UNIVERSIDAD POLITÉCNICA DE MADRID
ESCUELA TÉCNICA SUPERIOR
DE INGENIERÍA DE MONTES, FORESTAL Y DEL MEDIO NATURAL

DINÁMICA DE LOS PINARES DE MONTAÑA BAJO
GESTIÓN FORESTAL SOSTENIBLE EN UN CONTEXTO
DE CAMBIO GLOBAL

Tesis doctoral

DANIEL MORENO FERNÁNDEZ

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Sistemas Forestales

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*“Allá muevan feroz guerra,
ciegos reyes,
por un palmo más de tierra,
que yo tengo aquí por mío
cuanto abarca el mar bravío,
a quien nadie impuso leyes.”*

La Canción del Pirata. José de Espronceda

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Resumen

El principal objetivo de esta tesis doctoral es evaluar a distintas escalas, la influencia de la gestión forestal sostenible en la dinámica de los pinares de *Pinus sylvestris* L. (pino silvestre) en el Sistema Central el efecto del cambio global en los montes mediterráneos. En primer lugar se estudia a microescala la influencia de distintos factores ecológicos y de la intensidad de las cortas de regeneración en las primeras etapas de regeneración de *P. sylvestris*. Además, se comparan distintas técnicas estadísticas y se analizan las debilidades y las fortalezas de cada una de ellas. Las distintas técnicas estadísticas muestran que el número de plántulas del *P. sylvestris* está positivamente relacionado con la intensidad de las cortas y negativamente con el contenido de sodio en el suelo (**Capítulo 2**). A continuación, se plantea un modelo espacio-temporal para determinar la distribución espacial del número de pies menores en función del tamaño y de la distancia entre los pies adultos. Se encuentra una influencia negativa en la distancia de los pies adultos a los pies menores de hasta 7 m (**Capítulo 3**). En el **Capítulo 4** se trabaja a escala monte comparando el efecto de dos sistemas de gestión forestal en el carbono almacenado en los distintos compartimentos durante el periodo de rotación. El sistema de gestión menos intenso y con periodo de rotación más largo almacena, como media anual, más carbono que el sistema más intenso. Sin embargo, el carbono almacenado en los horizontes superficiales no se ve afectado ni por el sistema de gestión ni por la edad de la masa. Finalmente, se estudian los cambios de distribución y abundancia del *P. sylvestris* y del *Quercus pyrenaica* Willd. (rebollo) en los últimos 40 años en la Sierra de Guadarrama de la Comunidad de Madrid como consecuencia del cambio global (**Capítulo 5**). Además, se valida una metodología para determinar la significación de las variables auxiliares y la varianza asociada a la función principal, así como a la autocorrelación espacio-temporal en modelos de krigado y cokrigado universal. Los resultados indican que tanto la distribución y la abundancia del *P. sylvestris* se han mantenido constante mientras que la distribución y la abundancia del *Q. pyrenaica* han aumentado significativamente. Como consecuencia, la superficie donde ambas especies coexisten se ha triplicado.

Palabras clave: multiescala; mitigación; gestión forestal adaptativa; cambio climático; área Mediterránea; silvicultura; modelización forestal; ecología forestal; estructura de masa

Abstract

The main objective of this thesis is to assess the influence of sustainable forest management at different scales on the dynamics of *Pinus sylvestris* L. (Scots pine) stands in Central Spain as well as the effects of global change on Mediterranean forests. Firstly, the influence of ecological factors and of the intensity of regeneration fellings on the first stages of the regeneration of *P. sylvestris* at microscale are assessed. Additionally, several statistical approaches are used to model forest regeneration and the weaknesses and strengths of each are discussed. The alternative approaches show that the number of *P. sylvestris* seedlings is positively related to heavy fellings and negatively related to sodium content (**Chapter 2**). On a larger scale (plot level), a spatio-temporal recruitment model is proposed. This model determines the spatial distribution of the saplings as a function of the size of adult trees and the distance between adult trees and saplings. The model detects a negative association between the diameter of adult trees and number of saplings up to a distance of 7 m (**Chapter 3**). **Chapter 4** analyses the way in which two management systems affect the carbon stored in forest pools over the rotation period. The results reveal that less severe management systems with longer rotation periods increase carbon fixation. On the other hand, neither the forest management nor the stand age have a significant effect on the carbon stored in the soil. Finally, the shifts in distribution and changes in abundance of *P. sylvestris* and *Quercus pyrenaica* Willd. (Pyrenean oak) as a result of global change over the last 40 years are assessed in the Sierra of Guadarrama (Comunidad de Madrid) are assessed (**Chapter 5**). Furthermore, it is addressed the performance of a novel method to calculate the significance of climatic variables as auxiliary variables and to estimate which part of the variance is linked to the mean function and which part is linked to the space-time autocorrelation in space-time universal kriging and co-kriging distribution models. The results indicate that both the distribution and the abundance of *P. sylvestris* remained relatively constant, whereas the distribution and abundance of *Q. pyrenaica* increased significantly. As a consequence, the area where the two species coexist has increased three fold.

Key words: multiscale; mitigation; adaptive forest management; climate change; Mediterranean area; silviculture; forest modeling; forest ecology; stand structure

CHAPTER 1

General introduction

1.1. Global change in Mediterranean mountain forest systems

Human-induced climate change along with land use/land cover change are two of the drivers underlying global change (Hansen et al. 2001; Boysen et al. 2014). Related changes in climatic variables such as precipitation, temperature, water vapor, heat waves, and cloudiness are expected to occur extensively (Solomon et al. 2009). Moreover, many studies have already reported a decrease in precipitation and a rise in temperatures in some large regions such as the Mediterranean basin (Brunet et al. 2007; Gao and Giorgi 2008; Giorgi and Lionello 2008). Mountain forests are particularly vulnerable to climate change (Guisan et al. 1995; Theurillat and Guisan 2001) since they are isolated at high elevations (Beniston 2003). If they are unable to adapt to the new conditions, upward migration to more favorable sites may be the only possibility for their continued persistence (Hughes 2000; Jump et al. 2009; Lenoir et al. 2009). Migration of *Pinus sylvestris* L., *Fagus sylvatica* L. and *Quercus* species towards higher elevations has, in fact, already been detected in certain mountain systems in Spain (Peñuelas and Boada 2003; Hernández et al. 2014; Urli et al. 2014; Hernández et al. 2017).

Furthermore, land use and land cover changes commonly reflect the conversion of native grasslands, forests, and wetlands to croplands, tree plantations and urban areas (Weng 2002; Wright and Wimberly 2013; Lawler et al. 2014). Indeed, the modification of forest areas by humans is a major contributor to global change (Wimberly and Ohmann 2004) involving a reduction in global forest area (Foley et al. 2005). Nevertheless, due to the abandonment of agricultural land use (Peñuelas and Boada 2003; Améztegui et al. 2010; Kouba et al. 2012) the forested area in the European region has increased over the last 25 years, although the rate of expansion is currently decreasing. European forest expansion was greatest in South-West Europe with an annual increase of 242,000 ha (0.9% over the last 25 years, followed by South-East Europe at 166,000 (0.6%) and Central-Western Europe at 142,000 ha (0.4%) per year (Domínguez et al. 2015).

Finally, the severity, frequency and magnitude of biotic and abiotic disturbances in forests may increase (Brotons et al. 2013). For instance, increasing attacks of *Thaumetopoea pityocampa* (Denis and Schiff.) in populations of *P. sylvestris* in Andalusia have been identified as consequence of climate change (Hódar et al. 2003; Hódar and Zamora 2004). Furthermore, according to Vilà-Cabrera et al. (2012), as a result of climate change *P. sylvestris* may be more vulnerable to forest fires in the future.

In this context, direct services provided by montane forests such as wood production and indirect services such as watershed protection, are threatened (van Mantgem et al. 2009; Arnaez et al. 2011; Lü et al. 2012; Pretzsch et al. 2014). However, although wood growth rates in the Mediterranean basin are generally expected to decline, wood production may increase in some areas, as reported by Martin-Benito et al. (2011) for Spanish montane stands of *Pinus nigra* Arn. The role of montane ecosystems in biodiversity conservation should also be highlighted. In this regard, certain mountain stands, such as those in the Central Range forests, gain biological importance not only because of the rich diversity of endemic plant species they contain but also as part of a migratory route and speciation center (Médail and Quézel 1999; López-Sáez et al. 2014). Therefore, changes in the structure and composition of mountain forest can cause changes in habitat suitability and therefore in the distribution of associated species (Braunisch et al. 2014).

Several native pine species can be found in the mountains of the Iberian Peninsula, growing both in monospecific or in mixed forests: *Pinus halepensis* Mill., *Pinus pinaster* Ait., *P. nigra*, *P. sylvestris* and *Pinus uncinata* Ram. One of the most important species is *P. sylvestris*, which covers 1.28 million ha (Cañellas et al. 2000; Montero et al. 2001) and is highly appreciated in industry due to the quality of the wood and its relatively fast growth (Montero et al. 2001; Hermoso et al. 2002; Moreno-Fernández et al. 2014). *P. sylvestris* is the fourth most felled ($860000 \text{ m}^3 \text{ year}^{-1}$) species in Spain (MAGRAMA 2013) although forests of this species in the Iberian Peninsula tend to be relict, fragmented and mainly located in mountain regions (Cañellas et al. 2000; Robledo-Arnuncio et al. 2004).

The importance of *P. sylvestris*, or Scots pine, stretches beyond the Iberian Peninsula. In fact, it is the most widely distributed pine species in the world and the second most widespread conifer after *Juniperus communis* L. It grows naturally in Euroasia, from the Iberian Peninsula almost to the Pacific Ocean in Russia, and from above the Arctic Circle in Scandinavia to the Mediterranean Sea, occupying 28 million ha in Europe and Northwest Asia (Mason and Alía 2000; Houston Durrant et al. 2016). *P. sylvestris* is present in 7 forest categories and 13 European Forests Types (Table 1.1 and Fig. 1.1; Barbati et al. 2007; Barbati et al. 2014). The genuine Forest Type in the Mediterranean Basin is the 10.4 (Mediterranean and Anatolian Scots pine forest).

Because of the huge distribution area of *P. sylvestris*, it has high genetic variability and the number of separate subspecies which should be recognized continues to be debated

(Sinclair et al. 1999; Eckenwalder 2009). In this regard, the Iberian stands of *P. sylvestris* contain an important amount of the total genetic variability in this species, which is also well differentiated (Sinclair et al. 1999; Soranzo et al. 2000). Thus, from the perspective of genetic conservation, an appropriate conservation strategy for native populations of *P. sylvestris* in the Iberian Peninsula is imperative (Robledo-Arnuncio et al. 2004).

Table 1.1 European Forest Types in which *P. sylvestris* is present. Modified from (Pividori et al. 2016).

Category	Forest Type	Presence
1. Boreal forest	1.2. Pine and pine-birch boreal forest	
2. Hemiboreal forest and nemoral coniferous and mixed broadleaved-coniferous forest	2.1. Hemiboreal forest	
	2.2. Nemoral Scots pine forest	
	2.5. Mixed Scots pine-birch forest	
	2.6. Mixed Scots pine-pedunculate oak forest	
3. Alpine coniferous forest	3.2. Subalpine and mountainous spruce and mountainous mixed spruce-silver fir forest	
	3.3. Alpine Scots pine and Black pine forest	
7. Montaniuous beech forest	7.6. Moesian mountainous beech forest	
8. Thermophilous deciduous forest	8.1.1. Downy oak forest – western	
	8.1.2. Downy oak forest - Italian	
10. Coniferous forests of the Mediterranean, Anatolian and Macaronesian regions	10.1.1. Mediterranean pine forest – <i>Pinus pinaster</i>	
	10.4. Mediterranean and Anatolian Scots pine forest	
11. Mire and swamp forest	11.2. Pine mire forest	
	<i>P. sylvestris</i> is abundant and dominant	
	<i>P. sylvestris</i> is either secondary or predominant	
	Presence of <i>P. sylvestris</i> is both dominant and secondary in some cases	

1.2. Sustainable Forest Management: Adaptation and mitigation

Under the current scenario of global change, forests play a central role in climate change mitigation and adaptation (Canadell and Raupach 2008; FAO 2010) since they sequester one third of the total carbon emissions from fossil fuel every year (Denman and Brasseur 2007). It should be emphasized that under sustainable forest management, climate change mitigation and adaptation practices must be balanced with other objectives such as

production of goods and services like wood, soil protection, conservation of biodiversity and socio-cultural services (FAO 2010).

Figure 1.1 Distribution map estimating the relative probability of presence of *P. sylvestris* in Europe (Houston Durrant et al. 2016).

Mitigation of climate change by forests is tackled, on the one hand, by conserving the current forest carbon stocks. This is achieved through reducing deforestation and forest degradation by favoring health and vitality, biodiversity and fire prevention. On the other hand, carbon storage is enhanced through appropriate management practices and afforestation, reforestation and forest restoration (FAO 2010). In recent decades, research efforts have focused on quantifying the carbon stored in the different forest pools and on studying the effects of management on carbon stocks in mountain forests (Bravo et al. 2008a; Chiti et al. 2012; Ruiz-Peinado et al. 2013).

From a silvicultural perspective, in order to enhance the adaptive capacity of trees and forests it is necessary to reconsider forest strategies such as rotation periods, thinning intensity and regeneration methods (Sabaté et al. 2002; FAO 2010). For instance, reducing

competition through thinning has proved to be an effective forest management tool for reducing tree vulnerability to extreme droughts in both mixed forests (Aldea et al. 2017) and *P. sylvestris* monospecific stands (Ameztegui et al. 2017). Natural regeneration is a key stage in the spatial and temporal continuity of a forest after regeneration fellings (Lucas-Borja et al. 2017). Nevertheless, the establishment of new individuals in Mediterranean areas is threatened by summer drought, long intervals between large seed crops, presence of livestock and shrub, herb and litter layers (Calama and Montero 2007; Bravo Fernández et al. 2008). Hence, it would appear reasonable to re-evaluate the current methods used to achieve natural regeneration. In the case of *P. sylvestris*, for example, regeneration periods may be lengthened to favor more progressive establishment of regeneration (Barbeito et al. 2011). In this regard, more flexible management systems, such as the floating blocks approach, which allows the regeneration period to be extended, may substitute more rigid methods such as periodic blocks. Furthermore, the density of the remaining trees must be optimized according to the species, site conditions and regeneration stage, although depending on the precise objectives pursued, the most appropriate density and spatial pattern of the remaining trees over the regeneration period are often unknown (Barbeito et al. 2011).

1.3. Dynamics of *Pinus sylvestris* in Mediterranean mountains

The shade tolerance of *P. sylvestris* varies greatly across its distribution. This variation is associated with the latitudinal gradient. Whereas this species is classified as a light demanding species in Central and northern Europe (Mátyás et al. 2003), it is commonly considered to have a half-shade tolerant behavior in southern locations such as the Iberian Peninsula (Montes and Cañellas 2007). As a consequence of the variations in light tolerance across its distribution range, different regeneration methods are employed. While the shelterwood approaches are commonly used in the Mediterranean basin, clearcutting or seed tree methods are the main approaches used in northern and Central Europe (Mátyás et al. 2003).

Regeneration of *P. sylvestris* is often less successful than that of other Mediterranean species (Pardos et al. 2007; Barbeito et al. 2011). Hence, given the economic and ecological value of this species and the problems observed as regards the establishment of new individuals, several regeneration studies have been carried out at both small scales (González-Martínez and Bravo 2001; Pardos et al. 2007; Barbeito et al. 2009) and larger

scales (Montes and Cañellas 2007; Barbeito et al. 2011). Barbeito et al. (2011) and González-Martínez and Bravo (2001) highlighted the need for soil preparation to break up the grass and organic layer, thereby reducing competition with shrubs to facilitate seedling establishment. However, seedling establishment is affected by year-to-year conditions, such as meteorological conditions and variations in seed production (Pardos et al. 2007). Extending regeneration periods can therefore favor the establishment of new individuals. Additionally, fencing off regeneration areas could help to minimize herbivore grazing damage on seedlings (González-Martínez and Bravo 2001; Barbeito et al. 2011). As regards the spatial pattern of young individuals, both seedlings and saplings occur as clumped structures in favorable microsites (Barbeito et al. 2011). Another consideration is that while *P. sylvestris* seedlings in southern locations have been found to require moderate shade conditions (Pardos et al. 2007; Barbeito et al. 2009), the overstory canopy must be reduced in order to favor sapling development (Montes and Cañellas 2007). However, other questions such as the effect of canopy openness (level of canopy cover) on seedlings or the spatio-temporal relationships between the size of the adult trees and the number of saplings of *P. sylvestris* have not been investigated.

Regeneration failure due to inadequate forest management practices or climate change can lead to shifts in species distribution (Zhu et al. 2012; Vilà-Cabrera et al. 2012). Identifying and monitoring these effects poses a major challenge to forest managers and researchers (Hernández et al. 2014). Several authors (Benito Garzón et al. 2008; Ruiz-Labourdette et al. 2012) have predicted reductions in the Iberian populations of *P. sylvestris* and shifts towards higher elevations over the coming decades. However, retrospective analyses based on historical series are limited to local scales. Hernández et al. (2014) and Hernández et al. (2017), for example, reported that this pine species has moved towards higher elevations, increasing its distribution in the Western Pyrenees between 1971 and 2010. However, shifts in the distribution and abundance of *P. sylvestris* in southern locations, which are more susceptible to the effects of climate change, have scarcely been studied.

In the past, research concerning forest management and silviculture in Spanish *P. sylvestris* stands has mainly focused on maximizing wood production in the rotation period (Rojo et al. 2005; del Río and Sterba 2009). Hence, the effects of alternative thinning regimes on timber yield and growth have been extensively studied in the mountains of Central Spain (Montero et al. 2001; Río et al. 2008; Moreno-Fernández et al. 2014) as well as in other regions (Crecente-Campo et al. 2010), while increasing importance is being attached to other

management-related aspects, such as the determination of site quality. In this regard, site quality models have been developed for central Spain (Rojo and Montero 1996), northwestern Spain (Diéguez-Aranda et al. 2005), northern Spain (Bravo and Montero 2001; Bueis et al. 2016) and for the country as a whole (Moreno-Fernández et al. Under review) with the aim of optimizing forest management.

However, as previously mentioned, the mitigation of climate change through carbon sequestration in forest systems is a priority for foresters and researchers. Thus, recent lines of research have focused on quantifying forest carbon and the way in which carbon stocks are affected by management (Bravo et al. 2008a). Various studies addressing these issues have been undertaken in *P. sylvestris* stands located in Mediterranean mountains. Ruiz-Peinado et al. (2011) fit additive biomass equations to estimate the carbon stored in the stem, branches, needles and roots of *P. sylvestris*. Ruiz-Peinado et al. (2014) evaluated the effects of thinning on carbon stored in *P. sylvestris* tree biomass as well as in the mineral soil, concluding that unthinned stands store a greater amount of carbon in tree biomass while the carbon stored in the soil is not significantly affected by thinning intensity. Despite the current need for tools to mitigate the effects of climate change, scarce research has focused on the influence of forest management on carbon stocks in living tree biomass, coarse woody debris, forest floor and mineral soil or on carbon transference links over the complete rotation period.

1.4. Study area

1.4.1. Site characteristics

The research for this thesis was conducted in stands of *P. sylvestris* located in the Central Range (Central Spain). In this area, the annual rainfall is 1,100 mm and the annual mean temperature is about 7.5 °C with four months (June, July, August and September) of water deficit and two of a severe drought (July and August), which can cause complete seedling mortality (Pardos et al. 2007; Serrada and Bravo-Fernández 2011). The north-facing slopes of the Central Range are located in the region of Castilla y León, while the south-facing slopes are in the Comunidad de Madrid, each having different ecological characteristics. The south-facing slopes are drier and warmer than the north-facing slopes. Consequently, *P. sylvestris* occurs at lower altitudes on the north-facing slopes than on the south-facing ones.

The region has been exploited for timber for centuries (Rojo and Montero 1996; Franco Múgica et al. 1998). In addition to timber resources, this mountain system also has great biological importance as a migratory route and center of speciation (Peinado-Lorca and Rivas-Martínez 1987; López-Sáez et al. 2014). The Central Range also receives a large number of visitors, especially at weekends due to its proximity to Madrid, the most populated Spanish city. Hence, pressure from tourism is intense. Furthermore, the protected status of some of the mountain summits increased when the Guadarrama National Park was created in 2013 (BOE 2013). These conditioning factors mean that forest management planning must consider biological, economic, productive and social issues to guarantee the multifunctionality and sustainability of these stands.

Although *P. sylvestris* is native in the study area (Franco Múgica et al. 1998), the forestry administration reforested large areas at the beginning of the 20th century to stop deforestation, control soil erosion and increase wood production; *P. sylvestris* being favoured for this purpose over other species (Cañellas et al. 2000; Sánchez-Palomares et al. 2008). The first forest management plans for the region were also drawn up at the end of 19th century/beginning of the 20th century (Rojo et al. 2011). In Central Range, the regeneration of *P. sylvestris* stands is commonly achieved using the group shelterwood system (as in Valsaín) or the uniform shelterwood system (as in Navafría forest); whereas the selection system is only used in the protective working circles located close to the summits (Bravo-Fernández and Serrada Hierro 2011; Barbeito et al. 2011).

As mentioned above, forest management and silviculture differ in Valsaín and Navafría. Valsaín is managed using floating blocks with a rotation period of 120 years. The regeneration system employed is the group shelterwood method over a 40 year period. Management is more intensive in Navafría than in Valsaín and the rotation period is shorter (100 years). Additionally, thinnings are heavier in Navafría and the management system, periodic blocks, is stricter than in Valsaín. Uniform shelterwood fellings (Fig. 1.2) are used to regenerate this forest over a period of 20 years (Barbeito et al. 2011). Although the forestry is less intensive in Comunidad de Madrid, *P. sylvestris* is the most widely used species by the forestry industry in this region (CAM 2012).

Figure 1.2 Regeneration establishment under the uniform shelterwood felling system in Navafría forest.

1.4.2. Brief description of the data

Three types of plots were used, covering different spatio-temporal scales. Finer scale data were taken from temporal plots established in five regeneration blocks at Navafría forest after the first regeneration fellings. Nine square plots (64 m²) were installed in each regeneration block, 45 plots in total. In each plot, all the seedlings were measured and topsoil and light variables were taken. In addition, all the remaining trees within a 15-m radius from the center of each plot were mapped and their dbh and height was measured. These plots are of particular use for assessing the biotic and abiotic variables driving ecological processes at microsite scale (Pardos et al. 2007; Barbeito et al. 2009).

The second type of data consisted of two chronosequences. In forestry and forest ecology, chronosequences are used to study processes that take place over long periods (such as a complete forest cycle) in shorter periods through different plots that share similar ecological features but are of different ages. Therefore, the use of chronosequences is common in ecological succession studies (Foster and Tilman 2000) or when analyzing dynamics over the rotation period, such as carbon changes (Yanai et al. 2000). Two

chronosequences spanning the entire regeneration period in Valsaín (six 0.5 ha plots) and Navafría (five 0.5 ha plots) were installed in 2001. In each plot, all the trees ($\text{dbh} \geq 10$ cm) were mapped and the saplings ($\text{height} \geq 1.30$ m and $\text{dbh} \leq 10$ cm) were grouped into grids. Additionally, both trees and saplings were labelled and their dbh and height were measured. These measurements were repeated in 2006, 2010 and 2014.

Finally, the four Spanish National Forest Inventory cycles (NFI; from 1965 to 2012) in Comunidad de Madrid provide coarser scale data. NFIs record data on seedlings, saplings and trees in each plot and distinguish between species. The plots are also mapped. Thus, NFIs provide data for monitoring aspects such as tree mortality (Ruiz-Benito et al. 2013) or species distribution (Hernández et al. 2014). However, the design of the NFIs, plot locations, number of plots and plot design varied from one NFI cycle to another (Hernández et al. 2014), which complicates comparison between inventories.

1.5. Methodology

1.5.1. Statistical overview

Scientific analysis of data requires the use of an appropriate statistical approach according to the nature of the data and researcher's purposes. Advances in statistical science in conjunction with the progress in computer technology allow sophisticated models and large data sets to be fitted. Hence, the researcher has at his disposal a great variety of methods ranging from the simpler linear models to more complicated approaches, such as machine learning algorithms. Some studies have compared the strengths and weaknesses of different statistical methodologies in forestry or ecological fields. For instance, Segurado and Araújo (2004) and Dormann et al. (2007) evaluated alternative methods for modeling species distribution. Moreno-Fernández et al. (2014) compared linear mixed models with smooth penalized splines for assessing forest growth. Montes and Ledo (2010) explored the performance of different techniques to estimate the parameters of the variogram in universal kriging. However, the strengths and weaknesses of alternative statistical methodologies in other ecological processes such as regeneration phases have not been addressed.

According to Pretzsch (2009), the study of forest dynamics is concerned with the changes in forest structure and composition over time, including its behavior in response to anthropogenic and natural disturbances. Sustainable forest management must, as far as

possible, mimic natural forest dynamics. Therefore, understanding system dynamics is a key requirement of forest management (Kulakowski et al. 2016). Different variables can be used to account for the temporal component in forest models: age of the trees, stand or plots (Moreno-Fernández et al. 2013), year of the survey (Augustin et al. 2009) and tree or stand variables as proxy for the age (Manso et al. 2014).

The spatial component is crucial to understanding the relationships among individuals and the role of site conditions (Ledo et al. 2014). Alternative approaches can be used to consider the spatial component. In this regard, Ripley's K and related functions have been used to study the spatial pattern of individuals and the spatial relationships between two categories of individuals; for instance, the association and repulsion between two cohorts of pines (Montes and Cañellas 2007). Other techniques, such as geographical regression, incorporate spatial autocorrelation in the regression model. Geostatistical methods, such as kriging and cokriging, are spatial regression procedures that use the variogram in order to describe the degree of spatial dependence of a given variable (Hernández et al. 2014; Moreno-Fernández et al. Under review). These methods account for the spatial correlation among measurements introducing a spatial smooth term in site quality models. For a more in-depth understanding of methods considering spatial correlation, see the exhaustive review by Dormann et al. (2007).

The effect of adult trees on new individuals has been tackled by including local stand structure indices in models. Examples of local stand structure indices are the influence potential (Wu et al. 1985; Kuuluvainen and Pukkala 1989) and the index of influence (Woods and Acer 1984). These indices relate tree size features - height, dbh or crown diameter - and distances from trees to a given point and have been widely applied in different fields of forestry or ecology. For instance, Pardos et al. (2007) and Manso et al. (2014) used local stand structure to assess the influence of adult trees on seedlings. If the position of the adult trees over several inventories is known, then the spatio-temporal influence of adult trees on seedlings can be estimated easily.

In recent years, a need has arisen to develop tools (spatio-temporal models) to understand the occurrence of spatial processes over time (Gratzer et al. 2004). Thus, alternative approaches have been used to fit spatio-temporal models in different fields of forestry and forest ecology. Augustin et al. (2009), for example, developed a spatio-temporal model in a generalized additive framework to assess forest health. Jost et al. (2005) proposed

a spatio-temporal kriging approach to study the distribution of soil water storage in forest ecosystems over time. Similarly, Hernández et al. (2014) compared the four cycles of the NFI to assess shifts in the distribution of *F. sylvatica* and *P. sylvestris* in northern Spain using block kriging variances, fitting a universal kriging model per NFI cycle rather than a spatio-temporal model, considering all the NFI cycles. One weakness of universal kriging/cokriging techniques is the lack of statistical tests to check the significance of the auxiliary variables. Furthermore, the percentage of variance attributable to auxiliary variables and spatial autocorrelation has not been evaluated.

A new school of researchers have addressed the evolution of marked point pattern through time via growth interaction models (Renshaw and Särkkä 2001). These techniques simulate data, forest growth, interactions, mortality and arrival of new individuals through algorithms based on literature values rather than field data. Redenbach and Särkkä (2012) and Comas (2008) modified the original models to compare the regeneration patterns under two regeneration methods. Several software packages such as SILVA-ND or SORTIE-ND have been specifically designed to simulate tree spatial processes evolving through time. Both of these software packages have been employed in forest simulation studies, including regeneration and recruitment phases (Hanewinkel and Pretzsch 2000; Ameztegui et al. 2015).

Although there are a large number of techniques available, none of the statistical models address in sufficient depth the way in which the size of a given cohort is associated in space and time with the number of individuals of another cohort.

1.5.2. Multiscale framework

Different research goals, such as determining the ecological causes and consequences of global climate change, require the analysis of phenomena that occur at different spatial scales (Levin 1992). Moreover, a given ecological process might show alternative patterns when observed at different spatial scales (Barbeito et al. 2009; Barbeito et al. 2011). Furthermore, if the scale at which a system is studied is not appropriate, we may be unable to detect its actual dynamics (Wiens 1989).

In recent times, several authors have emphasized the necessity to analyze forest dynamics, integrating a multi-scale approach to anthropogenic and abiotic disturbances at

different scales (Ulanova 2000; Barbeito 2009). Abundant literature exists in relation to forestry or forest ecology studies based on small or medium scale data (Slodicak et al. 2005; Moreno-Fernández et al. 2013; Ledo et al. 2014; Ruano et al. 2015). However, although the impacts of human activity on ecosystem services, such as wood production, carbon sequestration and biodiversity are more clearly reflected at larger scales (Lü et al. 2012), published studies at this level are more scarce (e.g. Eid and Hobbelstad 2000) and broadly focus on climate change (Bala et al. 2007) and species distribution (Lenoir et al. 2008; Hernández et al. 2014). Therefore, since regional and global scales have become more important to researchers and managers, methods have been developed to use the existing fine-scale knowledge to predict larger-scale ecosystem services or products (Rastetter et al. 1992). For instance, García et al. (2009) integrated multi-scale data in a seed dispersal study using casual modeling and path analysis.

1.6. Objectives

The main objective of this thesis is to assess the influence of ecological factors and forest management at different scales on the multiple functions of *P. sylvestris* forests in Mediterranean mountains in order to ensure their sustainability and persistence over time under the current scenario of global change. This main objective can be split into the following specific objectives:

1. To identify the biotic and abiotic variables related to the development of *P. sylvestris* seedlings.
2. To assess the strengths and weaknesses of different statistical methods used to model forest regeneration.
3. To fit a spatio-temporal model to determine the effect of adult tree size on the number of *P. sylvestris* saplings as a function of the distance between saplings and adult trees.
4. To assess the way in which two management systems; one more intensive and the other more moderate, affect the carbon stored in the different forest pools over the rotation period.
5. To analyze shifts in the distribution and changes in the basal area of *P. sylvestris* and *Quercus pyrenaica* Willd. over the last 40 years and to assess the role of global change in these shifts.

6. To address the performance of a novel method to calculate the significance of climatic variables as auxiliary variables and to estimate which part of the variance is linked to the mean function and which part is linked to the space-time autocorrelation in space-time universal kriging and co-kriging distribution models.

1.7. Thesis structure

This doctoral dissertation is organized as follows: Chapter 1 (this chapter) is the general introduction to the thesis. Chapters 2, 3, 4 and 5 are original research studies tackling the objectives described in the previous section. These four chapters are entirely based on full, published articles in journals indexed in the Journal Citation Reports in the Web of Science and in Scopus databases (Fig. 1.3 and Appendix). Chapter 6 presents a general discussion of the thesis while Chapter 7 contains the main conclusions of this doctoral dissertation, both in English and in Spanish. Finally, the complete list of references can be found in Chapter 8.

A brief summary of the contents, objectives, spatial scale and remarks on the statistics presented in Chapters 2, 3, 4 and 5 follows (see also Fig. 1.3). The aim of Chapter 2 is to study the biotic and abiotic variables associated with the regeneration process of *P. sylvestris* at microsite scale, using data from temporal plots installed at Navafría (Objective 1). Additionally, alternative statistical methods are compared and their weaknesses and strengths are discussed (Objective 2).

Chapter 3 analyzes the spatial relationship between the size of the adult trees and the number of *P. sylvestris* saplings using a spatio-temporal model (Objective 3). In this study, we use two plots for the Valsaín chronosequence, i.e. this is conceived at plot scale. The statistical analysis is carried out fitting a spatio-temporal model with a functional predictor in a generalized additive model framework. Thus, our approach allows different growth patterns to be identified.

The main aim of Chapter 4 is to assess the influence of two forest management alternatives on carbon stocks in the living tree biomass, coarse woody debris, forest floor and mineral soil over the rotation period (Objective 4). To this end, the complete chronosequences installed in Valsaín and Navafría are used. Thus, the working spatial scale used in Chapter 4 is stand scale. The data analysis is performed using smooth penalized

splines in a linear mixed-effects modeling framework and general linear models. In addition to the direct application of this research in mitigating and adapting to the effects of climate change, this chapter also shows the forest growth trends associated with two management systems.

Finally, Chapter 5 analyzes the shifts in presence and changes in abundance of two representative tree species (*P. sylvestris* and *Q. pyrenaica*) in Comunidad de Madrid (Objective 5) using NFI data, i.e. landscape scale. This is achieved using space-time universal kriging and co-kriging distribution models, which allow us to determine the significance of the climatic variables as auxiliary variables and also to estimate the variance linked to the mean function and the part linked to the space-time autocorrelation (Objective 6).

Figure 1.3 Summary of contents, study scale and topics addressed in Chapters 2, 3, 4 and 5. REG=regeneration, FG= forest growth, CCA=climate change adaptation, CCM=climate change mitigation.

Finally, as the reader will observe, the temporal component is included in all of the chapters except for the case of Chapter 2. However, it should be noted that whereas Chapter 2 studies seedling development after regeneration fellings, Chapter 3 deals with saplings, i.e. both chapters follow a temporal line in the development of the new individuals.

CHAPTER 2

Alternative approaches to assessing the natural regeneration of Scots pine in a Mediterranean forest

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Abstract

The establishment of seedlings after regeneration fellings is key to guaranteeing the development and persistence of the forest. Depending on the objective pursued, data available, or type of forest, a number of different methods have been employed to assess the relationship between seedling establishment and both environmental and stand factors. Most authors have conducted their analyses using parametric regression or point pattern analysis. We analysed the way in which light, stand conditions, edaphic and topographic variables affect the regeneration of *Pinus sylvestris* L. in Central Spain. We used different methods to analyse the same data set. The strengths and weaknesses of each method were discussed. We used two parametric approaches: generalized linear mixed model regression using a negative binomial followed by the variant explanatory variables reduction prior to regression as well as three nonparametric approaches not commonly employed in forest regeneration: nonmetric multidimensional scaling, regression trees and Random Forests algorithm. The parametric regression identified a larger number of variables associated with the regeneration process and the inclusion of a random effect in the model allowed considering the spatial variability among plots. However, decision trees captured the complex interaction among variables, which typical parametric methods were unable to detect. Different statistical methods gave similar insights into the ecological process underlying. However, different statistical premises with inference implications can be noticed. This may give misinterpretation of the model depending on the nature of the data. The choice of a given method should be made according to the nature of the data and the achievement of desirable results.

Keywords: CHAID, Random Forests, PCA, NMDS, negative binomial, generalized linear mixed models

Abbreviations: CART, Classification and Regression Trees; CHAID, Chi-squared Automatic Interaction Detection; GLMM, Generalized Linear Mixed Model; GSF, Global Site Factor; INF, Index of Influence; IPOT, Influence Potential; NMDS, Nonmetric Multidimensional Scaling; OBB, out-of-bag; OOB-MSE, Mean Square Error from the OBB data; PCA, principal component analysis; SST, sum of squares.

2.1. Introduction

Natural forest regeneration is a key process in ensuring forest sustainability (Lucas-Borja 2014). However, in the Mediterranean basin, natural regeneration is hampered by the summer drought, high summer temperatures, long intervals between good seed crops, the presence of livestock and the existence of a too dense herb and litter layer (Barbeito et al. 2011; Calama and Montero 2007; Manso et al. 2013; Pardos et al. 2007). Therefore, understanding the dynamics, patterns, factors involved in the success or failure of regeneration and interactions at the seedling level, can provide foresters with the fundamental knowledge required for decision-making in forest management (Lucas-Borja 2014).

Regeneration in forest stands has been studied using different statistical methods depending on the aim, data available, or type of forest (Table 2.1). Analyses have been refined as statistical techniques have improved (Zuur et al. 2007). Regeneration studies often involve counts of the number of seedlings per sampling unit. However, a wider range of techniques can be applied to assess seedling abundance. An initial, simple approach is the linear model (del Cerro et al. 2009; Osem et al. 2013). However, regeneration data rarely satisfy the basic assumptions for linear models: normality of errors, linearity of parameters, homogeneity of variance and independence of the covariates (Zuur et al. 2010).

Explanatory spatial covariates that influence recruitment patterns have also been incorporated into different types of recruitment models, as explanatory variables. The covariates most used are: soil nutrients and/or soil moisture (Barbeito et al. 2009), light availability (Adili et al. 2013; Fyllas et al. 2008;), environmental conditions (Rathbun and Fei 2006) and stand structure (Manso et al. 2013a). Vertical and horizontal forest structure determines light availability and, therefore, regeneration dynamics (Catovsky and Bazzaz 2002; Montgomery 2004) and the development of the stand (Boyden et al. 2005; Montes and Cañellas 2007). Some authors have assessed the influence of the retained trees on regeneration through the inclusion of structure influence indices in the model (Barbeito et al. 2011; Kuuluvainen and Pukkala 1989; Paluch 2005).

Table 2.1 Methods used to study natural pine regeneration in Mediterranean mountains.

Study	Pine species studied	Methods
Barbeito et al. 2009	<i>P. sylvestris</i>	Point pattern
Barbeito et al. 2011	<i>P. sylvestris</i>	Generalized linear model after ordination method
Christopoulou et al. 2014	<i>P. nigra</i>	Mixed effect model and boosted regression trees
del Cerro et al. 2009	<i>P. nigra</i>	General linear model
Fyllas et al. 2008	<i>P. brutia</i> and <i>P. nigra</i>	Generalized linear model
Gómez-Aparicio et al. 2006	<i>P. nigra</i>	General linear model
González-Martínez and Bravo 2001	<i>P. sylvestris</i>	General linear model after ordination method
Lucas-Borja et al. 2012	<i>P. nigra</i>	General linear model
Montes and Cañellas 2007	<i>P. sylvestris</i>	Point pattern analysis
Osem et al. 2013	<i>P. halepensis</i>	General linear model
Pardos et al. 2007	<i>P. sylvestris</i>	Point pattern analysis and general linear model
Pausas et al. 2004	<i>P. halepensis</i>	General linear model
Prévosto et al. 2012	<i>P. halepensis</i>	Generalized and general linear model
Spanos et al. 2000	<i>P. brutia</i>	Linear and exponential regression

Regeneration studies often involve the consideration of a lot of explanatory variables that may be highly correlated. Collinearity among covariates increases the risk of inferring that these covariates have no explanatory power (increasing the risk of type I errors) and in addition, it can be especially problematic when ecological signals are weak (Zuur et al. 2010). Collinearity is often assessed through variance inflation factors, pairwise scatterplots comparing covariates or correlation coefficients (Zuur et al. 2010). In order to avoid correlation and to reduce the number of independent variables, scaling techniques can be used to create a dimensionally reduced dataset with uncorrelated variables (Borcard and Legendre 2002; Legendre and Legendre 1998; Strobl et al. 2009). The most widely used tools in this regard are principal component analysis (PCA) and factor analysis or nonmetric

multidimensional scaling procedure (NMDS). The obtained uncorrelated new covariates obtained can be then used in standard regression methods. The requirement of normality of the data in the PCA analysis is under discussion (Jolliffe 2002; Borcard and Legendre 2002; Zuur et al. 2010). In this respect, NMDS is not sensitive to normality, to outliers and homoscedasticity assumptions of classical metric scaling (Casini et al. 2004; Legendre and Legendre 1998). In addition, NMDS allows the identification of non-linear gradients of the environmental covariates. However, the disadvantage of using ordination methods is that the original input variables are projected into a reduced set of components or axes, so that their individual effect is no longer identifiable (Strobl et al. 2009).

This interpretability problem can be avoided using decision or regression trees, such as classification and regression trees (CART; Breiman et al. 1984), conditional inference trees (Hothorn et al. 2006) or Chi-squared automatic interaction detection (CHAID; Kass 1980). Besides allowing the use of multiple variables in the data set, these nonparametric procedures are capable of identifying interactions between the variables which are too complex to be captured by parametric regression models (Strobl et al. 2009). This can be especially useful in the field of ecology. Forest data have been analysed using regression trees (CHAID, Álvarez-Álvarez et al. 2011; conditional inference trees, Barbeito et al. 2012) but their use in regeneration studies is scarce (Fei 2010). However, simple tree models are vulnerable to small changes in the learning data (Strobl et al. 2008). Machine learning methods, such as the Random Forests algorithm (Breiman 2001) or boosted regression trees (Elith et al. 2008), solve the problem of instability by averaging an ensemble of trees into a more robust composite model (Cutler et al. 2007; Strobl et al. 2009).

Natural, rather than artificial, regeneration is the preferred option in Mediterranean areas. The shelterwood system is commonly employed to ensure the establishment of new Scots pine seedlings (*Pinus sylvestris* L.) in Central Spain (Cañellas et al. 2000). However, regeneration is sometimes hampered by excessively short regeneration periods or by a number of abiotic and biotic factors, such as competition from grass or the large fluctuation in cone production over the years (Barbeito et al. 2011; Cañellas et al. 2000; González-Martínez and Bravo 2001) which is especially notable in masting species such as *Pinus pinea* L. (Calama et al. 2011; Manso et al. 2013a). With regards the abiotic factors, the survival of *P. sylvestris* seedlings is closely linked to climate. In particular, summer drought can cause complete seedling mortality during the first summer after the regeneration fellings (Pardos et al. 2007). In addition, light availability has been shown to be relevant for regeneration on

a small scale, with moderate light conditions being optimum to maximize the regeneration density of Scots pine in the Central Mountain Range in Central Spain (Barbeito et al. 2009; Pardos et al. 2007). Topsoil variables, such as soil moisture and nutrients, as well as soil preparation have also been identified as important factors in forest regeneration (Barbeito et al. 2011).

The aim of this study is to employ and compare five different statistical techniques in order to evaluate the influence of environmental factors on natural regeneration, using as a case study a Scots pine forest in Central Spain. The techniques considered are (i) a generalized linear mixed model (GLMM) (ii) data reduction using the PCA ordination method prior to GLMM, (iii) ordination using the NMDS, (iv) CHAID algorithm and (v) Random Forests algorithm and the conditional inference trees. Additionally, we aimed to answer the following question: what is the most suitable method to evaluate tree recruitment and factors implicated? We compared the results obtained using the different methods, then assessed and discussed the strengths and weakness of each methodology. We calculated the goodness of fit for each methodology to assess how well the different models fit the observations. Measures of goodness of fit summarize the discrepancy between the observed values and the values expected under a statistical model (Maydeu-Olivares and García-Forero 2010). The importance of the methodology used in regeneration studies will be evident if not all the approaches identify the same biotic and abiotic variables that are associated with the regeneration abundance. Additionally, owing to the presence of complex interactive effects among the underlying variables and to correlations among the potential covariates used to represent those variables, it is expected that the parametric modeling strategies considered in this study would fail to identify the importance of covariates detected as important by decision trees.

2.2. Materials and methods

2.2.1. Study site

This study was conducted at the mountain forest of Navafría (41° 00'N, 3° 48'W), located on a north-facing slope in the Central Mountain Range in Spain. The altitude of this Scots pine forest ranges from approximately 1,200 to 2,200 m, and the altitudinal position of the timberline is around 1,800 m. Annual rainfall exceeds 730 mm and mean annual temperature is around 9.9 °C. These mountains are composed of granite and gneiss, with fairly

homogeneous soils throughout the pinewoods, predominantly humic cambisol type soils or leptosols at the higher sites (Forteza et al. 1988) according to the FAO taxonomic soil classification of 1989. The site index of these stands ranges between 21.4 and 29.9 m (Montes et al. 2007). Scots pine forms pure stands in the middle and high altitudes of the forest whereas in the lower parts of the forest this species grows alongside *Quercus pyrenaica* Willd. Some shrubs, such as *Genista florida* L., *Cytisus scoparius* (L.) Link and *Cistus laurifolius* L., appear in patches of forest which are at the reinitiation stage of the stand development.

The Navafría forest is managed using a permanent block plan with a 100 year rotation period. The management plans date from the end of the 19th century. The forest is divided into three working groups and these in turn into three wood production circles. Each wood production circle is made up of five blocks (García López 1994). Natural regeneration is achieved through the uniform shelterwood system over a 20 year regeneration period. Artificial regeneration is only employed in exceptional circumstances as a supplementary measure or aid. The silvicultural management applied consists of an intensive thinning from below regime from years 30 to 80 (removing subcanopy trees) or mixed (removing dominated and co-dominant trees). The canopy is then opened, leaving a density of 200-250 trees ha⁻¹ at the beginning of the regeneration period. Additional trees are subsequently removed in a uniform manner throughout the regeneration block in two or three harvests over the regeneration period, leaving a low residual tree density. Thus, the seedlings become established under the protection of the older trees (Loftis 1990). The remaining trees (30-40 trees ha⁻¹) are finally harvested at 100 years of age. In order to facilitate the establishment of the regeneration, soil preparation operations, subsoil and blade scarification are carried out before the final harvest. Through this management approach, natural regeneration of Scots pine throughout the forest is achieved successfully.

We installed a linear transect along a contour line in each of the five regeneration blocks. The five transects were installed after the first regeneration fellings and prior to the final felling, in the middle of the regeneration period. Square plots of 64 m² in size were established for regeneration inventory purposes at 50 m intervals along these transects, making a total of 45 plots across the five blocks (Table 2.2). Each plot was subdivided into 4 square subplots where seedlings (individuals shorter than 130 cm) were counted. Additionally, all the trees and the stumps within a 15 m radius from the centre of each regeneration plot were mapped. Measurements included: diameter at breast height (dbh) of

the trees, total tree height and diameter of the stumps at ground level. The topsoil characteristics of each plot were also recorded, consisting of a mixture of samples taken from a depth of 20 cm and collected at the centre of each subplot to obtain the following topsoil variables: soil pH (in distilled water), percentage of sand, lime and silt according to the International Society of *Soil Science*, the percentage of oxidizable organic matter (Walkey and Black method), available P (Olsen method), colloidal K, Ca, Mg, Na (all atomic absorption), the electrical conductivity (in distilled water) and the stoniness (percentage of stones in the uppermost 20 cm of the soil) (Table 2.2). We took a hemispherical photograph at the centre of each plot at a height of 1.30 m above the ground to measure light availability (Table 2.2). The Global Site Factor (GSF) was then calculated using HemiView Canopy Analysis software (Delta-T Devices Ltd.). The GSF is the proportion of total radiation under a plant relative to that in the open, ranging from 0 (completely closed canopy) to 1 (completely open canopy). We also measured plot slope, expressed as a percentage and the altitude (Table 2.2). We considered the same altitude for all the plots in each transect.

In order to assess the influence of local stand structure, two indices for the measured trees were calculated: the influence potential (IPOT) and the index of influence (INF; Woods and Acer 1984) of the retained trees at a given point. IPOT is based on the concept of ecological field theory (Wu et al. 1985), empirically modified by Kuuluvainen and Pukkala (1989):

$$IPOT_j = 1 - GPOT_j \quad (2.1)$$

where

$$GPOT_j = \prod_{i=1}^{n_j} (1 - \beta_{ij})$$

$$\text{and } \beta_{ij} = \left(dbh_{ij} / \max(dbh) \right) \exp(-b_{ij} \cdot s_{ij})$$

β_{ij} is the potential influence of tree i at plot centre j , s_{ij} is the distance from tree i to the plot centre, dbh_{ij} is the diameter of tree i at the plot centre j . $\max(dbh)$ is the maximum diameter at breast height in the dataset, 95 cm in our dataset. The parameter b_{ij} was replaced by $1/(a \cdot h_{ij})$, where h_{ij} is the height (m) of tree i at plot centre j and a is a parameter to be estimated. Alternative values of a from 0 to 1 by 0.1 based on the correlation between regeneration density and IPOT were tested. The highest correlation between a and regeneration density

was found for the value $a=0.4$. IPOT ranges from 0 (no competition) to 1 (maximum competition).

Table 2.2 Summary of the main characteristics of the study area.

Variables	Mean	Minimum	Maximum	Stand. Deviation
Number seedlings per subplot (4 x 4 m)	17	1	125	24
Edaphic variables				
pH	6.04	4.37	8.57	1.50
Electric conductivity (mS/cm)	0.11	0.03	0.48	0.09
Sand (%)	65.85	55.68	81.96	5.44
Silt (%)	13.91	5.64	23.64	3.74
Clay (%)	20.26	9.68	29.40	4.20
Organic matter (%)	10.86	4.75	21.97	3.58
Available P (mg/kg)	7.7	4.3	20.5	4.2
Available K (mg/kg)	181	87	379	61
Available Ca (meq/100g)	4.5	1.9	9.1	1.8
Available Mg (meq/100g)	0.85	0.25	2.50	0.45
Available Na (meq/100g)	0.06	0.01	0.16	0.03
Stoniness (%)	19.60	2.50	100	15.10
Light variable				
Global Site Factor (0-1)	0.62	0.22	0.94	0.16
Topographic variables				
Slope (%)	25	5	65	10
Elevation (m)	1540	1381	1730	138
Competition variables				
IPOT (0-1)	0.68	0.11	0.97	0.23
INF	39.24	0.01	152.80	33.41
Number of retained trees	6	0	15	4
Number of stumps	4	0	17	4

Stoniness: percentage of stones in the uppermost 20 cm of the soil. Global Site Factor: the proportion of total radiation under a plant. IPOT: influence potential (Wu et al. 1985; Kuuluvainen and Pukkala 1989) INF: index of influence (Woods and Acer 1984).

Moreover, the INF competition index was defined as:

$$INF_j = \sum_{i=1}^n dbh_{ij} \exp(-2s_{ij}^2 dbh_{ij}^{-1}) \quad (2.2)$$

where INF_j represents the index of influence in a plot centre j , and s_{ij} , dbh_{ij} are defined above. INF acquires low values in gaps and high values in dense overstory patches (Paluch 2005).

The target variable in our case study was the number of seedlings per plot, i.e. count data. This is an important attribute that should be considered in the method selection. All the measured variables (edaphic, light, topographic and stand condition variables; Table 2.2) were included as explanatory variables in the following fitted models.

2.2.2. Parametric regression: GLMM using a negative binomial

Generalized linear mixed models (GLMMs) extend linear regression mixed models to accommodate non-constant variance through a variance function, non-linear relationships and certain types of non-normally distributed errors (Bolker 2008; Hardin and Hilbe 2012; Venables and Ripley 2002). There are three steps in GLMMs: (1) choose a distribution function for the response variable, which is a function from the exponential family; (2) define a linear predictor function specifying the covariates; and (3) link the predictor function and the mean of the distribution (Zuur et al 2007). The connection of the mean of the distribution function to the linear predictor is done using link functions, e.g. logit, log or probit (Venables and Ripley 2002). Count data may be assumed to follow a Poisson distribution or a negative binomial distribution. However, in the Poisson distribution a single parameter quantifies both the mean and the variance, so the use of Poisson distribution is reduced to data that matches the requirement of having a value of variance similar to the mean value (Crotteau et al. 2014; Lawless 1987). When the variance values are higher than the mean, the negative binomial distribution is more appropriate than the Poisson distribution (Bliss and Fisher 1953; Venables and Ripley 2002). Although the negative binomial distribution cannot strictly be included in the exponential family, negative binomial models can be fitted using a small extension of the GLMs (Bolker 2008). The negative binomial distribution is characterized by a dispersion parameter, θ , which relates the mean (μ) of a response variable y and its variance: $V(y) = \mu + (\mu^2 / \theta)$ (Bolker 2008; Crotteau et al. 2014). This

parameterization of the variance, termed NB2 by Hardin and Hilbe (2012) or restricted negative binomial by Crotteau et al. (2014), assumes that the value of θ is constant across factors.

Observations recorded in forestry and ecology frequently present spatial or temporal correlation: several measurements are taken from the same subject or the sampling is carried out hierarchically. If these correlations are ignored, the assumption of independence of the observations and the error terms is violated and the standard error and p-values of the covariates might be affected (Zuur et al. 2007). The correlation among measurements can be taken into account by including random effects in the model (Fisher 1918; Henderson et al. 1959; Zuur et al. 2009). Pure spatial and temporal correlation can be addressed through semivariograms or correlograms, respectively (Zuur et al. 2009). Nevertheless, in our study, subplots are nested within the plots and the plots in turn nested within transect. Hence, a plot random intercept and a plot nested within transects random intercept effects were included in the model. Thus, the full negative binomial mixed model can be written as follows:

$$y = \text{negative binomial}(\mu, \theta) \quad (2.3)$$

$$\log(\mu) = X\beta + Zu \quad (2.4)$$

where X is the matrix of the covariates and β is the vector of the unknown (although estimable) parameters of fixed effects, Z is the random-effects design matrix; u is the vector of random effects with mean zero and variance to be estimated. After fitting the model, we used the McFadden's pseudo- R^2 to assess the goodness of fit (Domenich and McFadden 1975):

$$\text{Mc Fadden's } R^2 = 1 - \frac{-2 \log L_{Full}}{-2 \log L_{Null}} \quad (2.5)$$

where L_{Full} and L_{Null} are the likelihood of the full model and the likelihood of the null model. McFadden's pseudo- R^2 values can range between 0 and 1. Nevertheless, the resulting values are not equivalent to the classical R^2 values. Indeed, values of McFadden's pseudo- R^2 between 0.2 and 0.4 should be taken to represent a very good model fit (Louviere et al. 2000).

To avoid over parameterization, the inclusion of the random effects, the covariates (Table 2.2), the interaction of the variables in the model was carried out via a forward stepwise procedure according to the Likelihood Ratio test using a $[\text{Pr}>(\text{Chi})]=0.05$ as a

confidence level. This analysis was conducted by using the “glmmadmb” function of the “glmmADMB” package (Fournier et al. 2012) in R 3.0.2. (R Core Team 2013).

2.2.3. Including uncorrelated variables in the GLMM. PCA as ordination method

In the former section (2.2.), the explanatory variables were included sequentially to avoid collineality. A second option to deal with this problem is presented in this section. The measured covariates represent a multivariate data set, a collection of sites positioned in a space where each variable defines one dimension (Borcard et al. 2011). In this case, an ordination method can be used to reduce the number of variables to a new set of uncorrelated variables, which can be therefore included as explanatory variables in the GLMM fitting. The PCA is a classic multivariate technique (Legendre and Legendre 1998). It reduces the dimensionality of a group of variables into a new set of uncorrelated variables, called the principal components. The principal components retain all of the variable information, but weight linear combinations of the original variables (Abdi and Williams 2010; Jolliffe 2002; Legendre and Legendre 1998). The first principal-component axis a data set is the line that goes through the most explanatory dimension describing a multinomial distribution. The following axes are orthogonal to one another and explain successively less (Abdi and Williams 2010; Borcard and Legendre 2002). The PCA is an eigenvector-based method and requires the construction of a disperse matrix S , which assesses the distance among observations. The mathematical details are beyond the scope of this study, but this information can be found in Jolliffe (2002) and Legendre and Legendre (1998). The requirement of normality of the original variables in the PCA analysis has been widely discussed and some authors state that normality is not required (Jolliffe 2002; Zuur et al. 2010) whereas others argue that data must be normally distributed (Borcard and Legendre 2002).

We carried out two PCAs, one using edaphic variables and the other using the competition and light variables. The eigenvectors and the scores of the principal components were calculated after applying an orthogonal varimax rotation (Legendre and Legendre 1998). The PCA was conducted using the “principal” function of the “psych” package (Revelle 2013) in R. Seedling abundance was then modeled using eq (1). In this case, the predictors were the scores of the first and second principal components of each PCA and the topographic variables (slope and altitude). Two or three components are commonly used

following ordination methods (Barbeito et al. 2011; González-Martínez and Bravo 2001) because those components typically explain a large amount of the total variance. The criteria described in the previous section (2.2) were also used for the inclusion of covariates. As a measure of goodness of fit we used the statistics described in the previous section.

2.2.4. Ordination using NMDS

NMDS (Shepard 1962) is another ordination method. As with PCA, it is also an ordination technique, because it reduces a multivariable set into orthogonal univariate axes. However, unlike PCA and other ordination methods, NMDS is not based on an eigenvalue solution (Legendre and Legendre 1998). This method requires the construction of a community dissimilarity distance matrix (Legendre and Legendre 1998). For this purpose, any measure of association can be used, not only correlation, which sometimes is not the most appropriate measure (Zuur et al 2007). Several distance measures can be employed to build the dissimilarity distance matrix, e.g. Bray-Curtis, Manhattan or Jaccard. Measure selection depends on the availability and nature of the data. To calculate those dissimilarities, numerical optimization methods have to be used. NMDS is an iterative method. The iterative procedure attempts to position the objects in the three dimensions so as to minimize a stress function (scaled from 0 to 1), which measures how far the distances in the reduced-space configuration are from the original distances (Borcard et al. 2011; Legendre and Legendre 1998). The mathematical details can be found in Legendre and Legendre (1998).

We selected the Bray-Curtis empirical dissimilarity distance matrix (Bray and Curtis 1957) to reduce the observed 19 variables (Table 2.2) in three dimensions or axes. We selected this distance because it is one of the most appropriate metric distance for community ecology data (Legendre & Fortin 1989), and it has been used in recruitment patterns assessment before (Ledo et al. Accepted) We then plotted the Shepard diagram (Borcard et al. 2011; Legendre and Legendre 1998) to compare the original (empirical) distances with the ordination distances in the three dimensional space. The goodness of fit of the ordination is measured as the R^2 of both a linear and a monotone (nonparametric) regression of the NMDS distances on the original ones (Borcard et al. 2011).

We grouped the number of seedlings for each subplot into a categorical variable with two levels: one corresponding to the fourth quartile (Q4) and the other to the first, second and third quartiles (Q123) of the distribution of the number of seedlings. We chose this

division because the number of seedlings was relatively homogeneous in the first, second and third quartiles of the distribution, but increased greatly in the fourth quartile. We plotted the centroids of the quartiles to interpret the environmental variables with respect to the quartiles. We drew an ordination hull to enclose and cluster the environmental variables into the two levels (Q123 and Q4). Ellipses for the 95 % confidence areas of the class centroids were also calculated (Oksanen 2013). Furthermore, smooth surfaces of covariates to ordinations can be fitted using generalized additive models (Cayuela et al. 2006; Oksanen et al. 2013). NMDS was conducted using the function “metaMDS” implemented by the R package “vegan” (Oksanen et al. 2013).

2.2.5. Decision tree automatic classification method: CHAID algorithm

CHAID is a nonparametric procedure that splits a data set (root node) into groups, classes or segments that differ with respect to the response variable (Kass 1980; Kleppin et al. 2008). CHAID does not necessarily produce dichotomous categories and therefore a node can be split into more than two categories (Álvarez-Álvarez et al. 2011; van Diepen and Franses 2006). No distributional assumptions of the data are required in the CHAID, which implies a great advantage over other methods such as the GLMM parametric approach that we followed in section 2.2. The CHAID mode operates as follows: in a first step, continuous variables are divided into a number of categories with approximately equal numbers of observations, since the CHAID procedure operates on nominal variables (Álvarez-Álvarez et al. 2011; van Diepen and Franses 2006). CHAID then splits the data for the specific predictors which exhibit the strongest degree of association with the response variable (Álvarez-Álvarez et al. 2011; Kleppin et al. 2008; van Diepen and Franses 2006). Since CHAID is a forward stepwise approach, it is possible that a better segmentation solution can be found by using another variable at an earlier stage (Vriens 2001). Mathematical details of the method are in van Diepen and Franses (2006) and Kass (1980).

The root node in the present study is the seedling density. We used a significance level of 5% of the Chi-squared test of independence to decide which categories of each predictor to merge and which predictor to split. As the Chi-squared test is only approximately Chi-squared distributed, a large sample size is required (van Diepen and Franses 2006). CHAID was carried out using SPSS (IBM Corp 2012).

We evaluated the goodness of fit using the classic R^2 :

$$R^2 = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad (2.6)$$

where y_i is the observed density, $\hat{y}_i$ is the estimated seedling density, $\bar{y}$ is the mean of the density and n is the number of observations.

2.2.6. The Random Forests algorithm and conditional inference tree

The Random Forests algorithm (Breiman 2001) is a nonparametric technique that combines the prediction of many independent decision-tree models into a robust composite model (Cutler et al. 2007), thereby improving the accuracy of the prediction (James et al. 2013). To achieve this, the Random Forests procedure generated 500 bootstrapped data sets from the original data set. The procedure then constructs, by default, 500 bagged regression trees on the bootstrapped training samples and aggregates the bagged trees for prediction (James et al. 2013; Strobl et al. 2009). The remaining observations not used to fit a given bagged tree, referred to as out-of-bag (OOB) observations, are used to compute the prediction accuracy of the given tree (Strobl et al. 2009). In addition, the algorithm permutes a random sample of the predictors for determining each split in each tree, producing diverse uncorrelated trees (James et al. 2013; Strobl et al. 2009). Thus, the preference for certain predictors due to their scale of measurement or importance is avoided (Barbeito et al. 2012). The preference for a given predictor could result in the bagged trees being quite similar to each other and hence, highly correlated predictions (James et al. 2013). The predictor importance is the difference in prediction accuracy before and after permuting, averaged over all trees (Breiman 2001; Strobl et al. 2009). A conditional permutation scheme for the computation of the variable importance measure was used in order to account for the correlation among the variables (Strobl et al. 2008). The variable importance measure is based upon the mean decrease in accuracy of predictions on the out-of-bag samples when a given variable is excluded from the model (James et al. 2013). According to Grömping (2009), the prediction of the Random Forests algorithm can be estimated via Mean Square Error from the OOB data (OOB-MSE) as:

$$\text{OOB-MSE} = \frac{1}{n} \sum_{i=1}^n (y_i - \hat{y}_{i\text{OOB}})^2 \quad (2.7)$$

where $\hat{y}_{i\text{OOB}}$ denotes the average prediction for the i -th observation from all trees for which this observation has been OOB. As with linear regression, with the average of sum of squares

$$\text{SST} = \frac{1}{n} \sum_{i=1}^n (y_i - \bar{y})^2, \text{ OOB-}R^2 \text{ can be obtained as } 1 - \text{OOB-MSE/SST}.$$

Finally, we built an unbiased tree based on non-parametrical conditional inference procedures for testing independence between response and each predictor. The split selection criterion is based on conditional inference tests or permutation test (Hothorn et al. 2006). We used a significance level of 5% as a splitting node criterion in tree construction. The goodness of fit of the conditional inference tree was evaluated thorough the R^2 described in the CHAID section. We employed the functions cforest and ctree of the R package “party” (Hothorn et al. 2006; Strobl et al. 2008) to perform the Random Forests analysis and the conditional inference tree.

2.3. Results

2.3.1. Parametric regression: GLMM using a negative binomial

We assessed the influence of environmental variables on the number of seedlings per subplot through a negative binomial regression with a log link. Seedling distribution was explained through various models in which the different covariates were sequentially included (Table 2.3). The most accurate model (in terms of lower log-Likelihood) describing seedling abundance included the content of Na, P and the number of stumps within a 15 m radius (Table 2.3). The Na (estimation coefficient $\pm$ standard errors= -12.90 ± 3.20 , $p < 0.0001$) and P (estimation coefficient $\pm$ standard errors= -0.07 ± 0.029 , $p = 0.012$) content showed a negative association, while stump density had a positive association (estimation coefficient $\pm$ standard errors= 0.09 ± 0.028 , $p = 0.0001$) on regeneration density (Table 2.3). Altitude, GSF, the logarithm of electric conductivity and stoniness improved the model only very slightly ($0.05 < [\text{Pr} > (\text{Chi})] < 0.1$) in terms of log-likelihood, so these were not included in the model. GSF (estimation coefficient $\pm$ standard errors= 1.18 ± 0.71 , $p = 0.0941$) and altitude (estimation coefficient $\pm$ standard errors= 0.016 ± 0.0008 , $p = 0.0579$) were positively correlated with seedling density whereas the logarithm of electric conductivity (estimation

coefficient $\pm$ standard errors = -0.35 ± 0.20 , $p=0.0832$) and stoniness (estimation coefficient $\pm$ standard errors = -0.01 ± 0.01 , $p=0.0657$) were negatively correlated. As regards the interactions among variables, we did not find a significant effect of any of the three interactions tested (Table 2.3). The model including the plot random effect performed better, in terms of likelihood, than the model without random effects. This fact pointed out the importance of considering the spatial correlation within the plots in the model (Table 2.3). McFadden's pseudo- R^2 was 0.022, indicating poor model fit (Louviere et al. 2000).

2.3.2. Including uncorrelated variables in the GLMM. PCA as ordination method

The edaphic variables were reduced to two principal components, the first component was mainly related to the available Ca and Mg whereas the second component was related to the pH and the electric conductivity (Table 2.4). Together, the two components explained 32% of the total variance. Concerning the light and competition variables, the PCA reduced the number of variables to two principal components. The number of trees was related to the first component and the number of stumps to the second (Table 2.4). In this PCA, the two components explained 48 % of the total variance.

We found that the second component of the PCA of the light and competition variables (related to the number of stumps) was positively associated (estimation coefficient $\pm$ standard errors = 0.342 ± 0.119 , $p=0.004$) in terms of Likelihood Ratio test ($([Pr > (Chi)] < 0.05)$; Table 2.5) to the seedling density. We did not find a significant effect ($([Pr > (Chi)] > 0.05)$) of the two other components or the two topographic variables (slope and altitude) on the number of seedlings. In this regression, the variance of the plot random intercept was 0.45. Regardless of the goodness of fit, McFadden's pseudo- R^2 was 0.01 indicating quite poor model fit (Louviere et al. 2000).

Table 2.3 Summary of the selection process of the environmental variables and the fitting statistics of the forward stepwise regression. The chosen model in bold.

Model	Fixed effects	Random Effect	Log-Likelihood	Compared to model	Pr>(Chi)
(0)	Intercept	-	-543.56	-	-
(1)	Intercept	Plot	-512.74	(0)	<0.001
(2)	Intercept	Plot/Transect	-512.40	(1)	0.4124
(3)	Na	Plot	-508.77	(1)	0.0048
(4)	Na, P	Plot	-506.45	(3)	0.0312
(5)	Na, P, altitude	Plot	-504.71	(4)	0.0663
(6)	Na, P, GSF	Plot	-505.10	(4)	0.0999
(7)	Na, P, slope	Plot	-505.33	(4)	0.1340
(8)	Na, P, pH	Plot	-506.44	(4)	0.8993
(9)	Na, P, IPOT	Plot	-505.24	(4)	0.1201
(10)	Na, P, IFN	Plot	-505.31	(4)	0.1305
(11)	Na, P, organic matter	Plot	-506.29	(4)	0.5668
(12)	Na, P, Mg	Plot	-505.67	(4)	0.2114
(13)	Na, P, Ca	Plot	-505.29	(4)	0.1272
(14)	Na, P, K	Plot	-506.34	(4)	0.6375
(15)	Na, P, stumps	Plot	-501.28	(5)	0.0013
(16)	Na, P, stumps, trees	Plot	-501.21	(15)	0.7043
(17)	Na, P, stumps, Ln(electric conductivity)	Plot	-499.83	(15)	0.0889
(18)	Na, P, stumps, clay	Plot	-501.27	(15)	0.8580
(19)	Na, P, stumps, sand	Plot	-501.26	(15)	0.8415
(20)	Na, P, stumps, silt	Plot	-501.28	(15)	0.9383
(21)	Na, P, stumps, stoniness	Plot	-449.62	(15)	0.0681
(22)	Na, P, stumps, Na*stumps	Plot	-501.28	(15)	0.9643
(23)	Na, P, stumps, Na*P	Plot	-501.23	(15)	0.7567
(24)	Na, P, stumps, stumps*P	Plot	-501.24	(15)	0.7773

Table 2.4 Eigenvectors of the environmental variables obtained from the PCAs. In bold, the eigenvectors of the main variables related to each component.

Group of variables	Variables	Component 1	Component 2
Edaphic variables	pH	-0.10	0.95
	Electric conductivity	-0.04	0.94
	Sand (%)	0.11	0.03
	Silt (%)	0.18	-0.04
	Clay (%)	0.01	0.00
	Organic matter	0.02	-0.01
	K	0.10	0.02
	P	-0.14	-0.11
	Mg	0.85	-0.17
	Ca	0.96	-0.03
	Na	0.34	0.17
	Stoniness (%)	-0.02	-0.14
Light and competition variables	GSF	-0.40	0.36
	IPOT	0.40	-0.36
	IFN	0.24	-0.10
	Number of trees	0.89	-0.11
	Number of stumps	-0.11	0.95

Table 2.5 Summary of the selection process of the principal components and the fitting statistics of the forward stepwise regression. The chosen model in bold.

Model	Fixed effects	Random Effect	Log-Likelihood	Compared to model	Pr>(Chi)
(0)	Intercept	-	-543.56	-	-
(1)	Intercept	Plot	-512.74	(0)	<0.001
(2)	Intercept	Plot/Transect	-512.40	(1)	0.412
(3)	PC1 com	Plot	-512.55	(1)	0.540
(4)	PC2 com	Plot	-508.86	(1)	0.005
(5)	PC2 com + PC1 ed	Plot	-508.20	(4)	0.252
(6)	PC2 com + PC2 ed	Plot	-507.81	(4)	0.147
(7)	PC2 com + altitude	Plot	-508.86	(4)	0.950
(8)	PC2 com + slope	Plot	-508.07	(4)	0.209

PC1 ed: component related to the Ca and Mg. PC2 ed: component related to the pH and the electric conductivity. PC1 com: component related to the number of trees. PC2 com: component related to the number of stumps.

2.3.3. Ordination with NMDS

The NMDS (method section 2.2.4.) reduced the dimensionality of the 19 variables to three dimensions; one related to the light variables and to the indices of the influence of retained trees on regeneration; the second related to the soil variables; and the last related to the number of stumps. The R^2 of the linear ordination and the monotone of regression of the NMDS distances on the original ones were 0.88 and 0.98, respectively. The stress value was minimized to 0.14. The NMDS diagram shows that the entire hull of Q4 was enclosed by the hull of Q123 (Fig. 2.1). The ellipses for the 95 % confidence areas of both classes were almost overlapped, indicating only very slight differences between classes. IPOT and Mg centroids were enclosed by Q123 but not by Q4. The gradient (via contours) of the projected smooth surfaces of IPOT and Mg influenced regeneration density (Fig. 2.1). The projected smooth surfaces of the IFN and the number of trees followed the same pattern as the IPOT, parallel with the IPOT projected smooth surfaces; whereas the surfaces of the number of stumps was also parallel respect to the IPOT projected smooth surfaces but showed a positive association with the regeneration density. Moreover, both the contours of the projected smooth surfaces of the Ca and the Na followed the same pattern than the projected smooth

surfaces of the Mg, parallel to the latter and displaying a negative relationship with the regeneration density. The rest of the other variables overlapped each other and were very close to the centroids of Q4 and Q123. Therefore, we assumed that there was no association with the regeneration density; hence they are not shown in Fig. 2.1.

Figure 2.1 NMDS Ordination of the variables showing the centroids of the quartiles of the number of seedlings. Variables within Q4 hull not shown to facilitate the visualization. Red ellipse and red hull: Q4 (fourth quartile of the number of seedlings). Blue ellipse and blue hull: Q123 (first, second and third quartiles of the number of seedlings). Yellow smooth surfaces = IPOT gradient. Green surfaces = Mg gradient.

2.3.4. Decision tree automatic classification method: CHAID algorithm

The CHAID procedure split the data into two main branches according to the Na concentration. Thus, this variable played the most statistically important role ($p < 0.0001$) in the subplot seedling density (Fig. 2.2). The lowest concentrations of Na (≤ 0.030 meq/100g) were related to the highest number of seedlings. In the case of higher concentrations of Na (> 0.030 meq/100g) the algorithm split the data into six branches according to the number of retained trees ($P < 0.0001$). The distribution of the data in these six branches did not follow a linear pattern. The R^2 of the CHAID was 0.23, pointing to a poor model fit.

Figure 2.2 Regression tree as result of the CHAID algorithm for seedlings density. Mean indicates the mean number of seedlings per subplot and n the number of subplots per node.

2.3.5. Random Forests algorithm and conditional inference tree

Across all the trees considered in the Random Forests algorithm (method section 2.2.6.), the content of sodium and the number of stumps were the two most important variables since they reached the greatest values of conditional variable importance (Fig. 2.3). The OOB-MSE and the OOB- R^2 of the Random Forests algorithm were 434.77 and 0.17 respectively.

The first node of the conditional inference tree split the data according to the content of Na ($p<0.001$) (Fig. 2.4). The largest number of seedlings was related to the lowest concentrations of Na (≤ 0.040 meq/100g). For the highest concentrations of Na (>0.040 meq/100g), the branch was divided according to the number of stumps ($p=0.002$), which were positively related to the number of seedlings per subplot (Table 2.6). The R^2 of the conditional inference tree was 0.17, indicating a poor model fit.

Figure 2.3 Conditional variable importance measured following the “permutation principle of the mean” decrease in accuracy importance in the Random Forests algorithm. Larger values of conditional variable importance indicate more importance in the Random Forests model.

Figure 2.4 Implementation of conditional inference trees for seedlings density into the defined theory of conditional inference procedures. Mean indicates the mean number of seedlings per subplot and n the number of subplots per node.

Table 2.6 Significant variables involved in the regeneration process according to the alternative approaches employed. The effect of the variables is in brackets.

Method	Edaphic and topographic variables	Competition and stand variables
GLMM	Na (-); P (-)	Number of stumps (+)
GLMM after PCA	n.s.	Component related to the number of stumps (+)
NMDS	n.s.	n.s.
CHAID	Na (-)	Number of remaining trees (non-linear)
Random forest and conditional inference tree	Na (-)	Number of stumps (+)

n.s.: no statistically significant variables identified.

2.4. Discussion

2.4.1. Factors underlying Scots pine regeneration in Central Spain

A minimum of 2,000 ha⁻¹ (4 seedlings per subplot) denotes a sufficient regeneration density for Scots pine (e.g. Hyppönen et al. 2013). In our study we found that at least 4 seedlings per subplot (2,500 seedlings ha⁻¹) were present in 99% of the subplots suggesting regeneration success and good management practices. Therefore, we can state that the ranges of the measured variables are suitable for achieving natural regeneration. The current values of these variables are within a range that does not limit the regeneration process in the studied forest. Thus, some of the relationships found between the environmental variables and the regeneration density may be arbitrary rather than causal.

The different methods pointed to similar, although not identical factors underlying the regeneration process (Table 2.6). The models obtained using the different methods had low goodness of fit values. This indicates that the low association between the environmental variables and the seedling density may be due to the lack of limiting factors in the regeneration process.

The parametric regression, the CHAID, the Random Forests algorithm and the conditional inference tree found a negative association between available Na and the seedling density. This negative relationship can be explained by the salt sensitivity of Scots

pine (Bravo-Oviedo and Montero 2008). However, the sodium concentrations in the study area are lower than those found in other Scots pine forests (Bravo and Montero 2001). Furthermore, there was a positive relationship between the number of stumps and the seedling density according to the GLMM, the GLMM after PCAs reduction, the Random Forests algorithm and the conditional inference tree. The number of stumps is related to recently cut trees, so seedling density is directly related to canopy openness indicating that higher intensities in the regeneration fellings favoured the establishment of seedlings. In addition, the extraction of the wood resulted in a soil preparation effect, which facilitated the establishment of the Scots pine seedlings (Barbeito et al. 2011). The CHAID found an interaction between the highest levels of Na and the remaining trees. It indicates that the Na is the most important factor driving the regeneration and when its concentration increases over the optimum, other factor, the remaining trees also appeared as a driver. The NMDS placed the two classes (the fourth quartile and the first, second and third quartiles of the distribution of the number of seedlings) quite close to each other reporting a weak negative relationship between the number of remaining trees and the competition indices with the regeneration density. The remaining trees play an important role in the regeneration, as Scots pine seedlings prefer moderate light conditions in Mediterranean areas (Barbeito et al. 2009; Pardos et al. 2007) rather than intensive light conditions as in Northern countries (Valkonen 2000). Furthermore, in Mediterranean areas the success of Scots pine regeneration depends on summer droughts, so silviculture operations in our study area is also aiming at reducing the competition for resources thorough the soil preparation and thinnings (Barbeito et al. 2011).

2.4.2. Methods comparison

The variables used to predict the seedling recruitment were highly correlated. Including this in a regression model is a problem because it increases the risk of type I errors (Zuur et al. 2007). The PCA solved this problem reducing the data into uncorrelated components. Nevertheless, the full-dimensional GLMM had higher values of the goodness of fit statistics (McFadden's pseudo- R^2) than the GLMM including the components of the PCAs. In addition, the reduced components present another flaw, which is that the effect of the individual covariates is not fully identifiable (Strobl et al. 2009).

NMDS could also have been used to reduce the dimensionality of the data for the parametric regression. However, since the NMDS is based directly on the dissimilarities, it does not provide correlations between derived axis scores and the variables, whereas techniques based on the eigenvalues and eigenvectors allow the researcher to relate, at least in part, the original variables to the components (Quinn and Keough 2001). Therefore, if the objective of the ordination technique is to reduce the data to use the scores of the axes in a regression model, the eigenvalue techniques may be more useful, since the correspondence to the component-variables is maintained. However, eigenvalue techniques are based only on correlation or covariate coefficients and limited to Euclidean distances, and this may not be the most appropriate measure of association (Legendre and Legendre 1998; Zuur et al 2007). In addition, the method can also proceed with missing distance estimates as long as there are enough measures left to position each object with respect to a few of the others (Legendre and Legendre 1998). Furthermore, the NMDS allowed to fit non-linear relationships between the covariates to ordinations using generalized additive models whereas other methods, such as PCA, implies linear relationships and it cannot always be appropriate (Oksanen 2013).

As regards the regression trees, the R^2 of the CHAID was larger than that of the conditional inference tree. Additionally, the CHAID has the main advantage that split each node can be split into more than two branches, i.e., it is not a binary partitioning method (Kass 1980; Kleppin et al. 2008; van Diepen and Franses 2006) as the conditional inference tree (Hothorn et al. 2006). However, since the CHAID is a forward stepwise method, i.e. not all the variables are considered simultaneously but sequentially, there is the possibility that a better segmentation solution can be found using another variable at an earlier stage (Vriens 2001). Thus, CHAID cannot guarantee a single optimal solution (Perreault and Barksdale 1980). In relation to this, the bias in the variable selection is solved by the conditional inference trees using the permutation test principle (Hothorn et al. 2006). Both decision trees, the CHAID and the conditional inference tree, found second order interactions. In addition, decision trees may outperform the classical approaches if there is a non-linear and complex interaction between the variables and the results of the decision trees are easier to interpret than those of other regression models (James et al. 2013; Strobl et al. 2009). Nevertheless, the main weakness of simple tree models is their instability to small changes in the learning data (Strobl et al. 2008). The Random Forests algorithm solves the problem of instability by averaging an ensemble of trees into a more robust composite model (Cutler et al. 2007; Strobl

et al. 2009). However, the R^2 of the CHAID was larger than that of the Random Forests algorithm.

Forest regeneration studies in Mediterranean areas have often been conducted using parametric regression or point pattern analysis (Table 2.1). Despite all the assessed models performed in a similar way and gave similar ecological results, the election of the statistical technique must be done according to the characteristics and structure of the data. Ecological data often presents both spatial and temporal dependence among the observations. The hierarchical structure of our design indicates spatial dependence among measurements. The GLMM was the only method which allow the spatial correlation between subplots to be considered entering random effects (Fisher 1918; Henderson et al. 1959; Zuur et al. 2007). In studies with multiple hierarchies, like ours, random effects are specially important (Ten Have et al. 1999). We found a significant effect of the plot random effect indicating high correlation among subplots within the same plot. The model with the plot random effect captured more variability than the model without the random part. The other methods employed did not consider this correlation which can provide biased results and hide the effect of some explanatory covariates. Model misspecification is a frequent mistake disregarded in ecological modeling. Additionally, this method also identified the largest number of variables associated with seedling density. Thus, in studies with nested data, the parametric regression model is the most useful statistical approach. In studies with a large set of predictors, decision trees and the Random Forests algorithm through the conditional variable importance and ordination methods can be used to select and reduce the number of variables to be included in the model. If complex interactions are expected and the data set is large, then, decision trees are advisable (Strobl et al. 2009). Whether the researcher had to analyse data sets from a hierarchal design with complex interactions among variables, the parametric regression models could account both issues.

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CHAPTER 3

Modeling saplings distribution over time using a functional predictor in a generalized additive model

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Abstract

Spatial pattern of adult trees determines the number of new individuals after regeneration fellings, which modify the light and air temperature under tree canopy. We proposed a novel spatio-temporal model with a functional predictor in a generalized additive model framework to describe non linear relationships between the size of the adult trees and the number of saplings of *Pinus sylvestris* and to determine if the spatial pattern of the number of saplings remained constant or changed in time. In 2001, two plots (0.5 ha) were set up in two phases of regeneration fellings under the group shelterwood method. We mapped the trees and saplings and measured their diameter and height. The inventories were repeated in 2006, 2010 and 2014. We found a negative association between the diameter of adult trees and number of saplings up to 7 – 8 m. Beyond these distances, the diameter of adult trees was not associated with the number of saplings. Our results indicate that the spatial pattern of the number of saplings remained quite constant in time. The generalized additive models are a flexible tool to determine the distance range of inhibition of saplings by adult trees.

Keywords: edge effect; intra-specific competition; mountain forest; shade tolerance; Mediterranean areas

Abbreviations: AIC, Akaike's Information Criteria; GAM, Generalized additive model;

3.1. Introduction

Two main types of models can be used to explain or predict the renewal of a forest after regeneration fellings, seed dispersion and germination: regeneration and recruitment models. The former is related to the youngest individuals, seedlings, whereas the latter is related to larger stems, saplings, which reach or exceed a nominal size limit determined by the researcher (Vanclay 1992; Eerikäinen et al. 2007; Miina and Heinonen 2008). Since it is both difficult and expensive to obtain suitable data for modeling the regeneration, recruitment is more often modeled than regeneration. Both processes are influenced by the capacity of the soil to supply water and the amount of light that reaches the young seedlings. These are the most important factors for success in the establishment of new individuals (Kozłowski 2002). Hence, the summer drought in dry environments cause high mortality rates of seedlings over Mediterranean areas (Castro et al. 2004; Pardos et al. 2007; McDowell et al. 2008), where the water is a limited resource in the vegetative period.

Regeneration fellings can modify the effect of summer drought on seedlings and saplings by setting different target densities or spacing between remaining trees and, thus, modify the shade and the air temperature (Caccia and Ballaré 1998; Pardos et al. 2007). However, not all species can tolerate the same amount of shade and the shade tolerance behavior may vary with site conditions (Kobe and Coates 1997; Gómez-Aparicio et al. 2006). Additionally, the light requirement of plants varies with age. Indeed, the light requirement increases faster with plant age in light-demanding species than in shade tolerant species (Valladares and Niinemets 2008). This determines the density and spacing between remaining trees after regeneration fellings. Therefore, it is necessary to have a clear understanding of the effects of the density of residual trees on new individuals over the regeneration period in order to ensure the spatial continuity of the forest stand after the regeneration fellings.

In addition to the density and spacing between remaining trees after regeneration fellings, several features should be taken into account to model the number of saplings. The age of the stand should also be considered, particularly where shifts in the spatial relationship between trees and offspring over the stages of the forest renewal may occur (Wada and Ribbens 1997). Changes in spatial patterns of trees over time are determined by regeneration mechanisms, substrate characteristics, moisture and light availability as well as intra and inter specific competition (LeMay et al. 2009). Hence, the time perspective allows us to

distinguish between competition and the initial spatial pattern of individuals (Wolf 2005; Getzin et al. 2006), i.e., the initial distribution of seedlings as a consequence of the dispersion and germination of the seeds can vary with the development of the seedlings and competition for resources.

The spatial relationships between adult trees and new cohorts have previously been evaluated using different approaches. The bivariate Ripley's K and related functions have been used to determine if stems of two mapped cohorts of trees show spatial positive, negative or random association (see Montes and Cañellas 2007; Wild et al. 2014) by testing the spatial independence between the two cohorts. Ledo et al. (2014) used inhomogeneous Poisson process spatial models. These models allow the spatial distribution of new individuals to be defined in function of attributes of adult trees. Other authors used distance-dependent influence indices (Contreras et al. 2011) and available light under the forest canopy or the global site factor as explanatory variables in different models (Pardos et al. 2007; Moreno-Fernández et al. 2015a). Distance-dependent influence indices determine, at a given point, the influence of the tree size (such as diameter, height, or crown variables) and the distance between trees and the studied point whereas the global site factor measures the amount of light at a given point by analyzing hemispherical photographs. Influence indices and site factors can easily be entered in a time-dynamic model as additional variables (Eerikäinen et al. 2007; Manso et al. 2013b). However, the temporal modeling of Ripley's K and related functions over time is complex. LeMay et al. (2009) investigated the evolution of these functions in the regeneration of *Pseudotsuga menziesii* var *glauca* (Mirb.) Franco over time using a random coefficient mixed model. Furthermore, specific distance dependent models implemented using packages such as SILVA or SORTIE-ND have been used in forest development simulation studies which include the regeneration establishment phase (Hanewinkel and Pretzsch 2000; Ameztegui et al. 2015). These software packages are compounded of several submodels for the biological processes operating at individual tree level. Comas (2008) and Redenbach and Särkkä (2012) adapted the growth-interaction model proposed by Renshaw and Särkkä (2001) to develop a spatio-temporal regeneration model under two regeneration methods using values taken from the literature to estimate the parameters. This approach generates marked point configurations changing over time.

Generalized additive models (GAMs) may describe a complex relationship between the response and the predictors. This is especially useful in research fields such as ecology, biology or forestry in which simple models cannot capture the structure of the data and more

complex models may be required (Faraway 2006). Whereas GAMs have been used in different areas of forest science such as wood quality (Jordan et al. 2008), annual radial growth (Moreno-Fernández et al. 2014), mortality (Barbeito et al. 2012) or species distribution (Franklin 1998), their use in regeneration or recruitment studies is relatively scarce (Rabasa et al. 2013). Augustin et al. (2009) fit spatio-temporal models within a GAM framework to monitor forest health data. However, these techniques have never been used to assess the dynamics of forest regeneration.

Pinus sylvestris L. is the most widely distributed pine species in the world (Mason and Alía 2000). It can be found throughout Eurasia, stretching from Spain in the South-West to the far east of Russia (Houston Durrant et al. 2016). This pine species is commonly considered to be a light-demanding species in Central and northern Europe (Mátyás et al. 2003). However, it has a half-shade tolerant behavior in southern locations like Spain (Montes and Cañellas 2007), partially due to the high temperatures and drought conditions present during the summer months. Whereas during the early stages *P. sylvestris* seedlings prefer moderate light conditions (Pardos et al. 2007; Barbeito et al. 2009), the later development of saplings is inhibited by competition from the adult trees (Montes and Cañellas 2007). The variation on shade tolerance and climate conditions across its distribution condition the regeneration method; while seed tree and clear cutting are the main methods used in Central and Northern Europe, different alternatives of the shelterwood method are commonly used in Southern Europe (Mason and Alía 2000). In general, 2,000 seedlings per hectare are considered to be a sufficient natural regeneration density (Rodríguez-García et al. 2010; Hyppönen et al. 2013).

In this work, we propose a methodology to describe non-linear relationships between the size of the adult trees and number of saplings of *P. sylvestris* in Mediterranean mountains as a smooth function. We carried it out analyzing data from repeated measurements of two large plots at two stages of the regeneration period where all the stems were mapped. We modeled the spatio-temporal distribution of the number of saplings using a functional predictor (see for example Wood 2011) in a GAM framework (Hastie and Tibshirani 1989; Wood 2006). The functional predictor allowed us to weight the effect of every adult tree on the number of saplings per quadrat based on the distance between adult trees and saplings. In addition, the approach can deal with spatial correlation and a spatio-temporal trend, i.e. changes in the spatial pattern of number of saplings during the development of the stand. In

this regard, we fitted two models with different spatio-temporal structures to determine if the spatial pattern of the number of saplings remained constant or changed in time.

3.2. Material and methods

3.2.1. Study area and data

The study was carried out in a Scots pine forest (Pinar de Valsaín) located on the north facing slopes of the Central Range of Spain (40° 49' N, 4° 01' W). The elevation ranges from 1,200 to 1,600 m, the annual rainfall is about 1,000 mm and the mean temperature is around 9.8 °C. Regeneration is achieved using the group shelterwood method over a 40-year regeneration period. The regeneration fellings create small gaps (0.1-0.2 ha) for the establishment of the regeneration. As regeneration appears, subsequent harvests are carried out over the regeneration period to widen the gaps. The final fellings under the group shelterwood method take place at 120-140 years but some legacy trees are left for biodiversity conservation reasons at the end of the regeneration period.

In 2001, we set up a chronosequence of six plots (0.5 ha) covering all the rotation period (see Moreno-Fernández et al. 2015b for details) to study the dynamics and structure in Mediterranean forests of *P. sylvestris*. This chronosequence represents the management of *P. sylvestris* in the study area from the beginning to the end of the rotation period (Fig. 3.1) and it contains six plots. The plots were as homogeneous as possible in terms of altitude, exposure and site quality. Since we aim to address the influence of the adult trees on the saplings, we selected two plots at different stages of the regeneration period: at an intermediate stage of the regeneration period (100 x 50 m, Fig. 3.2, ca. 19-years-old) and at the end of the regeneration period (58.82 x 85 m, Fig. 3.3, ca. 32-years-old). Young individuals with different size were spread over the youngest studied plot. In this plot, regeneration fellings were done from 2010 to 2014 removing mainly trees located in the corners of the plot (Fig. 3.2). At the end of the regeneration period, the arrival of new individuals has almost been completed and the crown cover is getting closer. Additionally, some legacy trees (larger trees) appear in this plot (Fig. 3.3). Another plot, at the first stages of the regeneration period, was available. However, the arrival of new individuals has started as consequence of the natural dynamics but the number of saplings was still quite low (Fig. 3.1). Therefore, we did not include this plot in the analysis.

Figure 3.1 Position of adult trees ($\text{dbh} \geq 20$ cm; red circles), small trees ($10 \leq \text{dbh} \leq 20$ cm; green dots) and number of saplings per quadrat (darker tones indicate larger number of saplings) of the six plots of the chronosequence in 2001. Size of adult trees is proportional to dbh.

At the time the plots were set up, we carried out the first inventory in which all the stems higher than 1.30 m were labelled individually and their diameter at breast height (dbh) and height were measured. We numbered and classified the stems into the following: trees ($\text{dbh} \geq 10$ cm) and saplings ($\text{height} \geq 1.30$ m and $\text{dbh} < 10$ cm). We distinguished two cohorts of trees: adult trees ($\text{dbh} \geq 20$ cm) and small trees ($10 \leq \text{dbh} < 20$ cm). We mapped the position of every tree (adult and small trees) in each plot and additionally, we grouped the saplings into a 2×2 m quadrat grid. The coordinates of the center of each quadrat were used to determine the position of each quadrat. These measurements were repeated in 2006, 2010 and 2014.

Figure 3.2 Position of adult trees ($\text{dbh} \geq 20$ cm; red circles), small trees ($10 \leq \text{dbh} \leq 20$ cm; green dots) and number of saplings per quadrat (black and gray squares) at intermediate stages of the regeneration period in 2001 (upper left), 2006 (upper right), 2010 (bottom left) and 2014 (bottom right). Size of adult trees is proportional to dbh.

In order to model the sapling distribution, we used the number of saplings per quadrat (N_s) in each plot as response variable. We expected N_s to be highly related to the density of surrounding trees and distance to the surrounding trees, as well as to the time since the beginning of the regeneration fellings. However, the spatial dependence between the saplings and the two cohorts, adult and small trees, varies over stand development (Montes and Cañellas 2007). Thus, we considered as predictors the dbh of the adult trees ($\text{dbh} \geq 20$ cm), the distance in meters from adult tree to each sapling quadrat (considering all the adult trees within a maximum radius of 30 m from each sapling quadrat; Montes and Cañellas 2007) and the number of small trees (N_{small} ; $10 \leq \text{dbh} < 20$ cm) surrounding every sampling quadrat within a radius of 10 m and the inventory year. The distribution of N_s , number of small and adult trees over inventories is shown in Figs. 3.1, 3.2 and 3.3. We assume that at a given distance, larger dbh of the adult trees entails greater competition between adult trees and saplings. Furthermore, we consider that this competition effect between adult trees and N_s decreases with distance. Therefore, a model in which the coefficient of the dbh depends on the distance between adult trees and the sapling quadrat would be very suitable. These requirements can be taken into account using a linear functional predictor in a GAM. Thus,

this approach allowed us to weight the effect of every adult tree on the number of saplings per quadrat based on the distance between adult trees and saplings.

Figure 3.3 Position of adult trees ($\text{dbh} \geq 20$ cm; red circles), small trees ($10 \leq \text{dbh} \leq 20$ cm; green dots) and number of saplings per quadrat (black and gray squares) at the end of the regeneration period in 2001 (upper left), 2006 (upper right), 2010 (bottom left) and 2014 (bottom right). Size of adult trees is proportional to dbh.

3.2.2. Edge effect correction

The quadrats close to the boundaries of the plots are affected by the edge effect and this must be corrected (Ledo et al. 2014). Thus, the number of adult and small trees which surround a quadrat within 30 m and 10 m, respectively, can be underestimated because some of them may be located outside the plot (Goreaud and Pélissier 1999). Several authors (Lancaster and Downes 1998; Perry et al. 2006; Pommerening and Stoyan 2006) have investigated the edge effect and have analyzed the suitability of different edge-corrections for the calculation of the indices of spatial forest structure, Ripley's K and related second order functions.

In order to take account of the edge effect on the number of small and adult trees we used values per unit area, i.e., density. For each quadrat, we estimated the area of the 10 m radius circle within the plot (*AreaIn10* in m²). Therefore, *AreaIn10* changes with the distance between the quadrat and plot border, i.e., *AreaIn10* is smaller in the quadrats closer to the plot border. Then, we obtained the density of small trees as *Nsmall/AreaIn10*. We corrected the edge effect on adult trees by using the dbh density as *dbh/AreaIn30*. *AreaIn30* is the area (in m²) of the 30 m radius circle within the plot. Thus, we assume that the surrounding shelter trees outside the plot would be of similar density than within the area. *AreaIn30* is the area (in m²) of the 30 m radius circle within the plot.

3.2.3. Statistical analysis

For each of the two plots we modeled the expected number of saplings $E(Ns_{ij}) = \mu_{ij}$ in quadrat i and j -th inventory ($j=1, \dots, 4$) using the following GAM:

$$\log(\mu_{ij}) = \alpha + \beta \cdot \frac{Nsmall_{ij}}{AreaIn10_i} + \sum_{n=1}^N \left(f_1(Dist_{in}) \cdot \frac{dbh_{jn}}{AreaIn30_i} \right) + f_2(X_i, Y_i) + Time_j \quad (3.1)$$

with Ns_{ij} following a negative binomial distribution. This distribution is suitable for overdispersed counts such as those we are dealing with here. The variance function is $V(\mu_{ij}) = \mu_{ij} + \mu_{ij}^2 / \theta$, involving the extra parameter θ to be estimated. The greater θ is, the more similar the negative binomial distribution is to the Poisson distribution. Small values for θ indicate aggregation. The parameter α is the intercept of the model, β is the unknown but estimable parameter of the number of small trees. $Dist_{in}$ is a matrix which contains the distances (in m) from the adult tree ($n=1, \dots, N$) to the i -th quadrat, whereas dbh_{jn} is the matrix of the *dbh* of the adult tree ($n=1, \dots, N$). When the distance of the n -th adult tree to the i -th quadrat was greater than 30 m, the *dbh* was set to 0. $\sum_{n=1}^N (f_1(Dist_{in}) \cdot dbh_{jn} / AreaIn30_i)$ is functional predictor where $f_1(Dist_{in})$ is the smooth coefficient of dbh_{jn} . The function $f_2(X_i, Y_i)$ is a spatial smooth term to account the spatial trend and spatial correlation of the number of saplings. Any spatial trend will caused by other unmeasured environmental variables and hence the spatial smooth term is a proxy for other unmeasured environmental effects. X_i and Y_i are the coordinates of the i -th quadrat and $Time_j$ is the temporal factor referred to the j -th inventory.

Model 3.1 above separates the effects of space and time, i.e. the two effects are additive. The model can be made more flexible by allowing the spatial smooth to change in time, i.e., this model contains a spatial smooth per j -th inventory:

$$\log(\mu_{ij}) = \alpha + \beta \cdot \frac{Nsmall_{ij}}{AreaIn10_i} + \sum_{n=1}^N \left(f_1(Dist_{in}) \cdot \frac{dbh_{jn}}{AreaIn30_i} \right) + f_2^j(X_i, Y_i) \quad (3.2)$$

We used Akaike's Information Criterion (AIC) to select the variables by using backward stepwise procedure and choosing the best spatio-temporal structure.

Functions f_1 and f_2 were represented using thin plate regression splines (Wood 2003). Thin plate regression splines keep the basis and the penalty of the full thin plate splines (Duchon 1977) but the basis is truncated to obtain low rank smoothers. This avoids the problems of the knot placement of the regression splines and reduces the computational requirements of the smoothing splines (Wood 2003). Penalized regression smoothers such as thin plate regression splines are computationally efficient because their basis have a relatively modest size, k . In practice, k determines the upper limit on the degrees of freedom associated with the smooth function, hence k must be chosen when fitting models. However, the actual effective degrees of freedom of the smooth function are controlled by the degree of penalization selected during fitting. The degree of penalization determines how smooth the function is. So, k should be chosen to be large enough to represent the underlying process reasonably well, but small enough to ensure reasonable computational efficiency. The exact choice of k is not critical (Wood 2006).

The spatial smooth $f_2(X_i, Y_i)$ is confounded with the functional predictor term, $\sum_{n=1}^N (f_1(Dist_{in}) \cdot dbh_{jn} / AreaIn30_i)$, since both terms describe, in some way, the spatial pattern in the response. To avoid further confounding, we decided to include the effect of small trees in a linear form rather than a functional predictor. We used $k=10$ for f_1 since it was enough to represent the variation of the coefficient of dbh as the actual effective degrees of freedom for f_1 was between 3 and 4 - well below 10. As we are ultimately interested in estimating the f_1 of the functional predictor and f_2 is entered to eliminate the spatial correlation, we selected the smallest basis dimension (k) in f_2 that eliminated the spatial correlation. For the different values of k in f_2 , we checked whether the spatial correlation had been eliminated in the model by plotting semivariograms of the model residuals per inventory with envelopes

from 99 permutations under the assumption of no spatial correlation (see Augustin et al. 2009 for a description).

Table 3.1 Summary of the mean forest features in each plot during the four inventories. Trees (dbh $\geq$ 10cm), adult trees (dbh $\geq$ 20 cm), small trees (10 $\leq$ dbh<20 cm), saplings (dbh<10cm and height $\geq$ 1.30m). Standard deviation is within brackets.

Feature	2001	2006	2010	2014
Intermediate stage of the regeneration period				
Number of saplings	1,861	1,625	1,498	1,347
Mean diameter of saplings (cm)	3.68 (2.31)	4.42 (2.29)	4.61 (2.38)	4.77 (2.36)
Mean height of saplings (m)	4.20 (1.78)	4.86 (2.03)	5.38 (2.21)	5.76 (2.36)
Number of adult trees	80	62	75	102
Number of small trees	152	250	351	399
Number of trees	232	312	426	501
Mean diameter of trees (cm)	23.07 (14.75)	17.89 (11.30)	16.68 (8.89)	16.96 (8.72)
Mean height of trees (m)	15.00 (6.90)	12.46 (5.32)	12.31 (4.23)	13.26 (4.16)
End of the regeneration period				
Number of saplings	558	364	208	117
Mean diameter of saplings (cm)	5.54 (2.66)	6.43 (2.32)	6.55 (2.24)	6.97 (2.19)
Mean height of saplings	7.03 (3.27)	7.82 (3.32)	8.61 (3.44)	8.70 (3.55)
Number of adult trees	174	233	283	317
Number of small trees	568	492	434	366
Number of trees	742	725	717	683
Mean diameter of trees (cm)	16.88 (6.04)	17.77 (5.99)	19.15 (6.45)	20.30 (6.78)
Mean height of trees (m)	14.72 (3.06)	16.21 (3.44)	17.16 (3.13)	18.85 (3.33)

The statistical analyses were carried out in R 3.3.3. (R Core Team 2017) using the “gam” function of the package “mgcv” (Wood 2011) for fitting the models where we used the restricted maximum likelihood option. This means that the smoothness parameters are estimated using restricted maximum likelihood estimation and a penalized iterative re-weighted least squares algorithm is used to find all other parameters, i.e. the coefficients of basis functions and coefficients of linear terms. See Wood (2011) for the theory and Augustin et al. (2015) for a functional predictor example. For model checking we used the functions “variog” and “variog.mc.env” of the package “geoR” (Ribeiro and Diggle 2016) for estimating the semivariograms and the envelopes.

3.3. Results

3.3.1. Intermediate stages of the regeneration period

The total number of saplings was inversely related to the time whereas the mean size (dbh and height) of the saplings increased with time (Table 3.1). Saplings were spread around the plot except in the center and the bottom left corner (Fig. 3.2). Unlike the saplings, we found that the number of trees, both small and adult trees, increased with time, the mean dbh and size of this stratum decreasing with time due to ingrowth of individuals from the previous class (Table 3.1). During the study period, we found a great increase in small trees, especially in the lower right part of the plot (Fig. 3.2).

Both model 3.1 and model 3.2 explained a similar amount of deviance, almost 41%. However, the AIC of model 3.1 was lower than that of model 3.2 (Table 3.2). Therefore, we selected model 1, the more parsimonious model, with additive effects of space and time. This entails that the spatial distribution of the saplings remained constant over the time. The spatial smooth function (f_2) and the temporal factor (*Time*) improved the model in terms of AIC (Table 3.3). Fig. 3.4 shows the estimated spatial smooth function f_2 on the scale of the linear predictor. The estimate of the aggregation parameter θ of the negative binomial distribution is 1.5 and 1.4 in model 3.1 and 3.2, respectively. Our results show that we have chosen k large enough for both functions f_1 and f_2 , as we see that the effective degrees of freedom given in Table 3.2 are below $k-1$; the same applies to results for the other plot. The coefficients of *dbh* were robust to changes in k . This also applies to results of the other plot. Fig. 3.5 shows that the spatial correlation was eliminated.

Removing the term relating to the density of small trees increased the AIC (Table 3.3). The β of the density of small trees was negative ($\beta = -0.0004$) pointing towards competition between small trees and saplings. Furthermore, Fig. 3.6 shows the smooth coefficient of dbh (f_I) of adult trees over $Dist$. More saplings are expected to be found when the product of the smooth coefficient and the dbh is large, that is, the model predicts the greatest number of saplings for the largest trees located at the distances to which f_I is highest. f_I varied smoothly across the distances with significantly negative values from 0 m up to 7 m. From 7 m, f_I is not statistically different from zero as the 95 % confidence intervals contained zero. This suggests competition between adult trees and saplings at shorter distances (<7 m) and no relationship at larger distances between these two cohorts. From 13 to 20 m, the mean value of f_I turned positive and significant reaching the largest values of the smooth function. Beyond 20 m, the smooth function f_I started decreasing and it was not statistically different from zero.

Figure 3.4 Estimated $f_2(X_i, Y_i)$ spatial smooth function (continuous black contour lines) and standard errors (dashed red and green contour lines) on the scale of the linear predictor at intermediate stages of the regeneration period. Large values of $f_2(X_i, Y_i)$ indicate large number of saplings.

Table 3.2 Percentage of deviance explained, AIC (Akaike's Information Criterion), θ parameter in the variance of the negative binomial distribution, basis dimension (k) and effective degrees of freedom (e.df) of the functional linear predictor and the spatial smooth according to model 3.1 and model 3.2 in both plots. Inventory 2001, Inventory 2006, Inventory 2010 and Inventory 2014 indicate the effective degrees of freedom of the spatial smooth during the four inventories in model 3.2.

Feature	Intermediate stage of the regeneration period		End of the regeneration period	
	Model 3.1	Model 3.2	Model 3.1	Model 3.2
Deviance explained (%)	40.7	41.0	34.8	41
AIC	1,3120.98	1,3432.74	5,083.48	5,184.80
θ of variance	1.53	1.42	0.83	0.76
k of f_1	10	10	10	10
e.df of f_1	3.47	3.599	4.33	4.40
k of f_2	100	100	30	30
e.df of f_2 in model 3.1	90.42	-	24.50	-
Inventory 2001	-	69.60	-	19.47
Inventory 2006	-	65.64	-	17.30
Inventory 2010	-	63.42	-	16.28
Inventory 2014	-	63.11	-	13.15

f_1 : linear predictor. f_2 : spatial smoother

3.3.2. End of the regeneration period

The dynamics of the saplings and the trees followed the same trends as at intermediate stages of the regeneration period: the number of saplings decreased and their mean size increased with time. The number of trees decreased but the mean dbh and height increased over the four inventories because of fellings. However, in this plot there were less saplings and their mean size was larger than in the youngest studied plot. Additionally, there were more trees overall at the end of the regeneration period than in the previous stages. Nevertheless, Table 3.1 shows that the number of small trees reduced with time whereas the number of adult trees increased.

Table 3.3 Summary of the backward stepwise variables selection process according to the Akaike's Information Criterion (AIC). In bold, the selected model.

Variables included in the alternative models during backward stepwise selection process		AIC
Intermediate stage of the regeneration period		
(1) $\alpha + \beta \cdot \frac{N_{small_{ij}}}{AreaIn10_i} + \sum_{n=1}^N \left(f_1(Dist_{in}) \cdot \frac{dbh_{jn}}{AreaIn30_i} \right) + f_2(X_i, Y_i) + Time_j$		1,3120.98
(2) $\alpha + \sum_{n=1}^N \left(f_1(Dist_{in}) \cdot \frac{dbh_{jn}}{AreaIn30_i} \right) + f_2(X_i, Y_i) + Time_j$		1,3126.06
(3) $\alpha + \beta \cdot \frac{N_{small_{ij}}}{AreaIn10_i} + f_2(X_i, Y_i) + Time_j$		1,3125.11
(4) $\alpha + \beta \cdot \frac{N_{small_{ij}}}{AreaIn10_i} + \sum_{n=1}^N \left(f_1(Dist_{in}) \cdot \frac{dbh_{jn}}{AreaIn30_i} \right)$		1,500.13
(5) $\alpha + \beta \cdot \frac{N_{small_{ij}}}{AreaIn10_i} + \sum_{n=1}^N \left(f_1(Dist_{in}) \cdot \frac{dbh_{jn}}{AreaIn30_i} \right) + f_2^j(X_i, Y_i)$		1,3432.74
End of the regeneration period		
(1) $\alpha + \beta \cdot \frac{N_{small_{ij}}}{AreaIn10_i} + \sum_{n=1}^N \left(f_1(Dist_{in}) \cdot \frac{dbh_{jn}}{AreaIn30_i} \right) + f_2(X_i, Y_i) + Time_j$		5,083.94
(2) $\alpha + \sum_{n=1}^N \left(f_1(Dist_{in}) \cdot \frac{dbh_{jn}}{AreaIn30_i} \right) + f_2(X_i, Y_i) + Time_j$		5,083.48
(3) $\alpha + f_2(X_i, Y_i) + Time_j$		5,120.71
(4) $\alpha + \sum_{n=1}^N \left(f_1(Dist_{in}) \cdot \frac{dbh_{jn}}{AreaIn30_i} \right)$		5,387.18
(5) $\alpha + \beta \cdot \frac{N_{small_{ij}}}{AreaIn10_i} + \sum_{n=1}^N \left(f_1(Dist_{in}) \cdot \frac{dbh_{jn}}{AreaIn30_i} \right) + f_2^j(X_i, Y_i)$		5,184.80

As in the youngest studied plot, the model with the additive spatio-temporal structure (model 3.1), which assumes a constant spatial distribution of the saplings over the studied period, showed a lower AIC than model 3.2 (Table 3.2). We also found a significant effect of the spatio-temporal terms (f_2 and $Time$) in terms of AIC (Table 3.3). The map of the contour lines (Fig. 3.7) represents well the spatial distribution of the saplings during the last stages of the regeneration period (Fig. 3.3). The semivariograms showed that the spatial

structure eliminated the spatial correlation (Fig. 3.8). The estimate of the aggregation parameter θ of the negative binomial distribution is smaller than in the other plot, it is around 0.8 (Table 3.2). This indicates that saplings were more aggregated at the end of the regeneration period than in the previous stage, which is also confirmed by the visual inspection of the spatial distribution of saplings (Figs. 3.2 and 3.3) showing a more homogenous spread of saplings in earlier stages of the regeneration process.

Figure 3.5 Semivariograms (circles) and envelopes (dashed lines) of the Pearson residuals from the sapling distribution model at intermediate stages of the regeneration in 2001 (upper left), 2006 (upper right), 2010 (lower left) and 2014 (lower right).

In this plot, the β of density of small trees did not reduce the AIC whereas the rest of the terms reduced the AIC significantly (Table 3.3). Table 3.2 shows the effective degrees of freedom of the basis functions. The coefficient of the *dbh* of adult trees (f_i) took significant negative values from 0 to 8 m (Fig. 3.6). From 8 m, the 95 % confidence intervals contained the zero, and therefore we can state that the coefficient is not statistically different from 0.

This suggests competition between saplings and adult trees at very small distances and no effect beyond 8 m.

Figure 3.6 Estimated $f_I(Dist_{in})$ smooth coefficient function of the diameter at breast height of adult trees over the distance between adult trees and saplings (continuous lines) and 95% confidence intervals (dashed lines) at intermediate stages (upper) and the end (lower) of the regeneration period. Positive values of $f_I(Dist_{in})$ indicate positive effects of the diameter at breast height of adult trees on the number of saplings.

Figure 3.7 Estimated $f_2(X_i, Y_i)$ spatial smooth function (continuous black contour lines) and standard errors (dashed red and green contour lines) on the scale of the linear predictor at the end of the regeneration period. Large values of $f_2(X_i, Y_i)$ indicate large number of saplings.

Figure 3.8 Semivariograms (circles) and envelopes (dashed lines) of the Pearson residuals from the sapling distribution model at the end of the regeneration period in 2001 (upper left), 2006 (upper right), 2010 (lower left) and 2014 (lower right).

3.4. Discussion

We fitted a GAM with a functional predictor in the model to describe the influence of size of trees on the number of saplings by distance in two stages of the regeneration period. We have confirmed that the functional predictor is useful to achieve this aim. In GAMs explanatory variables may enter the model in many different forms: as variables with linear effects, smooth terms, tensor products of several variables, with varying coefficients or as functional predictors. Additionally, alternative response distribution families and link functions can be selected (see for example Wood 2006). Therefore, all this makes the approach employed suitable to be used in other fields of forestry or ecology in which the response variable depends on the size and distance of the neighbors. For instance, this approach could be useful to fit growth or mortality models instead of using competition indices in parametric models (Contreras et al. 2011).

In this work, we have studied the last stages of the renewal of a forest after regeneration fellings. Other authors have modeled the whole renewal of the forest using multistage models. For instance, Manso et al. (2014) proposed a multistage model based on partial studies or submodels in order to predict the regeneration occurrence of *Pinus pinea* L. in space and time. They considered different stages such as seed dispersal, seed germination, post-dispersal predation and seedling survival. Multistage models provide deeper ecological understanding than ours but the implementation is harder and requires stronger ecological hypotheses. However, our approach shows great flexibility and might be used to determine the effects of a limited number of factors on sapling distribution without making any assumptions about other factors involved on dispersion and survival processes.

As mentioned above, this methodology allows different types of variables to be included in the model. In this work, we included the density of small trees as a linear term and the spatio-temporal structure. It might be useful to use variables driving the regeneration as predictors in the model, like shrub cover, soil characteristics, cover and depth of litter or grass in each quadrat. However, gathering this data on large plots requires a great effort and the influence of these variables on the seedlings of *P. sylvestris* has already been studied at smaller scales (González-Martínez and Bravo 2001; Pardos et al. 2007; Barbeito et al. 2011; Moreno-Fernández et al. 2015a). On the other hand, new individuals of *P. sylvestris* are expected to be more affected by soil moisture than by other microsite characteristics (Barbeito et al. 2009; Moreno-Fernández et al. 2015a). However, because youngest

individuals – seedlings – are less resistant to drought than older – saplings (Maseda and Fernández 2006; Rodríguez-García et al. 2011; Manso et al. 2014), it seems it is more necessary to include environmental variables in models dealing with seedlings rather than in those dealing with older individuals – saplings. Moreover, it is likely the distance to adult trees is confounded with other local factors. Any residual spatial trend in a model without a spatial smooth term is caused by missing (unmeasured) environmental variables. Furthermore, the residual spatial trend could be due to the seedling spatial structure that would result from past dispersal events from adjacent mother trees. We have included the spatial smooth term as a proxy for effects of unmeasured environmental variables and for the spatial pattern of the new individuals during previous stages of the forest renewal. We have investigated goodness-of-fit thoroughly, and found that we did not have any spatial trend in residuals or residual spatial correlation. This means that the models fit well and there was no model mis-specification. Although we have only results from two plots, it is striking that the estimated functions f_l (of the effect of dbh) shown in Fig. 3.6 are very similar.

Our approach allows to test whether the spatial pattern remained constant over time by comparing model 3.1 which assumes a constant spatial pattern with model 3.2 which allows for a spatial pattern changing in time in the model selection. In our case, model 3.1 was selected suggesting that the spatial pattern of the saplings remained constant over time. If model 3.2 had been selected, the spatial pattern of saplings would have changed over the time. Due to the gradual low intensity fellings regime, which avoids damaging the established saplings clumps, these clumps persist and the spatial structure of the saplings remains fairly constant in each plot during the 15-year measurement period. On the other hand, if we were dealing with faster-growth species the saplings could move to the next cohort faster and then change the spatial pattern. Our results are consistent with LeMay et al. (2009) who reported that the spatial pattern of the new individuals of *P. menziesii* did not change very much over time.

Although we only analyzed data from two large plots (0.5 ha) we re-measured the plots four times, leading to four observations per plot. Large-sized plots with few sampling over time are common in regeneration studies describing spatial processes. These kind of plots have been used in tropical (Ledo et al. 2015), temperate (McDonald et al. 2003) and Mediterranean forests (Montes and Cañellas 2007; Ledo et al. 2014). Additionally, we modeled the number of saplings per 4 m² quadrat, i.e., we used 5 000 quadrats covering different competition conditions to fit every model. Moreover, the models presented in this

work were fitted for explanatory purposes rather than predictive purposes. If we had aimed to fit a predictive model, we would have needed more temporal measurements to cover all the regeneration period.

The underlying process studied here is the competition between trees and saplings. Our findings are in concordance with other studies: the saplings of *P. sylvestris* require high light conditions for successful development (Montes and Cañellas 2007). In Mediterranean areas, *P. sylvestris* seedlings require microsites with moderate light conditions (Pardos et al. 2007). These microsites ensure higher soil moisture than in open canopies but conserve enough level of sun radiation. In this regard, Castro et al. (2005) analyzed the growth of *P. sylvestris* seedlings in southern Spain under different light and water conditions concluding that the effects of water addition on seedlings growth are more evident in lightly microsites. Moreover, once the seedlings have stepped into saplings, the maintenance costs increase with size (Falster and Westoby 2003) and higher minimum light levels are required for survival (Williams et al. 1999). Additionally, their roots can reach deeper soil layers with more water availability (Ritchie 1981). Considering this, it seems it is necessary to reduce the canopy to favor the development of the saplings after seedling establishment under moderate light conditions in Mediterranean areas. However, the shade tolerance of *P. sylvestris* differ among regions. In northern locations where the summer drought is not a limiting factor for seedling development, natural regeneration takes place in open canopies by using the seed tree method (Hyppönen et al. 2013). In these latitudes, the negative spatial association between *P. sylvestris* adult trees and saplings may be even more pronounced than in our study.

The establishment of the new stand has been achieved successfully at the end of the regeneration period, the number of saplings decreased and the arrival of new individuals is no longer expected. Hence, the mean dbh of the saplings is getting close to 10 cm, the lower limit for small trees. In this plot, the number of small trees decreased over time due to the mortality as well as the growth and consequent reclassification of trees as adult trees. Most of the trees in this plot were not mother trees of the saplings but rather new cohorts of trees established at the first and intermediate stages of the regeneration period, such as those in our youngest studied plot. Therefore, the spacing between saplings and adult trees is a consequence of the competition between trees of different sizes.

3.5. Conclusions

We show that functional predictor in GAMs is a useful tool for modeling these kind of data as they allow to model nonlinear and linear relationships. In addition they allow to take account of the spatio-temporal structure of the data by inclusion of spatial and spatio-temporal smooth predictors. The methodology proposed has not been employed in forestry or ecology and can be broadly used in regeneration studies or in other fields of forestry or ecology dealing with spatio-temporal data. Therefore this methodology is potentially applicable in future ecological studies because of its flexibility. Additionally, this model can be used as a first step for a predictive model when more temporal data is available. We found that once the seedlings have become established, the density of the adult trees must be reduced heavily to allow the saplings to grow under high light conditions. In Mediterranean stands of *P. sylvestris*, the radius of the gaps created during the regeneration fellings under the group shelterwood should be always larger than 7-8 m in order to minimize the competition between adult trees and saplings; whereas if the radius is between 13 – 20 m the number of saplings will be maximized.

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CHAPTER 4

Temporal carbon dynamics over the rotation period of two alternative management systems in Mediterranean mountain Scots pine forests

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Abstract

Forests play an important role in the mitigation of global warming, acting as carbon sinks. However, the effects of forest management on the carbon pools over the rotation period in Mediterranean areas are scarcely understood. The objective of this chapter is to assess the way in which two alternative management systems; one more intensive and the other more moderate (with less severe harvesting and more spread over time) affect the carbon stocks in the living tree biomass, coarse woody debris, forest floor and mineral soil in Mediterranean forests. For this purpose, two chronosequences were established covering the whole rotation period in two *Pinus sylvestris* L. forests. We conducted four forest inventories over a period of 15 years, measuring the diameter and the height of all the trees higher than 1.3 m in order to calculate the carbon stored in the living parts of the tree. Soil pits were excavated and we collected soil samples to estimate the soil organic carbon. We found that the temporal trends for living tree biomass were similar in both forests. However, the total living tree carbon stored at the end of the rotation period was greater in the forest with the longer rotation period and lighter thinning regime (345.5 Mg ha⁻¹ of carbon) than in the intensively-managed forest (223.8 Mg ha⁻¹ of carbon). On average, more carbon was found to be stored in the forest floor under the more intensive management system, whereas more carbon was present in the first 20 cm of mineral soil under the moderate management system. Moreover, in each forest, the carbon stocks of the forest floor and in the uppermost cm of the soil remained constant over the rotation period. Therefore, management systems with longer rotation periods and moderate harvesting intensities are recommended to increase carbon fixation in Mediterranean forests.

Keywords: carbon stocks, climate change, adaptive forest management, silviculture

Abbreviations: AIC, Akaike's Information Criteria; C, Carbon; CWD, Coarse Woody Debris; SOC, Soil Organic Carbon; LTC: Living Tree Carbon

4.1. Introduction

Rising atmospheric concentrations of carbon dioxide contribute to global warming (IPCC 2013). Forests are considered to play an important role in mitigating this global warming through carbon (C) sequestration (Dixon et al. 1994; Lal 2004; Bravo et al. 2008b). Forests store between 40 % - 60 % of all terrestrial C (Bonan 2008; Pan et al. 2011) and sequester 33% of C emission from fossil fuels every year (Denman and Brasseur 2007). However, forests can become a net source of carbon dioxide, depending on the climatic conditions and the forest management employed, since both affect C gains and losses within the forest system (Kim Phat et al. 2004; Vayreda et al. 2012).

The quantification of forest C and the influence of management on C sequestration have become a focus of interest for both researchers and forest managers (Smith and Heath 2001; Jandl et al. 2007; Alvarez et al. 2014). In recent years, many studies have assessed the way in which C stocks are affected by various aspects of management such as thinning (Finkral and Evans 2008; Boerner et al. 2008; Ruiz-Peinado et al. 2013), length of the rotation period (Liski et al. 2001; Pohjola and Valsta 2007), different management systems (Balboa-Murias et al. 2006; Seidl et al. 2007), stand tree species composition (Kirby and Potvin 2007; Díaz-Pinés et al. 2011; Alvarez et al. 2014), harvesting technique (Johnson and Curtis 2001), the reproductive origin of the tree (Bruckman et al. 2011) and site preparation (Yildiz et al. 2010; Fonseca et al. 2014) among others.

Penman et al. (2003) defined five pools of C within forest ecosystems: living tree biomass –aboveground and belowground (roots), deadwood, forest floor and soil organic carbon (SOC). The living tree biomass and the SOC are the pools which store the most C in forest ecosystems (Peichl and Arain 2006; Nunes et al. 2010; Ruiz-Peinado et al. 2013). The C stored in the living parts of the trees, i.e. living tree carbon (LTC), is highly conditioned by the age of the stand, site index and management (De Simon et al. 2012; Ruiz-Peinado et al. 2013). However, SOC is more resistant to changes in forest management and disturbances than the LTC (Vesterdal et al. 2002; Peichl and Arain 2006; Bradford et al. 2008). Indeed, most studies have reported that management has no significant effect on SOC (Johnson and Curtis 2001; Ruiz-Peinado et al. 2014) or that harvesting only causes a small, temporal reduction in SOC after harvesting (Yanai et al. 2000; Peltoniemi et al. 2004; Nave et al. 2010). The effect of forest management on the forest floor is still somewhat debated. Nave et al. (2010) reported losses in forest floor C storage after harvesting operations whereas in

Mediterranean areas, Ruiz-Peinado et al. (2014, 2013) found that thinning had no significant impact on forest floor C stocks.

A better understanding of the dynamics of the different C pools throughout stand development is required in order to make a reliable assessment of the long-term effects of forest management on C (Kolari et al. 2004; Peltoniemi et al. 2004). Only a small number of studies have adopted a comprehensive approach embracing tree and SOC pools in the evaluation of C dynamics (Peichl and Arain 2006). Furthermore, most of the studies have been conducted in boreal and temperate forests, while information with regard to C dynamics in Mediterranean areas is scarce (Montes and Cañellas 2006; De Simon et al. 2012). In addition to determining how C stocks are distributed among the different pools and the way in which forest management affects these stocks, the mechanisms underlying C transfer among pools (Fig. 4.1) must also be identified in order to elucidate the impact of forest management on the C transference processes (e.g. Bradford et al. 2008).

Figure 4.1 C transfer links among forest pools.

Scots pine is the most widely distributed pine species in the world, ranging from the Iberian Peninsula to Siberia (Mason and Alía 2000). The importance of this species in Spain is due not only to its extensive distribution area and high quality wood, but also to its ecological value and protective function against soil erosion (Montero et al. 2001). The rotation period in Mediterranean pine forests is around 100-140 years, depending on the

intensity of the silvicultural operations. The establishment of new seedlings is often achieved under the shelterwood system and is sometimes aided by soil preparation (Cañellas et al. 2000; Barbeito et al. 2011). It is assumed that the group shelterwood system leads to an increase in structural biodiversity (Barbeito et al. 2009) and that it encourages more continuous establishment of regeneration to remain more constant over time. Under the shelterwood system the seedlings are also less affected by summer drought (Barbeito et al. 2011). However, the way in which the management alternative affects C sequestration in Mediterranean pine forests is still scarcely understood.

In this study, we used a chronosequence approach to quantify the LTC and soil carbon pool (SOC and forest floor C storage) over the rotation period in Scots pine Mediterranean forests under two management alternatives. The objective of this study is to assess the influence of the management regime on forest C dynamics over the rotation period. Three hypotheses were evaluated: i) long rotation length and a moderate thinning regime increase the LTC sequestration rate, ii) the SOC and the forest floor C pool are affected by the forest management regime and iii) SOC remains constant throughout the rotation period whereas forest floor C is affected by the silvicultural operations.

4.2. Materials and methods

4.2.1. Study areas

The study was conducted in two managed Scots pine forests, Navafría (41° 0'N, 3° 48'W) and Valsaín (40° 49'N, 4° 01'W), located in the Central Range of Spain. Both forests are located on north-facing slopes of the mountain range and they share similar ecological characteristics, with elevations ranging from 1,200 to 2,200 m above sea level, annual rainfall of about 730 mm, and mean annual temperature of around 9.8 °C. Despite these similarities, the average site quality is slightly higher in Valsaín than in Navafría (Rojo and Montero 1996). The management plans and harvest history of both forests date back 100 years and reveal several differences between the forests (Table 4.1). At Navafría, the thinning regime is more intense and begins at an earlier age. The uniform shelterwood system is used in this forest, consisting of two or three regeneration fellings over a 20 year regeneration period. In addition, in order to facilitate the establishment of the seedlings, mechanical soil tilling is carried out. At Valsaín, regeneration is achieved using the group shelterwood system, opening small gaps (0.1-0.2 ha) in the regeneration area over a 40 year

regeneration period. Thus, natural regeneration becomes established progressively under the protection of the remaining trees (Barbeito et al. 2009).

Table 4.1 Management characteristic in Navafría and Valsaín forests.

Management characteristic	Navafría forest	Valsaín forest
Management system	Permanent blocks	Floating periodic blocks
Rotation period	100 years	120 years
Thinning intensity	>30% G removed	20-30% G removed
Regeneration method	Uniform shelterwood	Group shelterwood
Regeneration period	20 years	40 years
Area of regeneration cuttings	20 ha	2-3 ha
Soil preparation	Ripper and blade scarification	No

G: basal area.

4.2.2. Sampling design and estimation of C fractions

4.2.2.1. Plot description and estimation of LTC and dead wood carbon

Two chronosequences spanning the whole rotation period in the two Scots pine forests were established in 2001: six 0.5 ha plots were set up in Valsaín and five in Navafría (Table 4.2). The plots were as homogeneous as possible in terms of altitude, exposure and site quality, the aim being to consider confounding factors other than stand age (Foster and Tilman 2000).

At the time of establishment (2001), all the trees higher than 1.30 m were labeled individually and their diameters at breast height (dbh) and heights were measured. The measurements were carried out again in 2006, 2011 and 2014. The main characteristics of the plots at the time of establishment are shown in Table 4.2. We applied the additive biomass models for Scots pine developed by Ruiz-Peinado et al. (2011) using data from our study area to estimate the biomass of stem, thick branches, medium branches, thin branches plus needles and roots of living Scots pine trees (Table 4.3). We then added up all the various components to obtain the living tree biomass. The LTC stock was calculated using a C weight / biomass weight ratio of 0.509 (Ibañez et al. 2002).

Table 4.2 Mean characteristics of the plots at the time of establishment (2001).

Plot	Age	N _{≥10cm}	N _{<10cm}	Dm _{≥10cm}	Dm _{<10cm}	G	Hm _{≥10cm}	Hm _{<10cm}
Navafria								
N1	10	810	4906	11.9	6.6	27.0	7.6	6.0
N2	28	2184	298	14.8	9.2	41.9	12.1	11.2
N3	65	680	-	32.9	-	60.6	22.0	-
N4	94	364	-	40.6	-	48.2	20.4	-
N5	110	304	-	42.5	-	44.2	22.1	-
Valsain								
V1	19	458	8876	23.2	5.5	37.0	15.1	3.2
V2	32	1484	1118	16.9	9.2	40.8	14.7	7.0
V3	49	1296	26	20.8	9.2	48.3	16.4	11.9
V4	75	686	-	30.5	-	53.3	23.5	-
V5	96	552	-	34.7	-	54.2	22.1	-
V6	115	332	516	38.9	1.5	54.2	24.0	2.0

Age in years; G= basal area (m² ha⁻¹); N= number of trees per hectare; Dm= mean diameter (cm); Hm= mean height (m); _{≥10cm} and _{<10cm} indicate attributes for trees with dbh equal or larger than 10 cm and trees with dbh of less than 10 cm.

Table 4.3 Biomass models and fitting statistics for Scots pine (Ruiz-Peinado et al. 2011) used in our study.

Component	Model	RMSE	ME
Stem	$W_s = 0.0154 d^2 h$	34.01	0.99
Thick branches	If $d \leq 37.5$ cm then $Z = 0$; If $d > 37.5$ cm then $Z = 1$; $W_{b7} = [0.540 (d-37.5)^2 - 0.0119 (d-37.5)^2 h] Z$	12.63	0.86
Medium branches	$W_{b2-7} = 0.0295 d^{2.742} h^{-0.899}$	10.83	0.87
Thin branches + needles	$W_{b2+n} = 0.530 d^{2.199} h^{-1.153}$	11.41	0.87
Roots	$W_r = 0.130 d^2$	110.17	0.98

W_s : Biomass of the stem fraction (kg). W_{b7} : Biomass of thick branch fraction (diameter larger than 7 cm) (kg). W_{b2-7} : Biomass of medium branch fraction (diameter between 2 and 7 cm) (kg). W_{b2+n} Biomass of thin branch fraction (diameter smaller than 2 cm) with needles (kg). W_r : Biomass of the roots (kg); d: dbh (cm). h: tree height (m). RMSE: Root Mean Square Error. ME: Model Efficiency.

Since each individual tree was numbered it was possible to monitor which trees had died or were harvested. Mortality rates were quite low, affecting mainly saplings. The sum of harvested and dead trees was referred to as “extracted trees” and was estimated in each plot between consecutive inventories. We calculated the total tree C at the end of the rotation period by summing the LTC in the oldest plot in each forest in 2014 plus the cumulative extracted C in each forest (sum of the C removed from the forest during the rotation period). In addition, we estimated the LTC growth rates ($\text{Mg ha}^{-1} \text{ year}^{-1}$ of C) for each plot and period between inventories.

Dead wood C was assessed using the coarse woody debris (CWD) data from a study by Montes and Cañellas (2006), recorded in our study plots in 2002. They classified the CWD into five decay classes and four elements: logs and branches (diameter at midpoint larger than 10 cm or between 5 and 10 cm) and stumps (cut surface diameter greater than 30 cm or between 5 and 30 cm). Detailed information on the sampling design is given in Montes and Cañellas (2006). The weight of the stumps was estimated using the biomass model for roots proposed by Ruiz-Peinado et al. (2011) (Table 4.3), assuming that the shape of the stem between dbh and the soil surface is cylindrical (i.e. dbh equals the stump diameter). We calculated the volume of logs and branches from their length and diameter, and then we converted the volume into biomass weight using empirical density data (unpublished data) according to decay class. Finally, the biomass of the stumps, branches and logs was transformed into C using a C weight / biomass weight ratio of 0.509 (Ibañez et al. 2002).

4.2.2.2. Sampling of soil pool C stock (Carbon stock in O-horizon and mineral soil)

Estimation of the forest floor C pool was performed in April 2009, using 4 replicates per plot. In each replicate, the whole forest floor down to the mineral soil was collected in a 1 x 1 m square. No differentiation was made between organic layers (O_l , O_h , O_f) when collecting the samples. The depth of the forest floor layer was measured on each side of the square and then averaged. The exact location of the square was marked appropriately by inserting wooden sticks into the soil.

Freshly incorporated material to the forest floor layer was collected between April 2009 and April 2010, following the same procedure in the same squares. It was decided to start and end the measurements in April since the late winter and spring periods present the lowest seasonal litterfall C rates in this area (Díaz-Pinés et al 2011b), hence potential bias

caused by seasonal variability was minimized. We took three measurements: in August and November 2009 and in April 2010. This allowed the annual aboveground litterfall C rates to be calculated.

To estimate SOC pools, five soil pits (70 cm x 70 cm x 50 cm, treated as replicates) were excavated at each of the plots. In each of the pits, genetic horizons were identified down to 50 cm. Soil samples were collected separately for each genetic horizon, beginning with the deepest one to avoid up-down soil contamination. In addition, intact soil cores (5 cm height, 5 cm diameter) were taken by triplicate at each of the soil horizons for soil bulk density determination. Stone content was estimated in the field for each horizon. A sampling approach based on genetic horizons was chosen to avoid potential bias associated with fixed depth approaches when the horizon development is markedly different among sites (Davidson and Ackerman 1993).

4.2.2.3. Laboratory analyses

The forest floor material was dried at 65 °C to constant weight and sieved (2 mm-mesh). Both fine and coarse fractions were weighed separately. Particles that passed through the sieve were milled and the total organic C in this fraction was determined using a Total Organic Carbon Analyzer (TOC 5000A, Shimadzu Corporation, Kyoto, Japan) equipped with a soil sample module (SSM-500, Shimadzu Corporation). Particles larger than 2 mm were assumed to have a content of 50.9 % organic C (Ibañez et al. 2002). The TOC 5000-A equipped with the SSM-500 was also used to determine the SOC content of the ground mineral soil samples.

Organic C stocks of the forest floor were calculated based on the weight of the layer per unit of area and the organic C content. Aboveground litterfall C rates were calculated by summing the amounts of litterfall collected during a time span of 12 months and expressed in $\text{Mg ha}^{-1} \text{ year}^{-1}$ of C. In the case of the mineral soil, organic C stocks were calculated according to the recommendations of the IPCC (Aalde et al. 2006), taking into account organic C content, soil bulk density, fine earth content and depth of each layer (Table 4.4). Since the mineral soils were collected according to genetic horizons, the depths were not consistent among different plots and replicates. Therefore, we calculated the SOC stocks per cm depth within the soil profile; for comparison purposes among plots, we virtually divided the soil profile into 10 cm deep layers.

Table 4.4 SOC concentration, bulk density and stone content in each plot.

SOC concentration (g kg ⁻¹ fine soil)					
Plot	0-10	10-20	20-30	30-40	40-50
10N	72.9 ± 6.3	72.9 ± 6.3	66.0 ± 2.7	57.6 ± 5.5	50.7 ± 10.6
30N	46.1 ± 4.5	39.9 ± 3.7	27.4 ± 4.1	17.8 ± 5.2	7.8 ± 1.9
50N	49.3 ± 4.0	40.2 ± 5.8	24.6 ± 7.2	20.6 ± 8.8	16.7 ± 9.7
70N	59.1 ± 5.1	59.1 ± 5.1	47.3 ± 5.7	41.7 ± 4.0	33.6 ± 2.0
90N	67.9 ± 4.7	62.8 ± 5.3	52.6 ± 4.8	48.8 ± 5.7	39.3 ± 7.0
10V	76.5 ± 7.2	65.5 ± 4.9	34.4 ± 11.3	12.6 ± 4.0	8.8 ± 0.5
30V	89.6 ± 11.7	68.2 ± 6.2	51.1 ± 4.3	35.7 ± 5.4	12.9 ± 3.1
50V	58.8 ± 7.8	59.1 ± 7.5	33.4 ± 2.7	30.0 ± 2.5	8.7 ± 1.8
70V	77.1 ± 4.8	60.5 ± 6.2	37.8 ± 3.7	15.2 ± 5.0	9.1 ± 2.7
90V	77.4 ± 10.4	61.5 ± 9.6	34.4 ± 6.3	18.2 ± 3.2	10.0 ± 2.0
110V	97.5 ± 12.0	81.5 ± 9.6	62.5 ± 11.7	27.0 ± 9.1	11.1 ± 1.8
Bulk density (g cm ⁻³)					
Plot	0-10	10-20	20-30	30-40	40-50
10N	0.80 ± 0.03	0.80 ± 0.03	0.92 ± 0.07	0.98 ± 0.08	1.03 ± 0.12
30N	0.88 ± 0.03	0.87 ± 0.02	0.96 ± 0.03	1.04 ± 0.07	1.19 ± 0.09
50N	0.89 ± 0.03	0.92 ± 0.03	0.96 ± 0.06	1.02 ± 0.06	1.08 ± 0.07
70N	0.83 ± 0.04	0.83 ± 0.04	0.90 ± 0.04	0.95 ± 0.04	1.00 ± 0.01
90N	0.74 ± 0.08	0.87 ± 0.06	0.89 ± 0.05	0.89 ± 0.05	0.92 ± 0.06
10V	0.83 ± 0.03	0.85 ± 0.03	0.89 ± 0.03	0.93 ± 0.02	0.95 ± 0.02
30V	0.72 ± 0.03	0.82 ± 0.06	0.88 ± 0.07	0.97 ± 0.04	1.07 ± 0.05
50V	0.82 ± 0.04	0.81 ± 0.04	0.84 ± 0.02	0.87 ± 0.03	1.08 ± 0.02
70V	0.80 ± 0.04	0.92 ± 0.08	0.97 ± 0.06	1.13 ± 0.04	1.18 ± 0.03
90V	0.88 ± 0.01	0.92 ± 0.03	0.96 ± 0.04	1.01 ± 0.01	1.02 ± 0.01
110V	0.86 ± 0.04	0.91 ± 0.03	0.94 ± 0.03	0.99 ± 0.01	1.03 ± 0.03
Stone content (%)					
Plot	0-10	10-20	20-30	30-40	40-50
10N	58 ± 5	58 ± 5	54 ± 4	52 ± 6	53 ± 6
30N	38 ± 4	40 ± 3	38 ± 3	40 ± 6	41 ± 6
50N	37 ± 2	41 ± 2	49 ± 4	53 ± 3	55 ± 3
70N	40 ± 3	40 ± 3	41 ± 4	42 ± 3	44 ± 4
90N	49 ± 3	48 ± 3	45 ± 4	43 ± 3	46 ± 3
10V	31 ± 2	33 ± 3	39 ± 5	48 ± 6	49 ± 5
30V	32 ± 2	37 ± 4	42 ± 6	48 ± 7	59 ± 8
50V	39 ± 4	42 ± 3	46 ± 3	46 ± 3	46 ± 15
70V	37 ± 4	35 ± 3	36 ± 4	37 ± 4	36 ± 4
90V	38 ± 5	40 ± 5	48 ± 11	56 ± 9	54 ± 10
110V	45 ± 6	54 ± 2	59 ± 2	72 ± 2	78 ± 1

4.2.3. Statistical analyses

4.2.3.1. *Living Tree Carbon*

In order to describe the LTC trends over the rotation period we fitted the data using an approach that ensured sufficient flexibility of the LTC trends. In this study we attempted to model the LTC trends over time using penalized smoothing splines or P-splines (Eilers and Marx 1996) in a mixed model-effects framework (Durbán et al. 2005). The P-splines are curves formed by joining together several low-order polynomials at specified locations known as knots (Eilers and Marx 1996; Durbán et al. 2005; Jordan et al. 2008). The penalty approach relaxes the importance of the number and location of the knots (Eilers and Marx 1996; Currie et al. 2004). We fitted a separate mean curve for each forest using a factor-by-curve interaction to assess the differences in the LTC trends between forests (Currie et al. 2004; Durbán et al. 2005; Jordan et al. 2008). The penalized spline formulation of the model is written as:

$$y_{ilj} = \alpha \cdot A_i + f_i(B_{lj}) + Z \cdot u + \varepsilon_{ilj} \quad (4.1)$$

where y_{ilj} is the LTC (in Mg ha⁻¹ of C), i is the forest stand number, l is the plot number and j is the age (years), A_i is a dummy variable for the forest, α is the forest fixed-effects parameter vector, and $f_i(\cdot)$ is a smooth function which reflects the trend of the LTC over each year B_{lj} . Detailed explanation of the smooth function $f(\cdot)$ is given further. Z is the random-effects matrix and u is the vector of random effects with mean zero and variance to be estimated. Given that the data available consisted of repeated measurements taken in the same plot and that such measurements are likely to be more correlated than measurements taken in different plots (Littell et al. 2000) we entered plot random intercept and slope effects. Due to the differences in the site quality of the plots according to the Rojo and Montero (1996) site index models, we included site quality random intercept and slope effects. ε_{ilj} is a random error term defining the within-subject pattern of variability. In the first instance we fitted the model without including random effects and compared it to models with more complicated random effects structures. The comparisons were performed according to Akaike's Information Criteria (AIC).

The smooth functions $f(\cdot)$ were represented by cubic B-splines and second order difference penalties (Eilers and Marx 1996; Currie et al. 2004). Eilers and Marx (1996) proposed a simple idea based on two main aspects: a regression basis and modifying the

likelihood function by adding a penalty term over adjacent regression coefficient to control the smoothness of the fit. There are several alternatives for choice of the regression basis, we used the B-spline basis due to their flexibility and ease of computation. The mixed model representation of the smooth function $f(\cdot)$ is Currie et al. (2004):

$$f_i(B_{lj}) = \beta \cdot x_{lj} + w_{lj} + z_i \cdot (\gamma \cdot x_{lj} + h_{lj}) \quad (4.2)$$

where $z_i = 1$ for Valsaín and $z_i = 0$ for Navafría, and w_{lj} and h_{lj} are the random effects of the nonlinear functions. The first two terms in Eq. (4.2) specify the fitted curve for the Navafría forest and the last term represents the deviation of the fitted curve for Valsaín as compared with Navafría. Both w_{lj} and h_{lj} are assumed to follow a normal distribution with mean zero and variances σ_w^2 and σ_h^2 . The smoothing parameter is given by the ratio of the variance components. We have assumed a common variance parameter for both curves but the random effects are independent from function to function, i.e., the curves are different but have the same amount of smoothing (Durbán et al. 2005).

Finally, we plotted the estimated smooth predictor trend with 95 % variability bands (Greven et al. 2006). All statistical analyses were conducted using SAS 9.2 (SAS Institute Inc 2009). Once the smooth trends were fitted we calculated the average C in each forest as the ratio of the areas under the curves and the rotation age.

4.2.3.2. Soil organic carbon pool

Soil organic C stocks at different depths were compared between the two forests under investigation as well as among different forest ages. Since the number of plots (6 plots for Valsaín, 5 for Navafría) and the ages of the plots differ between forests, we performed a nested analysis of variance, with the factor “plot age” nested in the factor “forests”. The following model was proposed:

$$s_{ijk} = \mu + F_i + C_{j(i)} + \varepsilon_{ijk} \quad (4.3)$$

where s_{ijk} is the soil C stock in the different soil layers (forest floor, 0-10 cm, 10-20 cm, 20-30 cm, 30-40 cm, 40-50 cm, 0-50 cm and 0-50 cm plus forest floor) of the k -th observation in the forest i -th in the plot age j -th, μ is the intercept of the model or overall mean; F_i is the effect of the i -th forest and $C_{j(i)}$ is the plot age effect of the j -th plot age nested in the i -th

forest; ε_{ijk} is the experimental error term of the k -th observation from the j -th plot age within the i -th forest. We assumed that $\varepsilon_{ijk} \sim N(0, \sigma^2)$. All analyses were carried out using the GLM procedure in SAS 9.2 (SAS Institute Inc 2009).

We applied linear regressions to look for relationships between different C pools, and used the coefficient of determination (R^2) as a metric for the goodness-of-fit. In order to compare the time evolution of different SOC stocks in different soil layers, we used standardized scores. Thus, for a specific soil layer, we standardized the SOC stocks with the mean SOC stocks over the whole rotation period

4.3. Results

4.3.1. LTC, extracted C and dead wood C

We fitted the LTC trends using B-splines of degree 3. We selected 6 knots in each smooth trend to ensure the flexibility of the curve. We found a significant effect of the forest on the LTC (p-value<0.0001). The Valsaín forest had a higher estimation coefficient than Navafría (Table 4.5) indicating that, on average, Valsaín stored more LTC than Navafría. In addition, the differences between the forests were statistically constant over the rotation period since the interaction forest x age emerged as non-significant (p-value=0.8997). The autocorrelation among the plots was accounted for by entering the random plot slope as a significant effect in terms of AIC. Both forests followed similar LTC smooth trends over time (Fig. 4.2) from the beginning of the rotation period (76.2 Mg ha⁻¹ of C in Navafría at an age of 10 years and 112.1 Mg ha⁻¹ of C in Valsaín at 19 years). The LTC trends increased up to an age of 80 years in Navafría (191.5 Mg ha⁻¹ of C) and up to 106 years in Valsaín (189.5 Mg ha⁻¹ of C). The LTC then fell after the last thinning and regeneration fellings. Prior to the regeneration fellings, the LTC in Navafría was 156.0 Mg ha⁻¹ of C (stand age=110 years) and in Valsaín 210.89 Mg ha⁻¹ of C (stand age=100 years). At the end of the rotation period, the estimated LTC was 99.3 and 160.0 Mg ha⁻¹ of C in Navafría and Valsaín, respectively. The ratio of the area under the curve and the rotation age was also smaller in Navafría than in Valsaín (148.9 and 162.9 Mg ha⁻¹ of C, respectively), indicating larger average LTC stocks in Valsaín than in Navafría over the rotation period.

Figure 4.2 Estimated smooth trends of the living tree carbon (LTC) in Navafría (solid blue line) and in Valsaín (dashed red line), the 95 % confidence limits (bands) and the observed values (blue circles in Navafría and red crosses in Valsaín).

Table 4.5 Estimates of the parameters of the fixed effects and covariance parameters of random effects for the living tree carbon model (see Equation 4.1).

Source	Effect	Estimate	Standard error	p-value
Forest	Navafría	108.39	20.13	<0.0001
Forest	Valsaín	136.97	21.58	<0.0001
Forest x Age	Navafría	-0.31	4.21	0.9428
Forest x Age	Valsaín	1.96	4.29	0.6589
Random slope plot effect		17.41	12.88	0.0882

In Navafría, N5 was the plot from which the most C was extracted. In this plot, regeneration fellings were carried out from 2001-2006 (stand age: 110 years), removing 95.93 Mg ha⁻¹ of C (Fig. 4.3). The remaining trees in N5 were removed at the end of 2014, before conducting our last forest inventory. The last thinning and regeneration felling

operations started at an age of 106 years (V5 and V6). Thinnings began in N1 in Navafría when the plot was 20 years old and were also carried out in N2 at 28 and 38 years. In Valsaín, first thinning was performed in V2 (32 years of age) and the second thinning was carried out 10 years later. Thinnings were carried out in V3 in the same forest from 2001-2006 and between 2012-2014, when the plot was 49 and 59 years old respectively. The silvicultural operations were quite light or null in N3, N4 and V4. In the youngest plot of the Valsaín forest (V1), a large amount of C was extracted between 2001 and 2011 (stand age: 19 years), mainly associated with the remaining trees from the regeneration fellings under the group shelterwood method. At the end of the rotation period, the amount of extracted C in Navafría was less than in Valsaín (161.79 and 218.40 Mg ha⁻¹ of C, respectively). The total tree carbon (cumulative extracted C plus LTC of the oldest plot in 2014) was greater in Valsaín than in Navafría (345.48 and 223.83 Mg ha⁻¹ of C, respectively). Prior to the regeneration fellings, the total tree carbon was 218.40 Mg ha⁻¹ of C in Valsaín at an age of 100 years and 217.65 Mg ha⁻¹ of C in Navafría at an age of 110.

Figure 4.3 Extracted C (Mg ha⁻¹ of C) in the periods between inventories in Navafría and Valsaín plots.

The LTC growth rates evolved differently over time in the two forests (Fig. 4.4). In Navafría, LTC growth rates were negatively related to plot age: the largest LTC growth rates were found in the youngest plot (average LTC growth rate in N1=3.98 Mg ha⁻¹ year⁻¹ of C) and the growth rates decreased as the stand got older (average LTC growth rate in N5=0.59

Mg ha⁻¹ year⁻¹ of C). In Valsaín, the LTC growth rate increased from V1 (average 1.90 Mg ha⁻¹ year⁻¹ of C) to V2 (average 4.50 Mg ha⁻¹ year⁻¹ of C), followed by a progressive decrease to the end of the rotation age (average LTC growth rate in V6=1.31 Mg ha⁻¹ year⁻¹ of C). Differences in LTC growth rates among observation periods for the same plot were usually moderate (Fig. 4.4).

Figure 4.4 Living tree carbon (LTC) growth rates (Mg ha⁻¹ year⁻¹ of C) in Navafría and Valsaín plots.

The CWD elements which stored the most C were the stumps of large trees ($d \geq 30$ cm) and the stumps of the rest of the trees ($5 \leq d < 30$ cm) whereas logs and branches represented a small part of the C stored in the CWD (Fig. 4.5). The smallest stumps ($5 \leq d < 30$ cm) were the main source of CWD in N2 and V3 (percentage of small stumps with $5 \leq d < 30$ cm in N2 and V3: 97.5% and 62.3%, respectively). Plot N5 presented the highest values for branches and logs (sum of all the branches and logs=1.6 Mg ha⁻¹ of C). Both in V6 and N5 (C in total CWD=16.6 and 26.2 Mg ha⁻¹ of C, respectively) presented an important increment in CWD C with respect to the next youngest plots (V5 and N4, both over 7 Mg ha⁻¹ of C) due to stumps of trees felled in the regeneration cuttings. The C stored in such stumps also made up an important part of the total CWD C of N1, V2 and V1 (13.6, 20.4 and 15.5 Mg ha⁻¹ of C, respectively). It is important to note that dead trees are extracted during the thinning operations and part of the felling residue is used as firewood.

Figure 4.5 Coarse woody debris in Navafría and Valsaín plots. d=diameter (cm).

4.3.2. Litterfall C rates

Aboveground litterfall rates showed a similar pattern for both the studied forests: from values of approximately 4 Mg ha⁻¹ year⁻¹ of C, litterfall rates increased up to about 6 Mg ha⁻¹ year⁻¹ of C at intermediate ages. As the regeneration period began, values dropped again to 3-4 Mg ha⁻¹ of C (Table 4.6).

Table 4.6 Average ($\pm$ standard error) aboveground litterfall C rates for Navafría and Valsaín estimated for the period April 2009-April 2010.

Plot	Aboveground litterfall rate (Mg ha ⁻¹ year ⁻¹ of C)
Navafría	
N1	4.05 $\pm$ 0.61
N2	5.06 $\pm$ 0.69
N3	6.67 $\pm$ 0.78
N4	5.35 $\pm$ 0.64
N5	2.90 $\pm$ 0.50
Valsaín	
V1	4.54 $\pm$ 0.65
V2	5.53 $\pm$ 0.75
V3	6.05 $\pm$ 0.18
V4	6.41 $\pm$ 0.99
V5	3.55 $\pm$ 0.51
V6	4.22 $\pm$ 0.39

4.3.3. Soil organic carbon stocks

Soil organic C stocks (forest floor + 50 cm) ranged from around 95 to 140 Mg ha⁻¹ of C for the two forests (Fig. 4.6), with no statistically significant differences between them (Table 4.7). However, differences were found when individual soil layers were compared. Navafría had larger C stocks in the forest floor and in the 30-40 and 40-50 cm soil layers, while Valsaín showed higher SOC storage values in the uppermost 20cm of the mineral soil, indicating a different vertical SOC distribution in each forest.

Figure 4.6 Mean ($\pm$ standard error) soil organic carbon stocks over the rotation period in Navafría (N) and Valsaín (V). FF=forest floor.

Age had a statistically significant effect on the SOC pool of both the whole soil profile (mineral soil + forest floor) and the mineral soil (Table 4.7). Layer-wise analyses indicated that the influence of age on the SOC stocks was due to differences in layers beyond 20 cm depth only.

We found no significant effect of plot age nested within the factor forest on forest floor C although the dynamics of forest floor C stocks exhibited slight differences between Navafría and Valsaín. In Navafría, the forest floor steadily increased its C storage from 12.2 ± 2.2 Mg ha⁻¹ of C in the youngest stand to 16.4 ± 1.5 Mg ha⁻¹ of C at the age of 65 years (N3). As tree density and LTC decreased (Fig. 4.2), forest floor C levels dropped slightly, resulting in 14.2 ± 0.6 Mg ha⁻¹ of C at the end of the rotation period (N5). Valsaín presented statistically significant lower overall forest floor C storage values (Table 4.7). The C stored

in the forest floor evolved from $6.3 \pm 1.3 \text{ Mg ha}^{-1}$ of C at the beginning of the rotation period (V1), to a maximum of $11.6 \pm 1.7 \text{ Mg ha}^{-1}$ of C at the age of 48 years (V3). A similar value was obtained at 75 years (V4), after which, and coinciding with the decrease in LTC, forest floor C pools declined to a value at the end of the rotation period of $7.1 \pm 2.0 \text{ Mg ha}^{-1}$ of C (V6).

Table 4.7 Model p-value, R^2 and p-values of the factors for the different soil layers (in cm).

Soil layer		p-value model	R^2	p-value forest	p-value plot age (forest)
Forest floor		0.0046	0.5004	0.0001	0.1594
Mineral soil	0-10	0.0002	0.5041	<0.0001	0.1967
	10-20	0.1566	0.2569	0.0017	0.8832
	20-30	0.0185	0.3610	0.7259	0.0122
	30-40	<0.0001	0.5812	<0.0001	0.0002
	40-50	<0.0001	0.5919	<0.0001	0.0008
	0-50	0.0415	0.3268	0.3846	0.0334
Soil profile	0-50 + Forest floor	0.0279	0.4224	0.7250	0.0191

Deeper soil layers generally exhibited greater variability between forests as well as among stand ages. For example, in Navafría, the lowest SOC stocks in N2 and N3 were found in deeper soil layers (20-30, 30-40 and 40-50 cm), with SOC concentrations two to four-fold lower than in the rest of the plots in Navafría, even though the bulk density and stone content values were similar (Table 4.4). In contrast, high stone content in Valsaín (up to 78 %) was responsible for lower SOC stocks in deeper layers. High within-plot SOC variability did not differ significantly when forest floor C stocks at different stand ages were compared.

4.3.4. Relationships between C pools

We found a positive relationship between the aboveground biomass C and the litterfall rates in Navafría ($R^2=0.90$), whereas no linear relationship could be established in Valsaín due to the low values for litterfall in V5 and V6.

A positive relationship between forest floor C and the C from the logs and branches fraction of the CWD was also found both in Navafría and in Valsaín ($R^2=0.77$ and $R^2=0.68$). In addition, in Navafría, the C stored in the stumps showed a positive association with the SOC in the first 30 cm of the soil profile ($R^2=0.56$). This association emerged between the stumps in plot j and the SOC of plot $j+1$.

In addition, we found a significant relationship between litterfall C rates and the forest floor C stocks ($R^2 = 0.20$ and 0.60 for Navafría and Valsaín, respectively). The regression was improved when plots from the regeneration period were taken out of it ($R^2 = 0.58$ and 0.78). In Navafría, we were able to establish a relationship between each soil layer and the underlying one, if a time offset was taken into account. This can be seen in the relationship between the SOC stocks of the forest floor in plot j and the SOC stocks in the 0-10 cm soil layer of plot $j+1$ ($R^2 = 0.57$). Forest floor C stocks increased between years 10 and 28 and then stabilized. In the underlying soil layer (0-10 cm), the increase in SOC stocks took place between years 28 and 60, the stocks then stabilizing (Fig. 4.6 and 4.7). Likewise, the increase in the SOC stocks of the 10-20 cm soil layer took place in the subsequent period (65-94 years). In Valsaín, no such time dynamics of the topsoil organic C stocks were detected (data not shown).

Figure 4.7 Standard scores of the SOC stocks for the three uppermost soil layers in Navafría.

4.4. Discussion

4.4.1. Living tree carbon

It is necessary to identify the way in which forest management affects C stocks in order to define management guidelines aimed at increasing these stocks (Schulze et al. 2000; Millar et al. 2007; Ruiz-Peinado et al. 2013). In this study, we evaluated two different management systems employed in Mediterranean Scots pine forests: one more intensive with a higher felling intensity and shorter rotation period, the other with a more moderate felling intensity and longer rotation period.

We identified an inflection point in LTC trends during the first part of the rotation period in both forests although this inflection point occurs at an earlier point in time in Navafría, probably because thinning operations take place at earlier development stages in this forest (Montero et al. 2001). This inflection point coincides with the maximum current annual increment. Maximum LTC levels were reached in both forests when stand density was more than 500 trees ha⁻¹ and the dbh was greater than 30 cm. The density was then reduced in order to promote the development of crop trees and further facilitate the regeneration (Lavender et al. 1990). Due to the higher intensity of regeneration fellings under the uniform shelterwood system (used in Navafría), the decline in LTC was more evident at the beginning of the regeneration period in Navafría than in Valsaín. Hence, the three last inventories for the oldest plot at Navafría (N5) were conducted when the regeneration fellings had almost finished and only the residual trees were still to be removed. Furthermore, the lower density of residual trees and the soil preparation carried out in Navafría allowed the regeneration to become established more quickly and favored the development of the seedlings (Barbeito et al. 2011).

Forest C stocks reported in different studies vary greatly due to differences in forest types, management systems, the monitoring methodology or because only certain parts of the C dynamics are taken into consideration. In long-term Mediterranean thinning experiments, Ruiz-Peinado et al. (2014, 2013) reported mean values for LTC ranging from 113.8 to 168.5 Mg ha⁻¹ of C in *Pinus pinaster* Ait. stands (from years 33 to 59) and 128.5 to 193.3 Mg ha⁻¹ of C in *P. sylvestris* (from years 22 to 52) stands depending on the thinning treatment. LTC values in Valsaín and Navafría fall well within these intervals. However, the LTC values found in the present study were greater than those reported in others papers. Nunes et al. (2010) found average LTC values of between 47.9 and 62.6 Mg ha⁻¹ of C in

young stands of *P. pinaster*. Xiao et al. (2003) estimated 176.4 Mg ha⁻¹ as the total tree biomass (89.8 Mg ha⁻¹ of C considering 0.509 as the factor to convert the biomass into C) in a 73 year-old Scots pine stand on a poor site in Belgium. Bascietto et al. (2012) reported 40.1 Mg ha⁻¹ of C stored in the aboveground biomass fraction of a Scots pine stand (80 years-old) in The Netherlands. The large difference with respect to our data is explained by the fact that the basal area of this Scots pine stand (24.4 m² ha⁻¹) was much lower than ours (basal area in Navafría and Valsaín=64.5 and 56.3 m² ha⁻¹, respectively) at an age of 80 years.

The total tree carbon (extracted and standing C) at the end of the rotation period and the ratio of the area below the smooth trends and the rotation age were larger in Valsaín, which is subjected to a more moderate management system (with less severe harvesting and more spread over time). Other studies have also found that longer rotation periods result in greater C accumulation, such as in Spanish stands of *Pinus radiata* D. Don and *P. pinaster* (Balboa-Murias et al. 2006), Finnish forests of *Picea abies* (L.) H.Karst (Pohjola and Valsta 2007), North American stands of *Pseudotsuga menziesii* (Mirb.) Franco and in *Tsuga heterophylla* (Raf.) Sarg. (Harmon and Marks 2002) and in US forests of *Pinus taeda* L. (Nepal et al. 2012). However, Pohjola and Valsta (2007) reported that thinnings account for a greater proportion (70-80 %) than the rotation period (20-30 %) in C sequestration in Finnish Scots pine forests. The fact that growth rates in Valsaín were more stable than in Navafría can be explained, on the one hand, by differences in the regeneration systems and on the other, by the lighter thinning regime in Valsaín.

The positive relationship found between aboveground C and litterfall rates in Navafría was expected and has already been reported in Mediterranean areas (Roig et al. 2005).

4.4.2. Mineral soil organic carbon and forest floor

Forest management comprises a number of different interventions affecting both the vegetation and the soil, with a specific time sequence over the rotation period. Each of these interventions (e.g. soil preparation, thinning, regeneration fellings) can influence the SOC stocks in different ways by altering the rate of soil C input as well as output (Jandl et al. 2007). Therefore, making an overall assessment of the effect of forest management on SOC stocks is highly complex. This complexity is further compounded by the generally high

spatial variability of Mediterranean forest soil characteristics (Rodeghiero et al. 2011). In the present study, the comparison involved differences in several aspects of forest management, hence differences were expected between forests.

Interventions in aboveground vegetation usually have a more evident effect on topsoil C stocks, these effects diminishing with increasing soil depth. However, since a significant amount of C is stored beyond 30 cm (Chiti et al. 2012) we considered it worthwhile investigating deeper layers in our study. Additionally, by computing SOC stocks down to 50 cm a more meaningful comparison can be made with other studies. At local to regional level, Díaz-Pinés et al. (2011a) found values of between 80 and 130 Mg ha⁻¹ of C for Scots pine forests in the same mountain range; Schindlbacher et al (2010) found slightly higher values for plots located in Navafría (up to 150 Mg ha⁻¹ of C for the first 36 cm of the soil profile + 20 in the forest floor); and Alvarez et al. (2014) found values of 100-120 Mg ha⁻¹ of C in a modeling study conducted for the Valsaín forest. Our results, therefore, fall well within the range of other observations in the same study area. In *P. pinaster* forests in southwestern France, C values ranged from 58 to 203 Mg ha⁻¹ of C for the entire soil pool (Augusto et al. 2010). Organic C stocks in forest floor ranged from 14.7 to 19.3 Mg ha⁻¹ of C in Scots pine and from 17.04 to 24.50 Mg ha⁻¹ of C in *P. pinaster*, whereas the 30 uppermost cm of mineral soil accounted for 85.9-88.9 Mg ha⁻¹ of C in Scots pine and 90.52-96.62 Mg ha⁻¹ of C in *P. pinaster* (Ruiz-Peinado et al. 2013; Ruiz-Peinado et al. 2014). Hence, our results are also similar to those reported for other study areas and/or species.

Navafría underwent soil preparation, causing a disturbance along the soil profile which is usually associated with the loss of a steady-state, therefore enhanced SOC losses were expected (Johnson and Curtis 2001; Jandl et al. 2007). No substantial SOC releases were observed. Our results showed indications of a buffering mechanism of C re-allocation from the forest floor to the underlying soil layers, curbing the loss of C from the system. Some of the C entering the forest floor via litterfall is incorporated into the mineral soil a few years after soil preparation. As a result, the equilibrium between SOC inputs and outputs is probably already achieved at the start of the rotation period, with the exception of small C flows between soil layers.

The topsoil in Valsaín may be less prone to exchanges in SOC stocks within the soil profile since a steady-state may already have been reached. Furthermore, since forest operations in Valsaín take place more gradually than in Navafría, mineralization conditions

have not changed dramatically over time (Jandl et al. 2007). Moreover, as could be the case of plot V3, spatial variability may play a greater role than forest management. With the exception of this plot, C pools in the mineral soil remained within a narrow threshold over the whole rotation period. In summary, the evolution over time of the SOC in the forest floor and the top mineral soil in both forests seems to be minimally affected over the rotation period, supporting the findings of previous investigations which suggest that forest management has either no effect at all or only a small, temporal effect on the SOC during the rotation period (Johnson and Curtis 2001; Peichl and Arain 2006; Bradford et al. 2008; Nave et al. 2010).

Deeper soil layers were found to be significant SOC pools, especially in Valsaín. However, it would be highly speculative to associate differences found in SOC over the rotation period with management operations given that, on the one hand, the influence of the vegetation on the soil usually decreases with increasing soil depth (Díaz-Pinés et al 2011b), and on the other, abiotic factors (mainly stone content) contributed as much as 80 % to the calculation of SOC stock, overshadowing the potential effects of forest management.

4.4.3. Conclusions

A complete analysis of C sequestration in forests requires all the different C pools to be taken into account. However, obtaining data for all the pools can be complicated and entails exhaustive sampling. On average, no significant differences were found in terms of the C stored in the whole soil profile of each system. However, the situation may be different in other areas under other climatic conditions. The main difference as regards carbon storage in the two management systems studied concerns the LTC pool. The system with longer rotation periods and more moderate harvesting intensity had higher LTC stocks. In addition, this management system also favors structural biodiversity, greater continuity of regeneration over time and lower susceptibility to drought. Therefore, if one of the management objectives pursued is C sequestration, we recommend management systems with longer rotation periods along with harvesting which is both less severe and more spread over time.

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CHAPTER 5

Space-time modeling of changes in the abundance and distribution of tree species

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Abstract

Land use change and global warming are important drivers in the distribution of tree species. The Mediterranean mountain forest ecosystems can be severely affected by climate change since an increment in temperature has been observed. The main aim of this chapter was to analyze shifts in the distribution and changes in the abundance of Pyrenean oak (*Quercus pyrenaica* Willd.) and Scots pine (*Pinus sylvestris* L.) in Mediterranean mountains over a period of 47 years (1965-2012) by using data from the National Forest Inventories, extending the Universal Kriging/Cokriging models to the space-time case for long-term forest inventory data analysis including climatic variables. Our results indicated that both the distribution and the abundance of Scots pine remained quite constant during the study period. Pyrenean oak increased its presence by 42 % whereas its abundance doubled between 1965 and 2012. This movement took place towards both higher and lower altitudes. With regard to climatic factors, the kriging models showed a negative association between the presence of Scots pine and the temperature. However, we found a quadratic relationship between the Pyrenean oak and temperature, pointing to the occurrence of at intermediate altitudes. Additionally, we found significant relationships between the rainfall and the abundance of both species. Rainfall was positively related to the abundance of Scots pine and negatively to that of Pyrenean oak. Our results indicate that there has been a threefold increase in the area covered by mixed stands. However, successive land use changes as well as forest policies related to conservation have played an important role in the distribution of both species and therefore are taken into account in the discussion of these results.

Key words: global change, land use, data autocorrelation, mixed stands, species distribution models.

Abbreviations: IRWGLS, Iteratively Reweighted Generalized Least Squares; VLS, Variance Least Square; ML, Maximum Likelihood; NFI, National Forest Inventory; SEE, Sum of estimations errors; UCK, Universal Cokriging; UK, Universal Kriging; VSEE, Variance of the Standardised Estimation Errors.

5.1. Introduction

Climate change and land use change are the main drivers of global change in ecological ecosystems (Hansen et al. 2001). The effects of both in forest ecosystems are associated with changes in species productivity (Boisvenue and Running 2006), species distribution (Hampe and Petit 2005; Aitken et al. 2008; Lenoir et al. 2008; Améztegui et al. 2010), forest dynamics (Kellomäki and Väisänen 1997; Palombo et al. 2013) and forest disturbances such as pest outbreaks (Kurz et al. 2008) or forest fires (Flannigan et al. 2009; Brotons et al. 2013), especially in the Mediterranean area (Hódar and Zamora 2004; Pausas 2004).

Mountain ecosystems exhibit high biodiversity because many species, often endemic, remain isolated at high elevations (Beniston 2003). This makes that high mountain systems are particularly vulnerable to climate change (Guisan et al. 1995; Theurillat and Guisan 2001). Three possibilities exist as regards the fate of mountain forest species in a rapidly changing environment: migration; persistence through adaptation to new conditions in current locations; and extirpation (Guisan et al. 1995; Aitken et al. 2008). During previous periods of climate change, species have tended to respond by migrating rather than adapting to new conditions (Huntley 1991). Hence, in mountain areas, forest species might migrate upward towards more favorable ecological niches in response to climate warming (Hughes 2000; Lenoir et al. 2008; Jump et al. 2009).

In particular, the montane species of the Iberian Peninsula can be especially vulnerable to climate change scenarios (Thuiller et al. 2005). In fact, changes in the distribution of the species have already been detected. Peñuelas and Boada (2003) found that the European beech (*Fagus sylvatica* L.) is occupying the summits of the mountains at the highest altitudes and it is being replaced at mid-altitudes in Northern Spain by the holm oak (*Quercus ilex* L.), which is a more xeritic species. Hernández et al. (2014) demonstrated that both Scots pine (*Pinus sylvestris* L.) and the European beech are shifting towards higher elevations in the Pyrenees. Similarly, Sanz-Elorza et al. (2003) reported movements in shrub species towards higher altitudes over recent decades, mainly associated with changes in climatic conditions. Furthermore, Améztegui et al. (2010) found an expansion in the distribution of mountain pine (*Pinus uncinata* Ram.) in the Pyrenees associated with the land use change (abandonment of rural communities and losses in the primary sector) rather than climate change. The effects of global change on the distribution of species must be understood by forest managers and policy-makers and taken into account in forest

management and decision making (Hernández et al. 2014). However, scarce information exists with regard to shifts in species distribution in other mountain areas of the Iberian Peninsula, such as Central Spain.

The broad scale response of species to environmental change has been often assessed by analyzing the distribution of the species (Lenoir et al. 2008; Ruiz-Labourdette et al. 2012; Hernández et al. 2014) since this is easy to measure providing that information is available regarding where a species is present and where it may interact with other species (Ehrlén and Morris 2015). Nevertheless, the absence/presence data may not provide a complete picture of the shifts in distribution of the species or detect changes in the size of the populations (Joseph et al. 2006). Hence, abundance will be much more useful as an indicator of the carry-on effects that one species will have upon interacting species in the community than presence alone (Ehrlén and Morris 2015). However, few studies to date have taken into account the abundance of tree species in population trends (Ficko et al. 2011; Caouette et al. 2015).

Alternative data sources have been used to model changes in species distributions, such as forest maps (Benito Garzón et al. 2008), National Forest Inventories (NFIs) (Hernández et al. 2014) or remote sensing techniques such as aerial photographs and satellite images (Wittmann et al. 2002; Blázquez-Casado et al. 2015). NFIs provide estimates of forest resources, growth, mortality, forest health and other valuable information (McRoberts and Tomppo 2007). Additionally, a large number of species are identified in the NFIs, allowing direct comparisons of species distribution among inventories. Different statistical methods have previously been used to model the distribution and identify the environmental factors that drive this process (reviews in Segurado and Araújo 2004; Miller et al. 2007; Osborne et al. 2007). Among these approaches, kriging techniques have been found suitable for determining species distribution by spatial interpolation from survey data (Carroll and Pearson 1998; Hernández et al. 2014). In this study, we take a step further in species distribution modeling by adding the temporal dimension to the Universal Kriging models (Matheron 1973). These models allow the space-time structure of the variance as well as the effects of climatic and geographical factors to be included in the model. Additionally, these techniques incorporate both spatial and temporal autocorrelation in the kriging prediction, so they are suitable for analyzing survey data when the locations of the samples vary temporally.

The main objective was to analyze shifts in the distribution and changes in the abundance of Scots pine and Pyrenean oak (*Quercus pyrenaica* Willd.) in Mediterranean mountain over the last 47 years. To achieve this objective we develop species dynamics space-time models integrating NFIs and climate data. These models can be an useful tool in order to understand the past distribution trends of tree species in order to develop forest policies in a global change context. The species studied spread from the lower montane broadleaved forests to the oromediterranean coniferous forest across the altitudinal gradient of the Mediterranean mountains of Central Spain. We hypothesized an upward altitudinal shift of the ecotone between Scots pine and Pyrenean oak that entails an increase in mixed stands. Additionally, we expected an increase in the presence and abundance of the Pyrenean oak and Scots pine.

5.2. Material and methods

5.2.1. Study area

This study was conducted in the Central Mountain Range, in Madrid province (Spain). The study area was delimited by 4,557N – 4,415S and 366E – 469W (UTM, ED50, zone 30N) covering 554,411 ha. The altitude ranged from 430 m asl in the lowest flattest areas to 2408 m asl in the mountains of the Central Range. The study area in the mountains mainly faces south and south-east. The climate of the region is continental Mediterranean with montane variations and is characterized by a severe summer drought and high seasonal temperature fluctuations. The total rainfall and annual mean temperature are respectively 535 mm and 15° C in the lowest areas and 1,340 mm and 7° C in the highest areas.

The lower altitudes (<1,000 m asl) are mainly dominated by Mediterranean forests of holm oak, and less frequent, stone pine (*Pinus pinea* L.) forest in the South-West. Between 1,000 m asl and 1,500 m asl sub-Mediterranean forests of Pyrenean oak and pinewoods of Maritime pine (*Pinus pinaster* Ait.) predominate. Scots pine dominates the mountain forests between 1,500 m asl and the timberline (2,000 m asl). In the transitional areas between the sub-Mediterranean and the mountain conifer belts, Scots pine is mixed with the Pyrenean oak, Maritime pine and black pine (*Pinus nigra* Arnold) (<1,700 m asl). Above the timberline, the common juniper (*Juniperus communis* L.), mixtures of broom leguminous bushes and open montane grasslands are the dominant plant communities (Franco Múgica et al. 1998; Cañellas et al. 2000; Benito Garzón et al. 2008; López-Sáez et al. 2014).

The stands of Scots pine have been subjected to long-term forest management and their range have been extended as a result of the forest policy (Gil and Aranzazu Prada 1993; Franco Múgica et al. 1998). Hence, this species is the widest used in the forestry industry in the study area (CAM 2012). The main traditional treatment in Pyrenean oak stands, the coppice management, was abandoned during the 1980s due to the decrease in use of firewood and charcoal as an energy source and to rural emigration to the cities (Gonzalez Molina 1995; Cañellas et al. 2004; Adame et al. 2008; Gea-Izquierdo et al. 2015). To a lesser extent, the Pyrenean oak makes up open woodlands (López Estébanez and Sáez Pombo 2002).

5.2.2. Forest inventory data and climate data

We used data from the four existing Spanish NFIs (Table 5.1; Alberdi Asensio et al., 2010) to evaluate the changes in the spatial distribution of Scots pine and Pyrenean oak. The number of trees per hectare of each species in the plots of the four NFI cycle can be found in Fig. 5.1. The NFI plots were only installed in woodland areas (i.e. none in non-forested areas). The highest altitude of NFI plots in the study area coincided with the uppermost limit of Scots pine.

Table 5.1 Year and type of the National Forest Inventory of the plots and number of plots in the study area.

NFI	Year	Type of forest inventory	Number of plots in the study area
First	1965	Relascope	693
Second	1990	Circular plots	1919
Third	2000	Circular plots	1783
Fourth	2012	Circular plots	1182

NFI: National Forest Inventory

We used two climatic variables to explain the space-time dynamics of Scots pine and Pyrenean oak: the annual average temperature (temperature, hereafter) and the yearly rainfall (rainfall, hereafter). The annual average temperature and the yearly rainfall are the variables most common used in species distribution models (Porfirio et al. 2014). We obtained the climatic data from the meteorological stations belonging to the Spanish Meteorological

Agency (www.aemet.es). We established 1950 as the beginning of the time series and 2014 as last year. The length of the climatic time series differed from one station to another. We used Universal Kriging (UK) with altitude as auxiliary variable to interpolate the temperature and rainfall in the NFI plots in the years of the four NFIs (305 meteorological stations for temperature data and 241 for rainfall data). Additionally, we calculated the annual average temperature and rainfall in the study area using block kriging (Isaaks and Srivastava 1989) to show the temporal trends of both variables.

Figure 5.1 Number of trees (trees ha⁻¹) of Scots pine (upper) and Pyrenean oak (lower) per diameter class in each inventory.

5.2.3. Statistical analysis: space-time models

5.2.3.1. Distribution (absence/presence) models: Space-time Universal Kriging

Environmental variables such as rainfall, temperature and elevation, as well as ecological processes such as dispersion or mortality, exhibit spatial dependence, some of which are responsible for spatial structure in the distribution of vegetation. Thus, the distribution of vegetation is not random and each observation is not independent (Segurado and Araújo 2004; Miller et al. 2007). The spatial autocorrelation must be accounted for in the model because otherwise the risk of Type I errors is increased (Legendre and Legendre 1998). The Kriging techniques used in this work incorporated spatial and temporal autocorrelation, and deals non-geostationarity through the mean function which depends on the auxiliary variables.

The distribution of the species was evaluated using an indicator variable that took a value 1 if the species was present in the plot and 0 if the species was absent in the plot. We defined a species as present in a given plot when trees, saplings or seedlings were registered in the plot. We used the space-time UK (De Iaco et al. 2002; Montes et al. 2011) to model and map the distribution of Scots pine and the Pyrenean oak in the study area.

$Z(s,t)$ being as the realization of a space-time random process, the UK model can be expressed as:

$$Z(s,t) = \sum_{k=0}^p \beta_k f_k(s,t) + \delta(s,t) \quad (5.1)$$

or, in matrix form:

$$Z = X\beta + \delta \quad (5.2)$$

where $s \in \mathbb{R}^2$ and $t \in T$, $f_k(s,t)$ are $p + 1$ functions of the auxiliary variables which estimate the space-time mean and $\delta(s,t)$ is an intrinsically stationary zero-mean residual random process.

The estimation of the optimal weights λ_i involves modeling the variogram. The generalized product-sum model (De Iaco et al. 2002) was used to fit the variogram $\gamma_{st}(h)$

$$\gamma(h_s, h_t) = \gamma(h_s, 0) + \gamma(0, h_t) - k\gamma(h_s, 0)\gamma(0, h_t) \quad (5.3)$$

We used a spherical variogram both for the temporal and spatial components assuming a common nugget effect for both components. We used two approaches to simultaneously estimate the variance-covariance matrix $\Sigma(\hat{\theta})$ (which depends on the variogram parameters $\hat{\theta}$) and the β_k coefficients of the auxiliary variables: the Iteratively Reweighted Generalized Least Squares (IRWGLS) (Neuman and Jacobson 1984) and the Variance Least Square (VLS) (Montes and Ledo 2010).

We fitted two absence/presence UK models, one for each species. We first used the IRWLS method to fit the models; however, we employed the VLS method when the convergence of the IRWLS could not be achieved. We predicted the distribution of both species at each inventory year in a 500 x 500 m grid covering the study area (22174 points per inventory year). The UK indicator predictions outside [0, 1] were set to the nearest bound, i.e., upward-downward correction (Deutsch and Journel 1992). Finally, we plotted maps for the dynamics of the mixed and pure stands of both species. We termed ‘pure stands’ those where only one of the two studied species occurred and ‘mixed stands’ those where both species coexisted.

5.2.3.2. Abundance models: Space-time Universal Cokriging

In order to complete the absence/presence analysis, we modeled the shifts of the distribution of Scots pine and Pyrenean oak over the study period using the basal area ($\text{m}^2 \text{ha}^{-1}$) as response variable. In this case, we used Universal Cokriging models (UCK), extending this technique to the space-time prediction.

Cokriging (Myers 1982) is an extension of kriging to the case of two or more spatial variables. These variables are not fixed variables that indicate the nature of a trend in the primary variable, but are themselves spatial random variables with expected values and variograms (Gotway and Hartford 1996). In the space-time UCK the value of the variables can be decomposed into a linear function of the auxiliary variables and a residual process with a space-time covariance structure defined by the variograms and cross-variograms of the variables:

$$Z_i(s, t) = \sum_{k=0}^p \beta_{ik} f_k(s, t) + \delta_i(s, t) \quad (5.4)$$

In our study we have two dependent variables ($i = 1, 2$), the basal area of the Scots pine and the basal area of the Pyrenean oak. The UCK prediction $p(Z_i, s_0, t_0)$ of the variable $Z_i(s_0, t_0)$ is a linear combination of the values of this variable in the n sampling points placed in $s_{11} \dots s_{n1}$ and the value of the other variable $Z_2(s_{j2})$ in the m points $s_{12} \dots s_{m2}$:

$$p(Z_1, s_0, t_0) = \sum_{i=1}^n \lambda_{11i} \cdot Z_1(s_i) + \sum_{j=1}^m \lambda_{12j} \cdot Z_2(s_j) \quad (5.5)$$

and analogously:

$$p(Z_2, s_0, t_0) = \sum_{i=1}^n \lambda_{21i} \cdot Z_1(s_i) + \sum_{j=1}^m \lambda_{22j} \cdot Z_2(s_j) \quad (5.6)$$

Each variable shows a space-time auto-semivariance function, which is modeled through the variograms γ_{11} and γ_{22} . The cross-variogram characterizes the space-time covariance between each pair of distinct variables (Clark et al. 1989; Cressie 1993):

$$\gamma_{12}(h) = \frac{1}{2 \cdot N(h)} \sum_{a=1}^{N(h)} (Z_1(u_a, t_a) - Z_2(u_a + h_s, t_a + h_t))^2 \quad (5.7)$$

The variables Z_1 and Z_2 were standardized to ensure the unbiasedness of the estimators (Deutsch and Journel 1992). In order to obtain a valid variance-covariance matrix, the variogram and cross-variograms should form a correlogram model, i.e., each variogram (or cross-variogram) is the linear combination of g spatial or temporal unitary variograms that stand for the different spatial structures i ($i = 1 \dots g$), multiplied by the correlogram coefficients b_{11i} y b_{22i} , which stand for the contribution of the spatial structure i to the variogram of the variable 1 and 2 respectively, and b_{12i} , which stands for the contribution of the spatial structure i to the cross-variogram.

We included two variograms in the model of correlogram ($g = 2$): a temporal spherical model and a spatial spherical model, plus a pure nugget effect variogram that stands for the variance which is neither associated to the auxiliary variables nor to associated to the temporal and spatial structures. The direct and cross variograms are linear combinations of variograms for each structure, that is, the variogram of a given variable is a linear combination of the nugget effect and the temporal and spatial variogram models. The correlogram model parameters (range and b coefficient of each elemental structure)

and mean function coefficients β were estimated through IRWGLS, analogously to the UK model.

We assumed that the abundance of one species is not independent of the abundance of the other. Thus, this technique would appear to be useful for modeling the basal area of both species. The basal area of each species was kriged at those prediction points where the presence/absence indicator UK was above 0.5.

5.2.3.3. Assessment of the statistical significance of the mean function coefficients

The covariance matrix $\hat{V}$ of the generalized least squares estimates $\hat{\beta}$ is obtained as follows:

$$\hat{V} = (X' \hat{\Sigma} X)^{-1} \quad (5.8)$$

We calculated the standard error estimates $s_k = \sqrt{\hat{v}_{kk}}$ for each beta parameter estimate, $\hat{\beta}_k$, $k=0,1,\dots,p$ to construct p-values for significance test of these coefficients based on the t -ratios:

$$t_k = \hat{\beta}_k / s_k, \quad k=0,1,\dots,p \quad (5.9)$$

the degrees of freedom for the t -tests being the difference between the number of observations and the number of auxiliary variables.

5.2.3.4. Relative structural correlation assessment

We can calculate the relative structural correlation to assess the correlation between the variables associated with each spatial or temporal structure i (Goovaerts and Webster 1994; Pelletier et al. 2009):

$$\rho_{12i} = \frac{b_{12i}}{\sqrt{b_{11i} \cdot b_{22i}}} \quad (5.10)$$

In order to quantify the part of the total correlation between variables associated with each structure, we propose the following definition of the relative structural correlation:

$$\rho_{12i}^r = \frac{b_{12i}}{\sqrt{\sum_{j=1}^g b_{11j} \cdot \sum_{j=1}^g b_{22j}}} \quad (5.11)$$

Positive values of the relative structural correlation indicate positive association between the variables and negative values indicate negative association between the variables.

5.2.3.5. Model selection: Cross-validation

Cross-validation was used to assess the performance of the UK and UCK model in term of bias and predicted variance. We selected randomly 500 points from data set to carry out the cross-validation of the UK and UCK. The sum of the estimation errors (SEE) was used to check for bias:

$$\text{SEE} = \frac{\sum_{i=1}^n (p^*(Z, s_i) - Z(s_i))}{n} \quad (5.12)$$

where n is the number of observations and $p^*(Z, s_i)$ is the prediction of $Z(s_i)$ leaving out the value observed at s_i . The variance of the standardised estimation errors (VSEE; which should be approximately 1 if the model performed well) was used to check the validity of the prediction error given by the kriging variance:

$$\text{VSEE} = \frac{\sum_{i=1}^n \frac{(p^*(Z, s_i) - Z(s_i))^2}{\sigma_{UK}^2(s_i)}}{n} \quad (5.13)$$

where $\sigma_{UK}^2(s_0)$ is the UK error variance (Cressie 1993).

The selected space-time UK and space-time UCK models presented SEE values closest to 0 and VSEE values closest to 1. All the statistical analyses were done using a MATLAB R2009a (MATLAB 2009) package developed by the authors. Maps were created using ArcGis 10.2.2. (ESRI 2014).

5.3. Results

5.3.1. Rainfall and temperature measurements

We employed the VLS method to fit the UK models for the rainfall and temperature. We found significant relationships between both variables and the altitude. As expected, the relationship temperature-altitude was negative and the relationship rainfall-altitude was positive. The spatial correlation was larger for the rainfall (104.16 km) than for temperature (8.67 km), i.e., the rainfall measurements were more constant over the study area than the temperature. Moreover, we found similar temporal ranges of both climatic variables, close to 1 year. Concerning the temporal trends of temperature and rainfall, the block kriging revealed great interannual variations in both variables. In addition, we found a rise in average temperatures and a slight decrease in average rainfall over the study period (Fig. 5.2).

Figure 5.2 Annual average values, variance and linear trendline of the temperature (upper) and rainfall (lower) over the study period after the performance of the block kriging.

5.3.2. Shifts in the absence/presence of Scots pine and Pyrenean oak

The UK model for the Scots pine distribution was fitted using the IRWLS and included the temperature as the auxiliary variable (Table 5.2). We found a negative relationship between temperature ($p < 0.0001$) and the distribution of Scots pine indicating that this species appeared in the coldest sites of the study area, i.e., at the highest altitudes. Both the temporal and spatial ranges of the Scots pine variogram, 47 years and 136.42 km respectively, were constrained by the fitting procedure to the maximum time difference and distance found in the data set, that is, the semivariance did not stabilize over the study period or the study area. The variance linked to the mean function was 49% (Supplementary Material: Fig. A.1, A.2 and A.3). The space-time autocorrelation explained 44% of the residual variation.

Table 5.2 Space-time UK models, estimations of the spherical variogram parameters and β coefficients of the auxiliary variables for the Scots pine and Pyrenean oak distributions (absence/presence). The p-values of the auxiliary variables are in brackets.

Parameter	Scots pine (IRWLS)	Pyrenean oak (VLS)
Variogram parameter		
Nugget	0.0600	0.0205
Sill XY	0.0183	0.1160
Range XY	136.3207	2.9682
Sill time	0.0284	0.0044
Range time	47.0000	12.6017
k coefficient	0.1373	0.1060
β coefficients of the auxiliary variables		
β_0	-0.7150 (0.4949)	-0.6348 (0.4953)
Temperature	-0.1358 (<0.0001)	0.2070 (<0.0001)
Temperature ²		-0.0111 (<0.0001)
Rainfall		
Cross-validation statistics		
SEE	-0.0065	0.0027
VSEE	0.9271	1.7776

IRWGLS: Iteratively Reweighted Generalized Least Squares. VLS: Variance Least Square. SEE: Sum of the Estimation Errors. VSEE: Variance of Sum of Estimation Errors.

We used the VLS method to fit the UK model for the absence/presence of Pyrenean oak (Table 5.2). The selected model included the temperature and the square of the temperature with positive and negative β coefficients, respectively, (p-value of both variables < 0.0001) indicating a quadratic relationship between the temperature and the presence of the Pyrenean oak. The negative β coefficient of the square of the temperature indicated that the curve opened downward; the presence of this species reaching a maximum at 9.3 °C. We found a spatial correlation among measurements of 3.0 km and a temporal correlation of 12.6 years. The mean function absorbed 14% of the variance (Supplementary Material: Fig. A.4, A.5 and A.6) and the space-time autocorrelation explained 63% of the residual variance. Additionally, in this case, the spatial sill was 26 times larger than the temporal sill, indicating larger variability in space than in time.

Table 5.3 Number of prediction points and proportion, between brackets, of pure stands of Scots pine, pure stands of Pyrenean oak and mixed stands. Mixed stands are where both species coexist. Scots pine and Pyrenean oak are pure stands of these species.

Type of stand	1965	1990	2000	2012
Mixed stand	191 (0.9)	384 (1.7)	471 (2.1)	626 (2.8)
Pyrenean oak stand	1,550 (7.0)	1,969 (8.9)	2,101 (9.5)	2,361 (10.6)
Scots pine pure stand	1,698 (7.7)	1,579 (7.1)	1,638 (7.4)	1,472 (6.6)
No presence	18,735 (84.5)	18,242 (82.3)	17,964 (81.0)	17,715 (79.9)
Total prediction points	22,174 (100)	22,174 (100)	22,174 (100)	22,174 (100)

According to the UK prediction maps (Fig. 5.3; Supplementary Material: Fig. A.7), the distribution of Scots pine has hardly changed over the study period. We found that the presence of Scots pine has increased by 11% during the period from 1965 to 2012 (Table 5.3). The altitudinal range of this species has remained constant over the study period (Table 5.4).

Figure 5.3 Distribution (absence/presence) of Scots pine pure stands (green), Pyrenean oak pure stands (blue) and mixed stands (red) in 1965 (upper left), 1990 (upper right), 2000 (lower left) and 2012 (lower right).

Furthermore, the UK revealed an expansion of Pyrenean oak in the study area (Table 5.3). This species increased its distribution by 42% from 1965 to 2012 (Fig. 5.3; Supplementary Material: Fig. A.7). In contrast to the distribution of Scots pine, the Pyrenean oak expanded its distribution both towards higher elevations and lower elevations, while the average altitude remained constant (Table 5.4). From 1965 to 2012, Pyrenean oak occupied new areas, creating pure stands (92%) rather than mixed stands (8%). In this respect, we found that there has been a threefold increase in mixed stands over the study period whereas the area occupied by pure stands of Scots pine has reduced by 14% and the area occupied by pure stands of Pyrenean oak has increased by 52%. In this regard, we found an increase in the altitude of the upper limit of the mixed pine-oak stands in 2012 compared to 1965 whereas the increment in altitude was less pronounced at the lower limit (Table 5.4).

Table 5.4 Average altitude (m asl) of the prediction points where Scots pine and Pyrenean oak occurred. In brackets, the 5th and the 95th percentiles. Mixed stands are where both species coexist.

Year	Scots pine	Pyrenean oak	Mixed stands
1965	1,646 (1,343-2,040)	1,195 (929-1,503)	1,474 (1,264-1,722)
1990	1,638 (1,338-2,034)	1,211 (929-1,582)	1,506 (1,262-1,780)
2000	1,619 (1,317-2,026)	1,203 (923-1,578)	1,490 (1,245-1,765)
2012	1,620 (1,322-2,024)	1,214 (911-1,617)	1,505 (1,272-1,783)

5.3.3. Shifts in the abundance of Scots pine and Pyrenean oak

The selected model included rainfall as explanatory variable, presenting a significant association with the basal area of both species (Table 5.5). The relationship between rainfall and the basal area of Scots pine was positive whereas it was negative in the case of the Pyrenean oak.

Table 5.5 β coefficients of the auxiliary variables of the space-time UCK model for the basal area of Scots pine and Pyrenean oak and the statistics of the cross-validation. The p-values of the auxiliary variables are in brackets.

Basal area of Scots pine	
β_0	-0.1264 (0.4200)
β of the rainfall	0.6111 (<0.0001)
β of the temperature	
β of the temperature ²	
Sum of the Estimation Errors	-0.0250
Variance of Sum of Estimation Errors	0.9733
Basal area of Pyrenean oak	
β_0	0.3798 (0.2906)
β of the rainfall	-0.4069 (<0.0001)
β of the temperature	
β of the temperature ²	
Sum of the Estimation Errors	-0.0272
Variance of Sum of Estimation Errors	0.9448

Figure 5.4 Basal area of Scots pine in 1965 (upper left), 1990 (upper right), 2000 (lower left) and 2012 (lower right). Yellow: (0-10 m² ha⁻¹], green: (10-20 m² ha⁻¹], red: (20-30 m² ha⁻¹], violet: (30-40 m² ha⁻¹] and purple: (40-50 m² ha⁻¹].

The ranges of the spatial and temporal spherical elemental variograms were the maximum distance among plots and the whole study period, respectively (Table 5.6). We found a positive value of relative structural correlation between the basal area of species in case of the spatial structure, whereas the relative structural correlation was negative for the temporal structure (Table 5.6, calculated in Eq. 5.11). This indicates a positive relationship between the basal area of both species in space and negative in time. Additionally, the absolute value of the relative structural correlation was larger in the time spherical structure than in the spatial one, highlighting that the species abundance for each of the two species has changed oppositely over the successive surveys, although the denser stands of both species tended to coincide geographically.

Figure 5.5 Basal area of Pyrenean oak in 1965 (upper left), 1990 (upper right), 2000 (lower left) and 2012 (lower right). Yellow: (0-4 m² ha⁻¹], blue: (4-8 m² ha⁻¹], green (8-12 m² ha⁻¹] and red (12-16 m² ha⁻¹].

Table 5.6 Ranges of the elemental variograms, coefficients of the coregionalization model of space-time UCK and relative structural correlations of the elemental variograms.

Elemental variogram	Range	Sills			Relative structural correlation
		Scots pine variogram	Pyrenean oak variogram	Cross-variogram	
Nugget	0.00	0.4652	0.6070	0.6680	0.4588
Spherical XY	136.32	0.2534	0.9417	0.1889	0.1300
Spherical time	47.00	0.5302	0.1485	-0.2806	-0.1927

We found great differences in the basal area of both species. Scots pine always displayed larger basal areas than the Pyrenean oak. The basal area of the Scots pine (Fig. 5.4) remained quite constant over the study period ($18.39 \text{ m}^2 \text{ ha}^{-1}$ in 1965, $16.14 \text{ m}^2 \text{ ha}^{-1}$ in 1990, $17.81 \text{ m}^2 \text{ ha}^{-1}$ in 2000 and $21.32 \text{ m}^2 \text{ ha}^{-1}$ in 2012). However, we found a reduction in the number of plots with the lowest basal area whereas the number of plots in the intermediate and uppermost ranges increased from the first NFI to the last (Table 5.7). The average basal area of the Pyrenean oak increased with time (Fig. 5.5). Hence, the average basal area of this species in 2012 ($4.00 \text{ m}^2 \text{ ha}^{-1}$) doubled compared to that in 1965 ($1.79 \text{ m}^2 \text{ ha}^{-1}$).

Table 5.7 Number of prediction points placed in each basal area range for the two species studied. The percentage of points in each basal area range is given in brackets.

Basal area range ($\text{m}^2 \text{ ha}^{-1}$)	1965	1990	2000	2012
Scots pine				
(0-10]	414 (21.9)	383 (19.5)	291 (13.8)	156 (7.4)
(10-20]	679 (36.0)	985 (50.2)	1055 (50.0)	876 (41.8)
(20-30]	575 (30.5)	552 (28.1)	627 (29.7)	702 (33.5)
(30-40]	213 (11.3)	43 (2.2)	135 (6.4)	349 (16.6)
(40-50]	7 (0.4)	0 (0.0)	1 (0.0)	15 (0.7)
Total (0-50]	1,888 (100.0)	1,963 (100.0)	2,109 (100.0)	2,098 (100.0)
Pyrenean oak				
(0-4]	1,515 (97.7)	1,590 (72.4)	1,552 (61.4)	1,584 (53.5)
(4-8]	16 (1.0)	571 (26.0)	887 (35.1)	1,208 (40.8)
(8-12]	19 (1.2)	30 (1.4)	72 (2.8)	144 (4.9)
(12-16]	0 (0.0)	5 (0.2)	18 (0.7)	27 (0.9)
Total (0-16]	1,550 (100.0)	2,196 (100.0)	2,529 (100.0)	2,963 (100.0)

5.4. Discussion

The methods used in these work, space-time UK and UCK, have been shown to be appropriate for monitoring changes in the distributions of forest species using long-term data. The space-time correlation allowed us to use the information from different inventories for data interpolation, thus improving the predictions where the location of the plots varied among inventories. We incorporate the climatic variables in the mean function, which can be interpreted as the climatic potential in basis to the species distribution (derived from the NFI samples over the forest area along the studied period). The spatial and temporal correlation determines the oscillations from this climatic potential in different areas along the period. Three novel approaches used in this work enhanced the model performance and provided a complete framework to understand the relationships between variables: i) the p-values estimation to calculate the significance of the coefficients of the auxiliary variables in the mean function, ii) the relative structural correlation based on the structural correlations proposed by Goovaerts and Webster (1994) and iii) the method proposed to determine the part of the variance linked to the mean function and the part linked to the space-time autocorrelation, based on Montes and Ledo (2010).

Our findings indicate a relatively steady distribution of Scots pine during the period analyzed in the study area. This is in contrast to the elevation shift of Scots pine towards high mountain grasslands and the reduction in the stands of Scots pine in the Iberian Peninsula predicted by species distribution models as a consequence of climate warming (Benito Garzón et al. 2008; Ruiz-Labourdette et al. 2012). Hernández et al. (2014) found that Scots pine shifted approximately 200 m towards higher elevations but increased its distribution in the Western Pyrenees between 1971 and 2010, stressing the importance of land use changes in species dynamics. However, in the study area the shallow and stony terrain impedes the establishment of trees above the tree line. Since the late 20th century, wood production has been reduced towards protective function in those Scots pine stands located at higher altitudes. This may explain the increasing trend in the basal area in the last inventory.

In contrast, the population of Pyrenean oak increased both in presence and abundance. From 1990 (Fig. 5.1, lower), a large number of trees of this species was incorporated to the upper diameter classes (diameter>55cm) entailing the increase in basal area. Ruiz-Labourdette et al. (2012) predicted that the Pyrenean oak would move slightly

towards higher elevations. However, our findings indicate that Pyrenean oak range has not shifted to higher elevations (in terms of average altitude) over the last 47 years but rather widen both upwards and downwards. The upwards expansion maybe related to climate factors, but also to changes in forestry policy that favored Scots pine stands over the oak woodlands at the uppermost limit of the Pyrenean oak altitudinal range at beginning of the 20th century (Cañellas et al. 2000; Sánchez-Palomares et al. 2008). The reduction of firewood exploitation, the conversion of the coppice into high forests, the decrease in human local population, the scarcity of recent large fires in the study area (differently to other Iberian mountains), the protection of Pyrenean oak by the forest policy led to expansion to lower elevation of this species, the increase of the basal area and, the shift of the diameter distribution towards larger sizes (Gómez et al. 2003; Cañellas et al. 2004; Pausas 2004; PORN 2010; Gea-Izquierdo et al. 2015).

The area where both species coexist has increased considerably. The Scots pine could facilitate the establishment and development of the Pyrenean oak as occurs with other pine and oak species in southern Spain (Urbietta et al. 2011). The positive spatial correlation between the basal area of both species found in the UCK model indicated that the areas where the basal area of both species is higher coincide. In fact, del Río and Sterba (2009) reported that the competition in mixed stands of Scots pine and Pyrenean oak is lower than in pure stands and the increase in stocking per occupied area is greater in mixed stands. The areas where both species coexist were mainly areas proximal to the ecotone between the pinewood and the oak woodland: the lowest areas Scots pine range and the uppermost range for Pyrenean oak. Current forestry policy promote mixed stands with complex structures to increase stability and biodiversity (e.g. Spiecker 2003). Some authors (Gimmi et al. 2010; Ruiz-Labourdette et al. 2012) predict that the Pyrenean oak and other broadleaf species will replace the stands of Scots pine since the increase in the intensity of the summer drought can cause a decrease in the regeneration and recruitment of Scots pine, therefore limiting its distribution (Martínez-Vilalta and Piñol 2002; Castro et al. 2004; Pardos et al. 2007; Fernández-de-Uña et al. 2015). In addition, a temperature rise may lead to a higher incidence of some outbreaks on pine forests (Hódar and Zamora 2004). Accordingly, the forecasted increase in temperatures, if not accompanied by an increase in rainfall, will threaten existing populations of Pyrenean oak at lower altitudes (Benito Garzón et al. 2008; de Dios et al. 2009; Ruiz-Labourdette et al. 2012; Gea-Izquierdo et al. 2013). However, despite the

climatic trends over the last 47 years (Fig. 5.2), the Pyrenean oak has expanded to lower altitudes as we discussed above.

Concerning the climatic variables, we found that temperature was negatively associated with the presence of Scots pine and rainfall was positively related to its abundance. The quadratic form of the mean function of the Pyrenean oak distribution model indicated that this species occurred at intermediate altitudes in our study area. At lower altitudes (warmer and drier areas), other species such as holm oak are the dominant species whereas Scots pine is established at higher altitudes with colder, more humid conditions (López-Sáez et al. 2014).

It is important not only to monitor the progress of these species but also to study their past and future dynamics in the context of global change in order to develop scientific tools for forest management. In our study area, the long life of these species combined with the changes in use seem to have contributed to the maintenance of Scots pine populations while the distribution range and density of Pyrenean oak as well as the coexistence areas have increased. This is not an equilibrium stage and future changes in the climate may lead to the retraction to the Scots pine with ongoing colonization of the Pyrenean oak (Gea-Izquierdo et al. 2015).

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Supplementary Material

Figure A.1 Variogram of the distribution of the Scots pine model.

Figure A.2 Trend function of the temperature for the distribution of the Scots pine model.

Figure A.3 Residual variogram of the distribution of the Scots pine model.

Figure A.4 Variogram of the distribution of the Pyrenean oak model.

Figure A.5 Trend function of the square of the temperature for the distribution of the Pyrenean oak model.

Figure A.6 Residual variogram of the distribution of the Pyrenean oak model.

Figure A.7 Distribution (absence/presence) of Scots pine (left) and Pyrenean oak (right) in the area of study in 1965 (red), 1990 (blue), 2000 (yellow) and 2012 (green).

CHAPTER 6

Discussion

6.1. Regeneration dynamics of *Pinus sylvestris* L. in Mediterranean areas

Regeneration, classified into seedlings and saplings, and its association with adult trees was studied at microscale (Chapter 2) and plot scale (Chapter 3), respectively. Hence, although the approach to regeneration differs between the uniform shelterwood and group shelterwood systems, these two studies together cover the whole process of the establishment of new individuals following seedling germination. We found that *P. sylvestris* seedlings require moderate light conditions for successful development in Mediterranean areas, which is in concordance with previous findings for this species (Pardos et al. 2007; Barbeito et al. 2009). The results of this study also show a positive relationship between the number of stumps and the number of seedlings. The number of stumps is a proxy of the intensity of the regeneration fellings and therefore, of the canopy openness. This suggests that higher intensities of regeneration fellings (cutting around 70 trees ha⁻¹, about 45 % of standing trees) promote the establishment of new individuals of *P. sylvestris*. In fact, the mean density of mother trees reported in this study (85 trees ha⁻¹) is within the tree density range after the seedling cuttings (70-100 trees ha⁻¹) proposed by García López (1995). In addition, the stem extraction operations may have a soil-preparation effect by removing the herb layer and facilitating the establishment of the *P. sylvestris* seedlings (Fig.1.1; Barbeito et al. 2011). Furthermore, the conditions at sites where *P. sylvestris* is found can vary greatly over its distribution range (Mason and Alía 2000; Mátyás et al. 2003). At sites with severe summer drought, such as those in this study, moderate canopy cover may ensure higher levels of soil moisture than open canopies, while also permitting a sufficient level of solar radiation. In contrast, at sites in northern latitudes the limiting factor is the amount of light, thus the regeneration appears in open gaps (Mátyás et al. 2003). Consequently, natural regeneration in northern countries is usually achieved using the seed-tree method, whereas in southern locations the different alternatives offered by the shelterwood approach tend to be employed (Mason and Alía 2000; Barbeito et al. 2008; Hyppönen et al. 2013). Our results confirm that natural regeneration in this forest is successfully achieved under the current management practices (uniform shelterwood), suggesting that, from a scientific perspective, the temporal and spatial continuity of the forest is ensured. In this regard, Montes et al. (2005) studied the historical records of the inventories (the first inventory took place in 1889) in Valsaín forest and concluded that despite changes in forest management, the continuity and sustainability of this forest is assured.

Once the factors underlying the establishment of seedlings has been analyzed, the dynamic of individuals at a later stage of development (saplings) was investigated on a larger scale. The exploration of the linear predictor function reveals a negative relationship between the diameter of adult trees and the number of saplings up to 7-8 m. This means that saplings prefer not to grow in close proximity to larger trees. Once the seedlings become saplings, the maintenance costs increase (Falster and Westoby 2003) and plants require higher minimum levels of solar radiation for survival (Williams et al. 1999). Additionally, their roots can penetrate into deeper and more humid soil layers (Ritchie 1981). The spatio-temporal structure selected means that the spatial distribution of the saplings remains constant over time. This may be due to the fact that our study only covers less than half of the regeneration period. As a consequence, given the growth rate of *P. sylvestris*, the length of the study period is insufficient for the saplings to move into the next cohort, changing their spatial distribution. Furthermore, the regeneration fellings are carried out in Valsaín forest using the group shelterwood system over a 40 year period, whereas the regeneration fellings in Navafría forest are more intense and take place over 20 years. Hence, the latter silvicultural approach entails more rapid establishment of the regeneration (Fig. 4.2) and therefore, it may have been easier to identify changes in the spatial pattern of the saplings. Finally, we can also confirm from a scientific perspective that the group shelterwood system is a suitable method for regenerating *P. sylvestris* in southern latitudes.

Our results with regard to regeneration suggest that it is necessary to reduce the density of the remaining trees after the establishment of seedlings in order to promote the growth of saplings in stands of *P. sylvestris* in Mediterranean mountains.

6.2. *Pinus sylvestris* L. forests as a climate change mitigation tool

Chapter 4 is related to the role of forests in global change mitigation. This chapter assesses the way in which two alternative management systems, one more intensive and the other more moderate (with less severe harvesting and more spread over time), affect the carbon stored in the five compartments in Mediterranean forests.

The biomass of living trees emerged as the compartment which stores the most carbon, followed by the mineral soil (SOC). Our results indicate that at the end of the rotation period, the amount of carbon stored in the living biomass of the forest subjected to a more

moderate management system (Valsaín forest) is greater than the amount stored in the forest subjected to a more intensive forest management system (Navafría forest). This agrees with previous findings of studies undertaken at different latitudes (Balboa-Murias et al. 2006; Pohjola and Valsta 2007; Nepal et al. 2012).

As regards the carbon stored in the mineral soil, our results show that the SOC stored in the uppermost layers (0-20 cm) – those more prone to be affected by interventions in aboveground vegetation – is more abundant in Valsaín than in the Navafría forest. In both of these forests, the SOC hardly changes over the rotation period. This is in accordance with the findings of previous studies which report that forest management has either null or only a small, temporal effect on the SOC during the rotation period (Johnson and Curtis 2001; Peichl and Arain 2006; Bradford et al. 2008; Nave et al. 2010).

It seems that management systems with longer rotation periods and harvests which are both less severe and spread over a longer period of time provide a valuable tool for global change mitigation. Additionally, the more moderate management system favors structural biodiversity, greater continuity of regeneration over time and lower susceptibility to drought. All of these concerns should be considered in forest planning. However, the regeneration fellings under the group shelterwood system and the floating periodic block method used in Valsaín create multi-layer forest structures, especially at the beginning of the regeneration period (see Figs. 3.1 and 4.2), increasing vertical fuel continuity and therefore, the intensity of forest fires (Vélez 2002). Although the number of large fires in the study area (such as the one which occurred at San Lorenzo de El Escorial in 1999) is relatively low, predictions point to an increase in fire risk in the Mediterranean basin (Moriendo et al. 2006).

6.3. Retrospective view of *Pinus sylvestris* L. in Central Spain: influence of global change

In order to gain a better understanding of the current state of forests and forest practices (Chapters 2, 3 and 4) it is necessary to analyze the previous state of forests and past forest management. Chapter 5 studies the shifts in distribution of two Mediterranean species, *P. sylvestris* and *Quercus pyrenaica* Willd., and the climatic variables driving these shifts. However, the absence/presence of a given species may not provide a complete picture of the shifts in its distribution or detect changes in population sizes (Joseph et al. 2006). In this

regard, Ehrlén and Morris (2015) suggest that abundance, rather than presence alone, is much more useful as an indicator of the effects that one species has upon interacting species in the community. Hence, changes in species abundance are also considered in our study. Additionally, the way in which the changes in land use and changes in forest policies can modify the dynamics of *P. sylvestris* and *Q. pyrenaica* at landscape scale are discussed.

The study has been developed in the Sierra de Guadarrama in Comunidad de Madrid over the last 37 years (from 1965 to 2012), using data from the National Forest Inventory (NFI). This area was selected as the four NFI cycles had been completed whereas the Northern slopes of the Sierra de Guadarrama (Segovia province) were not considered because the fourth cycle of NFI had not yet been completed when we were carrying out this research.

Our findings indicate that presence of *P. sylvestris* has increased by 11% in the study area between 1965 and 2012 but its altitudinal range has remained relatively constant over this period, in contrast to other regions in northern Spain where this species is moving towards higher elevations (Hernández et al. 2014). This underlines the suitability of the current forest management practices in terms of ensuring the spatial and temporal continuity of *P. sylvestris* forests, despite the more intensive management approach used on north-facing slopes (Segovia province, previous Chapters) in comparison to south-facing ones (Comunidad de Madrid). Hence, the reduction in wood production in this area may explain the rise in basal area reflected in the inventory for the period between 2000 and 2012. In the case of *Q. pyrenaica*, both its presence and basal area increased during the study period. Changes in forest policy may explain, at least in part, the shifts in presence and changes in basal area of *Q. pyrenaica*. At the beginning of the 20th century, *P. sylvestris* stands were favored at the uppermost limit of the *Q. pyrenaica* altitudinal range. However, forest policy supported the protection of broadleaf species, such as *Q. pyrenaica*, during the last part of the 20th century (Cañellas et al. 2000; Sánchez-Palomares et al. 2008). The expansion of *Q. pyrenaica* to higher altitudes led to an increase in the area where *P. sylvestris* and *Q. pyrenaica* coexist, especially in the areas adjoining the ecotone between the two species. The mortality of *P. sylvestris* seedlings associated with summer drought (Pardos et al. 2007) and the increase in the intensity of summer drought under the current climate change scenario could eventually result in the replacement of *P. sylvestris* by *Q. pyrenaica* (Gimmi et al. 2010; Ruiz-Labourdette et al. 2012). Therefore, taking into consideration the

abovementioned challenges, adaptive management is necessary to ensure the persistence of *P. sylvestris* forests in Mediterranean areas over time.

6.4. Methodological remarks

6.4.1. Multiscale framework

The assessment of several processes at four spatial scales has proved to be very useful to gain further insight into forest dynamics. Some of the processes studied at smaller scales, such as regeneration and recruitment, are strongly related to the temporal evolution of the carbon stored in forests or the past and future distribution of forests. Furthermore, the models developed at medium and intermediate spatial scales could provide the basis for a sub-model included in a more complex multistage model or simulation model which would function at larger scales, especially in the case of the sapling distribution model.

6.4.2. Statistical approaches

The data analyses were carried out using various statistical approaches taken from different branches of statistics: parametric, semiparametric and nonparametric methods implemented in R, SAS and SPSS (Table 6.1). Additionally, we propose novel approaches rarely used in forestry or ecology, but which help to further our methodological knowledge in these fields. All of these factors have contributed to improving the performance of the statistical analyses. In fact, three of the objectives (Objectives 2, 3 and 6) set out in this thesis are closely related to the advances in statistical methodologies.

In Chapter 2, the performance, weaknesses and strengths of alternative methods used to model forest regeneration are assessed (Objective 2). The generalized linear mixed model (GLMM) identified the largest number of variables associated with the response, seedling density. In addition, this approach allows nested designs be accounted for via random effect (Zuur et al. 2007), whereas the nonparametric approaches employed are not able to consider this type of correlation, which can lead to biased results and hide the effect of certain explanatory covariates. In any case, GLMM has two main weaknesses; it fits linear relationships between the response variable and the explanatory variables and it is necessary to address correlated variables. Nonparametric methods such as chi-squared automatic interaction detection (CHAID), nonmetric multidimensional scaling procedure (NMDS) and

Random Forest, can identify non-linear and complex relationships between the variables and, hence, have been used to make spatial predictions (Hengl et al. 2017). However, additive models or generalized additive models (GAM), depending on the distribution of errors, may also describe non-linear relationships between variables as smooth functions. In this thesis, additive models using penalized smoothing splines or P-splines (Eilers and Marx 1996) were employed to describe the living tree carbon trends over time whereas the sapling distribution was modeled by fitting GAMs, using thin plate regression splines (Wood 2003). Both P-splines and thin plate regression splines avoid the problems associated with knot placement of the regression splines and reduce the computational requirements of the smoothing splines (Wood 2003; Durbán et al. 2005). These semiparametric methods identified complex relationship between variables, which are too complicated to model parametrically. Additionally, additive models and GAM may consider correlation in hierarchical designs by including random effects as in the case of GLMM. Therefore, it would seem reasonable to conclude that GAM and additive models are highly applicable in ecological and forestry studies where the influence of one or a set of variables on the response may not be nonlinear (Faraway 2006; Wood 2006). However, GAMs present the same limitation as GLMs in terms of the correlation among explanatory variables. Including correlated variables simultaneously in a model increases the risk of type I errors (Zuur et al. 2007). Principal component analysis (PCA) and NMDS may reduce the dimensionality of the data, eliminating the correlation of the variables but the effect of the individual covariates is not fully identifiable (Strobl et al. 2009).

Objective 3 is to fit a model to determine the effect of adult tree size on the number of *P. sylvestris* saplings as a function of the distance between saplings and adults over time. This was successfully achieved using a functional predictor in a GAM (Wood 2006; Augustin et al. 2015). The model fitted allows the diameter of adult trees to vary smoothly over the distance between adult trees and saplings. The application of this technique has never been used in forestry or ecology and it is expected to become widely accepted.

One of the main drawbacks of universal kriging and universal cokriging is the lack of significance of the auxiliary variables. In this thesis, we test a methodology which eliminates this shortcoming by estimating the p-values associated with each auxiliary variable (Objective 6). However, the improvements in kriging performance are more far reaching. The estimation of the relative structural correlation based on the structural correlations (Goovaerts and Webster 1994) in universal cokriging allows the relationship

between the basal area of *P. sylvestris* and *Q. pyrenaica* to be described in space and time. Additionally, the method to determine which part of the variance is linked to the mean function and which the part is linked to the space-time autocorrelation is closer to the variance portioning variance-partitioning analysis (Legendre and Legendre 1998), thus making this approach even more applicable.

Table 6.1 Alternative methods used in the different Chapters according to the branch of statistics.

Chapter	Parametric methods	Semiparametric methods	Nonparametric methods
Chapter 2	Generalized linear mixed model		CHAID PCA NMDS Random Forests
Chapter 3		Generalized additive model	
Chapter 4	Nested ANOVA Linear regression	Additive model	
Chapter 5	Universal kriging Universal cokriging		

ANOVA: analysis of variance; CHAID: chi-squared automatic interaction detection; PCA: principal component analysis; NMDS: nonmetric multidimensional scaling procedure.

6.4.3. Spatio-temporal modeling

Certain data used in this work (both the location of the quadrats where saplings are grouped and the plots of the National Forest Inventory) are spatially correlated. Different techniques can take into account the spatial correlation such as autoregressive methods or geographical weighted regression (Segurado and Araújo 2004; Miller et al. 2007; Osborne et al. 2007). The remaining spatial correlation is eliminated (Fig. 3.5 and 3.8) by adding a spatial smooth function in the sapling distribution model (GAM), whereas the spatial correlation is addressed through the variograms of the universal kriging and universal cokriging (Fig. A3, A6). Another aim of this thesis is to develop models which help us to understand the occurrence of spatial processes over time. The GAMs fitted in Chapter 3 allow the temporal component to be included in the model in two ways; either by separating the time and the space, i.e., as additive effects, or by allowing the spatial component to change in time. The

selection process of the spatio-temporal structure determines whether the spatial pattern of the response variable (in this case the number of saplings) remains constant or whether it changes over time. In contrast, the temporal component is included in the kriging model as another coordinate. The spatio-temporal variograms appear to be quite flexible (Fig. A.3, A.6).

Therefore, Chapter 3 and Chapter 5 reveal that GAM and universal kriging/ universal cokriging are appropriate techniques for dealing with spatio-temporal data. However, explanatory variables can be included in many different forms in GAMs: as variables with linear effects, smooth terms, tensor products of several variables, with varying coefficients or as functional predictors, i.e., both linear and non-linear relationships between variables are allowed in this kind of model. On the other hand, the relationships between the auxiliary variables and the response variable are strictly linear in kriging techniques. This can be a drawback of kriging techniques as opposed to GAMs, especially when dealing with ecological data.

6.4.4. Alternative data sources

The data employed in this PhD thesis came from three kinds of plot: 1) temporal plots used to analyze processes at finer scales, 2) permanent plots grouped in a chronosquence and 3) NFI plots. Gadow et al. (2008) reviewed the main strengths and weaknesses of the temporal, interval and permanent plots in a production-modeling framework. According to these authors, temporal plots present certain important advantages in comparison to permanent plots in that the former allow data from different states of stand development to be gathered over short periods. Additionally, they state that information on previous silviculture in permanent plots is known whereas such data may not be available when using temporal plots. Hence, the data from permanent plots (where the size and the position of the trees removed during fellings is known) are used to model the sapling distribution and to model carbon trends, whereas the intensity of regeneration fellings was estimated through the number of stumps when using the temporal plots.

The NFI constitutes a powerful tool for monitoring forest state and forest dynamics. The position of the trees within the plots and their size is known and therefore growth, density or mortality are variables which can be easily quantified. Even though the location and design of the plots as well as the sampling method has varied from one NFI to another

(Hernández et al. 2014), with new plots being added in each inventory cycle (Alberdi Asensio et al. 2010), many of the plots have been re-measured several times.

Finally, it should be mentioned that other information, such as shrub or regeneration data, are also recorded in the NFIs. In this regard, a future line of research might include further development of *P. sylvestris* regeneration models for larger scales (landscape scale) using NFI data.

6.5. One step further: new challenges for the forestry sector

This thesis addresses different aspects of the wood-industry chain, in particular, the first steps; regeneration and stand growth. Under a classic and static scenario in the absence of global change, the next steps could be to assess the quality of the wood, its profitability and the by-products trade (Koga et al. 2002; Jaakkola et al. 2005; Mäkinen et al. 2015). However, under the current scenario of global change, causing a lack of regeneration as well as shifts in species distribution, the situation is far more complicated. In addition to the aforementioned effects of climate change, the increase in temperatures and reduction in rainfall are linked to a rise in the mortality rates of adult trees (Gea-Izquierdo et al. 2014; Prieto-Recio et al. 2015). Unfortunately, the forestry sector also has to face other kinds of threats.

The capacity to transport goods rapidly, wood among others, also entails the movement of organisms which are harmful to plants, such as insects or fungi. The damage caused by these organisms is often minimized in their natural distribution areas but they can cause dramatic losses in other areas due to the lack of adaptation of native plant species. This is the case of the nematode *Bursaphelenchus xylophilus* (Steiner & Buhrer 1934, Nickle 1970), known as the pine wood nematode, in the Iberian Peninsula and Asia (Mota et al. 1999). This agent causes mortality in pine trees (*P. sylvestris* being one of the species prone to attack) as a result of cavitation. Tackling this situation is an important challenge to managers and researchers (Abelleira et al. 2011). The damage caused by the seed bug *Leptoglossus occidentalis* (Heid.) in *Pinus pinea* L. cones (Lis et al. 2008) or infection by *Xylella fastidiosa* Wells. in agricultural trees (Olmo et al. 2017) are other examples of the impact of alien pathogens in plants species. Pathogen management, control and removal

requires an understanding of the biology and ecology of the pathogen, the interaction between agent and plant, as well as the ecology of the invaded forest (Rizzo et al. 2005).

All of this could lead to loss, or reduced quality, of services and wood along with non-wood products. Therefore, tools for adaptation to this scenario are required, such as optimizing regeneration fellings and thinnings (Aldea et al. 2017) along with mitigation, for instance through carbon sequestration. In addition to economic profit from wood and non-wood products or the adaptation to and mitigation of climate change, society demands other functions and services from forests. In this regard, conservationist groups and other stakeholders have highlighted the role of forests as biodiversity hotspots since the beginning of the 90s. These social demands were recorded in the management plans, considering the conservation and enhancement of biodiversity as other functions of forests (Kangas and Kuusipalo 1993). As a consequence, new lines of research concerned with assessing the impacts of forest management on biodiversity were initiated (Torras and Saura 2008).

From another perspective, the new paradigm of the bioeconomy and circular economy offers new opportunities to the forestry sector. The circular economy states that society is benefitted by minimizing the use of the environment as a sink for residuals and reducing the use of raw materials for economic activity. The benefits are based on the assumption that the loss of material residuals is minimized (e.g., Andersen 2007). Within the forestry sector, the bioeconomy and circular economy may play an important role, for example, in the production of renewable energy using forest biomass; in constructions employing wood as a building material, in industry by replacing synthetic fibers in textiles or the development of new products in the biorefinery field.

Forest biomass provides an option for producing renewable, sustainable, clean energy for communities, using wood and residues from cuttings operations in forests (Heikkilä et al. 2009; Hevia et al. 2017) and plantations (Oliveira et al. 2017). In contrast to other sources of energy, such as petrol, the carbon balance is almost neutral, since natural processes like plant decay would have released the carbon to the atmosphere in any case. Additionally, the carbon emitted when burning biomass is absorbed by other plants during their growth cycle. The use of forest biomass may also contribute to energy self-sufficiency in rural areas, helping rural populations to continue living in the countryside. Thanks to subsidies such as Kemera, some northern countries such as Finland have promoted the use of forest biomass as a source of energy.

Furthermore, through the integration of ‘green chemistry’ in biorefineries and the use of low environmental impact technology, biofuels and biochemicals provide alternatives which could replace, at least in part, the use of fossil fuels (Cherubini 2010; Ibarra et al. 2017)

The use of wood as building material presents certain advantages over other materials, such as the relatively low energy required to manufacture wood products compared with alternative materials; the reduction in carbon emissions associated with industrial processes such as cement manufacture; or the carbon stored in wood buildings (Eriksson et al. 2012). Hence, important innovations in timber construction have been developed in recent years, such as the use of Cross Laminated Timber for high rise construction (Guaita Fernández 2017).

Another use of forest biomass is as a raw material in the textile industry to replace, at least partially, synthesis and cotton production. The main advantage of cellulose over synthetics is the high availability of the former. In the case of cotton, production cannot be increased further as it competes with arable crops for cultivable land. However, the main weakness of cellulose as a raw material in textile production is that it is extremely difficult to process (Nykänen 2017).

The forestry sector, therefore, faces new challenges in a rapidly changing world, although a wide range of opportunities are emerging. It is essential for scientists, managers and social stakeholders to work together in order achieve their common goal.

CHAPTER 7

Conclusions

7.1. Conclusiones generales

1. Las plántulas de *Pinus sylvestris* tienden a aparecer en condiciones moderadas de luz en los sistemas montañosos de la cuenca mediterránea. Reducciones de densidad fuertes durante las cortas diseminatorias, apeando más de 70 pies por hectárea (45% del número de pies por hectárea de la masa remanente), maximizan la aparición de nuevos individuos de esta especie. Una vez instaladas las nuevas plántulas de *P. sylvestris* bajo condiciones moderadas de luz, es necesario abrir la masa para facilitar el desarrollo de las plántulas en estadíos superiores.
2. Las distintas aproximaciones estadísticas detectaron diferentes variables ambientales relacionadas con el proceso de regeneración en masas de *P. sylvestris*. El modelo lineal generalizado mixto fue la técnica que identificó un mayor número de relaciones significativas entre el número de plántulas y las variables ambientales considerando, además, la correlación espacial. Sin embargo, las técnicas semiparamétricas, como el escalamiento multidimensional no lineal o los árboles de decisión, permiten establecer relaciones no lineales entre la variable dependiente y las independientes. La elección de la técnica empleada para llevar a cabo los análisis estadísticos en estudios de dinámica forestal tiene que ir determinada por la naturaleza de los datos, la posible correlación espacial y temporal así como por la complejidad de las relaciones entre la variables dependiente e independientes.
3. Se ha identificado un efecto negativo del diámetro de los pies adultos en los pies menores de *P. sylvestris* en distancias inferiores a los 7-8 m. En distancias superiores no se detecta ningún efecto significativo. Esto indica que los pies menores necesitan condiciones de insolación elevadas para un correcto desarrollo. Además, el patrón espacial de distribución de los pies menores se mantiene bastante constante a lo largo del periodo de regeneración cuando las cortas se realizan mediante el método de aclareo sucesivo por bosquetes.
4. Los modelos semiparamétricos (modelos generalizados aditivos) han demostrado una gran flexibilidad al detectar relaciones no lineales complejas entre variables ambientales. Además, permiten considerar tanto correlación espacial como temporal incluyendo componentes aleatorias y distintas estructuras de correlación. Por lo tanto, su uso es altamente recomendable en estudios forestales y de ecología siempre y cuando se tenga en cuenta la correlación entre variables independientes.

5. Los sistemas de gestión forestal con turnos largos (120 años) y regímenes de claras moderadas almacenan, como media a lo largo del turno, más carbono en el arbolado vivo que sistemas de gestión con turnos algo más cortos (100 años) y claras más fuertes (162.9 y 148.9 Mg ha⁻¹ de C, respectivamente). Los efectos de la gestión forestal realizada en estas masas de pinares sobre el carbono almacenado en los horizontes superficiales del suelo son escasos, tanto si se analiza el turno completo dentro de un mismo sistema como si se comparan las dos alternativas de gestión forestal estudiadas. Por lo tanto, si el principal objetivo de la gestión del monte es el almacenamiento de carbono se recomienda usar esquemas selvícolas con turnos largos y regímenes de claras moderadas.
6. Tanto la presencia como la abundancia, cuantificada a través del área basimétrica, del *P. sylvestris* en la Comunidad de Madrid se ha mantenido relativamente constante desde 1965 hasta 2012, mientras que la presencia del *Quercus pyrenaica* ha aumentado 42 % y su área basimétrica se ha duplicado. Los aumentos significativos en la distribución del *Q. pyrenaica* están asociados al abandono de tierras de cultivo, a la reducción de demandas de leñas y a la política proteccionista para con esta especie. Cambios futuros en el clima pueden llevar asociados una reducción en la superficie ocupada por el *P. sylvestris*, así como un aumento de la distribución, especialmente hacia cotas más altas, del *Q. pyrenaica* en la Comunidad de Madrid.
7. El hecho de que la distribución del *P. sylvestris* apenas haya cambiado desde 1965 hasta 2012 y de que la distribución del *Q. pyrenaica* haya aumentado significativamente en ese periodo, unido a un posible efecto de facilitación entre ambas especies, se traduce en un incremento de la superficie donde las dos especies coexisten y se prevea una extensión de las masas mixtas de estas dos especies en el territorio de estudio.
8. Los avances en las técnicas de krigeado mostrados en esta tesis – la determinación de la significación de los coeficientes de las variables auxiliares en la función principal, la estimación de la varianza asociada a la función principal así como a la autocorrelación y la formulación de la correlación estructural relativa– han confirmado la utilidad de estas técnicas en los estudios de dinámica forestal.

7.2. General conclusions

1. *P. sylvestris* seedlings grow under moderate light conditions in Mediterranean mountains. It seems that more intensive regeneration cuttings, removing more than 70 trees ha⁻¹ (45 % of the remaining trees), maximizes the establishment of new individuals of this species. After the establishment of *P. sylvestris* seedlings under moderate light conditions, it is necessary to reduce the stand density to favor the development of *P. sylvestris* saplings.
2. Alternative statistical approaches have detected different environmental variables underlying the regeneration process in *P. sylvestris* stands. The approach that found the largest number of variables associated with the regeneration process was the generalized linear mixed model. Additionally, this method accounts for the spatial correlation. Nevertheless, semiparametric techniques, such as non-metric multidimensional scaling or decision trees, were able to detect non-linear relationships between the response and the predictors. The choice of a given method to perform statistical analyses in forest dynamics studies should be made according to the nature of the data, the spatial and temporal correlation and the complexity of the relationships among variables.
3. A negative association between the diameter of adult trees and the number of saplings up to 7 – 8 m was identified. Beyond this distance, the diameter of the adult trees shows no association with the number of saplings. This means that saplings require higher light conditions for successful development. The spatial pattern of the sapling distribution remains constant over time when the regeneration fellings are carried out using the group shelterwood method.
4. Semiparametric models (generalized additive models) present great flexibility, allowing complex non-linear relationships between environmental variables to be detected. Additionally, they can deal with spatially and temporally correlated data including random effects and several types of structures. Therefore, the use of this type of model is highly recommendable in forestry and ecological studies where the correlation between independent variables is considered.
5. The average of the total living tree carbon stored at the end of the rotation period is greater in the forest with the longer rotation period (120 years) and lighter thinning regime than in the intensively-managed forest (rotation period of 100 years and heavier thinning intensity), 162.9 and 148.9 Mg ha⁻¹ of C, respectively. The carbon

stored in the uppermost layers of the soil remains constant over the rotation period and is not affected by the management system. Therefore, if the main function of the forest is to maximize the carbon storage, the use of management systems with longer rotation periods and moderate harvesting intensities is recommended.

6. *P. sylvestris* populations in Comunidad de Madrid have remained constant between 1965 and 2012, both in presence and abundance (quantified through basal area), whereas the presence of *Q. pyrenaica* has increased by 42% and its basal area has doubled. The significant increment in *Q. pyrenaica* distribution is linked to the abandonment of crop lands and the protection of *Q. pyrenaica* through forest policy aimed at reducing the use of firewood. Future climate change may lead to a reduction in *P. sylvestris* distribution as well as an increase in *Q. pyrenaica* distribution, especially at higher altitudes.
7. The area in which both species coexist has increased three fold as a result of increased distribution of *Q. pyrenaica*, stable distribution of *P. sylvestris* and the possible facilitation phenomenon between the two species. The area in which both species coexist in Comunidad de Madrid is expected to continue increasing.
8. The methodological advances in kriging techniques shown in this thesis (estimation of the significance of the coefficients of the auxiliary variables in the mean function, the determination of the part of the variance linked to the mean function and the part linked to the space-time autocorrelation and the relative structural correlation) confirm the suitability of these techniques in studies assessing forest dynamics.

CHAPTER 8

References

The screenshot displays the Mendeley Desktop application window. The interface includes a menu bar (File, Edit, View, Tools, Help), a toolbar with icons for adding, organizing, and syncing documents, and a search bar. On the left, there is a sidebar with sections for 'Mendeley' (Literature Search, Mendeley Suggest), 'My Library' (All Documents, Recently Added, Recently Read, Favorites, Needs Review, My Publications, Unsorted, Create Folder...), 'Groups' (Create Group...), 'Trash' (All Deleted Documents), and a 'Filter by Authors' list. The main pane shows a table of documents with columns for Authors, Title, Year, and Published In. The document 'Regeneration dynamics of mixed stands of *Pinus pinaster* Ait. and *Pinus pinea* L. in Central Spain' by D. Moreno-Fernández, F. Montes, and M. Sánchez-González is selected. The right pane shows the details for this article, including the title, authors, journal name ('European Journal of Forest Research'), year (2017), volume, issue, pages, abstract, tags, author keywords, publisher (Springer Berlin Heidelberg), URL, catalog IDs (DOI, ISBN, ISSN, PMID), and files (Moreno-Fernández et al. 2017.pdf).

★	●	📄	Authors	Title	Year	Published In
★	●	📄	Muñoz, Alberto; Bonal, Raúl; Díaz, Mario	Ungulates, rodents, shrubs: interactions in a diverse Mediterranean ecosystem	2009	Basic and Ecology
★	●	📄	Ferretti, Marco	Forest health assessment and monitoring – Issues for consideration	1997	Environme Monitoring
★	●	📄	Gea-Izquierdo, Guillermo; Nicault, Antoine; Battipaglia...	Risky future for Mediterranean forests unless they undergo extreme carbon fertilization	2017	Global Ch Biology
★	●	📄	Domínguez, María T.; Pérez-Ramos, Ignacio M.; Murillo, ...	Facilitating the afforestation of Mediterranean polluted soils by nurse shrubs	2015	Journal of Environme
★	●	📄	Andriva, Enrique; Villar-Salvador, Pedro; Tovar, Lila...	Multiscale assessment of woody species recruitment in Mediterranean shrublands: facilitation and beyond	2017	Journal of Vegetatio
★	●	📄	Caldeira, Maria C.; Ibáñez, Inés; Nogueira, Carla; Bugal...	Direct and indirect effects of tree canopy facilitation in the recruitment of Mediterranean oaks	2014	Journal of Ecology
★	●	📄	Gómez-Aparicio, Lorena; Valladares, Fernando; Zamo...	Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: an experimental approach at...	2005	Ecograph
★	●	📄	Smit, Christian; den Ouden, Jany; Díaz, Mario	Facilitation of <i>Quercus ilex</i> recruitment by shrubs in Mediterranean open woodlands	2008	Journal of Vegetatio
★	●	📄	Castro, Jorge; Gómez, José M; Zamora, Regino; Hódar, ...	Use of shrubs as nurse plants: A new technique for reforestation in Mediterranean mountains	2002	Restoratio Ecology
★	●	📄	Gómez-Aparicio, Lorena; Zamora, Regino; Gómez, Jo...	Applying plant facilitation to forest restoration in Mediterranean ecosystems: A meta-analysis of the shrub...	2004	Ecological Applicatio
★	●	📄	Moreno-Fernández, Daniel; Montes, Fernando; Sánchez...	Regeneration dynamics of mixed stands of <i>Pinus pinaster</i> Ait. and <i>Pinus pinea</i> L. in Central Sp...	2017	European of Forest
★	●	📄	Ibarra, D.; Eugenio, M.E.; Cañellas, I.; Sixto, H.; Martí...	Potential of different poplar clones for sugar production	2017	Wood Sci and Techn
★	●	📄	Cherubini, Francesco	The biorefinery concept: Using biomass instead of oil for producing energy and chemicals	2010	Energy Conversio
★	●	📄	Gartner, Barbara L; North, Eric M; Johnson, G R; Single...	Effects of live crown on vertical patterns of wood density and growth in Douglas-fir	2002	Canadian of Forest
★	●	📄	Hevia, Andrea; Álvarez-González, Juan Gabriel; Maj...	Effects of pruning on knotty core taper and form of <i>Pinus radiata</i> and <i>Pinus pinaster</i>	2016	European of Wood z
★	●	📄	Nykanen, T	Fantastic fibres	2017	MetsaFibr
★	●	📄	Andersen, Mikael Skou	An introductory note on the environmental economics of the circular economy	2007	Sustainab Science
★	●	📄	Gea-Izquierdo, Guillermo; Viguera, Bárbara; Cabrera, ...	Drought induced decline could portend widespread pine mortality at the xeric ecotone in managed mediterranean ...	2014	Forest Eci and Mana
★	●	📄	Rizzo, David M; Garbelotto, Matteo; Hansen, Everett M	<i>Phytophthora ramorum</i> : Integrative research and management of an emerging pathogen in California and ...	2005	Annu . Re Phytopat
★	●	📄	Olmo, D.; Nieto, A.; Adrover, F.; Urbano, A.; Beidas, O.; ...	First Detection of <i>Xylella fastidiosa</i> Infecting Cherry (<i>Prunus avium</i>) and <i>Polygala myrtifol</i>	2017	Plant Dise
★	●	📄	Abelleira, A.; Picoaga, A.; Mansilla, J. P.; Aguín, O.	Detection of <i>Bursaphelenchus xylophilus</i> , causal agent of pine wilt disease on <i>Pinus pinaster</i> in northwestern Spain	2011	Plant Dise
★	●	📄	Mota, Manuel; Braasch, Helen; Bravo, Maria Antonia...	First report of <i>Bursaphelenchus xylophilus</i> in Portugal and in Europe	1999	Nematolo
★	●	📄	Gadow, K. v.; Alboreca, A. Rojo; Gonzalez, J. G. Alvare...	Ensayos de crecimiento. Parcelas permanentes, temporales y de intervalo	1999	Investigar Agraria. S
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CHAPTER 9

Curriculum Vitae

9.1. Personal data

Surname and name	Moreno Fernández, Daniel
Date of birth	23/09/1987
Place of birth	Madrid (Madrid)
Address	Avenida de Córdoba 2, 8º 13. 28026. Madrid
Telephone number	(+34) 686 35 46 50
e-mail	danielmorenofdez@gmail.com
ResearcherID	E-7958-2016
ORCID	0000-0002-9597-6609
Driving license	B and A

9.2. Education

9.2.1. University degrees

Title	Masters in Research in Engineering for the Conservation and Sustainable Use of the Forests Systems
University	University of Valladolid. School of Agrarian Sciences
Date	July 22 th , 2013
Grade (0-10)	8.89
Title	Forest Engineer
University	School of Forestry. Polytechnic University of Madrid
Date	July 20 th , 2011
Grade (0-10)	7.12

9.2.2. Awards

Award for the best academic performance of first-year students of the University School of Forestry Technical Engineering in the 2006-2007 academic year granted by the Polytechnic University of Madrid.

9.2.3. Other courses related to research

Title	Biostatistical analysis with regression models in R
University	Universidad Autónoma de Madrid
Duration	47 hours
Date	2014
Title	Training School on “Modelling nonwood forest products”
University	Cost Action FP1203. “European NWFPs Network”
Date	September 29 th – October 3 th , 2014

9.3. Fellowships and contracts

Institution	INIA-CIFOR. FPU Pre-doctoral contract supported by Ministry of Education, Culture and Sport and INIA-CIFOR
Date	September, 2014 – (April, 2018)
Institution	University of Valladolid. FPI Pre-doctoral contract supported by UVA and Banco Santander
Date	April, 2014 – September, 2014
Institution	Freelance
Date	April, 2013 – February, 2014
Institution	School of Forestry. Polytechnic University of Madrid. Fellow Collaboration in the Project of Educational Innovation Project of the School of Forestry coordinated by Dr. Yolanda Ambrosio Torrijos
Date	July, 2010 – November, 2010
Institution	School of Forestry. Polytechnic University of Madrid Fellow Collaboration in the informatics room of the School of Forestry
Date	October, 2009 – June, 2010

9.4. Publications

9.4.1. Scientific papers

1. **Moreno-Fernández D**, Álvarez-González JG, Rodríguez-Soalleiro R, Pasalodos-Tato M, Cañellas I, Montes F, Díaz-Varela E, Sánchez-González M, Crecente-Campo F, Álvarez-Álvarez P, Barrio-Anta M, Pérez-Cruzado C. Under review. National-scale assessment of forest site productivity using the National Forest Inventory. *Forest Ecology and Management*. FORECO_2018_37
2. **Moreno-Fernández D**, Hevia A, Majada J, Cañellas I. Under review. Do common silvicultural treatments affect wood density of Mediterranean montane pines? *Forests*. Forests-267775
3. **Moreno-Fernández D**, Augustin N, Montes F, Cañellas I, Sánchez-González M. 2018. Modeling sapling distribution over time using a functional predictor in a generalized additive model. *Annals of Forest Science*. DOI 10.1007/s13595-017-0685-3
4. **Moreno-Fernández D**, Montes F, Sánchez-González M, Gordo J, Cañellas I. In press. Regeneration dynamics of mixed stands of *Pinus pinaster* Ait. and *Pinus pinea* L. in Central Spain. *European Journal of Forest Research*. DOI 10.1007/s10342-017-1086-8
5. Hernández L, Jandl R, Blujdea V, Lehtonen A, Kriiska K, Alberdi I, Adermann V, Cañellas I, Marin G, **Moreno-Fernández D**, Ostonen I, Varik M, Didion M. 2017. Towards complete and harmonized assessment of soil carbon stocks and balance in forests: The Ability of the Yasso07 model across a wide gradient of climatic and forest conditions in Europe. *Science of the Total Environment* 599-600, 1171-1180. DOI 10.1016/j.scitotenv.2017.03.298
6. **Moreno-Fernández D**, Hernández L, Sánchez-González M, Cañellas I, Montes F. 2016. Space-time modeling of changes in the abundance and distribution of tree species. *Forest Ecology and Management* 372, 206-216. DOI 10.1016/j.foreco.2016.04.024
7. **Moreno-Fernández D**, Díaz-Pinés E, Barbeito I, Sánchez-González M, Montes F, Rubio A, Cañellas I. 2015. Temporal carbon dynamics over the rotation period of two alternative management systems in Mediterranean mountain Scots pine forests. *Forest Ecology and Management* 348, 186-195. DOI 10.1016/j.foreco.2015.03.043

8. **Moreno-Fernández D**, Cañellas I, Barbeito I, Sánchez-González M, Ledo A. 2015. Alternative approaches to assessing the natural regeneration of Scots pine in a Mediterranean forest. *Annals of Forest Science* 72, 569-583. DOI 10.1007/s13595-015-0479-4
9. **Moreno-Fernández D**, Sánchez-González M, Álvarez-González JG, Hevia A, Majada JP, Cañellas I, Gea-Izquierdo G. 2014. Response to the interaction of thinning and pruning of pine species in Mediterranean mountains. *European Journal of Forest Research* 133, 833-843. DOI 10.1007/s10342-014-0800-z
10. **Moreno-Fernández D**, Cañellas I, Calama R, Gordo J, Sánchez-González M. 2013. Thinning increases cone production of stone pine (*Pinus pinea* L.) stands in the Northern Plateau (Spain). *Annals of Forest Science* 70, 761-768. DOI 10.1007/s13595-013-0319-3

9.4.2. Science popularization articles

1. **Moreno Fernández D**, Montes F, Sánchez-González M, Alberdi I, Sánchez de Dios R, Cañellas I, Hernández L. 2016. Cambios en la distribución y abundancia de especies forestales a partir del Inventario Forestal Nacional. *Foresta* 66, 64-68.

9.4.3. Chapters in books

1. Cañellas I, Sánchez-González M, Bogino SM, Adame P, **Moreno-Fernández D**, et al. 2017. Carbon sequestration in Mediterranean oak forests. In *Managing Forest Ecosystems: The Challenge of Climate Change* (Eds: Bravo F, LeMay V, Jandl R, von Gadow K). Chapter 20. pp 403-427. Springer. ISBN 978-1-4020-8343-3
2. Del Río M, Barbeito I, Bravo-Oviedo A, Calama R, Cañellas I, Herrero C, Montero G, **Moreno-Fernández D**, et al. 2017. Mediterranean pine forests: management effects on carbon stocks. In *Managing Forest Ecosystems: The Challenge of Climate Change* (Eds: Bravo F, LeMay V, Jandl R, von Gadow K). Chapter 15. pp 301-327 Springer. ISBN 978-1-4020-8343-3

9.4.4. Conferences

1. **Moreno-Fernández D**, Cañellas I, Gordo J, Montero G, Nunes L, Piqué M, Calama R. 2017. Cone production of stone pine in Spain. Proceedings of the VIII Portuguese Forest Congress (Viana do Castelo, Portugal, October 11 – October 14, 2017). *Poster*
2. Rego F, Nunes L, **Moreno-Fernández D**, Alberdi I, Cañellas I. 2017. A procura de equações para estimar a produção de cortiça e de pinha na Península Ibérica a partir de variáveis de povoamento: um ensaio para Portugal. VIII Portuguese Forest Congress (Viana do Castelo, Portugal, October 11 – October 14, 2017). *Poster*
3. **Moreno-Fernández D**, Augustin NH, Montes F, Cañellas I, Bachiller A, Viscasillas E, Sánchez-González. 2017. Modelo espacio-temporal de regeneración del pino silvestre en la Sierra de Guadarrama. VIII Spanish Forest Congress (Plasencia, Spain, June 26 – June 30, 2017). *Oral presentation*
4. **Moreno-Fernández D**, Montes F, Sánchez-González M, Cañellas I. 2017. Regeneration in mixed-pinewoods in Mediterranean áreas. IV Jornadas de Jóvenes Investigadores de la ETSI Montes, Forestal y del Medio Natural. (Madrid, Spain, March 24, 2017). *Oral presentation*
5. **Moreno-Fernández D**, Hernández L, Sánchez-González M, Cañellas I, Montes F. 2016. Assesing shifts in the distribution and abundance of Mediterranean montane tree species in mountains using novel spatio-temporal kriging models. X Meeting of Young Researchers in Conservation and Sustainable Use of Forest Systems (Valsaín, Spain, January 25 – January 26, 2016). *Oral presentation*
6. **Moreno-Fernández D**, Díaz-Pinés E, Barbeito I, Sánchez-González M, Montes F, Rubio A, Cañellas I. 2015. Carbon temporal dynamics along the rotation period of two management systems in Mediterranean mountain forests. Mountain Forest Management in a Changing World conference (Smokovec, Slovakia, July 7 - July 9, 2015). *Oral presentation*
7. **Moreno-Fernández D**, Díaz-Pinés E, Barbeito I, Sánchez-González M, Montes F, Rubio A, Cañellas I. 2015. Trends of biomass carbon and soil organic carbon under two management systems in Mediterranean mountain forests. IX Meeting of Young Researchers in Conservation and Sustainable Use of Forest Systems (Valsaín, Spain, Januray 28 - Januray 29, 2015). *Oral presentation*

8. **Moreno-Fernández D**, Sánchez-González M, Cañellas I, Gea-Izquierdo G. 2014. Response to thinning and pruning of black pine. Medpine meeting 2014. (Solsona, Spain, September 22 –September 26, 2014). *Poster*
9. **Moreno-Fernández D**, Cañellas I, Sánchez-González M. 2014. Response to thinning and pruning of black pine. VIII Meeting of Young Researchers in Conservation and Sustainable Use of Forest Systems (Valsaín, Spain February 3 – February 5, 2014). *Poster*
10. **Moreno D**, Bachiller A, Calama R, Cañellas I, Gordo J, Sánchez-González M. 2013. Efecto de las claras tempranas en el crecimiento y la producción de piña en masas repobladas de *Pinus pinea* L. VI Spanish Forest Congress (Vitoria-Gasteiz, Spain, June 10 – June 14, 2013). ISBN: 978-84-937964-9-5 *Poster*
11. **Moreno D**, Calama R, Gordo J, Cañellas I, Sánchez-González M. 2013. Effect of the first thinning on cone production of stone pine (*Pinus pinea* L.) in the Northern Plateau (Spain). VII Meeting of Young Researchers in Conservation and Sustainable Use of Forest Systems (Valsaín, Spain, January 30 – February 1, 2013). ISBN: 978-84-695-8204-6 *Oral presentation*
12. **Moreno D**. 2012. Scots pine (*Pinus sylvestris* L.) management in Finland. VI Jornada de Jóvenes Investigadores en Conservación y Uso Sostenible de Sistemas forestales (Valsaín, Spain, March 27 – March 28, 2012). ISBN: 978-84-695-5280-3 *Poster*

9.4.5. Reviewer

I have reviewed manuscripts in the following journals (for confidential policies, the articles and authors are not shown):

1. Small-scale Forestry (1 paper)
2. Journal of Ecosystem & Ecography (1 paper)
3. Forests (1 paper)

9.5. Participation in research projects

AGL2016-76769-C2-1-R. Influencia del régimen de perturbaciones y la gestión en el balance de carbono, estructura y dinámica de las masas forestales. Project coordinator: Fernando Montes (INIA)

633464-DIABOLO H2020. DIABOLO. Distributed, integred and harmonised forest information for bioeconomy outlooks. Project coordinator: Tuula Packalen (Natural Resource Institute of Finland)

S2013/MAE-2760 BOSSANOVA-CM. Bosques Sanos y Variados: gestión sostenible en sistemas forestales de la CM en el contexto del cambio global. Project coordinator: Luis Gil (UPM)

388432-IGN EFDAC E-forest platform. Coordinator at INIA: Isabel Cañellas

AGL2013-46028-R La gestión forestal frente a los cambios en la dinámica de los ecosistemas forestales: un enfoque multiescala. Project coordinator: Fernando Montes (INIA)

9.6. Teaching

University	School of Forest Engineering and Natural Resources. Polytechnic University of Madrid
Academic year	2017-2018
Number of hours	30 hours
Subjects	Silviculture. Reforestations and nurseries.
University	School of Forest Engineering and Natural Resources. Polytechnic University of Madrid
Academic year	2016-2017
Number of hours	30 hours
Subjects	Silviculture. Reforestations and nurseries. Dasometry
University	School of Agrarian Sciences. University of Valladolid.
Academic year	2015-2016
Number of hours	30 hours
Subjects	Silviculture. Reforestations, nurseries and gardening

9.7. Short term missions

University	Department of Mathematical Sciences. University of Bath (England)
Date	April 16 th –July 14 th , 2016
Funding	FPU Short term program
Supervisor	Nicole H Augustin

9.8. Languages

Language	English
Reading	Good
Writing	Good
Speaking	Good

Appendix

Front page of articles published in SCI journals