40**	**10.32**	**16.88**	**-1.00**	**8.46**
RWI-SPEI	Model 2	17.12	16.29	10.57	15.35	11.92	17.98	0.27	10.46
RWI-SPEI	Model 3	18.94	17.99	12.24	17.29	13.46	19.06	1.97	12.32
Resistance	Model 1	**-32.60**	**-32.88**	**-27.77**	**-45.21**	**-32.42**	**-32.98**	**-37.01**	**-25.53**
Resistance	Model 2	-34.29	-32.35	-26.50	-44.05	-30.59	-32.64	-36.33	-23.53
Resistance	Model 3	-34.20	-32.94	-24.58	-42.13	-29.96	-31.05	-34.35	-22.24
Recovery	Model 1	**10.30**	**8.76**	**7.48**	**11.07**	**-0.47**	**13.49**	**-8.69**	**8.14**
Recovery	Model 2	12.17	10.58	9.10	12.51	1.53	15.29	-6.79	9.71
Recovery	Model 3	12.50	12.49	11.07	12.63	2.84	17.24	-6.32	11.59
Resilience	Model 1	-133.64	-129.10	**-90.36**	-168.05	**-97.39**	**-124.51**	**-86.02**	-86.02
Resilience	Model 2	**-139.43**	-128.36	-89.29	-166.72	-96.07	-122.57	-84.02	-81.54
Resilience	Model 3	-137.48	**-138.13**	-87.42	**-178.21**	-95.33	-121.03	-87.11	**-89.42**

Table S5. Comparison between number of droughts and number of chronologies weighted models for the relationship between Hydraulic Safety Margins (HSM), Resistance and Recovery.

Drought Index	**Weight**	**Estimate**	**Std. Error**	***p* value**
Resistance	Droughts	0.041	0.021	0.065
Recovery	Droughts	-0.072	0.038	0.068
Resistance	Chronologies	0.032	0.021	0.128
Recovery	Chronologies	-0.055	0.036	0.145

Figure S1. Relationship between Ring Width Indices (RWI) and the Standardized Precipitation and Evapotranspiration Index (SPEI). Top panels respresent northern hemisphere species, bottem panels represent southern hemispher species. Right panels show the relationship using the method “gam” in stat_smooth() ggplot, left panels show the relationshio using the “lm” method. Point color represent species.

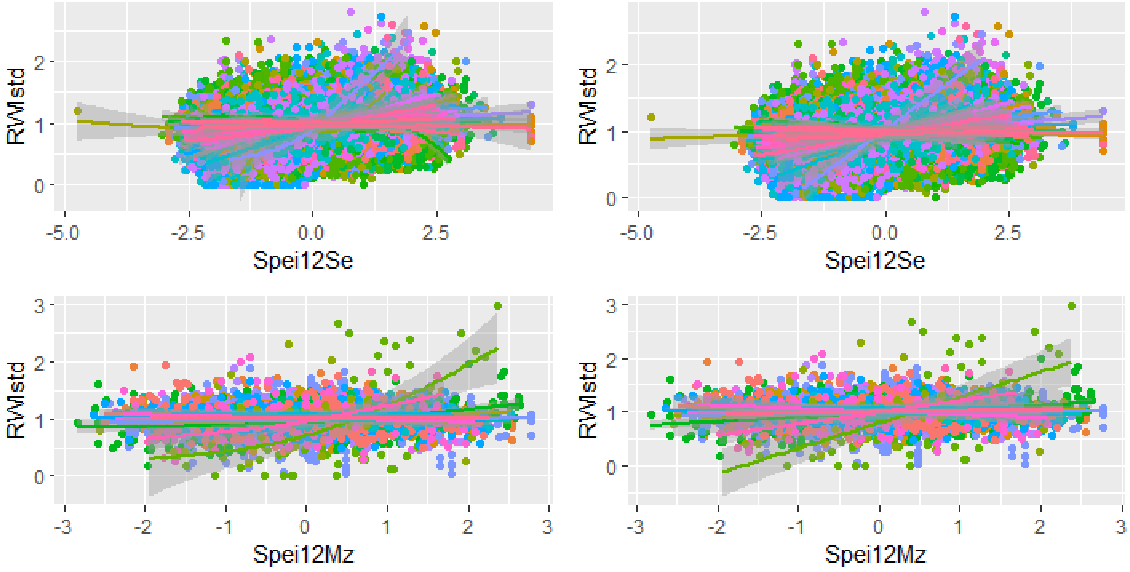


Figure S2. Scatter plot of the Ring-Width Indices-Standardized Precipitation and Evapotranspiration Index (RWI-SPEI relationship) measured with the residual RWI chronologies (x axis) and the standardized RWI chronologies (y axis).

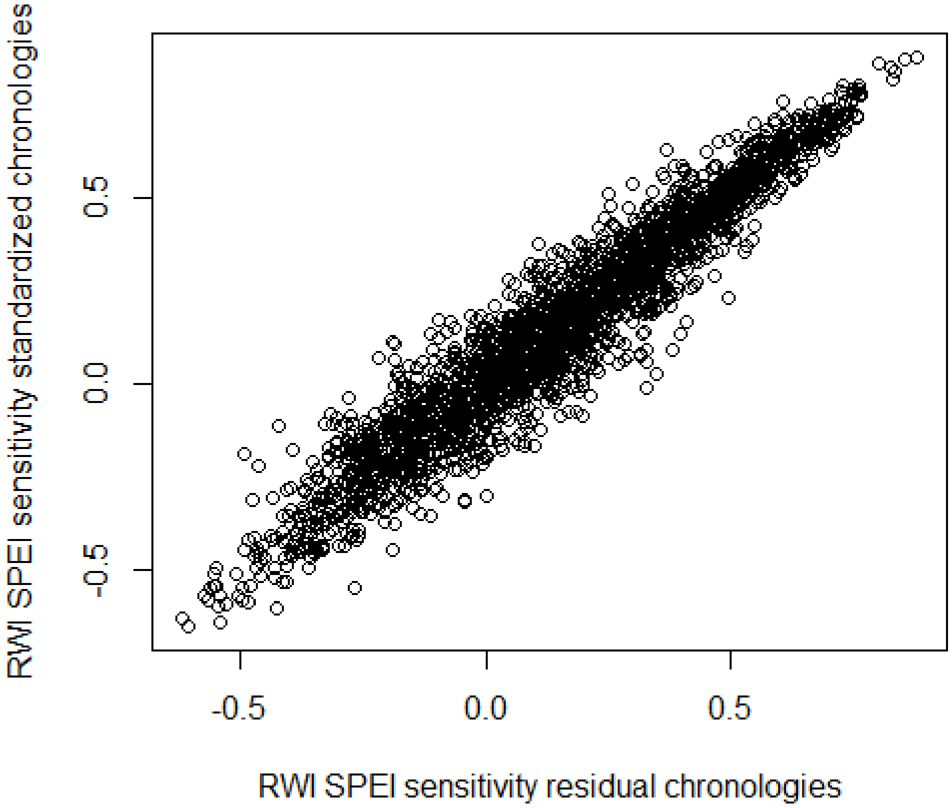


Figure S3. Weights used in the linear models to account for different proportion of chronologies and droughts in each species. (a) Histograms of number of chronologies per species and number of droughts per species. (b) Relationships between number of chronologies per species and number of droughts per species; both raw and log-transformed weights are plotted.

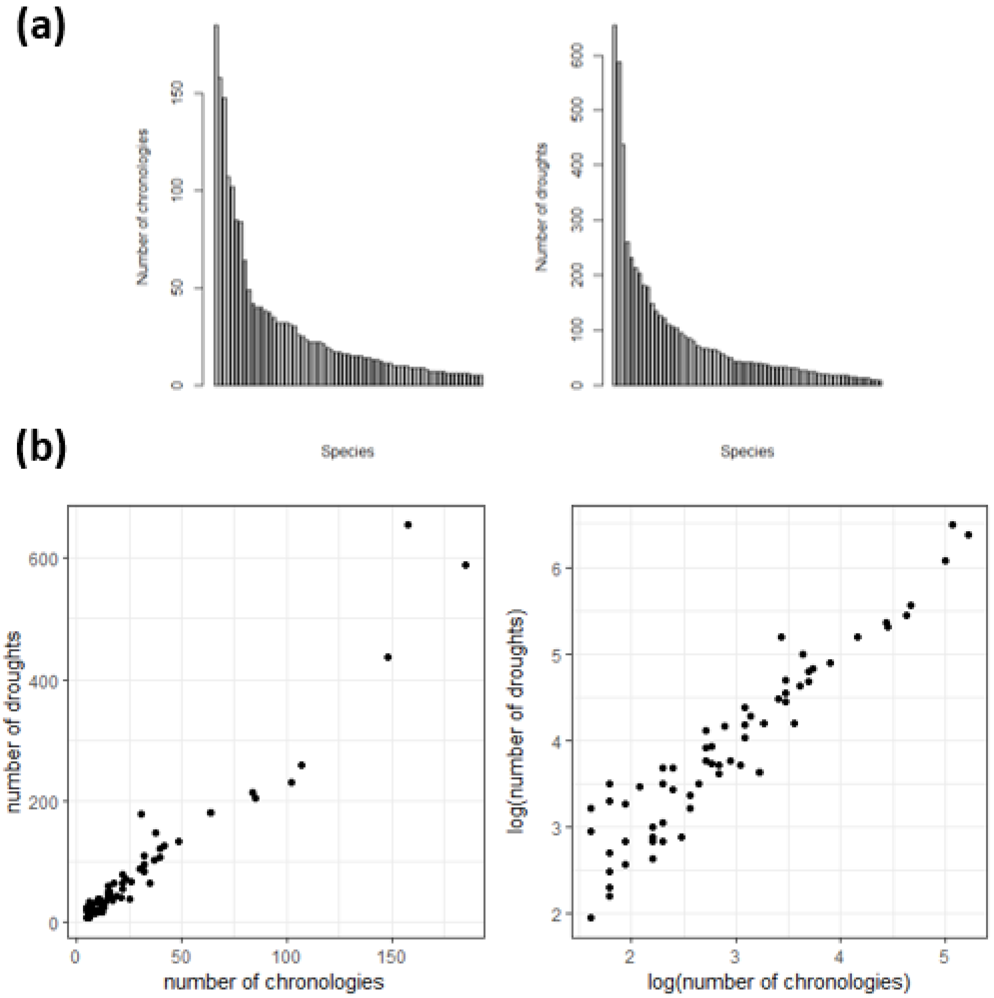


Figure S4. Maps of site mean Resistance (Rt), Recovery (Rc) and Resilience (Rs) for the tree-ring width chronologies used in the study.

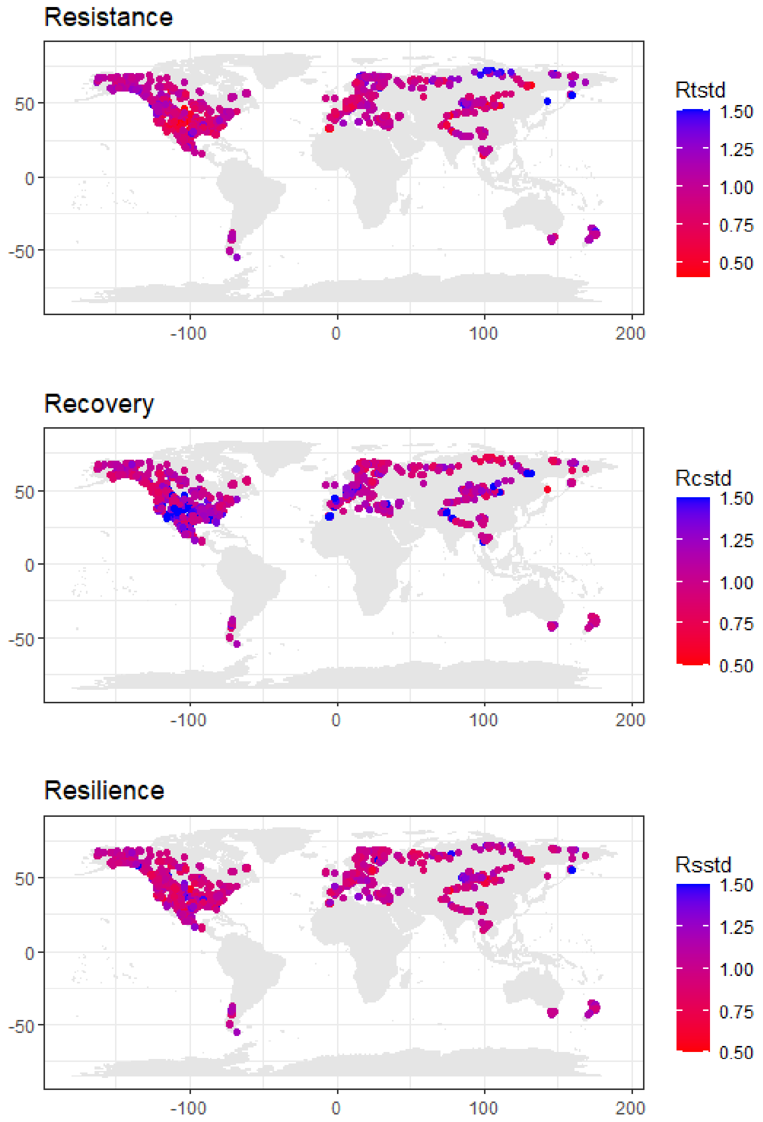


Figure S5. Relationships between the Lloret, Keeling & Sala, (2011) resistance, recovery and resilience indices. The ratios used to compute these indices make them non independent. The indices are calculated as follows: Resistance = Dr/PreDr, Recovery = PostDr/Dr and Resilience = PostDr/PreDr. In our case, Dr = ring-width index (RWI) during drought year, PreDr = mean RWI during the 4 years preceding the drought and PostDr = mean RWI during four years following the drought. Note that recovery has been log transformed to achieve normality.

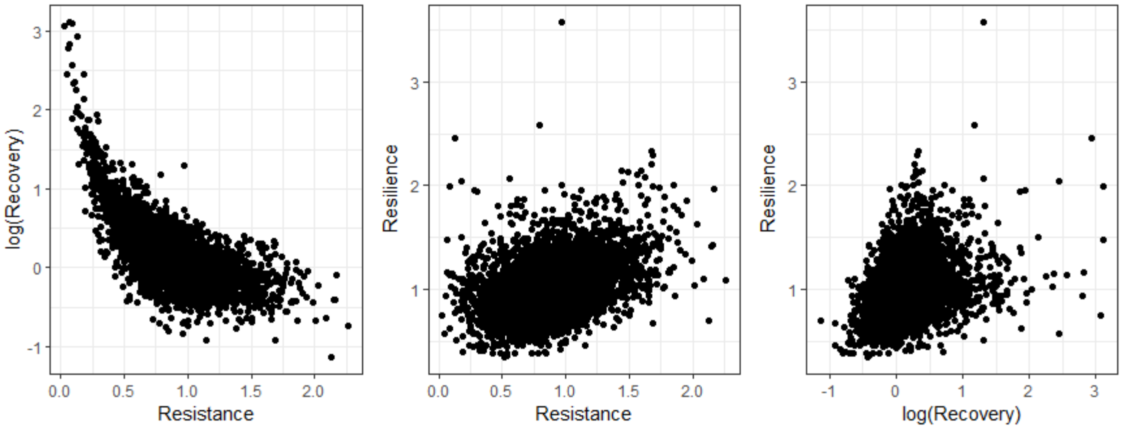


Figure S6. Relationship between RWI-SPEI relationship (Pearson correlation between RWI and SPEI), resistance (Rt), recovery (Rc) and resilience (Rs) indices at species level. Values are means and error bars are standard deviations.

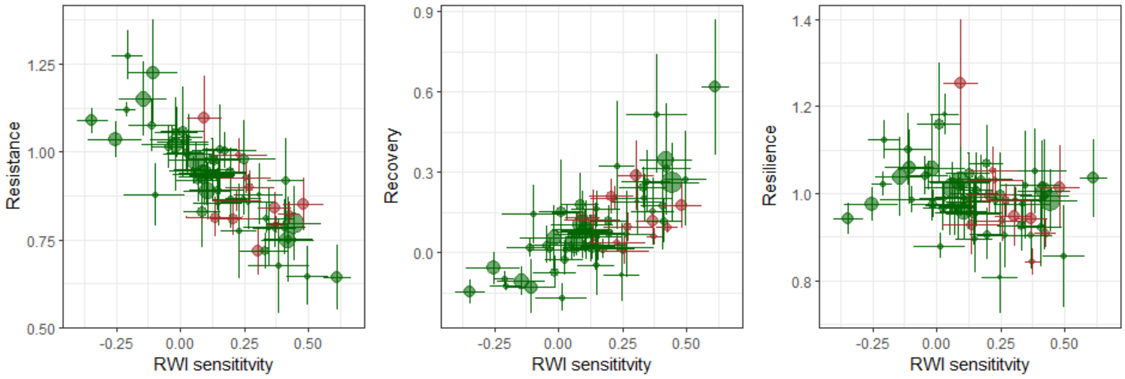


Figure S7. Relationship between Resistance and Recovery indices with species level Hydraulic Safety Margin (HSM). When models are weighted by number of droughts there is a significant relationship, while when models are weighted by number of chronologies the relationship is not significant.

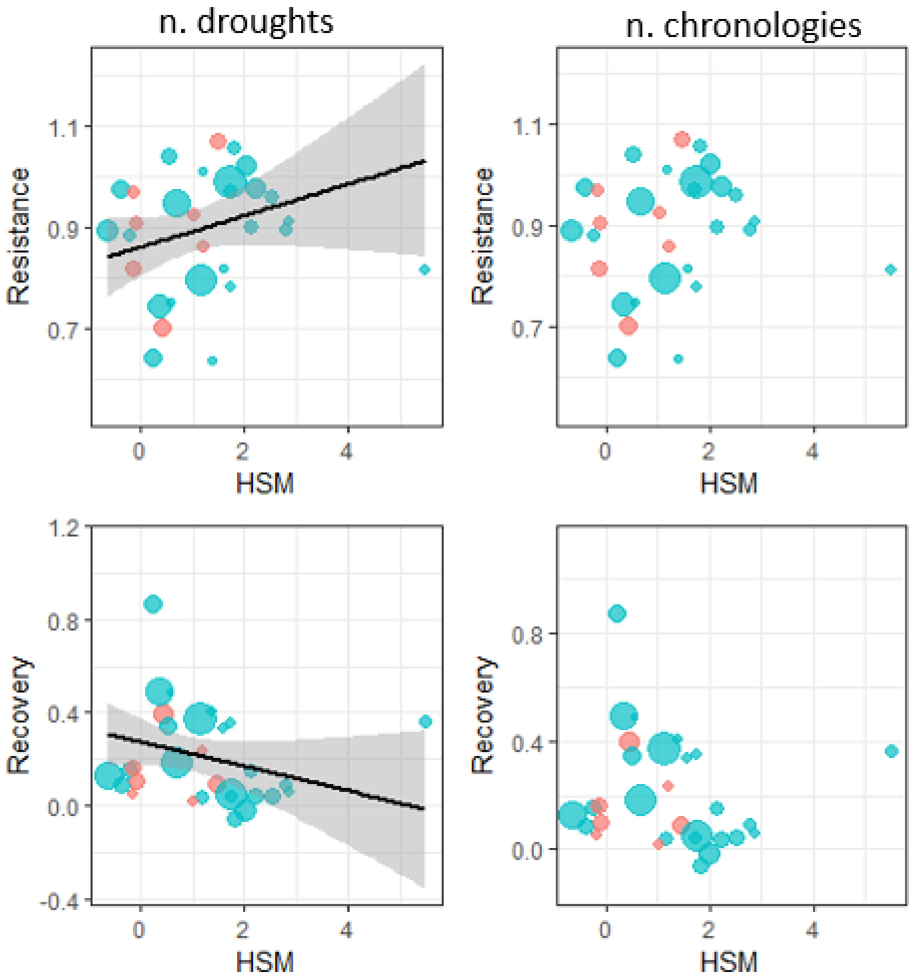
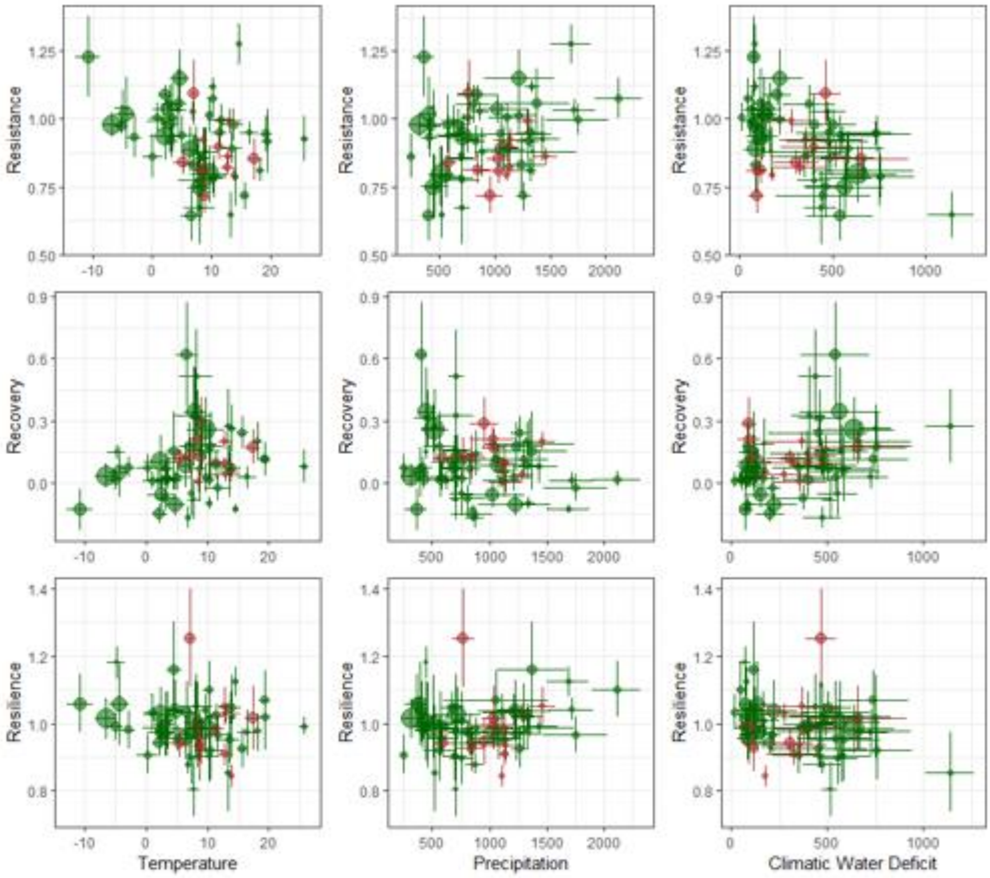


Figure S8. Relationships between Lloret resilience indices (Resistance, Recovery and Resilience) with mean species temperature, precipitation and climatic water deficit. Green points represent gymnosperm species and brown points represent angiosperm species. Point size is weighted by the number of chronologies per species. 0.5 * Standard deviations bars of resistance, recovery, resilience and temperature, precipitation and climatic water deficit are plotted



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