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New insights in the modeling and simulation of tree and stand level variables in Mediterranean mixed forests in the present context of climate change

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New insights in the modeling and simulation of tree and stand level variables in Mediterranean mixed forests in the present context of climate change

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LIST OF ACRONYMS

AIC	Akaike Information Criterion
BA	Stand basal area ($m^2 \cdot ha^{-1}$)
BAI	Tree basal area increment ($cm^2 \cdot yr^{-1}$)
BAL	Basal area of larger trees ($m^2 \cdot ha^{-1}$)
CEC	Competition Equivalence Coefficients
CMIP6	Sixth World Climate Research Programme
d	Diameter at breast height (cm)
Do	Dominant diameter (cm)
Dq	Quadratic mean diameter (cm)
EF	Expansion Factor
ER	Akaike Evidence Ratio
GCMs	Global Climate Models
h	Total tree height (m)
ha	Hectare
H-D	Tree Height-Diameter relationship
Ho	Stand dominant height (m)
M	De Martonne Index ($mm \cdot °C^{-1}$)
mi	Species proportion by area
MSDR	Maximum Size-Density Relationship
N	Stand Density ($tree \cdot ha^{-1}$)
REML	Restricted Maximum Likelihood
SDI_{max}	Maximum Stand Density Index
SNFI	Spanish National Forest Inventory
SRTM	Shuttle Radar Topography Mission
SSPs	Shared Socio-Economic Pathways

ABSTRACT

An increase of droughts intensity and frequency episodes combined with new extreme climate events are predicted to appear in the Mediterranean Basin due to global warming. In this context, mixed forests have become a sustainable opportunity to mitigate the effects of climate change. Species mixing may lead to the provision of a greater variety of ecosystem services and products while increasing temporal stability compared to pure forests. The development of new models that explain different tree and stand level variables may be vital to better understand the structure, composition and dynamics of this type of forests. In addition, it is essential to analyze how climate may influence these variables in order to design adaptive and sustainable management guidelines for mixed forests under future climate change scenarios.

In this study, we sought to advance in the modelization and simulation of different tree and stand level variables along a range of different forest and aridity conditions in Spain. To achieve that, climate-dependent models were fitted using data from the Spanish National Forest Inventory and the WorldClim databases. We focused our study on fifteen Mediterranean tree species from the *Pinus*, *Quercus,* and *Fagus* genus.

In our first study, we analyzed how climate may potentially influence the maximum stand carrying capacity, by terms of the maximum stand carrying capacity (SDI_{max}), for the species under study in pure stands. This variable was chosen because its importance in (1) managing density and (2) defining species mixing proportions in mixed forest stands. To do that, climate-dependent MSDR models were fitted for each species under study. 35 different climatic annual and seasonal variables (temperature, precipitation, evapotranspiration, aridity indexes) were simultaneously included into the models. In this study, climate was found to have significant influence on MSDR, and therefore on the maximum stand carrying capacity (SDI_{max}). The best climate-dependent MSDR models indicated that climatic variables related to temperature better explained the influence of climate on MSDR. Specifically, seasonal (MXT_i) and annual (MXT) maximum temperatures were the most representative climatic variables explaining changes in MSDR. Based on the selected seasonal variables, spring and summer were consistently appeared as key periods. A common trend in SDI_{max} variation for coniferous and broadleaf species was found, with higher SDI_{max} values negatively linked to temperature and positively linked to precipitation. This trend suggested that aridity may play a key role reducing the maximum stand

carrying capacity of the main Mediterranean tree species. In addition, the impact of climate on maximum stand carrying capacity was evaluated by the creation of the Q index. In general, broadleaved species presented higher values of Q indexes than coniferous species, suggesting that the maximum stand carrying capacity of the first ones would suffer more the influence of potential climate changes. Our findings highlight the importance of using specific climatic variables to better characterize how they affect MSDR.

Since we saw that aridity could play a key role influencing stand level variables such as SDI_{max}, we aimed to analyze how it may influence tree growth and tree allometry. Moreover, we aimed to analyze how species mixing effects may influence these variables on mixed forests. Thus, two more studies focused on 29 two-species Mediterranean mixtures were developed.

To study the influence of aridity and species mixing on tree growth, the basal area increment within a span of five years (BAI_5), was modelled based on individual tree size, stand development and other variables of site and competition. Two distance independent competition indexes were considered: total stand basal area (BA) representing size-symmetric competition, and the basal area of trees larger than the subject tree (BAL) representing size-asymmetric competition. To uncover the complex mixing effects on basal area increment at tree level, competition indexes were splitting into intraspecific and interspecific components. All possible combinations of competition structures were included and tested in the BAI models. Positive, negative or neutral mixing effects were determined by comparing the intraspecific and interspecific component of the selected models. Then, the biological interactions taking place between species were determined based on size-symmetric and size-asymmetric competition. Finally, the influence of aridity on basal area increment was studied including the De Martonne Index into the BAI models. A common trend among mixtures was found with higher productivity in mixed than pure stands, suggesting that BAI values may increase with the increment of species diversity. Based on model parameters, a novel approach to determine potential biological interactions between species in mixed forests was also presented in this study. Competition seemed to be the most representative biological interaction in conifer-conifer mixtures, since neutralism and facilitation may occur more frequently in conifer-broadleaved and broadleaved-broadleaved mixtures. Our findings also suggested that tree productivity may be significantly limited by arid conditions, excepting for *Pinus halepensis* and *Pinus pinea*.

In a third study, new height – diameter (H-D) models were fitted for 13 different Mediterranean species in mixed forest stands under different mixing proportions along an aridity gradient in Spain. Using Spanish National Forest Inventory data, different height-diameter base equations were initially fitted in order to select the best base models for each pair species-mixture. Then, the best models were expanded including species proportion by area (m_i) and the De Martonne Index (M). A general trend was found for coniferous species, with taller trees in pure than in mixed stands, being this trend inverse for broadleaved species. Regarding aridity influence on H-D relationships, humid conditions seem to beneficiate tree height for almost all the analyzed species and species mixtures. A different trend was found for *Pinus halepensis* and *Pinus pinea*, suggesting that these species dedicate more resources in promoting their radical systems instead of growing in height.

Finally, climate-dependent models developed in the previous studies were included in SIMANFOR platform to simulate CO_2 yield and growth of mixed forest stands each 5 years for the 2000-2100 period under different climate change scenarios (SSPs) In this final case study, we sought to compare the evolution of CO_2 yield and growth in pure and mixed stands under different climate change scenarios. We focused on *Pinus sylvestris* and its main mixtures (*Pinus nigra*, *Pinus pinaster*, *Fagus sylvatica* and *Quercus pyrenaica*). For each iteration, diameter at breast height and total height were estimated for each tree under study using models developed in this thesis. Mortality between iterations was estimated based on the maximum stand carrying capacity (SDI_{max}), since it defines the maximum number of trees per hectare where natural mortality takes place in a forest stand. Aboveground and belowground biomass was calculated for each tree under study and then turned into CO_2 values. We found a common and positive trend in CO_2 yield accumulations from 2000 to 2100 among the studied mixtures. A common trend was also found regarding SSPs scenarios, with higher yield values under the most optimistic scenario (SSP1) and lower values under the most pessimistic scenario (SSP5) in the following order: SSP1>SSP2>SSP3>SSP5. However, pure and mixed stands yields evolved differently along the simulated period of study. In the beginning of the simulation period, mixed stands generally presented smaller yields than the respective pure stands. However, our results showed that differences in yield between mixed stands and pure stands were drastically reduced at the end of the simulation period in favor of the first ones. Aboveground and belowground CO_2 were also simulated in our study, finding different trends based on species traits for the analyzed mixtures. In conifer-broadleaved mixtures, we found that aboveground CO_2 tended to increase along all the simulation periods in both pure and mixed stands. An opposite trend was found for conifer-conifer mixtures, with a constant diminution in aboveground biomass proportion between 2000 and 2100 under the different SSPs. For all the analyzed mixtures, growth rates for both pure and mixed stands experienced a significant reduction from the beginning to the end of the simulation period under all the different SSPs studied. Our results indicated that these reductions would be less drastic in mixed stands than in the pure ones. Here, it's important to highlight that growth rates for all mixed stands were higher than in pure stands at the end of the simulation period among all the analyzed mixtures, fractions (aboveground and belowground) and SSPs.

This thesis has analyzed how climate and species mixing influence tree and stand level variables, in order to provide management guidelines for the adaptation of Mediterranean mixed forests to climate change in future.

RESUMEN

El calentamiento global hará aumentar la intensidad y la frecuencia de los episodios de sequía en la cuenca mediterránea, así como la aparición de episodios climáticos extremos, en base a recientes previsiones. En este contexto, los bosques mixtos aparecen como en una oportunidad sostenible para mitigar los efectos del cambio climático. La mezcla de especies puede conducir a la provisión de una mayor variedad de servicios y productos ecosistémicos al tiempo que aumenta la estabilidad temporal en comparación con los bosques monoespecíficos. El desarrollo de nuevos modelos que incluyan diferentes variables a nivel de árbol y de rodal será vital para comprender mejor la estructura, composición y dinámica de este tipo de bosques. Por otra parte, resultará fundamental analizar cómo el clima puede influir en estas variables con el fin de diseñar directrices de gestión adaptativas y sostenibles para los bosques mixtos bajo futuros escenarios de cambio climático. En esta tesis, se pretende avanzar en la modelización y simulación de diferentes variables a nivel de árbol y rodal para un amplio rango de tipos forestales y climáticos en España. En un primer estudio, se analizó cómo el clima puede influir potencialmente en la máxima capacidad de carga de masas forestales puras pertenecientes a 15 especies forestales de los géneros *Pinus, Quercus y Fagus*. El Índice de Máxima Densidad (SDI_{max}) de Reineke fue elegido para tal objetivo debido a su importancia en (1) la gestión de la densidad y (2) la definición de las proporciones de mezcla de especies en las masas forestales mixtas. Se ajustaron modelos MSDR (Relación Máxima Densidad-Tamaño) dependientes del clima para cada especie de estudio utilizando datos del Inventario Forestal Nacional de España y WorldClim. Se incluyeron simultáneamente en los modelos 35 variables climáticas anuales y estacionales diferentes (temperatura, precipitación, evapotranspiración, índices de aridez). En este estudio, se encontró que el clima influye de forma significativa en la MSDR y, por tanto, en la máxima capacidad de carga de la masa (SDI_{max}). Los mejores modelos de MSDR dependientes del clima mostraron que las variables climáticas relacionadas con la temperatura explicaban mejor la influencia del clima en la MSDR. En concreto, las temperaturas máximas estacionales (MXT_i) y anuales (MXT) fueron las variables climáticas más representativas para explicar los cambios en la MSDR. Según las variables estacionales seleccionadas, la primavera y el verano aparecieron sistemáticamente como periodos clave. Se encontró una tendencia común en la variación del SDI_{max} para las especies de coníferas y frondosas, con mayores valores de SDI_{max} vinculados negativamente a la temperatura y positivamente a la precipitación. Esta tendencia sugiere que la aridez puede desempeñar un papel clave en la reducción de la máxima

capacidad de carga de los rodales de las principales especies arbóreas mediterráneas. El impacto del clima en la capacidad máxima de carga de los rodales se evaluó mediante la creación del índice Q. En general, las especies frondosas presentaron valores más altos de los índices Q que las especies de coníferas, sugiriendo que la máxima capacidad de carga de la masa de las primeras sufriría más la influencia de potenciales cambios climáticos. Los resultados de este primer estudio evidenciaron la importancia de utilizar variables climáticas específicas para caracterizar mejor cómo afectan a la MSDR y al SDI_{max}.

En este primer estudio se descubrío que la aridez podría desempeñar un papel clave en la influencia de variables a nivel de rodal como el SDI_{max}. Por ello, se realizaron dos estudios más centrados en analizar cómo dicha variable puede influir en el crecimiento y en la alometría a nivel de árbol. Además, se analizó cómo los efectos de la mezcla de especies pueden influir en estas variables en los bosques mixtos, estudiando un total de 29 composiciones de especies distintas en España.

Para analizar la influencia de la aridez y la mezcla de especies en el crecimiento de los árboles, se modelizó el incremento en área basimétrica en un lapso de cinco años (BAI_5) en base al tamaño individual de los árboles, el desarrollo del rodal y otras variables de sitio y competencia. Se consideraron dos índices de competencia independientes de la distancia: el área basimétrica total del rodal (BA), que representa la competencia asimétrica por tamaño, y el área basal de los árboles más grandes que el árbol sujeto (BAL), que representa la competencia asimétrica por tamaño. Para descubrir los complejos efectos de la mezcla en el incremento del área basimétrica a nivel de árbol, los índices de competencia se dividieron en componentes intraespecíficos e interespecíficos. Se incluyeron y probaron todas las combinaciones posibles de estructuras de competencia en los modelos BAI. Los efectos de mezcla positivos, negativos o neutros se determinaron comparando el componente intraespecífico e interespecífico de los modelos seleccionados. A continuación, se determinaron las interacciones biológicas que tienen lugar entre las especies basándose en la competencia simétrica y asimétrica en cuanto al tamaño. Por último, se estudió la influencia de la aridez en el incremento del área basal incluyendo el índice de Martonne en los modelos BAI. Se encontró una tendencia común entre las mezclas con una mayor productividad en los rodales mixtos que en los puros, sugiriendo que los valores del BAI pueden aumentar con el incremento de la diversidad de especies. Basándose en los parámetros del modelo, en este estudio se presentó un enfoque novedoso para determinar las posibles interacciones biológicas entre especies en los bosques mixtos. La competencia resultó ser la interacción biológica más representativa en las mezclas de coníferas-coníferas, ya que el neutralismo y la facilitación pueden darse con más frecuencia en las mezclas de coníferas-coníferas y de frondosas-coníferas. Los resultados obtenidos igualmente sugieren que la productividad de los árboles puede estar significativamente limitada por las condiciones de aridez, excepto para *Pinus halepensis* y *Pinus pinea*.

En un tercer estudio, se ajustaron nuevos modelos altura-diámetro (H-D) para 13 especies mediterráneas diferentes bajo las anteriores composiciones de especies y distintas proporciones de mezcla a lo largo de un gradiente de aridez en España. Utilizando los datos del Inventario Forestal Nacional de España, se ajustaron inicialmente diferentes ecuaciones base altura-diámetro con el fin de seleccionar los mejores modelos base para cada par especie-mezcla. A continuación, los mejores modelos se expandieron incluyendo la proporción de especies por área (m_i) y el índice de Martonne (M). Se encontró una tendencia general para las especies de coníferas, con árboles más altos en los rodales puros que en los mixtos, siendo esta tendencia inversa para las especies frondosas. En cuanto a la influencia de la aridez en las relaciones H-D, las condiciones de humedad parecen beneficiar la altura de los árboles para casi todas las especies analizadas y las mezclas de especies. Se encontró una tendencia diferente para *Pinus halepensis* y *Pinus pinea*, sugiriendo que estas especies dedican más recursos en promover sus sistemas radicales en lugar de crecer en altura.

En un último trabajo, los modelos dependientes del clima desarrollados en los estudios anteriores se incluyeron en la plataforma SIMANFOR para simular el stock y la productividad de masas puras y mixtas en términos de biomasa y CO_2 para el periodo 2000-2100 bajo diferentes escenarios de cambio climático (SSPs) en España. Este estudio estuvo centrado en la especie *Pinus sylvestris* y sus principales mezclas (*Pinus nigra*, *Pinus pinaster*, *Fagus sylvatica* y *Quercus pyrenaica*). En cada iteración (cada 5 años) se estimó el diámetro a la altura del pecho y la altura total de cada árbol en estudio mediante modelos desarrollados en esta tesis. La mortalidad entre iteraciones se estimó a partir de la máxima capacidad de carga de la masa (SDI_{max}), ya que define el número máximo de árboles por hectárea en el que se produce la mortalidad natural en una masa forestal. La biomasa aérea y subterránea se calculó para cada árbol estudiado y se convirtió en valores de CO_2. Se encontró una tendencia común y positiva en las acumulaciones de stock de CO_2 desde 2000 hasta 2100 entre las mezclas estudiadas. También se encontró una tendencia común en cuanto a los escenarios SSP, con producciones de carbono más altos bajo el escenario más optimista (SSP1) y valores más bajos bajo el escenario más pesimista (SSP5) en el siguiente orden SSP1>SSP2>SSP3>SSP5. Sin embargo, los stocks de las masas puras y mixtas evolucionaron de forma diferente a lo largo del periodo de estudio simulado. Al principio del periodo de simulación, las masas mixtas presentaban generalmente stocks menores que las respectivas masas puras. Sin embargo, los resultados mostraron que las diferencias de stock entre las masas mixtas y las puras se redujeron drásticamente al final del periodo de simulación a favor de las primeras. Igualmente se simularon los stocks de CO_2 por encima y por debajo del suelo, encontrando diferentes tendencias en función de los rasgos de las especies para las mezclas analizadas. En las mezclas de coníferas y frondosas, se encontró que el CO_2 sobre el suelo tendió a aumentar a lo largo de todos los periodos de simulación tanto en las masas puras como en las mixtas. En las mezclas de coníferas-coníferas se encontró una tendencia opuesta, con una disminución constante de la proporción de biomasa sobre el suelo entre 2000 y 2100 bajo los diferentes SSP. Para todas las mezclas analizadas, las tasas de crecimiento tanto de las masas puras como de las mixtas experimentaron una reducción significativa desde el principio hasta el final del periodo de simulación bajo todos los diferentes SSP estudiados. Nuestros resultados indicaron que estas reducciones serían menos drásticas en las masas mixtas que en las puras. En este sentido, es importante destacar que las tasas de crecimiento de todas las masas mixtas fueron superiores a las de las masas puras al final del periodo de simulación entre todas las mezclas, fracciones (aéreas y subterráneas) y SSPs analizados.

Esta tesis ha analizado cómo el clima y la mezcla de especies influyen en distintas variables a nivel de árbol y de rodal, con el fin de proporcionar directrices de gestión para la adaptación de los bosques mixtos mediterráneos al cambio climático en el futuro.

INTRODUCTION

1.1. Mixed forests in the context of climate change

An increase of droughts intensity and frequency episodes combined with new extreme climate events are predicted to appear in the future due to global warming (IPCC, 2018). Relevant projections suggest that climate change effects are expected to be harder in the Mediterranean region (Astigarraga et al., 2020), predicting an increase in mean seasonal temperature of up to 1.2°C in summer and 0.9°C in winter; mean seasonal precipitation is expected to increase by up to 25% in summer but decline by up to 20% in winter (IPCC, 2018). Forests are already experiencing alterations in composition, structure, and dynamics (Fernandez-de-Una et al., 2015).

In this context, mixed forest stands have become a sustainable opportunity to mitigate the effects of climate change. The wide variety of water-use strategies of Mediterranean species could play a key role in that context, enhancing the resilience of these forests to extreme drought episodes (Lindner et al., 2008; del Río et al., 2009; Fares et al. 2015; Bauhus et al., 2017; del Río et al., 2017; Muñoz-Gálvez et al., 2021; Pardos et al., 2021). This is allowed by the efficiency on resource use (Pretzsch, 2014; Pretzsch & Schütze, 2016; Riofrío et al., 2017), as well as their temporal and spatial resource complementarity (Toigo et al., 2015), like crown canopy packing (Pretzsch & Schütze, 2016); and stability (del Río et al., 2017; Riofrío et al., 2017).

Species mixing can also result in increased productivity (Forrester, 2014; Pretzsch, 2014; Pretzsch et al., 2015; Pretzsch & Schütze, 2016; Jactel et al., 2018) and also the provision of higher levels of multiple ecosystem services (Gamfeldt et al., 2013). Interactions between species may vary with climatic conditions (del Rio et al 2014) and, therefore, climate–growth sensitivity should be explicitly considered as part of the modelling and simulation process to consider climate change impacts.

Adapting forests to climate change is a critical component of forest management. This requires both an understanding of climate effects on forest systems and the ability to forecast how these effects may change over time (Keenan, 2015).

Numerous studies have examined the drivers of mixing effects in terms of competition, facilitation, and competitive reduction (Forrester and Bauhus, 2016).

These species interactions in mixtures are frequently dynamic, changing spatially and temporally as resource availability changes, as stands develop, or as a result of climate change (Forrester, 2014). This makes critical understanding the conditions under which species interactions may change for a particular species combination as a result of modifying growing conditions caused by global change. Due to the fact that the effects of climate change vary between species and thus with species composition, mixing proportions, and site conditions, the direction of interspecific competition may change as a result of climate change.

In summary, it is critical for forest managers to understand species interactions and, if necessary, adapt management practices in these mixed stands because of climate change.

1.2. Adaptive management of mixed forests. Forest simulators and models

a) Forest simulators

Forest simulators are computer models used to predict the state and dynamics of a forest (Pretzsch et al., 2008). These tools are commonly used to update previously measured forest data and forecast forest dynamics, allowing the implementation of adaptive forest management to improve the decision-making processes (Crookston and Dixon, 2005). They also can be used to develop and test new growth and yield models, to improve forest training among students and to evaluate clean development solutions for quantification and reduction of emissions (Bravo et al., 2012). Among the commonly used forest simulators, the most relevant are: PROGNOSIS (Wykoff et al., 1982), ORGANON (Hester et al., 1989; Hann et al., 1995), FVS (Dixon, 2002), CAPSIS (Coligny et al., 2004), TREEGROSS (Nagel, 2005), SExI-FS (Harja et al., 2006) and SIMANFOR (Bravo and Ordoñez, 2021).

SIMANFOR is an example of forest platform simulator which has been parameterized for many species and has been used to research the effects of climate on development. Outputs include tree volumes, biomass, density, canopy cover, harvest yields, fire effects, among others. Multiple sub-models, or growth equations, are commonly used in forest simulators to create a simplified representation of the forest ecosystem. This representation (model) depicts the various processes that occur in a forest, such as development, mortality, and other structural changes.

SIMANFOR has been commonly used in Spain for managing pure stands, albeit further work needs to be done regarding mixed forests. In this thesis, new climate-dependent models (MSDR, growth and H-D) for mixed forests have been developed and incorporated into SIMANFOR to allow the simulation and management of these forest under future climate change scenarios.

b) Models

Maximum Size-Density Relationship (MSDR)

Maximum stand carrying capacity is a key variable in forest management, commonly used to develop site resources for sustainable, healthy, and optimal stand growth. Reineke (1933) was the first who addressed this concept when he proposed the Maximum Stand Density Index (SDI_{max}), an attribute that determines full site occupancy (Zeide, 2005). Reineke discovered that for any given tree size (i.e. 25 cm), the physiological attributes of a species constrain the maximum number of trees that a fully stocked stand can support before natural mortality takes place. This relationship is widely recognized in forest science (Reineke, 1933) and ecology (Fowler,1981; Yoda et al., 1963) as the Maximum Size-Density Relationship (MSDR). Also known as the self-thinning line, its applications encompass studies related to habitat distribution (Moore and Deiter, 1992), risk assessment due to abiotic and biotic factors (Fettig et al., 2007; Ducey et al., 2017) or the carbon sink capacity of forests (Woodall et al., 2011; Brunet-Navarro et al., 2016). Its use also extends to the development of forest management tools, such as forest growth models (Makela et al., 2000; Yang and Titus, 2002), density management diagrams (Long and Shaw, 2005; Valbuena et al., 2008) and forest management plans (Jack and Long, 1996; Churchill et al., 2013).

Initially, Reineke (1933) and Yoda et al. (1963) claimed that the MSDR and the maximum stand carrying capacity might not be influenced by environmental conditions or site quality. However, recent studies showed that this relationship varies with site quality (Bi, 2001; Comeau et al., 2010), stand origin (Weiskittel et al., 2009), nutrient availability (Morris, 2003; Reyes-Hernandez et al., 2013) and stand age (Zeide, 2005). The influence of climate on MSDR deserves special attention, since it is widely accepted that climate is changing. Recent studies confirm that the size-density relationship is affected by climate, indicating an important decline in the maximum stand carrying capacity associated with potential drought conditions in different areas of the Mediterranean basin (Condés et al., 2017; Aguirre et al., 2018). These studies frequently use annual climatic variables, such as the De Martonne Index (1926), to study influences on MSDR. Studies involving more precise (monthly or seasonal) climatic variables are needed to better understand this relationship.

Tree growth models

Species mixing effects play a key role influencing tree and stand dynamics (Del Rio et al. 2016) in mixed forests. Contrary to monocultures, quantifying these effects in mixed stands is a key challenge since the presence of two or more species requires to estimate the degree of intra- and inter-specific competition among trees (Forrester & Bauhus 2016; Riofrio et al. 2017). A reduction in competition, or even facilitation may occur when inter-specific competition for a given tree species is lower than intra-specific competition (Mina et al. 2018), suggesting that the presence of one species has a beneficial complementary effect on the growth of the other. Mechanisms like niche complementarity or resources partitioning and use-efficiency could promote beneficial species mixing effects (Pretzsch 2014), although it's difficult to determine which of them is responsible for the facilitative or competitive effect since both mechanisms may occur simultaneously (Mina et al. 2018). Depending on whether resource uptake is proportional to size or not, competition could be divided in size-symmetric and size-asymmetric (Weiner, 1990), respectively. Based on that, trees may compete symmetrically for belowground resources such as water and soil nutrients and asymmetrically for light (Weiner 1990; Larocque et al. 2013). Several studies have followed this approach (Coates et al. 2009; Del Rio et al. 2014; Manso et al. 2014; Riofrio et al. 2017; Mina et al. 2018).

Tree growth is also influenced by environmental conditions (Vanclay, 1994; Pretzsch et al. 2009) both in pure and mixed forests. Previous research (Pretzsch et al., 2010; Río et al., 2014) suggested that complementarity occurs more often in stressful situations than in favorable conditions under the stress-gradient hypothesis. Aridity has also been shown to impact forest allometry (Fortin et al. 2015), growth (Condés and del Rio, 2015), mortality (Ruiz-Benito et al. 2013) or the maximum stand carrying capacity (Aguirre et al. 2018; Rodriguez-de-Prado et al. 2020), especially in the Mediterranean area.

In this scenario, future tree growth models for mixed forests should consider a wide variety of competition modes along an aridity gradient, to generate quantitative silvicultural guidelines adapted to future climate change scenarios.

Tree height-diameter relationship

Species mixing effects may also influence tree allometry in mixed forests (Temesgen et al. 2014; Sharma and Breidenbach, 2015; Liu et al., 2018; Riofrio et al. 2019; Xie et al., 2020). Estimating total tree height is fundamental for both developing and applying many growth and yield models in both pure and mixed forests (Sharma and Yin Zhang, 2004; Blozan, 2006). The height-diameter relationship (H-D) enables the description of stand characteristics and development over time, mean height estimation, stand stability, site index, and growth (Curtis, 1967). Many height-diameter equations have been developed using only diameter at breast height as the independent variable for estimating total height (Curtis, 1967; Wykoff et al., 1982; Huang et al., 1992; Zhang et al., 1997; Fang and Bailey, 1998; Peng, 1999; Jayaraman and Zakrzewski, 2001). However, the height-diameter relationship varies from stand to stand (Curtis, 1967), being significantly influenced by additional features, such as tree health and vigor, site quality and stand development stage, and stand density or competition, and species mixture in a stand (Calama et al., 2003; Sharma and Yin Zhang, 2004; Sharma and Yin Zhang, 2004). We refer to this type of model as "generalized H-D model" (Ciceu et al., 2020). Thus, the inclusion of additional explanatory variables in the H-D models would make the H-D relationships generalizable over large areas rather than having to fit individual relationships to different stands (Curtis, 1967; Sánchez et al., 2003; Sharma and Yin Zhang, 2004; Temesgen and Gadow, 2004; Mugasha et al., 2019). In Europe, generalized height–diameter models have been used since the 1930s (Lang, 1938; Kramer, 1964; Von Laer, 1964; Kennel, 1972; Nagel, 1991; Hui and Gadow, 1993; Diéguez-Aranda et al., 2005; Sanchez-Gonzalez et al. 2007). These models are usually designed to be climate-independent and for this reason they fail to evaluate future scenarios linked to climate change. There is need to assess whether the inclusión of additional factors, such as species proportions and climatic variables in mixed forests, may influence the H-D relationship.

In this context, this thesis has analyzed how climate and species mixing influence these tree and stand level variables, in order to provide management guidelines for the adaptation of Mediterranean mixed forests to climate change in future.

OBJECTIVES

2.1. Main Objective

The main objective of this study was to advance in the modelization and simulation of tree and stand-level variables to facilitate the management of mixed forest stands in the context of global change.

2.2. Specific Objectives

1. To research the climatic influence on the maximum size-density relationship (MSDR) in pure stands

2. To study the influence of competition and aridity in tree growth in mixed forests

3. To evaluate the influence of species mixing and aridity in the height-diameter relationship in mixed stands

4. To simulate CO_2 yield and growth in pure and mixed forests under different climate change scenarios

2.3. Graphical approach of the thesis

The research activity of the thesis is showed in Figure 1 as a linear process. The figure is divided into two main blocks. Black arrows indicate the direction followed in the research process, starting in the upper left corner and finishing in the lower right corner, to accomplish all the proposed objectives.

The upper block (light blue shading) focuses on satisfying specific objectives 1, 2, and 3 of the present thesis using present climate data. The lower block (dark blue shading) tries to satisfy specific objective 4 by using the models fitted in the upper block and future climate data.

The upper block is further divided into two different research stages. The first stage (left part) focuses on satisfying specific objective 1, which tries to analyze how climate influences the Maximum Size – Density Relationship (MSDR) and the maximum stand carrying capacity (SDI_{max}) of pure stands. The second stage (right part) focuses on satisfying specific objectives 2 and 3. To analyse how specific composition influences growth and allometry of species in mixed stands, the species proportion by area (m_i) was calculated from the Competition Equivalence Coefficients (CEC). CEC were calculated using SDI_{max} estimated with the MSDR models fitted previously for each species in pure stands.

The lower block corresponds to the last stage of research and addresses specific objective 4. For this purpose, the MSDR, H-D and BAI models developed in previous stages were included in the SIMANFOR simulator with the aim of analyzing the yield and growth of biomass and CO_2 in both pure and mixed stands under different climate change scenarios or Shared Socio Economic Pathways (SSPs).

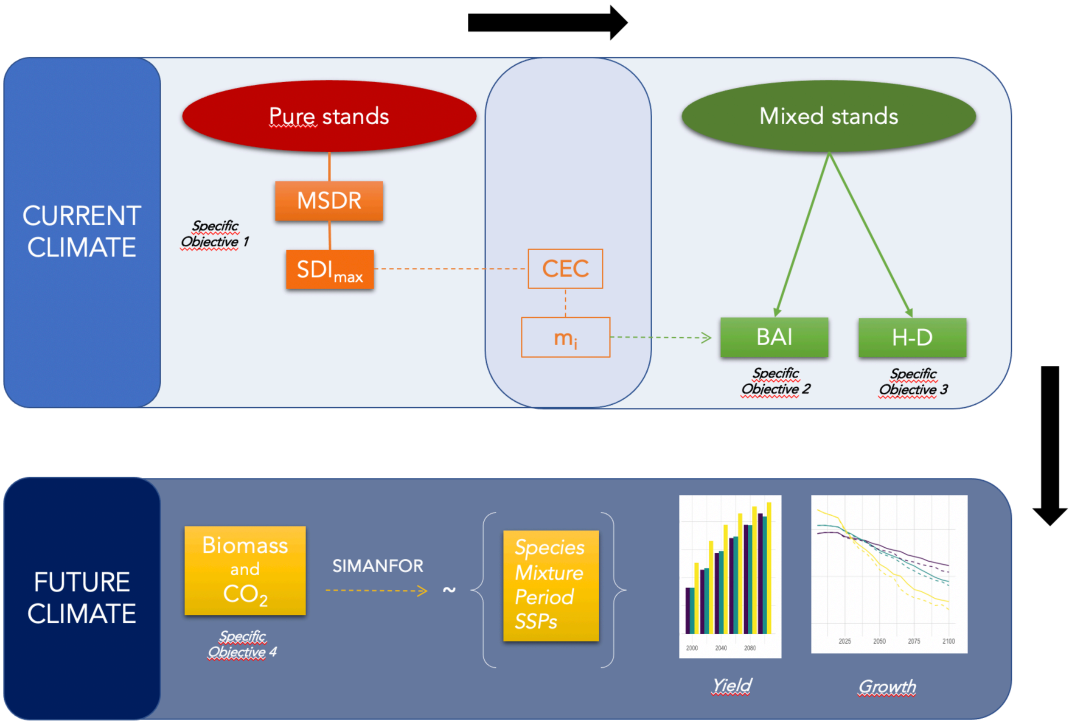


Figure 1. Thesis workflow process to advance in the analysis of tree and stand level variables to improve the management of mixed forest stands in the context of global change

Note: MSDR – Maximum Size-Density Relationship, SDI_{max} – Maximum Stand Density Index, CEC – Competition Equivalence Coefficient, m_i – Species proportion by area of species i, BAI – Basal Area Increment, SSPs – Shared Socio Economic Pathways.

DATA

3.1. Forest data. Spanish National Forest Inventory

Forestry data used for this study came from the Spanish National Forest Inventory (SNFI). SNFI was carried out using permanent plots located exclusively in forested areas (FAO, 2001) at a density of one sampling point per 1 km^2 (1x1 km grid), which were re-measured approximately every 10 years. SNFI plots consist of four concentric circles with radii of 5,10,15 and 25 meters, in each of which multiple tree level variables for all trees over 7.5, 12.5, 22.5 and 42.5 cm diameter at breast height (1.3 m), respectively, were recorded (Herrero and Bravo, 2012; Hernández et al., 2014; Alberdi et al., 2016). Stand level variables were computed from tree attributes measured in each concentric subplot using a different expansion factor (EF) for each subplot size as follows: $EF_r=10000/a_r$, where a_k denotes the area of each subplot with radii r. Therefore, EF_r is equal to the number of trees per hectare represented by every tree measured in each subplot with radii r (Moreno-Fernandez et al., 2018). The study focused on 15 Mediterranean tree species from Pinus, Fagus and Quercus genus distributed across the Iberian Peninsula, Balearic and Canary Islands: Scots pine (*Pinus sylvestris L.*), Beech (*Fagus sylvatica L.*), Maritime pine (*Pinus pinaster Ait.*), Stone pine (*Pinus pinea L.*), Aleppo pine (*Pinus halepensis Mill.*), Holm oak (*Quercus ilex L.*), Sessile oak (*Quercus petraea Matt. Liebl.*), Pyrenean oak (*Quercus pyrenaica Willd.*), Pedunculate oak (*Quercus robur L.*), Black pine (*Pinus nigra Arnold*), Cork oak (*Quercus suber L.*), Portuguese oak (*Quercus faginea Lam.*), Monterey pine (*Pinus radiata D.Don*), Pinus mugo (*Pinus uncinata Turra*) and Canary Island pine (*Pinus canariensis C.Sm.*).

From these species, pure and mixed SNFI plots were selected. SNFI plots were considered as pure if the proportion of basal area of the main species was 90% or higher. On the other hand, mixed plots (composed by two main species) were selected if (1) the proportion of both species being higher than 90% and (2) the proportion of each species being higher than 15%. In this study, data from the Second (2SNFI) and the Third Spanish National Forest Inventory (3SNFI) were used (Table 1). The following considerations were taking into account: (i) To study MSDR, low-density pure plots and those with quadratic mean diameter outside the 10-60 cm range were dismissed to avoid including under-represented stands, (ii) to study growth and allometry in mixed forests, similar site conditions between mixed and pure plots were guaranteed selecting only pure plots within a buffer of <3 Km from mixed plots, (iii) to consider a wide range of different species compositions in mixed forests, all possible two-species combinations were created based on the 15 species of study discarding non-representative mixtures (< 25 plots).

A summary of the tree and stand level variables used to accomplish specific objective 1 are shown in Table 2, since climatic variables are shown in Supplementary Tables 1 and 2. Supplementary Table 7 shows the initial variables and values used to accomplish specific objectives 2,3 and 4.

Table 1. Forestry and climatic data used to accomplish the different specific objectives of this study

Specific objective	Forestry data	Climatic data	Stand composition
1	3SNFI	*Historical (1970-2000)*	Pure
2	2SNFI + 3SNFI	*Historical (1970-2000)*	Pure + Mixed
3	2SNFI	*Historical (1970-2000)*	Pure + Mixed
4	2SNFI	*Future (2000-2100)*	Pure + Mixed

3.2. Climatic data. *WorldClim*

Climatic data were obtained from Worldclim 2 database (Fick and Hijmans, 2017), which is a high-resolution global geo-database (30 arc seconds or ~ 1km at equator) of monthly average data gathered from extensive climate observations and the NASA´s Shuttle Radar Topography Mission (SRTM). Worldclim includes monthly temperature (minimum, maximum and average), precipitation, solar radiation, vapour pressure and wind speed for different periods using data from between 9000 and 60000 weather stations. Weather station data were interpolated using thin-plate splines with covariates including elevation, distance to the coast and three satellite-derived covariates: maximum and minimum land surface temperature as well as cloud cover, obtained with the MODIS satellite platform. Historical and future climatic data were obtained from Worldclim 2 to analyze potential climatic influence on different tree and stand attributes. Historical data was obtained from 1970 to 2000, covering the period when 2SNFI and 3SNFI were developed. Future climatic data came from the Sixth World Climate Research Programme (CMIP6) future climate projections. Data downscaling and calibration (bias correction) were done with WorldClim 2 as baseline. Mean monthly values of the different climatic variables available in Worldclim were obtained for:

(1) Five global climate models (GCMs): BCC-CSM2-MR, CNRM-CM6-1, CanESM5, IPSL-CM6A-LR, MIROC6
(2) Four Shared Socio-economic Pathways (SSPs): 126, 245, 370 and 585.
(3) Four 20-year periods (2021-2040, 241-2060, 2061-2080, 2081-2100)

Potential evapotranspiration data from the Global Potential Evapotranspiration Geospatial Database (Trabucco and Zomer, 2009) were also used for the 1970-2000 period. All climatic data were derived from SNFI plots using QGIs software (QGis.org, 2021) and plot-specific latitude and longitude.

Table 2. Mean, standard deviation and range (minimum-maximum) of the main stand characteristics of the 3NFI plots selected

Functional group	Species	n	Elev (m)	N (trees·ha^{-1})	Dq (cm)	BA (m^{2}·ha^{-1})	Ho (m)
Conifers	*Pinus canariensis*	1158	1286 ± 349 (246-2317)	359 ± 298 (20-1984)	29.49 ± 8.57 (11.84-50.00)	1.93 ± 1.34 (0.11-9.30)	15.31 ± 4.12 (4.50-30.50)
	Pinus halepensis	6074	641 ± 307 (0-1559)	413 ± 309 (33-2387)	20.51 ± 5.89 (10.01-49.30)	0.60 ± 0.43 (0.05-4.03)	9.13 ± 2.50 (2.50-25.50)
	Pinus nigra	2321	1101 ± 324 (183-2141)	768 ± 577 (81-4623)	20.42 ± 6.19 (10.17-53.73)	1.13 ± 0.86 (0.06-8.02)	11.1 ± 3.38 (4.00-27.79)
	Pinus pinaster	4427	776 ± 371 (4-1842)	512 ± 404 (20-2886)	25.86 ± 6.97 (10.06-49.93)	1.61 ± 1.15 (0.23-12.79)	12.99 ± 4.16 (4.89-36.88)
	Pinus pinea	1352	513 ± 289 (0-1144)	336 ± 330 (31-3233)	26.95 ± 8.27 (11.21-49.66)	1.06 ± 0.71 (0.26-7.48)	9.70 ± 2.67 (3.42-22.45)
	Pinus radiata	874	412 ± 249 (8-2013)	430 ± 261 (10-1678)	33.85 ± 8.83 (10.01-54.92)	3.75 ± 2.32 (0.04-12.3)	23.89 ± 5.76 (5.00-38.42)
	Pinus sylvestris	4082	1302 ± 329 (282-2428)	786 ± 545 (15-4333)	23.46 ± 6.99 (10.15-49.74)	1.85 ± 1.36 (0.01-11.45)	13.01 ± 3.95 (2.50-30.48)
	Pinus uncinata	385	1899 ± 196 (1337-2456)	746 ± 478 (40-2430)	23.73 ± 6.04 (13.21-45.27)	1.89 ± 1.00 (0.57-6.94)	11.56 ± 2.81 (5.60-20.70)
Broadleaves	*Fagus sylvatica*	1117	999 ± 283 (143-1943)	561 ± 414 (82-2544)	29.02 ± 9.40 (11.07-54.97)	28.01 ± 10.28 (4.03-64.84)	18.97 ± 5.00 (5.05-36.35)
	Quercus faginea	685	869 ± 221 (146-1552)	643 ± 590 (28-3088)	17.18 ± 6.54 (10.01-39.94)	0.58 ± 0.75 (0.02-5.82)	7.89 ± 2.38 (2.50-20.46)
	Quercus ilex	3609	661 ± 309 (57-1980)	281 ± 333 (41-2005)	23.57 ± 10.09 (10.00-49.98)	6.85 ± 3.75 (1.39-22.78)	6.18 ± 1.38 (0.95-11.75)
	Quercus petraea	201	1006 ± 302 (112-1622)	697 ± 565 (38-3392)	24.17 ± 8.81 (10.58-48.02)	2.13 ± 1.82 (0.40-13.35)	12.86 ± 4.07 (5.54-28.82)
	Quercus pyrenaica	1879	1029 ± 247 (150-1898)	751 ± 664 (33-5125)	18.91 ± 7.79 (10.01-49.85)	0.80 ± 0.97 (0.08-9.84)	10.33 ± 2.90 (2.64-22.52)
	Quercus robur	560	495 ± 236 (31-1598)	403 ± 316 (52-1791)	29.01 ± 9.59 (11.07-54.92)	20.42 ± 9.71 (3.75-61.49)	13.97 ± 4.11 (1.85-28.98)
	Quercus suber	687	398 ± 211 (18-1065)	243 ± 228 (41-1287)	31.9 ± 10.31 (12.06-54.09)	14.12 ± 6.92 (3.16-41.87)	8.13 ± 2.11 (2.38-15.55)

Note: n - Number of plots; Elev - Plot altitude (m), N - Stand density (trees ha^{-1}), Dq - Quadratic mean diameter (cm), BA - Basal area (m^{2} ha^{-1}), H_o - Dominant height (m).

METHODS

4.1. Climatic influence on the maximum carrying capacity of Mediterranean tree species

4.1.1. Climate-dependent Maximum Size-Density Relationship (MSDR) models

Firstly, basic MSDR models (without climatic influence) were fitted using Reineke´s (1933) equation (Eq.1) after natural logarithmic transformation (Eq.2), to obtain species-specific coefficients:

$$N_{max} = \alpha'_0 \cdot Dq^{\beta 0} \qquad [1]$$

$$\log(N_{max}) = \alpha_0 + \beta_0 \cdot \log(Dq) \qquad [2]$$

where **N_{max}** is the maximum density (trees ha $^{-1}$), **Dq** is the quadratic mean diameter (cm), **α_0** is the species-specific intercept and **β_0** is the species-specific slope to be estimated.

Basic MSDR coefficients were estimated by linear quantile regression (Koenker & Basset, 1978) for each species, using the quantreg R package (Koenker, 2015) on R software (R Core Team, 2018). Models were fitted for the upper quantiles (95th, 97.5th and 99th) since the MSDR is a limiting boundary (Ducey and Knapp, 2010; Aguirre et al., 2018).

Secondly, climate-dependent MSDR models were then fitted by species, to analyze the influence of climate on MSDR and maximum stand carrying capacity. Climate-dependent coefficients were obtained for each climatic variable (Table 3) using linear quantile regression, by expanding the coefficients in Eq.(2) as a function of climate:

$$\ln(N_{max}) = \alpha_0 + \alpha_1 \cdot \log(Clim) + (\beta_0 + \beta_1 \cdot Clim) \cdot \log(Dq) \qquad [3]$$

where: **Clim** is a climatic variable and **α_0**, **α_1**, **β_0** and **β_1** are the model parameters to be estimated.

Table 3. List of climatic variables used to fit the MSDR models

Variable	Definition
T	Annual Mean Temperature (Kelvin degrees)
Ti	Mean Temperature (Kelvin) of the i Season (i = 1,2,3,4)
MNT	Annual mean Minimum Temperature (Kelvin degrees)
MNT_i	Minimum Temperature (Kelvin degrees) of the i Season (i = 1,2,3,4)
MXT	Annual Mean Maximum Temperature (Kelvin degrees)
MXT_i	Maximum Temperature (Kelvin degrees) of the i Season (i = 1,2,3,4)
MXTWM	Maximum Temperature of Warmest Month (Kelvin degrees)
MNTCM	Minimum Temperature of Coldest Month (Kelvin degrees)
TAR	Temperature Annual Range (Kelvin degrees) (MXTWM - MNTCM)
P	Total Annual Precipitation (mm)
P_i	Total Precipitation (mm) of the i Season (i = 1,2,3,4)
PWM	Precipitation of Wettest Month (mm)
PDM	Precipitation of Driest Month (mm)
M	Annual De Martonne Index (mm $°C^{-1}$)
M_i	De Martonne Index (mm $°C^{-1}$) of the i Season (i = 1,2,3,4)
PET	Annual Potential Evapotranspiration (mm)
PET_i	Potential Evapotranspiration (mm) of the i Season (i = 1,2,3,4)

Note: i - 1=Autumn (October, November, December), 2=Winter (January, February, March), 3=Spring (April, May, June), 4=Summer (July, August, September)

In total, 35 climate-dependent models were fitted for each species at the same quantiles as the basic MSDR models. The F-test, based on the extra sum of squares principle (Ratwosky, 1983), was used to test any statistically significant improvement (at α=0.05 significance level) of these models over the basic models. Finally, significant climate-dependent models were arranged based on the Akaike Information Criterion (Akaike, 1973; Bozdogan,1987) and pseudo-R^2 for quantile regression (Koenker and Machado,1999), to determine the climatic variables that most affect MSDR by species.

4.2.2. Climatic effect on Maximum stand density index (SDI_{max}). Q_{index}

Maximum stand carrying capacity was expressed as the Maximum Stand Density Index (SDI_{max}), derived from Reineke´s (1933) equation. Reference values for SDI_{max} (SDI_{maxREF}) were calculated by species, using estimated coefficients from basic MSDR models (Eq.2).

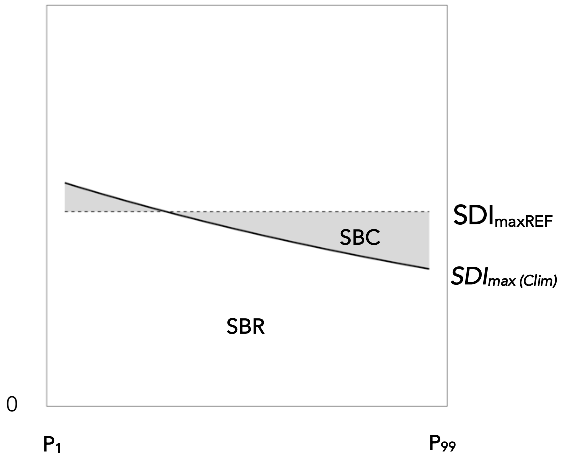
$$SDI_{maxREF} = e^{[\alpha 0 \ + \ \beta 0 \cdot \log(25)]} \qquad [4]$$

In a similar way, estimated coefficients from the selected climate-dependent models were used to calculate the climate-dependent SDI_{max} by species (Eq.5):

$$SDI_{max}(Clim) = e^{[(\alpha 0 + \alpha 1 \cdot \log(Clim)) + (\beta 0 + \beta 1 \cdot Clim) \cdot \log(25)]} \qquad [5]$$

where **SDI_{max} (Clim)** is the function of the maximum stand carrying capacity for each species and climatic variable **Clim** and **α_0**, **α_1**, **β_0** and **β_1** are the estimated coefficients from climate-dependent MSDR models.

To visually detect trends in SDI_{max} variation, *SDI_{max} (Clim)* values were obtained and plotted along the range of values (percentiles 1 to 99) for each climatic variable selected. Then, to quantify the SDI_{max} variation a species experiences in a region along a range of different climatic conditions the Q index was proposed. It was calculated as follows: First, the difference between *SDI_{max} (Clim)* values obtained from the climate-dependent models (Eq. 5) with respect to species-specific SDI_{maxREF} obtained from (Eq. 4) was considered (Figure 2). By integrating them between the 1st and the 99th percentile of each climatic variable, the area between the *SDI_{max} (Clim)* function and the y = SDI_{maxREF} line was then determined. This area is known as the Surface Between Curves (SBC). Finally, the Q index was calculated using (Eq.6) to relativize the SBC to the SDI_{maxREF} reference value, making it comparable among species and climatic drivers. Higher Q index values indicate greater variation (by excess or defect) in the range of estimated SDI_{max} across the climatic distribution of a species. On the other hand, lower Q index values represent less SDI_{max} variation.



$$Q\ index = \frac{SBC}{SBR} \qquad [6]$$

Figure 2. Graphical representation of the Q index

Note: SBR (Surface Below Reference) represents the area below the reference line y = SDImaxREF, i.e., SBR = SDImaxREF · (P99 – P1) and P1 and P99 are the 1st and the 99th percentile of the climatic variable.

4.2. Climatic and competition influence on tree growth in mixed forests

4.2.1. Modelling approach

In this study, the basal area increment (BAI), has been modelled based on individual tree size, stand development, site, competition and climatic variables (Wagenmakers et al. 2004, Wykoff et al. 1982) to analyze the influence of competition and the aridity on tree growth. Diameter at the breast height (d) and height (h) were used as the explanatory variables indicating tree size. Developmental stand stage was represented by the mean quadratic diameter (Dq). Similarly, the De Martonne index (M) was selected as climatic variable to define an aridity gradient. To analyze the influence of competition on the basal area increment, two distance independent competition indexes were considered: total stand basal area (BA) and the basal area of trees larger than the subject tree (BAL). Here, size symmetric competition was represented by BA, whereas BAL portrays size-asymmetric competition. To uncover the complex mixing effects on basal area increment at tree level, competition indexes were splitting into intraspecific (BA_{intra}, BAL_{intra}) and interspecific (BA_{inter}, BAL_{inter}) components. All possible combinations of competition structures were tested using the competition term (C) of the BAI models (Eq 7). Thus, positive, negative, or neutral mixing effects could be determined by comparing the intraspecific and interspecific component of the resultant models. Positive species mixing effect was considered when parameter estimates for interspecific competition was lower than intraspecific competition term. Negative species mixing effect was considered when parameter estimates for interspecific competition was higher than intraspecific competition term. Neutral species mixing effect was considered when the intraspecific, interspecific or both components were non-significant in BAI models.

These mixing effects ultimately allowed us to determine the biological interactions taking place between species based on size-symmetric and size-asymmetric competition. These interactions could be categorized into four different biological interactions (Competition, ammensalism, commensalism and neutralism) as represented in Figure 3.

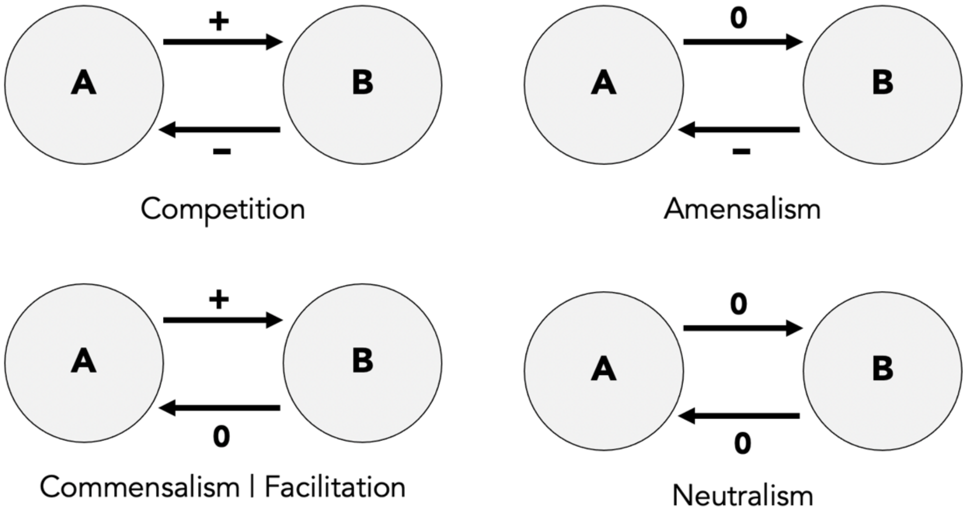


Figure 3. Different biological interactions between species derived from BAI models based on intra and inter-specific competition components

Note: "+" indicates a positive species mixing effect, "-"indicates a negative species mixing effect and "0" indicates no significant species mixing effect.

Due to the hierarchical nature of the inventory data, BAI models were fitted using a linear mixed effect approach with lme4 package (Bates et al. 2015) in R (R core Team, 2020). For accounting to possible autocorrelation among trees within plots, we included plot as random effect in the intercept (a_0) of the fitted model. The significance of the random plot effect was based on the likelihood ratio test ($p < 0.05$). Furthermore, a natural logarithmic transformation of the original dependent variable was applied to attain normal distribution of the residuals and reduce heteroscedasticity. Thus, the final form of the model for BAI_5 of tree i in a plot j is presented in (Eq.7):

$$log\;(BAI_{5,ij}) \;=\; (a_0 + a_{oj}) + a_1 d_i + a_2 log(d_i) + a_3 h_i + a_4 Dq_j + a_5 M_j + \sum \quad (b_k C_{ik}) + e_{ij}$$

[7]

where $\mathbf{BAI_{5,ij}}$ is the 5-year periodic mean annual basal area increment of the tree *i* within plot *j*, in $cm^2 \cdot 5yrs^{-1}$;$\mathbf{d}_i$ is the diameter at breast height, in cm; $\mathbf{h}_i$ is the total tree height, in m; $\mathbf{Dq}_j$ is the plot quadratic mean diameter, in cm; and $\mathbf{M}_j$ is the De Martonne index, in $mm \cdot °C^{-1}$. $\mathbf{a_0}$, $\mathbf{a_1}$, $\mathbf{a_2}$, $\mathbf{a_3}$, $\mathbf{a_4}$ and $\mathbf{a_5}$ are the parameters estimated from the model. $\mathbf{C_{i,k}}$ are the k different terms of the different competition structures for tree *i*, with $\mathbf{b_k}$ being the corresponding parameters to be estimated, $\mathbf{a_{0j}}$ is the random plot effect; and $\mathbf{e_{ij}}$ is the error term. Random effect $\mathbf{a_{0j}}$ and error term $\mathbf{e_{ij}}$ are assumed to be normally distributed with a mean of zero and a variance σ_i^2 and σ_ε^2, respectively.

4.2.2. Model selection

Model selection was carried out according to the following approach. First, parameter estimations were obtained for all possible species, mixtures and combinations of competition structures by Maximum Likelihood (ML) in order to allow the comparison of the results. Only models with all the coefficients being significant ($p < 0.05$) were selected. Among these models, an information-theoretic approach for selecting the best one by species for each mixture was carried out. In a first step, models were arranged by descending AIC_c (Second-order Akaike Information Criterion). Since differences in AIC_c between the best models were too low in some cases, the final selection on Akaike Evidence Ratios (Wagenmakers and Farrell, 2004) was considered. Akaike Evidence ratios (ER) indicated the number of times the model with the lowest AICc was likely to be the best model in terms of Kullback-Leibler discrepancy (Kullback and Leibler, 1951; Burnham and Anderson, 2001), being calculated as follows:

$$ER_i = \frac{w_i}{w_j} \qquad [8]$$

where $\mathbf{ER_i}$ is the evidence ratio of model i; being $\mathbf{W_i}$ and $\mathbf{W_j}$ the Akaike weights of the models with the lowest and the second lowest AIC_c, respectively.

Models with ER >2 were selected for each species and mixture. In the case of having several models satisfying this condition, models with more complete competition structure were prioritized for further evaluation and analysis.

4.2.3. Model evaluation

The selected models were evaluated performing a 10-fold cross validation procedure. First, the original dataset was split into 10 subsamples of approximately equal size and the selected models were fitted for each fold. One of the subsamples was omitted at each fit for training the model. Each of the 10 fitted models was tested with the observation of the omitted subsample. The excluded subsample observation was used to evaluate each of the ten models. Differences between the expected and observed values across all plots were used to calculate statistics such as the Akaike Information Criterion Index (AIC), mean bias, root mean square error (RMSE), model performance (EF), marginal and conditional R^2 (Riofrio et al. 2019).

4.3. Climatic and species composition influence on tree allometry in mixed forests

4.3.1. Modeling approach

Base H-D model selection

Model fitting was carried out in two steps. In a first step, basic height-diameter (H-D) models were fitted for each species and species compositions studied. A total of 14 expressions of H-D equations most used from the forestry literature (Table 4) were considered. These base candidate models were fitted for each species and mixture composition using the *optimize.curve_fit* function from the scikit-learn (Pedregosa et al. 2011) library in Python.

To validate models and check overfitting, a cross validation bootstrap process was carried out. Data was splitted into train and test sets in an 80-20 proportion for each pair of mixture composition. Train set was used to obtaining parameter estimates, since test set was used for model evaluation performance. Confidence intervals for each parameter were obtained by using a nonparametric bootstrap procedure, as described by Robinson and Froese (2004). The number of bootstrap replicates was set to 1000. Following this bootstrap procedure, root mean squared error (RMSE) and Akaike Information criterion (AIC) were obtained for each model. The best H-D base model was selected for each species in a mixture composition based on parameter significance and model performance (lower AIC and RMSE). Then, selected H-D base models were expanded to allow the inclusion of competition and climate variables in the H-D relationships.

Table 4. Base H-D equations used in this study

Model	Reference	Formula
Generalized H-D models		
M1	CAÑADAS et al (1999) (IV)	$h=1{,}3+\left(\beta_0\left(\frac{1}{d}-\frac{1}{d_0}\right)+\left(\frac{1}{H_0-1{,}3}\right)^{1/2}\right)^{-2}$
M2	DEL RIO (1999)	$h=\beta_o\, e^{\beta_1\,(\frac{1}{d}-\frac{1}{d_0})}$
M3	GAFFREY (1988) (modified by DIÉGUEZ et al. (2005))	$h=1{,}3+(H_0-1{,}3)e^{\beta_0\left(1-\frac{do}{d}\right)+\beta_1\left(\frac{1}{do}-\frac{1}{d}\right)}$
M4	MICHAILOFF (1943)	$h=H_o\, e^{\beta_0\,(\frac{1}{d}-\frac{1}{d_0})}$
M5	MONNESS (1982)	$h=1{,}3+\left(\beta_0\left(\frac{1}{d}-\frac{1}{d_0}\right)+\left(\frac{1}{H_0-1{,}3}\right)^{1/3}\right)^{-3}$
M6	NILSON (1999) (modified by DIÉGUEZ et al. (2005))	$h=\frac{H_0}{1-\beta_0\left(1-\left(\frac{d_0}{d}\right)^{\beta_1}\right)}$
Basic (only diameter) H-D models		
M7	HUANG y TITUS (1992) (II)	$h=\beta_0 e^{-\beta_1 e^{(-\beta_2 d)}}$
M8	MEYER (1940)	$h=\beta_0\left[1-e^{(-\beta_1 d)}\right]$
M9	PEARL y REED (1920)	$h=\frac{\beta_0}{\left(1+\beta_1 e^{-\beta_2 d}\right)}$
M10	RATKOWSKY y REEDY (1986)	$h=\frac{\beta_0}{\left(1+\beta_1{}^{-1} d^{-\beta_2}\right)}$
M11	RICHARDS (1959) (I)	$h=\beta_0(1-e^{\beta_1 d})^{\beta_2}$
M12	SCHUMACHER (1939)	$h=1{,}3+\beta_o\, e^{\frac{\beta_1}{d}}$
M13	SEBER y WILD (1989) (I)	$h=\beta_0 e^{-e(-\beta_1(d-\beta_2))}$
M14	ZEIDE (1992)	$h=\beta_0 e^{\left(-\beta_1 e(-\beta_2 d^{\beta_3})\right)}$

Note: h - Total tree height (m), d - Diameter at breast height (cm), H_o *- Dominant height of the plot (m),* d_o *- Dominant diameter of the plot (cm),* β_0, β_1, *and* β_2 *- Model parameters to be estimated*

Extension of base H-D models

In a second step, the previously selected H-D base models were expanded including several independent variables representing stand development (Dq, Ho), competition (BAL), species proportion (m), and climatic conditions (M). Since we considered these variables to mostly affect asymptotic parameter (β_o) of the base H-D models, this parameter was further expanded both as a linear (Eq.9) and multiplicative (Eq.10) form as follows:

$$\beta_o = \alpha_0 + \alpha_1 \cdot BAL + \alpha_2 \cdot Dq + \alpha_3 \cdot m_i + \alpha_4 \cdot M + \alpha_5 \cdot Ho \qquad [9]$$

$$\beta_o = \alpha_0 \cdot BAL^{\alpha_1} \cdot Dq^{\alpha_2} \cdot m_i^{\alpha_3} \cdot M^{\alpha_4} \cdot Ho^{\alpha_5} \qquad [10]$$

where **β_0** is asymptotic parameter of base H-D models presented in Table 3; **BAL** is the basal area of trees larger than a subject tree, in $m^2 \cdot ha^{-1}$; **Dq** is the quadratic mean diameter, in cm; **m_i** is the species proportion by area for species i; **M** is the De Martonne aridity index, in mm·°C^{-1}; and **Ho** is the dominant height, in m. Note that Dq and Ho were tested both at plot and species (**Dq_i**, **Ho_i**) level since preliminary analysis showed a high correlation between these variables at species level with height estimation, especially for *Quercus* species.

Mixed effects models

The best H-D model was selected considering variable significance and model parsimony using AIC_c. After that, we fitted non-linear mixed effects models to correct hierarchical and spatial data structure of forest inventory data. Numerous studies have applied the mixed-effects models to describe H–D relationships and have alleviated this lack of independence of error terms, improving the model fitting and prediction accuracy (Pinheiro, 2000; Vargas-Larreta et al., 2009; Crecente-Campo et al., 2014; Harrison et al. 2018). To consider random effects in the expanded H-D models, the following procedure was carried out:

Firstly, we tested plot as random variable based on a similar study (Riofrio et al. 2019) This variable was included iteratively into the different parameters of the expanded H-D models to determine the best model for each pair species-triplet. To allow their comparison, models were fitted using maximum likelihood (ML). Secondly, among the pool of fitted models, we identified the best expanded mixed-effects H-D model for each pair species-mixture composition considering model parsimony using an information-theoretic approach. The model with the lowest AIC_c (Second-order

Akaike Information Criterion) and greater Akaike weight (W_i) was considered the best and most parsimonious model for the observed data relative to the set of alternative models. Finally, the best-fitting expanded H-D functions were re-fitted using the unbiased restricted maximum likelihood method (REML) with R-package 'nlme' (Pinheiro et al. 2021). To ensure that our modelling strategy has accounted for heteroscedasticity, models were assessed using residuals plots. We assessed the contribution of forest stand and climate variables by looking at the significance of their respective parameters.

4.3.2. Mixing proportion influence on H-D relationships in mixed forest stands

We used species proportion by area (m_i) to define stand composition and to identify the significant effects of species interactions on H-D relationships in mixed stands. The species-specific growing space occupied is relevant for calculation of the mixing proportions, stand density, and quantification of mixing effects on growth (Sterba et al., 2014). Thus, species mixing proportions might be calculated to avoid bias in the quantification of the net total mixing effect, as well as in the relative importance of under- or overyielding by species, due to differences in the potential densities of the species (Kearsley et al., 2017). Competition equivalence coefficient (CEC) compares species-specific growing space requirements of a species with their value in mixed stands, and it is calculated as the ratio of potential carrying capacity of both species in pure stands (by means of maximum stand density index (Reineke, 1933) – SDI_{max}). Since recent studies have shown evidence that SDI_{max} varies with climate (Bravo-Oviedo et al., 2018; Aguirre et al. 2018), in this study we obtained climate-dependent CECs (Supplementary Table 8) to calculate species mixing proportions for each species in mixed stands using climate-dependent MSDR models presented by Rodriguez-de-Prado et al. (2020). Therefore, species proportion by area was calculated for each species based on SDI and equivalence coefficients following similar studies (Sterba et al., 2014; Del Río et al., 2016; Pretzsch, 2016; Riofrío et al., 2017).

$$m_i = \frac{SDI_i}{SDI_i + SDI_j \cdot CEC_{j,i}} \quad [11]$$

$$CEC_{j,i} = \frac{SDI_{max,j}}{SDI_{max,i}} \quad [12]$$

where $\mathbf{m_i}$ is the species proportion by area of species I; $\mathbf{SDI_i}$ is the stand density index of species I; $\mathbf{SDI_j}$ is the stand density index of species j; $\mathbf{CEC_{j,I}}$ is the competition equivalence coefficient for species j, taking as reference species I; $\mathbf{SDI_{max,I}}$ is the climate-dependent maximum stand density index of species I; and $\mathbf{SDI_{max,j}}$ is the climate-dependent maximum stand density index of species j

To compare total tree height estimations in mixed and pure stands, the M_{ratio} was introduced. M_{ratio} was calculated as the ratio between the estimated height in mixed (H_{mix}) and monospecific (H_{pure}) stands. H_{mix} was estimated along a gradient of different mixing proportions (m_i), since H_{pure} was estimated at $m_i = 1$. Therefore, when $M_{ratio} > 1$, the estimated total tree height would be higher in mixed than in pure stands.

4.3.3. Aridity influence on H-D relationships in mixed forest stands

The De Martonne Aridity Index (M) was included in the models as a measure of aridity ($M = P/(T+10)$; mm $°C^{-1}$) (De Martonne, 1926). Including this index into H-D models allowed us to estimate total tree height along an aridity gradient. In this context, the C_{ratio} (H_{arid}/H_{humid}) was introduced to analyze whether height is higher in arid ($C_{ratio} < 1$) or in humid ($C_{ratio} > 1$) conditions. While H_{arid} corresponds to the total tree height estimated along the aridity gradient of each species and mixture (from smallest value of the De Martonne Index to the highest one), H_{humid} corresponded to the estimated height at the highest De Martonne Index found.

4.4.CO_2 stock simulation in Spanish mixed forests. A case study for *Pinus sylvestris* mixtures

4.4.1. Species and mixtures of study

In this study, we focused on *Pinus sylvestris* in four different mixtures (*Pinus sylvestris – Pinus nigra, Pinus sylvestris – Pinus pinaster, Pinus sylvestris – Fagus sylvatica and Pinus sylvestris – Quercus pyrenaica*) to simulate CO_2 yield and growth under different climatic scenarios.

Scots pine (*Pinus sylvestris L.*) is a tree species with a huge importance on the European region, due to the huge extension and distribution that occupies all over Europe (Durrant et al., 2016; Pretzsch et al., 2020) and their commercial and ecological importance (del Río et al., 2009; Durrant et al., 2016; de Rigo et al. 2016;

Riofrío et al., 2017;). Scots pine is a light-demanding and evergreen conifer widespread across temperate and boreal European forests (Toigo et al., 2015; Durrant et al., 2016), linked to continental climate areas and with a good adaptation to cold and poor-nutrient areas and different altitude ranges (Fernandez-de-Una et al., 2015; Durrant et al., 2016b ; Pretzsch et al., 2020; Muñoz-Gálvez et al., 2021), being at the Mediterranean area at the limit of his natural distribution (Fernandez-de-Una et al., 2015). In Spain, Scots pine was favored by large-scale afforestation policies across the 19th and 20th centuries (Vadell et al., 2016), which favored the area occupied in this region. Although it frequently grows in pure stands (Durrant et al., 2016), both in natural and afforestation, it can be found in mixing with different coniferous and broadleaved species. Among them, we highlighted the following:

Maritime pine (*Pinus pinaster Ait.*)

It is an interesting species mixed with Scots pine due to the complementarity of their behaviors, even taking into account their similarities. Both of them are two of the main conifers in Spain (Serrada et al., 2008; Riofrío et al., 2017), growing on pure and mixed stands, naturally or planted for afforestation (Serrada et al., 2008; Riofrío et al., 2019). Overyielding was reported from this mixed stands (Riofrío et al., 2017), and also a high influence of aridity as an environmental gradient affecting productivity (Carrión et al., 2010). These mixed forests are interesting from the economic point of view (Riofrío et al., 2017), and their crown complementarity and vertical stratification in the canopy make that mixture more productive due to the higher light interception and use (Riofrío et al., 2017), comparing with pure stands. Also, a positive effect of that mixed stands was found regarding understory richness and tree regeneration comparing to monospecific stands (López-Marcos et al., 2020).

Black pine (*Pinus nigra J.F.Arnold*)

It is linked to intermediate altitude forests, usually appearing on mixed forests with Scots pine closer to the southern distribution of that specie, which is the ecological optimum for black pine (Barbéro et al., 1998). Due to the high affection of climate change to the Mediterranean basin (Martín-Benito et al., 2010), Black pine was reported as the most affected pine species in this area (Martin-Benito et al., 2011). Also, Martin-Benito et al. (2011) reported precipitation from previous autumn to summer and winter temperature with a positive effect, and temperature in spring-summer with negative effect over black pine growth. In addition, drought was found as the main climatic driver affecting tree radial growth (Martin-Benito et al., 2013), strengthen the previous finding. Although different models were created for Black and Scots pine mixed stands in Spain (Trasobares et al., 2004a, 2004b, 2004c), also taking into account non-wood products like fungi (de Aragón et al., 2007; Palahí et al., 2009), a few knowledge about the species complementarity and interactions are available.

Pyrenean oak (*Quercus pyrenaica Willd.*)

It is another common species mixed with Scots pine, interesting due to their complementarity on the long-term stability to average climate conditions (Muñoz-Gálvez et al., 2021). While Pyrenean oak shows low resistance to drought with high recovery rates, Scots pine has the opposite behavior (Muñoz-Gálvez et al., 2021). Regarding productivity, higher growth rates were found on mixed comparing to monospecific stands, having Pyrenean oak higher rates under wet and Scots pine under dry conditions (Muñoz-Gálvez et al., 2021), founding the same results on volume increment per occupied area (del Río et al., 2009), but with the opposite trend to the total volume growth, which is lower due to the low growth rate of Pyrenean oak, depending on the mix proportions (del Río et al., 2009). That results are expected due to the differences of this species into shade tolerance, leaf habits, and rooting deep (Martín-Gómez et al., 2017), which suppose a higher resource use efficiency in mixed stands comparing to pure ones (Forrester, 2014). Furthermore, this complementarity is also interesting on forest fire regenerations due to the seed dispersal (Scots pine) and resprouting (Pyrenean oak) abilities (del Río et al., 2009)

Sessile oak (Quercus petraea (Matt.) Liebl.), a mid-successional broadleaved specie widespread over western Europe (Toigo et al., 2015), is another specie that usually creates mixed forests with Scots pine across Europe. Sessile oak has a high summer drought tolerance (Pretzsch et al., 2020; Toigo et al., 2015) due to its deep-reaching rooting systems (Steckel et al., 2019), while Scots pine performs better on spring droughts (Pretzsch et al., 2020; Steckel et al., 2019). Overyielding on mixed forests was found with different results (Steckel et al., 2020; Toïgo et al., 2015), which variation is attributed to differences in site conditions, with a stronger and positive effect of overyielding in mixture on low productive areas (Toïgo et al., 2015), letting us understand the higher resistance of that species mixture (Pretzsch et al., 2020), and also in wet conditions (Jucker et al., 2014). Besides, in the cases when overyielding was found, it was reported a complimentary light use for both species according to their differences in shade tolerance, leaf phenology, and crown architecture (Steckel et al., 2019).

European beech (*Fagus sylvatica L.*)

It is one of the main tree species in Europe due to their high economic importance and huge distribution, both in pure and mixed stands frequently joined with Scots pine (Pretzsch et al., 2015), and probably being the mixed forests more studied in Europe. Their huge mixed stands distribution is due to the species niche complementarity (del Río et al., 2017; Pretzsch & Schütze, 2016) due to their different behaviors on factors like space occupancy efficiency (Pretzsch & Schütze, 2009), light tolerance, and light use complementarity (del Río et al., 2014; Pretzsch et al., 2015), structural and vertical heterogeneity (Pretzsch & Schütze, 2016; del Río et al., 2017), and root systems (del Río et al., 2014; Pretzsch et al., 2015; Yeste et al., 2021). Also, an improvement of soil characteristic of that mixed forest was reported by Yeste et al. (2021) comparing with pure pine stands, and a nursery effect of Scots pine over European beech seedling were noticed by Aranda et al. (2004) and Pretzsch et al. (2015), even reducing the drought stress of European beech at the more fragile growing moments. That species complementarity is translated on higher productivity of mixed comparing to pure stands, being true that stand structure and climatic conditions have complex influences over it (Condes et al., 2013; Pretzsch et al., 2015; del Río et al., 2017; Condés et al., 2018).

4.4.2. CO_2 yield simulation in Spanish mixed forests

In this study, CO_2 yield each five years for the 2000-2100 period under four different SSPs (SSP1, SSP2, SSP3 and SSP5) was carried out with SIMANFOR platform (Bravo and Ordoñez, 2021). SIMANFOR is a platform developed to simulate sustainable forest management alternatives, allowing users to compare different silvicultural scenarios and choose the one which better adjusts to their management purpose. Its workflow consists in a forest inventory and silvicultural scenario as inputs, processing inventory data by using equations of the selected model and following the scenario steps, in order to return an output to the user with the information of each tree and stand "evolution" at each step of the planned scenario. In this study, SIMANFOR simulator was adapted to simulate forest dynamics in mixed forest stands. Thus, new tree growth distance-independent models were included in the platform. Tree growth, characterized by tree basal area increment (BAI), was estimated using models from *Section 5.2*. Diameter at breast height was derived from BAI estimations, so it could be used for predicting total tree height using H-D models presented in *Section 5.3*. We controlled mortality based on the maximum stand carrying capacity (SDI_{max}), since it defines the maximum number of trees per hectare where natural mortality takes place in a forest stand. At each iteration, Stand Density Index (SDI) (Reineke, 1933) and SDI_{max} were estimated using the climate-dependent MSDR models presented in *Section 5.1* for each species inside each SNFI sample plot. Thus, while SDI_{max} < SDI, mortality does not take place in a specific plot for a specific species; nonetheless, when. In the moment SDI_{max} > SDI for a specific species, expansion factor expansion of all the trees from that species experience a 2% reduction. As a consequence, stand density (trees · ha^{-1}) would decrease 2% of the specific species value below the limit defined by SDI_{max}, and stand will continue its dynamics. Aboveground and belowground biomass was calculated for each tree using Ruiz-Peinado et al. (2011, 2012) equations. Biomass estimations were transformed into CO values using the corresponding conversion factors for each species of study: *Fagus sylvatica* (0.486), *Pinus nigra* (0.464), *Pinus pinaster* (0.468), *Pinus sylvestris* (0.459) and *Quercus pyrenaica* (0.457). Finally, CO values were multiplied by 3.67 to obtain CO_2 values. We assumed null incorporated forest mass or regeneration process into the simulations. SIMANFOR simulations were developed by using the supercomputational Scayle services due to the higher computational capacity compared to the desktop version, which means higher velocity on the simulation process. After that, all the generated outputs (at tree and plot level) were joined, re-structured and analyzed using R language programming (R Core Team, 2019). Figure 4 shows the location of the SNFI selected plots for each mixture.

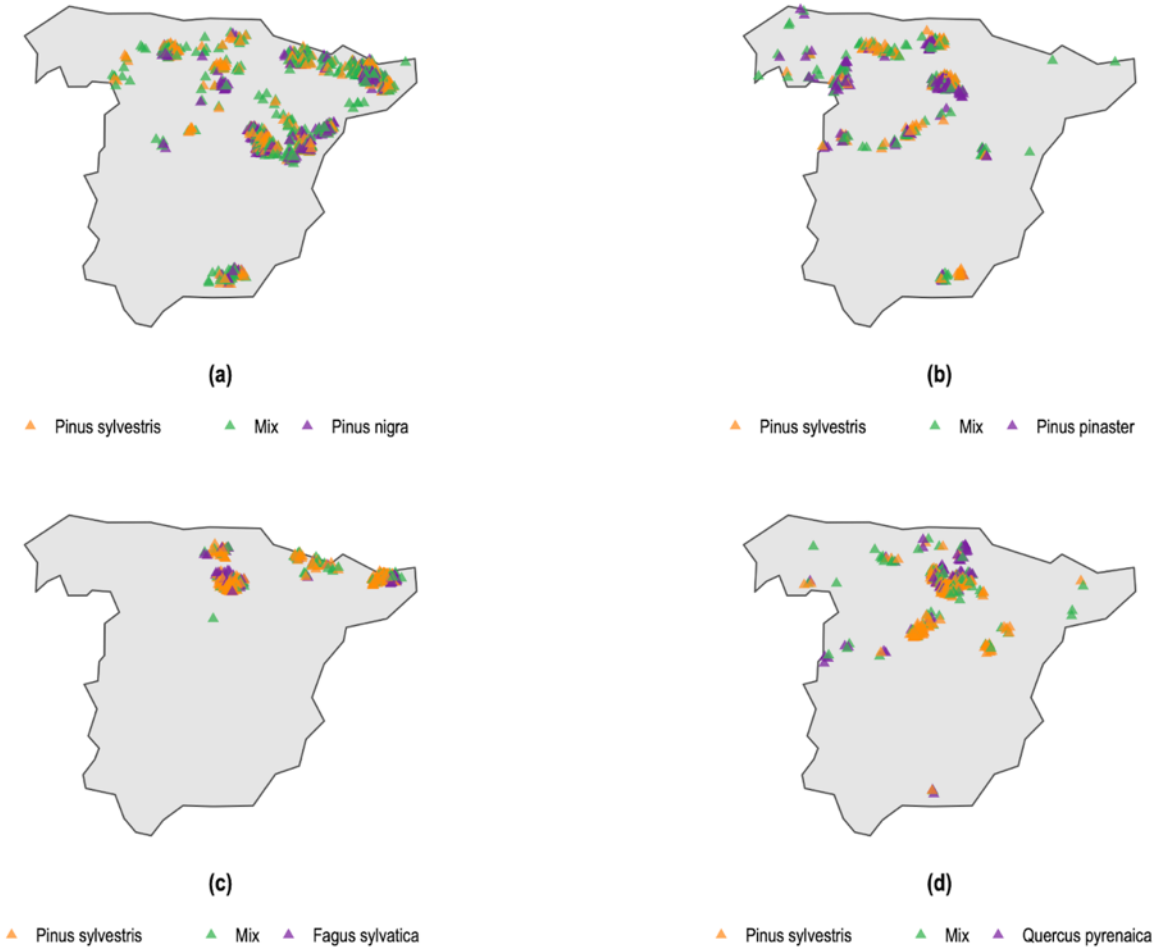


Figure 4. SNFI plots distribution in Spain to the four simulated mixtures

Note: a: Pinus sylvestris – Pinus nigra, b: Pinus sylvestris – Pinus pinaster, c: Pinus sylvestris – Fagus sylvatica, d: Pinus sylvestris – Quercus pirenaica mixture

4.4.3. Shared Socio-Economic Pathways (SSPs)

SSPs are scenarios describing how the world would look in the absence of climate policy and allow researchers to examine barriers and opportunities for climate mitigation and adaptation in each possible future world when combined with mitigation targets (Riahi et al. 2017; Meinshausen et al. 2020). They are based on five narratives (Figure 5), which intend to span the range of plausible futures each of which represents a different future socio-economic projection and political environment:

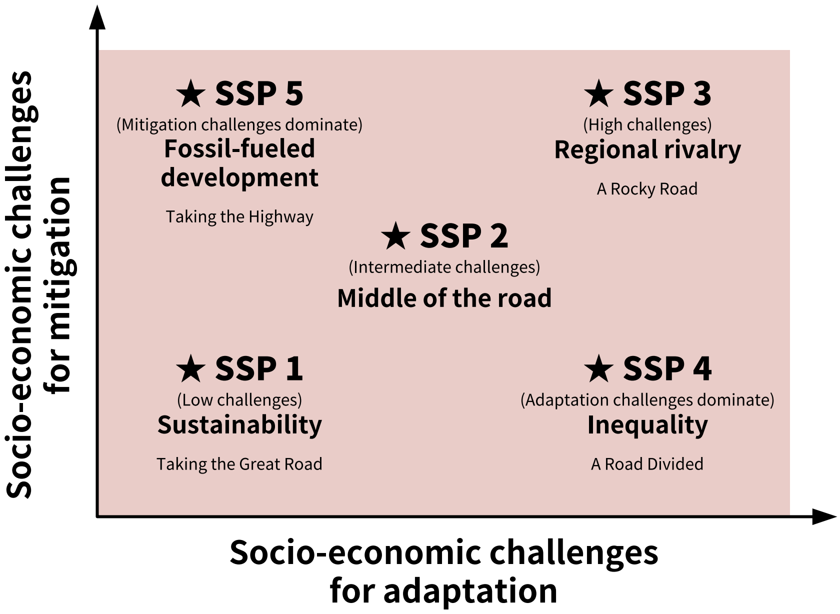


Figure 5. Overview of Shared Socio-Economic Pathways (SSPs) representing combinations of challenges to mitigation and adaptation (from O'Neill et al. (2017))

SSP1 and SSP5 anticipate reasonably positive patterns in human development, including "significant investments in education and health, robust economic growth, and well-functioning institutions." However, they differ in that SSP5 assumes this would be powered by an energy-intensive, fossil-fuel economy, while SSP1 assumes a gradual transition toward sustainable practices. SSP3 and SSP4 are more negative about the potential economic and social growth of their nations, citing low investment in education and health in poorer countries, as well as a rapidly rising population and growing disparities. SSP2 is a "middle of the road" scenario in which historical trends of growth are maintained into the twenty-first century.

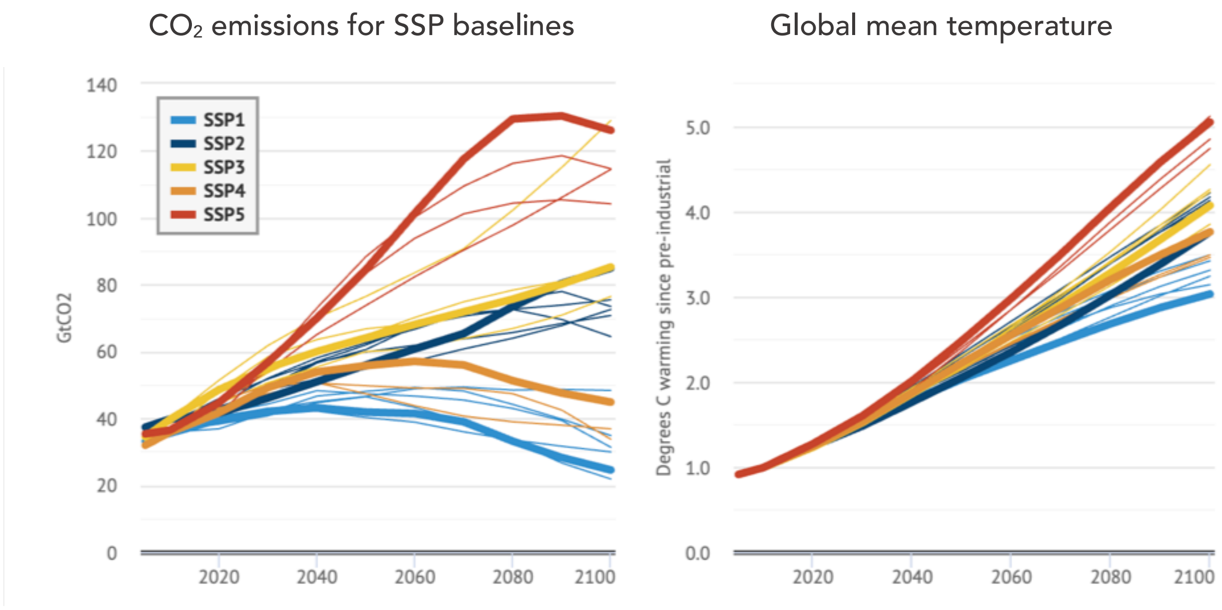


Figure 6. CO_2 emissions (left) in gigatonnes (Gt CO_2) and global mean surface temperature change relative to pre-industrial levels (right) in degrees C across all models and SSPs for baseline no-climate-policy scenarios (Carbon Brief website: www.carbonbrief.org)

CO_2 emissions vary dramatically across SSP baselines, as shown in Figure 6. One of the SSP framework's main advantages is that it stresses the importance of baseline assumptions in determining the emissions and temperatures that result. Even in the absence of specific climate legislation, SSP1 emissions peak between 2040 and 2060, before declining to around 20 to 50 gigatonnes of CO_2 (Gt CO_2) per year by 2100. By 2100, the global temperature will have risen by 3-3.5 degrees Celsius. In the "middle of the road" SSP2, emissions continue to climb through the end of the century, reaching between 65 and 85 Gt CO_2, leading in a temperature increase of 3.8 to 4.2 degrees Celsius. For the "regional rivalry" SSP3, models indicate a wide range of baseline emissions, with most runs showing rises of roughly 76-86 Gt CO_2 by 2100. In SSP3, warming is anticipated to range between 3.9 and 4.6 degrees Celsius by 2100. SSP4 has low emissions despite its high inequality, thanks to rapid technical developments in low-carbon energy sources. SSP4 emissions are predicted to range between 34 and 45 Gt CO_2 by 2100, resulting in a 3.5-3.8 °C temperature increase. Finally, the SSP5 produces the largest overall emissions of any SSP, ranging from 104 Gt CO2 to 126 Gt CO_2 in 2100, resulting in 4.7-5.1°C warming. In this study, we simulated and analyzed how CO_2 stock varies in Spanish mixed forests under four different SSPs (SSP1, SSP2, SSP3 and SSP5). Data from SSP4 was not available in WorldClim, so this scenario was not analyzed in our study.

RESULTS

5.1. Maximum Size-Density Relationship and SDI_{max} response to climate

5.1.1. Basic MSDR models

The intercept (α_0) and slope (β_0) of the basic MSDR models were highly significant ($p < 0.001$) for all the coniferous (Table 5) and broadleaf species (Table 6) studied. Since SDI_{maxREF} estimate results were very low for the 95th and very high for the 99th quantiles compared to similar studies, the 97.5th quantile was selected as the reference for each model, to allow for comparison of results among all the species studied. The results of the basic MSDR models fitted at these quantiles are available in Supplementary Table 3. Of the coniferous species, *Pinus pinea* (-2.1855) and *Pinus pinaster* (-1.9063) presented the steepest slopes of the basic MSDRs, while *Pinus sylvestris* (-1.7524) and *Pinus uncinata* (-1.7336) presented the flattest slopes. Estimated SDI_{maxREF} values for the coniferous species ranged from 526 (*Pinus halepensis*) to 1178 (*Pinus radiata*) trees per hectare (Table 7).

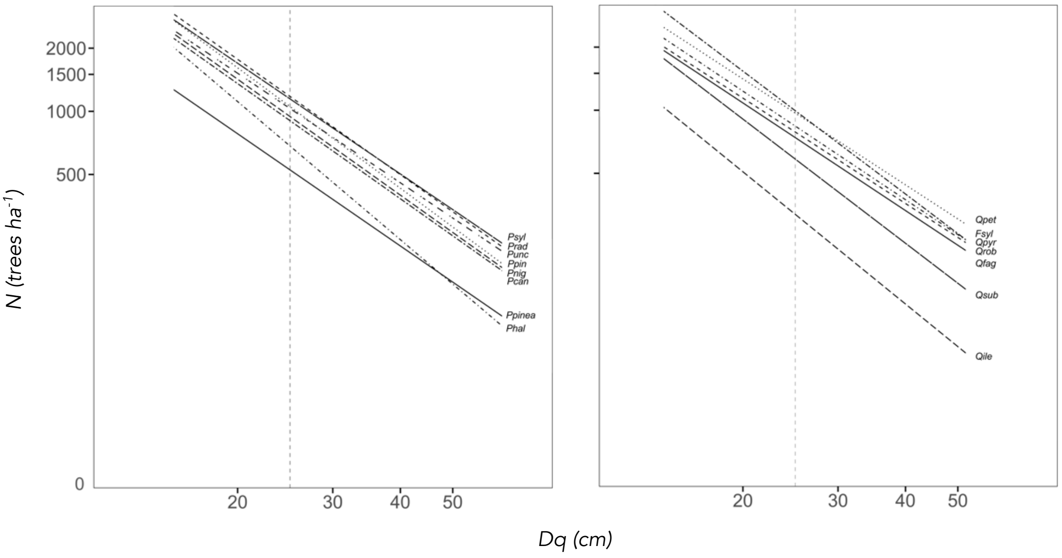


Figure 7. Basic MSDR fits plotted on a log-log scale for the (a) coniferous and (b) broadleaf species studied

Note: Pcan - Pinus canariensis, Phal – Pinus halepensis, Pnig – Pinus nigra, Ppin – Pinus pinaster, Ppinea – Pinus pinea, Prad – Pinus radiata, Psyl – Pinus sylvestris, Punc – Pinus uncinata, Fsyl – Fagus sylvatica, Qfag – Quercus *faginea, Qile – Quercus ilex, Qpet – Quercus petraea, Qpyr – Quercus pyrenaica, Qrob – Quercus robur, Qsub – Quercus suber*

In general, broadleaf species presented smaller maximum stand carrying capacities (from 319 to 995 trees per hectare) than coniferous species. Results for these species fell along a gradient; *Quercus ilex* (-2.0951) had higher intercepts and shallower slopes, followed by *Quercus suber*, *Fagus sylvatica*, *Quercus pyrenaica*, *Quercus faginea*, *Quercus petraea*, and finally *Quercus robur* with the least pronounced slope (-1.6698) (Table 7). Basic MSDR trajectories are shown by species in Figure 7 and Supplementary Figure 1.

5.1.2. Climate-dependent MSDR models

Coefficients for the best climate-dependent MSDR models are presented in Table 5 (coniferous species) and Table 6 (broadleaved species). Results indicated that climatic variables related to temperature better explained the influence of climate on MSDR, for both conifers and broadleaf species. Specifically, seasonal (MXT_i) and annual (MXT) maximum temperatures were the most representative climatic variables among the 35 studied. Climate-dependent models including Maximum Summer Temperature (MXT4) were selected in 8 (4 conifer and 4 broadleaf) of the 15 species, followed by models including Maximum Spring Temperature (MXT3), Maximum Temperature of the Warmest Month (MXTWM) and Maximum Annual Temperature (MXT). Based on the climatic variables selected in the best climate-dependent models, spring and summer consistently appeared as key periods.

Among the conifers studied, the models selected for *Pinus halepensis*, *Pinus nigra*, *Pinus pinaster* and *Pinus sylvestris* presented maximum temperatures as key variables for explaining climatic influence on MSDR. In contrast, aridity, precipitation, and potential evapotranspiration were the variables that most influenced MSDR for *Pinus canariensis, Pinus pinea*, *Pinus radiata* and *Pinus uncinata* (Table 5). Only three climatic models were significant for *Pinus radiata*, which may be due to a high concentration of selected monospecific plots in a specific area without a wide climatic variability. Among the broadleaved species studied, temperature was also found to be a key driver affecting MSDR, since most of the climate-dependent models selected were related to these variables (Table 6).

Table 5. Species-specific coefficients, SDI_{max} estimates and goodness of fit in terms of Akaike's Information Criterion (AIC) and pseudo-R^2 coefficient for the basic and the top five climate-dependent MSDR models fitted by linear quantile regression (97.5th quantile) for coniferous species

Species	Model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2	Q index
Pinus canariensis	**basic**	**12.672 *****	**-**	**-1.8226 *****	**-**	**2616.9**	**0.3378**	**-**
	P1	3.639 ***	2.448 ***	-2.0891 ***	-	2320.8	0.4178	0.305
	PWM	4.176 ***	2.059 ***	-1.9567 ***	-	2347.4	0.4111	0.251
	P	13.161 ***	-	-2.6082 ***	0.0015 ***	2364.4	0.4067	0.245
	P2	12.989 ***	-	-2.3961 ***	0.0075 ***	2420.9	0.3921	0.189
	M1	11.738 ***	1.061 ***	-1.8500 ***	-	2431.5	0.3893	0.189
Pinus halepensis	**basic**	**11.982 *****	**-**	**-1.7760 *****	**-**	**12622.5**	**0.3388**	**-**
	M	9.241 ***	0.886 ***	-1.5559 ***	-0.0095 **	12325.5	0.3549	0.063
	MXT3	96.948 ***	-14.977 ***	-1.7045 ***	-	12368.1	0.3526	0.079
	MXT4	105.595 ***	-16.445 ***	-1.7171 ***	-	12383.7	0.3517	0.077
	MXTWM	100.504 ***	-15.542 ***	-1.7134 ***	-	12394.4	0.3512	0.073
	PWM	8.722 ***	0.784 ***	-1.6057 ***	-0.0026 *	12401.9	0.3509	0.051
Pinus nigra	**basic**	**12.756 *****	**-**	**-1.8346 *****	**-**	**5117.9**	**0.2965**	**-**
	MXT3	140.953 ***	-22.536 ***	-1.9324 ***	-	5010.9	0.3128	0.123
	MXT	154.667 ***	-24.995 ***	-1.9154 ***	-	5028.5	0.3102	0.119
	MXT4	104.610 ***	-16.094 **	-1.9119 ***	-	5045.9	0.3076	0.091
	MXT2	13.019 ***	-	5.7005 ***	-0.0268 ***	5046.7	0.3075	0.119
	P2	11.821 ***	0.290 ***	-1.8973 ***	-	5047.8	0.3073	0.098
Pinus pinaster	**basic**	**13.096 *****	**-**	**-1.9063 *****	**-**	**10593,0**	**0.2716**	**-**
	MXT	13.446 ***	-	4.1770 ***	-0.0213 ***	10229,0	0.3011	0.129
	MXT3	13.365 ***	-	3.5759 ***	-0.0190 ***	10241.6	0.3001	0.128
	T3	13.324 ***	-	3.9110 ***	-0.0206 ***	10296.4	0.2958	0.121
	MXT4	13.462 ***	-	2.6955 ***	-0.0159 ***	10307.5	0.2949	0.114
	MXT2	13.389 ***	-	3.3318 ***	-0.0187 ***	10317.1	0.2941	0.114
Pinus pinea	**basic**	**13.562 *****	**-**	**-2.1855 *****	**-**	**3270.9**	**0.3887**	**-**
	P4	15.072 ***	-0.460 *	-2.4379 ***	0.0093 ***	3139.5	0.4185	0.262
	M4	13.531 ***	-0.467 **	-2.4556 ***	0.2919 ***	3144,0	0.4176	0.257
	P	13.213 ***	-	-2.2271 ***	0.0003 **	3210.7	0.4026	0.131
	TAR	77.368 **	-11.127 *	-2.2790 ***	-	3213.2	0.4020	0.143
	M	13.304 ***	-	-2.2518 ***	0.0077 *	3216.7	0.4013	0.155
Pinus radiata	**basic**	**12.947 *****	**-**	**-1.8254 *****	**-**	**1432.8**	**0.3723**	**-**
	PET3	110.968 ***	-21.507 ***	-8.0490 ***	0.0652 ***	1402.4	0.3845	0.058
	PET4	88.959 ***	-16.269 **	-6.5496 ***	0.0441 **	1409.2	0.3821	0.062
	PET1	6.920 **	1.675 *	-1.3894 ***	-0.0119 **	1421.2	0.3778	0.020
Pinus sylvestris	**basic**	**12.685 *****	**-**	**-1.7524 *****	**-**	**7718.9**	**0.368**	**-**
	TAR	66.470 ***	-9.442 ***	-1.7478 ***	-	7594.7	0.3777	0.078
	MNTCM	617.791 ***	-108.147 ***	-40.0934 ***	0.1425 ***	7630.1	0.3751	0.109
	MXTWM	74.540 ***	-10.872 ***	-1.7675 ***	-	7637.6	0.3744	0.075
	MXT4	71.686 ***	-10.376 ***	-1.7699 ***	-	7643.9	0.3739	0.073
	MXT3	58.945 ***	-8.154 ***	-1.7767 ***	-	7653,0	0.3732	0.064
Pinus uncinata	**basic**	**12.519 *****	**-**	**-1.7336 *****	**-**	**556.6**	**0.4414**	**-**
	PET3	12.918 ***	-	-1.6378 ***	-0.0031 **	534.6	0.4586	0.068
	PET4	16.777 ***	-0.838 ***	-1.8979 ***	-	535.5	0.4580	0.063
	PET	12.899 ***	-	-1.6288 ***	-0.0004 **	535.6	0.4578	0.108
	PET2	12.908 ***	-	-1.6784 ***	-0.0077 **	536.7	0.4571	0.062
	P2	11.386 ***	0.364 ***	-1.9112 ***	-	538.1	0.4561	0.052

****$p<0.001$; **$p<0.01$; *$p<0.05$; - non significant*

Note: Fewer than 5 significant climate-dependent MSDR models were found for Pinus radiata and Pinus uncinata.

Table 6. Species-specific coefficients, SDI_{max} estimates and goodness of fit in terms of Akaike's Information Criterion (AIC) and pseudo-R^2 coefficient for the basic and the best climate-dependent MSDR models fitted by linear quantile regression (97.5th quantile) for broadleaved species

Species	Model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2	Q index
Fagus sylvatica	**basic**	**13.170 *****	**-**	**-1.9471 *****	**-**	**1577.1**	**0.5137**	**-**
	MXT3	12.870 ***	-	2.0880 ***	-0.0137 ***	1507.5	0.5290	0.085
	T3	12.813 ***	-	2.0872 *	-0.0138 ***	1510.2	0.5285	0.085
	MXT2	75.624 ***	-11.138 ***	-1.8360 ***	-	1512.2	0.5281	0.070
	PET1	12.911 ***	-	-1.5935 ***	-0.0085 ***	1514.5	0.5276	0.061
	M1	12.133 ***	0.671 ***	-2.0013 ***	-	1514.9	0.5275	0.135
Quercus faginea	**basic**	**12.097 *****	**-**	**-1.7055 *****	**-**	**2003.5**	**0.1811**	**-**
	MXTWM	247.037 ***	-41.233 ***	-1.7874 ***	-	1883.7	0.2508	0.315
	TAR	12.606 ***	-	12.9044 ***	-0.0495 ***	1886.9	0.2490	0.350
	MXT4	254.074 ***	-42.519 ***	-1.7485 ***	-	1899.6	0.2420	0.315
	T4	271.627 ***	-45.750 ***	-1.6856 ***	-	1910.6	0.2359	0.303
	M	9.667 ***	0.812 ***	-1.8657 ***	-	1915.9	0.2329	0.188
Quercus ilex	**basic**	**12.508 *****	**-**	**-2.0951 *****	**-**	**8099.8**	**0.5025**	**-**
	PET3	11.777 ***	-	-1.3094 ***	-0.0044 ***	7398.6	0.5487	0.211
	PET	11.773 ***	-	-1.4050 ***	-0.0004 ***	7449.7	0.5455	0.207
	MXT3	11.899 ***	-	5.0064 ***	-0.0234 ***	7474.1	0.5440	0.215
	MXTWM	11.969 ***	-	4.7651 ***	-0.0223 ***	7484.2	0.5433	0.172
	PET2	11.865 ***	-	-1.5025 ***	-0.0087 ***	7491.1	0.5429	0.159
Quercus petraea	**basic**	**12.277 *****	**-**	**-1.6777 *****	**-**	**431.3**	**0.3877**	**-**
	MXT	-489.861 ***	88.759 ***	36.5003 ***	-0.1334 ***	357.6	0.4954	0.242
	MXT4	12.593 ***	-	9.0312 ***	-0.0370 ***	358.5	0.4917	0.247
	MXT3	12.615 ***	-	7.5139 ***	-0.0323 ***	360,0	0.4899	0.230
	MXTWM	12.382 ***	-	8.8624 ***	-0.0360 ***	360.8	0.4889	0.227
	T4	12.674 ***	-	11.0925 ***	-0.0446 ***	361.6	0.4878	0.240
Quercus pyrenaica	**basic**	**12.271 *****	**-**	**-1.7203 *****	**-**	**4718.4**	**0.2962**	**-**
	T4	-187.581 *	35.255 *	17.946 ***	-0.0679 ***	4537.2	0.3300	0.213
	MNT4	12.312 ***	-	7.1163 ***	-0.0309 ***	4566.5	0.3244	0.186
	MXTWM	12.335 ***	-	5.6320 ***	-0.0250 ***	4570,0	0.3238	0.191
	MXT3	-310.973 *	57.023 *	24.1039 **	-0.0892 ***	4577.6	0.3228	0.204
	MXT4	12.328 ***	-	5.5596 ***	-0.0248 ***	4578.1	0.3223	0.182
Quercus robur	**basic**	**12.043 *****	**-**	**-1.6698 *****	**-**	**1017.7**	**0.4394**	**-**
	MNT3	-795.789 ***	143.317 ***	49.1578 ***	-0.1812 ***	974.7	0.4624	0.120
	MNT	-820.659 ***	147.740 ***	51.1787 ***	-0.1885 ***	981.1	0.4594	0.125
	MNT2	-605.574 ***	109.939 ***	37.8316 ***	-0.1435 ***	985.5	0.4572	0.123
	MNT4	-1112.201 ***	198.611 ***	70.2864 ***	-0.2505 ***	989.2	0.4554	0.131
	MNT1	-624.820 **	113.08 **	39.0364 **	-0.1458 **	993.6	0.4533	0.115
Quercus suber	**basic**	**12.704 *****	**-**	**-1.9674 *****	**-**	**1340.2**	**0.4839**	**-**
	PET3	11.948 ***	-	-1.2349 ***	-0.0043 ***	1233.6	0.5231	0.176
	MXTWM	12.097 ***	-	9.7879 ***	-0.0385 ***	1235.9	0.5223	0.208
	PET4	11.846 ***	-	-1.3656 ***	-0.0025 ***	1239.2	0.5211	0.150
	MXT4	-670.091 **	119.608 **	43.6583 ***	-0.1515 ***	1239.5	0.5217	0.147
	MXT3	12.343 ***	-	9.4775 **	-0.0384 ***	1243.8	0.5195	0.185

***p<0.001; **p<0.01; *p<0.05; - non-significant

Maximum temperatures were found to be key drivers for *Quercus petraea and Quercus pyrenaica*, while *Quercus robur* was affected by minimum temperatures. The best models for *Quercus ilex* and *Quercus suber* indicated that potential evapotranspiration played an important role in explaining changes in MSDR and SDI_{max} for these species. Aridity also influenced the MSDR of *Fagus sylvatica* and *Quercus faginea* according to the best models for these species. However, the other selected models for *Quercus faginea* were related to changes in summer temperatures. For all species, selected climate-dependent MSDR significantly improved the goodness of fit, in terms of AIC and pseudo-R^2, compared to the basic models. Among the coniferous species, *Pinus pinea* and *Pinus radiata* selected models showed the highest pseudo-R^2 with values close to 0.40 (Table 5). *Pinus canariensis* models showed the highest AIC reduction (Δ AIC ranging -7 and -11.3%) with respect to the basic MSDR model. For *Pinus nigra, Pinus sylvestris and Pinus radiata*, however, inclusion of a climatic variable in the basic MSDR model did little to improve its efficiency (Δ AIC close to -2%). Compared to conifers, broadleaf results generally presented higher pseudo-R^2 values and greater differences in AIC with respect to the basic MSDR models (Table 6). Climate-dependent models for *Fagus sylvatica*, *Quercus ilex* and *Quercus suber* presented the highest pseudo-R^2 values among the 15 species. A complete list of all fitted climate-dependent MSDR models is available in Supplementary Table 4.

5.1.3. Climatic influence on the maximum stand carrying capacity

In this study, climate was found to have significant influence on MSDR, and therefore on the maximum stand carrying capacity (SDI_{max}). The best climate-dependent models for each species revealed a common trend in SDI_{max} variation for coniferous and broadleaf species (Figure 8). The results indicated that higher SDI_{max} values were negatively linked to temperature and positively linked to precipitation (Table 7). Accordingly, higher maximum temperatures led to smaller SDI_{max} values for *Pinus nigra*, *Pinus pinaster*, *Fagus sylvatica*, *Quercus faginea* and *Quercus petraea*, while increments in precipitation led to higher SDI_{max} values for *Pinus canariensis* and *Quercus pinea*. A particular trend of SDI_{max} variation was found for *Pinus pinea* and *Pinus radiata*, with a $SDI_{max}(Clim)$ distribution presenting a parabolic shape with a minimum reached close to the median of the P4 (*Pinus pinea*) and PET3 (*Pinus radiata*) range.

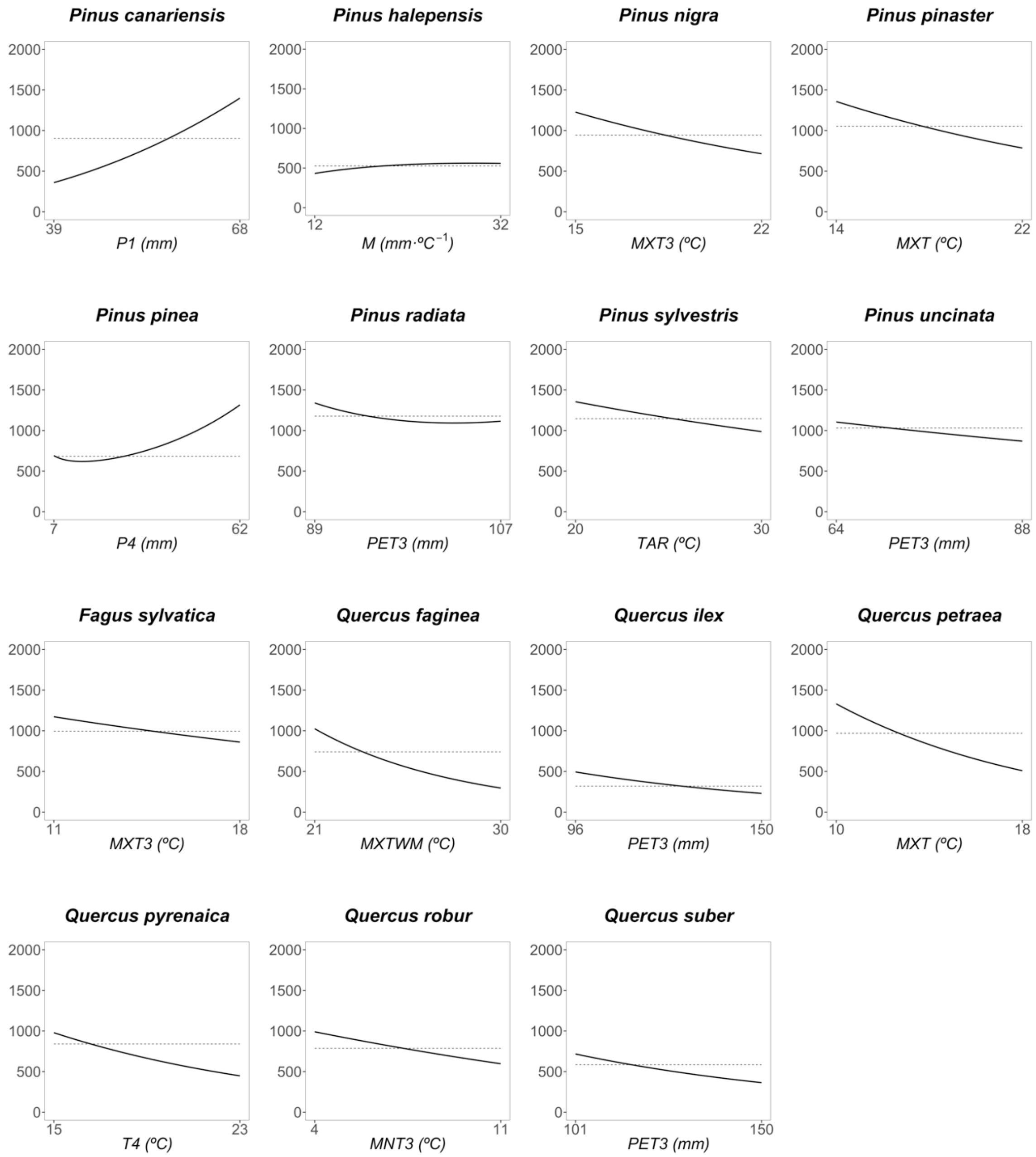


Figure 8. Climatic influence on the maximum stand carrying capacity (expressed as SDI_{max}) for coniferous and broadleaved species. Solid line corresponds to $SDI_{max\,(Clim)}$ prediction estimates using the best climate-dependent MSDR model by species. Dashed horizontal line represents the reference value of SDI_{maxREF}

Note: Temperature has been transformed to degrees Celsius (ºC).

Q indexes obtained for conifers (Tables 5, 6, 7) showed that the highest variations in SDI_{max} across different climatic conditions were obtained for *Pinus canariensis* (0.305), followed by *Pinus pinea* (0.262). On the contrary, the lower values of Q index were found for *Pinus halepensis* (0.063) and *Pinus radiata* (0.058). Among broadleaf species, the lowest Q index was found for *Fagus sylvatica* (0.085) and the highest for *Quercus faginea* (0.315). The rest of the *Quercus* species presented similar values ranging from 0.11 to 0.24.

Table 7. SDI_{max} estimates for the different percentiles of the selected climate variable (best climate-dependent model) and Q index for the species studied

Functional Group	Species	Clim	SDI_{maxREF}	$SDI_{max\ (Clim)}$					Q index
				P_1	P_{25}	P_{50}	P_{75}	P_{99}	
Conifers	*Pinus canariensis*	P1	903	351	536	768	1051	1388	0.305
	Pinus halepensis	M	526	422	500	543	559	558	0.063
	Pinus nigra	MXT3	944	1204	1064	941	832	737	0.123
	Pinus pinaster	MXT	1053	1353	1190	1046	920	809	0.129
	Pinus pinea	P4	683	700	632	756	982	1325	0.262
	Pinus radiata	PET3	1178	1355	1197	1116	1093	1120	0.058
	Pinus sylvestris	TAR	1146	1342	1241	1148	1063	984	0.078
	Pinus uncinata	PET3	1031	1109	1043	981	923	869	0.068
Broadleaves	*Fagus sylvatica*	MXT3	995	1188	1093	1005	924	850	0.085
	Quercus faginea	MXTWM	740	999	725	527	384	281	0.315
	Quercus ilex	PET3	319	496	409	337	278	229	0.211
	Quercus petraea	MXT	969	1268	1001	787	616	480	0.242
	Quercus pyrenaica	T4	840	1021	838	686	561	458	0.213
	Quercus robur	MNT3	787	993	888	790	699	616	0.120
	Quercus suber	PET3	585	721	608	512	432	364	0.176

Pi: Percentile, for i = (1,25,50,75,99)

5.2. Tree growth response to aridity and competition in mixed forests

5.2.1. Basal area increment models for mixed stands in Spain

Results for the fitted BAI models indicated that basal area growth increased with the initial tree diameter and total tree height, being the effect of the latter more frequently present for broadleaved than coniferous species (Table 8). On the other hand, quadratic mean diameter, as a surrogate of stage development, showed a negative effect on BAI. This effect was most visible for species composing conifer-

conifer admixtures, while being too low for broadleaved-broadleaved ones. The inclusion of competition in the model structure considerably improved the BAI models for both species. Models including size-symmetric for predicting the basal area increment in mixed and pure stands were more repeated in the best ranked ones than models including only size-asymmetric competition terms across all admixtures. Particularly, intra-specific basal area (BA_{intra}) appears to be the most influential competition variable than BA to explaining BAI in mixed stands. The inclusion of the De Martonne Index in the models was mainly significant in widely distributed species composition, due to differences in environmental conditions. For most species, a negative relationship between BAI and aridity was found. The inclusion of random effects greatly improved the goodness-of-fit indicators, decreasing AIC and producing significant differences in the likelihood ratio test compared to only fixed-effects models (Table 9). Differences between marginal and conditional R^2 quantified the improvement resulting from including the plot random effect in the model structures. The greatest improvements found being that for conifer-conifer admixtures while the least improvements were found for broadleaved-broadleaved admixtures, with mean values of 0.23 and 0.11, respectively. In general, higher marginal R^2 values were found for *Pinus nigra*, *Pinus pinaster* and *Fagus sylvatica* models, while *Quercus ilex* models obtained the lowest R^2 values among the studied species.

5.2.2. BAI response to different competition modes in mixed forests

We found an overall pattern of basal area increment increased with species mixing, which can be observed across the diverse species compositions stands across Spain., i.e, in mixed stands tree growth seemed to be higher than the pure one. Such observation could result from either facilitation interactions or complementarity of niches between different species in a mixed strand. Figure 9 depicts the effects of species composition of size-symmetric competition (BA) on BAI. We compared different scenarios when trees were influenced by intraspecific competition only, pure stands (BA_{intra} proportion = 1), and when size-symmetric competition was the combination of intraspecific and interspecific competition, mixed stands (BA_{intra} proportion < 1). We observed that species mixing had a positive effect on BAI in Pinus species mixed with broadleaved species and other conifers, except for *Pinus nigra-Pinus halepensis*, *Pinus pinaster-Pinus nigra*, *Pinus pinaster-Pinus halepensis,* and *Pinus uncinata-Pinus sylvestris mixtures* (Fig 9, a~f).

Table 8. Estimated model coefficients (standard error) for the selected BAI models for the different species and species composition studied

Species composition	Species	Intercept	d	log (d)	h	Dq	BA	BA$_{intra}$	BA$_{inter}$	BAL	BAL$_{intra}$	BAL$_{inter}$	M
Pinus halepensis – Pinus nigra	*Pinus halepensis*	2.7944 (0.2262)	0.0522 (0.0032)	-	0.0725 (0.0108)	-0.029 (0.0076)	-	-0.0344 (0.0053)	-	-	-	-	0.0131 (0.0063)
	Pinus nigra	-2.1909 (0.3825)	-0.0399 (0.0068)	2.0757 (0.1388)	0.0334 (0.0093)	-0.0291 (0.0077)	-	-0.0208 (0.0053)	-0.0325 (0.0088)	-	-	-	0.0347 (0.0076)
Pinus halepensis – Pinus pinaster	*Pinus halepensis*	-1.0381 (0.366)	-0.0373 (0.0072)	1.9721 (0.148)	0.0262 (0.0093)	-0.0205 (0.0056)	-	-0.0343 (0.0051)	-	-	-	-	0.0238 (0.0089)
	Pinus pinaster	-1.6673 (0.544)	-0.0363 (0.0084)	1.9709 (0.2014)	-	-0.0252 (0.0073)	-	-0.0181 (0.0065)	-0.0283 (0.0111)	-0.0063 (0.0032)	-	-	0.0581 (0.015)
Pinus halepensis – Pinus pinea	*Pinus halepensis*	-1.4508 (0.4396)	-0.047 (0.0101)	2.4045 (0.207)	0.0573 (0.0124)	-0.0449 (0.0079)	-	-0.0348 (0.0054)	-	-	-	-	-
	Pinus pinea	0.8052 (0.2996)	-	1.2766 (0.0902)	-	-0.0335 (0.0124)	-	-0.0154 (0.0069)	-	-	-	-0.0266 (0.0114)	-
Pinus nigra – Pinus pinaster	*Pinus nigra*	-2.3026 (0.2779)	-0.0365 (0.0039)	2.3215 (0.0945)	-	-0.0466 (0.0051)	-	-0.0234 (0.0039)	-0.0127 (0.0045)	-	-	-	0.0448 (0.0057)
	Pinus pinaster	-1.1313 (0.3304)	-0.0323 (0.0053)	2.0101 (0.1274)	-	-0.0308 (0.0051)	-	-0.016 (0.003)	-0.0257 (0.0048)	-	-0.0051 (0.0016)	-	0.0314 (0.0054)
Pinus nigra – Pinus sylvestris	*Pinus nigra*	-1.7176 (0.1807)	-0.0495 (0.0029)	2.3873 (0.0641)	0.0187 (0.0041)	-0.0464 (0.0032)	-	-0.0255 (0.0023)	-0.0095 (0.0035)	-	-	-0.0087 (0.0028)	0.0158 (0.0031)
	Pinus sylvestris	-1.3287 (0.1753)	-0.044 (0.0033)	2.2713 (0.0683)	-	-0.0382 (0.0035)	-	-0.0181 (0.0021)	-0.0218 (0.0037)	-	-0.0018 (0.001)	-0.008 (0.0034)	0.0081 (0.0024)
Pinus pinaster – Pinus sylvestris	*Pinus pinaster*	-0.6012 (0.2454)	-0.0249 (0.0041)	2.1674 (0.104)	-	-0.0419 (0.004)	-0.0149 (0.002)	-	-	-	-0.0033 (9e-04)	-	-
	Pinus sylvestris	-1.4576 (0.2163)	-0.0393 (0.0033)	2.3275 (0.0887)	0.0225 (0.0047)	-0.0441 (0.0033)	-	-0.0205 (0.002)	-0.013 (0.0028)	-	-0.0016 (8e-04)	-	0.01 (0.0023)
Pinus pinea – Pinus pinaster	*Pinus pinaster*	-1.2902 (0.3162)	-0.044 (0.0055)	2.3163 (0.1357)	-	-0.0148 (0.0047)	-0.0154 (0.0037)	-	-	-	-	-	-
	Pinus pinea	1.8982 (0.2735)	-	1.1735 (0.0432)	-	-0.0185 (0.0052)	-	-0.0329 (0.0047)	-	-	-	-	-0.0261 (0.0093)
Pinus sylvestris – Pinus uncinata	*Pinus sylvestris*	-0.4978 (0.279)	-0.0257 (0.0034)	1.6305 (0.0965)	0.0151 (0.0051)	-0.019 (0.0048)	-	-0.0175 (0.0023)	-0.0134 (0.0038)	-	-	-	0.0106 (0.0028)
	Pinus uncinata	-0.7357 (0.3403)	-0.0236 (0.0052)	1.627 (0.1222)	-	-0.0178 (0.0054)	-	-0.0183 (0.0024)	-0.023 (0.0041)	-	-	-	0.0088 (0.003)
Fagus sylvatica – Quercus petraea	*Fagus sylvatica*	-2.2101 (0.3218)	-0.0266 (0.0054)	2.0872 (0.1468)	0.0434 (0.0071)	-	-	-0.0339 (0.0041)	-0.0117 (0.0053)	-	-	-	-
	Quercus petraea	-1.439 (0.372)	-0.0205 (0.0046)	1.7953 (0.1621)	0.0428 (0.0116)	-	-0.0191 (0.0053)	-	-	-	-	-	-
Fagus sylvatica – Quercus pyrenaica	*Fagus sylvatica*	-1.3884 (0.3222)	-0.0199 (0.0046)	1.9848 (0.138)	0.0309 (0.0064)	-0.0194 (0.005)	-	-0.0282 (0.0038)	-	-	-0.0045 (0.0023)	-	-
	Quercus pyrenaica	-2.8565 (0.3207)	-0.0519 (0.0051)	2.3692 (0.1269)	0.06 (0.0084)	-0.0218 (0.0056)	-	-0.0243 (0.0047)	-0.0404 (0.0073)	-	-	-	0.0158 (0.0057)
Fagus sylvatica – Quercus robur	*Fagus sylvatica*	-3.3249 (0.4815)	-0.0386 (0.0057)	2.8025 (0.2007)	0.0148 (0.0081)	-	-	-0.0423 (0.0067)	-	-0.0057 (0.0029)	-	-	-
	Quercus robur	-3.0948 (1.1315)	-0.0385 (0.0121)	2.8737 (0.4474)	-	-	-0.0482 (0.0101)	-	-	-	-	-	-
Quercus faginea – Quercus ilex	*Quercus faginea*	-2.2426 (0.3102)	-0.0361 (0.006)	1.8621 (0.1469)	0.0827 (0.0118)	-	-	-0.0292 (0.0054)	-	-	-	-	0.0129 (0.0047)
	Quercus ilex	-1.8672 (0.3091)	-0.0319 (0.0066)	1.7637 (0.1433)	0.0652 (0.0186)	-	-0.0161 (0.005)	-	-	-	-	-	0.0114 (0.0052)
Quercus ilex – Quercus pyrenaica	*Quercus ilex*	-0.2648 (0.3873)	-	1.3493 (0.1279)	-	-	-0.0275 (0.0084)	-	-	-	-	-	-
	Quercus pyrenaica	-1.3431 (0.6327)	-0.0425 (0.0148)	1.7239 (0.324)	0.1162 (0.0182)	-	-	-0.0433 (0.0088)	-	-	-	-0.0414 (0.0141)	-
Quercus ilex – Quercus suber	*Quercus ilex*	-0.8205 (0.3071)	-0.0294 (0.0064)	1.3885 (0.1514)	0.1355 (0.0136)	-	-	-0.0364 (0.0048)	-	-	-	-	-
	Quercus suber	0.1117 (0.3273)	-0.0093 (0.0054)	0.9492 (0.1434)	0.0924 (0.0124)	0.0185 (0.0047)	-	-0.0296 (0.0042)	-0.0141 (0.0072)	-	-	-	-
Quercus pyrenaica – Quercus robur	*Quercus pyrenaica*	0.1827 (0.8946)	-0.0209 (0.0186)	1.4183 (0.4333)	-	-	-0.0284 (0.0085)	-	-	-	-	-	-
	Quercus robur	-1.3817 (0.7193)	-0.0311 (0.0119)	2.1817 (0.3285)	-	-	-	-0.0433 (0.0092)	-0.0319 (0.0111)	-	-	-	-

Table 8 *Cont.*. Estimated model coefficients (standard error) for the selected BAI models for the different species and species composition studied

Species composition	Species	Intercept	d	log (d)	h	Dq	BA	BA_{intra}	BA_{inter}	BAL	BAL_{intra}	BAL_{inter}	M
Pinus halepensis – Quercus faginea	*Pinus halepensis*	-1.91 (0.7511)	-0.0545 (0.0152)	2.2627 (0.3074)	0.0505 (0.0199)	-0.036 (0.0176)	-	-0.0232 (0.0093)	-	-	-	-	0.0296 (0.0154)
	Quercus faginea	-3.3523 (1.128)	-0.0824 (0.0316)	2.9723 (0.5926)	-	-	-	-0.0523 (0.0247)	-	-	-	-0.043 (0.0231)	-
Pinus halepensis – Quercus ilex	*Pinus halepensis*	-1.7286 (0.2872)	-0.0513 (0.006)	2.3588 (0.1247)	0.0469 (0.0067)	-0.0382 (0.0061)	-	-0.0284 (0.0036)	-	-	-	-	0.0114 (0.0044)
	Quercus ilex	-1.1688 (0.2458)	-	1.0882 (0.0782)	0.1416 (0.0145)	-0.0232 (0.0097)	-	-0.0405 (0.0063)	-0.0133 (0.0071)	-	-	-	0.0289 (0.0055)
Pinus nigra – Quercus faginea	*Pinus nigra*	-2.5009 (0.4671)	-0.0607 (0.0058)	2.4259 (0.1256)	0.0389 (0.0085)	-0.0421 (0.0075)	-	-0.0305 (0.0052)	-	-	-	-	0.0325 (0.0121)
	Quercus faginea	-1.7441 (0.4554)	-0.0312 (0.0125)	1.7971 (0.2452)	0.098 (0.0206)	-	-0.0269 (0.0067)	-	-	-	-	-	-
Pinus nigra – Quercus ilex	*Pinus nigra*	-2.1206 (0.2149)	-0.0559 (0.004)	2.518 (0.0921)	0.0217 (0.0058)	-0.0268 (0.0055)	-0.022 (0.0034)	-	-	-	-0.0052 (0.0014)	-	-
	Quercus ilex	-1.2536 (0.3297)	-0.0288 (0.0104)	1.5467 (0.1818)	0.0988 (0.0181)	-	-	-0.0411 (0.0065)	-	-	-	-	-
Pinus pinaster – Quercus ilex	*Pinus pinaster*	-0.7777 (0.4396)	-0.0245 (0.0081)	1.7932 (0.1996)	-	-	-	-	-	-	-0.0055 (0.0023)	-	-
	Quercus ilex	-1.6101 (0.4255)	-0.0381 (0.0114)	1.5558 (0.2249)	0.1836 (0.0254)	-	-	-0.0227 (0.0105)	-	-	-	-	-
Pinus pinaster – Quercus pyrenaica	*Pinus pinaster*	-0.597 (0.2555)	-0.0404 (0.0046)	2.1635 (0.1145)	-	-	-	-0.0255 (0.0036)	-	-	-	-	-
	Quercus pyrenaica	-2.7258 (0.5561)	-0.0527 (0.0133)	2.7721 (0.2832)	-	-0.0139 (0.0102)	-	-0.035 (0.0096)	-0.0204 (0.0077)	-	-	-	-0.0059 (0.0047)
Pinus pinaster – Quercus suber	*Pinus pinaster*	-0.9839 (0.4757)	-0.0287 (0.0098)	2.1165 (0.2067)	-	-0.0184 (0.0093)	-	-0.0285 (0.0057)	-	-	-	-	0.0136 (0.0052)
	Quercus suber	0.2845 (0.3104)	-	0.9688 (0.1229)	0.0612 (0.0234)	-	-	-0.0234 (0.0078)	-	-	-	-0.026 (0.0104)	-
Pinus pinea – Quercus ilex	*Pinus pinea*	0.4764 (0.2389)	-	1.5955 (0.0827)	-0.0449 (0.0148)	-0.0236 (0.0077)	-0.032 (0.006)	-	-	-	-	-	-
	Quercus ilex	-1.053 (0.4358)	-0.0315 (0.0114)	1.4928 (0.2246)	0.1113 (0.0197)	-	-0.023 (0.0085)	-	-	-	-	-	-
Pinus pinea – Quercus suber	*Pinus pinea*	0.6606 (0.2569)	-	1.3249 (0.0737)	-	-	-	-0.0427 (0.0067)	-0.0187 (0.0099)	-	-	-	-
	Quercus suber	0.9728 (0.3972)	-	0.811 (0.0936)	0.1237 (0.02)	-	-0.0282 (0.0061)	-	-	-	-	-	-0.0244 (0.0119)
Pinus sylvestris – Fagus sylvatica	*Fagus sylvatica*	-3.0448 (0.356)	-0.0378 (0.0047)	2.3552 (0.1264)	0.0421 (0.0062)	-0.0159 (0.0054)	-	-0.0361 (0.0042)	-0.0214 (0.0048)	-	-	-	0.0178 (0.0044)
	Pinus sylvestris	-1.9057 (0.2338)	-0.0366 (0.003)	2.2551 (0.0805)	0.0173 (0.0042)	-0.0224 (0.0034)	-	-0.0162 (0.002)	-0.0305 (0.005)	-	-	-	0.0083 (0.0028)
Pinus sylvestris – Quercus faginea	*Pinus sylvestris*	-1.4388 (0.3248)	-0.0384 (0.0056)	1.9542 (0.1269)	0.015 (0.0077)	-0.0237 (0.0066)	-	-0.0207 (0.0035)	-	-	-	-	0.019 (0.005)
	Quercus faginea	-2.2906 (0.4362)	-0.045 (0.0086)	1.9224 (0.1931)	0.078 (0.0141)	-	-0.0232 (0.0049)	-	-	-	-	-	0.0149 (0.0075)
Pinus sylvestris – Quercus ilex	*Pinus sylvestris*	-0.7816 (0.2614)	-0.0299 (0.0055)	1.7776 (0.1234)	0.0202 (0.0069)	-	-0.0199 (0.0034)	-	-	-	-	-	-
	Quercus ilex	-0.8542 (0.3397)	-0.0239 (0.0112)	1.3615 (0.1923)	0.1229 (0.0159)	-	-	-0.0315 (0.0058)	-	-	-	-0.0206 (0.0063)	-
Pinus sylvestris – Quercus petraea	*Pinus sylvestris*	-0.0273 (0.2082)	-	1.2849 (0.0754)	0.0264 (0.0094)	-	-	-0.0158 (0.0042)	-	-	-	-	-
	Quercus petraea	-1.5479 (0.7548)	-0.0401 (0.019)	1.8118 (0.4116)	0.0827 (0.0263)	-	-	-0.0522 (0.015)	-	-	-	-	-
Pinus sylvestris – Quercus pyrenaica	*Pinus sylvestris*	-1.1121 (0.1985)	-0.0374 (0.0028)	2.2161 (0.0776)	0.0191 (0.0044)	-0.0447 (0.0032)	-	-0.0206 (0.002)	-	-	-0.0024 (7e-04)	-	0.0133 (0.0027)
	Quercus pyrenaica	-2.2915 (0.2656)	-0.0568 (0.006)	2.2302 (0.1369)	0.0671 (0.0094)	-	-	-0.0258 (0.0045)	-0.0174 (0.0056)	-	-	-0.0132 (0.0057)	-

Note: d - Diameter at breast height (cm), h - total tree height (m), dq - quadratic mean diameter (cm), BA - stand basal area ($m^2 \cdot ha^{-1}$), BAL - basal area of larger trees ($m^2 \cdot ha^{-1}$), subscripts inter and intra designate interspecific and intraspecific BA or BAL, M - The De Martonne Aridity Index ($mm \cdot °C^{-1}$)

Table 9. Model evaluation for the selected BAI models for the different species and species composition studied

		Variance parameters		*Fit statistics*				
Species composition	**Species**	**Plot**	**Error**	**RMSE**	**bias**	**EF**	**Marginal R²**	**Conditional R²**
Pinus halepensis – Pinus nigra	*Pinus halepensis*	0,1153	0,3496	0,5660	-4,16968E-15	0,5365	0,5116	0,3506
	Pinus nigra	0,2116	0,2856	0,5089	5,63236E-16	0,6479	0,6315	0,3584
Pinus halepensis – Pinus pinaster	*Pinus halepensis*	0,1250	0,3445	0,5624	5,98145E-15	0,5515	0,5255	0,3534
	Pinus pinaster	0,2991	0,4924	0,6684	-1,58243E-15	0,5194	0,5147	0,2200
Pinus halepensis – Pinus pinea	*Pinus halepensis*	0,1308	0,3900	0,6000	-8,81579E-15	0,5641	0,5455	0,3930
	Pinus pinea	0,1903	0,2800	0,4994	-3,20492E-15	0,5556	0,5610	0,2628
Pinus nigra – Pinus pinaster	*Pinus nigra*	0,2533	0,3240	0,5476	-2,15073E-16	0,6378	0,6349	0,3493
	Pinus pinaster	0,2099	0,4014	0,6116	1,09424E-14	0,5477	0,5238	0,2749
Pinus nigra – Pinus sylvestris	*Pinus nigra*	0,2386	0,3236	0,5474	-8,7654E-15	0,6211	0,6150	0,3310
	Pinus sylvestris	0,2551	0,3650	0,5841	-1,2119E-14	0,5772	0,5642	0,2596
Pinus pinaster – Pinus sylvestris	*Pinus pinaster*	0,2060	0,3829	0,6026	1,45744E-14	0,5394	0,5378	0,2891
	Pinus sylvestris	0,1665	0,3825	0,6040	1,91436E-14	0,4928	0,5059	0,2909
Pinus pinea –Pinus pinaster	*Pinus pinaster*	0,2120	0,2917	0,5200	4,31763E-15	0,5847	0,5738	0,2639
	Pinus pinea	0,1742	0,2740	0,4986	3,2391E-15	0,6384	0,6238	0,3845
Pinus sylvestris – Pinus uncinata	*Pinus sylvestris*	0,1468	0,4498	0,6544	4,32571E-15	0,4527	0,4349	0,2505
	Pinus uncinata	0,1094	0,5566	0,7299	1,36498E-15	0,3681	0,3610	0,2354
Fagus sylvatica – Quercus petraea	*Fagus sylvatica*	0,1661	0,6285	0,7745	-2,19159E-15	0,6024	0,6042	0,4997
	Quercus petraea	0,1653	0,4558	0,6505	3,75485E-15	0,5896	0,5904	0,4418
Fagus sylvatica - Quercus pyrenaica	*Fagus sylvatica*	0,1416	0,5286	0,7090	-5,24436E-15	0,6148	0,6081	0,5031
	Quercus pyrenaica	0,1380	0,4759	0,6705	1,00452E-14	0,5300	0,5512	0,4211
Fagus sylvatica - Quercus robur	*Fagus sylvatica*	0,1864	0,5979	0,7525	1,28217E-14	0,6499	0,6650	0,5606
	Quercus robur	0,1932	0,4947	0,6660	1,86258E-15	0,5877	0,6063	0,4551
Quercus faginea - Quercus ilex	*Quercus faginea*	0,1142	0,3533	0,5663	8,12019E-16	0,6534	0,6427	0,5272
	Quercus ilex	0,1896	0,5018	0,6766	-4,98527E-15	0,5640	0,5302	0,3529
Quercus ilex - Quercus pyrenaica	*Quercus ilex*	0,1264	0,4921	0,6712	1,75285E-16	0,5287	0,5034	0,3759
	Quercus pyrenaica	0,1488	0,3846	0,5951	-1,28878E-15	0,5666	0,5744	0,4098
Quercus ilex - Quercus suber	*Quercus ilex*	0,1036	0,5344	0,7037	2,48688E-15	0,5145	0,4653	0,3616
	Quercus suber	0,1585	0,6163	0,7576	6,61427E-15	0,4793	0,4704	0,3342
Quercus pyrenaica - Quercus robur	*Quercus pyrenaica*	0,0272	0,6141	0,7636	-1,73421E-16	0,2976	0,2726	0,2405
	Quercus robur	0,0588	0,6902	0,8098	2,05617E-15	0,4316	0,4404	0,3929
Pinus halepensis - Quercus faginea	*Pinus halepensis*	0,1836	0,4137	0,6188	7,85235E-15	0,5236	0,5046	0,2848
	Quercus faginea	0,1079	0,3127	0,5123	3,30058E-16	0,7026	0,6528	0,5333
Pinus halepensis - Quercus ilex	*Pinus halepensis*	0,1274	0,3682	0,5840	4,89413E-16	0,5678	0,5604	0,4084
	Quercus ilex	0,1406	0,5063	0,6794	-1,14436E-15	0,4894	0,4496	0,2966
Pinus nigra - Quercus faginea	*Pinus nigra*	0,2386	0,3392	0,5615	5,9539E-15	0,6110	0,6211	0,3546
	Quercus faginea	0,1451	0,3193	0,5285	5,83924E-15	0,6364	0,6125	0,4364
Pinus nigra - Quercus ilex	*Pinus nigra*	0,2897	0,4136	0,6210	1,00989E-14	0,6097	0,6185	0,3514
	Quercus ilex	0,1383	0,4838	0,6624	4,88825E-16	0,4901	0,4609	0,3069
Pinus pinaster - Quercus ilex	*Pinus pinaster*	0,2938	0,4490	0,6453	-1,55197E-15	0,4764	0,5489	0,2538
	Quercus ilex	0,2610	0,4032	0,5997	6,16285E-16	0,6043	0,5777	0,3045
Pinus pinaster - Quercus pyrenaica	*Pinus pinaster*	0,2010	0,2742	0,5082	7,24603E-15	0,5363	0,6443	0,3835
	Quercus pyrenaica	0,1285	0,3765	0,5850	9,40262E-15	0,6336	0,6099	0,4769
Pinus pinaster - Quercus suber	*Pinus pinaster*	0,2256	0,2852	0,5123	-2,77332E-15	0,6335	0,6457	0,3656
	Quercus suber	0,2026	0,6404	0,7651	1,84381E-15	0,4695	0,4375	0,2595
Pinus pinea - Quercus ilex	*Pinus pinea*	0,2286	0,2447	0,4674	6,58037E-15	0,7100	0,7181	0,4549
	Quercus ilex	0,1946	0,4970	0,6673	1,84364E-17	0,5373	0,4879	0,2875
Pinus pinea - Quercus suber	*Pinus pinea*	0,1297	0,2796	0,5025	-2,42195E-15	0,6228	0,6173	0,4398
	Quercus suber	0,1050	0,5857	0,7414	1,75853E-15	0,3877	0,3856	0,2756
Pinus sylvestris - Fagus sylvatica	*Fagus sylvatica*	0,1584	0,5014	0,6885	-4,19866E-15	0,6332	0,6161	0,4949
	Pinus sylvestris	0,1774	0,4350	0,6450	1,08383E-14	0,5047	0,5009	0,2975
Pinus sylvestris - Quercus faginea	*Pinus sylvestris*	0,1595	0,3882	0,6049	-3,50927E-15	0,5043	0,4879	0,2775
	Quercus faginea	0,1108	0,3958	0,6017	-1,9287E-15	0,5773	0,5665	0,4452
Pinus sylvestris - Quercus ilex	*Pinus sylvestris*	0,1812	0,4249	0,6318	1,75409E-17	0,4980	0,4852	0,2657
	Quercus ilex	0,1225	0,5222	0,6964	-3,27228E-15	0,4582	0,4312	0,2977
Pinus sylvestris - Quercus petraea	*Pinus sylvestris*	0,1749	0,3610	0,5849	2,34267E-15	0,5250	0,5449	0,3244
	Quercus petraea	0,0380	0,5377	0,7108	1,00385E-15	0,5051	0,4858	0,4494
Pinus sylvestris - Quercus pyrenaica	*Pinus sylvestris*	0,2010	0,4104	0,6268	-1,37497E-14	0,4899	0,5305	0,3006
	Quercus pyrenaica	0,1519	0,4245	0,6286	-3,28094E-15	0,5640	0,5703	0,4166

Regarding broadleaved species, only *Quercus pyrenaica* mixed with *Fagus sylvatica* showed a decrease in BAI as result of species interactions, opposite to the predominant trend than species mixing increased BAI in broadleaved-broadleaved and broadleaved-cofiner mixtures (Fig 9 g~m).

Potential biological interactions that can be take place in a mixed stand as result of size-symmetric competition has been represented in Figure 10. These biological interactions have been categorized into four main groups as described in the Material and Methods section. Figure 10 has been divided in three quadrants *(*Q_1 *[upper left]: conifer-conifer,* Q_2 *[upper right and down left]: conifer-broadleaved and* Q_3 *[down right]: broadleaved-broadleaved)*, representing the different types of mixtures analyzed in this study.

According to our results, competition and amensalism seem to be key processes controlling growth dynamics in coniferous-coniferous forests, while commensalism (or facilitation) and neutralism better reflects biological interactions in conifer-broadleaved and broadleaved-broadleaved forests. At species level, *Pinus halepensis*, *Pinus nigra* and *Fagus sylvatica* are the most competitive species, producing more frequent negative growth effects on competitors species in mixtures. A similar negative effect exerts *Pinus nigra* mixed with *Pinus pinaster* and *Pinus sylvestris*. Conversely, *Pinus pinaster* and *Pinus sylvestris* seemed to be good facilitators since they have a positive effect on both conifers and broadleaved mixed with. For most of the *Quercus* species studied, neutralism is the most repeated biological interaction when mixed with conifers or other broadleaved species. Among them, results indicate that *Quercus pyrenaica* and *Quercus suber* promote facilitation when mixed with other conifers and broadleaved species.

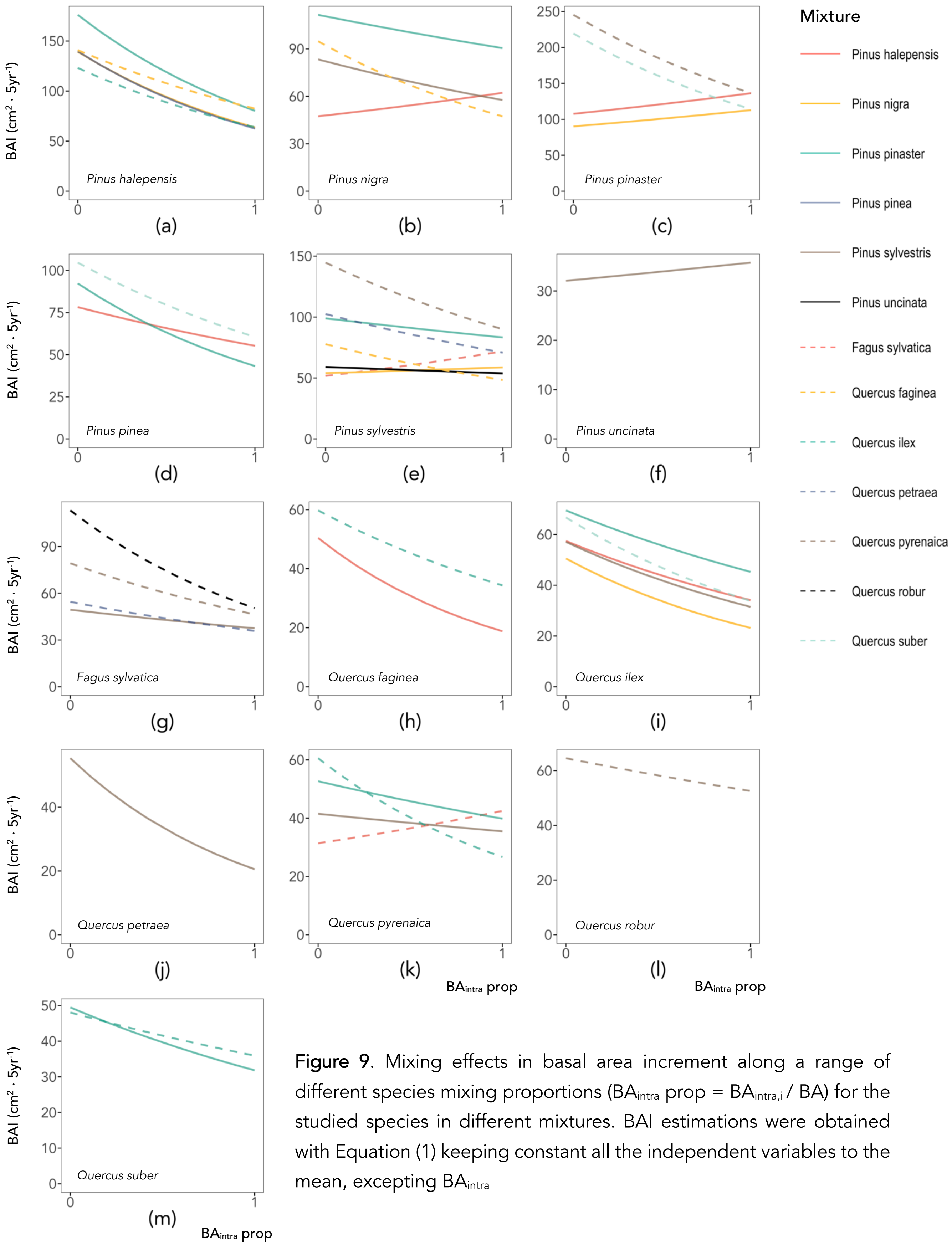
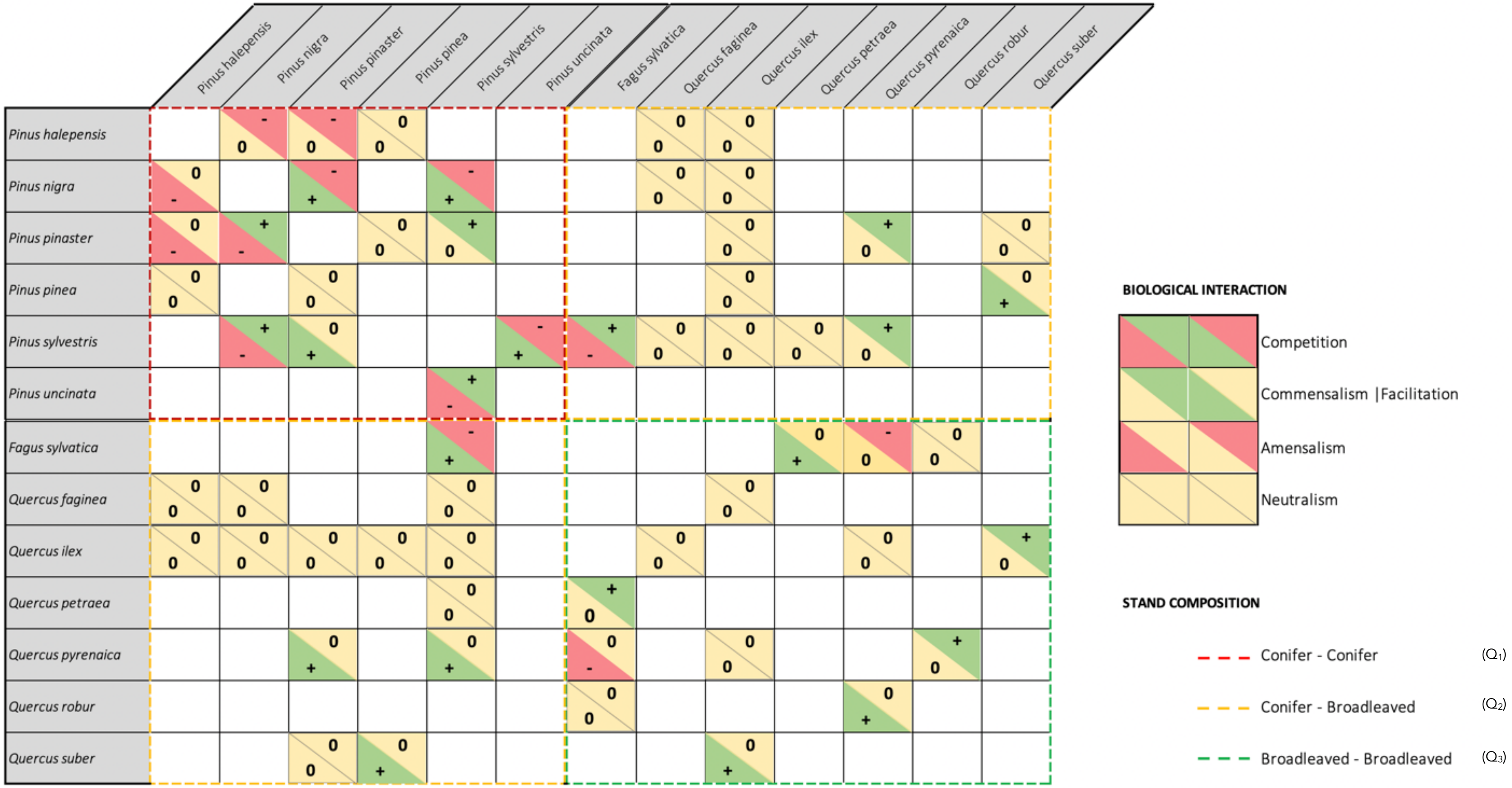


Figure 9. Mixing effects in basal area increment along a range of different species mixing proportions (BA$_{intra}$ prop = BA$_{intra,i}$ / BA) for the studied species in different mixtures. BAI estimations were obtained with Equation (1) keeping constant all the independent variables to the mean, excepting BA$_{intra}$



	Pinus halepensis	Pinus nigra	Pinus pinaster	Pinus pinea	Pinus sylvestris	Pinus uncinata	Fagus sylvatica	Quercus faginea	Quercus ilex	Quercus petraea	Quercus pyrenaica	Quercus robur	Quercus suber
Pinus halepensis		- 0	- 0	0 0				0 0	0 0				
Pinus nigra	0 -		- +		- +			0 0	0 0				
Pinus pinaster	0 -	+ -		0 0	+ 0				0 0		+ 0		0 0
Pinus pinea	0 0		0 0						0 0				0 +
Pinus sylvestris		+ -	0 +			- +	+ -	0 0	0 0	0 0	+ 0		
Pinus uncinata					+ -								
Fagus sylvatica					- +					0 +	- 0	0 0	
Quercus faginea	0 0	0 0			0 0				0 0				
Quercus ilex	0 0	0 0	0 0	0 0	0 0			0 0			0 0		+ 0
Quercus petraea					0 0		+ 0						
Quercus pyrenaica			0 +		0 +		0 -		0 0			+ 0	
Quercus robur							0 0				0 +		
Quercus suber			0 0	0 +					0 +				

Figure 10. Potential biological interactions between tree species in mixed forest stands emerged as effect of size-symmetric competition

5.2.3. Influence of aridity on tree growth in mixed forests

Regarding the aridity influence on tree growth, for the majority of the studied species, growth increased as the aridity decreased,i.e. higher values of BAI for higher values of the De Martonne Index were found (Figure 11). An exception for this pattern was found for *Pinus pinea* and *Quercus pyrenaica* coexisting with *Pinus pinaster*, as well as *Quercus suber* mixed with *Pinus pinea*. In these cases, the model coefficient for the De Martonne Index indicates that higher values of BAI are found in more arid places (Table 8). Figure 11 shows how BAI varies along the aridity gradient across species distribution within each species composition. We also noticed that the magnitude of the climatic effects differs among species and mixtures. Our results support the idea that aridity play a key role explaining changes in BAI for *Pinus nigra*, *Pinus pinaster* and *Pinus sylvestris* in different mixtures composition (Fig 11b, c, and e). Model predictions for these species indicated wide differences in BAI between the most arid and humid conditions along their geographical distribution. These species, being three of the most distributed species in Spain, presented the highest values of BAI (close to 100 $cm^2 \cdot 5yrs^{-1}$) among the studied species and mixtures. Conifers such as *Pinus halepensis*, *Pinus uncinata* (Fig 11a and f) and broadleaved species such as *Fagus sylvatica*, *Quercus faginea* and *Quercus pyrenaica* (Fig 11g, h and k) also showed higher values of BAI in more humid places. This pattern contrasted with that found for *Pinus pinea* when mixed with *Pinus pinaster*, where BAI drastically descend from arid to humid places. Similar effects also could be observed in stands composed by *Quercus pyrenaica* and *Pinus pinaster* and *Quercus suber* mixed with *Pinus pinea*, though the effect is less severe for *Pinus pinea*. *Quercus petraea* and *Quercus robur* presented a constant BAI along their distribution, indicating no climatic influence on productivity for these species.

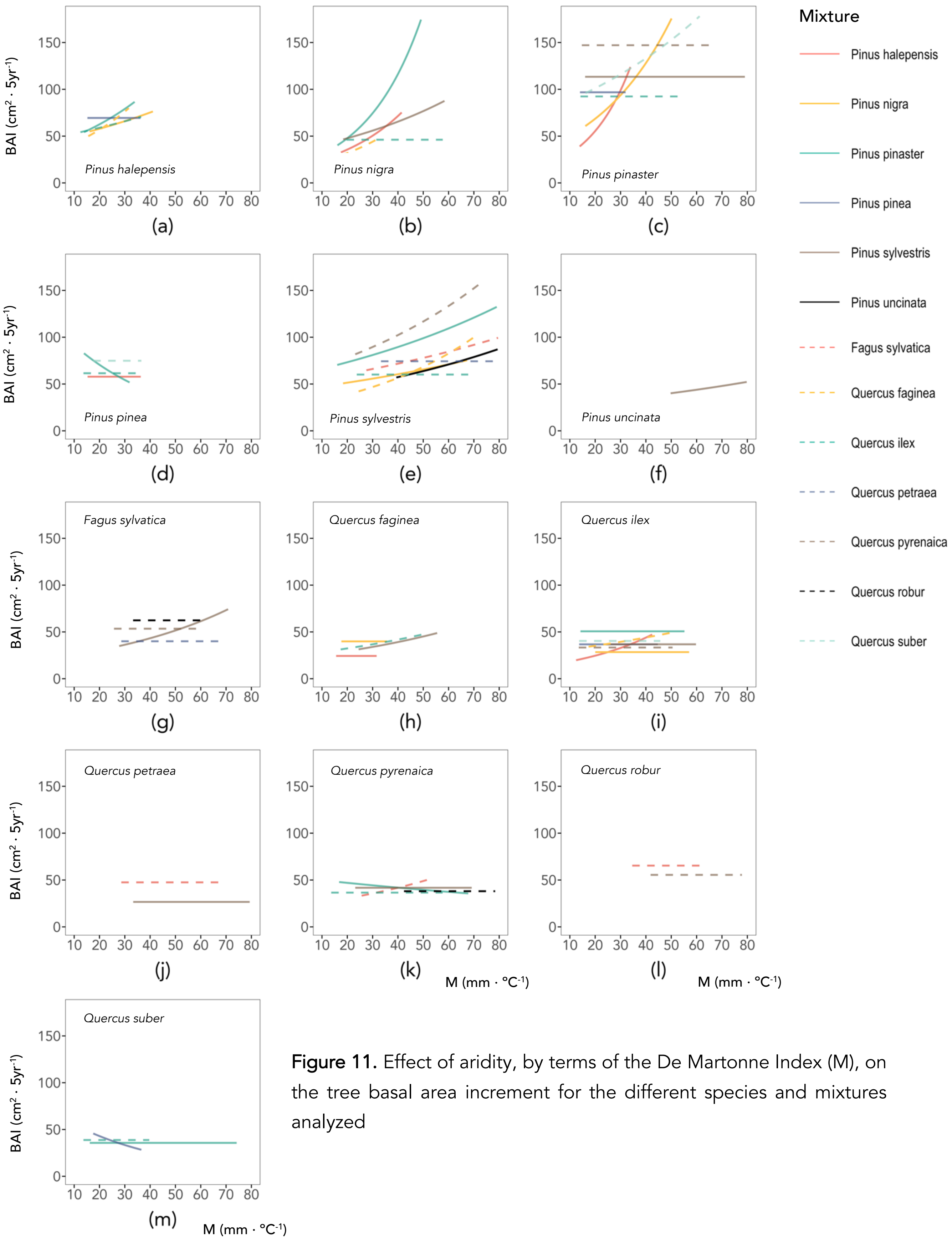


Figure 11. Effect of aridity, by terms of the De Martonne Index (M), on the tree basal area increment for the different species and mixtures analyzed

5.3. Tree allometry response to aridity and species mixing in mixed forests

5.3.1. New H-D models for mixed forests in Spain

Coefficients for the final best generalized mixed-effects H-D models for each species and mixture are presented in Table 10. Results indicated that M1 (Cañadas et al.; 1998) was the most frequently chosen base H-D model among conifers, while M12 (Schumacher; 1939) was the most chosen among broadleaves. An exception was found for *Pinus sylvestris* and *Pinus uncinata*, where M3 (Gaffrey; 1998) and M5 (Monness; 1982) shown better fits H-D relationships. All the parameters of the expanded H-D models obtained by bootstrap procedure were significant ($p\text{-value} < 0.05$), finding some differences between regarding the independent variables entering the models for coniferous and broadleaves. For the coniferous species, competition (BAL) and species proportion by area (m_i) had a significant effect explaining height in the models. For these species, the developmental stage at plot level (by means of Dq) was more times included into the models when mixed with conifers, but Dq_i (at species level) was included more often when mixed with broadleaves. Indeed, for all the Quercus species analyzed, Dq_i and Ho_i were were included into the H-D expanded models as independent variables. Note that, for almost all the species and species compositions of broadleaved species, the De Martonne Index (M) was significant with positive sign, meaning a height growth increment by humid conditions. For all pairs species-mixture, expanded H-D models significantly improved the goodness of fit, in terms of AIC and RMSE, compared to the base H-D models. Among the analyzed species, *Pinus pinea* and *Quercus ilex* selected models showed the smallest RMSE with values ranging 0.80-1.06 m. On the contrary, the highest RMSE values were found for *Pinus sylvestris*, *Pinus uncinata*, *Quercus petraea*, *Quercus pyrenaica* and *Quercus robur* with values close to 1.5 m.

5.3.2. Species mixing influence on H-D relationships

Figure 12 shows the height variation under different species mixing proportions in mixed forest stands for the studied species. A general trend was found for *Pinus* species (Figure 12, a~f), with taller trees in pure than in mixed stands ($M_{ratio} < 1$). However, an exception was found in for *Pinus sylvestris* in *Pinus sylvestris*-*Pinus pinaster* mixture (Figure 12e), with slightly higher trees in mixture than pure stands of this species. *Pinus uncinata* height was nearly insensitive to proportional area change and mixed and pure forest allometry (Figure 12f).

Table 10. Estimated model coefficients for the selected H-D models for the different species and species compositions

Species	Mixture	Model	Form	α_0 (Int)	α_1 (BAL)	α_2 (Dq)	α_2 (Dq$_i$)	α_3 (m$_i$)	α_4 (M)	α_5 (Ho)	α_5 (Ho$_i$)	β_0	β_1	RMSE	AIC
Pinus halepensis	*Pinus nigra*	M3	A	0,8740	-0,0097	-	-0,0092	0,1385	-	-	-	-	-5,6254	1,0762	5950,45
	Pinus pinaster	M1	A	1,2130	-0,0402	-	0,0431	-	-	-	-	-	-	1,2008	6675,29
	Pinus pinea	M1	A	-	-0,0125	-	0,0390	1,2598	-	-	-	-	-	1,0623	5022,50
	Quercus faginea	M1	A	-	-	-	0,0294	1,0935	-	-	-	-	-	1,0467	2319,73
	Quercus ilex	M1	A	1,3583	-0,0151		-0,0200	1,4876	-0,0307	-	-	-	-	1,1195	12939,80
Pinus nigra	*Pinus halepensis*	M5	A	0,9181	-0,0168	0,0797	-	-	-	-	-	-	-	1,1218	6870,48
	Pinus pinaster	M1	A	1,0318	-0,0112	0,0440	-	0,6216	-	-	-	-	-	1,2479	12652,84
	Pinus sylvestris	M1	A	1,4454	-0,0137	0,0474	-	-	-	-	-	-	-	1,2510	35767,45
	Quercus faginea	M1	A	0,7447	-	-	-0,0319	2,1911	-	-	-	-	-	1,2586	8690,03
	Quercus ilex	M1	A	-	-0,0068	-	-0,0209	2,8952	-	-	-	-	-	1,3745	19658,38
Pinus pinaster	*Pinus halepensis*	M1	A	-	-0,0173	0,0734	-	1,5235	-	-	-	-	-	1,2239	5962,40
	Pinus nigra	M1	A	1,8800	-0,0183	0,0499	-		-	-	-	-	-	1,0761	12580,34
	Pinus pinea	M1	M	-	-	-	0,2314	0,3722	-	-	-	-	-	1,0464	10159,86
	Pinus sylvestris	M1	A	2,7801	-0,0132	-0,0203	-	-	-	-	-	-	-	1,2119	21720,17
	Quercus ilex	M1	M	-	-	-	-	2,8266	0,3382	-	-	-	-	1,1813	5850,48
	Quercus pyrenaica	M1	A	-	-0,0104	-	0,0319	1,6618	-	-	-	-	-	1,0701	8513,35
	Quercus suber	M3	A	-0,6969	-	-	0,0137	0,1964	-	-	-	-	13,9493	1,0751	4130,34
Pinus pinea	*Pinus halepensis*	M5	M				0,0997							0,81	1898,24
	Pinus pinaster	M1	A	4,0383	-0,0221			1,5266	-0,1198					0,98	6111,83
	Quercus ilex	M3	A	1,3421			-0,0162		-0,0079				-8,4247	0,88	3512,50
	Quercus suber	M1	A	2,1130	-0,0258		-0,0460	1,2023						0,93	1979,70
Pinus sylvestris	*Fagus sylvatica*	M3	A	-0,1063					0,0037				7,1987	1,61	33678,46
	Pinus nigra	M5	A	0,8792	-0,0068	0,0465								1,19	42508,63
	Pinus pinaster	M3	A	0,1674				-0,0846					5,7848	1,34	29369,08
	Pinus uncinata	M5	A						0,0271					1,62	22112,05
	Quercus faginea	M5	M				0,1286	0,6005						1,25	11709,53
	Quercus ilex	M1	A	-1,1988	-0,0104		0,0241	1,6356	0,0178					1,33	14518,65
	Quercus petraea	M5	A									1,3877		1,53	5481,21
	Quercus pyrenaica	M3	A						0,0038				4,3652	1,40	33274,37
Pinus uncinata	*Pinus sylvestris*	M5	A						0,0244					1,52	16426,61

Table 10 *Cont.*. Estimated model coefficients for the selected H-D models for the different species and species composition

Species	Mixture	Model	Form	α_0 (Int)	α_1 (BAL)	α_2 (Dq)	α_2 (Dq_i)	α_3 (m_i)	α_4 (M)	α_5 (Ho)	α_5 (Ho_i)	β_0	β_1	RMSE	AIC
Fagus sylvatica	*Pinus sylvestris*	M5	A		-0,0049		0,0243	0,6819						2,08	11466,10
	Quercus petraea	M5	A	0,9408	-0,0066	0,0184								1,93	9802,89
	Quercus pyrenaica	M1	M				0,3293	0,5965	-0,2352					2,10	9292,34
	Quercus robur	M12	M			-0,1038		-0,0509	0,1244	1,0300			-9,4827	2,46	5726,19
Quercus faginea	*Pinus halepensis*	M12	M				-0,2481				1,3855		-4,2707	1,09	355,92
	Pinus nigra	M12	M				-0,3677		0,2853		1,1564		-7,0128	1,05	1709,34
	Pinus sylvestris	M12	M				-0,3601		0,3284		1,0817		-8,4275	1,34	3439,68
	Quercus ilex	M1	A	0,7578				0,8303						1,24	4311,78
Quercus ilex	*Pinus halepensis*	M12	M				-0,2772	-0,0425	0,1651		1,1925		-6,0763	0,96	5638,96
	Pinus nigra	M12	M				-0,3333		0,1989		1,2466		-6,5164	0,85	4446,14
	Pinus pinaster	M12	M				-0,1802		0,1547		1,0835		-5,9781	0,89	2131,00
	Pinus pinea	M12	M				-0,1910		0,1413		1,1488		-6,6968	0,95	2836,90
	Pinus sylvestris	M12	M				-0,3877	-0,0143	0,2363		1,2026		-6,3941	0,98	5086,48
	Quercus faginea	M1	A		-0,0282			1,1636	0,0407					0,87	4927,66
	Quercus pyrenaica	M12	M				-0,2510				1,4862		-6,8655	0,93	838,59
	Quercus suber	M12	A				-0,2571	-0,0324	0,2214		1,0963		-7,2568	1,07	5404,67
Quercus petraea	*Pinus sylvestris*	M12	M				-0,3962		0,3045		1,1671		-9,1325	1,48	986,33
	Fagus sylvatica	M12	M				-0,2111	-0,0364	0,1916		1,0490		-7,3359	1,69	3202,77
Quercus pyrenaica	*Fagus sylvatica*	M1	M			0,1170								1,51	9281,96
	Pinus pinaster	M1	A		-0,0368	0,1155								1,26	1811,55
	Pinus sylvestris	M1	A		-0,0091		0,0163	1,2693						1,39	8372,09
	Quercus ilex	M5	A					1,4330						1,32	1653,03
	Quercus robur	M12	M				-0,2799		0,2404		1,0418		-7,7023	1,80	883,50
Quercus robur	*Fagus sylvatica*	M12	M				-0,2329		0,3245		0,9650		-11,7381	2,58	1000,90
	Quercus pyrenaica	M12	M				-0,2167		0,1838		1,0630		-8,1876	1,98	2032,19
Quercus suber	*Pinus pinaster*	M1	A		-0,0332			2,6535	0,0252					1,09	2779,01
	Pinus pinea	M1	M				0,3620	0,8264						0,99	3862,59
	Quercus ilex	M1	A	1,4835	-0,0386	0,0578		0,8232						1,12	8671,20

Note: Form refers to the way whether the asymptotic parameter (β_0) is expanded in an Additive (A) or Multiplicative (M) way. See Section 4.3.1. for further explanation.

On the other hand, an inverse trend was found for broadleaved species, where trees were comparatively taller (~2-8%) in mixed stands than in pure ones (Figure 12, g~m). Among them, *Fagus sylvatica*, *Quercus faginea* and *Quercus robur* height was comparatively stable under different species mixing, finding similar estimated tree heights both in pure and mixed forests (Figure 12 g,h,l). Among the conifers, the highest differences in height between mixed and pure stands were observed for *Pinus nigra* (Figure 1; b), when mixing with *Quercus faginea* and *Quercus ilex* (~10%). Regarding broadleaved species, *Quercus ilex* showed a high difference between mixed and pure stands when mixing with *Pinus halepensis* (Figure 12i), with taller trees in mixed stands. This trend was also found for *Quercus suber* and *Pinus pinaster* mixture (Figure 12m) *Quercus petraea* also presented significant differences in height respecting pure stands when mixing with *Fagus sylvatica* (Figure 12j).

5.3.3. Aridity influence on H-D relationships

The variation of height under different aridity conditions, by terms of the De Martonne Aridity Index, is presented in Figure 13. According to our results, taller trees could be found in more humid conditions for almost all the analyzed species and species mixtures. Based on estimated height along an aridity gradient, results also indicated that conifers are more insensitive to changes in aridity than broadleaved species (Figure 13). Among the studied species and species compositions, aridity influence was nearly insignificant for *Pinus nigra*, *Pinus pinaster* and *Quercus suber* (Figure 13; b,c,m). Two different trends were found regarding climatic influence on height for conifers. On one hand, Mediterranean conifers such as *Pinus halepensis* (Figure 13a) and *Pinus pinea* (Figure 13d) are approximately 5% higher in more arid than humid conditions ($C_{ratio} < 1$).

Oppositely, estimated heights for species living at higher altitudes such as *Pinus sylvestris* (Figure 13e) and *Pinus uncinata* (Figure 13f) presented higher values at more humid environments ($C_{ratio} > 1$), although these differences were nearly insignificant (~1-2%). Broadleaved species (Figure 13, g~m) seemed to be highly influenced by aridity according to their height estimations, excepting *Quercus sube*r. Among them, the highest differences in height between arid and humid conditions were found for *Quercus faginea* in mixture with *Pinus sylvestris* (Figure 13h) and *Quercus robur* in mixture with *Fagus sylvatica* (Figure 13l), with values close to 15%.

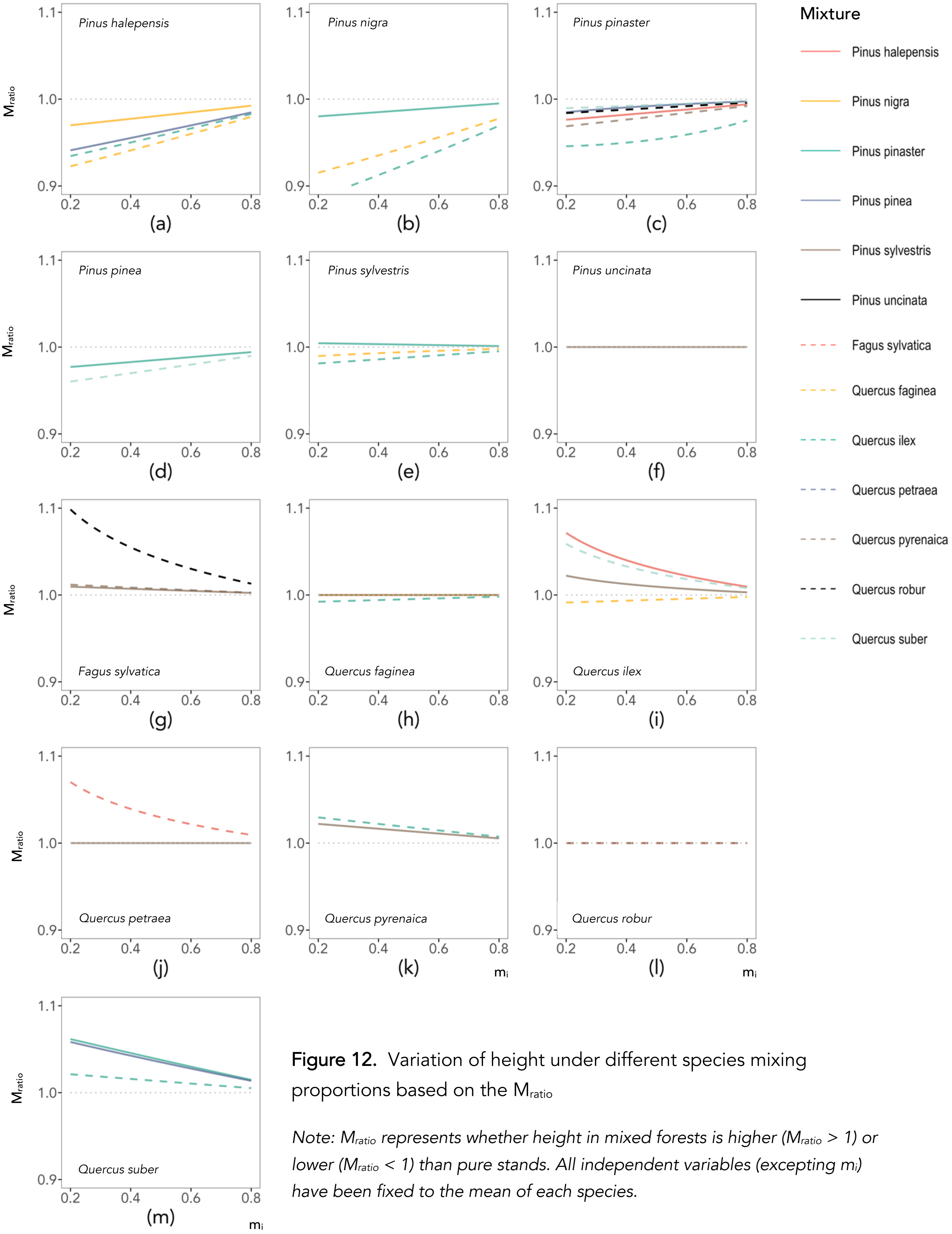


Figure 12. Variation of height under different species mixing proportions based on the M_{ratio}

Note: M_{ratio} represents whether height in mixed forests is higher (M_{ratio} > 1) or lower (M_{ratio} < 1) than pure stands. All independent variables (excepting m_i) have been fixed to the mean of each species.

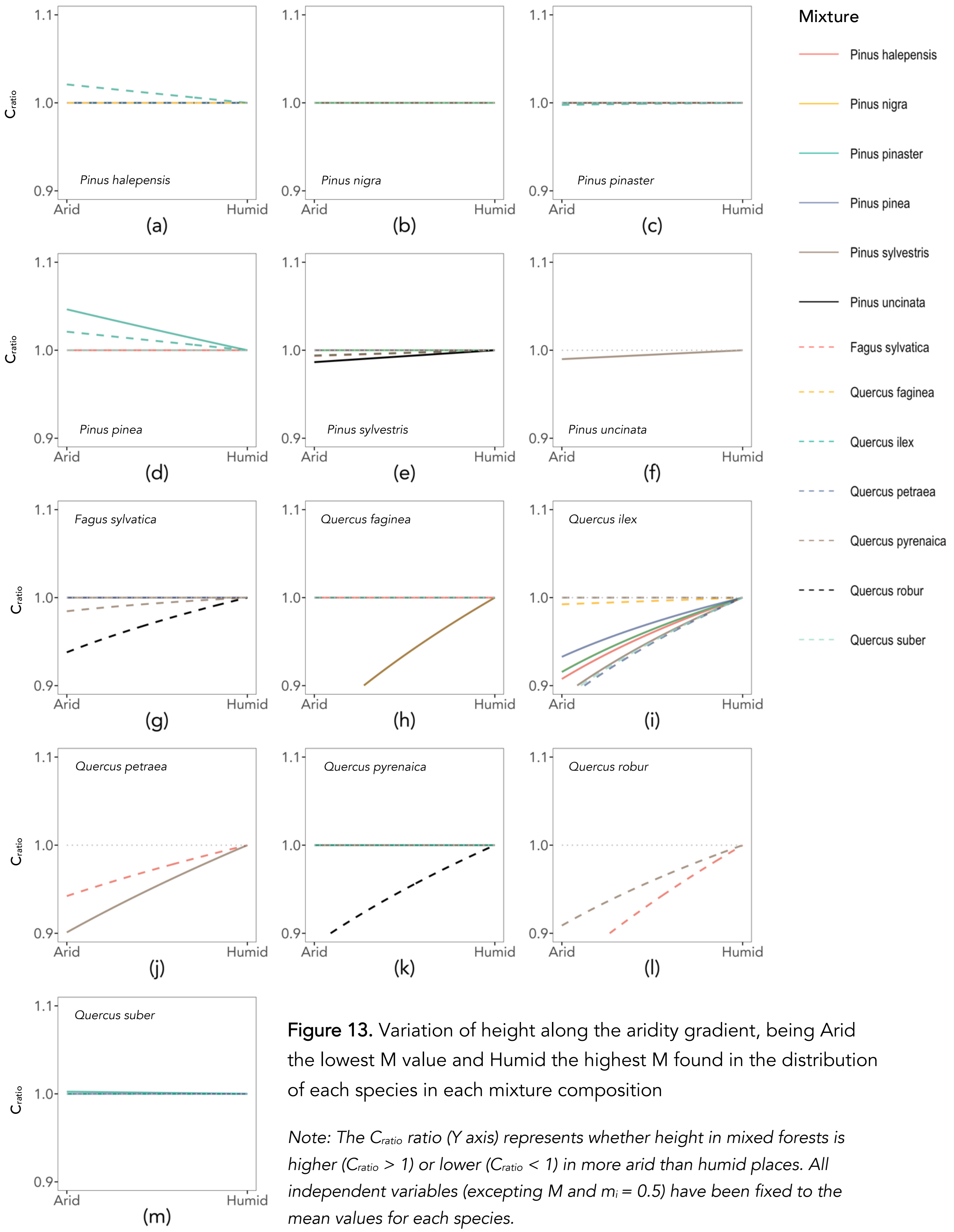


Figure 13. Variation of height along the aridity gradient, being Arid the lowest M value and Humid the highest M found in the distribution of each species in each mixture composition

Note: The C_{ratio} ratio (Y axis) represents whether height in mixed forests is higher ($C_{ratio} > 1$) or lower ($C_{ratio} < 1$) in more arid than humid places. All independent variables (excepting M and $m_i = 0.5$) have been fixed to the mean values for each species.

Figure 14 shows total tree height estimations (y axis) along the diameter distribution of each species in each mixture (y axis) under different values of dominant height. Here, we can see that trends in aridity-height found for each species and mixture are constant under different tree sizes and stand developmental stages. In the case of *Quercus robur*, taller trees were found in more humid than in less humid places for all sizes and developmental stages. On the other hand, height estimations for *Pinus uncinata* experienced a change in the trend at a diameter of 27 cm. Under the three simulated stand developmental stages, taller trees were found in less humid places below this point. Opposite to this trend, taller trees were found in more humid places above this point. Aridity-Total height relationship for different sizes and developmental stages were also plotted for the remaining species of study and they are available in Supplementary Figure 4.

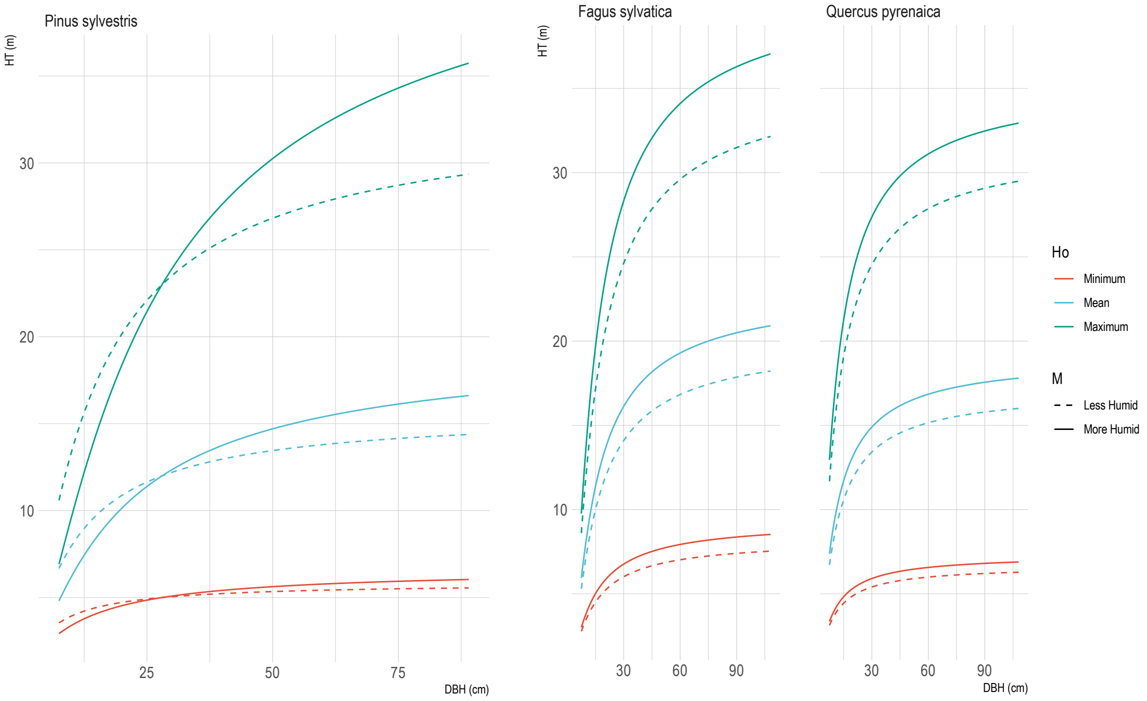


Figure 14. Aridity influence at different stand developmental stages along the diameter distribution for (a) *Pinus uncinata* and (b) *Quercus robur*

Note: The developmental stage is represented as stand dominant height (Ho) or species dominant height (Hoi), depending on parameter significance from selected H-D models

5.4. Forest CO_2 yield and growth simulation under different climate change scenarios

5.4.1. Forest CO_2 yield simulation for Pinus sylvestris mixtures along the 2000-2100 period

Simulated CO_2 yield for the 2000-2100 period under different SSPs for different *Pinus sylvestris* mixtures in Spain is shown in Table 11. We found a common and positive trend in CO_2 yield accumulations from 2000 to 2100 among the studied mixtures. A common trend was also found regarding SSPs scenarios, with higher yield values under the most optimistic scenario (SSP1) and lower values under the most pessimistic scenario (SSP5) in the following order: SSP1>SSP2>SSP3>SSP5. However, pure and mixed stands yields evolved differently along the simulated period of study. In the beginning of the simulation period, mixed stands generally presented smaller yields than the respective pure stands. However, our results showed that differences in yield between mixed stands and pure stands were drastically reduced at the end of the simulation period in favor of the first ones.

Based on the SSP2, mixed stands in *Pinus sylvestris* – *Fagus sylvatica* mixture presented less yield than *Pinus sylvestris* (4%) and *Fagus sylvatica* (53%) pure stands in the year 2000 (Figure 15). By the year 2100, these differences were reduced to 0.8% and 7.22%, respectively. *Pinus sylvestris* and *Pinus nigra* mixture showed similar yields on pure and mixed stands, being 17% higher in pure than in mixed ones. For this mixture, yield of mixed stands overpassed in 6% the yield of *Pinus sylvestris* pure stands, since the difference respecting *Pinus nigra* monocultures was reduced by 10% at the end of the simulation period. Regarding the *Pinus sylvestris-Pinus pinaster* mixture, mixed stands initially presented more yield (11%) than the *Pinus pinaster* pure stands. By the year 2100, mixed stands presented more yield (6-16%) than both pure stands.

A similar trend was found on *Quercus pyrenaica* mixed stands, finding initially higher CO_2 yield on *Pinus sylvestris* pure stands compared to mixed stands, which differences periodically were reduced until the point that mixed stands CO_2 stock got over the pure ones. At the end of the simulation period, mixed stands presented around 11-25% more yield than pure stands.

Table 11. Total CO_2 yield ($Mg \cdot ha^{-1}$) simulated for the 2000-2100 period under different SSPs, showing the data corresponding to each 20 years period

SSP	Species composition	Type	2000	2020	2040	2060	2080	2100
SSP1	*Pinus sylvestris - Fagus sylvatica*	*Pinus sylvestris*	248.36 (70)	350.77 (70.4)	442.11 (70.8)	516.94 (71.2)	578.39 (71.6)	625.34 (71.9)
		Fagus sylvatica	387 (83.6)	504.39 (83.9)	592.73 (84.1)	652.48 (84.2)	691.13 (84.4)	716.23 (84.5)
		Mix	245.77 (78.2)	342.23 (78.5)	432.61 (78.8)	514.26 (79)	586.82 (79.1)	650.79 (79.3)
	Pinus sylvestris - Pinus nigra	*Pinus sylvestris*	186.77 (82.1)	266.67 (81.5)	329.6 (81)	377.04 (80.6)	411.09 (80.4)	434.85 (80.1)
		Pinus nigra	188.73 (67.7)	277.34 (68.3)	353.82 (68.7)	414.77 (69.1)	461.65 (69.4)	497.38 (69.7)
		Mix	159.69 (75.1)	239.97 (75.1)	310.47 (75.1)	370.7 (75)	421.19 (75)	463.51 (75)
	Pinus sylvestris - Pinus pinaster	*Pinus sylvestris*	286.41 (70.9)	377.74 (71)	448.29 (71.2)	500.58 (71.4)	537.98 (71.6)	564.89 (71.8)
		Pinus pinaster	199.44 (78.2)	300.18 (77)	381.66 (76.2)	441.24 (75.5)	484 (75)	514.61 (74.5)
		Mix	224.09 (73)	329.41 (72.8)	420.44 (72.7)	497.2 (72.6)	560.19 (72.5)	613.08 (72.4)
	Pinus sylvestris - Quercus pyrenaica	*Pinus sylvestris*	305.41 (70.6)	410.29 (70.7)	485.02 (70.9)	534.88 (71.2)	568.69 (71.4)	592.93 (71.6)
		Quercus pyrenaica	186.88 (70.9)	268.39 (71.3)	346.16 (71.6)	410.29 (71.7)	461.74 (71.8)	500.74 (71.9)
		Mix	206.99 (69)	339.03 (69.6)	453.66 (70.1)	543.14 (70.5)	611.85 (70.9)	667.14 (71.2)
SSP2	*Pinus sylvestris - Fagus sylvatica*	*Pinus sylvestris*	248.36 (70)	350.77 (70.4)	441.89 (70.8)	516.06 (71.2)	575.4 (71.6)	620.82 (71.9)
		Fagus sylvatica	387 (83.6)	504.39 (83.9)	592.17 (84.1)	650.05 (84.2)	684.78 (84.4)	707.19 (84.5)
		Mix	245.77 (78.2)	342.23 (78.5)	432.27 (78.8)	512.56 (78.9)	582.67 (79.1)	644.01 (79.2)
	Pinus sylvestris - Pinus nigra	*Pinus sylvestris*	186.77 (82.1)	266.67 (81.5)	329.44 (81)	376.3 (80.6)	408.53 (80.4)	430.72 (80.1)
		Pinus nigra	188.73 (67.7)	277.34 (68.3)	353.63 (68.7)	414.17 (69.1)	460.14 (69.4)	495.1 (69.7)
		Mix	159.69 (75.1)	239.97 (75.1)	310.32 (75.1)	370.02 (75)	419.21 (75)	460.43 (75)
	Pinus sylvestris - Pinus pinaster	*Pinus sylvestris*	286.41 (70.9)	377.74 (71)	448.07 (71.2)	499.78 (71.4)	535.91 (71.6)	562.18 (71.8)
		Pinus pinaster	199.44 (78.2)	300.18 (77)	381.66 (76.2)	441.1 (75.5)	483.81 (75)	514.15 (74.5)
		Mix	224.09 (73)	329.41 (72.8)	420.32 (72.7)	496.6 (72.6)	559.07 (72.5)	611.5 (72.4)
	Pinus sylvestris - Quercus pyrenaica	*Pinus sylvestris*	305.41 (70.6)	410.29 (70.7)	484.75 (70.9)	533.91 (71.2)	566.07 (71.4)	589.09 (71.6)
		Quercus pyrenaica	186.88 (70.9)	268.39 (71.3)	346.16 (71.6)	410.29 (71.7)	461.64 (71.8)	500.34 (71.9)
		Mix	206.99 (69)	339.03 (69.6)	453.34 (70.1)	541.79 (70.5)	608.95 (70.8)	663.14 (71.1)
SSP3	*Pinus sylvestris - Fagus sylvatica*	*Pinus sylvestris*	248.36 (70)	350.77 (70.4)	441.63 (70.8)	515.35 (71.2)	573.31 (71.6)	617.6 (71.9)
		Fagus sylvatica	387 (83.6)	504.39 (83.9)	590.36 (84.1)	646.69 (84.2)	677.94 (84.3)	697.61 (84.5)
		Mix	245.77 (78.2)	342.23 (78.5)	431.86 (78.8)	511.39 (78.9)	579.11 (79.1)	638.45 (79.2)
	Pinus sylvestris - Pinus nigra	*Pinus sylvestris*	186.77 (82.1)	266.67 (81.5)	328.92 (81)	374.95 (80.6)	405.51 (80.4)	426.71 (80.1)
		Pinus nigra	188.73 (67.7)	277.34 (68.3)	353.34 (68.7)	413.55 (69.1)	458.72 (69.4)	493.04 (69.7)
		Mix	159.69 (75.1)	239.97 (75.1)	309.98 (75.1)	369.2 (75)	417.22 (75)	457.55 (74.9)
	Pinus sylvestris - Pinus pinaster	*Pinus sylvestris*	286.41 (70.9)	377.74 (71)	447.92 (71.2)	499.3 (71.4)	534.43 (71.6)	560 (71.8)
		Pinus pinaster	199.44 (78.2)	300.18 (77)	381.66 (76.2)	440.95 (75.5)	483.53 (75)	513.69 (74.5)
		Mix	224.09 (73)	329.41 (72.8)	420.27 (72.7)	496.44 (72.6)	558.23 (72.5)	610.15 (72.4)
	Pinus sylvestris - Quercus pyrenaica	*Pinus sylvestris*	305.41 (70.6)	410.29 (70.7)	484.35 (70.9)	533.07 (71.2)	563.81 (71.4)	585.82 (71.6)
		Quercus pyrenaica	186.88 (70.9)	268.39 (71.3)	346.16 (71.6)	410.29 (71.7)	461.25 (71.8)	499.61 (71.9)
		Mix	206.99 (69)	339.03 (69.6)	452.94 (70.1)	540.92 (70.5)	606.44 (70.8)	659.63 (71.1)
SSP5	*Pinus sylvestris - Fagus sylvatica*	*Pinus sylvestris*	248.36 (70)	350.77 (70.4)	441.4 (70.8)	514.27 (71.2)	571.15 (71.5)	614.73 (71.9)
		Fagus sylvatica	387 (83.6)	504.39 (83.9)	589.68 (84.1)	643.79 (84.2)	672.27 (84.3)	690.45 (84.5)
		Mix	245.77 (78.2)	342.23 (78.5)	431.52 (78.7)	509.61 (78.9)	575.52 (79)	633.43 (79.2)
	Pinus sylvestris - Pinus nigra	*Pinus sylvestris*	186.77 (82.1)	266.67 (81.5)	328.88 (81)	373.95 (80.6)	403.5 (80.4)	423.79 (80.1)
		Pinus nigra	188.73 (67.7)	277.34 (68.3)	353.24 (68.7)	412.86 (69.1)	457.45 (69.4)	491.24 (69.7)
		Mix	159.69 (75.1)	239.97 (75.1)	309.89 (75.1)	368.37 (75)	415.58 (75)	455.22 (74.9)
	Pinus sylvestris - Pinus pinaster	*Pinus sylvestris*	286.41 (70.9)	377.74 (71)	447.62 (71.2)	498.46 (71.4)	532.98 (71.6)	558.17 (71.8)
		Pinus pinaster	199.44 (78.2)	300.18 (77)	381.66 (76.2)	440.68 (75.5)	483.17 (75)	513.13 (74.5)
		Mix	224.09 (73)	329.41 (72.8)	420.05 (72.7)	495.88 (72.6)	557.14 (72.5)	609 (72.4)
	Pinus sylvestris - Quercus pyrenaica	*Pinus sylvestris*	305.41 (70.6)	410.29 (70.7)	483.99 (70.9)	531.83 (71.2)	561.85 (71.4)	583.44 (71.6)
		Quercus pyrenaica	186.88 (70.9)	268.39 (71.3)	346.16 (71.6)	409.99 (71.7)	460.88 (71.8)	498.91 (71.9)
		Mix	206.99 (69)	339.03 (69.6)	452.47 (70.1)	539.6 (70.5)	604.34 (70.8)	656.9 (71.1)

Note: Data in brackets correspond to the amount of aboveground biomass comparing to the total (%)

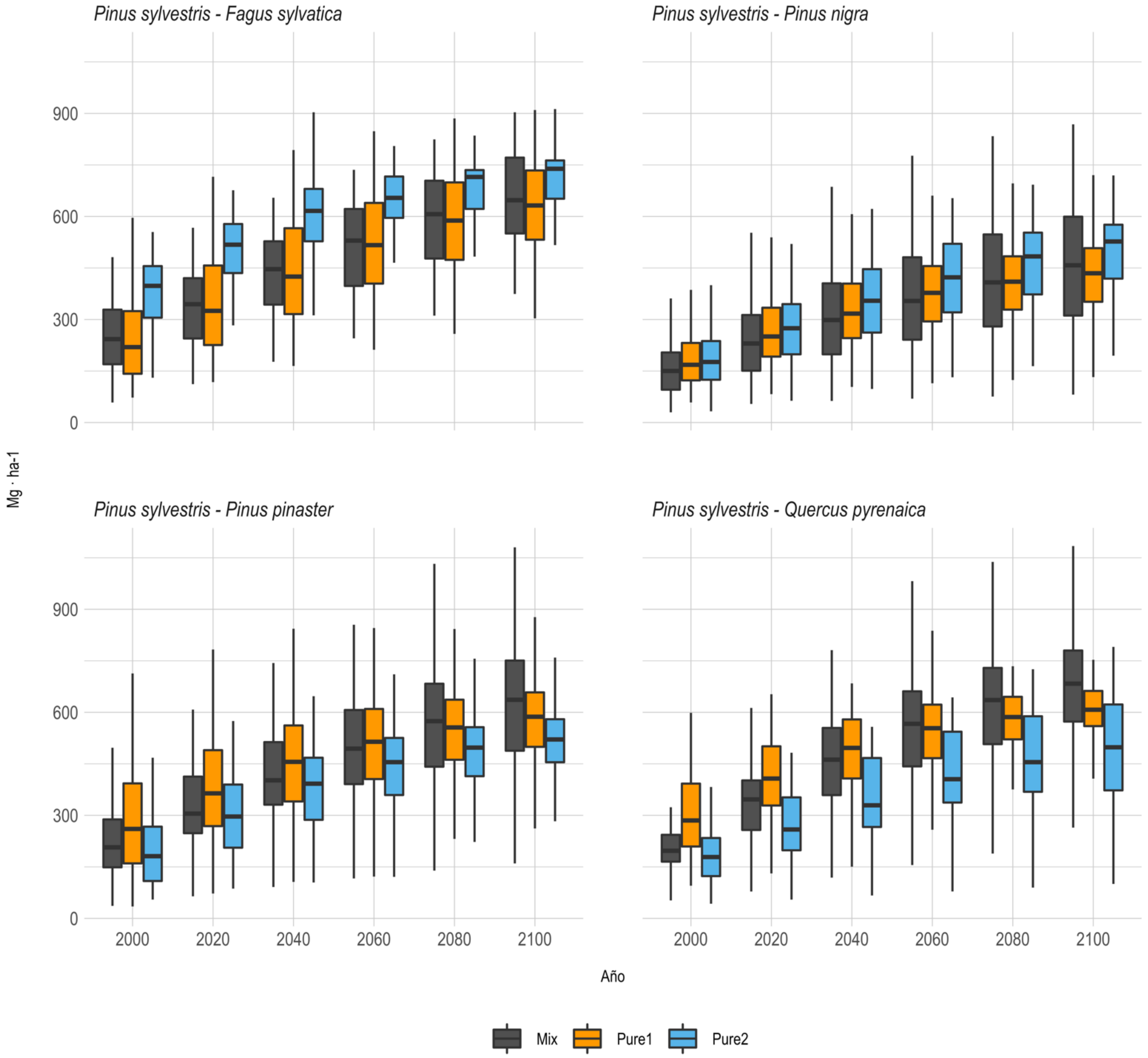


Figure 15. Total CO_2 yield (Mg · ha^{-1}) simulation for the 2000-2100 period under the most realistic SSP (SSP2) under study

Aboveground and belowground CO_2 were also simulated in our study (Table 12), finding different trends based on species traits for the analyzed mixtures. In conifer-broadleaved mixtures, we found that aboveground CO_2 tended to increase along all the simulation periods in both pure and mixed stands.

For these mixtures, *Pinus sylvestris-Fagus sylvatica* mixed stands experienced an increment of 1% in the aboveground biomass, where an increment of 2.2% was found for *Pinus sylvestris-Quercus pyrenaica* mixed stands.

An opposite trend was found for conifer-conifer mixtures, with a constant diminution in aboveground biomass proportion between 2000 and 2100 under the different SSPs. Although this decrement was too light for both *Pinus sylvestris-Pinus nigra* and *Pinus sylvestris-Pinus pinaster*, differences were found among pure and mixed stands of these mixtures. In the first one, *Pinus sylvestris* pure stands showed a reduction (2%) in aboveground CO_2 proportion in time, since *Pinus nigra* pure stands experienced an increment in the same amount. On the other mixture, while *Pinus pinaster* pure stands experienced a great reduction (~4%) in aboveground CO_2 proportion, aboveground CO_2 in *Pinus sylvestris* pure stands increased between 2000 and 2100.

Results presented in this section are also available, in terms of biomass (Mg·ha^{-1}), in Supplementary Table 9.

5.4.2. Forest CO_2 growth simulation for the period 2000-2100

Based on simulated CO_2 yield values, growth in terms of tons of CO_2 per hectare and year was determined for different periods between 2000-2100 (Table 12).

At the initial period, total growth rates for *Pinus sylvestris* in mixed stands ranged from 4-6.6 Mg·ha^{-1}·yr^{-1}, finding differences among the studied mixtures in comparison with the pure ones. In the case of *Pinus sylvestris – Pinus nigra*, similar growth rates (4-4.5 Mg·ha^{-1}·yr^{-1}) between mixed and pure stands were found. Mixed stands of *Pinus sylvestris-Fagus sylvatica* presented higher growth rates than *Pinus sylvestris* pure stands, but slightly lower (~12%) than *Fagus sylvatica* pure stands. On the other hand, when *Pinus sylvestris* was in mixture with *Pinus pinaster* and *Quercus pyrenaica*, mixed stands presented higher growth rates than pure stands (~2 Mg·ha^{-1}·yr^{-1}). These patterns were also found for the aboveground and belowground fractions, with some exceptions: (i) *Pinus sylvestris* pure stands growth was initially lower than *Fagus sylvatica* and mixed stands on the aboveground fraction (64.12% and 12.27%, respectively) but lower on belowground growth (33.33% and 28.20%, respectively); (ii) *Pinus sylvestris* pure stands showed slightly higher growth rates in the aboveground fraction than *Pinus nigra* pure stands, but this pattern was the opposite regarding belowground growth.

Table 12. Forest CO_2 growth (Mg · ha^{-1}· $year^{-1}$) calculated for the Reference period (Ref:2000-2005) and the last simulation period (2095-2100). In brackets, the difference in percentage between CO_2 growth in both moments for the different SSPs and tree fractions

Mixture	Variable	Type	Ref	SSP1	SSP2	SSP3	SSP5
Pinus sylvestris – Fagus sylvatica	Aboveground	*Pinus sylvestris*	2.62	1.3 (-50.38%)	1.25 (-52.29%)	1.23 (-53.05%)	1.21 (-53.82%)
		Fagus sylvatica	4.30	1.01 (-76.51%)	0.9 (-79.07%)	0.79 (-81.63%)	0.74 (-82.79%)
		Mix	3.83	2.58 (-32.64%)	2.46 (-35.77%)	2.38 (-37.86%)	2.33 (-39.16%)
	Belowground	*Pinus sylvestris*	1.04	0.41 (-60.58%)	0.39 (-62.5%)	0.38 (-63.46%)	0.38 (-63.46%)
		Fagus sylvatica	0.78	0.14 (-82.05%)	0.12 (-84.62%)	0.1 (-87.18%)	0.1 (-87.18%)
		Mix	1.00	0.62 (-38%)	0.6 (-40%)	0.58 (-42%)	0.57 (-43%)
	Total	*Pinus sylvestris*	3.67	1.71 (-53.41%)	1.65 (-55.04%)	1.62 (-55.86%)	1.58 (-56.95%)
		Fagus sylvatica	5.08	1.14 (-77.56%)	1.02 (-79.92%)	0.9 (-82.28%)	0.83 (-83.66%)
		Mix	4.82	3.2 (-33.61%)	3.07 (-36.31%)	2.97 (-38.38%)	2.89 (-40.04%)
Pinus sylvestris – Pinus nigra	Aboveground	*Pinus sylvestris*	3.19	0.9 (-71.79%)	0.84 (-73.67%)	0.8 (-74.92%)	0.77 (-75.86%)
		Pinus nigra	3.08	1.31 (-57.47%)	1.29 (-58.12%)	1.27 (-58.77%)	1.25 (-59.42%)
		Mix	3.02	1.58 (-47.68%)	1.54 (-49.01%)	1.5 (-50.33%)	1.47 (-51.32%)
	Belowground	*Pinus sylvestris*	0.80	0.29 (-63.75%)	0.27 (-66.25%)	0.26 (-67.5%)	0.25 (-68.75%)
		Pinus nigra	1.35	0.48 (-64.44%)	0.46 (-65.93%)	0.45 (-66.67%)	0.45 (-66.67%)
		Mix	1.00	0.54 (-46%)	0.52 (-48%)	0.52 (-48%)	0.5 (-50%)
	Total	*Pinus sylvestris*	4.00	1.19 (-70.25%)	1.11 (-72.25%)	1.06 (-73.5%)	1.02 (-74.5%)
		Pinus nigra	4.44	1.79 (-59.68%)	1.75 (-60.59%)	1.72 (-61.26%)	1.69 (-61.94%)
		Mix	4.01	2.12 (-47.13%)	2.06 (-48.63%)	2.02 (-49.63%)	1.98 (-50.62%)
Pinus sylvestris – Pinus pinaster	Aboveground	*Pinus sylvestris*	2.32	0.74 (-68.1%)	0.72 (-68.97%)	0.7 (-69.83%)	0.69 (-70.26%)
		Pinus pinaster	3.16	0.84 (-73.42%)	0.83 (-73.73%)	0.82 (-74.05%)	0.82 (-74.05%)
		Mix	3.82	1.89 (-50.52%)	1.88 (-50.79%)	1.85 (-51.57%)	1.85 (-51.57%)
	Belowground	*Pinus sylvestris*	0.94	0.23 (-75.53%)	0.22 (-76.6%)	0.22 (-76.6%)	0.22 (-76.6%)
		Pinus pinaster	1.05	0.4 (-61.9%)	0.4 (-61.9%)	0.4 (-61.9%)	0.4 (-61.9%)
		Mix	1.44	0.76 (-47.22%)	0.75 (-47.92%)	0.74 (-48.61%)	0.74 (-48.61%)
	Total	*Pinus sylvestris*	3.25	0.97 (-70.15%)	0.95 (-70.77%)	0.92 (-71.69%)	0.91 (-72%)
		Pinus pinaster	4.21	1.24 (-70.55%)	1.23 (-70.78%)	1.23 (-70.78%)	1.22 (-71.02%)
		Mix	5.27	2.64 (-49.91%)	2.62 (-50.28%)	2.6 (-50.66%)	2.6 (-50.66%)
Pinus sylvestris – Quercus pyrenaica	Aboveground	*Pinus sylvestris*	3.73	0.93 (-75.07%)	0.89 (-76.14%)	0.85 (-77.21%)	0.84 (-77.48%)
		Quercus pyrenaica	2.94	1.42 (-51.7%)	1.41 (-52.04%)	1.4 (-52.38%)	1.38 (-53.06%)
		Mix	4.66	2.06 (-55.79%)	2.02 (-56.65%)	1.98 (-57.51%)	1.96 (-57.94%)
	Belowground	*Pinus sylvestris*	1.52	0.28 (-81.58%)	0.26 (-82.89%)	0.25 (-83.55%)	0.25 (-83.55%)
		Quercus pyrenaica	1.14	0.53 (-53.51%)	0.52 (-54.39%)	0.52 (-54.39%)	0.52 (-54.39%)
		Mix	1.94	0.7 (-63.92%)	0.7 (-63.92%)	0.68 (-64.95%)	0.68 (-64.95%)
	Total	*Pinus sylvestris*	5.25	1.22 (-76.76%)	1.15 (-78.1%)	1.1 (-79.05%)	1.08 (-79.43%)
		Quercus pyrenaica	4.08	1.95 (-52.21%)	1.94 (-52.45%)	1.92 (-52.94%)	1.9 (-53.43%)
		Mix	6.6	2.76 (-58.18%)	2.71 (-58.94%)	2.66 (-59.7%)	2.63 (-60.15%)

For all the analyzed mixtures, growth rates for both pure and mixed stands experienced a significant reduction from the beginning to the end of the simulation period under all the different SSPs studied (Table 12). Our results indicated that these reductions would be less drastic in mixed stands than in the pure ones. Here, it's important to highlight that growth rates for all mixed stands were higher than in pure stands at the end of the simulation period among all the analyzed mixtures, fractions (aboveground and belowground) and SSPs.

Differences in growth rates between 2000 and 2100 ranged from 30% to 50% in mixed stands, where pure stands experienced higher differences (from 50% to 80%). In conifer-conifer mixtures, *Pinus sylvestris* mixed stands experienced a similar growth reduction (50%). In conifer-broadleaved mixtures, when mixed with *Fagus sylvatica* these reductions were approximately 35% since these were close to 60% when mixed with *Quercus pyrenaica*. Consistently with our results for CO_2 yield simulations (Table 11), higher growth rates under the most optimistic scenario (SSP1) and lower values under the most pessimistic scenario (SSP5) were obtained in the following order: SSP1>SSP2>SSP3>SSP5.

Comparing the rate of change of the reduction in growth between the SSP5 and SSP1 conditions, we found that in the *Pinus sylvestris-Fagus sylvatica* mixture the rate of reduction of *Pinus sylvestris* increased by 6.63% and by 7.86% of *Fagus*, while the mixed stand increased by 19.13%. In the group of *Pinus sylvestris-Quercus pyrenaica* the rate of reduction of *Pinus sylvestris* increased by 3.48% and by 2.34% of *Fagus*, and the mixed stands increased by 3.39%. Figure 16 shows the simulated growth rates for the different mixtures and forest types (pure and mixed) in the 2000-2100 period. Mixed stands conifer-broadleaved species followed different initial trends in growing terms, but both of them derived to the same result. *Fagus sylvatica* pure stands growth was initially higher than *Pinus sylvestris* and mixed stands on aboveground production (64.12% and 12.27% on CO_2, respectively) and lower on belowground production (33.33% and 28.20% on CO_2, respectively). Nevertheless, its growth was reduced faster than in the other cases, staying under *Pinus sylvestris* and mixed stands values around 2050 and 2090 for above- and belowground CO_2 production, respectively. On the other hand, mixed stands production was higher during all the studied period than *Pinus sylvestris* pure stands, and growth reduction across time had a lower slope.

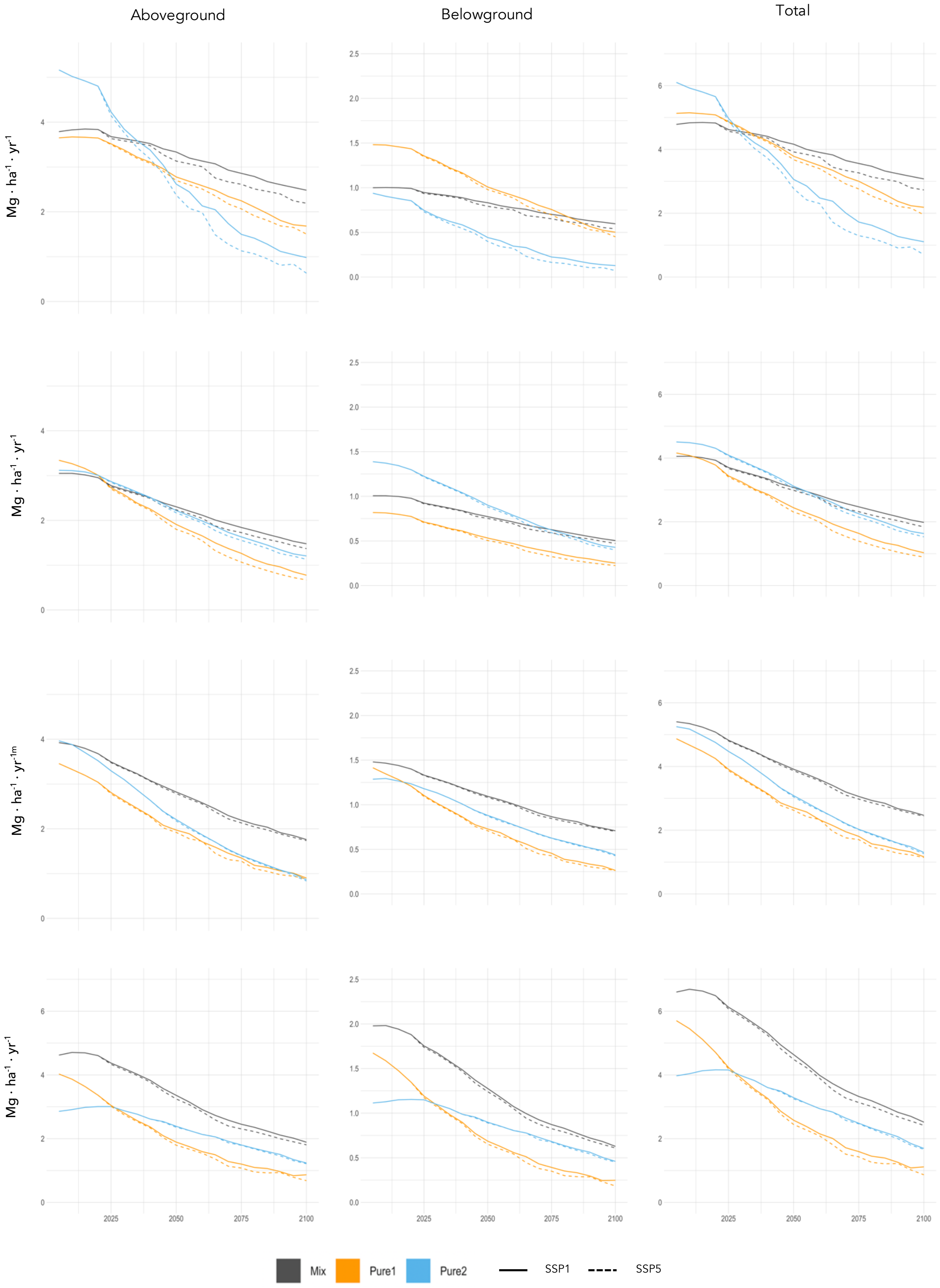


Figure 16. Mean CO_2 growth (Mg · ha^{-1}·$year^{-1}$) for the different studied mixtures (a: *Pinus sylvestris – Fagus sylvatica*, b: *Pinus sylvestris – Pinus nigra*, c: *Pinus sylvestris – Pinus pinaster*, d: *Pinus sylvestris – Quercus pyrenaica*) and tree fractions for the 2000-2100 period based on the most optimistic (SSP1) and pessimistic (SSP5) scenarios

At the end of the simulation, total growth reductions on mixed stands were lower (33.61%) than in pure *Fagus sylvatica* (77.59%) and *Pinus sylvestris* (53.41%) stands for CO_2 production. Initial growth of *Pinus sylvestris* pure stands was higher (28.68%) than *Quercus pyrenaica* pure ones but growing process of both species experienced a change into the final production at the end of the studied period, being *Quercus pyrenaica* pure stands more productive (59.84%) than *Pinus sylvestris* pure ones, consistently to above- (52.69%) and belowground (89.29%) growth. In this case, mixed stand growth was higher than *Pinus sylvestris* and *Quercus pyrenaica* pure stands during all the studied period, being this significantly higher at 2100 with differences of 121.50% and 45.07% for above- and 150% and 32.07% for belowground growth respecting *Pinus sylvestris* and *Quercus pyrenaica* pure stands.

The behavior of conifer mixtures in terms of growth showed many similarities with yield results. *Pinus nigra* tends to have lower growth reduction in pure stands than *Pinus sylvestris* (10.57% less reduction), excepting in the first period referring aboveground growth. Pure *Pinus nigra* stands growth was 10.72% higher on the initial periods compared to mixture, while finally mixed stands overpassed them by 18.44%, as in *Fagus sylvatica* mixture happened to the case of aboveground fraction. On the other conifer mixture, *Pinus pinaster* pure stands demonstrated to be more productive than *Pinus sylvestris* pure stands for both above- and belowground production both at initial (36.21% and 11.70%) and final time (13.51% and 73.91%), although these differences were reduced over time until the point to be very close. Mixed stands growth was always above both pure stands, and the growth reduction during time is also softer (~20% less CO_2 growth reduction). Comparing both mixtures, while the starting growth point was different, the trends described in both cases were quite similar. In addition, a harder decreasing slope was appreciable on aboveground growth compared to belowground.

Although in some cases a pure stand initial production was higher than their mixture, mixed stands slope tended to be softer across all studied mixtures compared with pure stands (47.21% and 66.32% growing reduction, respectively), surpassing on the studied period the productivity, both above- and belowground, of the corresponding pure stands. Another interesting finding was the fact that mixtures with a broadleaved species showed higher production reductions on below- than in aboveground CO_2 (50.96% and 44.21%), while conifer mixtures had the contrary behavior (46.61% on belowground and 49.10% on aboveground to CO_2 production, respectively. Differences between extreme SSPs on mixture ranged from 1.54% to 10.73% on total

CO_2 growth, being the last one the mixture with *Fagus sylvatica*, which supposed the most extreme case of all the studied here.

Results presented in this section are also available, in terms of biomass ($Mg \cdot ha^{-1} \cdot yr^{-1}$), in Supplementary Table 10.

DISCUSSION

6.1. Potential climatic influence on maximum stand carrying capacity of Mediterranean forests

In this study, a significant influence of climate on the MSDR was found for the 15 Mediterranean species studied. Our results highlighted the need to consider different specific climatic variables to better predict this climatic influence as previous researchers (Aguirre et al. 2018; Condés et al. 2017; Brunet-Navarro et al. 2016; Charru et al., 2012). However, exact agreement with previously published studies (Aguirre et al. 2018; Brunet-Navarro et al. 2016) could not be expected for the same species and areas regarding the key drivers affecting the MSDR and the way they impact the maximum stand carrying capacity estimations. In addition, different approaches (Condés et al., 2017; Riofrio et al. 2017) in selecting monospecific plots could derive in a different plot samples and therefore in different results. As well as this, regarding the climate database, although other databases could also be used such as Gonzalo Jimenez (2010), the most updated (1970-2000) time period offered by WorldClim2 available for the whole study area was selected in order to consider a suitable range of different climatic conditions with high resolution (Abatzoglou et al. 2018; Poggio et al. 2018; Panagos et al. 2017).

6.1.1. Basic MSDRs and SDI_{max} reference values

Our findings showed significant differences in the coefficients of the basic MSDRs (Tables 5 and 6), confirming intra- and inter-specific variability among the selected coniferous and broadleaf species (Vospernik and Sterba, 2015). The range of the slopes fitted in the basic MSDR models for the coniferous species agreed with findings reported by Charru et al. (2012) and Aguirre et al. (2018). Those authors found shallower slopes for *Pinus sylvestris* than for other pines in Spain and France, showing the great ability of this species to grow and survive amidst intra-specific competition (Zeide, 1987; Pretzsch and Biber, 2005). The development of wide crown areas at older ages could explain the extreme value of the slope for *Pinus pinea* (Barbeito et al., 2008). Among the broadleaf species, *Quercus suber* (-1.9674) and *Quercus ilex* (-2.0951) presented the steepest MSDR slopes and the smallest SDI_{max} estimates. These outputs may be due to the ability of these species to support a great leaf area, so that fewer individuals are needed to fully occupy a stand (Woodall et al., 2005). SDI_{maxREF} values estimated in this study were compared to prior reference values from published studies in similar areas, to test the consistency of our models (Supplementary Table 5). Agreement was generally good, as stands dominated by conifers showed relatively higher SDI_{maxREF} values when compared to those dominated by broadleaf species. The distinct values obtained in other studies for the same species may be due to the use of different approaches, methodologies and datasets (Hann, 2014). SDI_{maxREF} values were obtained by quantile regression in this study, whereas other relevant studies used different methodologies and types of statistical analysis, such as stochastic frontier analysis (e.g. Charru et al., 2012) or simple linear regression (e.g. Brunet-Navarro et al., 2012). Our findings were consistent with the theory that maximum stand density is known to be positively related to species shade tolerance (Jack and Long 1996, Woodall et al., 2005) (Supplementary Table 6). However, SDI_{maxREF} values for light-demanding coniferous species such as *Pinus pinaster*, *Pinus uncinata* and *Pinus sylvestris* were unexpectedly high (Table 5), given their low shade-tolerance (Niinemets and Valladares, 2006). A similar trend was found by Andrews et al. (2018), who obtained smaller SDI_{maxREF} values for shade-tolerant species such as *Fagus grandifolia* and *Acer saccharum* than other light-demanding species in the northeastern United States. Prior to that, Dixon and Keyser (2017) reported similar results when analyzing the maximum stand density of 15 coniferous and broadleaf species in the same area. Higher maximum carrying capacities for light-demanding species such as *Pinus sylvestris* than for *Fagus sylvatica* or *Quercus petraea* were also obtained by Charru et al. (2012) and Toigo et al. (2018) in France. These results suggest the existence of other drivers affecting the maximum carrying capacity of the species studied, such as silvicultural objectives, plant phenology, crown allometry, available growing space or climate.

6.1.2. Climatic drivers influencing MSDR and SDI_{max}

In this study, a significant influence of climate in the MSDR and the maximum stand carrying capacity of 15 Mediterranean tree species was found. Reductions in the maximum carrying capacity were generally linked to warmer and drier conditions, though the climatic drivers that best explained the influence of the climate on MSDR and SDI_{max} varied for conifer and broadleaf species.

Coniferous species

Results from the climate-dependent MSDR models suggest that temperature could be the main driver affecting the maximum stand carrying capacity for conifers (Table 7). For *Pinus nigra, Pinus pinaster* and *Pinus sylvestris*, most of the selected climate-dependent models included seasonal temperatures, especially seasonal maximum (MXTi) temperatures. *SDI_{max} (Clim)* estimates for these species suggest that significant reductions in the maximum carrying capacity might be expected as temperatures increase, especially during the spring season (Figure 8).

Contrary to this trend, recent research on climate change and coniferous forest dynamics (Martin-Benito et al., 2008; Kurz-Besson et al., 2016) suggest that reducing the number of days below 5°C could also improve the growth and vitality of these species by enhancing processes such as winter photosynthesis (Rathgeber et al., 2005), cambium and xylem formation (Vieira et al., 2014) and the development of deeper roots during the colder months of the year (Hansen and Beck, 1994). An increase in minimum temperatures could also boost the growth of individuals in mountainous areas. Smaller snowpack has been linked to higher soil water availability (Kreyling, 2010), lower mortality from root damage (Peterson and Peterson, 2001; Gedalof and Smith, 2001) and less foliar erosion from wind-blown snow (Kajimoto et al., 2002). The best climate-dependent models for *Pinus halepensis* indicated that seasonal maximum temperatures (MXT_i), precipitation during the warmest month (PWM) and aridity (expressed as M) were the key drivers affecting SDI_{max}. Small Q indexes were obtained for this species based on these models (Table 5), leading to small SDI_{max} variations along its climatic range (Table 7). These results go in line with previous studies showing the high resilience and adaptation to extreme drought and heat conditions of this Mediterranean species (Baquedano and Castillo, 2007; Benito-Garzón et al., 2011; de Luis et al., 2013; Aguirre et al. 2018). *Pinus uncinata* and *Pinus radiata* also showed small variations in SDI_{max} *(Clim)* along their distribution area according to their best climate-dependent MSDR models and Q indexes (Table 7). Particularly, the best climate-dependent model (PET3) for *Pinus radiata* presented an atypical behavior in which *SDI_{max} (Clim)* was found to decrease between percentiles 75 and 99 of this variable. This effect was also visible for *Pinus pinea*, which showed enhanced functioning at the highest values of P4. This might be explained by the link between climate and species traits, which is often too complex to adequately capture in a linear form (Reich, 2012; Craigmile, 2017). For this reason, further studies should test alternative model structures (i.e. multiple regression) with different combinations of climatic variables in order to better capture climate influences on MSDR and SDI_{max}. Results for *Pinus canariensis and Pinus pinea* revealed that seasonal (Pi) and annual precipitation (P) seemed to be key variables affecting their maximum stand carrying capacity. Indeed, these species showed the highest variation in SDI_{max} according to their Q index values (close to 0.3), suggesting that their maximum stand carrying capacity would be very sensitive to potential changes in precipitation regimes. In this context, climate change projections for the lower areas of the Mediterranean basin emphasize that precipitation will continue to decrease, especially during the warmest season (IPCC, 2018). Vitality (Sabaté et al., 2002; Climent et al., 2006; Sanchez-Salguero et al., 2012), growth reduction (Pasho et al., 2012; Gazol et al., 2017; Navarro-Cerillo et al., 2018; Peña-Gallardo et al., 2018) and even death from xylem embolism (López et al., 2013) due to increasing extreme drought events would be expected for Mediterranean conifers and would indirectly influence the maximum number of trees a stand could fully support in the future.

Broadleaved species

Similar to conifers, the influence of climate on MSDR was also found to be significant for all broadleaf species (Table 6). Selected climate-dependent models for *Fagus sylvatica* showed that higher SDI_{max} values were linked to wetter and milder conditions. This result corroborates results obtained previously by Condés et al., (2017), who found a similar pattern when studying the influence of aridity on MSDR in *Fagus sylvatica* and *Pinus sylvestris* stands across a wide environmental gradient in Europe. Other studies (Friedrichs et al., 2009; Zimmermann et al., 2015) on growth dynamics have reported similar climatic impacts for this species.

For *Quercus* species, temperature was found to be the key driver affecting the maximum stand carrying capacity (Table 7). Based on the selected climate-dependent models by species, maximum temperatures in spring (MXT3) and summer (MXT4) influenced SDI_{max} for all *Quercus* species except *Quercus robur*, which was more affected by potential changes in minimum temperatures (Table 6). Similar to the results obtained for *Pinus* species, higher temperatures (both maximum and minimum) were linked to smaller SDI_{max} estimates (Table 7). This is consistent with what has been found in previous studies (Fernandez-Marin et al., 2017; Gentilesca et al., 2017; Gil-Pelegrín et al., 2017; Kunz et al., 2018), suggesting that extreme heat and heat-induced drought conditions in the future would affect the vitality of oak stands in the Mediterranean basin. However, different responses in SDI_{max} variation as effect of potential changes in temperature were obtained among the *Quercus* species. The best climate-dependent models for *Quercus faginea and Quercus pyrenaica* suggest that a small increment in the temperatures of the warmest months would lead to a great decrease in the SDI_{max} of this species (Figure 8). Indeed, *Quercus faginea* presented the highest Q index (0.315) among the studied oak species (Table 7) due to changes in MXTWM. Expected reductions in soil water reserves in the distribution area of this species could also foster its progressive substitution in the future by more drought-resistant species such as *Quercus suber* or *Quercus ilex* (Peñuelas et al., 2001). However, previous studies have revealed the great resilience and adaptability of *Quercus faginea* for surviving in extreme conditions, such as those expected in the Mediterranean Basin (Camarero et al., 2015). For this area, a pronounced warming is also predicted, giving rise to higher rates of evapotranspiration with subsequent decreases in soil water availability and increases in drought episodes (IPCC,2018). Several authors have shown that these new conditions will drastically affect the growth and vitality of the main Mediterranean broadleaved species (Sabaté et al., 2002; Baquedano and Castillo, 2007; Gea-Izquierdo et al. 2013; Gentilesca et al., 2017; Peña-Gallardo et al., 2018). In this context, different adaptation mechanisms such as leaf area reduction may be decisive for these oak species in order to reduce water loss and survive under these new conditions (Peguero-Pina et al., 2016). For *Quercus petraea*, maximum temperatures seemed to be also relevant climatic variables explaining potential reductions on the SDI_{max} (Figure 8) according to the best climate-dependent MSDR models obtained for this species (Table 6). Similar climatic influence was also reported by Michelot et al. (2012), who studied growth dynamics for *Quercus petraea* in France. However, positive impacts on growth (Kellomäki et al., 2008) and seed production (Caignard et al., 2017) could be expected in cold and mild areas, such as boreal and temperate forests, as an effect of global warming. As Spain is the western limit of *Quercus petraea* distribution, future climate change impacts could be more determinant for this oak species. As cited before, differences in SDI_{max} *for Quercus robur* could well be explained by changes in seasonal minimum temperatures (Table 6). However, a small climatic impact on SDI_{max} could be expected for this species linked to potential increments of minimum temperatures, according to its Q index (Table 7). In this study, new climate-dependent MSDR models have been fitted and new SDI_{maxREF} and SDI_{max} *(Clim)* for different broadleaf species have been estimated.

However, further studies focused on these species are needed in order to better understand and predict potential changes in the maximum stand carrying capacity under different climate change scenarios.

6.2. Tree productivity variation in mixed forest along a gradient of different climatic and competition conditions

This study presents new basal area increment (BAI) models for mixed and pure stands of a total twenty-nine different species compositions across Spain. Estimates of BAI from the models developed here providing new evidence about how productivity is influenced by competition and aridity. Furthermore, models for each admixture accurately represent the species interactions effects on tree growth.

6.2.1. Basal area increment response to competition. Emerging biological interactions between species in mixed forests

Based on competition symmetry, our results suggest that trees compite for horizontal (BA: size-symmetric) more than vertical (BAL: size- asymmetric) space. Depending on the genus of the species in mixture, the analyzed species compositions can be divided into three main groups: conifer – conifer, conifer – broadleaved and broadleaved – broadleaved. Regarding species compositions composed by two coniferous species, our results suggested that competition is the most representative biological interaction taking place in these mixtures (Figure 10, Q_1). Among these species, *Pinus halepensis* and *Pinus nigra* seem to impart a high level of competition over other *Pinus* species in a mixed stand (Palahí et al. 2006).

In both cases, the predominant mode of competition is size-symmetric (De Luis et al. 1998; Trasobares et al. 2004; Cattaneo et al. 2018, Aguirre et al. 2019, Helluy et al. 2020). Though the productivity of *Pinus halepensis* is known to be influenced by the stand structure in the Mediterranean ecosystem (Moreno-Gutiérrez et al. 2011). In agreement to our results, Martin-Benito et al. (2011) showed that growth responses of West-Mediterranean *Pinus nigra* to climate change are modulated by competition and productivity. *Pinus sylvestris* and *Pinus uncinata* also have a competitive interaction as observed in our result and reported by Camarero et al (2019). For *Pinus pinaster* – *Pinus pinea* mixtures, previous studies (Vergarechea et al. 2021) shown that differences in growth synchrony in monospecific and mixed stands indicates temporal niche complementarity between these two species. The association of *Pinus sylvestris* in other pine species in mixed stand has been previously described elaborately (Weber et al. 2007; Primicia et al. 2013; Navarro et al. 2019, Jaime et al. 2019). Accordingly to our results, a facilitation could occur with *Pinus pinaster* that derived in a positive effect on BAI for *Pinus sylvestris* as observed by other authors (Bravo-Oviedo et al. 2006; Navarro-Cerrillo et al. 2016; Riofrio et al. 2017; Aguirre et al 2019; Lopez et al. 2020).

Broadleaved-Conifer mixed stands are predominantly affected by neutralism and commensalism as observed in our results (Figure 10,Q_2). Predominantly Oak - Pine mixtures are undergone with such mixing effects as spatiotemporal niche separation and below ground portioning lead their coexistence (Pretzsch et al. 2020). Specifically, in various combinations of conifers with *Quercus ilex* and *Quercus faginea*, we could clearly observe neutralism (Aguade et al. 2015, Prévosto et al. 2011, de-Dios-García et al. 2015, Grossiord et al. 2015). Whereas *Quercus pyrenaica* was mostly involved in commensal or facilitation interactions as were also observed by other authors (Aldea et al. 2017; Del Río et al. 2019; Muñoz-Galvez et al. 2021; Aldea et al. 2021). Though in some studies there is a clear indication of the positive mixing effect of *Pinus sylvestris* and *Quercus robur* in mixed stand in various climatic conditions (Paluch et al. 2004; Steckel et al. 2019; Steckel et al. 2020) such indication was absent in our study. Differences in site conditions with respect to humidity and fertility in this mixture distribution may explain this pattern. Our results indicate competition between *Fagus sylvatica* and *Pinus sylvestris* (Figure 10). However, literature indicates a positive mixing effect which is also modulated by a specific climatic condition like humidity (Aranda et al. 2004; Condes et al. 2013; Forrester et al. 2013; Condes et al. 2018, Yeste et al. 2021). For this species composition, we found a positive effect of pine on beech basal area growth. On the contrary, beech generally had a negative effect on pine basal area growth being these mixing effects modulated by site humidity as a measure of climatic conditions (Condés et al. 2018). Finally, our results suggest that neutralism and facilitation are the most representative interactions in broadleaved - broadleaved mixtures (Figure 10, Q_3). In line with previous studies, *Quercus ilex* imparts a positive effect on *Quercus suber*, whereas conveying a neutral effect on *Quercus faginea* (Plieninger et al. 2010). Our results suggest that *Fagus sylvatica* could experience a neutral effect when growing with *Quercus robur*. However, it was previously shown that this species may experiences a facilitation relationship when mixed with *Quercus petraea* (Pretzsch et al. 2013; Manso et al. 2015; Maleki et al. 2020) and an ammensal relationship when mixed with

Quercus pyrenaica (Aranda et al. 1996). This latter mixture was also studied by del Río et al. (2014), indicating that there is a negative mixing effect on *Quercus pyrenaica* productivity growing with *Fagus sylvatica* in the mixed stand (Pardo et al. 1997).

6.2.2. Basal area increment response to aridity

Tree growth in terms of basal area increment not only depends on competition driven by intra and inter species interactions, but also climate can influence the magnitude and direction of species mixing effects as reported in some recent studies (Forrester et al. 2013; Condés and Del Rio, 2015; Manso et al. 2015; Zell 2018; Pretzsch et al. 2020; Vergarechea et al. 2021; Vospernik 2021). In this study, the inclusion of the De Martonne Index as independent variable in BAI productivity models allowed us to analyze how basal area increment varies along an aridity gradient in Spanish mixed stands. Our results suggest that productivity is negatively influenced by aridity, finding higher BAI rates at more humid places, in agreement with decreasing growth rate in dryer conditions (Aldea et al. 2017, Marqués et al. 2016). Specifically, in pine-oak mixed stands where the effect of water and light availability on the radial increment is significantly notable (Aldea et al. 2017). However, exceptionally we also found a positive relationship between aridity and tree growth, as observed for *Pinus pinea* mixed with *Pinus pinaster*, and for *Quercus suber* mixed with *Pinus pinea* (Figure 11) (Sabaté et al. 2002, Manrique-Alba et al. 2017), being these species and their mixtures are located in the most arid conditions of Spain. In the case of Pinus *halepensis* the effect of water stress also may play a crucial role mainly in the productivity (Manrique-Alba et al. 2017; Helluy et al. 2020), contrary to our findings where tree growth was unaffected along the aridity gradient. In addition, in *Quercus suber* - *Pinus pinea* mixtures higher productivity rates were previously observed in more arid than humid places (Pardos et al. 2021, Steckel et al. 2020). Among the studied species, previous studies shown that *Fagus sylvatica* had the most complex growth response towards availability of ground water (Kint et al. 2012). However, only a significant negative effect of aridity on BAI was found when mixed with *Pinus sylvestris* (Figure 11g), being this effect no significant when mixed with oak species like *Quercus pyrenaica*, *Quercus petraea* or *Quercus robur*. A similar trend was previously found by many authors analyzing the climatic influence on productivity of both species in mixture along a climatic gradient in Europe (Medlyn et al.,2011; Michelot et al. 2012; Pretzsch et al. 2015; Pretzsch et al 2016; Aguirre et al. 2019).

6.3. Tree allometry variation in mixed forest along a gradient of different climatic and species mixing conditions

This study presents novel non-linear height-diameter models for predicting tree height in Mediterranean mixed forests under different species mixing proportions and aridity conditions. The results obtained here could be important to support management and policy decision for Mediterranean forests under the context of climate change.

6.3.1. Total tree height response to species mixing proportions

We showed that the species identity would define differences between the height in mixed and pure stands. In addition, taking into account species mixing proportions in mixed forest studies is key to understand differences in tree and stand variables of a specific species (Riofrío et al., 2017a). Our first results suggested that conifers could be higher in pure than in mixed forest stands (Figure 12, a~f). We hypothesize that it may be caused by specific-species traits, such as pines are pioneer and shade intolerant species, so they are very sensitive to growing under broadleaves cover. This depends primary on species identity, i.e., shade tolerance is caused for plant ontogeny and influenced by numerous biotic and abiotic factors (Valladares and Niinemets, 2008). Among the conifers studied here, *Pinus nigra* showed the highest differences in height between mixed and pure stands (Figure 12b), especially when mixed with oaks. It is known that, although this is a high shade tolerant species compared to other Mediterranean pines, water limitation could drastically limit its distribution in Mediterranean plant communities (Martin-Benito et al. 2008; Savi et al. 2020). An exception among conifers was found in *Pinus sylvestris* mixed with *Pinus pinaster*, with higher trees found in mixed than in pure stands, although the M_{ratio} keeps close to 1 along all the mixing proportions gradient (Figure 12e). A similar trend was found by Riofrio et al. (2019) for this species and mixture composition from NFI data in Spain.

Another related explanation to these patterns could be due to differences in species growth rates. When the mixture occurs between two species with different growth rates, the estimated height for pure stand may be higher at the same stage of development. This seems logical because all trees in a regular pure stand grow very similar and in a regular way, maintaining the upper average. This is much more evident for pine in conifer-broadleaved mixtures, where the latter do not grow as much in height and the crown structure is not pyramidal (Liu et al., 2018), increasing inter-specific competition for pine species. Competition may also explain our results found for *Quercus petraea* when mixed with *Fagus sylvatica* (Figure 12j), with great differences in height between mixed and pure stands for oak species. In mixture, we hypothesize that the growth rate of the light-demanding oak is supposed to be higher than the shade tolerant beech. Thus, an increase of beech proportion in mixture could reduce intra-specific competition for oak and enhance height growth for this species. However, this contradicts Ligot et al (2013) observations in forest of Central Europe , where oak trees were systematically outcompeted by beech in mixture, preventing also the oak regeneration. Focusing on broadleaved species, and contrary to conifers, a common trend was found where higher trees were found in mixed stands (Figure 12,g~m). Among other reasons, this inverse trend could be due to stand stratification promoted by silvicultural history. Silviculture can accelerate growth of different species in admixtures, affecting stand composition, structure and dynamics (Pretzsch et al., 2010). In some stands, one of the species in the mixture may historically experience repeated fires, grazing or silvicultural treatments (cutting) to favor the other species. This can be the case of *Quercus* - *Pinus* mixtures analyzed, where H_{mix}/H_{pure} ratios higher than 1 for broadleaved in mixed stands may suggest a positive effect of mixture. As broadleaves coppice forests are wide extended in Mediterranean areas, we think that the mixture with conifers, may reduce the intra-specific competition and, hence, promote height growth. In this sense, our results may have a relevant importance for Mediterranean coppice stands, suggesting that introducing or combing conifers in broadleaves forests, could enhance height growth for coppice species. This practice would also increase the ecosystem services and productivity, so it has been commonly used in reforestation (Pausas et al. 2004). Differences in trends between conifers and broadleaved species could be also explained based on initial SNFI selected plots, which could have different stand structures and developmental stage of the species, as shown in Supplementary Figures 2 and 3. It seems that in conifer mixtures, the size (height and diameter) of the trees seems to be greater in strict Mediterranean species (*Pinus halepensis, Pinus pinaster, Pinus pinea*) than in montane species (*Pinus sylvestris, Pinus nigra, Pinus uncinata*), probably as a consequence of the character of greater shade intolerance. In addition, as the stand distribution for a species moves away from its ideal ecological niche, competition with other more adapted and opportunistic species appears. If the second or third species is equally or better adapted, it leads to the formation of mixed stands. This can be the reason why *Quercus* species may perform better in mixtures (mainly conifer-broadleaved as *Quercus ilex* - *Pinus halepensis* or *Quercus suber* –

Pinus pinaster) than pines, since they naturally form this kind of mixed forests. Differences in the water uptake depth appears to be stimulated in mixed forests because *Quercus ilex* surrounded by *Pinus halepensis* explores deeper water sources than in monospecific formations (Vicente et al. 2018). We observed that shade-tolerant species as *Fagus sylvatica*, *Quercus robur* and *Pinus uncinata*, were no affected by mixture, regardless species composition. This may be due to shade tolerant species have high plasticity for certain traits, particularly for morphological features which optimizing light capture (Valladares and Niinemets, 2008), so a high canopy cover promoted by mixed stand seems to be practically irrelevant.

6.3.2. Total tree height response to aridity

We observed a significant climatic influence on HD relationship for the mostly species under study, in line with similar research in the topic (Fortin et al. 2019). Including climatic related variables in the H-D models could be the key to design forest prescriptions under different present and future environmental conditions (Pan et al., 2011). A basic assumption in tree allometry studies is that, as long as site conditions are homogenous, trees of a given species, at a given location, with the same DBH, would have the same height (Ng'andwe et al., 2019). But climatic conditions change over locations and time, and they could contribute towards specific species dynamics (Ng'andwe et al., 2019; Ruiz-Peinado et al., 2021). In this context, it is well known that height–diameter relationships depend heavily on local environmental conditions (Özçelik et al., 2014). In the present scenario of climate change, the fluctuating climatic conditions may have a positive or negative influence in the HD relationship influence positively (Fortin et al., 2019). We observed that for most of the mixtures analyzed here, total tree height was reduced under drought conditions (Figure 13). However, we identify two mixtures in which in the stress-gradient hypothesis (Maestre et al. 2009) was observed: *Pinus halepensis* – *Quercus ilex* (Figure 13a) and *Pinus pinea* – *Pinus pinaster* (Figure 13d). While in the first case it may be due to a reduction of intra-specific competition for *Pinus halepensis* during drought conditions, in the second one, it could be due to a facilitation process, i.e., a complementarity in the use of resources (Grossiord, 2018). Due to its stronger plastic character and its potential adaptability, *Pinus halepensis* has been demonstrated to be the most suitable species in terms of tree growth in arid sites of Spain (Martinez del Castillo et al., 2018). A more efficient use of below-ground water resources due to different root stratification could be also speculated for these mixtures, which allows for a better exploration of the soil profile (Vergarechea et al. 2021, Vicente et al. 2018). Therefore, these species could use more resources to strengthen the root system than the aerial system as aridity increases.

Potential changes in height due to changes in aridity may be higher in broadleaved than conifers, suggesting that allometry of oaks species in Spain may be highly affected by future climate change scenarios. We hypothesize that the differences between species on water use efficiency may underlay this process. *Pinus* species can maintain a relatively stable leaf water potential by strict stomatal control during drought events (isohydric strategy). On the other hand, broadleaves have not a discernible threshold of minimum water potential response, i.e., a light stomatal control under drought conditions (anisohydric behavior) (Grossiord, 2018; Grossiord et al. 2014). Consequently, higher competition for water use resources in arid sites are expected for broadleaves when are mixed with conifers (Fernandez-de-Uña et al. 2017). Our results are in line with this hypothesis, as shown especially for *Quercus faginea* when mixed with *Pinus sylvestris* (Figure 13h). As previously observed in other oak-pine mixture compositions (Toigo et al. 2015), the impact of soil water deficit on species may be worsened in mixtures, but mixture of species with different growth sensitivities to the seasonality of the drought periods might help to buffer these effects.

Climate change predictions for the Mediterranean basin forecast an increase in the frequency and intensity of drought events. Therefore, it seems to be counterproductive to promote most of mixed forests studied here for productive goals under the ongoing climate change scenario. However, pines could be beneficiated in some mixtures, as *Pinus halepensis – Quercus ilex*, *Pinus pinea - Quercus ilex*, *Pinus pinea - Pinus pinaster*, which is of great relevance given the extension of these species' distribution in Spain.

6.4. CO_2 yield and growth simulation in pure and mixed stands for the 2000-2100 period under different climate change scenarios

We found consistent differences between climate scenarios on both growth and yield CO_2 and biomass accumulated to the forests studied. While specific behaviors were found depending on the species mixture, a common trend reporting higher yield and growth in terms of fixed CO_2 and biomass in mixed stands was found, suggesting the activation of complementary mechanisms to fight drought stress (Muñoz et al., 2021; Pardos et al., 2021).

6.4.1. Total CO_2 yield in pure and mixed stands of Pinus sylvestris in Spain

As we initially hypothesized, a higher CO_2 yield was found to all the cases (pure and mixed stands) at the end of the studied period, because of the continuous stand growth accumulation. Another expected trend with higher yields on the most optimistic climate scenario (SSP1) comparing to the most pessimistic one (SSP5), consistent to all the study cases, was also found. However, in this case an opposite finding was previously reported on Swedish boreal forests (Poudel et al., 2010) and on the subtropical monsoon climate area (Wu and Xi, 2016), with higher production reported on the climate change scenarios comparing to control ones. These results could be supported by the local climate initial conditions. While in those forests the climate change effect is favorable due to a low or null rainfall reduction and the increase in temperature, in Mediterranean area it supposes an increasing drought stress situation, causing a reduction on their growth and, as consequence, CO_2 yields. Nevertheless, although a yield increasing trend was reported on climate change scenarios at short time periods, in longer time periods that trend turns down and their effects turned negative, showing a reduction on production when the climate conditions started to be more intense (Ma et al.,2014; Steenberg et al.,2011) reported in similar areas. Based on the type of forests we studied, a higher CO_2 yield in pure stands was found at the start of the studied period, while its difference was reduced to the end of the period or even surpassed by mixed stands. Although different responses depending on the species mixtures were found, a clear tendency to higher yields of mixed stands is clear at long time simulation periods, consistent with previous studies (Wu and Xi, 2016). That result is consistent with the higher resistance and resilience reported on mixed comparing to pure stands (Pardos et al., 2021; Muñoz et al., 2021), being that fluctuation very similar under all the studied climate scenarios, as Wu and Xi (2016) also found on their case.

Our results indicated that *Pinus sylvestris* mixed stands with *Fagus sylvatica* and *Pinus nigra* reduced the differences with the pure ones of the second species. Previous studies reported higher growth rate of *Fagus sylvatica* mixed stands comparing to the pure ones (Del Río et al., 2014) in terms of overyielding (Condes et al., 2013) and even transgressive overyielding (Preztsch and Schütze, 2009), attributed to niche complementarity of both species (Del Río et al., 2017). Results obtained to *Pinus nigra* are quite similar, although differences between pure and mixed stands were lower during all the period, which could be explained by the similar behavior of both species. In both cases, even not founding overyielding in the studied period, our findings suggested that both mixtures could show a reduction in their yield differences with pure *Fagus sylvatica* and *Pinus nigra* stands if a longer period of time were simulated. On the other hand, mixtures with *Quercus pyrenaica* and Pinus pinaster reported overyielding at the end of the studied period. This result was consistent with previous studies focused on the *Pinus sylvestris* - *Pinus pinaster* (Riofrío et al., 2017) and the *Pinus sylvestris* - *Quercus pyrenaica* mixtures (Muñoz et al., 2021). In conifer-conifer mixtures, the complementarity into vertical structure due to the different growth velocity could derive in a higher efficiency in light use, while on the conifer-broadleaved mixtures, their complementarity into crown and root systems may suppose a higher resource efficiency belowground (Forrester et al., 2014; Forrester and Bauhus, 2016), in both cases resulting on overyielding at mixed stands. Also, in both mixtures a positive effect on stand regeneration were found (López-Marcos et al., 2020; Del Río et al., 2009), which suggests a positive effect on the stand long-term stability.

6.4.2. CO_2 growth under different SSPs for the 2000-2100 period

Our findings indicated that overyielding in terms of CO_2 growth could appear in the four mixtures analyzed in this study. One of the main findings was that the mixed stands showed a lower decline over time. This trend has provoked that mixed stands outstripped pure stands or gradually widen the gap with the pure stands. It appeared that all four mixtures underwent a period in which the CO_2 growth remained high and stable, or increased slightly, at the very beginning (Figure 13). This may be related to the initial conditions. These initial forests are still at a time when SDI are not at their maximum and competition between trees is less intense, when forests are growing faster. Note that in our simulations we set a 2% reduction in all trees when SDI reaches a constant SDI_{max}. This allows for a relatively high growth in theory until the forest reaches SDI_{max}. After SDI> SDI_{max}, for pure stands the CO_2 growth would theoretically repeat a period of years in which there will be a short abrupt increase, followed by a decrease, and then remain very flat and stable (regardless of climate, i.e. M, variability). For mixed stands each 2% reduction had the potential to change the composition of the two species, driving the forest to the most stable species ratio, a process in which the change in growth is greater than the stable period for pure stands, but still very gentle. So, in contrast we have not reached this stage in 100 years of simulation. There is another detail that we can see, the curve for the mixed forests had a small abrupt change at the horizontal coordinate of 2020, which was due to the fact that the De Martonne aridity index, M, does not vary continuously in our simulations, but is updated every 20 years, thus causing the CO_2 production rate to receive a small fluctuation (Figure 14). Our results may suggest also that the different combinations of tree species analyzed may respond differently to the harsh living conditions in the future. There was a trend in the simulations for M to decrease with SSP, meaning that SSP5 has a lower M than SSP1. This trend was also reflected in our simulations, where the total growth of all subjects, whether pure stands or mixture stands, eventually decreases as the SSP becomes more severe (M decreases). However, the growth of the mixture stands was significantly higher than those of their pure stands counterparts under either SSP. An important hypothesis used to explain the advantages of such mixed stands over monoculture stands is the "complementary effects hypothesis"(Aarssen 1997; Huston 1997; Loreau 2000; Steckel et al 2019). It is mainly composed of two parts: competition reduction and facilitation. Take the forest we studied as an example. Different species of trees in a mixed stands do not require the same resources, so that competition for a particular resource that occurs between trees of the same species is reduced. In addition, the inter-specific needs for the same resource do not overlap exactly in time or space. Inter-specific differences may be due to shade tolerance, phenology, crown structure or the root system (Kelty, 1992; Man and Lieffers, 1999; Pretzsch et al., 2015). For example, light is a very important resource. According to (Jucker et al., 2014b), there is enough light to pass through the canopy of the *Pinus sylvestris* to allow the broadleaf plants below it to grow. At the same time, the morphological differences in the canopies of *Pinus sylvestris* and oak also complement each other and increase light utilisation throughout the whole forest (Pretzsch et al., 2015).

For the two mixed coniferous forests, the growth of pure stands of the three conifers *Pinus sylvestris*, *Pinus pinaster*, and *Pinus nigra* were very similar, and as can be seen in Figure 13, their growth curves are almost parallel. Those mixture stands of two conifer species also show a relatively similar growth which at the end of the simulation were reduced by almost the same value, about 50%. Exhibited relatively small overyielding, about 28%, compared with the pure stands of *Pinus sylvestris*.

In a recent study, Aguirre et al. (2019) showed that, in general, when two *Pinus* species form a mixed stand, they have a neutral or negative effect on each other, making the productivity of the mixed stand similar or lower than that of the monoculture stand. Toïgo et al., 2015 also suggested that overyielding would be exhibited in some cases and underyielding in others. This depends on the degree of complementarity and competition between the two *Pinus*. However, in general the combination of two conifers does not lead to significant overyielding, which is broadly in line with our simulation results.

There is a clear difference between the results obtained for the mixture of *Pinus sylvestris* with two broad-leaved species, where mixing with Fagus increased the CO_2 growth of the mixture forest by 30-37% relative to a pure *Pinus sylvestris* stand. In contrast, mixed stands with *Quercus* produced only 24% of overyielding relative to pure *Pinus sylvestris* stands, which was the lowest of the four groups. Although the growth of pure stands of *Fagus* declined rapidly, its high initial value may suggest that it could be able to rapidly occupy a proportion of the mixed stands. This means that the mixed forest is not dominated by any one of these species. Both contribute to the overproduction. The same is true in the mixed forest with *Quercus*. It is clear from our simulations that *Fagus sylvatica* is well suited to *Pinus sylvestris* to form a mixed forest, which also corresponds to reality. In addition to being complementary by the shape of the canopy, the spatial use of the root system of both is also complementary according to Bonnemann (1939, fig. 20). *Pinus sylvestris* roots usually occupy only the upper 0-40 cm of soil, whereas *Fagus sylvatica* roots can reach depths of 40-80 cm and can help *Pinus* to bring water from the deep to the shallow layers. The Fagus also brings minerals from the deeper layers to the surface through its own circulation in the form of leaf litter etc., improving the humus layer, the upper mineral soil and optimizing soil environment for the *Pinus*. However, the drought tolerance of *Pinus-Fagus* mixture stands is a concern and in the future this may be a limiting factor for their viability. According to Martín-Gómez et al., 2017, *Quercus* trees may have a significant survival advantage over *Pinus* trees under prolonged drought conditions. Even the decline and conversion of Pinus forests to *Quercus* forests has been observed in many locations. The same result can be seen in our simulations comparing the performance of *Quercus* in SSP1 and SSP5, where its growth in the more arid SSP5 conditions is not much reduced. *Pinus-Quercus* mixture could be much more drought tolerant than *Pinus-Fagus mixture*.

CONCLUSION

1. A significant climatic influence on the Maximum Size-Density Relationship and the maximum stand carrying capacity was found for fifteen Mediterranean tree species in Spain. A general trend linking smaller SDI_{max} values to warmer and drier conditions was found, suggesting that potential increments in temperatures and drought episodes would limit the maximum stand carrying capacity for these species. Among the climatic variables studied, maximum temperatures, especially those related to spring and summer seasons, were found to be key drivers affecting the MSDR in most of the species studied.

2. Tree growth was significantly found to be influenced by competition and aridity in mixed forests. For the majority of the mixtures studied, higher productivity rates were found in mixed than pure stands, suggesting that BAI values may increase with the increment of species diversity. Size-symmetric competition seemed to be more determinant than size-asymmetric competition in Spanish mixed forests. Based on that, competition seemed to be the most representative biological interaction in conifer-conifer mixtures, since neutralism and facilitation may occur more frequently in conifer-broadleaved and broadleaved-broadleaved mixtures. Tree growth was also found to be significantly limited by arid conditions, excepting for *Pinus halepensis* and *Pinus pinea*.

3. Height-diameter relationship was found to be significantly influenced by species proportions and climate in mixed forest stands. Regarding mixing proportions, taller trees were found in pure for conifers and mixed stands for broadleaved. Based on aridity conditions, in general, taller trees are supposed to be found in more humid conditions, with exceptions found for some mixtures considering *Pinus pinea* and *Pinus halepensis* species. The broadleaved and conifer mixed stands showed different patterns. Broadleaves species are more sensitive to prone drought sites.

4. A common and positive trend in CO_2 yield accumulations was found from 2000 to 2100 for different mixtures of *Pinus sylvestris*. Higher yield values were under the most optimistic scenario (SSP1) and lower values under the most pessimistic scenario (SSP5). However, pure and mixed stands yields evolved

differently along the simulated period of study. In the beginning of the simulation period, mixed stands generally presented smaller yields than the respective pure stands. However, our results showed that differences in yield between mixed stands and pure stands were drastically reduced at the end of the simulation period in favor of the first ones.

5. Growth rates for both pure and mixed stands of Pinus sylvestris experienced a significant reduction from 2000 to 2100 under different climate change scenarios. These reductions would be less drastic in mixed stands than in the pure ones. Growth rates for all mixed stands were higher than in pure stands at the end of the simulation period among all the analyzed mixtures, fractions (aboveground and belowground) and SSPs.

CONCLUSIONES

1. Se encontró una influencia climática significativa en la relación tamaño-densidad máxima y en la máxima capacidad de carga de la masa para quince especies arbóreas mediterráneas en España. Se encontró una tendencia general que relaciona los valores más pequeños de SDI_{max} con condiciones más cálidas y secas, sugiriendo que los incrementos potenciales de las temperaturas y los episodios de sequía limitarían la capacidad máxima de carga de la masa para estas especies. Entre las variables climáticas estudiadas, las temperaturas máximas, especialmente las relacionadas con las estaciones de primavera y verano, resultaron ser los factores clave que afectan a la SDI_{max} en la mayoría de las especies estudiadas.

2. El crecimiento de los árboles se vio significativamente influenciado por la competencia y la aridez en los bosques mixtos. Para la mayoría de las mezclas estudiadas, se encontraron mayores tasas de productividad a nivel de árbol en las masas mixtas que en puras, lo que sugiere que el crecimiento puede verse favorecido por la diversidad de especies. La competencia asimétrica por tamaño pareció ser más determinante que la competencia asimétrica por tamaño en los bosques mixtos españoles. En base a ello, la competencia parece ser la interacción biológica más representativa en las mezclas de coníferas-coníferas, ya que el neutralismo y la facilitación pueden ocurrir con más frecuencia en las mezclas de coníferas-coníferas y de frondosas-coníferas. También se encontró que el crecimiento de los árboles estaba significativamente limitado por las condiciones de aridez, a excepción de *Pinus halepensis* y *Pinus pinea*.

3. La relación altura-diámetro resultó estar significativamente influenciada por las proporciones de las especies y el clima en las masas forestales mixtas. En cuanto a las proporciones de mezcla, se encontraron árboles más altos en las masas puras para las coníferas y en las mixtas para las frondosas. En base a las condiciones de aridez, en general, se supone que los árboles más altos se encuentran en condiciones más húmedas, con excepciones encontradas para algunas mezclas que consideran las especies *Pinus pinea* y *Pinus halepensis*. Las especes de frondosas y coníferas mostraron patrones diferentes. Las

especies de frondosas parecen ser más sensibles a los sitios propensos a la sequía.

4. Se encontró una tendencia común y positiva en las acumulaciones de stock de CO_2 desde 2000 hasta 2100 para diferentes mezclas de *Pinus sylvestris*. Los valores de rendimiento fueron más altos en el escenario más optimista (SSP1) y más bajos en el escenario más pesimista (SSP5). Sin embargo, los stocks de las masas puras y mixtas evolucionaron de forma diferente a lo largo del periodo simulado de estudio. Al principio del periodo de simulación, las masas mixtas presentaban generalmente rendimientos menores que las respectivas puras. Sin embargo, nuestros resultados mostraron que las diferencias de stock entre las masas mixtos y las puras se redujeron drásticamente al final del periodo de simulación a favor de los primeras.

5. Las tasas de crecimiento tanto de las masas puras como de las mixtas de *Pinus sylvestris* experimentaron una reducción significativa entre 2000 y 2100 bajo diferentes escenarios de cambio climático. Estas reducciones serían menos drásticas en las masas mixtas que en las puras. Las tasas de crecimiento para todas las masas mixtas fueron mayores que en las masas puras al final del periodo de simulación entre todas las mezclas, fracciones (sobre y bajo el suelo) y SSPs analizadas.

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Appendix A: Supplementary Tables

Supplementary Table 1: Mean ± standard deviation and range (minimum-maximum) of the climatic variables used to fit the climate-dependent MSDR models for coniferous species.

	Pinus canariensis	*Pinus halepensis*	*Pinus nigra*	*Pinus pinea*	*Pinus pinaster*	*Pinus radiata*	*Pinus sylvestris*	*Pinus uncinata*
Plots	1158	6074	2321	4427	1352	874	4082	385
T (°C)	14.1 ± 1.8 (10-18.9)	14.1 ± 1.5 (10.5-18.1)	10.7 ± 1.1 (6.7-14.3)	12.4 ± 1.6 (7.9-17.4)	14.7 ± 2 (11.3-18.1)	12.6 ± 0.9 (9.5-17.2)	8.7 ± 1.4 (3.6-13.7)	5.2 ± 1 (2.5-7.7)
T1 (°C)	13.3 ± 2.1 (7.9-18.9)	10.4 ± 1.9 (6.4-16)	7.3 ± 1.2 (3.6-11)	9.2 ± 2 (4.7-15.2)	11.2 ± 2.5 (7.6-16.4)	10.7 ± 1.2 (7-17.2)	5.9 ± 1.4 (1.5-10.4)	3 ± 0.9 (0.7-5.3)
T2 (°C)	10.4 ± 2.1 (5.2-16.1)	7.7 ± 1.7 (3.4-12.6)	4.3 ± 1.2 (0.3-8.3)	6.6 ± 2.1 (1.6-12.3)	8.6 ± 2.4 (4.9-13.2)	7.9 ± 1.2 (4.2-14.2)	2.8 ± 1.5 (-1.8-7.7)	-0.1 ± 0.9 (-2.5-2.5)
T3 (°C)	13.8 ± 1.7 (10.2-18.3)	15.9 ± 1.3 (12.2-19.3)	12.1 ± 1.2 (7.1-15.9)	13.7 ± 1.6 (8.9-18.5)	16.3 ± 1.8 (12.9-19.2)	13.3 ± 0.7 (10.6-16.7)	9.8 ± 1.6 (3.1-15.4)	5.3 ± 1.3 (1.5-8.4)
T4 (°C)	19 ± 1.3 (16-22.7)	22.5 ± 1.3 (18.4-25.5)	19.1 ± 1.3 (13.2-23.1)	19.9 ± 1.9 (15.9-25.3)	22.7 ± 1.8 (19.5-25.7)	18.3 ± 0.7 (15.7-22)	16.4 ± 1.3 (11.1-21.3)	12.6 ± 1.1 (9.5-15.2)
MNT (°C)	10.5 ± 1.8 (6.2-15.6)	8.2 ± 1.9 (3.9-13.6)	5 ± 1.2 (1.8-9)	7.2 ± 2 (2.4-13.8)	9.1 ± 2.3 (5.4-14.7)	8.6 ± 1 (5.4-13.9)	4 ± 1.3 (0.2-8.5)	1.7 ± 0.8 (-0.6-3.9)
MNT1 (°C)	9.9 ± 2.2 (5.1-15.8)	5.6 ± 2.2 (1.4-12.6)	2.6 ± 1.2 (-0.3-7.5)	5 ± 2.3 (0.2-11.6)	6.6 ± 2.6 (2.8-13.1)	7.3 ± 1.2 (3.4-14.4)	2 ± 1.2 (-1-6.9)	0.4 ± 0.7 (-1.8-2.5)
MNT2 (°C)	6.4 ± 2.2 (0.6-12.8)	0.7 ± 2.4 (-4.6-8.2)	-2.3 ± 1.6 (-6.8-3.6)	0.5 ± 3 (-5.5-8.7)	2 ± 3 (-2.1-10)	3.4 ± 1.5 (-0.4-10.4)	-2.7 ± 1.5 (-7.5-3.6)	-4.5 ± 1.2 (-7.7--1.6)
MNT3 (°C)	9.8 ± 1.7 (5.6-15)	8.9 ± 1.8 (4.2-14.3)	5.5 ± 1.5 (1.6-10)	7.6 ± 2 (2.1-14.5)	9.7 ± 2.2 (6-15.3)	8.8 ± 0.9 (5.7-12.8)	4.2 ± 1.5 (-0.6-9.4)	0.9 ± 1 (-1.5-3.4)
MNT4 (°C)	15.7 ± 1.3 (13.3-19)	17.7 ± 1.5 (13.2-21)	14.3 ± 1.2 (10.6-18)	15.6 ± 1.7 (12.1-20.2)	18.1 ± 1.8 (14.6-20.6)	14.9 ± 0.6 (12.4-18.1)	12.5 ± 1.1 (8.9-16.9)	9.9 ± 0.8 (7.9-12.2)
MXT (°C)	17.8 ± 1.8 (12.9-22.7)	20 ± 1.3 (16-23.8)	16.4 ± 1.3 (9.9-20.1)	17.6 ± 1.6 (12.7-23.2)	20.3 ± 1.9 (16.9-24)	16.6 ± 0.9 (13.5-20.6)	13.5 ± 1.7 (6.2-18.9)	8.7 ± 1.4 (4.7-12.2)
MXT1 (°C)	16.6 ± 2.1 (10.7-22.2)	15.3 ± 1.7 (11.1-20.9)	12 ± 1.3 (6.9-15.6)	13.5 ± 1.7 (8.3-18.8)	15.9 ± 2.5 (11.8-20.4)	14.1 ± 1.2 (10.3-20.3)	9.8 ± 1.7 (3.4-14.9)	5.6 ± 1.3 (2.2-9.1)
MXT2 (°C)	14.4 ± 2.1 (9-19.8)	14.6 ± 1.4 (10.2-18.4)	11 ± 1.2 (5.5-14.3)	12.7 ± 1.6 (7.3-18)	15.2 ± 2 (11.3-19.2)	12.5 ± 1.1 (8.7-18.1)	8.4 ± 1.7 (1.9-13.6)	4.3 ± 1.1 (1.1-7.1)
MXT3 (°C)	17.9 ± 1.8 (12.9-22.8)	22.8 ± 1.4 (17.5-26.1)	18.8 ± 1.4 (10.9-23.4)	19.9 ± 1.9 (14.5-26)	22.8 ± 1.7 (19.1-26.5)	17.9 ± 0.9 (14.4-21.7)	15.3 ± 2 (6.5-21.4)	9.7 ± 1.8 (4.5-13.7)
MXT4 (°C)	22.3 ± 1.4 (17.9-26.7)	27.4 ± 1.3 (22.4-30.8)	23.8 ± 1.6 (15.9-28.2)	24.1 ± 2.2 (19.2-30.7)	27.4 ± 1.9 (23.7-30.9)	21.7 ± 0.8 (18.7-26.5)	20.3 ± 1.7 (13.1-26.1)	15.2 ± 1.6 (10.9-19)
MXTWM (°C)	23.1 ± 1.4 (18.7-27.3)	28.8 ± 1.3 (23.5-32.1)	25.3 ± 1.8 (17-30)	25.3 ± 2.5 (20-32.1)	28.7 ± 1.9 (24.9-32.3)	22.4 ± 0.8 (19.7-27.7)	21.5 ± 1.7 (14.6-27.2)	16.5 ± 1.5 (12.3-20.3)
MNTCM (°C)	5.9 ± 2.4 (-0.1-12.6)	-0.9 ± 2.7 (-6.1-7.6)	-3.8 ± 1.5 (-8.1-2.9)	-1 ± 3.2 (-7-7.8)	0.3 ± 3.3 (-4.1-9)	2.5 ± 1.7 (-1.9-10.2)	-3.9 ± 1.3 (-8.2-3)	-5 ± 1.2 (-8.2--2.1)
TAR (K)	290.3 ± 2 (285.2-294.6)	302.7 ± 2.9 (289.3-307.3)	302 ± 2.3 (291.9-307.2)	299.3 ± 4.8 (287.6-307.1)	301.4 ± 3 (291.8-306.4)	293 ± 1.7 (285.9-299.6)	298.4 ± 1.9 (290.6-305)	294.6 ± 1.8 (291.4-299.1)
P (mm)	406.8 ± 46.2 (258-516)	453.8 ± 99.6 (273-868)	599.6 ± 126.4 (373-1364)	769.9 ± 436.5 (329-1988)	489.4 ± 108.9 (326-891)	1120.2 ± 214.7 (318-1802)	799.6 ± 187.9 (393-1597)	1222.4 ± 109.8 (683-1474)
P1 (mm)	54.5 ± 6.7 (34.3-69.3)	48.6 ± 13.2 (28-109.7)	59.7 ± 13.6 (28.3-149.7)	90 ± 55.4 (30.3-252)	61.3 ± 17.6 (36.3-121.3)	116.8 ± 25.2 (46-211.7)	80.7 ± 23.2 (31-190.7)	121.9 ± 12.4 (59-153)
P2 (mm)	59.5 ± 7.3 (37-75.7)	35.5 ± 12.2 (18-119.7)	45.8 ± 13.6 (17-128)	76 ± 53.2 (20-236.7)	45.6 ± 16.6 (24-136.3)	100.8 ± 22.6 (45-213)	63 ± 19.7 (21.7-171.3)	96.8 ± 11.6 (47.7-124)
P3 (mm)	15.5 ± 1.7 (9.7-19.7)	42.6 ± 8.9 (15.7-81.7)	59.8 ± 11 (39-115.3)	60.5 ± 23.4 (30-128.3)	39.6 ± 7.4 (27.3-76.3)	91.3 ± 18 (10-119.3)	76.1 ± 13.6 (40-122)	110 ± 8.8 (77-129.7)
P4 (mm)	6.2 ± 0.9 (3.7-9.7)	24.6 ± 12.1 (6-72)	34.7 ± 16.2 (10.7-90.3)	30.1 ± 17.4 (7.3-94.7)	16.7 ± 11.6 (6.3-69.7)	64.5 ± 15.5 (4.7-99.3)	46.8 ± 16.7 (12-86)	78.8 ± 5.3 (44-88)
PWM (mm)	73.4 ± 8.7 (46-90)	59.3 ± 14.5 (37-129)	73 ± 12.6 (43-178)	104.3 ± 64.5 (38-303)	70.3 ± 21.9 (38-147)	129.3 ± 28.8 (63-260)	94 ± 22 (45-220)	131.9 ± 11.8 (91-163)
PDM (mm)	1.1 ± 0.6 (0-2)	13.5 ± 7.7 (0-46)	24.2 ± 11.6 (5-79)	19.5 ± 11.3 (1-83)	9.7 ± 8 (0-46)	53.7 ± 14.9 (0-86)	36.9 ± 13.6 (5-73)	66 ± 4.8 (37-74)
M (mm °C^{-1})	17 ± 2.9 (9.1-24.9)	18.9 ± 4.5 (10.1-39.8)	29 ± 6.3 (16.7-61.8)	34.2 ± 18.7 (13.3-84.4)	19.8 ± 4 (13.4-36.7)	49.8 ± 9.8 (11.7-81)	43.1 ± 11.7 (18.3-98.6)	81.3 ± 12.1 (40.9-118)
M1 (mm °C^{-1})	2.4 ± 0.4 (1.3-3.5)	2.4 ± 0.6 (1.3-6)	3.6 ± 0.9 (1.5-8.9)	4.7 ± 2.6 (1.7-12.5)	2.9 ± 0.6 (1.8-5.4)	5.8 ± 1.3 (1.7-10.8)	5.3 ± 1.7 (1.8-13.4)	9.7 ± 1.6 (4.3-14.3)
M2 (mm °C^{-1})	3 ± 0.6 (1.5-4.6)	2 ± 0.7 (1-7.8)	3.3 ± 1.1 (1.1-8.9)	4.5 ± 2.8 (1.2-12.4)	2.5 ± 0.7 (1.4-6.6)	5.7 ± 1.3 (1.9-11.7)	5.1 ± 1.8 (1.5-12.9)	10 ± 1.9 (4.5-15.4)
M3 (mm °C^{-1})	0.7 ± 0.1 (0.4-1)	1.7 ± 0.4 (0.7-3.6)	2.8 ± 0.5 (1.6-5.6)	2.7 ± 1 (1.1-5.5)	1.6 ± 0.3 (1-3.3)	4.1 ± 0.8 (0.4-5.3)	4.1 ± 1 (1.8-10.1)	7.7 ± 1.3 (4.6-12.4)
M4 (mm °C^{-1})	0.2 ± 0 (0.1-0.4)	0.8 ± 0.4 (0.2-2.5)	1.2 ± 0.6 (0.4-3.2)	1.1 ± 0.6 (0.2-3.4)	0.5 ± 0.4 (0.2-2.3)	2.3 ± 0.5 (0.2-3.5)	1.8 ± 0.7 (0.4-4)	3.5 ± 0.4 (1.8-4.5)
PET (mm)	963.8 ± 44.5 (849-1095)	1068.5 ± 96 (817-1298)	974 ± 84.4 (747-1183)	1011.3 ± 131.5 (754-1340)	1129.6 ± 110.9 (827-1370)	839.1 ± 50.6 (748-1116)	860.9 ± 78.4 (592-1132)	640.8 ± 44.6 (522-831)
PET1 (mm)	56 ± 3.5 (47.7-65.7)	45.8 ± 5.5 (32.7-59.7)	38.4 ± 3.8 (28.3-49)	39.8 ± 5 (31-54.7)	46.1 ± 6.2 (33-57.3)	35.9 ± 4.8 (31-61)	32.4 ± 3 (22-46.7)	24.2 ± 1.8 (19.7-32.3)
PET2 (mm)	55.3 ± 3.7 (46-65.7)	47.5 ± 4.9 (35-62)	39.5 ± 3.3 (29.3-50.7)	41.8 ± 4.7 (32.7-56.3)	47.8 ± 5.4 (35.3-59)	38.4 ± 4.2 (32.7-61)	33.7 ± 3 (22-46.7)	24.3 ± 2.2 (18.7-31)
PET3 (mm)	95.9 ± 4.5 (83.7-109)	121.8 ± 8.9 (96.7-145.7)	112.1 ± 7.5 (89-132.3)	116.9 ± 13.7 (88.3-152)	129.8 ± 11.4 (98.3-154.3)	97.2 ± 4.8 (87-122)	100.2 ± 8.3 (69-128.3)	75.2 ± 5.4 (60.3-95.7)
PET4 (mm)	114.1 ± 3.6 (104.3-124.7)	141.1 ± 15.1 (108-178.7)	134.7 ± 14.6 (100-166.3)	138.6 ± 22.1 (92.3-184.7)	152.9 ± 18.3 (108.7-186.3)	108.2 ± 6.8 (92.3-148.7)	120.7 ± 12.9 (84.3-161)	90 ± 5.6 (75.3-121.7)

Supplementary Table 2: Mean ± standard deviation and range (minimum-maximum) of the climatic variables used to fit the climate-dependent MSDR models for broadleaved species.

	Fagus sylvatica	*Quercus faginea*	*Quercus ilex*	*Quercus petraea*	*Quercus pyrenaica*	*Quercus robur*	*Quercus suber*
Plots	1117	685	3609	201	1879	560	687
T (°C)	9.4 ± 1.3 (5.1-14)	11.2 ± 1.3 (8.2-17.6)	14 ± 2.2 (6.6-17.7)	9.5 ± 1.4 (6.5-14.6)	10.4 ± 1.5 (6-15.7)	12.1 ± 1.2 (6.1-14.5)	15.5 ± 1.3 (11.4-18)
T1 (°C)	7 ± 1.4 (2.9-12.4)	8 ± 1.2 (5.5-15)	10.5 ± 2.2 (3.4-15.2)	7 ± 1.4 (4-11.3)	7.4 ± 1.5 (3.2-12.2)	10 ± 1.4 (3.8-13.5)	12.7 ± 1.7 (7.8-16.2)
T2 (°C)	4 ± 1.4 (-0.3-9.6)	5.2 ± 1.2 (2.3-11.9)	7.7 ± 2.2 (0.1-12)	4 ± 1.4 (1-8.7)	4.7 ± 1.6 (0.1-9.7)	7.5 ± 1.4 (0.8-11)	9.8 ± 1.6 (5.3-13.1)
T3 (°C)	10.4 ± 1.5 (5.2-14.5)	12.6 ± 1.4 (9.1-18.4)	15.5 ± 2.2 (7.6-19.1)	10.6 ± 1.6 (6.8-16.1)	11.6 ± 1.6 (6.9-17.2)	12.9 ± 1.2 (6.2-15.8)	16.7 ± 1.1 (12.9-18.9)
T4 (°C)	16.2 ± 1.2 (12.5-19.4)	19 ± 1.7 (15.7-25)	22.4 ± 2.3 (14.5-25.7)	16.3 ± 1.5 (13.2-22.2)	17.9 ± 1.7 (13.3-24.3)	17.8 ± 1 (13.5-20.5)	23 ± 1.2 (18.3-25.9)
MNT (°C)	5.3 ± 1.2 (1.6-10.3)	5.8 ± 1.3 (2.7-11.9)	8.2 ± 2.1 (2-13.3)	5.2 ± 1.1 (2.7-9.4)	5.6 ± 1.5 (1.8-10.3)	7.8 ± 1.1 (2.5-11.2)	10.5 ± 1.6 (6.1-14.4)
MNT1 (°C)	3.4 ± 1.3 (0.1-8.8)	3.5 ± 1.3 (0.6-10.3)	5.8 ± 2.2 (0.4-11.4)	3.3 ± 1.1 (0.8-6.9)	3.4 ± 1.5 (-0.4-8)	6.4 ± 1.3 (0.9-10.5)	8.5 ± 1.8 (3.9-12.3)
MNT2 (°C)	-0.8 ± 1.4 (-4.9-5.9)	-1 ± 1.4 (-4.8-6.5)	0.8 ± 2.2 (-6.4-7.7)	-0.9 ± 1.3 (-4-3.9)	-1 ± 1.7 (-5.9-4.5)	2.6 ± 1.5 (-4-7.5)	4 ± 2.3 (-1.3-9.9)
MNT3 (°C)	5.7 ± 1.4 (0.9-10.7)	6.4 ± 1.4 (2.7-12.6)	8.6 ± 2 (1.3-13.9)	5.6 ± 1.3 (2.7-10.6)	6 ± 1.5 (1.8-10.7)	8 ± 1.2 (1.8-11.3)	10.9 ± 1.6 (6.3-15.2)
MNT4 (°C)	12.7 ± 1 (10.1-15.8)	14.5 ± 1.6 (11.5-20.3)	17.7 ± 2.2 (10.8-20.6)	12.7 ± 1.1 (10.7-17.3)	13.9 ± 1.6 (10.6-20)	14.2 ± 0.8 (10.9-16.2)	18.8 ± 1.1 (14.3-20.7)
MXT (°C)	13.5 ± 1.6 (8.6-18.3)	16.6 ± 1.6 (12.9-23.5)	19.8 ± 2.4 (11.2-24)	13.8 ± 1.9 (9.8-19.8)	15.3 ± 1.7 (9.8-21.3)	16.4 ± 1.4 (9.6-19.2)	20.6 ± 1.4 (16.6-24.2)
MXT1 (°C)	10.5 ± 1.6 (5.4-16)	12.5 ± 1.3 (9.7-19.7)	15.1 ± 2.3 (6.3-19.9)	10.6 ± 1.8 (6.9-16.3)	11.4 ± 1.6 (6.1-16.8)	13.7 ± 1.5 (6.4-16.8)	16.9 ± 1.7 (11.7-20.1)
MXT2 (°C)	8.7 ± 1.6 (4-14.3)	11.5 ± 1.4 (7.6-19)	14.7 ± 2.4 (6.4-19.1)	9 ± 1.8 (5.6-14.2)	10.4 ± 1.8 (5.1-16.3)	12.5 ± 1.6 (5.3-15.3)	15.6 ± 1.5 (11.8-19.4)
MXT3 (°C)	15.2 ± 1.7 (9.4-19.4)	18.9 ± 1.8 (14.5-25.6)	22.5 ± 2.5 (13.1-26.3)	15.5 ± 2.1 (10.8-21.6)	17.3 ± 1.9 (11.1-23.7)	17.9 ± 1.4 (10.7-21.5)	22.5 ± 1.5 (19.1-26.5)
MXT4 (°C)	19.8 ± 1.4 (14.8-23.4)	23.5 ± 2 (19.6-30.2)	27 ± 2.5 (18.1-31.2)	20 ± 2 (15.6-27.1)	21.9 ± 1.9 (16.1-28.6)	21.4 ± 1.2 (16.2-24.8)	27.2 ± 1.5 (22.3-31.1)
MXTWM (°C)	20.8 ± 1.4 (15.9-24.1)	24.7 ± 2.1 (20.7-31.7)	28.4 ± 2.5 (19.4-32.7)	21 ± 1.9 (16.7-28.3)	23 ± 2 (17.3-30)	22.2 ± 1.1 (17.5-25.5)	28.3 ± 1.5 (22.9-32.2)
MNTCM (°C)	-1.9 ± 1.3 (-5.7-5.2)	-2.7 ± 1.4 (-5.9-5.4)	-0.9 ± 2.2 (-7.2-6.6)	-2 ± 1.1 (-5.1-2.7)	-2.4 ± 1.7 (-7.5-4.1)	1.5 ± 1.6 (-5.1-6.8)	2.7 ± 2.5 (-3.2-8.9)
TAR (K)	295.7 ± 1.5 (290.9-299.4)	300.4 ± 2.4 (294-306.5)	302.3 ± 2 (290.4-307.4)	296 ± 2 (292.2-300.5)	298.4 ± 2.2 (290.1-303.9)	293.6 ± 1.4 (288-298)	298.5 ± 3.1 (292.6-304.8)
P (mm)	1009.1 ± 122.6 (702-1396)	643.4 ± 173.2 (381-1041)	557.8 ± 142.3 (317-1567)	927 ± 155.5 (492-1405)	764.5 ± 244 (339-1763)	1371.7 ± 274.7 (753-1827)	683.8 ± 137.1 (359-1665)
P1 (mm)	101.2 ± 12.7 (68.7-161.3)	65.7 ± 17.9 (32-129)	67.9 ± 19.4 (30.7-199.7)	95.3 ± 21.6 (47.3-162.7)	86.8 ± 33.6 (37-218)	158 ± 40.8 (80.3-220.7)	89.3 ± 21.1 (40-205)
P2 (mm)	85.6 ± 12.6 (53.3-135)	52 ± 17.8 (20.3-119.7)	52.7 ± 18.5 (20.7-169.7)	77.1 ± 18.9 (39.3-138.3)	70.8 ± 30.3 (25.7-194.7)	139.6 ± 41.1 (64.3-216.7)	76.8 ± 27.7 (25.3-182.7)
P3 (mm)	90.5 ± 8.9 (67.7-117.7)	61.3 ± 14.4 (32.7-93.7)	46 ± 11.4 (30.3-99.7)	81.8 ± 9.9 (51-107)	65.1 ± 13.5 (30.7-114.7)	98.5 ± 10.7 (62.3-122.3)	43.6 ± 10.4 (29.7-108)
P4 (mm)	59.1 ± 9.5 (35-93.7)	35.5 ± 14.2 (7.7-76)	19.4 ± 13.2 (7.3-77)	54.7 ± 10.9 (26-85)	32.1 ± 11.1 (11-71.3)	61.1 ± 8.6 (39.7-102)	18.2 ± 16.6 (7-65)
PWM (mm)	109.1 ± 11.9 (84-174)	74.9 ± 18.4 (42-159)	78.5 ± 23.3 (38-216)	104.9 ± 20.1 (58-176)	98.4 ± 37.3 (40-251)	179.1 ± 51.8 (88-268)	105.7 ± 25.5 (44-240)
PDM (mm)	51.7 ± 8.3 (26-80)	28.7 ± 12.9 (1-59)	12 ± 10.9 (1-64)	45.1 ± 8.2 (19-71)	24.7 ± 10.5 (5-59)	43.5 ± 11.2 (22-87)	8.2 ± 10.8 (0-42)
M (mm °C^{-1})	52.1 ± 6.4 (40-82.7)	30.5 ± 8.8 (16.9-53.8)	23.5 ± 7.1 (12.5-65.8)	47.9 ± 9.4 (24.7-81.1)	37.6 ± 11.9 (14.1-80.2)	62.2 ± 12.1 (37.3-83.9)	26.9 ± 5.8 (14-72.9)
M1 (mm °C^{-1})	6.2 ± 0.8 (4.3-10.4)	3.7 ± 1 (1.8-7)	3.4 ± 1 (1.6-9.6)	5.8 ± 1.5 (2.9-11.4)	5.2 ± 1.9 (1.8-11.5)	8.1 ± 2.1 (4.3-11.8)	4 ± 0.9 (2-10)
M2 (mm °C^{-1})	6.2 ± 1 (3.7-11)	3.5 ± 1.1 (1.3-7.4)	3.1 ± 1.1 (1.3-9.9)	5.6 ± 1.5 (2.6-11.5)	4.9 ± 1.9 (1.5-11.8)	8 ± 2.3 (4-12.1)	3.9 ± 1.3 (1.4-10)
M3 (mm °C^{-1})	4.6 ± 0.5 (3.5-8.2)	2.8 ± 0.8 (1.2-4.8)	1.9 ± 0.6 (1.1-5.3)	4.2 ± 0.7 (2.5-6.2)	3.2 ± 0.8 (1.2-6.4)	4.5 ± 0.5 (2.5-7.1)	1.7 ± 0.5 (1.1-4.7)
M4 (mm °C^{-1})	2.3 ± 0.3 (1.4-3.7)	1.3 ± 0.5 (0.2-2.9)	0.6 ± 0.5 (0.2-3)	2.1 ± 0.4 (1-3.3)	1.2 ± 0.4 (0.4-2.6)	2.2 ± 0.3 (1.5-3.6)	0.6 ± 0.5 (0.2-2.3)
PET (mm)	848.4 ± 41.8 (645-937)	957.5 ± 93.7 (782-1332)	1132.9 ± 132.6 (719-1373)	850.8 ± 45.9 (727-952)	963.6 ± 80 (748-1215)	860.1 ± 47.6 (674-982)	1094.3 ± 125.3 (837-1379)
PET1 (mm)	32.7 ± 2.1 (24.3-38)	36.8 ± 3.9 (29.3-54)	44.8 ± 6.4 (27-57)	32.7 ± 2 (27.7-38)	35.9 ± 3.2 (28.3-48.3)	35.1 ± 1.7 (25.3-39.3)	47.8 ± 5.8 (34-58)
PET2 (mm)	34 ± 2.5 (24.3-41)	38.5 ± 4 (31.3-55.7)	46.6 ± 6 (28.3-59)	33.9 ± 2.4 (28.7-39)	37.5 ± 3.5 (29-49.7)	37.9 ± 2.2 (26-42.7)	49.4 ± 5.5 (36-59.7)
PET3 (mm)	99.1 ± 4.8 (76-109.7)	111.7 ± 10.1 (92.7-150.7)	130.1 ± 13.8 (85-154.7)	100 ± 5.2 (86-111)	112.1 ± 8.8 (87.7-140.7)	101 ± 5.9 (79.7-117)	123.5 ± 13.7 (99.3-155)
PET4 (mm)	117 ± 5.9 (90.3-129.7)	132.2 ± 14.3 (102.7-183.7)	156.2 ± 19 (99.3-187)	117 ± 6.9 (100-136)	135.7 ± 11.9 (96.3-172.3)	112.7 ± 7.7 (91-131)	144 ± 21.8 (109.3-187)

Supplementary Table 3: Species-specific coefficients, goodness of fits in terms of Akaike's Information Criterion (AIC) and pseudo-R^2 coefficient and SDI_{max} estimations for the basic MSDR models fitted by linear quantile regression at the 95th and 99th quantiles.

Functional group	Species	tau	α_0	β_0	SDI_{max}	AIC	pseudo-R^2
Coniferous	*Pinus canariensis*	0.95	12.694 ***	-1.8631 ***	810	2514.7	0.3210
		0.99	12.493 ***	-1.7431 ***	975	2710.5	0.3676
	Pinus halepensis	0.95	11.971 ***	-1.8037 ***	476	12307.3	0.3151
		0.99	11.738 ***	-1.6708 ***	578	12867.2	0.3665
	Pinus nigra	0.95	12.516 ***	-1.7924 ***	851	4807.8	0.2971
		0.99	12.892 ***	-1.8327 ***	1089	5484.2	0.2965
	Pinus pinaster	0.95	13.213 ***	-1.9787 ***	938	10046.5	0.2744
		0.99	13.065 ***	-1.8502 ***	1223	11170.9	0.2724
	Pinus pinea	0.95	13.645 ***	-2.2517 ***	600	3002.5	0.3876
		0.99	13.558 ***	-2.1227 ***	833	3599.1	0.3769
	Pinus radiata	0.95	12.498 ***	-1.7161 ***	1069	1305.9	0.3624
		0.99	13.233 ***	-1.8652 ***	1379	1571.5	0.3846
	Pinus sylvestris	0.95	12.471 ***	-1.7118 ***	1055	7229.2	0.3550
		0.99	12.736 ***	-1.7337 ***	1281	8307.9	0.3794
	Pinus uncinata	0.95	13.332 ***	-2.0183 ***	930	539.7	0.4171
		0.99	12.197 ***	-1.6159 ***	1092	572.0	0.4470
Broadleaf	*Fagus sylvatica*	0.95	13.283 ***	-2.0057 ***	922	1435.9	0.5188
		0.99	13.030 ***	-1.8756 ***	1089	1774.1	0.4990
	Quercus faginea	0.95	12.307 ***	-1.8437 ***	585	1902.5	0.2057
		0.99	12.224 ***	-1.6850 ***	898	2129.0	0.1389
	Quercus ilex	0.95	12.483 ***	-2.1209 ***	286	7723.4	0.5099
		0.99	12.439 ***	-2.0294 ***	367	8503.5	0.4919
	Quercus petraea	0.95	12.077 ***	-1.6479 ***	874	387.8	0.3990
		0.99	12.974 ***	-1.8351 ***	1173	479.4	0.3702
	Quercus pyrenaica	0.95	12.291 ***	-1.7838 ***	699	4565.1	0.2974
		0.99	12.182 ***	-1.6603 ***	932	4848.3	0.3151
	Quercus robur	0.95	12.241 ***	-1.7466 ***	749	965.7	0.4265
		0.99	12.066 ***	-1.6576 ***	837	1101.9	0.4214
	Quercus suber	0.95	12.530 ***	-1.9372 ***	542	1272.9	0.4834
		0.99	12.319 ***	-1.8162 ***	647	1424.5	0.4731

****p<0.001; **p<0.01; *p<0.05*

Supplementary Table 4.1: Climate-dependent MSDR models for *Pinus canariensis* fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2
T	107.072 ***	-16.757 ***	-1.6999 ***	-	2524.8	0.3642
T1	76.138 ***	-11.314 ***	-1.6712 ***	-	2554.2	0.3560
T2	81.878 ***	-12.343 ***	-1.6815 ***	-	2547.8	0.3578
T3	126.032 ***	-20.086 ***	-1.7406 ***	-	2502.1	0.3704
T4	206.414 ***	-34.143 ***	-1.8183 ***	-	2447.6	0.3850
MNT	96.203 ***	-14.857 ***	-1.7213 ***	-	2546.1	0.3583
MNT1	79.203 ***	-11.873 ***	-1.6778 ***	-	2559.4	0.3546
MNT2	68.779 ***	-10.070 ***	-1.6443 ***	-	2575.4	0.3501
MNT3	12.204 ***	-	3.2524 ***	-0.0175 ***	2542.7	0.3592
MNT4	159.366 ***	-25.941 ***	-1.7586 ***	-	2473.7	0.3781
MXT	111.833 ***	-17.545 ***	-1.7230 ***	-	2513.5	0.3673
MXT1	83.453 ***	-12.568 ***	-1.6919 ***	-	2555.3	0.3558
MXT2	96.515 ***	-14.864 ***	-1.7412 ***	-	2524.3	0.3643
MXT3	137.266 ***	-21.979 ***	-1.8149 ***	-	2478.6	0.3767
MXT4	192.808 ***	-31.680 ***	-1.8256 ***	-	2482.7	0.3756
MXTWM	231.904 ***	-38.519 ***	-1.8596 ***	-	2466.4	0.3800
MNTCM	261.436 **	-44.206 *	-12.8800 *	0.0398 *	2582.9	0.3486
TAR	-552.597 *	99.707 *	28.9155 *	-0.1061 *	2600.4	0.3436
P	13.161 ***	-	-2.6082 ***	0.0015 ***	2364.4	0.4067
P1	3.639 ***	2.448 ***	-2.0891 ***	-	2320.8	0.4178
P2	12.989 ***	-	-2.3961 ***	0.0075 ***	2420.9	0.3921
P3	12.954 ***	-	-2.2695 ***	0.0217 ***	2447.3	0.3851
P4	11.513 ***	0.739 ***	-1.8848 ***	-	2528.0	0.3633
PWM	4.176 ***	2.059 ***	-1.9567 ***	-	2347.4	0.4111
PDM	13.025 ***	0.071 **	-1.8108 ***	-0.1100 ***	2555.4	0.3563
M	10.028 ***	0.940 ***	-1.8486 ***	-	2435.8	0.3882
M1	11.738 ***	1.061 ***	-1.8500 ***	-	2431.5	0.3893
M2	12.005 ***	0.544 ***	-1.8100 ***	-	2488.1	0.3742
M3	12.646 ***	-	-2.0458 ***	0.3009 ***	2452.8	0.3836
M4	13.555 ***	0.576 ***	-1.8333 ***	-	2509.1	0.3685
PET	37.144 ***	-3.559 ***	-1.8398 ***	-	2488.2	0.3741
PET1	22.219 ***	-2.401 ***	-1.7990 ***	-	2496.4	0.3719
PET2	20.601 ***	-2.013 ***	-1.7907 ***	-	2499.1	0.3712
PET3	27.754 ***	-3.298 ***	-1.8447 ***	-	2504.4	0.3698
PET4	50.420 ***	-7.841 ***	-2.0254 ***	-	2479.2	0.3766

****p<0.001; **p<0.01; *p<0.05*

Supplementary Table 4.2: Climate-dependent MSDR models for *Pinus halepensis* fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2
T	262.676 **	-44.319 **	-14.2340 *	0.0435 *	12539.9	0.3435
T1	234.196 **	-39.372 **	-13.7142 **	0.0423 **	12598.1	0.3403
T2	236.144 **	-39.788 **	-13.6817 **	0.0426 **	12588.7	0.3408
T3	378.851 ***	-64.788 ***	-19.9687 ***	0.0632 ***	12491.2	0.3461
T4	367.474 ***	-62.531 ***	-18.0298 **	0.0552 **	12431.1	0.3493
MNT	223.305 ***	-37.485 ***	-13.5951 ***	0.0421 ***	12605.5	0.3399
MNT1	124.575 **	-20.006 *	-8.0578 **	0.0226 *	12617.0	0.3393
MNT2	-	-	-	-	-	-
MNT3	210.862 ***	-35.261 ***	-13.0329 ***	0.0400 **	12606.1	0.3399
MNT4	406.012 ***	-69.505 ***	-22.6423 ***	0.0720 ***	12525.2	0.3442
MXT	96.070 ***	-14.848 ***	-1.7000 ***	-	12406.5	0.3505
MXT1	49.417 ***	-6.642 ***	-1.7142 ***	-	12572.9	0.3416
MXT2	78.396 ***	-11.777 ***	-1.6945 ***	-	12448.3	0.3483
MXT3	96.948 ***	-14.977 ***	-1.7045 ***	-	12368.1	0.3526
MXT4	105.595 ***	-16.445 ***	-1.7171 ***	-	12383.7	0.3517
MXTWM	100.504 ***	-15.542 ***	-1.7134 ***	-	12394.4	0.3512
MNTCM	-	-	-	-	-	-
TAR	31.561 ***	-3.436 ***	-1.7624 ***	-	12562.0	0.3421
P	10.155 ***	0.280 ***	-1.7468 ***	-	12412.3	0.3502
P1	11.330 ***	0.155 ***	-1.7620 ***	-	12518.5	0.3445
P2	11.966 ***	-	-1.8124 ***	0.0010 ***	12530.6	0.3438
P3	10.919 ***	0.231 ***	-1.7162 ***	-	12497.5	0.3456
P4	12.249 ***	-0.117 *	-1.8022 ***	0.0022 **	12527.8	0.3441
PWM	8.722 ***	0.784 ***	-1.6057 ***	-0.0026 *	12401.9	0.3509
PDM	12.074 ***	-0.108 ***	-1.7813 ***	0.0043 ***	12510.0	0.3451
M	9.241 ***	0.886 ***	-1.5559 ***	-0.0095 **	12325.5	0.3549
M1	11.764 ***	0.216 ***	-1.7732 ***	-	12459.3	0.3477
M2	11.871 ***	0.157 ***	-1.7808 ***	-	12492.2	0.3459
M3	11.632 ***	0.227 ***	-1.7060 ***	-	12476.9	0.3467
M4	11.827 ***	-	-1.7531 ***	0.0295 ***	12533.5	0.3437
PET	28.421 ***	-2.389 *	-2.3564 ***	0.0006 *	12466.9	0.3474
PET1	13.155 ***	-0.378 ***	-1.6926 ***	-	12486.4	0.3462
PET2	13.676 ***	-0.505 ***	-1.6990 ***	-	12446.1	0.3484
PET3	24.672 ***	-2.670 **	-2.4245 ***	0.0056 *	12467.3	0.3474
PET4	25.074 ***	-2.671 ***	-2.5475 ***	0.0057 **	12498.1	0.3457

_***p<0.001; **p<0.01; *p<0.05_

Supplementary Table 4.3: Climate-dependent MSDR models for *Pinus nigra* fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2
T	871.072 ***	-151.945 ***	-48.8820 ***	0.1657 ***	5074.5	0.3036
T1	-	-	-	-	-	-
T2	-	-	-	-	-	-
T3	815.154 ***	-141.912 ***	-44.8688 ***	0.1507 ***	5066.2	0.3048
T4	119.527 ***	-18.797 ***	-1.8521 ***	-	5063.2	0.3050
MNT	-	-	-	-		
MNT1	568.796 ***	-98.980 ***	-35.8929 ***	0.1237 ***	5087.6	0.3016
MNT2	12.811 ***	-	-3.8799 ***	0.0075 **	5104.9	0.2987
MNT3	512.297 *	-88.755 *	-31.7062 *	0.1074 *	5089.2	0.3014
MNT4	748.493 **	-129.947 **	-40.9041 **	0.1358 **	5083.3	0.3023
MXT	154.667 ***	-24.995 ***	-1.9154 ***	-	5028.5	0.3102
MXT1	573.278 **	-99.152 **	-32.7777 **	0.1085 *	5085.6	0.3019
MXT2	13.019 ***	-	5.7005 ***	-0.0268 ***	5046.7	0.3075
MXT3	140.953 ***	-22.536 ***	-1.9324 ***	-	5010.9	0.3128
MXT4	104.610 ***	-16.094 **	-1.9119 ***	-	5045.9	0.3076
MXTWM	93.760 ***	-14.174 **	-1.9164 ***	-	5057.3	0.3059
MNTCM	12.800 ***	-	-4.1847 ***	0.0087 **	5100.9	0.2993
TAR	53.820 **	-7.171 *	-1.8746 ***	-	5067.2	0.3044
P	-	-	-	-	-	-
P1	11.568 ***	0.347 ***	-1.9117 ***	-	5056.4	0.3060
P2	11.821 ***	0.290 ***	-1.8973 ***	-	5047.8	0.3073
P3	-	-	-	-	-	-
P4	-	-	-	-	-	-
PWM	12.803 ***	-	-1.9221 ***	0.0010 *	5096.1	0.3001
PDM	-	-	-	-	-	-
M	11.963 ***	0.268 **	-1.8700 ***	-	5072.0	0.3037
M1	12.447 ***	0.334 ***	-1.8756 ***	-	5048.1	0.3072
M2	12.575 ***	0.282 ***	-1.8877 ***	-	5050.5	0.3069
M3	12.807 ***	-	-1.9221 ***	0.0246 *	5085.0	0.3017
M4	-	-	-	-	-	-
PET	-	-	-	-	-	-
PET1	-	-	-	-	-	-
PET2	-	-	-	-	-	-
PET3	-	-	-	-	-	-
PET4	-	-	-	-	-	-

***$p<0.001$; **$p<0.01$; *$p<0.05$

Supplementary Table 4.4: Climate-dependent MSDR models for *Pinus pinaster* fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2
T	13.283 ***	-	3.6017 ***	-0.0195 ***	10357.7	0.2909
T1	70.461 ***	-10.167 ***	-1.9061 ***	-	10445.6	0.2838
T2	346.791 *	-59.217 *	-17.0639 *	0.0541 *	10449.5	0.2836
T3	13.324 ***	-	3.9110 ***	-0.0206 ***	10296.4	0.2958
T4	13.362 ***	-	2.8886 ***	-0.0167 ***	10360.4	0.2906
MNT	-	-	-	-		
MNT1	329.208 ***	-56.126 **	-16.9772 **	0.0539 **	10523.2	0.2777
MNT2	333.907 ***	-57.140 ***	-17.7443 ***	0.0577 **	10522.1	0.2777
MNT3	74.361 ***	-10.863 ***	-1.9146 ***	-	10458.3	0.2828
MNT4	-435.827 **	79.282 **	26.8313 ***	-0.0998 ***	10430.3	0.2852
MXT	13.446 ***	-	4.1770 ***	-0.0213 ***	10229.0	0.3011
MXT1	99.279 ***	-15.226 ***	-1.9214 ***	-	10335.1	0.2927
MXT2	13.389 ***	-	3.3318 ***	-0.0187 ***	10317.1	0.2941
MXT3	13.365 ***	-	3.5759 ***	-0.0190 ***	10241.6	0.3001
MXT4	13.462 ***	-	2.6955 ***	-0.0159 ***	10307.5	0.2949
MXTWM	13.492 ***	-	2.3540 ***	-0.0147 ***	10329.3	0.2931
MNTCM	341.604 ***	-58.565 ***	-18.3189 ***	0.0601 ***	10531.9	0.2769
TAR	-440.516 ***	79.590 ***	23.5515 ***	-0.0852 ***	10489.8	0.2804
P	-	-	-	-	-	-
P1	-	-	-	-	-	-
P2	-	-	-	-	-	-
P3	8.636 ***	1.167 ***	-1.6924 ***	-0.0048 ***	10517.0	0.2782
P4	11.446 ***	0.556 ***	-1.8094 ***	-0.0048 ***	10492.2	0.2802
PWM	-	-	-	-	-	-
PDM	13.124 ***	0.106 ***	-2.0045 ***	-	10513.0	0.2783
M	11.641 ***	0.489 **	-1.8491 ***	-0.0035 **	10542.3	0.2761
M1	-	-	-	-	-	-
M2	-	-	-	-	-	-
M3	-	-	-	-	-	-
M4	12.712 ***	0.866 **	-1.8330 ***	-0.0752 **	10483.1	0.2809
PET	13.329 ***	0.461 ***	-1.8409 ***	-0.1135 ***	10475.7	0.2815
PET1	13.246 ***	-	-1.8523 ***	-0.0001 *	10569.4	0.2737
PET2	13.306 ***	-	-1.7219 ***	-0.0062 ***	10432.2	0.2849
PET3	13.340 ***	-	-1.7265 ***	-0.0061 ***	10430.2	0.2850
PET4	-27.039 ***	8.433 ***	0.7719 *	-0.0228 ***	10403.1	0.2874

***p<0.001; **p<0.01; *p<0.05

Supplementary Table 4.5: Climate-dependent MSDR models for *Pinus pinea* fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2
T	-	-	-	-	-	-
T1	-	-	-	-	-	-
T2	13.505 ***	-	-4.4234 ***	0.0080 *	3257.7	0.3921
T3	-	-	-	-	-	-
T4	-	-	-	-	-	-
MNT	-	-	-	-		
MNT1	13.650 ***	-	-4.5010 ***	0.0082 *	3250.2	0.3938
MNT2	13.763 ***	-	-4.7594 ***	0.0091 ***	3235.8	0.3970
MNT3	13.565 ***	-	-5.1013 ***	0.0103 **	3245.7	0.3948
MNT4	-	-	-	-	-	-
MXT	-	-	-	-	-	-
MXT1	-	-	-	-	-	-
MXT2	-	-	-	-	-	-
MXT3	-	-	-	-	-	-
MXT4	-	-	-	-	-	-
MXTWM	-	-	-	-	-	-
MNTCM	-29.493 *	7.684 **	-2.2089 ***	-	3228.5	0.3986
TAR	77.368 **	-11.127 *	-2.2790 ***	-	3213.2	0.4020
P	13.213 ***	-	-2.2271 ***	0.0003 **	3210.7	0.4026
P1	-	-	-	-	-	-
P2	-	-	-	-	-	-
P3	13.465 ***	-	-2.4048 ***	0.0063 ***	3226.9	0.3990
P4	15.072 ***	-0.460 *	-2.4379 ***	0.0093 ***	3139.5	0.4185
PWM	-	-	-	-	-	-
PDM	14.023 ***	-	-2.3647 ***	0.0039 *	3228.1	0.3987
M	13.304 ***	-	-2.2518 ***	0.0077 *	3216.7	0.4013
M1	-	-	-	-	-	-
M2	-	-	-	-	-	-
M3	13.649 ***	-	-2.3483 ***	0.0875 *	3249.1	0.3940
M4	13.531 ***	-0.467 **	-2.4556 ***	0.2919 ***	3144.0	0.4176
PET	20.341 ***	-0.887 *	-2.3588 ***	-	3232.4	0.3978
PET1	-	-	-	-	-	-
PET2	-	-	-	-	-	-
PET3	14.074 ***	-	-2.0350 ***	-0.0024 *	3238.5	0.3964
PET4	17.595 ***	-0.713 **	-2.3301 ***	-	3226.0	0.3992

_***p<0.001; **p<0.01; *p<0.05_

Supplementary Table 4.6: Climate-dependent MSDR models for *Pinus radiata* fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2
T	-	-	-	-	-	-
T1	-	-	-	-	-	-
T2	-	-	-	-	-	-
T3	-	-	-	-	-	-
T4	-	-	-	-	-	-
MNT	-	-	-	-	-	-
MNT1	-	-	-	-	-	-
MNT2	-	-	-	-	-	-
MNT3	-	-	-	-	-	-
MNT4	-	-	-	-	-	-
MXT	-	-	-	-	-	-
MXT1	-	-	-	-	-	-
MXT2	-	-	-	-	-	-
MXT3	-	-	-	-	-	-
MXT4	-	-	-	-	-	-
MXTWM	-	-	-	-	-	-
MNTCM	-	-	-	-	-	-
TAR	-	-	-	-	-	-
P	-	-	-	-	-	-
P1	-	-	-	-	-	-
P2	-	-	-	-	-	-
P3	-	-	-	-	-	-
P4	-	-	-	-	-	-
PWM	-	-	-	-	-	-
PDM	-	-	-	-	-	-
M	-	-	-	-	-	-
M1	-	-	-	-	-	-
M2	-	-	-	-	-	-
M3	-	-	-	-	-	-
M4	-	-	-	-	-	-
PET	-	-	-	-	-	-
PET1	6.920 **	1.675 *	-1.3894 ***	-0.0119 **	1421.2	0.3778
PET2	-	-	-	-	-	-
PET3	110.968 ***	-21.507 ***	-8.0490 ***	0.0652 ***	1402.4	0.3845
PET4	88.959 ***	-16.269 **	-6.5496 ***	0.0441 **	1409.2	0.3821

***p<0.001; **p<0.01; *p<0.05

Supplementary Table 4.7: Climate-dependent MSDR models for *Pinus sylvestris* fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2
T	-	-	-	-	-	-
T1	-	-	-	-	-	-
T2	-	-	-	-	-	-
T3	-	-	-	-	-	-
T4	55.518 **	-7.547 *	-1.7711 ***	-	7697.6	0.3698
MNT	-	-	-	-		
MNT1	-	-	-	-	-	-
MNT2	322.444 *	-55.329 *	-21.8988 *	0.0746 *	7673.7	0.3718
MNT3	-	-	-	-	-	-
MNT4	-	-	-	-	-	-
MXT	65.896 ***	-9.391 ***	-1.7774 ***	-	7664.1	0.3724
MXT1	54.869 ***	-7.463 ***	-1.7703 ***	-	7679.3	0.3712
MXT2	41.879 **	-5.164 *	-1.7745 ***	-	7696.3	0.3699
MXT3	58.945 ***	-8.154 ***	-1.7767 ***	-	7653.0	0.3732
MXT4	71.686 ***	-10.376 ***	-1.7699 ***	-	7643.9	0.3739
MXTWM	74.540 ***	-10.872 ***	-1.7675 ***	-	7637.6	0.3744
MNTCM	617.791 ***	-108.147 ***	-40.0934 ***	0.1425 ***	7630.1	0.3751
TAR	66.470 ***	-9.442 ***	-1.7478 ***	-	7594.7	0.3777
P	-	-	-	-	-	-
P1	-	-	-	-	-	-
P2	12.110 ***	0.107 **	-1.7104 ***	-	7675.6	0.3715
P3	-	-	-	-	-	-
P4	-	-	-	-	-	-
PWM	-	-	-	-	-	-
PDM	-	-	-	-	-	-
M	12.579 ***	-	-1.7462 ***	0.0007 *	7704.4	0.3693
M1	12.390 ***	0.107 **	-1.7119 ***	-	7684.3	0.3708
M2	12.375 ***	0.115 ***	-1.7107 ***	-	7670.7	0.3719
M3	-	-	-	-	-	-
M4	-	-	-	-	-	-
PET	-	-	-	-	-	-
PET1	12.675 ***	-	-1.6454 ***	-0.0031 *	7709.1	0.3689
PET2	-	-	-	-	-	-
PET3	-	-	-	-	-	-
PET4	-	-	-	-	-	-

***p<0.001; **p<0.01; *p<0.05

Supplementary Table 4.8: Climate-dependent MSDR models for *Pinus uncinata* fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2
T	65.799 ***	-9.413 **	-1.8310 ***	-	541.6	0.4536
T1	72.583 **	-10.637 *	-1.8259 ***	-	542.5	0.4530
T2	62.186 **	-8.808 *	-1.8206 ***	-	550.6	0.4472
T3	-	-	-	-	-	-
T4	-	-	-	-	-	-
MNT	-	-	-	-	-	-
MNT1	-	-	-	-	-	-
MNT2	-	-	-	-	-	-
MNT3	65.683 **	-9.395 *	-1.8730 ***	-	544.1	0.4518
MNT4	73.860 **	-10.813 *	-1.8292 ***	-	548.7	0.4486
MXT	-	-	-	-	-	-
MXT1	74.959 ***	-11.002 **	-1.9032 ***	-	539.0	0.4555
MXT2	55.316 **	-7.575 *	-1.7969 ***	-	542.7	0.4528
MXT3	52.975 ***	-7.087 **	-1.8875 ***	-	540.9	0.4541
MXT4	60.606 ***	-8.384 ***	-1.9346 ***	-	539.5	0.4551
MXTWM	56.182 **	-7.606 *	-1.9176 ***	-	540.0	0.4547
MNTCM	-	-	-	-	-	-
TAR	57.065 **	-7.756 *	-1.8802 ***	-	546.6	0.4500
P	9.699 ***	0.451 *	-1.8620 ***	-	542.5	0.4530
P1	11.168 ***	0.363 *	-1.8635 ***	-	540.0	0.4548
P2	11.386 ***	0.364 ***	-1.9112 ***	-	538.1	0.4561
P3	-	-	-	-	-	-
P4	-	-	-	-	-	-
PWM	-	-	-	-	-	-
PDM	-	-	-	-	-	-
M	11.993 ***	0.228 *	-1.8876 ***	-	541.0	0.4541
M1	12.856 ***	-	-1.9196 ***	0.0077 **	539.0	0.4555
M2	12.364 ***	0.203 **	-1.8344 ***	-	540.6	0.4543
M3	-	-	-	-	-	-
M4	-	-	-	-	-	-
PET	12.899 ***	-	-1.6288 ***	-0.0004 **	535.6	0.4578
PET1	12.896 ***	-	-1.6636 ***	-0.0082 *	538.6	0.4558
PET2	12.908 ***	-	-1.6784 ***	-0.0077 **	536.7	0.4571
PET3	12.918 ***	-	-1.6378 ***	-0.0031 **	534.6	0.4586
PET4	16.777 ***	-0.838 ***	-1.8979 ***	-	535.5	0.4580

****p<0.001; **p<0.01; *p<0.05*

Supplementary Table 4.9: Climate-dependent MSDR models for *Fagus sylvatica* fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2
T	84.978 ***	-12.783 ***	-1.8450 ***	-	1520.2	0.5264
T1	69.028 ***	-9.970 **	-1.8495 ***	-	1528.6	0.5246
T2	71.240 ***	-10.382 **	-1.8500 ***	-	1524.0	0.5255
T3	12.813 ***	-	2.0872 *	-0.0138 ***	1510.2	0.5285
T4	12.771 ***	-	3.2512 ***	-0.0176 ***	1521.3	0.5261
MNT	72.193 ***	-10.536 ***	-1.8614 ***	-	1533.1	0.5236
MNT1	61.002 ***	-8.555 ***	-1.8669 ***	-	1537.9	0.5226
MNT2	60.650 ***	-8.525 **	-1.8516 ***	-	1542.0	0.5217
MNT3	76.863 ***	-11.370 ***	-1.8514 ***	-	1531.2	0.5240
MNT4	100.456 ***	-15.481 **	-1.8687 ***	-	1529.6	0.5244
MXT	84.592 ***	-12.675 ***	-1.8615 ***	-	1515.0	0.5275
MXT1	70.247 ***	-10.155 ***	-1.8648 ***	-	1523.2	0.5257
MXT2	75.624 ***	-11.138 ***	-1.8360 ***	-	1512.2	0.5281
MXT3	12.870 ***	-	2.0880 ***	-0.0137 ***	1507.5	0.5290
MXT4	12.966 ***	-	1.9497 ***	-0.0131 ***	1523.2	0.5257
MXTWM	12.952 ***	-	2.4228 ***	-0.0147 ***	1528.7	0.5245
MNTCM	49.285 **	-6.485 *	-1.8831 ***	-	1551.5	0.5197
TAR	-	-	-	-	-	-
P	-	-	-	-	-	-
P1	13.387 ***	-	-2.1378 ***	0.0012 ***	1564.8	0.5168
P2	-	-	-	-	-	-
P3	-	-	-	-	-	-
P4	-	-	-	-	-	-
PWM	11.163 ***	0.469 ***	-2.0059 ***	-	1563.5	0.5171
PDM	-	-	-	-	-	-
M	13.279 ***	-	-2.1438 ***	0.0031 ***	1529.2	0.5244
M1	12.133 ***	0.671 ***	-2.0013 ***	-	1514.9	0.5275
M2	12.406 ***	0.450 ***	-1.9686 ***	-	1528.0	0.5247
M3	13.290 ***	-	-2.1362 ***	0.0326 **	1539.8	0.5222
M4	13.488 ***	-	-2.1392 ***	0.0421 *	1563.7	0.5171
PET	13.036 ***	-	-1.5861 ***	-0.0004 ***	1533.2	0.5236
PET1	12.911 ***	-	-1.5935 ***	-0.0085 ***	1514.5	0.5276
PET2	12.851 ***	-	-1.6180 ***	-0.0068 **	1517.0	0.5270
PET3	13.018 ***	-	-1.6126 ***	-0.0029 ***	1545.1	0.5210
PET4	-	-	-	-	-	-

***p<0.001; **p<0.01; *p<0.05

Supplementary Table 4.10: Climate-dependent MSDR models for *Quercus faginea* fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2
T	12.436 ***	-	8.7757 *	-0.0374 **	1970.3	0.2019
T1	-	-	-	-	-	-
T2	-	-	-	-	-	-
T3	233.156 ***	-38.984 **	-1.9505 ***	-	1960.8	0.2073
T4	271.627 ***	-45.750 ***	-1.6856 ***	-	1910.6	0.2359
MNT	-	-	-	-	-	-
MNT1	-1047.998 **	188.507 **	63.4382 **	-0.2352 **	1991.1	0.1908
MNT2	-	-	-	-	-	-
MNT3	-	-	-	-	-	-
MNT4	275.616 ***	-46.563 ***	-1.7134 ***	-	1934.1	0.2227
MXT	204.087 **	-33.789 **	-1.9014 ***	-	1944.0	0.2170
MXT3	12.416 ***	-	7.8794 *	-0.0340 *	1977.7	0.1975
MXT4	190.412 **	-31.459 **	-1.9219 ***	-	1968.4	0.2029
MXTWM	202.428 **	-33.429 **	-1.9483 ***	-	1934.4	0.2225
MNTCM	254.074 ***	-42.519 ***	-1.7485 ***	-	1899.6	0.2420
TAR	247.037 ***	-41.233 ***	-1.7874 ***	-	1883.7	0.2508
P	-	-	-	-	-	-
P1	12.606 ***	-	12.9044 ***	-0.0495 ***	1886.9	0.249
P2	7.655 ***	0.703 ***	-1.7754 ***	-	1933.3	0.2231
P3	9.939 ***	0.568 **	-1.8101 ***	-	1959.9	0.2079
P4	9.747 ***	0.686 ***	-1.8566 ***	-	1940.6	0.2190
PWM	8.949 ***	0.800 ***	-1.7900 ***	-	1930.8	0.2245
PDM	10.242 ***	0.542 ***	-1.7612 ***	-	1952.0	0.2124
M	8.663 ***	0.813 ***	-1.7536 ***	-	1960.1	0.2078
M1	13.080 ***	-0.249 *	-2.0875 ***	0.0095 ***	1928.2	0.2271
M2	9.667 ***	0.812 ***	-1.8657 ***	-	1915.9	0.2329
M3	11.463 ***	0.645 *	-1.8078 ***	-	1948.8	0.2142
M4	11.662 ***	0.691 ***	-1.8910 ***	-	1922.7	0.2291
PET	11.375 ***	0.838 ***	-1.7905 ***	-	1919.0	0.2312
PET1	12.083 ***	0.516 ***	-1.7726 ***	-	1943.5	0.2173
PET2	12.066 ***	-	-0.8581 ***	-0.0009 ***	1944.3	0.2169
PET3	20.420 ***	-2.270 ***	-1.8082 ***	-	1957.5	0.2093
PET4	20.828 ***	-2.343 ***	-1.8209 ***	-	1949.2	0.2140

****p<0.001; **p<0.01; *p<0.05*

Supplementary Table 4.11: Climate-dependent MSDR models for *Quercus ilex* fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2
T	11.966 ***	-	5.4244 ***	-0.0256 ***	7614.5	0.5350
T1	11.99 ***	-	4.3763 ***	-0.0223 ***	7761.6	0.5254
T2	11.959 ***	-	4.5974 ***	-0.0232 ***	7718.4	0.5283
T3	-203.752 **	38.076 **	18.6551 ***	-0.0713 ***	7548.9	0.5393
T4	12.000 ***	-	5.1724 ***	-0.0241 ***	7517.9	0.5412
MNT	12.059 ***	-	4.3424 ***	-0.0224 ***	7785.8	0.5238
MNT1	12.064 ***	-	3.5385 ***	-0.0197 ***	7880.2	0.5176
MNT2	12.221 ***	-	2.3123 ***	-0.0158 ***	7950.2	0.5129
MNT3	-183.104 *	34.619 *	15.2413 **	-0.0612 ***	7786.2	0.5239
MNT4	-171.905 **	32.405 **	16.2231 ***	-0.0624 ***	7576.3	0.5376
MXT	11.882 ***	-	5.3381 ***	-0.0248 ***	7523.0	0.5409
MXT1	11.963 ***	-	4.5508 ***	-0.0225 ***	7671.1	0.5313
MXT2	127.035 ***	-20.350 ***	-1.8931 ***	-	7568.2	0.5380
MXT3	11.899 ***	-	5.0064 ***	-0.0234 ***	7474.1	0.5440
MXT4	11.963 ***	-	5.0802 ***	-0.0234 ***	7491.1	0.5429
MXTWM	11.969 ***	-	4.7651 ***	-0.0223 ***	7484.2	0.5433
MNTCM	59.321 ***	-8.377 ***	-2.0487 ***	-	8017.5	0.5083
TAR	12.342 ***	-	2.9730 ***	-0.0166 ***	7749.4	0.5262
P	12.474 ***	-	-2.2131 ***	0.0002 ***	7877.8	0.5177
P1	-	-	-	-	-	-
P2	-	-	-	-	-	-
P3	10.088 ***	0.559 ***	-2.0213 ***	-	7640.1	0.5333
P4	11.433 ***	0.220 ***	-1.9687 ***	-	7634.6	0.5337
PWM	-	-	-	-	-	-
PDM	12.004 ***	-	-1.9947 ***	0.0037 ***	7635.8	0.5336
M	12.379 ***	-	-2.1959 ***	0.0054 ***	7747.0	0.5264
M1	12.342 ***	0.267 ***	-2.1479 ***	-	8013.3	0.5086
M2	12.387 ***	0.220 ***	-2.1347 ***	-	7997.2	0.5097
M3	11.702 ***	0.541 ***	-1.9684 ***	-	7549.0	0.5392
M4	12.139 ***	0.215 ***	-1.9555 ***	-	7588.7	0.5367
PET	11.773 ***	-	-1.4050 ***	-0.0004 ***	7449.7	0.5455
PET1	11.881 ***	-	-1.5566 ***	-0.0078 ***	7564.1	0.5382
PET2	11.865 ***	-	-1.5025 ***	-0.0087 ***	7491.1	0.5429
PET3	11.777 ***	-	-1.3094 ***	-0.0044 ***	7398.6	0.5487
PET4	11.909 ***	-	-1.5462 ***	-0.0024 ***	7510.4	0.5417

****p<0.001; **p<0.01; *p<0.05*

Supplementary Table 4.12: Climate-dependent MSDR models for Quercus petraea fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2
T	12.404 ***	-	11.6926 ***	-0.0475 ***	369.3	0.4779
T1	12.335 ***	-	12.6721 ***	-0.0513 ***	378.7	0.4656
T2	12.338 ***	-	10.9878 ***	-0.0458 ***	380.4	0.4633
T3	12.429 ***	-	9.9918 ***	-0.0414 ***	364.9	0.4836
T4	12.674 ***	-	11.0925 ***	-0.0446 ***	361.6	0.4878
MNT	-1169.241 ***	209.898 ***	82.0857 ***	-0.3009 ***	385.4	0.4593
MNT1	12.140 ***	-	12.0032 **	-0.0493 **	397.8	0.4396
MNT2	12.380 ***	-	11.4710 ***	-0.0484 ***	411.1	0.4207
MNT3	12.308 ***	-	10.6062 ***	-0.0441 ***	388.8	0.4519
MNT4	12.689 ***	-	13.1134 ***	-0.0523 ***	371.1	0.4756
MXT	-489.861 ***	88.759 ***	36.5003 ***	-0.1334 ***	357.6	0.4954
MXT1	12.623 ***	-	10.8801 **	-0.0447 ***	369.6	0.4775
MXT2	-348.430 *	63.966 *	28.0916 ***	-0.1058 ***	363.2	0.4883
MXT3	12.615 ***	-	7.5139 ***	-0.0323 ***	360.0	0.4899
MXT4	12.593 ***	-	9.0312 ***	-0.0370 ***	358.5	0.4917
MXTWM	12.382 ***	-	8.8624 ***	-0.0360 ***	360.8	0.4889
MNTCM	12.602 ***	-	10.6650 ***	-0.0459 ***	429.1	0.3942
TAR	157.524 **	-25.493 **	-1.7459 ***	-	381.0	0.4625
P	-	-	-	-	-	-
P1	-	-	-	-	-	-
P2	4.285 *	1.879 ***	-1.2898 ***	-0.0054 ***	419.1	0.4120
P3	-	-	-	-	-	-
P4	12.565 ***	-	-1.3686 ***	-0.0075 ***	398.0	0.4392
PWM	32.910 ***	-4.432 **	-2.9490 ***	0.0119 **	419.5	0.4114
PDM	12.808 ***	-	-1.4380 ***	-0.0088 ***	415.9	0.4137
M	-	-	-	-	-	-
M1	10.500 ***	0.818 ***	-1.5610 ***	-	416.1	0.4135
M2	10.786 ***	0.818 **	-1.6339 ***	-	410.9	0.4209
M3	23.887 ***	-8.481 ***	-4.2699 ***	0.6577 ***	398.5	0.4414
M4	12.167 ***	-	-1.3617 ***	-0.1387 ***	427.3	0.3969
PET	12.289 ***	-	-0.8605 *	-0.0009 *	421.7	0.4053
PET1	12.013 ***	-	-0.4393 *	-0.0345 ***	401.2	0.4349
PET2	12.283 ***	-	-0.6573 **	-0.0298 ***	385.2	0.4568
PET3	22.509 ***	-2.189 *	-1.7088 ***	-	421.0	0.4062
PET4	11.831 ***	-	-2.1149 ***	0.0049 **	431.4	0.3907

***p<0.001; **p<0.01; *p<0.05

Supplementary Table 4.13: Climate-dependent MSDR models for *Quercus pyrenaica* fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	**AIC**	**pseudo-R^2**
T	-287.444 **	53.090 **	23.9132 ***	-0.0906 ***	4589.0	0.3207
T1	-320.175 **	58.994 ***	25.2750 ***	-0.0964 ***	4636.4	0.3121
T2	-	-	-	-		
T3	-296.017 **	54.575 **	24.1656 ***	-0.0912 ***	4593.5	0.3199
T4	-187.581 *	35.255 *	17.9460 ***	-0.0679 ***	4537.2	0.330
MNT	-328.016 **	60.450 ***	25.9570 ***	-0.0994 ***	4641.4	0.3112
MNT1	12.287 ***	-	3.0745 *	-0.0174 ***	4669.0	0.3057
MNT2	62.927 **	-9.041 *	-1.7177 ***	-	4702.2	0.2996
MNT3	12.300 ***	-	3.0244 *	-0.0171 ***	4676.4	0.3044
MNT4	12.312 ***	-	7.1163 ***	-0.0309 ***	4566.5	0.3244
MXT	-255.561 *	47.321 *	20.7678 **	-0.0783 **	4578.4	0.3226
MXT1	12.178 ***	-	3.1939 ***	-0.0172 ***	4640.7	0.3110
MXT2	12.309 ***	-	3.8858 ***	-0.0199 ***	4616.6	0.3154
MXT3	-310.973 *	57.023 *	24.1039 **	-0.0892 ***	4577.6	0.3228
MXT4	12.328 ***	-	5.5596 ***	-0.0248 ***	4578.1	0.3223
MXTWM	12.335 ***	-	5.6320 ***	-0.0250 ***	4570.0	0.3238
MNTCM	-	-	-	-	-	-
TAR	64.485 ***	-9.175 ***	-1.7080 ***	-	4679.1	0.3039
P	-	-	-	-	-	-
P1	-	-	-	-	-	-
P2	-	-	-	-	-	-
P3	10.821 ***	0.320 *	-1.6870 ***	-	4686.2	0.3026
P4	11.172 ***	0.297 ***	-1.7067 ***	-	4629.3	0.3130
PWM	-	-	-	-	-	-
PDM	11.570 ***	0.234 ***	-1.7462 ***	-	4608.1	0.3169
M	9.809 ***	0.677 **	-1.5369 ***	-0.0047 *	4697.6	0.3008
M1	-	-	-	-	-	-
M2	-	-	-	-	-	-
M3	11.766 ***	0.371 ***	-1.7009 ***	-	4647.6	0.3097
M4	12.156 ***	0.275 ***	-1.7087 ***	-	4617.2	0.3153
PET	12.270 ***	-	-1.2285 ***	-0.0005 ***	4584.9	0.3211
PET1	12.222 ***	-	-1.2564 ***	-0.0130 ***	4599.0	0.3186
PET2	12.364 ***	-	-1.3735 ***	-0.0105 ***	4593.1	0.3196
PET3	12.306 ***	-	-1.1779 ***	-0.0052 ***	4584.0	0.3213
PET4	12.269 ***	-	-1.2806 ***	-0.0034 ***	4596.3	0.3190

****p<0.001; **p<0.01; *p<0.05*

Supplementary Table 4.14: Climate-dependent MSDR models for *Quercus robur* fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2
T	-658.148 *	118.548 *	41.3317 *	-0.1508 *	1001.0	0.4497
T1	-602.202 ***	108.830 ***	37.3468 ***	-0.1381 ***	996.3	0.4520
T2	76.724 ***	-11.442 ***	-1.7353 ***	-	1002.7	0.4479
T3	92.442 ***	-14.184 ***	-1.7317 ***	-	1007.5	0.4455
T4	81.830 ***	-12.287 ***	-1.7053 ***	-	1011.0	0.4437
MNT	-820.659 ***	147.740 ***	51.1787 ***	-0.1885 ***	981.1	0.4594
MNT1	-624.820 **	113.080 **	39.0364 **	-0.1458 **	993.6	0.4533
MNT2	-605.574 ***	109.939 ***	37.8316 ***	-0.1435 ***	985.5	0.4572
MNT3	-795.789 ***	143.317 ***	49.1578 ***	-0.1812 ***	974.7	0.4624
MNT4	-1112.201 ***	198.611 ***	70.2864 ***	-0.2505 ***	989.2	0.4554
MXT	63.703 ***	-9.108 ***	-1.6903 ***	-	1011.8	0.4433
MXT1	74.444 ***	-11.004 ***	-1.7205 ***	-	1004.9	0.4468
MXT2	61.685 ***	-8.777 ***	-1.6824 ***	-	1011.1	0.4437
MXT3	-	-	-	-	-	-
MXT4	-	-	-	-	-	-
MXTWM	-	-	-	-	-	-
MNTCM	81.360 **	-12.334 *	-1.6887 ***	-	994.4	0.4519
TAR	-537.820 *	96.848 *	25.9075 *	-0.0944 *	1005.4	0.4475
P	-	-	-	-	-	-
P1	12.261 ***	-	-1.7063 ***	-0.0002 *	1015.6	0.4415
P2	-	-	-	-	-	-
P3	12.295 ***	-	-1.6408 ***	-0.0011 **	1009.6	0.4445
P4	12.181 ***	-	-1.5798 ***	-0.0022 **	1001.3	0.4485
PWM	-	-	-	-	-	-
PDM	9.142 ***	0.737 *	-1.3696 ***	-0.0059 **	1006.7	0.4468
M	-	-	-	-	-	-
M1	-	-	-	-	-	-
M2	-	-	-	-	-	-
M3	-	-	-	-	-	-
M4	12.233 ***	-	-1.5876 ***	-0.0623 **	1008.3	0.4451
PET	-	-	-	-	-	-
PET1	15.108 ***	-0.749 *	-1.7925 ***	-	1013.5	0.4425
PET2	-	-	-	-	-	-
PET3	-	-	-	-	-	-
PET4	11.979 ***	-	-1.7983 ***	0.0013 *	1011.8	0.4433

****p<0.001; **p<0.01; *p<0.05*

Supplementary Table 4.15: Climate-dependent MSDR models for *Quercus suber* fitted at the 97.5th quantile arranged by AIC

model	α_0	α_1	β_0	β_1	AIC	pseudo-R^2
T	55.009 **	-7.508 *	-1.9023 ***	-	1337.2	0.4857
T1	-	-	-	-	-	-
T2	-	-	-	-	-	-
T3	101.496 **	-15.722 **	-1.8724 ***	-	1326.9	0.4896
T4	12.040 ***	-	6.6223 **	-0.0284 ***	1285.4	0.5047
MNT	-	-	-	-	-	-
MNT1	578.103 *	-100.247 *	-33.3097 **	0.1113 *	1326.3	0.4905
MNT2	557.855 ***	-96.901 ***	-32.6036 ***	0.1104 ***	1313.2	0.4954
MNT3	-	-	-	-	-	-
MNT4	12.231 ***	-	3.3563 *	-0.0178 ***	1318.1	0.4928
MXT	12.122 ***	-	4.2310 ***	-0.0206 ***	1301.1	0.4991
MXT1	473.409 *	-81.306 *	-25.7606 *	0.0823 *	1336.4	0.4868
MXT2	12.247 ***	-	3.0873 *	-0.0171 ***	1317.3	0.4931
MXT3	12.343 ***	-	9.4775 **	-0.0384 ***	1243.8	0.5195
MXT4	-670.091 **	119.608 **	43.6583 ***	-0.1515 ***	1239.5	0.5217
MXTWM	12.097 ***	-	9.7879 ***	-0.0385 ***	1235.9	0.5223
MNTCM	511.050 **	-88.657 **	-30.2000 ***	0.1022 ***	1302.8	0.4992
TAR	12.922 ***	-	2.2551 **	-0.0144 ***	1248.3	0.5179
P	24.550 ***	-1.802 *	-2.7602 ***	0.0011 **	1254.7	0.5164
P1	-	-	-	-	-	-
P2	17.454 ***	-1.033 **	-2.4402 ***	0.0048 **	1283.4	0.5062
P3	-	-	-	-	-	-
P4	-	-	-	-	-	-
PWM	27.431 ***	-3.154 ***	-3.0211 ***	0.0096 ***	1310.9	0.4962
PDM	-	-	-	-	-	-
M	13.048 ***	-	-2.2457 ***	0.0061 ***	1264.9	0.5121
M1	12.923 ***	0.347 ***	-2.1668 ***	-	1321.2	0.4917
M2	14.486 ***	-1.064 *	-2.4802 ***	0.1007 **	1295.3	0.5019
M3	-	-	-	-	-	-
M4	-	-	-	-	-	-
PET	11.606 ***	-	-1.1484 ***	-0.0005 ***	1269.5	0.5104
PET1	-	-	-	-	-	-
PET2	-	-	-	-	-	-
PET3	11.948 ***	-	-1.2349 ***	-0.0043 ***	1233.6	0.5231
PET4	11.846 ***	-	-1.3656 ***	-0.0025 ***	1239.2	0.5211

***$p<0.001$; **$p<0.01$; *$p<0.05$

Supplementary Table 5: Comparison of the MSDR slope and SDI$_{maxREF}$ values obtained for the species studied in this research and in similar works.

Functional Group	Species	β_0	SDI$_{maxREF}$	Area	Statistical analysis	Reference
Conifers	*Pinus halepensis*	-1.881	637	France	SFA	Charru et al., 2012
		-1.777	732	Catalonia	SLR	Brunet-Navarro et al., 2016
		-1.829	619	Spain	QR (97.5th percentile)	Aguirre et al., 2018
		-1.920	780	France	QR	Toigo et al., 2018
		-1.776	***526***	***Spain***	**QR (97.5th percentile)**	***This study***
	Pinus nigra	-1.653	881	France	SFA	Charru et al., 2012
		-1.787	600	Catalonia	SLR	Brunet-Navarro et al., 2016
		-1.794	960	Spain	QR (97.5th percentile)	Aguirre et al., 2018
		-1.810	1181	France	QR	Toigo et al., 2018
		-1.835	***944***	***Spain***	**QR (97.5th percentile)**	***This study***
	Pinus pinaster	-1.711	648	France	SFA	Charru et al., 2012
		-1.929	1104	Spain	QR (95th percentile)	Riofrio et al., 2016
		-1.983	1053	Spain	QR (97.5th percentile)	Aguirre et al., 2018
		-1.860	807	France	QR	Toigo et al., 2018
		-1.906	***1053***	***Spain***	**QR (97.5th percentile)**	***This study***
	Pinus pinea	-1.857	1040	South Spain	SLR	Montero et al., 1998
		-2.122	702	Spain	QR (97.5th percentile)	Aguirre et al., 2018
		-2.186	***683***	***Spain***	**QR (97.5th percentile)**	***This study***
	Pinus sylvestris	-1.750	1444	Central Spain	NLR	Rio et al., 2001
		-1.615	893	France	SFA	Charru et al., 2012
		-1.750	1297	Navarra. Spain	NLR	Condés et al., 2013
		-1.789	1144	Spain	QR (95th percentile)	Riofrio et al., 2016
		-1.647	579	Catalonia. Spain	SLR	Brunet-Navarro et al., 2016
		-1.634	1078	Europe*	NLQR (97.5th percentile)	Condés et al., 2017
		-1.726	1154	Spain	QR (97.5th percentile)	Aguirre et al., 2018
		-2.020	1000	France	QR	Toigo et al., 2018
		-1.752	***1146***	***Spain***	**QR (97.5th percentile)**	***This study***
	Pinus uncinata	-1.665	581	Catalonia	SLR	Brunet-Navarro et al., 2016
		-1.734	***1031***	***Spain***	**QR (97.5th percentile)**	***This study***
	Pinus canariensis	***-1.823***	***903***	***Spain***	**QR (97.5th percentile)**	***This study***
	Pinus radiata	***-1.825***	***1178***	***Spain***	**QR (97.5th percentile)**	***This study***
Broadleaves	*Fagus sylvatica*	-1.941	814	France	SFA	Charru et al., 2012
		-1.943	1184	Europe*	NLQR (97.5th percentile)	Condés et al., 2017
		-1.923	952	Spain	NLQR (97.5th percentile)	Condés et al., 2017
		-1.790	991	France	QR	Toigo et al., 2018
		-1.947	***995***	***Spain***	**QR (97.5th percentile)**	***This study***
	Quercus petraea	-1.911	685	France	SFA	Charru et al., 2012
		-2.080	776	France	QR	Toigo et al., 2018
		-1.678	***969***	***Spain***	**QR (97.5th percentile)**	***This study***
	Quercus robur	-1.758	651	France	SFA	Charru et al., 2012
		-1.540	760	France	QR	Toigo et al., 2018
		-1.670	***787***	***Spain***	**QR (97.5th percentile)**	***This study***
	Quercus faginea	***-1.706***	***740***	***Spain***	**QR (97.5th percentile)**	***This study***
	Quercus ilex	***-2.095***	***319***	***Spain***	**QR (97.5th percentile)**	***This study***
	Quercus pyrenaica	***-1.720***	***840***	***Spain***	**QR (97.5th percentile)**	***This study***
	Quercus suber	***-1.967***	***585***	***Spain***	**QR (97.5th percentile)**	***This study***

Note: SFA – Stochastic Frontier Analysis; QR – Quantile Regression; NLQR – Non-Linear Quantile Regression; SLR – Simple Linear Regression; NLR – Non-Lineal Regression

** Europe: Austria, France, Spain, Germany and Poland*

Supplementary Table 6: Functional traits and climatic requirements for the 15 species studied

Functional group	Species	ST	T (°C)	MTWM (°C)	MTCM (°C)	DT	P (mm)	RSP (mm)
Coniferous	*Pinus canariensis*	1	13-17	18-25	7-14	Very tolerant	400-1000	No limit
	Pinus halepensis	1.35	12-16	21-26	3-8	4.97 (0.03)	300-700	20-132
	Pinus nigra	2.1 (0.43)	9-12	20-23	1-4	4.38 (0.47)	600-1200	60-130
	Pinus pinaster	1.89 (0.21)	12-16	18-27	1-7	3	400-1600	70-150
	Pinus pinea	1	11-18	21-16	3-11	High	430-800	15-125
	Pinus radiata	2.97 (0.03)	10-13	16-20	4-8	3	1000-2000	100-290
	Pinus sylvestris	1.67 (0.33)	6-12	15-20	0-3	4.34 (0.47)	600-1200	> 100
	Pinus uncinata	1.2	4	< 15	< 0	3.88	> 800	> 200
Broadleaf	*Fagus sylvatica*	4.56 (0.11)	7.3-10	18	0	2.4 (0.43)	600-900	150-200
	Quercus faginea	-	8-16	15-26	(-3)-5	-	350-1400	> 100
	Quercus ilex	3.02 (0.19)	10-18	14-28	(-3)-11	4.72	> 450	75-100
	Quercus petraea	2.73 (0.27)	5-15	15-25	(-3)-7	3.02 (0.15)	600	150
	Quercus pyrenaica	2.55 (0.11)	11-16	12-22	(-5)-7	4.29 (0.21)	600	> 125
	Quercus robur	2.45 (0.28)	10	14-25	-10	2.95 (0.31)	600	200
	Quercus suber	-	13-16	20-26	4-5	-	> 500	23-165

Note: ST - Shade Tolerance, T - Mean Annual Temperature (°C), MTWM - Mean Temperature of the Warmest Month (°C), MTCM - Mean Temperature of the Coldest Month (°C), P - Mean Annual Precipitation (mm), and RSP - Required Summer Precipitacion (mm). Data obtained from Niinemets and Valladares (2006) and Serrada et al. (2008). Shade tolerance is ranked as proposed by Baker (1949): 1 = Very intolerant, 2 = intolerant, 3 = moderately tolerant, 4 = tolerant, 5 = very tolerant.

Supplementary Table 7: Mean (standard error) values used in the fitting on BAI and H-D models by species for the different species compositions analyzed

Mix Type	Species composition	Species	Plots	BAI$_5$	DBH	H	N	DG	HO	BA	BAintra	BAinter	BAL	BALintra	BALinter	M
Conifer – Conifer	*Pinus halepensis – Pinus nigra*	*Pinus halepensis*	227	65.56 (44.57)	20.1 (7.8)	8.7 (2.6)	679 (392)	17.3 (4.2)	8.5 (2)	13.98 (5.88)	11.5 (5.75)	2.49 (3.32)	7.61 (5.53)	6.32 (5.06)	1.29 (2.16)	25 (5)
		Pinus nigra	222	39.6 (28.58)	18.9 (8)	8.6 (3.1)	813 (513)	17.1 (5.1)	9.1 (2.7)	16.07 (7.96)	13.64 (8.77)	2.42 (3.79)	9.37 (7.09)	7.78 (7.04)	1.58 (2.96)	28 (5)
	Pinus halepensis – Pinus pinaster	*Pinus halepensis*	210	66.82 (48.65)	21.4 (8.6)	9.4 (3)	625 (355)	19.3 (5.6)	9.4 (2.5)	15.65 (6.74)	12.57 (6.11)	3.08 (4.9)	8.86 (6.34)	6.96 (5.44)	1.9 (3.49)	19 (3)
		Pinus pinaster	197	63.87 (50.64)	25.7 (10.6)	9.3 (3.5)	594 (381)	22.6 (7.4)	9.7 (3)	19.15 (8.39)	16.33 (8.79)	2.82 (4.11)	10.6 (7.68)	9.11 (7.44)	1.49 (2.6)	20 (3)
	Pinus halepensis – Pinus pinea	*Pinus halepensis*	160	70.53 (51.28)	21.1 (7.8)	9.5 (2.8)	642 (420)	18.9 (4.8)	9.4 (2.3)	15.58 (7.22)	13.52 (7.51)	2.06 (3.88)	8.67 (6.48)	7.53 (6.33)	1.15 (2.51)	27 (5)
		Pinus pinea	99	54.83 (35.21)	23 (7.1)	8.6 (2.4)	626 (417)	20.2 (4.2)	9.1 (2.1)	19.12 (11.88)	14.49 (12.48)	4.62 (4.23)	10.51 (9.35)	7.8 (8.98)	2.71 (3.19)	25 (5)
	Pinus nigra – Pinus pinaster	*Pinus nigra*	293	48.98 (36.93)	22.1 (11.2)	10.1 (4.3)	903 (565)	20.2 (7)	10.7 (3.9)	23.29 (10.33)	17.6 (9.54)	5.7 (7.6)	13.7 (9.71)	9.91 (7.97)	3.78 (6.06)	26 (5)
		Pinus pinaster	310	72.75 (52.61)	24.5 (9.9)	9.4 (3.2)	914 (608)	20.7 (6.3)	9.8 (2.9)	25.63 (12.99)	21.44 (13.07)	4.19 (6.06)	14.18 (10.97)	12.06 (10.45)	2.12 (3.84)	25 (5)
	Pinus nigra – Pinus sylvestris	*Pinus nigra*	832	50.55 (38.1)	21.3 (9.5)	10.1 (3.8)	969 (591)	18.7 (6)	10.5 (3.3)	21.91 (9.98)	17.38 (9.82)	4.53 (6.21)	12.44 (9.07)	9.79 (8.13)	2.64 (4.43)	33 (6)
		Pinus sylvestris	903	48.91 (37.94)	20.6 (8.2)	10 (3.4)	1036 (617)	18.4 (5.3)	10.4 (3.1)	23.36 (10.29)	19.82 (10.76)	3.54 (5.56)	13.26 (9.35)	11.17 (8.97)	2.09 (3.81)	37 (8)
	Pinus pinea – Pinus pinaster	*Pinus pinaster*	268	86.99 (60.49)	24.7 (9.1)	10.3 (3)	693 (487)	22.9 (6.7)	10.5 (2.6)	22.34 (9.12)	20.27 (10)	2.06 (3.48)	12.51 (8.62)	11.26 (8.69)	1.25 (2.47)	20 (3)
		Pinus pinea	221	87.91 (60.35)	26.8 (11.2)	8.8 (2.8)	525 (443)	24.2 (7.4)	9.1 (2.4)	17.92 (7.79)	14.12 (7.91)	3.8 (5.78)	9.94 (7.57)	7.79 (6.76)	2.14 (4.16)	20 (4)
	Pinus pinaster – Pinus sylvestris	*Pinus pinaster*	360	85.41 (62.74)	26.8 (10.1)	11.6 (3.9)	952 (569)	23 (7.1)	12.1 (3.5)	33.46 (14.59)	29.54 (15.26)	3.92 (6.44)	18.28 (13.16)	16.44 (12.83)	1.84 (3.78)	32 (11)
		Pinus sylvestris	409	57.69 (42.64)	25.8 (10.9)	13.4 (4.9)	912 (572)	23.8 (8)	13.9 (4.7)	32.92 (13.56)	29.27 (14.87)	3.65 (7.28)	19.05 (12.73)	16.57 (12.61)	2.48 (5.55)	32 (9)
	Pinus sylvestris – Pinus uncinata	*Pinus sylvestris*	305	68.52 (48.34)	26.8 (11)	12.1 (3.7)	841 (491)	22.6 (5.8)	12.6 (3.2)	29.88 (13.33)	26.97 (14.12)	2.91 (5.84)	16.64 (12.08)	15.3 (12)	1.33 (3.22)	61 (9)
		Pinus uncinata	238	42.85 (34.3)	23.1 (9.2)	10.7 (3.4)	988 (579)	20.9 (4.8)	11.6 (2.7)	29.64 (11.96)	25.71 (12.92)	3.93 (6.55)	17.39 (11.55)	14.64 (11.13)	2.75 (5.15)	75 (9)

Supplementary Table 7 *Cnt.*: Mean (standard error) values used in the fitting on BAI and H-D models by species for the different species compositions analyzed

Mix Type	Species composition	Species	Plots	BAI_5	DBH	H	N	DG	HO	BA	BAintra	BAinter	BAL	BALintra	BALinter	M
Conifer – Broadleaved	*Pinus halepensis – Quercus faginea*	*Pinus halepensis*	63	61.7 (44.14)	19.8 (7.2)	8.5 (2.3)	774 (381)	16.7 (3.7)	8.4 (1.8)	15.66 (7.31)	14.48 (7.52)	1.18 (1.95)	8.89 (6.59)	8.15 (6.48)	0.74 (1.42)	25 (4)
		Quercus faginea	26	20.17 (19.56)	13.9 (6.7)	7.1 (2.1)	933 (635)	14.3 (3)	8.3 (1.5)	12.19 (4.56)	6.44 (4.69)	5.75 (3.17)	6.9 (4.93)	3.5 (3.74)	3.4 (2.85)	24 (4)
	Pinus halepensis – Quercus ilex	*Pinus halepensis*	393	68.6 (50.75)	20.9 (7.7)	9.6 (3)	811 (452)	16.7 (3.8)	9.1 (2.4)	15.94 (6.78)	13.84 (7.19)	2.1 (3)	8.81 (6.45)	7.71 (6.26)	1.1 (1.95)	25 (5)
		Quercus ilex	286	18.87 (17.08)	13.9 (5.1)	6.4 (2)	1049 (620)	14.3 (3.5)	7.8 (2.2)	14.75 (6.57)	10.33 (7.04)	4.42 (4.63)	8.73 (6.21)	5.75 (5.57)	2.97 (3.72)	29 (6)
	Pinus nigra – Quercus faginea	*Pinus nigra*	187	40.51 (30.7)	20.7 (10.1)	10 (4.1)	939 (530)	17.5 (6.1)	10.2 (3.6)	18.94 (8.39)	17.18 (8.74)	1.77 (3.51)	10.92 (7.83)	9.91 (7.67)	1 (2.56)	28 (3)
		Quercus faginea	97	23.11 (18.67)	15.1 (6.5)	7.3 (2.1)	940 (558)	15 (4)	8.5 (2.1)	15.44 (9.73)	8.64 (8.06)	6.8 (5.52)	9.12 (8.01)	4.82 (6.16)	4.3 (4.6)	29 (4)
	Pinus nigra – Quercus ilex	*Pinus nigra*	410	43 (36.77)	22 (9.9)	9.9 (3.8)	1012 (600)	17.9 (5.3)	10.2 (3.4)	22.07 (11.16)	20.47 (11.9)	1.6 (3.17)	12.51 (9.64)	11.65 (9.72)	0.86 (2.03)	27 (4)
		Quercus ilex	248	18.17 (16.7)	14.5 (6.8)	5.7 (1.8)	946 (508)	14.3 (3.8)	7 (2.3)	13.98 (7.47)	9.16 (5.92)	4.82 (5.04)	8.3 (6.68)	5.04 (4.76)	3.26 (4.12)	28 (6)
	Pinus pinaster – Quercus ilex	*Pinus pinaster*	141	78.55 (54.16)	24.9 (10)	9.5 (3.3)	851 (622)	20.8 (6.3)	9.6 (2.8)	23.68 (12.29)	22.24 (13.1)	1.43 (2.38)	13.33 (10.48)	12.56 (10.63)	0.77 (1.56)	26 (8)
		Quercus ilex	101	22.69 (21.78)	14.8 (7)	6.1 (1.7)	1099 (695)	14.3 (4.5)	7 (1.6)	14.56 (6.76)	11.09 (7.01)	3.47 (5.16)	8.53 (6.29)	6.31 (5.77)	2.21 (3.78)	28 (8)
	Pinus pinaster – Quercus pyrenaica	*Pinus pinaster*	162	106.97 (69.33)	23.1 (10.7)	9.6 (3.9)	1042 (665)	19.9 (7.9)	9.9 (3.6)	25.24 (12.3)	23.42 (11.91)	1.82 (3.17)	14.26 (10.71)	13.13 (10.08)	1.13 (2.36)	28 (10)
		Quercus pyrenaica	64	29.16 (24.4)	17.8 (9.1)	10.1 (3.8)	1117 (668)	17.1 (6.3)	10.8 (3.6)	20.04 (8)	13.24 (7.39)	6.8 (7.74)	11.55 (7.82)	7.39 (6.21)	4.16 (5.49)	35 (14)
	Pinus pinaster – Quercus suber	*Pinus pinaster*	114	89 (63.16)	20.9 (7.5)	9.7 (3.5)	832 (475)	19 (5.4)	9.5 (3)	20.65 (9.59)	17.38 (9.44)	3.27 (4.95)	11.62 (8.44)	9.55 (7.76)	2.06 (3.59)	24 (9)
		Quercus suber	112	39.9 (42.98)	21.9 (10.2)	6.9 (2.4)	792 (503)	18.8 (6.8)	7.6 (2.5)	17.67 (8.39)	13.78 (7.61)	3.89 (6.08)	9.91 (7.61)	7.74 (6.5)	2.17 (4.03)	27 (7)
	Pinus pinea – Quercus ilex	*Pinus pinea*	157	78.7 (58.44)	25.1 (10.2)	8.3 (2.7)	673 (496)	19.8 (5.7)	7.9 (2.2)	17.54 (11.48)	15.09 (12.16)	2.45 (3.26)	9.34 (8.84)	8.23 (8.89)	1.11 (1.91)	22 (6)
		Quercus ilex	150	24.77 (23.06)	16 (8)	6.3 (2.1)	916 (545)	15.5 (4.9)	7.1 (2.1)	13.83 (5.92)	10.09 (5.67)	3.75 (4.61)	8.35 (5.96)	5.59 (4.88)	2.76 (3.97)	26 (9)
	Pinus pinea - Quercus suber	*Pinus pinea*	87	78.63 (53.61)	23.7 (7.9)	8.7 (2.5)	705 (383)	19.4 (3.9)	8.4 (2.2)	18.98 (8.04)	13.32 (8.28)	5.66 (4.77)	9.99 (7.38)	7.14 (6.47)	2.84 (3.31)	27 (5)
		Quercus suber	126	27.24 (28.55)	18.9 (7.3)	6.2 (1.7)	822 (469)	17.2 (4)	6.8 (1.4)	16.69 (6.79)	13.39 (6.73)	3.3 (4.83)	9.72 (6.74)	7.51 (5.92)	2.21 (3.87)	28 (3)
	Pinus sylvestris - Fagus sylvatica	*Fagus sylvatica*	169	54.55 (60.1)	24.6 (12.4)	15.1 (4.8)	943 (568)	21.4 (7)	16.1 (4)	27.13 (9.31)	22.19 (10.21)	4.95 (7.93)	16.13 (10.08)	12.79 (9.27)	3.34 (6.06)	44 (8)
		Pinus sylvestris	401	65.04 (47.34)	27.1 (11.3)	13.7 (4.5)	885 (547)	23.8 (7.9)	14.2 (4.2)	32.57 (14.01)	31.05 (14.59)	1.52 (3.78)	18.32 (12.87)	17.54 (12.85)	0.78 (2.21)	44 (8)
	Pinus sylvestris - Quercus faginea	*Pinus sylvestris*	224	50.41 (39.46)	22.2 (8.8)	10.1 (3.4)	910 (535)	19.1 (5.5)	10.2 (3.1)	23.22 (10.85)	21.14 (10.98)	2.08 (3.76)	13.24 (9.69)	11.98 (9.36)	1.26 (2.6)	40 (7)
		Quercus faginea	125	25.87 (23.15)	16.3 (9.1)	7.7 (2.8)	1107 (631)	15 (4.5)	8.4 (2.5)	17.21 (8.93)	10.7 (5.72)	6.51 (7.29)	10.16 (8.11)	6.01 (4.98)	4.15 (5.66)	38 (6)
	Pinus sylvestris - Quercus ilex	*Pinus sylvestris*	288	54.37 (42.71)	21.9 (8.5)	10.4 (3.2)	915 (482)	18.4 (5)	10.4 (2.8)	21.66 (9.33)	19.54 (9.89)	2.13 (3.49)	12.15 (8.72)	10.98 (8.58)	1.17 (2.27)	42 (8)
		Quercus ilex	188	20.29 (19.09)	14 (6.1)	6.3 (1.9)	1352 (652)	13.4 (3.5)	7.3 (2)	17.07 (6.78)	12.5 (6.7)	4.57 (5.66)	10.02 (6.84)	7.04 (5.8)	2.97 (4.4)	38 (5)
	Pinus sylvestris - Quercus petraea	*Pinus sylvestris*	80	62.65 (44.81)	23.7 (8.9)	12.5 (3.9)	954 (534)	20.5 (5.8)	12.8 (3.4)	27.78 (12.58)	26.07 (13.25)	1.71 (2.85)	15.63 (11.22)	14.65 (11.23)	0.98 (1.95)	45 (9)
		Quercus petraea	34	28.96 (26.52)	17 (8.2)	8.5 (2.9)	895 (512)	16.5 (4.5)	9.6 (2.7)	16.16 (6.23)	9.47 (3.96)	6.7 (6.09)	9.37 (6.39)	5.21 (3.83)	4.16 (4.59)	44 (10)
	Pinus sylvestris – Quercus pyrenaica	*Pinus sylvestris*	403	65.57 (47.08)	27 (12.6)	13.4 (5.3)	995 (628)	23.7 (9.3)	13.9 (5.1)	33.68 (14.1)	32.38 (14.99)	1.3 (3.37)	19.17 (13.1)	18.4 (13.29)	0.77 (2.29)	36 (9)
		Quercus pyrenaica	199	26.77 (22.28)	17.2 (9.3)	9.5 (3.1)	1320 (674)	15.5 (6)	10.2 (3)	20.78 (8.65)	16.14 (8.18)	4.65 (7.53)	12.37 (8.59)	9.43 (7.4)	2.94 (5.57)	34 (7)

Supplementary Table 7 ***Cnt.*****:** Mean (standard error) values used in the fitting on BAI and H-D models by species for the different species compositions analyzed

Mix Type	Species composition	Species	Plots	BAI_5	DBH	H	N	DG	HO	BA	BAintra	BAinter	BAL	BALintra	BALinter	M
Broadleaved – Broadleaved	*Fagus sylvatica – Quercus petraea*	*Fagus sylvatica*	121	46 (60.79)	24 (12.3)	13.6 (4.7)	1068 (542)	20.7 (6.6)	14.4 (3.8)	30.51 (11.53)	26.3 (10.7)	4.21 (7.97)	19.03 (12.27)	15.58 (10.36)	3.45 (7.5)	51 (7)
		Quercus petraea	73	51.47 (48.4)	24.9 (16.7)	12.4 (4.4)	1013 (523)	19.2 (5.7)	12.8 (4)	25.56 (10.23)	19.55 (10.73)	6.01 (7.43)	14.62 (9.68)	11.42 (8.96)	3.2 (4.75)	46 (6)
	Fagus sylvatica – Quercus pyrenaica	*Fagus sylvatica*	124	66.87 (71.23)	28 (14)	16.1 (5.5)	880 (532)	23.2 (8.6)	16.5 (5)	28.27 (10.03)	25.82 (11.56)	2.45 (4.71)	16.3 (10.35)	14.92 (10.47)	1.38 (3.18)	41 (9)
		Quercus pyrenaica	160	33.05 (25.54)	18.7 (9.8)	10.8 (3.6)	1253 (709)	16.6 (6.4)	11.5 (3.4)	21.57 (8.22)	19.59 (8.59)	1.98 (4.27)	12.78 (8.19)	11.43 (8.01)	1.34 (3.22)	34 (6)
	Fagus sylvatica – Quercus robur	*Fagus sylvatica*	68	92.97 (99.55)	33.4 (16.1)	18.9 (6.3)	647 (461)	28.8 (9.9)	19.6 (5.1)	30.17 (9.12)	26.23 (8.04)	3.94 (7.15)	17.95 (11)	15.28 (9.11)	2.66 (6.06)	47 (7)
		Quercus robur	27	93.47 (78.75)	34.7 (16.9)	17.8 (5.1)	560 (372)	29.6 (12)	18.8 (4.1)	27.99 (10.03)	15.82 (7.05)	12.17 (9.72)	15.73 (9.95)	8.77 (6.68)	6.93 (6.96)	47 (7)
	Quercus faginea – Quercus ilex	*Quercus faginea*	184	27.04 (26.52)	17.1 (10.3)	7.9 (3.5)	1276 (754)	14.1 (5.3)	7.8 (3.4)	17.08 (10.25)	12.06 (8.72)	5.02 (4.81)	9.87 (8.5)	6.88 (6.87)	2.99 (3.61)	30 (7)
		Quercus ilex	219	25.91 (25.59)	16.7 (9.6)	5.9 (1.9)	1212 (777)	14.7 (6)	6.4 (1.9)	16.38 (8.52)	13.01 (8.5)	3.37 (4.89)	9.64 (7.37)	7.47 (6.84)	2.16 (3.49)	31 (7)
	Quercus ilex – Quercus pyrenaica	*Quercus ilex*	38	34.23 (30.6)	19.3 (9.1)	6.1 (1.6)	858 (555)	17.2 (5.9)	7.2 (2.5)	16.59 (10.14)	11.39 (6.01)	5.2 (7.57)	9.58 (8.15)	6.3 (5.17)	3.27 (5.23)	30 (10)
		Quercus pyrenaica	43	25.09 (20.63)	17.9 (8.6)	8.7 (2.9)	1184 (634)	15.5 (4.7)	8.6 (2.6)	20.32 (12.07)	16.71 (10.14)	3.61 (5.67)	11.96 (9.99)	9.7 (8.36)	2.26 (3.96)	36 (11)
	Quercus ilex – Quercus suber	*Quercus ilex*	228	31.94 (28.29)	19.2 (10.7)	7.2 (2.1)	963 (749)	18.6 (7.9)	7.6 (1.7)	17.09 (8.51)	12.17 (7.95)	4.92 (5.82)	10.33 (7.66)	6.86 (6.4)	3.46 (4.77)	30 (6)
		Quercus suber	289	44.9 (45.68)	24.2 (11.5)	7.3 (2.2)	854 (588)	19.6 (6.9)	7.5 (1.6)	19.59 (8.81)	16.53 (8.47)	3.05 (4.28)	10.89 (8.02)	9.38 (7.37)	1.51 (2.7)	29 (4)
	Quercus pyrenaica – Quercus robur	*Quercus pyrenaica*	36	42.42 (28.26)	24.4 (11.4)	11.8 (4.6)	653 (464)	23.4 (8.6)	12.3 (3.9)	20.82 (7.97)	11.25 (5.79)	9.57 (5.54)	12.15 (7.99)	6.17 (5.16)	5.97 (4.48)	66 (8)
		Quercus robur	45	79.9 (69.93)	28.8 (14.3)	12.9 (4.1)	684 (505)	23.3 (8.9)	13 (3.4)	21.11 (6.62)	15.95 (6.55)	5.16 (5.55)	11.79 (7.33)	8.98 (6.32)	2.81 (3.66)	66 (7)

Note: BAI_5 – Basal area increment in five years ($cm^2 \cdot 5\ yrs^{-1}$), DBH – Diameter at breast height (cm), H – Total tree height (m), N –Density ($trees \cdot ha^{-1}$), DG - Mean quadratic diameter (cm), HO – Dominant height (m), BA – Basal area ($m^2 \cdot ha^{-1}$), BAintra – Intraspecific basal area ($m^2 \cdot ha^{-1}$), BAinter – Interspecific basal area ($m^2 \cdot ha^{-1}$), BAL – Basal area of larger trees ($m^2 \cdot ha^{-1}$), BALintra – Intraspecific BAL ($m^2 \cdot ha^{-1}$), BALinter – Interspecific BAL ($m^2 \cdot ha^{-1}$), M – De Martonne Index ($mm \cdot {}^{\circ}C^{-1}$)

Supplementary Table 8: Competition Equivalence Coefficients (e2-1 = $SDI_{max,sp1}/SDI_{max,sp2}$ | e1-2 = $SDI_{max,sp2}/SDI_{max,sp1}$) for the most representative species compositions in Spain

Species 2

Species 1

	Fagus sylvatica	*Pinus halepensis*	*Pinus nigra*	*Pinus pinaster*	*Pinus pinea*	*Pinus sylvestris*	*Pinus uncinata*	*Quercus faginea*	*Quercus ilex*	*Quercus petraea*	*Quercus pyrenaica*	*Quercus robur*	*Quercus suber*
Fagus sylvatica	1.00	0.54	1.04	1.16	0.61	1.20	0.86	0.76	0.45	0.89	0.81	0.79	0.64
Pinus halepensis	1.85	1.00	1.73	1.96	1.31	2.11	1.60	1.02	0.65	1.31	1.31	1.44	1.09
Pinus nigra	0.97	0.58	1.00	1.12	0.78	1.20	0.86	0.68	0.41	0.74	0.77	0.77	0.63
Pinus pinaster	0.87	0.51	0.89	1.00	0.69	1.10	0.77	0.55	0.35	0.66	0.67	0.68	0.57
Pinus pinea	1.65	0.77	1.31	1.48	1.00	1.66	1.28	0.68	0.45	0.93	0.96	1.23	0.83
Pinus sylvestris	0.85	0.47	0.84	0.91	0.61	1.00	0.77	0.58	0.33	0.69	0.65	0.64	0.49
Pinus uncinata	1.17	0.63	1.16	1.31	0.78	1.30	1.00	0.84	0.47	1.05	0.96	0.91	0.74
Quercus faginea	1.36	1.08	1.50	1.95	1.61	1.81	1.20	1.00	0.66	1.10	1.13	1.06	1.20
Quercus ilex	2.29	1.59	2.50	2.92	2.27	3.10	2.12	1.55	1.00	1.81	1.85	1.79	1.73
Quercus petraea	1.15	0.83	1.41	1.58	1.21	1.60	0.96	0.92	0.56	1.00	1.03	0.95	0.93
Quercus pyrenaica	1.24	0.78	1.32	1.52	1.11	1.59	1.04	0.89	0.55	0.98	1.00	0.97	0.88
Quercus robur	1.27	0.69	1.32	1.46	0.81	1.59	1.11	0.96	0.57	1.05	1.03	1.00	0.83
Quercus suber	1.58	0.92	1.59	1.75	1.21	2.03	1.36	0.91	0.59	1.11	1.15	1.22	1.00

Supplementary Table 9: Total (aboveground + belowground) biomass yield (Mg · ha^{-1}) simulated for the 2000-2100 period under different SSPs, showing the data corresponding to each 20 years period.

SSP	Mix	Type	2000	2020	2040	2060	2080	2100
SSP1	*Pinus sylvestris - Fagus sylvatica*	*Pinus sylvestris*	147.44 (70)	208.23 (70.4)	262.46 (70.8)	306.88 (71.2)	343.36 (71.6)	371.22 (71.9)
		Fagus sylvatica	216.97 (83.7)	282.79 (83.9)	332.32 (84.1)	365.82 (84.2)	387.48 (84.4)	401.56 (84.5)
		Mix	141.32 (78)	196.77 (78.3)	248.76 (78.6)	295.75 (78.8)	337.55 (79)	374.44 (79.1)
	Pinus sylvestris - Pinus nigra	*Pinus sylvestris*	110.87 (82.1)	158.31 (81.5)	195.66 (81)	223.82 (80.6)	244.04 (80.4)	258.14 (80.1)
		Pinus nigra	110.83 (67.7)	162.87 (68.3)	207.78 (68.7)	243.57 (69.1)	271.1 (69.4)	292.08 (69.7)
		Mix	94.31 (75.1)	141.74 (75.1)	183.39 (75.1)	218.98 (75.1)	248.8 (75)	273.79 (75)
	Pinus sylvestris - Pinus pinaster	*Pinus sylvestris*	170.02 (70.9)	224.24 (71)	266.12 (71.2)	297.16 (71.4)	319.37 (71.6)	335.34 (71.8)
		Pinus pinaster	116.12 (78.2)	174.77 (77)	222.21 (76.2)	256.9 (75.5)	281.8 (75)	299.62 (74.5)
		Mix	131.86 (72.9)	193.8 (72.8)	247.32 (72.7)	292.43 (72.6)	329.46 (72.5)	360.55 (72.4)
	Pinus sylvestris - Quercus pyrenaica	*Pinus sylvestris*	181.3 (70.6)	243.56 (70.7)	287.92 (70.9)	317.53 (71.2)	337.6 (71.4)	351.99 (71.6)
		Quercus pyrenaica	111.42 (70.9)	160.02 (71.3)	206.39 (71.6)	244.63 (71.7)	275.31 (71.8)	298.56 (71.9)
		Mix	123.07 (69)	201.53 (69.6)	269.64 (70.1)	322.81 (70.5)	363.65 (70.9)	396.51 (71.2)
SSP2	*Pinus sylvestris - Fagus sylvatica*	*Pinus sylvestris*	147.44 (70)	208.23 (70.4)	262.32 (70.8)	306.35 (71.2)	341.58 (71.6)	368.54 (71.9)
		Fagus sylvatica	216.97 (83.7)	282.79 (83.9)	332 (84.1)	364.46 (84.2)	383.93 (84.4)	396.49 (84.5)
		Mix	141.32 (78)	196.77 (78.3)	248.56 (78.6)	294.79 (78.8)	335.2 (78.9)	370.6 (79.1)
	Pinus sylvestris - Pinus nigra	*Pinus sylvestris*	110.87 (82.1)	158.31 (81.5)	195.57 (81)	223.38 (80.6)	242.52 (80.4)	255.69 (80.1)
		Pinus nigra	110.83 (67.7)	162.87 (68.3)	207.67 (68.7)	243.22 (69.1)	270.21 (69.4)	290.74 (69.7)
		Mix	94.31 (75.1)	141.74 (75.1)	183.3 (75.1)	218.57 (75.1)	247.62 (75)	271.97 (75)
	Pinus sylvestris - Pinus pinaster	*Pinus sylvestris*	170.02 (70.9)	224.24 (71)	265.99 (71.2)	296.69 (71.4)	318.14 (71.6)	333.73 (71.8)
		Pinus pinaster	116.12 (78.2)	174.77 (77)	222.21 (76.2)	256.82 (75.5)	281.68 (75)	299.35 (74.5)
		Mix	131.86 (72.9)	193.8 (72.8)	247.25 (72.7)	292.07 (72.6)	328.79 (72.5)	359.61 (72.4)
	Pinus sylvestris - Quercus pyrenaica	*Pinus sylvestris*	181.3 (70.6)	243.56 (70.7)	287.77 (70.9)	316.95 (71.2)	336.04 (71.4)	349.71 (71.6)
		Quercus pyrenaica	111.42 (70.9)	160.02 (71.3)	206.39 (71.6)	244.63 (71.7)	275.25 (71.8)	298.32 (71.9)
		Mix	123.07 (69)	201.53 (69.6)	269.45 (70.1)	322.01 (70.5)	361.92 (70.8)	394.14 (71.1)
SSP3	*Pinus sylvestris - Fagus sylvatica*	*Pinus sylvestris*	147.44 (70)	208.23 (70.4)	262.17 (70.8)	305.93 (71.2)	340.34 (71.6)	366.63 (71.9)
		Fagus sylvatica	216.97 (83.7)	282.79 (83.9)	330.99 (84.1)	362.57 (84.2)	380.09 (84.4)	391.12 (84.5)
		Mix	141.32 (78)	196.77 (78.3)	248.33 (78.6)	294.12 (78.8)	333.18 (78.9)	367.44 (79)
	Pinus sylvestris - Pinus nigra	*Pinus sylvestris*	110.87 (82.1)	158.31 (81.5)	195.26 (81)	222.58 (80.6)	240.73 (80.4)	253.31 (80.1)
		Pinus nigra	110.83 (67.7)	162.87 (68.3)	207.49 (68.7)	242.85 (69.1)	269.38 (69.4)	289.53 (69.7)
		Mix	94.31 (75.1)	141.74 (75.1)	183.1 (75.1)	218.09 (75.1)	246.45 (75)	270.26 (75)
	Pinus sylvestris - Pinus pinaster	*Pinus sylvestris*	170.02 (70.9)	224.24 (71)	265.9 (71.2)	296.4 (71.4)	317.26 (71.6)	332.44 (71.8)
		Pinus pinaster	116.12 (78.2)	174.77 (77)	222.21 (76.2)	256.73 (75.5)	281.52 (75)	299.08 (74.5)
		Mix	131.86 (72.9)	193.8 (72.8)	247.22 (72.7)	291.98 (72.6)	328.29 (72.5)	358.81 (72.4)
	Pinus sylvestris - Quercus pyrenaica	*Pinus sylvestris*	181.3 (70.6)	243.56 (70.7)	287.53 (70.9)	316.45 (71.2)	334.7 (71.4)	347.76 (71.6)
		Quercus pyrenaica	111.42 (70.9)	160.02 (71.3)	206.39 (71.6)	244.63 (71.7)	275.01 (71.8)	297.89 (71.9)
		Mix	123.07 (69)	201.53 (69.6)	269.21 (70.1)	321.49 (70.5)	360.44 (70.8)	392.05 (71.1)
SSP5	*Pinus sylvestris - Fagus sylvatica*	*Pinus sylvestris*	147.44 (70)	208.23 (70.4)	262.03 (70.8)	305.29 (71.2)	339.06 (71.5)	364.93 (71.9)
		Fagus sylvatica	216.97 (83.7)	282.79 (83.9)	330.61 (84.1)	360.95 (84.2)	376.92 (84.3)	387.1 (84.5)
		Mix	141.32 (78)	196.77 (78.3)	248.14 (78.6)	293.11 (78.8)	331.14 (78.9)	364.6 (79)
	Pinus sylvestris - Pinus nigra	*Pinus sylvestris*	110.87 (82.1)	158.31 (81.5)	195.24 (81)	221.99 (80.6)	239.53 (80.4)	251.58 (80.1)
		Pinus nigra	110.83 (67.7)	162.87 (68.3)	207.44 (68.7)	242.45 (69.1)	268.64 (69.4)	288.48 (69.7)
		Mix	94.31 (75.1)	141.74 (75.1)	183.05 (75.1)	217.6 (75.1)	245.48 (75)	268.88 (75)
	Pinus sylvestris - Pinus pinaster	*Pinus sylvestris*	170.02 (70.9)	224.24 (71)	265.72 (71.2)	295.9 (71.4)	316.4 (71.6)	331.35 (71.8)
		Pinus pinaster	116.12 (78.2)	174.77 (77)	222.21 (76.2)	256.57 (75.5)	281.31 (75)	298.76 (74.5)
		Mix	131.86 (72.9)	193.8 (72.8)	247.08 (72.7)	291.65 (72.6)	327.65 (72.5)	358.13 (72.4)
	Pinus sylvestris - Quercus pyrenaica	*Pinus sylvestris*	181.3 (70.6)	243.56 (70.7)	287.31 (70.9)	315.71 (71.2)	333.54 (71.4)	346.35 (71.6)
		Quercus pyrenaica	111.42 (70.9)	160.02 (71.3)	206.39 (71.6)	244.45 (71.7)	274.79 (71.8)	297.47 (71.9)
		Mix	123.07 (69)	201.53 (69.6)	268.93 (70.1)	320.71 (70.5)	359.18 (70.8)	390.43 (71.1)

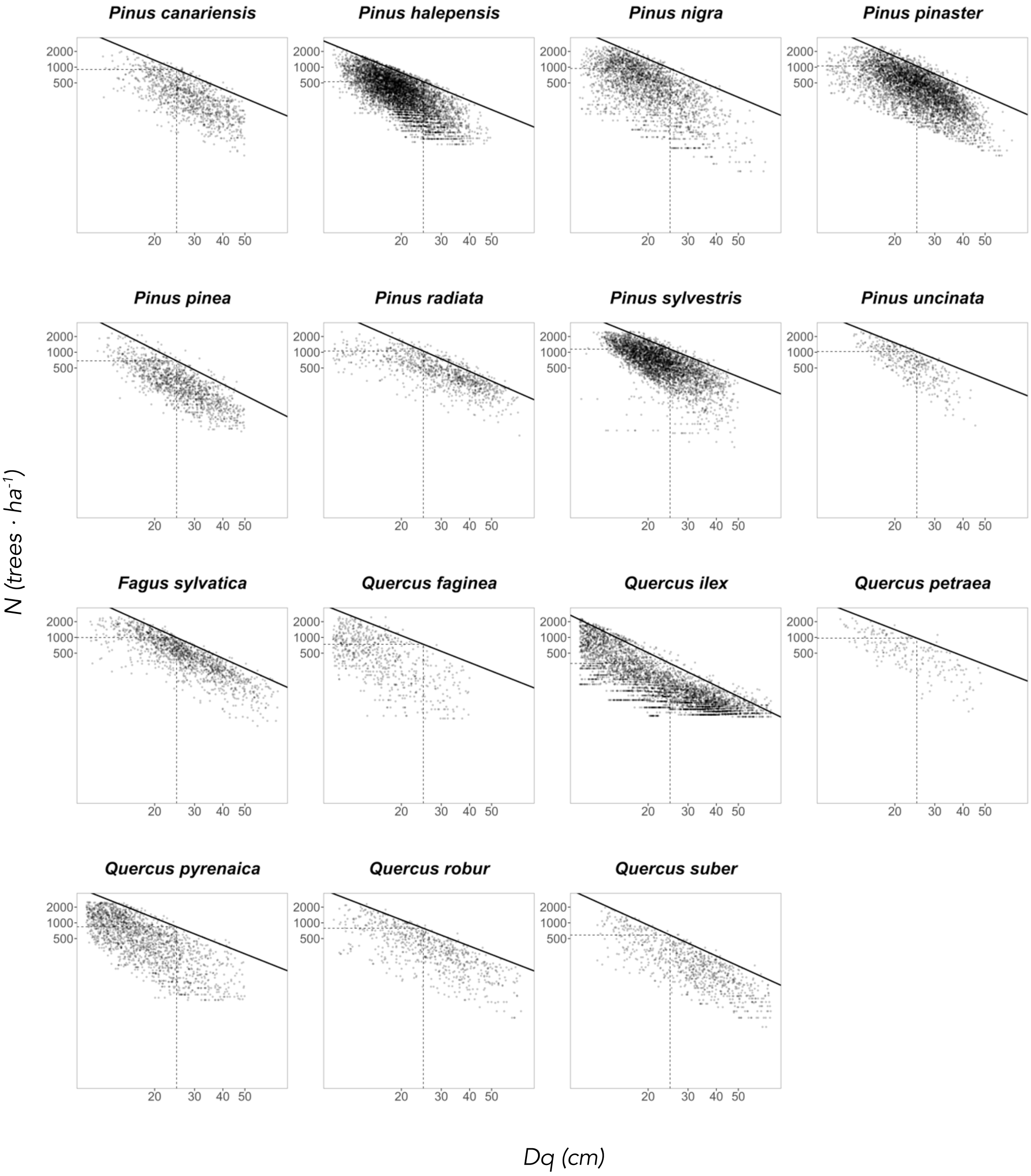
Note: Data in brackets correspond to the amount of aboveground biomass comparing to the total (%)

Supplementary Table10: Forest biomass growth (Mg · ha^{-1}· yr^{-1}) simulated for the Reference period (Ref:2000-2010) and 2100.

Mixture	Variable	Type	Ref	SSP1	SSP2	SSP3	SSP5
Pinus sylvestris – Fagus sylvatica	Aboveground	*Pinus sylvestris*	1,56	0.77 (-50.64%)	0.74 (-52.56%)	0.72 (-53.85%)	0.72 (-53.85%)
		Fagus sylvatica	2,41	0.56 (-76.76%)	0.5 (-79.25%)	0.44 (-81.74%)	0.41 (-82.99%)
		Mix	2,19	1.48 (-32.42%)	1.42 (-35.16%)	1.38 (-36.99%)	1.34 (-38.81%)
	Belowground	*Pinus sylvestris*	0,62	0.24 (-61.29%)	0.23 (-62.9%)	0.22 (-64.52%)	0.22 (-64.52%)
		Fagus sylvatica	0,44	0.08 (-81.82%)	0.07 (-84.09%)	0.06 (-86.36%)	0.06 (-86.36%)
		Mix	0,58	0.36 (-37.93%)	0.35 (-39.66%)	0.34 (-41.38%)	0.34 (-41.38%)
	Total	*Pinus sylvestris*	2,17	1.01 (-53.46%)	0.98 (-54.84%)	0.96 (-55.76%)	0.94 (-56.68%)
		Fagus sylvatica	2,85	0.64 (-77.54%)	0.57 (-80%)	0.5 (-82.46%)	0.46 (-83.86%)
		Mix	2,77	1.84 (-33.57%)	1.77 (-36.1%)	1.71 (-38.27%)	1.68 (-39.35%)
Pinus sylvestris – Pinus nigra	Aboveground	*Pinus sylvestris*	1,9	0.53 (-72.11%)	0.5 (-73.68%)	0.48 (-74.74%)	0.45 (-76.32%)
		Pinus nigra	1,81	0.77 (-57.46%)	0.76 (-58.01%)	0.74 (-59.12%)	0.73 (-59.67%)
		Mix	1,78	0.94 (-47.19%)	0.9 (-49.44%)	0.88 (-50.56%)	0.87 (-51.12%)
	Belowground	*Pinus sylvestris*	0,48	0.17 (-64.58%)	0.16 (-66.67%)	0.15 (-68.75%)	0.15 (-68.75%)
		Pinus nigra	0,8	0.28 (-65%)	0.27 (-66.25%)	0.27 (-66.25%)	0.26 (-67.5%)
		Mix	0,58	0.32 (-44.83%)	0.31 (-46.55%)	0.3 (-48.28%)	0.3 (-48.28%)
	Total	*Pinus sylvestris*	2,38	0.7 (-70.59%)	0.66 (-72.27%)	0.63 (-73.53%)	0.6 (-74.79%)
		Pinus nigra	2,6	1.05 (-59.62%)	1.02 (-60.77%)	1 (-61.54%)	1 (-61.54%)
		Mix	2,38	1.25 (-47.48%)	1.21 (-49.16%)	1.19 (-50%)	1.17 (-50.84%)
Pinus sylvestris – Pinus pinaster	Aboveground	*Pinus sylvestris*	1,38	0.44 (-68.12%)	0.43 (-68.84%)	0.42 (-69.57%)	0.41 (-70.29%)
		Pinus pinaster	1,84	0.48 (-73.91%)	0.48 (-73.91%)	0.48 (-73.91%)	0.48 (-73.91%)
		Mix	2,25	1.11 (-50.67%)	1.1 (-51.11%)	1.09 (-51.56%)	1.08 (-52%)
	Belowground	*Pinus sylvestris*	0,55	0.14 (-74.55%)	0.14 (-74.55%)	0.13 (-76.36%)	0.13 (-76.36%)
		Pinus pinaster	0,61	0.24 (-60.66%)	0.24 (-60.66%)	0.23 (-62.3%)	0.23 (-62.3%)
		Mix	0,86	0.44 (-48.84%)	0.44 (-48.84%)	0.44 (-48.84%)	0.44 (-48.84%)
	Total	*Pinus sylvestris*	1,94	0.57 (-70.62%)	0.56 (-71.13%)	0.54 (-72.16%)	0.53 (-72.68%)
		Pinus pinaster	2,46	0.73 (-70.33%)	0.72 (-70.73%)	0.71 (-71.14%)	0.71 (-71.14%)
		Mix	3,09	1.55 (-49.84%)	1.54 (-50.16%)	1.52 (-50.81%)	1.52 (-50.81%)
Pinus sylvestris – Quercus pyrenaica	Aboveground	*Pinus sylvestris*	2,21	0.55 (-75.11%)	0.52 (-76.47%)	0.5 (-77.38%)	0.5 (-77.38%)
		Quercus pyrenaica	1,75	0.84 (-52%)	0.84 (-52%)	0.84 (-52%)	0.82 (-53.14%)
		Mix	2,76	1.23 (-55.43%)	1.2 (-56.52%)	1.18 (-57.25%)	1.16 (-57.97%)
	Belowground	*Pinus sylvestris*	0,9	0.17 (-81.11%)	0.16 (-82.22%)	0.15 (-83.33%)	0.15 (-83.33%)
		Quercus pyrenaica	0,68	0.32 (-52.94%)	0.32 (-52.94%)	0.31 (-54.41%)	0.31 (-54.41%)
		Mix	1,16	0.42 (-63.79%)	0.41 (-64.66%)	0.4 (-65.52%)	0.4 (-65.52%)
	Total	*Pinus sylvestris*	3,12	0.72 (-76.92%)	0.68 (-78.21%)	0.66 (-78.85%)	0.64 (-79.49%)
		Quercus pyrenaica	2,43	1.17 (-51.85%)	1.16 (-52.26%)	1.15 (-52.67%)	1.13 (-53.5%)
		Mix	3,92	1.64 (-58.16%)	1.61 (-58.93%)	1.58 (-59.69%)	1.56 (-60.2%)

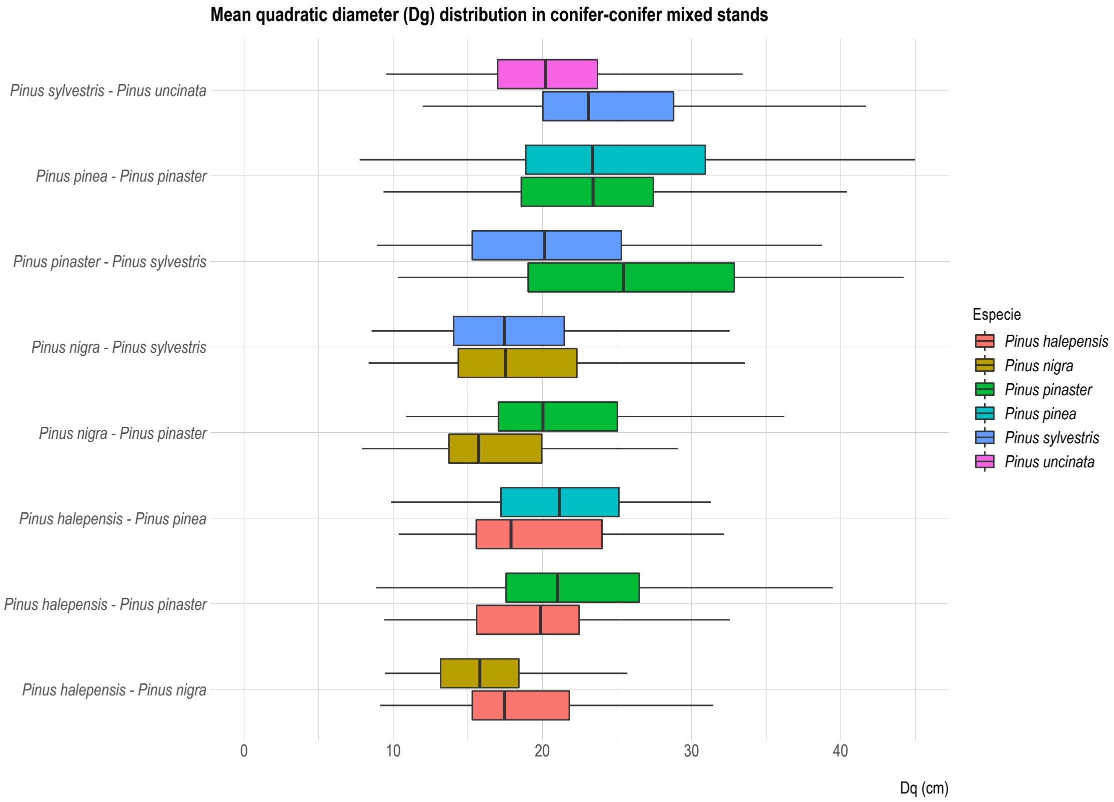
Note: In brackets, the difference in percentage between Ref and 2100 production values for the different SSPs

Appendix B: Supplementary Figures

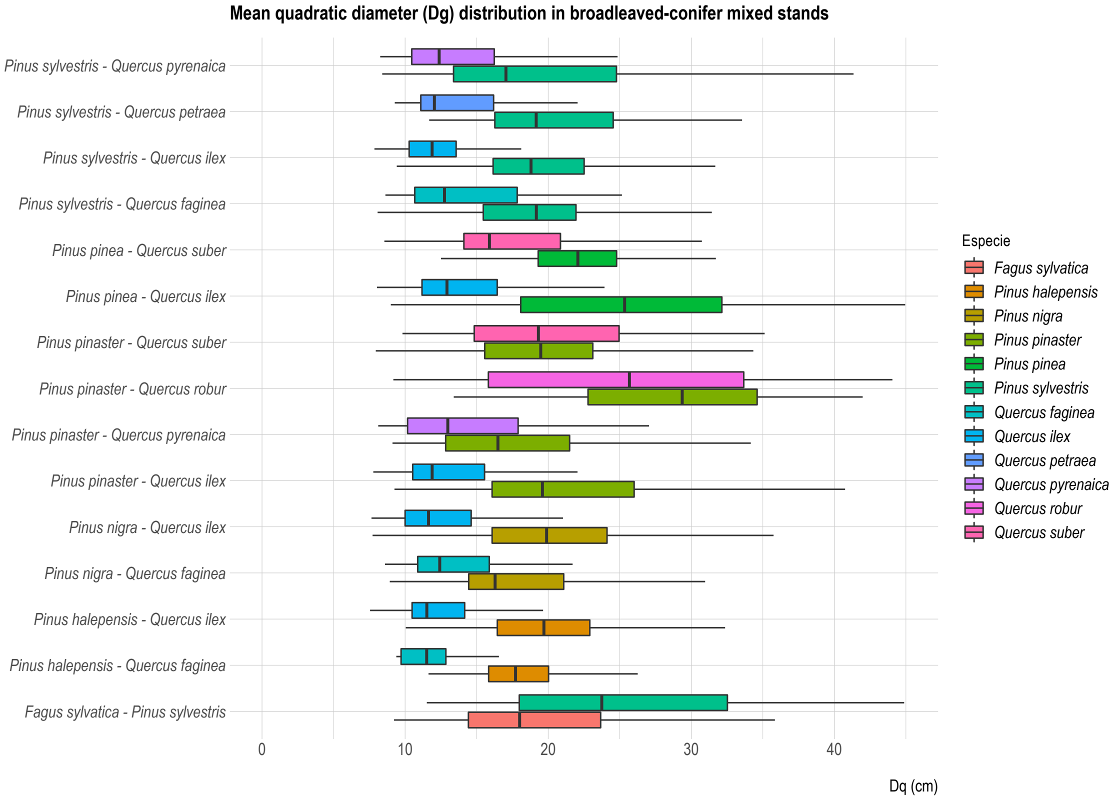


Supplementary Figure 1: Maximum Size-Density Relationships (MSDR) for the 15 coniferous and broadleaf species studied, plotted on a log-log scale for the selected monospecific stands.

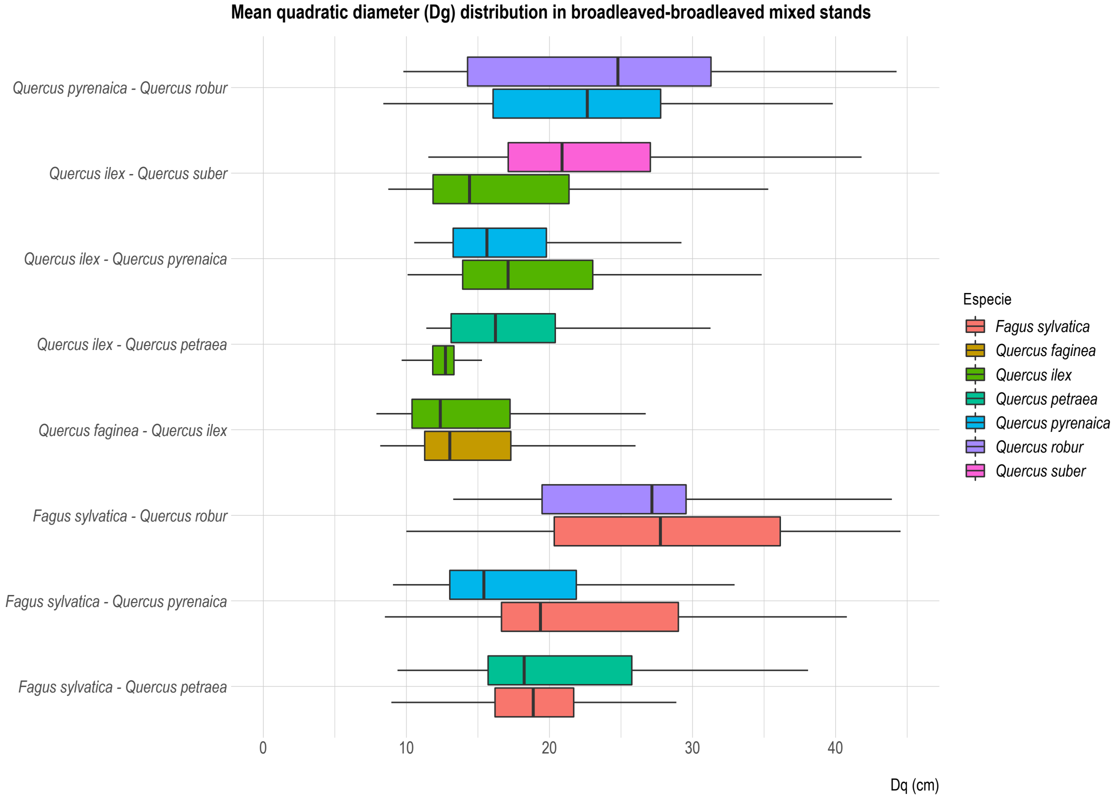
Note: Self-thinning boundary lines fitted by quantile regression (97.5th quantile) are represented by solid lines. Dashed lines represent the SDI_{maxREF} *(maximum number of trees at a Dq reference of 25 cm).*


Mean quadratic diameter (Dg) distribution in conifer-conifer mixed stands
Pinus sylvestris - Pinus uncinata
Pinus pinea - Pinus pinaster
Pinus pinaster - Pinus sylvestris
Pinus nigra - Pinus sylvestris
Pinus nigra - Pinus pinaster
Pinus halepensis - Pinus pinea
Pinus halepensis - Pinus pinaster
Pinus halepensis - Pinus nigra
0
10
20
30
40
Dq (cm)
Especie
Pinus halepensis
Pinus nigra
Pinus pinaster
Pinus pinea
Pinus sylvestris
Pinus uncinata

(a)

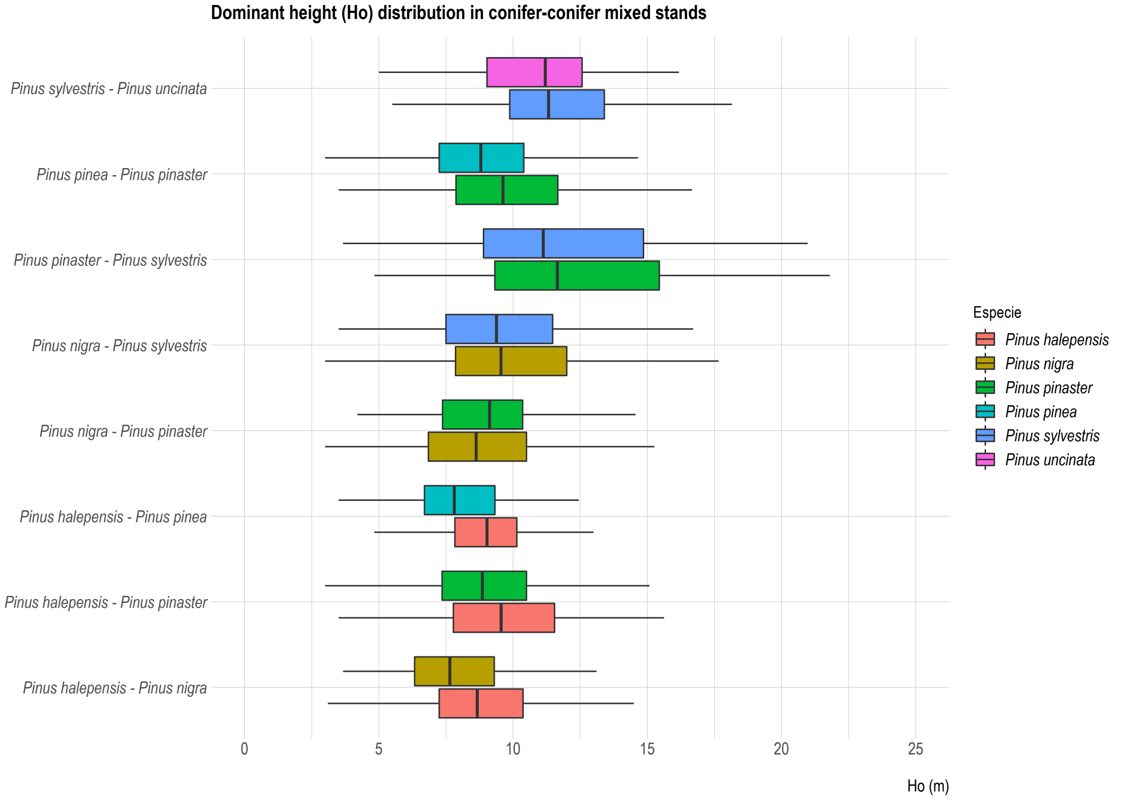

Mean quadratic diameter (Dg) distribution in broadleaved-conifer mixed stands
Pinus sylvestris - Quercus pyrenaica
Pinus sylvestris - Quercus petraea
Pinus sylvestris - Quercus ilex
Pinus sylvestris - Quercus faginea
Pinus pinea - Quercus suber
Pinus pinea - Quercus ilex
Pinus pinaster - Quercus suber
Pinus pinaster - Quercus robur
Pinus pinaster - Quercus pyrenaica
Pinus pinaster - Quercus ilex
Pinus nigra - Quercus ilex
Pinus nigra - Quercus faginea
Pinus halepensis - Quercus ilex
Pinus halepensis - Quercus faginea
Fagus sylvatica - Pinus sylvestris
0
10
20
30
40
Dq (cm)
Especie
Fagus sylvatica
Pinus halepensis
Pinus nigra
Pinus pinaster
Pinus pinea
Pinus sylvestris
Quercus faginea
Quercus ilex
Quercus petraea
Quercus pyrenaica
Quercus robur
Quercus suber

(b)

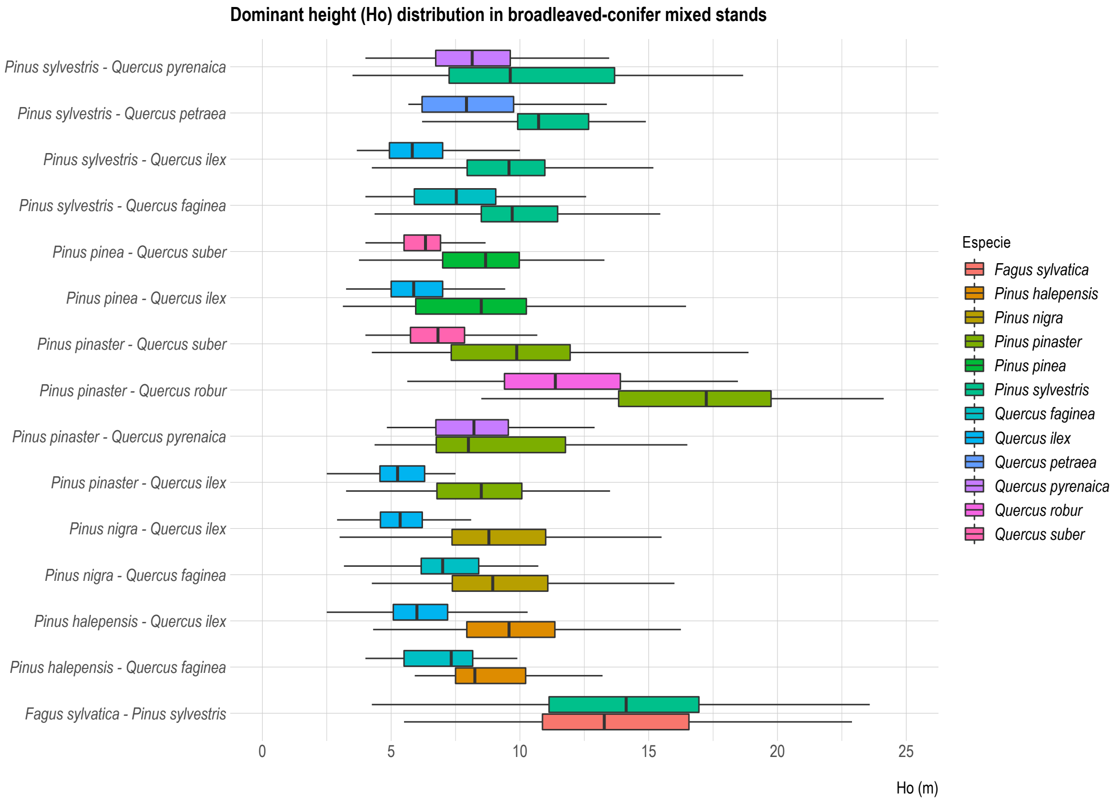


(c)

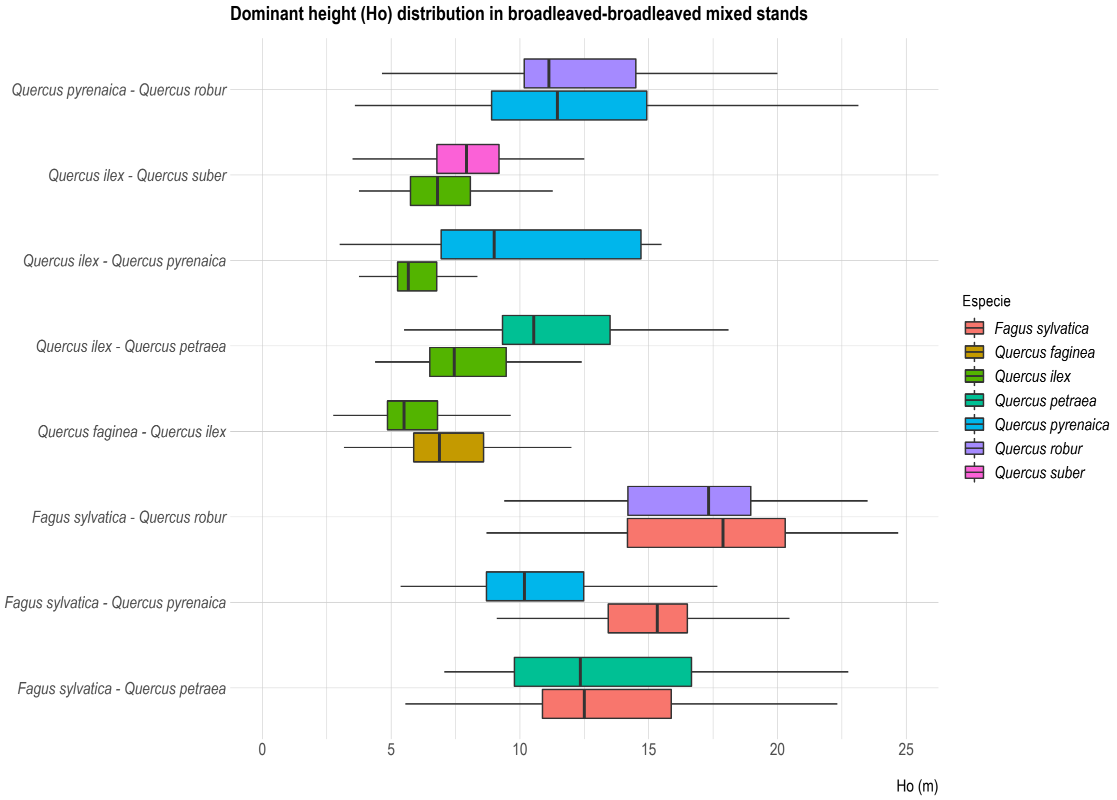
Supplementary Figure 2: Mean values of mean quadratic diameter by species (Dg_i) for the selected SNFI plots for the different conifer-conifer (a), conifer-broadleaved (b) and broadleaved-broadleaved (c) mixtures analyzed



(a)

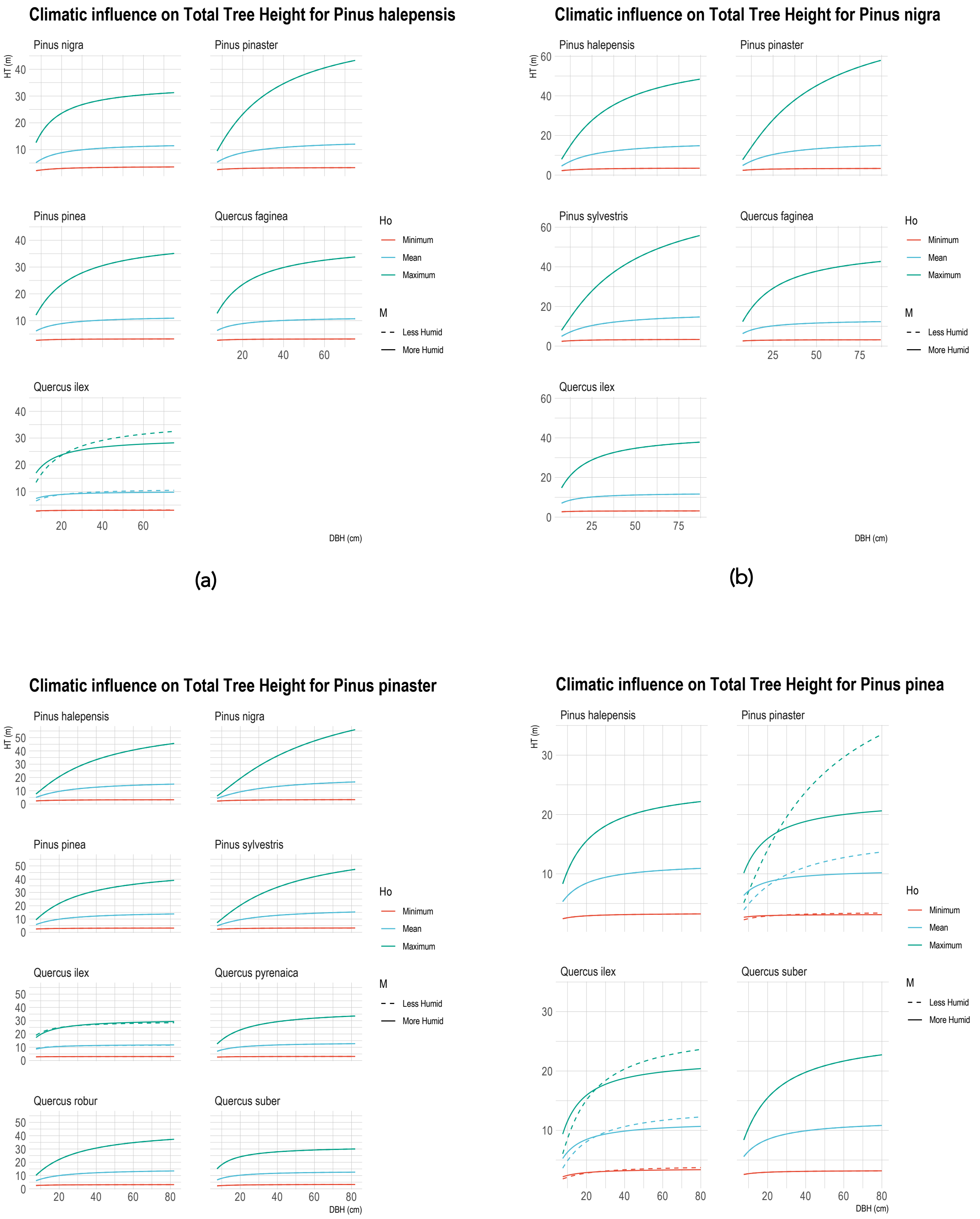

Dominant height (Ho) distribution in broadleaved-conifer mixed stands
Pinus sylvestris - Quercus pyrenaica
Pinus sylvestris - Quercus petraea
Pinus sylvestris - Quercus ilex
Pinus sylvestris - Quercus faginea
Pinus pinea - Quercus suber
Pinus pinea - Quercus ilex
Pinus pinaster - Quercus suber
Pinus pinaster - Quercus robur
Pinus pinaster - Quercus pyrenaica
Pinus pinaster - Quercus ilex
Pinus nigra - Quercus ilex
Pinus nigra - Quercus faginea
Pinus halepensis - Quercus ilex
Pinus halepensis - Quercus faginea
Fagus sylvatica - Pinus sylvestris
0
5
10
15
20
25
Ho (m)
Especie
Fagus sylvatica
Pinus halepensis
Pinus nigra
Pinus pinaster
Pinus pinea
Pinus sylvestris
Quercus faginea
Quercus ilex
Quercus petraea
Quercus pyrenaica
Quercus robur
Quercus suber

(b)


Dominant height (Ho) distribution in broadleaved-broadleaved mixed stands
Quercus pyrenaica - Quercus robur
Quercus ilex - Quercus suber
Quercus ilex - Quercus pyrenaica
Quercus ilex - Quercus petraea
Quercus faginea - Quercus ilex
Fagus sylvatica - Quercus robur
Fagus sylvatica - Quercus pyrenaica
Fagus sylvatica - Quercus petraea
0
5
10
15
20
25
Ho (m)
Especie
Fagus sylvatica
Quercus faginea
Quercus ilex
Quercus petraea
Quercus pyrenaica
Quercus robur
Quercus suber

(c)

Supplementary Figure 3: Mean values of dominant height by species (Ho$_i$) for the selected SNFI plots for the different conifer-conifer (a), conifer-broadleaved (b) and broadleaved-broadleaved (c) mixtures analyzed


Climatic influence on Total Tree Height for Pinus halepensis

Climatic influence on Total Tree Height for Pinus nigra

Climatic influence on Total Tree Height for Pinus pinaster

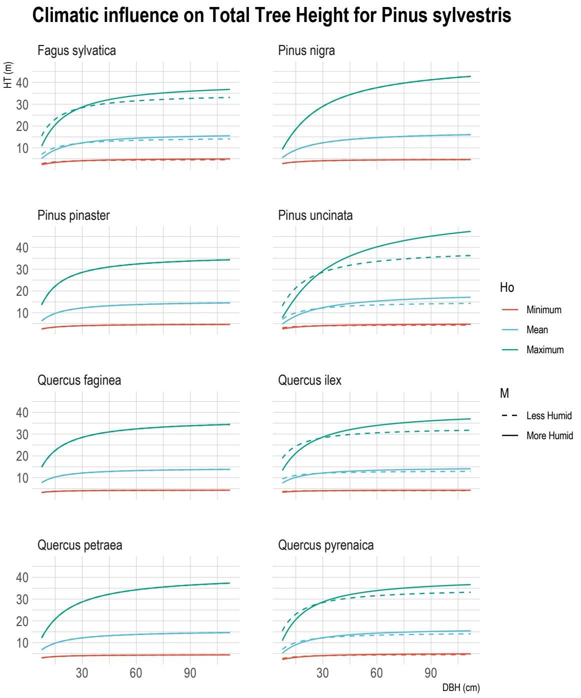
Climatic influence on Total Tree Height for Pinus pinea

(a)

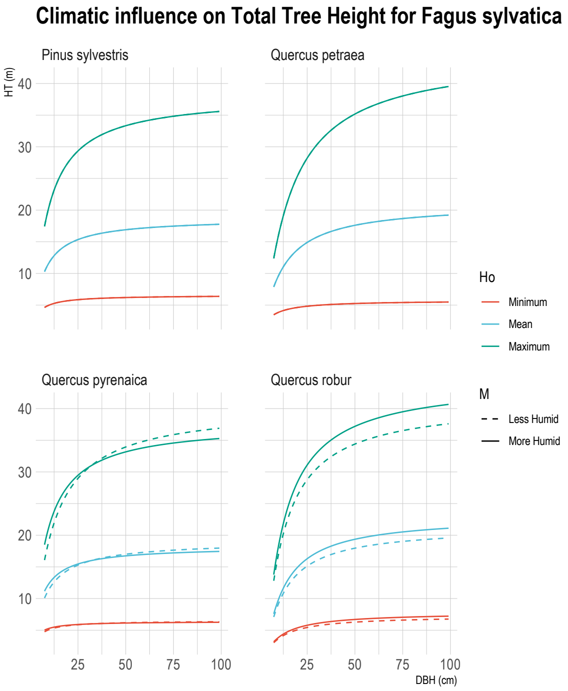
(b)

(c)

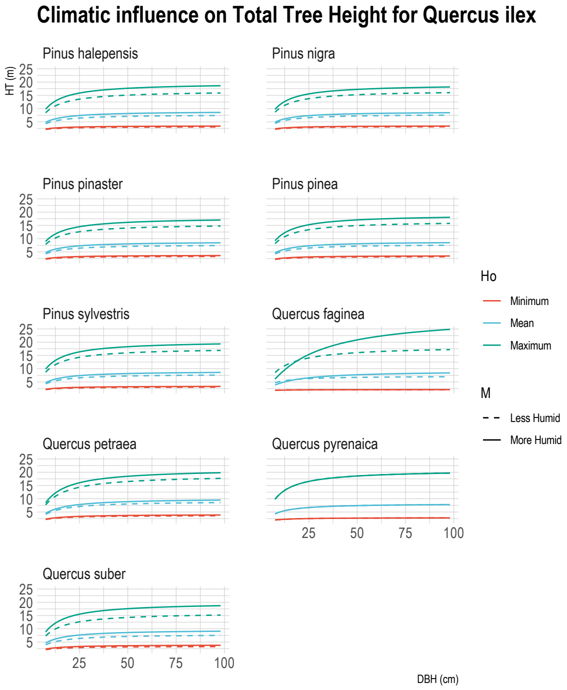
(d)


Climatic influence on Total Tree Height for Pinus sylvestris
HT (m)
Fagus sylvatica
Pinus nigra
Pinus pinaster
Pinus uncinata
Quercus faginea
Quercus ilex
Quercus petraea
Quercus pyrenaica
10
20
30
40
30
60
90
DBH (cm)
Ho
Minimum
Mean
Maximum
M
Less Humid
More Humid

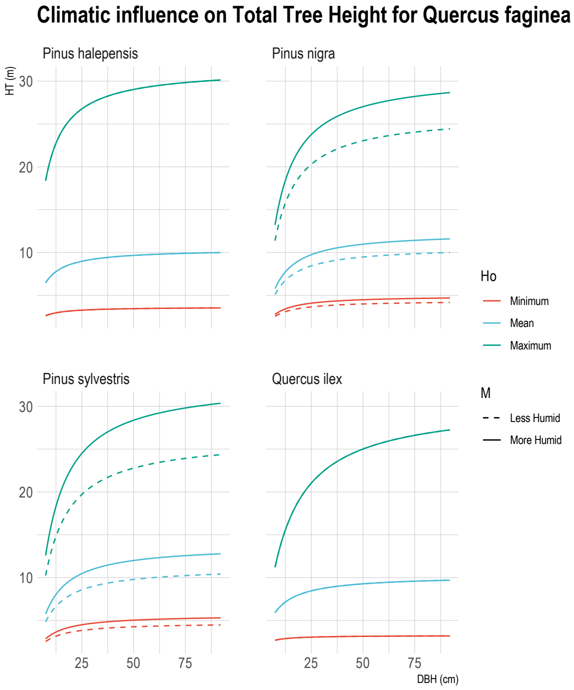
(e)


Climatic influence on Total Tree Height for Fagus sylvatica
HT (m)
Pinus sylvestris
Quercus petraea
Quercus pyrenaica
Quercus robur
10
20
30
40
25
50
75
100
DBH (cm)
Ho
Minimum
Mean
Maximum
M
Less Humid
More Humid

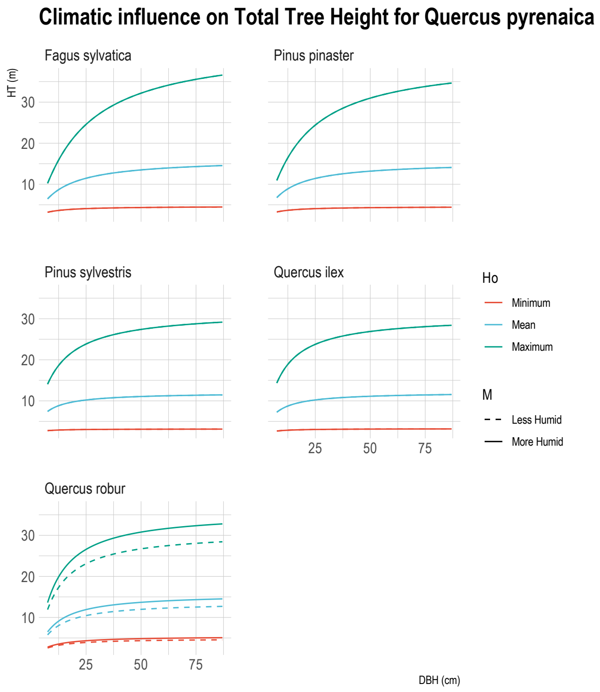
(f)


Climatic influence on Total Tree Height for Quercus ilex
HT (m)
Pinus halepensis
Pinus nigra
Pinus pinaster
Pinus pinea
Pinus sylvestris
Quercus faginea
Quercus petraea
Quercus pyrenaica
Quercus suber
5
10
15
20
25
25
50
75
100
DBH (cm)
Ho
Minimum
Mean
Maximum
M
Less Humid
More Humid

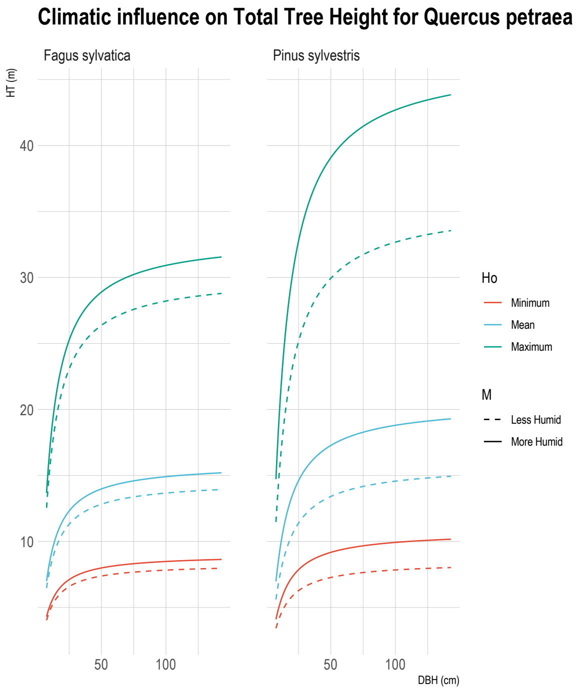
(g)


Climatic influence on Total Tree Height for Quercus faginea
HT (m)
Pinus halepensis
Pinus nigra
Pinus sylvestris
Quercus ilex
10
20
30
25
50
75
DBH (cm)
Ho
Minimum
Mean
Maximum
M
Less Humid
More Humid

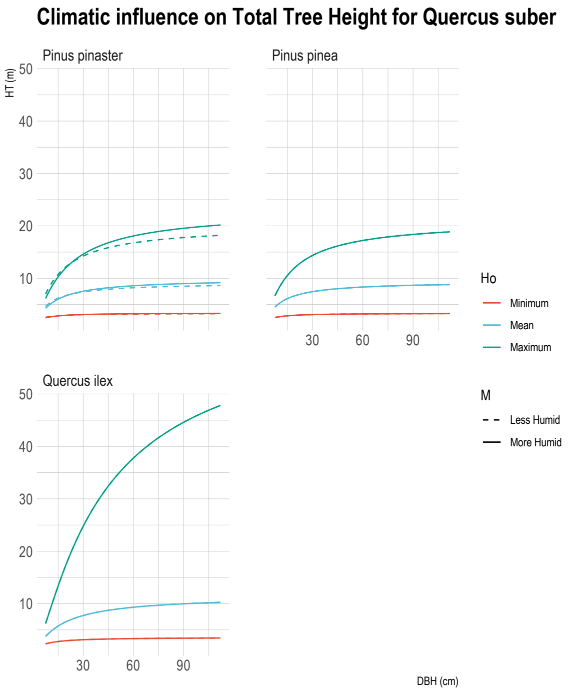
(h)



(i)



(j)



(k)

Supplementary Figure 4: Aridity influence at different stand developmental stages along the diameter distribution of the analyzed species-mixtures. The developmental stage is represented as stand dominant height (Ho) or species dominant height (Hoi), depending on parameter significance from selected H-D models

Appendix C: Scripts

Statistical analyses of present study were performed using the R (R Development Core Team, 2020) and Python (Van Rossum & Drake, 1995) language programme.

All the developed scripts are available on my personal GitHub profile: ***DiegoRP90***

Appendix D: Peer-reviewed articles

This thesis is based on four original works published or under revision in an international journal. These manuscripts are the following:

- Rodriguez-de-Prado,D.,San Martín,R.,Bravo, F., de Aza, C.H., 2020. Potential climatic influence on maximum stand carrying capacity for 15 Mediterranean coniferous and broadleaf species. Forest. Ecol. Manag. 460, 117824.

- Rodriguez-de-Prado,D.,Riofrio,J.,Aldea,J.,Bravo,F.,McDermott,J.,Herrero-de-Aza,C., 2021.Species mixing proportion and climate influence in the height-diameter relationship for different species mixtures in Mediterranean forests. Forest. Ecol. Manag. *Under review*

- Rodriguez-de-Prado,D.,Riofrio,J.,Aldea,J.,Bravo,F.,Herrero-de-Aza,C.,2021. Competition and climate influence in the basal area increment models for Mediterranean mixed forests. Forest. Ecol. Manag. *Under review*

- Rodriguez-de-Prado,D., Quian,Y.F.,Vazquez-Veloso,A., Bravo,F.; Herrero-de-Aza,C., 2021. CO_2 stock simulation in Spanish mixed forests under different climate change scenarios. A case study for *Pinus sylvestris* mixtures. Forest. Ecol. Manag. *Under review*