



Universidad de Valladolid



PROGRAMA DE DOCTORADO EN CONSERVACIÓN Y USO  
SOSTENIBLE DE SISTEMAS FORESTALES

DOCTORAL THESIS:

**Dynamics of *P. pinea* and *P. pinaster* forests:  
Implications for adaptive management in a  
climate change context**

Presented by Marta Vergarechea  
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Dr. Rafael Calama

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TESIS DOCTORAL:

**Dinámica de los bosques de *P. pinea* y *P. pinaster*: implicaciones para el manejo adaptativo en un contexto de cambio climático**

Presentada por Marta Vergarechea para optar al grado de doctora por la Universidad de Valladolid

Dirigida por:  
Dra. Miren del Río  
Dr. Rafael Calama

2020





*“La imaginación -también lo decía Borges- “está hecha de convenciones de la memoria” y por eso crear consiste principalmente en copiar, repetir, recombinar... en apropiarse de todo un bagaje cultural previo y, sólo a veces, lograr hacer brillar algo que no estaba allí ya.”*

Almudena M. Castro



Para el desarrollo de la tesis doctoral, la autora ha contado con una beca predoctoral del Programa de Formación de Personal Investigador (FPI) del Ministerio de Economía Competitividad (Ref. ayuda: BES-2015-073943). Esta tesis se ha realizado bajo la supervisión de la Dra. Miren del Río y el Dr. Rafael Calama, dentro del Departamento de Dinámica y Gestión Forestal del Centro de Investigación Forestal del Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA-CIFOR).

El proyecto dentro del cual se enmarca la tesis doctoral lleva como título “Complejidad y Sostenibilidad en bosques mixtos: dinámica, selvicultura y herramientas de Gestión Adaptativa”.

Finalmente, indicar que la autora opta con la presente tesis al título de Doctora dentro del programa de doctorado “Doctorado en Conservación y Uso Sostenible de los Sistemas Forestales”.

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## Abstract

Over the last decades, climate change has been particularly severe in the Mediterranean basin, where the intensity and frequency of drought events had a significant effect on forest dynamics. As a consequence, tree allometry is modified, reducing tree and stand growth, provoking tree or stand decay and dieback and altering plant recruitment. In this context, differences in structural and physiological strategies of tree species, could mitigate the damage inflicted by climate change and reduce risk. Programs aiming to adapt forests to climate-changing conditions should take profit from the knowledge of these strategies, and propose a set of actions oriented to emulate or enhance the inherent capacity of the forest for adaptation. Between these actions, this thesis highlights the promotion of natural regeneration or the increase of intra and interspecific diversity. A most diverse ecosystem could help to reduce vulnerability and increase resistance against the lack of water availability. In addition, tree species interactions could lead to complementary effects during low-growth years by the optimization of resources.

This thesis provides a variety of methodologies based on analyzing how different factors control the response dynamics of *P. pinea* and *P. pinaster* in mixed and monospecific Mediterranean forests throughout stand development, from regeneration to adult stages. The main hypothesis was that species responses, could help to cope with climatic variability and that the composition, mixed or monospecific, could attenuate these responses. The thesis used data from a network of 1936 plots of 0.02 ha to study natural regeneration, and a network of 75 mixed and monospecific temporal plots on adult stands, both installed in the Northern Plateau of Spain. In this last group of plots, the use of tree-ring width series permitted us to evaluate species-mixing effects on inter-annual and intra-annual tree growth dynamics.

The study of natural regeneration showed that regeneration of *P. pinea* was more successful than that of *P. pinaster* over the whole studied period, at both seedling and sapling stages. We found that *P. pinaster* regeneration was associated with conspecific adult trees, while the relationship between *P. pinea* regeneration and adult trees varied depending on the regeneration development stage, i.e., seedling or sapling. Furthermore, the presence of mixtures of adult trees enhanced the natural regeneration in both species. On the other hand, we observed that while seedlings occurrence was more conditioned by the annual climate, saplings establishment were more conditioned by site conditions. Here, the maximum summer temperature was the climate variable which had the greatest influence on natural regeneration, especially in *P. pinaster*.

Different attributes of the adult stands of *P. pinea* and *P. pinaster*, such as age, size, composition as well as the stand density seem to act synergistically and compensate drought stress in different ways. Here, larger and/or older trees often appear more prone to drought impacts, especially in the case of *P. pinaster*. The comparison between the interspecific - synchrony in growth in mixed composition and monospecific composition showed the existence of interrelationship between both species in these mixtures. Thus, we observed that species exhibited an unbalanced competitive relationship for aboveground and belowground resources, and while *P. pinea* is mainly controlled by intraspecific competition, especially by the size-asymmetric competition, *P. pinaster* is strongly competing with *P. pinea* for below resources.

The findings obtained in the present thesis could help to identify problematic areas with regard to natural regeneration. Here, the appropriate management of forest could make a significant contribution, such as maintaining the appropriated stand density along with the different ontogeny states. Similarly, the control of stand structure or the increase in stand heterogeneity (i.e. size, age, and species) could result in increased resistance and resilience to

climate change for both *P. pinea* and *P. pinaster*, as well as a reduction in the competitive status.





## Resumen

Durante las últimas décadas, el cambio climático ha sido particularmente severo en la cuenca Mediterránea, donde la intensidad y la frecuencia de los eventos de sequías ha afectado significativamente a la dinámica de los bosques. Como consecuencia, se ha modificado la alometría de los árboles, reduciendo el crecimiento tanto de los árboles individuales como de los rodales en su conjunto, provocando la muerte de los mismos y afectando al reclutamiento de nuevos individuos. Bajo esta situación, las diferentes estrategias estructurales y fisiológicas de las especies arbóreas podrían mitigar el daño y reducir los riesgos ocasionados por el cambio climático. Los programas orientados a adaptar los bosques a estas nuevas condiciones climáticas, deben aprovechar estas estrategias y promover un conjunto de acciones orientadas a emular o a promover la capacidad inherente que tienen los bosques para adaptarse a estas condiciones cambiantes. La presente tesis destaca alguna de estas acciones, como la promoción de la regeneración natural o el aumento de la diversidad intra e interspecifica. Se sabe, que un ecosistema más diverso podría ayudar a reducir la vulnerabilidad y aumentar la resistencia, por ejemplo, ante la falta de disponibilidad de agua. Además, las interacciones entre las especies arbóreas podrían generar efectos complementarios durante los años de bajo crecimiento mediante la optimización de recursos.

De esta manera, presentamos una variedad de metodologías enfocadas en analizar como diferentes factores controlan la dinámica de las respuestas de *P. pinea* y *P. pinaster* en bosques Mediterráneos mixtos y monoespecíficos a lo largo de diferentes estados de desarrollo del rodal, es decir, desde la etapa de regeneración hasta la etapa adulta. El hecho de que las respuestas de las especies pueden ayudar a hacer frente a la variabilidad climática era la hipótesis principal manejada, sin embargo también esperamos que la composición, mixta o el monoespecífica, pudiera atenuar estas respuestas. Para ello utilizamos datos de una red de 1936 parcelas de 0.02 ha para estudiar la regeneración natural, y una red de 75 parcelas temporales, mixtas y monoespecíficas, instaladas en el norte de la meseta de España. En este

último grupo de parcelas, se evaluó también el efecto de la mezcla de especies en la dinámica interanual de crecimiento de los árboles a través del uso de series de ancho de anillos.

A través del estudio de la regeneración natural pudimos observar que durante todo el periodo estudiado la regeneración de *P. pinea* siempre tuvo más éxito que la regeneración de *P. pinaster*, tanto en la etapa de plántula como en la etapa de regeneración avanzada. Observamos que la regeneración de *P. pinaster* se asoció principalmente a la presencia de árboles adultos conspecificos, mientras que la relación entre la regeneración natural de *P. pinea* con los árboles adultos varió en función de la etapa de desarrollo de la regeneración. Sin embargo, en ambos casos, la presencia de mezcla de especies en el estrato arbóreo mejoró la probabilidad de regeneración natural. Las características del clima anual condicionó principalmente la presencia de plántulas, aquí, se encontró que la temperatura máxima de verano fue la variable que más influenció (negativamente) sobre la regeneración natural, especialmente en el caso *P. pinaster*. El regenerado avanzado, por el contrario, estuvo más condicionado por las condiciones del sitio.

A lo largo de la tesis, se ha observado que diferentes atributos de los rodales de *P. pinea* y *P. pinaster*, como la edad, el tamaño, la composición o la densidad, parecen actuar de forma sinérgica y compensar el estrés por sequía de diferentes maneras. Así los árboles más grandes y/o más viejos a menudo parecen más propensos a los impactos de la sequía, especialmente en el caso de *P. pinaster*. Los resultados de la sincronía interespecifica, que comparó el crecimiento en composición mixta y en composición pura, mostró la existencia de relaciones entre ambas especies en mezclas. También observamos que las especies mostraron una relación competitiva desbalanceada en relación a los recursos disponibles. De esta forma, los individuos de *P. pinea* están controlados principalmente por la competencia intraespecífica, especialmente por la competencia asimétrica, mientras que los individuos de *P. pinaster* compiten fuertemente con *P. pinea* por los recursos hídricos.

Los resultados obtenidos en la presente tesis podrían ayudar a identificar áreas problemáticas con respecto a la regeneración natural. En este caso, el manejo apropiado del bosque podría contribuir de manera significativa, por ejemplo, mediante el mantenimiento adecuado de la densidad del rodal durante las diferentes etapas ontogénicas de las especies. De la misma manera, el control de la estructura de los rodales o el aumento de la heterogeneidad de los mismos (es decir, tamaño, edad y especies) podrían conllevar una mayor resistencia y resiliencia al cambio climático de las especies, así como una reducción en el estado de competencia de las mismas.



## 1. Introduction

### *1.1. Climate change and its effects on forest ecosystems*

Many of the projected future changes in climate are likely to have a negative impact on forest systems (Keenan, 2015). The increase in air temperatures and the change in precipitation regimes are the main threats affecting the long-term persistence of the forests as well as the individuals that compose them. As a consequence of the drier and warmer climate, many forests around the world are changing their dynamics and composition (Trenberth et al., 2014) and although these projections may be positive for some species in specific locations where higher temperatures extend the growing season and benefit tree growth (Pretzsch et al., 2014), most of the forecasted future changes are likely to have negative consequences for forests ecosystems (Keenan, 2015).

Among the different bioclimatic regions, the Mediterranean region is considered one of the most vulnerable to climate change (Palahi et al., 2008). The role of water as a limiting resource is the main aspect determining the vulnerability of the Mediterranean ecosystem. In addition, studies available to date project large increases in the frequency, duration, and severity of droughts in the Mediterranean area, involving potential risk to forest species (Trenberth et al., 2014). These climatic trends will make Mediterranean forests more vulnerable to these extreme events. For this reason, the way in which forest dynamics are changing as climate changes has become one of the main scientific issues over recent decades.

Drought is a complex multi-dimensional climatic phenomenon with a significant effect on social and natural systems (Mishra and Singh, 2010; Obasi, 1994), causing forest disequilibrium. As a consequence of severe droughts tree growth decreases, often triggering tree dieback, plant recruitment is frequently limited, and susceptibility to biotic damages increases, which results in forest decline (Lloret et al., 2004; Trenberth et al., 2014). Additionally, due to the close succession of drought events, it is expected that the impact on

forest ecosystems will be greater than that of other factors that involve more gradual shifts (Jentsch and Beierkuhnlein, 2008; Lindner et al., 2010).

In the Mediterranean region, extended droughts will exacerbate moisture limitations leading to decreased forest regeneration while negatively affecting tree growth and inducing species die-off (Halofsky et al., 2018; Restaino et al., 2016). In this regard, widespread die-off of many tree species as a consequence of increasing temperatures and/or water stress has recently been observed in certain regions (Vilà-Cabrera et al., 2018). However, in some instances, it can be very difficult to interpret the patterns of drought-related impacts, due to the lagged responses in some species, with mortality often occurring years or decades after drought stress events (Allen et al., 2010).

Forest species display different strategies to cope with climate stress which result in different sensitivities and, therefore, different vulnerability to drought and climate variability (Martínez-Vilalta et al., 2012; McDowell et al., 2008, 2013). Differences in structural and physiological acclimation of tree species, such as xylem anatomy (e.g. vessel/tracheid area and length), plant allometry (e.g. ratio between evaporative/conductive or aboveground/belowground structure), stomatal behavior or rooting strategies (e.g. rooting depth, rooting forms) can help to mitigate drought-induced limitations or growth reduction (Grossiord, 2019). Furthermore, positive interactions between several cohabiting tree species could help different species to cope with drought events (Lebourgeois et al., 2013; Pretzsch et al., 2013; Pretzsch et al., 2014). Other factors, such as tree size, the competitive status of the tree in terms of stand stocking, age, or site conditions also modulate the response of trees to drought (Lloret et al., 2011; Merlin et al., 2015). All the above factors can also act synergistically and may be dynamic; varying with changes in stand characteristics, resource availability or climate conditions (Belote et al. 2011). Management strategies that result in adjustments in response to exposure to stress have been conceived as 'adaptation' (Smit and Wandel, 2006). Consequently, different perspectives have been considered as regards the adaptation of forest ecosystems to these

changing and uncertain future conditions, such as mitigation of the impact of climate-related events or the increase in resilience and capacity of forest ecological systems to recover from climate "shocks".

### ***1.2. Adaptation strategies***

Several authors emphasize the vulnerability of forest ecosystems to climate change. The main manifestations of this vulnerability, as identified by different authors, are reduced growth rates (Bravo-Oviedo et al., 2010; Cailleret et al., 2017), increased disturbances due to fire and pests (Robinet et al., 2014), substitution and extinction of species (García-Valdés et al., 2015), reduced regeneration success (Manoso et al., 2014b), changes in wood quality and quantity (Solomon et al., 1995) or increased competition from exotics (García-Valdés et al., 2015).

Adaptation constitutes one of the main strategies for coping with climate change (IPCC, 2014), and includes a whole set of measures and actions aimed at minimizing the potential negative effects of climate change on the systems, reducing vulnerability and increasing their resistance and resilience in the presence of changing conditions (Calama, 2017). In this context, tree species responses are always dynamic, adapting to their local conditions and involving mechanisms to deal with the vagaries of natural climate. However, with only a few generations or often only one generation per century, this inherent adaptation capacity of tree species may be too slow to successfully respond to the present rapid rate of climate change (Allen et al., 2010). Through the application of different adaptive actions, forest managers have the opportunity to mitigate the effects of climate change and adapt forests to that change (Spittlehouse and Stewart, 2003). These adaptive actions must take into account the risk and probability of the occurrence of the different expected impacts. It is important that signs of the occurrence of such impacts are recognized at an early stage and therefore it is necessary to develop models capable of predicting the expected impacts on the systems and to have adequate, accessible tools for monitoring both the climate and the impacts on forests (Swanston and Janowiak, 2012). Besides, in the application of such measures, it is important to

take advantage of the processes of autonomous adaptation inherent in forest systems, which should be encouraged. For this reason, some authors recommend that forest managers should promote measures that facilitate adaptation through natural processes (Colombo, 2008).

Consequently, different adaptation strategies have been considered in order to adapt forest ecosystems to climate change. For instance, Calama et al (2017) highlight the need to take advantage of the natural dynamics of regeneration, promoting the growth of groups of advanced regeneration. As observed in several cases, changes in the composition of mature forests could also guarantee the persistence of the ecosystem by aiding regeneration processes. Other authors have noted that high intra and interspecific diversity allows the forest ecosystem to recover more quickly than monospecific forests following the occurrence of disturbance events (Grossiord, 2019). A more diverse ecosystem provides a greater guarantee of recovery, for example, where phenomena of decay occur in adult woodland as a response to drought events (Jactel et al., 2009), this situation being particularly common in Mediterranean forests. In fact, the application of thinning regimes in these Mediterranean ecosystems has been found to reduce vulnerability and increase resistance against the most limiting stress factor, the lack of water availability. In this case, thinning allows the water resource to be optimized by regulating the inter and intraspecific competition (Lindner and Calama, 2013; Vericat et al., 2012). Above all, under a scenario of continuous change, adaptive actions need to be flexible enough to incorporate new information and perspectives on the future climate and forest vulnerability (Spittlehouse and Stewart, 2003). In the following sections, three key aspects for developing adaptive strategies are revised with special emphasis on Mediterranean forest systems: regeneration, species resilience to climate events, and effects of mixing species forest resilience.



### **1.2.1 Forest natural regeneration**

According to Colombo (2008) and Kolström et al. (2011) the promotion of natural regeneration can be used as a strategy to facilitate species adaptation to climate change since, as long as the species-specific properties allow it, the natural regeneration of native tree species offers the best guarantee for the evolutionary development of genetic information (Spathelf, 2010). Thus, over recent years, the proposed silvicultural practices have been aimed at natural regeneration (Finkeldey and Ziehe, 2004) in order to achieve high genetic variation in forests. In this context, the future ecological conditions present a challenging scenario in terms of implementing appropriate management practices to sustain current and future tree regeneration. In this regard, the success of natural regeneration depends on the individual success of different, well-defined and sequential stages, such as seed dispersal, predation, germination, emergence and establishment (Calama et al., 2017; Manso et al., 2014a). During this process, the ontogenetic developmental stages, in which natural regeneration is recognized and identified (e.g. seedling or sapling), are influenced differently by the vegetation structure, species composition and functional attributes (Walker et al., 2007). In this context, the species-specific requirements and limitations (light, site and climate conditions, competition, etc.) play a key role, which may explain the success of the regeneration of one species compared to the others and subsequent shifts in the specific composition of forest stands.

Thus, it is essential to take into account the species-specific regeneration strategies (the degree of shade tolerance, water use efficiency or resistance to drought of the species) in order to determine how silvicultural treatments contribute to and interact with the regeneration process (Stancioiu and O'hara, 2006; Webb and Jarrett, 2013; Yoshida et al., 2005). In those areas, such as the Mediterranean region, where the establishment of natural regeneration is expected to be less successful due to climate change, this knowledge may be crucial. For instance, it has been observed that the role of tree canopy protection will be more

important as the climatic conditions become more stressful, especially in extremely dry, hot summers (Valladares et al., 2005). It has also been well documented that some species require a progressive release of overstory cover, probably due to an increase in light requirements (Manso et al., 2014b). However, to promote favorable conditions for the occurrence and development of natural regeneration and to reduce risks, the exact moment at which these silvicultural treatments must be applied varies depending on the species, site and climate conditions (Calama et al., 2017). Therefore, the modeling of these responses to ecological drivers, such as incoming light, temperature, etc. can be useful to improve management methods and expand our understanding of the regeneration processes of tree species.

Modeling of natural regeneration has mainly been addressed using two different approaches (Kolo et al., 2017): (i) Recruitment models, which evaluate the established regeneration as a function of the environmental characteristics (Eerikäinen et al., 2007; Fortin and DeBlois, 2007); and (ii) Multistage models, which consider regeneration as a multistage process consisting of underlying consecutive sub-processes –flowering & fruiting, seed dispersal, predation, germination and survival (Manso et al., 2014a; Ordóñez et al., 2006; Pukkala and Kolström, 1992). While the usefulness of these models has been widely demonstrated, current environmental concerns, as well as new management challenges related to global change, species interactions, and larger management scales, demand the development of new modeling tools (Costanza et al., 1990). These models should allow the integration of new tangible information at larger scales that can be used by managers to examine more complex, spatial scientific questions (Mladenoff, 2004). Through the re-measurement of permanent sample plots, regeneration occurrence can be defined as the number of new seedlings that emerge in a specific plot within a given time interval. For instance, modeling the probability of regeneration at large scales could be used to define new strategies for regional conservation and management planning. Survival or lifetime analyses comprise many methods for modeling the probability of occurrence of a particular event after time  $t$  (Lawless, 2003). In addition,

survival models allow us to predict the probability of regeneration occurrence when the exact date of the regeneration occurrence is unknown and data records are compiled in annual-intervals, minimizing uncertainties in the estimation process (Yu et al., 2013). Hence, it is necessary to use an annual resolution to evaluate the effect of climate on the regeneration process.

### ***1.2.2. Species-resilience and changes associated with climate variability in *P. pinea* and *P. pinaster* stands***

Maintaining forest resilience has been also identified as an important mechanism to mitigate and adapt to climate change (Chapin et al., 2007; Millar et al., 2007) since it is related to the capacity of an ecosystem, community or individual to absorb disturbances and reorganize so as to retain, essentially, its pre-disturbance structure and functions (Lloret et al., 2011). Currently, there is a general interest in understanding the mechanism associated with resilience, as it relates to the way in which forest ecosystems respond to disturbances and climate change (Kinzig et al., 2001; Scherer-Lorenzen et al., 2005). As it has been observed, when species interactions help to reinforce each other and to reduce the impact of disturbances over time, ecosystems are both temporally and spatially resilient. This condition can be achieved through a range of mechanisms, for example, offsetting differences among species (Thompson et al., 2009).

The effect of climate, and especially of droughts, on forest systems may last for several years, since dry conditions reduce tree growth and often weaken trees by deteriorating their vigor (Camarero et al., 2018). This fact could mean that forest stands may change continuously as a result of small-scale periodic disturbances, or they may change considerably owing to severe disturbances.

In addition, the legacy of past land-use policies and practices may exacerbate the impacts of drought on forests (Vernon et al., 2018) and lead to dieback due to continuous drought-induced conditions (Gazol et al., 2018). Inadequate management, such as focusing on the negative selection of slow-growing trees (more vulnerable to recent droughts), could lead to a

greater predisposition of the species to decay. Fortunately, during recent years, forest management goals have shifted more generally towards enhancing ecosystem resilience (Nocentini et al., 2017).

The analysis of tree growth based on annual rings provides a suitable approach for reconstructing the long-term effects of environmental variables on growth (González de Andrés et al., 2018), along with a record with annual resolution of growth response to climate, which is also highly useful for the study of past known disturbances such as drought events (Fang and Zhang, 2019). The combination of long and short-term temporal studies, taking into account the role of different factors, like composition, tree size, age and density on annual growth, could provide valuable insight into the species-specific responses to stress events and strategies to adapt forest management to climate change.

### ***Forest growth responses to climate at short-term scales***

In response to disturbances, the ecosystem may shift to a different state, and this new state may or may not supply the same goods and services as the original state (Thompson et al., 2009). Therefore, analysis of resilience generally involves quantitative estimations which are mainly based on comparisons between pre and post-disturbance states (DeClerck et al., 2006; Orwin and Wardle, 2004). In the quantification of forest resilience, three basic aspects have been considered in order to assess specific responses to extreme events: resistance, recovery, and resilience (Grimm and Wissel, 1997). These three aspects can be evaluated through several indices using ring-width data from individual trees (Lloret et al., 2011), and may be used to infer the underlying patterns of the adaptation mechanisms of tree species. In this way, the resistance of trees to drought is determined as the ratio between growth during the drought and growth during the respective pre-drought period. The ratio between the post-drought growth and the growth during the respective drought period is denoted as tree recovery, and finally, tree resilience is estimated as the ratio between the performance after and before drought disturbance (Lloret et al., 2011; MacGillivray and Grime, 1995).

Furthermore, at individual level, it has been observed that resistance, recovery and resilience of trees to drought in terms of growth depends on factors such as species (Zang et al., 2011), competitive status of the tree within the stand (Zang et al., 2012), age and size (Lloret et al., 2011), as well as site conditions (Pretzsch and Dieler, 2011). For instance, Lloret et al. (2004) found that the greater the size and age the greater the resilience, while Mueller et al. (2005) and Kolb et al. (2007) observed precisely the opposite trend. Moreover, it has been observed that the distinct ecological needs of the species could modulate species responses and strategies in the presence of drought. Thus, Gomes et al. (2018) found that the resistance response to severe drought was of a stand level nature, whereas resilience, in contrast, was mainly species-specific.

#### ***Forest growth responses to climate at long-term scales***

The cumulative effect of climatic factors has been observed to lead to effects on species growth (Gomes Marques et al., 2018). In this regard, synchrony in tree growth patterns among trees from the same species and from different species, as well as the dependence of these patterns on climate events, have been used to analyze species response to climatic restrictions, since these constraints tend to strengthen growth–climate relationships, resulting in enhanced common ring-width signals (Shestakova et al., 2016). This type of analysis is highly relevant since a certain relationship has been observed between spatial synchrony and the persistence of populations; the greater the synchrony between population dynamics, the greater the probability of extinction (Heino et al., 1997). Although few methodological approaches currently exist to unravel the complexities of tree-ring signals (Alday et al., 2018), Shestakova et al. (2014) presented a sound methodology to interpret synchrony patterns in tree-ring networks, ranging from local (Shestakova et al. 2018) to sub-continental scales (Shestakova et al., 2016). Through this approach, it is possible to test the presence of contrasting tree-ring patterns in pre-established groups of chronologies, so it can be very useful to detect common temporal signals between different species across time and space.

### ***1.2.3. Mixing species as a strategy to enhance ecosystem resilience***

Several studies have identified the use of mixed forest as a management strategy to enhance ecosystem resilience (Forrester, 2015; Pretzsch et al., 2013). The increase in tree species diversity has been demonstrated to have positive effects on productivity (Jactel et al., 2018; Pretzsch et al., 2013; Pretzsch and Schütze, 2016; Riofrío et al., 2017; Zeller et al., 2018), improve temporal stability of forest ecosystems (Griess and Knoke, 2011; Jactel and Brockerhoff, 2007), reduce vulnerability to drought (Forner et al., 2018; Grossiord, 2019), and increase the probability of natural regeneration occurrence (Moreno-Fernández et al., 2017).

Today, it is widely accepted that species diversity mediates ecosystem functioning (Hooper et al., 2005; Kinzig et al., 2001; Tilman and Snell-Rood, 2014), and several studies have reported benefits to tree growth from interspecific interactions in mixed stands compared to monospecific stands (de-Dios-García et al., 2015; Pretzsch et al., 2013). For instance, the coexistence of two or more species in the same niche permits different species to access resources in spatially and temporally different ways (Bauhus et al., 2017). This variation in the use of resources by the species in a mixed stand has been observed to result in more elastic responses to disturbances (Yachi and Loreau, 1999). However, the generalization of the benefits of mixed forest due to positive species interaction is inaccurate, since strong niche similarities between coexisting species can sometimes increase competition (del Río et al., 2014a). Moreover, interspecific interaction can be moderated by stand density (Condés et al., 2013), site conditions (Huber et al., 2014) and climate (Manso et al., 2015a). Here, spatial gradients (a proxy of resource availability gradients) can also affect interactions between any given pair of species, and evidence exists of both increasing (Forrester, 2014; Jactel et al., 2018) and decreasing (Jucker et al., 2014; Aguirre et al., 2019) complementarity with the decrease in resource availability. Hence, species interaction becomes a dynamic phenomenon that needs to be addressed in a broad sense by considering the main factors that can modulate it.

The use of competition indices in individual tree growth models, comparing intra and inter-specific competition indices, can reveal different types of interaction between tree species (Canham and Uriarte, 2006; Cattaneo et al., 2018; Forrester et al., 2013). While strong niche complementarity tends to relax inter-specific competition, the opposite is true when ecological niches between coexisting species bear greater similarity (Pretzsch, 2009). Moreover, as pointed out by Pretzsch and Biber (2010), the reaction of growth to competition can also be heavily influenced by the prevailing limiting factor (i.e. the main contested resource), and that can be further explored by analyzing intra and inter-specific competition based on the *mode* of competition, i.e. size-asymmetric or size-symmetric competition (del Río et al., 2014a). Here, Schwinning and Weiner (1998) described the size-asymmetric competition as a process where larger individuals use resources in ways that are disproportional to their size, making those resources unavailable to smaller individuals, and size-symmetric competition as that which occurs when competitors share resources equally or in ways that are proportional to their size. While most studies support the generalization that competition for light is almost always size-asymmetric (Cattaneo et al., 2018; del Río et al., 2014a; Pretzsch and Biber, 2010), available data suggest that competition for belowground resources is often size-symmetric (Weiner and Damgaard, 2006).

Although the effect of competition could be quantified directly by using individual-tree growth models and different formulations of competition indices, some authors have pointed out that the potential impact of climate in these models has commonly been ignored (Calama et al., 2019). However, Gómez-Aparicio et al. (2011) found that the sensitivity of different species to competition varied markedly along climatic gradients. Similarly, Condés and del Río (2015) reported different inter-specific competition effects on tree growth and mortality under different climates.

In the Mediterranean ecosystem, the effects of local climate variability on the competition-growth relationships are of particular interest. In this regard, the negative impacts of climate

change on forest growth dynamics are predicted to be aggravated due to more frequent heat-waves, increased frequency, and intensity of drought, and the general decrease in precipitation (Pachauri et al., 2014). In this context, it is expected that competition will significantly mediate the effect of site and/or climate on growth and other forest dynamic processes in this region (Calama et al., 2019; de-Dios-García et al., 2015; Wang et al., 2016). Most findings with regards to species interactions and their dependence on site conditions are based on the net long-term performance of trees. However, species interactions that influence the performance of growth in mixed stands versus monospecific stands in the long term, especially in poor sites such as Mediterranean ecosystems, can also be assumed to be relevant in the short term, e.g. in dry years (del Río et al., 2014, 2014a). Thus, Pretzsch et al. (2013) found that in drought years, such as 1976 and 2003, trees in mixed stands performed better than those trees of the same species growing in pure stands. Nevertheless, in order to examine the relationships linking climate, competition, and growth, it is necessary to use repeated measurements of growth at a temporal scale. Such information can be obtained, for example, from dendrometer measurements (Aldea et al., 2018) or by examining the climatic signal in tree ring chronologies (Linares et al., 2010; Martin-Benito et al., 2011). Moreover, the inclusion of climate drivers as an explanatory covariate in empirical growth and yield models has been found to be a good approach to evaluate potential shifts in competition patterns depending on the availability of spatially and temporally varying resources (Calama et al., 2019).

### ***1.3. Case study: P. pinea and P. pinaster Mediterranean forests***

Mediterranean forests are ecosystems with high ecological, economic and social values, which provide multiple wood and non-wood products (firewood, resin, pine nuts, etc.), and services (biodiversity conservation, soil protection, water regulation, recreation possibilities, etc) (Palahi et al., 2008). According to the FAO definition of forests, there were around 88 million ha of forest area in the Mediterranean region in 2015, which represent 2.20 percent of the world's total forest area. In Spain, this value is of particular relevance, since the percentage of



Mediterranean forested area (with respect to total land area) is 37% (FAO and Plan Bleu, 2018), reflecting the importance of these ecosystems in the country. It is in the Mediterranean basin where we find the woodlands referred to as "Tierra de Pinares". This area is located within the Spanish Northern Plateau, an inland plateau of about 50,000 km<sup>2</sup> with a mean altitude of 700 m above sea level. The Mediterranean- dominant climate, determined by the latitude of the plateau, is characterized by the occurrence of severe, four-month summer droughts. The low mean precipitation values (ranging from 300 to 500 mm) and the extreme absolute temperatures, ranging from 40 °C (summer) to -10 °C (winter) are due on the one hand to its sheltered physiographic situation, beyond the humid influence of the ocean, and on the other to the conditions associated with its high altitude. The lack of availability of water is one of the main limitations in the area, aggravated by the overexploitation of the water table and the increasingly irregular distribution of rainfall due to climate change (Gordo et al., 2012). The main forest species in the territory are stone pine (*Pinus pinea* L.) and maritime pine (*Pinus pinaster* Ait.) (Fig. 1.1), and in this case, the different ecological conditions modulate the level of presence of each of the two species in the area.

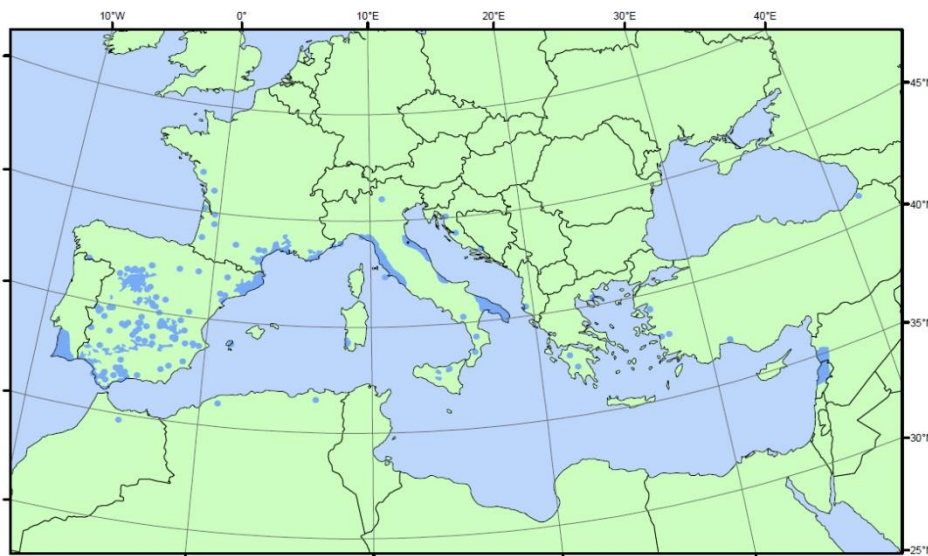


**Figure. 1.1.** General view of one of the mixed permanent plots located in the province of Valladolid

These forests have also been subjected to intensive management in order to produce wood, resin, and pine nuts, throughout history. The fluctuation in the prices of these products in the international markets has significantly affected the management of the area, which has focused on one or other species alternately. This intensive management, together with the more recurrent recent drought episodes in the area, has resulted in serious problems for natural regeneration (Ledo et al., 2014) as well as forest decline (Prieto-Recio et al., 2015).

The stone pine (*Pinus pinea* L) is a valuable Mediterranean pine species due to the potentiality of its products in the national and international markets, its capacity to grow in poor and sandy soils, as well as to withstand severe and persistent droughts and relatively extreme temperatures. The wide use of pine nuts from this species over the course of human history makes it difficult –if not impossible- to establish with exactitude the original distribution area (Caudullo et al., 2016). In this context, there is no general agreement on the naturalness of *P. pinea* in the Northern Plateau of Spain, despite existing palynological records confirming the presence of the species dating back 13.000 years (Stevenson, 1985, 1984). The current geographical distribution area of *P. pinea* includes the Mediterranean basin (Fig. 1.2), from

Portugal to Syria, with greater abundance in south-western Europe (Iberian Peninsula, Southern France, and Italy). In Spain, the species occupies more than 400,000 ha, which constitutes 50% of the total area of this species in the world (Montero et al., 2008). In the studied area, *Tierra de Pinares*, the 2009 Catalogue of Public Forests indicates 75,000ha of public forests in which *P. pinea* is present. However, this estimation (occupied area) is complex, since the growth of this species tends to be intimately associated with that of *Pinus pinaster* Ait. on sandy soils and mixed with *Quercus ilex*, *Quercus faginea*, *Juniperus thuriphera* and *Juniperus communis* on limestone uplands (Clément, 1993; Franco-Múgica et al., 2005; Múgica et al., 2001).



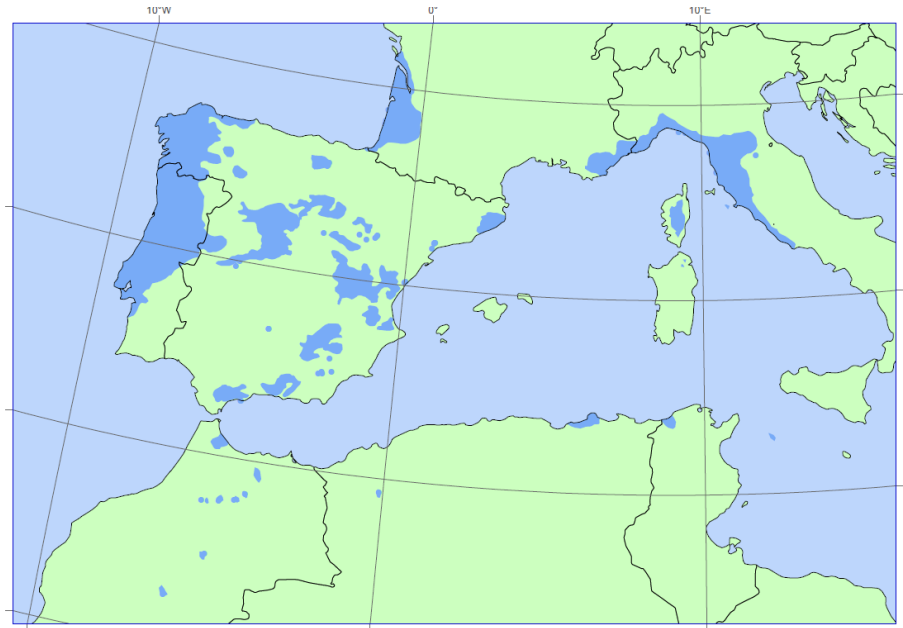
**Figure 1.2.** Distribution of stone pine (*Pinus pinea*) in the Mediterranean area. Source: EUFORGEN 2009, [www.euforgen.org](http://www.euforgen.org)

*P. pinea* is considered a heliophilous, xerophilous and thermophilous pine species, and although it can withstand shade conditions during the early stages, it requires abundant light for fructification in maturity (Montero et al., 2004). Generally, the optimum requirement as regards annual average precipitation ranges from 400 to 800 mm, although it is possible to find *P. pinea* trees in areas with annual average precipitation of 250 mm. The species can withstand periods of summer droughts, with summer rainfall of less than 50 mm. In addition,

with adequate humidity conditions, *P. pinea* is able to tolerate minimum temperatures down to -14 °C.

Maritime pine (*Pinus pinaster* Aiton) is a conifer from the western Mediterranean Basin with a distribution area that exceeds 4 million ha, across which there are a variety of origins and environmental conditions (Fernandes and Rigolot, 2007). The current geographic distribution of *P. pinaster* includes the Iberian Peninsula, Southern France, Western Italy, western Mediterranean isles, North Morocco, Algeria and Tunisia (Fig. 1.3). In the southern hemisphere, intensive plantations were established with both economic and environmental objectives. In Spain, Maritime pine is the most widespread conifer and it can be found in both natural (1 million ha) and planted forests (0.6 million ha) (DGCONA, 2004). In the studied area, this species is especially abundant, where it occupies more than 114,000 ha, representing approximately 7.5% of the European distribution of the species. It grows in warm, temperate regions and although it is possible for trees to survive in areas with only 400 mm annual precipitation, the species prefers more humid or sub-humid areas where annual rainfall is greater than 600 mm.

This species is highly versatile and shows certain resistance to winter frost, summer droughts, and limestone substrates (Bravo-Oviedo et al., 2011; Prieto-Recio, 2016). Moreover, it does not tolerate shade and prefers siliceous soils with a coarse texture, such as sandy soils, dunes, and other poor substrates.



**Figure 1.3.** Distribution of maritime pine (*Pinus pinaster*) in the Mediterranean area. Source: EUFORGEN 2009, [www.euforgen.org](http://www.euforgen.org)

This species has a high economic value due to the characteristics of its timber as well as the extraction of resin in order to obtain turpentine and rosin (Praciak, 2013). In addition, due to its ecological characteristics, fast growth and tolerance to poor soils, maritime pine has been widely used to consolidate dunes or slopes, for sanitation plantations (Farjon, 2010), or for protection of agricultural crops against salt spray (Pereira, 2002).

Thus, both species are found in monospecific and mixed stands, sharing territory as well as ecological conditions (Calama et al. 2017), and both have been intensively managed in the area since ancient times (Prieto-Recio et al. 2015). Several studies have demonstrated that precipitation is the main growth-driving factor for the two species in these Mediterranean forests (Calama et al., 2019; Gea-Izquierdo et al., 2019) although the effect of water scarcity is more evident in *P. pinaster*, which seems to display worse adaptation to the current environmental conditions than *P. pinea*. The expected future climate conditions and resultant periods of drought could affect the availability of water in Mediterranean pinewoods and induce severe growth decline and tree dieback.

### **1.3.1. Natural regeneration in *P. pinea* and *P. pinaster* mixed and monoespecific forests**

Natural regeneration of Mediterranean pine forests is often unsuccessful due to the presence of certain limiting factors. The main bottlenecks for regeneration are directly linked to either the intrinsic characteristics of the species (e.g., seed size, masting), to those of the habitat (e.g., soil compaction) or to climatic conditions (mainly summer drought). Unfortunately, the natural regeneration of both species is often unsuccessful under the current regeneration methods (Manso, 2013). Under future climatic scenarios, this situation could become worse with even lower rates of natural regeneration occurrence (Manso et al., 2014b; Ruano et al., 2015). Various studies have been undertaken in this field in order to identify the main limitations affecting natural regeneration (Gordo et al. 2012). Manso et al. (2014a, 2014b) observed that the regeneration of *P. pinea* is limited by the mast-year occurrence, seed dispersal limitations and seed predation, all of which are influenced by climatic conditions. Furthermore, Calama et al. (2015) found that the joint occurrence of severe water stress and negative rates of net assimilation (circumstances commonly found during the summer), result in *P. pinea* seedling mortality. In the case of *P. pinaster*, several authors have suggested that natural regeneration is suitable, although the functioning of the factors underlying this process remains unclear since some areas present null or scarce regeneration while others show abundant regeneration (Miguel Pérez et al., 2002; Rodríguez-García et al., 2007). In a recent study conducted in the same area, Ruano et al. (2015) found that seed rain, the first summer after emergence and the microsite conditions are significant factors affecting *P. pinaster* natural regeneration. Moreover, they found that cutting intensity could seriously limit the regeneration rates of this species.

Therefore it is important to consider the initial conditions required by each species, in accordance with the species-specific shade needs for germination and initial seedling growth and survival. In this regard, regeneration in both species is highly favored by water availability in soils (Rodríguez-García et al. 2011a, b). Mid-shade positions provide the optimal conditions

required by *P. pinaster* regeneration (Ruano et al. 2009), while *P. pinea* regeneration is favored by the presence of dense shade environments during the first stages of regeneration, followed by the progressive and flexible release of the seedlings (Manso et al., 2014b). These conditions are especially important during the hot, dry summer, since shade and adequate levels of water availability in soils prevent water stress conditions, reducing the air temperature and evaporative demand (Valladares et al. 2005).

Thus, to enhance the capacity of this Mediterranean forest to regenerate, management efforts must be aimed at reducing the risks during this stage, taking into account these species-specific regeneration limitations and strategies (the degree of shade tolerance, water use efficiency or resistance to drought). These new paradigms make it necessary to reconsider forest strategies, which have been defined by human pressures throughout history in the studied area (Gordo et al., 2012).

### **1.3.2. Forest management for *P. Pinea* and *P. pinaster* in the Northern Plateau of Spain**

Due to the poor degree of conservation of the public forests as a consequence of intensive grazing along with abusive pruning and debarking (Gordo, 1999), at the end of the 19th century, the first management strategies for pinewoods in the studied area were defined. The main objective of these strategies was the transformation of these depauperated forests into monospecific even-aged stands. To achieve this objective, the main method used was the strip clearcutting system, followed by either lateral seed dispersal (*P. pinaster*) or artificial sowing (*P. pinea*) using local seeds (Calama et al., 2017; Gordo et al., 2012). Using this method, managers were able to change the species focus at stand level depending on the main product being favored: cones and nuts (*P. pinea*) or resin (*P. pinaster*).

In this way, up until the decade of the 1960's, *P. pinaster* was traditionally favored to *P. pinea*, due to the economic importance of resin (Gordo, 1999). As a consequence, the management of the area was conditioned by the production of resin, resulting in clearcutting methods with

short rotation (80 years) and regeneration periods (10 years). However, this management, together with grazing and the keeping of mature resin, did not achieve the expected objectives. Therefore, in order to ensure the homogeneity of the stand, artificial sowing was necessary (Calama et al., 2017). In 1970's the resin crisis lead to a change in the focus species in the area. There was a shift towards favoring *P. pinea* stands, a situation that has continued until the present for several reasons. On the one hand, this species provides very important benefits for the local population associated with the production of pine nuts and timber, and on the other hand, this species has been observed to be better adapted to summer droughts (Gandía et al., 2009). Up until the 1970s, clearcuttings were successfully conducted in *P. pinea* stands, but then a uniform shelterwood system was proposed based on experience from other regions (e.g. Andalusia) (Montero et al., 2008). This method involves a preparatory cutting during the first three to four years of the regeneration period, which ranges from 20 to 25 years in the studied area (Montero et al., 2008). During this phase stand density is reduced to 100-150 stems·ha<sup>-1</sup>, when the stocking is superior to this density. In a second step, secondary fellings are applied every 5–10 years over the following 20 years (Montero et al. 2008), aiming to completely regenerate the stand in a period of 20 years at maximum. During this procedure, cone collection should also be restricted, at least during the initial phases of the regeneration process. Rotations in monospecific stands of *P. pinea* currently range from 100 to 120 years, while for monospecific stands of *P. pinaster* the rotation is around 80–100 years (Calama et al. 2017). In mixed stands, regeneration fellings tend to mimic the practices proposed for the dominant species, since no specific guidelines for these mixtures are currently available. However, throughout the sandiest areas within the Northern Plateau, this system has widely failed. As a consequence, large areas have remained without regeneration, years after the fellings, while other areas have been occupied by advanced regeneration, leading to non-viable, badly-shaped trees, with low potential as cone producers. An alternative approach



which has been successfully applied in these latter areas is the conversion to uneven-aged stands by means of group selection (Calama et al., 2005).

#### **1.4. Thesis Focus**

In order to unify efforts and aims, forest management needs to incorporate a holistic perspective in its strategies. Although extensive information is available in the literature on the ecological processes involved at the different stages of development of forest ecosystems, most of this information only provides a fragmented view of the overall process.

##### **1.4.1. Methodological approach**

A wide variety of statistical methodologies are currently in use in forest or ecological research (Zimmermann and Guisan, 2000). In recent years, the advances in statistical methodologies, the progress in computer technology, and the greater availability of large field data sets have allowed the development of more complex approaches.

The methodologies presented in this thesis are generally based on analyzing how different factors control the response dynamics of *P. pinea* and *P. pinaster* in these Mediterranean monospecific and mixed forests throughout stand development, from regeneration to mature trees. In this regard, we combined different multivariate methods, such as contingency tables, principal components analysis, etc. to understand and identify underlying and hidden patterns in the data set. We subsequently built several statistical models to assess the effect of stand structure and climate change on natural regeneration occurrence, forest growth, and competitive species-relationships in mixed and monospecific Mediterranean forests. In this context, models have been widely used to predict the spatial and temporal variability in terms of growth as well as other ecosystem functions and the interactions between different environmental factors (Pretzsch et al., 2017).

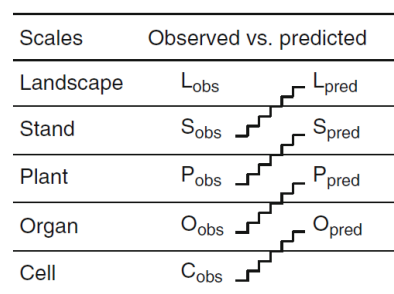
In this way, multivariate statistical methods provide numerous tools to interpret the relationship between groups of variables (Manly, 2005). Principal component analysis (PCA) is very useful to reduce the number of analyzed variables to a small number of indices that are

linear combinations of the original variables. Contingency tables are one of the most common ways to summarize categorical data. Using this method, we can observe whether or not there is an association between the row variable and the column variable that comprise the table, as well as the strength of that association (Stokes et al., 2008). The analysis of the Tau-Kendall coefficient of concordance, however, is very useful to evaluate hierarchical patterns of decreasing similarity between different, previously established groups (Farnsworth and Ellison, 1996), through a set of rankings.

Several authors have distinguished two distinct types of models; those that are intended to inform us on the configuration of a process or those that are capable of predicting the response from plausible causal relations (Leohle, 1983; Peters, 1991). However, what is essential in both types is to define specific research goals when selecting a model approach. In our context, the model formulation should be silviculture-oriented through appropriate variables and additionally, it should be flexible enough to provide new frameworks that can be used as a decision-making tool for forest managers (Manso, 2013). In the present thesis, we combined different modeling approaches in order to study forest dynamics under changes in forest structure and environmental conditions over time. These modeling tools include i) survival models, used to deal with response time data (or events), which in our context, is the occurrence of regeneration, ii) linear mixed models, which allow us to analyze data with a hierarchical spatial structure through the fixed and random effects (Zuur et al., 2009) and iii) logistic regression models, where the logit transformation, widely used in percentages and ratios, allows us to model values between 0 and 1 (Pampe, 2000).

Furthermore, a matter of primary interest is to define the appropriate scale at which a system should be studied in order to determine the ecological causes and consequences of global climate change for this system (Levin, 1992). If this scale is not adequate, the dynamics being studied may not be detected (Wiens, 1989). Recent studies have highlighted that researching forest stand dynamics requires multi-level analyses involving individual tree level, size

distribution and stand level analyses since the processes in forest ecosystems occur at vastly different temporal and spatial scales (Fig. 1.4) (Forrester and Pretzsch, 2017). Each organizational level provides distinct insights and reveals emerging properties that are unattainable at higher or lower levels. However, feedback between processes, either within the same level or between different hierarchical levels, influences the characteristic behavior of ecosystems, which cannot be understood by considering the sub-processes in isolation.



**Figure 1.4.** Forest research through scale-overlapping analysis of patterns and processes from cell to landscape. The observed (obs) system variables at a certain level (Cell, Organ, Plant, Stand and Landscape) can be used to predict (pred) the expected behavior for the next level (Opred, Ppred, Spred, and Lpred) through linear temporal or spatial upscaling (symbolized by the ladders) (Pretzsch 2009, p30)

This is especially important for mixed-species stands, where a solid understanding of mixed-stand dynamics requires measurement at multiple hierarchical levels, e.g. landscape, stand and tree (Forrester and Pretzsch, 2017). Thus, while landscape and stand levels could lead to the identification of patterns at regional levels, which are useful for defining strategic regional conservation and management planning, the combination of stand and individual tree level dynamics allows us to identify the relationships between tree species that depend on both spatiotemporal variability of resource availability and abiotic conditions (Cattaneo et al., 2018; Forrester, 2014).

However, the integration of mixing effects in these types of models has proved challenging for forest managers and scientists, since the silvicultural guidelines in mixed-species stands are still largely based on monospecific even-aged stands (Bravo et al., 2011; Forrester and Pretzsch, 2015). In spite of the numerous studies that have analyzed species-mixing effects on

tree and stand productivity, tree allometry, mortality, etc, tools for evaluating the long-term sustainability of mixed forests are still lacking. In addition, to ensure that mixtures are used appropriately, it is critical to understand how climatic variability influences species interactions (Forrester, 2017). In this regard to understand the relationship between species and the role of climate conditions, the combination of short-term perspectives (1-5 years) and long-growth term responses is crucial. The combination of both approaches allows us to infer the functional traits which best characterize the different species-specific responses to climate restrictions (Camarero et al., 2018; Gazol et al., 2017) and give us a retrospective assessment of forest sensitivity to climate.

### **1.5. Objectives**

The main objective of this thesis is to evaluate the processes involved in the dynamics of the *P. pinea* and *P. pinaster* Mediterranean forests located in the Northern Plateau of Spain under the current scenario of global change. We define the adaptation strategies aimed at reducing the vulnerability of these Mediterranean forests and enhancing their resilience and resistance to changing conditions. Therefore, to provide an overview of the ecosystem situations and threats, we analyze the main strategies and limitations of the species during different developmental stages. Questions arising on how and why the species interactions change, both spatially and temporally, are therefore evaluated.

The specific objectives of this work were:

1. To analyze the spatial patterns of recruitment of seedlings and saplings of both species, depending on adult stand composition, and stocking.
2. To identify whether there is intra and interspecific synchrony in regeneration establishment and changes from one developmental stage to another as well as to determine how temporal variation in the establishment is related to climatic conditions.

3. To develop a probabilistic model based on survival analysis techniques in order to predict *P. pinea* and *P. pinaster* natural regeneration occurrence in the Northern Plateau of Spain, taking into account the time elapsed since regeneration felling as well as different climate and stand level conditions.
4. To explore the vulnerability of the two cohabiting species, at maturity, to drought-related stresses, and the role of different factors such as species composition, tree size, age, and density.
5. To analyze common associations (synchrony) between indexed ring-width series in *P. pinea* and *P. pinaster* in mixed and monospecific stands, as an indicator of the strength of climate influence on tree growth.
6. To explore the size-symmetric and size-asymmetric and intra and inter-specific competition in *P. pinea* and *P. pinaster* stands to gain a better understanding of the interaction between both species and test whether climatic variability over the studied years modifies competition-growth relationships.

### **1.6. Research questions and thesis structure**

The main hypothesis of this thesis is that differences in structural and functional traits between *P. pinea* and *P. pinaster* could reduce the vulnerability of mixed stands to climate variability in comparison to monospecific stands. We hypothesize that species-specific strategies and species interactions vary over space and time in association with spatial and temporal changes in the different drivers (climate, stand attributes, site) that govern the processes. To test the different hypotheses we have organized the thesis into four different studies (Fig. 1.5), according to the theoretical framework for analyzing species dynamics in the *P. pinea* and *P. pinaster* forests.

Study I analyzes the spatio-temporal patterns of natural regeneration in these *P. pinea* and *P. pinaster* mixed and monospecific Mediterranean forests. We hypothesize that: (i) *P. pinea* and *P. pinaster* seedlings and saplings have different ecological requirements and

limitations, which could result in interspecific differences in the rate of establishment and success of the natural regeneration; (ii) the occurrence and the abundance of adult trees of one of the species could have a significant effect on the natural regeneration not only of that species but also of the other species; hence, regeneration fellings could be regulated to modify future stand composition. Finally, during this Study, we also tested whether (iii) the effect of climatic drivers on natural regeneration is constant across species and/or regeneration stages.



Figure 1.5. Summary of the study and topics addressed in the studies I, II, III and IV

In Study II, we used all the information obtained during the previous one to develop a statistical model based on survival analysis techniques in order to predict the occurrence of natural regeneration. Our main hypotheses here were that; (i) dryer conditions in the Mediterranean area, characterized by the increase in temperatures as well as the decrease in precipitation, hamper the occurrence of *P. pinea* and *P. pinaster* natural regeneration; (ii) in this regard, different climate scenarios could lead to differences in the probability of success in the natural regeneration process; and (iii) species-specific requirements, as well as stand-related variables, could contribute to increasing, or decreasing, the occurrence of natural regeneration.

In Study III, we explore the vulnerability of the two cohabiting species, at maturity, to drought-related stresses, and the role of different factors such as the composition, tree size, age, and density. Our main hypotheses here were that: (i) mixed composition improves the ability of *P. pinea* and *P. pinaster* to cope with extreme climate conditions, such as summer droughts; (ii) other factors, such as tree size, tree age or stand density influence the growth response in both species in the presence of drought events; (iii) on the other hand, interaction between species in mixtures could lead to differences in long-term growth variation between *P. pinea* and *P. pinaster* due to the species-specific growth requirements.

Finally, in Study IV we tested the main mode of competition and intra and inter-specific competition in each of the two species in mixed and monospecific stands by using competition indices integrated within growth models. We also evaluated whether different climate conditions, i.e. dry or wet years, modify the mode of competition. Therefore, we hypothesize that (i) tree level competition in *P. pinea* and *P. pinaster* differs between mixed and monospecific stands. Furthermore, due to the low resource availability in the study area, (ii) we expect that size-symmetric competition will be more important than size-asymmetric competition both in mixtures as well as in monospecific stands. Finally, in accordance with previous studies that found a differential effect of mixture on species-competition in dry and

wet years (de-Dios-García et al., 2015), we expect that (iii) *P. pinea* and *P. pinaster* mixtures will lead to improved tree growth in the driest years in comparison with monospecific stands.



## 2. Data

Hence, in the development of this thesis, it has been used information from two different networks. Both are located in the Northern Plateau of Spain, in the area previously defined as *Tierra de Pinares*. The first group of plots, henceforth called the *regeneration plots*, was used in Study I and Study II, in order to evaluate the dynamics of natural regeneration, while the second network of plots, named as *permanent plots*, was used in the development of study III and study IV.

### 2.1. Study area

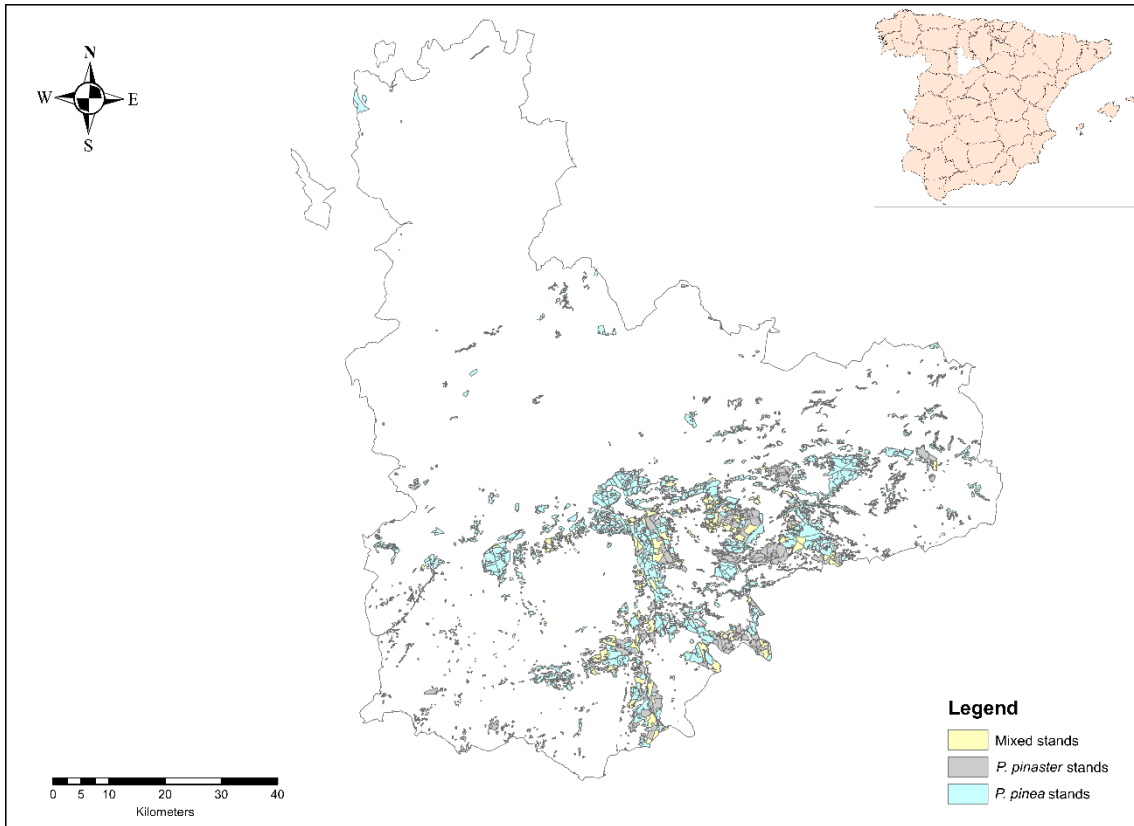
The focus study area of this thesis includes mixed and monospecific forests of *P. pinea* and *P. pinaster* located at 700 m a.s.l. on the Northern Plateau of Spain in the Valladolid province, within the region that previously we defined as “Tierra de Pinares”. In Valladolid, the two species cover approximately 68.000 ha, with monospecific *P. pinea* stands covering 70% of the area, monospecific *P. pinaster* 10% and mixed forest of the two species, 20% (PORF, 2008) (Fig.2.1). This region is defined by the river Duero Basin with typical soils presenting a large percentage of sand and low content of nutrients.

From an ecological perspective, Calama et al. (2008) proposed a stratification for the region based on soil, lithology and climatic attributes, resulting in ten groups denominated natural units. Hence, the study area is distributed among three very homogenous natural units 6, 7 and 8, whose characteristics are presented in Table 2.1.

**Table 2.1.** Main characteristics of natural units

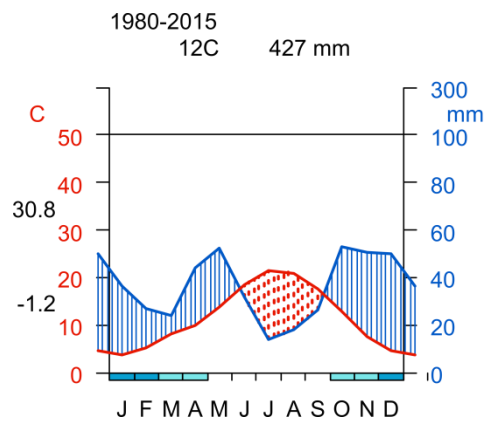
Unit	Name	Total area (ha)	Altitude (m)	Annual rainfall (mm)	SI (m)	Geology texture	Soil origin	Water retention (mm)
6	Viana de Cega	7211	707	369	15.1	Quartz sands	Wind deposits	80-150
7	Iscar	2945	745	380	16.7	Quartz sands-Clays	Alluvial-wind	>300
8	Medina	4044	746	371	12.5	Quartz sands	Wind deposits	75-130

Where SI is site index, as stated by Calama et al. (2013)



**Figure 2.1.** Distribution of the monospecific and mixed stands of *P. pinea* and *P. pinaster* in Valladolid province. The upper right corner of the figure shows the location of the province of Valladolid in Spain.

The climate is continental-Mediterranean characterized by absolute temperatures in summer and winter of 40 °C and – 10 °C, respectively, with a mean annual temperature of 11.2 °C. Mean annual precipitation is 435 mm, and there is a period of summer drought (July to September) with mean precipitation of 66 mm (Fig. 2.2). Frosts may occur from September to May.



**Figure 2.2.** Climodiagram for the 1980-2015 period in the study area (Valladolid province). Digits sited on the left side of the y-axis are average daily maximum temperatures of the warmest month and average of daily minimum temperatures of the coldest month from top to bottom respectively. Climate data from Valladolid meteorological station.

For Study I and Study II, climate data were obtained from the nearby meteorological stations (Valladolid, 04 ° 46' 27" W; 41° 38' 402 N; 735 m and Olmedo 04° 41' 15" W; 41°17' 19" N; 769 m [data available at [www.inforiego.org](http://www.inforiego.org)]). In this case, seasonal and yearly precipitation and mean temperatures were calculated for the study period (2001-2015) (Table 2.2).

**Table 2.2.** Summary of the climate variables of interest for the study period (2001 – 2015). Mean ( $\pm$ SE)

Code	Variable Units	
<i>Temporal variation</i>		
T_spring	Mean spring temperature (°C)	10.73 (0.23)
T_summer	Mean summer temperature (°C)	20.59 (0.20)
T_autumn	Mean autumn temperature (°C)	11.62 (0.38)
T_winter	Mean winter temperature (°C)	3.57 (0.25)
T_anual	Mean annual temperature (°C)	11.62 (0.13)
P_spring	Mean spring precipitation sum (mm)	427.58(35.91)
P_summer	Mean summer precipitation(mm)	184.36 (23.06)
P_autumn	Mean autumn precipitation (mm)	471.22 (41.95)
P_winter	Mean winter precipitation (mm)	404.80 (44.21)
P_anual	Mean annual precipitation (mm)	374.57 (17.30)

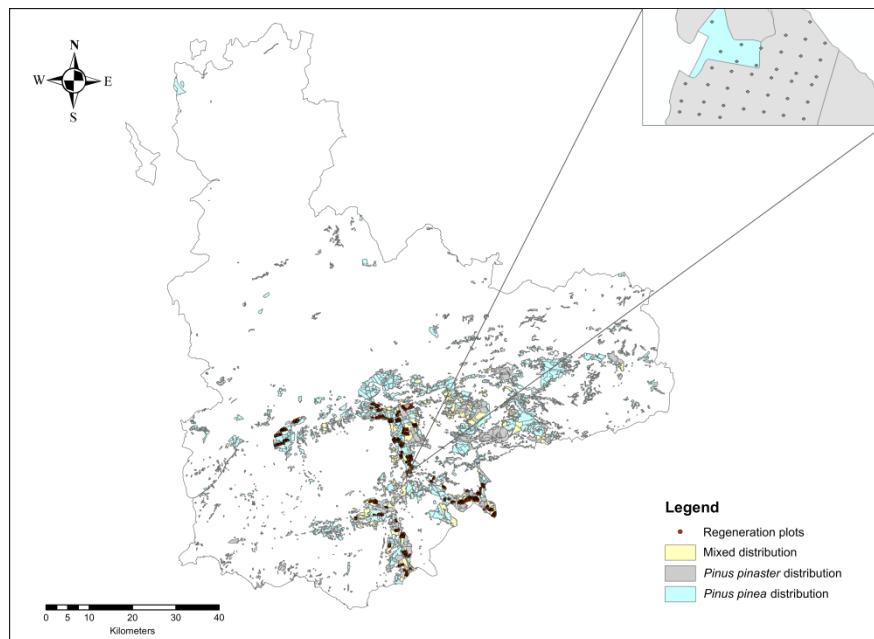
However, during Study III and Study IV, due to the homogeneity of the climate over the whole studied area, we uniquely used climate data from a single meteorological station (Valladolid, 04 ° 46' 27" W; 41° 38' 402 N; 735 m a.s.l) for all the analyses. In addition to monthly data for mean, maximum and minimum temperature and precipitation, we calculated the Standardized Precipitation Evapotranspiration Index-SPEI (Vicente-Serrano et al., 2010) to estimate drought intensity according to its strength and length in the studied area. Negative values below -1 and positive values above 1 for this index correspond to dry and wet periods respectively. To better identify the temporal variability of the SPEI in the studied area and its potential influence on tree growth we then calculated the SPEI for three accumulated periods: 6, 9 and 12 months, obtaining three SPEI values for each month of the year. For further analysis, monthly SPEI values were aggregated into a single yearly value using: a) the period from 1<sup>st</sup> October of the previous year to 30<sup>th</sup> September of the current year (hydrological year in the region) and b) from January to December (chronological year).

## ***2.2. Network of natural regeneration plots (Study I and Study II)***

The installation of this network of plots started in 2001 by the Forest Service of the Junta de Castilla y León in the province of Valladolid. Today, the installation of new plots keeps on going, however, for the development of the thesis we used the data available until 2015.

### ***2.2.1. Experimental design***

The network consisted of 1936 systematically distributed permanent plots for monitoring natural regeneration, with a sampling intensity of one plot every 2 ha in 120 blocks where regeneration fellings had been carried out. The complete network is located in 32 publicly owned, managed forests (Fig. 2.3) (13,951 ha). Plot installation followed the Stock Quadrant method (Stein, 1992), consisting a fixed radius (8 m, equivalent to 0.02 ha) circular plots, divided into four quadrants where natural regeneration was annually monitored. The first regeneration plots were installed in autumn 2001 in stands where regeneration fellings had already been applied during the previous years. The rest of the plots were gradually installed in accordance with the regeneration fellings, i.e., as soon as cuttings were performed in the blocks, these were included in the experimental design.

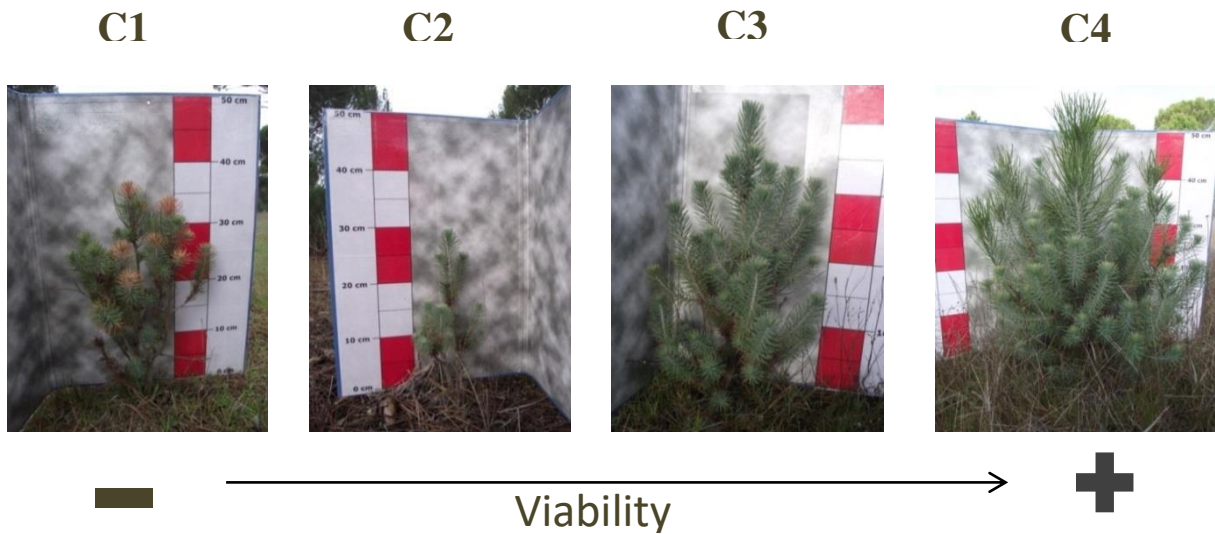


**Figure 2.3.** Distribution of the monospecific and mixed stands of *P. pinea* and *P. pinaster* as well as the distribution of the regeneration plots that comprise the dataset from Valladolid province. The upper right corner of the figure shows a zoom of the systematic distribution of the plots

### 2.2.2. Dataset

Seedlings and saplings of each species, *P. pinea* or *P. pinaster*, were counted and classified into four different categories (C1, C2, C3 and C4) depending on the size and viability of the plant. C4 was the most viable and durable, and C1 the least (see Fig 2.4). However, in the present thesis, we organized these four categories in two stages of development: well-established plants with adult needles, hereafter termed “saplings”; and young plants with uncertain future and without significant growths, hereafter termed “seedlings”. The number of plants of each category in each quadrant of the plot was recorded annually, between October and December from 2001 to 2015, along with the level of grass cover (high, medium and low) and the number of adult trees per species in each plot. The proportion of monospecific adult *P. pinea* plots was 56.8 % while the proportion of monospecific adult *P. pinaster* plots was considerably lower at 16.4 %. In the case of plots with mixed composition, the proportion was 5.9%. The remaining 20.9% corresponds to plots where no adult trees of any of the species remain standing after regeneration fellings were applied. In addition, other general information (number of adult trees and basal area of *P. pinea* and *P. pinaster*, Age, Dominant height, etc ) as regards stand

structure was obtained from the Forest Management inventories at block and stand level – i.e. forest management unit –.



**Figure 2.4.** Categories in which natural regeneration was classified based on its size and viability

#### **Data used in the study of Spatio-temporal patterns of natural regeneration (Study I)**

In addition to the number of seedlings and saplings per species and plot as well as the climate variables, other general information as regards structure was obtained from the forest management inventories at block and stand level-i.e., forest management unit. Between these variables there are, age, dominant height, quadratic mean diameter, basal area and number of adult trees per ha by species, along with the Reineke stand density index (SDI). Finally we used the number of years since the regeneration felling as a potential explanatory covariable (Table 2.3).

#### **Data structure for modeling the probability of regeneration occurrence (Study II)**

Here, we used the same dataset used in the study I. The objective of study II was to model the probability of regeneration occurrence at *P. pinaster* and *P. pinea* in each plot after time  $t$  (years) since the first regeneration felling had been carried out, considering both the characteristics of the plot as well as the climatic conditions observed during the period. For this purpose, measurements taken from the same plot were organized into annual successive intervals.

**Table 2.3.** Description of stand level variables. Mean ( $\pm$ SE)

Code	Variable	Units	Mean ( $\pm$ SE)
<b>Spatial variation</b>			
Age	Age of adult trees	(years)	82.39 (0.16)
Ho	Dominant height	(m)	14.60 (0.02)
Dg	Quadratic mean diameter of adult trees	(cm)	49.36 (0.18)
BA Pp	<i>P. pinea</i> adult trees Basal Area	(m <sup>2</sup> /ha)	7.74 (0.06)
N Pp	<i>P. pinea</i> number of adult trees	(trees/ha)	50.14 (0.45)
BA Pt	<i>P. pinaster</i> adult trees Basal Area	(m <sup>2</sup> /ha)	3.39 (0.04)
N Pt	<i>P. pinaster</i> number of adult trees	(trees/ha)	25.93 (0.30)
SDI	Reineke Stand Density Index		325.79 (1.46)
Years since Reg.	Number of years since regeneration	fellings (years)	1-24
Feelings			High (1) Medium (2) Low (3)
Level of grass	Factor of level of grass on soil		

In this study, we found some plots in which there was no information about the moment in which the first regeneration felling had been carried out. Taking into account that this information is essential for the purpose of study II we decided not to use these plots. Consequently, the total number of plots used in this study was 1,703.

Therefore, for each plot, we identified the first annual intervals where the regeneration of each species occurred. The flexibility of survival analysis methods allows this factor to be taken into consideration so that each plot can be entered in the model in the corresponding year.

In accordance with the structure of our dataset, as well as the monitoring design, the following issues had to be considered:

- Experiments ending prior to seedling regeneration occurrence, in other words, there may be some plots with no regeneration at all for one or other of the species during the study period. These are referred to as “right censored” observations (Lawless, 2003).
- When the first measurements were recorded (2001), regeneration may have already taken place in some plots. In these cases, we only know that seedling emergence occurred prior to the first measurement date; at some time between the year in which the regeneration felling was carried out and 2001. These are “left censored” observations.

- Furthermore, the exact moment at which seedling regeneration occurred was not determined. We only know that a given plot displayed no natural regeneration until the beginning of year  $i$  and that natural regeneration had occurred (or not) in the plot at the end of the interval  $i+1$ .

The above issues are represented in Figure 2.5. In the center is the zone which coincides with the studied period, 2001-2015, while at the extremes we can see the different types of censoring.

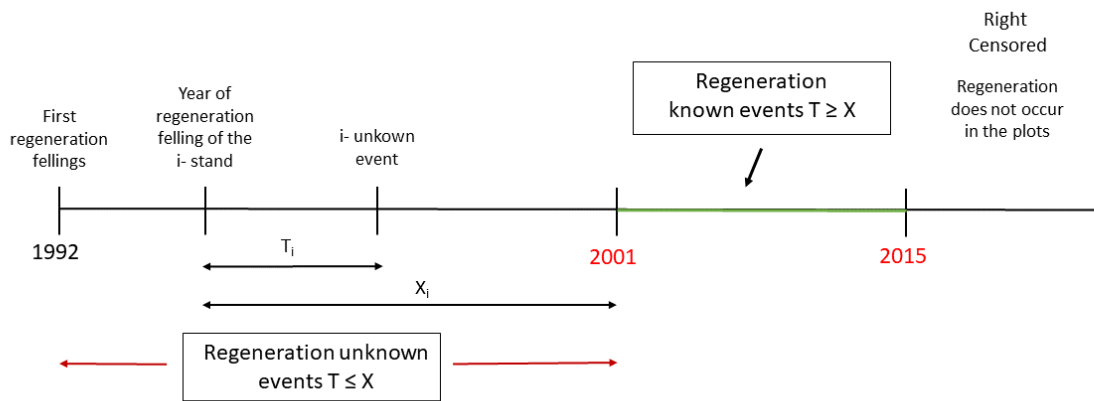


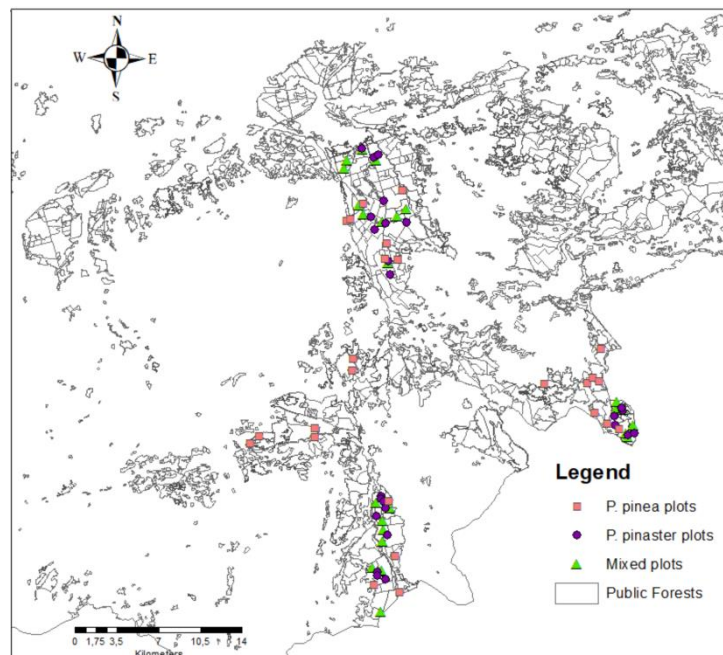
Figure 2.5. Data structure about time of regeneration occurrence in plots.

### 2.3. Network of permanent plots (Study III and Study IV)

#### 2.3.1. Experimental design

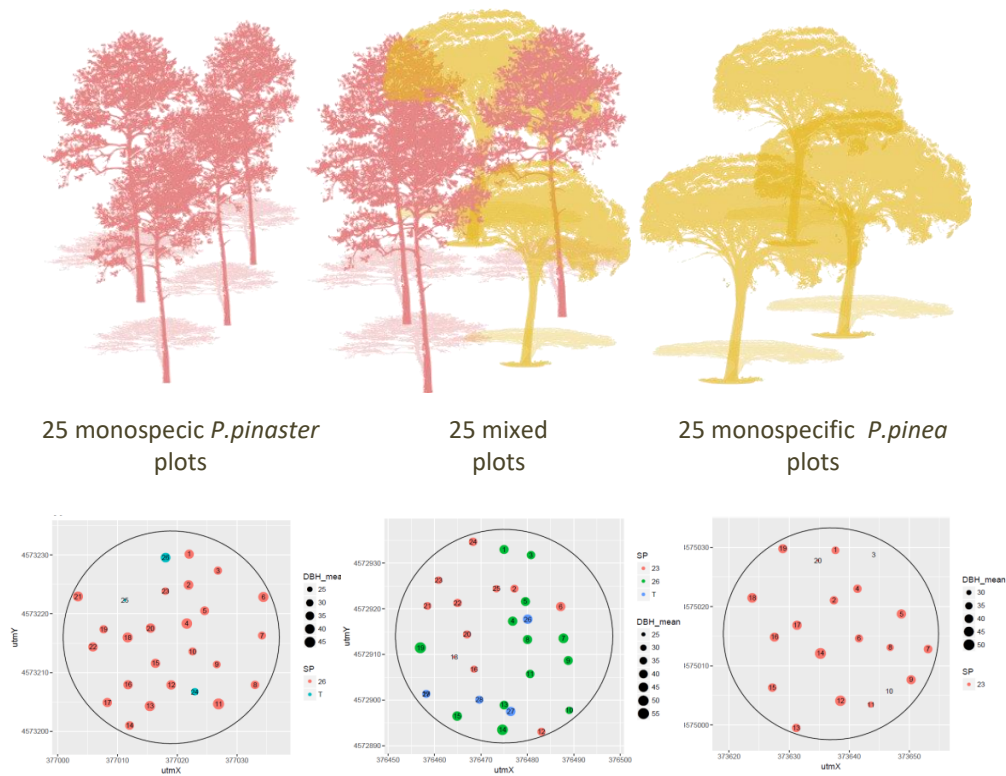
The second type of data used in the development of this thesis consists of 75 permanent plots installed by INIA-CIFOR in 18 public forests, located in the same region where natural regeneration plots were installed, that is the province of Valladolid (Fig 2.6).





**Figure 2.6.** Distribution of the monospecific and mixed *Pinus pinea* and *Pinus pinaster* permanent plots comprising our dataset for Valladolid province.

Monospecific, even-aged *P. pinea* plots (25 plots) were set up in 1996 in cooperation with the Forest Service of Valladolid (Junta de Castilla y León) and are regularly monitored (the most recent inventory was carried out in 2016). Mixed (25 plots) and monospecific *P. pinaster* plots (25 plots) were installed between the summer of 2015 and the spring of 2016 (Fig.2.7, Fig.2.8). In order to achieve uniform spatial distribution of the plot network, plots were established such that the whole range of stocking, age and site conditions in the area were covered. These plots cover include also non-tapped and resin tapped trees mixed. Moreover, the plots were installed in stands with no signs of recent (< 5 years) thinnings, regeneration cuttings or pruning. Plots are circular, with a variable radius ranging from 9 to 36 m to include at least 20 trees in monospecific plots, and at least 10 trees of the less represented species in mixed plots. In each plot, tree measurements included tree coordinates, species, diameter at breast height (DBH, cm), total height (Height, m), height to crown base (Live\_Branch, m) and four crown radius measurements (Crown Radius m). In addition inside each plot, all stumps coordinates and diameters were measured.



**Figure 2.7.** Example of the distribution of the trees inside of the mixed and monospecific *Pinus pinea* and *Pinus pinaster* permanent plots of our dataset.

Table 2.4 shows the main stand characteristics of the plots depending on the composition and species: monospecific *P. pinea*, mixed *P. pinea*, monospecific *P. pinaster* and mixed *P. pinaster*.

Two radial increment cores were extracted perpendicularly at breast height (1.30 m) from a subset of five trees per plot (the five closest to the center of the plot) in monospecific *P. pinea* and *P. pinaster* plots and of ten trees per plot (five of each species) in mixed plots. In order to calculate the stand age one increment core per plot and species was taken from the base of the tree. Total final number of cored trees was 250 in *P. pinaster* and 223 in *P. pinea*. The difference in the number of cores in *P. pinea* is related with the fact that *P. pinea* plots were initially installed in 1996. As a consequence, some *P. pinea* trees have died or have been cut in 2016, that is when cores were extracted. However, we decided to core uniquely the remaining trees from the original five closest-to-the-center of the plot trees. Therefore the number of *P. pinea* cores is unbalanced, i.e. we have not the same number of *P. pinea* cores per plot

**Table 2.4.** Main stand variables for *P. pinea* and *P. pinaster* in mixed and monospecific plots. Mean ( $\pm$ SD)

Composition	N(Trees/ha)	BA (m <sup>2</sup> /ha)	DG (cm)	Ho (m)	SDI	Age	SI
Monospecific <i>P. pinea</i>	162.14 (72.13)	7.49(2.47)	41.26 (10.26)	13.25 (9.80)	316.10 (104.33)	88.12 (29.7)	14.16 (2.51)
Monospecific <i>P. pinaster</i>	181.38 (107.99)	22.92 (11.39)	40.81 (6.70)	16.62 (1.56)	374.82 (179.86)	57.66 (18.7)	11.48 (1.08)
Mixed <i>P. pinea</i>	58.22 (19.12)	7.35 (2.40)	41.15 (7.38)	13.90 (2.47)	121.84 (37.31)	63.04 (28.7)	17.15 (4.18)
Mixed <i>P. pinaster</i>	66.15(18.31)	19.27 (6.99)	37.74 (4.51)	15.11 (2.20)	123.74 (36.03)	51.64 (17.7)	10.34 (1.45)

N:number of trees; BA: basal area; DG: mean square diameter; Ho: Dominant height; SDI: standar density index; SI:site index

### 2.3.2. Dendrochronological data

Increment cores were mounted on wooden supports and sanded until tree-ring boundaries were clearly visible and later measured using a LINTAB measuring table (Rinntech, 2003) with an accuracy of 0.01 mm. The quality of cross-dating and synchronization of the growth series were then assessed using the “*dplR*” R package (Bunn, 2010) (Fig. 2.9). This package was also used to calculate the mean series of annual radial increment for each individual, which were then transformed into series of basal area increment (BAI) since this variable is preferable for analyzing growth trends (Biondi and Qeadan, 2008):

$$BAI = \pi(r_t^2 - r_{t-1}^2) \quad [2.1]$$

Where  $r_t$  and  $r_{t-1}$  represent the stem radius at the end and the beginning of a given annual ring increment corresponding to rings formed in  $t$  and  $t-1$  years. To eliminate the biological growth trends and to produce stationery and residual tree ring width chronologies (Fritts, 1976) we applied a detrending procedure and autocorrelation removal using the Friedman supersmoother spline (Friedman, 1984) and autocorrelation modeling.

Through this procedure we obtained chronologies of dimensionless indices (CDI), preserving a common variance with interannual time scales. These chronologies have been used in Study III in order to evaluate the species responses to climate. However, in the development of Study IV, these procedures (detrending and autocorrelacion removal) have not been applied since

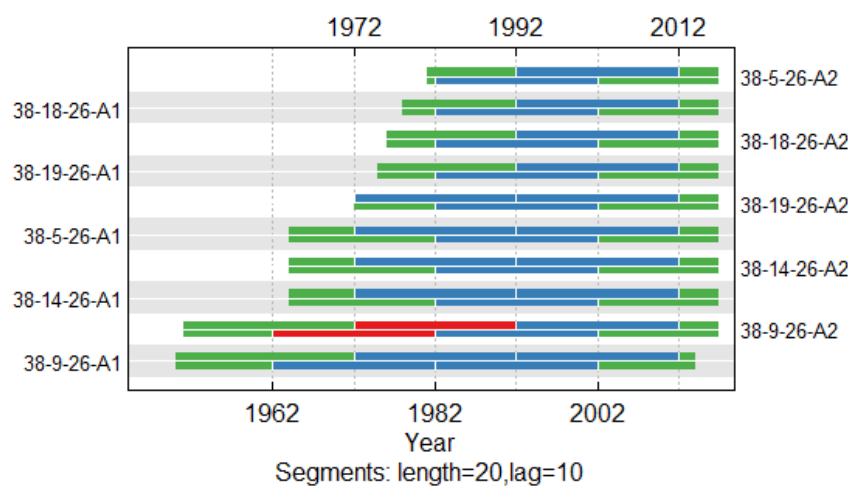




Figure 2.8. Mixed and pure stands of *P. pinea* and *P. pinaster*

we considered that these procedures will eliminate the competition effect, which is what we aim to analyze in the Study IV.

To observe the reliability of the chronologies, we calculated standard dendrochronological statistics (mean tree-ring width, mean correlation with master series, mean sensitivity, expressed population signal (EPS), etc.) (Speer, 2010; Wigley et al., 1984), grouped by species and composition.



**Figure 2.9.** Cross-dating between each segment (10 years) of each sample in a plot with the master chronology, blue segments showed significant correlation to the master chronology (critical value=0.35), red segments indicated the segment with potential dating problems (Bunn, 2010).

### 2.3.3. Backdating

In order to calculate competition indices values prior to the sampling date, the diameters of all trees in the plots were reconstructed for the last 15 years. To do this, ring widths of cored trees were converted to annual diameter increments. Then we follow the next steps:

- 1) We calculated the diameter increment for these 15 years for each of the cored trees. Using these increments and the diameters of the cored trees in 2015 we fitted linear models for each species and plot (Eq. 2.2).

$$id_{2001-2015} = a + b * Dn_{2015} \quad [2.2]$$

In this way, we have a specific equation [2.2] for each pure plot and a specific equation for each species and plot in mixed plots.

- 2) We applied the previous equations to the rest of non-cored trees (separately by plot and species). So, we can calculate the diameter increment  $id_{2001-2015}$  for these 15 years, based on the diameters in 2015 ( $Dn_{2015}$ ) for all non-cored trees.
- 3) For each cored tree (i) of species (s) in plot (j), we estimated the annual diameter growth rate in year (k) as the diameter increment in this year in relation to the total growth of the period 2001-2015 ( $Growth\ rate_{ikjs} = id_{ikjs} / id_{ijs2001-2015}$ ). Then, we averaged the annual diameter growth rates for each of the year (k) (period 2001-2015) by plot (j) and species (s) ( $Growth\ rate_{kjs}$ ). For example, tree 1 of plot 1, had an annual increment of 2 mm during 2001. In total this tree has grown 20 mm during the period 2001-2015. So, the growth of 2001 represents the 10% of the growth of the period 2001-2015 for tree 1 in plot 1. We repeated this procedure for each cored tree (i) in the plot 1 for the different fifteen years (k). After that, we calculated the species-specific annual series of plot diameter growth rates, i.e. we calculated the average annual diameter growth rates for each plot and species and year ( $Growth\ rate_{kjs}$ ).
- 4) Now, with the step 2 we know how much the non-cored trees have grown in 15 years ( $id_{i2001-2015}$ ). With steps 3, we know the percentage of growth for the different years, for the different species in each of the plots. So the diameter increment for a non-cored tree i of species s in year k and plot j is computed multiplying diameter increment for the interval ( $id_{ij2001-2015}$ ) per the mean diameter growth rate for that year, species and plot ( $Growth\ rate_{kjs}$ ).

[2.3]

$$id_{ikj} = Growth\ rate_{kjs} * id_{ij2001-2015}$$







### 3. Methods

#### 3.1. Spatio-Temporal variation of natural regeneration

##### 3.1.1. Regeneration occurrence and success

The occurrence of regeneration during the studied period was analyzed as a proxy to evaluate the capacity of the territory to produce regeneration. For this purpose, plots were classified into: Pp, plots where only *P. pinea* regeneration has been identified during the studied period; Pt, plots in which only *P. pinaster* regeneration has occurred; Mixed, plots where regeneration of both species has taken place; and No\_Reg, plots in which no regeneration has been recorded during the studied period. In this analysis, the identification of a single plant during the whole period was sufficient to consider that regeneration had occurred.

In addition, to evaluate the success of the regeneration at the end of period (2001-2015), we studied the presence of saplings of both species in the last year of the study (2015), analyzing the distribution of observed frequencies and presenting the percentage of plots in which saplings of *P. pinea*, *P. pinaster*, both species, or no saplings at all were present.

##### 3.1.2. Statistical analysis

The spatial pattern of natural regeneration was studied using the records from the last year of the study (2015) in order to observe the most recent spatial relationships at two different spatial scales: plot and forest stand. Spearman's correlation analysis was carried out to determine whether there was a significant correlation among the two species and developmental stages at plot level. To this end, we applied the analysis in plots where recruitment of at least one of the species is present, leaving out the 0, 0 combinations (no presence of regeneration at all) which could obscure the results. We also analyzed the association at plot level between the presence/absence of natural regeneration of *P. pinea* and *P. pinaster* and the composition of the stratum of adult trees by means of  $\chi^2$  contingency tables. Here, the composition of the adult tree stratum was classified into four categories: (i)

pure *P. pinea* (ii) pure *P. pinaster*, (iii) mixed and (iv) plots without adult trees. This analysis was carried out separately for seedlings and saplings.

Principal component analysis (PCA) was used to determine the dependence between adult stand characteristics and the natural regeneration of both species at stand level. Variables included in the PCA were the stand variables presented in Table 2, the number of years since regeneration fellings started, the level of grass, and the average number of seedlings and saplings of each species recorded in the last year of the study period (2015).

We also used PCA to identify the main temporal-varying factors influencing natural regeneration. In this case, we used the annual ingrowth, defined as the observed difference between the number of plants recorded in two consecutive years for each developmental stage and species. In the case of seedlings, this value can be interpreted as an indicator of seedling recruitment, whereas for saplings it is an indicator of the change from seedling to sapling. As potential temporal influencing factors, we evaluated the annual and seasonal averaged values of the different climatic variables corresponding to the current and the previous year (Table 2.2).

The Kendall coefficient of concordance,  $W$ , (Sokal and Rohlf, 1995) was used to evaluate the degree of concordance in inter-annual variation of regeneration (synchrony). Kendall's  $W$  is a nonparametric measure of agreement among several complete sets of rankings of a number of objects, in this case, series of a number of individuals by species or development stages - seedlings or saplings-. Kendall's  $W$  ranges from 0 (no association) to 1 (perfect association). In order to determine the existence of a common temporal pattern, the analysis was performed in three different ways. First, we calculated the Kendall coefficient of concordance,  $W$ , to determine whether each regeneration stage, seedlings or saplings, of each of the two species follows the same temporal pattern between the three natural units (Case A). Here, the p-value indicates whether synchrony exists (or not) between the three natural units in each of the analyzed cases. Subsequently, within each natural unit, we used Kendall's  $W$  to study: i)

whether the two developmental stages of regeneration of the same species shared the same temporal pattern (intraspecific synchrony, Case B); and ii) the occurrence of an interspecific synchrony between species at the same developmental stage (Interspecific synchrony, Case C).

### **3.2. Modeling natural regeneration occurrence**

#### **3.2.1. Survival analysis**

Allison (1982) and Lawless (2003) described the underlying concepts of this type of analysis. To illustrate the basis of this technique, we defined  $T$  as a non-negative random variable that represents the precise time at which the event of interest occurred. In our case,  $T$  is the moment at which natural regeneration (of each species separately) occurs in a particular plot, defined as the instant when we observe regeneration of the subject species for the first time. We defined a binary variable  $y_{ijk}$  which adopts the value 1 if the plot has regenerated during the studied period or 0 if the plot had not taken place during this interval. The block, plot and year are defined by the  $i$ ,  $j$  and  $k$  indices, respectively. Hence, the probability that natural regeneration occurred at or before time  $t$ , is defined by the cumulative distribution function of  $T$  at time  $t$ , i.e.  $F(t) = P(T \leq t)$  while the probability of a particular plot remaining without regeneration after time  $t$  is represented by what is called the survival function  $S(t)$ , i.e.  $S(t) = 1 - F(t)$  (Lawless, 2003). Thus, the marginal probability that the regeneration occurs between  $t_1$  and  $t_2$  is defined by  $S(t_1) - S(t_2)$ .

Another fundamental concept of survival analysis is the hazard function  $h(t)$ , which specifies the probability of regeneration at time  $t$ , provided that the event has not occurred in a previous period. The hazard function and the survivor function are related as follows (Lawless, 2003, p.10):

$$S(t) = \exp\left(-\int_0^t h(x)dx\right) \quad [3.1]$$

Through this function, we can assume that the probability of a plot remaining without regeneration at time  $t$  is a decreasing function of the sum of all instantaneous hazards that occurred prior to time  $t$ .

### 3.2.2. Hazard function definition

There are many different formulations for the hazard function in survival analysis (Singer and Willett, 1993). In this study, we used a formulation that is commonly known as proportional hazards (PH). This type of model leaves the baseline hazard function  $h_0$  unspecified, obtaining a semi-parametric model where the covariates enter linearly. This baseline hazard function is multiplicatively affected by a proportional effect.

The expression for the PH model was given by:

$$h_{ijk} = h_0(t, g_{ijk}, \gamma) e^{x_{ijk}\beta} \quad [3.2]$$

In this study, we considered the baseline hazard function  $h_0$  as being linearly affected by time-varying covariates, mainly climatic variables such as mean, minimum and maximum seasonal and annual temperatures as well as mean seasonal precipitation, which vary within the intervals on an annual basis. In the expression given above, this baseline hazard function  $h_0$  is defined by the vectors  $g_{ijk}$  (explanatory variables) and  $\gamma$  (estimable parameters). In addition to this, plot-related variables were considered to affect the proportional effect over the baseline hazard function. In this case,  $x_{ijk}$  is the vector related with the fixed constant on-time explanatory variables while  $\beta$  is the vector of the estimable parameters. Among these, we tested the potential number of *P. pinea* and *P. pinaster* adult trees growing in the plot and the grass cover on the forest floor (three levels; high, medium and low). Similarly, another dummy variable (Mix) was created to include the effect of the mixture (the presence of both *P. pinea* and *P. pinaster* adult trees in the plot) in the model. The value 1 indicates the existence of adult trees mixture in the plot, while 0 indicates an absence of mixture in the plot.

Besides, to take into account the existence of spatial dependence between the regeneration of *P. pinea* and *P. pinaster*, we modeled both species simultaneously. Then, in order to include the effect of the species we created a variable (*Sp*) which adopts the value 1 if the observed regeneration is of *P. pinaster* or 0 if the regeneration is *P. pinea*. This was done by simultaneously modeling parameters  $\gamma$  and  $\beta$  for both species, obtaining specific parameters (for *P. pinea* and *P. pinaster*) affecting each variable included in the model:

$$\begin{aligned} \gamma_i * g &= (\gamma_m + \gamma_{msp} * Sp) * g_{ijk} \\ \beta_i * X &= (\beta_m + \beta_{msp} * Sp) * X_{ijk} \end{aligned} \tag{3.4}$$

The estimation of the vector of parameters  $\gamma$  and  $\beta$  is based on the maximization of the likelihood function.

We also assumed the existence of spatial correlations due to the hierarchical structure of the data. In this context, the probabilities of regeneration occurrence in plots belonging to the same forest block during the same interval could be correlated. In order to deal with this violation of the assumption of independence, random effects  $u_j$  accounting for the block level entered the model affecting the intercept of the baseline.

$$h(x_{ijk}, g_{ijk}, \beta, \gamma, u_i) \tag{3.5}$$

This random effect  $u_i$  was assumed to be normally distributed with mean zero and variance  $\sigma_u^2$ . The final expression of the model was the following:

$$F(t) = 1 - e^{\left(-\sum_1^t \gamma_0 + \gamma_o * Sp + (\gamma_m + \gamma_{msp} * Sp) * g_{ijk} + u_i * e^{((\beta_m + \beta_{msp} * Sp) * X_{ijk})}\right)} \tag{3.6}$$

### 3.2.3. Model fitting

We tested different models, from the simplest (null model), without covariates, to the most complex (including all the potential covariates). Starting with the null model, we first tested the plot-related covariates. In a second step, the covariates representing the mixture effect were tested. Then we tested the climate covariates. When this selection procedure was complete, we tested the presence of a block random effect in the model. We used the Akaike information criterion (AIC), the Bayesian information criteria (BIC) as well as the level of significance of the parameter estimates for model comparison. All calculations were carried out using PROC NL MIXED in SAS 9.2 (SAS Institute Inc, 2009).

### 3.2.4. Model evaluation

Here, regeneration occurrence predictions are conditional on the expectation of the block random effect  $u_i$ , which enters in the hazard function  $h(x_{ijk}, g_{ijk}, \beta, \gamma, u_i)$ . However, these random effects are usually unknown. If the model is not linear, as in our case, population-averaged predictions cannot be computed from the marginal response given by the fixed effects alone, otherwise, population-averaged predictions cannot be directly obtained by setting the random effects to their expectations, i.e., zero (Fortin, 2013; McCullagh, 2008). In this context, the population-averaged predictions can be computed from the conditional expectation of  $y_{ijk}$  marginalized over the distribution of  $u_i$ , which is given by the following integral:

$$E[y_{ijk} | x_{ijk}, g_{ijk}] = \int h(x_{ijk}, g_{ijk}, \beta, \gamma, u_i) \text{pdf}(u_i, \sigma_u^2) du_i \quad [3.7]$$

Where  $\text{pdf}(u_i, \sigma_u^2)$  is the probability density function of a normal distribution with mean 0 and variance  $\sigma_u^2$ . This integral has no closed form solution, although it can be approximated through numerical integrations. In this case, we used the Gauss-Hermite quadrature, which is used to approximate integrals of functions by a weighted average of the integrand over a predetermined grid (Pinheiro and Bates, 1995). This technique allows us to evaluate the predictive ability of the model for new locations.

To perform the evaluation of the model, we ran a cross-validation. The dataset was split into 122 groups, omitting the plots belonging to a different block in each of the groups. We then fitted the model 122 times. The fitted models were subsequently used to predict the probability of regeneration occurrence of each species at the end of the studied period in each of the omitted plots, using the abovementioned Gauss-Hermite quadrature. These probabilities were then averaged for each omitted block and compared with the corresponding percentage of plots actually presenting regeneration in those management units. To evaluate the accuracy of the model we performed a linear regression between observed and predicted values:

$$\textit{Observed} = a + b * \textit{predicted} \quad [3.8]$$

We determined the level of agreement between the model predictions and the observations in the forest management unit, testing if  $a = 0$  and  $b = 1$ . In addition, we used graphical methods for improved visualization of the results.

Finally, to determine the sensitivity of the model to a particular climate covariate (mean spring and autumn temperature and maximum summer temperature), we changed its value within the range observed in the dataset, maintaining the other variables constant on their mean value. We then simulated the probability for the occurrence of natural regeneration within the ranges delimited for each climate variable.

### **3.2.5. Natural regeneration projection under future climate scenarios**

To illustrate the regeneration success which could be expected at the end of the 21<sup>st</sup> century, we used the model to simulate the probability of regeneration occurrence in both species under two different climate scenarios. To generate the simulations we used all the plots, taking the stand variables observed for each plot in the last inventory (2015) and maintaining these constant while varying the climate variables. The probability of regeneration occurrence was then evaluated for different compositions in the stratum of seed trees, pure *P. pinea*, pure *P. pinaster* and mixed. The predictions were calculated for 10-year intervals at the end of the

21st century (2071-2080). The first climate scenario was provided by the IPCC as the representative concentration pathways (RCP) 8.5 (Pachauri et al., 2014). The second scenario represents a constant climate with respect to the 1971 – 2001 period and is termed the historical scenario. Climate data projections for the RCP 8.5 and the historical scenarios were obtained from the AdapteCCa project (<https://www.adaptecca.es/>), which implements the climate projections provided by the Spanish Meteorological Agency ([www.aemet.es](http://www.aemet.es)). This source of information provides daily precipitation and temperature of observational data as well as regional projections for different climate scenarios on the same grid of 0.11° as that used in the EURO-CORDEX models. Climate variables included in the regeneration model were then calculated from the daily data of the two scenarios for the ten years used in the simulations.

### **3.3. Growth responses to climate**

#### **3.3.1. Impact of drought on tree growth. Selection of pointer years**

In order to evaluate the most important reductions in BAI during the 20<sup>th</sup> century, we determinate the “pointer years” (years with a notable increase or decrease in growth at individual level) using the pointRES R package (Van Der Maaten-Theunissen et al., 2015). This method relates tree growth in a particular year to the average growth of a specific number of preceding years. In this thesis, we determined the common pointer years as those years in which at least 60 % of the *P. pinea* and *P. pinaster* trees showed a BAI decrease of at least 60 % relative to the average BAI in the 3 previous years. To define these pointer years we used data exclusively from monospecific plots, in order to analyze whether mixed composition changes the growth pattern, and we selected the years in which both species showed this BAI decrease. To ensure that these periods corresponded to droughts, and were not caused by other local drivers, we then compared those negative pointer years with negatives values of previously calculated Palmer drought severity index (SPEI). Selected years were used to evaluate the relationship between the reduction in tree growth and the intensity of drought.



### 3.3.2. Quantification of growth responses to drought (Resistance, recovery and resilience)

In order to evaluate the performance of individual trees under episodic drought stress, we calculated numerical indices for resistance, recovery, and resilience (Lloret et al. 2011) for all sampled cored trees. The indices were obtained through the annual basal area increment indices (IBAI) ( $\text{cm}^2 \cdot \text{year}^{-1}$ ) for all individual trees, i.e. after eliminating the biological growth trends to produce the stationary and residual chronologies (Study III). We then averaged the relative IBAI values for a period of 3 years prior to the drought period (*PreDr*), for the year of drought (*Dr*) defined previously, and for a period of 3 years following the drought period (*PostD*). These values were used to calculate the Resistance index,  $R_t = \text{Dr}/\text{PreDr}$ , to quantify the decrease from the pre-drought period to the drought period. Values of for  $R_t$  close to 1 indicate complete resistance, while values falling below 1 indicate lower resistance. The growth reaction following the drought event is explained by the Recovery index,  $R_c = \text{PostDr}/\text{Dr}$ . Here,  $R_c = 1$  implies the persistence of a low level of growth even after the drought,  $R_c < 1$  implies further decline and  $R_c > 1$  can be interpreted as recovery after the drought period. Finally, the ratio between post-drought and pre-drought increment is represented by the Resilience index,  $R_s = \text{PostDr}/\text{PreDr}$ . In this case, full recovery or even an increase after the episodic stress is indicated by values of  $R_s \geq 1$ , while  $R_s < 1$  reveals growth decline and low resilience. We evaluated through t-tests the existence of differences, on the one hand, between species, and on the other hand, between mixed and monospecific composition both in *P. pinea* and *P. pinaster*.

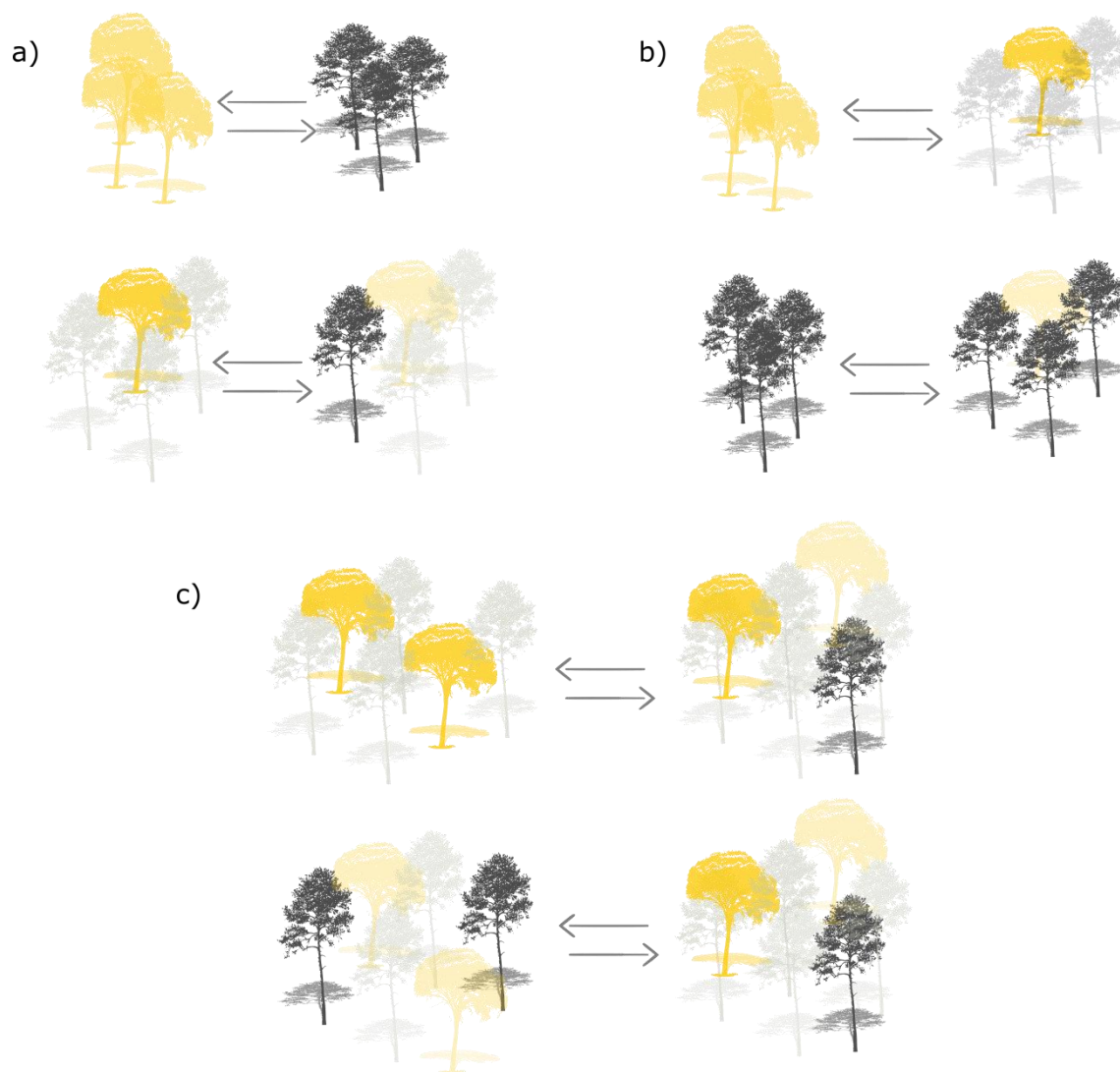
### 3.3.3. Tree growth synchrony

On the other hand, we define synchrony,  $\hat{a}_c$ , as the presence of a relevant common signal for a time-varying trait (in our case annual indices of basal area increment) in a group of tree-ring chronologies. As we want to study the behavior of the two species growing in mixed and monospecific stands, we estimated synchronies at plot level, that is, the synchrony between the tree-ring chronologies in a specific plot, for a period covering 30 years. Therefore, we

obtained a synchrony value for each monospecific *P. pinea* and *P. pinaster* plot, whereas for each mixed plot we estimated the intra and inter-specific synchronies, evaluating the degree of common signal within and between species (grouping factor), thereby obtaining three synchrony values for each mixed plot ( $P.pinea - P. pinea / P. pinea - P. pinaster / P.pinaster - P.pinaster$ ).

Synchrony was estimated as the inter-chronology temporal correlation. In this case, to analyze the pattern of covariation among the tree ring chronologies by plot, between and within species in the case of mixed plots, we used different variance-covariance (VCOV) mixed models according to the approach by Shestakova et al. (2016). The different VCOV models for each plot were then compared using standard criteria for model selection (Akaike and Bayesian information criteria) (Burnham et al., 2002). We obtained the synchrony values ( $\hat{\alpha}_c$ ) from the VCOV of the best mixed model (Alday et al., 2018; Shestakova et al., 2018b). Values close to 1 represent a near-perfect synchrony between chronologies while values close to 0 indicate asynchrony. As for the Lloret indices, we tested differences between groups using 5 groups of synchronies according to the species and composition (*P. pinea* intra-specific in monospecific / *P. pinaster* intra-specific in monospecific / *P. pinea* intra-specific in mixed / *P. pinaster* intra-specific in mixed / *P.pinea-P.pinaster* inter-specific in mixed). We compared:

- i) The synchronies between the two species, differentiating those trees that grow in mixed composition versus those that grow in monospecific composition (i.e. monospecific *P. pinea* versus monospecific *P. pinaster* and mixed *P. pinea* versus mixed *P. pinaster*) (Fig 3.1, a)
- ii) The intra-specific synchronies for each species growing in monospecific and mixed composition ( i.e. monospecific *P. pinea* versus mixed *P. pinea* and monospecific *P. pinaster* versus mixed *P. pinaster*) (Fig 3.1, b)
- iii) Finally, for each mixed plot, the intra and inter-specific synchronies for both *P. pinea* and *P. pinaster* (Fig 3.1, c).



**Figure 3.1.** Schematic representation of the synchrony analysis comparing a) synchronies of *P. pinea* and *P. pinaster* in monospecific (above) and mixed (below) composition; b) synchronies in mixed and monospecific composition, separately for *P. pinea* (above) and *P. pinaster* (below); c) intra and inter-specific synchronies in mixed plots.

### 3.3.4. Modeling approaches

We used models to evaluate the effects of different factors, apart from composition, on the Lloret indices values as well as on the synchrony values. Hence, we used linear mixed models to evaluate whether  $R_b$ ,  $R_c$  and  $R_s$  were related to any of the following explanatory variables ( $X$ ): tree age, size, stand density (estimated by the Reineke Stand Density Index, SDI), composition (mixed or monospecific) and a selected pointer year (categorical). We fitted the models separately for each of the species. We also assumed the existence of spatial correlations due to the hierarchical structure of the data since it is expected that a correlation will exist

between the measurements of the trees belonging to the same plot. Thus, in order to deal with this violation of the assumption of independence, random effects accounting for the plot level were included in the model.

The expression of the models was then formulated as:

$$I_{ij} = X_{ij}\beta + u_i + \varepsilon \quad [3.9]$$

Where  $I_{ji}$  is the observation for the response variable (one of the three indices) recorded for the  $i^{\text{th}}$  tree within the  $j^{\text{th}}$  plot. In this case  $X_{ij}$  is the vector containing the observed values for the explanatory covariates while  $\beta$  is the vector of the estimable parameters. Finally,  $v_j$  represents the plot random effect, normally distributed with mean zero and variance  $\sigma_u^2$ , and  $\varepsilon$  represents the independent and identically distributed residual error.

The sequential procedure used in the model construction was as follows: first, we fitted the complete model including all the explanatory variables in the fixed part, and we defined the best structure for the random components, finally selecting the inclusion of a single plot random effect affecting the intercept of the model. We then used a backward procedure for the selection of fixed effects in each model. During this procedure, we used the Akaike information criterion (AIC) as well as the significance of the parameter estimates to select the best model.

In order to quantify the effects of stand characteristics on synchrony in *P. pinea* and *P. pinaster*, we built a logistic regression model for each species. We used the logit transformation as it is widely used to model percentages and ratios with values ranging between 0 and 1. We related the  $\hat{a}_c$  values previously obtained in the monospecific and mixed plots for each species to the different stand characteristics, such as age, the composition of the plot (mixed or monospecific), stand density index (SDI), and quadratic mean diameter. The expression of the models was the following:

$$\text{logit}(\hat{a}_j) = \ln\left(\frac{a}{1-a}\right) = X_j\beta \quad [3.10]$$

Where  $\hat{a}_j$  is the observation for the response variable (Synchrony) recorded in the  $j^{\text{th}}$  plot. In this case  $X_j$  is the vector containing the observed values for the explanatory covariates while  $\beta$  is the vector of the estimable parameters. As previously mentioned, we fitted one model separately for *P. pinea* and *P. pinaster*.

In order to avoid collinearity between all the explanatory variables included in the model, we checked the correlation between them. This procedure was performed both for the variables included in the Lloret model (linear mixed model) and for the variables included in the synchrony model (logistic model).

The DendroSync package was used to calculate synchronies at plot level (Alday et al., 2019). All models were processed using R (Team R Core, 2018) and the lme4 package (Bates et al., 2015). Normality and homogeneity of the residual variance were checked by visual inspections of diagnostic plots of residuals against fitted values (Zuur et al., 2010).

### **3.4. Analysis of tree interactions**

#### **3.4.1. Competition indices**

The literature divided the competition indices in two classes; (i) distance-independent indices that are simple functions of stand level variables and/or size of the subject tree and do not require individual tree coordinates, and (ii) distance-dependent indices that incorporate the spatial information of neighboring trees within the area (Contreras et al., 2011; Soares and Tomé, 1999). Therefore, the selection of competition indices is based on their favorable performance in previous studies, on the nature of the competition they represent, as well as the type of data available, which it is always a determining factor (del Río et al., 2014a; Riofrío et al., 2017). In the development of this thesis, we used distance-independent competition indices based on the stand density index concept.

In this way, we compute a) the stand density index (SDI) (Reineke, 1933); b) and the stand density index of trees larger than the target tree (SDIL) (Pretzsch and Biber, 2010). The SDI was used as a proxy of the size-symmetric competition and determines the degree of crowding

through comparing with standards conditions. On the other hand, SDIL is frequently used as a proxy of size-asymmetric competition to inspect how larger (SDIL) trees compete for resources. These indices were calculated using the following equations:

$$SDI = N \left( \frac{25}{Dg} \right)^E \quad [3.11]$$

$$SDIL = N_l \left( \frac{25}{Dg_l} \right)^E \quad [3.12]$$

Where  $N$  is the number of trees per hectare and  $N_l$  is the number of trees larger than the target tree per hectare. Similarly,  $Dg$  is the quadratic mean diameter of the trees in the plot, and  $Dg_l$  the quadratic mean diameter of trees larger than the target tree in the plot. Finally, we used the generic figure proposed by Reineke  $E = -1.605$  for the coefficient  $E$  in eq. [3.11-3.12] for both species. Competition indices were computed for every tree in the plots, at the beginning of each growth period analyzed (from 2001 to 2015). In this way, SDI and SDIL were calculated for each tree as a whole, and also separated as inter and intraspecific competition. Therefore, the subscripts *intra* y *inter* refer to the competition indices calculated only with competitor trees of the same species only or with competitor trees of the other species, respectively. In the Table 3.1 is shown a description of the individual tree data at the beginning of the studied growth period for different species along with the stand composition.

### 3.4.2. Model structure

In order to test several hypotheses regarding individual tree growth, we use a modeling approach with multilevel linear mixed models (MLMM), with the aim to take into account the spatiotemporal structure of the data, since the observations coming from the same tree, plot and year are likely to be more similar among them than the average. Through this approach, we included different random effects action at tree ( $i$ ), plot ( $j$ ) and year ( $k$ ). The basic structure for our model was:

$$y_{ijk} = x_{ijk}\beta + u_i + v_j + w_k + e_{ijk} \quad [3.13]$$

**Table 3.1.** Tree characteristics and competition status, total and by species.

		DBH (cm)	BAI (cm <sup>2</sup> year <sup>-1</sup> )	SDI <sub>intra</sub> (stem ha <sup>-1</sup> )	SDI <sub>inter</sub> (stem ha <sup>-1</sup> )	SDI <sub>intra</sub> (stem ha <sup>-1</sup> )	SDI <sub>inter</sub> (stem ha <sup>-1</sup> )
<i>P. pinea</i> in mixed plots	Mean	40.19	2.62	66.18	49.70	127.63	120.13
	Desv	9.45	1.5	45.13	49.77	40.57	40.34
	Min	19.16	0.19	0.0	0.0	50.95	46.56
	Max	63.3	15.51	183.89	192.05	196.13	199.32
<i>P. pinea</i> in monospecific plots	Mean	40.24	1.71	167.88		325.78	
	Desv	10.90	1.17	121.12		116.40	
	Min	18.86	0.03	0.0		155.03	
	Max	84	11.78	630.70		648.90	
<i>P. pinaster</i> in mixed plots	Mean	36.94	2.17	62.57	86.99	120.07	113.19
	Desv	6.79	1.53	40.37	55.40	31.95	34.46
	Min	21.80	0.004	0.0	0.0	46.56	50.95
	Max	66.8	13.25	192.05	196.13	199.32	196.13
<i>P. pinaster</i> in monospecific plots	Mean	39.46	2.19	208.02		383.76	
	Desv	10.97	1.93	160.37		177.91	
	Min	21.38	118.61	0.0		190.69	
	Max	244.5	0.02	1055.99		1085.46	

desv – standard deviation; min – minimum value; max – maximum value.

Here,  $y_{ijk}$  is the observation for the response variable,  $\log(BAI)$  in our case, recorded in the  $i^{\text{th}}$  tree, within the  $j^{\text{th}}$  plot in the  $k^{\text{th}}$  year. In the expression given above  $x_{ijk}$  is the vector containing the observed values for the explanatory covariates (the section of the tree, climate variables, competition terms, etc.) in the  $ijk^{\text{th}}$  observation while  $\beta$  is the vector of the estimable parameters. In order to deal with the departure of the assumption of independence,  $u_i$ ,  $v_j$ ,  $w_k$  represent the random effects acting a tree, plot and year scales of variability. These random effects are distributed following a normal distribution with mean zero and variance  $\sigma_u^2$ ,  $\sigma_v^2$  and  $\sigma_w^2$  respectively. Finally,  $e_{ijk}$  is the error term such that  $e_{ijk} \sim N(0, \sigma^2)$ , with  $\sigma^2$  the residual variance. Apart from these random effects, specific year random effects ( $p_k$ ,  $x_k$ ,  $m_k$ ,  $n_k$ ,  $r_k$  and  $q_k$ ) affecting the slope of the model associated with different competition indices (SDI, SDIL, SDI<sub>inter</sub>, SDI<sub>intra</sub>, SDIL<sub>inter</sub>, SDIL<sub>intra</sub>) were also included.

The statistical method used for model fitting followed the next steps: first, we started to fit the complete model, including all the explanatory in the fixed part in order to define the best

structure for the random effect. Later we used the backward procedure to explore the effect of tree size attributes, competition indices as well as climate variables in order to test different hypotheses.

### 3.4.3. Competition hypothesis

Different models were used to test the following hypothesis i) the individual basal area increment of each of the two species was explained by size-symmetric and size- asymmetric competition; ii) there is an effect of the mixture, i.e. intra and inter-specific competition are different, iii) the effect of competition in dry and wet years is not constant in monospecific and mixed stands. Model comparisons to contrast the different hypotheses were carried out separately for each species.

For contrasting the first hypothesis, we compared three different models (3.14 – 3.16) including only size-symmetric competition (SDI, model [3.14]), only size-asymmetric competition of larger trees (SDIL, model [3.15]) or a both indices (3.16), jointly considering in this case the competition exerted by trees irrespective of its species:

$$\log(BAI_{ijk}) = \alpha + u_i + v_j + w_k + g_{ijk} + pp_k + [c + p_k] * SDI + e_{ijk} \quad [3.14]$$

$$\log(BAI_{ijk}) = \alpha + u_i + v_j + w_k + g_{ijk} + pp_k + [c + x_k] * SDIL + e_{ijk} \quad [3.15]$$

$$\log(BAI_{ijk}) = \alpha + u_i + v_j + w_k + g_{ijk} + pp_k + [c + p_k] * SDI + [c + x_k] * SDIL + e_{ijk} \quad [3.16]$$

Here,  $g_{ijk}$  is the section of the tree ( $\text{cm}^2$ )  $i$  in the plot  $j$  during the year  $k$ , and  $pp_k$  refers to the different precipitations (mm) tested in the models (annual precipitation and the different seasonal precipitation).

To analyze the effect of the mixture on tree growth, we compared two different models including competition indices formulated considering the species. Therefore, SDI and SDIL indices were split into intra-specific and inter-specific competition components, following a similar approach to that proposed by del Río et al. (2014). Our hypothesis of mixture effect



was contrasted by comparing models 3.14-3.15 (considering the effects of intra-and interspecific competition to be equivalent) against those models where we considered that intra-and interspecific competition effects were different (eqs. 3.17 – 3.18):

$$\log(BAI_{ijk}) = \alpha + u_i + v_j + w_k + g_{ijk} + pp_k + [c + m_k] * SDI_{intra} + [d + n_k] * SDI_{inter} + e_{ijk} \quad [3.17]$$

$$\log(BAI_{ijk}) = \alpha + u_i + v_j + w_k + g_{ijk} + pp_k + [c + r_k] * SDIL_{intra} + [d + q_k] * SDIL_{inter} + e_{ijk} \quad [3.18]$$

To test whether species tree basal area increment is better explained by size-symmetric and/or size-asymmetric competition and whether overall competition or intra and inter-specific competition separately are better in explaining, we fitted the following models (eqs. 3.19 – 3.21):

$$\log(BAI_{ijk}) = \alpha + u_i + v_j + w_k + g_{ijk} + pp_k + [c + m_k] * SDI_{intra} + [d + n_k] * SDI_{inter} + [c + x_k] * SDIL + e_{ijk} \quad [3.19]$$

$$\log(BAI_{ijk}) = \alpha + u_i + v_j + w_k + g_{ijk} + pp_k + [c + p_k] * SDI + [c + r_k] * SDIL_{intra} + [d + q_k] * SDIL_{inter} + e_{ijk} \quad [3.20]$$

$$\log(BAI_{ijk}) = \alpha + u_i + v_j + w_k + g_{ijk} + pp_k + [c + m_k] * SDI_{intra} + [d + n_k] * SDI_{inter} + [c + r_k] * SDIL_{intra} + [d + q_k] * SDIL_{inter} + e_{ijk} \quad [3.21]$$

In order to evaluate the effects of the different modes of competition, i.e. size-symmetric, size-asymmetric, and intra and inter-specific competition, each of the 8 models 3.14 – 3.21 were fitted separately for *P. pinea* and *P. pinaster*.

To allow comparisons of the results, models were fitted by using ML (maximum likelihood) method of the 'lmer' function in the "lme4" package (Pinheiro et al., 2018). Model comparison

to contrast hypotheses was carried out by means of AIC. Through the t-test it was also checked whether all the fixed regression parameters were significant at level  $P = 0.05$ .

Finally, for testing hypothesis (iii), the effect of competition in dry and wet years in mixed and monospecific stands, specific year random effects ( $p_k, x_k, m_k, n_k, r_k$  and  $q_k$ ) affecting the slope of the model associated with different competition indices (SDI, SDIL, SDI<sub>inter</sub>, SDI<sub>intra</sub>, SDIL<sub>inter</sub>, SDIL<sub>intra</sub>) were plotted jointly to the selected precipitation for the whole period of study.

All models were evaluated by checking the distribution of residuals to confirm error independence in residual versus fitted values plots, equal variance of the error (stand residuals) versus fitted values plots, and normal distribution of the residuals in QQ plots (Draper et al., 1998).

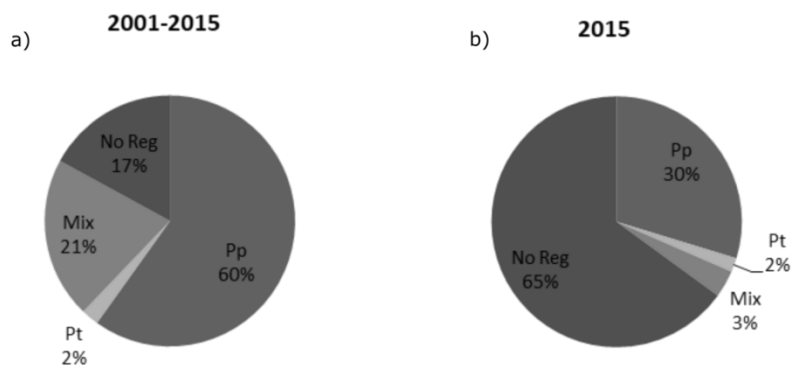
## 4. Results

### 4.1. Development of *P. pinea* and *P. pinaster* natural regeneration

During the whole studied period (15 years), natural regeneration of either of the two studied species at any developmental stage was recorded in 83% of the sampling plots. Hence, 332 out of the 1,939 plots (17 %) showed no regeneration at all of either *P. pinea* or *P. pinaster* during the whole period (Figure 4.1a).

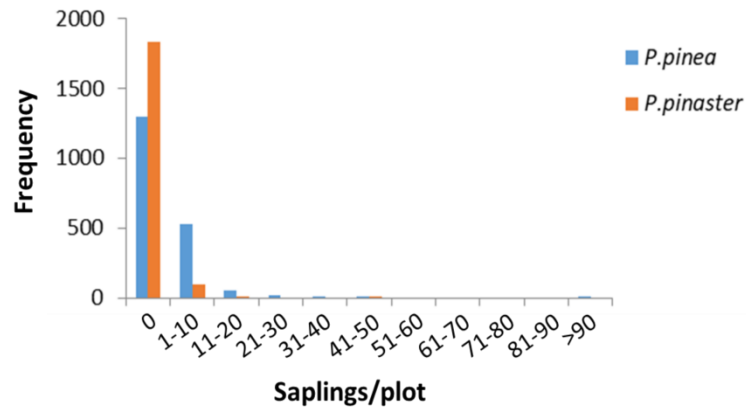
When each species was analyzed separately, the number of plots with *P. pinea* regeneration was 1,598 plots, while *P. pinaster* regeneration was recorded in 445 plots (23% of the plots) during this period (Fig 4.1a). Only 40 (2%) of these plots presented pure *P. pinaster* regeneration while in the rest of plots, 405 (21%), the natural regeneration observed was of mixed composition (Fig 4.1a).

As regards successfully established saplings, only 35% of the plots had established saplings of any species at the end of the monitoring period (Fig 4.1b).



**Figure 4.1.** Diagrams showing frequencies of occurrence of regeneration for (a) seedlings and saplings during the complete study period and (b) saplings during the last studied year, 2015. (Pp) refers to plots where only regeneration of *P. pinea* has been observed; (Pt) refers to plots where only regeneration of *P. pinaster* has been observed; (Mix) plots where regeneration of both species has been observed; (No Reg) plots without regeneration.

*P. pinaster* saplings were only observed in 5% of the plots, while the figure was 33% in the case of *P. pinea*. In this regard, it was possible to identify a pattern of zero



**Figure 4.2.** Histogram of frequencies for the number of *P. pinea* and *P. pinaster* saplings observed per plot in the last year of the study (2015).

and asymmetry in the distribution of frequencies for the number of established saplings per plot, which would indicate that most of the successful natural regeneration occurred in only a few parts of our study area (Fig 4.2).

#### 4.1.1. Spatial association at plot level and stand level

Using Spearman's rank correlation coefficient to check for significant spatial correlation between the regeneration stages and species at plot level, we identified a significant negative correlation between the number of *P. pinea* seedlings and *P. pinaster* seedlings and saplings. Conversely, we found a significant positive correlation between the number of *P. pinea* and *P. pinaster* saplings. Moreover, a significant positive, strong correlation was observed between seedlings and saplings belonging to the same species (Table 4.1).

**Table 4.1.** Correlation matrix between the numbers of plants of the different regeneration development stages of each species during the last year of the study, 2015.

	<i>P. pinea</i> (Seedlings)	<i>P. pinea</i> (Saplings)	<i>P. pinaster</i> (Seedlings)	<i>P. pinaster</i> (Saplings)
<i>P. pinea</i> (Seedlings)	1			
<i>P. pinea</i> (Saplings)	<b>0.21</b>	1		
<i>P. pinaster</i> (Seedlings)	-0.09	-0.01	1	
<i>P. pinaster</i> (Saplings)	<b>-0.06</b>	<b>0.13</b>	<b>0.42</b>	1

Significant correlations in bold ( $P \leq 0.05$ )

The association between natural regeneration and the composition of the stratum of adult trees at plot level is presented in Table 4.2. The significant values indicate the existence of

dependence between different natural regeneration stages and the presence of adult trees. In the case of *P. pinaster*, a strong association was observed between the natural regeneration and the composition of the adult stratum, specifically with conspecific adult trees (203 plots with regeneration vs 63.4 expected plots under a random distribution of regeneration). Moreover, there was scarce presence of *P. pinaster* regeneration in plots with only *P. pinea* adult trees (66 observed plots vs 219.4 expected under a random distribution). As regards *P. pinea*, the contingency table showed no significant differences among observed and expected values for saplings, while an influence of conspecific adult trees over the presence of *P. pinea* seedlings was observed. A mixed composition of adult trees had a beneficial effect on natural regeneration, especially in the case of *P. pinaster*.

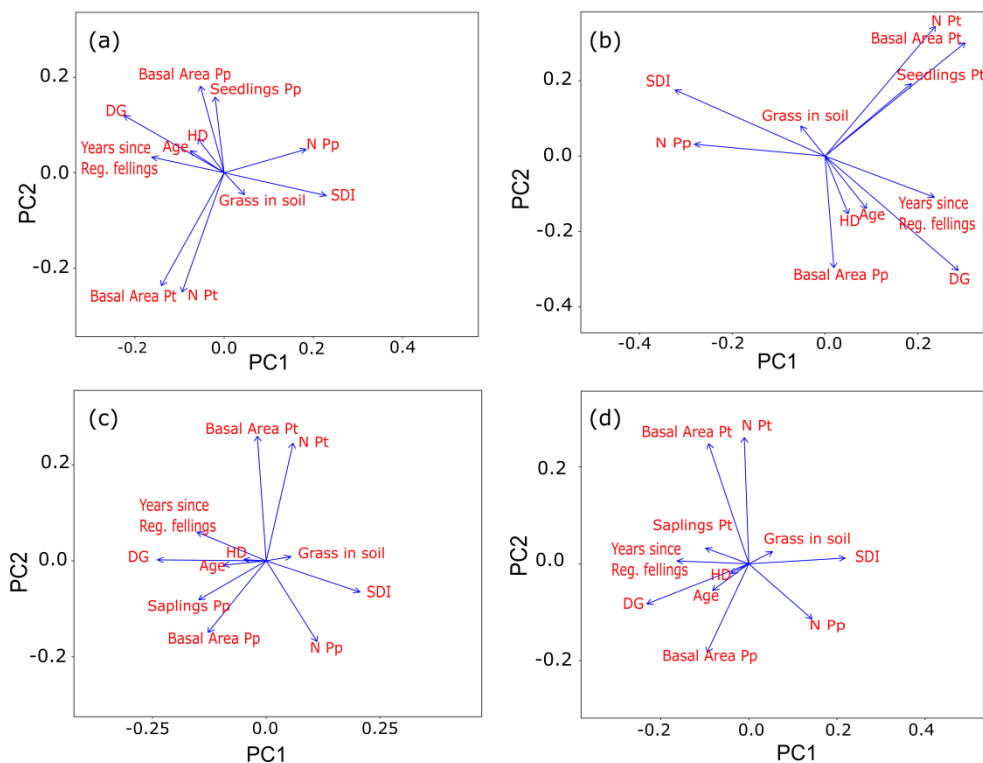
**Table 4.2.** Contingency Table Analysis for the presence of regeneration and composition of the stratum of adult trees.

Species	Regeneration stages	Regeneration	Mix	Na	Pp	Pt	Total	$\chi^2$	df	P-value
<i>P. pinea</i>	Seedlings	Presence	<b>84</b>	<b>235</b>	<b>724</b>	<b>184</b>	1227	16.08	3	<b>0.00109</b>
		Absence	72.9	255.4	697.2	201.5	709			
	Saplings	Presence	<b>46</b>	<b>143</b>	<b>340</b>	<b>114</b>	643			
		Absence	38.2	133.6	365.5	105.7	1292			
<i>P. pinaster</i>	Seedlings	Presence	<b>42</b>	<b>42</b>	<b>46</b>	<b>153</b>	283	431.74	3	<b>2.2e-16</b>
		Absence	16.8	58.9	160.8	46.5	1653			
	Saplings	Presence	<b>12</b>	<b>21</b>	<b>20</b>	<b>50</b>	103			
		Absence	6.1	21.4	58.6	16.9	1832			
			<b>103</b>	<b>381</b>	<b>1080</b>	<b>268</b>		101.03	3	<b>2.20E-16</b>
			109.9	380.6	1041.4	301.1				

Observed values are presented in bold, the rest are expected values. (Pp) Pure *P. pinea* (Pt) pure *P. Pinaster* (Mix), mixed and (Na) plots without adult trees. Significant correlations ( $P$ -value  $\leq 0.05$ )

The PCA analysis showed that in the four analyzed cases – *P. pinea* seedlings and saplings/ *P. pinaster* seedlings and saplings - the PC1 explained approximately 25% of the variability and the PC2 around 20%. In the analysis, we observed that seedlings of both species showed a close, positive relationship with the basal area of conspecific adult trees (Fig 4.3 a, b). For *P. pinaster* seedlings, we also found a positive influence of the number of *P. pinaster* adult trees

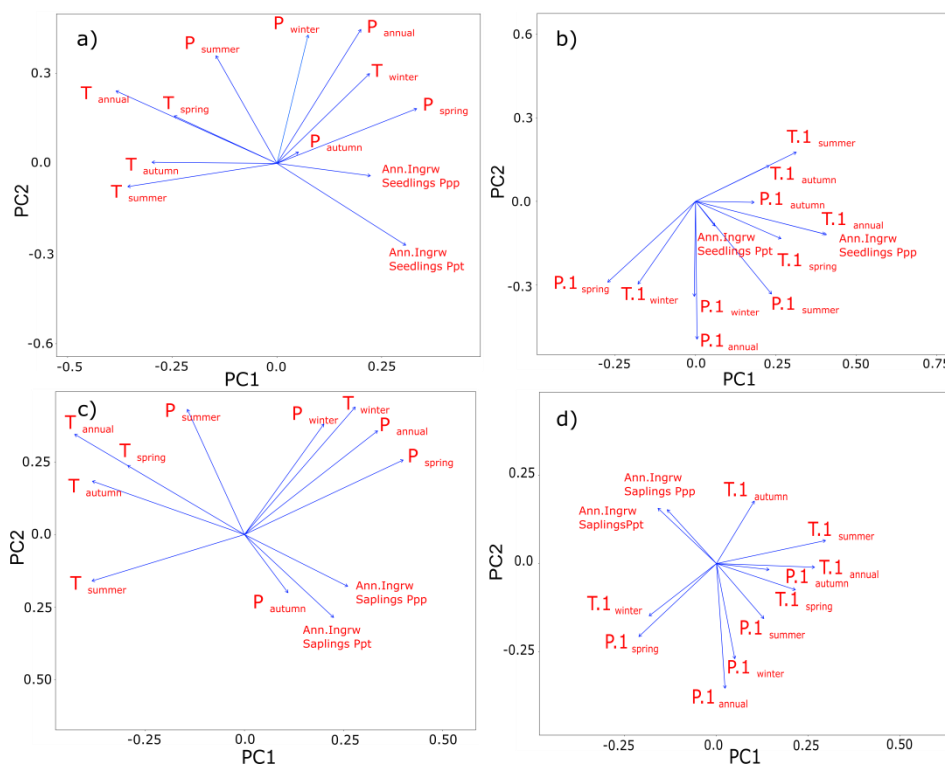
(Fig 4.3 b). In the case of saplings, these variables -basal area and number of conspecific adult trees- had less impact (Fig 4.3 c, d). Moreover, negative relationships were observed between the number of seedlings of each species and the stand density index (SDI). Similarly, saplings of the two species displayed negative relationships with this variable, although in the case of *P. pinaster* this relationship was closer. Other variables that seemed to have an influence on natural regeneration were the number of years since fellings had been carried out as well as the age of the stand and the mean squared diameter of adult trees. In this case, the magnitude of the variables used in the analysis is related to the degree of relevance of these same variables in the PC1 and PC2. Thus, it is likely that SDI, which is at least one order of magnitude larger than all the other variables, will also have a large variance and therefore, a greater probability of becoming highly relevant in the first component. This could also occur with the basal area and the number of trees in conspecific situations in the second component.



**Figure 4.3.** Results for the first two axes of the PCA combining stand variables and natural regeneration; **(a)** *P. pinea* seedlings; **(b)** *P. pinaster* seedlings; **(c)** *P. pinea* saplings; and **(d)** *P. pinaster* saplings. Abbreviations as shown in Table 2.3

#### 4.1.2. Natural regeneration dynamics in function of climate

The percentage of variability explained by PCA using climatic variables was around 30% for the first axis and 20% for the second, both for *P. pinea* and *P. pinaster*. It was observed that the association between climate and natural regeneration changed depending on the time lag used for the climatic variable as well as on the species (Fig 4.4). PCA analysis revealed that there was a perfect, opposite relationship between the annual ingrowth (observed difference in the number of seedlings or saplings between two consecutive years) in both species and the mean annual and spring temperature of the current year (Fig 4.4 a and c). In this regard, sapling ingrowth also showed a negative relationship with the mean autumn temperature and a positive, close relationship with the autumn precipitation of the current year.



**Figure 4.4.** Results for the first two axes of the PCA combining climatic variables and annual ingrowth natural regeneration; **(a)** *P. pinea* and *P. pinaster* seedlings and current year climatic variables **(b)** *P. pinea* and *P. pinaster* seedlings and previous year climatic variables **(c)** *P. pinea* and *P. pinaster* saplings and current climatic variables **(d)** *P. pinea* and *P. pinaster* saplings and previous year climatic variables. Abbreviations as shown in Table 2.3.

Interestingly, summer precipitation of the previous year seems to have a perfect, positive relationship with the annual ingrowth of seedlings, especially for *P. Pinaster* seedlings. In

contrast, an opposite relationship was found between the current value of this variable and the annual ingrowth of saplings. Similar relationships (positive association with the value for the previous year and opposite relationship with the value for the current year) were observed for the rest of the analyzed climatic variables (Fig 4.4 b and c).

The Tau-Kendall analysis revealed an intraspecific regeneration synchrony between the three natural units for the variation in the number of seedlings of the two species (p-value <0.05, Case A of Table 4.3). In the case of *P. pinaster*, the value of W (0.851) reveals almost perfect synchrony over the studied period. In contrast, in the case of saplings, we only observed this intraspecific synchrony among natural units in *P. pinea*.

**Table 4.3.** Parameter estimates for the Tau-Kendall analysis applied in three different cases. A) Between the three natural units by species and category; B) between seedling and saplings by natural units and species; and C) between both species by natural unit and category.

	Case	Unit of comparison	Time series	First year	Last year	N	W	r	Chi-Square	P-value
Intraspecific synchrony	A	<i>P. pinea</i>	Seedlings	2004	2015	12	0.517	0.360	22.74	<b>0.020</b>
			Saplings	2003	2015	13	0.504	0.340	24.21	<b>0.020</b>
		<i>P. pinaster</i>	Seedlings	2003	2015	13	0.851	0.780	30.63	<b>0.002</b>
			Saplings	2004	2015	12	0.396	0.009	13.08	0.288
	B	UN6	<i>P. pinea</i>	2001	2015	14	0.540	0.080	15.15	0.368
			<i>P. pinaster</i>	2001	2015	14	0.528	0.290	14.77	0.390
		UN7	<i>P. pinea</i>	2003	2015	12	0.660	0.320	15.92	0.190
			<i>P. pinaster</i>	2003	2015	12	0.651	0.300	15.60	0.201
		UN8	<i>P. pinea</i>	2003	2015	12	0.530	0.061	19.03	0.080
			<i>P. pinaster</i>	2003	2015	12	0.558	0.116	13.39	0.340
Interspecific synchrony	C	UN6	Seedlings	2001	2015	14	0.838	0.680	23.47	<b>0.050</b>
			Saplings	2001	2015	14	0.662	0.490	18.53	0.180
		UN7	Seedlings	2003	2015	12	0.688	0.377	16.53	0.168
			Saplings	2003	2015	12	0.668	0.336	16.03	0.189
		UN8	Seedlings	2003	2015	12	0.881	0.770	21.29	<b>0.049</b>
			Saplings	2003	2015	12	0.650	0.301	15.71	0.205

Where n: number of years; W: Kendall statistic parameter; r: Spearman rank correlation coefficient test.  
p<0.05 indicates the existence of a temporal pattern

No synchronized temporal patterns were observed within each natural unit between seedlings and saplings belonging to the same species (Case B of Table 4.3). Lastly, the analysis revealed interspecific synchrony in the variation of the number of seedlings in two of the natural units



(six and eight), with values of  $W$  (0.838 and 0.881) close to 1. No interspecific synchrony was observed in the case of saplings (Case C of Table 4.3).

## **4.2. Contribution of climatic factors and stand structure to the success of regeneration occurrence**

### **4.2.1. Building approach**

The sequential steps to construct the model for the occurrence of natural regeneration are shown in Table 4.4. The number of adult trees per species, the level of grass cover and the mixture effect entered in the proportional part of the model, thus modulating the baseline regeneration occurrence. The baseline  $h_0$  of the hazard model was finally defined by the mean spring and autumn temperatures as well as the maximum summer temperatures. We detected problems of convergence when entering the precipitation-related covariates and consequently, these variables were excluded. The inclusion of a block random effect resulted in a significant improvement in terms of AIC and BIC (with a reduction of 53), which indicated a better fit when block random effects were included. The final model was the following:

$$F(t) = 1 - e^{(-\sum_1^t \text{hazard.baseline} \cdot e^{(\text{Proportionalpart})})} \quad [4.1]$$

Where:

*Proportionalpart*

$$\begin{aligned} &= (\beta_1 + \beta_{1Sp} * Sp) * Nsp_{ij} + (\beta_2 + \beta_{2Sp} * Sp) * Nosp_{ij} + (\beta_{3.2} + \beta_{3.2Sp} * Sp) \\ &* Lgrass.Medium_{ij} + (\beta_{3.3} + \beta_{3.3Sp} * Sp) * Lgrass.High_{ij} + (\beta_4 + \beta_{4Sp} * Sp) \\ &* Mix_{ij} \end{aligned}$$

*hazard.baseline*

$$\begin{aligned} &= \gamma_0 + \gamma_o * Sp + (\gamma_1 + \gamma_{1Sp} * Sp) * T_{spr_k} + (\gamma_2 + \gamma_{2Sp} * Sp) * T_{fall_k} \\ &+ (\gamma_3 + \gamma_{3Sp} * Sp) * T_{max.summ_k} + u_i \end{aligned}$$

**Table 4.4.** Model evaluation indexes for the different regeneration occurrence models tested.

Modeling step	1	2	3	4	5
Intercept	$\mu$	$\mu$	$\mu$	$\mu$	$\mu$
Plot variables		$N_{sp}, N_{osp}, LG$	$N_{sp}, N_{osp}, LG$	$N_{sp}, N_{osp}, LG$	$N_{sp}, N_{osp}, LG$
Mixture effect			Mix	Mix	Mix
Climate variables				$T_{spr},$ $T_{fall}, T_{max.sum}$	$T_{spr},$ $T_{fall}, T_{max.sum}$
Random effect					block
AIC	8883	8439	8359	8280	7726
BIC	8895	8500	8456	8390	7785

Where  $N_{sp}$ : number of adult trees of the same species;  $N_{osp}$ : number of adult trees of the other species indicated by the regeneration variable;  $Lgrass$ : levels of grass;  $Mix$ : presence or not of mixture in the adult trees of the plot;  $T_{spr}$ : mean spring temperatures for year  $k$ ;  $T_{fall}$ : mean autumn temperatures for year  $k$ ;  $T_{max.sum}$ : Maximum summer temperatures for year  $k$ ;  $block$ : block random effect.

Here,  $Sp$  is the dummy variable related with species regeneration (1 for *P. pinaster*, 0 for *P. pinea*);  $N_{sp\ ij k}$  (stems. plot<sup>-1</sup>) is the number of adult trees of the same species, (i.e. for *P. pinea* regeneration, the number of *P. pinea* adults trees) in plot  $j$  in block  $i$  during year  $k$ ;  $N_{osp\ ij k}$  (stems. plot<sup>-1</sup>) is the number of adult trees of the other species indicated by the regeneration variable (i.e. for *P. pinea* regeneration, the number of *P. pinaster* adults trees);  $Lgrass.Medium_{ijk}$  is the dummy variable related with the presence (1) of a medium level of grass in plot  $j$  in block  $i$  for year  $k$ ;  $Lgrass.High_{ijk}$  is the dummy variable related with presence (1) of a high level of grass in plot  $j$  in block  $i$  for year  $k$ ; when the level of grass in plot  $j$  in block  $i$  for year  $k$  was low, the previous variables adopt a value of 0;  $Mix_{ijk}$  is a dummy variable related with the presence (1) or not (0) of mixture in the stratum of seed trees in plot  $j$  in block  $i$  for year  $k$ ;  $T_{spr,k}$  is the mean spring temperatures for year  $k$ ;  $T_{fall,k}$  is the mean autumn temperatures for year  $k$ ;  $T_{max.sum,k}$  is the mean maximum summer temperatures for year  $k$ ; and  $u_i$  is the block random effect.

#### 4.2.2. Factors affecting natural regeneration occurrence

Through the final model, we can infer species-specific responses to the different factors. Natural regeneration patterns were characterized by a cumulative probability curve, both in *P. pinea* and *P. pinaster*. The parameter estimates of the final model are presented in Table 4.5. The sign and magnitude of the estimates define the influence of these parameters over the predicted probabilities, with positive values indicating higher probability of regeneration.

The presence of conspecific adult trees significantly increased the probability of regeneration occurrence for a given species in a plot. This variable was found to have greater influence over *P. pinaster* ( $\beta_{1Pt} = 0.165 + 0.349$  than *P. pinea* ( $\beta_{1Pp} = 0.165$ ). The presence of adult trees of the other species, however, decreased the probability of regeneration occurrence, and, as in the previous case, the influence was greater on *P. pinaster* ( $\beta_{2Pt} = -0.119 - 0.403$ ) than on *P. pinea* ( $\beta_{2Pp} = -0.119$ ). Our results also indicated that the presence of mixture in the plot led to a greater occurrence of regeneration in both species, this effect being greater for *P. pinaster* ( $\beta_{4Pt} = 0.468 + 0.540$  than for *P. pinea* ( $\beta_{4Pp} = 0.468$ ). The level of grass was found to be an important predictor of regeneration occurrence. As the degree of grass cover increases, the probability of occurrence of natural regeneration decreases similarly in both species.

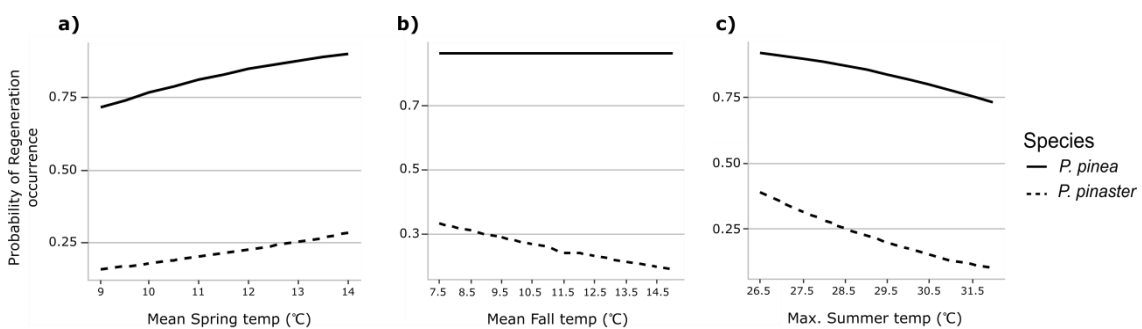
**Table 4.5.** Summary of final parameterization of the regeneration occurrence model

Effect	Parameter	Estimate	Standar error	DF	t values	Pr > t
<b>Baseline</b>						
<b>Intercept</b>	$\gamma_0$	1.571	1.084	121	1.45	<b>0.1488</b>
	$\gamma_{0sp}$	4.682	2.024	121	2.31	<b>0.0224</b>
<b>T<sub>spr</sub></b>	$\gamma_1$	0.296	0.039	121	7.50	<b>&lt;0.0001</b>
	$\gamma_{1sp}$	-0.075	0.082	121	-0.92	0.3615
<b>T<sub>fall</sub></b>	$\gamma_2$	0.002	0.023	121	0.06	0.9491
	$\gamma_{2sp}$	-0.121	0.057	121	-2.11	<b>0.0371</b>
<b>T<sub>max.sum</sub></b>	$\gamma_3$	-0.213	0.035	121	-6.16	<b>&lt;0.0001</b>
	$\gamma_{3sp}$	-0.169	0.068	121	-2.47	<b>0.0148</b>
<b>Proportional part</b>						
<b>N<sub>sp</sub></b>	$\beta_1$	0.165	0.032	121	5.16	<b>&lt;0.0001</b>
	$\beta_{1sp}$	0.349	0.049	121	7.14	<b>&lt;0.0001</b>
<b>N<sub>osp</sub></b>	$\beta_2$	-0.119	0.042	121	-2.84	<b>0.0053</b>
	$\beta_{2sp}$	-0.403	0.106	121	-3.81	<b>0.0002</b>
<b>Lgrass.Medium</b>	$\beta_{3,2}$	-0.183	0.079	121	2.31	<b>&lt;0.0224</b>
	$\beta_{3,2sp}$	0.009	0.145	121	0.06	0.9529
<b>Lgrass.High</b>	$\beta_{3,3}$	-0.895	0.101	121	-8.88	<b>&lt;0.0001</b>
	$\beta_{3,3sp}$	0.022	0.195	121	0.11	0.9096
<b>Mix</b>	$\beta_4$	0.468	0.144	121	3.25	<b>0.0015</b>
	$\beta_{4sp}$	0.540	0.234	121	2.31	<b>0.0227</b>
<b>Variance random effect</b>	$\sigma_1$	0.667	0.106	121	6.31	<b>&lt;0.0001</b>

Where  $N_{sp}$ : number of adult trees of the same species;  $N_{osp}$ : number of adult trees of the other species indicated by the regeneration variable; Lgrass: levels of grass; Mix: presence or not of mixture in the adult trees of the plot;  $T_{spr}$ : mean spring temperatures for year k;  $T_{fall}$ : mean autumn temperatures for year k;  $T_{max.sum}$ : Maximum summer temperatures for year k; block: block random effect.

As regards climate variables, we found that mean spring temperatures significantly affected the probability of regeneration occurrence in a similar way for both species (Table 4.5; Fig.

4.5a). However, autumn mean temperatures were only significant in the case of *P. pinaster* (Table 4.5; Fig. 4.5b). The probability of *P. pinaster* regeneration occurrence decreased with increasing mean autumn temperatures ( $\hat{\gamma}_{Pt} = -0.002 - 0.121$ ). Finally, the increase in maximum summer temperatures significantly decreased the probability of occurrence of regeneration in the plots, both for *P. pinea* ( $\hat{\gamma}_{Pp} = -0.213$ ) and *P. pinaster* ( $\hat{\gamma}_{Pp} = -0.213 - 0.169$ ) (Table 4.5; Fig. 4.5c).



**Figure 4.5.** Marginal effect of the different covariates included in the model on *P. pinea* (solid line) and *P. pinaster* (dashed line).

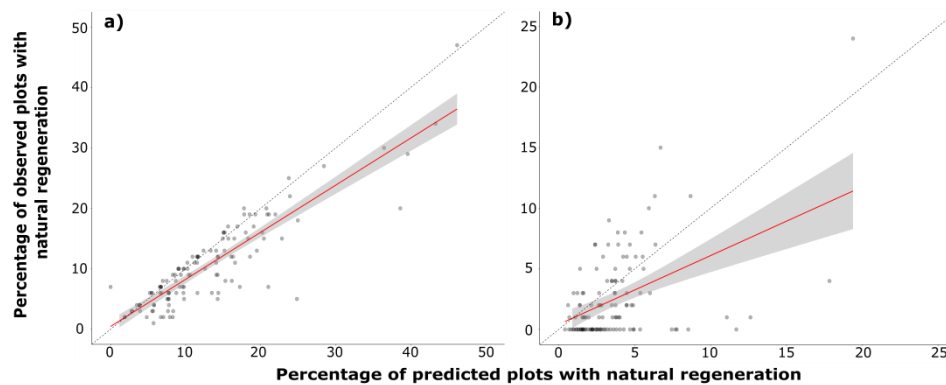
### 4.2.3. Model evaluation

The model validation revealed high agreement between the number of plots in which natural regeneration occurrence was predicted and the number of plots in which natural regeneration was observed for both species in the regeneration management units (Fig 4.6). In this case, each point in the graph represents the management unit- block- in which plots were grouped. However, the values obtained for a and b parameters through the evaluation of the linear regression indicate a slight overestimation (Table 4.6) for both *P. pinea* and *P. pinaster*.

**Table 4.6.** Estimates of the parameters in the linear regression for the evaluation of the model

		Estimate	SE	p value	CI
<i>P. pinea</i>	Intercept	0.463	0.583	0.429	(-0.692, 1.618)
	Pred	0.779	0.037	< 0.0001	(0.704, 0.854)
<i>P. Pinaster</i>	Intercept	0.415	0.472	0.381	(-0.519, 1.350)
	Pred	0.568	0.099	< 0.0001	(0.370, 0.764)

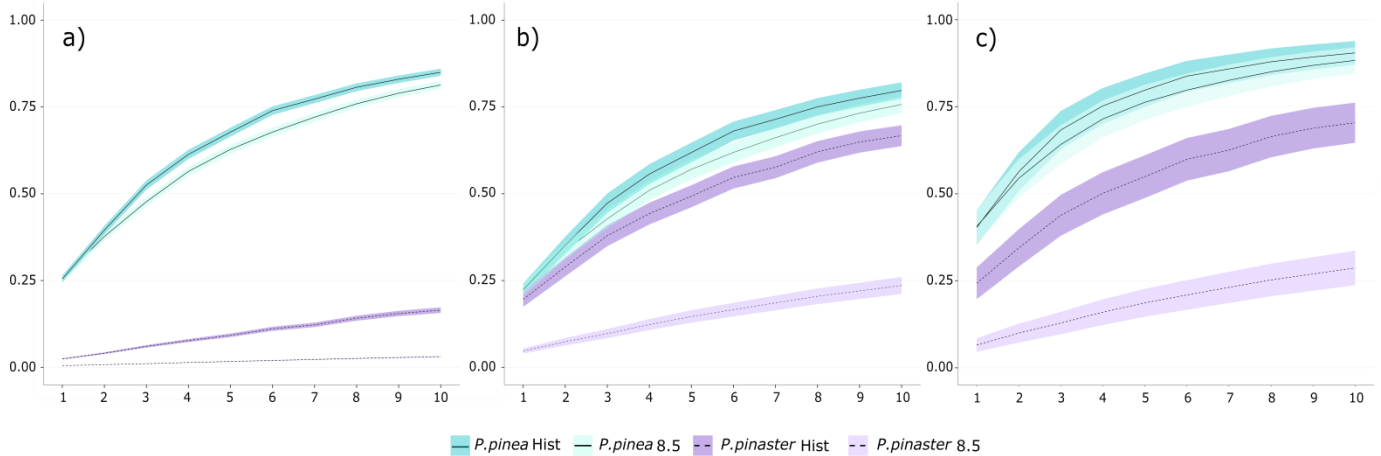
Where SE: standar error; p-value: level of significance; CI: confidence interval.



**Figure 4.6.** Observed and predicted number of plots showing natural regeneration for (a) *P. pinea* and (b) *P. pinaster* per regeneration management unit during the studied period.

#### **4.2.4. Natural regeneration projection under future climate scenarios**

The results of the simulations showed small differences between the RCP 8.5 and historic scenarios for the probability of *P. pinea* natural regeneration occurrence. In this case, we also observed no significant differences in the probability of *P. pinea* regeneration under the different compositions of the stratum of seed trees (Fig. 4.7). However, the probability of *P. pinaster* natural regeneration occurrence showed significant differences between both climatic scenarios, the historic (current) scenario being the most favorable and RCP 8.5 the least favorable. In contrast to the results obtained for *P. pinea*, *P. pinaster* showed differing behavior under different compositions of the stratum of seed trees, with very low probability of regeneration under pure *P. pinea* adult trees (Fig. 4.7a). Finally, in both cases, the simulations showed that under mixed composition (Fig. 4.7c) there was a greater probability of regeneration occurrence than under conspecific composition.



**Figure 4.7.** Mean (higher lines) and 0.95 confidence interval (shaded areas) probability of regeneration occurrence for a 10 year period at the end of XXIst century under (a) *P. pinea* pure adult tree plots (b) *P. pinaster* pure adult tree plots and (c) mixed adult tree plots under RCP 8.5 and Historic climate scenarios.

### 4.3. Signals of climate on Mediterranean pine forest

#### 4.3.1. Tree growth and selection of drought events

We found a higher increment in the mean tree basal area for both species in mixed composition compared to monospecific plots. Similar results were obtained when we compared the mean tree-ring width in mixed and pure compositions. The mean length of annual series, which are related to the age of the trees, is similar for both species in both compositions, so we can assume that there are no age differences between the mixed and monospecific plots (Table 4.7).

The values of the expressed population signal (EPS) as well as the high correlation between the master chronologies (mean site series), both in monospecific and mixed compositions (Table 4.7), reveal that all chronologies can be considered reliable and well replicated (EPS > 0.85) (Wigley et al., 1984).

**Table 4.7.** Description of structural and dendrochronological variables for cored trees in mixed and monospecific plots.

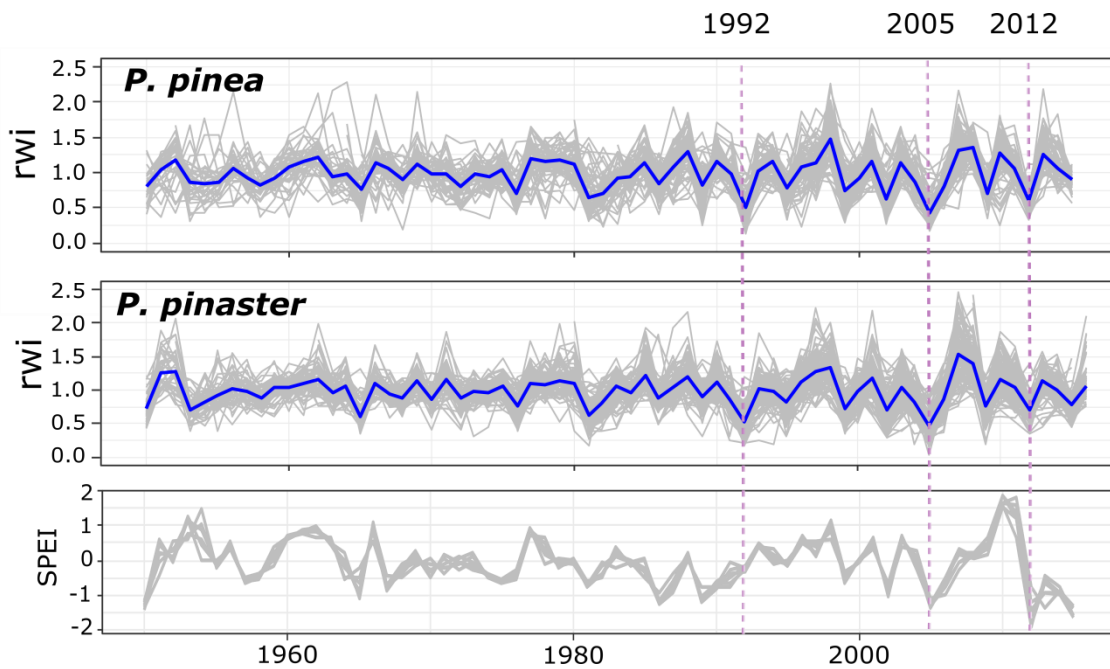
	Pure_ <i>P.pinea</i>	Mixed_ <i>P.pinea</i>	Pure_ <i>P.pinaster</i>	Mixed_ <i>P.pinaster</i>
Number of cored trees	98	125	125	125
Number of sampled cores	195	375	375	375
Mean length of series (years)	53	60	59	52
Maximum length of series (years)	117	151	127	120
Mean tree-ring width (mm)	1.83	2.52	2.11	2.6
Mean basal area increment (cm <sup>2</sup> )	3.87	5.67	4.75	6.18
Mean correlation with master series	0.5	0.61	0.63	0.62
Mean sensitivity	0.41	0.38	0.35	0.34
Expressed population Signal	0.98	0.99	0.98	0.98

Although the results of the Pearson correlations between the master chronologies and the different options for computing for the Standardized Precipitation Evapotranspiration Index-SPEI were quite similar in all cases, the highest correlation was found for the SPEI calculated using the hydrologic year and an accumulation period of 6 months (Table 4.8), both in *P.pinea* and *P. pinaster*. Therefore, this is the SPEI value which was used during the rest of the study to evaluate drought severity in the studied area.

**Table 4.8.** Correlation values between master chronologies and SPEI calculated for the natural (Ann) or the hydrologic (Hydr) year considering a temporal window of 6, 9 or 12 months.

	SPEI6.Ann	SPEI9.Ann	SPEI12.Ann	SPEI6.Hydr	SPEI9.Hydr	SPEI12.Hydr
<b><i>P. pinea</i></b>	0.44	0.45	0.42	<b>0.54</b>	0.47	0.40
<b><i>P. pinaster</i></b>	0.46	0.46	0.42	<b>0.52</b>	0.45	0.38

In order to compare the behavior of the two species, we selected the years 2012, 2005 and 1992 to evaluate the performance of individual trees under episodic drought stress. These years coincide with negative SPEI values -for all evaluated options-, which are associated with extremely dry conditions (Fig 4.8) and characterized by warm spring-summer (Fig 4.9) and severe droughts.

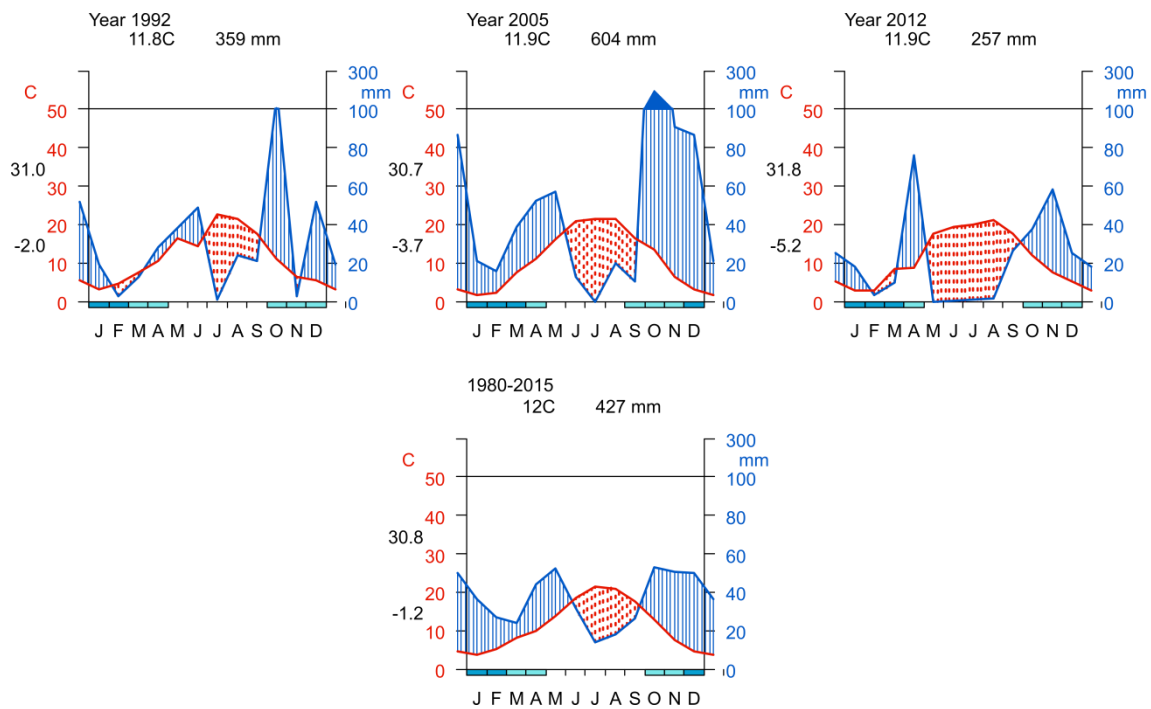


**Fig. 4.8.** ring width index for each sample (grey lines) of *P. pinea* and *P. pinaster*. Mean fluctuation of *P. pinea* (a) and *P. pinaster* (b) in monospecific stands. Different values for the Index-SPEI (c) computed using various temporal windows (6, 9 and 12 months) and two options for the growth period (hydrologic and natural year).

#### 4.3.2. Tree resistance, recovery and resilience to drought events

Through the t-test we observed significant differences in the Resistance  $R_t$  (p-value < 0.0001) and the Recovery  $R_c$  (p-value < 0.008) indexes between both species, although not in the Resilience index  $R_s$  (p-value < 0.417). *P. pinea* showed lower  $R_t$  (0.536) than *P. pinaster* (0.633). In contrast, recovery in *P. pinea* was greater (2.43) than that of *P. pinaster* (2.11).





**Figure 4.9.** Climograms for the selected pointer years and average climograms for the 1980-2015 period in the study area (Valladolid province). Digits sited on the left side of the y-axis are average daily maximum temperatures of the warmest month and average of daily minimum temperatures of the coldest month from top to bottom respectively.

When we applied the t-test separately in mixed and monospecific compositions, we found similar results for the resistance index but not for the other two. In the case of the Recovery and Resilience indices, there were only differences between species in mixed composition, with *P. pinaster* showing lower  $R_c$  and  $R_s$  than *P. pinea* (Table 4.9).

**Table 4.9.** T-test results for the Lloret indices comparing both species in mixed and monospecific composition.

		P-value	Mean <i>P. pinea</i>	Mean <i>P. pinaster</i>
Rt	Mixed	< 0.0001	0.523	0.644
	Monospecific	< 0.0002	0.558	0.622
Rc	Mixed	< 0.0001	2.490	2.024
	Monospecific	0.1014	2.357	2.201
Rs	Mixed	0.0021	1.183	1.111
	Monospecific	0.0980	1.134	1.182

The selected models for the Lloret indices are shown below. We found different variables to be significant in each index and for each species, which highlights the species-specific strategies of *P. pinea* and *P. pinaster*.

$R_t$  index:

$$R_{tPa} = \alpha_0 + \beta_1 * DroughtYear_t + \beta_2 * DBH_{ijt} + \beta_3 * Mix_i + \beta_4 * (DBH_{ijt} * Mix_i) + \varepsilon \quad [4.2]$$

$$R_{tPp} = \alpha_0 + \beta_1 * DroughtYear_t + \beta_2 * DBH_{ijt} + \beta_3 * Age_{ijt} + u_i + \varepsilon \quad [4.3]$$

$R_c$  index:

$$R_{cPa} = \alpha_0 + \beta_1 * DroughtYear_t + u_i + \varepsilon \quad [4.4]$$

$$R_{cPp} = \alpha_0 + \beta_1 * DroughtYear_t + \beta_2 * \log(SDI_{it}) + \beta_3 * DBH_{ijt} + u_i + \varepsilon \quad [4.5]$$

$R_s$  index:

$$R_{sPa} = \alpha_0 + \beta_1 * DroughtYear_t + u_i + \varepsilon \quad [4.6]$$

$$R_{sPp} = \alpha_0 + \beta_1 * DroughtYear_t + u_i + \varepsilon \quad [4.7]$$

$DBH_{ijt}$  is the diameter at breast height of tree  $i$  in plot  $j$  for each of the selected drought year  $t$ .  $Age_{ijt}$  is the age of tree  $i$  in plot  $j$  in the year  $t$ .  $SDI_{it}$  is the Reineke stand density index of plot  $j$ .  $Mix$  is a dummy variable related to the presence (1) or not (0) of mixture in plot  $j$  and finally,  $DroughtYear_t$  is also a dummy variable associated with the selected pointer year.

The estimated parameters for the six Lloret indices models are shown in Table 4.10. Through these models we can infer species-specific responses to the drought events. Thus, we found that 2012 was the best year in terms of resistance, however, this year was the worst in terms of recovery both in *P. pinea* and *P. pinaster*. In this case, we identify 2005 as the best year in terms of recovery for both species. Note also that 1992 was the most negative year in terms of resilience while 2005 was the most positive.

Our results also indicated a positive effect of mixture on resistance capacity in *P. pinea*, although it seems to be mediated by the negative interaction between mixture and tree diameter at breast height, leading to lower large trees. In the case of *P. pinaster* the increase in diameter at breast height led to lower resistance to drought events but also greater recovery. In this case, mixture did not interact with any other variable. As regards the Reineke stand

density index, we detected that this variable negatively affected recovery capacity in *P. pinaster*, thus the greater the plot density the greater the impact of extreme droughts.

**Table 4.10.** Summary of final parameterization of the Lloret indices models for *P. pinea* and *P. pinaster*.

Model	Sp	Effect	Parameter	Estimate	Standar error	t value	Pr >  t		
Resitance	<i>P. pinea</i>	Intercept	$\alpha_0$	0.721	0.043	16.498	< 0.0001		
		DroughtYear_2005	$\beta_{1\_2005}$	-0.070	0.016	-4.887	< 0.0001		
		DroughtYear_1992	$\beta_{1\_1992}$	-0.106	0.018	-5.476	< 0.0001		
		DBH	$\beta_2$	0.00005	0.0004	0.426	0.670		
		Mixed	$\beta_3$	0.245	0.073	3.354	0.001		
		DBH x Mixed	$\beta_{2\_m}$	-0.0004	-0.0001	-3.786	0.0001		
		Variance of random effects							
	plot	$\sigma_1$	0.008						
Resitance	<i>P. pinaster</i>	Intercept	$\alpha_0$	0.976	0.053	15.461	< 0.0001		
		DroughtYear_2005	$\beta_{1\_2005}$	-0.211	0.020	-10.326	< 0.0002		
		DroughtYear_1992	$\beta_{1\_1992}$	-0.226	0.023	-9.593	< 0.0003		
		DBH	$\beta_2$	-0.0003	-0.0005	-2.599	0.009		
		Age	$\beta_3$	-0.0015	-0.0001	-2.710	0.007		
		Variance of random effects							
			plot	$\sigma_1$	0.004				
Recovery	<i>P. pinea</i>	Intercept	$\alpha_0$	1.539	0.218	7.042	< 0.0001		
		DroughtYear_2005	$\beta_{1\_2005}$	0.974	0.088	10.867	< 0.0001		
		DroughtYear_1992	$\beta_{1\_1992}$	0.605	0.099	6.009	< 0.0001		
		Variance of random effects							
			plot	$\sigma_1$	0.162				
		Recovery	<i>P. pinaster</i>	Intercept	$\alpha_0$	-1.478	0.995	-1.485	0.1433
				DroughtYear_2005	$\beta_{1\_2005}$	1.625	0.093	17.451	< 0.0001
DroughtYear_1992	$\beta_{1\_1992}$			0.652	0.105	6.208	< 0.0001		
log (SDI)	$\beta_2$			0.396	0.172	2.311	0.025		
DBH	$\beta_3$			0.002	0.0006	2.684	0.007		
Variance of random effects									
	plot			$\sigma_1$	0.116				
Resilience	<i>P. pinea</i>	Intercept	$\alpha_0$	1.066	0.021	48.823	< 0.0001		
		DroughtYear_2005	$\beta_{1\_2005}$	0.285	0.023	12.141	< 0.0001		
		DroughtYear_1992	$\beta_{1\_1992}$	-0.028	0.025	-11.25	0.261		
		Variance of random effects							
			plot	$\sigma_1$	0.009				
		Resilience	<i>P. pinaster</i>	Intercept	$\alpha_0$	1.020	0.025	40.166	< 0.0001
				DroughtYear_2005	$\beta_{1\_2005}$	0.418	0.027	15.277	< 0.0001
DroughtYear_1992	$\beta_{1\_1992}$			-0.052	0.027	-1.901	0.058		
Variance of random effects									
	plot			$\sigma_1$	0.013				

Where DBH: diameter at breast height of the tree; Age: age of the tree; SDI: reineke index in the plot; Mix: dummy variable related to the presence or not of mixture; SPEI: Standardized Precipitation Evapotranspiration Index. Parameters with a p value lower than 0.05 are in bold.

### 4.3.3. Long-term effect of climate across species

As we hypothesized (Study III), when comparing the intra-specific synchronies of the two species, the results of the t-test showed that they were significantly different in mixed composition, but not in monospecific composition (Table 4.11,A). Intra-specific synchrony in tree growth series was lower for *P. pinaster* than for *P.pinea* in mixed stands. Furthermore, it was noted that there were significant differences in the synchrony values for *P. pinaster* between monospecific and mixed composition, with lower values for the former, whereas this difference was not observed in the case of *P. pinea* (Table 4.11, B). Finally, the analysis of the inter-specific versus intra-specific synchrony in mixed composition only revealed significant differences in the case of *P. pinea*, with lower inter- than intra-specific synchrony (Table 4.11, C).

**Table 4.11.** Results for the T-test analysis to evaluate different synchrony patterns. (A) Comparing the intra-specific synchrony in mixed and monospecific composition. (B) Comparing, separately for each species, the synchrony between mixed and monospecific composition. (C) Comparing, for each species, the intra-specific with inter-specific synchrony in mixed plots. Means of the two options in each case (i.e, in case A, mean of *P. pinea* synchrony values and mean of *P. pinaster* synchrony values in the first line in monospecific composition and in the second line in mixed composition).

Case	Unit of comparison	p-value	Mean	Mean
(A) <i>P. pinea</i> vs <i>P. pinaster</i>	Monospecific	0.745	0.533	0.548
	Mixed	0.001	0.5407	0.4317
(B) Mixed vs Monospecific	<i>P. pinea</i>	0.882	0.534	0.533
	<i>P. pinaster</i>	< 0.0001	0.433	0.548
(C) Inter vs intra	<i>P. pinea</i>	0.0007	0.435	0.534
	<i>P. pinaster</i>	0.947	0.435	0.433

The variation in synchrony among plots for both species was explored through various models. However, none of the available covariables was found to be significant in the case of *P. pinea*. In the case of *P. pinaster*, the final model was as follows:

$$\text{logit}(\hat{a}_{i\ sp}) = \alpha_0 + \beta_1 * \text{Mix}_i + \beta_2 * \text{Age}_i + \beta_3 * \text{DG}_i \quad [4.8]$$

$\text{Mix}_j$  is a dummy variable related to the presence (1) or not (0) of mixture in the plot  $j$ ,  $\text{Age}_j$  is the average age of the *P. pinaster* trees in plot  $ij$  and  $\text{DG}_i$  is the quadratic mean diameter of *P.*

*pinaster* trees in plot  $j$ . We also scrutinized whether there were any interactions among covariables, but no significant interactions were found.

The parameter estimates of the final model are presented in Table 4.12. Our results indicate that both age and quadratic mean diameter significantly increased the intra-specific synchrony, although the presence of mixture in the plot led to lower synchrony in this species, as shown in Table 4.11, B.

**Table 4.12.** Summary of final parameterization of the synchrony model for *P. pinaster*

Effect	Parameter	Estimate	Standar error	t value	Pr >  t
Intercept	$\alpha_0$	0.290	0.069	4.153	< 0.0001
Mixed	$\beta_1$	-0.103	0.019	-5.357	< 0.0001
Age	$\beta_2$	0.002	0.0005	2.105	0.041
DG	$\beta_3$	0.005	0.002	2.649	0.011

Where Mix: presence or not of mixture in the plot; Age: average age of the trees in the plot; DG: the quadratic mean diameter of the trees in the plot.

#### 4.4. Analyzing tree level competition structures in mixed stands

##### 4.4.1. Model structure

The sequential procedures to construct the final competition structure of the model are shown in Table 4.13. This table shows the results for the fitted models, with size-symmetric competition model (SDI), size-asymmetric competition (SDIL), and the combination of both size-symmetric and size-asymmetric competition (SDI + SDIL), also split into intra and inter-specific competitors. Having chosen the best competition structure (Table 4.13), climate-related variables, such as the different seasonal precipitations or the annual precipitation were included in the model. The final structure of the model (Tables 4.14) is similar for both species and includes the section of the tree, spring precipitation, and both size-symmetric and size-asymmetric competition, split into intra and interspecific competitors.

$$\log(BAI_{ijk}) = \alpha + u_i + v_j + w_k + g_{ijk} + ppspr_k + [c + m_k] * SDI_{intra} + [d + n_k] * SDI_{inter} + [c + r_k] * SDIL_{intra} + [d + q_k] * SDIL_{inter} + e_{ijk} \quad [4.9]$$

**Table 4.13.** Comparison in terms of Akaike's Information Criterion (AIC) of growth models including stand density index, calculated both for size-symmetric (SDI) and/or size-asymmetric competitors (SDIL), split into intra and inter-specific competitors for *P. pinea* and *P. pinaster*. Parameter estimations corresponding to density indices are shown. The AIC of the best model are shown in bold.

		All competitors together		Competitors separate ofr intra and inter-specific neighborhood				
		SDI	SDIL	SDI <sub>intra</sub>	SDI <sub>inter</sub>	SDIL <sub>intra</sub>	SDIL <sub>inter</sub>	AIC
<i>P. pinea</i>	[1] SDI	-0.00347*						4850.5
	[2] SDI <sub>intra</sub> + SDI <sub>inter</sub>			-0.0031*	-0.001			4760.6
	[3] SDIL		-0.002*					4818
	[4] SDIL <sub>intra</sub> + SDIL <sub>inter</sub>					-0.0025*	0.0003	4699.4
	[5] SDI + SDIL	-0.001*	-0.003*					4707.5
	[6] SDI <sub>intra</sub> + SDI <sub>inter</sub> + SDIL		-0.002*	-0.0014*	-0.0001			4615.6
	[7] SDI + SDIL <sub>intra</sub> + SDIL <sub>inter</sub>	-0.001*				-0.002*	0.0003	4611.9
	[8] <b>SDI<sub>intra</sub> + SDI<sub>inter</sub> + SDIL<sub>intra</sub> + SDIL<sub>inter</sub></b>			<b>-0,001*</b>	<b>-0.0003</b>	<b>-0,0024*</b>	<b>0.0001</b>	<b>4526.5</b>
<i>P. pinaster</i>	[1] SDI	-0.001*						8459.2
	[2] SDI <sub>intra</sub> + SDI <sub>inter</sub>			-0.001*	-0.004*			8273.3
	[3] SDIL		-0.001*					8558
	[4] SDIL <sub>intra</sub> + SDIL <sub>inter</sub>					-0.001*	-0.002*	8422.1
	[5] SDI + SDIL	-0.0003	-0.001*					8360.8
	[6] SDI <sub>intra</sub> + SDI <sub>inter</sub> + SDIL		-0.001*	-0.0008	-0.003*			8177.2
	[7] SDI + SDIL <sub>intra</sub> + SDIL <sub>inter</sub>	-0.0005				-0.001*	-0.0024*	8249.2
	[8] <b>SDI<sub>intra</sub> + SDI<sub>inter</sub> + SDIL<sub>intra</sub> + SDIL<sub>inter</sub></b>			<b>-0.0008</b>	<b>-0.003*</b>	<b>-0.001*</b>	<b>-0.001</b>	<b>8152.4</b>

Significant parameters are indicated with \*

In addition, the inclusion of the random effects in the model, acting at tree,  $u_i$ , plot,  $v_j$ , year  $w_k$  and the year x competition index specific random parameters ( $m_k$ ,  $n_k$ ,  $r_k$  and  $q_k$ ) led to an improvement in the variance explained by the models for both species. Hence, while the proportion of variance explained by the fixed factors alone in *P. pinea* was 0.455, the proportion of variance explained by both the fixed and random factors was 0.834. In the case of *P. pinaster*, the proportion of variance explained by the fixed factors was slightly lower, 0.222, although the proportion explained by the combination of fixed and random factors was similar to that of *P. pinea*, 0.856.

#### 4.4.2. Size-symmetric and size-asymmetric competition

When two competition effects were included together in the model (Table 4.13 [model 5 vs model 1 and model 3]), SDI and SDIL (without splitting into inter and interspecific competitors), the effect of size-asymmetric competition for larger trees was more significant than that of size-symmetric competition. In both species, the inclusion of two competition effects

improved the AIC of the models. In the case of *P. pinea*, both size-symmetric (SDI) and size-asymmetric (SDIL) terms were statistically significant (Table 4.13 [model 5]). However, in the case of *P. pinaster*, when the two competition indices were included in the model, the effect of size-symmetric competition (SDI) remained statistically non-significant (p-value= 0.387).

**Table 4.14.** Parameter estimates for the definitive model for *P. pinea* and *P. pinaster*.

		<i>P.pinea</i>				<i>P.pinaster</i>			
		Estimate	Std error	t-value	p-value	Estimate	Std error	t-value	p-value
Fixed effects	Intercerp	-8.8760	0.2049	-43.324	< <b>0.0001</b>	-8.596	0.2498	-34.417	< <b>0.0001</b>
	g	1.2420	0.4082	3.044	<b>0.0025</b>	0.5162	0.0843	6.119	< <b>0.0001</b>
	PpSpr	0.0004	0.0001	4.854	<b>0.0003</b>	0.00037	0.0001	3.13	<b>0.0145</b>
	SDI <sub>intra</sub>	-0.0011	0.0004	-2.418	<b>0.0193</b>	-0.0008	0.0004	-1.86	0.0693
	SDI <sub>inter</sub>	-0.0002	0.0009	-0.308	0.7593	-0.0035	0.0013	-2.56	<b>0.0127</b>
	SDIL <sub>intra</sub>	-0.0024	0.0001	-13.362	< <b>0.0001</b>	-0.0013	0.0001	-9.752	< <b>0.0001</b>
	SDIL <sub>inter</sub>	0.0001	0.0006	0.279	0.7805	-0.0014	0.0007	-1.845	0.0655
variance random effects	$\sigma_j$ (Plot)	0.0715				0.184			
	$\sigma_i$ (Tree)	0.0053				0.124			
	$\sigma_k$ (Year)	0.0383				0.063			
	$\sigma_e$ (error)	0.080				0.092			

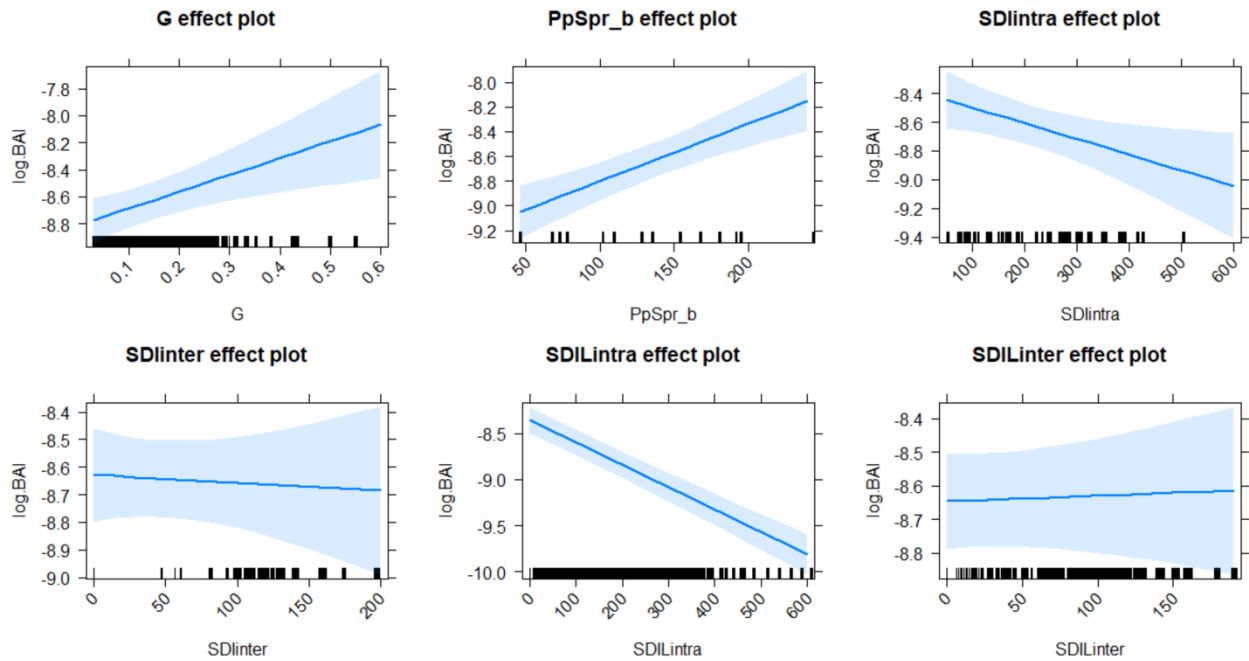
Where g: tree section (m<sup>2</sup>); PpSpr: spring precipitation (mm); SDI<sub>intra</sub> intra size-symmetric competition effect for each species; SDI<sub>inter</sub> inter size-symmetric competition effect for each species; SDIL<sub>intra</sub> size-asymmetric competition effect for each species; SDIL<sub>inter</sub> size-asymmetric competition effect for each species. Significant parameters are in bold.

#### 4.4.3. Intra and inter-specific competition

In both species, when the competition is divided into intra and inter-specific competitors, the inclusion of indices combining size-symmetric and size-asymmetric competition, i.e. SDI<sub>intra</sub>, SDI<sub>inter</sub>, SDIL<sub>intra</sub>, and SDIL<sub>inter</sub>, resulted in the best models, with lower AIC values (Table 4.13). The results showed that in both species, there is a differential effect of between species and within species-competition on growth.

Although in *P. pinea* model the inclusion of intra and inter-specific effects resulted in an improvement of the model, only the intra-specific competition terms were statically significant. The lack of significance of the inter-specific competition terms in all the fitted models (Table 4.13) indicates that the presence of *P. pinaster* trees has neither a positive nor negative influence on *P. pinea* growth, at least for the degree of mixture found within the studied area. However, the negative effect of the intra-specific competition detected,

especially that associated with the larger trees, points to *P. pinea* growth decreased as in the proportion of *P. pinea*  $SDI_{intra}$  and  $SDIL_{intra}$  increases. In Figure 4.10 the marginal effect of these competition terms on *P. pinea* growth can be observed. Thus, as intra-specific competition increases, the increase in BAI gets smaller. In this regard, in each case the rest of the variables in the model remained constant and equal to the average.

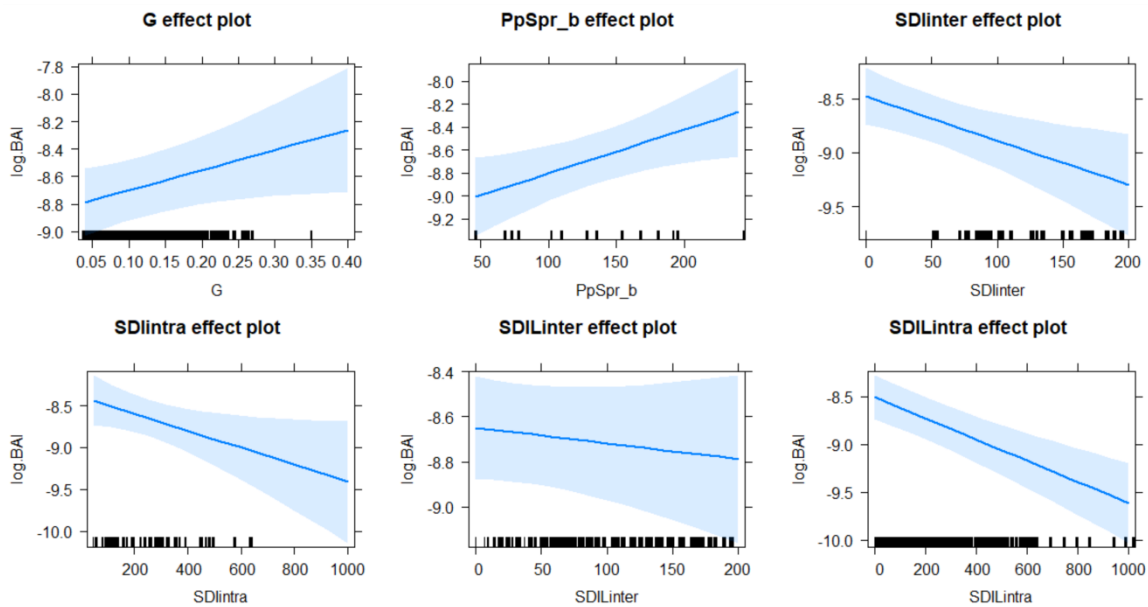


**Figure 4.10.** Marginal effect of the different covariates included in the model for *P. pinea*

Different results were obtained in the case of *P. pinaster*. For this species, the inclusion of intra and inter-specific effects also resulted in an improvement of the model (Table 4.13). However, unlike the case of *P. pinea*, different inter and intra-specific effects of competition were observed. Here, the value of the parameters was significantly negative for the inter-specific size-symmetric competition terms ( $SDI_{inter}$ ) and for the intra-specific size-asymmetric competition terms ( $SDIL_{intra}$ ), although the other two competition terms were close to be significant ( $P < 0.07$ ). In this case, the parameter of the inter-specific size-symmetric competition was greater than that of intra-specific size-asymmetric competition, which indicates that the presence of *P. pinea* trees, regardless of the size, has a more negative influence on the *P. pinaster* secondary growth than the presence of larger *P. pinaster* trees. As



with *P. pinea*, the marginal effect of the different competition terms on the BAI of *P. pinaster* can be observed in Figure 4.11.



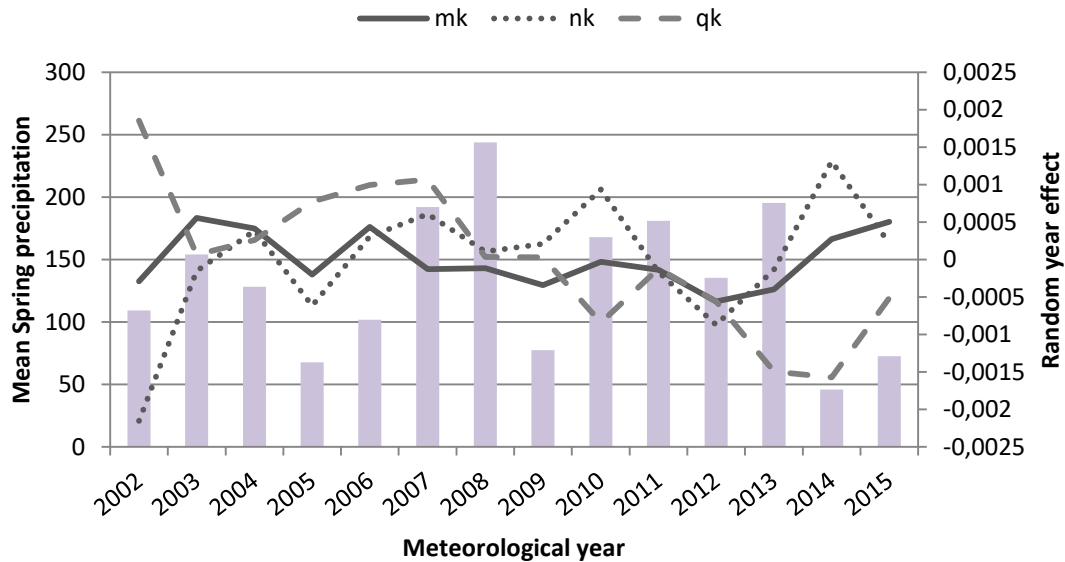
**Figure 4.11.** Marginal effect of the different covariates included in the model for *P. pinaster*.

#### 4.4.3. Impact of climate variability on secondary annual growth

As shown in the model results (Tables 4.14) and in the above Figures (4.10 and 4.11), spring precipitation had a significant effect on BAI in both *P. pinea* and *P. pinaster*. These results again highlight the importance of climate on the secondary growth of the two Mediterranean species and reinforce the different results obtained throughout the present thesis on the climate as a driving factor in Mediterranean forests. However, growth response to climate in both species has been analyzed in depth in the previous section. Here, we focus on the specific competition response of *P. pinea* and *P. pinaster* in dry and humid years, and on the role that different competitor structures (size-symmetric, size-asymmetric and intra or interspecific) played during these years.

The following Figures, 4.12 and 4.13, show the EBLUP's (empirical best linear unbiased predictors) for annual random parameter affecting the intra size-symmetric competition ( $m_k$ ), the inter size-symmetric competition ( $n_k$ ) and the inter size-asymmetric competition ( $q_k$ ),

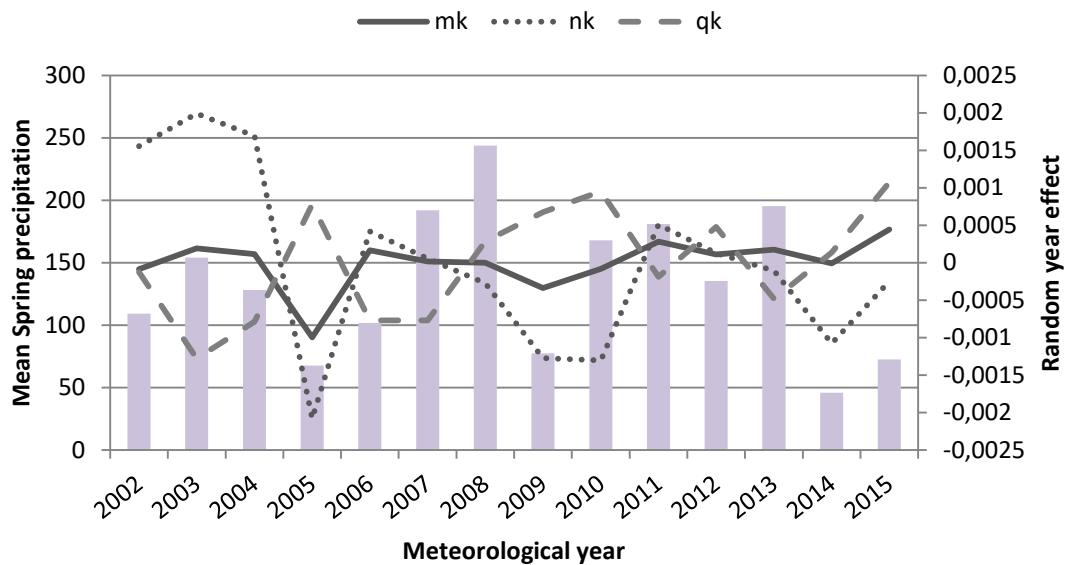
plotted against the spring precipitation for both *P. pinea* and *P. pinaster*. Curiously, in both cases we observed that the variance component associated with the intra-asymmetric competition was null, and therefore, their  $r_k$  were 0. These parameters point to a specific annual response in BAI of the trees in a given year to a specific competition structure, indicating whether the effect of the type of competition is attenuated or enlarged in a given year. According to Figures 4.12 and 4.13, positive values for the random effect indicate that for that particular year, growth is greater than that expected according to the model, given the current level of competition. Taking this into consideration, different patterns are observed between the two species.



**Figure 4.12.** Empirical best linear unbiased predictors (EBLUPS) for *P. pinea* associated with each competition term plotted against spring precipitation. Spring precipitation (mm), competition term associated with intra size-symmetric competition ( $m_k$ ), competition term associated with inter size-symmetric competition ( $n_k$ ) and competition term associated with inter size-asymmetric competition ( $q_k$ ). Here, the variance component associated with inter-asymmetric competition was null, and therefore, its  $r_k$  were 0.

The *P. pinea* results showed that random year effect influencing intra size-symmetric competition ( $m_k$ ) and inter size-symmetric competition ( $n_k$ ), were negative during the 2005 and 2012 droughts, indicating that in these dry years, the negative effect of size-symmetric competition is aggravated. However, this was not observed during the 2009 drought. This may be because the previous year, 2008, was a very wet year, which would have buffered the

negative effect of the drought. On the other hand, the positive value of the random effect influencing inter size-asymmetric competition ( $q_k$ ) shown in the 2005 drought indicates that for that year, size-asymmetric competition was attenuated if compared with the average. However, it can be observed that  $q_k$  shows a declining trend after 2007 (and especially after 2012), which indicates an increased and maintained negative effect of inter-specific size-asymmetric competition on the growth of *P. pinea* in recent years.



**Figure 4.13.** Empirical best linear unbiased predictors (EBLUPS) for *P. pinaster* associated with each competition term plotted against spring precipitation. Spring precipitation (mm), competition term associated with intra size-symmetric competition ( $m_k$ ), competition term associated with inter size-symmetric competition ( $n_k$ ) and competition term associated with inter size-asymmetric competition ( $q_k$ ). As in the previous case, the variance component associated with intra-asymmetric competition was null, and therefore, its  $r_k$  were 0.

*P. pinaster* shows a different pattern. In this case, the random year effects influencing intra size-symmetric competition ( $m_k$ ) and inter size-symmetric competition ( $n_k$ ), showed negative values during the 2005 and 2009 drought episodes, especially the second one. These results indicate that for those years, the negative effect on growth of both intra size-symmetric competition ( $m_k$ ) and inter size-symmetric competition ( $n_k$ ) was aggravated. In addition, it can be observed that during 2009, this effect is extended up to one year. As with *P. pinea*, the results show a positive value of the random effect influencing inter size-asymmetric competition ( $q_k$ ) during the 2005 and 2009 droughts. As explained above, positive values

during these years seem to indicate that there was an attenuation of the effect of the competition exerted over *P. pinaster* individuals by larger trees of *P. pinea*. However, these findings could also indicate that size-symmetric competition ( $m_k$  and  $n_k$ ) is generally limiting the *P. pinaster* basal area growth of the studied species more strongly than inter size-asymmetric competition ( $q_k$ ) during these driest years.

## 5. Discussion

### **5.1. Dynamics of natural regeneration in *P. pinea* and *P. pinaster* Mediterranean forest**

Natural regeneration in pinewood forests on the Northern Plateau of Spain exhibited large heterogeneity linked to density and composition of adult stands as well as to inter-annual variability in climatic conditions. Although the density of established saplings was at a critical level for the two studied species, our results related with the spatio-temporal analyses show that regeneration success was greater for *P. pinea* than for *P. pinaster* regardless of the structure of the adult stand (Table 4.2), confirming our first hypothesis and pointing to the better adaptation of *P. pinea* to current climatic conditions. Hence, this could lead to a shift in species composition, which is likely to involve the conversion of mixed *P. pinea* and *P. pinaster* stands into pure stands of *P. pinea*, which already cover 70% of the study area. The large scale used in our study for the analysis of the spatial and temporal regeneration variability complements the findings obtained in previous studies, mainly designed at smaller scales, allowing us to generalize the observed regeneration patterns at forest management scale.

#### **5.1.1. Drives of spatial variation in regeneration success**

The significant negative spatial correlation between *P. pinea* and *P. pinaster* seedlings indicates differences related to the initial conditions required by each species, in accordance with the species-specific shade needs for germination and initial seedling growth and survival (Manso et al., 2014b; Ruano et al., 2009). However, the observed positive correlation between saplings of both species suggests similar requirements for sapling development. These requirements could be related with a similar demand for light at this stage, but also to the density of adult trees in the plot. This idea is supported by Barbeito et al. (2008) and Rodríguez-García et al. (2011a), who conducted studies concerning *P. pinea* and *P. pinaster* and found similar requirements at more advanced stages of regeneration. Furthermore, we must consider the existence of other uncontrolled factors, such as soil water retention, which could have a significant influence on regeneration success under these Mediterranean conditions.

Surprisingly, we detected a significant negative correlation between the presence of *P. pinea* seedlings and *P. pinaster* saplings, but a nonsignificant relationship between *P. pinaster* seedlings and *P. pinea* saplings. This finding could be related to the fact that the denser and more shaded conditions required for *P. pinea* seedling establishment prevent not only the establishment of *P. pinaster* seedlings but also the transition to the sapling developmental stage of the established *P. pinaster* seedlings. All these results confirm our first hypothesis, by defining how the different light and shade requirements of the species affect the establishment and success of the natural regeneration.

As stated in the second hypothesis of Study II, the presence and composition of adult trees had a significant influence over the two regeneration stages. *P. pinea* seedlings were mainly favored by the presence of conspecific adult trees (Table 4.2), in accordance with previous findings in monospecific stands at smaller scales. Calama et al. (2015) found that crown cover favors the survival of *P. pinea* seedlings, mitigating the negative effects of high irradiance and drought. In this species, the primary dispersal agent is gravity (Manso et al., 2012), which could also explain this positive association. However, the results for *P. pinea* saplings revealed that presence was only lower than expected under conspecific conditions, suggesting that *P. pinea* saplings must be progressively released from the overstory cover, probably due to an increase in light requirements. Manso et al. (2014b) found that as seedlings grow, their performance is optimized in more exposed environments. The observed negative relationship of *P. pinea* saplings with the SDI variable in the PCA analysis reinforces this idea. In addition, *P. pinea* recruits manage to survive beneath *P. pinaster* crowns, probably as a consequence of the higher light availability under *P. pinaster* as opposed to *P. pinea* crowns (Barbeito et al., 2008), suggesting that the mixed composition of adult trees is a plausible alternative.

In the case of *P. pinaster*, we found that both seedling and sapling establishment occurred in close proximity to conspecific adult individuals (Table 4.2; Fig. 4.2), and even though regeneration in *P. pinaster* is generally less successful recruits of this species were still found in

about half of the 318 pure conspecific plots. Although *P. pinaster* generally exhibits a shade-intolerant behavior, our results suggest that under the light and climate conditions present in the study site, canopy protection by conspecific trees against the extreme summer drought favors regeneration in this species. Rodríguez-García et al. (2011a) and Ruano et al. (2009) reported that a certain level of canopy cover is required for *P. pinaster* seedling survival and establishment, particularly during the water stress season. However, despite the fact that *P. pinaster* seeds may be able to reach *P. pinea* stands as they are mainly wind-dispersed, we found limited *P. pinaster* regeneration under non-conspecific trees. This fact could be related also to the dense shade conditions caused by *P. pinea* crowns, which are much denser than those of *P. pinaster* crowns and therefore probably hamper successful natural regeneration in the latter species. Rodríguez et al. (2008) confirm the shade-intolerant nature of this species, providing examples of greater seedling densities at sites with open rather than closed canopies. These somewhat contradictory results highlight the importance of considering foliar distribution and overstory canopy structure to characterize species as shade-tolerant or not, according to abiotic conditions (Martínez and Tapias, 2005). Given the positive influence of *P. pinaster* adult trees over conspecific regeneration, retaining a sufficient number of *P. pinaster* adult trees to ensure successful regeneration should be considered when performing regeneration fellings.

The positive effect of mixed composition in adult stands on natural regeneration of the two species is noteworthy, even though this mixed composition was only observed in a few plots. Canopy cover comprising species with different crown features can create different light and environmental conditions, allowing the development of species with distinct shade tolerances (Stancioiu and O'hara 2006). Note also that this situation could be advantageous over pure composition due to differences in existing seed sources. These facts would explain the results obtained in mixed plots. In the studied mixtures, light availability can differ considerably from that of monospecific stands due to the differences in crown widths and foliar densities of the

two species, providing different niches for the development of each (Moreno-Fernández et al. 2017). However, quantifying light availability and its effect on natural regeneration in complex stands requires detailed measurements (Lochhead and Comeau, 2012), often carried out at local scales (Moreno-Fernández et al. 2017). Such measurements are not feasible at large scales like that of our study. Conversely, by exploring relationships between observed regeneration and adult stand characteristics at landscape scale it would be possible to provide meaningful information regarding the role of mixed species composition on natural regeneration.

#### **5.1.2. Intra and interspecific synchrony**

The results of the Kendall coefficient of concordance,  $W$ , (Table 4.3) highlight the important role of climate variation on the success of natural regeneration in Mediterranean pinewoods (Calama et al. 2017). The synchrony found in the seedling and sapling time series for each species among the three natural units, with the exception of *P. pinaster* saplings, suggests that temporal variation in the number of seedlings and saplings per species was mainly driven by inter-annual climatic conditions, which are similar across the three natural units. Conversely, the lack of synchrony among natural units in *P. pinaster* saplings (case A, table 4.3) may indicate a stronger dependence at this stage of regeneration on other factors apart from annual climatic conditions. However, this result could be affected by the large number of plots that presented no natural regeneration at all (Fig 4.1a and Fig 4.1b), making it difficult to detect synchrony. Accordingly, the lack of intra-specific synchrony between young seedlings and saplings in these two species, analyzed inside each natural unit (case B, Table 4.3), underlines the different climatic requirements shown by the two regeneration stages, as has been reported for other Mediterranean species (Davis et al., 2011). As regards interspecific synchrony, our results again highlight the difference between regeneration stages (Table 4.3). In the two natural units with lower water retention (6 and 8), there was synchrony between the seedling time series of the two species (case C), suggesting a similar dependence on



climatic conditions, probably linked to successful germination and seedling emergence in the previous year, as well as summer drought survival in the current year (Calama et al. 2017). These findings highlight the complexity of the natural regeneration process, since our observations suggest that regeneration in *P. pinea* and *P. pinaster* presents similar dependence on climatic conditions while at the same time displays differences with regard to the initial spatial conditions. In this sense, the probability of natural regeneration occurring in one or other species could be more related with the presence/absence of adult trees, i.e. with a spatial requirement. After this initial life stage, both species seem to display similar variations with climate, revealing the dependence of these developmental stages on climatic conditions. In contrast, the lack of interspecific synchrony in the sapling stage, could suggest that this stage is more closely related with stand characteristics than with climatic drives.

### **5.1.3. Climatic drivers**

The results of the PCA analysis support our third hypothesis of Study I, suggesting that the effect of climatic drivers is not constant across species and/or regeneration stages. Favorable conditions as regards annual and spring mean temperatures could promote seedlings establishment and the transition to the next regeneration stage. Calama et al. (2015) highlighted the importance of optimum root system development in *P. pinea* seedlings during the period prior to summer to improve water uptake in the summer months. Our findings may reflect this theory in the sense that an increase in spring temperatures and scarce spring precipitation could limit the development of the root system, affecting water uptake during the following months and therefore hindering the transition to the next ontogenetic stage. In addition, a notable positive relationship was observed between warmer winters and ingrowth for both seedlings and saplings, which given the high frost tolerance observed for pine species in the region (Pardos et al., 2014) may be related to a lengthening of the period with optimal conditions for seedling and sapling growth (Calama et al., 2015). Furthermore, the relationship with the annual and spring mean temperatures was stronger in the case of *P. pinaster* than for

*P. pinea*, possibly due to the better adaptation of *P. pinea* to sandy soils (Moreno-Fernández et al., 2017), which restrict the natural establishment and development of *P. pinaster* in years with extreme climatic conditions such as high temperatures and severe drought (Rodríguez-García et al. 2011b; Calama et al. 2017). In general, this climatic effect may be more direct at the seedling stage, since seedlings are more sensitive to extreme climatic conditions than saplings (Castro et al., 2004a; Cavender-Bares and Bazzaz, 2000).

Overall, *P. pinaster* is a species with a narrow range of optimal precipitation conditions (Gandullo and Sánchez-Palomares, 1994). The significance of this climatic variable on natural regeneration of *P. pinaster* has been addressed in previous studies (Rodríguez-García et al., 2011a; Rodríguez et al., 2008). Ruano et al. (2009) observed that summer rainfall had a significant influence on germination, early development, and on total and viable seedling density in *P. pinaster*; the availability of water being of greater influence than light on the growth of *P. pinaster* regeneration. These authors also found differing effects of water supply on seedling development according to the time lag used. We detected a significant positive relationship between current year seedling ingrowth and the precipitation of the summer and fall seasons of the previous year, probably due to the positive effect that this water availability has on the emergence and survival of recently emerged seedlings which, in the following year, will enter the seedling stage. In contrast, precipitation of the previous year has no effect on sapling ingrowth, indicating that changes in ontogeny from seedling to sapling are mainly linked to current year conditions. According to future climate scenario predictions for the Mediterranean basin (Brunet et al., 2009) it is likely that this narrow range of optimal precipitation conditions will be reduced, which could seriously limit the long-term establishment of *P. pinaster* in the study area.

### ***5.2. Contribution of climatic factors and stand structure to the success of regeneration occurrence***

The results Study II support our hypothesis that climatic factors control regeneration occurrence and point to the contribution of stand structure and composition to the success of

this process. Taking into account these climatic and stand-structural drivers, we also identified those future climate scenarios where natural regeneration of the studied species is expected to be an issue.

As expected, the presence of conspecific adult trees promotes about an increase in natural regeneration occurrence in both species. In the case of *P. pinaster*, this effect was more important than for *P. pinea* (Table 4.5). This finding is consistent with studies by Calama et al. (2015), Manso et al. (2014a), Rodríguez-García et al. (2011a), and Ruano et al. (2009), which evaluated the effect of the overstory cover on pine seedlings in pure stands of *P. pinea* and *P. pinaster* at local scale, as well as the importance of seed sources. As noted by these authors, extreme summer droughts are frequent in the study area, and the canopy protection offered by conspecific trees favors the regeneration of both species. The negative impact of heterospecific trees on the occurrence of *P. pinea* and *P. pinaster* regeneration has also been reported in previous studies (Ledo et al., 2014; Moreno-Fernández et al., 2017). This covariate had a significant negative effect on both species, although again, the magnitude of this effect was greater in the case of *P. pinaster*. As stated by Rodríguez et al. (2008), the shade-intolerant behaviour of *P. pinaster* could explain this relationship. The dense crowns of *P. pinea* provide more shade than those of *P. pinaster* and this probably hinders the regeneration of *P. pinaster*. In the case of *P. pinea* regeneration occurrence, the significant negative effect of heterospecific trees might be explained by the low dispersal capacity of *P. pinea* (Barbeito et al., 2009; Manso et al., 2012), limiting the seedbed beneath conspecific crowns or adjacent areas (Rodrigo et al., 2007).

Although mixed composition of the tree canopy was only observed in a few plots (5.2 %) the positive effect that this variable had over the probability of regeneration occurrence is worthy of note. The influence of this variable was again greater in the case of *P. pinaster*. Different natural regeneration responses in the presence of mixture have been reported in the literature. For example, Kolo et al. (2017) reported that regeneration of spruce species is more

likely to occur in pure stands than in mixed stands. In contrast, Stancioiu and O'hara (2006) and Moreno-Fernandez et al. (2017), in a previous study focusing on the same species, reported that light availability in mixtures can differ from that of monospecific stands, allowing the development of species with different requirements. Our results corroborate this idea, in which the different levels of shade created by mixtures increase the probability of the natural regeneration occurrence. In a recent research, Pardos and Calama (2018) observed that optimal conditions for regeneration in *P. pinea* were mainly found in mid-shade environments, where the influence of the crown reduces the negative effect of extremely high irradiance and temperatures during summer. In this regard, mixed forest with a greater variation in shade and other stand conditions, could provide more opportunities for the occurrence of regeneration.

It has been widely observed that competition between herbaceous and tree species can be an important issue for tree natural regeneration establishment and growth (Götmark et al., 2011; Jensen et al., 2012; Jensen et al., 2011). The main reason seems to be the competition for available resources, especially in sites where resources are scarcer such as the Mediterranean basin (Jensen and Löf, 2017). In line with this assumption, we detected a negative effect of the presence of a high level of herbaceous cover on the regeneration occurrence in both species, being the effects similar for both *P. pinea* and *P. pinaster*. However, other studies have reported that herbaceous vegetation may offer protection to seedlings by alleviating microclimatic extremes, such as solar radiation and soil temperature (Castro et al., 2004b; Löf, 2000). In our case, despite extreme temperatures in summer (40 °C) and winter (-10 °C), the negative effect of competition from high levels of herbaceous vegetation would appear to be greater than the attenuating effect of this vegetation on extreme microclimatic conditions.

One of the main limitations on measuring the effect of climate on regeneration occurrence is the scarcity of long-term time series. In our case a 15-year series was used, which is close to the usual regeneration period for the studied species, and thus giving strength and robustness to the results obtained and allowing us to confirm our hypothesis of climate-mediated annual

regeneration occurrence. Depending on the magnitude and sign of the parameter estimates in the model, mean spring temperatures, mean autumn temperatures, and maximum summer temperatures play a critical role in regeneration occurrence. The differences found with regard to the effects of mean spring temperatures (positive and equal for both species) and mean autumn temperatures (negative and only significant for *P. pinaster*) reflect the complex interactions which exist between environmental factors and optimum conditions for natural regeneration. Temperatures and precipitation during the months previous to spring and autumn may be linked to these findings. Blanco et al. (2015) found that cold soil temperatures can reduce water uptake, organic matter decomposition and limit root penetration. In our study area, Pardos et al. (2010) demonstrated that extremely low winter temperatures resulted in a limitation of photosynthetic and respiratory activity in *P. pinea* regeneration. Thus, it is possible that the increase in temperatures in spring help the seedlings to recover from the cold winter months, leading to better conditions for regeneration occurrence.

Autumn temperatures may have the opposite effect. After the summer season, during which seedlings are subjected to a high level of stress due to extreme temperatures and lack of precipitation, the decrease in temperatures could aid regeneration recovery. The fact that this variable only affects *P. pinaster* regeneration occurrence may support the theory that *P. pinea* is better adapted to sandy soil texture and extreme drought conditions (Calama et al., 2017; Rodriguez-Garcia et al., 2011b). Maximum summer temperature was found to be the climatic variable that had the greatest influence on natural regeneration, especially in *P. pinaster*. This result is in line with previous studies carried out in this study area (Calama et al., 2017, 2013; Cavender-Bares and Bazzaz, 2000; Moreno-Fernández et al., 2017; Ruano et al., 2015). Although the latter studies focused on a more local scale and the monitoring period was shorter, the results highlighted the strong interaction between summer stress conditions (extreme temperatures, higher rates of light irradiance and a drastic decline in soil water content) and the failure of natural regeneration. In the present thesis, despite identifying

summer precipitation as one of the driving factors of natural regeneration (Rodríguez-García et al., 2011b; Ruano et al., 2009) we did not manage to include this variable in the model. As evidenced, regeneration processes are highly stochastic phenomena in forest dynamics, the interactions of which with the different environmental parameters vary from one year to the next (Paluch, 2005) and from one regeneration stage to another. Because in this thesis, we excluded the first-year seedlings, which show a high level of mortality during summer, so regeneration occurrence might be less dependent on precipitation events. Our inability to include the precipitation in the model may also be attributed to species-specific strategies to cope with dry summer periods, by adjusting their life cycle or investing more in those traits that increase resistance to drought (Unger et al., 2018). Thus, it is possible that these seedlings are more adapted to drought conditions as maximum summer precipitation is more important in the emergence stage than in the establishment stage. This is in agreement with observations made by Calama et al. (2015) and Moreno-Fernández et al. (2017) who found higher mortality rates in younger seedlings in comparison to older ones as a result of summer drought.

Generating projections of natural regeneration processes under future climate scenarios could be a useful tool for exploring the consequences of different hypotheses on regeneration dynamics (Koniak and Noy-Meir, 2009; Peng and Apps, 1997). In this regard, a major challenge in modeling the climate effects on regeneration occurrence is to capture the integrative nature of all relevant climatic predictors. For this reason, our results may be subject to uncertainties associated with the complexity of future climate trends, where the role of interactions and extreme events are likely to be closely associated with the occurrence of natural regeneration. In this sense, the results obtained in the present study must be interpreted with caution when speculating about future events.

Despite these uncertainties, a general pattern emerges from our regeneration projections under the two climate scenarios analyzed (IPCC RCP 8.5 and Historic scenarios): the ability of *P.*

*pinaster* to regenerate will be lower than that of *P. pinea*, regardless of the scenario or the composition of the stratum of adult trees (Fig. 4.7). In this regard, the greater negative effects of mean autumn temperatures and maximum summer temperatures on *P. pinaster* could explain the differences found in the simulations between the probabilities of natural regeneration occurrence in *P. pinaster* and *P. pinea*. Bearing in mind that the mean and maximum temperatures are expected to increase in the future in Spain (De Castro et al., 2005), it can reasonably be assumed that suitable conditions for natural regeneration occurrence will decrease, especially in the case of *P. pinaster*. In addition, the findings of the simulations again emphasize the importance of mixed composition, since the projections for both species seem to be better in mixtures than in conspecific situations. This result is of particular importance since it may allow us to improve the probability of regeneration occurrence in these Mediterranean pine forests, especially in the case of *P. pinaster* species, and to maintain a certain level of species biodiversity in the region. In addition, they highlight the importance of promoting mixed forest as a strategic measure for adapting these forests to climate change (Kolström et al., 2011).

Different approaches to modeling regeneration success can be found in the literature. For instance, Canham and Murphy (2017) assume the existence of a 5-yr survival probability which can be extended or reduced to longer or shorter time intervals through a power function of the survival probability, in the same way as a composite interest rate. Under this framework, there is a strong assumption that annual survival does not change over time. This might be the case if the interval length does not vary much as in Fortin et al. (2008). In other contexts, it was found that this assumption does not hold (e.g. Manso et al., 2015b). Fortin et al. (2008) provide a methodology to test this assumption of survival probability acting like a composite interest rate.

The proportional hazards model does not fit this assumption. On the contrary, it assumes that the annual survival probabilities can change through the hazard function. Moreover, the

hazard function makes it possible to account for time-varying covariates, which is not the case for other likelihood-based models. For instance, our model takes into account the changes in the spring and autumn mean temperature on an annual basis. Because they cannot consider time-varying covariates, other likelihood-based approaches such as in Canham and Murphy (2017) have to rely on the maximum, minimum or mean temperatures over the interval. This can obviously hide some drastic year-to-year changes.

Thus, although these adverse climatic factors predicted for the studied area are not controllable, stand management could be used to facilitate natural regeneration. Our results could help managers to decide when and how to open the forest, releasing regeneration in order to favor different species in the future stand. Hence, to favor *P. pinaster* regeneration it would be necessary to maintain an adequate number of *P. pinaster* trees when regeneration fellings are performed. To favor *P. pinea* regeneration, however, it would be necessary to maintain denser conditions, provided mainly by conspecific crown cover, along with the progressive release of the overstory cover once the establishment of *P. pinea* seedlings is observed.

### ***5.3. Effect of species dynamic in the temporal response to climate in mature trees***

Study III provides a new perspective on the analysis of species-response to climate by introducing different temporal-scale approaches, with short-term impacts and long-term periods. Our results corroborate our main hypothesis on the existence of different behaviors in *P. pinea* and *P. pinaster* to cope with drought stress based on variables such as age, composition, density, size or drought intensity. Moreover, by comparing the growth of both species in mixed and monospecific compositions through synchrony patterns, we were able to gain a perspective on long-term forest response to climate variability.

#### ***5.3.1. Factors influencing tree response to extreme drought***

As expected, the results for the analysis of pointer years (i.e., anomalously wide or narrow rings), originating from extreme events, are in agreement with the peaks obtained in the SPEI



values (Fig 4.8). The integrative analysis of the different components of disturbance allows us to compare the performance during or immediately after the event (resistance), the impact of the change induced by the event (recovery) as well as the post and pre-disturbance states (resilience). The results obtained through the models fitted for the Lloret indices suggest a trade-off between resistance and recovery after the drought episodes, so that high resistance could result in low recovery or vice-versa. This is in line with the results of Galiano et al. (2011) who also observed similar trade-offs in the presence of limited stored reserves. Similarly, Thurm et al. (2016) found that in years with low average water supply the recovery capacity in European beech was more pronounced.

However, different characteristics of the species could act synergistically and may compensate drought stress in different ways, leading to several uncertainties. For instance, in the case of *P. pinaster*, young trees are more resistant than older trees. Different sensitivity to drought with age has been observed in other trees species, with responses depending on the species and age range used. Thurm et al. (2016) observed a significant, positive effect of this covariable in their models and similarly, Carrer and Urbinaty (2006) found that drought stress sensitivity in European Larch (*Larix decidua* Mill.) and Swiss stone pine (*Pinus cembra* L.) increase with tree age. They hypothesized that hydraulic constraints increase with tree age and this leads to an increase in drought stress sensitivity of tree species. Water requirements of the tree could also be related to this observation, since it is likely that older trees, which have higher rates of respiration, requires more water than young trees (Cavender-Bares and Bazzaz, 2000). Interestingly, higher stand density (SDI) improves the ability to regain growth (Recovery) to pre-drought levels in *P. pinaster*. However, the literature on this issue generally points to a negative effect of high stand densities on the resistance capacity of tree species due to decreased availability of resources (Lebourgeois et al., 2014; Rais et al., 2014; Thurm et al., 2016). This density effect would be in line with the abovementioned theory concerning the

existence of a trade-off between resistance and recovery after the drought episodes (Cavender-Bares and Bazzaz, 2000; Sun et al., 2018; Thomas and Winner, 2002).

In terms of resistance capacity, the worst year was 1992 and the best 2012. These results do tie in with the SPEI values, as the most severe drought occurred in 2012. However, it has been demonstrated that the time at which the drought event occurs has significant importance as regards the vulnerability of tree species (Eilmann et al., 2009; Michelot et al., 2012). In our case, the two years prior to 2012 were very wet, so these years probably influenced the resistance capacity of the species, improving the accumulated reserves. In contrast, the years prior to 2005 were also characterized as dry years, with an important heat wave in 2003. It is likely that this had an effect on tree growth and vigor, leaving the trees more vulnerable to the impact of drought. Merlin et al. (2015) reported opposite results for resistance and recovery, depending on when the drought occurs (summer or spring). Thus, some species have been found to be more sensitive to spring conditions and particularly to water availability during spring than to summer conditions, since the radial growth would have mainly occurred during the months preceding the drought (Morán-López et al., 2014; van der Werf et al., 2007; Zang et al., 2012). In this thesis, we have not specifically taken into account the moment at which the drought event occurs. Nevertheless, we observed that during the year 1992, spring precipitation was lower than during 2005 and 2012 (Fig. 4.9). Consequently, we assume that this could have influenced the responses of the two species to the drought events. Similarly, the worst recovery capacity was in 2012 and the best in 2005, in concordance with the autumn precipitation patterns (Fig. 4.9), reflecting the importance of the intra-annual precipitation pattern for tree growth in the Mediterranean region (Natalini et al., 2015) and the variability of growth responses to climate (Carrer and Urbinati, 2006).

The *drought Year* was the only covariable affecting the resilience capacity of the two species, which reflect the importance of climate conditions on tree growth in the Mediterranean region. Similar findings have been observed in other Mediterranean forests (Natalini et al.,

2015), suggesting a reaction to warming and increased water stress in tree species. In addition, these results highlight the inappropriateness of considering a numerical index which summarizes all the climatic variations for a given year, since we are not observing the non-stationary nature of the growth responses of trees to climate, as for example the precipitation patterns in spring and autumn.

The results also reveal opposite effects of increasing DBH in *P. pinaster*, with resistance decreasing but increasing recovery capacity. These findings agree with Merlin et al. (2015), who observed better response of small trees in terms of resistance to drought, and, as in our case, a faster recovery in larger trees. Similarly, as explained above, trees with larger diameters are subject to higher hydraulic constraint, which could decrease the resistance while larger root system might improve their recovery (Hacke et al., 2001). In line with this assumption, Thurm et al. (2016) suggested that older trees with smaller DBH had better resistance under drought, since these trees produced wood with higher density, forming stronger hydraulic pathways. However, the findings of Pichler and Oberhuber (2007) appear to contradict our results, since they found that small trees are more affected by drought events than larger trees, as a result of the shallow root system. That suggests that a size effect to more extent than an age effect on sensitivity to drought, while temperature to sensitivity, more related to transpiration rates and photosynthetic efficiency, suggests a true aging effect.

Moreover, although the results seem to indicate that *P. pinea* trees in mixtures have a higher resistance to drought than trees in monospecific composition, the negative interaction of DBH with mixtures attenuates this effect. In this context, a positive effect of mixtures associated with drought episodes could indicate higher within-population competition than between-species-competition, with smaller differences for larger trees, in drought years. In the case of our mixtures, it could be argued that tree diversity contributes to reducing vulnerability to drought in *P. pinea*, as supported by numerous studies in recent years (del Río et al., 2014b; Grossiord, 2019; Pretzsch et al., 2013), although this is not the case for *P. pinaster*. In this

regard, Grossiord (2019), in a recent review, reported that although positive effects of mixture are more commonly observed in relation to drought events, neutral and negative effects are also possible for some species. Other authors have also noted that tree diversity is not a fixed modulator of drought events and that the influence of mixture on tree response can shift from negative to positive (Forrester, 2014) under, for example, more benign climate conditions (Belote et al., 2011; Jucker et al., 2014). This fact makes it difficult to describe a specific directionality of mixed forest responses to drought. Furthermore, other factors apparently related to the environmental conditions have been observed to influence the relationships between diversity and the impacts of drought (Grossiord, 2019).

### **5.3.2. Drivers of synchrony and long-term temporal response**

The results obtained in the synchrony reveal that growth patterns are more affected by the forest structure, at least for *P. pinaster* that is less synchronous when growing mixed with *P. pinea*. Here, the significant p-value (0.0013) observed in the comparison between the intersynchrony in mixed compositions and monospecific compositions (Table 4.11, A), confirms our hypothesis of the existence of interactions between the two species in mixtures, and highlights the importance of competition-facilitation processes in a restrictive habitat, such as the Mediterranean pinewoods studied. The results presented in Table 4.11 reveal lower climate synchrony of *P. pinaster* in mixtures compared to monospecific stands. Therefore, it is likely that in mixed plots, the growth of *P. pinaster* is more influenced by interspecific interactions than that *P. pinea* growth and less conditioned by climatic conditions than in monospecific conditions, i.e. mixed compositions could reduce *P. pinaster* tree-ring sensitivity to climate. However, this effect was not identified during extreme events, possibly because growth in those extreme years was more limited by climate conditions than by competition.

The presence of age and quadratic mean diameter as covariates in the final model reflects the influence of other variables as modulators of synchrony patterns in the studied forests. In this regard, findings in community ecology have led to disagreement on the role of age in the

relationships between climate and radial growth. While some studies have assumed that, once the biological growth function has been removed, these relationships are independent of tree age (Fritts et al., 1990; Van Deusen, 1988), other studies maintain that trees respond in different ways to climate depending on their age (Szeicz and MacDonald, 1994; Thurm et al., 2016). Our results seem to be in agreement with the second assumption, since the significant positive effect of this covariate in the synchrony model for *P. pinaster* suggests greater sensitivity to climate variability in older trees than in younger trees. This greater sensitivity could also determine a greater response (increased water stress) to warming and increased water stress in older trees, which has already been observed in the results of the Lloret index models (Table 4.10). This finding is in accordance with the study of Natalini et al. (2015) in which it was observed that younger Mediterranean trees were less sensitive to climatic variability than older trees. However, research conducted by Vieira et al. (2009) under the Mediterranean climate of central Portugal, revealed that young *P. pinaster* trees responded faster to climate than older trees in the same climatic conditions. This lack of uniformity in the response of trees of different ages reflects the complexity of the climate-growth relationship. At the same time, the increase in drought frequency and intensity over the second half of the twentieth century ties in with the increase in growth synchrony in trees, in agreement with the results reported by Andreu et al. (2007).

Equally, the results of the model show that in the case of *P. pinaster*, larger trees were more sensitive than small trees to climate, which seems to be in agreement with the previously mentioned findings on the size-resistance relationship. As has been demonstrated, small trees are less able to obtain resources, nutrients, and light (Dhôte, 1994) due to their shallow root system, although it should be taken into account that they also require fewer resources than larger trees. This fact probably results in lower sensitivity to climate variability since they are likely to be more dependent on resource availability than on climate conditions. Nevertheless, it is important to consider that different soil or competition conditions within a stand can also

modify the response thresholds of individual trees (Merlin et al., 2015; Orwig and Abrams, 1997; Pichler and Oberhuber, 2007).

As regards *P. pinea*, the inability to perform a model suggests a common response to climate variability in the region, regardless of stand characteristics. The low genetic variability of *P. pinea* can reduce the individual response to climate and stand conditions, thus reducing variability and increasing synchrony (Mutke et al., 2019).

#### **5.4. Study of tree interactions**

Study IV offers insights into the tree interactions in mixed and monospecific *P. pinea* and *P. pinaster* forests by using empirical growth models and competition indices. This approach, based on the proxy variables of size-symmetric and size-asymmetric competition, differentiating between intra and interspecific competition, provides valuable information on the interactions between these two Mediterranean species. We found contrasting effects of mixing on both species; while *P. pinea* always benefits in mixed stands, the magnitude of the negative effect on *P. pinaster* growth depends on the relative sizes of the two species, reflecting the complexity of competitive interactions (Larocque et al., 2013). In addition, the inclusion of annual random effects in the different competition terms could help us to infer whether between-species interactions change during the most limiting years, for example during drought years (de-Dios-García et al., 2015).

Although there are several ways to evaluate competition measurements (Burkhardt and Tomé, 2012), competition indices have proved to be a suitable method to predict growth when other important predictors (age, size, density) are available. In this context, despite the fact that distance-dependent indices seem to be more effective due to the inclusion of inter-tree distances (Cattaneo et al., 2018), several authors have concluded that size ratio distance-independent indices can perform as well or better than distance-dependent indices (Ledermann, 2010; Pukkala and Kolström, 1987; Rivas et al., 2005). In the case of the studied species, previous studies have obtained satisfactory results by using distance-independent

indices (Calama et al., 2003; Riofrío et al., 2017), although for more complex structures, distance-dependent indices have delivered better results (Calama et al., 2008; Cattaneo et al., 2018; de-Dios-García et al., 2015).

Our competition indices provide empirical estimates of the effects of size-symmetric competition (SDI) and the effects of size-asymmetric competition (SDIL) as well as reflect the importance of plant interactions (intra o interspecific) in determining the growth response of trees to environmental changes (de-Dios-García et al., 2015). The findings obtained in this study reveal different competition patterns in *P. pinea* and *P. pinaster* in these Mediterranean forests.

In this regard, we found that stem growth in *P. pinea* was controlled by both intra size-asymmetric competition and intra size-symmetric competition (Table 4.13 [model 8]), although in this case, the effect of the size-asymmetric competition from larger *P. pinea* trees was more significant than the size-symmetric effect of the same species. These results reveal that *P. pinea* trees are not equally affected by the scarcity of resources, and that, smaller pine neighbors are suppressed by the larger individuals that obtain the majority of the contested resources (de-Dios-García et al., 2015; Schwinning and Weiner, 1998). Although there is no general relationship between the degree of size symmetry or asymmetry and the particular growth limiting resources, many studies (Weiner et al., 1990; Wichmann, 2001) have pointed to an association between size-symmetric competition and competition for below-ground resources on the one hand, and between size- asymmetric competition and above-ground competition for light on the other. Therefore, our results suggest that intra-specific competition in *P. pinea* may be controlled by both light and water resources. This Mediterranean pine is a highly light-demanding species and has adapted to the arid environments that characterize the study area (Niinemets and Valladares, 2006). However, water limiting situations, such as the typical Mediterranean summer droughts, could increase

competition for belowground resources among *P. pinea* trees (Cattaneo et al., 2018; Grams and Andersen, 2007).

Several authors have pointed to advantageous complementarity between species in the presence of reduced resource availability (Garber and Maguire, 2004; Perot and Picard, 2012; Pugnaire et al., 2000). In our case, although the effect of interspecific competition is not significant in our final *P. pinea* growth model, in relative terms, these results indicate the positive effects of mixtures. In this respect, the higher growth in mixed stands, when stand density levels are similar, is related to the non-significant effect of interspecific competition. Previous authors have related this complementarity to root stratification (de-Dios-García et al., 2015), since the root system of *P. pinea* is able to access deeper soil water (Mutke et al., 2012). Similarly, for a given level of competition between larger trees (SDIL), *P. pinea* benefits when there is a greater proportion of *P. pinaster* trees (non-significant effect of inter-specific size-asymmetric term), which may be due to the greater crown transparency of *P. pinaster* in comparison to *P. Pinea* (Barbeito et al., 2008).

In *P. pinaster*, the increased competitiveness detected in the presence of size-asymmetric competition, with a significant effect of the intra-specific term, led to an increase in the degree of asymmetry and consequently, an increase in tree size differentiation within the stand. Therefore, as in the previous case, smaller *P. pinaster* neighbours are suppressed by the larger individuals of the same species (de-Dios-García et al., 2015; Schwinning and Weiner, 1998), which obtain the majority of the contested resources. We also found that the admixture effect was significant (and negative), in symmetric mode of competition. Following the same idea presented above, our results suggest that in mixed stands, *P. pinaster* competes strongly with *P. pinea*, particularly for belowground resources. Several studies have pointed to *P. pinaster* as a species which is seriously affected by water availability in these Mediterranean forests as a result of climate change and/or overuse of aquifers (Prieto-Recio et al., 2015). Bearing in mind that *P. pinea* seems to be best adapted to sandy soil conditions, as widely reported (Manso et



al., 2014b; Moreno-Fernández et al., 2017), the existence of high belowground competition for *P. pinaster* in this area would appear to make sense. On the other hand, the non-significant effect of the inter-specific size-asymmetric competition could suggest certain niche complementarity in the crown architecture, since we obtain the same results (lack of significance and therefore absence of competition) in both species. This type of complementarity has previously been observed for *P. pinaster* - *P. sylvestris* mixtures by Riofrío et al. (2017, 2016), who provided evidence that species mixing increased structural heterogeneity and may induce over-yielding in mixed-species stands compared to monospecific stands.

The signal contribution of the random term in the models, both in *P. pinea* and *P. pinaster*, suggests that our results regarding plot, individual tree and year are robust with respect to spatial and temporal variability (Calama et al., 2019; Natalini et al., 2016), described in factors “plot”, “tree” and “year”, respectively. The initial breakdown of the observed variability (Table 4.14) reveals that pure spatial effects (plot and tree) in both species are quite high. In this case, the observed variability associated with the plot level is very similar in both cases, with 36.6% of the variability in *P. pinea* and 39.9% in *P. pinaster*. However, the variability associated with tree level was much higher in *P. pinaster* (26.9%) than in *P. pinea* (2.7%). Furthermore, the values associated with pure temporal-spatial effects (19.6% and 13.6%) highlight the importance of considering patterns of temporal variation in this type of studies. The important role of these random terms in the model suggests that other drivers such as microclimatic or edaphic variations, within-plot structure variability or anthropic factors linked to forest management, among others, could affect the relationship between tree secondary growth with respect to competition.

The findings point to a significant growth response to climate, as expected in this type of Mediterranean ecosystem (Calama et al., 2019; Madrigal-González and Zavala, 2014). We detected a positive relationship between spring rainfall and growth. Similar findings have been

reported for other Mediterranean pines (de Luis et al., 2009; Natalini et al., 2015; Novak et al., 2013; Piraino et al., 2013) as well as for other Mediterranean species (Campelo et al., 2009; Gea-Izquierdo et al., 2011).

In addition, in the case of *P. pinea* we detected an increment in the intense, negative effect of the intra-specific size-symmetric competition ( $m_k$ ) and inter-specific size-symmetric competition ( $n_k$ ) in 2005 and 2012 years, indicating that under such conditions, the BAI tends to be lower than predicted by the model (Fig. 4.12) and pointing to stronger competition for belowground resources under extreme droughts. Opposite results were found in relation to the inter-specific size-asymmetric competition effect ( $q_k$ ) for 2005, which could be related with the proposed stress gradient hypothesis, postulating positive interactions under harsher conditions (Bertness and Callaway, 1994). However, these findings are not consistent across all the drier years. For example, for 2009, the effect of the parameters is significantly attenuated (close to 0 and positive in the case of inter-specific size-symmetric competition), and in 2012, all the random effects related with the different modes of competition were again negative, indicating that in that year, competition was again accentuated.

In the case of *P. pinaster* we found that in 2005 and 2009 the negative effect of inter-specific size-symmetric competition ( $n_k$ ) over growth was especially aggravated, which is consistent with the situation described previously with regard to the negative effect of competition from *P. pinea* for the belowground resources (Fig. 4.13). These results would also indicate that under conditions of limited resources, such as a drought year, the competition status of *P. pinaster* versus *P. pinea* could be seriously aggravated. However, the positive effect of inter-specific size-asymmetric competition ( $q_k$ ) observed during these drought years (2005, 2009 and 2012) suggests a lower level of asymmetric competition during dry years, which is consistent with the theory of the different modes of competition (Pretzsch et al 2018). This theory suggests that under water limiting conditions, the size-asymmetric competition and therefore, the over-proportional growth of tall trees compared with small trees, may become

more symmetric. Thus, greater size may become a disadvantage, as large trees are more exposed to heat and hydraulic stress than their smaller neighbors (Pretzsch et al., 2018). These results have already been mentioned in the previous section (5.3.1), when we evaluated factors influencing tree response to extreme drought. However, while this pattern of species-specific reactions seems to be clear, no significant differences between monospecific and mixed-species stands as regards the dependency of growth partitioning on water availability have been observed (Pretzsch et al., 2018). In this respect, in our case, tree response to drought years seems to be more influenced by size-structure than by species composition, as observed in other studies (de-Dios-García et al., 2015; Raynaud and Leadley, 2005). However, detecting the mode of competition is not straightforward given the difficulty involved in direct measurement of the amounts of different types of resources used by individuals (Larocque et al., 2013).

Finally, as noted by Larocque et al. (2013), stands in which mixtures lead to reduced competition for one component species but not for the other would not necessarily be easy to manage, since extra effort would be required to maintain the least competitive of the species (*P. pinaster* in our case). In this context, stable coexistence in the same ecosystem requires that differences in ecological niches overcome differences in competitive ability (Mayfield and Levine, 2010). However, as shown in this study and in others previously (Grossiord, 2019), the influence of competition on tree response can easily shift from negative to positive. As a strategy to prevent great differences in growth and in order to capitalize the positive influence of mixture, Cattaneo et al. (2017) suggested avoiding notable differences between species in the initial size of the trees. For instance, in our case, favoring the *P. pinaster* growth rate could delay the appearance of intense interspecific competition processes and therefore the exclusion process.

### ***5.5. Synthesis***

The findings obtained in this thesis are of relevance for designing specific adaptation strategies tailored for this Mediterranean system and oriented towards increasing its resistance and resilience to concomitant climatic changes. As we explained before, adaptation to climate change refers to different adjustments in ecological, social and economic systems in response to the effect of climate change (Smit et al., 2000; Smit and Pilifosova, 2001). In this context, there are no global rules, since these adaptation strategies must respond to the occurrence of impacts and the vulnerability of each system to these impacts. This implies that adaptation measures must be designed at a local scale. To achieve it, an accurate assessment of forest system conditions constitutes a preliminary basic requirement.

Until date, there exist several evidences showing that the effects of mixing different tree species over ecosystem functioning go beyond the sum of the individual effect of each species (additive effect). However, the current available knowledge is so far rather fragmented that prevents providing a holistic picture of mixed species forests functioning. The research questions addressed in the different studies that compose this thesis are combined to describe how species-specific traits could reflect its evolutionary adaptation to environmental conditions such as temperature, and the availability of water, light and nutrients along with different ontogeny states (Bauhus et al., 2017). In addition, the approach established for this thesis confirmed the importance of combining different levels and scales in the analysis of Mediterranean forest stands dynamics. The results presented in this thesis provided useful information about species interactions at different levels and scales, as well as their consequences on pure and mixed forest stand dynamics regarding natural regeneration, responses to climate and drought, as well as temporal variability of their intra and interspecific interactions.

### **5.5.1. The process of natural regeneration: Success and projection under future scenarios**

It has been observed that during the regeneration process of these Mediterranean pines there are many influential factors, acting at both different spatial and temporal scales. In addition, as pointed by (Poorter, 2007), the fundamental regeneration niche of the different tree species is not constant and may change with the ontogeny of the individuals. The findings of the Study I could constitute a starting point for future studies on the role of ontogeny in the regeneration process. In this sense, the identification of the spatial and temporal factors controlling the establishment, growth, and survival of each ontogenic phase and triggering the change from seedling to sapling is considered a key issue in the studies of natural regeneration on forest tree species. One of the main aspects that contribute to the originality of this thesis is the regional scale used in the study of natural regeneration, allowing us to generalize the observed regeneration patterns at forest management scale. Upscaling to landscape scales has been considered a critical issue, since from manager's perspectives the main part of the adaptation strategies proposed by forest researchers refer either to detailed studies at a very local scale, very heterogeneous in their approach, or to very global scale studies based mainly on model predictions. As Calama et al (2017) reflected, both cases seem to move away from the work scale of the forest manager. In this sense, the results presented in this thesis can be useful for supporting the implementation of adaptive management practices under a climate change context. By the modeling approach, performed in Study II, we are able to identify the problematic areas with regards to natural regeneration. Therefore, despite the uncertainties associated with the complexity of future trends and according to the results of the simulations carried out under different climate scenarios, the promotion of mixed composition could be an adequate approach to increase the probability of natural regeneration occurrence in the Northern Plateau of Spain. However, as a negative point, the results of the regeneration studies clearly show regeneration problems for *P. pinaster* in the study area. This fact – together with the apparent success of *P. pinea* regeneration even beneath pure *P. Pinaster*

patches - could lead to a shift in species composition, with the conversion of the mixed stands of *P. pinea* and *P. pinaster* into pure stands of *P. pinea*, leading to a loss of biodiversity.

#### **5.5.2. Linking of species-mixing effects: drought responses and competition**

In order to obtain a better knowledge of the current and future state of the forests, understanding the potential effect of future climate scenarios over ecosystem functioning is one of the greater challenges in forest science (Allen et al., 2010). Here, differences in structural and physiological adaptation strategies of tree species could mitigate the expected negative impacts associated with climate change and reduce vulnerability of forests. Nonetheless, tree response to drier conditions is an eco-physiological process depending on both extrinsic and intrinsic factors, which can be observed at different temporal scales. The approach established in Study III assessed the short and long term responses in order to obtain a retrospective assessment of forest sensitivity to climate. This is especially important when the climatic conditions correspond to the driest (for both species) and colder (in the case of *P. pinea*) conditions in the distribution range of the two species. In this way, the observed changes in the relationship between climate and growth responses reflect the non-stationary nature of tree growth response to climate and disturbances, in our case drought events. In addition, the evaluation of these responses in function of variables such as age, size, density or composition reflects the complexity of species strategies to withstand the negative impact of climate. The results of Study III, corroborate findings from other studies (Carrer and Urbinati, 2006; Thurm et al., 2016) and support the hypothesis about the occurrence of different strategies in *P. pinea* and *P. pinaster* facing drought stress in function of the variables previously mentioned (age, size, density or composition). Among these findings, we could highlight the existence of a trade-off between resistance and recovery, widely observed in other trees species (Galiano et al., 2011). In addition, larger and/or older trees often appear more vulnerable to drought impacts, especially in the case of *P. pinaster*. Although this relationship has been observed to be species-dependent, some authors (Cavender-Bares and

Bazzaz, 2000) hypothesized that hydraulic constraints increase with tree age and/or size, leading to an increase in drought stress sensitivity in tree species.

Since the effect of drought on tree species can last for several years and decades, the proposed synchrony analysis provides us insights into long term effects of climate variability. In this case, the results of the interspecific synchrony in mixed and monospecific composition reveal that growth patterns are also affected by the forest structure, at least for *P. pinaster* that is less synchronous when growing mixed with *P. pinea*. This hypothesis will be also reinforced in the results of Study IV, which deep into the interactions in mixed and monospecific *P. pinea* and *P. pinaster* forests and where we found that even when similar species are combined, the outcome still depends on the set of current environmental conditions, including resource availability and climate constraints. In this context, Larocque et al. (2013) pointed out that few attempts have been performed to better understand the complete range of interactions in mixed stands using well-replicated experimental designs. The number of plots used here (25 monospecific *P. pinea* plots, 25 monospecific *P. pinaster* plots and 25 mixed plots), contributes also to the soundness of this study and helps us to generalize the results about the competitive relationship between the species in the studied area. On the other hand, the concept of mode of competition used in Study IV is helpful to a better understanding of how competing tree species share resources. Interestingly, our results showed that species exhibited unbalanced competitive relationships for above-ground and below-ground resources. Thus, we found that *P. pinea* is mainly controlled by intraspecific competition, especially by the size-asymmetric competition. In addition, the results indicate that *P. pinea* growth is enhanced by the presence of *P. pinaster* trees. However, this relationship seems to be complex, since for instance, Lloret indices reflect a positive effect of the mixture in the resistance capacity of *P. pinea* while growth models indicate that under extreme drought there is stronger competition for below-ground resources. *P. pinaster* is negatively affected by the intraspecific size-asymmetric competition, while strongly competing

with *P. pinea* for belowground resources. Curiously, under water-limited conditions, the size-asymmetric competition and therefore, the over-proportional growth of larger trees compared with smaller ones may become more symmetric in this species, suggesting that tree response to drought years seems to be more influenced by size-structure than species composition, as has been observed through the model fitted for the Lloret indices and in others studies (de Dios-García et al., 2015; Raynaud and Leadley, 2005).

### **5.5.3. Current and future implication for forest management**

The combination of all of these results shows that individuals and populations of different species experience a range of different interactions (Larocque et al., 2013), especially under critical events including extreme climate or disturbances. In this context, the net effect of these interactions (loss or gain) may shift on time (Cavard et al., 2011) and the new state of the ecosystem may or not warrant the supply of the expected ecosystem services. Here, the appropriate management of a given forest ecosystem could make a significant contribution, since as it has been observed through the thesis, characteristics such as age, size, stand density or species composition could lead to variations among species in the ability to capture resources and improve their resistance to climate change. In the studied area, current management has a long tradition of promoting nut production in *P. pinea* and resin production in *P. pinaster*, and to date, these productions are still quite important for local populations. This fact, together with the advantages associated with the complexity and diversity of mixed stands, as described in this thesis, have encouraged forest managers to demand general management prescriptions for mixed forests. As we observed, the specific adaptation measures tailored for this ecosystem must be oriented towards promoting and ensuring natural regeneration as well as increasing its resistance and resilience to concomitant climatic changes. In this way, a number of actions within current silvicultural prescriptions can be implemented. In this sense, it is recommended to ensure initial protection to the emerged seedlings, by maintaining a coverture of adult trees. Subsequently, at some point, parent trees



should be progressively removed to release from shade those cohorts with increasing light requirements. However, this temporal point is not necessarily the same in both species, so the species-specific requirements for the change to the next ontogeny stage (seedling to sapling) should be taken into account. In the case of adult stands, an increase in stand heterogeneity (i.e. size and species) could help *P. pinea* and *P. pinaster* species to increase resistance and resilience to climate change, with special attention to drought events. A greater heterogeneity could also help to decrease competition intensity and compensate for the losses on the growth of tall trees in the benefit of small trees (Pretzsch et al., 2018), stabilizing stand growth under drought events. This recommendation of increasing stand heterogeneity (i.e. size and species) to strengthen resistance and resilience to climate change, could be complemented with examples of possible silvicultural options (e.g. shelterwood with artificial sowing) taking into account the precipitation/temperature levels of previous years when planning harvesting, in order to favor optimal natural regeneration establishment.

Because holistic management of climate change effects over forest ecosystems is paramount, this thesis compiles and summarizes useful management options for evaluating risk and reducing the vulnerability of Mediterranean *P. pinea* and *P. pinaster* forests in the current era of changing climate. Our results show that management strategies are reasonably good and applicable and may achieve the previously mentioned adaptation objectives. At the next step, it is necessary the transfer of this knowledge to the practical management of forests, because adaptation objectives will only be possible through a cooperation between researchers, forest managers and policymakers.



## 6. Conclusions

1. Natural regeneration in *P. pinea* is more successful than that of *P. pinaster* in the studied area, at both seedling and sapling stages. However, for both species, the step from seedlings to saplings is critical, since only 35% of the plots had established saplings of any species at the end of the studied period. In this case, *P. pinaster* saplings were only observed in 5% of the plots.
2. *P. pinea* seedlings were favored by the presence of conspecific adult trees, likely due to the low dispersal capacity of the species. However, saplings must be progressively released from *P. pinea* overstory cover. In *P. pinaster*, both seedlings and saplings occurred in close proximity to conspecific adult individuals. In this case, the shade-intolerance of the species could explain the limited *P. pinaster* regeneration observed under nonconspecific trees. Although both species regenerate better under the cover of their own species, there is a positive effect of mixture, especially in *P. pinea*.
3. Seedlings occurrence is more conditioned by the annual climate while the success of saplings establishment is more related to the site conditions.
4. An optimal regeneration establishment was related to favorable conditions as regards annual and spring mean temperatures. Precipitation levels of the summer and fall seasons of the previous and current year were found to have different effects on seedling and sapling ingrowth.
5. The summer maximum temperature was the climate variable which had the greatest influence (negative in this case) on natural regeneration, especially in *P. pinaster*. Under more adverse climate change scenarios the regeneration of *P. pinaster* is seriously threatened.
6. To promote and ensure natural regeneration silvicultural practices may be oriented to protect the emerged seedlings by maintaining a crown cover of adult

trees (of both species) and remove progressively and timely adult trees to release seedlings and saplings from shade.

7. In adult trees of both species, it was observed a trade-off between resistance and recovery capacities. In the case of *P. pinaster*, young trees were more resistant than older trees. In addition, curiously the increase in stand density (SDI) improves the ability to recover. *P. pinea* in mixtures have a higher resistance to drought, however, the negative interaction of DBH with mixtures attenuate this effect. In this last case, the recovery capacity seems to be dependent of the moment in which the drought event occurs.
8. In order to increase resistance and resilience to climate change forest management practices must be oriented to increase stand heterogeneity (size and species), i.e. aim at multi-cohort mixed pine stands.
9. The significant differences between the synchrony in mixed and monospecific compositions seem to indicate the existence of interactions between both species in mixtures. In *P. pinaster*, the significant positive effect of age and quadratic mean diameter in the synchrony model suggest a higher sensitivity to climate variability in older trees than in younger trees. On the contrary, the inability to fit a model for *P. pinea* suggests a common response to climate variability in the region.
10. Intra-specific size-asymmetric and size-symmetric competitions determine *P. pinea* tree growth, indicating that intra-specific competition is controlled by both light and water resources. The competition for below resources is aggravated under extreme droughts. The mixture with *P. pinaster* reduces both size-symmetric and size-asymmetric competition, resulting in a positive effect on *P. pinea* tree growth.

11. In *P. pinaster* the admixture effect was significant and negative in symmetric competition, which suggests a strong competence for belowground resources with *P. pinea*. However, small *P. pinaster* trees are suppressed only by larger conspecific individuals, reflecting some degree of niche complementarity between species at aboveground level.
12. Species mixing effects in *P.pinea* - *P pinaster* forests vary between forest dynamic stages and along spatio-temporal scales, with some trade-offs among them, highlighting the complexity of species interactions. However, in the absence of management or favored by it, these Mediterranean forests will very likely be transformed into a *P. pinea* pure forests.



## 6. Conclusiones

1. Dentro de la zona de estudio, la regeneración natural de *P. pinea* es más exitosa que la regeneración de *P. pinaster*. Sin embargo, en ambas especies el paso de plántula hacia el regenerado avanzado es crítico, ya que solamente el 35% de las parcelas presentaron regenerado establecido al final del periodo. En el caso de *P. pinaster* este porcentaje fue solo del 5%.
2. Las plántulas de *P. pinea* se vieron favorecidas por la presencia de árboles adultos de su misma especie, probablemente debido a la baja capacidad de dispersión de la especie, sin embargo, se observó que el regenerado avanzado debe liberarse para su óptimo desarrollo. En *P. pinaster*, ambas fases del regenerado ocurren en la proximidad de individuos adultos de la misma especie. En este caso, la intolerancia a la sombra podría explicar limitada regeneración observada de *P. pinaster* bajo arboles adultos de *P. pinea*. Aunque ambas especies se regeneran mejor bajo la cobertura de la misma especie, existe un efecto positivo de la mezcla, especialmente en *P. pinea*.
3. La presencia de plántulas está más condicionada por las condiciones climáticas anuales, mientras que la presencia de regenerado avanzado está más condicionado por las condiciones del sitio.
4. Las condiciones óptimas para el establecimiento de la regeneración natural se relacionó con temperaturas medias anuales y de primavera favorables. Se observó que los niveles de precipitación de las temporadas de verano y otoño, tanto del año anterior como del actual, tienen diferentes efectos sobre el regenerado.
5. La temperatura máxima del verano fue la variable climática que tuvo la mayor influencia (negativa en este caso) en la regeneración natural, especialmente en *P.*

*pinaster*. En escenarios de cambio climático más adversos, la regeneración de *P. pinaster* está seriamente amenazada.

6. Para promover y asegurar la regeneración natural, la silvicultura debe orientarse a proteger las plántulas que emergen, a través de un mantenimiento adecuado de la cobertura de los árboles adultos (de ambas especies). Sin embargo, una vez que estas plántulas alcanzan el estado de regenerado avanzado, se debe eliminar el arbolado adulto de manera progresiva, al objeto de permitir la liberación del mismo.
7. Existe una compensación entre la resistencia y la capacidad de recuperación de los árboles adultos en ambas especies. En el caso de *P. pinaster*, los árboles jóvenes mostraron más resistencia, y curiosamente, el aumento de la densidad del rodal mejoró la capacidad de recuperación de esta especie. *P. pinea* mostró una mayor resistencia a la sequía en mezclas, sin embargo, la interacción negativa de la mezcla con el DBH atenuó ese efecto positivo. En este último caso, la capacidad de recuperación parece depender más del momento en que ocurre el evento de sequía.
8. Para aumentar la resistencia y la resiliencia frente al cambio climático, se deben plantear prácticas silvícolas orientadas a aumentar la heterogeneidad de los rodales (tamaño y especies), es decir, fijar como objetivo alcanzar rodales mixtos de múltiples cohortes.
9. Las diferencias significativas observadas al comparar la inter-sincronía en composiciones mixtas y monoespecíficas, parece indicar la existencia de interacciones entre ambas especies en mezclas. En el caso de *P. pinaster*, el efecto positivo de la edad y del diámetro medio cuadrático en el modelo, sugieren una mayor sensibilidad de los árboles más viejos a la variabilidad climática. Por el



contrario, la incapacidad de ajustar un modelo de sincronía para *P. pinea* sugiere una respuesta común por parte de los árboles de la especie al clima.

10. La competencia intraespecífica, tanto simétrica como asimétrica, determina el crecimiento de los árboles de *P. pinea*, indicando que esta competencia intraespecífica está controlada tanto por luz como por la disponibilidad de los recursos hídricos. Sin embargo, esta última se ve agravada durante las sequías extremas. La mezcla con *P. pinaster* reduce la competencia tanto simétrica como asimétrica, lo que resulta en un efecto positivo en el crecimiento del árbol de *P. pinea*.
11. En *P. pinaster*, el efecto de la mezcla fue significativamente negativo en la competencia simétrica, lo que sugiere una fuerte competencia por los recursos hídricos con *P. pinea*. Sin embargo, los árboles de menor tamaño de *P. pinaster* son suprimidos principalmente por individuos conspecíficos más grandes, lo que refleja cierto grado de complementariedad de nicho entre especies a nivel del suelo.
12. El efecto de la mezcla de especies entre *P. pinea* y *P. pinaster* varía entre las diferentes etapas ontogénicas y a lo largo de diferentes escalas espacio-temporales, con algunas compensaciones entre ellas, lo que pone de relieve la complejidad de las interacciones entre las especies. Sin embargo, se observa que ante la ausencia de un manejo óptimo es probable que estos bosques mediterráneos se transformen en bosques puros de *P. pinea*.



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## Appendix A: Scientific Studies

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## **Study I**

Based on: **Spatio-temporal variation of natural regeneration in *Pinus pinea* and *Pinus pinaster* Mediterranean forests in Spain (2019). European Journal of Forest Research.**

Marta Vergarechea, Miren del Río, Javier Gordo, Rebeca Martín, David Cubero, Rafael Calama

DOI: 10.1007/s10342-019-01172-8

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### **SPECIFIC OBJETIVES**

1. Evaluating the establishment and success of natural regeneration in mixed and monospecific forests.
  2. Analyzing the recruitment of both species in function on adult stand composition
  3. Identifying whether there is intra-and interspecific synchrony in regeneration
  4. Determining how temporal variation is related to climate
- 

### **DATA**

#### **Experimental design**

- Inventories of INIA-CIFOR and forest service of Valladolid
- 1936 circular plots with a radius of 8 m (0.02 ha) following the stock quadrant methods.
- Natural regeneration of *P. pinea* and *P. pinaster* identify and classify in 4 categories in function of the viability

#### **Spatial scale**

- Plot and stand scale

#### **Time scale**

- Period: 2001-2015
- 

### **METHODOLOGY**

#### **Spatial variation**

- Exploratory analysis (Spatial correlation and frequency tables)
- Contingency tables
- Principal components analysis (Spatial scale)

#### **Temporal variation**

- Principal components analysis (Temporal scale)
  - Tau Kendall analysis (Synchrony patterns)
- 

### **MAIN FINDINGS**

- Natural regeneration show species-specific differences during the seedling stage
- The composition of the stratum of adult trees play a significant role in the successful of regeneration
- Higher seedlings sensitivity to extreme climatic conditions
- At landscape scale, seedlings are more dependent on site and spatially explicit attributes
- Optimal regeneration establishment seems to be related to annual and spring mean temperatures

## **Study II**

Based on: **Climate-mediated regeneration occurrence in Mediterranean pine forests: A modeling approach (2019). Forest Ecology and Management.**

Marta Vergarechea, Rafael Calama, Mathieu Fortin, Miren del Río

DOI: 10.1016/j.foreco.2019.05.023

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### **SPECIFIC OBJETIVES**

5. Developing a probabilistic model based on survival analysis techniques in order to predict *P. pinea* and *P. pinaster* natural regeneration occurrence
  6. Selecting variables to include in the model that are easily-accessible by forest managers
  7. Identify the limitations that could affect natural regeneration, taking into account the species-specific traits as well as the silvicultural practices
- 

### **DATA**

#### **Experimental design**

- Inventories of INIA-CIFOR and forest service of Valladolid
- 1703 circular plots with a radius of 8 m (0.02 ha) following the stock quadrant methods.
- Natural regeneration of *P. pinea* and *P. pinaster* identify and classify in 4 categories in function of the viability

#### **Spatial scale**

- Landscape scale

#### **Time scale**

- Period: 2001-2015
- 

### **METHODOLOGY**

- Proportional-hazards mixed model
- 

### **MAIN FINDINGS**

- The presence of conspecific adult trees brought about an increase in natural regeneration occurrence in both species
- Heterospecific adults trees have a negative impact on the occurrence of regeneration, especially in *P. pinaster*
- The positive effect of mixed composition is worthy of note
- There are a high competition between herbaceous and seedlings, which can be an issue for regeneration establishment and growth
- Maximum summer temperature is the climate variable that has the greatest influence of regeneration. Temperature in spring and autumn also affect regeneration, but in different way

## **Study III**

Based on: **Effect of species dynamic in the temporal response to climate in *Pinus pinea* and *Pinus pinaster* Mediterranean forests (2019). Forest Ecology and Management (Under review).**

Marta Vergarechea, Rafael Calama, Hans Pretzsch, Josu G. Alday, Miren del Río

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### **SPECIFIC OBJETIVES**

8. Observing common associations (synchrony) between indexed ring-width
  9. Analyzing species responses to drought events using Lloret indices at individual tree scales
- 

### **DATA**

#### **Experimental design**

- Inventories of INIA-CIFOR and forest services of Valladolid
- 75 permanent plots. 25 monoespecific *P. pinea* plots, 25 monoespecific *P. pinaster* plots and 25 mixed plots

#### **Measurements**

- Tree coordinates, DBH, Height, Live\_Branch, Crown Radius and three increment cores

#### **Spatial scale**

- Plot scale (Synchrony)
- Individual tree scale (Lloret indices)

#### **Time scale**

- > 30 years (Synchrony)
  - Annual scale (Lloret indices)
- 

### **METHODOLOGY**

- Logit models using tree growth synchrony
  - Mixed models using Lloret indices (Resistance, recovery and resilience)
- 

### **MAIN FINDINGS**

- Tree diversity contributes to reducing vulnerability to drought in *P. pinea* as well as tree-ring sensitivity to climate in *P. pinaster*
- The age and quadratic mean diameter influence the synchrony patterns in Mediterranean forests
- In *P. pinaster*, larger and older trees were more susceptible to climate than smaller and young trees
- The worst recovery capacity was in 2012 and the best in 2005, in concordance with the autumn precipitation patterns



## **Study IV**

Based on: **Is the effect of inter and intraspecific competition on radial growth mediated by climate events? (In preparation)**

Marta Vergarechea, Rafael Calama, Nicolas Cattaneo, Miren del Río

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### **SPECIFIC OBJETIVES**

10. Analyzing size-symmetric and size-asymmetric competition effects in mixed and monospecific *P.pinea* and *P. pinaster* forests
- 

### **DATA**

#### **Experimental design**

- Inventories of INIA-CIFOR and forest services of Valladolid
- 75 permanent plots. 25 monoespecific *P. pinea* plots, 25 monoespecific *P. pinaster* plots and 25 mixed plots

#### **Measurements**

- Tree coordinates, DBH, Height, Live\_Branch, Crown Radius and tree ring width data

#### **Spatial scale**

- Individual tree

#### **Time scale**

- Annual scale
- 

### **METHODOLOGY**

- Distance-independent competition indices based on the stand density index (SDI) and the stand density index of trees larger than the target tree (SDIL)
  - Multilevel linear mixed models (MLMM)
- 

### **MAIN FINDINGS**

- Intra-specific size-asymmetric and size-symmetric competition determines *P. pinea* tree growth.
- The mixture with *P. pinaster* reduces both size-symmetric and size-asymmetric competition, resulting in a positive effect on *P. pinea* tree growth.
- In *P. pinaster* have a strong competence for belowground resources with *P. pinea*
- small *P. pinaster* trees are suppressed only by larger conspecific individuals



## **Appendix B: Peer-reviewed articles**

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Front page of articles published in SCI journals



# Spatio-temporal variation of natural regeneration in *Pinus pinea* and *Pinus pinaster* Mediterranean forests in Spain

Marta Vergarechea<sup>1,2</sup> · Miren del Río<sup>1,2</sup> · Javier Gordo<sup>3</sup> · Rebeca Martín<sup>3</sup> · David Cubero<sup>3</sup> · Rafael Calama<sup>1,2</sup>

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## Abstract

Recent research undertaken in Mediterranean pine forests suggests that the establishment of *Pinus pinea* L. and *Pinus pinaster* Ait. natural regeneration is determined by different spatial and temporal factors. In this context, we analyzed the establishment and success of natural regeneration in these two species and we examined the hypothesis that the spatial pattern of natural regeneration depends on adult tree presence, density or stand composition, while temporal patterns are typically driven by climatic conditions. For the purposes of the experiment we used 1936 plots of 0.02 ha established in mixed and pure forests of *P. pinea* and *P. pinaster* in the Northern Plateau of Spain. Plots were installed following regeneration fellings, and regeneration was monitored annually between 2001 and 2015. We used contingency tables and principal component analysis (PCA) to evaluate the main factors affecting the spatial distribution of the regeneration. PCA was also used to assess the temporal variation as a function of climatic variables. Finally, we checked for the existence of interspecific and intraspecific synchrony through Tau-Kendall synchrony analysis. We found that natural regeneration of *P. pinea* was more successful than that of *P. pinaster* over the whole of the studied period. Contingency tables showed that *P. pinaster* regeneration was associated with conspecific adult trees, while the relationship between *P. pinea* regeneration and adult trees varied depending on the regeneration development stage, i.e., seedling or saplings. Furthermore, we found that natural regeneration in both species could be enhanced through the presence of mixtures of adult trees. The spatial variability, analyzed through PCA, showed similar responses in both species, although temporal variability associated with climate variables differed between *P. pinea* and *P. pinaster*. Finally, we found different synchrony patterns affecting natural regeneration, depending on the species and the regeneration stages. In this context, temporal patterns seem to be species specific during the sapling stage of regeneration. These findings allow the observed regeneration patterns in Mediterranean pinewoods to be generalized at forest management scale.

**Keywords** Regeneration establishment · Ontogenic development · Temporal synchrony · Principal component analysis

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# Climate-mediated regeneration occurrence in Mediterranean pine forests: A modeling approach



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## ARTICLE INFO

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## ABSTRACT

The generation of projections under different climate scenarios and stand conditions provides a useful tool to explore the consequences of climate change on ecosystem dynamics and to define possible interventions to ensure their persistence over time. Over recent decades, climate change has been particularly severe in the Mediterranean basin, where a lack of natural regeneration is one of the main limitations threatening Mediterranean forests. In this context, in order to define the main drivers affecting this process, we evaluated the occurrence of regeneration in *P. pinea* and *P. pinaster* forests, taking into account the stand-structure as well as climate conditions. The regeneration data is taken from a network of 1703 plots located on the Northern Plateau of Spain and monitored over 15 years. Through survival analysis we modeled the probability of regeneration occurrence after a time  $t$  (years since regeneration fellings were carried out) at regional level. The model was then used to simulate regeneration success under two climatic scenarios. According to the modeling results, the ability of *P. pinaster* to regenerate was always lower than that of *P. pinea*, regardless of the scenario and stand conditions. The relationship between regeneration success and presence of adult trees varies depending on the species composition. Higher probabilities of regeneration occurrence were positively associated with mixed species composition in adult trees for both species, while *P. pinaster* exhibited significantly lower regeneration under monospecific *P. pinea* adult trees. Regeneration probability was negatively associated with increasing levels of grass cover on soils. The results also pointed to the existence of climate-mediated annual regeneration occurrence, reflecting the complex interaction which exists between environmental factors and the optimum conditions for natural regeneration. The findings obtained in the present study could help us to identify problematic areas with regard to natural regeneration so that appropriate management can be defined to favor the different species in future stands.

## 1. Introduction

Natural regeneration is a key element in the evaluation of long-term sustainability of forest systems. The success of natural regeneration is dependent on different well-defined stages such as seed dispersal, predation, germination, emergence and establishment (Calama et al., 2017; Manso et al., 2014a) whereby the degree of success of one of these stages has a direct effect on the success of the next. Hence, regeneration establishment is directly dependent on the success of the regeneration emergence phase (Hunziker and Brang, 2005). Furthermore, during the change in ontogeny (seedlings to saplings), the species are influenced differently by the vegetation structure, species composition, functional attributes as well as climate conditions (Walker et al.,

2007), developing different species-specific regeneration strategies (degree of shade tolerance, water use efficiency or resistance to drought). This fact, may explain the regeneration success of one species over the other and subsequent shifts in the specific composition of forest stands.

Taking into account the species-specific regeneration strategies is essential in order to determine how regeneration fellings contribute to and interact with the regeneration process (Stancioiu and O'Hara, 2006; Webb and Jarrett, 2013; Yoshida et al., 2005). In those areas where the establishment of natural regeneration is expected to be less successful due to climate change, this knowledge may be crucial. For instance, it has been observed that the role of tree canopy protection will be more important as the climatic conditions become more stressful, especially

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