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USO SOSTENIBLE DE SISTEMAS FORESTALES

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Mixed stands growth dynamics of Scots pine and Maritime pine: species complementarity relationships and growth effects

presented by José Guillermo Riofrío Salazar

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Advisors:

Prof. Dr. Felipe Bravo

Dra. Miren del Río

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TESIS DOCTORAL

Dinámica de crecimiento masas mixtas de pino silvestre y pino negral: relaciones de complementariedad y efectos en el crecimiento

Presentada por José Guillermo Riofrío Salazar para optar
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[*A mis padres*]

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List of Acronyms

Arel	Relative species profile index
BA	Stand basal area (m2 ha-1)
BAI	Tree basal area increment (cm2)
CR	Tree crown ratio
d	tree diameter at breast height (cm)
dq	Quadratic mean diameter (cm)
Do	Dominant diameter (cm)
Ho	Dominant height (m)
h	total tree height (m)
hcb	tree height to crown base (m)
m_i	Species proportion by area
NFI	Spanish National Forest Inventory
GC	Gini coefficient
PAIBA	periodic annual basal area growth ($m^2 ha^{-1}$ year)
PAIV	periodic annual volume growth (m^3ha^{-1} year)
PS	Scots pine
PT	Maritime pine
rHo	Relative ratio between the species dominant height in mixed stands
SDI	Stand density index
SDI	Stand density index
SDIL	Stand density index of larger trees
SDImax	Maximum stand density index
SDIR	Relative stand density index
SDIRL	Relative stand density index of larger trees
SI	Site index
SPEI	Standardized Precipitation Evapotranspiration Index
V	Total stand volume

Abstract

Mixed-species forests are becoming more prominent in forest management due to increasing evidence of their greater potential to supply ecosystem functions and services. Given the recognized multifunctionality of mixed forests, it is essential to generate knowledge that provides forest managers with evidence-based silvicultural guidelines. However, species interactions and their impacts on forest dynamics are anything but simple. The functioning of mixed-species stands is modulated mainly by potential niche differentiation, the ability to share available resources and competition dynamics among species. Moreover, species interactions can also change according to environmental spatial gradients and temporal scales. Consequently, analysis of species interactions must include different levels and scales to form a solid working knowledge of mixed-species stand dynamics, which cannot be understood by looking at isolated sub-processes.

This thesis provides a multilevel analysis, from tree to stand-level and along temporal and spatial scales, of how species interaction affects the growth and yield processes of Scots pine (*Pinus sylvestris* L.) and Maritime pine (*Pinus pinaster* Ait.) mixed stands in a Mediterranean ecosystem. The leading hypothesis was that differences in structural and functional traits between the two species could induce interactions capable of altering stand productivity, above-ground species allometries, species crown dominance, stand structural traits and forest stand dynamics. The study used data from Spain's National Forest Inventory (NFI) and temporal plots grouped in triplets as primary input in the analysis of species-mixing effects at the three organizational levels: individual tree, tree size distribution, and stand. Additionally, tree-ring width series and band dendrometer measurements from pure and mixed plots made it possible to evaluate species-mixing effects on inter-annual and intra-annual tree growth dynamics.

NFI data showed that species-mixing effects at stand level differ from the effects of intra- and inter-specific competition at tree level. Growth efficiency increased in both species according to admixed species proportions at stand level. Intra-specific competition at tree level was higher than inter-specific competition in Scots pine tree growth, indicating a benefit from the mixture. In contrast, Maritime pine showed greater adverse effects of size-asymmetric inter-specific competition. In this species, tree growth was more strongly influenced by the competition structure (size-symmetric and size-asymmetric) than by the species of the competitors.

Stand composition influenced intra-specific variation in tree crown allometry. Species-specific traits and species interactions altered vertical structure and size-

distribution in mixed stands. Greater vertical structural heterogeneity was related to the relative productivity increment of mixed stands. Crown complementarity and vertical stratification in the canopy space were proposed as crucial mechanisms related to light interception and light-use that enhance ecosystem productivity in mixed stands composed of light-demanding species.

Both Scots pine and Maritime pine exhibited species-specific growth fluctuations in response to drought severity as well as different resilience values for drought events. While Maritime pine had a stronger temporal growt*h-d*rought correlation and lower resistance to extreme drought than Scots pine, it showed greater resilience and recovered better from drought. The long-term fluctuations and species-specific responses during the drought spells analyzed indicated that species interaction in mixed stands did not affect drought-growth relationships.

The two species presented distinct cumulative radial increment patterns in pure stands and species-mixing accentuated these differences. While species mixing did not affect maritime pine patterns, changes in intra-annual radial increment patterns for Scots pine in mixed versus pure stands increased temporal niche complementarity in mixed stands. The intra-annual growing period for Scots pine became longer in mixed stands, but the radial increment rate decreased compared to monospecific stands.

Finally, combining mixed-effect models and including parameters that express species-mixing enhanced the estimation performance for tree height and basal area growth, compared to the available models for pure stands. Models for mixed-species stands can be integrated into tree-level models as a planning and evaluation tool for assessing the impact of different management options and determining mixing proportions that maximize performance.

Resumen

Los bosques mixtos son cada vez más relevantes en el manejo forestal debido a la creciente evidencia de su mayor potencialidad para suministrar servicios ecosistémicos. Además de su reconocida multifuncionalidad, se requiere generar mayor conocimiento sobre su dinámica y funcionamiento, que permita diseñar herramientas para definir propuestas de gestión adaptativa. Sin embargo, las interacciones entre especies y sus consecuencias en la dinámica de los bosques no son para nada simples. El funcionamiento de los bosques mixtos está definido principalmente por diferenciación de nichos, que permite compartir los recursos disponibles, y la capacidad competitiva entre las especies. Además, las interacciones entre especies pueden cambiar por el efecto de diferentes gradientes ambientales y escalas temporales. En consecuencia, es necesario considerar diferentes niveles de análisis y escalas como base para una comprensión sólida de la dinámica y funcionamiento de los bosques mixtos, lo que no podría lograrse si se consideran los subprocesos del sistema de forma aislada.

En esta tesis se analiza cómo la interacción de especies afecta los procesos involucrados en el crecimiento y producción de masas mixtas de pino albar (*Pinus sylvestris* L.) y pino negral (*Pinus pinaster* Ait.) en un ecosistema mediterráneo. Para ello el análisis se realizó a múltiples niveles, desde rodal hasta árbol, así como a diferentes escalas temporales y espaciales. La hipótesis principal fue que las diferencias en los rasgos estructurales y funcionales entre ambas especies podrían inducir interacciones que generan cambios en la productividad, alometría de las especies, dominancia copa de las especies, características estructurales a nivel el rodal y dinámica del crecimiento. El estudio se basó en datos del Inventario Forestal Nacional (NFI) y parcelas temporales agrupadas en tripletes, que fueron la principal fuente de datos para el análisis del efecto de mezcla de especies en tres niveles de trabajo, árbol, distribución del tamaño y rodal. Además, se usaron series de ancho de anillo y mediciones de dendrómetros de banda, de parcelas mixtas y puras de los tripletes, para evaluar a escala interanual e intra-anual el efecto de la mezcla en la dinámica de crecimiento a nivel de árbol.

Usando los datos del NFI, los efectos de la mezcla de especies mostraron distintos resultados entre el nivel de rodal y el efecto de las estructuras de competencia intra e intre-específica a nivel de árbol. La eficiencia de crecimiento en ambas especies aumentó con la proporción de la mezcla de especies a nivel de rodal. A nivel de árbol, el efecto de la competencia intraespecífica fue mayor que la competencia interespecífica sobre el crecimiento del pino albar, lo que significa un beneficio en el crecimiento debido a la mezcla. Sin embargo, para pino negral el efecto fue contrario, la competencia interespecífica asimétrica fue mayor que la

competencia intraespecífica. Además, para esta especie el crecimiento se vio más afectado por la estructura de competencia (simétrica y asimétrica) que por la composición de especies (intraespecífica e interespecífica).

La interacción entre especies influyó en la variación intraespecífica de las relaciones alométricas de la copa a nivel de árbol entre parcelas puras y mixtas. Tanto las características morfológicas y estructurales específicas, así como las interacciones entre ambas especies causaron cambios en la estructura vertical y en la distribución de tamaño observados en los rodales mixtos. Este incremento en la heterogeneidad estructural vertical estuvo relacionado con el aumento de la productividad relativa de los rodales mixtos. La complementariedad de copas entre especies y la estratificación vertical del dosel se han propuesto como mecanismos relacionados con la intercepción y uso eficiente de luz que aumentan de productividad en masas mixtas.

Tanto pino albar como pino negral exhibieron respuestas específicas en las fluctuaciones del crecimiento respecto a la severidad de la sequía. Además, mostraron distinta tolerancia y resiliencia a los eventos de sequía extrema. El pino negral mostró una correlación temporal más fuerte en las fluctuaciones crecimiento-sequía que el pino albar. Por otro lado, durante eventos de sequía extrema, el pino negral fue menos resistente, pero se recuperó mejor y fue más resiliente a la sequía que el pino albar. La interacción de especies en rodales mixtos no afectó las relaciones sequía-crecimiento tanto en las fluctuaciones a largo plazo, como en las respuestas específicas a los años de sequía analizados.

El patrón de incremento radial intra-anual fue diferente entre las dos especies en rodales puros. Además, la mezcla de especies acentuó estas diferencias, incrementando la complementariedad temporal de nicho entre especies debido a modificaciones en el patrón de incremento radial acumulado para de pino albar entre parcelas puras y mixtas. En cambio, la mezcla de especies no afectó el patrón de pino negral. La duración del período de crecimiento intra-anual de pino albar se incrementó y la tasa de incremento radial disminuyó en rodales mixtos en comparación a los rodales monoespecíficos.

Finalmente, el uso de modelos de efectos mixtos y la inclusión de parámetros que expresen la mezcla de especies mejoró los errores de estimación de altura y crecimiento en área basimétrica en comparación con los modelos disponibles para rodales puros. Estos nuevos modelos que consideran la interacción de especies pueden integrarse en modelos de árbol individual como herramientas de planificación y gestión de rodales mixtos.

1. Introduction

Forests worldwide are experiencing alterations in dynamic growth patterns, structural composition, and functional integrity due to climate change (Allen et al., 2010). The impacts of climate change on forest ecosystems differ among regions depending on their limitations for forest production (Lindner et al. 2010). Higher temperatures in northern latitudes extend the growing season, which benefits tree growth (Pretzsch et al., 2014). In regions such as the Mediterranean, where water availability restricts productivity, a wide range of severe and negative impacts are expected (Gómez-Aparicio et al., 2011). However, warmer winters are driving positive growth trends in Mediterranean mountain forests, where temperature can be a more predominant constraint to tree growth than drought, (Sánchez-Salguero et al., 2015a).

Today, the main concerns for forest managers include strategies to promote resistance, resilience and adaptability in the face of abiotic and biotic stressors and disturbances to forest ecosystems (Puettmann et al., 2015). These strategies prioritize maintaining an ample range of ecosystem services within the framework of sustainable forest management, emphasizing species diversification as an adaptive forest management option (Ammer, 2016). Compared to pure forests, mixed forests have potential to deliver a greater variety of ecosystem functions and services at higher levels (Gamfeldt et al., 2013; Isbell et al., 2017; Van Der Plas et al., 2016) while also reinforcing resilience to disturbances (Jactel et al., 2017) and growth stability (del Río et al., 2017).

The multifunctionality of mixed forests is widely recognized (Van Der Plas et al., 2016). Currently, around 19% of European forests are dominated by two or more tree species, while the area of forest covered by a single tree species has been decreasing over the last 15 years at a rate of around 0.6% annually (FOREST EUROPE, 2015, pag 28). This tendency underscores the essential task of generating additional knowledge to provide forest managers with evidence-based silvicultural guidelines (Coll et al., 2018).

Numerous studies have described the complexity of mixed-species stands and species interactions, demonstrating the inability to simulate the dynamics of stand-level attributes of mixed-species stands by applying weighted means of the same attributes from pure stands of the constituent species (Pretzsch et al., 2017). Classical coexistence theories establish that each species inhabits a particular niche. Functional traits such as rooting depth, shade tolerance, phenology, wood density or specific leaf area determine the niches that species can occupy (fundamental niche). Similarly, ecological interactions such as competition or responses to environmental gradients determine the actual niche of a species within a community at a given site (realized niche) (Kelty, 1992; Pretzsch et al., 2017). Complementary traits between species result in niche differentiation, which tends to stabilize their coexistence (Pretzsch, 2009a; Valladares et al., 2015). However, other mechanisms such as competition, facilitation, intra-specific variability and environmental heterogeneity play a more relevant role as niche differences diminish (Valladares et al., 2015). For example, differences in competitive ability (differences in species fitness) favor dominance of the more competitive species, those that will exclude the others in the absence of niche differences (Chesson, 2000).

The relationship between tree diversity and forest productivity is mostly positive across the major biomes, despite some geographic variation (Forrester and Bauhus, 2016; Liang et al., 2016). One explanation for increased stand productivity and resource efficiency in mixed stands compared to monocultures suggests that complementarity of structural and functional traits between species could reduce competition for above-ground and below-ground resources (Dănescu et al., 2016; Pretzsch, 2014; Williams et al., 2017). However, adverse or non-significant effects have also been reported for diversity-productivity relationships (Bourdier et al., 2016; Grossiord et al., 2014). In other words, the type and intensity of interactions, along with species functional traits and stand structure, drive the effects of tree species richness on ecosystem functioning for a particular species mixture at a given site (Forrester and Bauhus, 2016). For example, complementary traits and functions among species are likely to be higher in forests with shade-tolerant and deep-rooting deciduous species – which cover a wide range of functional types – than in forests with the same number of species but consisting only of coniferous evergreens (Bauhus et al., 2017a).

1.1 Problem statement

Most studies on mixed forests in temperate zones focus on mixtures that combine species with more diverse traits (shade tolerance, height growth rate, crown structure, leaf phenology, root depth) (Forrester, 2014; Pretzsch and Schütze, 2016), due to the higher probability of complementarity (reduced competition and facilitation) in the allocation and efficient use of available resources among species (Bauhus et al., 2017a; Forrester, 2014; Kelty, 2006). Since competition among species increases as species niches overlap, when organisms occupy the same spatial and temporal habitats and use the same resources, the strength of inter-specific competition is affected and they could interact as if they were the same species (functional redundancy concept) (Naeem, 1998; Rosenfeld, 2002). A positive diversity-productivity relationship has been observed in discrete species functional groups or homogeneous forest types, such as alpine coniferous, Mediterranean conifer or Mountain pine forests, with higher wood production in mixed-species stands than in monospecific stands (Jucker et al., 2014b; Ruíz-Benito et al., 2014; Vilà et al., 2013). However, the ecological mechanisms underlying the positive relationship between tree species richness and wood production remain unclear.

Comparison of mixed stands with neighboring pure stands in analogous environmental and silvicultural conditions makes it possible to detect positive or negative species-mixing effects. Quantitative information about how species diversity influences forest functioning can be obtained from forest inventory analyses that capture large-scale effects (del Río and Sterba, 2009; Gamfeldt et al., 2013; Mina et al., 2017; Vilà et al., 2013), controlled experiments, research comparing monospecific and mixed stands (especially two-species mixtures) long-term forest plots (Forrester et al., 2004; Pretzsch et al., 2015a, 2010) or experiments involving a greater range of species richness levels and functional diversity (Bruelheide et al., 2014; Jucker et al., 2014a; Tobner et al., 2014). Other sources include simulations that model dynamics (Bohn and Huth, 2017; Morin et al., 2011) and meta-analyses (Liang et al., 2016; Zhang et al., 2012).

Methodologically, researching the dynamics in mixed-species stands requires multi-level analysis involving tree, size distribution/structure and stand levels. Such work might even include zooming in closer (lower) to leaf level or farther out (higher) to landscape level (Forrester and Pretzsch, 2015). Each organizational level provides distinct insights and reveals emerging properties that are unattainable at higher or lower levels. Discrepancies between predictions and observations when comparing different levels can also be used to formulate new hypotheses concerning the mechanisms that drive species interactions or for scaling up and down between levels (del Río et al., 2016; Pretzsch et al., 2015b). Analyzing processes and species interactions between levels and scales provides a solid base for understanding mixed-species stand dynamics, which cannot be understood by observing the subprocesses in isolation. The following paragraphs describe the most important theoretical and methodological issues involved in the analysis of species-mixed stands.

1.1.1 Evaluation of species-mixing effects at the stand and tree level

The fact that mixed forests can be more productive than single-species stands has been observed in many species combinations and ecosystems (Forrester, 2014; Kelty, 2006; Vilà et al., 2013). However, the generalization that forest productivity increases with species mixture is inaccurate. For example, greater stand density leads to increased complementarity for some species combinations but decreases complementarity for others (Condés et al., 2013; Forrester et al., 2013; Garber and Maguire, 2004). Other factors such as site conditions (Mina et al., 2017; Toïgo et al., 2015), climate (Forrester et al., 2016; Manso et al., 2015) or species assemblage (Mina et al., 2017; Pretzsch and Schütze, 2016) may modulate the effect of species interactions, thereby affecting stand productivity (Forrester and Bauhus, 2016), mortality (Condés and del Río, 2015) or resource-use efficiency (Forrester, 2015; Richards et al., 2010). Consequently, interactions between any two species can also change along spatial gradients, with temporal scales and development stand stages adding further complexity (Cavard et al., 2011; del Río et al., 2014b; Forrester, 2014).

Combining tree- and stand-level analysis may help to trace the effects and determine the relevance of species interactions in forest functioning and dynamics (del Río et al., 2016; Forrester and Pretzsch, 2015). For instance, tree level models can represent size-distribution heterogeneity that emerges from species interaction, something that is scarcely captured in stand-level models. Moreover, while tree-level analysis can be directly carried out through regression techniques where the response is single-tree growth, mixing effects at stand-level are usually analyzed through possible growth deviations in mixtures compared to neighboring pure stands. In this respect, species proportion is used as a proxy for the partitioning of growing space: the allocation of resources such as light, water, and nutrients among the species in the stand (del Río et al., 2016).

The species proportion may vary considerably depending on how it is defined, leading to variations in the net species-mixing effects on stand growth (Dirnberger et al., 2017; Pretzsch, 2009b; Sterba et al., 2014). Selecting a species proportion definition that considers different potential densities between species might be more advisable than comparison based on species basal area or volume (Sterba et al., 2014). Species proportion in terms of maximum stand density index provides a better estimate of occupied growing space for each species and avoids incorrect interpretations stemming from different species-specific growth rates (Dirnberger and Sterba, 2014). This method is used extensively to analyze mixture effects at stand and tree level based on forest inventory data or to compare temporally plots in mixed and pure stands (Condés et al., 2013; del Río and Sterba, 2009; Huber et al., 2014; Pretzsch and Schütze, 2009). However, it requires potential density estimates for each species (Pretzsch and Biber, 2005) instead of using the generic self-thinning allometric coefficient established by Reineke (1933).

Competition from neighbors is an essential driver of tree growth and might cause much more substantial reductions in potential growth than climate or tree size (Sánchez-Salguero et al., 2015b). Moreover, target tree sensitivity to competition (competitive response) can vary markedly along environmental gradients, leading to significant rank reversals in species performance (Gómez-Aparicio et al., 2011). Competition indices reveal differences between intra- and inter-specific competition effects, thus making it possible to evaluate the influence of the species-mixture on tree growth (del Río et al., 2014a). They show adverse, neutral, or even positive effects of the inter-specific competitive environment on tree growth, such as when inter-specific competition coefficient term values are non-significant or lower than the intra-specific coefficient. Analyzing both tree and stand levels to determine the species-mixing effect may be the first step to understanding species-specific interactions that favor higher profitability in mixed stands compared to monospecific stands.

1.1.2 Tracing the effects of species mixing from stand to tree level

The tree size distribution of a stand can be understood as a property that emerges from the demographics of individual trees and therefore represents an intermediate scale between the tree and stand levels (del Río et al., 2016). Research into size structure dynamics can also link findings at both levels and help trace the effects of species mixing (Pretzsch and Schütze, 2016). Stand structure is usually described in terms of stand density, size distribution, horizontal and vertical tree distribution patterns or combinations of several attributes (Gadow et al., 2012; McElhinny et al., 2005). Mixing species with complementary structural and functional traits may enhance structural complexity above and below-ground, which can increase stand production through more efficient use of resources compared to single-species stands (Dănescu et al., 2016; Pretzsch, 2014; Pretzsch and Schütze, 2016). However, negative or non-significant effects have also been reported for structural diversity-productivity relationships (Bourdier et al., 2016).

Structural attributes such as crown morphology and the resulting canopy structure drive stand dynamics, which may be crucial to determining productivity and a broad range of ecosystem services (Gadow et al., 2012). This applies to mixed-species stands where inter- and intra-specific interactions may increase structural heterogeneity (Pretzsch, 2014). Inter-specific differences in morphological and physiological traits among coexisting species may enhance complementarity mechanisms, such as the filling of canopy space, leaf area index (LAI), light capture and light use efficiency, all of which can contribute to explaining greater productivity in more diverse forests (Jucker et al., 2015; Larocque et al., 2012; Pretzsch, 2014; Toïgo et al., 2017; Williams et al., 2017). Recent studies have also found that intra-specific differences in the allometric scaling of tree crowns in mixed stands were dependent on the competitive environment and competitive species composition of the stand (Barbeito et al., 2017; Forrester et al., 2017), which are directly related to canopy structure. In some mixtures, even small differences in species structural traits can trigger positive inter-specific interactions through complementarity or competition reduction mechanisms (Jucker et al., 2014b). However, the role of species-specific trait differences in mixed-stand functioning is not yet fully understood.

When mixed-species stands are more productive than monocultures, higher light absorption is often suggested as a cause. However, few studies have quantified this effect, and even fewer have examined light-related interactions (Forrester et al., 2018). A key question is whether differences in structural attributes between mixed and pure stands result from a merely ‘additive effect’, i.e., the combination of the different species-specific morphological traits in a mixed stand, or if species interactions trigger species traits that surpass their behavior in pure stands and modify outcomes such as productivity, stability, and resilience in a ‘multiplicative effect’ (Forrester and Pretzsch, 2015; Loreau and Hector, 2001; Morin et al., 2011). Multiplicative effects are highly relevant for understanding changes in forest functioning and for modeling and predicting mixed-stand dynamics and productivity (Pretzsch et al., 2015b).

1.1.3 Inter- and intra-annual radial growth dynamics in mixed-species stands

Analysis of inter-annual and intra-annual temporal scales might reveal the degree of asynchrony between species in resource capture and growth, as well as growth pattern responses to variation in environmental conditions in mixed and monospecific stands. Inter-specific differences can lead to temporal complementarity/reduced competition or to competition for resources when species coexist (Kelty, 1992). However, species interactions can be altered intra- and inter-annually by temporal changes in climatic conditions and resource availability (Forrester, 2014). Intra-annual patterns define the species-specific timing and magnitude of growth rhythms, which can provide insight into climate impacts on tree physiology and growth processes (Aldea et al., 2018; de-Dios-García et al., 2015; Rossi et al., 2012; Swidrak et al., 2013). For their part, inter-annual fluctuations in tree ring measurements in response to climate variability and specific disturbances (del Río et al., 2014b; Gazol and Camarero, 2016) are especially interesting for looking at productivity stability over time (del Río et al., 2017; Jucker et al., 2014a).

Tree-ring width series make it possible to quantify and compare climate-growth relationships and growth trend dependency on stand development or specific site conditions, thus providing long-term information with annual resolution (Fritts, 1976). Tree-rings data analysis must disentangle ontogenetic and short-term environmental signals from changes in long-term trends driven by gradually shifting environmental conditions (Peters et al., 2015; Speer, 2010). However, traditional dendro-climatic analysis and detrending methods are not always considered in the sampling design (e.g., hierarchical sources of variability from sample, tree, stand, forest and ecoregion). Different levels of variation in tree-ring series might include important biases in the extracted fluctuations (Bowman et al., 2013; Lara et al., 2013; Peters et al., 2015).

Most studies on mixed-species stands focus on finding how differences in species sensitivity affect tree growth and productivity in relation to specific disturbances. An example would be comparing species resistance or resilience to extreme drought events (Gazol and Camarero, 2016; Granda et al., 2018a; Pretzsch et al., 2013). However, drought resistance and post-drought resilience may also involve other factors, such as tree and stand features (Merlin et al., 2015; Thurm et al., 2016) or age and size (Pretzsch et al., 2013). To address these sources of variability and account for the intrinsic sampling schemes of dendrochronological data, algorithms based on multilevel modeling and multivariate comparison have recently been developed (Lara et al., 2018, 2013). Multilevel analyses – such as mixed-effects models – consider random effects for sampling designs (Bolker et al., 2009; Galecki and Burzykowski, 2013), while multivariate comparison – such as dissimilarity analysis – can contrast and organize dendroclimatic fluctuations into common ecological-factor levels (Borcard and Legendre, 2012; Goslee and Urban, 2007; Legendre and Legendre, 1998). This method can be implemented to better understand the role of species interactions in the long-term dendroclimatic relationships that affect forest-ecosystem dynamics.

Intra-annual growth patterns, or the daily course of growth, can also differ considerably among species (Camarero et al., 2010). The effects of species interactions on seasonal tree growth dynamics in mixed-species stands are even less well understood than long-term effects during rotation (Pretzsch et al., 2017). Measurements from band dendrometers on trees in monospecific and mixed-species stands make it possible to adjust the growth function to describe the accumulated radial increment pattern (McMahon and Parker, 2015; Oberhuber et al., 2014). From this, the critical phenological stages within the intra-annual pattern can be identified as the onset, end, rate and moment of maximum growth in seasonal dynamics and growth phenology (Swidrak et al., 2013). Such information could reveal how intra-annual and daily growth courses are modulated through species mixing (Schäfer et al., 2018), tree size and climate conditions (Camarero et al., 2010; Pacheco et al., 2018).

As with other scales and levels, analysis of species temporal complementarity in mixed stands involves defining whether the intra-annual radial growth and inter-annual growth variation between species results from a merely ‘additive effect’ – combining species with different seasonal growth or climate-growth behaviour, for example – or if species interactions have a ‘multiplicative effect’ on individual tree species growth dynamics that modifies outcomes such as productivity, stability and resilience to drought.

1.1.4 Modeling mixed-species stands

Despite evidence that mixed-species forests offer greater potential to supply ecological and socio-economic services of than monospecific forests, quantitative silvicultural guidelines that facilitate efficient management that facilitate efficient management of mixed-species stands are still largely based on pure even-aged stands (Bravo et al., 2012; Forrester and Pretzsch, 2015). The lack of tools for evaluating the long-term sustainability of silvicultural systems proposed for mixed-species stands hinders acceptance of these systems by stakeholders, practitioners and scientists concerning ecosystem services and the benefits of heterogeneous mixed forests compared to single-species stands (Carnol et al., 2014; Coll et al., 2018). Models that incorporate known species-mixing effects on tree and stand productivity, tree allometry, mortality, and maximum density are essential for proper design, the initial composition, spatial arrangement and management of mixed-species stands (Pretzsch and Zenner, 2017).

A critical issue for representing species mixing in forest growth models is the transition from the tree to the stand level, which involves introducing tree size structure, crown morphology, canopy structure and growth differences that might emerge from species interactions (del Río et al., 2016; Fichtner et al., 2017).. This is especially important for mixed-species stands where structural and environmental heterogeneity affects productivity at stand level (Dănescu et al., 2016; Forrester et al., 2018). Thus, individual tree models provide a better balance alternative between adequately representing the effects of species interactions and the integration of ecological processes in mixed-species stands into silvicultural guidelines (Pretzsch and Zenner, 2017).

Crown size and relative height of species in a mixed stand may be more relevant for growth and potential over-yielding than the given site conditions (Pretzsch, 2014; Pretzsch et al., 2015b). Productivity at the mixed-stand level might be influenced by the tree-level functions used, such as tree volume or biomass allometric equations, height-diameter and crown size functions, diameter or height increment models, mortality rates and ingrowth models, particularly if any or all are influenced by species composition and resulting stand structure. As these functions are seldom available for mixed stands, functions developed for pure stands are commonly used (del Río et al., 2016). The effects of either using functions developed from pure stands, or from a mix of pure and mixed stands may be significant depending on the covariates used in the model. For example, crown ratio accounts for some additional variability in stem form and stem volume when its marginal effect on a function containing tree diameter and total tree height is considered (Burkhart and Walton, 1985; Hann et al., 1987); hence, if tree diameter-height-crown ratio combination reflects local stand structure in complex mixed species stands, the models developed should perform well as long as the modelling data included the appropriate tri-variate distribution of these covariates. The extent to which additional information on species composition would affect stem form is largely unknown. Limited evidence suggests the effects would be small (Garber and Maguire, 2003), but this working hypothesis should be further tested.

Pretzsch et al., (2015b) describes three approaches to representing species-mixing effects in empirical models: i) computing stand-level attributes as the weighted mean attribute of the monospecific stands, ii) adding covariates that represent the almost infinite range of stand structures in mixed species stands, or iii) including modifiers to represent the departure of mixed species stand attributes from pure stands attributes as a function of species composition. Forest growth models that are directly parameterized or adapted to more complex stands (uneven-aged or mixed stands) from existing functions for even-aged stands could use correction factors or include specific variables to express the multi-species condition (Calama et al., 2008; Forrester and Tang, 2015; Pukkala et al., 2009; Sterba et al., 2002; Trasobares et al., 2004). Thus, models of species growth rates, tree allometry, maximum density or mortality could be sensitive to intra- and inter-specific competition environments (Condés and del Río, 2015; del Río et al., 2014a; Temesgen et al., 2014).

1.2 Mediterranean mixed-pine forests

The 3.5 million ha of mixed forests in Spain represent 19% of total forest surface (MAGRAMA, 2012) and are mainly formed by combinations of broadleaf-broadleaf or broadleaf-conifer species. Mixtures of pines with *Fagus sylvatica* or Quercus species are the most frequent in Mediterranean areas (MAGRAMA, 2012). However, forests with coexisting pine species are also common in Spain, covering almost 0.5 million ha (Montero and Serrada, 2013). Several studies have focused on inter-specific interactions and effects in pine-pine mixtures in different regions of the Iberian Peninsula, such as *Pinus sylvestris - Pinus nigra* (Trasobares et al., 2004), *Pinus halepensis - Pinus nigra - Pinus sylvestris* (Granda et al., 2018a) in the northeast, *Pinus halepensis - Pinus pinea* (Cattaneo et al., 2018) and *Pinus pinaster - Pinus pinea* (Ledo et al., 2014) in the northern plateau, *Pinus sylvestris - Pinus nigra* in the Southern Iberian Range (Jucker et al., 2014b) or *Pinus pinaster-Pinus sylvestris* with *Abies pinsapo* in the Cádiz Mountain Range. These studies reported positive, negative or neutral effects, which varied according to species assemblage and site conditions, for pine-pine interactions on wood production.

Scots pine (*Pinus sylvestris* L.) and Maritime pine (*Pinus pinaster* Ait.) are two of the main forest species in Spain (covering 1.20 and 0.68 million ha, respectively). They grow in pure and mixed stands, either naturally or through species selection for afforestation (Serrada et al., 2008). The two species co-exist on moderate slopes, mainly in the Iberian and Central Mountain Range in approximately 120000 ha (Figure 1.1), where their natural ecological distributions overlap: in the colder and higher areas of Maritime pine distribution and close to the southern latitudinal limit of Eurasian distribution for Scots pine. These mixed stands are particularly interesting because of their location at the edges of the *P. sylvestris* range distribution, where ecological conditions (high temperatures, frequent droughts) approach the species tolerance limit and the most drastic effects of climate change are expected (Matías and Jump, 2012). Meanwhile, Maritime pine in a dynamic and continuous process expand into the natural distribution areas of Scots pine, especially in more xeric site conditions (García-Güemes and Calama, 2015).

Outside the areas where their distribution ranges overlap, Scots pine and Maritime pine have different life histories and ecological requirements (Richardson, 2000; Tapias et al., 2004). In the Mediterranean region, Scots pine and Maritime pine present differences in growth phenology (Camarero et al., 2010; Vieira et al., 2014) and climate-growth responses (Bogino et al., 2009; Bogino and Bravo, 2008; Lara et al., 2013) that might enhance species complementarity. For instance, different intra-annual growth patterns have been described for the two species in Mediterranean environments. Scots pine shows a unimodal pattern, with photoperiod and temperature changes as the main environmental factors that condition the beginning and end of xylem growth (Camarero et al., 2010). In contrast, Maritime pine shows a bimodal intra-annual growth pattern that is typical of xeric regions (Vieira et al., 2014), though with a second (autumn) radial increment period explained as rehydration after summer contraction (Aldea et al., 2017; Vieira et al., 2013).

Scots pine is the most widely distributed pine species in the world, ranging from the Iberian Peninsula to Siberia. In Spain, Scots pine is mainly found in montane climates: 800-2000 m.a.s.l., 600-1200 mm mean annual precipitation and summer precipitation above 100 mm. In addition to the high-quality wood obtained from this species, it has great ecological value and a protective function against soil erosion. The rotation period in Mediterranean pine forests is around 100–140 years, depending on the intensity of silvicultural operations (Montero et al., 2008). Scots pine is a light-demanding pioneer species that can grow in half-light conditions. New seedlings are often established under the shelterwood system, thereby maximizing regeneration density in moderate light conditions (Barbeito et al., 2011). Because of its deep root system with dominant oblique and long secondary roots, this species can tolerate frost and drought and grows in ecologically diverse habitats with very poor soils.

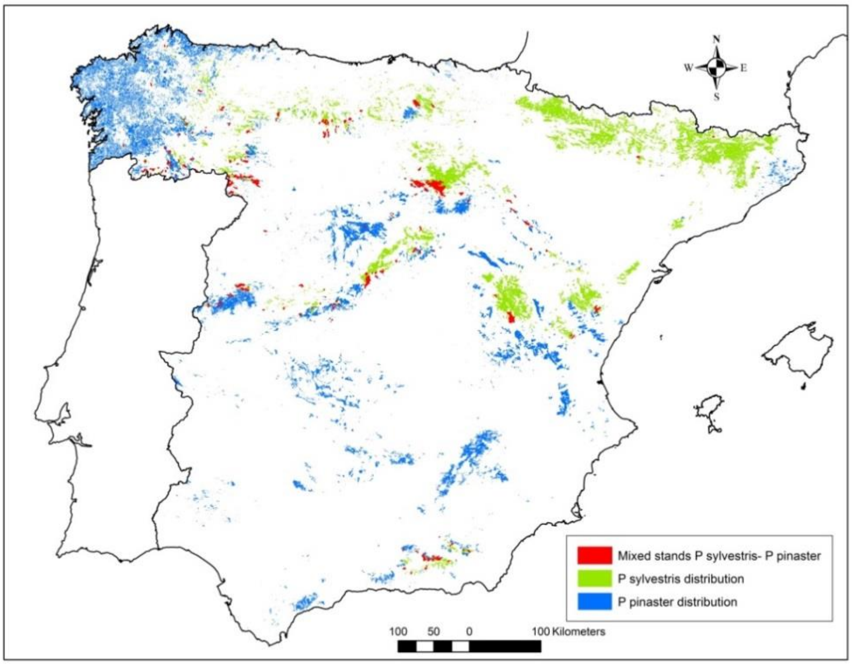

Figure 1.1. Distribution of Scots pine and Maritime pine in pure and mixed stands in Spain.

Maritime pine is widely distributed throughout the western Mediterranean basin (southwest Europe and northwest Africa), but not continuously, due to geographic isolation and human activity since ancient times. In Spain, Maritime pine grows in sub-humid and continental Mediterranean climates: 600-1300 m.a.s.l., 400-800 mm mean annual precipitation and 20-125 mm summer precipitation (Serrada et al., 2008). Maritime pine is a light demanding, shade intolerant, fast-growing species that occupies very diverse sites, showing high genetic diversity within populations and important genotype-by-environment interactions (Alía et al., 1997). It is also frost-resistant and tolerant to summer drought, which favors adaptation to local ecological conditions (Rodríguez et al., 2008). Natural regeneration occurs most commonly by means of the seed tree method (Rodríguez-García et al., 2010) and the survival of the new individuals is more related to light than to summer precipitation (Ruano et al., 2009). Traditionally, Maritime pine silviculture has focused on resin extraction, but the species has also been used for soil protection, reforestation of degraded areas and dune stabilization.

Growth and yield models for both species are available for different management purposes and regions, and at different scales (from whole stand to individual tree models), however, most models and tools were developed for pure even-aged stands (Bravo et al., 2012). For instance, IBERO is a distance-independent tree-level model for the simulation of different forest management scenarios in Spain. It predicts five-year growth for each tree in even-aged monospecific *Pinus sylvestris* L. stands (IBERO^{PS}) in the Iberian and Central Range (Lizarralde et al., 2010a) and for *Pinus pinaster* Ait. (IBERO^{PT}) in the Southern Iberian Range (Lizarralde et al., 2010b). IBERO is structured by modules that represent process driving stand dynamic , including initialization and complementary models (height-diameter model and functions of crown features)(Lizarralde, 2008; Lizarralde et al., 2004), productivity (side index) (Bravo-Oviedo et al., 2004; Bravo and Montero, 2001; Rojo and Montero, 1996), mortality/ingrowth (Bravo-Oviedo et al., 2006; Bravo et al., 2008), growth (diameter and height growth projection models) and stem-taper equations (Lizarralde, 2008).

Finally, despite ongoing development of growth and yield models in Spain during recent decades (Bravo et al., 2012), there is still a clear and urgent need for silvicultural and forest management information for mixed Scots and Maritime pine stands. Accurate tools must be generated to inform the structural development and maintenance of mixed stands, tools that address the expansion of mixed forest surface due to changes or abandonment of forest management and the impact of global change.

1.3 Research questions and hypothesis

The main hypothesis in this thesis is that differences in structural and functional traits between Scots pine and Maritime pine could induce species interactions that can produce changes in stand productivity, above-ground species allometries, crown dominance, stand structural traits and forest stand dynamics. This thesis tests the hypothesis using a multi-level analysis (tree to stand level) that includes temporal and spatial scales, to understand how species interaction affects growth and yield processes in Scots pine - Maritime pine mixed stands in a Mediterranean ecosystem. The following research questions were set:

- When both species coexist, can competition relationships between species and stand attributes favor higher productivity at tree and stand levels compared to neighboring pure stands?
- Are the differences in structural and functional traits between Scots pine and Maritime pine enough to reveal species interactions and induce changes in above-ground species allometries, crown dominance, and stand structural attributes?
- Is there evidence of temporal species interaction dynamics on intra- and inter-annual scales that could modulate species-mixing effects?
- Do the available models for pure stands need to be adapted to mixed-species stands to improve mixed-stand growth estimates?

In concordance with these questions, the following hypotheses were formulated:

- Species-mixing effects can be traced at different organizational levels, from trees to stands. If inter-specific competition is less intense than intra-specific competition for the available above-ground or below-ground resources, then an increase in productivity (overyielding) in mixed stands compared to monospecific stands is expected. Combining tree- and stand-level analysis makes it possible to infer complementarity mechanisms between these pine species.

- Changes in structural heterogeneity may be associated with the effects of species mixing on productivity in Mediterranean mixed-pine stands. If the differences in structural attributes at tree and stand levels in mixed stands emerge from species interactions, then they are not a simple effect of mixture species with differing structural traits. Increased structural heterogeneity in mixed stands results in vertically structured canopies or crown complementarity among species, which is related to increased overyielding in mixed stands.
- Differences in intra- and inter-annual growth patterns could change temporal competition or complementarity relationships between species in mixed stands. Together, intra-annual cumulative radial increment patterns and inter-annual growth responses to drought could contribute to niche complementarity in the use of available resources by separating the temporal niche and stabilizing species coexistence.
- Integrating modifiers or parameters reflecting inter-specific competition into the structure of models adapted for mixed stands could improve their predictive capacity, thereby making them more useful than the parametrized functions available for each species in monospecific stands.

1.4 Thesis focus and contributions

Complexity in forest systems is expected to increase with the number of interacting species. Interactions between two species are often dynamic and result from processes and factors operating at different scales, none of which are mutually exclusive (Valladares et al., 2015). Additionally, species interactions can change along spatial and temporal gradients depending on resource availability and climate conditions (Forrester, 2014). To simplify complex systems (e.g., mixed-species stands), components are studied separately and then integrated to a whole system. However, this approach must take into account the emergent properties (e.g., species-mixing effects) resulting from component interactions (Messier et al., 2014) in the whole system. Analyzing these processes and species interactions at different levels and scales forms the basis for a solid understanding of forest dynamics in Scots pine-Maritime pine mixed-species stands, dynamics that cannot be predicted by studying isolated individual components.

The research activities in this thesis are based on the modeling approach proposed by Pretzsch et al., (2015b) and were modified to include tree-to-stand hierarchical levels along with spatial and temporal scales. Figure 1.2 describes the components (central cycle), level and scales that were analyzed according to the research questions formulated in Section 1.3. Theoretical modeling frameworks for deriving and predicting growth dynamics in mixed stands rely on the species-mixing effects of the main interacting components. Solid arrows (Figure 1.2) connect the components between the tree and stand-level, indicating species-mixing (composition) effects on stand structure and the influence of the competition environment (species interactions) on tree growth. Dashed arrows indicate the spatial and temporal scales used when species-mixing effects were analyzed at different levels. Feedback between stand structure and tree growth using competition indices shows that species interactions can significantly affect stand development (Pretzsch, 2014). Components and system inputs outside the scope of this thesis are in bold grey.

This thesis is organized into five studies according to the theoretical framework for analyzing mixed species depicted in Figure 1.2, within the scope of the research questions identified in Section 1.3.

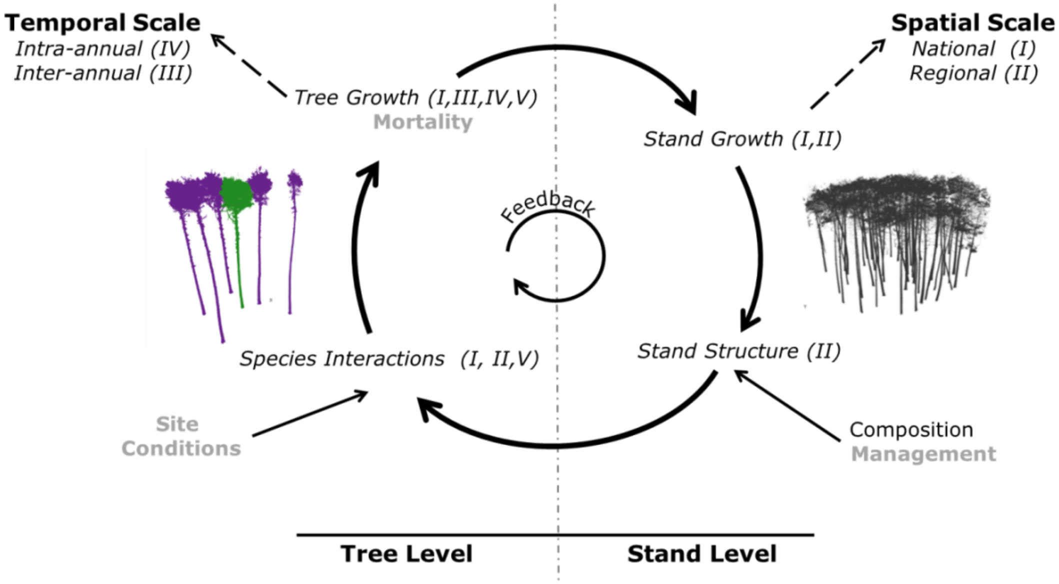

Figure 1.2. Theoretical framework for modeling mixed-species stands, modified from Pretzsch et al., (2015b). Sub-components of the conceptual system within the levels and scales analyzed throughout this research are highlighted with the 'Study number' in roman numerals. Sub-modules and inputs outside the scope of this thesis are in bold grey. Bold arrows connect tree and stand levels. Dashed arrows indicate the spatial and temporal scales used when species-mixing effects were analyzed at different levels.

Study I combines tree- and stand-level analysis to evaluate species-mixing effects of Scots pine and Maritime pine on a national scale using Spanish National Forest Inventory data (NFI). To understand the species-specific interactions that favor higher profitability of mixed stands over monospecific stands, the following approach was used: (i) determine species-specific potential density and space occupancy, (ii) evaluate if growth efficiency at the stand level is modified by mixture in terms of the growing space occupied, and (iii) test different competition structures to evaluate the influence of intra-specific and inter-specific competition on tree growth. This analysis provides a general overview of the behavior of this species mixture in an unbiased and systematic sample distributed across the complete range of mixture proportions.

Study II explores net species-mixing effects on stand productivity and stand structure in mixed forests composed of Scots pine and Maritime pine, compared to homologous monospecific stands, in a triplets assay in the Northern Iberian Range (Spain). The main objective of this study was to analyze mixture effects at three organizational levels – individual tree, tree size distribution, and stand – to develop hypotheses about possible complementarity mechanisms between these pine species. The following working questions were set for this purpose: i) to what extent does mixing modify structural attributes at the stand and species levels compared to pure stands?, (ii) how does volume production of mixed-species stands differ from that of neighboring pure stands?, and (iii) are mixing effects on stand productivity related to structural heterogeneity?

Study III includes modeling long-term growth fluctuations related to drought severity time series and comparing species-specific growth resilience to drought events in Scots pine and Maritime pine. The inter-annual niche differentiation of both co-existing pine species might be explored by combining both approaches. Our specific objectives were to (i) determine the long-term correlation between growth fluctuations and aridity index for each species, (ii) explore how stand composition and age might influence correlation in growt*h-d*rought fluctuations, (iii) quantify mean species-specific growth response and resilience to drought events in pure stands, and (iv) determine to what extent species responses to drought are influenced by stand composition.

Study IV focuses on comparing the intra-annual radial increment patterns of Scots pine and Maritime pine for mixed and pure stands. To quantify how species mixing influences cumulative radial increment patterns, the following objectives were established: (i) to compare the fitted functions for cumulative radial increment of each species in pure stands; (ii) to evaluate species-mixing effects on the intra-specific deviation of cumulative radial increment patterns between mixed stands and pure stands.

Study V applies the knowledge gained in the previous studies to develop generalized height-diameter and basal area tree growth models adapted to mixed stands for each species. First, for adapting these models, species-mixing effects were integrated through modifiers or parameters that reflect inter-specific competition. Estimates from the adapted models were then compared to predictions based on available functions for monospecific stands.

2. Data

2.1 Experimental units and databases

In this thesis, two data sources were the primary input to analyze, at multiple levels and spatial and temporal scales, the mixing-species effects of Scots pine and Maritime pine mixtures compared to their respective monocultures.

One dataset consisted of the Spanish National Forest Inventory (NFI). Data from the Second (1986–96) and Third NFI (1997– 2007) were used to analyze at the tree- and stand-level the species-mixing effect in Scots pine and Maritime pine mixed stands at large spatial range, to understand the species-specific interactions that favor higher profitability in the mixture than in monospecific stands (Study I). NFI was also used to validate the performance of generalized height-diameter functions developed for both species in mixed stands (Study V). NFI data offered the advantageous possibility to obtain a general overview of the behavior of this mixture in an unbiased and systematic sample distributed across the complete range of mixture distribution and proportions. However, using NFI data have some constraints due to the uncertainty related with data characteristics and methodological approach: stand age information is unavailable, uncertainty about past silvicultural treatments. Although estimates of stand variables using expansion factors could generate unbiased errors (Bravo et al., 2002).

Although, the strength of inventory datasets is the representativeness of the inferences, e.g., comparison of stand productivity of mixed versus monospecific stands and the correlation with site conditions is representative of a population (del Río and Sterba, 2009; Toïgo et al., 2015). The comprehensive quantification of the system properties and process in mixed stands from the analysis of inventory data is limited by the abovementioned data constraints and possible confounding factors that require particular attention when analyzing species-mixing effects (Bauhus et al., 2017a; Vilà et al., 2005). As a complementary alternative, observational studies based on temporary plots can help to exclude or control the influence of other factors in the analysis. Also, they allow ensuring a desire environmental gradient in the design (Bauhus et al., 2017a).

For this thesis, temporally plots grouped in a triplet design were established by the Sustainable Forest Management Research Institute (iuFOR). Typically triplets, a set of one plot in a mixed-species stand and two plots in the respective monospecific stands, are used to study species-mixing effects because this design allows for more control of some stand conditions, avoiding confounding factors at least for part of the stand development (Forrester and Pretzsch, 2015; Vallet and

Perot, 2016). These parameters include climate, soil conditions, stand structure, age, and forest practices.

The Triplets Research Network using in this thesis was located in a Mediterranean mixed pine forests area of Scots pine and Maritime pine that cover approximately 50 000 ha in the Northern Iberian Range. This design facilitates a pair-wise plausible comparison of mixed versus pure stands (Pretzsch and Schütze, 2009). Data from the tree and stand measurements were used to analyze changes in stand structure related with species mixing, as well as the relationship between the increase of stand productivity and differences in the canopy structure in mixed stands compared to pure stands (Study II). Dendrochronological data (tree-rings width) from tree cores taken in all the triplets and data from measurements of band dendrometers installed some of the triplets, allowing to evaluate the effect of species-mixing in the inter-annual growth responses to drought with the former (Study III) and intra-annual increments patterns with the latter (Study IV). Finally, dendrometric data from the triplets and diameter increment measurements from the cores were used to fit predictive generalized height-diameter functions and tree basal area growth models that consider the effects of the species-interactions (Study V).

2.1.1 Spanish National Forest Inventory

2.1.1.1 Description of the NFI

NFI is a systematic sample of permanent plots distributed across the forested area of Spain following the UTM square grid of 1 km, with a ~10-year re-measurements interval. NFI plots consist of four circular concentric subplots with radii of 5, 10, 15 and 25 meters, where species, diameter (d) and height (h) of all trees over 7.5, 12.5, 22.5 and 42.5 cm breast height diameter respectively are recorded.

Estimated stand variables included the number of trees (N), basal area (BA), dominant height (Ho), quadratic mean diameter (dq) and total stand volume (V) in pure and mixed plots; they were calculated using adequate expansion factors. Individual-tree stem volume over bark was estimated from volume equations proposed by the Second NFI (ICONA, 1990) and measures of diameter and height of each tree recorded in NFI. The origin of the stands, natural (Nt) or plantation (Pl) was considered in the analysis; available at SIG-FOREST (Auñon et al., 2011).

2.1.1.2 Plots selection criteria and mixed plots definition

NFI plots were selected rely on species composition. In pure plots of Scots pine and Maritime pine stands, the target species had at least 90% of the total BA of the plot. Plots were defined as mixed when the combined BA of both species in the plot had a minimum of a 90% of the total BA, and the proportion of BA of each target species in the mixed plots was higher than 15%. Thus, the proportion of other species remained lower than 10% (Figure 2.1). Pure plots without evidence of thinning (BA reduction) between inventories were used to fit the self-thinning boundary line for each species (Table 2.1). Plots with dq under 10cm were removed to avoid including under-represented stands due to NFI lower threshold diameters. Thus we estimated the self-thinning line and maximum stand density index value (SDImax) for each species, as described in section 3.1.

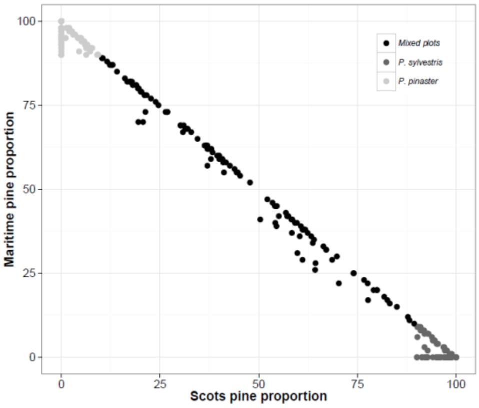

Figure 2.1. Range of mixture proportions in selected plots from NFI.

Table 2.1. Main stand variables of pure plots used to fit the self-thinning boundary line.

		Scots pine		Maritime pine	
		Nt	**Pl**	**Nt**	**Pl**
Nº of plots		379	142	170	283
N	mean	965.0	1472.7	826.2	1087.5
(trees ha^{-1})	max	3939.9	3480.1	2567.7	4916.0
	min	65.2	187.5	117.9	88.3
	sd	585.5	734.1	502.7	659.7
dq (cm)	mean	22.4	18.0	24.4	20.0
	max	40.4	40.8	41.8	42.3
	min	10.5	10.0	13.3	10.4
	sd	6.4	5.6	5.9	6.2

N: stems per hectare; dq: quadratic mean diameter; Nt: Natural stands; Pl: Plantation stands

2.1.1.3 Data used in the analysis of species-mixing effects at stand and tree level

Only plots measured in both inventories were considered to analyze the effect of the mixture on growth efficiency at stand level (section 3.2.1). Plots, where total BA or BA of each species decreased more than 5% between inventories were excluded. Plots lacking continuous measurement, stand origin data, with damages due to biotic or abiotic factors (BA>40% affected) or with recorded growth anomalies were also rejected. Finally, to reduce the effects of different abiotic growing conditions between mixed and pure plots: only pure plots within a buffer of <5km from the mixed plots were included (Figure 2.2). Plots with relative stand density index (SDIR) below 0.15 were excluded (see Eq. [3.2] in section 3.1.1) to avoid the use of plots with very low density. A total of 115 mixed plots, 210 pure Scots pine plots, and 148 pure Maritime pine plots were finally selected (Table 2.2). Volume increment was calculated by the difference in standing volume between inventories, extracting natural mortality and including in-growth from the Third NFI.

A data subset was selected to evaluate the species-mixing at tree-level from the same plots used to assess species-mixing effects at the stand level (section 3.2.2). Trees were selected regardless of the plot mixture proportion. Dead trees and trees registering anomalous growth data were excluded. Individual tree data for both species at the beginning of the studied growth period is shown in Table 2.3.

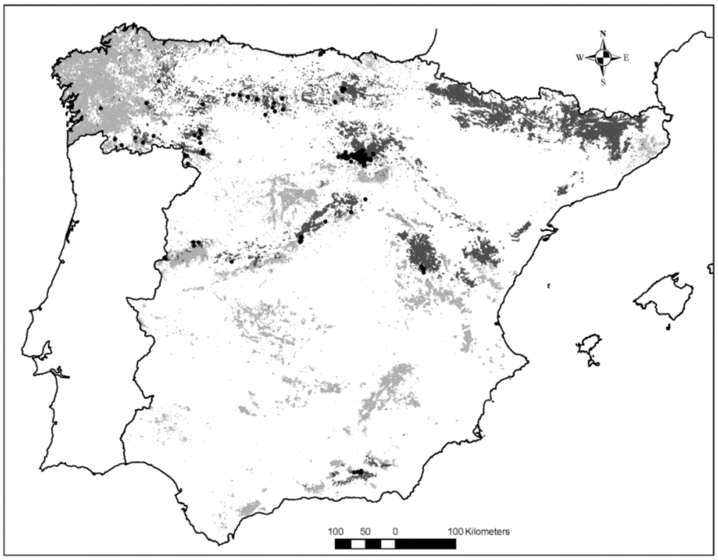

Figure 2.2. Location of mixed and pure plots selected from NFI (black dots) and the distribution of Maritime pine (gray) and Scots pine (dark gray) in Spain.

2.1.1.4 Data used for the evaluation of generalized height-diameter functions

Selected plots of the Third NFI located in the Northern Iberian Range were used to evaluate the performance of estimates of generalized *h-d* function fitted for both species in mixed stands (*Study V*). A total of 213 permanent plots of mixed and pure stands were used for this purpose, 47 mixed plots and 109 pure plots of Scots pine and 57 of Maritime pine, respectively.

Table 2.2. Main stand variables for mixed and pure plots at the beginning of the growth period (used to fit the growth models).

		Mixed plots						**Pure plots**			
		Total stand		***P. sylvestris***		***P. pinaster***		***P. sylvestris***		***P. pinaster***	
		Nt	**Pl**	**Nt**	**Pl**	**Nt**	**Pl**	**Nt**	**Pl**	**Nt**	**Pl**
Nº of plots		82	33	82	33	82	33	165	45	106	42
N	mean	564.5	1023.6	309	590	264	423	667.9	1293.3	796.5	863.6
(trees ha^{-1})	max	1479.9	3087.5	1322.7	1987.6	1177.7	1481.9	2893.0	3755.9	2291.8	1955.8
	min	87.1	226.4	14.2	88.4	19.2	28.3	65.1	240.5	104.1	283.0
	sd	312.5	744.6	241.4	500.1	218.1	398.5	468.6	678.6	558.3	450.7
BA	mean	26.8	21.6	12.7	9.7	14.3	11.7	31.9	21.2	30.3	23.7
(m^2 ha^{-1})	max	53.7	41.4	35.4	22.9	44.8	31.9	68.9	54.0	67.4	48.0
	min	8.4	7.9	1.5	1.5	0.8	1.9	8.9	7.4	8.0	8.1
	sd	12.3	9.5	8.3	5.3	9.3	7.5	14.2	10.7	15.5	10.3
Ho	mean	14.0	9.8	13.3	8.9	13.3	9.8	15.4	8.7	12.0	9.7
(m)	max	22.3	13.6	21.0	14.1	21.3	13.2	27.9	19.2	20.1	14.3
	min	6.3	5.3	5.8	4.2	4.8	5.6	6.1	4.7	5.1	5.5
	sd	3.4	2.2	3.5	2.6	3.8	2.0	4.0	3.2	3.2	2.3
dq	mean	26.3	18.0	25.1	17.0	28.9	21.5	27.7	15.1	24.3	19.6
(cm)	max	39.5	33.6	50.7	35.8	41.6	31.7	51.5	32.5	46.1	33.5
	min	11.7	10.7	9.8	8.8	10.3	11.2	10.5	8.9	10.0	10.7
	sd	7.0	5.3	7.8	6.8	8.9	5.5	8.7	4.6	7.6	5.0
PAIV	mean	5.1	7.4	2.3	3.2	3.1	4.1	4.6	6.7	5.0	7.7
(m^3 ha^{-1} yr^{-1})	max	12.5	17.6	8.5	7.5	9.2	14.4	14.0	16.6	14.4	19.1
	min	0.3	1.4	0.1	0.6	0.1	0.6	0.1	1.6	0.7	1.0
	sd	2.8	4.1	1.7	1.8	2.3	3.2	3.1	3.5	3.1	4.8
Total stand density (SD)	mean	0.48	0.41	0.23	0.19	0.25	0.22	0.55	0.41	0.56	0.44
	max	0.99	0.76	0.62	0.47	0.81	0.60	1.17	1.00	1.2	0.88
	min	0.17	0.16	0.03	0.03	0.01	0.03	0.15	0.15	0.15	0.15
	sd	0.23	0.18	0.15	0.11	0.17	0.14	0.24	0.19	0.28	0.19

N: trees per hectare, *BA*: basal area per hectare, *Ho*: dominant height, *dq*: quadratic mean diameter; N: Natural stands; P: Plantation stands; SD: Total stand density as the sum of the relative stand density of each species SD=SDIRi+SDIRj.

Table 2.3 Tree characteristics and competition status by stand origin in selected plots at the beginning of the growth period (used to fit tree-growth models).

	Origin	**n**		**d (cm)**	**h (m)**	**iv (dm^3 yr^{-1})**	**SDIR**	**SDIRL**	**SDIR$_{intra}$**	**SDIR$_{inter}$**	**SDIRL$_{intra}$**	**SDIRL$_{inter}$**
Scots pine	Nt	1317	mean	27.2	14.1	11.12	0.52	0.30	0.33	0.19	0.16	0.14
			min	7.5	3.0	0.01	0.09	0.00	0.01	0.01	0.00	0.00
			max	54.1	24.0	68.15	1.06	1.04	0.97	0.94	0.96	0.94
	Pl	419	mean	17.5	8.9	9.16	0.36	0.23	0.19	0.18	0.09	0.14
			min	7.5	3.5	0.20	0.07	0.00	0.01	0.01	0.00	0.00
			max	55.8	18.0	74.89	0.65	0.62	0.39	0.49	0.35	0.49
Maritime pine	Nt	1367	mean	32.3	14.0	18.69	0.54	0.23	0.38	0.16	0.18	0.05
			min	7.65	2.0	0.01	0.09	0.00	0.01	0.01	0.00	0.00
			max	73.2	25.5	120.51	1.06	0.98	0.94	0.97	0.92	0.44
	Pl	523	mean	22.3	9.6	17.53	0.39	0.15	0.26	0.13	0.13	0.02
			min	7.7	4.0	0.15	0.07	0.00	0.01	0.01	0.00	0.00
			max	54.5	19.0	76.54	0.65	0.63	0.49	0.39	0.48	0.26

d: diameter at breast height; iv: tree volume growth; sd: standard deviation, min: minimum value, max: maximum value. Nt: Natural stands; Pl: Plantation stands. Competition indices are described at section 3.2.2, SDIR: size-symmetric competition index; SDIRL: size-asymmetric competition index for larger trees; intra: intra-specific competition, inter: inter-specific competition

2.1.2 Triplets network

2.1.2.1 Study area

Triplets were established during 2014-2015 in mixed pine forests of Scots pine and Maritime pine that cover approximately 50 000 ha in the Northern Iberian Range. The climate is subhumid Mediterranean continental with a mean annual temperature of 9.0ºC and mean annual precipitation approximately of 800 mm with frost occurring from September to May. Plots are located at an elevation ranged from 1090 to 1277 m a.s.l. Soils are acidic (pH 3.9–5.4) with sandy loam to sandy texture, low cation exchange capacity (2.4 – 18.1 cmolC kg^{-1}) and medium to lower water-retention capacity (1.5 – 18 g cm^{-2}) (López Marcos et al., 2017).

In the region, forest management has divided the forest cover into even-aged sections and compartments. Traditionally, the even-aged stands management applied strip clear-cutting with soil movement and sowing when necessary, followed by natural regeneration. The main objective is timber production, but with a clear multifunctional approach. For instance, mushroom production and the recreational activities related are considered as highly relevant economic incomes from forestry resources (Aldea et al., 2014; de Frutos et al., 2009). Forest management of mixed stands of Scots pine and Maritime pine commonly favor the former due to its better wood quality. However, environmental conditions have benefited the progressive establishment of Maritime pine into forest areas covered by Scots pine (García-Güemes and Calama, 2015). Moreover, Maritime pine stands historically were slightly tapping for resin extraction in this area due to resin productions constraints by low temperatures (Rodríguez et al., 2008)

2.1.2.2 Triplets design

A total of 36 plots, grouped into 12 triplets of mixed plots (PS,PT) and their corresponding pure plots of Scots pine (PS) and Maritime pine (PT) (Figure 2.3). Plots within triplets had similar site conditions, age, and density and belonged to the same management compartments where the same silviculture regime had been applied; facilitating a pair-wise plausible comparison of mixed versus pure stands (Table 2.4).

Table 2.4. Description of mixed-species and monospecific plots included in the triplet design.

Composition		**N** (trees ha^{-1})	**dq** (cm)	**BA** (m^2 ha^{-1})	**Ho** (m)	**V** (m^3 ha^{-1})	**PAIV** (m^3 ha^{-1} year^{-1})	**Prop** (% BA)	**Age**	**SI**
Maritime pine mixed	mean	286	37.9	31.2	21.5	282.5	4.2	53.5	100	22
	max	538	48.0	49.3	26.9	429.3	7.0	67.0	49	27
	min	127	27.5	11.1	15.0	79.7	2.2	28.6	140	16
Scots pine mixed	mean	398	29.5	26.7	20.2	237.4	2.8	46.5	100	22
	max	594	40.6	45.9	26.7	473.2	6.9	71.4	44	29
	min	241	20.5	13.0	15.0	86.3	0.9	33.0	138	14
Total mixed	mean	685		57.9		519.9	7.0			
	max	1103		75.7		700.2	9.2			
	min	523		33.3		234.3	4.4			
Maritime pine pure	mean	724	33.1	59.3	19.0	476.7	6.9	98.7	98	20
	max	1259	40.3	70.3	22.5	632.6	9.2	100.0	45	28
	min	410	22.0	37.5	14.9	249.6	4.2	95.0	130	16
Scots pine pure	mean	709	30.8	50.3	21.5	453.3	5.8	94.3	105	22
	max	1217	39.3	66.3	25.7	652.8	11.3	100.0	44	31
	min	410	21.5	33.3	16.5	236.4	3.1	93.3	140	17

N, tree number (ha^{-1}); dq, quadratic mean diameter (cm); Ho, dominant height (m); BA, stand basal area (m^2 ha^{-1}); V, standing stem volume (m^3 ha^{-1}); PAIV, periodic annual volume growth (m^3 ha^{-1} year^{-1}) for the period 2004-2014; Prop, proportion of species stand basal area; SI, site index as the dominant height (m) at age 100 based on the site index curves developed by Rojo and Montero (1996) and Bravo-Oviedo et al. (2007) for Scots pine and Maritime pine, respectively.

The stands were approximately full stocked, stocked above 60% relative to or even exceed the maximum, and none of the plots had been thinned for at least 10 years. In most of the triplets, both species were in the same age phase comparing monoculture and mixed-species stands, ranging from mature (45-50 years) to old stands (120-140 years). Site quality estimated as the dominant height at age 100 years indicated moderate to low growth conditions according to specific curves of pure stands (Bravo-Oviedo et al., 2007; Bravo and Montero, 2001; Rojo and Montero, 1996). Some variations in stand age and site conditions were tolerated among triplets to cover stand variability in the study area (Table 2.4).

Each triplet consisted of three circular plots of 15m radius, including one pure plot of Scots pine, one pure plot of Maritime pine and one mixed plot that contained both species. Mixed plots had varying individual tree mixtures, and the mixing proportion between species had a combination of at least 75-25% of the total basal area. Pure plots were located within 1 km of the mixed plots. Pure plots stands were considered only when the total basal area of the target species was higher than 90% and was used as a reference to evaluate mixing effects on stand structure, growth, and yield.

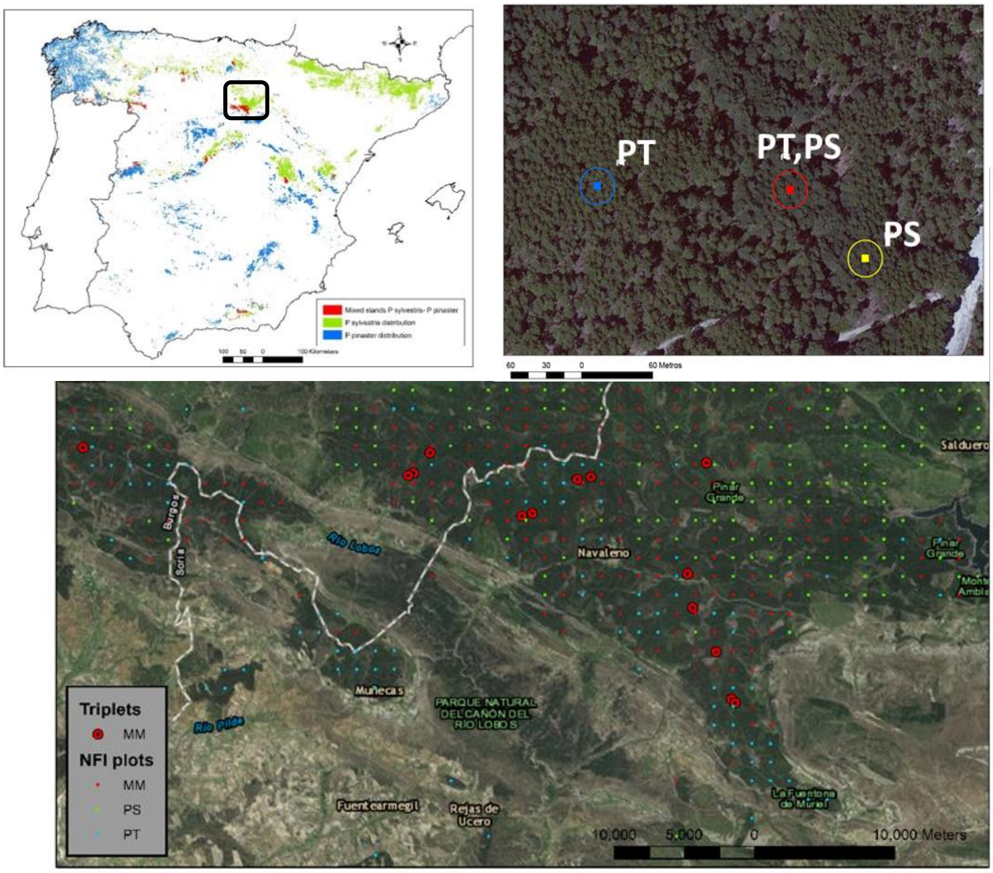

Figure 2.3. Left above: Distribution of Maritime pine (blue), Scots pine (green) and mixed stands (red) in Spain, black frame marks the study area. Below: The locations of the 12 triplets (red circles with black center) respecting to the NFI plots. Right above: location of monospecific and mixed plots in one triplet (PS -green circle- for Scots pine and PT -blue circle for Maritime pine) and mixed stands (PS,PT -red circle-).

Figure 2.4. Mixed (above) and pure stands of Scots pine (middle) and Maritime pine (below).

2.1.2.3 Triplets inventory and cores sampling

All stems > 7.5cm in diameter were positioned ('x, y' coordinates) and measured the diameter at breast height (*d*). Tree total height (*h*) and height to crown base (*hcb*, height of the crown's lowest primary branch) were measured for all trees using a vertex hypsometer. A crown class was assigned to each tree (dominant, co-dominant, dominated and suppressed).

Increment cores at stem height of 1.30 m covering at least the last 15 years were taken from all trees avoiding dead or suppressed individuals. A total of 736 from Scots pine and 693 from Maritime pine trees in mixed and pure plots were sampling. All cores were mounted, sanded till tree-ring boundaries were clearly visible and scanned at 1800ppi image resolution. For each cored tree, tree ring widths (mm year^{-1}) were dated and measured from the scanned images using the *measuRing* package (Lara et al., 2015), Figure 2.5. We performed cross-dating using species-specific marker years, narrow rings, followed by statistical confirmation of quality tree-ring series synchronization using the *dplR* package (Bunn, 2010), Figure 2.6.

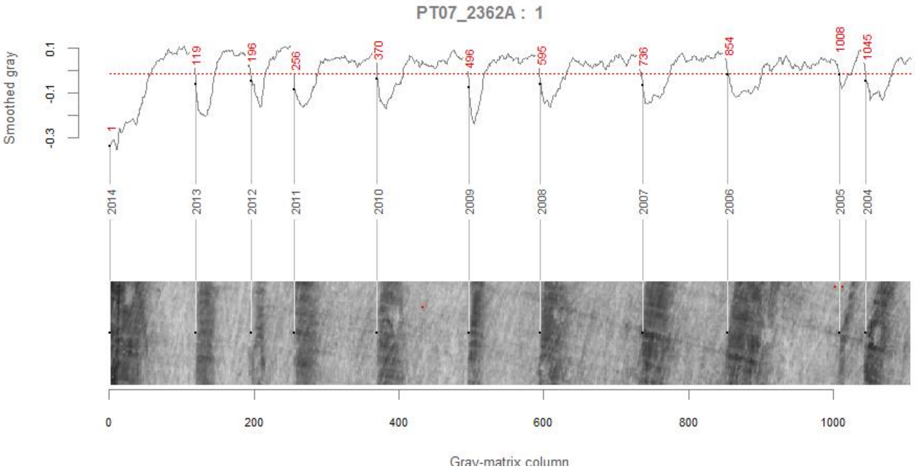

Figure 2.5. Segment from a scanned core sample 'PT07_2362A' of Maritime pine processed with *measurRing* R-package. Tree-ring detection was a combination of automatic and visual selection from the sampling year 2014. Numbers on vertical segments 'gray-matrix column' are the formation years. The position of the dotted red line over the smoothed grays correspond to a constant across which the ring borders were detected (default origin = 0), details in Lara et al., (2015).

Stand variables and tree measurements were used to analyze to what extent mixing modifies the structural attributes in the stand and species crown allometric relationships compared to pure stands (Study II). Tree-rings width was the main input to evaluate growth at tree level and scale up to stand level (Study II and V). Tree rings measurements were used to backdate tree size (*d* and volume) and stand variables (BA and dq) to the beginning of the evaluation period. Tree-ring series after detrending were used to evaluate the responses and long-term drought effects in both species in mixed and pure stands (Study III).

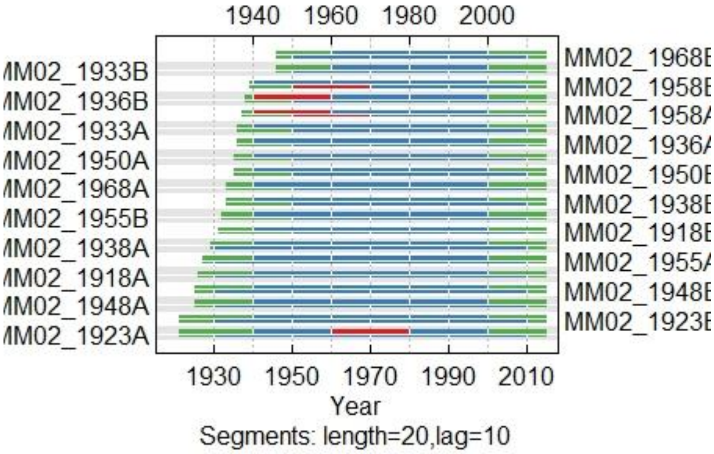

Figure 2.6. Cross-dating between each segment (10 years) of each sample in a plot with the master chronology, blue segments showed significative correlation to the master chronology (critical value=0.35), red segments indicated the segment with potential dating problems (Bunn, 2010).

2.1.3 Backdating

Reconstruction of diameter and height of all trees to the beginning of the evaluation period (2004, t_1) is necessary to relate past growth to initial condition, '*backdating*' (Bravo et al., 2001, Hann and Hanus, 2001). Diameter over bark at breast height for time t_1 (d_1) for all cored trees was calculated using the diameter measured at 2014 (d_2), the tree ring width measurements from each core sampled and the species-specific bark factors (Bravo et al., 2007; Lizarralde, 2008). The diameter increments of all non-cored trees for this evaluation period were calculated by fitting diameter increment functions for each plot and species based on the diameter measured at 2014 (d_2).

$$id = \beta_0 + \beta_1 d_2 \qquad [2.1]$$

where *id* is the stem diameter increment for the period, and β_0 and β_1 are intercept and slope of the linear model. Diameter increment estimation of non-cores trees and backdated data of cored trees were used to calculate the diameter over bark at the beginning of the evaluation period for all trees (d_1). Stand variables such as quadratic mean diameter and stand basal area directly derived from the backdating. This data was used to evaluate the effect of mixing species on stand productivity (Study II) and tree growth (Study V).

Specific height-diameter functions parameterized for the same study region (Lizarralde, 2008) were used to reconstruct individual tree heights. However, this required estimates past dominant height in each plot (Ho_1). Ho_1 was calculated using species-specific site index curves and the mean stand age. Age was determined relies on cores to the pith took from dominant trees of both species in each plot. We used site index curves developed by Rojo and Montero (1996) and Bravo-Oviedo et al. (2007) for Scots pine and Maritime pine, respectively. Once Ho_1 was estimated, tree height ($\hat{h}_1$) at the beginning of the growth period was calculated using the generalized specific height-diameter functions (Lizarralde, 2008). Then past tree height (h_1) was calculated by multiplying the 2014 measured tree height (h_2) by the proportional difference between estimated past and current tree height, $\hat{h}_1$ and $\hat{h}_2$ respectively, thereby avoiding negative height growths in the h_1 reconstruction. Tree height reconstruction in mixed plots was based on the species-specific dominant height and quadratic mean diameter in the stand.

$$h_1 = h_2 \frac{\hat{h}_1}{\hat{h}_2} \qquad [2.2]$$

Individual tree diameter and height reconstruction data and species-specific volume functions (Rodríguez and Broto, 2014) were used to estimate stand volume (V). Annual volume increment was calculated by differences between the stand volume at 2014 (V_2) and stand volume at the beginning of the period evaluation, 2004 (V_1), as $PAIV=(V_2-V_1)/t$, analogously annual basal area increment was calculated as $PAIBA=(BA_2-BA_1)/t$. Removed volume and basal area from the stand were not considered since the triplets were established in stands that had not been thinned during the study period at least. In pure plots, stems of the coexisting species were assigned as Scots pine or Maritime pine, respectively. Volume increment was used to evaluate the effect of mixing species on stand productivity and stand structure (Study II).

2.1.4 Band dendrometers

Band dendrometers (DB 20, EMS Brno) were placed on one triplet from the Triplets Research Network of pinewood forest during autumn and winter 2015. Stand variables, age and site index, were similar between mixed and pure plots (Table 2.5). Tree dead bark was removed and circumference measured previous mounted the dendrometers at breast height (1.3m) on 32 trees, 8 trees per species and plot (16 trees in mixed stands). Trees were selected to obtain a balanced representation of the diameter distribution of each tree species in mixed and pure stands (d >17cm). Band dendrometers were measured biweekly from March to December 2016 with a precision of 0.1mm. To avoid diurnal biases due to changes in tree water status, all measurements were taken in the afternoon around 4 p.m. Girth increment data were transformed to radial increments based on a cylindrical tree shape (Table 2.6). We used girth increment measurements of band dendrometers to analyze the intra-annual radial increment pattern of both species in mixed and pure stands (Study IV).

Table 2.5. Description of the triplet used to install band dendrometers.

Composition	**N (trees ha^{-1})**		**BA (m^2 ha^{-1})**		**dq (cm)**		**Ho (m)**		**Prop (%BA)**		**Age**		**Site index**	
	PS	PT	PS	PT	PS	PT	PS	PT	PS	PT	PS	PT	PS	PT
Mixed plot	396	283	13.0	20.2	20.5	30.2	15.0	16.1	0.39	0.61	44	49	23	23
Scots pine pure	778	42	30.8	2.6	22.4	27.7	17.8	19.5	0.92	0.08	44		26	
Maritime pine pure	0	594	0	37.5	0	28.4	0	16.9	0	1.00		49		23

PT: *P. pinaster*; PS: *P. sylvestris*; BA: stand basal area; Ho: dominant height

Table 2.6. Main characteristics of Scots pine and Maritime pine trees with band dendrometers in mixed and pure plots. Mean and standard deviation in brackets of tree diameter and intra-annual cumulative radial increment measured at 2016.

Composition	**Tree diameter (cm)**		**Cumulative radial increment (mm)**	
	PS	**PT**	**PS**	**PT**
Mixed plot	21.05 (3.11)	28.79 (4.41)	1.462 (0.38)	1.828 (0.72)
Scots pine pure	22.76 (4.30)		1.609 (0.38)	
Maritime pine pure		30.47 (6.58)		1.808 (0.73)

2.2 Climate data

Climate data were extracted from available raster maps (at 1x1 km scale) of the functional phytoclimatic model (Gonzalo Jiménez, 2010). Mean monthly, seasonal and annual temperature and precipitation values from 1951 to 1999 and the corresponding phytoclimatic regions were assigned to each selected plot from the NFI dataset according to their coordinates. These variables were used to test if the main environmental conditions influenced the mixture effects in the stand model (Study I).

Standardized Precipitation Evapotranspiration Index–SPEI (Vicente-Serrano et al., 2010) was used to estimate the drought intensity at triplets plots. The SPEI is a multi-scalar drought index based on a simple climatic water balance (monthly differences between precipitation and reference evapotranspiration), which is intended to determine the onset, duration and magnitude of drought conditions with respect to normal conditions in a given area. Negative and positive values below or above 1 correspond, respectively, to dry and wet periods. In this study, we considered a 12 months long September SPEI (i.e., the cumulative water deficit from October of the previous year to September). Based on analyses reported by Camarero et al., (2015) showing the most robust SPEI-growth relationships for both species. We used specific coordinates of each plot to extract SPEI time series for the period 1961–2015 from the gridded Dataset of Drought Indices for Spain (spatial resolution 1.1 km^2) (Vicente-Serrano et al., 2017). From 1961 to 2015, seven years showed SPEI values lower than -1 (Figure 2.8), considered as drought years (Potop et al., 2014). Strongest drought event in 2005 (SPEI = -2.20) and an increment of drought events in the last 30 years.

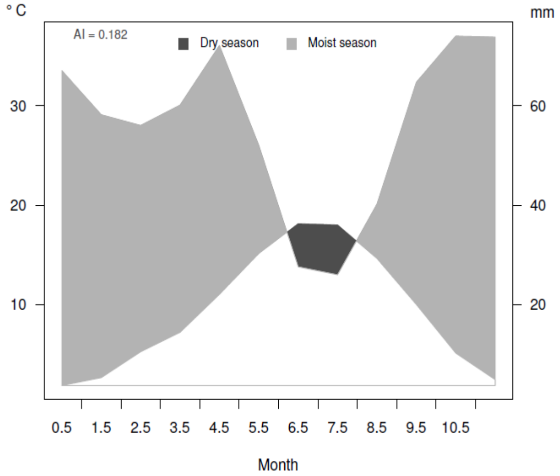

Figure 2.7. Walter-Lieth Diagram of the study area where Triplets Research Network was established. Aridity Index (AI)=0.182. Monthly mean temperature and precipitation calculated using Gonzalo Jiménez, (2010) dataset, 1951 – 1999.

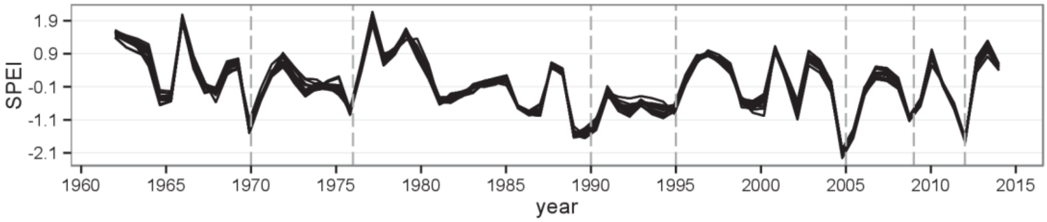

Figure 2.8. Standardized Precipitation–Evapotranspiration Index (SPEI), drought index accumulated during 12 months (from February to September). SPEI time series extracted for each plot in the Triplets (black lines). Positive and negative SPEI values indicate wet and dry conditions, respectively. Vertical dashed lines highlight drought years.

3. Methods

During the development of this thesis, species-mixing effects on processes involved in growth and yield mixed stands (Figure 1.2) were progressively analyzed at three organizational levels, stand, individual tree and tree size distribution level. NFI and temporal plots grouped in triplets were the primary data used for these analyses. Additionally, tree growth dynamics and temporal variation were studied at long-term inter-annual and short-term intra-annual scale. Tree-ring width series and band dendrometers measurements were used for this purpose. In the following sections, the methodological aspects considered and analytical procedures used for developing each study are widely described. Data sources and analysis methods used in the different studies are summarized in Table 3.1.

Table 3.1. Summary of data sources and analytical approaches used in relation to each study in this thesis.

Study/Objective	**Data source**				**Analysis method**	
	NFI	**Triplets and backdating**	**Tree-ring series**	**Band dendrom.**	**Statistical procedure**	**R Package**
Study I: Mixing effects at stand and tree-level						
Maximum stand density	●				Quantile regression	*quantreg*
Comparison of mixing effects between stand and tree-level	●				Linear mixed model Model selection	*nlme* *MuMIn*
Study II: Species-mixing effects on stand productivity and stands structure						
Intra-specific differences in tree allometry		●			Major axis regression	*smatr*
Evaluation of stand structure heterogeneity		●			t.test wilcox.test	*stat*
Overyielding and stand structure relationship		●			Linear models	*stat*
Study III: Dendroclimatic responses of mixed and pure stands						
Growt*h-d*rought long-term fluctuations			●		Linear mixed model Mantel correlograms	*nlme* *BIODry*
Tree growth responses to drought events			●		Linear mixed model	*nlme*
Study IV: Temporal complementarity intra-annual increment patterns						
Mixture effects in intra-annual growth patterns				●	Non-linear model Generalized linear model	*FlexParamCurve* *nlme*
Study V: Adapting tree-level model IBERO to mixed species stands						
Generalized *h-d* model for mixed stands	●	●			Non-linear mixed model	*nlme*
Basal area growth model for mixed stands		●			Linear mixed model Model selection	*nlme* *MuMIn*

3.1 Mixing proportion and maximum stand density

3.1.1 Mixing proportion

Comparison of growth in mixed and pure stands, negative or positive interaction effects on growth must be related to the area occupied by the respective species. The area available for a species in a mixed stand (species proportion by area) can be defined as the ratio of the observed space occupancy and the potential (maximum) space occupancy for this species and site. The maximum stand density index (Reineke, 1933) and the maximum basal area (Sterba, 1987) have well-developed theories that describe potential density which can be used to estimate species proportion by area, and can be estimated from large inventory data (Río and Sterba, 2009; Condés et al., 2013). They are expressions of the same ecological principal (Vospernik and Sterba, 2015) and both approaches produced similar estimations of mixture effects when the potential densities of the species did not differ by much (Sterba et al., 2014). In this way, the *stocking proportion* or species proportion by area (m_i) Eq. [3.1] were estimated in this study using the respective relative stand density index of the target species (SDIR_i) Eq.[3.2] (Sterba et al., 2014).

$$m_i = \frac{SDIR_i}{SDIR_i + SDIR_j} \qquad [3.1]$$

$$SDIR_i = \frac{SDI_i}{SDI_{max}} = \frac{N_i\left(\frac{25}{dq_i}\right)^{E_i}}{C_i \cdot 25^{E_i}} \qquad [3.2]$$

where m_i is the proportion of species i by area, SDIR_i is the observed relative stand density of species i, SDI_i is the stand density index of species i and index j is referred to coexisting species. The denominator in Eq. [3.2] represents the maximum or potential stand density index (SDImax) of species i in a fully stocked pure stand. Thus, mixing proportion was adjusted to take account inter-specific differences in carrying capacity at a given site and allowing a plausible comparison of productivity per hectare between pure and mixed stands (del Río et al., 2016; Forrester and Pretzsch, 2015).

3.1.2 Maximum stand density

In order to use the stocking proportion approach, the maximum stand density had to be determined for both species. To derive the potential density of the species in pure stands, we used the maximum stand density index SDImax as the self-thinning rule (Reineke, 1933) Eq. [3.3]. Species-specific parameters C and E were estimated with a log-linear quantile regression (QR) in Eq. [3.4] using the *quantreg* R-package (Koenker, 2015; R Develomment Core Team, 2015).

$$N_{max} = C_0 \cdot dq^{E_0} \qquad [3.3]$$

$$\ln N = C_0 + E_0 \ln dq + \varepsilon \qquad [3.4]$$

where C_0 and $E_0$are species-specific parameters of the self-thinning line to be estimated. The parameters obtained in the outermost quantiles (90–99th) were compared with the slope and intercept fitted by OLS. Additionally, we tested whether other independent variables such as stand origin might significantly affect the intercept value in the self-thinning line. This robust method is especially useful for estimating rates of change along or near the upper limit of the functional size-density relationship (Cade and Noon, 2003; Zhang et al., 2005). Several studies have demonstrated the suitability of using National Forest Inventory data for estimating self-thinning lines (Charru et al., 2012; Valbuena et al., 2008) and evaluating the influence of species-specific traits to predict maximum size-density relationship (Bravo-Oviedo et al., 2018).

3.2 Mixing effects at stand level and tree level using NFI data

3.2.1 Mixing effects at the stand level

Effects of species-mixing at the stand-level are usually analyzed through the possible growth deviations in mixtures as compared to neighboring pure stands. In this respect, species proportion was used as a proxy for the partitioning of growing space: the allocation of resources such as light, water, and nutrients among the species in the stand (Río et al., 2016). The growth efficiency at stand level for species i (IVm_i), was defined as the volume increment of species per hectare $PAIV_i$ (m3 ha-1 year-1) divided by the stocking proportion (Eq.[2.1]), $IVm_i = PAIV_i/m_i$, e.g. species volume growth up-scales to the hectare, being $m_i = 1$ in pure stands. The volume increment per hectare (PAIV) is the volume difference between the two inventories divided by the time span between them. The period between measurements varied among plots (10 - 13 years). To test if the species mixture affects growth efficiency and study the density-growth relationships, the following general model was fitted for Scots pine and Maritime pine, respectively.

$$\ln(IVm_i) = \beta_0 + \beta_1 \ln(Ho) + \beta_2 \ln(dq_i) + \beta_3 \ln(SD) + \beta_4 m_j + \beta_5 ORIG_i + \varepsilon \qquad [3.5]$$

where the dependent variable is the volume growth efficiency of species i . Dominant height (Ho) of the stand, the quadratic mean diameter (dq) of the species i and total stand density (SD) are the independent variables. Stand variables such as Ho and dq were included in the model as surrogate variables to account for the high variability in the site qualities and ages presented in NFI data. Total stand density (SD) was used to compare growth in pure and mixed stands. SD was calculated based on the relative total stand density concept, $SD = SDIR_i + SDIR_j$ (Sterba et al., 2014).

To test if species-mixing affects growth, we included the species proportion by area of the coexisting species (m_j). A positive and significant coefficient for this variable would indicate that growth efficiency of the species i increases with an increasing proportion of species j, e.g. positive species-mixing effect. Additionally, a dummy variable for each origin was included ORIG (0 for natural plots or 1 for plantation plots) and interactions between species proportion by area and independent variables were also tested. Finally, we tested the benefit of including the set of climate variables (Gonzalo Jiménez, 2010; section 2.2) in the model structure.

Linear regression was fitted using the least squares approach establishing significance at $p<0.05$. The relevance of the species proportion in the growth efficiency model was tested using the F-statistic to compare equation Eq. [3.5] (mixture model) against a null model (without the m_j parameter).

3.2.2 Mixing effects on inter-tree competition

Single-tree models are a very effective tool for exploring the effect of competition on growth. An adequate individual tree growth model must include both an expansion and decline component to represent the growth pattern (Zeide, 1993). Equation [3.6] includes both components as a function of tree size. The competition status of the tree was included as a modifier component (e^{Comp}) that reduces the potential growth rate to the actual growth rate (Bravo et al., 2001; del Río et al., 2014a; Pretzsch and Biber, 2010).

$$iv_i = \beta_0 \cdot e^{\beta_1 d_i} \cdot d_i^{\beta_2} \cdot h_i^{\beta_3} \cdot e^{Comp} \qquad [3.6]$$

where iv_i is the volume increment of a tree with a given diameter d_i and tree height h_i. The species-specific parameters are β_0, β_1, β_2 and β_3. $Comp$ is the competition term. Because in NFI trees are recorded according to diameter classes over circular concentric plots is not possible to use a distance independent approach to quantify tree competition. We used the stand density index concept (Eq. [3.2]) as a measure of size-symmetric competition. To analyze size-asymmetric competition, we used the stand density index of trees larger than the target tree (SDIL) Eq. [3.7] as an indicator of asymmetric competition for light (Pretzsch and Biber, 2010).

$$SDIL = N_L \left(\frac{25}{dq_L}\right)^E \qquad [3.7]$$

where N_L and dq_L, are the number of stems per hectare and quadratic mean diameter of trees larger than the target tree, respectively, and E is maximum stand density exponent. We used species-specific values of E fitted using the QR technique (section 3.1.2).

Both size-symmetric (SDI) and size-asymmetric (SDIL) competition were calculated in relative terms Eq. [3.2] to take into account species-specific site occupancy (Condés and del Río, 2015; Sterba et al., 2014). Relative size-symmetric (SDIR) and relative size-asymmetric (SDIRL) competition indices attributed for each species were calculated following a similar approach to that of Río et al., (2014). SDIR and SDIRL were split into intra-specific and inter-specific competition components for evaluating the influence of the mixture on tree growth. If inclusion of SDIR or SDILR in the growth model results in a better fit than the use of the intra- and inter-specific indices, it may indicate similar intra- and inter-specific competition or no species-mixing effect (del Río et al., 2014a). The performance of the different competition structures was analyzed in the tree volume growth model Eq. [3.8] using the information-theoretic approach (Anderson, 2007), section 3.8.

The original dependent variable was logarithmically transformed to attain normal distribution of the residuals and reduce heteroscedasticity. Linear mixed-models were fitted considering random effects at two nested levels: phytoclimatic region and plot-in-region. However the inclusion of the phytoclimatic region in the hierarchical structure did not improve models performance; thus, we only used plot as the grouping structure of the random effects. We included random effects in both intercept and logarithm diameter terms.

$$\ln(iv_{ij}) = (a_0 + u_{0j}) + a_1 \cdot d_i + (a_2 + u_{2j}) \cdot \ln(d_i) + a_3 \cdot \ln(h_i) + a_4 ORIG + \sum \beta_k \, Comp_{ijk} + \varepsilon_{ij} \qquad [3.8]$$

where iv_{ij} is the volume increment of the tree j measured in the plot i, u_{0j} and u_{2j} are plot level random effects and ε_{ij} the error term. $Comp_{ijk}$ represents the k different competition structures for tree j in plot i. a_0, a_1, a_2, a_3, a_4 and β_k are parameters to be estimated. All errors terms were assumed to be normally distributed with mean $0, (u_{0j}) \sim N(0, \sigma_0^2)$, $(u_{2j}) \sim N(0, \sigma_2^2)$ and $\varepsilon_{ij} \sim N(0, \sigma_{res}^2)$.

3.3 Stand structure and species functional traits in mixed versus pure stands

3.3.1 Intraspecific differences in tree allometry

Stand density and competition can considerably modify crown allometry and tree morphology. Species-specific characteristics of crown shape and allometric scaling are relevant for understanding the tree species size development, especially in mixed stands (Pretzsch, 2014). The influence of species mixing on the *h-d* and hcb-d allometric relationships were assessed using h, hcb and d measurements from 938 and 858 trees of Maritime pine and Scots pine, respectively. Tree allometry relationships were fitted by log-transforming h–d and hcb-d, assuming that above-ground allometry follows a power-law function or allometric relation, $y = \alpha x^{\beta}$. Stand composition was treated as a factor for each species model (mixed or monospecific stand). Then, likelihood ratio test was used to ascertain whether the slope of the allometric functions differed according to stand composition (Warton et al., 2006). Significant differences between model parameters indicate in what extent inter- vs. intraspecific environment influence above-ground allometry. h–d and hcb-d relationships were fitted with standardized major axis regression (SMA) in R package *'smatr'* (Warton et al., 2012). SMA regression is preferable to ordinary least squares regression when neither variable is clearly the dependent variable, and the objective is estimating how one variable scales against another. Such a line is a summary in the sense that a single dimension is used to describe two-dimensional data (Warton et al., 2006).

3.3.2 Stand structure on mixed and pure stands

In order to characterize structural traits and compare mixed and monospecific stands, we considered a set of attributes related to horizontal size distribution patterns and vertical structure as measures of stand structure, Table 3.2., as well as quadratic mean diameter and dominant height. For analyzing differences in size distributions, we calculated the mean, minimum and maximum values of tree diameter, height and volume for each plot (x_{mean}, x_{min}, x_{max} where x is the d, h or tree volume (v), respectively). We also considered the vertical species profile index (A_{index}) according to (Pretzsch, 2009b), that allows for comparison of vertical structure differentiation between mixed and pure stands. Gini coefficient for tree volume (GC_v) and tree volume growth (GC_{iv}) were used to quantify inequalities in volume distribution and growth allocation among trees within a stand, respectively (Binkley et al., 2006).

The A_{index} quantifies the vertical stand structuring of each tree species within different height zones. Any deviation from a single-layered pure stand is reflected as a distinct increase in the species profile index. The more heterogeneous the vertical profile, the higher A_{index} becomes (Pretzsch, 1998).

$$A_{index} = -\sum_{i=1}^{S}\sum_{j=1}^{Z} p_{ij} \times \ln p_{ij} \qquad [3.9]$$

where S represents the number of species in the stand, Z the number of height zones, and p_{ij} the proportion of a species in the height zone, $p_{ij} = n_{ij}/N$, being N the total number of individuals and n_{ij} the number of individuals of each species i in zone j. Thus the overall species diversity and the vertical spatial occupancy of the species present in the forest stand were quantified. We calculated A_{index} dividing each plot into three height zones j=(1, 2, 3), which constituted 0–50%, 50–80% and 80–100% of the maximum stand height, respectively.

A_{index} was standardized to relative vertical species profile index (A_{rel}) facilitating comparisons between stands with differing numbers of species. A_{rel} quantifies the relative degree of structural diversity, e.g., the observed diversity in relation to the maximum structural diversity for the given number of species and number of zones distinguished (Pretzsch, 2009b).

$$A_{rel} = A_{index} \times \ln(S \times Z) \times 100 \qquad [3.10]$$

Gini coefficient was used to evaluate whether mixing modifies the size and growth hierarchy among trees in a population. GC = 0.0 represents a homogeneous distribution and means that all trees are equal in size or growth. Higher GC corresponds to greater size or growth inequality among trees. These have been used to compare how species-mixing can modify the hierarchy between trees in mixed compared with pure stands (Pretzsch and Schütze, 2014).ç

$$GC = \frac{\sum_{i-1}^{n}\sum_{j=1}^{n}|x_i - x_j|}{2n\,(n-1) \times \bar{x}} \qquad [3.11]$$

for quantifying the relative distribution of tree volume (GC_v) and tree volume growth (GC_{iv}), respectively, between the trees in mixed versus pure stands of all 12 triplets. Variables x_i and x_j denote tree volume or tree volume growth for the *i*th, respectively the *j*th tree in the stand with i =1…n trees (Pretzsch and Schütze, 2014). GC_v and GC_{iv} were calculated separately for both species of each triplet.

Table 3.2. Mean values and standard error of structural measures for monospecific and mixed-species stands of Scots pine and Maritime pine.

Structure traits	**PS_{pure}**		**PT_{pure}**		**PS_{mix}**		**PT_{mix}**		**Mix_{obs}**	
	mean	**SE**	**mean**	**SE**	**mean**	**SE**	**mean**	**SE**	**mean**	**SE**
d_{mean}	30.06	1.49	32.52	1.56	28.81	1.64	37.63	2.02	32.31	1.96
d_{min}	14.58	1.18	17.46	1.68	14.88	1.97	25.78	2.38	14.54	1.71
d_{max}	46.83	2.17	49.22	1.88	44.61	2.18	51.14	2.17	52.68	1.80
h_{mean}	19.89	0.80	17.59	0.78	18.94	1.04	20.48	1.18	19.55	1.04
h_{min}	13.03	1.25	12.34	1.38	13.28	1.25	17.04	1.49	12.80	1.36
h_{max}	24.35	1.03	21.18	0.85	23.02	1.05	23.62	1.22	24.18	1.10
v_{mean}	0.71	0.08	0.74	0.08	0.64	0.09	1.13	0.15	0.82	0.09
v_{min}	0.14	0.03	0.20	0.05	0.18	0.07	0.54	0.11	0.16	0.05
v_{max}	1.72	0.18	1.72	0.17	1.45	0.17	2.05	0.23	2.16	0.22
A_{rel}	49.25	20.71	54.04	19.13	62.54	8.30	51.04	11.77	69.64	8.75
GC_v	0.27	0.02	0.26	0.02	0.27	0.02	0.22	0.02	0.30	0.02
GC_{iv}	0.29	0.02	0.28	0.02	0.29	0.02	0.24	0.02	0.36	0.02

PS, *Pinus sylvestris* and PT, *Pinus pinaster*; mean, minimum (min) and maximum (max) values of tree diameter in cm (d); height in m (h); volume in m^3(v); relative species profile index (A_{rel}); Gini coefficient for tree volume (GC_v) and volume growth (GC_{iv}).

3.3.3 Evaluation of species-mixing effects stand structural heterogeneity

We calculated ratios ($R_x = x_{mixed}/x_{pure}$) of tree size distribution traits, inequality growth indices and vertical structure between mixed (x_{mixed}) and pure (x_{pure}) stands separately for both species in each triplet. The mean ratios ($\bar{R}_x$) provide a simple basis for testing whether species mixing alters stand structural characteristics compared to monocultures (Pretzsch and Schütze, 2016). $\bar{R}_x$ significantly different from 1 (1.0 is beyond the confidence intervals) can be considered a mixture effect. We used the *t.test* and *wilcox.test* functions for normally and non-normally distributed $\bar{R}_x$, respectively.

Differences in any structural attributes between mixed and pure stands may be due to an additive or a multiplicative effect (Forrester and Pretzsch, 2015; Loreau and Hector, 2001). Additive effects quantify heterogeneity when both species retain the same structural behavior in mixed stands as in monocultures. They represent how complementary species traits would be in a mixture if their size or shape did not vary from those grown in a monoculture (Pretzsch and Schütze, 2016). Multiplicative effects arise from facilitation and/or niche partitioning between species that modify structural attributes and cannot be predicted by only studying the species in their monocultures (Pretzsch et al., 2016). Both mechanisms are not mutually exclusive and could act simultaneously increasing ecosystem function (Loreau and Hector, 2001; Ruíz-Benito et al., 2014). The expected additive effect was quantified as the weighted mean of the pure stand characteristics; any deviations in mixed stands from this weighted mean were considered multiplicative or complementarity effects.

Therefore, after comparing the inter-specific structural differences of species growing in mixed stands or monocultures, we explored both additive and multiplicative mixing effects. In order to reveal any additive effects, we compared the weighted mean expected of the structural traits of the two monocultures (x_{exp}) with both monocultures (x_{exp}/x_{pure}). This may indicate how species selection alone can modify mixed stand traits with respect to monocultures. The weighted mean of both monocultures ($\widehat{D}_{PS,PT}$) represents the expected distribution of each structural trait under the assumption that mixing causes an additive effect. They were calculated by multiplying the monospecific stand size distributions (D_{PS} and D_{PT}) in such a way that the observed species mixing proportion of the mixed stands was reproduced. This resulted in $\widehat{D}_{PS,PT} = D_{PS} \cdot m_{PS(PT)} + D_{PT} \cdot m_{(PS)PT}$, where $m_{PS(PT)}$ and $m_{(PS)PT}$ are the proportions calculated based on the species stand density index, weighted by equivalence coefficients (section 3.3.4.1).

We used structural traits Table 3.2 to test for a multiplicative mixing effect on the Scots pine, and Maritime pine mixed stands. At the stand level, this was done by comparing the observed distribution of mixed stands $D_{PS,PT}$ with the weighted mean distribution $\hat{D}_{PS,PT}$. Analogously, the contribution of each species to a multiplicative mixing effect was analyzed, and the structural traits of a species in the mixture ($D_{(PS)PT}$ and $D_{PS(PT)}$) were compared to those in monoculture (D_{PS} and D_{PT}). Again, the species distribution of structural traits in mixture had to be scaled up to a unit area of 1 ha using the species mixing proportions (Pretzsch et al., 2016).

3.3.4 Stand productivity related to structural heterogeneity

3.3.4.1 Quantification of overyielding in mixed stands

Quantity the net effects on stand growth is a key question when comparing growth and yield in pure and mixed stands and may result in under-, neutral-, or over-yielding or even transgressive over-yielding (Pretzsch and Schütze, 2009). In addition to whole-stand analysis, we explored species-specific growth in mixed and compared monospecific stands, applying the nomenclature and algorithm used by Pretzsch et al., (2015) and del Río et al., (2016).

Species-mixing effects at stand level were evaluated as stand productivity for the period from 2004-2014. In order to determine whether mixing affects productivity at the stand level, relative productivity ($RP_{PS,PT} = P_{PS,PT}/\hat{P}_{PS,PT}$) was used as the ratio of observed productivity in a mixed stand ($P_{PS,PT} = pp_{PS(PT)} + pp_{(PS)PT}$) divided by the expected productivity from the mixed stand ($\hat{P}_{PS,PT} = P_{PS} \cdot m_{PS(PT)} + P_{PT} \cdot m_{(PS)PT}$). The total productivity of the mixed stand was the shared productivity of Scots pine ($pp_{PS(PT)}$) and Maritime pine ($pp_{(PS)PT}$), while the expected productivity for the mixed stand was obtained from the productivity of both species in the neighboring pure stands (P_i) and their mixing portions (m_i). In the same way, relative productivity was used to compare species performance in mixed versus pure stands. For Scots pine, ($RP_{PS(PT)} = pp_{PS(PT)}/m_{PS(PT)}/P_{PS}$; notice that $pp_{PS(PT)}/m_{PS(PT)}$ is the contribution of Scots pine in the mixed stand scaled up to 1 ha using the mixing proportion. Relative productivity for Maritime pine ($RP_{(PS)PT}$) was established in the same way.

To measure productivity, we used the mean periodic stand basal area growth ($PAIBA$, m^2 ha^{-1} $year^{-1}$) and mean periodic stand volume growth ($PAIV$, m^3 ha^{-1} $year^{-1}$) for the period 2004 – 2014. If the mean ratio of relative productivity at stand ($RP_{PS,PT}$) or by species ($RP_{PS(PT)}$,$RP_{(PS)PT}$) significantly differed from 1, productivity in mixed and pure stands differs. Mean ratio higher than 1 indicates positive species-mixing effect or over-yielding, whereas the opposite indicates under-yielding. The same statistical test applied in section 3.3.3 was used.

In this section mixing proportions (m_i) were calculated rely on SDI concept to consider species-specific growing space occupied. Analogously as in section 3.1.1, but weighting by equivalence coefficients in order to compare species-specific growing space requirements of a species with their value in mixed stands (del Río et al., 2016; Pretzsch and Biber, 2016; Sterba et al., 2014). Maximum stand density for each species (SDImax) was calculated using the species-specific function fitted in section 3.1.2. Equivalence coefficient using Scots pine as reference species was 1.03 ($e_{PT \Rightarrow PS} = SDImax_{PS}/SDImax_{PT}$). The resulting species SDI values transformed by the equivalence coefficients were used to calculate density in mixed stands ($SDI_{PS,PT} = SDI_{PS,(PT)} + SDI_{(PS),PT} \cdot e_{PT \Rightarrow PS}$) and the relative density ($RD_{PS,PT} = SDI_{PS,PT} / SDI_{PS}$), which measures over/understocking in the mixed-species stands in relation to neighboring monocultures within each triplet (Pretzsch and Biber, 2016). 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 over-yielding by species, due to differences in the potential densities of the species. The mixing proportions for both species were calculated as follows:

$$m_{PS(PT)} = SDI_{PS(PT)}/(SDI_{PS(PT)} + SDI_{(PS)PT} \cdot \mathrm{e}_1) \qquad [3.12]$$

$$m_{(PS)PT} = (SDI_{(PS)PT} \cdot \mathrm{e}_1)/(SDI_{PS(PT)} + SDI_{(PS)PT} \cdot \mathrm{e}_1) \qquad [3.13]$$

3.3.4.2 Relationships between mixing effects at different levels of organization. Relative productivity with structural heterogeneity

Finally, we used linear regression to attempt explaining the relationship between the species-mixing effect on relative productivity at the stand level ($RP_{PS,PT}$) and species level ($RP_{(PS)PT}$ and $RP_{PS(PT)}$) with variability in stand structural trait ratios between mixed and pure stands. OLS linear regression was used to reveal the relevance of observed changes between species tree crowns and canopy structures in terms of productivity gains or losses at stand level.

3.4 Modeling of dendroclimatic responses of mixed pines stands

3.4.1 Growt*h-d*rought long-term correlations

The standard dendrochronological analysis can be improved with new advances in time-series modeling, e.g., using mixed-effects models and multivariate ordination techniques (Lara et al., 2018). Considering the hierarchical structure of tree-ring series and adequately handling the pseudoreplication, autocorrelation, and nested random effects underlying in sampling design and modeling of tree-ring data (Bowman et al., 2013; Hughes, 2002). BIOdry algorithm (Lara et al., 2018) was used to modeling the non-linear relationships between long-term growth fluctuations and drought severity (SPEI time series, 2.2) in mixed and pure stands. Modeling scheme in BIOdry mainly consists in: i) multilevel normalization of tree-ring series, and ii) multivariate comparison between residual variances (tree growth and drought).

3.4.1.1 Multilevel normalization of tree-rings series

Basal area increment (BAI) series were used instead of ring width series to extract the climate-related growth reaction. BAI is calculated directly from tree-ring width series and could reflect the whole tree volume (Biondi and Qeadan, 2008). BAI was preferable instead of volume or biomass estimations derived from allometric models (parameterized species in monospecific stands) because these models could induce bias in the comparison between growth patterns in mixed and monospecific stands (del Río et al., 2016).

Growth equation developed by Zeide (1993) was used to normalize BAI series Eq.[3.14] and extract the ontogenetic growth trend for each species. Random effects were progressively included in the growth model accounting for hierarchical structures of the data, enhancing residual variances due to the sampling design: sample replicate (core), core nested in the tree (tree/), core in tree nested in the stand (plot/) and core in tree in plot nested in the triplet (site/) Eq. [3.15]. Triplet level diminished he performance of random structure and was excluded. Significances of fixed effects were tested with t-tests, and the best random structure was selected based on the likelihood ratio test. Serial autocorrelation and heteroscedasticity of residuals were assessed by inspecting diagnostic plots of the normalized residuals and by evaluating their empirical autocorrelation functions (Pinheiro and Bates, 2000).

$$ln(BAI) = \beta_0 + \beta_1\, ln(g) - \beta_2 f(t) \qquad [3.14]$$

where $\ln(BAI)$ is the natural logarithm of annual tree basal area increments (cm^2 yr^{-1}); g is the cumulative tree basal area (cm^2), β are parameters to be fitted; t is the time. $f(t)$ is a function of time which can be $\ln(t)$ called Logarithmic Time-Decline Form (LTD), or t called a Time-Decline Form (TD) (Zeide, 1993). This growth model form represents the expansion and decline components present in tree growth pattern. The expansion component is proportional to $ln(g)$. Whereas the decline from could be LTD or TD depending of the declining is proportional to the logarithm of age (t) or directly proportional to age, respectively (Zeide, 1993). Taking into account the random structure considered the following model was used:

$$ln(BAI_{ijk,t}) = A_{ijk} + B_{ijk}\, ln(g_{ijk,t}) - C_{ijk} f(t) + \epsilon_{ijk,t} \qquad [3.15]$$

$$A_{ijk} = \beta_0 + u_{i,0} + u_{ij,0} + u_{ijk,0} \qquad [3.16]$$

$$B_{ijk} = \beta_1 + u_{i,1} + u_{ij,1} + u_{ijk,1} \qquad [3.17]$$

$$C_{ijk} = \beta_2 + u_{i,2} + u_{ij,2} + u_{ijk,2} \qquad [3.18]$$

where β are the model parameters, $u_i = (u_{i,0}, u_{i,1}, u_{i,2})^T$ is the vector of plot random effects, u_{ij} is a vector of tree random effects nested in the plots, and u_{ijk} is a vector of core random effects nested in trees that are nested in the plots. The vector $\epsilon_{ijk,t}$ contains the within-core residual errors and follows a multivariate normal distribution $\epsilon_{ijk,t} \sim N(0, R)$. The residuals of BAI (rBAI) contain valid fluctuations of tree growth (Lara et al., 2018) to computes multivariate correlograms between rBAIs and Standardized Precipitation Evapotranspiration Index–SPEI (Vicente-Serrano et al., 2010).

3.4.1.2 Multivariate comparison

Mantel correlograms are the extension of 'Mantel test' plotted against spatial/temporal distance classes (lags) (Legendre and Legendre, 1998). The 'Mantel test' is the correlation between two similarity or dissimilarity matrices obtained independently (Goslee and Urban, 2007; Lichstein, 2007). To test the significance of coefficients of correlation, both matrices need to being first detrended to make the data second-order stationary, mean and variance should be constant and finite along series. Hence the covariance (or correlation) function depends only on the distance (lags) between observations along the series. In other words, temporal variation of the data should be adequately described by the same single temporal correlation function in all sections of the analyzed period (Borcard et al., 2011; Legendre and Legendre, 1998).

We used BIOdry algorithm (Lara et al., 2018) to compute 'Mantel correlograms' that depict patterns between residual variances of rBAI and SPEI with magnitudes and significances of the relationships. Allowing identify changes in the intensity of temporal patterns at different distances (lags). We compared patterns between rBAI and SPEI of Maritime pine and Scots pine in mixed and pure stands and explored how stand intrinsic factors such tree ontogeny could influence correlation in the growt*h*-*d*rought fluctuations. In mantel correlogram, the shape of the significant values along the distance classes might show nonlinear patterns. Positive and significant values indicate that for the given distance class, the multivariate similarity between rBAI and SPEI is higher than expected by chance (i.e., the mean within-class similarity is higher than the mean among-class similarity). The reverse is true for negative and significant values (Borcard and Legendre, 2012).

Mantel correlograms between rBAI and SPEI were established considering a common classification factor, for this case plot. Mantel correlograms for each plot allowed comparison of rBAI fluctuation between species and stand composition exposed to common climate conditions for each site (triplet). Standard Euclidean distances (z scores) of rBAI were compared with binary model matrices specifying membership in particular classes of z scores of SPEI. The Mantel statistic was:

$$r(d) = \frac{\sum_i^n \sum_j^n w_{ij} z_{ij}}{\sum_i^n \sum_j^n w_{ij}} \qquad [3.19]$$

where d is the distance class from SPEI; z_{ij} is the distance between each pair i and j from basal area residuals; w_{ij} is a weight for the pair: typically 1 if z_{ij} is in d and 0 if it was not. The number of classes is calculated with the Sturges rule and the significance of Mantel statistic for each distance class was tested using 1000 permutation (Goslee and Urban, 2007; Legendre and Legendre, 1998).

3.4.2 Tree growth resilience to drought events

Resilience indices (Lloret et al., 2011) have been successful used to quantify forest growth response to drought across varying spatial scales (Gazol et al., 2018, 2016) and to assess whether species-mixing alters a given species growth stability (resilience) related to drought (Merlin et al., 2015; Pretzsch et al., 2013). We calculated four resilience components: resistance (Rt), recovery (Rc), resilience (Rs), and relative-resilience (rRs = Rs–Rt) indices for all sampled trees using BAI time series. We selected the last 30 years (1984-2014) in the analysis to excluding the juvenile period in the younger stands, avoiding a strong age-related trend in the BAI time series. To identify when a drought event had an impact on tree growth, we considered only years when SPEI was lower than -1. Then, negative pointer years were defined when at least 45% of the BAI series of both species displayed a noticeable BAI drop of at least 50% relative to the average BAI in the four preceding years (Schweingruber et al., 1990). Thus in this analysis, we selected 2005 and 2012 as pointer years.

The Rt index quantifies the decrease in BAI from the preceding drought years (PreDr) to the dry year (Dr), Rt= Dr ⁄ PreDr. It measures the capacity of trees to resist disturbing events; trees are less resistant as the Rt value fall below 1, Rt = 1 is complete resistance. Rc index describes the difference in BAI between the dry year and the subsequent years (PostDr), Rc=PostDr/Dr. It describes the tree ability to restore a level of growth after disturbance; Rc > 1 indicates a tree growth recovery; Rc < 1 indicates a growth decline and Rc = 1 indicates a persistent low level of growth in the subsequent years. The Rs index is the ratio between the BAI values of the subsequent drought years (PostDr) and preceding drought years (PreDr), Rs = PostDr ⁄ PreDr. It quantifies the capacity of trees to return the growth rates observed before the disturbing event; Rs > 1 indicates full recovery, while Rs < 1 indicates a growth decline and low resilience. Finally, the rRs index is the resilience weighted by the growth decrease experienced during the disturbance, rRs= (PostDr - Dr)/PreDr (Lloret et al., 2011; Pretzsch et al., 2013). To quantify these resilience indices, the mean annual BAI was calculated for the three years before and after the drought period, except for 2012, where we defined two years before and after the drought event.

We used linear mixed-effect models to assess whether Rt, Rc, Rs and rRs indices differ between species and to analyze the influence of species mixing on growth resilience. Resilience indices were log transformed when necessary for ensuring the assumption of normality. We used triplet as a random factor to consider the hierarchical nature of the data. Separate models were fitted for each of resilience index and given drought event. Tree diameter, stand density, tree age, and site index were selected as covariates in the model. First, we tested the species-specific response to drought for each drought event in pure stands, with Maritime pine as the reference group. Second, we analyzed the influence of stand composition on tree response during drought years using pure stands as the reference group for both species. Species or stand composition effect was removed from each model if it was not significant, as well as the tree and stand covariates. When significant differences between tree species or pure vs. mixed stands were found, we used least-squares means based on Tukey HSD tests for post-hoc analysis between marginal means. To calculate the resilience indices we used the *'pointRes'* R-package (van der Maaten-Theunissen et al., 2015).

3.5 Intra-annual radial increment patterns

Asymptotic functional models can adequately represent the intra-annual radial increment pattern (McMahon and Parker, 2015; Zeide, 1993). The advantage that parameters have biological meaning, allowing identify the critical phenological stages within the intra-annual pattern. For the selection of the non-linear model that better describes the intra-annual pattern, we used *FlexParamCurve* R-package (Oswald et al., 2012). A set of models based on a flexible single-Richards function Eq.[3.20] were tested. The most suitable model (number of necessary parameters) was selected considering the lowest mean square error value (RMSE) penalized by the sample size of the fitted models.

$$y = \frac{Asym}{\left(\left[1+M\times e^{(-K(t-I))}\right]^{\frac{1}{M}}\right)} \qquad [3.20]$$

where y is the cumulative radial increment for tree, $Asym$, I , K and M are the asymptote, inflection point (Julian days), rate parameter and shape parameter of Richards curve; t is time variable (days). The shape parameter (M) allows modifying the asymmetric form of the function. If M =1 the function is symmetric or logistic, if M ≈0 is similar than a Gompertz function and when M =-0.3 is a Von Bertalanfy function (Oswald et al., 2012).

First, the parameters of Eq. [3.20] were obtained for each individual tree, as well as a general model by species and type of composition. Second, parameters obtained for each tree were used to compare differences between species in pure stands and then the effect of the stand composition. Additionally, effects of tree size and the interaction *Composition x Size* were tested using generalized linear models (GLM). GLM was fitted using monospecific stand as the reference group in both species. Significant differences in parameters between mixed and pure stands by species indicate a deviation from the expected pattern in pure stands.

3.6 Adapting he tree-level model IBERO to mixed species stands

This section aimed to develop generalized height-diameter and basal area growth models for mixed-species of Maritime pine and Scots pine that considering the effect of species interaction on the estimations. Both models could be potentially integrated as the initialization and growth sub-modules within tree-level models IBERO parameterized for Maritime pine (IBERO^{PT}, Lizarralde et al., 2010a) and Scots pine (IBERO^{PS}, Lizarralde et al., 2010b) in monospecific stands. These components were considered because results from previous sections showed that crown allometric plasticity and vertical stratification can vary in response to inter-specific competitive environmental conditions (section 3.3), and tree-growth efficiency increased in mixed stands compared to monocultures (section 3.2).

3.6.1 Generalized height-diameter functions

In the first step, we considered generalized height-diameter equations used previously to fit the height-diameter relationships for both species in the model IBERO for mono-specific stands (Lizarralde, 2008). These models have the advantage that include stand variables in their formulation, which is a particular interest for their use in a given region and also require a medium sampling effort for their application.

Models were modified for including a term that reflects interspecific competition environments in the model structure (Table 3.3). Two modifications on the base structure were tested; i) only adding the species-mixing effect term (BASE + mix) and ii) considering the target species stand variables instead of the corresponding whole stand values plus the species-mixing effect term ($\text{BASE}_{\text{sp}} + mix$). As indicators for the species-mixing effect term (mix), we tested the proportion of admixed species (m_{sp2}) and ii) the relative ratio between the dominant height of both species in mixed stands, $rHo = Ho_{PS}/Ho_{PT}$. Where, Ho_{PS} and Ho_{PT} are the species-specific dominant height for Scots pine and Maritime pine, respectively.

Mixing proportions as described in Section 3.3.4.1 were used to calculate m_{sp2}. When both species have the same species-specific dominant height ($rHo = 1$) none of the species is dominant in the canopy; as relative ratio decreases or increases from 1, larger difference between species dominant height. Values above 1 indicate a dominance of Scots pine over Maritime pine, the opposite for values lower than 1; in pure stands $rHo = 0$.

Table 3.3. Generalized height-diameter equations modified to include species-mixed effect.

Function number	Function form	Source base function
M1	$h = 13 + \left[\alpha_0 \cdot \left(\frac{1}{d} - \frac{1}{Do}\right) + \left(\frac{1}{Ho-13}\right)^{0.5}\right]^{-2} + \beta_1 \cdot mix$	Cañadas et al. IV (1999)
M2	$h = 13 + \left[\alpha_0 \cdot \left(\frac{1}{d} - \frac{1}{Do_{sp}}\right) + \left(\frac{1}{Ho_{sp}-13}\right)^{0.5}\right]^{-2} + \beta_1 \cdot mix$	Cañadas et al. IV (1999)
M3	$h = 13 + (\alpha_0 + \alpha_1 \cdot Ho - \alpha_2 \cdot dq) \cdot e^{\left(\frac{-\alpha_3}{\sqrt{d}}\right)} + \beta_1 \cdot mix$	Schöder & Álvarez (2001)
M4	$h = 13 + (\alpha_0 + \alpha_1 \cdot Ho_{sp} - \alpha_2 \cdot dq_{sp}) \cdot e^{\left(\frac{-\alpha_3}{\sqrt{d}}\right)} + \beta_1 \cdot mix$	Schöder & Álvarez (2001)
M5	$h = \alpha_0 \cdot Ho^{\alpha_1} \cdot BA^{\alpha_2} \cdot e^{\left(\frac{\alpha_3}{d}\right)} + \beta_1 \cdot mix$	Rio (1999)
M6	$h = \alpha_0 \cdot {Ho_{sp}}^{\alpha_1} \cdot BA_{sp}^{\alpha_2} \cdot e^{\left(\frac{\alpha_3}{d}\right)} + \beta_1 \cdot mix$	Rio (1999)
M7	$h = \alpha_0 \cdot Ho^{\alpha_1} \cdot BA^{\alpha_2} \cdot e^{\alpha_3\left(\frac{1}{d} - \frac{1}{Do}\right)} + \beta_1 \cdot mix$	Rio I (1999)
M8	$h = \alpha_0 \cdot {Ho_{sp}}^{\alpha_1} \cdot BA_{sp}^{\alpha_2} \cdot e^{\alpha_3\left(\frac{1}{d} - \frac{1}{Do_{sp}}\right)} + \beta_1 \cdot mix$	Rio I (1999)
M9	$h = Ho \cdot e^{(\alpha_1 \cdot Ho + \alpha_2 \cdot dq)\left(\frac{1}{d} - \frac{1}{Do}\right)} + \beta_1 \cdot mix$	Michailoff I (1943)
M10	$h = Ho \cdot e^{(\alpha_1 \cdot Ho_{sp} + \alpha_2 \cdot dq_{sp})\left(\frac{1}{d} - \frac{1}{Do_{sp}}\right)} + \beta_1 \cdot mix$	Michailoff I (1943)
M11	$h = Ho \cdot e^{\left(\alpha_0 + \alpha_1 \cdot Ho + \alpha_2 \cdot \frac{N}{1000}\right)\left(\frac{1}{d} - \frac{1}{Do}\right)} + \beta_1 \cdot mix$	Michailoff II (1943)
M12	$h = Ho \cdot e^{\left(\alpha_0 + \alpha_1 \cdot Ho_{sp} + \alpha_2 \cdot \frac{N_{sp}}{1000}\right)\left(\frac{1}{d} - \frac{1}{Do_{sp}}\right)} + \beta_1 \cdot mix$	Michailoff II (1943)

h: tree height (m), d: diameter at breast height (cm), m_j: proportion of complementary species j. α_0, α_1, α_2, α_3 and $\beta_1$are parameters. dq: quadratic mean diameter (cm), Ho: dominant height (m), Do: dominant diameter (cm), BA: basal area (m^2 ha^{-1}), N: tree number (ha^{-1}), subheading $'sp'$ is the species-specific stand variables value for the target species, Scots pine or Maritime pine.

A total of 12 equations with a combination of species-specific or whole stand covariates and the expression of species mixture were evaluated (Table 3.3). Non-significant parameters (p-value <0.05) were set to zero, and the remaining parameter were re-estimated. We used ordinary non-linear least squares (ONLS) to fit each of the equations with the function nls in R (R Develomment Core Team, 2015). Once the best generalized h–d models were selected based on the lower AIC, nonlinear mixed-effect modeling framework (NLME) was used to consider the hierarchical levels of the data (multiple trees in a plot, plots nested in triplets). Triplet level was non-significant in the nested random structure rely on the likelihood ratio test. A general multilevel nonlinear mixed-effects model (Pinheiro and Bates, 2000) can be defined as follow:

$$h_{ij} = f(x_{ij}, \varphi_i) + \varepsilon_{ij},\ \varepsilon_{ij} \sim N(0, R_{ij}) \qquad [3.21]$$

where h_{ij} is the observed height of tree j within plot i; f is a nonlinear function of the covariate matrix x_{ij} with a parameters vector φ_i; ε_{ij} is the within tree error term that is assumed to be independent and normal distributed; and R_{ij} is a positive-definite variance–covariance matrix for the error term. In this study, $f$is the best selected model of the 12 equations listed in

Table 3.3. Moreover the parameter vector φ_i can be expressed with their fixed and random components, as follow:

$$\varphi_i = A_i\lambda + B_i b_i \qquad [3.22]$$

where φ_i is the parameter vector r × 1 (r is the total number of parameters in the model) specified for the i-th plot; λ is the vector p × 1 of the common fixed parameters (p is the number of fixed parameters in the model), b_i is the vector q × 1 of the random parameters associated with the i-th plot (q is the number of random parameters in the model), A_i and B_i are matrices of size r × p and r × q for fixed and random effects for the *i* plot, respectively.

3.6.2 Tree basal area growth model

Increment basal area (Δg) calculated from each cored tree from the last 5 years (2009-2014) were used to fit basal area increment models of Scots pine and Maritime pine mixed stands. Stand variables were calculated including total stand basal area (BA), quadratic mean diameter (dq), dominant diameter (Do) and dominant height (Ho). Further, crown ratio (CR), as the proportion of crown length to total tree height, and the ratio of target tree height to stand dominant height (Rh), were calculated as measurements of vigor and competitive status of tree in the stand (Yang et al., 2009). Except for crown ratio (CR), all variables values were backdated (section 2.1.3) to the beginig of the growth period (year=2009). Crown ratio changes slowly over time and bias introduced by not backdating is probably negligible (Sterba et al., 2002; Wykoff, 1990). Rh was backdated using the height-diameter function fitted in section 3.6.1.

The basal area increment model followed the same basic form of previous growth models for mono-specific stands for both species in the region (Lizarralde, 2008). The basic equation has been commonly used in modeling diameter or basal area increments in pure (Wykoff, 1990) and mixed stands (Bravo et al., 2001; Sterba et al., 2002). The log transformation of the original dependent variable was applied to homogenize the variance, linearize the parameters and attain normal distribution of the residuals.

$$ln(\Delta g) = ln(d) + d^2 + ln(CR) + Rh + ln(SI) + COMP \qquad [3.23]$$

where Δg is the 5-year basal area increment of a tree (cm^2) and depends on the following tree and stand attributes; d is the diameter at breast height (mm); d^2 is the square diameter and the declining term that prevents unlimited growth for large-diameter trees (Zeide, 1993); CR is the crown ratio; Rh is the relative tree height; SI is the site index (m) for stand productivity , which was calculated as the dominant height at age 100 years according to specific site index curves for both species (Bravo-Oviedo et al., 2007; Rojo and Montero, 1996). We considered the SI in pure stands, which is used for each species and by triplet as reference for the mixed-species stands.

$COMP$ is the competition term as a combination of both a one-sided (asymmetric) and a two-sided (symmetric) competition used to adjust potential to actual growth. We considered two metrics to evaluate the effect of competition, both distance-independent measures of competition that do not require a tree's spatial coordinates which are usually not available in most of the stand inventories in the region. First, we used the basal area of trees larger than the target tree (BAL) as size-asymmetric competition and total stand basal area (BA) as size-symmetric competition. Both were used in the growth model developed for these species in pure stands (Bravo, 2005) and they are frequently included in tree increment models for uneven-aged and mixed species stands (Bravo et al., 2012, 2001; Yang et al., 2009). Second, we analyzed the competition rely on the SDI concept, that characterizes the degree of crowding with reference to standard conditions (del Río et al., 2014a). Competition based on SDI was calculated in relative terms as described in section 3.2.2.

Both measures of competition, based on BA and SDI, were compared to determine the most suitable explanatory variable for competition. To evaluate the influence of the species-mixture on tree growth, competition indices for each species were calculated with individuals of both species together and then split into intra- and interspecific components (del Río et al., 2014a), similar as in section 3.2.2. Thus, the resulting competition structures for each species might express the adverse, neutral, or even reduced interspecific competitive effects, e.g., when values of interspecific competition coefficient term are non-significance or lower than the intraspecific coefficient means positive species interaction on tree growth. The performance of the different competition structures were analyzed using information- theoretic approach (Anderson, 2007), section 3.8.

We used a linear mixed-model approach to predict the basal area growth and account for possible correlation among grouping levels. For both species, triplet level was non-significant in the nested random structure. We included plot as random effects in the intercept term first, and then in the initial diameter term, the latter instance did not improve the models. The linear mixed-effects models for tree increment had the following form:

$$ln(\Delta g_{ij}) = (\alpha_0 + u_i) + \alpha_1 ln(d_{ij}) + \alpha_2 d^2 + \alpha_3 ln(CR_{ij}) + \alpha_4 Rh_{ij} + \alpha_5 ln(SI_i) + \sum \beta_k \, COMP_{ijk} + \varepsilon_{ij} \quad [3.24]$$

where Δg_{ij} is the basal area increment of tree j within plot i; α are parameters to be estimated, $COMP_{ijk}$ represents the k different terms of the competition for tree j in plot i according to the different structures mentioned and β_k their corresponding parameters to be estimated. Moreover, u_i as the random effects at plot level and ε_{ij} is the error term. Random effects u_i and error term ε_{ij} are normally distributed with a mean of zero and a variance σ_i^2 and σ_ε^2 , respectively.

Fitted models showed non-constant variance in the residuals for both species. This problem was addressed by modeling residual variance with weights arguments. We used an exponential variance function(Var), which is useful for relax normality assumptions in variables which may take the value 0 (Pinheiro and Bates, 2000):

$$Var\left(\varepsilon_{ij}\right) = \sigma_\varepsilon^2\ exp^{(2\delta\ x_{ij})} \qquad [3.25]$$

where ε_{ij} are the residuals within the innermost level of grouping; σ_ε^2 is the initial variance for the innermost residual; δ is the parameter to be estimated and x_{ij} is the variance covariate. We test d, BAL, SDIRL and BA to modeling residual variance. We verified mixed-model assumptions graphically (quantile-quantile and residual plots).

3.6.3 Models evaluation

Predictions of *h-d* function and basal area increment model for both species were examined for assessing their predictive ability. We used the Third Spanish National Forest Inventory data (IFN) as an independent data source for quantifying models error of the *h-d* generalized functions. Mixed and pure plots were selected according to section 2.1.1.2. Predictions from the best parsimonious generalized *h-d* functions that express species-mixing effect in their structure were compared with the predictions of the models proposed by Lizarralde (2008) for these species parameterized for monospecific stands.

There were some limitations using the NFI data to evaluate the basal area increment models. Stand age and height to the crown base are missing in NFI data. Consequently, site index and CR could not be calculated. Instead, we evaluated the predictive quality of the basal area increment models using a ten-fold block cross-validation procedure. The original data set was split at the plot level into ten subsamples approximately of equal size. Final models were fitted ten times, with one of the subsamples omitted at each fit for training the model. Each of the re-calibrated models was testing with observation of the omitted subsample, thus a population-averaged predictions were generated (Dănescu et al., 2017; Manso et al., 2015) These predictions provided a pseudo-independent measure of the mean bias, root mean square error (RMSE) and model efficiency (EF), computed as follows:

$$bias = \frac{\sum_{i=1}^{n}(O_i - P_i)}{n} \qquad [3.26]$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(O_i - P_i)^2}{n}} \qquad [3.27]$$

$$EF = 1 - \frac{\sum_{i=1}^{n}(O_i - P_i)^2}{\sum_{i=1}^{n}(O_i - \bar{O}_i)^2} \qquad [3.28]$$

Where, O_i and P_i are the observed and predicted values for the ith observations respectively, n in the total number of observations, $\bar{O}$ is the mean of the observed variable. In the models that included random effects, the predicted value P_i denotes the population-averaged predictions (outermost residuals).

We used a log-transformed of tree basal area growth to attain normal distribution of the residuals Eq.[3.24]. This induces a bias proportional to the model semivariance terms when the predictions are back-transformed to the original scale (Calama and Montero, 2005; Manso et al., 2015). To correct for this bias, population-averaged predictions were calculated as follows:

$$\Delta g_{ij} = e^{\,ln(\Delta g_{ij}) + 1/2(\sigma_i^2 + \sigma_\varepsilon^2)} \qquad [3.29]$$

where, $ln(\Delta g_{ij})$ is the model basal area predicted on the log-transformed scale and σ_i^2 and σ_ε^2 are the maximum likelihood estimators of the plot and residual variance, respectively.

3.7 Linear and non-linear mixed models

Mixed-models approach was used when the data source presented a clear hierarchical structure due to sampling design, e.g., plot-in-phytoclimatic region in the model evaluating the effect of intra and inter-specific competition on tree volume growth using NFI (Study I) in section 3.2.2; core-in-tree-in-plot-in-triplet in the detrending procedure to extract growth fluctuations, and comparison of resilience indices between species and stand composition (*Study III*) in section 3.4.1 and 3.4.2 and tree-in-plot-in-triplet to fit the *h-d* and tree basal area growth models adapted to mixed species stands (Study V) in section 3.6.1 and 3.6.2.

The inclusion of random effects alleviated the lack of independence of models residuals, as they would absorb the unaccounted variability at the above mentioned levels due to growing conditions. The significance of the random structure was based on the likelihood ratio test ($p < 0.05$) between nested models in the presence of all non-collinear fixed predictors (Pinheiro and Bates, 2000). Multicollinearity of model variables was controlled by variance inflation factor values. We assumed that the random effects are independent; in this case, we used a diagonal form for variance-covariance matrix. Models were fitted using *nlme* R-package (Pinheiro and Bates, 2000) and the ML (maximum likelihood) method to allow comparison among different candidate model structures. The unbiased restricted maximum likelihood (REML) method was then used to fit the parameter estimates and variance components for the final model selected. Additionally, we calculated conditional R^2 values, which account for the explanatory power of both fixed and random effects and marginal R^2 to describe the proportion of variance explained by the fixed factors alone, both as a measure of goodness-of-fit of mixed models (Nakagawa and Schielzeth, 2013).

When non-linear mixed models were used, we tested different combinations of random parameters to determine which parameters should be modeled as mixed effect. First, all parameters were assumed random, with a general positive definite variance-covariance structure for the random effects. If this model failed to converge, then the number of random parameters was reduced to achieve convergence. Non-nested fitted models were compared according to the Akaike information criterion (AIC) using ML fits. In addition, we verified correlations between estimated random-effects parameters to evaluate whether the NLME model was appropriately parameterized. A high correlation coefficient between two estimated random parameters is an indication that the model is not correctly parameterized regarding setting random effects (Lindstrom and Bates 1990).

3.8 Model selection

Information-theoretic approach was used in the model selection procedure among candidate models (Anderson, 2007). Allowing evaluate multiple non-nested models relative to each other and quantify the relative support for multiple models simultaneously (Zuur et al., 2009). Fitted models were ranked by their AICc value (Second-order Akaike Information Criterion, Eq. [3.30]). Model with the lowest AICc could be considered most parsimonious *"best model"*. The absolute magnitude of the differences in AICc between alternate models (ΔAICc) and Akaike weights (w_i in Eq.[3.31]) provides an objective index of the strength of empirical support for the competing models or alternate hypothesis (Anderson, 2007). The multi-model inference procedure was performed with *MuMIn* R-package (Bartó, 2016).

$$AICc = -2\log(L) + 2K + \left(\frac{2K(K+1)}{n-K-1}\right) \qquad [3.30]$$

where L is the likelihood of the fitted model, K is the total number of parameters in the model and n is the sample size.

$$w_i = \frac{exp\left\{-\frac{1}{2}\Delta_i(AICc)\right\}}{\sum_{k=1}^{R} exp\left\{-\frac{1}{2}\Delta_r(AICc)\right\}} \qquad [3.31]$$

where Δ is the differences in AICc between the model i and the best candidate model and r ranges from 1 to the total number of candidate models compared R. Therefore, the final output is a set of candidate models rather than a single model.

4. Results

4.1 Mixing effects at stand level and tree level

4.1.1 Self-thinning boundary line and maximum stand density

A maximum size-density relationship was clearly identified using NFI data (Figure 4.1). No effects from stand origin were detected in the self-thinning limit parameters. We chose the 0.95 quantile because it showed significant parameters and the closest 95% confidence intervals of the highest quantiles. The intercept and slope of the self-thinning relationship for both species are given in Table 4.1. These parameters were used in Eq.[3.1] to estimate the SDI and SDImax values.

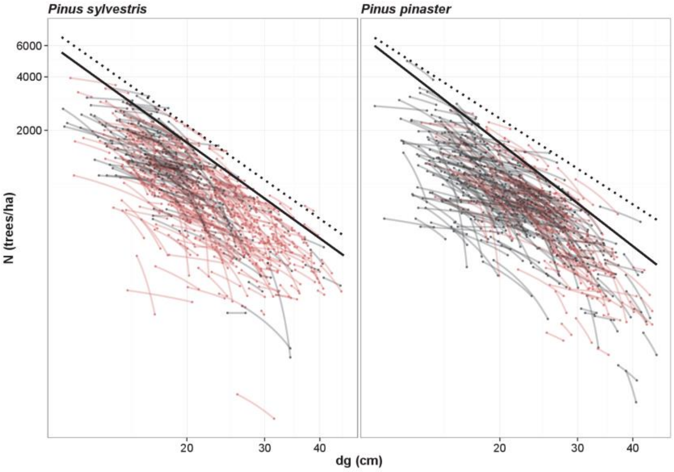

Figure 4.1 Self-thinning boundary line using NFI data plotted on a log-log scale. Lines by joining dots represent the ongoing density-related mortality within plots between the second and third NFI, red lines natural (Nt) and black lines plantation stands (Pl). Straight lines represent maximum size-density lines (solid = fitted by QR regression, dotted = functions fitted by del Río et al., (2006, 2001).

Table 4.1. Quantile regression parameters and standard errors (in parentheses) for linear models of self-thinning relationships of pure stands (Eq. [3.4]).

Species	**Intercept**	**Slope**	**SDI$_{max}$**
Scots pine	12.801 (0.192)	-1.789 (0.061)	1143.65
Maritime pine	13.218 (0.278)	-1.929 (0.088)	1103.64

SDImax: maximum stand density index estimated using *dq*=25.

4.1.2 Growth efficiency and species-mixing effects at the stand level

Table 4.2 shows the estimated parameters and regression statistics of the growth efficiency models for both species. All coefficients were significant in the final models ($p < 0.05$). Similar relationship between growth efficiency and predicted variables was found between species: a positive relationship with Ho, SD and stocking proportion of admixture species, but a negative relationship with the dq of the target species. Dominant height and quadratic mean diameter were used as surrogate variables of site quality and age respectively. Thus, the results in Table 4.2 might indicate an increase in growth efficiency with increasing site quality and a decrease in growth efficiency with aging.

Growth efficiency increased with total stand density and obtained maximum volume increment in fully stocked stands (SD=1), as expected. The significant difference with the null model (F-statistic and ΔAIC) revealed the influence of species proportion in the final model, indicating that both species grew better in mixed stands than in pure stands. The interaction between stand density and mixing proportion did not improve the growth efficiency models in either species. Additionally, the stand origin was statistically significant, indicating that a model is required for each origin and species. The inclusion of climatic variables did not prove to be statistically significant.

Table 4.2. Estimated coefficients (SE) of the stand volume growth efficiency models Eq.[3.5] for both species.

Species	**Intercept**	**ln (Ho)**	**ln (dq_i)**	**ln (SD)**	**m_{PT}**	**m_{PS}**	**Origin$_i$**	**RSE**	**Adj.R^2**	**F.**	**ΔAIC**
Scots pine	3.516	0.626	-1.076	0.238	0.341		-0.306	0.735	0.222	5.12	3.2
	(0.461)	(0.244)	(0.176)	(0.117)	(0.148)		(0.122)				
Maritime pine	3.782	0.530	-0.971	0.331		0.355	-0.338	0.623	0.228	5.63	3.7
	(0.475)	(0.209)	(0.150)	(0.090)		(0.149)	(0.094)				

Ho: Dominant height; dq: quadratic mean diameter; SD: total stand density, m: stocking proportion of Maritime pine (PT) and Scots pine (PS). Origin: dummy variable (0=natural stands, 1=plantation stands) RSE: residual standard error; Adj.R^2: adjusted coefficient of determination R^2; and F: F-statistic; Δ AIC: delta AIC between mixture versus null model.

4.1.3 Comparison of tree-level competition structures in mixed stands

Table 4.3 compares the different models that include size-symmetric or size-asymmetric competition structures and assumes different composition in the competition structures. Models that simultaneously included size-symmetric and size-asymmetric terms (SDIR + SDIR) outperformed the models than used only SDIR or SDIRL in both species. Further, models expressed only by size-asymmetric competition resulted better, and the parameter was larger than the size-symmetric competition, which denotes the importance of light competition in these species. The combination of size-symmetric and size-asymmetric terms with different species composition (intra+inter) emerged as the best competition structure model, with the lowest AICc values.

Table 4.3. Ranking of volume tree growth models comparing competition structures and their parameters estimated. The competition status was defined as the relative stand density index calculated for size-symmetric (SDIR) and/or size-asymmetric competitors (SDRIL) and for trees of all species or divided by intra- and inter-specific competitors.

	SDIR	**SDIRL**	**$\text{SDIR}_{\text{inter}}$**	**$\text{SDIR}_{\text{intra}}$**	**$\text{SDIRL}_{\text{inter}}$**	**$\text{SDIRL}_{\text{intra}}$**	**AICc**	**ΔAICc**	w_i
Scots pine			ns	-0.8558	-0.8312	-1.0079	3077.7	0	0.801
	-0.4552	-0.8943					3081.0	3.25	0.158
		-1.0860					3083.6	5.91	0.042
					-0.8985	-1.1969	3104.6	26.92	0.000
			-0.7641	-1.3640			3118.8	41.08	0.000
	-0.9990						3120.7	43.04	0.000
Maritime pine			ns	-0.6262	-1.614	-0.7307	3202.9	0	0.535
	-0.5251	-0.8650					3203.3	0.44	0.429
					-1.669	-0.9077	3209.0	6.12	0.025
		-1.0120					3210.6	7.68	0.012
	-0.8950						3233.1	30.17	0.000
			-0.7357	-0.9379			3234.9	32.02	0.000

SDIR: size-symmetric competition index; SDIRL: size-asymmetric competition index for larger trees; intra: intra-specific competition; inter: inter-specific competition; AICc Second-order Akaike Information Criterion; ΔAICc difference between the model i and the best candidate model; w_i Akaike weights. Significance of coefficients $p \leq 0.05$, ns: not significant.

Contrasting results were observed between species when best competition structures were compared. In the case of Scots pine, intra and inter-specific competition were significant in size-asymmetric competition terms with a higher coefficient value of intra-specific term that means that inter-specific competition was less intense for Scots pine. In size-symmetric competition, the variable related to Maritime pine competition was found to be non-significant, which means no effect of inter-specific competition on tree growth.

For Maritime pine, the same pattern was observed than in Scots pine for size-symmetric competition structure. On the other hand, for size-asymmetric competition the intra-specific parameter was lower than the Scots pine competition term. However, this model was slightly better (ΔAICc = 0.44) than the second best-ranked model (without distinguishing species composition in the competition). Despite the uncertainty to define the 'best model', both models indicate no benefit from the mixture in the size-asymmetric competition, which is more intense for tree growth than that of size-symmetric competition. However, in the first model species interaction have a positive effect in the size-symmetric competition, revealing that both relationships (competition and complementarity) could be observed simultaneously in Maritime pine. The volume growth models with the lowest AICc value were fitted with the REML procedure (Table 4.4). Parameters were significant at 95% probability.

Table 4.4. Estimated coefficients for the best tree growth model Eq.[3.8] of the two species (standard errors in parentheses), including competition structures. Conditional R^2 values are showed as a measure of goodness-of-fit.

	Scots pine	**Maritime pine**
Intercept	-4.0212 (0.417)	- 3.0889 (0.392)
d	-0.0465 (0.009)	-0.0242 (0.006)
ln (d)	2.2426 (0.209)	1.8626 (0.178)
ln (h)	0.3951 (0.105)	0.3854 (0.093)
Origin	-0.3493 (0.089)	-0.3442 (0.082)
$SDIR_{intra}$	-0.8606 (0.264)	-0.6377 (0.209)
$SDIR_{inter}$	*ns*	*ns*
$SDIRL_{intra}$	-1.0020 (0.205)	-0.7242 (0.163)
$SDIRL_{inter}$	-0.8196 (0.320)	-1.6234 (0.385)
AIC	3104.13	3230.74
R^2 conditional	0.62	0.60
R^2 marginal	0.43	0.46
Variance of random effects		
σ_{u0}^2	0.3637	0.3229
σ_{u2}^2	8.479×10^{-7}	0.0403
σ_{ε}^2	0.0003	0.0086

R^2 conditional: variance explained by both fixed and random effects; R^2 marginal: describes the proportion of variance explained by the fixed factors alone. Significance of coefficients $p \leq 0.05$, *ns*: not significant.

Figure 4.2 depicts the effects of size-symmetric and size-asymmetric competition analyzed independently, when the target tree was influenced by intra-specific competition only (pure stand) and when the competition was the combination of intra- and inter-specific competition structures (mixed stands). To illustrate the different effect of competition structures, simulations of tree volume growth were based on fitted models (Table 4.4). Simulations depending of the amount of size-symmetric (Figure 4.2 left) and size-asymmetric competition (Figure 4.2 right) for an average tree with d=30 cm and h=14 m in a natural stand. Results show that the stronger the size-symmetric inter-specific competition, the higher the growth benefit from the mixture of both species (Figure 4.2, left) when size-asymmetric competition was fixed to 0, for example dominant trees. However, when asymmetric competition was split by species and symmetric competition was fixed to 1, for example full-stocked stands. Positive mixture effect on tree growth was only evident for Scots pine (Figure 4.2, right).

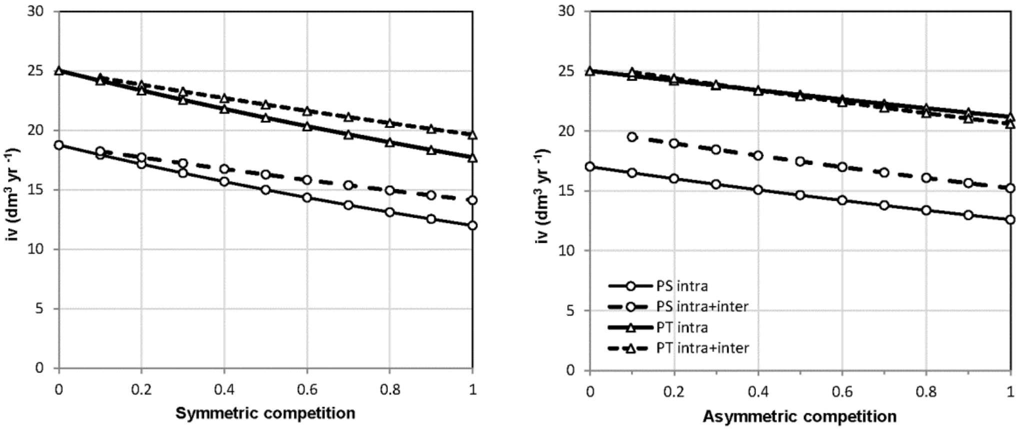

Figure 4.2. Volume growth as a function of size-symmetric competition (left, asymmetric competition = 0) and size-asymmetric competition (right, symmetric competition = 1) in Scots pine (PS, circles) and Maritime pine (PT, triangles) for a tree with d=30cm and h=14m in a natural stand and using mean competition status values (Table 2.3). Solid lines indicate results for intraspecific competition only (pure stand); dashed lines indicate results for a combination of intraspecific and inter- specific competition structures (mixed stand).

4.2 Comparison of stand structure in mixed versus pure stands

4.2.1 Species-mixing influence in tree allometry

Height-diameter relationships varied significantly between stand compositions in both species (Figure 4.3 and Table 4.5). The *hcb-d* allometry relationship, in contrast, remained constant for Maritime pine but differed for Scots pine trees growing in mixture versus monocultures. Parameters and statistical tests of the fitted functions are shown in Table 4.5. Maritime pine trees growing in mixture tended to be significantly higher, presented a considerably steeper slope in the *h-d* relationship and had longer crowns as size increased compared with trees in pure stands. Despite the slope differences in both functions for Scots pine, vertical crown extension was similar in mixture that than in monospecific stands. This pattern concurs with intra-specific stand structural traits ratios (Figure 4.4).

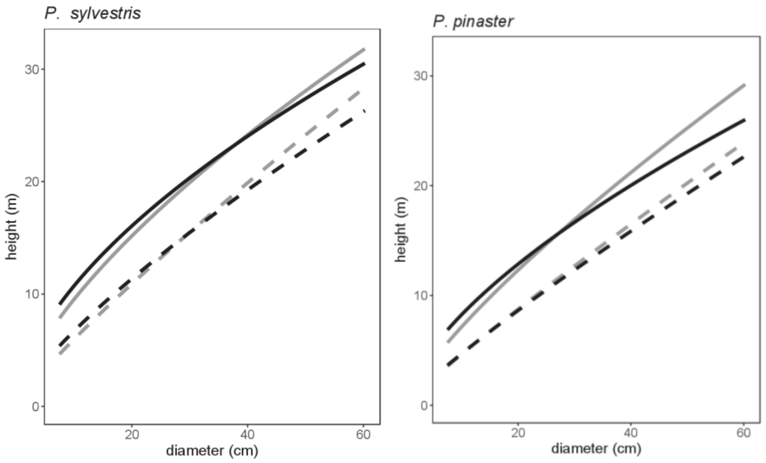

Figure 4.3. Crown and height tree allometry of Scots pine and Maritime pine in mixed and pure stands. Solid lines represent *h-d* functions and dashed lines represent hcb-d functions. Grey lines indicate trees in mixture; black lines indicate trees growing in monocultures.

Table 4.5. Crown allometry functions of Scots pine and Maritime pine. SMA log-linear regression parameters (confidence intervals) of height – diameter (*h-d*) and height to crown base – diameter (hcb-d) functions by species and composition.

Species	**Model**	**composition**	**intercept**	**Slope**	**R^2**	**p-value**
Scots pine	*h-d*	mixed	0.307	0.672	0.57	0.003
			(0.24 - 0.38)	(0.64 - 0.72)		
		pure	0.448	0.583	0.51	
			(0.40 - 0.50)	(0.55 - 0.62)		
	hcb-d	mixed	-0.914	0.868	0.56	0.017
			(-0.19 - 0.06)	(0.80 – 0.94)		
		pure	0.064	0.76	0.31	
			(-0.02 – 0.14)	(0.71 – 0.82)		
Maritime pine	*h-d*	mixed	0.071	0.783	0.68	<0.001
			(-0.03 - 0.17)	(0.72 - 0.85)		
		pure	0.279	0.639	0.59	
			(0.23 - 0.33)	(0.60 - 0.68)		
	hcb-d	mixed	-0.246	0.914	0.51	0.509
			(-0.40 - -0.10)	(0.82 – 1.02)		
		pure	-0.203	0.876	0.42	
			(-0.30 - -0.11)	(0.82 - 0.94)		

Significant differences in slope between fitted composition models (mixed vs. pure), p-value <0.05.

4.2.2 Structural attributes between species and stand composition

Inter-specific comparison of stand characteristics between pure and mixed stands (Figure 4.4) showed that dq was significantly greater for Maritime pine than for Scots pine in mixed stands, whereas between pure stands did not differ from 1. The opposite was observed for *Ho,* Scots pine in pure stands was on average about 19% taller than pure Maritime pine stands, while in mixed stands both species reached similar dominant height. However, these mean relationships varied due to differences in site conditions and age prevailing among triplets. SDI was about 24 % higher in pure Maritime pine than in pure Scots pine stands (Figure S1). Despite the lower dominant height of pure Maritime pine, the higher SDI and dq resulted in 20% and 8% higher basal area, and standing volume compared to pure Scots pine stands. Greater differences, 37% and 43%, were observed for PAIBA and PAIV, respectively.

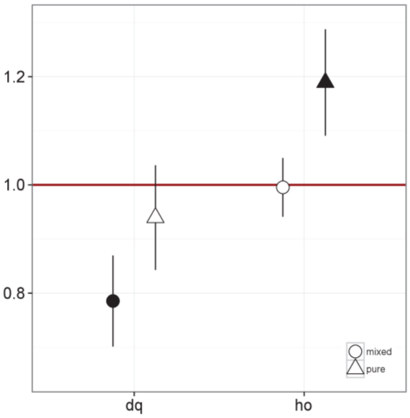

Figure 4.4. Inter-specific ratio of quadratic mean diameter and dominant height between mixed or pure stands (PS_{mix}/PT_{mix} and PS_{pure}/PT_{pure}). Filled symbols indicate mean ratio significantly different from one ($p < 0.05$).

In addition, some shifts in size distribution traits emerged when we compared species-specific ratios in mixed stands with pure stands (Figure 4.5). Values of mean diameter, height, and volume, as well as minimum diameter and volume, were higher for Maritime pine than Scots pine in mixture (Figure 4.5). Significant differences were also observed in vertical structure and grow inequality indexes and were greater for Scots pine in mixture. These differences show an overview of the stands characteristics and reveal which role each species plays in the mixture as an indication of their competitive status.

Intra-specific comparison showed that *dq* of Maritime pine in mixed stands was 16 % higher and *Ho* was 18 % higher than in pure stands (Table 4.6). For Scots pine, quadratic mean diameter and dominant height were 3 % and 4 % lower in mixed stands, respectively, but the differences were not significant. SDI in mixed stands increased for Scots pine but maintained similar for Maritime pine compared to pure stands. Although the stands represent fully stocked and almost unthinned conditions, SDI values varied considerably among triplets due to the wide range in site conditions and the variation in stand age.

Table 4.6. Comparative statistics (mean and standard error) of the ratios between of observed mixed stand (Mix$_{obs}$) over expected mixed stand (Mix$_{exp}$) and by species in pure vs. mixed stands. Bold values indicate significant differences in ratios, $p \leq 0.05$.

	Mix$_{obs}$/Mix$_{exp}$		**PS$_{mix}$/PS$_{pure}$**		**PT$_{mix}$/PT$_{pure}$**	
	mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
N (trees ha^{-1})	0.96	0.05	**1.35****	**0.14**	**0.72*****	**0.03**
dq (cm)			0.97	0.04	**1.16*****	**0.03**
Ho (m)			0.96	0.03	**1.15*****	**0.03**
BA (m^2 ha^{-1})	1.05	0.04	**1.20*****	**0.05**	0.97	0.05
V (m^3 ha^{-1})	**1.12***	**0.05**	**1.16****	**0.07**	**1.11*****	**0.07**
SDI	1.06	0.04	**1.21*****	**0.05**	0.96	0.05
PAIBA (m^2 ha^{-1} yr^{-1})	1.08	0.07	1.06	0.08	1.09	0.08
PAIV (m^3 ha^{-1} yr^{-1})	**1.14***	**0.07**	1.11	0.11	**1.19***	**0.08**

N, trees per hectare; dq, quadratic mean diameter; ho, dominant height; BA, stand basal area; V, stand standing volume; SDI, stand density index; PAIBA, periodic annual basal area growth; PAIV, periodic annual volume growth. In bold, significant differences in mixed-species versus monoculture stands at: $^*p < 0.05$, $^{**}\ p < 0.01$ and $^{***}\ p < 0.001$.

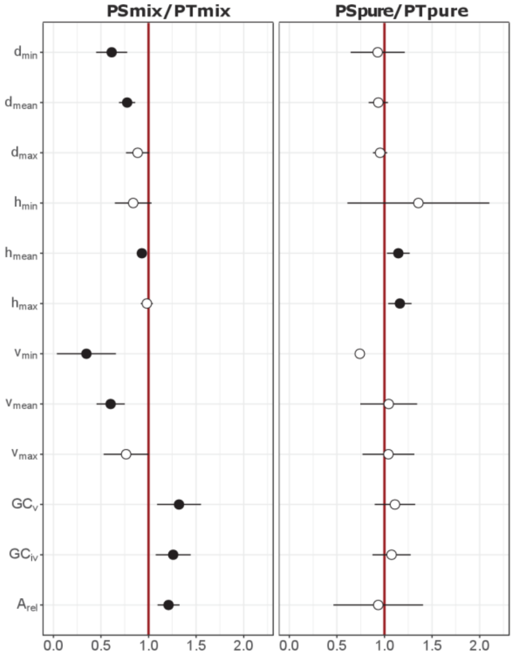

Figure 4.5. Mean of the ratio resulting from the pair-wise division of the structural traits between species growing in mixed stands and monocultures. PS: *Pinus sylvestris* and PT: *Pinus pinaster*. Filled circles indicate mean ratio significantly different from one ($p < 0.05$).

4.2.3 Additive and multiplicative effects of species mixing on structural traits

Table 4.7 showed a weak additive effect on structural traits of mixture compared to Scots pine pure stands and a moderate effect compared to Maritime pine: Species structural indices differed between weighted stands (Mix_{exp}) and monocultures for 4 out of 12 in the former and 6 out of 12 in the latter. Scots pine monoculture compared with the expected mixed stand (weighted mean of both monocultures) showed higher diameter and volume maximum values. However, mean and minimum heights were reduced by the component of Maritime pine in the expected mixed stand. Maritime pine monoculture showed significantly higher mean and maximum height values compared to the weighted mean of both monocultures, and lower minimum diameter, height and volume values than expected in mixed stands. These indicate that a broader size distribution range was expected in mixed stands than in monospecific stands, especially with regard to tree height size distribution. The higher GC_v means greater inequality in the standing stand volume for the weighted mean of the two monocultures than in the Maritime pine monoculture. All these comparative differences in structural traits for both species imply that structural heterogeneity may increase just by mixing.

Table 4.7. Mean of the ratio resulting from the pair-wise division comparing the structural traits of the mixed-species stands (Mix_{obs}) and monocultures, and of the expected mean of the monocultures ($Mix_{exp,}$ weighted mean pure stands by mixing proportions) with the neighboring monocultures.

		Structure traits											
		d_{mean}	d_{min}	d_{max}	h_{mean}	h_{min}	h_{max}	v_{mean}	v_{min}	v_{max}	A_{rel}	GC_v	GC_{iv}
Mix_{exp} vs. PS_{pure}	mean	1.03	0.92	**1.12****	**0.94***	**0.65***	1.01	1.04	0.85	**1.25****	1.15	1.07	1.08
	SE	0.03	0.05	**0.03**	**0.03**	**0.05**	0.01	0.06	0.1	**0.08**	0.68	0.06	0.04
Mix_{exp} vs. PT_{pure}	mean	0.96	**0.79*****	1.07	**1.06****	**0.89***	**1.17****	0.98	**0.60****	1.59	1.02	**1.14***	1.12
	SE	0.02	**0.05**		**0.02**	**0.06**	**0.05**	0.05	**0.09**		0.42	**0.05**	0.06

PS, *Pinus sylvestris* and PT, *Pinus pinaster*. In bold, significant differences in mixed-species stand versus monoculture at: *$p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

The multiplicative mixing effects observed by comparing the structural traits between species in mixed and pure stands are shown in Figure 4.6. Differences between observed mixed-stand structural indexes and the weighted mean of both monocultures (Mix_{obs} vs. Mix_{exp}) are also displayed. No shifts in structural traits for Scots pine were observed in mixtures compared to monocultures, PS_{mix}/PS_{pure}. In contrast, most of the size distribution traits were significantly higher for

Maritime pine in mixed-species stands. Only GC_V was lower compared to Maritime pine monocultures (PT_{mix}/PT_{pure}). We might consider these changes in the structural indexes of Maritime pine growing in mixture versus monoculture to be closely related to shifts in structural traits patterns when species coexist in mixing (PS_{mix}/PT_{mix}) or to comparison of species in pure stands (PS_{pure}/PT_{pure}), Figure 4.4 and Figure 4.5. However, the multiplicative effect of species mixing at the stand level (Mix_{obs} vs. Mix_{exp}) does not always emerge from patterns at the species level.

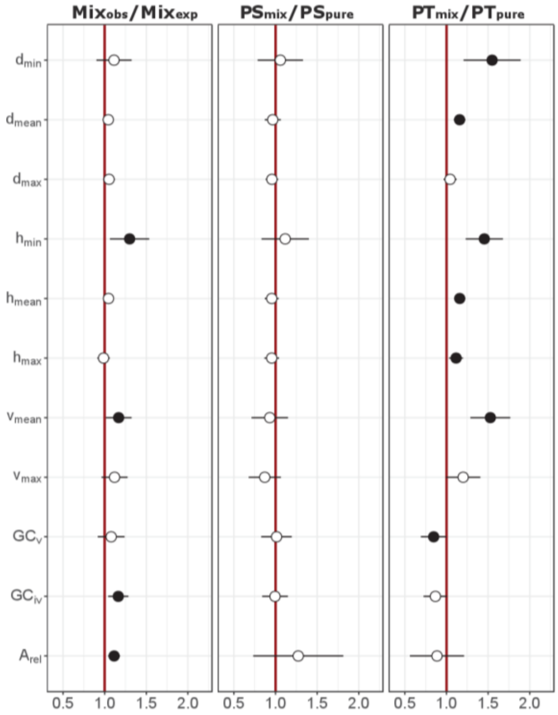

Figure 4.6. Multiplicative mixing effects on the structural traits of Scots pine and Maritime pine in mixed stands compared with monocultures. Circles are the mean of the ratio resulting from the pair-wise division of the structural traits of the mixed-species stands by the respective value of the neighboring monocultures. Filled circles indicate mean ratio significantly different from one ($p < 0.05$).

4.2.4 Over-yielding and structural heterogeneity relationships

Table 4.6 shows that standing volume and PAIV values were an average of 12 % and 14% higher in mixed stands than in pure stands, respectively. However, BA, PAIBA, and SDI were similar in mixed and pure stands. Greater volume in mixed stands was caused by the larger volume (RP $V_{(PS)PT}$ = 1.11) and mean annual volume growth (RP $PAIV_{(PS)PT}$ = 1.19) of Maritime pine in mixed stands compared to pure stands. Though PAIBA was higher for Maritime pine in mixed stands (1.09), the effect was not significant at the total mixed-stand level.

The variability of relative stand productivity at the stand and species levels was related to specific stand characteristics and the intra-specific ratio of structural traits between mixed and pure stands. We focused on the whole stand ($RP_{PS,PT}$) and Maritime pine relative productivity in mixed stands ($RP_{(PS)PT}$) since both showed significant effects of mixture on the PAIV (Table 4.6, Figure S2). Accordingly, we explored the significant ratios of the structural traits between Maritime pine in mixed-species stands and monocultures (PT_{mix} vs. PT_{pure}) as explanatory variables (Figure 4.5). In both cases, we accounted for relative stand density ($SD_{PS,PT}$), site index (dominant height of Maritime pine at age 100 in mixed stand) and age (age of Maritime pine in mixed stand).

Relative stand productivity increased significantly with relative stand density, $SD_{PS,PT}$ (Figure S3). However, site index and age had non-significant effects on relative productivity, though they presented a slightly positive correlation. Both the over-yielding observed at stand level and species level for Maritime pine were related to structural ratios describing tree height differences between Maritime pine in mixed-species stands and monocultures (Table 4.8). $RD_{PS,PT}$ and $RP_{(PS)PT}$ increased as the difference in maximum tree height of Maritime pine trees in mixed stands increased with respect to monocultures (Rh_{max}).

Table 4.8. Linear model of the relative productivity in mixed-species versus monocultures at the stand and species levels as a function of changes in structural attributes.

	$RP_{PS,PT}$	$RP_{(PS),PT}$
Intercept	-0.178 (0.26)	-0.887(0.53)
Rh_{max} (PT_{mix}/PT_{pure})	1.126 (0.2)	1.924 (0.47)
R^2 adjusted	0.710	0.669
RSE	0.078	0.159
p-value	0.001	0.003

$RP_{PS,PT}$, Relative productivity of mixed-species stands versus monocultures; $RP_{(PS),PT}$, Relative productivity of Maritime pine mixed-species stands versus monocultures; Rh_{max} (PT_{mix}/PT_{pure}), ratio between the maximum tree height of Maritime pine in mixed versus monospecific stands. (Standard error in brackets)

4.3 Relationships between drought and tree-growth

4.3.1 Temporal fluctuations of drought-growth relationship

For both species, the inclusion of random effects in the extraction of the ontogenetic trend from BAI series improved the fitted models compared to fixed effect only. The final random structure included plot/tree/core levels as random effects, considering triplet in the random structure did not improve the model based on likelihood ratio test (Table S1). Further modeling the variance and accounting for autocorrelation enhanced models parameters of both species. All parameters were significant ($p<0.05$) in the fitted model derived from Eq.[3.16]. Residuals were generally scattered symmetrically around zero for both species (Figure 4.7) within some variation among triplets. Superimposing tree growth residuals, the rBAI fluctuations were generally similar in both species between plot composition (mixture vs. pure), with some differences across triplets. However, rBAIs of Maritime pine exhibited higher deviations below the threshold of −1 than rBAI of Scots pine during the drought events in the last 20 years.

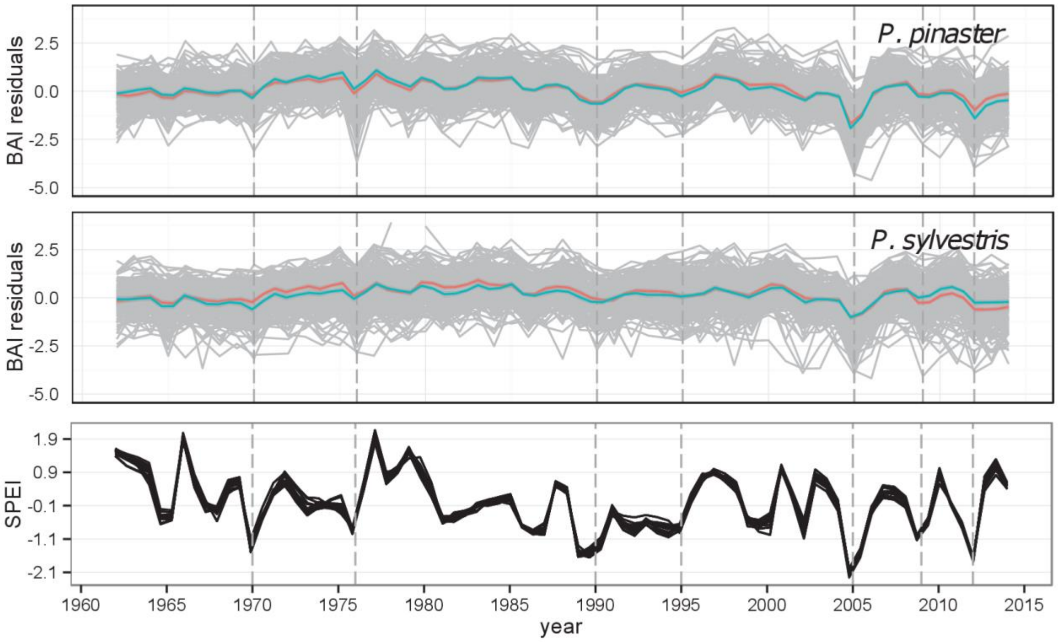

Figure 4.7. rBAI for each sample (grey lines) of *P. pinaster* (above) and *P. sylvestris* (middle). Mean fluctuation of trees in mixed stands (red line) and pure stands (green line). (Below) Standardized Precipitation–Evapotranspiration Index (SPEI), drought index accumulated over 12 months (from October to September). SPEI time series extracted for each plot in the triplets (black lines). Positive and negative SPEI values indicate wet and dry conditions, respectively. Vertical dashed lines highlight the drought years, SPEI<-1.

Mantel correlograms between rBAI and SPEI show a clear nonlinear pattern of the computed correlations, but different oscillating patterns over time between species (Figure 4.8). Maritime pine showed a stronger temporal correlation than Scots pine, which was progressively reducing from positive in the first distance classes to negative for distance classes around 3. This general pattern was also observed across triplets (sites) (Figure S4 and Figure S5), moreover, differences between stand composition (mixture vs. pure) were not evidently noticed.

Species identity defined the patterns of the computed correlations over time, while the variability within-site and among-plots influenced the correlation trends and scales across the calculated distance classes. Maritime pine trees showed a generally consistent symmetric pattern over distance classes across sites and within plots. The response pattern was more irregular among Scots pine trees within plots, and the correlation of the closer temporal classes vary widely depending on the site. In other words, Maritime pine trees were more sensitive, but they disassembled faster from the drought long-term effects than Scots pine trees.

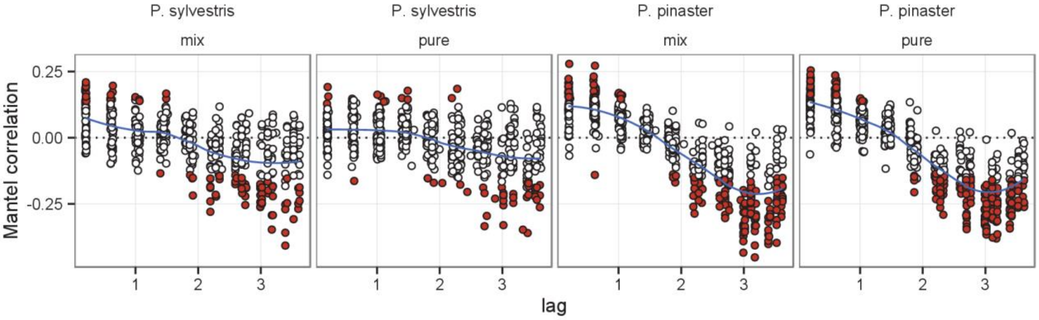

Figure 4.8. Mantel correlograms showing the extent of temporal similarities between of rBAI and SPEI along distance classes (lag). Filled and open symbols indicate the significant and non-significant Mantel statistic ($p < 0.05$). Blue line illustrated the overall pattern.

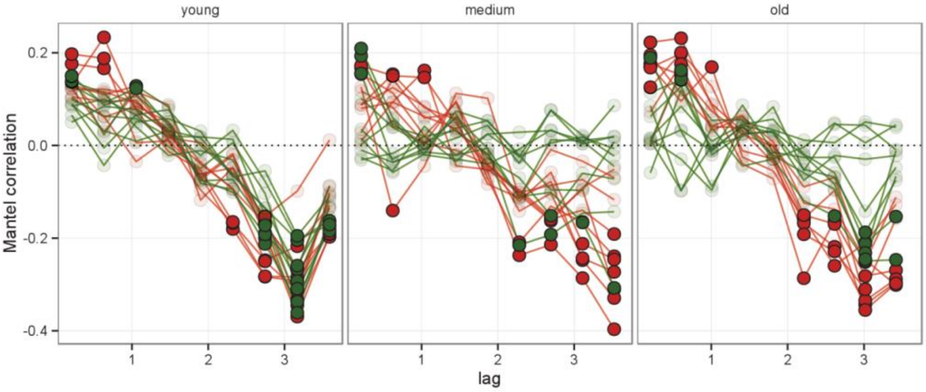

Figure 4.9. Mantel correlograms representing individual tree responses to drought rely on BAI residuals and SPEI synchrony for age classes. Filled and transparent open symbols indicate the significant and non-significant Mantel statistic ($p \leq 0.05$) for both species in mixed plots, Scots pine in green and Maritime pine in red.

We found that differences in dendroclimatic relationships between species depending on the tree age. Figure 4.9 illustrates those differences in mixed stands. In young stands (45 years) both species showed similar response patterns. However, Scots pine trees responded less intense and frequent to drought that Maritime pine trees in closer temporal classes. In mature and old stands (80 and >110 years, respectively) changes in the intensity of temporal patterns between species were notorious. While Maritime pine trees followed similar response pattern among age classes, discrepancies among age classes were more evident for

Scots pine. Weaker correlations and less frequent significant responses to drought were observed for closer distance classes in Scots pine trees, moreover, trees without any response across all distance classes were more common in mature and old stands.

4.3.2 Differences in responses to drought events between species and stand composition

Species-specific response to drought differs among drought events and varies depending on the index (Table 4.9 and Figure 4.10). During the extreme drought in 2005, Maritime pine was less resistant than Scots pine, while in 2012 both species had a similar level of growth reduction. Generally, Maritime pine recover better was more resilient and showed higher relative resilience to drought than Scots pine. Tree and stand covariates did not show a consistent pattern between drought events. Tree age showed a negative relationship with Rc and rRs indices in 2005, but positive with Rt in 2012. SDIR and tree size were never significant for the selected drought events. Analysis of Rt, Rc, Rs and rRs depending on stand composition between the two dry years showed a dominance of no significant differences in mixed versus pure stands (Table S2 and Figure S7). However, only Rs in 2012 for Maritime pine showed differences depending on species-mixing (Table S2). In this case, Maritime pine was more resilient to drought in mixed stands than in pure stands.

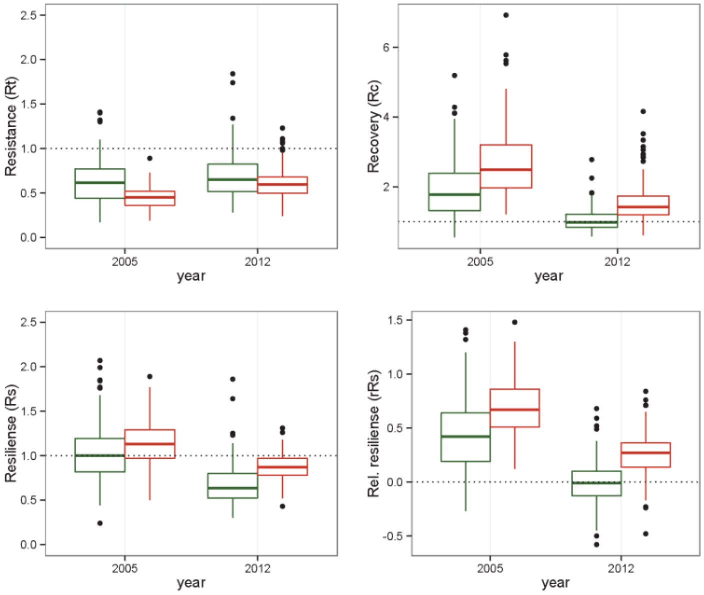

Figure 4.10. Variation in growth responses to drought at tree level (Rt, Rc, Rs, and rRs) between species growing in pure stand for each drought event. Scots pine in green and Maritime pine in red.

Table 4.9. Results from the linear mixed models of the resistance Rt, recovery Rc, resilience Rs and relative resilience rRs indices for Maritime pine and Scots pine trees growing in pure stands in all the selected drought events. ($p < 0.05$).

	Resistance		**Recovery (*ln*)**		**Resilience**		**Relative resilience**	
	2005	**2012**	**2005**	**2012**	**2005**	**2012**	**2005**	**2012**
Intercept	0.617	-0.407	1.099	0.008	1.085	0.687	0.798	-0.001
Maritime pine	-0.171		0.333	0.381		0.174	0.220	0.262
Age		0.004	-0.005				-0.004	
SI		0.029						
ΔAICc	3.816	6.019	2.704	1.941	3.643	2.676	1.886	1.276

ΔAICc: second-order Akaike Information Criterion (AICc) difference between the actual and full model. *ln* next to recovery index indicates a logarithmic transformation of the response variable.

4.4 Intra-annual complementarity relationships

The mean radial-annual increment was greater for Maritime pine than in Scots pine, in both mixed and pure stands (Table 2.6). The single-Richards function Eq.[3.20] was the best model that fitted the data. This model described a unimodal pattern for both species and by stand composition (Figure 4.11). The double-Richards function did not converge with our data, thus we were not able to distinguish the second peak of growth or radial increase in autumn after summer season (bi-modal pattern).

The parameters of the single-Richards models fitted for each tree were used to evaluate the inter- and intra-specific differences in the cumulative intra-annual radial increment pattern between species and by stand composition. Maritime pine presented higher asymptote ($Asym$), and greater radial increment rate (K) and shape (M) parameters than Scots pine, regardless of stand composition (Figure 4.11 and Figure 4.12). There was a not significant difference in the intra-annual pattern between mixed and pure stands for Maritime pine. While, for Scots pine the inflection point was greater and the increment rate lower in trees growing in mixed compared to pure stands. This means that for Scots pine trees in mixed stands, the intra-annual growing period became longer although the radial increment rate decreases compared to monospecific stands.

Tree size affected the shape of the intra-annual pattern for Scots pine, increasing the value of M related with tree diameter. In addition, *size x Composition* interaction showed that for a given diameter M was lower in pure stands compared to mixed stands (Table 4.10). The inflection point was lower in Scots pine growing in pure stands, but no-size dependency was observed. For Maritime pine the *size x*

Composition interaction was significant only for the value of the asymptote, increasing with the tree diameter in pure stands

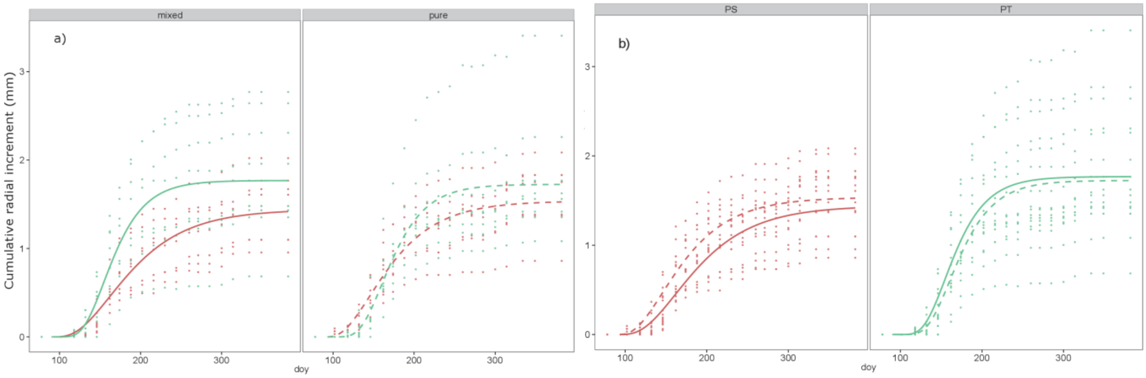

Figure 4.11. Intra-annual cumulative radial increment pattern during 2016 from single-Richards fitted model for Maritime pine (green line) and Scots pine (red line) in mixed (solid line) and pure stands (dashed line). a) Inter-specific comparison of patterns in mixed and pure stands. b) Intra-specific comparison of intra-annual pattern between trees growing in pure or mixture conditions, (PT: *P. pinaster*; PS: *P. sylvestris*).

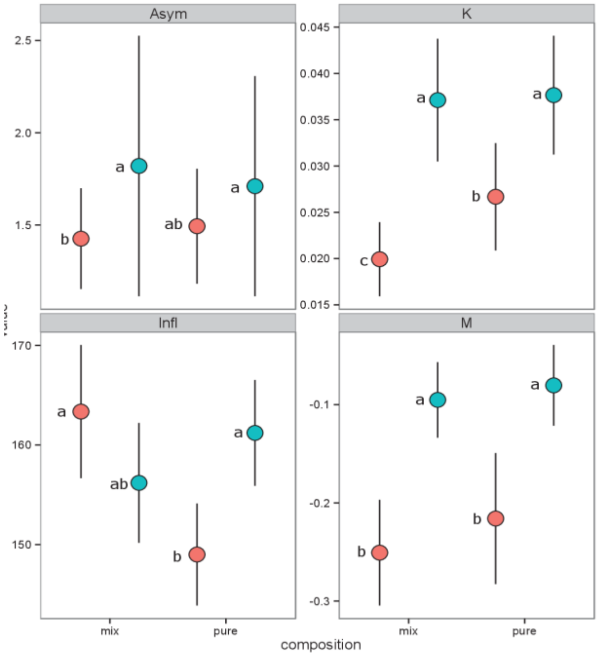

Figure 4.12. Differences of parameters from the cumulative intra-annual radial increment model fitted for Scots pine (red symbols) and Maritime pine (green symbols) trees in mixed and pure stands. Different letters denote significant differences (p-value <0.05). $Asym$ is the asymptote; $Infl$ is the inflection point; K is the rate or slope at the inflection point and M is the shape parameter of the model.

Table 4.10. Cumulative intra-annual radial increment pattern for Scots pine and Maritime pine as a function of tree size and stand composition (pure or mixed stands).

	Scots pine				**Maritime pine**			
	$Asym$	K	$Infl$	M	$Asym$	K	$Infl$	M
Composition (pure stand)	ns	ns	-14.458**	0.618*	-5.253*	ns	ns	ns
d	ns	ns	ns	0.021*	ns	ns	ns	ns
d x Composition	ns	ns	ns	-0.027*	0.175*	ns	ns	ns
AIC			112.5	-29.7	33.09			
Deviance			643.83	0.077	4.096			

Parameters of single-Richards function: A asymptote;. $Infl$ inflection point; K rate or slope at infection point and M shape parameter; d: tree diameter; *p< 0,05; ** p < 0,01; *** p < 0,001; ns: not significant.

4.5 Integration of species- mixing effects in empirical models

4.5.1 Height-diameter generalized model

Table 4.11 shows the best fitted models for Scots pine and Maritime pine that including the species-mixing effects parameter in their structure and yielded better goodness of fit than the base models fitted without considered the species interaction (Table S3). Just considering the species-specific stand variables ($Ho_{sp}, BA_{sp}, dq_{sp}$ or N_{sp}) instead of the total stand values, the performance of the models increased (Table 4.11 and Table S3). The relative ratio of the species-specific dominant height (rHo) showed lower AICc and less bias than the proportion of admixed species, therefore the former was selected as an indicator of species-mixing effects and intrer-specific competition environment in the fitted models. Functions M8 for Scots pine and M6 for Maritime pine showed the best performance among all the proposed functions, as measured by lower ACIc values and higher model efficiency. On inspecting the residuals versus predicted height by the best models for each species, we observed a homogeneous variation of the residuals over the full range of the predicted values (Figure S6), which would suggest compliance with the assumption of homogeneity of variance.

The performance of models for both species was improved when sample plot-level was included as random effects (Table 4.12). When all parameters in selected models were considered random, the final NLME *h-d* model failed to converge in both species. Convergence was possible when only one or two parameters of the model were treated as random. However, most of the models with two parameters specified as random showed high correlations between the random parameters; this indicates over parameterized random-effects that can produce poor estimates of the standard errors on the fixed-effects in the model (Pinheiro and Bates, 2000).

The best random structure treated α_3 as random parameter at the plot level for both species. The following mixed-effects model formulations, which showed the smallest Akaike's information criterion (AIC) were finally selected for Scots pine Eq. [4.1] and Maritime pine Eq. [4.2], respectively:

$$h_{ij} = \alpha_0 \cdot {Ho_{sp}}^{\alpha_1} \cdot BA_{sp}^{\alpha_2} \cdot e^{(\alpha_3+u_i)\left(\frac{1}{d}-\frac{1}{Do_{sp}}\right)} + \beta_1 \cdot rHo \qquad [4.1]$$

$$h_{ij} = \alpha_0 \cdot {Ho_{sp}}^{\alpha_1} \cdot BA_{sp}^{\alpha_2} \cdot e^{\left(\frac{\alpha_3+u_i}{d}\right)} + \beta_1 \cdot rHo \qquad [4.2]$$

where α_0 to α_3 and $\beta_1$are considered fixed parameters; u_i is the random plot effects on parameter α_3, and all other variables were previous specified in Table 3.3. The NLME *h-d* generalized models supposed a reduction in the RMSE of 5.11% in Scots pine and 4.08% in Maritime pine compared with the fixed-effects models fitted by ordinary non-linear least squares (Table 4.11).

Table 4.11. Summary statistics and ranking of generalized height-diameter models for Scots pine and Maritime pine considering the species-mixing effects. Models number according to Table 3.3.

Scots pine					**Maritime pine**				
model	**AICc**	**ΔAICc**	**w_i**	**EF**	**model**	**AICc**	**ΔAICc**	**w_i**	**EF**
m8	7595.11	0.00	1.00	0.820	m6	6687.69	0.00	0.870	0.848
m7	7611.43	16.32	0.00	0.817	m8	6691.51	3.81	0.129	0.846
m11	7629.94	34.83	0.00	0.812	m2	6703.39	15.70	0.000	0.843
m9	7635.56	40.45	0.00	0.811	m9	6703.76	16.07	0.000	0.843
m6	7644.02	48.91	0.00	0.810	m10	6718.30	30.60	0.000	0.841
m2	7645.67	50.57	0.00	0.808	m11	6720.76	33.07	0.000	0.840
m11	7658.18	63.07	0.00	0.806	m4	6738.52	50.83	0.000	0.837
m5	7663.97	68.86	0.00	0.806	m12	6742.19	54.50	0.000	0.836
m4	7678.41	83.30	0.00	0.802	m7	6744.31	56.62	0.000	0.836
m12	7687.51	92.41	0.00	0.800	m1	6751.12	63.43	0.000	0.834
m10	7692.94	97.84	0.00	0.798	m5	6757.30	69.61	0.000	0.834
m3	7724.38	129.27	0.00	0.792	m3	6781.27	93.58	0.000	0.828

AICc: Second-order Akaike Information Criterion; ΔAICc: difference between the best model and the ith model; w_i: Akaike weights.

The species mixing effects varied between the species in the fitted models. Figure 4.4 seems to support the tendency of Maritime pine to overtop Scots pine, suggesting that most increases in rHo are associated with an increase in relative height of Scots pine while this species is still in an inferior crown class within the stand at a fixed age. Thus, within the stand a larger diameter is associated with a relatively small increase in height for Scots pine. In contrast, a decrease in rHo implies an increase in the dominance of Maritime pine, so heights associated with a given d are greater, and a given decrease in rHo is associated with a greater increase in height for a *P. pinaster* tree of given d within the stand at a fixed age.

Table 4.12. Parameter estimates and goodness-of-fit statistics for the generalized *h-d* model selected (all parameters were significant at p <0.05; standard errors in brackets)

Species	**Estimated parameters (and standard errors)**							**NLME performance**	
	α_0	α_1	α_2	α_3	β_1	σ^2_u (plot)	σ^2_ε (error)	**RMSE**	**% RMSE reduct.**
Scots pine	0.9928	0.9732	0.0271	-7.284	0.2908	3.644	2.464	1.654	5.107
	(0.081)	(0.035)	(0.002)	(0.502)	(0.027)				
Maritime pine	2.5348	0.8356	-0.0630	-8.165	-0.643	0.521	1.888	1.374	4.795
	(0.325)	(0.033)	(0.018)	(0.417)	(0.344)				

% RMSE; Percentage of RMSE reduction with regards to RMSE obtained using ordinary non-linear least squares fitting method.

4.5.2 Height-diameter function validation

The most parsimonious generalized *h-d* functions (Table 4.12) were validated based on the independent dataset, a set of pure and mixed plots selected from the third NFI plot network. Validation statistics were calculated and compared with the performance of the equations proposed by Lizarralde et al., (2010a, 2010b) for monospecific stands of both species (Table 4.13). When the fitted models were applied to trees in mixed stands, the Scots pine *h-d* function had larger model efficiency and lower RMSE of those of Maritime pine. Results were consistent across stand composition when predictions bias were compared between the models fitted in this research and the proposed by Lizarralde et al., (2010a, 2010b). For both species, the fitted models that included mixed-species stands attributes reduced the total prediction error in the mixed stands, increasing the model efficiency by 6% and 1%, for Scots pine and Maritime pine, respectively. The gain in efficiency in pure stands was only 2% for Scots pine, and for Maritime pine a loss in efficiency of 1% was observed.

Table 4.13. Performance of generalized *h-d* fitted models and the equations proposed by Lizarralde et al., (2010a, 2010b) applied to data from National Forest Inventory of the in the Northern Iberian Range.

Stand Composition	**Species**	**n**	**Fitted models**		**Lizarralde (2010a, 2010b)**	
			RMSE	**EF**	**RMSE**	**EF**
Mixed	Scots pine	721	1.69	0.74	1.88	0.68
	Maritime pine	738	1.88	0.66	1.89	0.65
Pure	Scots pine	3983	1.73	0.81	1.79	0.79
	Maritime pine	2089	1.71	0.75	1.68	0.76

The fitted models reduced the mean bias of tree height predictions for both species regardless of stand composition across medium to small trees (*d* <25 cm, Figure 4.13). Bias from both models in other diameter classes followed the same pattern. However, bias was evident and sizable in larger diameter classes (*d* >65 cm) for Maritime pine when the models were applied to both mixed and monospecific stands.

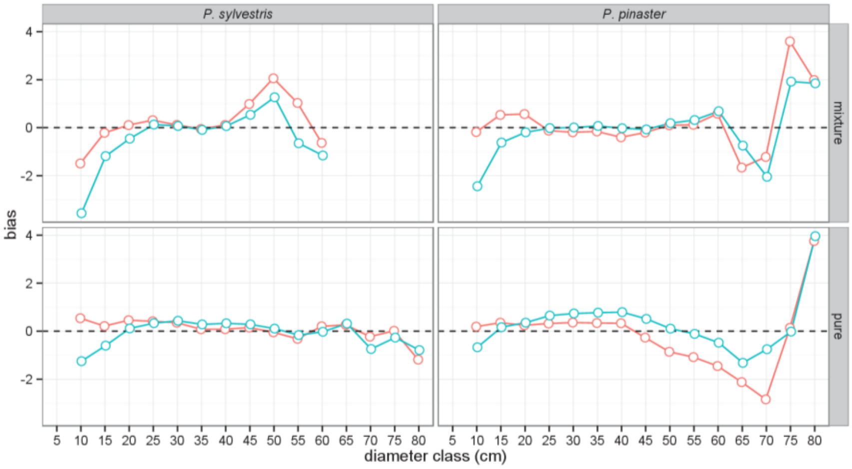

Figure 4.13. Mean bias (m) by diameter classes of the generalized *h-d* fitted models (red circles and lines) compared with models by Lizarralde (2008) (green circles and lines) in mixed and pure stands using NFI data.

4.5.3 Basal area increment model

Differences in growth rates between mixed and pure stands were more evident and variable among triplets in Maritime pine that in Scots pine. In the fitting model, the inclusion of random effects greatly improved the goodness-of-fit indicators, decreasing AIC and producing significant differences in likelihood ratio. For both species, a random intercept at the plot level and an exponential variance function (function of SDIRL) was selected as most appropriate random model structure for the data. A visual check of the model residuals indicated no major departures from the assumptions of normality and homogeneity of variance.

According to the base model structure, basal area growth (log-transformed) increased with tree size and crown ratio with the differing magnitude depending on species identity. The d^2 term was non-significant in the base model structure. Site index did not improve the performance of the models in either species, as indicated by non-significant differences by the likelihood ratio test, so it was not included in the base model. Rh had high collinearity with the diameter (variance inflation factor, VIF>10) so was also excluded. The inclusion of competition in the model structure improved considerably the basal area increment models for both species. Competition terms relying on SDIR yielded the most parsimonious models compared to competition expressed in terms of stand basal area (BA or BAL), so the former were used in the subsequent model selection.

Table 4.14 compares the different models that include symmetric or asymmetric competition structures. Not all the possible combinations of competition structure are listed because non-significant parameters were excluded from the models and the remaining parameters were re-estimated. Clear differences between species in terms of competition structure were observed after ranking the best models by AICc and w_i.

Table 4.14. Ranking of basal area increment models comparing competition structures and their respective parameters estimated. Competition status was compared for the size-symmetric (SDIR) and/or size-asymmetric competitors (SDIRL) and divided by intraspecific and interspecific competitors. Significant parameters, p-value <0.05.

	SDIR	**SDIR$_{\text{intra}}$**	**SDIR$_{\text{inter}}$**	**SDIRL**	**SDIRL$_{\text{intra}}$**	**SDIRL$_{\text{inter}}$**	**AICc**	**ΔAICc**	w_i
Scots pine	-1.669						1107.8	0	0.674
		-1.818	-1.645				1109.3	1.53	0.314
		-1.138				-1.132	1115.9	8.13	0.012
						-0.5957	1123.8	16	0
				-0.3128			1127.2	19.39	0
Maritime pine	-0.941				-0.2561		926.8	0	0.332
		-0.9415	-0.836		-0.2521		927.2	0.39	0.273
	-0.917			-0.271			928.9	2.05	0.119
		-0.4815		-0.397			929	2.22	0.109
	-1.192						929.1	2.3	0.105
		-1.188	-1.048				930.6	3.75	0.051
				-0.410			934.5	7.72	0.007
					-0.385		935.6	8.75	0.004

SDIR, size-symmetric competition index; SDIRL, size-asymmetric competition index for larger trees; subheading inter and intra are the interspecific and intraspecific competition structures, respectively; AICc, Second-order Akaike Information Criterion; ΔAICc, difference of AICc values between the best model and the ith model; ωi, Akaike weights.

For Scots pine, the size-symmetric competition indices were the most relevant predictors of basal area tree growth in mixed and pure stands. The index measuring size-symmetric competition without considering species composition of competitors was the best-ranked model. The model containing size-symmetric competition and accounting for different levels of competition by species was the second-best model according to AICc ranking. Here, the symmetric intra-specific competition (SDIR$_{\text{intra}}$) was greater that inter-specific competition term (SDIR$_{\text{inter}}$), implying a reduced competition effect when the competitor was Maritime pine rather than Scots pine competing against itself. Even though the difference in AICc between the two highest-ranking models is small, Akaike weights endorsed the relative superiority of the model containing the SDIR competition index without discriminating among competitors by species.

These results for Scots pine contrasted with the best basal area increment model for Maritime pine. Here, the effects of competition on basal area growth rate in the most parsimonious model are most accurately predicted by the combination of size-symmetric and size-asymmetric indices. Thus, the asymmetric competition was mainly affected by the competition neighborhood with other Maritime pine trees, and the effect from the inter-specific competition with Scots pine was not significant. On the other hand, the symmetric competition had a similar effect on Maritime pine basal area growth as that the observed for Scots pine, with no species-mixing effects. When the size-symmetric competition effect was separated into species effects in the second best ranked model, a positive species interaction was observed, with size-symmetric intra-specific competition (SDIRintra) greater than the inter-specific competition term. Differences between the two best ranked models were smaller than in Scots pine, and both models showed species-mixing effects of competition

Table 4.15. Estimated parameters (standard errors) and fitting statistics for the selected basal area increment models of both species (Table 4.14). Parameter estimates rely on REML.

		Scots pine	**Maritime pine**
Fixed parameters	α_0	-1.4119	-3.1198
		(0.5434)	(0.9136)
	α_1	1.1894	1.4201
		(0.0895)	(0.1635)
	α_3	0.4897	0.3171
		(0.0723)	(0.0732)
	SDIR	-1.6751	-0.9524
		(0.3078)	(0.2909)
	$\mathrm{SDIRL}_{\mathrm{intra}}$		-0.2447
			(0.1282)
Variance components	$\sigma^2_{i\ (plot)}$	0.0592	0.0589
	$\sigma^2_{\varepsilon\ (error)}$	0.1965	0.1071
Variance function	δ	0.2880	0.5166
	R^2 marginal	0.4963	0.5695
Cross-evaluation	Bias	0.1246	0.8255
	EF	0.2825	0.3680
	RMSE	15.9205	20.9099

σ^2_ε, residual variance; σ^2_i, variances for the plot random effects; δ, parameters of the variance function (Eq. [3.25]); Marginal R^2, values correspond to the proportion of variance explained by the fixed effects (Nakagawa and Schielzeth, 2013). Bias, EF and RMSE are mean bias model efficiency and root mean square (Eq.[3.26]-[3.28]), respectively, calculated with back-transformed data Eq. [3.29].

The cross-validation gave satisfactory results, the model being reasonably accurate and unbiased. The basal area growth models with the lowest AICc value were fitted with the REML procedure (Table 4.15) and all parameters were significant. Figure 4.14 depicts the effects of size-asymmetric competition on basal area increment of Maritime pine, comparing when trees were influenced by intraspecific competition only, pure stands (Proportion PT=1), and when competition was the combination of intraspecific and interspecific interactions, mixed stand (Proportion PT <1). The effect of competition reduction on tree growth was greater as the proportion of Scots pine in size-asymmetric competition increase, however, these effects was reduced as total size-asymmetric competition decreased, e.g., dominant trees.

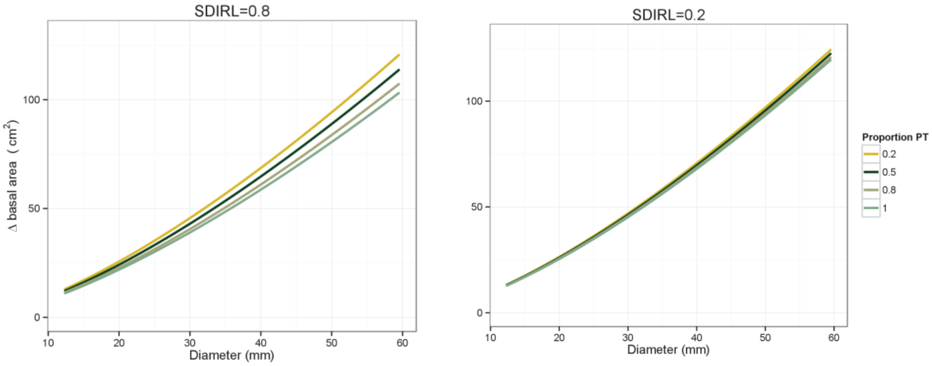

Figure 4.14. Variation of Maritime pine basal area increment with tree diameter depending on the amount of total size-asymmetric competition (SDIRL), and according to Maritime pine proportion in SDIRL (SDIL$_{intra}$/SDIL). In pure stands proportion PT =1 and decreased as the asymmetric competition of Scots pine increased (SDIRL$_{inter}$). All the other explanatory variables were fixed at their mean values, CR=0.25 and SDIR=0.8.

5. Discussion

5.1 National scale mixing effects on growth at stand and tree level

5.1.1 Feasibility of maximum size-density estimation with NFI

Appropriate estimation of potential or maximum density is a crucial step in determining the stocking proportion of species in mixed stands (Sterba et al., 2014). Self-thinning fitted models reached a lower maximum size-density line and SDImax value than the upper limiting boundary lines fitted in previous studies for these species in this region (del Río et al., 2006, 2001) (Figure 4.1). This was mainly due to different intercept values, which can vary with site conditions. The same has been reported in other studies, where larger intercept values in stands growing on more productive sites (Bi, 2004; Weiskittel et al., 2009) led to considerable differences in density. It is important to note that both the methodology and the type of data used for analysis may explain the distinct values of the maximum size-density relationships compared to previous studies (Hann, 2014). Here, the 95% quantile of the selected NFI plots was used to fit the size-density relationship, thereby providing a genuine reflection of the wide range of stand conditions in the national distribution of the species. Stand origin had also been associated with significant changes in the intercept on the self-thinning boundary line in prior research (Weiskittel et al., 2009). However, we did not observe differences between natural stands and plantations in our results, which concur with those of Puettmann et al. (1993).

The species-specific slope observed for Scots pine was similar to that estimated by del Río et al., (2001) from non-thinned permanent plots, suggesting quantile regression as an appropriate approach for estimating the self-thinning boundary line using inventory data. The self-thinning coefficient determined for Maritime pine in this study supports the idea of using a species-specific slope rather than a constant coefficient among species (Charru et al., 2012). However, del Río et al. (2006) used the slope stated by Reineke to fit the self-thinning line for Maritime pine, so comparison of the fitted self-thinning line was not possible. Recently, Aguirre et al. (2018) developed climate-dependent maximum size-density models for pine species in Spain. Using these models could help to deal with the potential variability of the size-density relationship on environment and site conditions (Condés et al., 2017). Such models may also generate more accurate species-specific carrying capacities and subsequent calculations of mixing proportions.

5.1.2 Species-mixing effects on growth efficiency at stand level

The criteria used to select the pure and mixed plots made it possible to reduce the shift in ecological variables between pure and mixed stands and control the effects of silvicultural practices (level of growing stock) that might alter or mask mixture effects (Forrester and Pretzsch, 2015). However, the low variability explained by the growth efficiency models in both species may be due to uncertainty regarding NFI data characteristics and methodological approach. When highly accurate predictions are required, methods for dealing with bias in predictions can be used, such as marginalization of predictions over the error term distribution through numerical integration (Fortin, 2013). Furthermore, the self-thinning law is hard to verify, and we have assumed that mixed-stand density can be estimated from the relative densities of both species, though this implies a risk of introducing bias into yield estimates in mixed stands. Nevertheless, estimating species occupancy, and therefore species proportion, by area in mixed stands has often provided good results (Huber et al., 2014; Sterba et al., 2014).

National Forestry Inventory data made it possible to obtain a general overview of the behavior of this mixture type in an unbiased and systematic sample distributed across the complete range of mixture proportions. Thus, we compared the 'true mixture effect' (Forrester and Pretzsch, 2015) independently of the mixture proportion, revealing apparent profit at the stand scale and the mutual benefit of both species from the mixture. Given that complementarity processes require species niche differentiation (Kelty, 1992), complementarity is less likely to occur when light-demanding species with potentially similar crown architectures coexist, as is the case with these two pines (Crecente-Campo et al., 2013). Hence, the mutual facilitation we observed, in which both species gained (Larocque et al., 2012), is an unexpected indication of a complementary relationship between Scots pine and Maritime pine. These results suggest that slight differences in species traits, even small differences in shade tolerance, can trigger positive inter-specific effects through competition reduction or complementarity mechanisms. Species mixture can induce changes in crown dominance, above-ground species allometries and structural stand traits (Pretzsch et al., 2016; Williams et al., 2017) according to how light is distributed among the trees, which affects productivity. This applies to light-demanding species mixtures with notable effects on tree growth and stand productivity (Jucker et al., 2014b).

Potential growth gain for Scots pine was also found in mixture with *Quercus pyrenaica* (Río and Sterba, 2009) and *Fagus sylvatica* (Condés et al., 2013; Pretzsch et al., 2015b), and *Pinus nigra* (Jucker et al., 2014b), but no such effect was reported in mixture with *Quercus petraea* (Toïgo et al., 2015). To our knowledge, no prior research has reported mixture effects on growth efficiency for Maritime pine. Despite the mixture effect observed in this study, the mechanisms that trigger species interactions are not easy to disentangle in a stand-level analysis, because some factors may act simultaneously. In most cases, complementary strategies for light interception or light use efficiency between species were the main drivers of positive mixing effects. However, in climatically stressful Mediterranean conditions there is evidence of higher wood production in mixed forests due to species niche partitioning in water use (Vilà et al., 2007).

Site quality is a trigger factor and could determine the effect of species mixing (Huber et al., 2014; Toïgo et al., 2015). Because stand age is missing in NFI data, the age-related site index could not be estimated in this study. Instead, we used Ho and dq as surrogate variables for site quality and stand age or development stage, respectively, in the growth efficiency model. Additionally, since dominant height cannot be directly associated to site quality class, mixture effects at stand level could not be assessed along a productivity gradient (Condés et al., 2013). The traditional use of Eichorn's rule for calculating side index might not be appropriate for mixed stands due to inter-specific interactions that could modify the expected side index, as calculated from pure stands (del Río et al., 2016). However, site index for pure stands (Pretzsch et al., 2015b) or abiotic gradients to describe site productivity (Dănescu et al., 2017; Toïgo et al., 2015) are commonly used to analyze the relationship between total yield and site conditions in mixed forests.

5.1.3 Competition effects on tree growth

Unlike the stand-level results, response to both structure and species composition of the competition varied significantly between Scots pine and Maritime pine at the tree level. This demonstrates the importance of looking at tree-specific competition relationships in multi-level analyses of mixed-species forests (Pretzsch et al., 2015a).

Symmetric and asymmetric competition have frequently been related to below-ground and above-ground resources, respectively (Larocque et al., 2012; Weiskittel et al., 2011). The fitted single-tree volume growth models revealed that asymmetric competition was stronger than symmetric competition, suggesting light competition (above-ground resources) as the main driver limiting growth in these mixtures. This was expected as both species are considered light demanding, though Scots pine is relatively more shade tolerant.

Differentiation of intra- and inter-specific competition has also provided useful information for inferring species interactions that influence tree growth (Manso et al., 2015) and whether niche complementarity occurs above-ground or below-ground (Río et al., 2014). For Scots pine, competition with Maritime pine was less intense than intra-specific asymmetric competition. This indicates a degree of complementarity or reduced competition for above-ground niche occupation or light interception, especially if we consider that Maritime pine mainly occupies the dominant canopy layer and larger size-distribution class (Table 2.3) and that Scots pine can grow in half-light conditions (Gaudio et al., 2011). In contrast, Maritime pine tree growth was more strongly influenced by the competition structure (symmetric and asymmetric) than by the specific composition of the competition (intra- and inter-specific), indicating that growth depends more on size than on species identity. This is explained by the greater shade intolerance of Maritime pine, which as mentioned dominates the canopy layer and the larger size-distribution classes in mixture stands, where access to light is less affected by species-mixing (lower SDIRLinter values, Table 2.3). The effect of intra-specific symmetric competition was more intense than that of inter-specific symmetric competition (lower and non-significant) in both species. This may explain the results at the stand level, as it indicates reduced competition for belowground resource extraction for both species in the mixture.

Combining both competition structure models resulted in a clearly positive mixture effect for Scots pine, while the mixture effect could be overridden at tree level for Maritime pine. This might apply to dominant trees especially, due to the stronger and negative effects of inter-specific asymmetric competition (Figure 4.2). It also means that inter-specific competition and complementarity co-occur. However, we think that upscaling these interactions to stand level would depend on size distribution, which should be considered to understand the extent to which the specific mixture effect deviates stand growth in mixtures as compared to pure stands. The differences detected in our study may correspond to the fact that Maritime pine occupied the dominant social classes in the mixtures. Thus, any neutral or negative mixing effect on suppressed trees would have little influence and result in a positive net effect when aggregated at the stand level.

Differences in species-mixing effects at stand and tree levels have also been found in other mixtures, such as *Pinus sylvestris* – *Quercus petraea* L. (Perot and Picard, 2012) and *Pinus sylvestris – Fagus sylvatica* (Condés et al., 2013; del Río et al., 2014a). Tree size distribution is a crucial issue when upscaling from tree to stand level (Pretzsch and Schütze, 2016, 2014); mortality differences between mixed and monospecific stands can modify size distribution and influence upscaling. For instance, mixing might increase mortality in suppressed trees of the more light-demanding species, while decreasing mortality in the less light-demanding one (Condés and del Río, 2015).

Regarding the reliability of results at the two levels studied (tree and stand), it is important to note that tree-level results might be influenced by functions used (tree volume allometric equations, height-diameter relationships) for upscaling from tree to and level. Since these functions are usually not available for mixed stands, the functions developed for pure stands are commonly used (del Río et al., 2016) and add uncertainty to the results.

5.2 Emerging differences: species-mixing and stand structural attributes

5.2.1 Crown allometry plasticity

Tree crown morphology was significantly influenced by interspecific competition. Vertical crown extension of Maritime pine was greater in mixed versus pure stands, especially in larger trees (Figure 4.3), which is consistent with studies showing that interspecific interactions affect species-specific allometric relationships (Forrester et al., 2017a; Pretzsch, 2014). This may signify niche partitioning processes resulting from the slow, continual feedback between structure, environment and tree growth in mixed stands (Pretzsch, 2014). Crown plasticity, or the ability of trees to develop complementary crown morphologies in response to changes in their local competitive environment, is a critical element that promotes efficient canopy packing and reduces the intensity of light competition in mixed forests (Ishii and Asano, 2010; Jucker et al., 2015).

Though the variability of allometric relationships was partially explained by the inclusion of stand composition in the model (Table 4.5), the intra-specific differences of tree height for given diameter in monspecific versus mixed stands could not be attributed to species-mixing alone. Density and canopy structures across plots, which can be partially attributed to interspecific interactions, might also modify crown allometry and tree morphology. Thus, including stand structural variables in allometric equations could help account for variability in stand densities (Calama and Montero, 2004). In addition, Vizcaíno-Palomar et al., (2016) observed variation in the inter-population tree height allometry of both Maritime pine and Scots pine, resulting from adaptive responses to local environments (climate and geographical sites of origin) or their past genetic background. This indicates that allometric relationships are not a static trait for any species (Forrester et al., 2017) and underscores the need to develop individual tree-based growth models for mixed stands.

5.2.2 Changes in structural heterogeneity driven by species-mixing

Stand structure and species diversity are crucial drivers that affect most forest functions and services (Gadow et al., 2012; Pretzsch, 2014). Detailed information on stand structures and size-distribution is needed for upscaling mixing effects from the individual tree to the species or stand level, thereby improving our understanding and modeling of mixed-species stand dynamics (Forrester and Pretzsch, 2015; Pretzsch, 2014).

For some structural traits (Table 4.7 Mix_{exp}/Pure), differences between the two species (monoculture compared to the weighted mean of both monocultures) were enough to increase structural heterogeneity through species-mixing alone, resulting in an additive effect. This implies that these species can show complementary traits in vertical stand structure related to crown architecture and differences in their ability to grow in low light conditions (Gaudio et al., 2011; Sánchez-Gómez et al., 2006). However, information about the differences between species morphology and stand structure in pure stands is insufficient for predicting crown vertical extension, crown packing or structural heterogeneity resulting from emerging species-mixing effects. This multiplicative effect revealed new structural and morphological aspects resulting from species interactions (Forrester, 2014; Pretzsch, 2014). At the stand level, vertical stratification and volume growth inequality emerged as the most meaningful multiplicative effects of species interaction in mixed stands (Figure 4.6: Mix_{obs}/Mix_{exp}). However, most of the mixed-species size-distribution ratios that differed significantly from pure stands at this level showed opposite species reaction traits, which counteracted each other and overrode the mixing effects at the whole stand level. Counterbalancing effects at the species level was also observed in mixtures with more contrasting morphological traits between species (Pretzsch et al., 2016).

Enhanced vertical layering through species-mixing could be traced to structural trait shifts in Maritime pine growing in mixture versus pure stands, which contrasts with the steady structural performance of Scots pine in mixed versus pure stands. Vertical heterogeneity (Figure 4.6), differences in allometric equations (Figure 4.3) and mixing effects on mean tree sizes (Table 4.6) resulted in stand structures in which Maritime pine tended to occupy the dominant canopy layer and larger size-distribution classes more in mixtures, compared to inter-specific size-distribution and vertical structure in monospecific stands. . Previous studies analyzed the mixture effect on dominant height (Menalled et al., 1998; Pinto et al., 2008; Pretzsch et al., 2015a), their results shows that inter-specific competition for light in mixed forests can modify tree height growth, mean height or dominant. However, the magnitude of the mixture effect on dominant height depending on species interactions (Vallet and Perot, 2016) as well as stand density (Amoroso and Turnblom, 2006).

Complementarity or reduced competition due to the space released by Scots pine for above-ground niche occupation is probably enabled by the slight differences in light-use strategies between the two species. This has implications for crown architecture in species subjected to heavy competition for light (Ishii and Asano, 2010; Jucker et al., 2015). Jucker et al. (2014) reported that shifts in size distribution and crown structure in mixed versus pure stands acted as mechanisms for inducing the positive effects of species-mixing by enhancing light use efficiency in *Pinus sylvestris* and *Pinus nigra* mixtures.

5.2.3 Ecological explanation of mixing effects on productivity and structure

We observed greater relative volume productivity in mixed stands compared to pure stands (Table 4.6 and Figure S2), derived from the significant over-yielding of Maritime pine; whereas the relative productivity of Scots pine remained steady and was unaffected by mixing. These results partially agreed with the results of *Study I* (Section 5.1.2), where species-mixing increased productivity at the stand level and large-scale mutual benefits were observed for both species. This might be due to differences in environmental conditions between the two studies, which may cause spatial variations in over-yielding or mixing effects (Forrester, 2014; Toïgo et al., 2015).

Despite the over-yielding observed, the variability in relative productivity among triplets (Figure S2) highlights the complexity of the different processes that influence net complementarity effects between species. Mixing effects depend on stand development stage, stand density and site conditions (Cavard et al., 2011; Condés et al., 2013; Mina et al., 2017). In some cases, opposite patterns even appear between species in the same mixture (Amoroso and Turnblom, 2006; Pretzsch et al., 2010; del Río, et al., 2014; Toïgo et al., 2015). It is also relevant to note that though the stands had not been managed for about ten years, some of the crown architectural and stand structural traits observed in mixed stands might represent earlier silviculture interference more than the species-specific ability to appropriate resources or adapt to competition. Uncertainty in the observed mixing effect due to past management could not be quantified here.

Some degree of niche partitioning is required for coexisting species and can be reflected in crown characteristics, vertical leaf profiles, shade tolerance or differences in growth phenology (Aldea et al., 2018; Jucker et al., 2015; Toïgo et al., 2017). Nonetheless, small differences in species structural traits can trigger positive interspecific effects through complementarity or competition reduction mechanisms (Jucker et al., 2014b). In this study, over-yielding at the stand level was related to vertical structural heterogeneity resulting from species interaction (Table 4.8), which increased mixed-species stand productivity compared to monocultures. In other words, crown complementarity in canopy space can be thought of as a mechanism that links biodiversity with ecosystem productivity (Forrester et al., 2018). Similar relationships have been observed in recent studies for mixtures involving the main Central European temperate (Dănescu et al., 2016; Pretzsch and Schütze, 2016) and North American temperate-boreal tree species (Williams et al., 2017).

Vertical structure has notable effects on light-demanding species such as pines, which in single-species stands tend to exhibit suppressed growth due to light competition (Gómez-Aparicio et al., 2011). The processes involved in the positive relationship between crown complementarity and over-yielding in mixed stands have been associated with maximized light capture and/or light-use efficiency (Forrester et al., 2018; Williams et al., 2017). Both processes are closely related to crown size characteristics (Binkley et al., 2013). For example, crown projection area has been used to measure species growing-space occupancy and to study growing-space efficiency as a proxy for light interception in mixed stands (Dirnberger et al., 2017; Mainwaring and Maguire, 2004). Using this approach on the same Scots pine-Maritime pine triplets, Cattaneo et al. (2017) observed that the tree level growth efficiency of *P. pinaster* increased in mixture, while *P. sylvestris* showed no benefits from admixture. Their findings concur with the differences in relative productivity described in Section 4.2.4 of the present work (Table 4.6). Consequently, relationships between crown characteristics and tree growth or canopy characteristics and stand growth in mixed stands indicate that, for these trees, crown allometric plasticity and vertical stratification in the canopy can vary in response to local competitive environmental conditions. This is highly relevant in terms of productivity gains or losses.

Species-specific physiological and morphological plasticity responses to shade conditions allow light-demanding species to coexist (Gratani, 2014; Valladares et al., 2002). In experimental trials with seedlings, Scots pine was able to grow in low light conditions (Gaudio et al., 2011) due to greater total carotenoid concentration and higher chlorophyll ratios in response to shade than Maritime pine (Sánchez-Gómez et al., 2006)., The combination of higher crown plasticity in Maritime pine (Vizcaíno-Palomar et al., 2016), slight differences in shade tolerance between species (Poorter et al., 2012) and the higher physiological plasticity of Scots pine (Gaudio et al., 2011; Sánchez-Gómez et al., 2006) might allowed the two species to develop a multi-layered vertical structure and complementary crown architectures when they grew in mixtures. Thus, intercepted light could also be used more efficiently, suggesting that light-related interactions may contribute to the mixing effect on stand productivity.

5.3 Inter-annual differentiation of species sensitivity to drought

Both Scots pine and Maritime pine exhibited species-specific growth fluctuations in response to drought severity and nonlinear response variation among subject trees within species. These differences were captured in the multilevel analysis by assessing responses at successive levels of drought sensitivity. Differences in drought sensitivity between the two species have been observed in various Mediterranean environments (Lara et al., 2013; Sánchez-Salguero et al., 2012) due to species-specific responses to climatic conditions. For instance, climate growth association in the Iberian Range indicated that Scots pine growth depended mainly on summer rainfall (Bogino et al., 2009), while water availability in spring and early summer were the main growth predictors for Maritime pine (Bogino and Bravo, 2008). Moreover, correlations between growth and spring precipitation, as well as sensitivity to drought, have been increasing since the 1980s (Bogino and Bravo, 2008; Lara et al., 2013). The two species also displayed different physiological mechanisms related to their hydraulic capacity to deal with water deficits (Martínez-Vilalta et al., 2004). Maritime pine shows better water-use efficiency than Scots pine (Martínez-Vilalta and Piñol, 2002), which has less geographical plasticity in xylem traits for stomatal control (leaf-to-sapwood area ratio) (Martínez-Vilalta et al., 2009; Martínez-Vilalta and Piñol, 2002).

Irregular response patterns for Scots pine among plots and among trees within plots suggest that factors other than drought – such as genetic adaptations, competition, soil types, and physiographic position (elevation, slope, and aspect) – might also constrain growth and growth response to climate (Benito Garzón et al., 2011; Lara et al., 2013). For instance, competition seems to be a much more relevant driver for growth than drought for Scots pine at high altitudes, where low temperatures mainly limit growth (Sánchez-Salguero et al., 2015b). Our results also indicate that sensitivity decreased with increasing age in Scots pine, while fluctuation patterns remained similar across age classes for Maritime pine. However, we cannot attribute this effect directly to age; it is likely an indirect age-related effect of different competition levels among plots. Younger stands with less inter-tree competition that are exposed to more severe and frequent drought events in early development stages could become more sensitive to climate variability than older stands, where competition constrains growth dynamics.

Our findings confirm that severe droughts negatively impact tree growth in both species. Maritime pine showed greater growth reduction during the extreme drought events, but greater recovery indices compared to Scots pine. The greater resilience of Maritime pine was expected, since this and other Mediterranean pine species can experience higher recovery rates after strong drought stress and thereby avoid catastrophic xylem embolism (Martínez-Vilalta et al., 2004). Maritime pine exhibits extensive local adaptive variability and resilience to drought across its distribution area (Sánchez-Salguero et al., 2018). Scots pine, however, was found to have less growth resilience when it co-existed with other pines, such as Aleppo pine and Black pine (Granda et al., 2018a; Marqués et al., 2016). Although size-dependence on growth resilience to drought was reported (Ding et al., 2017; Merlin et al., 2015), the fact that only dominant trees were considered in this study might explain why tree size had no apparent effect during the drought years analyzed. Moreover, older trees recovered less well after extreme drought events, which coincides with findings of previous studies (Bogino and Bravo, 2009; Martínez-Vilalta et al., 2012).

The species-specific oscillating patterns over time between rBAI and SPEI and tree-growth resilience to drought events observed in this section support the hypothesis that temporal species niche differentiation could contribute to species coexistence. However, species-mixing effects were absent in growt*h-d*rought fluctuations and reactions to drought, when comparing mixed and pure stands. This is in line with studies showing that species mixing does not necessarily reduce drought stress on growth (Grossiord et al., 2014) and that physiological characteristics, in terms of water-related interactions, can be helpful for analyzing the potential complementarity of species in mixed stands (Forrester et al., 2016; Grossiord et al., 2015). Our results show an additive or selection effect (Kelty, 1992; Loreau and Hector, 2001) of sensitivity to drought when both species coexist.

Extrinsic factors or microsite conditions such as soil depth, water-holding capacity, water table depth, organic matter or nutrient content may alter drought resilience and growt*h-d*rought fluctuations in these two pines. López-Marcos et al. (2017) found higher levels of carbon stock and water holding capacity above the 50 cm soil profile in mixed and pure stands of these species. This is directly related to soil water available and would affect tree growth. The subject requires attention in future research.

5.4 Intra-annual radial growth complementarity

The intra-annual unimodal pattern for both species was confirmed using the single-Richard function fitted with dendrometer records. The result matched the intra-annual growth pattern for Scots pine observed by Camarero et al. (2010), but differed from the bi-modal pattern reported by Aldea et al. (2017) and Vieira et al. (2014) for Maritime pine in other locations. These differences could be partially explained by the annual water balance in the study area, which indicated a slight summer drought (Walter & Lieth index= 0.18, Figure 2.7) compared to the drier Mediterranean environments studied by Aldea et al. (2017) and Vieira et al. (2014). In colder mesic conditions, a bimodal pattern is less likely than in xeric sites because cambial activity is concentrated in the spring (Camarero et al., 2010). This might also explain the failure convergence of the double-Richard function, especially for the inflection point and increment rate corresponding to cumulative radial increase during the autumn.

Intra-annual cumulative radial increment functions showed species-specific patterns and intra-specific differences for some function parameters depending on stand composition (Figure 4.12). Differences in inter-specific intra-annual patterns in pure stands result from each species' particular growth strategies and responses to growth conditions. The radial growth asynchrony between species indicates temporal niche complementarity and supports the explanation of the mechanisms involved in the over-yielding observed in mixed stands (del Río et al., 2017). In both species, temperature and water availability are the main factors that determine the onset and duration of xylogenesis (Camarero et al., 2010; Vieira et al., 2014). However, their responses to climatic conditions, even intra-specific sensitivity to drought (Lara et al., 2013; Sánchez-Salguero et al., 2018), vary across the Mediterranean region (Bogino et al., 2009; Bogino and Bravo, 2008).

Species-mixing accentuated the asynchrony of intra-annual growth patterns between Scots pine and Maritime pine in mixed stands. This implies greater temporal niche complementarity than would be expected based on species behavior in monospecific stands: a multiplicative effect. Such asynchrony in intra-annual growth patterns may lead to reduced competition for resources during part of the growing season. For example, Rötzer et al. (2017) explain the intra-annual growth asynchrony between Norway spruce and European beech as temporal diversification of below-ground resource exploitation. Temporal niche complementarity in mixed stands has been also observed at inter-annual scale in different mixtures (del Río et al., 2017, 2014b).

In this study, the cumulative intra-annual radial pattern was not controlled exclusively by species identity or stand composition. Tree size determined the value of the asymptote for Maritime pine and altered the function symmetry for Scots pine, which is related to the inflection point of the intra-annual pattern. The size distribution differences between species in pure and mixed stands that were observed in *Study II* (section 5.2) could explain the effect of tree size on the intra-annual pattern.

Using results from band dendrometers to determine the timing of phenology phases can be inaccurate or misleading in some cases. For example, radial growth onset in early spring can be confused with stem rehydration after frost-induced shrinkage during winter (Turcotte et al., 2011; Zweifel and Hasler, 2000). However, studies combining xylogenesis with dendrometer measurements have described comparable radial growth patterns from both methods (Deslauriers et al., 2007; Oberhuber and Gruber, 2010; Swidrak et al., 2013), though functions relying on dendrometer data may generate greater asymptotes than functions based on cell production data (Cocozza et al., 2016).

5.5 Performance of empirical models for mixed stands

Species mixing had contrasting effects between species in both the generalized *h-d* and basal area growth models. Models adapted to mixed stands rely on data from temporally plots grouped in triplets and located along the overlapping distribution area of Scots pine and Maritime pine in the Northern Iberian Range (Figure 2.3). Mixed and pure plots covered the prevalent stand development stages, site conditions and mixing proportions in the region, and were exposed to same silviculture regime within triplets. This design is effective because it allows control of some stand conditions analogous to blocking, avoiding confounding factors at least for part of the stand development (Forrester and Pretzsch, 2015; Vallet and Perot, 2016). In this way, estimates of tree height and basal area growth would accurately represent the species interaction effects in the adapted models for mixed stands.

5.5.1 Influence of species-mixing in tree height estimation

For both species, *h-d* models described a large proportion of the variation in tree height among plots and exhibited no substantial trends in the residual that indicated bias (Figure S6). This result suggested that the selected base model (Eq. [4.1] and [4.2]) fit the data appropriately. The final fitted models for mixed species stands differed from the basic formulation of the models developed by Lizarralde et al. (2010a, 2010b) for the same species in pure stands , both included stand variables that reduced bias and increased the precision of the model estimates (Calama and Montero, 2004). Testing predictions from these new equations on an independent dataset showed modest increases in the accuracy of height estimates for trees growing in mixed and pure stands (Table 4.13 and Figure 4.13).

Species dominant height and basal area for Maritime pine and Scots pine were significant in the generalized *h-d* models. Though the same variables have already been used in several *h-d* functions for mixed species stands (Temesgen et al., 2014; Vargas-Larreta et al., 2009), the stand dominant height and total basal area are polled over all species were considered rather than species-specific values. Dominant height is important to site quality as defined by stand growth and yield capacity, while stand basal area measures competition and density (Zeide and VanderSchaaf, 2002). Particularly for mixed stands, including species-specific Ho and BA could be advantageous for modelling the more complex effects of the vertical structure compared to pure stands (Pretzsch, 2014), as well as the differential influence of the inter-specific competitive environment (Huang et al., 2009; Sharma et al., 2017). However, though other tree and stand variables such as stand age or spatially explicit competition indices may also improve the predictive capacity of the *h-d* relationships (Weiskittel et al., 2011), these were not included because they require a substantial increase in the cost of forest inventory, which restrict the practical application of the developed predictive functions.

The structure of Eq. [4.1] and [4.2] consider Ho_{sp} and rHo as complementary parameters that describe the canopy structure and species dominance in the generalized *h-d* function. Thus, Ho_{sp} defines the position of the species in the canopy and act as asymptote in the model. Meanwhile, rHo reflects the inter-specific competition environment for light in mixed stands and reducing the total height of Scots pine, as Maritime pine trees overtop Scots pine. The varying magnitude of the effects of species-mixing in the *h-d* relationship observed for other mixtures (Erickson et al., 2009; Huang et al., 2009; Thurm and Pretzsch, 2016) , suggest that the degree of differences in the *h-d* relationships might also depend on shade tolerance and stand density.

Predictions from the *h-d* models to the triplets data for both species performed better than the estimates from the available *h-d* models for pure stands (Lizarralde et al., 2010a, 2010b). Besides the inclusion of the terms that express the species-mixing effect in the structure of *h-d* models, the application of the NLME modeling approach considers the hierarchal structure of the data and increased proportion of variation in height accounted for compared to estimates from fixed-effects non-linear least squares models (Calama and Montero, 2004; Pinheiro and Bates, 2000). Increasing the accuracy of tree height estimations in mixed stands has important implications, as differences in tree morphology directly affect crown competition, stem volume, biomass production, mechanical stability and wood quality predictions.

Section 5.2 showed that changes in the vertical structure of mixed stands, compared to pure stands, resulted from species interaction rather than the simple combination of species with different traits and structural morphology. The heterogeneity in vertical structural of mixed stands has been related to over-yielding at the stand level (Section 5.2.3) or greater stand productivity than in single-species stands, which has also been observed in other studies (Dănescu et al., 2016; Pretzsch and Schütze, 2016; Vallet and Perot, 2016). These results underscore the need to generate reliable models that account for species interactions in mixed-species stand dynamics.

5.5.2 Adapting the tree basal area growth model for mixed stands

Size-symmetric and size-asymmetric competition had different effects on basal area growth rates of the two species. Maritime pine was more sensitive to asymmetric competition than Scots pine, suggesting greater sensitivity to competition for light (Pretzsch and Biber, 2010). In contrast, size-symmetric competition described with SDIR was the predominant competitive driver in Scots pine in regard to restricting tree growth and representing below-ground competition (Weiskittel et al., 2011). However, our analysis showed clearly different inter-specific competition effects on basal area growth rates for the two species. The empirical models showed that a reduction in inter-specific competition for light was only relevant for Maritime pine, whereas Scots pine growth was relatively unaffected by mixing. This competition reduction implies an increased tree growth rate for Maritime pine growing in mixture with Scots pine, compared to homogeneous pure stands. These results are consistent with the species competitive relationships observed for Maritime pine using NFI data (section 4.1.3 and 5.1.3) but diverge in the case of Scots pine. The different spatial scale of the data used in both analyses might explain these discrepancies.

Although deciphering the ecological causes of these interactions were not the aim of this section, we can suggest some possibilities. For example, species-specific plastic response of physiological and morphological traits to shade conditions (Gaudio et al., 2011; Sánchez-Gómez et al., 2006) or responses of crown plasticity to competitive pressure (Vizcaíno-Palomar et al., 2016) might be associated with light mediated interactions. Navarro-Cerrillo et al. (2016) found greater growth gain of Maritime pine over Scots pine when a change of light conditions was induced by thinning in mixed stands. However, in mixed stands with light-demanding species such as pines, the degree of differential preferences for light is probably not the single controlling mechanism in positive (Jucker et al., 2014b), negative (Liang et al., 2007) or null (Garber and Maguire, 2004) growth effects observed. Complementarity traits for securing below-ground resources, such as differences in water use efficiency (Navarro-Cerrillo et al., 2016) or growth responses to drought (Granda et al., 2018b), need special attention. These were analyzed and discussed in Sections 5.3 and 5.4.

Though site index is frequently used in growth models to account for site-related variation in inherent productivity (Wykoff, 1990), the fact that the age-dependent site index was not significant in any final basal area growth models could be advantageous. Species-specific site index equations based on stand age are usually not available for multi-species stands (del Río et al., 2016) because, as our findings confirm, interspecific competition may suppress top height growth for different stand stages in stand development (Jucker et al., 2015; Pretzsch, 2014) altering the height-age relationships and bias SI estimations (Dănescu et al., 2017; Pinto et al., 2008). Although site index based on reference diameter are available in Spain (Moreno-Fernández et al., 2018), caution is advised in their application because of inherent greater sensitivity of diameter growth to stand density relative to height growth (Wang, 1998; Weiskittel et al., 2011). This applies especially to mixed-species stands, where stand density can alter growth dynamics (Condés et al., 2013; Forrester et al., 2013; Garber and Maguire, 2004).

5.5.3 Implications for tree-level model for mixed stands

The generalized *h-d* and individual-tree basal area increment models developed in this study can be used for Scots pine and Maritime pine trees growing in pure and mixed stands. The effect of the inter-specific competitive environment was successfully represented in the structure of the models. Combining the mixed-effect models approach with parameters expressing species mixing enhanced the performance of tree height and basal area growth estimates compared to previous models that had been fitted for pure stands (Lizarralde et al., 2010a, 2010b). The superior performance of multilevel mixed models over fixed-effects models fitted to more complex sampling designs in which plots can be considered to impose random effect, has already been widely discussed in the literature (Calama and Montero, 2004; Pinheiro and Bates, 2000). However, the magnitude of variations in allometric relationships and tree growth due to species-mixing is a subject of intense debate, with evidence of adverse and positive effects that depend on multiple, simultaneously driven factors (Chamagne et al., 2017; Forrester et al., 2017; Jucker et al., 2014b; Mina et al., 2017; Pretzsch, 2014). Therefore, application of these models is restricted to the data range as well as to the Northern Iberian Range, since species-mixing effects can vary among regions. This was demonstrated by the results comparing the different spatial scales analyzed in this thesis.

The adaptation of IBERO model to mixed species stands can be used as a decision-support tool for evaluating the impact of different silvicultural options in a context of sustainable forest management. In this Section, species-specific new models are proposed for adapting *h-d* function and growth sub-modules of the tree-level IBERO model to mixed stands of Scots pine and Maritime pine in the Northern Iberian Range. Both height-diameter relationships and basal area growth equations might have greater effects on tree-level models in terms of gains or losses in productivity due to species interactions, as demonstrated in Section 5.1.3 and 5.2.3.

Obviously, other IBERO sub-modules require analysis to determine the species-mixing effects on the complete model structure and evaluate the performance of growth estimates on mixed stands simulations. Several studies have demonstrated that species mixing can have significant effects on species crown size and shape (Barbeito et al., 2017; Sharma et al., 2017), taper equations, height growth (Pinto et al., 2008; Russell et al., 2014) and mortality rates (Condés and del Río, 2015; Rathbun et al., 2010), all of which could influence mixed-species stand productivity. The IBERO site quality sub-module interrelates with a different component in the model structure and relies on age-related site index curves developed for both species in monospecific conditions. Although site index was not included in the structure of the model developed in this study, several authors have demonstrated that species interaction effects change according to site conditions (Forrester and Bauhus, 2016; Mina et al., 2017; Toïgo et al., 2015). Hence, alternative methods for evaluating site quality based on geocentric measures (Bravo-Oviedo and Montero, 2005; Bravo and Montero, 2001; Bueis et al., 2016) could be used to establish a suitable productivity index for mixed-species stands (Dănescu et al., 2017).

5.6 Synthesis

The study of mixed-stand dynamics for Scots pine and Maritime pine provided information about species interactions at different levels and scales, as well as their consequences on mixed-stand functioning and dynamics regarding to growth and yield. Analyses of the processes and components involved in mixed-stand dynamics were integrated according to the theoretical framework established in Figure 1.1. Hence, this thesis evaluated the hypothesis that species interactions and their specific functional traits produce changes in stand productivity, stand and tree structure, and tree growth dynamics compared to monospecific stands. Additionally, this work has contributed to the adaption of the tree-level IBERO model to mixed stands. Further effort is certainly needed to arrive at a comprehensive representation of mixed-stand dynamics, which would better inform evaluation of the suitability of alternative forest management strategies for promoting and maintaining mixed stands in the Northern Iberian Range.

In the following sections, the main findings are discussed to provide an overview of the effects of species interaction on the functioning of mixed stand dynamics. The research questions addressed in the different studies that compose this thesis are combined to describe how the observed species-mixing effects were linked from stand to tree level (*Study I, II* and *V*) and how tree growth dynamics were used to analyze temporal complementarity between species (*Study III* and *IV*). We highlight the uncertainty related to the results and research questions directly derived from these studies. Lastly, we look at implications for forest management and draft some recommendations for future research.

5.6.1 Linking of species-mixing effects among levels and scales

The approach established for this research confirmed the importance of combining different levels and scales in the analysis of mixed-stand growth dynamics. Results were consistent between stand and tree levels within both national and regional spatial scales analyzed. At national scale, species-mixing affected productivity at stand-level and growth at tree-level in both species (*Study I*), while at regional scale species-mixing effects were only observed for Maritime pine from tree to stand level (*Study II*). The clear discrepancies between national and regional scales could be attributed to the intrinsically greater environmental variability of NFI data compared to the triplets data used in the regional analysis. In the analysis at national scale, we did not detect a climate gradient that altered species-mixing effects on stand productivity. However, several other studies have shown that site quality and climatic conditions can change the effects of species interaction in positive or negative directions depending on the environmental gradient analyzed and the species combination (Huber et al., 2014; Mina et al., 2017; Toïgo et al., 2015). This issue requires further analysis to explore the site-dependent conditions of species interactions in relation to forest productivity for this mixture, mainly because growth of both species can vary along environmental gradients. For example, rising temperatures across the distribution range of both species in Iberian forests had more negative effects on mountain pines – like Scots pine – than Maritime pine (Gómez-Aparicio et al., 2011). Similarly, growth sensitivity was found to differ between the species observed in *Study III*. Furthermore, the method for quantifying the effects of species-mixing depends on the maximum stand density of each species, which vary along an aridity gradient in Iberian pinewoods (Aguirre et al., 2018), thereby influencing in the results between national and regional scales.

The competitive relationship between species that affected tree growth differed between the scales analyzed, in *Study I* and *II*. Species competitive responses are not constant and can vary spatially along ecological gradients in mixed stands (Pretzsch and Biber, 2010). Interestingly, our results showed that inter-specific competition and complementarity relationships co-occur, when comparing size-symmetric and size-asymmetric competition, for example. This indicates that regardless of the scale analyzed, species exhibited unbalanced competitive relationships for above-ground and below-ground resources, though the magnitude and direction of positive or negative net effects varied among levels. Additionally, climate or site conditions can modify competitive interactions between species (Ammer, 2016; Condés and del Río, 2015). Analyzing the dependence of intra- and inter-specific competition on site conditions might improve understanding of how niche differentiation and the species-specific requirements of coexisting trees can improve access to limiting site resources. This knowledge is also essential for developing tools such as climate-sensitive growth models for evaluating forest management options under different climate scenarios.

The results for species-mixing effects among levels at regional scale (*Study II and Study V*) corroborated findings from other studies (Pretzsch and Schütze, 2016; Williams et al., 2017) and support the hypothesis set in this thesis, that differences in species structural traits trigger positive interspecific effects through complementarity or competition reduction. Species-mixing increased structural heterogeneity, leading to greater productivity and over-yielding compared to neighboring monocultures of Scots pine and Maritime pine (*Study II*). Species-mixing effects at regional scale were also coherent between stand and tree level (*Study II* and *V*). Competition reduction implied an increase in tree growth and stand productivity for Maritime pine only, while growth of Scots pine remained steady and unaffected by mixing at both levels.

The findings presented in this work highlight the relevance of analyzing size distribution and canopy structure to improve understanding of how the effects of species interactions, or emerging properties from species-mixing, affect productivity and can be adequately transmitted from tree to stand level. These outcomes reinforce the idea that the ability to develop an environment of crown complementarity, attributable to both intra-specific and inter-specific differences in crown size plasticity and size-distribution differentiation, is a crucial mechanism for enhancing productivity (Ishii and Asano, 2010; Jucker et al., 2015; Pretzsch, 2014), especially in mixtures of light-demanding species.

In *Study III* and *IV*, analyses of growth patterns at inter- and intra-annual scales depicted temporal complementarity traits for resource uptake and use between species that help explain the effects of species mixing. While it is well known that water shortage during the growing season reduces secondary growth, the short- and long-term consequences of drought on forest growth and tree vigor require greater attention in the current context of climate change (Camarero et al., 2018). *Study III* short-term analysis showed the impact of dry spells on tree growth by assessing species drought tolerance and resilience to drought, whereas long-term growth trends revealed responses to continuous processes such as climate warming or decreasing water availability. Clearly, both species displayed specific long-term fluctuations and different short-term reactions of tree growth to drought, which were unaffected by species-mixing. In other words, Maritime pine trees disassembled faster from the effects of long-term drought and they recovered better dry spells than Scots pine trees. Previous studies have demonstrated an increase in drought sensitivity over the last 50 years, partially due to the carry-over effects of depleted soil water reserves and long-term morphological and/or physiological effects on plants (Lara et al., 2013), which can also trigger declines in forest productivity (Camarero et al., 2018; Prieto-Recio et al., 2015). This is especially important for Scots pine populations located near the southern-edge of species distribution, where they may face significant declines in productivity due to the more frequent and severe droughts predicted for the Mediterranean region (Sánchez-Salguero et al., 2017).

Intra-annual growth pattern variations between species revealed complementarity relationships or differentiated use of resources within the season when the two species coexist (*Study IV*). Species-mixing also modified the intra-annual growth patterns in Scots pine compared to pure stands. This accentuates the asynchrony between species, which may imply variations in phenology or physiological plasticity in the use of resources. However, this analysis only represents behavior during one growing season. Including multi-annual measurements could make it possible to test how climate variables affect change in intra-annual patterns. Extending the study to stands with different endogenous conditions (age, density, site quality) may also help to improve the accuracy of the results. Analysis of both inter-annual and intra-annual temporal scales highlighted the degree of temporal complementarity between Scots pine and Maritime pine in mixed stands. Inspection of within-season and multiannual climate variability would require extra consideration in the analysis of mixed stand dynamics for sites where such information could determine forest composition and productivity.

Altogether, these results contribute critical new knowledge to our understanding of important ecological questions and methodological approaches for the analysis of species interactions and mixed-stand dynamics in Scots pine-Maritime pine mixtures. It will also inform and assist the development of new guidelines for maintaining and managing mixed-species stands.

5.6.2 Implications for forest management and future research questions

In the Northern Iberian Range, forest management has a long tradition of promoting timber production and nature conservation, which are the most important ecosystem services for local communities. Though Scots pine wood has higher economic value and silviculture practices mainly focus on maintaining this species, the advantages associated with the complexity and diversity of mixed stands, as described in this thesis, have encouraged forest managers to demand general management standards for mixed forests. However, species-mixing and changes in structural heterogeneity may modify tree morphology, thereby altering wood quality (Pretzsch and Rais, 2016; Zeller et al., 2017). Hence wood quality is a relevant attribute that must be addressed because harvesting Scots pine provides income for landowners in the region.

Species selection and control of stand density through thinning are the main management decisions taken at strategic and operational levels, respectively. However, information regarding thinning of mixed-species stands is scarce. Traditionally, silvicultural practices in mixed stands of Scots pine and Maritime pine favored the former due to its better wood quality. In this research, the main uncertainty was related to the impact of past management on species-mixing effects, because altering stand density through thinning could increase or reduce complementary effects. Hence, future studies that describe how management practices modify interactions between species would provide a key piece to complement the development of sound management prescriptions for mixed stands.

Additionally, silvicultural regimes for mixed stands are inevitably more challenging compared with those developed for monospecific stands, and their complexity and operation cost typically increases with the compositional and stand structural heterogeneity (Bauhus et al., 2017b; O'Hara, 2014). However, tree species mixtures with similar growth rates and shade tolerance, as the species analyzed in this thesis, could require less silvicultural interventions through repeated thinning for maintaining the benefit of species interactions than for example mixtures with light- demanding species that grow slower or reach a lower maximum height than competing shade-tolerant species (Kerr, 2004). Thus, maintain the desired structure and composition of mixed stands will require similar management cost that pure stands of Scots pine and Maritime pine but potentially improving productivity and ecosystem services that might promote their implementation rather than simply considering the economic returns.

As mentioned in previous sections, other components of mixed stand dynamics that require attention include mortality, recruitment and regeneration. These processes have long-term effects and contain information for understanding the temporal development of mixed stands beyond one rotation. Defining the impact of forest management on the persistence of tree species in mixtures for longer than one rotation and the extent to which mixture transcendence requires substantial intervention to maintain species coexistence (Cordonnier et al., 2018). Long-term experiment plots would help forest managers to assess practices for maintaining mixed stands and avoiding that forest dynamics that can derive in monospecific scenarios.

Finally, this thesis corroborates the positive species-mixing effects observed for different species mixture assemblage and environmental conditions. Scots pine-Maritime pine mixed stands showed increased productivity (>10%) compared to pure stands and demonstrated greater resilience due to the temporal complementarity of the two species. Consistently, this has significant implications for forest management in the region, because maintaining and promoting mixed-species stands presents multiple benefits for the provision of ecosystem services, such as timber production and biodiversity conservation, as well as carbon storage and protection against natural hazards (e.g., drought), though the last was only additive, it constitutes an advantage over pure stands.

6. Conclusions

1. Analysis of NFI data showed an increase in productivity at stand and tree level in mixed stands of Scots pine and Maritime pine compared to monospecific stands. Species mixing produced a mutual gain in productivity at stand level for both species in mixture stands, but different tree growth responses to inter-specific competition for each species. NFI data made it possible to identify the main large-scale interactions between the two species in mixture and suggests that light competition is the main driver limiting growth.

2. Mixing species induced greater vertical structure heterogeneity and size-distribution changes in mixed stands, compared to the structural traits observed in pure stands. Differences were observed in tree crown allometry and vertical stratification in the canopy, in response to the inter-specific competitive environment. These changes result from Scots pine-Maritime pine interactions rather than the simple combination of two species with different traits and structural morphology in pure stands. In other words, the effect is multiplicative rather than additive.

3. Data from the triplets assay indicated increased relative volume productivity in mixed stands compared to pure stands. This is directly derived from the significant over-yielding of Maritime pine, whereas the relative productivity of Scots pine remained steady and unaffected by species mixing. Increased vertical structural heterogeneity in mixed stands was also related to over-yielding at the stand level.

4. Species-specific oscillations between tree growth fluctuations and drought severity over time, as well as indicator values comparing the resilience of Scots pine and Maritime pine to drought events, suggest species niche complementarity involving an efficient inter-annual use of resources. Both growth dynamics were unaffected by species interaction in mixed stands, showing that sensitivity to drought emerges as an additive mixing effect when both species coexist.

5. Cumulative intra-annual radial increment patterns for each species in pure stands result from species-specific growth strategies and responses to growth conditions. This points to potential temporal niche complementarity in intra-annual radial increment patterns between species. Species mixing also influenced intra-specific intra-annual patterns, accentuating the asynchrony between Scots pine and Maritime pine in mixed stands. The greater asynchrony of intra-annual growth patterns compared to the patterns expected for these species in monospecific stands may lead to reduced competition for resources in mixed stands during part of the growing season.

6. Integrating the variables that reflect species-mixing effects in the structure of models for estimating tree height and basal area increment in mixed stands enhanced the prediction performance compared to available models that had been parameterized for Scots pine and Maritime pine in pure stands. Both models could be incorporated into the tree-level IBERO model for estimating growth dynamics in mixed stands.

7. Finally, the results demonstrate a complexity of species-mixing effects that confirms the importance of considering different levels and scales in the analysis of growth dynamics for mixed stands. Competition and complementarity between species, as well as additive or multiplicative effects, may occur simultaneously in different aspects of mixed stand dynamics.

Conclusiones

1. El análisis con los datos de Inventario Forestal Nacional mostró un aumento en la productividad a nivel de rodal y árbol en masas mixtas de pino silvestre y pino negral en comparación con masas mono-específicas. Se observó que la mezcla de especies produce un incremento de la productividad a nivel de rodal para ambas especies, sin embargo, a nivel de árbol las respuestas del crecimiento a la competencia inter-específica fueron distintas entre ambas especies. Los datos de Inventario Forestal Nacional permitieron identificar las principales interacciones a gran escala cuando ambas especies coexisten, lo que sugirió que el principal factor limitante en el crecimiento en estas especies es la competencia por luz.

2. La mezcla de especies indujo cambios en la estructura vertical y en la distribución de tamaños en rodales mixtos en comparación con los rasgos estructurales esperados de las masas puras. Las principales diferencias en respuesta al entorno competitivo inter-específico se observaron en la alometría de la copa a nivel de árbol y la estratificación vertical del dosel. Estos cambios son el resultado de un efecto multiplicativo más que un efecto aditivo, es decir que los cambios observados en la estructura de las masas mixtas son el efecto de las interacciones entre el pino silvestre y pino negral en lugar de una simple combinación de especies con diferentes características estructurales y rasgos morfológicos.

3. El análisis de los datos de los tripletes mostró que la productividad relativa en volumen de las masas mixtas aumentó en comparación con las masas puras. Las diferencias se deben al incremento de productividad del pino negral cuando se encuentra en mezcla, mientras que la productividad relativa de pino albar se mantuvo estable en ambos tipos de masa, tanto puras como mixtas. El incremento de productividad en rodales mixtos se relacionó con el aumento de la heterogeneidad estructural vertical debido a la interacción entre especies.

4. Cada una de las especies comparadas reveló patrones específicos entre las fluctuaciones del crecimiento y la severidad de la sequía, y además mostraron diferentes valores de respuesta, recuperación y resiliencia a los

eventos específicos de sequía. La combinación de ambos resultados sugiere una complementariedad de nicho entre las especies, lo que implica un uso potencial más eficiente de recursos a escala interanual. La mezcla de especies no afectó la sensibilidad a la sequía en ninguna de los dos casos (fluctuaciones inter-anuales y respuestas específicas) y se entiende que es un efecto aditivo de la mezcla.

5. Los diferentes patrones de incremento radial intra-anual en ambas especies en las masas puras son el resultado de estrategias de crecimiento específicas de cada especie y de sus distintas respuestas a condiciones de crecimiento. Esto demuestra que las especies presentan una complementariedad potencial de nicho a escala temporal debido a patrones específicos de incremento radial intra-anual. Además, la mezcla de especies acentuó la asincronía de los patrones intra-anual de pino silvestre entre rodales puros y mixtos. Esta mayor asincronía entre especies observada en masas mixtas en comparación con los patrones esperados en rodales monoespecíficos se interpreta como una reducción de la competencia por los recursos en parte de la estación de crecimiento en rodales mixtos.

6. Los modelos de altura-diámetro e incremento de área basimétrica para ambas especies en masas mixtas incluyeron variables que reflejan los efectos de la interacción especies, esta estructura mejoró las estimaciones en comparación con los modelos disponibles para pino silvestre y pino negral parametrizados para rodales puros. Estos modelos pueden incorporarse dentro del modelo de árbol individual IBERO para simular de dinámica de crecimiento de ambas especies en masas mixtas.

7. Finalmente, los resultados demuestran la complejidad de los efectos de la mezcla de especies, y, confirma la importancia de considerar diferentes niveles y escalas en el análisis. Se destaca que las relaciones de competencia y complementariedad en la dinámica de crecimiento de las masas mixtas, así como efectos aditivos y multiplicativos debido a la mezcla de especies pueden ocurrir simultáneamente en diferentes componentes y a distintos niveles.

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8. Appendix

8.1 APPENDIX A: Peer-reviewed articles

As output of this thesis, two original articles were published in SCI journals, one congress proceeding and two more manuscripts in preparation:

— **Riofrío, J.**, del Río, M., Bravo, F., 2017. Mixing effects on growth efficiency in mixed pine forests. *Forestry* 90, 381–392.

— **Riofrío, J.**, del Río, M., Pretzsch, H., Bravo, F., 2017. Changes in structural heterogeneity and stand productivity by mixing Scots pine and Maritime pine. *For. Ecol. Manage*. 405, 219–228.

— **Riofrío, J.**, del Río, M., Maguire, D., Bravo F. Generalized height-diameter and basal area increment models for mixed stands of Scots pine and Maritime pine. *Submitted*.

— **Riofrío, J.**, del Río, M., Aldea, J., Bravo, F., 2017. Relaciones de complementariedad en masa mixtas de pinos mediterráneos: un análisis de los patrones de incremento radial intra-annual, in: Sociedad Española de Ciencias Forestales (Ed.), 7º Congreso Forestal Español. Plasencia.

— **Riofrío, J.**, Lara, W., Bravo, F., del Río, M. Long term responses and tree growth sensitivity to drought in mixed pines stands. *In preparation*.

8.2 APPENDIX B: Supplementary figures

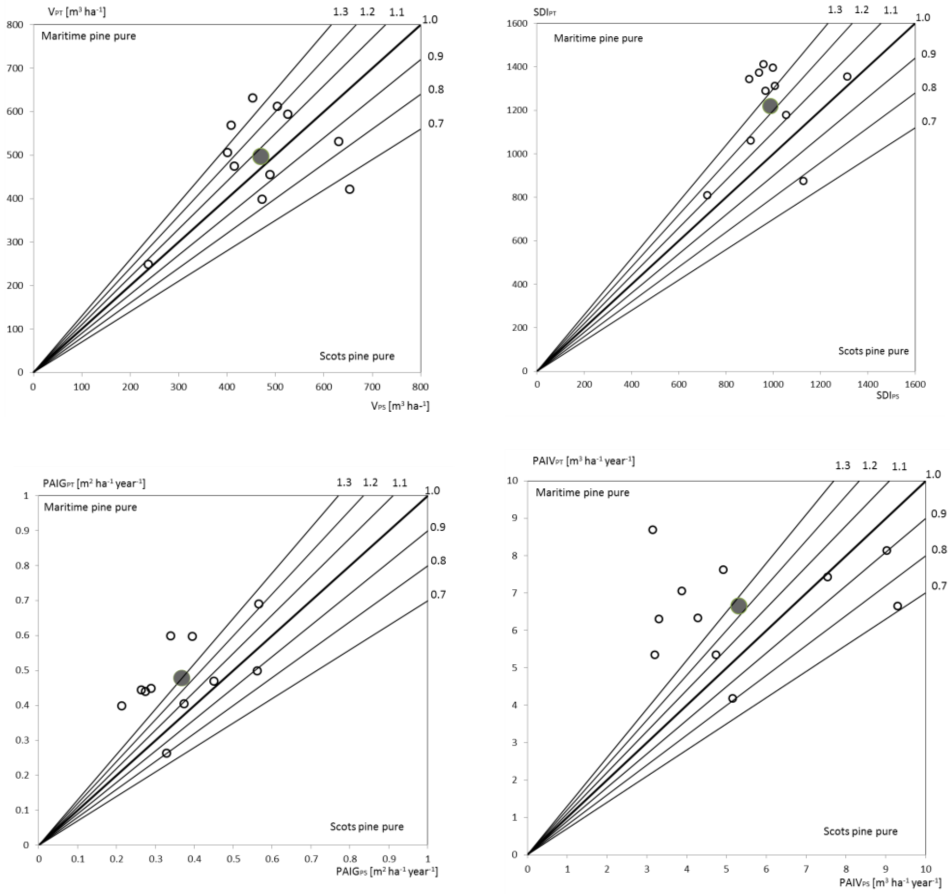

Figure S1. Comparison of main stand traits for pure Scots pine (x-axis) and pure Maritime pine stands (y-axis). Values closer to the bisector line indicate greater equality of pure-stand traits for both species. White circles represent observed values and the large gray circle indicates the mean values of all triplets.

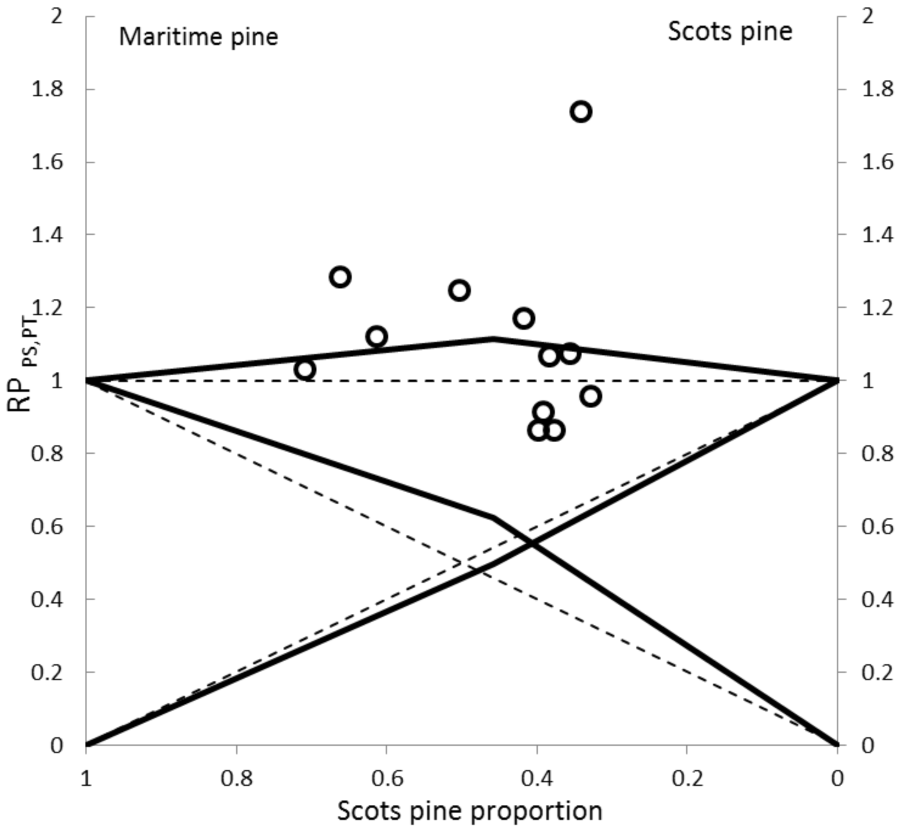

Figure S2. Cross diagram showing the mixing effect on relative productivity for annual volume increment for Maritime pine and Scots pine and total mixed stand in relation to the productivity of the neighboring pure stands. The points represent the observed relative volume productivity of mixed versus pure stands. The left (Maritime pine) and right (Scots pine) ordinates in the cross diagrams represent species relative productivity (RPPS,(PT) and RP(PS),PT) and the abscissa the mixing portion of Scots pine (mPS,(PT)). Solid lines indicate growth in mixtures and the corresponding broken lines show the expected growth in monocultures. The upper lines show whole stand and crossing lines species-specific productivity.

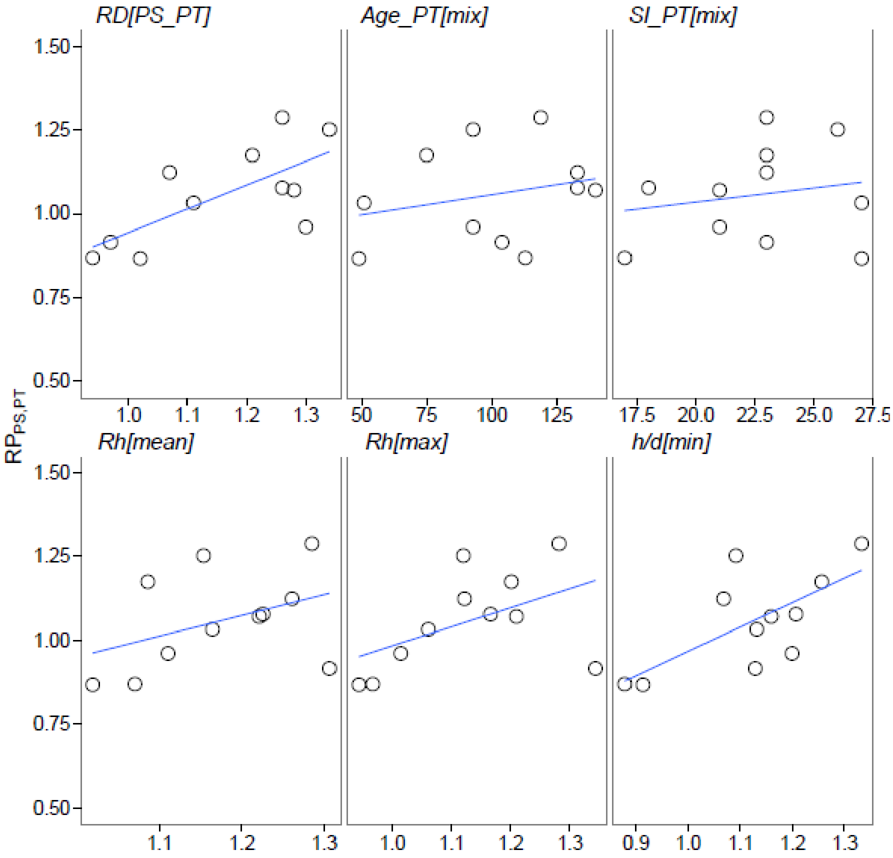

Figure S3. Relationship between relative productivity at stand level ($RP_{PS,PT}$) and relative stand density ($RD_{PS,PT}$), age and site index for *P. pinaster* in mixture, and selected ratios (Rd_{mean}, Rd_{max}, and Rh/d_{min}) indicating the multiplicative mixing effect for Maritime pine at the species level.

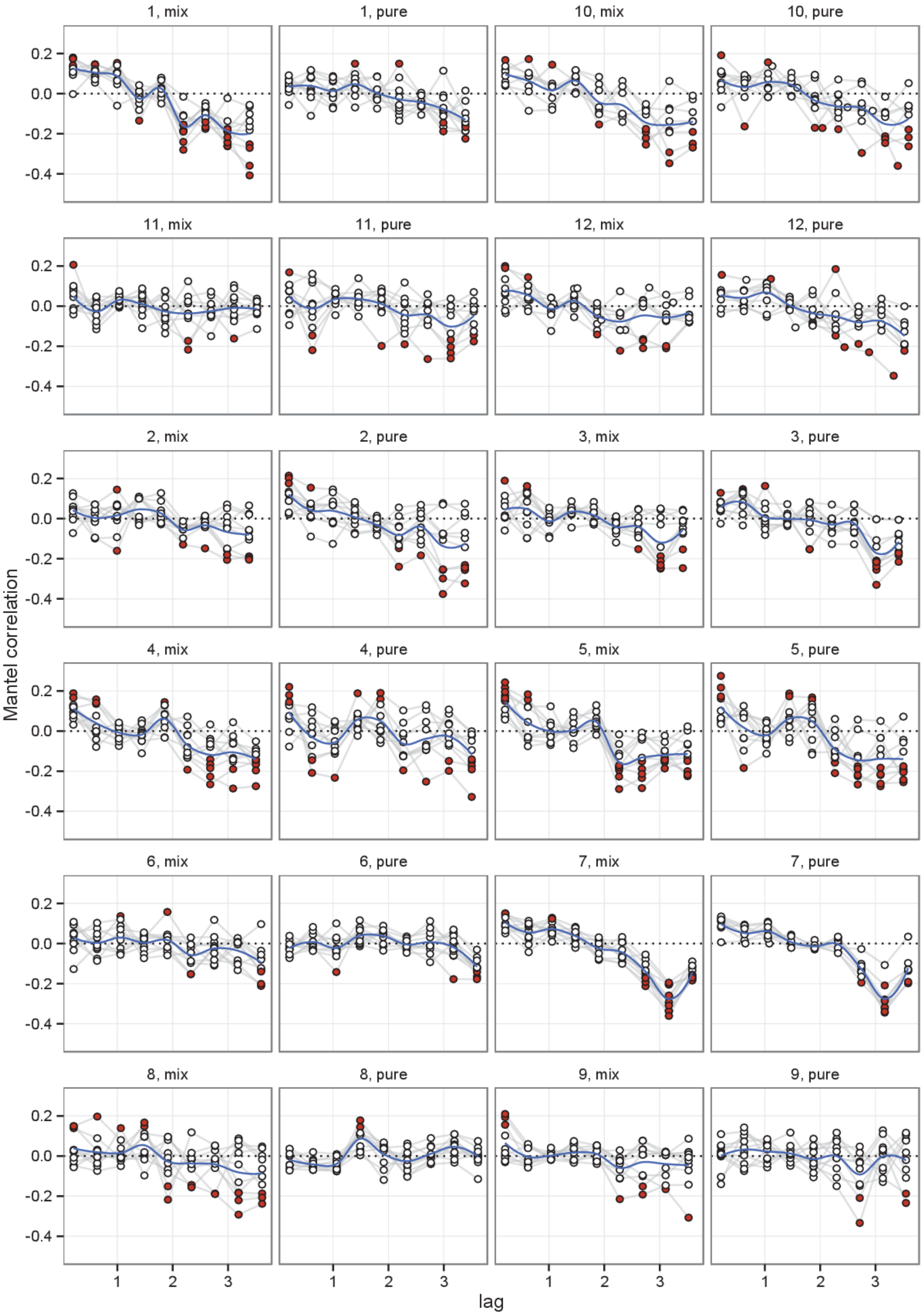

Figure S4. Mantel correlograms showing the extent of temporal similarities between of rBAI and SPEI along distance classes (lag) for Scots pine in mixed and pure stands by triplets (number above each panel plot). Filled and open symbols indicate the significant and non-significant Mantel statistic ($p < 0.05$). Blue line illustrated the overall pattern.

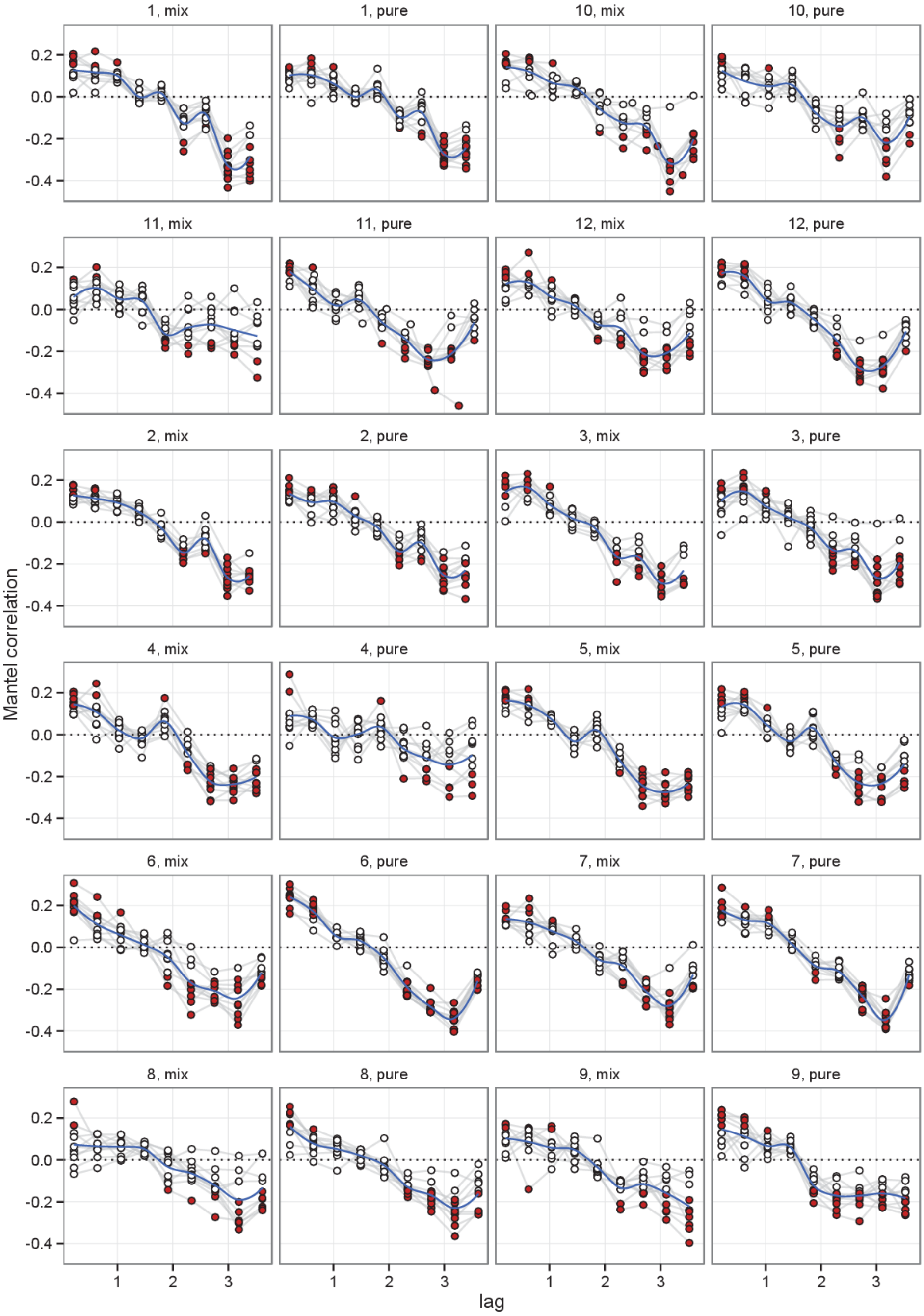

Figure S5. Mantel correlograms showing the extent of temporal similarities between of rBAI and SPEI along distance classes (lag) for Maritime pine in mixed and pure stands by triplets (number above each panel plot). Filled and open symbols indicate the significant and non-significant Mantel statistic ($p < 0.05$). Blue line illustrated the overall pattern

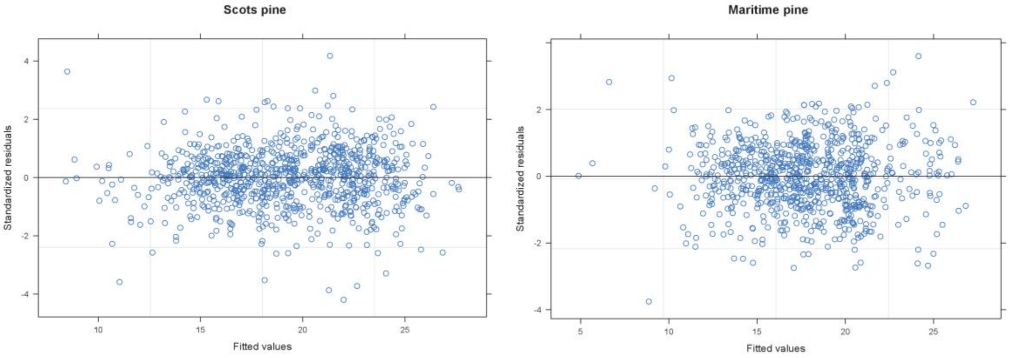

Figure S6. Standardized residuals of generalized non-linear mixed-effects *h-d* model (Eq [4.1] and [4.2]).

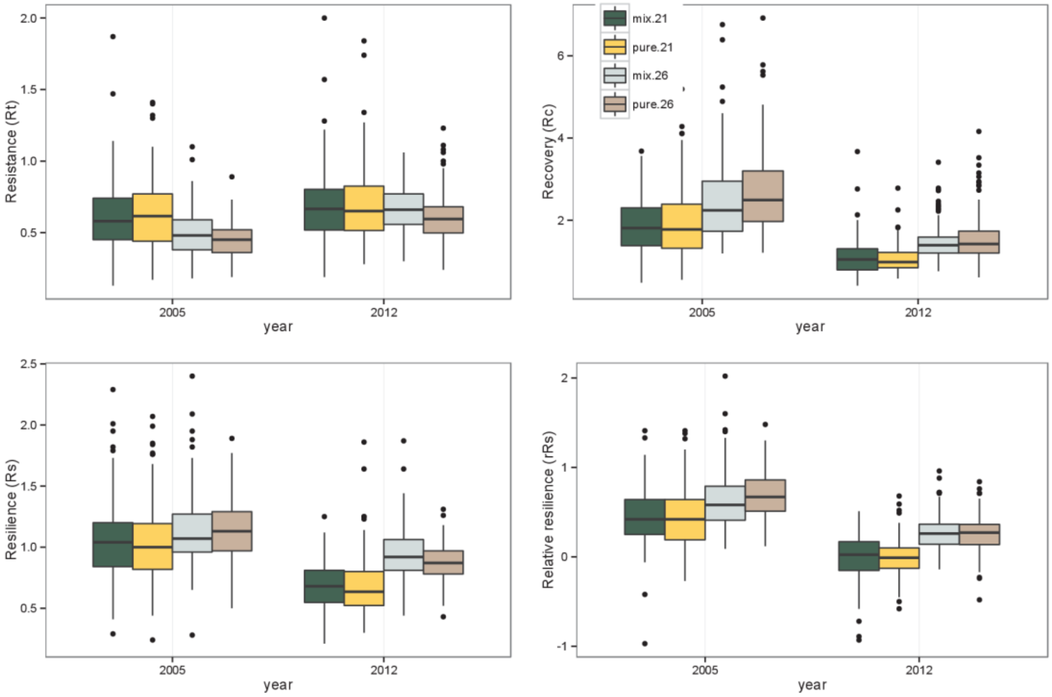

Figure S7. Comparison of growth responses to drought at tree level (Rt, Rc, Rs and rRs) between species growing in pure stands vs. mixed stands for each drought event. Green boxes for Scots pine (21) in mixed stands, yellow boxes for Scots pine in pure stands, grey boxes for Maritime pine (26) mixed stands and brown boxes for Maritime pine in pure stands.

8.3 APPENDIX C: Supplementary tables

Table S1. Estimated parameters (standard error) for fixed effects and variance components of random effects models to detrending basal area increments (BAI) using the restricted maximum likelihood method.

	Fixed effects		**Variance components (σ^2)**		
Specie	**Parameter**	**value**	**core**	**tree**	**plot**
Scots pine	intercept	-1.2980 (0.120)	0.000	0.021	0.114
	log (g)	0.6470 (0.027)	0.000	0.000	0.000
	(time)	-0.0227 (0.002)	0.000	0.000	0.000
	Error		0.000		
Maritime pine	intercept	-0.5610 (0.099)	0.0029	0.001	0.043
	log (BA)	0.6512 (0.028)	0.000	0.000	0.000
	log (time)	-0.4602 (0.023)	0.000	0.002	0.003
	Error		0.000		

g is the tree basal area. σ^2 is the variance component for the random effects at plot, tree nested in the plots (tree) and core nested in tree that are nested in the plots (core). Error is the residual variance σ^2.

Table S2**.** Results from the linear mixed models of the effect of stand composition on resistance Rt, recovery Rc, resilience Rs and relative resilience rRs indices for both species trees growing in mixed and pure stands. Significant parameters of covariates and species reference group (pure stands) for each model are shown in bold characters (p <0.05).

	Maritime pine		**Scots pine**	
	2005	**2012**	**2005**	**2012**
Resistance				
Intercept	**0.472**	**0.631**	**0.612**	**0.691**
pure stand				
dbh				
Age				
SI				
ΔAICc	7.397	7.258	10.165	8.785
Recovery (ln)				
Intercept	**0.886**	**0.374**	**0.575**	**0.015**
pure stand				
dbh				
Age				
SI				
ΔAICc	8.411	5.998	7.569	3.611
Resilience				
Intercept	**1.125**	**0.939**	**1.536**	**0.686**
pure stand		**-0.078**		
dbh			**-0.001**	
Age				
SI				
ΔAICc	1.620	5.143	7.817	5.766
Relative resilience				
Intercept	**0.654**	**0.269**	**0.915**	**-0.005**
pure stand				
dbh			**-0.001**	
Age				
SI				
ΔAICc	6.680	6.613	7.777	1.614

Table S3. Ranking and summary statistics for generalized height–diameter models fitted without considered the mixture effects for both species.

Scots pine				Maritime pine			
Model	**AICc**	**ΔAICc**	**EF**	**Model**	**AICc**	**ΔAICc**	**EF**
Michailoff II	7634.26	0.00	0.812	Michailoff I	6703.76	0.00	0.843
Rio I	7641.63	7.37	0.810	Michailoff II	6720.76	17.00	0.840
Michailoff I	7641.84	7.58	0.809	Rio I	6751.37	47.61	0.835
Cañadas IV	7661.39	27.12	0.805	Rio	6754.79	51.03	0.833
Rio	7675.60	41.34	0.803	Cañadas IV	6759.01	55.25	0.833
Schöder & A	7730.77	96.51	0.791	Schöder & A	6782.37	78.61	0.828
Cañadas I	7867.34	233.08	0.755	Cañadas II	6894.58	190.82	0.802
Cañadas II	8010.04	375.78	0.712	Cañadas I	6946.94	243.18	0.788
Cox	8342.36	708.10	0.585	Cox	7297.56	593.80	0.677
Cañadas III	8907.57	1273.31	0.218	Cañadas III	7573.10	869.34	0.545

AICc: Second-order Akaike Information Criterion; ΔAICc: difference between the best model and the ith model, EF: model efficiency.