Universitat de Lleida

Forest dynamics at the montane-subalpine ecotone in the Eastern Pyrenees

Dinámica de bosques del ecotono montano-subalpino en el Pirineo oriental

Aitor Ameztegui Gonzalez

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UNIVERSITAT DE LLEIDA
Departament de Producció Vegetal i Ciència Forestal

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TESIS DOCTORAL

Aitor Ameztegui Gonzalez

SOLSONA, 2013

CENTRE TECNOLÒGIC
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Universitat de Lleida

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Dinámica de bosques del ecotono montano-subalpino en el Pirineo oriental

Tesi presentada per **Aitor Ameztegui** per a optar al grau de Doctor per la Universitat de Lleida

El present treball ha estat realitzat sota la direcció del **Dr. Lluís Coll** (Centre Tecnològic Forestal de Catalunya) i tutorat pel **Dr. José Antonio Bonet** (Universitat de Lleida)

Solsona, Maig de 2013

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ABSTRACT

In recent decades, the Pyrenean forests have been exposed to changes in both land-use patterns and climate, which are expected to have profound implications on their future dynamics. The main objective of this thesis is to gain a better understanding of the dynamics of mixed-conifer forests constituting the montane-subalpine ecotone of the Pyrenees. For this, we identified the main environmental factors that drive the dynamics of these communities to then assess how changes in these factors may affect their future structure and composition. This work was done using a multiscale approach that allowed detecting the key factors determining the dynamics of these systems across different biological scales.

At a mountain-range scale, socioeconomic factors emerged as the main drivers of forest dynamics, leading to a high increase in forest cover (*encroachment*) and a severe canopy closure of the pre-existing stands (*densification*) (Chapter 2). In this context of change and at stand-scale, light availability appeared as the major factor driving the growth, mortality and morphological response of the three main conifer species in the Pyrenees: *Pinus uncinata*, *Pinus sylvestris* and *Abies alba* (Chapter 4). Moreover, we observed that aspect played an important role in defining the crown morphology and architecture of these species, affecting in turn light transmission through the canopy and light availability in the understory (Chapter 3). Short periods of extreme climate (drought, cold temperatures) critically affected the seedling performance of the abovementioned species, in particular for those growing at the extremes of their current elevational range. However, this effect was found to be mediated by abiotic and biotic factors acting at a microsite scale (Chapter 5). Finally, in Chapter 6 we used all the information gathered in previous chapters to parameterize an individual-based, spatially-explicit model of forest dynamics (SORTIE-ND) in order to simulate the future dynamics of the studied forests. The results of the simulations support the predictions of future biome changes in the Pyrenean subalpine forests, since *A. alba* and *P. sylvestris* may find appropriate conditions for colonizing mountain pine dominated stands due to land-use change-related forest densification and climate warming, respectively.

Keywords: forest dynamics, Pyrenees, global change, modeling, *Pinus uncinata*, *Pinus sylvestris*, *Abies alba*, montane-subalpine ecotone

RESUMEN

En las últimas décadas, los bosques del Pirineo han estado expuestos a importantes cambios – tanto en el clima como en los usos del territorio – que pueden tener profundas implicaciones en su dinámica futura. El objetivo último de esta tesis es comprender mejor la dinámica de los bosques mixtos de coníferas del ecotono entre los pisos montano y subalpino del Pirineo. Se pretende, en primer lugar, identificar los principales factores ambientales que controlan la dinámica de estas comunidades para, posteriormente, evaluar cómo afectará a su composición y estructura futuras los cambios en dichos factores. Para todo ello, se ha utilizado una aproximación a diferentes escalas espaciales.

A escala de cordillera, se pudo determinar que los factores socioeconómicos fueron los principales responsables de la expansión del bosque observada en las últimas décadas, provocando una sustancial colonización de zonas abiertas y una importante densificación de los bosques (Capítulo 2). En este contexto, la disponibilidad de luz en el sotobosque es el principal factor que rige el crecimiento, mortalidad y morfología de juveniles de las tres principales especies de coníferas en el Pirineo: *Pinus uncinata*, *Pinus sylvestris* y *Abies alba* (Capítulo 4). Además, se observó que la orientación juega un papel importante en la morfología y arquitectura de copa de estas especies, afectando a su vez a la transmisión de luz a través de la cubierta y a los valores de disponibilidad de luz en el sotobosque (Capítulo 3). Breves episodios de meteorología extrema (sequía, bajas temperaturas) pueden jugar un papel crítico en la supervivencia de plántulas de estas especies en los límites de su actual área de distribución, pero también se observó que este efecto puede ser amortiguado por factores, tanto bióticos como abióticos, que actúan a escalas espaciales más pequeñas, de microhábitat (Capítulo 5). En el Capítulo 6 se utilizó toda la información recopilada en los capítulos previos para parametrizar un modelo de dinámica forestal espacialmente explícito (SORTIE-ND) con el fin de simular la evolución de los bosques objeto de estudio de esta tesis. Los resultados de las simulaciones predicen un futuro cambio en la composición de estos bosques, ya que tanto *A. alba* como *P. sylvestris* podrían encontrar condiciones adecuadas para colonizar áreas actualmente ocupadas por *P. uncinata*, debido a la densificación del bosque o a un mayor crecimiento relacionado con un aumento de las temperaturas, respectivamente.

Palabras clave: dinámica forestal, Pirineos, cambio global, modelización, *Pinus uncinata*, *Pinus sylvestris*, *Abies alba*, ecotono montano-subalpino

RESUM

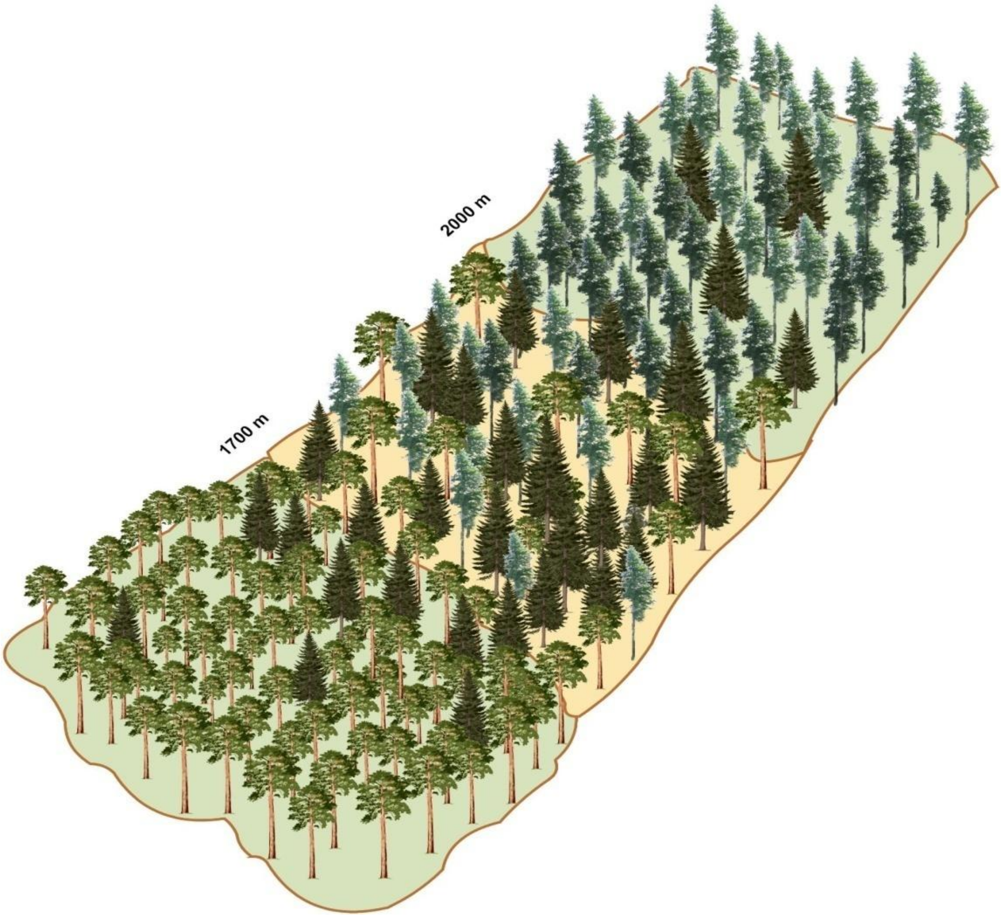
En les darreres dècades, els boscos del Pirineu han estat sotmesos a canvis importants – tant a nivell climàtic com en els usos del territori—que poden tenir profundes implicacions en la seva dinàmica futura. L'objectiu principal d'aquesta tesi és avançar en la comprensió de la dinàmica dels boscos mixtos de coníferes de l'ecotò que conformen els estatges montà i subalpí del Pirineu català. Es pretén, en primer lloc, identificar els principals factors ambientals que controlen la dinàmica d'aquestes comunitats per, posteriorment, avaluar com afectaran els canvis que es preveuen en aquests factors a la seva composició i estructura futura.Per assolir aquests objectius, la tesi utilitza diverses aproximacions a diferents escales espacials.

A nivell de paisatge, es va poder determinar l'important paper que diferents factors d'ordre socioeconòmic (èxode rural i abandó de les activitats agrosilvopastorals tradicionals) han jugat en la marcada expansió del bosc observada en les darreres dècades, i que s'ha traduït en una substancial colonització d'àrees obertes i una important densificació dels boscos (Capítol2). En aquest context, la disponibilitat de llum al sotabosc esdevé el principal factor que regeix el creixement, mortalitat i morfologia de juvenils de les tres principals espècies de coníferes del Pirineu: *Pinus uncinata*, *Pinus sylvestris* i *Abies alba* (Capítol 4). A més, es va observar que l'orientació juga un paper important en la morfologia i arquitectura de la capçada d'aquestes espècies, afectant a la transmissió de llum a través de la coberta i als valors de disponibilitat de llum al sotabosc (Capítol 3). Breus episodis meteorològics extrems (sequera continuada, fortes gelades) poden induir mortalitats importants en les plàntules d'aquestes espècies quan es desenvolupen als límits de la seva àrea de distribució actual. No obstant, s'ha observat que aquests efectes poden ser esmorteïts per factors, tant biòtics com abiòtics, que actuen a escales espacials més petites, de microhàbitat (Capítol 5). Finalment, en el Capítol 6 es va utilitzar tota la informació recopilada en els capítols previs per parametritzar un model de dinàmica forestal espacialment explícit (SORTIE-ND) per tal de simular l'evolució dels boscos objecte d'estudi d'aquesta tesi. Els resultats de les simulacions prediuen un futur canvi en la composició d'aquests boscos, ja que tant *A. alba* com *P. sylvestris* podrien trobar condicions adequades per colonitzar àrees actualment ocupades per *P. uncinata* a causa, respectivament, de la progressiva densificació del bosc i d'un major creixement relacionat amb un augment de les temperatures, respectivament.

Paraules clau: dinàmica forestal, Pirineus, canvi global, modelització, *Pinus uncinata*, *Pinus sylvestris*, *Abies alba*, ecotó montà-subalpí

1

Introduction



1. Introduction

1.1. Mountains and mountain forests

Mountains cover between a fifth and a quarter of the Earth's land surface, depending upon the criterion used to define them (Kapos *et al.*, 2000), and twenty percent of the human population live in mountains or in their near vicinities (UNEP-WCMC, 2002). The importance of mountainous areas is yet even greater, and over a half of the Earth's 7 billion people have been considered to depend on them for their subsistence (Price *et al.*, 2011). Mountain forests occupy a total of 9 million km^2, which represents a remarkable 23% of the Earth's forest cover (Price *et al.*, 2011). They cover a significant part of most mountain regions and represent the main forest reservoirs in mountainous countries where land conversion for agriculture, pasture and urbanization has significantly denuded lowland areas (Körner & Ohsawa, 2005).

Mountain forests provide a variety of essential goods and services including timber, fuelwood and non-timber forest products. They also play an important role for climate regulation and for the global C cycle as they store a considerable amount of terrestrial carbon (EEA, 2012). Due to their location in mountainous and hilly areas, the greatest value of mountain forests at the European scale is probably their role as regulators of the hydrological cycle (intercepting and retaining water and releasing it gradually, thus reducing peak stream flows) and as protectors of soil from erosion and degradation (EEA, 2012). Moreover, mountain ecosystems have high biodiversity, in terms of habitat and species richness and degree of endemism, in comparison with adjacent lowlands (UNEP-WCMC, 2002; European Commission, 2004; Price *et al.*, 2011). Finally, mountain forests also hold considerable spiritual, cultural and aesthetic values that make them very appreciated for recreation and tourism by an increasingly urban population. The variety of functions and services delivered by mountain forests demand a multifunctional approach that accounts for the different objectives and endures the sustainability of their management (Regato & Salman, 2008).

1.2. Mountain forests in the eastern Pyrenees: a case study

The Pyrenees extend in a west-east direction from the Atlantic Ocean to the Mediterranean Sea, covering 500 km^2 between France and Spain. This mountain range constitutes a transition zone between the Eurosiberian and the Mediterranean biogeographic regions of Europe. The western part of the range is affected by the mild and humid Atlantic air streams, whereas the central sector has more continental, cold, and dry climate, and the eastern area has an evident Mediterranean influence particularly at lower elevations, where many valleys evidence different degrees of summer drought.

As in every mountain system, the abrupt terrain of the Pyrenees induces strong changes in climate and an elevational zonation of vegetation, with aspect emerging as one of the main sources of environmental variation (Bugmann *et al.*, 2005). Furthermore, their position as a transition area between the two abovementioned biogeographic regions reinforces the differences in climate and land-cover between shade and sun slopes. According to Ninot *et al.* (2007), six main elevational vegetation units can be distinguished in the Pyrenees, with lower belts showing a clear Mediterranean character whereas higher elevations have equivalent conditions to most Medioeuropean mountains. In the Eastern Pyrenees, the basal belt (up to 800-900 m) is characterized by a mosaic of farmlands, meadows and forests (mainly composed by sclerophyllous and deciduous oak species such as *Q. ilex* ssp. *ballota, Q. humilis* and *Q. petraea)*, whereas the alpine and subnival belts are located, by definition, above the treeline. Conversely, forests are the most abundant land cover in the montane and subalpine belts, between 1200 and 2200 m (Burriel *et al.*, 2004), with three coniferous species (*Pinus sylvestris*, *Pinus uncinata* and *Abies alba*) constituting more than 80% of these forests. These species, and more precisely the mixed-conifer forests they constitute, are the object of study of the present work (Figure 1.1).

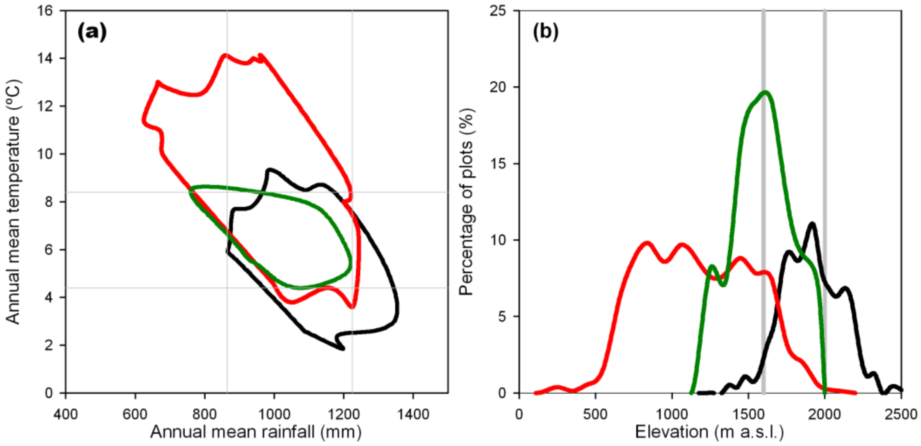


Figure 1.1 (a) Temperature and precipitation requirements of *Pinus uncinata* (black), *P. sylvestris* (red) and *A. alba* (green) based on their presence according to the Third Spanish Forest Inventory (b) Elevational histogram of the distribution of plots with presence of the same species according to the same data source. Own-made figures based on data available at the Third Spanish Forest Inventory (Direccion General para la Biodiversidad, 2007)

1.2.1. *Pinus uncinata* Ram. (mountain pine)

Mountain pine is the second most abundant tree species in the Catalan Pyrenees, where it covers around 70.000 ha (Piqué *et al.*, 2011b). It is a Eurosiberian, subalpine species that finds in the Pyrenees its greater distributional area (it is also present in the Jura, Vosges and western Alps). As a pioneer species (Niinemets & Valladares, 2006), it is able to grow on a wide range of soil conditions and is capable of colonizing open areas such as abandoned pastures and farmlands (Blanco *et al.*, 2005; Centre Tecnològic Forestal de Catalunya *et al.*, 2012). It tolerates cold, winter desiccation and frost better than the rest of the Pyrenean tree species (Cantegrel, 1983; Camarero & Gutiérrez, 1999; Ruiz de la Torre, 2006). Consequently, *P. uncinata* is the species with the highest elevational limit of the Pyrenees, reaching up to 2400-2500 m, and constitutes most of the Pyrenean timberlines, although it shows optimum performance at about 1800 m (Ninot *et al.*, 2007, 2008). The harsh environmental conditions that prevail on its distributional range usually limit the performance of other species, and thus more than 80% of the forests where this species is present are monospecific, particularly in the subalpine belt, above 2000 m (Burriel *et al.*, 2004; Piqué *et al.*, 2011b). Below this elevation, it progressively looses dominance in favor of other species, mainly Scots pine (*Pinus sylvestris* L.) and, in the most humid, north-facing slopes, silver fir (*Abies alba* Mill.).

1.2.2. *Pinus sylvestris* L. (Scots pine)

Scots pine is the most widely distributed conifer in the world, with a range that spreads through more than 14,000 km and covers more than 30º in latitude and 130º in longitude (Mason & Alía, 2000). The wide distributional range of Scots pine is a consequence of its high ecological adaptability, being able to survive on a wide range of substrates, soil types and climates (from cold, continental - to cool, wet, Atlantic and even Mediterranean) (Cañellas *et al.*, 2000; Ruiz de la Torre, 2006). Its fast-growing, heliophilous character has also contributed to the wide spread of this species, enabling it to outcompete other more demanding species and to colonize cleared lands to form second-growth forests (Cañellas *et al.*, 2000). Its morphological and physiological traits and ecological requirements significantly vary across its distributional range, and several sub-species and clima-types have been defined (Rehfeldt *et al.*, 2002; Ruiz de la Torre, 2006). For instance, *P. sylvestris* is the dominant species in the Alpine and Arctic treelines of Northern Europe (Kullman, 1987, 2005), where it is considered as a completely shade-intolerant species. In the most continental areas of its southern limit it is usually restricted to the montane belt and requires some lateral protection to regenerate

(Serrada *et al.*, 2008). In the Pyrenees, Scots pine is the most common tree species, covering more than 400,000 ha, one third of them in the Catalan Pyrenees (Piqué *et al.*, 2011b). In this area, it dominates the montane belt (between 1000 and 2000 m) mainly constituting regular, pure stands. At the extremes of its elevational range, *P. sylvestris* mixes with other species, mainly *P. uncinata* and *A. alba* at high elevation and *Pinus nigra* and several oak species (*Quercus ilex*, *Q. pubescens* and, less often, *Q. petraea*) in lower, humid areas (Ninot *et al.*, 2007).

1.2.3. *Abies alba* Mill. (silver fir)

Silver fir is a shade-tolerant, drought-sensitive species whose main distribution area is located in Central Europe, and that finds its southern limit of distribution in the Iberian peninsula (Aussenac, 2002; Blanco *et al.*, 2005). In the Pyrenees, it is mostly found on the northern side, whereas in the Spanish Pyrenees it covers 60,000 ha and is usually restricted to humid sites on north-facing, shady slopes with relatively deep soils and always above 1200 m a.s.l., where the risk of water stress is lower than in the surroundings (Aussenac, 2002; Macias *et al.*, 2006). Between 1400 and 1800 m a.s.l. *A. alba* tends to form dense, monospecific stands in the best sites (Aunós *et al.*, 2007). Nevertheless, silver fir forests have been subjected to intensive logging in the recent past, in some cases up to the late 1970s, and as a consequence its distribution area has been significantly reduced in favour of pioneer species such as pines (Macias *et al.*, 2006; Aunós *et al.*, 2007; Camarero *et al.*, 2011). Currently, the reduction in logging pressure and the shade-tolerant character of this species are promoting an expansion of silver fir by colonization of the understory of pine forests, and almost half of the Pyrenean forests where silver fir is present are mixed stands (Aunós *et al.*, 2007; Piqué *et al.*, 2011b). In the southernmost Pyrenean ranges, signs of climatically-driven silver decline are more and more reported (Macias *et al.*, 2006; Peguero-Pina *et al.*, 2007; Linares *et al.*, 2009; Camarero *et al.*, 2011).

1.2.4. Mixed-conifer forests

Despite the different elevational ranges and ecological requirements of *A. alba*, *P. sylvestris* and *P. uncinata* , the three species coexist in a strip located in the ecocline between the montane and subalpine elevational belts (between 1,600 and 2,000 m a.s.l., see Figure 1.1), constituting the mixed-conifer forests that are the object of study in this work. According to Piqué *et al.* (2011b), there are 21,898 ha in the Catalan Pyrenees in which at least two of these three species are present. The combination of *Pinus uncinata* and *P. sylvestris* is the most common mixed forest in the area, covering more than 15,000 ha (Figure 1.2). These forests are commonly located between 1,500 and 1,800 m a.s.l. (slightly above in the south-facing slopes), in areas with intermediate ecological conditions to those preferred by both species (Piqué *et al.*, 2011b). The phylogenetic proximity between these two species (Gernandt *et al.*, 2005; Climent *et al.*, 2010) and the coincidence of their floration period leads to the existence of morphologically intermediate forms between *P. uncinata* and *P. sylvestris* sometimes described as the hybrid *Pinus* x *rhaetica* Brügger (Probst & Rouane, 1984; Plumettaz Clot *et al.*, 1996; Jasinska *et al.*, 2010). However, recent studies show that introgression would only be possible via pollen flow from *P. uncinata* to *P. sylvestris* populations (Boratyńska & Boratyński, 2007; Jasinska *et al.*, 2010), and that hybrids are not frequent in natural conditions (Neet-Sarqueda, 1994; Boratyńska & Bobowicz, 2001; Centre Tecnològic Forestal de Catalunya *et al.*, 2012). Although there is great variability in the composition and structure of these forests, both species are often evenly represented in number and age classes. In the absence of large-scale disturbances, cuttings or environmental changes, this formation can be stable in time (Piqué *et al.*, 2011a).

The second most common mixed-forest is the combination of *P. uncinata* and *A. alba* (4,298 ha), whereas the *P. sylvestris* – *A. alba* forests cover 2,446 ha. These two types of forests are often the result of similar processes, and the presence of fir indicates either an advanced step in the recolonization of open areas by the pioneer pines or a reduction in cutting pressure after decades of intensive logging in pine stands. When the ecological conditions are optimal for the fir, this species tends to dominate due to the deep shade it casts, under which pines have difficulties to regenerate (Burriel *et al.*, 2004; Aunós *et al.*, 2007). According to Aunós *et al.* (2007), these mixed formations are often located in sites where the ecological conditions are suboptimal for a complete development of fir. Depending on the environmental conditions, these forests may ultimately evolve towards a fir-dominated, a pine-dominated or a mixed forest.

These mountain mixed-conifer forests fulfill a multitude of functions. Silver fir, mountain and Scots pine are among the most productive species of Catalonia in terms of growth and timber production (Burriel *et al.*, 2004). They also constitute favorable habitats for a wide community of plant and animal species that have been catalogued as of Communitary Interest by the European Union: for instance, this is the preferred habitat for endangered species such as western capercaillie (*Tetrao urogallus*), brown bear (*Ursus arctos*), black woodpecker

(*Dryocopus martius*) or Tengmalm's owl (*Aegolius funereus*). Ultimately, they are vital as regulators of the hydrological cycle and act as protectors from natural risks, and are also largely appreciated by their landscape and aesthetic values. The fulfillment of all these functions is largely dependent on the structure and composition of the forests. At present, there are many uncertainties on how the different components of global change will affect the future evolution of these ecosystems. A better understanding of their functioning and dynamics constitutes a first step to anticipate and adapt to these changes.

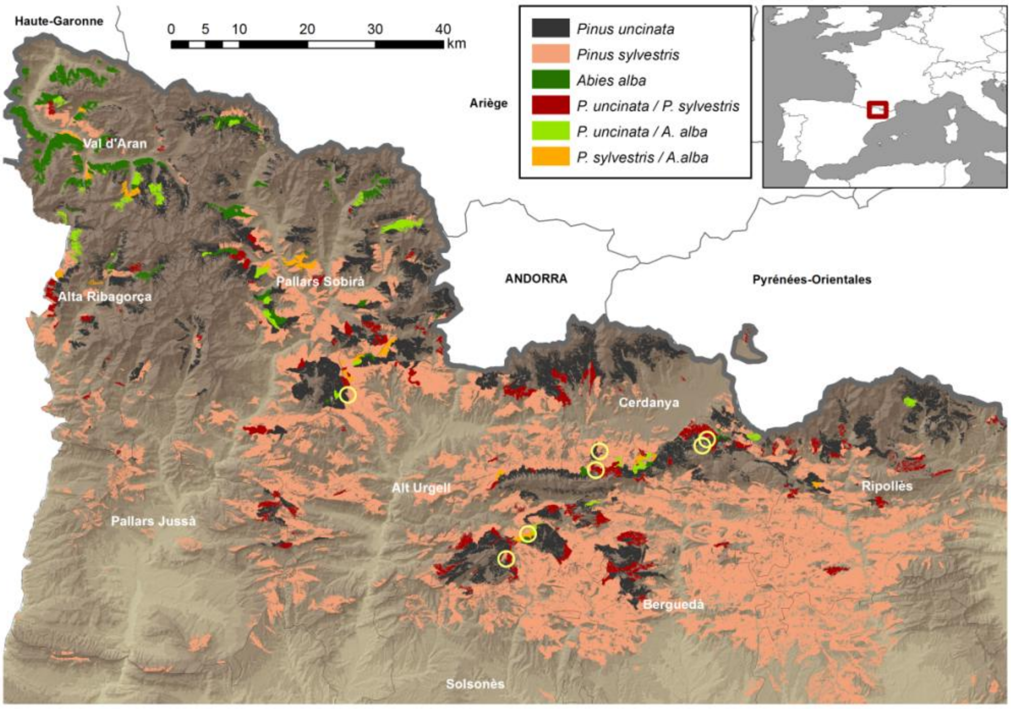


Figure 1.2. Distribution of the main forests of the studied species over the Catalan Pyrenees, and location of the study plots used for these work (yellow circles). Source: own elaboration based on data from Vericat *et al.*, (2010)

1.3. Drivers of change in the Pyrenean forests

Environmental and economic changes have been a constant in mountain areas, particularly in a region with such a long-history of anthropogenic influence as the Mediterranean basin (Körner & Ohsawa, 2005; Regato, 2008). Nevertheless, in the present global change context, the magnitude and the rate of change threaten to overcome mountain ecosystems, which are changing more rapidly than at any time in human history (Körner & Ohsawa, 2005). Changes in atmospheric CO_2 concentration, nitrogen deposition and acid rain, biotic interactions (mainly invasive species), climate and land use are considered as the major components of global change. All of them can have significant effects on forests, but their relative importance varies across biomes (Sala *et al.*, 2000; Chapin III *et al.*, 2001). For instance, mountain and alpine ecosystems are particularly susceptible to climate change (Beniston *et al.*, 1997; Theurillat & Guisan, 2001; Beniston, 2003), whereas land-use changes and invasive species may be more important factors of change in Mediterranean ecosystems (Regato & Salman, 2008; Lindner *et al.*, 2010). The Pyrenees show mixed characteristics of both Mediterranean and Alpine biogeographic regions of Europe and constitute a transition area between them. Consequently, both changes in land-use and climate can be expected to be the major drivers of biological change in these areas (Lindner *et al.*, 2010).

1.3.1. Climate change

The average temperature in Europe for the last decade was more than 1ºC above the pre-industrial values, and the rhythm of change has accelerated during the last decades, reaching 0.17 - 0.22ºC per decade over the last 20 years (IPCC, 2007; EEA, 2012). The change in temperatures has been particularly intense in high-elevation areas, where increases in the minimum daily temperature of more than 2ºC have been recorded over the last century (Bucher & Dessens, 1991; Beniston *et al.*, 1997; Diaz & Bradley, 1997). In contrast, annual precipitation records across Europe show no significant changes since 1950, although seasonal precipitation trends show an increase in winter precipitation in northern Europe and a decrease in southern Europe (EEA, 2012).

These abovementioned patterns are expected to intensify during next decades, and the IPCC Fourth Assessment predicts an increase in European average temperatures by 2.5ºC to 4ºC for the end of the 21st century (IPCC, 2007). Climatic models also predict changes in precipitation patterns, with a trend for humid areas to become more humid and for dry areas to become even drier (Figure 1.3). However, there is still a high degree of uncertainty in these projections, particularly in mountainous areas where the spatial resolution of general circulation models (GCMs) does not allow to capture the considerable regional and seasonal variability (IPCC, 2007).

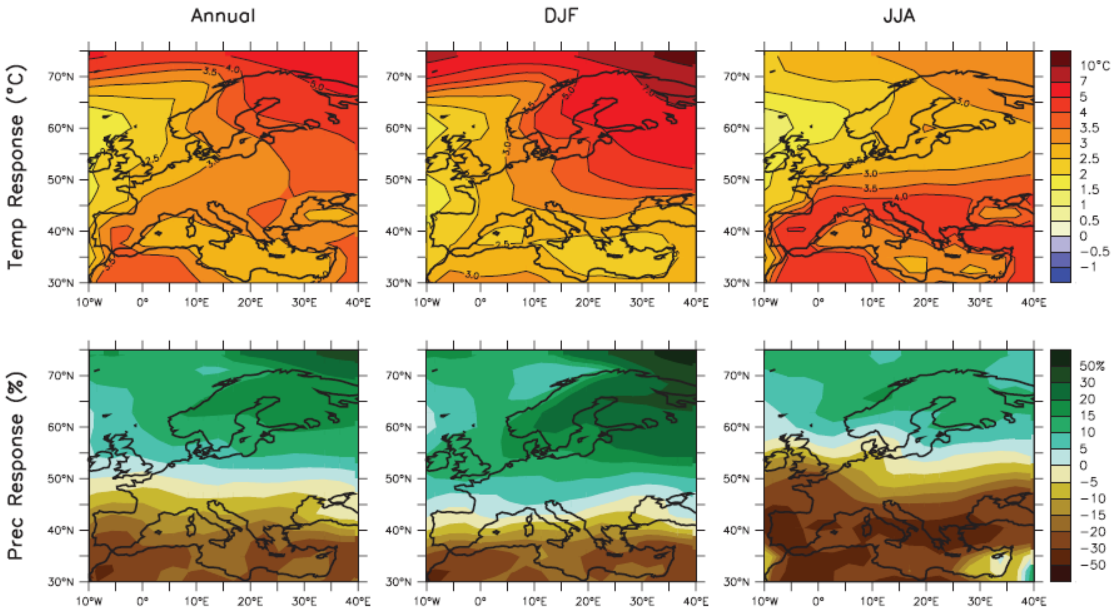


Figure 1.3. Temperature and precipitation changes over Europe from the MMD-A1B simulations. Top row: Annual mean, DJF and JJA temperature change between 1980 to 1999 and 2080 to 2099, averaged over 21 models. Bottom row: same as top, but for fractional change in precipitation. Source: IPCC (2007)

In recent years, the development of regional climatic models and downscaling methods has allowed to generate regionally-specific forecasts. This approach has been recently implemented in Catalonia using the MM5 mesoscalar model, leading to climatic projections at 15 km of spatial resolution (Grell *et al.*, 1994; Barrera-Escoda & Cunillera, 2011). For the Pyrenees, these models predict increases by 2.6ºC to 3.8ºC in mean annual temperature and reductions of 13.5% to 21.7% in precipitation by the end of the 21st century, depending on the considered socio-economic scenario (Barrera-Escoda & Cunillera, 2011).

1.3.2. Land-use changes

Mediterranean landscapes have been shaped by humans at least since the beginning of the Holocene, and from the Neolithic period, the cycles of forest expansion and regression have been coupled with human demography (Barbero *et al.*, 1990; Blondel, 2006). The Pyrenees are not an exception, and there are evidences of an intensive use of fire as a tool for creating pastures for at least the last three millennia (Bal *et al.*, 2011; Rius *et al.*, 2012). For centuries, cultivation was necessary to ensure food production for the population, and agriculture reached its maximum expansion at the end of the nineteenth century, the period with the greatest population density, when up to 35% of the Pyrenean landscape was cultivated (Garcia-Ruiz *et al.*, 1996; Lasanta, 2002; Vicente-Serrano *et al.*, 2005). Under the traditional system of land management, the need to reach self-sufficiency forced the societies to use all the available land resources by means of different cultivations and types of livestock (Lasanta *et al.*, 2005; Blondel, 2006). Farmlands were established in all the possible locations, even in steep slopes and poor soils (Garcia-Ruiz *et al.*, 1996). During summer, herds of cattle, sheep and horses grazed extensively summer pastures, which in some valleys comprised more than 30% of the territory. In these times, forest was thus restricted to the shady slopes between these two areas, and was intensively used as a source of timber and fuelwood and as a grazing area by transhumant herds in their way to the alpine grasslands.

From the beginning of the twentieth century, and particularly since the 1950's, the Pyrenees went through significant socioeconomic changes as a consequence of the development and liberalization of the Spanish economy and the integration of the mountain regions on the market economy (Lasanta, 2002). The development of communications between mountains and flat areas made difficult for the mountain products to compete with lowlands in the national economy (Garcia-Ruiz, 1988; Domínguez, 2002), leading to a sharp depopulation process (some municipalities lost more than 50-60% of their inhabitants in less than 30 years) (Lasanta, 1990; Molina, 2002)). As a consequence, the Pyrenees experienced a rapid transformation of exploitation systems and socio-economic organization of the landscape, similar to that previously experienced by other mountain systems of Western Europe, such as the Alps (MacDonald *et al.*, 2000; Chauchard *et al.*, 2007; Gellrich *et al.*, 2007). Within the new system, the most fertile areas (valley bottoms) are intensively exploited with important external economic and energy inputs (Lasanta, 2002), whereas the less accessible or productive farmlands – mostly slopes - are abandoned. The lack of workforce induces a progressive substitution of sheep herds by cattle, while the overall livestock pressure significantly declined (Lasanta, 1990).

The result of all these changes led to a progressive increase of scrubland and woodland areas by colonization of abandoned lands (Debussche *et al.*, 1999; Molina, 2002; Poyatos *et al.*, 2003; Lasanta *et al.*, 2005; Vicente-Serrano *et al.*, 2005). At the same time, population decline and replacement of forest resources by other sources of energy and materials also led to an accumulation of biomass in forests, leading to higher density and canopy closure (Poyatos *et al.*, 2003).

1.4. Responses of mountain forests to global change: the role of ecotones

Mountain areas are considered to be very sensitive to environmental changes, particularly to climate change (Grabherr *et al.*, 1994; Theurillat & Guisan, 2001; Beniston, 2003). There are three main ways in which tree populations can respond to rapid environmental changes: (i) persistence in the new conditions through genetic adaptation, phenotypic plasticity or ecological buffering; (ii) migration to track new conditions and (iii) extinction due to progressive reductions of growth rate and/or regeneration success (Aitken *et al.*, 2008).

The ability of trees to adjust their morphology or physiology, i.e. their plasticity, is one of the key processes that allows plants to survive and develop in different environments (Delagrange *et al.*, 2004; Vitasse *et al.*, 2010). Since environmental conditions, mainly resource availability, change continuously during the life-span of a plant, all species have developed some degree of acclimation potential (Bazzaz, 1979; Messier *et al.*, 1999). The ability to grow and survive in a given environment can be achieved by alternative combinations of physiological, morphological and architectural traits (Claveau *et al.*, 2002; Valladares & Niinemets, 2008) and being plastic has some associated metabolic costs and may not always be the most adequate way to ensure that a species will survive and compete in all possible environments. However, populations with a higher phenotypic plasticity are likely to have greater tolerance to changing environments and thus, in a global change context, plasticity can be decisive in their ability to adapt to the new conditions resulting from climate change (Aitken *et al.*, 2008).

Studies of range shifts over the last millennia show that tree species have migrated in latitude or elevation following changes in climate (Davis & Shaw, 2001), and most predictive models forecast significant upward or poleward shifts in species ranges over the next decades, along with the predicted increase in temperatures (Guisan *et al.*, 1998; Malcolm *et al.*, 2002; Thomas *et al.*, 2004; Guisan & Thuiller, 2005). In the last decades, considerable research effort has been devoted to assess if range shifts associated with climate change are yet occurring. Ecotones, as transition areas between adjacent biomes, are considered as the best zones to seek for early signs of responses of vegetation to changes in climate, and have consequently received much attention by ecologists (di Castri *et al.*, 1988; Neilson, 1993; Malanson, 1997). Most of this attention initially focused on treeline ecotones (*i.e.* the ecotone between subalpine forests and alpine or boreal grasslands), because the boundary between trees and grasslands is relatively easy to detect and their limits are in general thermally-defined (Kupfer & Cairns, 1996). Evidences of a northward or upward displacement of the treeline are numerous at high latitudes, both in North America (Lescop-Sinclair & Payette, 1995; Szeicz & Macdonald, 1995; Gamache & Payette, 2005) and Northern Europe (Kjällgren & Kullman, 1998; Juntunen *et al.*, 2002; Kullman, 2002). In mountain areas of southern Europe such as the Alps and the Pyrenees, upward displacement of some species has been reported (Lenoir *et al.*, 2008; Pauli *et al.*, 2012; Gottfried *et al.*, 2012), although the treeline seems to be more unresponsive and the effects of the increases in temperature are often more evident in terms of growth and changes in structure and density of trees in the ecotone than in a detectable movement of treeline position (Camarero & Gutiérrez, 2001, 2004; Dullinger *et al.*, 2004; Ninot *et al.*, 2008; Batllori *et al.*, 2009). This relative unresponsiveness may be related to the high intensity of human activities in the recent past (Grace *et al.*, 2002). In effect, it is now widely accepted that changes in anthropogenic pressure (mainly abandonment of pastures) have driven treeline position at least as much as climate(Cairns & Moen, 2004; Gehrig-Fasel *et al.*, 2007).

More recently, an increasing number of studies have focalized on montane-subalpine ecotones, considering that their position would mostly be associated with climatic gradients controlled by elevation (the role of anthropogenic disturbances being less important than in the treeline) (Noble, 1993; Kupfer & Cairns, 1996; Loehle & LeBlanc, 1996). In these areas, some studies have observed an upward displacement of montane species associated with climate warming (Peñuelas & Boada, 2003; Berger *et al.*, 2007; Lenoir *et al.*, 2008) and this pattern has been predicted for the next decades by most models, in particular those based on climate envelopes (Theurillat & Guisan, 2001; Malcolm *et al.*, 2002). However, the inverse, *i.e.* a downslope movement of subalpine forests into the montane belt, has also been reported (Hättenschwiler & Körner, 1995; Lenoir *et al.*, 2008; Bodin *et al.*, 2013), suggesting that climate is not the only factor driving the dynamics of these systems (Lenoir *et al.*, 2010)

The upper and lower limits of species' range are often not driven by the same ecological factor: for most mountain trees, temperature is the limiting factor at the upper limit, whereas competitive interactions or moisture are usually limiting at the lower boundary (Theurillat & Guisan, 2001; Vetaas, 2002; Lenoir *et al.*, 2010). On water-limited sites, growth and regeneration of the most drought-sensitive species is expected to decrease as a consequence of increased drought stress (Lindner *et al.*, 2010). This process has already been observed in some Mediterranean mountains, where the increase in temperatures experienced during the last decades has induced a progressive replacement of European beech (*Fagus sylvatica* L.) by Holm oak (*Quercus ilex* L.) (Peñuelas & Boada, 2003). In addition, signs of drought-induced decline has been recently reported for drought-sensitive species such as silver fir (*Abies alba* Mill.) growing in their southernmost distributional area (Macias *et al.*, 2006; Peguero-Pina *et al.*, 2007; Camarero *et al.*, 2011). Nevertheless, in ecosystems where water is not limitant, such as the montane-subalpine forests, the rear edge of species distribution is likely to be driven by competition with species from lower elevation (Vetaas, 2002; Lenoir *et al.*, 2010). In these areas, species currently limited by temperature can expect growth increases as a result of warming, whereas subalpine populations are unlikely to decline quickly due to climate warming (Lindner *et al.*, 2010). Consequently, the ability of species to migrate upwards tracking climate changes can be restricted by the slow upward retreat of subalpine species, whose decline, if existent, would come from unbalances in the dynamics of interspecific competition (Walther *et al.*, 2002; Aitken *et al.*, 2008).

Furthermore, human activities not linked to climate change can also drive the future dynamics of the montane-subalpine forests. For example, the drastic reduction in logging experienced during the last decades has caused an increasing lag between forest growth and timber uptake (Poyatos *et al.*, 2003; Bodin *et al.*, 2013). As a consequence, many mountain forests have experienced a process of maturation and canopy closure that has favored the establishment of advanced regeneration of shade-tolerant species (Poyatos *et al.*, 2003; Aunós *et al.*, 2007).

In short, the ecological implications of climate and land-use changes and their effects on mountain forest ecosystems are difficult to assess and quantify. A thorough assessment of the future dynamics of these forests may require, first, to distinguish the main factors that create and maintain the position of the ecotone and then, to assess how the different components of global change may affect the main processes within the ecotone (Weinstein, 1992). In most cases, vegetation belts would probably not migrate as a whole entity, and individual species will respond in different ways to the several factors that condition them, changing plant species competitiveness and probably leading to disruption in community compositions (Parmesan, 2006; Lindner *et al.*, 2010; Lenoir *et al.*, 2010). Thus, predicting the fate of these forests in a rapidly changing environment may require the integration of knowledge on the effects of different factors acting across several biological scales (Aitken *et al.*, 2008).

1.5. **Modeling as a tool to study forest dynamics**

During the last decades, an impressive number of models (with different degrees of complexity) have been developed with the objective of better assessing the future dynamics of forest ecosystems at stand-scale (Canham *et al.*, 2003; Aitken *et al.*, 2008). Most of these models can be considered as derived from JABOWA, initially developed by Botkin *et al.* (1972) for hardwood forests of North America, and FORET, created by Shugart & West (1977). The "JABOWA-FORET" family of models, also called "gap models" simulate the fate of a forest as a composite of many small patches of land, each of them being able to have a different age and successional stage (Bugmann, 2001). In this type of models, the position of individual trees within a patch is not considered and successional processes are described on each patch separately (Bugmann, 2001). Although some more recent versions of the FORET models, such as ZELIG (Urban *et al.*, 1991), include the effects of local competition by tracking individuals inside each patch, the spatial interaction is not complete, and processes such as seed dispersal are still simulated globally.

More recently, with the progressive increase in computational power, forest models have become increasingly detailed in their description of local interactions among trees. For example, individual-based, spatially-explicit models such as SORTIE (Pacala *et al.*, 1993, 1996) can incorporate functions for local competition and dispersal, as they predict the fate of every individual tree in the stand throughout its life. In this type of models, trees occupy individual spatial positions, and processes of tree birth, growth and mortality are simulated on an individual-by-individual basis using species-specific characteristics (Pacala *et al.*, 1993; Kupfer & Cairns, 1996). This permits a better simulation of fine-scale spatial processes such as the death of an individual tree, neighborhood competition for resources (Canham *et al.*, 2004, 2006; Canham & Uriarte, 2006), seed dispersal (Ribbens *et al.*, 1994) or seedling establishment (Papaik & Canham, 2006), which are all important drivers of forest dynamics (Canham *et al.*, 1990, 1994; Pacala & Deutschman, 1995). This type of models allows simulating the effects of large-scale disturbances such as windthrow (Canham *et al.*, 2001; Papaik & Canham, 2006), insect outbreaks (LeGuerrier *et al.*, 2003; Coates & Hall, 2005; Papaik *et al.*, 2005) or even hurricanes (Uriarte *et al.*, 2005; Uriarte & Papaik, 2007; Canham *et al.*, 2010). Yet more interestingly, they can be used to assess the role that silvicultural treatments of different intensity and spatial organization can have on forest dynamics, as well as their interaction with the abovementioned disturbances (Beaudet & Messier, 2002; Beaudet *et al.*, 2002, 2011).

Although they were not initially conceived and designed with this purpose, distance-dependent, individual-based models have also been successfully used to assess the dynamics of forest communities under diverse scenarios of climate and land-use change (Loehle, 2000).

It has been argued that mechanistic or process-based models, which are able to determine how ecosystem functions (physiology, growth, carbon allocation, etc.) vary over time when affected by climate may be more suitable to test the responses of plant communities to changes in environment (Loehle & LeBlanc, 1996; Pitelka *et al.*, 2001). Indeed, these models are more realistic in simulating the physiological processes involved in ecosystem functions, but as a counterpart they are usually more complex, difficult to parameterize, time-demanding to run, and often harder to interpret and analyze (Pitelka *et al.*, 2001; Reynolds *et al.*, 2001; Didion *et al.*, 2009). The need to optimize among generality, realism and accuracy has been a constant in ecological modeling since the early times of the discipline (Levins, 1966; Didion *et al.*, 2009), and it is clear now that higher complexity does not always lead to higher accuracy (Astrup *et al.*, 2008; Kimmins *et al.*, 2008). Both simplest and most complex models commonly perform poorer predictions, the former due to a poor approximation to the modeled system and the latter for the bias in parameter estimation (Pacala *et al.*, 1996; Astrup *et al.*, 2008).

In summary, individual-based models have a number of qualities that make them suitable for examining forest responses to global change (Kupfer & Cairns, 1996). Their main strength is that they provide scientists with useful research tools to increase our understanding of forest dynamics, identify uncertainties and future experiments to cover these uncertainties (Pitelka *et al.*, 2001), which makes them valuable tools for both scientific and management purposes.

1.6. **Objectives and structure of the doctoral thesis**

The main objective of the doctoral thesis is to deepen the knowledge on the main factors that drive the dynamics of mixed-conifer forests in the eastern Pyrenees. Since these drivers can be different across spatial and temporal scales, this objective has implied working at different scales, from micro-habitats to landscape and regional levels, consequently using different approaches and tools. The thesis has been organized in chapters, written in the format of scientific articles, with the aim of publishing them in international, peer-reviewed, scientific journals. The first study (Chapter 2) consisted on a regional-scale analysis of the patterns and drivers of forest expansion using aerial photographs. Chapter 3 aimed at assessing how aspect can induce changes in the crown and canopy of the main species dominating the Pyrenean mountain forests (*Abies alba, Pinus sylvestris* and *Pinus uncinata*), leading to variations in the availability of resources at the understory. In Chapters 4 and 5 we assessed the effects of light availability, temperature and other biotic and abiotic factors on the performance of juveniles (seedlings and saplings) of the three studied species. Finally, in Chapter 6 we used a model of forest dynamics to determine the role of temperature-induced variations of growth and initial composition in the future dynamics of mixed-conifer forests.

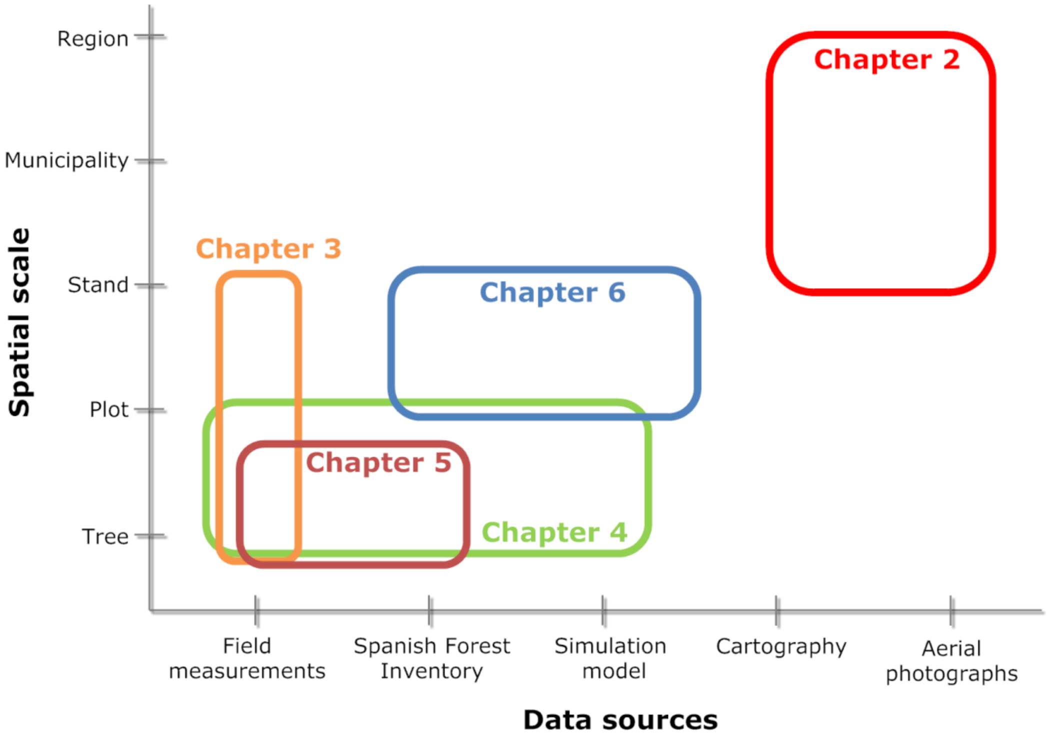


Figure 1.4. Data source and spatial scale of the thesis chapters

At the moment, 4 of the chapters have already been published (Chapters 2, 3, 4 and 5) and the last one will be sent for publication within the next weeks.

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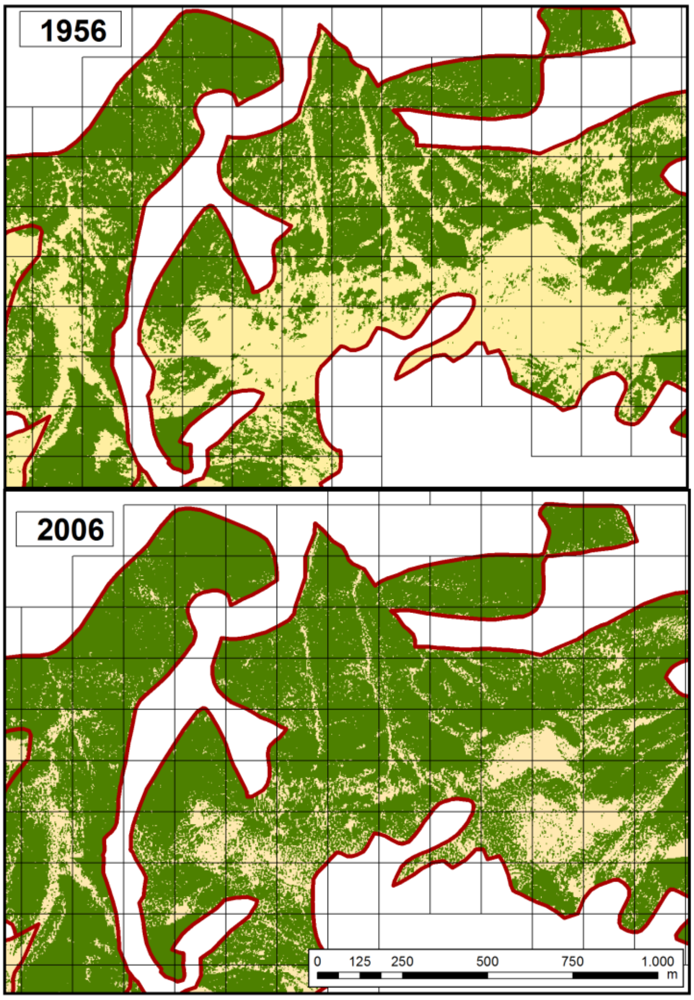
Land-use changes as major drivers of mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees

2



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2. Land-use changes as major drivers of mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees

Abstract

Aim To assess the spatial patterns of forest expansion (encroachment and densification) for Mountain pine (*Pinus uncinata* Ram.) during the last 50 years in a whole mountain-range scale by the study of different topographic and socio-economic potential drivers in the current global-change context.

Location The study area includes the whole distributional area of Mountain pine in the Catalan Pyrenees (NE Spain). This represents more than 80 municipalities, covering a total area of 6,018 km^2.

Methods Forest cover was obtained by image reclassification of more than 200 pairs of aerial photographs taken in 1956 and 2006. Encroachment and densification were determined according to changes in forest cover, and were expressed as binary variables on a 150x150m cell-size grid. We then used logistic regression to analyze the effects of several topographic and socio-economic variables on forest expansion.

Results In the period analyzed, Mountain pine increased its surface coverage by 8,898 hectares (an increase of more than 16%). Mean canopy cover rose from 31.0% in 1956 to 55.6% in 2006. Most of the expansion was found on north-facing slopes and at low altitudes. Socio-economic factors arose as major factors of Mountain pine expansion, as encroachment rates were higher at municipalities with greater population losses or weaker primary sector development.

Main Conclusions The spatial patterns of Mountain pine expansion highly matched the main patterns of land-use change in the Pyrenees, suggesting that land-use changes have played a more determinant role than climate in driving forest dynamics at landscape scale over the period studied. Further studies on forest expansion at regional scale should incorporate patterns of land-use changes to correctly interpret drivers of forest encroachment and densification.

Keywords: Mountain pine, Pyrenees, encroachment, densification, land-use changes, global warming, canopy cover, image reclassification

2.1. **Introduction**

Despite the high rates of deforestation measured worldwide, forest cover in most developed countries is on the increase (Coop and Givnish, 2007; Gellrich et al., 2007a; Gellrich and Zimmermann, 2007). Although this increase is mainly caused by forest encroachment into open areas, there has also been an increase in canopy cover of pre-existent forests, either through enhanced growth of pre-existent individuals or the recruitment of new ones (densification) (Poyatos *et al.*, 2003; Gehrig-Fasel *et al.*, 2007). Forest expansion (including both encroachment and densification) does not occur homogenously at the local scale, as it is determined by both natural and cultural factors, such as local recent livestock pressure (Dirnböck et al., 2003; Lasanta-Martinez et al., 2005; Coop and Givnish, 2007), topographic factors (Poyatos et al., 2003; Gellrich and Zimmermann, 2007) and locally dominant ecological and socio-economic conditions, among others (Debussche *et al.*, 1999). However, these drivers usually act at different scales: for example, the decision to abandon a farmland depends on socio-economic factors, and subsequent changes in land cover will be modulated by ecological processes, which in turn are associated with environmental and climatic conditions (Rutherford *et al.*, 2008). Therefore, researchers have studied land-cover change at a wide range of spatial scales, from small plots to entire mountain ranges. Local-scale approaches based on the study of plots usually employ dendrochronology methods (Camarero and Gutierrez, 2007; Chauchard et al., 2007), while at larger spatial scales, land-cover changes have mainly been assessed by comparison of aerial photographs (Miller, 1999; Coop and Givnish, 2007; Gellrich et al., 2008). Lastly, changes in large areas (covering thousands of square kilometres) have mainly been analyzed using remote sensing techniques (Gellrich and Zimmermann, 2007; Millington et al., 2007). Although attempts have been made to integrate these scales (Jump et al., 2006; Lasanta and Vicente-Serrano, 2007; Gellrich et al., 2008; Rutherford et al., 2008), this is still one of the major challenges facing the study of forest expansion, since a holistic view is required in order to better understand the drivers underlying these processes.

Many European mountain areas have recorded a significant increase in temperatures since the 1940s (Diaz and Bradley, 1997). Mountain ecosystems, especially areas located at high altitude, are considered particularly vulnerable to climate change (Dirnböck *et al.*, 2003; Camarero *et al.*, 2006). Forest encroachment in these systems has often been attributed to global warming, which may favour conditions for tree recruitment and growth near or beyond the tree line (MacDonald et al., 1998; Peñuelas and Boada, 2003b; Camarero and Gutierrez, 2004; Camarero et al., 2006; Batllori and Gutierrez, 2008). Nevertheless, over the last century, European mountain systems have suffered not only global warming but also major demographic, economic and organizational changes (Garcia-Ruiz *et al.*, 1996; Hofgaard, 1997; Dirnböck *et al.*, 2003). Therefore, land-use changes must be considered as a major potential factor driving forest expansion, especially in areas exposed to significant human influence, such as north-Mediterranean basin (Dale, 1997; Sala *et al.*, 2001; Chauchard *et al.*, 2007; Gehrig-Fasel *et al.*, 2007; Gellrich *et al.*, 2007b; Millington *et al.*, 2007).

In order to integrate the different scales at which forest expansion acts and segregate climate change from land-use change as drivers of forest expansion, we performed the analysis on Mountain pine (*Pinus uncinata* Ram.), a species that grows in the subalpine belt of the Central and Eastern Pyrenees, where it constitutes most of the tree lines. We employed a multi-scale approach comparing hundreds of pairs of aerial photographs. Though this technique is widely used for assessing forest encroachment (Poyatos et al., 2003; Coop and Givnish, 2007; Gellrich et al., 2008), it has rarely been employed for regional-scale studies. Furthermore, the densification process has been extensively studied along the tree line from a dendro-ecological, climate-related standpoint (Szeicz and Macdonald, 1995; MacDonald et al., 1998; Camarero and Gutierrez, 2004; Batllori and Gutierrez, 2008) but has never, to our knowledge, been quantified at landscape scale, despite reports establishing its important role in land-cover change contexts (Poyatos et al., 2003; Gehrig-Fasel et al., 2007; Lasanta and Vicente-Serrano, 2007).

The main objectives of this study were (i) to assess spatial patterns of Mountain pine encroachment and densification in the Eastern Pyrenees at both local and regional scale, and (ii) to infer the main factors driving these processes. Our main hypothesis is that if climate change is the main driver of Mountain pine expansion, encroachment and densification will be more evident at high altitudes, near the tree line. In contrast, if the primary drivers are changes in land-use, then spatial patterns of expansion should match reported spatial patterns of land-use changes.

2.2. Materials and methods

2.2.1. Study area

2.2.1.1. Location and description of the study area

The Pyrenees is a mountain range that spreads from east to west along the French and Spanish border, with an extension of more than 50,000 km^2. The study area is located southeast of the axial zone of the range, and includes the 83 municipalities of Catalonia with current presence of Mountain pine, thus covering a total area of 6,018 km^2 (Fig. 2.1).The abrupt terrain of the study area, with altitude ranging from 500 to more than 3,000 m a.s.l., in conjunction with the proximity of Mediterranean Sea creates significant climatic variation. Thus, the highest areas are representative of mountain climate (mean annual temperature below 3ºC, precipitation over 1400 mm), while the valley bottoms present much temperate conditions (mean annual temperature over 12ºC, precipitations below 700 mm), and show some traits of mediterraneity in the eastern zone. Vegetation is also strongly influenced by this double altitude-mediterraneity gradient. With valley bottoms supporting most conventional human activities, the montane belt (600-1600 m a.s.l.) is dominated by beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) in humid areas, while Scots pine (*Pinus sylvestris* L.) dominates the dryer ones. The Alpine belt (over 2300 m a.s.l.) is highly conditioned by cold temperatures and only supports herbaceous vegetation, while the subalpine belt (1600-2300 m a.s.l.) is dominated by Mountain pine (*Pinus uncinata* Ram.), which can grow in all kinds of soils and forms most of the central and eastern Pyrenean tree lines.

2.2.1.2. Climatic and land-use changes in the Pyrenees

Over the last 50 years, the Pyrenees have gone through major changes in land-organisation (Garcia-Ruiz, 1988; Garcia-Ruiz and Lasanta, 1990). Until the mid-20th century, all the resources needed by local societies had to be obtained locally, and thus landscapes were highly influenced by human activities (Lasanta, 2002; Lasanta and Vicente-Serrano, 2007). Since then, strong depopulation trends in rural areas led to many farmlands being abandoned, while the crisis affecting the transhumance system led to a sharp decline in livestock (Garcia-Ruiz, 1988; Domínguez, 2001). Therefore, human-driven pressure concentrated on the most productive areas, especially valley bottoms, while the hillslopes were exposed to high risk of abandonment (Garcia-Ruiz, 1988; Garcia-Ruiz and Lasanta, 1990). Along with these land-use changes, climate in the Pyrenees has also changed during the last century, with annual mean temperature and annual mean minimum temperature increasing by 0.83ºC and 2.11ºC, respectively (Bucher and Dessens, 1991). These temperature increases are similar to those measured in other European mountain ranges, including the Alps (Dirnböck *et al.*, 2003).

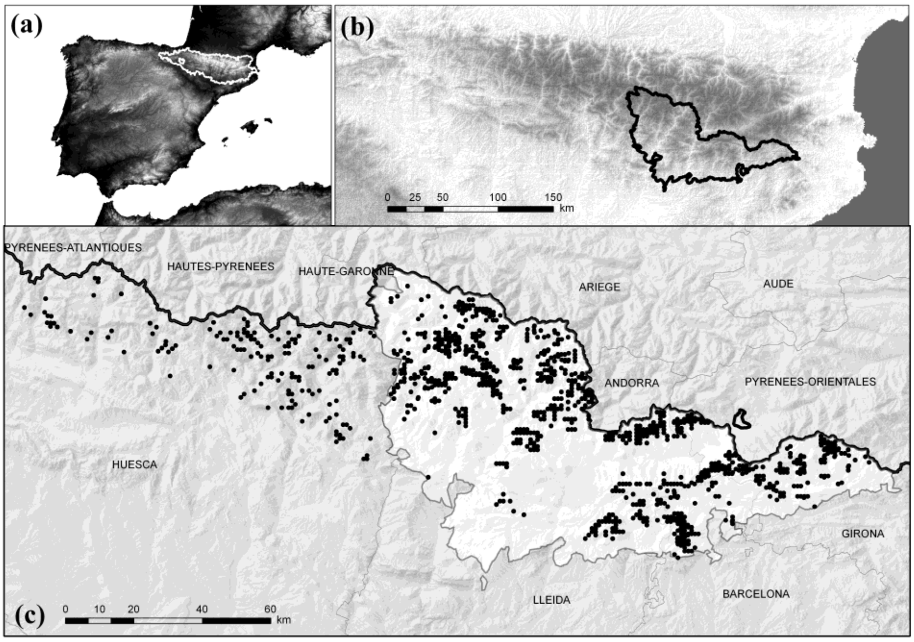

Figure 2.1 Location of study area showing (a) Pyrenees mountain range; (b) study area inside the Pyrenees; (c) current distribution of Mountain pine in Spanish Pyrenees and in study area (white shaded) according to Third National Forest Inventory (Direccion General para la Biodiversidad, 2007).

2.2.2. Data preparation and determination of forest cover

To investigate changes in Mountain pine distribution and canopy cover, we conducted a GIS analysis by comparing more than 200 pairs of aerial photographs taken in 1956 and 2006 and covering the whole surface of the study area. The 1956, grey-scale photographs (with a resolution of 1 m)) were geo-referenced and orthorectified. For each 1956 photo, at least 15 ground control points were identified, and a digital elevation model (DEM) was added in order to incorporate altitude coordinates. Each 1956 and 2006 image was semi-automatically reclassified into a binary raster with ’tree’ and ‘non-tree’ values, and with a resolution of 1 meter (Fig. 2.2), and all the 1956 and 2006 reclassified images were stitched into mosaics. A 150x150 m sampling grid was created covering the whole 6,018 km^2 study area, as this cell size (2,25 ha) matches the minimum area considered in the Map of Habitats of Catalonia (MHCat) (ICC, 2004). For each cell of the sampling grid, canopy cover in 1956 and 2006 were determined as the ratio between the amount of ‘tree’ pixels and the total number of pixels in the cell, expressed as percentage. A threshold of 10% canopy cover was used to distinguish 'forested' from 'not-forested' cells. This threshold is also used in the Spanish National Forest Inventory (Direccion General para la Biodiversidad, 2007).

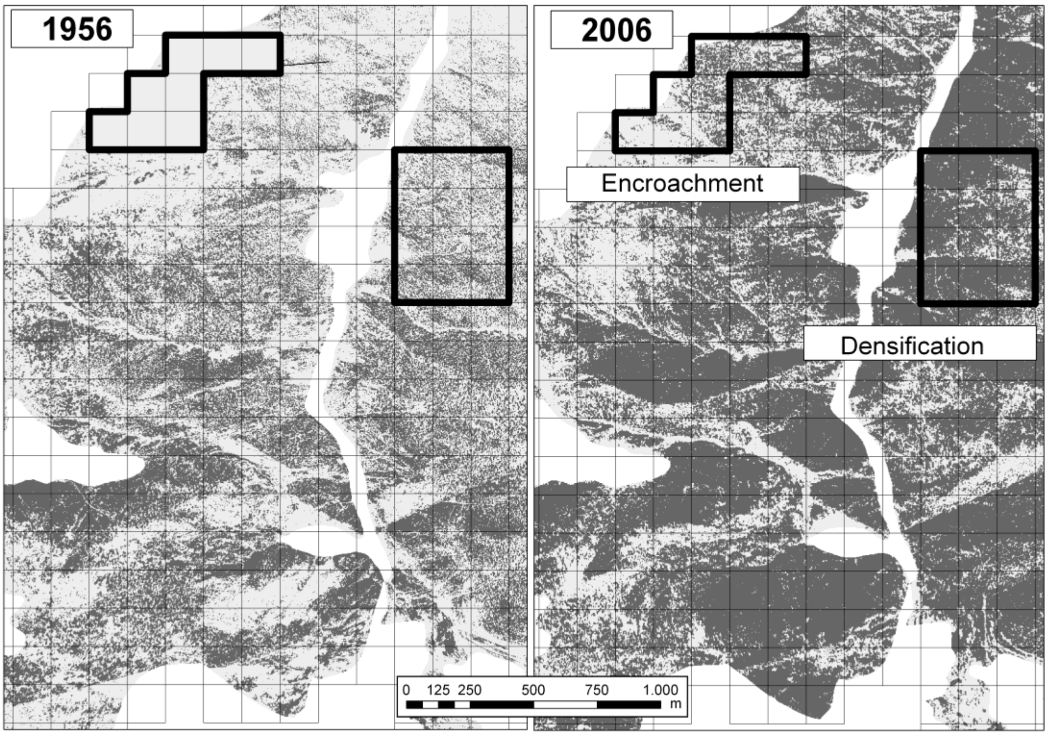

Figure 2.2 Example of 1956 (left) and 2006 (right) aerial photographs, reclassified into a binary variable to show Mountain pine distribution. Thin solid lines correspond to 150x150 m sampling grid, while thick solid lines correspond to examples of encroachment and densification processes.

2.2.3. Dependent variables

2.2.3.1. Encroachment (Colonization)

Current distribution of Mountain pine (Mp06) was obtained by intersecting the sampling grid with the MHCat, while distribution of Mountain pine in 1956 (Mp56) was obtained by removing those sampling-grid cells qualified as 'not forested' in 1956. Encroachment was assessed by establishing a 200 meters buffer around each Mp56 patch, as seed dispersion is unlikely to occur beyond this distance (Dullinger *et al.*, 2004). All land-cover types where encroachment was not possible (*e.g.* lakes, rivers, reforested and stony areas) were excluded from the analysis. Encroachment was then assessed using a binary approach. To minimize sampling errors associated to the use of aerial photographs, we only defined as encroached those cells with no tree cover in 1956 (i.e. tree cover = 0) and with more than a 10% increase in canopy cover in the studied period (Fig. 2.2). Deforestation processes (areas covered by

Mountain pine in 1956 but not in 2006) were not taken into account, as clear-cuts and deforestation are scarce, with shelterwood, group and selection systems being the only treatments applied on Mountain pine forests since the early 20th century (Gonzalez, 2008).

2.2.3.2. Densification

Forest canopy cover can increase due to growth of pre-existent individuals as well as recruitment of new ones (densification). Our focus was on densification, so in order to separate these two processes, only those cells with a 1956 canopy cover of between 10% and 40% were considered in the analysis. Cells with a canopy cover lower than 10% were considered as 'not forested' and therefore not susceptible to undergo densification processes. Areas with canopy cover greater than 40% were also excluded on the basis that recruitment was impossible. In fact, a Mountain pine stand with a canopy cover of 40% corresponds to an average density of 600 trees·ha^{-1}, which is the recommended threshold to start selection thinning (Gonzalez, 2008) and therefore wholly unsuitable for recruitment of new individuals. Furthermore, as a conservative measure aimed at assuring that only recruitment processes were taken into account, only areas showing more than a 30% increase in canopy cover were considered as densified due to recruitment (Fig. 2.2).

2.2.4. Potential factors driving land-use changes

A set of topographic and land-use variables were selected as potential drivers of Mountain pine encroachment and densification. The topographic variables included *altitude*, *slope* and *aspect*. These three variables were obtained from a Digital Elevation Model (DEM) with a resolution of 150 meters, as expansion was assessed on a 150x150 m grid. *Aspect* was pre-transformed into a *shade index* to more adequately reflect variation between north and south aspects (Table 2.1). Thus, shade index increased from 0º at south aspects to 180º at north aspects, with east and west aspects given a value of 90º.

Land-use changes have affected forest expansion by two main processes: land abandonment and reduction of livestock density (Lasanta, 2002). However, these processes cannot be directly determined, as there is no local-level information on farmland extension or livestock densities for 1956. Indirect measures or proxies based on current available indicators provide an alternative approach. *Farmland abandonment* during the second half of the 20th century is strongly tied to depopulation and to changes in economic structure (Lasanta, 2002). Therefore, the variable *population change*, defined as the ratio between population in 2001 and population in 1951, was included in the models. In addition, *population density*, defined as the total population in 2001 in relation the municipality's surface area in square kilometers; and *importance of primary sector*, defined as the proportion of primary-sector-dedicated employees (agriculture and stockbreeding) were used to assess differences in economic structure among municipalities (Table 2.1). As mentioned above, current livestock density is also a determinant of forest expansion. Garcia-Ruiz & Lasanta (1990) observed that, at municipality level, livestock density was highly correlated with the extension of both subalpine pastures and lowland meadows. Therefore, influence of current livestock density on forest expansion was assessed by incorporating *proportion of meadows* and *proportion of pastures* for each municipality into the models (Table 2.1).

Table 2.1 Covariates included in the model, indicating source, resolution and descriptive statistics

Variable	Source	Resolution	Mean	Std. Dev.	Min.	Max.	Range
Topographic							
Altitude	DEM	150 m	1984.3	256.1	1340.2	2514.9	1174.7
Slope	DEM	150 m	44.5	20.5	0.0	146.0	146.0
Shade Index	DEM	150 m	70.2	45.2	0.0	180.0	180.0
Socio-economic							
Proxies for farmland abandonment							
Population change	INE	Municipality	84.5	46.6	16.0	214.0	198.0
Population density	INE	Municipality	7.7	17.5	0.7	371.0	370.3
Imp. Primary Sector	IDESCAT	Municipality	13.9	8.9	0.0	53.0	53.0
Proxies for reduction of livestock density							
% meadows	IDESCAT	Municipality	1.7	3.5	0.0	29.7	28.0
% pastures	IDESCAT	Municipality	42.4	18.4	2.4	80.2	77.8

DEM: Digital elevation model; INE: Spanish National Statistics Institute; IDESCAT: Catalan Statistics Institute

2.2.5. Statistical analyses

As both response variables (encroachment and densification) were represented using a binary approach, they were modeled by logistic regression. This kind of model has been extensively used to assess land-cover changes, as they are commonly expressed as discrete variables (Carmel et al., 2001; Serneels and Lambin, 2001; Munroe et al., 2004). Since logistic regression is based on the assumption of independence among observations, spatial autocorrelation for both response variables was tested using Moran's *I* statistic. Since both response variables showed high autocorrelation, regular subsampling tools were applied. Subsampling is based on a sample-size reduction that causes distance between observations to increase, so only spatially-independent data are analyzed (Munroe *et al.*, 2004).

Semivariograms were constructed, and the range (the distance after which semivariance stabilizes) was determined as approximately 400 m for both datasets. Therefore, as the sample grid was 150x150 m, only one of each three points in both the *x* and *y* axis was sampled.

Given that most socio-economic variables were taken at municipality level and that these factors may have an influence on both response variables, observations belonging to the same municipality may not be independent from one another (cluster-correlated data), so we followed the recommendations of Muller & Munroe (2005) and used a robust estimator based on the Huber-White or 'sandwich' estimator (Williams, 2000).

Low levels of collinearity were found among the covariates. The coefficients of determination (R^2) of one variable against all the others ranged from 0.02 to 0.59, which are in all cases below the critical value of 0.80 set by Menard (2002). All independent variables were therefore used in the models. Evidence of non-linearity between the independents and the logit of the dependent were not found for any of the models, and thus variable transformation was not required. In order to get the most parsimonious models, a stepwise procedure was performed to remove non significant variables. Significance of covariates was tested using Wald statistic, and odds-ratios for each covariate were estimated. Model accuracy was tested by Nagelkerke's R^2 and area under the receiver operating characteristic (ROC curve). The area under the ROC curve (AUC) gives the probability that the model will properly distinguish between presence and absence of the studied process, so predictions by chance would correspond to a value of approximately 0.5 (Gellrich *et al.*, 2007a).

2.3. **Results**

2.3.1. Changes in Mountain pine forests

In 1956, Mountain pine covered 55,196 ha, with an average canopy cover of 54.3%. By 2006, it had colonized 8,898 new hectares to reach a total of 64,074 ha, *i.e*. a 16.1% increase in surface area. Mean canopy cover in 2006 had reached 60.9%. However, to assess this process correctly, changes in canopy cover should only be considered for the areas susceptible to densification (canopy cover lower than 40% but higher than 10% in 1956, see methods for further detail). Taking this into account, mean canopy cover in 1956 was 31.0%, and by 2006 it has increased up to 55.6%, so canopy cover almost doubled in open Mountain pine forests between 1956 and 2006.

2.3.2. Variables driving Mountain pine encroachment and densification

Both logistic models for encroachment and densification were significant ($p<0.001$). However, their overall explanatory power was considerably low, as indicated by Nagelkerke's pseudo-R^2, with values of 0.123 for the encroachment model and 0.101 for the densification model, while AUC was 0.699 for the encroachment model and 0.656 for the densification model.

The variable *altitude* contributed significantly ($p<0.05$) to both response variables, and the relationship was in both cases negative (Table 2.2), with forest expansion (*i.e.* encroachment or densification) more likely to occur at low altitudes. The odds of finding forest expansion were 2.7 times higher at 1500 meters than at 2500 meters, near the tree line. Therefore, the probability of forest encroachment varied from 0.50 at 1500 meters to 0.27 at 2300 meters, while the probability of densification varied between 0.80 and 0.60 for the same altitude range (Fig.2.3). *Shade index* also contributed significantly and positively to both the encroachment and densification models ($p<0.05$; Table 2.2). Thus, these processes were more likely to occur on northern rather than southern slopes. Odds-ratio was 1.010 and 1.011 for encroachment and densification, respectively. This means that the odds of finding forest encroachment or densification were nearly 6 times higher on northern slopes (shade index of 180) than on southern slopes (shade index of 0). Probability of encroachment therefore varied between 0.24 on south-facing slopes and 0.65 on northern aspects, while probability of densification varied between 0.55 and 0.90 for the same cases (Fig.2.3). On the contrary, s*lope* had no significant relationship with the response variable neither for the encroachment nor densification models (data not shown).

Table 2.2 List of main parameters of both encroachment and densification logistic models. Only variables included in the model after stepwise procedure are showed ($p<0.05$).

Variable	Coefficient	Wald Statistic	p	Odds-Ratio
Encroachment				
Intercept	1.173	13.92	<0.001	-
Altitude	-0.001	74.04	<0.001	0.999
Shade Index	0.010	117.60	<0.001	1.010
Population change	-0.005	28.79	<0.001	0.995
Pop. Density	0.008	22.32	<0.001	1.008
Densification				
Intercept	2.170	4.50	0.038	-
Altitude	-0.001	7.92	0.006	0.999
Shade Index	0.011	31.25	<0.001	1.011

None of the socio-economic variables showed significant relationships at $p<0.05$ with the densification response variable (data not shown), meaning that either densification occurs independently of socio-economic conditions or that our proxy variables were unable to capture the ultimate driving factors for densification. However, the case was different for the encroachment model, in which *population change* and *population density* appeared to be significantly related to the observed changes in Mountain pine forests ($p<0.05$) while *importance of primary sector, proportion of pastures* and *proportion of meadows* were not (Table 2.2). The relationship between *population change* and encroachment was negative, showing that forests were more likely to encroach in municipalities with declining populations. For example, probability of encroachment was 0.45 for a municipality experiencing a 50% drop in population, but only 0.25 for a municipality doubling its population (Fig. 2.3). On the other hand, *population density* had a significant and positive relationship with changes in forest cover ($p<0.05$; Table 2.2), thus encroachment was more likely to occur in municipalities with higher population density. The odds of finding encroachment in dense-populated municipalities (200 inhabitants per hectare) were 4.6 times higher than for a municipality with only 10 inhabitants per hectare, and probabilities of encroachment varied, for the same cases, from 0.74 to 0.38 (Fig. 2.3). On the other hand, no significant relationship was found between encroachment and the proxies for the reduction of livestock density (data not shown).

2.4. **Discussion**

During the last half of the 20th century, there has been a significant expansion of Mountain pine forests in the Eastern Pyrenees. This process has not occurred in a homogeneous way, and has been strong in the low, north-facing slopes, although there is also a significant influence of some of the socio-economic indicators. The major influence of topographic variables on encroachment processes seems to indicate an effect of site conditions in Mountain pine expansion. The greatest probabilities of encroachment corresponded to low altitudes and to north-facing aspects, where neither thermal nor hydric limitations could condition the development of Mountain pine (Thuiller et al., 2003; Camarero and Gutierrez, 2004; Batllori and Gutierrez, 2008). Other studies conducted in Mountain areas (Poyatos et al., 2003; Coop and Givnish, 2007; Lasanta and Vicente-Serrano, 2007) have also reported lower encroachment rates in south-facing slopes associated with water stress. However, to correctly assess the importance and meaning of topographic variables, it is important to understand that they are not independent of patterns of land abandonment and livestock grazing in the Pyrenees, and therefore these results have to be reframed in a context of land-use changes (Poyatos *et al.*, 2003). In the mid-19th century, when the population of the Pyrenees was at its peak, farmlands spread into hillslopes, occupying higher altitudes and slopes. Garcia-Ruiz (1988) points out that farmlands came to cover up to 30% of all land below 1600 meters. However, profitability limitations meant that cultivation only rarely rose above these altitudes. Along with the important changes on land-organisation during the 20th century, agriculture concentrated in the valley-bottoms, leaving most hillslopes abandoned, especially those situated on higher altitudes (Poyatos *et al.*, 2003). Since only 10% of the Mountain pine stands are located on altitudes below 1,600 m, areas with higher abandon rate would correspond to the lowest altitudes in the study area. Aspect is also not independent of land abandonment patterns, since farmlands were primarily located on south-facing slopes, with better conditions for cultivation. Therefore, after the maximum expansion of farmlands, those located on north-facing aspects were the first to be abandoned. Furthermore, the south-facing slopes had been cultivated for thousands of years, causing a loss of fertility that could limit or delay forest encroachment especially in highest and steepest areas, where no soil conservation techniques or fertilization were implemented (Garcia-Ruiz, 1988; Garcia-Ruiz et al., 1996; Lasanta and Vicente-Serrano, 2007).

Patterns of livestock grazing are also related to topographic variables, especially altitude. When transhumance was still practiced, livestock grazed subalpine grasslands during the summer and moved to the Ebro valley in the winter (Garcia-Ruiz *et al.*, 1996; Domínguez, 2001), while low and mid-range forests and scrublands were grazed in the intermediate periods, accounting for 17% of the total livestock food sources in Central Pyrenees (Garcia-Ruiz *et al.*, 1996; Lasanta, 2002). More recent farming practices only use summer grasslands, while autumn, winter and spring food is obtained from lowland meadows, and forest and scrublands only account for 2% of the total food supply (Domínguez, 2001). Therefore, there has been a significant reduction in livestock density on low and mid-range land, which have almost disappeared as grazing areas, while grazing in subalpine summer pastures, although at lower livestock density, remains important.

Mountain pine encroachment was also significantly affected by patterns of farmland abandonment on the municipality level, as indicated by its relationship with the analyzed proxies. However, it was not the case for proxies of livestock density. Probability of encroachment was higher in municipalities experiencing greater population losses and in municipalities with higher population density. These findings reflect two extreme cases of changes in population structure in the Pyrenees. On one hand, small villages, where the economy was highly dependent on agriculture and stockbreeding, suffered strong depopulation over the 20th century, as traditional activities lost profitability (Molina, 2002; Gellrich *et al.*, 2008). In these municipalities, rate of land abandonment (and associated forest encroachment) is highly related to depopulation (Lasanta, 1990).

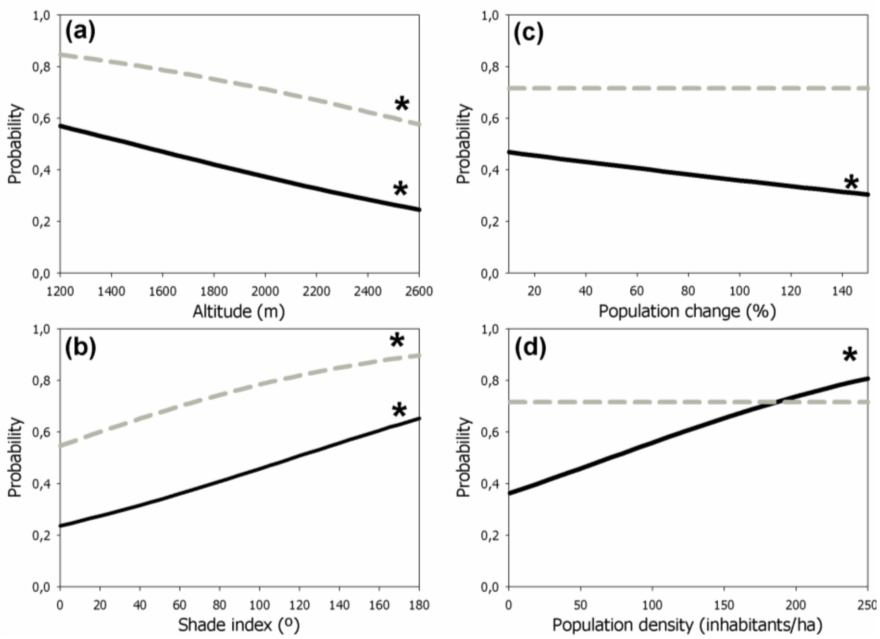

Figure 2.3 Effect of altitude (a), shade index (b) population change (c) and population density (d) (c) on the probability of encroachment (black solid line) and densification (grey dashed line), according to developed models (Table 2.2). Variables other than the one on the *x* axis are equal to their mean value in the modeling data (Table 2.1). Significant relationships are indicated by an asterisk (*) above the curve.

On the other hand, the biggest villages had developed a trade and industry network, so instead of losing population they actually recruited part of the exodus from the smaller villages (Lasanta, 1990; Molina, 2002). Furthermore, the 1970s marked the growth of tourism as an important economic sector in the Pyrenees. Most of the tourist facilities were located in the most populated villages in each valley, where tourists could find the services they demanded (Molina, 2002), further consolidating the population differences between small and big villages. However, in these municipalities, a greater population density does not necessarily correspond to a greater pressure on the territory, as their economy is not based on primary sectors. In fact, most of the tourist facilities (apartments, camp sites and hotels) were sited on valley-bottoms, where they directly compete for space with meadows and farmlands, causing opportunity costs for agriculture and stockbreeding to increase, and therefore contributing to land abandonment. Lasanta (2002) found a positive and significant correlation between tourist development and rates of farmland abandonment and livestock density decline in several municipalities in the Pyrenees, while other authors report correlations between high population densities and rates of forest encroachment (Gellrich *et al.*, 2007a; Gellrich *et al.*, 2008). Surprisingly, the variable *primary sector* showed a non-significant relationship with encroachment probability. This is likely related to the increasing number of part-time farms (*i.e.* where the farmer is not exclusively dedicated to agriculture or stockbreeding) established in the area over the last few decades. Gellrich *et al*. (2007a) highlighted the importance of part-time farms in determining forest encroachment in the Alps. Therefore, the lack of significance for primary sector activity could be due to these part-time farmers, who are not included in the agrarian census.

Unlike encroachment, densification was not significantly influenced by any of the socio-economic covariates. According to Poyatos *et al*. (2003), forest densification reflects the decreasing use of fuelwood and timber as a result of population decline and the shift towards other energy sources and materials. However, Mountain pine timber has never been extensively used as fuelwood in the Pyrenees, where other species, such as beech or oak, were preferred due to their better properties and proximity to village centres. Nevertheless, densification is significantly related to altitude and, above all, to aspect. This could imply that climatic conditions may limit this process, either by temperature constraints at higher altitudes or by drought conditions on south-facing slopes. In any case, our analysis of Mountain pine densification focuses exclusively on the period 1956-2006. However, land abandonment, and hence forest encroachment, has started before 1956. Indeed, Lasanta (2002) points out that most of the non-permanent and low-fertility farmlands had already been abandoned by 1936. Thus, many of these areas could have undergone encroachment processes in the following years and therefore, by 1956, would present low canopy cover susceptible to densificate in the following years. Hence, patterns of densification may depend on encroachment patterns prior to 1956. Our results agree with this premise since densification processes were found to be more important in north-facing exposures and low altitudes (between 1200-1600 m) home to the first farmlands to be abandoned during the first half of the century (Garcia-Ruiz, 1988; Poyatos *et al.*, 2003).

To recap, over the last 50 years, alpine forests in the Eastern Pyrenees have undergone significant encroachment and densification. On a regional scale, these patterns are highly related to patterns of farmland abandonment. Forest has colonized most of the abandoned fields, and therefore forest encroachment has been more important at low and medium altitudes than close to the tree line, indicating that land-use changes have a greater influence on forest expansion than climate changes. However, this does not mean climate has no influence on forest dynamics, as the response of forest-grassland ecotones to climate changes depends on several factors, including autoecological characteristics, phenotypic plasticity and availability of regeneration niches, among others (Camarero and Gutierrez, 1999; Holtmeier and Broll, 2005). Therefore, influence of climate change is not necessarily reflected as tree line displacements, as changes in stand density and recruitment or in growth form are more likely to occur (Szeicz and Macdonald, 1995; Camarero et al., 2000b; Camarero and Gutierrez, 2004; Gehrig-Fasel et al., 2007; Batllori and Gutierrez, 2008). In fact, Camarero & Gutierrez (1999, 2004) studying a Mountain pine stand in the Pyrenees, found significant changes in recruitment and tree growth inside the stand, despite a reduced or even null altitudinal rise of the tree line. However, even considering the influence of climate on tree line dynamics, our results indicate that, in the Pyrenees, land-use changes are the main drivers of recent Mountain pine encroachment at regional scale. Therefore, future research on tree line dynamics in the Pyrenees should explicitly consider the influence of land-use changes in order to correctly estimate the net contribution of climate-change associated processes.

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Understory light predictions in mixed-conifer forests: role of aspect-induced variation in crown geometry and openness

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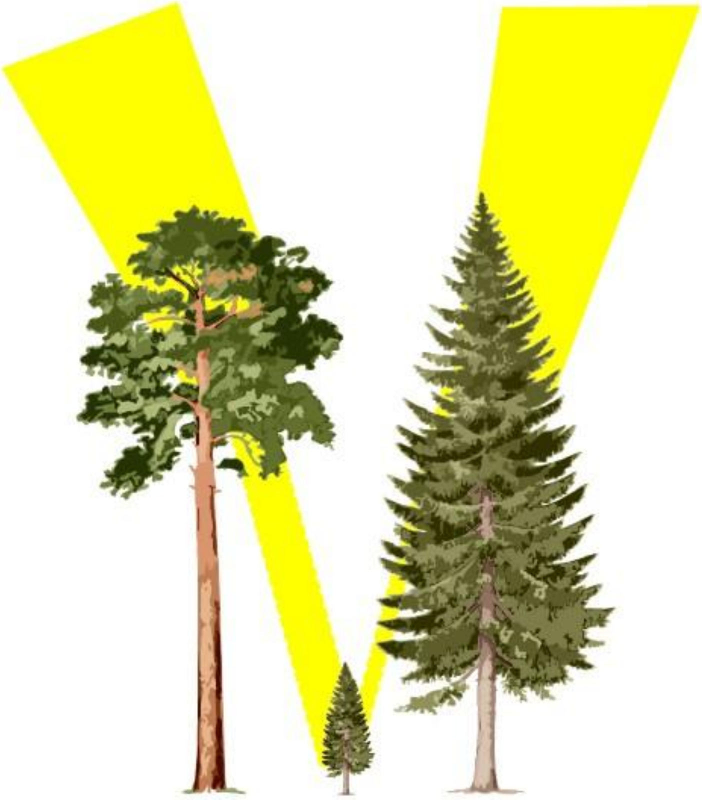

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3. Understory light predictions in mixed-conifer mountain forests: role of aspect-induced variation in crown geometry and openness

Abstract

Predicting light availability in forest understory is a key step in the modeling of forest dynamics. Aspect is often the main source of environmental variation in mountain forests, and so aspect-induced differences in crown geometry and transparency can be expected to affect light transmission through the canopy and modify understory light predictions. To gain a better understanding of the effects of aspect on the light interception capacity of forest trees, we determined crown allometry and crown openness (CO) in 120 adult trees of three common conifer species in the Pyrenees (mountain pine, Scots pine and silver fir), sampled in eight montane-subalpine forests that each included two contrasting aspects. CO was calculated from digital photographs and several crown outlines were automatically determined to prevent user bias. We also calculated crown irregularity as the difference between crown surface area for the tightest and loosest outlines. Predictions of understory light availability obtained from a forest dynamics model were compared with actual values obtained from 115 hemispherical photographs. Crown length and CO varied across species following previous rankings of shade tolerance. Both pines had longer and wider crowns in the north aspect, whereas fir crown geometry was not affected by aspect. CO depended largely on the method chosen for determining crown outline, ranging from 0.10 to 0.56, and the tightest outline provided the best predictions of understory light (slope = 0.89, R^2 = 0.46). CO was also significantly affected by tree size and plot aspect ($p < 0.001$): crowns in southern-oriented plots were more open for mountain pine and silver fir, whereas Scots pine showed the opposite trend. Predictions of understory light were significantly improved when crown geometry and openness were allowed to vary according to plot aspect (slope of the regression: 0.95, R^2 = 0.50). Our results suggest that aspect should be explicitly considered when modeling ecological processes and dynamics in mixed mountain forests given its influence on both abiotic conditions and crown responses to them.

Keywords: crown openness, crown irregularity, aspect, Pyrenees, SORTIE-ND, light understory

3.1. **Introduction**

Understory light plays a crucial role in forest dynamics, often being the most limiting resource for growth and survival of juveniles (Bazzaz, 1979; Kobe et al., 1995; Lefrançois et al., 2008). Also, modifying light regimes is frequently the only way in which managers can intervene in the forest to favor some species over others (Lieffers et al., 1999). Accordingly, the study and modeling of light transmission through the forest canopy has received much attention (Pacala et al., 1993; Brunner, 1998; Stadt and Lieffers, 2000; Groot, 2004). Since the seminal work by Monsi and Saeki (1953), most models of light transmission have been based on Beer's law, and assume that the forest canopy is a homogeneous layer that attenuates light transmission exponentially (Brown and Parker, 1994; Larsen and Kershaw, 1996; Stadt and Lieffers, 2000). These models adduce two important limitations: (*i*) they require large amounts of data input (leaf area density, inclination angles, etc.) that is not directly applicable in forest management (Lieffers et al., 1999; Stadt and Lieffers, 2000; Astrup and Larson, 2006); and (*ii*) they cannot predict light regimes in heterogeneous forests where regeneration dynamics are dependent on small-scale processes (Canham et al., 1994). In this last case, the use of spatially explicit models that include individual representation of crowns are much more appropriate to predict the light transmitted through the canopies (Brunner, 1998; Boivin et al., 2011). Some of these models simulate individual crowns as 3-D objects and estimate light attenuation as a function of the distance traveled by rays through the crowns (Brunner, 1998; Stadt and Lieffers, 2000). Simpler models that reduce light by a given amount for each hit 2-D crown (Canham et al., 1994; Canham et al., 1999a) have also been shown to predict understory light levels successfully in very different environments (Pacala et al., 1993; Beaudet et al., 2002; Astrup and Larson, 2006; Uriarte et al., 2009; Thorpe et al., 2010). Spatially explicit 2-D models are easily parameterized and are faster to run, as they only require estimation of the crown size, generally determined from allometric relationships and the attenuation factor assigned to each crown, which can be empirically obtained as crown openness (CO), *i.e.* the fraction of sky that on average can be seen through the crown of an individual tree (Boivin et al., 2011).

Crown openness varies substantially among species (see Beaudet et al. (2002), Astrup and Larson (2006)). In general, shade-tolerant species present lower CO than shade-intolerant ones, which in part may explain their reported higher ability to intercept light (Valladares and Niinemets, 2008). Astrup and Larson (2006) and Lefrançois *et al.* (2008) reported variations in CO along environmental gradients, but Sonohat et al. (2004) and Stadt et al. (2005) could not find a clear relationship, and the effect of these variations on understory light predictions remains unclear. Also, Lefrançois *et al.* (2008) and Boivin *et al.* (2011) showed that differences in methodology, *e.g.* angle of transmission through zenith and delimitation of crown outline, can lead to marked differences in CO, therefore affecting light predictions. CO can vary as a result of changes in crown porosity (proportion of hollows inside the crown) and in crown irregularity (understood as the existence of dents and bulges in tree crown profile). The use of different crown outlines can provide information on the role of each of these processes. Moreover, it can be combined with the study of the effect of environmental factors to assess the architectural response of tree crowns to changes in the environment. Crown geometry (crown width and length) also has a marked effect on spatial variation in understory light (Canham et al., 1999a), and some models have demonstrated more sensitivity to variation in crown geometry than to variations in crown openness (Beaudet et al., 2002). However, the effect of environmental gradients on crown geometry has received little attention to date. In mountain systems, where most forests are located on hillslopes, aspect is usually one of the main sources of environmental variation. Solar energy regimes differ according to aspect (Hicks and Frank, 1984) and this causes differences in site characteristics such as evapotranspiration and hydrologic regimes (Garcia-Pausas et al., 2007; Navas et al., 2007), soil and nutrient dynamics, species composition and abundance and forest growth and productivity (Verbyla and Fisher, 1989; Bale and Charley, 1994). Hence aspect might also be expected to induce variation in crown morphology and openness, and so differential parameterization of crown characteristics according to aspect may be needed to correctly simulate light transmission through canopies and forest dynamics in mountain systems. To gain a fuller understanding of the potential role of aspect on crown characteristics and light interception we conducted a study in different Pyrenean mixed-conifer forests to (*i*) estimate crown geometry, openness and irregularity and their variation with aspect for the three main species composing these forests (*Pinus sylvestris* L., *Pinus uncinata* Ram. and *Abies alba* Mill.), (*ii*) predict understory light in mixed-conifer mountain forests using a spatially explicit model of forest dynamics and (*iii*) assess how aspect-induced differences in the parameterization of the model affected the predictions of understory light levels. Our main hypothesis was that higher evaporative demand on southern aspects would increase crown openness, but would also induce changes in crown geometry, therefore affecting light transmission through forest canopy and the simulations of the SORTIE-ND model (Canham et al., 2005).

3.2. Materials and methods

3.2.1. Study area and species

Data were collected from eight montane-subalpine forests in the Catalan Pyrenees (NE Spain; Figure 3.1). All the selected stands were dominated by one or more of the studied species: mountain pine (*P. uncinata*), Scots pine (*P. sylvestris*) and silver fir (*A. alba*). Mountain pine is the dominant species in the Pyrenean subalpine belt, whereas Scots pine and fir dominate the montane areas, although the three species mix in the montane-subalpine ecotone (Ameztegui and Coll, 2011). We used four of the stands to determine the tree allometry and crown openness (sampling sites). The remaining four were physically separate from the sampling sites and were used to validate the model (Figure 3.1). Each sampling site included two different, contrasting aspects that were classified either as north-facing (N, NW and NE) or south-facing slopes (SE, S, SW; Table 3.1) for analysis. In the southern Pyrenees, fir usually grows in the most humid, northern-exposed sites and is absent in full sun-exposed slopes. This caused limitations in the selection of sampling sites, and the two aspects in each site were not as strongly opposed for silver fir as for pines (Table 3.1). All the stands had been thinned in the previous 3 years, allowing an easier determination of crown openness due to the greater separation between trees, while avoiding the special characteristics of trees grown without competence (Lefrançois et al., 2008).

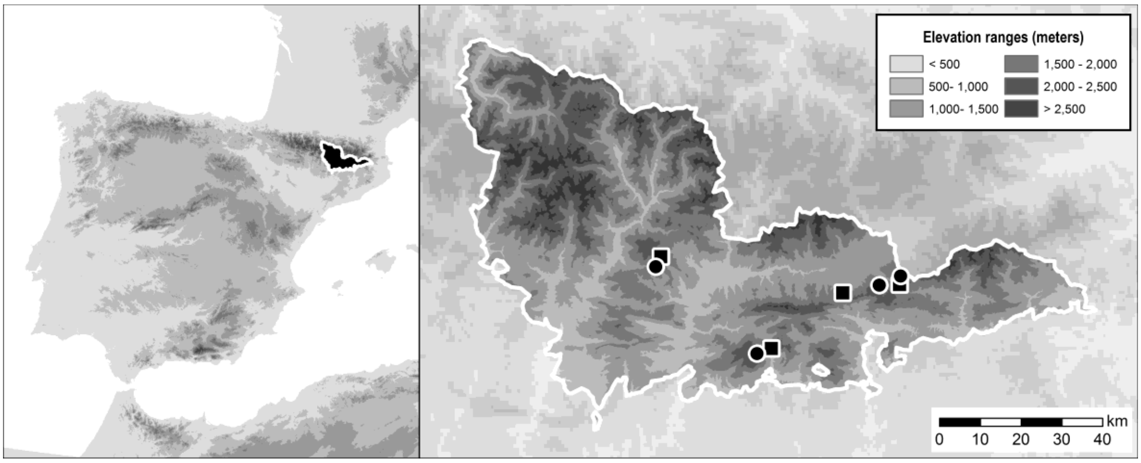

Figure 3.1 Location of the study area and the sampling (circles) and validation sites (squares)

Table 3.1. Summary of site characteristics

Sites	Site Coordinates	Elevation (m)	Aspects	Species Composition*	Mean tree DBH (cm) ± SD
Sampling sites					
Pallerols 1	42º23'N, 1º15'E	1850	NE, SE	Pu, Aa, Ps	34.6 ± 16.3
Riu de Cerdanya	42º19'N, 1º48'E	1800	NW, E	Aa, Pu	27.4 ± 13.0
Serra del Verd	42º12'N; 1º35'E	1770	N, S	Ps	24.6 ± 8.9
Paborde	42º21'N, 1º58'E	1750	NE, SW	Ps, Pu	31.0 ± 11.8
Validation sites					
Pallerols 2	42º23'N, 1º23'E	1940	NE, SE	Pu, Aa, Ps	31.1 ± 14.6
Port del Comte	42º11'N, 1º33'E	1700	NE, S	Ps, Pu	27.0 ± 8.3
Massella	42º20'N, 1º54'E	2000	N, NE	Pu	28.0 ± 9.6
Salteguet	42º21'N, 1º59'E	1750	N	Pu, Aa	23.4 ± 12.5

*Species composition is given in decreasing order of dominance: Pu, mountain pine (*Pinus uncinata)*; Aa, silver fir (*Abies alba);* Ps*, Scots pine (Pinus sylvestris).*
SD: standard deviation

3.2.2. Crown geometry

We sampled at least 30 adult trees (diameter at breast height > 75 mm) per species and aspect at each sampling site. Data were collected to ensure a wide range of diameters and a good distribution among diameter classes. For saplings (height > 0.5 m, diameter at breast height < 75 mm), we used data collected from a previous study (Ameztegui and Coll, 2011). For each adult tree, we measured diameter at breast height (DBH), tree height and crown radius and length. Crown radius was defined as the average of two perpendicular crown radii and crown length as the distance from the top of the tree to the base of the living crown. A total of 232 Scots pines, 225 mountain pines and 207 silver firs were sampled, ranging from 1 to 84 cm in DBH and from 0.6 to 27 m in height. We used three allometric equations to define crown geometry for each species: (*i*) tree height as a function of DBH, (*ii*) crown length as a function of tree height and (*iii*) crown radius as a function of DBH. To predict tree height as a function of DBH we used a nonlinear exponential curve that saturates at a maximum height (Canham et al., 1999a; Beaudet et al., 2002):

$$\text{Tree height} = 1.3 + (\text{Max. height} - 1.3) \cdot \left[1 - e^{(-b \cdot \text{DBH})}\right] \tag{1}$$

where DBH is in centimeters and tree height in meters. Maximum height was determined from the Spanish National Forest Inventory in Catalonia (Skelly et al., 2007) as the average height of the 5% tallest trees for each species. The slope of the curve *b* was estimated by nonlinear least-square regression (Table 3.2). We also used nonlinear regression to estimate crown radius and crown length, as saplings usually have wider and longer crowns per unit of DBH that adult trees (Beaudet et al., 2002)

$$Crown\ radius = c \cdot DBH^{d} \quad (2)$$

$$Crown\ length = f \cdot TH^{g} \quad (3)$$

where crown radius, crown length and TH (tree height) are expressed in meters and DBH in cm. *c*, *d*, *f* and *g* are estimated parameters (Table 3.2). To assess the effect of aspect on crown geometry, we estimated the parameters for northerly and southerly slopes separately, and differences in estimated parameters were determined by examining the significance of the interaction between aspect and the other explanatory variable (DBH or TH).

3.2.3. Crown openness

We took pictures of the crown of every measured adult tree (120 trees per species) with a Nikon Coolpix 995 digital camera. To eliminate the effect of angle in the determination of crown openness (Lefrançois et al., 2008) we attached a clinometer to the camera to ensure that all photographs were taken at a 45º angle relative to the top of the tree. We selected only undamaged individuals with regular crowns and with no signs of having developed free from competition. Crown openness (CO) was determined as described by Canham *et al*. (1999a). Images were transformed according to a defined threshold, so that all the “shading” elements (trunk, branches and leaves) were set to black and the background to white. Image reclassification was later corrected by hand to eliminate effects of light reflection.

CO was determined as the ratio of the surface occupied by white pixels (sky area visible through the crown) to the total surface of the 2D projected silhouette the crown. Hence the values estimated with this method are highly dependent on the determination of the crown outline, and due to the fractal nature of the outline projection of a tree crown, large user bias can be expected (Canham et al., 1999a; Boivin et al., 2011). To minimize this bias, crown outline was automatically determined using Crown Delineator, a Python script specifically written for this task and developed by Boivin *et al.* (2011). We used the software to delineate seven different crown outlines: five geometrical buffers with different adjustment sensitivities to crown shape (from tightest to loosest: Out20, Out40, Out80, Out160, Out 320,) together with the smallest convex hull (OutCH) and the smallest rectangle perpendicular to the horizon that includes the entire crown (OutRec; Figure 3.2). A thorough description of the functioning of the script and the outlines produced can be found in Boivin *et al.* (2011). CO was calculated for each of the seven outlines, named accordingly CO20, CO80, CO160, CO320, COCH and CORec. We estimated crown irregularity as the difference in crown area between OutCH and Out20, divided by the former. This crown irregularity index takes values close to 0 for dense, compact conic crowns, and values close to 1 for highly irregular crown shapes that include large void spaces between branches. To assess the variations in CO and irregularity with DBH and aspect we used generalized linear models, setting the seven CO values and irregularity as dependent variables, aspect as a factor (two levels: north- and south-facing) and DBH as covariate. All statistical analyses were performed using R (R Development Core Team, 2010). Unless otherwise specified, the significance level was set to alpha = 0.05.

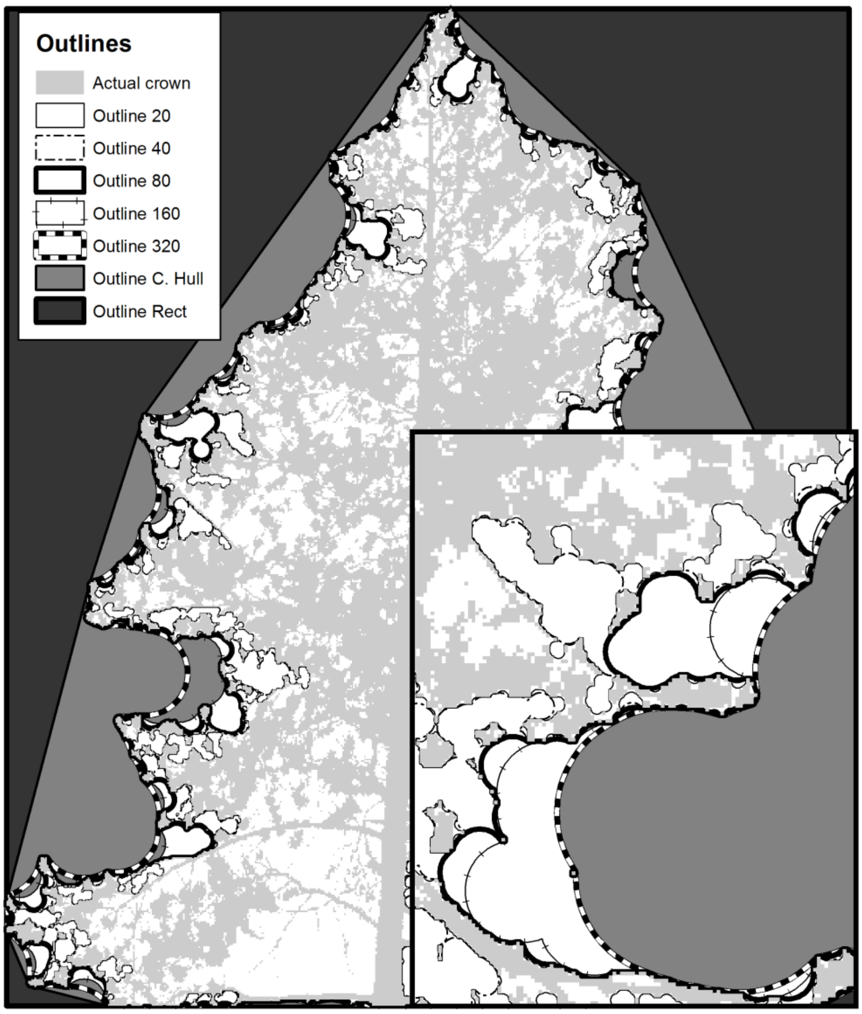

Figure 3.2. Example of the different outlines created by the Crown delineator for a Scots pine (*Pinus sylvestris*) crown. Tighter outlines produce lower CO values, whereas crown irregularity can be determined as the difference in crown area calculated for the outline 20 and the Convex Hull algorithms, divided by the latter.

3.2.4. Prediction of understory light and role of aspect

Predictions of understory light were carried out using the “GLI light behavior” developed in SORTIE-ND (Canham et al., 2005), a spatially explicit individual tree model where tree growth is mainly driven by light availability, which in turn is determined by shading of neighboring trees (Pacala et al., 1993; Pacala et al., 1996; Canham et al., 2005). The “GLI light behavior” simulates the movement of the sun throughout the growing season to determine the total, seasonally averaged light that reaches a given point expressed as Gap Light Index (GLI), an index equivalent to the percentage of photosynthetically active radiation (PAR) on a horizontal plane compared with above-canopy levels (Canham, 1988b; Gendron et al., 1998). For a given point, available light is determined by finding all neighboring trees that shade that point. In SORTIE-ND, calculations are normally restricted to zenith angles within 45º of vertical to optimize computation time, since little illumination comes from angles close to the horizon (Canham et al., 1990; Pacala et al., 1996). In SORTIE-ND, individual crowns of all the neighboring trees are modeled as cylinders and light attenuates by a given factor for each crown it encounters (Boivin et al., 2011). Therefore, each tree must be defined by its location, DBH, crown geometry and CO. We obtained the data to make the predictions from the 24 validation plots (6 plots in 4 validation sites). Each plot was composed of two concentric circles of radius 10 and 20 m, respectively. In the first one, all trees with DBH > 7.5 cm were mapped and measured. In the second one, only those trees with DBH > 20 cm were considered. For every tree measured we determined the species, DBH and its distance and azimuth from the plot center. We created a parameter file for each of the 24 validation plots. For each species, the obtained average values of crown allometry and CO were used (species-specific constants). As SORTIE-ND simulates crowns as cylinders, and because of the conical shape of the crowns of the three species studied, crown radius was set at 50% of the actual values measured in the field (Rautiainen and Stenberg, 2005). This rescale makes the area of the modeled crown closer to the real crown area and has been shown to improve light predictions (Canham et al., 1999a; Rautiainen et al., 2008). Simulations were performed eight times for each plot, once for each average CO value obtained from the defined outlines and once assigning a CO of zero to all species (opaque crowns). All the other parameters involved in light calculations (crown geometry, tree location, etc.) were kept constant.

These simulated GLI values were compared with observed values obtained from a series of hemispherical photographs taken at each validation plot: one in the center of the plot, and four at 5 m from the center in each cardinal direction. Photographs were taken on overcast days using a leveled tripod at height 1 m. After discarding all the photographs where branches, leaves or shrubs were too close to the camera we analyzed a total of 114 photographs. Light availability for each photograph was determined by calculating GLI using Gap Light Analyzer v. 2.0 (Frazer et al., 2000), which works in an analogous way to the GLI light behavior in SORTIE. To ensure that observed and simulated GLI values were directly comparable, we set temporal and spatial resolution and the characteristics of the incident radiation in exactly the same way as for the GLI light behavior, and we created a topographic mask that covered the lower 45º from horizon. GLI was thus calculated as the ratio between transmitted and incident light in the area not covered by the mask.

To identify the outline that produced the best fit to observed data we used both the slope of the regression (with a zero intercept) to measure bias and the R^2 value of the regression as a measure of goodness of fit. Once identified, we performed three different simulations. In the first one, we used a single averaged species-specific CO, while two different values of crown allometry were assigned for each species according to the aspect of the validation plots. In the second, crown allometry remained a species-specific constant, but CO varied depending on aspect. Finally, in the third simulation, both crown allometry and CO were allowed to vary for each species according to the aspect of the validation plot. We compared bias and goodness of fit of the models to assess the influence of aspect on predictions of understory light values.

3.3. Results

3.3.1. Crown geometry

DBH and TH explained more than 85% of the variability in crown geometry for the three species studied (Table 3.2). Pine height increased sharply with DBH (high *b* parameter), and both pines rapidly reached the asymptotic maximum height, whereas fir had a greater maximum height but also a lower slope for the height-DBH relationship (Table 3.2). We observed that aspect did not affect this relationship (data not shown), so all the data available for each species were modeled together. Average crown ratio ranged from 50% of tree height for Scots pine to more than 90% for silver fir. This ranking in crown ratio matched the observed rankings in shade tolerance for these species in the Pyrenees (Ameztegui and Coll, 2011), with shade-tolerant species having deeper, longer crowns. However, at comparable aspects Scots pine had wider crowns than mountain pine for any given DBH (Figure 3.3). Crown geometry of both pines significantly varied with aspect, as pines had wider and longer crowns on north-facing slopes (Figure 3.3). Conversely, fir showed the longest and widest crowns all along the size gradient, but no effect of aspect was observed.

Table 3.2. Parameter estimates by nonlinear least squares regression of tree height, crown radius and crown length as a function of tree size for three conifer species in the Pyrenees: silver fir (*Abies alba*); Scots pine (*Pinus sylvestris*) and mountain pine (*Pinus uncinata*). All regressions were highly significant ($p < 0.001$). Parameters are shown separately for north-facing and sun-exposed slopes except for silver fir, for which no differences were found in the parameters estimated for the two aspects.

		Tree Height			**Crown radius**			**Crown length**		
Species	**Aspect**	Max. Height* (m)	b	R^2	c	d	R^2	f	g	R^2
Silver fir	N,S	29.2	0.020	0.952	0.533	0.488	0.932	0.781	1.056	0.991
Scots pine	N	22.6	0.034	0.872	0.214	0.708	0.889	1.143	0.796	0.867
	S				0.270	0.626	0.891	0.723	0.885	0.848
Mountain pine	N	20.4	0.030	0.897	0.244	0.650	0.911	1.189	0.805	0.927
	S				0.287	0.566	0.912	1.129	0.753	0.863

*Maximum height was obtained from the Spanish National Forest Inventory in Catalonia (Skelly et al., 2007) as the average height of the 5% tallest trees for each species

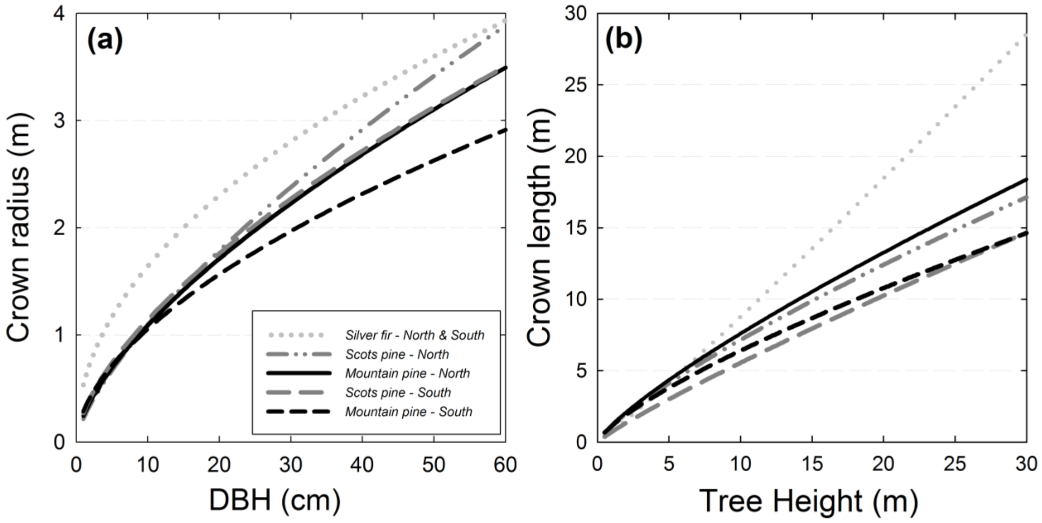

Figure 3.3 Allometric relationships for the determination of crown geometry as a function of tree size for three conifer species in the Pyrenees: silver fir (*Abies alba*); Scots pine (*Pinus sylvestris*) and mountain pine (*Pinus uncinata*). (a) Crown radius as a function of DBH. (b) Crown length as a function of tree height. Equations are adjusted separately for north-facing and south-facing slopes except for fir, for which we found no differences in the parameters estimated for the two aspects.

3.3.2. Crown openness

Crown openness ranged from 0.101 to 0.422 for silver fir, from 0.186 to 0.559 for Scots pine and from 0.113 to 0.439 for mountain pine (Figure 3.4) depending on the selected outline. CO differed among species for any given outline, but pairwise comparisons indicated that there were no differences in CO between silver fir and mountain pine ($P > 0.12$ for all the outlines). For the tightest outlines (CO20, CO40, CO80), Scots pine CO was almost twice that of the other species, but this difference decreased for looser outlines (Figure 3.4). Nevertheless, Scots pine showed a significantly higher CO than the other two species for any outline ($P < 0.001$). For all three species, CO increased as looser outlines were used, as expected. However CO values for a given outline were not much different from the immediately higher and lower outline (data not shown). Hence we selected CO20, CO80, CO320; COCH and CORec to assess the influence of aspect and DBH and to validate the model for light availability in the understory. Mean crown irregularity was 0.172 for silver fir and 0.178 for mountain pine, whereas Scots pine presented a much more irregular crown, with a mean value of 0.275.

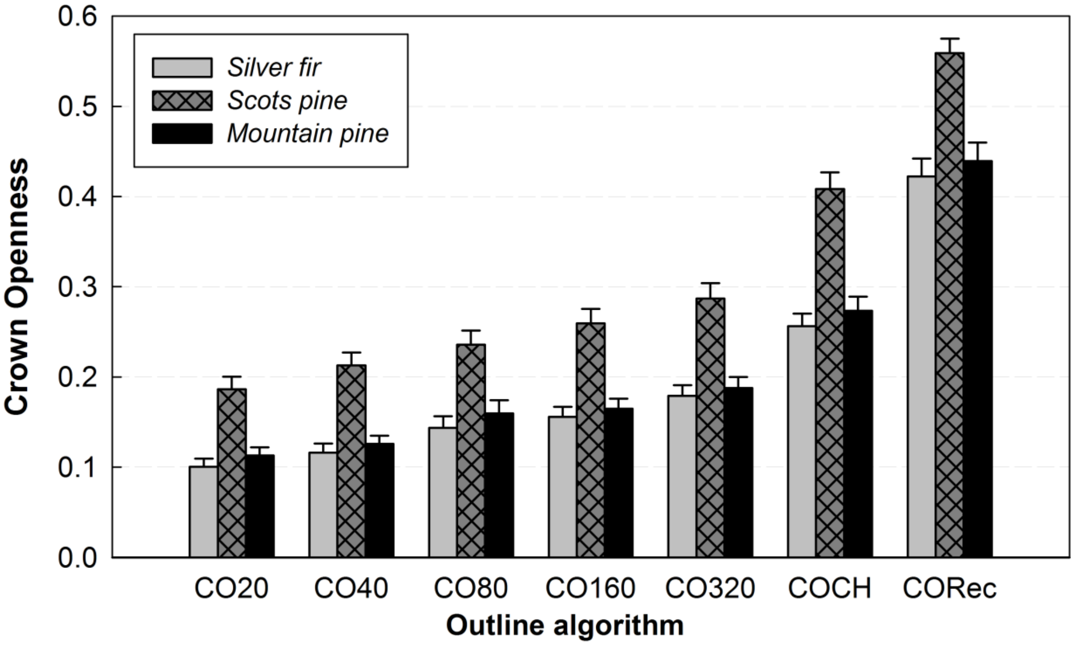

Figure 3.4 Values of crown openness (CO) for three conifer species in the Pyrenees as obtained by seven different algorithms included in the Crown Delineator. Bars indicate upper 95% confidence intervals. N = 104 for silver fir (*Abies alba*), 119 for Scots pine (*Pinus sylvestris*) and 106 for mountain pine (*Pinus uncinata*).

CO was significantly affected by DBH and aspect in all cases analyzed except for the tightest outlines for mountain pine (Table 3.3). The effect of DBH, when significant, was always negative, *i.e.* CO decreased with increasing DBH. In pines, we found DBH to influence CO for loose outlines but also crown irregularity. For example, CORec in Scots pine decreased from 0.62 for a 10 cm DBH tree to 0.48 for a 60 cm DBH tree, whereas in mountain pine it varied between 0.33 and 0.19 for the same range of tree sizes. Conversely, the effect of DBH on fir CO was only significant for the tightest outlines (Figure 3.5). The effect of aspect varied across species: silver fir and mountain pine had higher CO in south-exposed slopes, but the opposite effect was found for Scots pine (Table 3.3). The same species-specific effect of aspect was also observed for crown irregularity (Table 3.3, Figure 3.6). In the case of DBH, its effect varied across species: it did not have a significant effect on silver fir irregularity, whereas both pines showed more regular crowns for bigger diameters (Table 3.3).

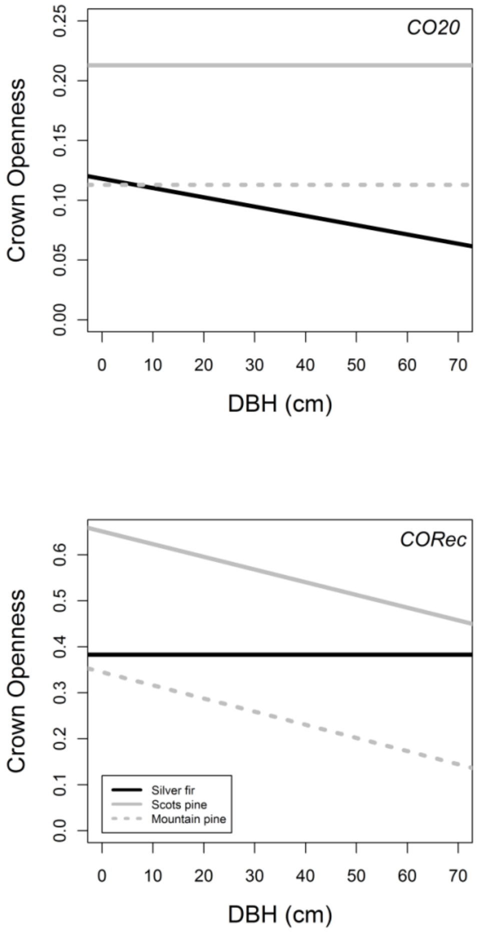

Figure 3.5. Effect of DBH on crown openness as determined for the tightest (CO20) and loosest (CORec) outlines using the parameters reported in Table 3.3. For silver fir, DBH only affected CO for the tightest outlines, denoting variation in crown porosity with DBH. For pines, DBH made CO to decrease only for loosest outlines, thus indicating a major role of crown irregularity. Horizontal lines denote no effect of DBH on CO, and are included only for comparative purposes.

Table 3.3. Results of the generalized linear model (GLM) predicting crown openness (CO) as a function of tree size (DBH) and aspect for three montane-subalpine conifers in the Pyrenees: silver fir (*Abies alba*); Scots pine (*Pinus sylvestris*) and mountain pine (*Pinus uncinata*). Parameter estimates and significance of both predictive variables are shown, and model significance is indicated by "Model *p*-value". Positive values of aspect parameter indicate an increase in the dependent variable for south slopes.

	Aspect estimate	p-value (aspect)	DBH estimate	p-value (DBH)	Model p-value
Silver fir					
CO20	0.021	0.026	- 7.65 e-04	0.005	<0.001
CO80	0.040	<0.001	-6.47e-04	0.033	<0.001
CO320	0.051	<0.001	-6.85e-04	0.049	<0.001
COCH	0.066	<0.001	-0.77e-04	0.008	<0.001
CORec	0.083	<0.001	n.s.	0.571	<0.001
Irregularity	0.048	<0.001	n.s.	0.416	<0.001
Scots pine					
CO20	-0.047	<0.001	n.s.	0.053	<0.001
CO80	-0.064	<0.001	-2.02 e-03	0.005	<0.001
CO320	-0.072	<0.001	-2.71 e-03	0.001	<0.001
COCH	-0.074	<0.001	-3.05 e-03	<0.001	<0.001
CORec	-0.049	0.001	-2.56 e-03	0.004	<0.001
Irregularity	-0.053	0.001	-2.71 e-03	0.004	<0.001
Mountain pine					
CO20	n.s.	0.806	n.s.	0.149	0.322
CO80	n.s.	0.166	n.s.	0.357	0.378
CO320	n.s.	0.367	n.s.	0.768	0.650
COCH	0.043	0.003	n.s.	0.165	0.003
CORec	0.051	0.011	- 2.56 e-03	0.007	<0.001
Irregularity	0.043	0.001	-1.57 e-03	0.014	<0.001

3.3.3. Prediction of understory light

The regression between observed and predicted values of light availability in the understory was significant for all the simulations ($P < 0.001$), and the explained variance ranged between 0.43 and 0.50. However, slopes of the regression ranged from 0.69 to 0.89, indicating that predictions of light in the understory overestimated observed values for any outline used (Figure 3.7). Predictions using COCH and CORect provided an acceptable fit, but the greatest bias, and so were discarded. Although there were no marked differences in goodness of fit between values obtained using CO320, CO80 and CO20, the latter provided less biased predictions ($y = 0.887x$; $R^2 = 0.46$) and was therefore selected as the reference model. When aspect was explicitly considered*, i.e.* when CO and allometry were allowed to vary according to plot aspect, regression of observed *vs.* predicted values produced a better fit and lower bias than the reference model ($y = 0.951x$; $R^2 = 0.50$).

In stands where mountain pine or Scots pine were the dominant species, allowing CO and crown geometry to vary depending on the aspect of the validation plot greatly improved the fit of the models, and the slope of the regression was close to 1. A much poorer fit was obtained in silver fir stands, and variation of parameters according to aspect did not result in substantial improvement of predictions (Figure 3.8). Most of the improvement in light predictions when considering the aspect was caused by variation in crown geometry, as variation of crown openness without changing crown geometry caused no or little improvement in predictions compared with the reference model (Table 3.4).

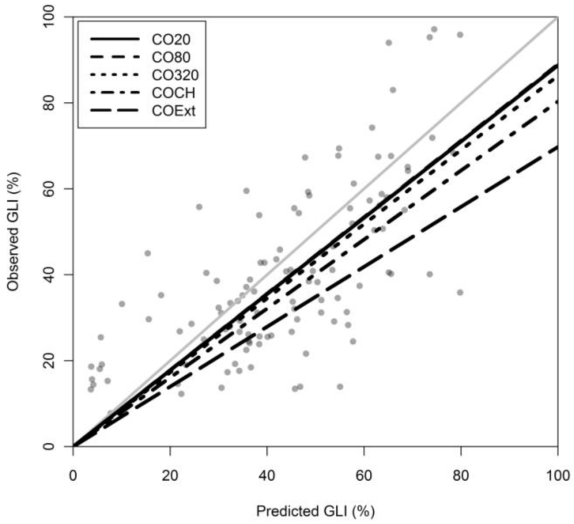

Figure 3.6.Boxplot of distribution of crown irregularity determined for the three species: silver fir (*Abies alba*); Scots pine (*Pinus sylvestris*) and mountain pine (*Pinus uncinata*)), and two aspects: N: north-facing; S: south-facing slopes

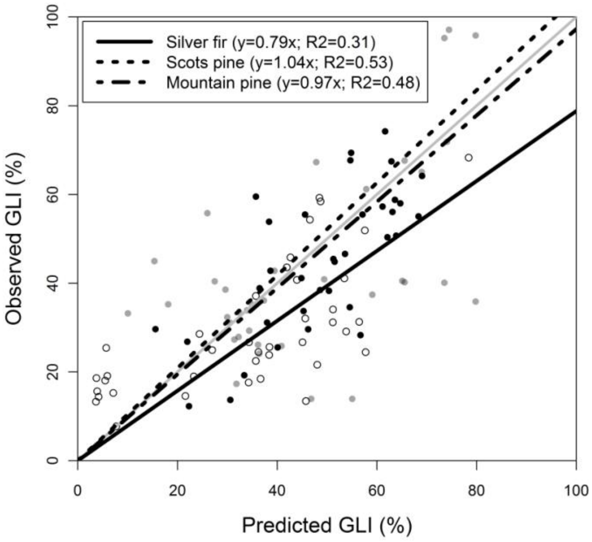

Figure 3.7 Test of the model's ability to predict understory light levels in 24 plots in montane-subalpine forests in the Pyrenees. Predicted GLI values are simulated by SORTIE-ND using different crown openness (CO) as calculated from five different outlines, and observed GLI values are obtained from hemispherical photographs. The gray points represent the values obtained for outline CO20, and the gray solid line represents 1:1 relationship.

3.4. Discussion

3.4.1. The role of aspect on crown geometry and openness

We hypothesized that aspect would exert a significant influence on the crown architecture and openness of the studied species, thereby affecting light transmission through their canopies. Our results support this hypothesis, but interestingly, we found the effect of aspect on crown geometry and openness to be highly species-specific. Fir crown allometry was not affected by aspect and showed the largest crown dimensions and little crown rise, so that crowns extended almost the entire length of the tree (Figure 3.3). The lack of response of silver fir allometry to aspect may be caused by limited morphological response of the species to changes in environmental conditions, as previously observed for silver fir saplings (Ameztegui and Coll, 2011). Its large crown, along with the observed low CO value (0.1) are characteristic of shade-tolerant species, which in general present dense crowns and cast deep shade in the understory (Canham et al., 1999a; Valladares and Niinemets, 2008), a strategy that prevents the establishment of pioneer species (Ameztegui and Coll, 2011). Scots pine had the shortest and most open crown for any adopted outline (Figure 3.3), also matching previous reports (Petersson, 1997; Rouvinen and Kuuluvainen, 1997; Rautiainen and Stenberg, 2005). Unlike fir, both pine species had wider and longer crowns on northern slopes (Table 3.3). Better soil quality and higher water availability could explain the observed aspect-related differences in crown geometry (DeLucia et al., 2000; Lang et al., 2010), but changes in architectural traits to optimize light interception can also play a role, as longer and wider crowns allow trees to forage better for light (Falster and Westoby, 2003; Purves et al., 2007).

We observed similar CO values for silver fir and mountain pine (Figure 3.4), a species that has been described in the botanic literature as having a narrow, deep, “fir-like” crown (Ruiz de la Torre, 2006). Comparison of the ranking of CO and crown ratio matched shade-tolerance rankings for these species: fir > mountain pine > Scots pine (Ameztegui and Coll, 2011) (Figure 3.4). Previously reported CO values range between 0.05 for shade tolerant species to more than 0.2 for shade intolerant ones, but CO values derived from crown photographs largely depend on the method chosen for the determination of crown outline (Boivin et al., 2011). The divergence in our results, with CO values ranging from 0.1 to more than 0.5 (Figure 3.4), stresses the importance of standardizing the methodology for CO determination. The fractal nature of tree crowns makes the definition of their outline a very uncertain and subjective task (Mandelbrot, 1983; Zeide and Pfeifer, 1991), but the method chosen can give not merely different numeric results, but also different biological interpretations. If defined by hand, it is common to define a serrated outline following all the cavities and gaps, so that CO is determined by the proportion of leaves and hollows within the crown. However, there is an inherent problem in deciding the smallest cavity that must be taken into account (Zeide, 1998). On the other hand, the use of objective geometrical conventions (convex hull or the circumscribed rectangle) leads to high values of CO where openness is mainly influenced by the existence of dents and bulges in the crown profile, *i.e.* crown irregularity (Mizoue and Dobbertin, 2003). However, the combined study of crown porosity (the value of CO for tight outlines) and irregularity (the difference in CO between tight and loose outlines) can be of interest for assessing the patterns of leaf distribution. This is related to the light interception efficiency, which has commonly been assessed in terms of the silhouette-to-total-area ratio (STAR) (Sinoquet et al., 2005; Delagrange et al., 2006). In turn, STAR depends on crown density (the ratio of leaf area to crown area) and leaf dispersion (Duursma et al., 2011) and can be related to CO as: STAR=SA·(1-CO)/LA, where SA is the projected silhouette leaf area and LA is the crown leaf area. Thus assessment of crown porosity and irregularity can lend insight into the study of leaf distribution throughout the crown and the effect of environmental factors on it.

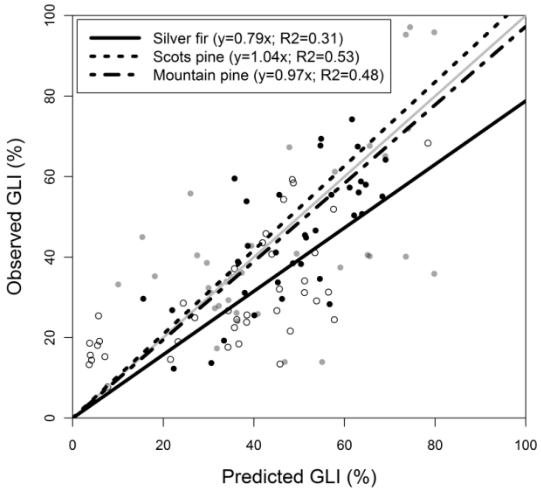

Figure 3.8 Test of the model's ability to predict understory light levels in montane-subalpine forests in the Pyrenees depending on the dominant species. Silver fir (*Abies alba*): white dots; Scots pine (*Pinus sylvestris*): grey dots, and mountain pine (*Pinus uncinata*): black dots. Equations and dashed lines correspond to models in which crown openness and crown allometry were allowed to vary as a function of plot aspect. The gray solid line represents 1:1 relationship.

Table 3.4. Slope and goodness-of-fit of equations relating predicted and observed GLI values in montane-subalpine forests in the Pyrenees. The reference model was adjusted with species-specific constants for crown openness and allometry: silver fir (*Abies alba*); Scots pine (*Pinus sylvestris*) and mountain pine (*Pinus uncinata*). Subsequent models allowed CO, crown geometry and both parameters to vary depending on the species and the aspect of the validation plot.

	Silver fir		Scots pine		Mountain pine	
	Slope	R^2	Slope	R^2	Slope	R^2
Reference model (CO20)	0.767	0.33	0.937	0.32	0.915	0.49
Variable CO	0.773	0.32	1.028	0.48	0.913	0.49
Variable crown geometry	0.781	0.30	1.018	0.53	0.973	0.49
Both	0.788	0.30	1.044	0.54	0.971	0.49

In our study, the lower CO we observed for bigger trees (Table 3.3) agrees with previous reports that related this effect to a higher foliage accumulation in the top layer of the canopy and to lower branchiness and sparse display of foliage in smaller trees (Lefrançois et al., 2008; Boivin et al., 2011; Duursma et al., 2011). In pines, we found DBH to influence CO for loose outlines but also crown irregularity (Table 3.3). Small pines have fewer and less uniformly distributed branches than fir, and so the bigger spaces between branches contribute to higher CO and irregularity. Conversely, the effect of DBH on fir CO was only significant for the tightest outlines, suggesting that differences would be mainly a consequence of changes in the proportion of leaves and hollows within the crown. The rank of crown regularity observed for the three species also matched ranks of shade tolerance (Ameztegui and Coll, 2011). Our results agreed with previous studies that have already found a relationship between shade tolerance and the regularity in the distribution of foliage, assessed by means of the fractal dimension of the crown (Zeide and Pfeifer, 1991; Osawa, 1995; Boudon et al., 2006).

Crowns in southern-oriented plots were more open for mountain pine and silver fir, while we observed the opposite trend for Scots pine (Table 3.3). Within-species regional differences in CO have been suggested to vary with water availability, whether from annual precipitation or actual evapotranspiration (Messier et al., 1998; Astrup and Larson, 2006). Lefrançois *et al*. (2008) showed enhanced CO values in plants growing in drier conditions that were ascribed to a decrease in the quantity of foliage supported by plants. Analyses compiled from 25 studies and including 17 species found that higher vapor pressure deficit (VPD) caused reduction in leaf/sapwood area ratio in pines, but not in other conifer species, including *Abies* (DeLucia et al., 2000). Our observed species-specific changes in CO with aspect cannot be completely explained by either the decrease in the total amount of foliage or by the changes in leaf distribution patterns associated with shade tolerance alone. We found crown regularity to vary with aspect in the same direction as CO (Table 3.3), suggesting that changes in CO with aspect would be mainly caused by variation in the distribution patterns of branches and foliage.

Increasing light interception efficiency allows plants to increase carbon assimilation, but this can only be achieved at high metabolic cost associated with the construction and maintenance of the woody structures needed (Duursma et al., 2011). Thus the optimal metabolic option is frequently not the one that maximizes light interception, and some degree of leaf clumping is commonly observed (Pearcy et al., 2005). In addition, leaf self-shading prevents leaves warming above air temperature (de Castro and Fetcher, 1999; Falster and Westoby, 2003; Valiente-Banuet et al., 2010), limits evapotranspiration losses and can also help trees to avoid photo-damage caused by excessive radiation (Valladares et al., 2005). This is particularly important in seedlings of plants growing at high altitudes such as mountain pine and silver fir, but has also been observed in adult trees (Germino and Smith, 1999; Grace et al., 2002; Handa et al., 2005). This could explain the observed increase in CO that both species experience in sun-exposed slopes. In the case of Scots pine, its lower crown porosity in southern aspects may be a consequence of its strategy to face higher evaporative demand. In this species, increased VPD has been observed to cause little variation in the leaf/sapwood area ratio but a marked enhancement of tree branchiness as a strategy to avoid catastrophic cavitation in trees (Berninger et al., 1995; DeLucia et al., 2000).

3.4.2. Prediction of understory light

Average GLI values in the understory of the forests studied ranged from 7.7 to 97.1%, with an average of 39.7%. In our study area, the SORTIE-ND model slightly overestimated the amount of light reaching the understory. This overestimation may be caused by the effect of slope, which causes a distortion between the actual and the modeled relative position of trees in SORTIE-ND, thus causing changes in shade cast by neighbor trees. However, the potential biasing effect of slope was minimized by restricting calculations to the sky region within 45º from vertical. Light predictions can be considered more than acceptable and regression fits were comparable to previously validated forests (Beaudet et al., 2002; Boivin et al., 2011). The least biased predictions of GLI were obtained using CO20, *i.e.* the tightest crown outline. These results agree with those of Boivin *et al*. (2011), who also found CO20 to give the best fit in adult poplar plantations. However, we observed few differences in the estimated parameters for different outlines. Only the loosest outlines (COCH and CORec) produced significantly less accurate predictions and slopes different from 1. The weak influence of different crown outlines in predicting GLI suggests a low influence of CO in forest understory light availability. Canham *et al*. (1999a) and Beaudet *et al*. (2002) have already suggested that the size, distribution and geometry of tree crowns are the most important factors regulating spatial variation in understory light availability. Our results support these findings, as the marked improvement of light predictions obtained when crown parameters were allowed to vary depending on the aspect of the validation plot was mainly caused by variation in crown geometry (Table 3.4).

3.4.3. Conclusions

In summary, the effect of slope aspect on tree crowns was found to be highly species-specific. Aspect influenced both crown transparency and irregularity of the species studied and, as a consequence, changes in crown openness may be a combined effect of changes in total leaf area and patterns of leaf distribution. The observed species-specific variation in crown geometry and openness with aspect resulted in differences in understory light predictions that were large enough to warrant explicit consideration when studying and modeling the ecological processes driving the dynamics of these forests.

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Tree dynamics and co-existence in the montane-sub-alpine ecotone: the role of different light-induced strategies

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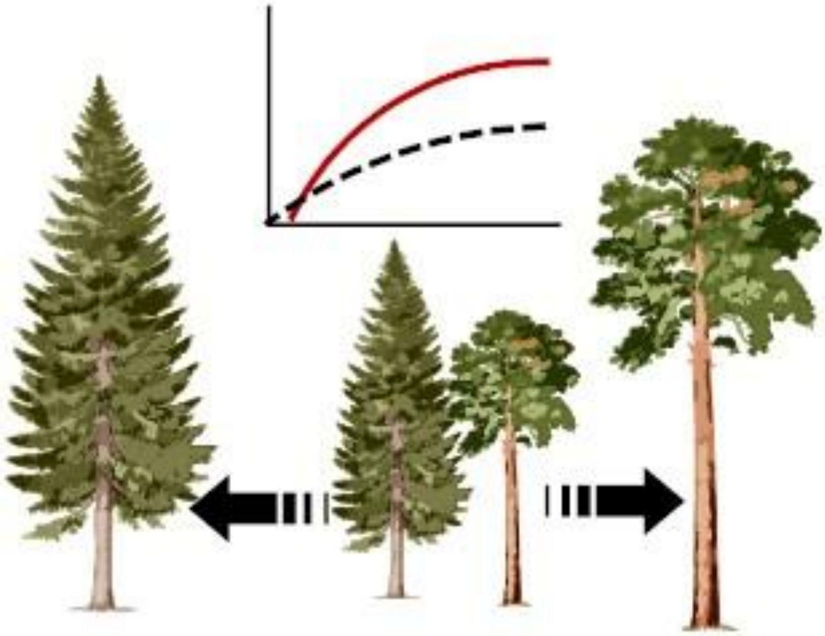

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Aitor Ameztegui & Lluís Coll

4. Tree dynamics and co-existence in the montane-subalpine ecotone: the role of different light-induced strategies

Abstract

Questions: Is light availability the main factor driving forest dynamics in the Pyrenean subalpine forests? Do pines and firs differ in their growth, mortality and morphological response to low light availability? Can differences in shade tolerance affect the predictions of future biome changes in the Pyrenean subalpine forests in the absence of thermal limitation?

Location: Montane-subalpine ecotones of the Eastern Pyrenees (NE Spain)

Methods: We evaluated the morphological plasticity, survival and growth response of saplings of Scots pine, mountain pine and silver fir to light availability in a mixed-forest ecotone. For each species, we selected 100 living and 50 dead saplings and measured their size, crown morphology and light availability. A wood disk at root collar was then removed for every sapling, and models relating growth and mortality to light were obtained.

Results: Fir showed the lowest mortality rate (< 0.1) at any given light condition. Pines showed comparable responses to light availability although in deep shade Scots pine faced a higher risk of mortality (0.35) than mountain pine (0.19). Pines and fir developed opposing strategies to face light deprivation: fir employed a conservative strategy based on sacrificing height growth, whereas pines enhanced height growth to escape from shade, but at the expense of higher mortality risk. Scots pine showed higher plasticity than mountain pine on all architectural and morphological traits analyzed, showing a higher adaptive capacity to a changing environment.

Conclusions: Our results support the prediction of future biome changes in the Pyrenean subalpine forests as silver fir and Scots pine may find appropriate conditions for colonizing mountain pine dominated stands due to land-use change-related forest densification and climate warming-related temperature increases, respectively.

Keywords: shade tolerance; montane-subalpine ecotone; morphological plasticity; forest dynamics; *Pinus uncinata*; *Pinus sylvestris*; *Abies alba*; Pyrenees.

4.1. Introduction

Mountain pine (*Pinus uncinata* Ram.) is the dominant species in the subalpine belt of the Pyrenees, whereas Scots pine (*Pinus sylvestris* L.) and silver fir (*Abies alba* Mill.) dominate the montane belt. However, these three species coexist in the ecotone between the upper-montane and lower-subalpine belts, constituting a mixed-conifer forest (Mason and Alía, 2000; Aunós et al., 2007). The rise in temperatures associated to climate change has prompted predictions of species displacement in mountain areas (Walther et al., 2002; Resco et al., 2006), meaning an upward encroachment of montane species (silver fir and Scots pine) into the subalpine belt can be expected (Walther et al., 2002; Peñuelas and Boada, 2003a; Resco et al., 2006; Peñuelas et al., 2007). Upward spread of species into existing forests is driven not only by climate, but also by interspecific competition for resources and dispersal and establishment patterns (Woodward and Williams, 1987; Vetaas, 2002), as species-specific adaptive responses to the environment and homeostatic effects may modulate changes in community composition (Neilson, 1993; Walther et al., 2002; Valladares et al., 2006). Together with increasing temperatures, mountain forests in Spain have also experienced a drastic reduction in logging in recent decades thanks to environmental concerns and the drop in timber profitability. In the absence of large-scale disturbances, this has promoted severe canopy closure and establishment of advanced regeneration of shade-tolerant species such as silver fir (Robakowski et al., 2004; Aunós et al., 2007). In this context, and in the absence of water deficit, interspecific differences in performance under contrasting light conditions can sharply affect the dynamics of these transition areas (Neilson, 1993; Delagrange et al., 2004). Light is a highly temporally- and spatially-heterogeneous resource in the forest (Canham, 1988a; Gravel et al., 2010), and species have developed different abilities to adjust their morphology and physiology to different sets of light conditions (Messier et al., 1999; Delagrange et al., 2004). The way in which species allocate their resources will determine their ability to perform in sun conditions and shade conditions, the latter ability being traditionally dubbed ‘shade tolerance’ (Canham, 1988a; Valladares and Niinemets, 2008). Early classifications of shade tolerance were constructed as relative rankings among species or discrete classes (Baker, 1949; Anderson et al., 1969; Whitmore, 1989; Ellenberg, 1992). The first attempts at quantification related shade tolerance to the ability to maximize carbon gain and growth in shady environments (Bazzaz, 1979; Givnish, 1988), but more recent studies have reported a trade-off between survival and radial growth at low light (Kobe et al., 1995; Lin et al., 2002; Kunstler et al., 2005). Thus, shade tolerance has been quantified by estimating the relationship between growth and probability of mortality (Kobe, 1996; Wyckoff and Clark, 2000, 2002), producing quantitative estimates of shade tolerance that generally match the previously accepted ranks (Kneeshaw et al., 2006). Accordingly, in low-light ambiances, shade-tolerant species do not necessarily grow faster that shade-intolerants (Canham, 1989; Pacala et al., 1994), but will be more likely to survive (Kobe and Coates, 1997; Canham et al., 1999b). Furthermore, shade tolerance has also been suggested to be related to the ability to reduce height growth to avoid the increased respiration and maintenance costs associated with larger size (Messier et al., 1999; Kneeshaw et al., 2006). Overall, the ability to grow and survive in the understory can be achieved by alternative combinations of physiological, morphological, allocational and architectural traits that can be species- and/or environment-specific (Claveau et al., 2002; Delagrange et al., 2004; Valladares and Niinemets, 2008) and that are in turn affected by ontogenetic effects, i.e. by the plant size (Niinemets, 2006; Sánchez-Gómez et al., 2006b; Lusk et al., 2008).

This study aimed to advance in understanding the different light-induced strategies developed by three conifers (silver fir, mountain pine and Scots pine) in order to coexist in the montane-subalpine ecotones of the Catalan Pyrenees (NE Spain). In today's changing context, potential structure and composition changes are of major concern in these forests, as they constitute the southern distribution limit of endangered plant and animal species, such as the Western capercaillie (*Tetrao urogallus*) or Tengmalm's Owl (*Aegolius funereus*) that are particularly sensitive to changes in their habitat (Camprodon, 2001; Gracia et al., 2007). We hypothesize that in the absence of thermal limitation, silver fir and Scots pine would develop more efficient strategies than mountain pine to respond to light variations, which if true would lead to an upward displacement of the montane-subalpine transition zone.

4.2. **Materials and methods**

4.2.1. Study area and species

The study area is located on the Pallerols Valley in the Alt Pirineu Natural Park, Catalonia, NE Spain (42º23' N; 1º15' E). Mean annual rainfall at the study site is slightly below 1000 mm, distributed equally among seasons. Mean annual temperature is 6.1ºC and, in general, summers are relatively cool (mean temperature around 15ºC), meaning there is no summer drought. Winters are long and cold, with a growing period of 173 days and only 150 frost-free days. Forests in the montane belt are occupied by Scots pine (*Pinus sylvestris* L.), a shade-intolerant species that find its optimum at about 1500 m, and by silver fir (*Abies alba* Mill.), one of the most shade-tolerant conifers in the Pyrenees, which grows in the more humid areas between 1200 and 1900 m. Mountain pine (*Pinus uncinata* Ram.), also traditionally considered as a shade- intolerant species, dominates the subalpine belt (1700-2400 m), with its optimum performance at about 1800 m (Blanco et al., 2005; Ruiz de la Torre, 2006). Our study site was located between 1700 and 1850 m, in the montane-subalpine ecotone where these three conifer species (silver fir, Scots pine and mountain pine) co-exist. No logging, silvicultural treatments or major disturbances affecting canopy have occurred in the last decade in the study area. The plots were all located on uneven-aged stands characterized by a high horizontal and vertical heterogeneity, therefore presenting gaps alternating with heavily-shaded areas.

4.2.2. Data collection

Samples were taken along six transects crossing the montane-subalpine ecotone. All transects were located in mixed-conifer stands, with different slopes and aspects. A total of 94 silver fir, 98 Scots pine and 96 mountain pine saplings were sampled, with a sapling defined as a tree above 50 cm in height but below 7.5 cm in diameter at breast height (Camarero et al., 2000a). For each sapling, we measured diameter at 10 cm, total sapling height, crown height and crown diameter. Apical growth was determined as the mean value of the length of the last three shoots of the main axis. We also measured lateral growth as the mean length growth of the last three years for at least four branches per tree, two in the upper third of the sapling and two in the lower one. A wood disk from the root collar of every sapling was removed, dried, sanded and scanned, and annual radial growth was determined as the mean for the last three years according to the method described at Lussier et al. (2004).

Light measurements were taken during September and October 2009, under completely overcast conditions, as proposed by Messier and Puttonen (1995) and Parent and Messier (1996). The percentage of above-canopy light (photosynthetic photon flux density; PPFD) at the top of each sapling was used to describe its light environment. Above-canopy PPFD was measured with a Li-190SA Quantum sensor (Li-COR, Nebraska, USA) placed on an open area adjacent to the study site and connected to a data-logger that recorded readings every 10 seconds. A second quantum sensor was used to measure PPFD at the top of each sapling, and time of the measurement was recorded. Light availability for each sapling was then determined as %PPFD.

4.2.3. Growth and mortality as a function of light

To obtain the relationship of growth and mortality with light, we employed the two-step approach originally developed by Kobe et al. (1995) for the SORTIE model. Thus, we first modeled the relationships between growth and light availability and between mortality risk and past growth, and then combined them to determine the relationship between mortality and light. Radial and apical growth were modeled against light availability (Figure 4.1). The relationship between growth and light availability was established by a Michaelis-Menten function, which is widely used for modeling tree growth (Pacala et al., 1994; Wright et al., 1998; Lin et al., 2002; Kunstler et al., 2005). According to this function, growth can be expressed as:

$$G = size^{d}\ \frac{a * L}{{}^{a}\!/\!{}_{s} + L} \qquad (1)$$

where G is the growth of an individual of a given size at a light level L (%PPFD), while *a* and *s* are the parameters of the Michaelis-Menten function, which can be interpreted as asymptotic growth rate and slope at zero light, respectively. Size was defined as radius (in mm) in the case of radial growth and as tree height (in cm) in the case of length growth, and *d* is a parameter which describes the changes in growth rate with tree size. To estimate the maximum likelihood parameter values, we used simulated annealing (Goffe et al., 1994). A series of alternate models were fitted to each dataset. The simplest model (null model) only considered the effect of size on tree growth, and was used to assess the influence of light availability on growth. We also fitted a linear and power model to the data available for each species. The R^2 of the observed *vs*. predicted regression was used as a measure of goodness of fit of each model, and alternative models were compared using ΔAICc, the difference in corrected Akaike Information Criterion (Burnham and Anderson, 2002).

Mortality as a function of radial growth was estimated according to Wyckoff and Clark (2000), who in turn modified the method originally proposed by Kobe et al. (1995). Implementing this method requires the growth rates of live and recently dead saplings together with an estimation of annual mortality rate. Growth rates of living saplings were obtained from the sample collected for growth-light relationships. To obtain the growth rate of dead saplings, 50 recently dead saplings of each species were randomly harvested from the transects, and growth rate was obtained using the method given above for living saplings. The criterion used to consider a sapling as 'recently dead' was twig suppleness and the maintenance of some needles. We used a parametric option to allow for comparison among species (Kunstler et al., 2005), where the growth-mortality function for each species can be calculated as:

$$p(d|g) = \frac{\theta}{\left[\theta + {(1-\theta)}/{Q}\right]} \tag{2}$$

where p(d|g) is the growth-mortality function, θ is the overall mortality rate, and Q is the ratio of the growth rates (g_i) of living (g_l) and dead (g_d) saplings. These growth rates were estimated by adjusting the dataset to a gamma density distribution using the maximum likelihood method, with the likelihood of the gamma density being:

$$L(G_d \mid \lambda_d, \rho_d) = \prod_{i=1}^{D} \frac{\lambda^{\rho_d}}{\Gamma(\rho_d)} g_i^{(\rho_d - 1)} \exp(-\lambda_d g_i) \tag{3}$$

where G_d represents the data set for the growth rates of dead saplings and Γ is the gamma function, while λ_d and ρ_d are *shape* and *scale*, the fitted parameters for the gamma density. The same approach was used for live saplings, but likelihood took parameters λ_l and ρ_l and the dataset was G_l. Overall mortality rate ϑ was estimated, for each species, from 100x5 m transects in which all recently dead and living saplings were counted. Parameters were estimated using simulated annealing, as specified above. Mortality as a function of light availability was obtained by combining equations [1] and [2]. For a given light availability, growth was estimated from equation [1] for an individual with a radius of 20 mm (the dataset average). Then, growth ratio *Q* was estimated, and annual probability of mortality was obtained from equation [3]. To assess sapling performance, probability of survival as a function of light availability was calculated for an average-size sapling and for two situations, i.e. *i*) over five years and *ii*) over the number of years needed to become adult (diameter > 75 mm).

4.2.4. Architecture and crown morphology

For the data set of living saplings, a set of architectural traits was calculated: apical and lateral average growth and slenderness (as the ratio between tree height and diameter). Crown morphology was assessed by crown depth (the ratio between crown height and total tree height), crown slenderness (the ratio between crown height and crown diameter) and apical dominance, estimated by plagiotropy index (the ratio between apical and lateral growth). The influence of light availability and ontogenetic effects on these morphological and architectural traits was determined by analysis of covariance, where species was a factor and %PPFD and tree size were covariates. %PPFD was transformed to its logarithm when necessary to achieve normality of residuals and homoscedasticity. Differences in slope coefficients between species were tested by examining the significance of the interaction term between species and %PPFD or tree size, respectively. Unless otherwise specified, significance was set at *P*-value < 0.05.

4.3. **Results**

4.3.1. Growth and mortality as a function of light availability

The key role of light in both apical and radial growth was strongly supported by our data, the full Michaelis-Menten model presenting in all cases a much lower AICc value than the null model, in which no influence of light was considered (Table 4.1). Furthermore, the Michaelis-Menten model fitted well for all the datasets (R^2 ranging between 0.53 and 0.8; Table 4.1). At low light levels, the slope of the function relating apical growth and light was similar for the three species. However, fir rapidly reached its asymptotic growth and thus both pines outgrew fir growth as light availability increased above 15% (Figure 4.1). At full sun, Scots pine showed higher maximum apical growth rate than mountain pine, the differences between the two species becoming important for light values above 40%. Both pines increased their radial growth almost linearly in response to light availability (Table 4.1; Figure 4.1). In contrast, fir reached its maximum growth rate at a light availability of 20%.

In all cases, radial growth over the last three years was consistently higher for living saplings than for dead saplings (Table 4.2). Silver fir had the lowest probability of mortality for any given growth rate or light level, with almost no variation across the entire data range (Figure 4.2). Scots pine showed the greatest probability of mortality at low and intermediate growth rates, clearly above that observed for mountain pine, but its mortality rate dropped below mountain pine's for growth rates higher than 0.9 $mm \cdot year^{-1}$ (Figure 4.2).

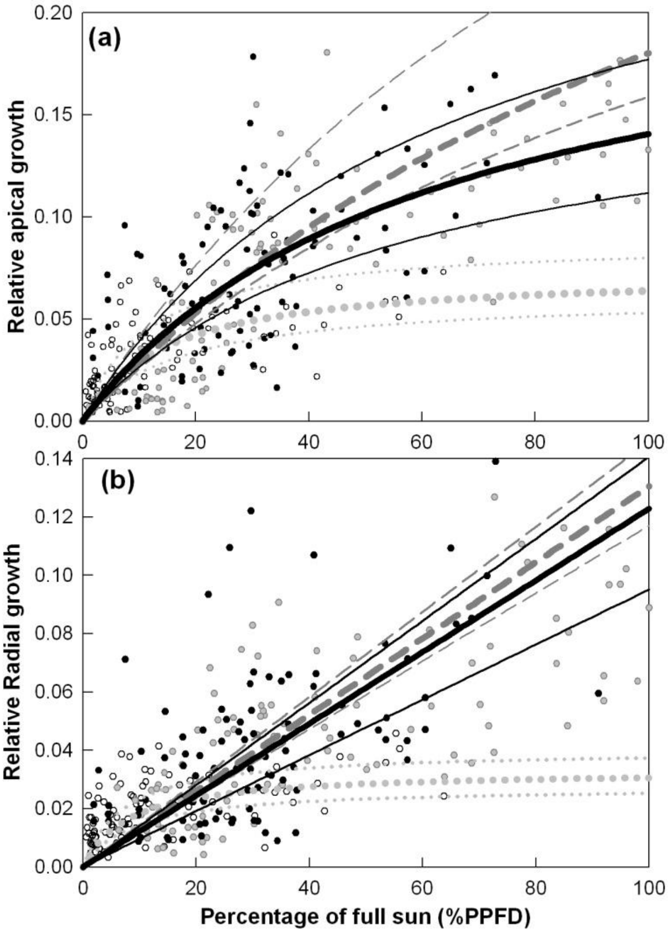

Figure 4.1 Response of (a) relative apical growth and (b) relative radial growth to increases in light availability. Dots represent observed values for 94 *Abies alba* (unfilled dots), 98 *Pinus sylvestris* (grey dots) and 96 *Pinus uncinata* (black dots) saplings. Thick lines correspond to the adjusted Michaelis–Menten function for a sapling with average radius (20 mm) and height (180 cm), with the parameters shown in Table 4.1 for *Pinus uncinata* (black), *Pinus sylvestris* (dark-grey) and *Abies alba* (light-grey). Dashed lines represent upper and lower growth predictions constructed with minimum and maximum values of the two-unit support intervals for parameter estimates.

Among-species trends in mortality for different light levels were similar to those observed for different growth rates (Fig.4.3a). Thus, while silver fir consistently showed the highest likelihood of survival (above 0.8) at any given light level, both pines sharply increased their probability of survival as light availability increased. Survival rates for mountain pine and Scots pine reached 50% at 12% and 20% of full sun, respectively. However, the Scots pine survival likelihood surpassed that of mountain pine at light levels above 40%. At full light, mountain pine and silver fir showed a similar maximum survival rate of 0.9 over a period of five years (Fig 4.3.a), whereas the survival rate of Scots pine sapling with no light limitation reached values up to 99%. Maximum survival probability did also differ among species when considering time needed to reach adulthood (defined as a tree with dbh > 7.5 cm), mainly as a consequence of differential growth rates (Fig. 4.3b). At low light levels, fir showed the highest survival rates, but as it took more than 25 years for a fir to become an adult (data not shown), its survival rate never reached more than 60%, whatever the light level. In the case of pines, their high mortality rate at low light conditions almost prevented them reaching adulthood at any given light level below 15%. Above this value, their probabilities of reaching adult size rapidly increased, driven by a lower mortality rate associated with higher radial growths. Both pines showed similar survival trends at light levels below 50%. Differences between Scots pine and mountain pine at low light were lower than observed for a five-year period due to the accumulated effect of lower mortality for Scots pine at any growth rate above 1 mm·year^{-1} (Fig. 4.3b), but differences in full sun were bigger as a consequence of the higher radial growth rate of Scots pine

Table 4.1. Parameter estimates for Michaelis-Menten growth-light function for (a) apical growth; (b) radial growth.

Apical growth						
Species	N	a	s	d	R^2	ΔAICc
A. alba	94	0.445	0.029	0.656	0.691	79.17
		[0.396; 0.498]	[0.024; 0.035]	[0.642; 0.668]		
P. sylvestris	98	6.428	0.043	0.488	0.842	136.89
		[5.564; 7.486]	[0.040; 0.046]	[0.483; 0.493]		
P. uncinata	96	0.809	0.013	0.756	0.535	35.54
		[0.669; 0.977]	[0.011; 0.015]	[0.741; 0.767]		
Radial growth						
Species	N	a	s	D	R^2	ΔAICc
A.alba	94	17.43	2.16	0.449	0.591	66.10
		[15.63; 19.41]	[1.73; 2.70]	[0.421;0.473]		
P. sylvestris	98	4031.8	0.0071	0.436	0.802	148.49
		[40.30; 10000.0]	[0.0068; 0.0076]	[0.418; 0.449]		
P.uncinata	96	3069.8	0.0015	0.93	0.579	88.53
		[0.23; 10000.0]	[0.0013; 0.0016]	[0.90; 0.96]		

Note:Parameter estimates for radial growth of *Abies alba* cannot be directly compared with the rest of species as the dependent variable was multiplied by 100 to avoid anormal residual behavior. N is sample size and *a*, *s* and *d* are the fitted parameters of the Michaelis-Menten functions. R^2 is the regression coefficient of the observed vs. predicted equation and ΔAICc is the decrease in AICc for the selected Michaelis-Menten model as compared with a null model in which no light effect on growth is considered. Values in brackets are the 2-unit support intervals for the parameter estimates.

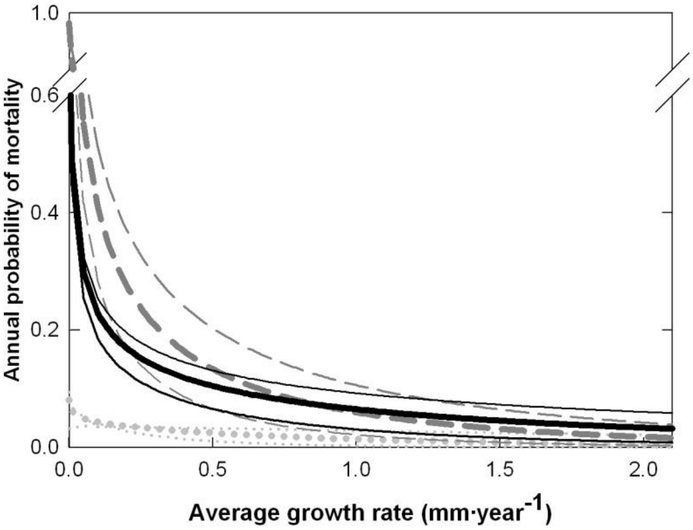

Figure 4.2 Annual probability of mortality for a sapling as a function of average radial growth rate. Growth rate was calculated for a sapling with average radius (20 mm). Thick lines represent modelled annual probability of mortality, while dashed lines represent upper and lower growth predictions constructed with minimum and maximum values of the two-unit support intervals for parameter estimates: *Pinus uncinata* (black), *Pinus sylvestris* (dark-grey) and *Abies alba* (light-grey).

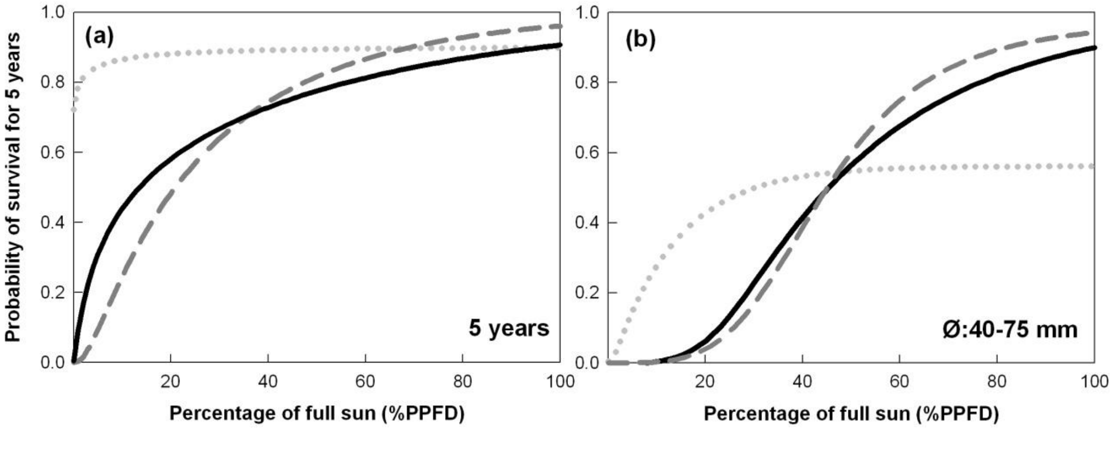

Figure 4.3 Probability of survival for an average sapling over (a) a 5-year period; and (b) the time needed to reach a diameter of 75 mm (the average sapling had a diameter of 40 mm). Species are: *Pinus uncinata* (black lines), *Pinus sylvestris* (dark-grey lines) and *Abies alba* (light-grey lines).

Table 4.2. Estimated parameters of shape (ρ) and scale (λ) for the adjusted gamma distribution of radial growth for live and dead saplings

	Live			Dead			
Species	Growth rate ($mm \cdot y^{-1}$)	λ	ρ	Growth rate ($mm \cdot y^{-1}$)	λ	ρ	**Annual Mortality Rate**
A. alba	0.30	0.11 [0.09;0.14]	2.62 [2.17; 3.07]	0.17	0.10 [0.08-0.13]	2.50 [1.89; 3.10]	0.033
P. sylvestris	1.26	1.06 [0.86; 1.26]	1.892 [1.56; 2.22]	0.33	0.60 [0.41-0.79]	1.13 [0.80; 1.46]	0.066
P. uncinata	0.77	0.45 [0.38; 0.53]	1.71 [1.40; 2.03]	0.25	0.39 [0.27-0.50]	1.22 [0.89; 1.55]	0.110

Values in brackets are the 2-unit support intervals for the parameter estimates.

4.3.2. Architectural and morphological plasticity in response to light availability

The models explained more than a half of total observed variability for all the architectural and morphological variables analyzed (R-squared ranging from 0.59 to 0.81), except for slenderness (R-squared = 0.29; Figure 4.4). All architectural traits significantly changed with variation in light availability and the response was species-specific (Table 4.3). In effect, response of apical and lateral growth to changes in light environment was significantly higher for Scots pine than the other two species ($P < 0.001$, data not shown), while no significant differences in growth rate variation were observed between mountain pine and silver fir (apical growth: $P = 0.09$; LG: $P = 0.96$; data not shown). Growth curves for Scots pine intersected the x- axis at %PPFD = 10, demonstrating almost no apical or lateral growth below that light level (Figure 4.4a). In contrast, mountain pine and silver fir showed positive growth values even at very low light levels, but the apical growth of Scots pine rapidly overgrew both of them (at %PPFD = 9 and 22, respectively).

Growth of lateral branches tended to follow the same pattern, but in this case the growth of fir was the highest at low light and Scots pine only became the fastest-growing species at light levels above 25%, while mountain pine could not rival with fir growth even at full sunlight (Figure 4.4a). Slenderness was significantly reduced with increasing light conditions for all three species (Figure 4.4c), but the decrease was significantly sharper for Scots pine, which decreased slenderness by more than 50%, than for the other two species, whose response was not statistically different ($P = 0.270$; data not shown). All three architectural variables increased with tree size (Figure 4.4), but species-specific differences in response were only observed for apical growth (Table 4.3). Silver fir showed a weak response in apical growth with increasing tree size, whereas both pines showed a significantly higher response (*P* < 0.01), but without significant between-pine differences (*P* = 0.237; data not shown).

Table 4.3. Summary of ANCOVA P values (values in bold indicate significance at α =5 %) for the relationship between plant architecture, crown morphology and tree size (TH), light (L) and species (SP) and interactions.

Variable	**SP**	**L**	**TH**	**SPxL**	**SPxTH**
Architecture					
Apical growth	<0.001	<0.001	<0.001	<0.001	0.002
Lateral growth	<0.001	<0.001	<0.001	<0.001	0.188
Slenderness	<0.001	<0.001	<0.001	<0.001	0.172
Crown Morphology					
Plagiotropy index	<0.001	<0.001	<0.001	0.089	0.018
Crown Depth	<0.001	<0.001	0.201	<0.001	<0.001
Crown Slenderness	0.001	0.132	<0.001	0.263	0.002

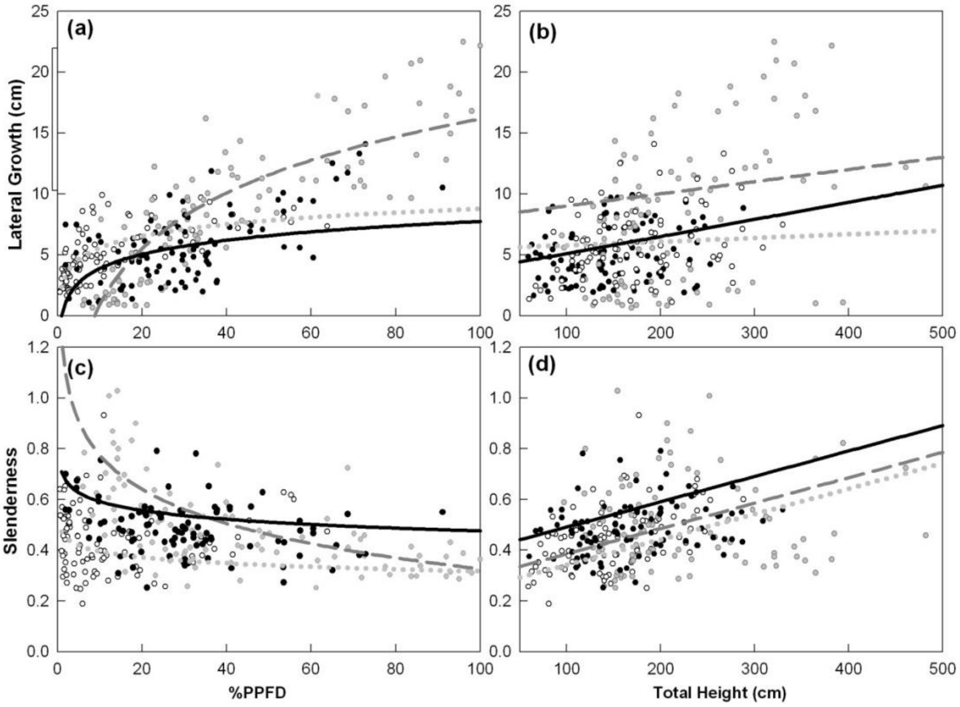

Figure 4.4 Effect of light availability and sapling size on sapling architecture. Dots represent observed values, while lines correspond to ANCOVA models. Explanatory variable not indicated in the x-axis is set to the average for each species. Species are: *Pinus uncinata* (black solid dots and black lines), *Pinus sylvestris* (grey dots and dashed lines) and *Abies alba* (unfilled dots and dotted lines).

Crown morphology also varied among species. Mountain pine and silver fir showed a slight yet significant increase in crown depth as light availability increased, without difference between the two species (P = 0.205; data not shown). However, Scots pine gave a significantly higher response slope (P < 0.001; data not shown), as its crown depth increased from 0.31 at 10% PPFD to over 0.85 at full-sun (Fig. 4.5a). Both pines showed two-fold higher crown slenderness values than silver fir, but no effect of light availability on crown slenderness was observed (Table 4.3; Fig. 4.5c. Silver fir presented a significantly lower plagiotropy index than both pines at any light level. Even though differences were bigger at deep shade as fir reduced its apical dominance to less than one (Fig. 4.5e), no species-specific responses to light variations were observed (P = 0.089; Table 4.3). Size also induced variation in crown morphology variables. Mountain pine and fir increased the depth of their crown as saplings got bigger, but with no significant difference in their response (P = 0.101; data not shown). However, Scots pine showed the opposite trend (Fig. 4.5b). Crowns also tended to be slenderer as tree size increased, whatever the species considered (Fig. 4.5d). In the case of plagiotropy index, fir values decreased as saplings got bigger, whereas both pines showed the opposite trend (Fig. 4.5e).

4.4. **Discussion**

Our results correctly matched previously established classifications of shade tolerance proposed by Ellenberg (1992), who assigned a value of three (shade-tolerant, the minimum value for tree species) to silver fir and eight (half-light to full-light species) to Scots pine and mountain pine. Radial growth in deep shade conditions (below 10% of full sun) was almost double for silver fir than for pines, but fir reached its maximum growth at around 20% of incident light, as observed by Robakowski et al. (2003). Hence, both pines rapidly outgrew fir as more light became available. However, although differences between fir and pines were especially important in low light conditions, silver fir showed the lowest annual mortality rate for any given light level. Therefore our results confirm that the higher survival ability of silver fir in low light conditions is due to its ability to maintain a higher radial growth in light-limiting environments, which has traditionally been considered the main general explanation of shade tolerance (Bazzaz, 1979; Givnish, 1988; Pacala et al., 1993; Wright et al., 1998; Lin et al., 2002), but also to an intrinsic ability to withstand low radial growth rates, as more recently suggested for shade-tolerant species (Pacala et al., 1994; Kobe and Coates, 1997; Vieilledent et al., 2010). Although differences in tolerance were much slighter between pine species than between genera, Scots pine showed a higher mortality risk in shaded environments than mountain pine, despite no significant differences in relative growth. Therefore, differences in mortality between both pines are due to lack of ability of Scots pine to survive at low radial growth rather than to any enhanced growth ability of mountain pine.

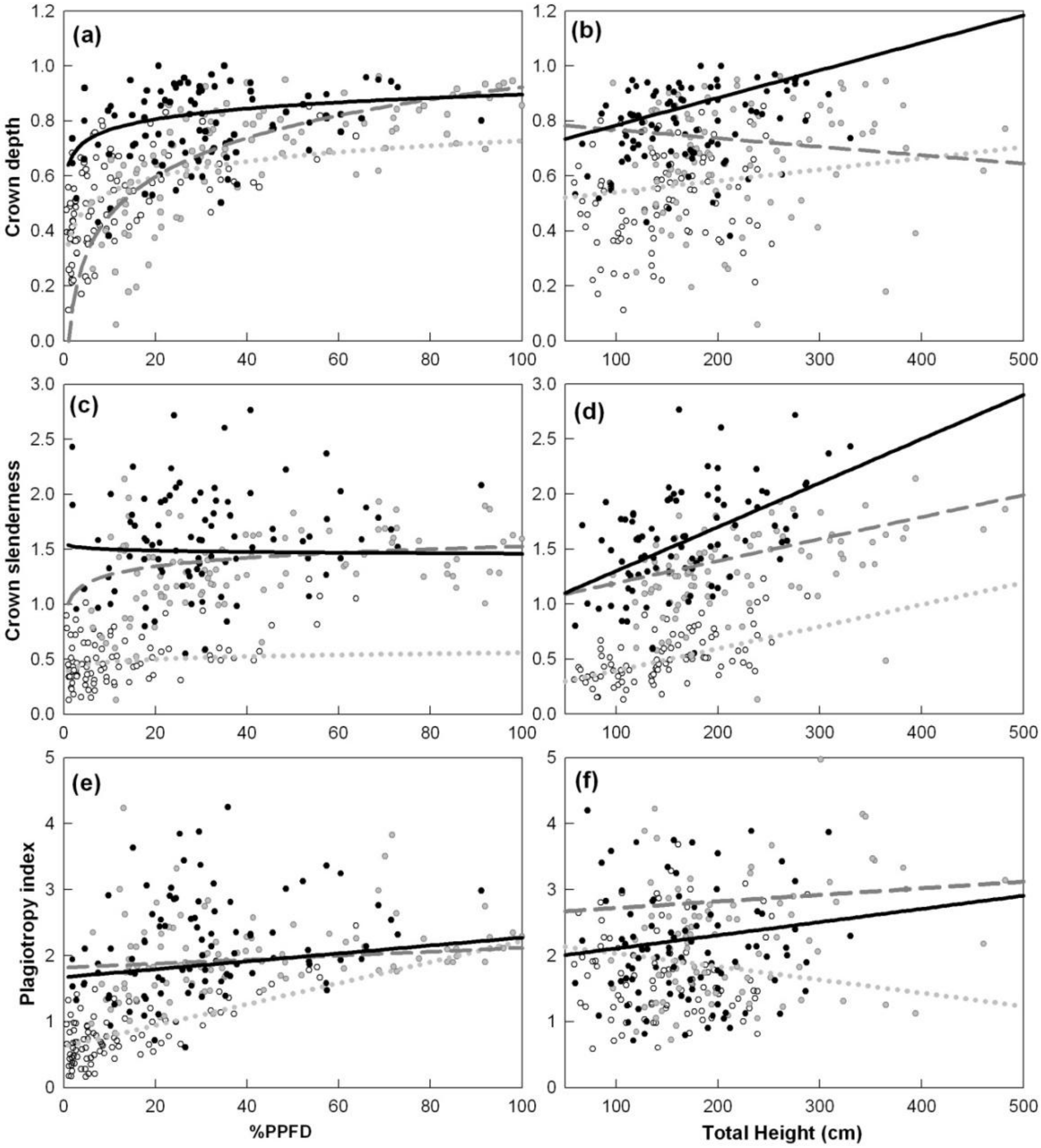

Figure 4.5 Effect of light availability and sapling size on crown morphology traits. Dots represent observed values, while lines correspond to ANCOVA models. Explanatory variable not indicated in the x-axis is set to the average for each species. Species are: *Pinus uncinata* (black solid dots and black lines), *Pinus sylvestris* (grey dots and dashed lines) and *Abies alba* (unfilled dots and dotted lines).

Recently, a series of studies have suggested a relationship between shade tolerance (understood as survival at deep shade) and the ability to suppress height growth when faced with shade conditions (Messier et al., 1999; Williams et al., 1999; Kneeshaw et al., 2006). These studies assert that shade-intolerant species would favor height growth, even in shade conditions. If the enhanced growth results in a greater light availability, for example by rapidly attaining the forest canopy, it will favor sapling performance. Conversely, if it does not result in an advantage in light interception, then the increase in height would cause the saplings to incur higher respiration and maintenance costs that would subsequently increase mortality rate (Givnish, 1988; Messier et al., 1999; Claveau et al., 2002). The patterns of maximum height for live and dead saplings observed in our study agree with this hypothesis, and reveal two opposite behaviors when having to withstand shade conditions. Both pine species show a "shade-escaping" strategy, maintaining an enhanced height growth (much higher than silver fir) even in shade. However, only pines not growing above a determined height – slightly above three meters – are likely to survive (Fig.4.6). In contrast, silver fir appears to develop a conservative resource-use strategy in which growth is reduced to increase the chances of survival, a typical "shade-tolerant" strategy (Canham, 1988a; Beaudet and Messier, 1998; Claveau et al., 2002; Sánchez-Gómez et al., 2006a).

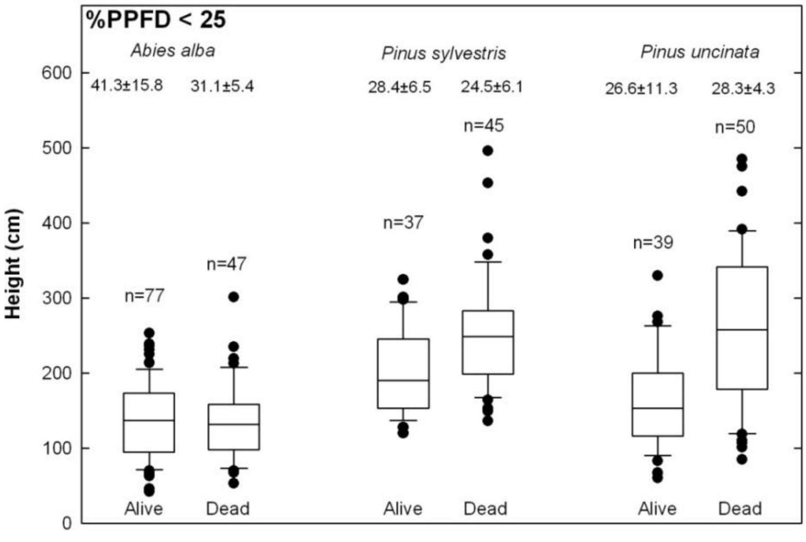

Figure 4.6. Box-plots for total height of living and dead saplings of the three studied species in shade conditions (below 25% PPFD). N represents the sample size, while numbers below species name are the mean Æ SD of sapling age in years.

Silver fir showed little variation in its architectural and crown morphological patterns, *i.e*. low plasticity to changes in available light, except for plagiotropy index. The observed weak apical dominance in the shade was caused by fir's ability to reduce height growth and is a common trait in shade-tolerant firs (Fig.4.7). Nevertheless, low plasticity in crown depth conflicts with the observed patterns for other *Abies* species which usually vary their crown shape from a conical form in full sun to a flat-topped form in understory shade (Kohyama, 1980; O'Connell and Kelty, 1994). If the observed crown depth values at low light matched previous findings reported elsewhere (Fig.4.7), the scant maximum crown depth revealed a limited ability of *Abies alba* saplings to exploit high-light conditions, as observed by Grassi and Bagnaresi (2001). Conversely, *Pinus sylvestris* showed the highest plasticity in apical growth, lateral growth, slenderness and crown depth, conflicting with patterns of low plasticity commonly observed for pines (Fig.4.7). High slenderness values were probably a consequence of the "shade-escaping" strategy of Scots pine and its sharp reduction of crown depth in shade may be interpreted as an attempt to increase survival chances by reducing maintenance costs associated with non-photosynthetic tissues (Beaudet and Messier 1998; Givnish 1988). Finally, mountain pine showed an intermediate and moderate behavior matching previous results for *Pinus* species (Fig.4.7).

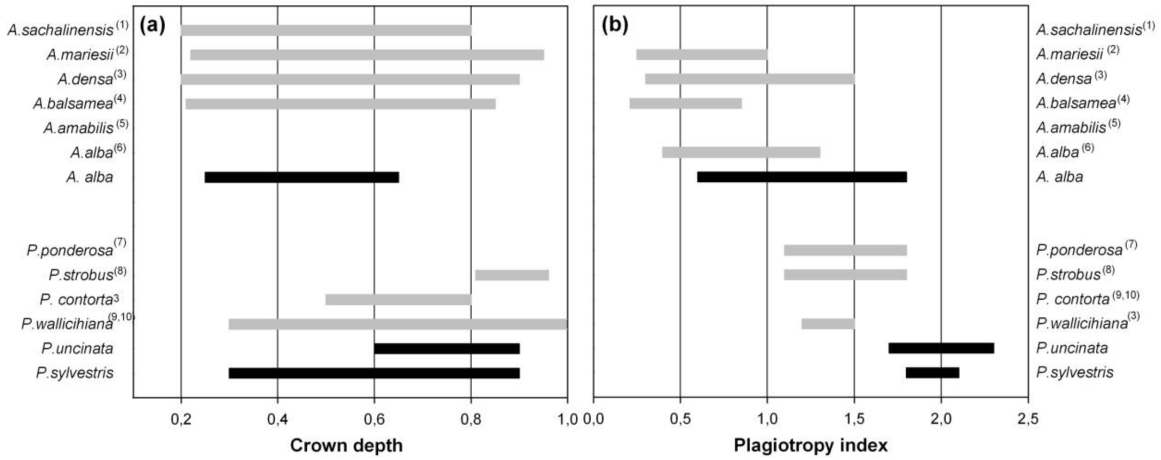

Figure 4.7.Minimum (at deep shade) and maximum (in full sunlight) values of (a) crown depth and (b) plagiotropy index for several Abies and *Pinus* species. Black bars represented observed values in this study. Grey bars represent values obtained from literature review: (1) Takahashi (1996); (2) Kohyama (1980); (3) Gratzer et al. (2004); (4) Gilmore and Seymour (1997); (5) Tucker et al. (1987); (6) Robakowski et al. (2004); (7) Chen (1997); (8) O'Connell and Kelty (1994) ; (9) Chen et al. (1996); (10) Williams et al. (1999)

The negative correlation between morphological plasticity and survival in deep shade that we observed in this study has already been linked in Mediterranean areas to the high costs of the "shade-escaping" strategy for intolerant species (Sánchez-Gómez et al., 2006a). Simultaneous adaptation of plants to a combined gradient of different ecological factors requires compromises that can restrict the competitive success of the species (Valladares et al., 2002; Sánchez-Gómez et al., 2008). Since both Scots pine and silver fir find their upper limit of distribution in the studied ecotone, deviations from expected patterns may also correspond to species-specific responses to these compromises. In Mediterranean areas, for example, drought-induced stress caused little change in Scots pine response to light , whereas limited morphological and physiological plasticity in *Abies alba* has been related to its low drought resistance (Grassi and Bagnaresi, 2001; Robakowski et al., 2003; Robakowski et al., 2004).

Sapling size also modulated the architectural response of the three species to changing light conditions. Both pines showed a high response in apical growth as saplings got bigger. This could be related to existence putative correlation between apical growth and sapling size, but as saplings of all sizes were sampled in every light ambiance, it could also imply a higher selective pressure against pines with greater growth, whereas moderate or limited growth for firs would be part of a strategy to avoid growing above the maximum sustainable height (Messier et al., 1999; Claveau et al., 2002; Kneeshaw et al., 2006).

4.4.1. Ecological implications

Brokaw and Busing (2000) defined three premises to coexistence through niche partitioning in gaps: (*i*) the existence of a light availability gradient; (*ii*) specific differential distribution along that transect and (*iii*) a species-specific trade-off in performance along the gradient. All the three were accomplished by the ecotones studied here. Furthermore, light availability explained a major part of observed variability in growth and mortality for the three studied species, thus emphasizing the important role of light in the demographic processes in the studied forests. Pines growth patterns were adapted to maximize performance in high light ambiances, yet incurring high mortality in closed understory. Conversely, fir optimizes performance in shade but cannot compete with pines in light levels above 60%. The generalized densification of mountain forests caused by reduced logging can nevertheless favor the progressive establishment of advanced regeneration of fir in the understory (Robakowski et al., 2004; Aunós et al., 2007). Although fir presented the lowest annual mortality rate for any given light level, its limited radial growth makes it incur higher accumulated mortality risk during its lifespan. Both pines only showed slight differences in growth and mortality, even though the observed differences in plasticity could imply a higher adaptative potential for Scots pine to a changing environment. If the minimum temperatures currently acting as a barrier to upward spread of Scots pine were to rise as expected (Ipcc, 2007), subsequent enhanced growth would mean a competitive advantage for this species. Furthermore, as mountain pine has had to adapt its morphology and physiology to tough environmental conditions this could constrain its ability of responding to changes in light availability. In short, if silver fir is the species most favored by a lack of management (that creates shaded understories where pine has few opportunities to regenerate), and if temperature no longer limits Scots pine performance (favoring its colonization of open areas), the current land-use and climate change context are expected to culminate in a progressive upward shift of the lower distribution limit of *Pinus uncinata* stands.

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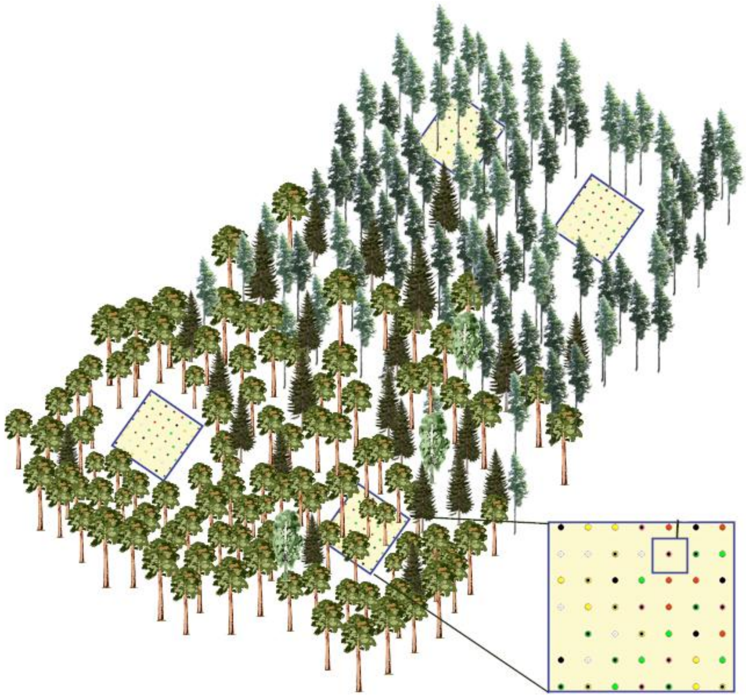
Unraveling the role of light and biotic interactions on seedling performance of four Pyrenean species along environmental gradients

5



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Aitor Ameztegui & Lluís Coll

5. Unraveling the role of light and biotic interactions on seedling performance of four Pyrenean species along environmental gradients

Abstract

The predicted upward displacement of forest species due to climate warming is expected to be modulated by a medley of abiotic and biotic factors acting at microsite level. Species-specific differences in plantresponses to this set of environmental factors can thus have strong implications in the future dynamics of forest ecosystems. To gain a better understanding of the main fine-scale factors and processes driving present and future species performance in the montane and subalpine belt of the Eastern Pyrenees (NE Spain), we established a set of experimental mixed plantations along elevational and environmental gradients using the four tree species dominating these areas (*Pinus sylvestris*, *Pinus uncinata*, *Abies alba* and *Betula pendula*). Once the plantations had been established, the performance and growth of 72 seedlings of each species was monitored and linear and non-linear models were fitted to identify the main factors controlling their survival and growth.

We found most of the mortality to occur during the third growing season, following a harsh winter and a drought period during summer. Mortality patterns were highly species- and site-specific. At the subalpine belt, shrubs were found to have a facilitative effect on winter survival of *P. sylvestris* (mortality < 10%) but not on the other species. At the montane belt, *A. alba* mortality during the summer increased in areas with high light exposure and herbaceous cover (mortality > 30%). All species except *P. uncinata* showed lower height growth at high elevation, with differences between sites matching differences in growing season duration (20%).

Our results underline a potentially critical role played by short periods of extreme climate in the performance of plants developing in mountainous areas far from their optimal elevational range. However, they also underline a potentially critical role played by biotic and abiotic microsite factors in mediating speciesresponsesto these climatic events.

Keywords: Seedlings, plant-plant interactions, elevational gradient, climate change, Pyrenees, facilitation

5.1. Introduction

The predicted increase in temperatures caused by global warming (IPCC, 2007) is expected to have large effects on mountain ecosystems, where the elevational ranges of trees are mainly controlled by temperature (Grabherr et al., 1994; Walther et al., 2002; Peñuelas and Boada, 2003; Lenoir et al., 2008). Accordingly, most simulations based on ‘climate envelopes’ predict upward or poleward displacement of species under future warming scenarios (Guisan et al., 1998; Dullinger et al., 2004),with some species even becoming extinct if the rate of change exceeds their pace of biological response (Thomas et al., 2004; Thuiller et al., 2005). However, realized ecological niches are multidimensional, and species distribution is not only explained by macro-climate but also by species-specific responses to a medley of abiotic and biotic factors that often operate at finer temporal and spatial scales (Vetaas, 2002; Walther et al., 2002; Dullinger et al., 2004; Holtmeier and Broll, 2005). The effects of these factors are often not adequately captured by the ‘climate envelope’ models, sometimes leading to unrealistic predictions of species distributional changes (Randin et al., 2009; Willis and Bhagwat, 2009; Martínez et al., 2012).

In many mountain ecosystems, abiotic stresses are considered the major mechanism setting the upper limit of species’ elevational ranges. To successfully migrate upwards, tree species must be able to grow and survive outside their current elevational range, thus facing climatic conditions that are at the limits of their physiological tolerance (Lenoir et al., 2009; 2010), particularly at their younger stages (Germino et al., 2002; Gómez-Aparicio et al., 2008a). Therefore, in these areas, short periods of extreme climatic conditions (e.g. extreme cold or freezing events) play a critical role in shaping future species composition (Schneider, 2004; Lindner et al., 2010). However, some recent studies have shown that micro-topographical factors can buffer or even override the effects of harsh climate on plant survival (Willis and Bhagwat, 2009; Ackerly et al., 2010; Scherrer and Körner, 2011). Positive plant—plant interactions could also play a major role in these stressful environments, as postulated by the ‘stress-gradient hypothesis’ (SGH; Bertness and Callaway, 1994; Maestre et al., 2009). Shrubs for example are known to facilitate the survival of young plants of species growing at their upper elevational limit by reducing wind abrasion, mitigating the minimum temperatures to which they are exposed, protecting them from radiation, or reducing snowdrift (Batllori et al., 2009; Barbeito et al., 2012).

Conversely, competitive effects are considered the major mechanism setting the lower limit of species' elevational ranges (Lenoir et al., 2010). However, this might not occur when environmental severity increases at low elevation. In such cases, species' sensitivity to the main stress factor (e.g. drought in Mediterranean mountains) would significantly define its lower range margin (Macias et al., 2006; Candel-Pérez et al., 2012; Linares and Camarero, 2012). Other processes not directly related to climate, such as habitat modification due to changes in human activities have led to severe canopy closure in many European forests (Poyatos et al., 2003; Ameztegui et al., 2010), which can also induce significant shifts in species distribution, even favoring downslope displacement of some species (Lenoir et al., 2010; Bodin et al., 2013).

In the Pyrenees, the rise in temperatures associated to climate change has prompted predictions of species displacements (Resco de Dios et al., 2006) with a progressive upward encroachment of montane species into the subalpine belt (Ameztegui and Coll, 2011). However, these areas are characterized by a high variability of abiotic and biotic factors acting at local scale, whose role in these apparently climate-driven processes remains unclear. With the ultimate aim of advancing understanding of the relative impact of these factors in the future dynamics of the Pyrenean mountainous forests, we set up a 4-year field experiment in which seedlings of the 4 most widespread tree species in the montane and subalpine belt of the Eastern Pyrenees (*Pinus sylvestris* L., *Pinus uncinata* Ram, *Abies alba* Mill. and *Betulapendula* Roth.) were planted along gradients of elevation and microsite conditions (light availability and herbaceous and shrub cover). Specifically, we aimed to answer the following questions: (i) how does the performance (survival and growth) of these species vary along environmental gradients including variation in climate, light availability and biotic interactions?; (ii) what role do short extreme climatic events play in seedling survival and growth?; (iii) are the intensity and sign of biotic interactions (competitive vs. facilitative) species-specific?; and (iv) can plant-plant interactions favor or limit species range expansion by modulating the effects of climate change through facilitation and competition?

We hypothesized that climate (minimum temperatures at high elevation and drought at low elevation) wouldplay a determinant role in seedling mortality, but that biotic interactions may play a role in partially buffering this effect, especially for those species established far from their optimal elevational range.

5.2. **Methods**

5.2.1. Study area

The experiment was conducted at two different elevations in the northern slopes of the Serra del Cadí, a Pyrenean mountain range in the Cadí-Moixerò Natural Park (42º17'N; 1º42'E). The "low-elevation" plots were located in the montane belt, slightly below the *P. sylvestris–P. uncinata* transition zone (around 1500 m a.s.l.). The forest overstory in this site was dominated by *P. sylvestris* (more than 75% of total basal area) with some *P. uncinata* and *B. pendula* individuals, whereas the main species in the understory were common box (*Buxus sempervirens* L.) and common juniper (*Juniperus communis* L.). The "high-elevation" plots were located in the subalpine belt (around 2000 m a.s.l.), close to the optimum elevational distribution for *P. uncinata*. In this site, the overstory was overwhelmingly dominated by *P. uncinata*, although some disperse individuals of *A. alba* and *B. pendula* could be found. The shrub layer was almost exclusively composed by *J. communis*. These two areas (located in the same valley but set 12 km apart) present contrasting climates associated to the abrupt terrain involving marked elevational zonation of the vegetation (Ninot et al., 2007).

5.2.2. Species selection and characteristics

This study focused on the 4 most widespread tree species in the area: Scots pine (*P. sylvestris*), a shade-intolerant species that in the Pyrenees can be found between 1000 and 1800 m a.s.l., thus dominating the montane belt of the Pyrenees; mountain pine (*P. uncinata*), a shade-intolerant conifer that reaches its southern distributional limit in the Iberian Peninsula and constitutes most of the treelinesin the Pyrenees as it is restricted to the subalpine belt (between 1600 and 2300 m a.s.l.); silver fir (*A. alba*), the most shade-tolerant conifer species in the Pyrenees, usually restricted to humid sites on north-facing, shady slopes between 1200 and 2000 m a.s.l. where the risk of water stress in summer is lower (Macias et al., 2006); and silver birch (*B. pendula*), a shade-intolerant pioneer species that usually colonizes disturbed areas between 1000 and 1800 m a.s.l. but only rarely reaches the canopy (Ruiz de la Torre, 2006). These species differ in their ecological requirements, and they can be ordered from most (rank = 5) to least (rank = 1) shade tolerant following the ranking system developed by Niinemets and Valladares(2006): *A. alba* (4.6 ± 0.06; mean ± SE), *B. pendula* (2.03 ± 0.09), *P. sylvestris* (1.67 ± 0.33), and *P. uncinata* (1.2). Moreover, the drought tolerance ranking order according to the same authors would be: *P. sylvestris* (4.34 ± 0.47); *P. uncinata* (3.88), *B.*

pendula (1.85 ± 0.21) and *A. alba* (1.81 ± 0.28). Despite their different ecological requirements, these four species are able to coexist in a strip between 1600 and 2000 m a.s.l. constituting the local montane-subalpine mixed forest.

5.2.3. Experimental design

At each one of the two sites, 72 two-year-old seedlings of each of the 4 studied species were distributed into 12 plots and planted in early summer 2008. Plot size varied between 40 and 50 m² and each plot included 24 seedlings (6 per species) planted at least one meter apart to avoid interaction between them. Half of the plots were located in the forest understory and the other half in naturally-occurring gaps (Figure 5.1). Gap surface was between 150 and 350 m^2 (196.0 ± 33.4 m^2; mean ± SE). Seedlings were randomly distributed across each plot, and were carefully planted to minimize alteration of the micro-environment. As domestic herds of cattle and horses are led into these forests during the summer, the seedlings were protected from browsing with an individual protector with a 20 x 20 mm mesh net (Nortène, Lille, France) to exclude the influence of animal damage. All the seedlings were 2 years old at the time of planting and had been grown in a local nursery (ForestalCatalana, Pobla de Lillet, Spain) from seeds collected in neighboring forests. For all species, seedling source, nursery and plantation area were all inside the same region of provenance (Alía et al., 2005).

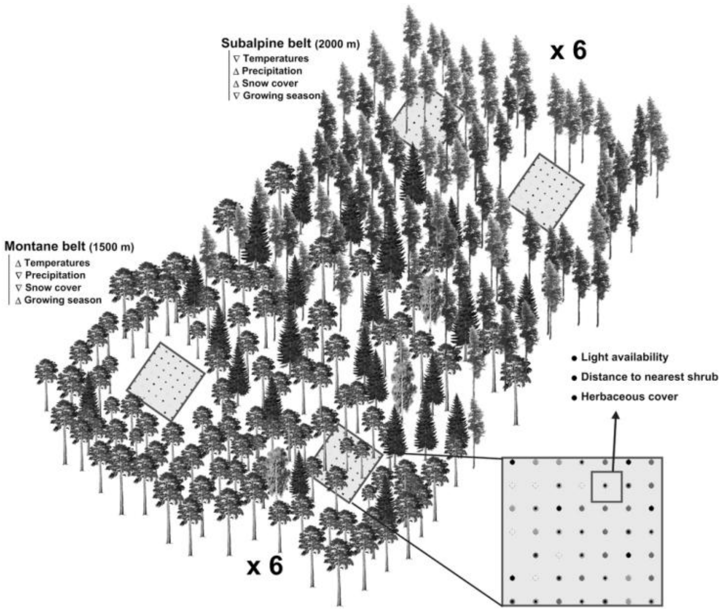

Figure 5.1 Representation of the experimental design and the measured abiotic and biotic variables. At each of the two sites (montane and subalpine belt), 6 plots were located in the forest understory and 6 in naturally-occurring gaps. At each plot, 24 seedlings (6 per species) were planted, and environmental variables at the microsite scale (light availability, herbaceous cover, and distance to nearest shrub) were measured.

5.2.4. Characterization of the environment

To better characterize climatic differences between the two sites, two meteorological stations were installed (one per site), and air temperature (at 1 m height), below-ground soil temperature (at 10 cm depth) and precipitation were measured continuously using ECH2O sensors (Decagon Devices, Pullman, WA, USA; see Table 5.1). Data from the *in situ* meteorological stations registered high climatic variability over the 4 years of the study. In August and early September 2011, there was a rather warm and dry period (with 60% less precipitation than the average for the last 10 years, Figure 5.2) that exposed the vegetation to a significant drought stress that was visually appreciable even in the adult stand. The winters of 2009 and 2010 were particularly cold, with minimum temperatures reaching –15.8ºC in the high-elevation sites. In early winter 2010, the cold period coincided with low precipitations, resulting in the shallowest snow layer seen in recent years (Figure 5.2). Throughout the duration of the study, the seedlings established at high elevation (subalpine sites) were exposed to lower mean temperatures, higher precipitations, higher Thornthwaite index and a 20% shorter growing period than the seedlings established at lower elevation (Table 5.1).

To characterize the microsite conditions of the planted seedlings, light availability, percentage of herbaceous cover and distance to nearest shrub were measured for each of the seedlings (Table 5.1). Light availability was measured using two Li-190SA quantum sensors (Li-COR, Lincoln, NE, USA). The sensors were used in paired mode, *i.e.* one of the sensors was placed at the top of each seedling and the other in an adjacent open area, following standard procedure (see Messier &Puttonen (1995) and Parent & Messier (1996) for a complete description of the method). This approach makes it possible to calculate light availability as a percentage of transmitted photosynthetic photon flux density (%PPFD), and consequently ranged from 0 (complete obstruction) to 100 (open sky). The measurements showed mean light availability to be slightly higher in the subalpine plantations, but the range was similar at both elevational sites, with a maximum of about 60% (Table 5.1). Percentage of herbaceous cover surrounding the seedlings was visually estimated to the nearest 5% using an 80 x 80 cm grid centered on each seedling, and was found to be higher overall at the subalpine belt (although extremely variable, with values ranging from 0% to 90—95% at both sites). Finally, distance from each seedling to the nearest shrub was measured with a tape meter. We defined a shrub as any woody plant with several stems arising from the base, so other elements such as neighbor seedlings, adult trees, logs or rocks were not considered. The montane sites showed higher shrub density, resulting in a lower mean distance of seedlings to the nearest shrub (Table 5.1).

Table 5.1 Main abiotic and biotic characteristics of the studied stands

Variable	Montane sites	Subalpine sites
Latitude (N) / Longitude (E)	42º19’/ 1º43’	42º18’ / 1º42’
Elevation (m a.s.l.)	1550	1955
Aspect/Slope (degrees)	NE / 39	NE / 53
Bedrock	Limestone	Limestone
Mean annual/summer temperature (ºC)	7.4 / 14.8	4.9 / 11.7
Total annual/summer precipitation (mm)	992 / 271	1118 / 327
Thornthwaite Index[1]	70.3	120.7
Length of the growing season[2] (days)	194	147
Mean Summer Maximum Temperature (ºC)	21.0	17.3
Mean Winter Minimum Temperature (ºC)	-3.4	-4.6
Dominant species[3]	Ps, Pu, Bp	Pu, Aa, Bp
Light availability (%PPFD)	19.3 ± 9.8 [2.8-55.1]	23.9 ± 13.3 [5.4-58.6]
Herbaceous Cover (%)	39.1 ± 23.1 [0-95]	51.1 ± 30.6 [0-100]
Distance to nearest shrub (cm)	56.5 ± 45.8 [10-350]	118.9 ± 76.3 [20-430]

Values for light availability, herbaceous cover, and distance to nearest shrub are means ± SD (n=286). Values in brackets are minimum and maximum observed values. The number of decimal positions indicates precision of the variable when measured.

[1] Calculated as the ratio between precipitation and potential evapotranspiration (Thornthwaite et al., 1957)

[2] Calculated as in Körner and Paulsen (2004)

[3] Listed for each site in decreasing order of dominance: Pu: *Pinus uncinata*; Aa: *Abies alba*; Ps: *Pinus sylvestris*; Bp: *Betula pendula.*

5.2.5. Seedling monitoring

Seedling mortality was regularly monitored throughout the duration of the experiment. With the aim of disentangling the main climatic variables driving mortality for each species at each elevation, we divided the observed mortality into either summer mortality (occurring during the growing season) or winter mortality (occurring during the winter). The plots were frequently visited, and we only assigned mortality to a given period (summer or winter) when plants were found to be dead in the beginning of a period but had been recorded as healthy (absence of any symptom of disease) at the end of the previous one. Despite the protective net, seven seedlings were damaged by animals, mainly by trampling, and were subsequently excluded from the analysis. Furthermore, 13 seedlings died due to small disturbances (e.g. stones falling, small landslides, etc.) and were also excluded, giving a total of 552 seedlings analyzed. Seedling size was monitored by measuring total height and diameter at the root collar at the end of every growing season. Using this dataset, we determined the following response variables: (1) survival rate along the 39 months of the study; (2) winter and summer mortality; (3) height at the end of the study period; and (4) diameter at the end of the study period.

5.2.6. Data analyses

For each species and site (montane vs. subalpine), survival function curves were developed based on Kaplan—Meier estimates, and the Mantel—Cox log-rank test was used to determine significant differences between sites. To test the effect of categorical or continuous covariates on our censored survival data, we used a Mixed Effects Cox model (Therneau and Grambsch, 2000), which is a modification of the commonly used Cox's Proportional Hazards (coxPH) model (Cox, 1972) that allows for inclusion of random covariates. For each combination of response variable (summer and winter mortality) and species, we fitted a separate model in which the effects of the three explanatory variables at microsite level (herbaceous cover, distance to shrubs, and light availability) and elevation (site) were introduced as fixed factors, whereas plot was introduced as a random factor. The equation fitted by the model was:

$$\lambda(t) = \lambda_0(t)\ e^{X\beta+Zb}$$

$$b \sim G(0, \Sigma(\theta))$$

where $\lambda_0(t)$ is an unspecified baseline hazard function, X and Z are the design matrices for the fixed and random effects, respectively, β is the vector of fixed-effects coefficients, and b is the vector of random effects coefficients. When comparing two groups, the hazard ratio (e^{β}) is the quotient of the hazard functions for each of the groups. For a continuous variable, the hazard ratio indicates the change in the risk of mortality if the parameter in question rises by one unit. The random effects distribution G is modeled as Gaussian with mean zero and a variance matrix Σ, which in turn depends on a vector of parameters θ. To test the significance of each variable, we performed a likelihood ratio test (LRT) to compare deviances of a pair of nested models: a null model (in which the variable was absent) and an alternative model including it. Interactions between variables were only included if the LRT of the model indicated significant difference with both the simpler models. Goodness-of-fit of the models was assessed through the concordance statistic *(C)*, which is analogous to Kendall's tau between the prediction and the outcome but can be used with censored data.

Several model formulations (linear, exponential, power and Michaelis—Menten; see Appendices for details on the model equations) were used to analyze the effect of the different explanatory variables (light availability, herbaceous cover and distance to nearest shrub) on seedling size (height and diameter) at the end of the study period (39 months). Initial seedling size was introduced as a covariate with an exponent α to allow for non-linear relationships between final and initial size. The maximum likelihood parameter values were estimated using simulated annealing (Goffe et al., 1994) and the asymptotic 2-unit support intervals were used to assess the strength of evidence for individual maximum likelihood parameter estimates. The $R^2$of the regression of observed *vs.* predicted values provided a measure of the goodness-of-fit of each model, and alternative models were compared using ΔAICc, the difference in corrected Akaike information criterion (Burnham and Anderson, 2002). Following the likelihood approach, we used comparison of alternate models to test our hypotheses. For each explanatory variable, the best of the 4 formulations (linear, exponential, power and Michaelis—Menten) was compared (in terms of ΔAICc) to a null model in which there was no effect of the independent variable, and we considered that an effect of this variable was supported when $\Delta AICc > 2$. When there was substantial support for more than one independent variable, we also tested a bivariate model in which both variables were included, and the strength of evidence for this model was compared with univariate models. Finally, when the best model had been identified, we also tested for an effect of elevation by comparing the strength of evidence of a model in which parameters were estimated separately for low- and high-elevation sites against another model in which all the data were pooled together, and we retained the first model only if it was substantially supported by the data ($\Delta AICc > 2$).

All analyses were performed using R 2.14.1 software (R Development Core Team, 2011) and the 'likelihood' v. 1.5 (Murphy, 2012), 'survival' v. 2.37—2 (Therneau, 2011) and 'coxme' v.2.2—3 (Therneau, 2012) packages for R.

5.3. Results

5.3.1. Seedling survival

Survival rate after three growing seasons was significantly different among species ($P <$ 0.001) and ranged from more than 80% for *P. uncinata* to less than 65% for *P. sylvestris*. For the three conifer species (*A. alba*, *P. sylvestris* and *P. uncinata*), most of the mortality at both elevations (more than 60% of total dead seedlings) was observed during the third year. Between-site differences in survival rates were only significant for *P. sylvestris* ($P < 0.001$) and *A. alba* ($P = 0.044$; Figure 5.3). These species presented opposite patterns, with *P. sylvestris* showing higher mortality in subalpine sites and *A. alba* showing higher mortality in montane sites. The seasonal patterns of mortality were also species-specific. While most of the *P. uncinata* and *A. alba* mortality occurred during the growing season, for the other two species it occurred during the winter (Figure 5.3).

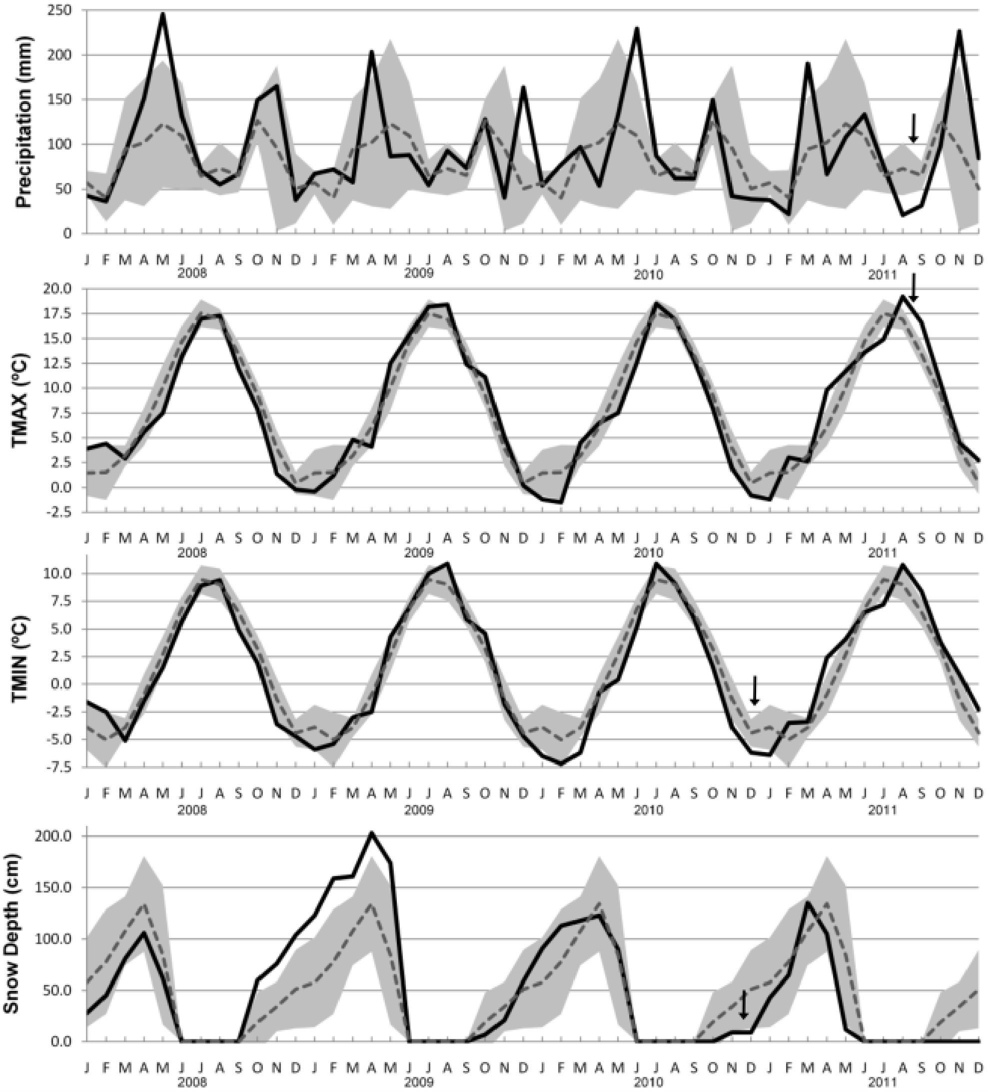

Figure 5.2. Evolution of precipitation, monthly average of the maximum (TMAX) and minimum (TMIN) temperatures and snow depth in the study area over the four-year study period (2008-2011). Dashed lines and shaded areas indicate mean ± SD during the last 10 years, whereas solid lines indicate measured values. Data are from the Pratd'Aguiló meteorological station (2138 m a.s.l.), located less than 1 km away from the high-elevation site. Vertical arrows indicate the extreme climatic events that occurred during late-autumn 2010 and summer 2011 (see text for further details).

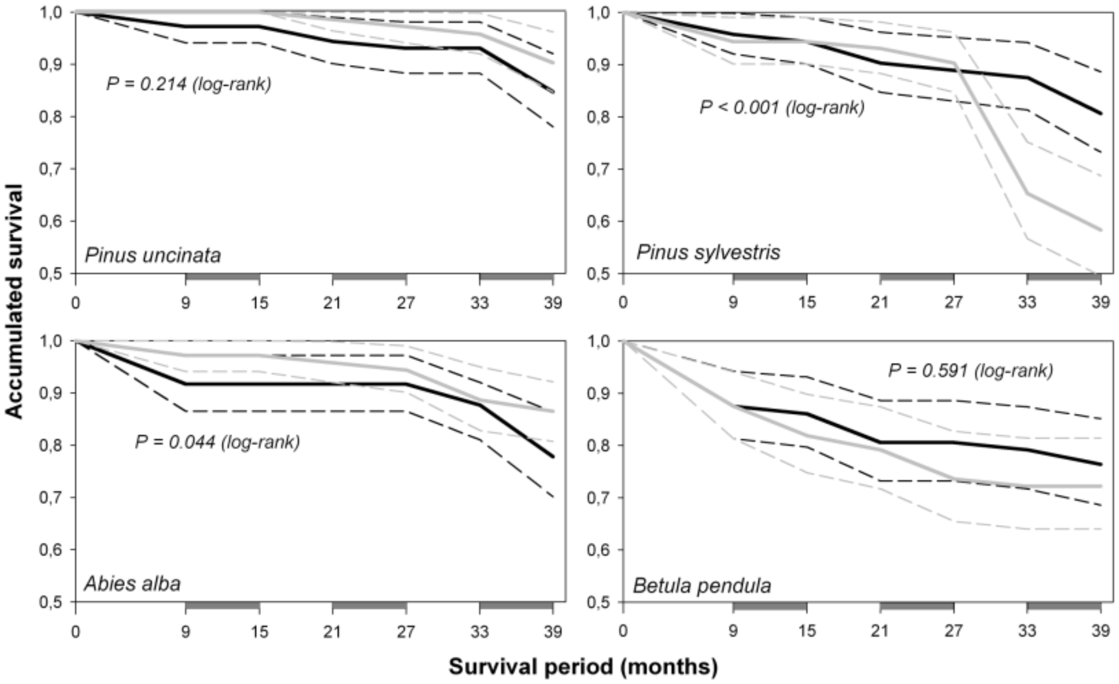

Figure 5.3 Survival curves for seedlings of the four species of trees planted at the two experimental sites over the course of the study period, based on Kaplan-Meier estimates. Black and grey lines represent seedlings in the montane and subalpine belts, respectively. Solid lines represent Kaplan-Meier estimates whereas dashed lines are 95% confidence intervals. *P*-values indicate significance of the log-rank test between sites for each species. Shaded areas in the x-axis correspond to the vegetative period (from May to October). Note that the *y*-axis starts at 0.5 for greater clarity and easier comparison among species.

P. sylvestris was the only species that showed an effect of the explanatory variables on winter mortality. The winter mortality of *P. sylvestris* was found to be positively associated with elevation (hazard ratio [HR] = 4.13; 95% CI: 2.15 – 7.95; P < 0.001) and with seedling distance to the nearest shrub (HR = 1.004; 95% CI: 1.002 – 1.007; *P* < 0.001; Figure 5.4). At the subalpine belt, mortality rate for seedlings planted at less than 0.5 m from a shrub was 0.11, whereas mortality rate for the rest of the seedlings ranged between 0.28 and 0.44. The positive effect of the shrubs on winter survival was not as marked at the montane belt, where mortality rates ranged from 0 to 0.13, but we did not find a significant effect of the interaction between distance to nearest shrub and elevation (*P* = 0.112). For the other three species (*P. uncinata*, *B. pendula* and *A. alba*), we could not detect an effect of any of the explanatory variables (including elevation) on winter mortality (Appendix A).

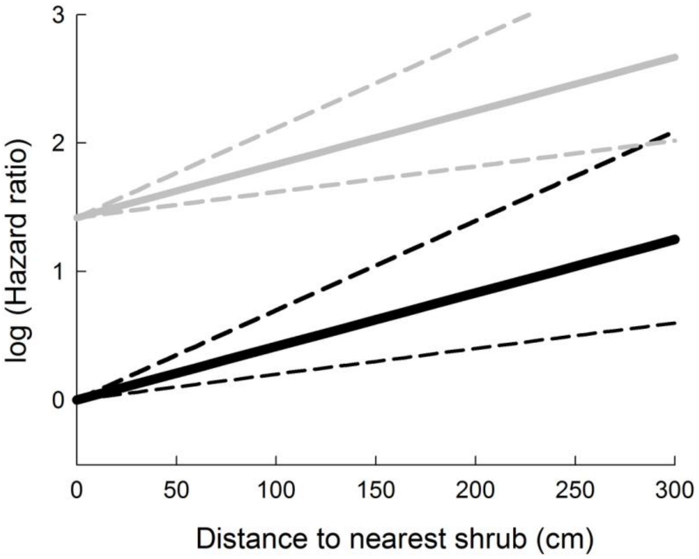

Figure 5.4 Predicted variation in the log hazard ratio for winter mortality as a function of distance to nearest shrub for *P. sylvestris* seedlings planted at montane (black) and subalpine (grey) sites in the Eastern Pyrenees. Solid lines represent predicted models whereas shaded areas correspond to 95% confidence intervals.

A.alba was the only species that showed a significant effect of the analyzed abiotic and biotic factors on summer mortality. For *A. alba*, both herbaceous cover and light availability (*P* = 0.036) were positively associated with mortality. The analyses also revealed a significant correlation between both variables (Pearson correlation coefficient = 0.21 for the montane belt; 0.42 for the subalpine belt) and the bivariate model including them was not significantly better than the univariatemodels. Herbaceous cover showed the most significant effect on mortality (*P* < 0.001), and we found a significant interaction between this variable and site (P < 0.001): the effect of herbaceous cover on mortality wasonly significant at the montane belt, where the observed mortality rate ranged from 0.08 for low classes of herbaceous cover (<20%) to 0.33 for seedlings planted in sites with more than 80% herbaceous cover (HR = 1.120; 95% CI: 1.047 – 1.198; *P* < 0.001; Figure 5.5). Light availability was also positively associated with a higher mortality rate (HR = 1.056; 95% CI: 1.017 – 1.097; *P* = 0.036), with a maximum of 0.25 for seedlings with more than 40% PPFD available, but without significant effect of elevation in this trend (*P* = 0.882; Figure 5.5). An effect of herbaceous cover in the mortality of *B. pendula* was also detected, although the model including this variable was only marginally significant compared to the null model (HR = 1.020; 95% CI: 0.998 – 1.043; *P* = 0.055; Appendix B).

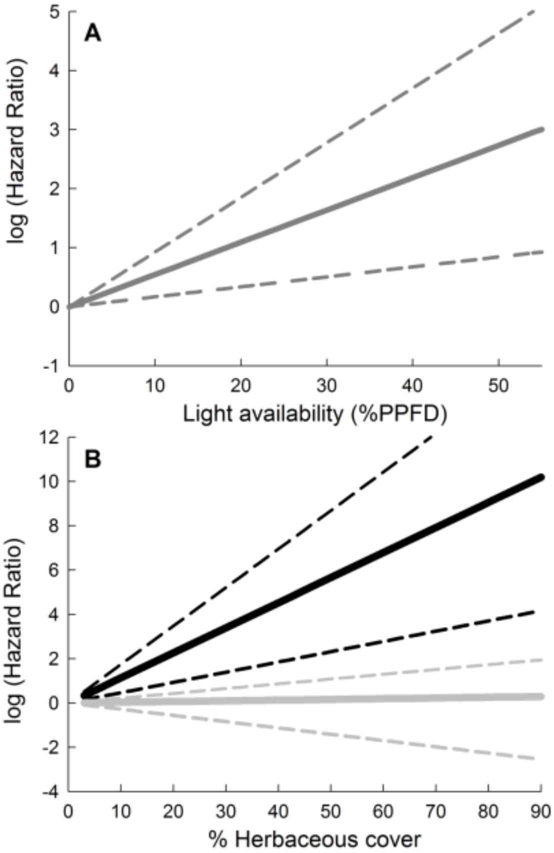

Figure 5.5. Predicted variation in the log hazard ratio for summer mortality as a function of (a) light availability and (b) percentage of herbaceous cover, for *A. alba* seedlings planted at montane (black) and subalpine (grey) sites in the Eastern Pyrenees. In (a), no significant effect of site was detected, and pooled data for both sites are represented in dark grey. Solid lines represent predicted models whereas shaded areas correspond to 95% confidence intervals.

5.3.2. Seedling growth

There were significant among-species differences in absolute height growth, which ranged from 15 mm·y^{-1} for *A. alba* to more than 70 mm·y^{-1} for *B. pendula* (Table 5.3). These differences were weaker when considering relative height growth, but *B. pendula* still had higher growth than both pines, which in turn grew faster in height than *A. alba*. All species showed higher relative height growth at low-elevation sites, but the differences were not significant for *P. uncinata (P* = 0.73). In contrast, all species showed higher relative radial growth at the subalpine site, but the differences were only significant for the two pine species (Table 5.3). However, measured radial growth over the 3 years was rather low (annual relative radial growth <0.1 mm for all species), and we discarded it from further analyses as these values were below the measurement accuracy.

Light availability was the main environmental factor controlling height of the three conifer species (*P. uncinata*, *P. sylvestris* and *A. alba)*. For *A. alba* and *P. sylvestris*, the effect of light availability on growth was modulated by elevation, with seedling growth showing lower response to enhanced light (or almost null response in the case of *A. alba*) at low elevation than at high elevation (Figure 5.6). For *A. alba*, the observed response was linear, whereas for *P. sylvestris* it followed a power equation (Table 5.2; Figure 5.6). These differences in response with elevation were not observed for *P. uncinata*, for which relative height growth increased with light availability but was saturated at %PPFD > 40%, following a Michaelis—Menten equation (Table 5.2; Figure 5.6). For these species, the exponent of the initial height (introduced as a covariate in the model) ranged between 0.4 and 0.6, thus indicating a non-linear relation between this variable and final height. In contrast, the relation between initial and final height growth was linear for *B. pendula* ($\alpha = 1.01$), which was the only species for which there was no detectable effect of microsite factors or elevation on height (Appendix C).

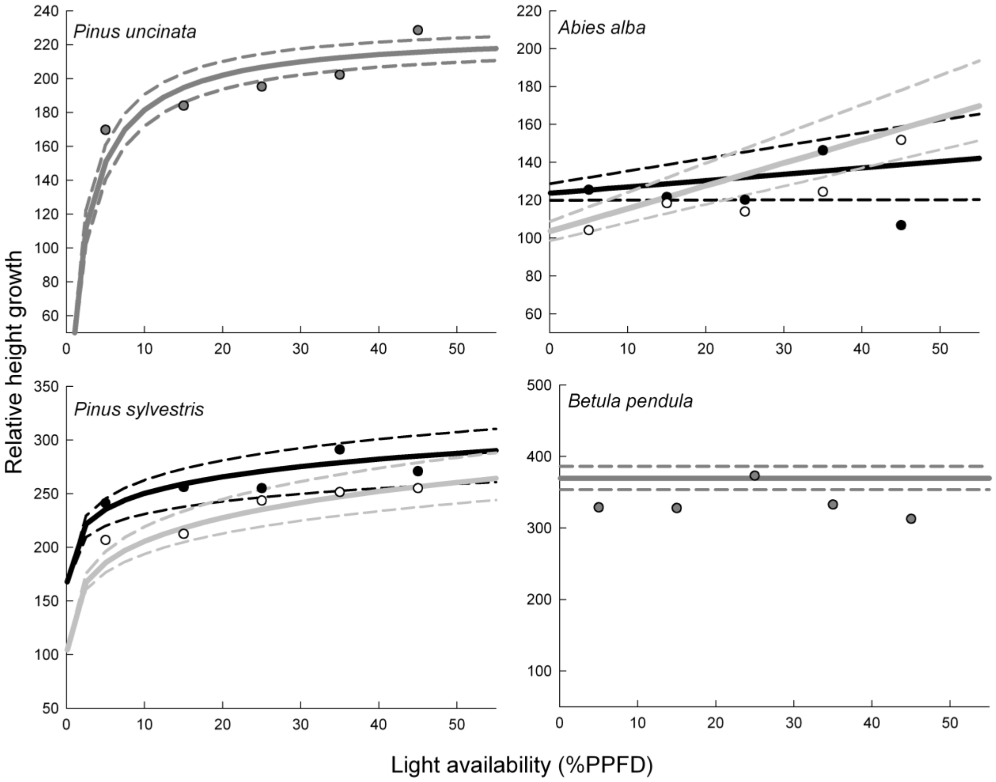

Figure 5.6 Predicted variation in height as a function of initial height and light availability for seedlings of the 4 studied species planted at montane (black) and subalpine (grey) sites in the eastern Pyrenees.When no effect of elevation was predicted, data were pooled together, and symbols are represented in dark grey. Solid lines represent predicted models whereas shaded areas correspond to 2-unit support intervals. Horizontal lines indicate lack of effect of the predictive variable for that species, and are shown for comparative purposes.

5.4. **Discussion**

Mortality events in the established plots took place at different periods of the year in the two studied elevations. At the subalpine belt, a majority of mortality occurred during winter, whereas at the montane belt a majority of mortality occurred during the growing season. Although mortality was relatively low for all species during the first two years after plantation, it sharply increased during the third year when the area was exposed to a particularly cold late-autumn and early-winter followed by a drought episode during summer. The potentially strong impact of short events of extreme climatic conditions on juvenile tree mortality has already been observed elsewhere (Schneider, 2004; Saccone et al., 2009; Lindner et al., 2010), and in our sites we observed marked species-specific responses to these events. The harsh winter particularly affected *P. sylvestris* plants growing in the subalpine belt, where this species ranked as the least adapted to the climatic conditions, whereas as expected, summer drought mainly affected *A. alba*, which is the least drought-tolerant of the four studied species. Interestingly, the negative effect of drought in *A. alba* survival was only observed in the montane sites.

Table 5.2 Summary of the models predicting seedling height as a function of microsite conditions and initial height for seedlings of four species of trees planted at two experimental sites in the Eastern Pyrenees. For each species and explanatory variable, the AIC of the best-fit model is provided for all seedlings pooled together (AIC_P) and separated into two groups (montane vs. subalpine, AIC_S)

	Model	AIC_P	AIC_S	R^2
Pinus uncinata				
Light	MM	2113.58	2123.75	0.33
Herb. cover	Lin	2136.17	2141.73	0.21
Null	Null	2207.46	2201.72	0.12
Abies alba				
Light	Lin	1669.49	1673.84	0.41
Herb. cover	Lin	1676.75	1679.01	0.30
Null	Null	1688.31	1688.16	0.25
Pinus sylvestris				
Light	Pow	2067.94	2055.57	0.36
Herb. cover	Lin	2076.28	2063.71	0.22
Null	Null	2085.66	2078.33	0.18
Betula pendula				
Null	Null	1771.06	1775.33	0.22

Factors are ranked from highest to lowest support according to AIC_P. For each species, only models with stronger empirical support than the null model (i.e. an AIC_P at least two units lower) are provided. Models are: Lin = linear; Exp = exponential, Pow = power, MM = Michaelis—Menten; see Appendix C for details on the equations. Lower AIC_S values than AIC_P values indicate stronger empirical support for separated data than for pooled data, i.e. an elevational effect.

Positive plant-plant interactions were found to be species-specific and to vary with elevation, being particularly important for the survival of species establishing at the extremes of their elevational range. This was the case for *P. sylvestris* seedlings, a species typical of the montane belt and consequently the least adapted to the harsh climate of the high-elevation plots. Our results agreed with the stress-gradient hypothesis (Bertness and Callaway, 1994) and are consistent with previous research showing facilitation to be more important for species planted at experimental sites located at higher elevations than their distributional mean (Batllori et al., 2009). Our results also stress the major role that facilitation could play in modulating the effects of extreme climatic events such the extremely cold late-autumn and winter of 2010 in our experimental sites (Brooker et al., 2008; Saccone et al., 2009). We did not find a facilitative effect of shrubs on *B. pendula, A. alba* or*P. uncinata* plants. For the first two species, this could be explained by the fact that they are less drought-tolerant than pines (in particular *A. alba*), and competition for water from the neighboring shrubs may probably overcome their positive nurse effect. As pointed out by Maestre et al. (2009), in extremely severe environmental conditions, resource uptake by facilitators can overcome their positive effect if the stress is resource-based and the beneficiary species are not stress-tolerant.The lack of facilitative effects of *P. uncinata* was not surprising, given that this species is the best adapted to climate at the subalpine belt and presented relatively low overall mortality over the course of the experiment.

At the montane belt, most of the mortality occurred during summer, and more specifically during the third year's growing season when the area was exposed to a major drought episode. This event mainly affected *A. alba,* a species well-known to be highly sensitive to water deficit, being negatively affected by high temperature conditions and the related drought stress (Rolland et al., 1999; Pagès et al., 2003; Peguero-Pina et al., 2007; Toromani et al., 2011). The positive effect of light closure on *A. alba* survival might indicate a facilitative effect of tree cover on *A. alba* seedlings by reducing the Vapor Pressure Deficit to which the seedlings were exposed and thus indirectly limiting the development of competitive herbaceous neighbors (Pagès et al., 2003; Saccone et al., 2009). This indirect facilitative effect of canopy cover seemed to be particularly important in our study sites given the marked negative relationship found between herbaceous cover and *A. alba* survival, that was probably associated to competition for water. The herbaceous cover also increased mortality of *B. pendula* in the montane belt, although this effect was only marginally significant. In general, *B. pendula* is considered to tolerate drought much better than *A. alba* but shows a lower ability to compete for water than pines (Prevosto and Balandier, 2007).

In the montane sites, we expected to find a positive effect of shrubs on plant survival (at least for the most drought-sensitive species) after the marked drought period that occurred during the third growing season. In the drier areas of Mediterranean mountains, seedlings frequently benefit from habitat amelioration by shrubs which reduce the radiation and temperature to which they are exposed and thereby improve their water status (Castro et al., 2002; 2004; Gómez-Aparicio et al., 2004; 2008b). However, we did not detect any positive effect of shrubs on plant survival, indicating that in this relatively mesic area, the net effect of the and negative interactions occurring above- and below-ground between the shrubs and the seedlings was neutral.

Table 5.3 Absolute and relative height growth at the end of the study period for seedlings of four species of trees planted at two experimental sites (montane and subalpine) in the Eastern Pyrenees. Absolute growth is expressed as average annual growth, and relative growth is annual growth relative to the initial state.

Species	Abs. height growth (mm·y-1)		Rel. height growth	
	Montane belt	Subalpine belt	Montane belt	Subalpine belt
Betulapendula	76.23 ± 4.44 a	69.73 ± 5.45 a	0.381 ± 0.024 a	0.305 ± 0.027 a
Pinus sylvestris	40.76 ± 1.91 b	34.98 ± 2.14 b	0.289 ± 0.018 b	0.232 ± 0.016 b
Pinus uncinata	30.48 ± 1.71 c	30.28 ± 2.04 b	0.283 ± 0.021 b	0.267 ± 0.021 b
Abies alba	16.48 ± 1.10 d	13.98 ± 1.18 c	0.207 ± 0.016 c	0.160 ± 0.016 c

Values are means ± SE. Values with the same letter indicate lack of significance between species. Values in bold indicate significant differences in relative growth between sites for a given species ($P < 0.05$).

Interestingly, we did not observe a higher mortality of *P. uncinata*in the montane belt, where this species was planted below its current elevational range, and neither biotic nor abiotic factors exerted any influence on the rate of *P. uncinata* mortality. Although the lower limit of species' elevational ranges in Mediterranean mountains is often considered to be set by drought-induced stress (Macias et al., 2006; Candel-Pérez et al., 2012; Linares and Camarero, 2012), our results suggest that this might not be the case for *P. uncinata*. It is possible that the current low elevational limit of *P. uncinata* is not climatically-driven but is instead set by other factors, such as competitive interactions with low-elevation species, mainly *P. sylvestris*(Callaway et al., 2002; Ameztegui and Coll, 2011).

In contrast to the abovementioned species-specific and temporal patterns, all the species studied grew faster in height in the montane belt than in the subalpine belt. Growth is known to be mainly limited by duration of the growing season in high-elevation forests (Grace and Norton, 1990; Grace et al., 2002; Hoch and Körner, 2003; Cailleret and Davi, 2010). Here, the average reduction in growth (20%) found in *P. sylvestris, A. alba* and *B. pendula* seedlings matched the average difference in length of the growing season observed between both sites during the experiment(Table 5.3). In contrast, *P. uncinata* (the species currently dominating the subalpine belt) presented the same height growth—light relationship at both elevations, following the typical saturating curve for environments where light is the most limiting factor (Ameztegui and Coll, 2011). However, the height growth of all species increased with higher light availability, thus indicating that the microsite requirements for seedling survival were different from those required for growth, as observed in the Alps by Barbeito et al. (2012).

In summary, this study showed that short periods of extreme climate can have a strong impact on the mortality of species growing far from their mean elevational range (e.g. *P. sylvestris* in the subalpine belt; *A. alba* at the montane belt). We found that positive plant—plant interactions can play a critical role in mediating the effects of these unfavorable climate conditions on the performance of these species when growing above their current limits. In contrast, in the lower limit of species' elevational ranges, competition plays a more important role. Overall, we conclude that species-specific differences in performance under different environmental conditions and the role of plant—plant interactions should be explicitly considered when making predictions of climate change-induced species displacement and when designing or implementing management plans to contend with the impacts of climate change.

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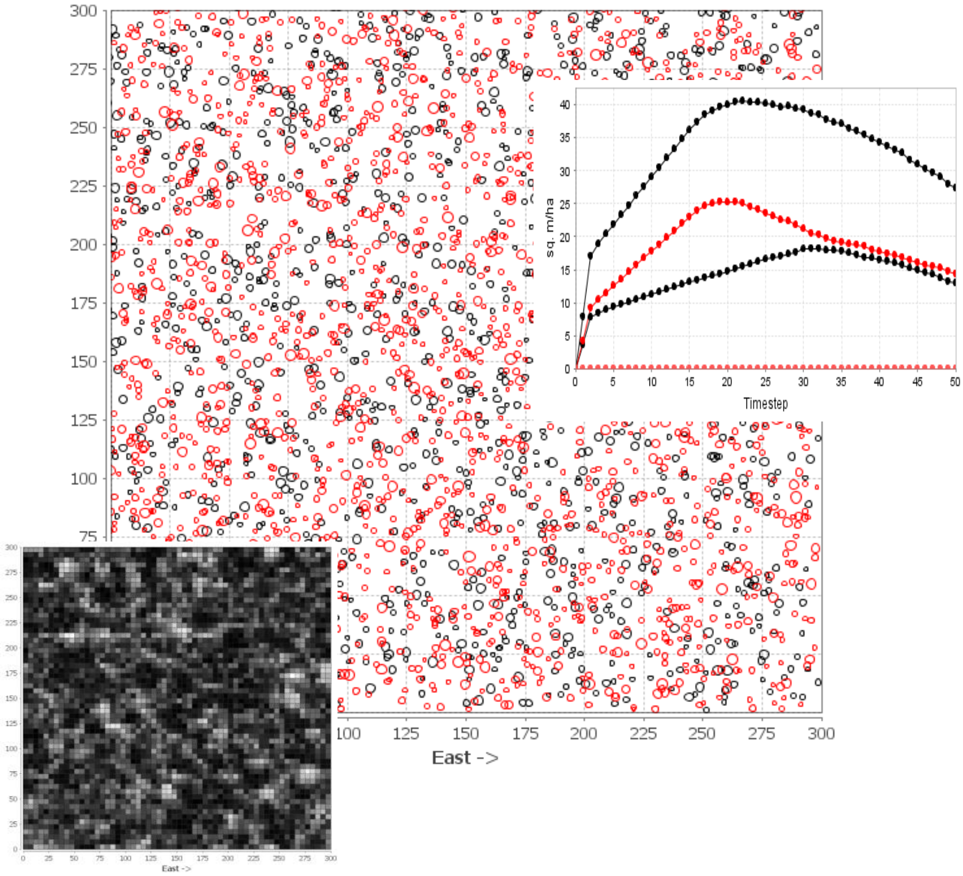
6

Relative importance of climatic-induced variations in juvenile growth and initial composition in the future dynamics of the Pyrenean montane-subalpine ecotone



6. Relative importance of climatic-induced variations in juvenile growth and initial composition in the future dynamics of the Pyrenean montane-subalpine ecotone

Abstract

Most predictive models forecast significant upward displacement of forest ecotones tracking increases in temperatures. However the predicted upward spread of species into existing forests is driven not only by climate but also by other demographic processes operating at a lower scale. In this study, we parameterized and used an individual-based, spatially-explicit model of forest dynamics (SORTIE-ND) to investigate the role of species-specific differences in juvenile growth and recruitment in the evolution of the Pyrenean conifer montane-subalpine ecotone under a climate change context.

Predicted estimates of total biomass and tree size distribution of adult stands were consistent with observed values from mixed-conifer stands in the study area (composed by *Pinus sylvestris, Abies alba* and *Pinus uncinata*). Our results show that for ecologically similar species (i.e. both pines), even small differences (10%) in the response of sapling growth to climate change can lead to significant differences in the future species composition of these forests (increase in abundance of *P. sylvestris* from 42% to 50.3%). Conversely, in the transition areas composed by species with contrasted ecological requirements (i.e. *P. uncinata* and *A. alba*) other factors such as shade-tolerance emerge as more decisive than temperature-induced changes in driving the future composition of these forests.

Keywords: SORTIE-ND; *Pinus uncinata*, *Pinus sylvestris*, *Abies alba*, modeling, forest dynamics, climate change, juvenile growth, recruitment

6.1. **Introduction**

Mountain ecosystems are considered to be particularly sensitive to the effects of climate change due to the existing sharp climatic variation along short distances, which drives the elevational distribution of species (Grabherr *et al*., 1994; Theurillat and Guisan, 2001). Most of the research on the effects of global change on mountain areas has been devoted to the study of treeline dynamics (Camarero & Gutiérrez, 2001, 2004; Gottfried *et al.*, 2012) because the tree limit is relatively easy to detect and species develop there at the extremes of their physiological tolerance (Kupfer and Cairns, 1996). However, at most European treelines, changes in anthropogenic pressure - mainly abandonment of pastures - have proven to be at least as important as climate in setting the treeline position (Gehrig-Fasel *et al.*, 2007; Ameztegui *et al.*, 2010).

Comparatively, the lower limit of distribution of subalpine species, i.e. the montane-subalpine ecotone, has received much less attention, despite some authors consider it as more adequate for tracking changes derived from climatic warming (Noble, 1993; Kupfer and Cairns, 1996; Loehle, 2000). Most predictive models, particularly those based on climatic envelopes, forecast significant upward displacement of this ecotone tracking increases in temperatures due to the spread of montane species into the subalpine belt (Theurillat and Guisan, 2001; Malcolm *et al*., 2002). This behavior has already been described in some European mountains (Peñuelas & Boada, 2003; Lenoir *et al.*, 2008) but the inverse, i.e. a downslope movement of subalpine forests into the montane belt, has also been reported (e.g. Hättenschwiler and Körner, 1995; Lenoir *et al*., 2010; Bodin *et al*., 2013), suggesting that drivers other than temperature may also play a determinant role in the dynamics of these systems It should also be noted that in mountain areas the upper and lower limits of species' ranges are often not driven by the same environmental factor: it is generally accepted that the upper limit of species distribution is mainly controlled by temperature (Rickebusch *et al.*, 2007), whereas the lower extreme is commonly set by competitive interactions with other species or by drought-related limitations, depending on the species and the environment considered (Loehle, 1998; Lenoir *et al.*, 2010).

Predicting the future composition and structure of forest transition areas requires first identifying the main environmental factors that create and maintain the limits of each species, and then determining how variations in these factors associated to the future climate are expected to affect their dynamics (Weinstein, 1992; Loehle, 1998). However, not all the processes that can be affected or constrained by climate have been equally studied. For example, there is a considerable amount of research devoted to the relationship between climate and adult tree growth and mortality (Andreu *et al.*, 2007; Gómez-Aparicio *et al.*, 2011; Ruiz-Benito *et al.*, 2013), whereas the factors controlling juvenile performance (recruitment, growth and mortality) are much less understood, even though juveniles are more susceptible to climate and more responsive to environmental changes (Lenoir *et al*., 2009; Benavides *et al*., 2013; Rabasa *et al*., 2013).

In this context of uncertainty and complexity of the processes driving forest dynamics, simulation models represent an interesting tool to help researchers and managers to identify the main bottlenecks in the dynamics of mixed forests and to predict the behavior of these forests under changing scenarios (Weinstein, 1992; Loehle & LeBlanc, 1996). In this study, we used a spatially-explicit, individual-based model of forest dynamics (SORTIE-ND) to assess the fate of the montane-subalpine ecotones in the Eastern Pyrenees (NE Spain). These ecotones are defined by the conjunction of *Pinus uncinata*, the dominant species in the subalpine elevational belt, with *Pinus sylvestris* and *Abies alba*, two species with contrasting drought- and shade-tolerances that dominate the montane belt (Niinemets and Valladares, 2006; Ninot *et al*., 2007). This ecotone is considered to be temperature-based, with cold temperatures limiting the upper range of *P. sylvestris* and *A. alba*, whereas *P. uncinata* finds its low distributional limit when facing species with higher competitive ability (Loehle, 2000; Blanco *et al.*, 2005). Climate change predictions in the area for the end of the century include increases in temperatures, a slight reduction in precipitation and increases in the intensity and length of drought periods (Barrera-Escoda & Cunillera, 2011). On the other hand, significant land-use changes (including agricultural land abandonment, reduction in livestock pressure and logging intensity) have occurred in the area in the last decades, leading to a marked increase in forest extent, stand density and mean canopy cover, thus favoring more shade-tolerant species (Poyatos *et al.*, 2003; Ameztegui *et al.*, 2010). Consequently, simultaneous effects of climate and stand-structure can be expected to drive the dynamics of these forests in the next decades.

The main objective of this study is to evaluate the relative importance of both (1) climatic-induced variations in juvenile growth and (2) initial composition of the stand in the future dynamics of the Pyrenean montane-subalpine conifer ecotone. For this we calibrated and used the model SORTIE-ND. We expected that species-specific differences in the growth response of juveniles to climate change will be particularly important for the future dynamics of the ecotone when it is composed by species with similar successional status species (i.e. both pines). In contrast, differences in initial composition would overcome the potential climatic-induced variations in growth when the ecotone is composed by species with different successional status (i.e. *P. uncinata* and *A. alba*).

6.2. **Methods**

6.2.1. Study area and species

We studied the three most common tree species in the Eastern Pyrenees: *Pinus uncinata* Ram., an intolerant to mid-tolerant conifer that reaches its southern distributional limit in the Iberian Peninsula and in the Pyrenees is restricted to the subalpine belt (between 1700 and 2300 m a.s.l.); *Pinus sylvestris* L. a shade-intolerant, widespread species that tolerates certain degree of drought and dominates the montane belt of the Pyrenees; and *Abies alba* Mill., which is also distributed along the montane belt, but it is usually restricted to humid sites on north-facing, shady slopes where the risk of water stress in summer is lower (Macias *et al.*, 2006). These species differ in their successional status and ecological requirements, and they can be ordered from most (rank = 5) to least (rank = 1) shade tolerant following the ranking system developed by Niinemets and Valladares (2006): *A. alba* (4.6 ± 0.06; mean ± SE), *P. sylvestris* (1.67 ± 0.33) and *P. uncinata* (1.2). Both pines present also a higher degree of drought-tolerance than silver fir i.e. ranking order according to the same authors: *P. sylvestris* (4.34 ± 0.47); *P. uncinata* (3.88) and *A. alba* (1.81 ± 0.28). The three species co-exist in a strip located between 1600 and 2000 m a.s.l. constituting the conifer montane-subalpine ecotone. Nevertheless, the presence of the three species in the same stand is not common, so we chose as study-cases the two most common associations of these species: (i) a pine mixed forest (*P. uncinata - P. sylvestris)* and (ii) pine-fir forest (*P. uncinata - A. alba)*. Both forests types are characterized by a different composition and structure and are the result of different land-use legacies.

The first case study, the combination of *Pinus uncinata* and *Pinus sylvestris,* is the most common mixed-forest in the area, covering more than 15,000 ha (Vericat *et al.*, 2010). These forests present a great variability in composition and structure depending on local environmental conditions, climate and the type of management applied. Although this formation is composed by relatively early-successional species, in the absence of large-scale disturbances, cuttings or environmental changes, it is considered to be potentially stable in time.

The second case study (combination of *P. uncinata* with *A. alba)* covers 4,298 ha in the study area. In many cases, the presence of fir is restricted to the lowest diametric classes and indicates either an advanced successional stage of forests that have recolonized open areas or the result of a reduction in cutting pressure after decades of intensive logging (Aunós *et al.*, 2007; Camarero *et al.*, 2011). When the ecological conditions are adequate for the fir, this species tends to dominate because pines have difficulties to regenerate under the deep shade it casts.

6.2.2. Model description

To perform the simulations we used SORTIE-ND version 7.01 (http://www.sortie-nd.org) (Canham *et al.*, 2005), a spatially explicit, individual-based model of forest dynamics based on the model SORTIE, firstly developed by Pacala *et al.* (1993) for temperate hardwood forests of the northern US. SORTIE-ND simulates the architecture, recruitment, growth and mortality of individuals in a plot, recording the specific location of each tree. Although initially developed to simulate the dynamics of forests where light availability is the main limiting resource, successive new versions have incorporated more detail on other issues such as management, disturbances and the effect of climate change. SORTIE-ND is considered to be especially suitable to model the dynamics of complex, mixed forests. It has been successfully used to simulate fine-scale spatial processes such as neighborhood competition for resources (Canham *et al.*, 2004, 2006), spatial patterns of seed dispersal (Ribbens *et al.*, 1994) and the effect of substrate availability on seedling recruitment (Papaik and Canham, 2006). It has also been used to assess the effects of different types of natural or anthropogenic disturbances such as windthrow, silvicultural treatments, insect outbreaks and hurricanes (Canham *et al.*, 2001; LeGuerrier *et al.*, 2003; Uriarte *et al.*, 2005; Beaudet *et al.*, 2011).

The main structure of SORTIE-ND is composed by 4 submodels: (i) allometry and resource availability (Canham *et al.*, 1994), (ii) seed dispersal and recruitment (Ribbens *et al.*, 1994) and (iii) growth and (iv) mortality of seedlings, saplings and adults (Pacala *et al.*, 1994; Kobe *et al.*, 1995). Each of these submodels has been parameterized in this study for the three studied species in the Pyrenees.

6.2.3. Model parameterization

6.2.3.1. Allometry and light availability submodel

Allometric equations in SORTIE-ND define relationships between stem diameter and tree height, crown depth and crown width. The size, shape and openness of the crown of a given tree define the amount of light that it is able to intercept. The sum of the light intercepted by all the trees in a forest determines the patterns of light availability, which in turn drive tree growth and mortality. The parameterization of this submodel for the studied species was carried out in a previous study in which more than 200 saplings and adults of each species were sampled to obtain allometric equations (Ameztegui *et al.*, 2012). Species-specific crown openness was determined from pictures of the crown of 120 adult trees per species following the methodology described by Canham *et al.* (1999) and Boivin *et al*. (2011). Predictions of light transmission to the understory were evaluated against understory light measurements in 96 validation plots (Ameztegui *et al.*, 2012).

6.2.3.2. Dispersal and recruitment submodel

Seedling dispersal and recruitment are modeled in SORTIE-ND using a seed dispersal kernel, in which the probability of seedling establishment in a given point is related to the distance to conspecific adults, whereas the number of seeds produced by an adult tree varies with species and size (Pacala *et al.*, 1996). For every tree above a given DBH, SORTIE-ND simulates the production and dispersal of seeds based on the species-specific parameter *Standardized Total Recruits* (STR), defined as the number of new seedlings produced by a tree with a DBH of 30 cm. Field determination of these processes often requires the disposal of long-term, large-scale datasets that are commonly not available. In this study, we followed the approach by Papaik and Canham (2006), who calculate *STR* as the result of two components: (i) tree fecundity; *i.e.* the average seed production of a tree and (ii) seed germination and 1-year seedling survival. We obtained tree fecundity from the empiric equations formulated by Greene and Johnson (1994, 1998), that inversely relate seed production and seed mass, with values of seed mass for each species coming from Alía *et al*. (2005). Seedling survival was determined as a function of substrate availability as follows: first, we compared the relative abundance of six different seedbed substrate types (mineral soil, forest floor, fresh logs, decayed logs, herbaceous layer and mosses) and the number of recruits (1-2 years old) by species and substrate type in 500 sampling quadrats placed across 5 different mixed forests. Then, each substrate type was classified as either favorable or unfavorable for establishment of each species, and finally we determined seed germination and 1-year seedling survival based on equations from Papaik and Canham (2006).

The parameters for the growth and mortality submodels were obtained separately for juveniles and adults, thus taking into account the different drivers of these processes in each life stage. Juvenile radial growth was determined as a function of light availability by fitting a Michaelis-Menten function for 150 seedlings and saplings of each studied species sampled under a gradient of light conditions (Ameztegui and Coll, 2011). The growth of adults (DBH > 7.5 cm) for both pine species was determined from Gómez-Aparicio *et al*. (2011), who estimated radial growth as a function of species-specific potential radial growth and scalars that reduce this maximum growth as a function of tree size, climate (temperature and precipitation) and neighborhood competition (Canham *et al.*, 2004). In the case of *A. alba*, parameter values were estimated specifically for this study using the same approach and the Spanish Forest Inventory (SFI) as data input (this species was not included in the original work of Gómez-Aparicio *et al*. (2011)) (Appendix 1).

Since the function describing the growth of the adults depends on temperature and precipitation values, current climate and a rate of variation must be defined. We characterized the current climatic parameters from the Digital Climatic Atlas of Catalunya (Ninyerola *et al.*, 2000), taking the average temperature and precipitation values recorded for the plots where each type of forest was present (according to the SFI). The rate of expected climatic variation was obtained from the regionalized predictions for the Pyrenees based on IPCC predictions and the MM5 mesoscale atmospheric circulation model (Grell *et al*., 1994; Barrera-Escoda and Cunillera, 2011). We used predictions for a moderate emission scenario (B1), which forecasts an increase in the average temperatures of 2.6 ºC and a decrease in precipitation of 13.5% by the end of the century (Appendix 2).

Seedling and sapling mortality were determined as a function of recent radial growth history, assuming that growth is an integrated measure of whole-plant carbon assimilation (Kobe *et al.*, 1995) and using field-data from 150 living and dead saplings of each species (Ameztegui and Coll, 2011). We tried to obtain senescence patterns of mortality from repeated-measures from the SFI (Direccion General para la Biodiversidad, 2007), but the young age of most Pyrenean forests did not allow us obtaining good estimators (as acknowledged by Ruiz-Benito *et al*. (2013)). Nevertheless, running the simulations without setting a maximum potential DBH resulted in unrealistic slow dynamics. For this, we decided to assign a maximum value of tree size for each species combining data from the SFI and expert knowledge.

6.2.4. Model input and simulations

6.2.4.1. Initial stand structure and composition

For each case study described above, the initial composition and structure of the forests used for the simulations (i.e. tree density per DBH classes and species) were defined from previous works on forest typologies for these species (Aunós *et al.*, 2007; Martín-Alcon *et al.*, 2012). In the case of the *P. uncinata* – *P. sylvestris* forest, the initial stand was composed by saplings of both species (1,000 individuals·ha^{-1} per species). This kind of structure is rather common in even-aged pine stands managed with shelterwood systems (just after the last cut is made). The simulations were started from bare ground, with the only presence of juveniles (Table 1). This approach allowed us to use baseline simulations as an evaluation test of the predictive ability of the model under current conditions (Bugmann, 2001).

Table 6.1 Main dasometric and climatic characteristics of the simulated stands

Variable	***P. uncinata – P. sylvestris***			***P. uncinata – A. alba***		
	Pinus uncinata	*Pinus sylvestris*	*Total*	*Pinus uncinata*	*Abies alba*	*Total*
BA (m2·ha-1)	-	-	-	8.5	4.7	15.0
N (stems·ha-1)	-	-	-	215	135	330
Mean DBH (cm)	-	-	-	22.5	17.7	21.0
Nreg (stems·ha-1)		2000			300	
Mean annual temp. (ºC)		6.4			6.2	
Annual prec. (mm)		1027.4			1045.0	

BA: basal area; N: stem density, Nreg: regeneration stem density (DBH < 7.5 cm)

This initial structure would not be realistic in the case of pine-fir forests, since fir is known for not being able to withstand complete or sudden exposition to full-light conditions at young ages. Therefore, for the *P. uncinata* – *A. alba* forest, we defined as starting point a stand structure defined by a typical diameter distribution of an adult pine stand with a high presence of fir in the understory (low diameter classes) and abundant regeneration (300 seedlings·ha^{-1}). This type of forests is relatively common in our study area, being the result of densification processes due to forest maturation and lack of management. To accelerate forest succession, we decide to remove from the starting “scene” large trees (mainly pines) (Figure 6.1). This approach allowed us to test the role of fir juvenile performance on forest dynamics. In both study cases, the position of each tree was randomly assigned by the model.

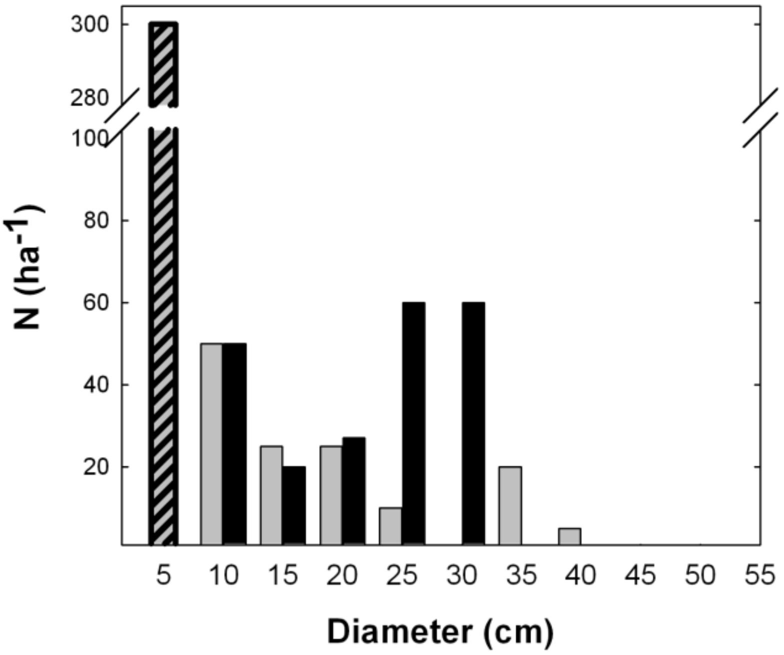


Figure 6.1 Diameter distribution for the fir-mountain pine mixed forest as reconstructed based on the information obtained from the Spanish Forest Inventory. Black bars correspond to mountain pine (*Pinus uncinata*) and grey bars to silver fir (*Abies alba*). Dashed bars indicate the total amount of regeneration (DBH < 7.5 cm) for both species, with proportion variable among scenarios.

6.2.4.2. Variation in recruitment ability

For each case study, we first defined a baseline simulation in which regeneration (DBH < 7.5 cm) was balanced between species (i.e. 50% of juveniles corresponded to each species). Then, we changed the initial proportion of regeneration between species to test the sensitivity of the model to changes in this parameter. For the pine-mixed forest we simulated five initial conditions: (i) 90% of regeneration *P. sylvestris* and 10% of *P. uncinata*; (ii) 70% *P. sylvestris* and 30% *P. uncinata*; (iii) 50% of each species (baseline); (iv) 30% - 70% and (v) 10% - 90%. Only three initial conditions were defined for the pine-fir forest: (i) 90% *A. alba* – 10% *P. uncinata*; (ii) 70%-30% and (iii) 50% of each species (baseline). The other two initial conditions, in which *P. uncinata* was dominant, were discarded for considering them unrealistic due to the higher regeneration capacity of fir in the understory.

6.2.4.3. Variation in juvenile growth

To assess the role of climatically-induced variation in juvenile growth in the future dynamics of these forests we defined, for each of the initial conditions described above, different scenarios in which all the parameters but juvenile radial growth were kept constant. The effect of future climatic conditions on juvenile growth was introduced as scalars that modified the growth-light availability equation developed in a previous work (Ameztegui & Coll, 2011). Nevertheless, the values of the scalars were different for each species, matching the expected species-specific responses to changes in climate.

The current upper elevational limit of *P. sylvestris* is commonly considered to be climatically driven (Hättenschwiler and Körner, 1995; Ninot *et al.*, 2007) so we hypothesized that this species may benefit from a future increase in temperatures. Consequently, we tested scenarios in which juvenile growth rate of *P. sylvestris* increased by 0% (i.e. current measured growth rate), 10%, 25% and 50%. More uncertainties exist in the possible response of *A. alba* juveniles to predicted changes in climate. On one hand, its growth and recruitment ability could be favored by warmer temperatures (Lenoir *et al.*, 2009; Rabasa *et al.*, 2013) but, as a drought-sensitive species, it may also suffer drought-induced decline, as already observed in its southernmost distribution limit in the Peripheral ranges of the Pyrenees (Macias *et al.*, 2006). Therefore we tested three scenarios in which growth was enhanced by 10, 25 and 50% and three other scenarios in which its growth was reduced in the same proportions. Finally, we expected a small effect of climate change on *P. uncinata* juvenile growth, since this species has shown little responses in performance to increases in temperature (Gómez-Aparicio *et al.*, 2011; Ameztegui and Coll, 2013; Ruiz-Benito *et al.*, 2013). Therefore, we decided to not vary its observed current growth rate.

6.2.5. Model runs and statistical analyses

The combination of different initial proportions in regeneration (5 for the pine-mixed forest; 3 for the pine-fir forest) and scenarios of juvenile growth rate (4 and 7, respectively) produced a total of 41 different initial conditions to simulate. We ran each model for 40 timesteps, i.e. 200 years, and each scenario was simulated ten times to account for the effect of spatial distribution of trees and for the stochasticity of some of the submodels in SORTIE-ND (Deutschman *et al.*, 1997; Vanhellemont *et al.*, 2011). To test for the effect of regeneration composition and juvenile growth on forest dynamics, we defined two response variables: total basal area of the plot ($m^2 \cdot ha^{-1}$) and basal area of *P. sylvestris* or *A. alba*, depending on the case. For each case study, differences between growth rates for each initial regeneration composition were evaluated with one-way ANOVA and post-hoc Tukey mean comparisons using R statistical software (R Development Core Team, 2010).

6.3. Results and discussion

6.3.1. Case study 1: *P. uncinata – P. sylvestris* forests

The baseline simulation performed with the *P. uncinata – P. sylvestris* mixed forest predicted an asymptotic growth of the stand, which reached a maximum basal area of 40 $m^2 \cdot ha^{-1}$ at around year 100-120 (Figure 6.2). Then the total basal area of the plot remained relatively stable during some years and started to decrease from year 150 due to senescence of the oldest trees. Stem density continuously decreased throughout the simulated period, the number of trees decreasing from 1400 $stems \cdot ha^{-1}$ at year 20 to 500 $stems \cdot ha^{-1}$ at the end of the simulation. The density and basal area estimated by the model were consistent with observed values from mixed-conifer forests in the Catalan Pyrenees and with management guides for the area, which report similar values for a mature forest of these species (Piqué *et al.*, 2011; Centre Tecnològic Forestal de Catalunya *et al.*, 2012).

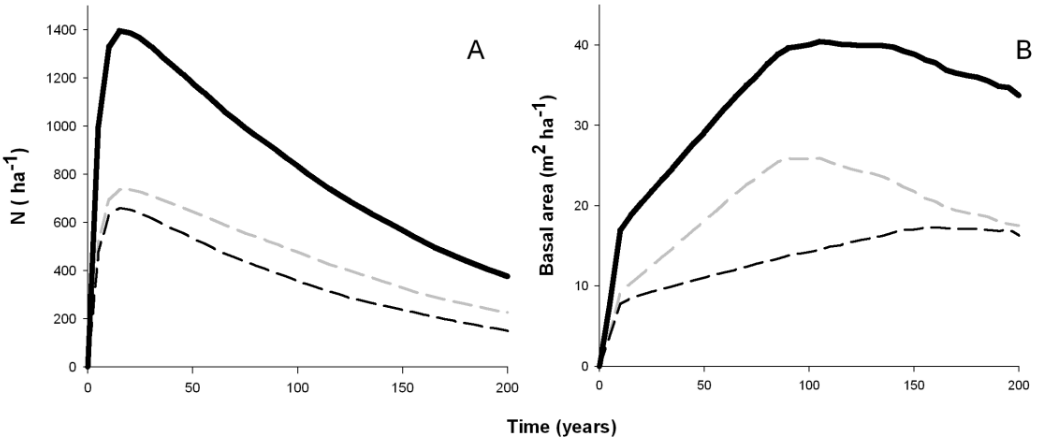


Figure 6.2 Output of the SORTIE-ND baseline simulations for the pine-mixed forest over a 200-year simulation period showing (a) the stem density (ha-1) and (b) the basal area (m2·ha-1) of the adult trees (DBH > 7.5 cm). Species are represented as follows: *Pinus sylvestris* (grey dashed line), *Pinus uncinata* (black dashed line), and the total for the plot is represented by the black bold line. The baseline simulations represent the dynamics of a forest with a balanced initial composition of regeneration and no climatic constraints to juvenile growth. The values shown for each figure are the mean output for the ten repetitions run for each scenario.

Regarding the composition of the stand, the higher growth rate of *P. sylvestris* led to higher initial basal area of this species during the first 100 years, but its dominance began to decrease from year 110 (Figure 6.2B). Under conditions of balanced composition of regeneration (i.e. 50% of each species) and current growth rates the model predicted a balanced between-species repartition of basal area for the year 200. Although the interpretation of the results obtained beyond the year 100 should be done with caution because it represents an extrapolation of climate predictions, this would mean that both species would be able to coexist in the mid-term.

All the tested scenarios showed a clear dominance of *P. sylvestris* at the short-, mid-term (Figure 6.3). These results agree with previous works that reported higher growth rate for *P. sylvestris* than for *P. uncinata* when both species grow in non-limited environmental conditions (Camarero *et al.*, 1998; Climent *et al.*, 2010). Nevertheless, the abundance of *P. sylvestris* tended to decrease after the first 100 years, no matter the tested scenario, whereas *P. uncinata* continued to increase its basal area. This would indicate that if *P. sylvestris* is not able to improve its ability to regenerate or increase its growth rate in response to climate change, its presence in the ecotone may be conditioned to the existence of large-scale disturbances or active management, as already suggested in the Alps (Hättenschwiler and Körner, 1995).

Variations in juvenile growth and recruitment ability produced significantly different results depending on the scenario considered. The initial composition of the regeneration was the most important factor driving the proportion of *P. sylvestris* after 100 years of simulation. However, juvenile growth rate did also significantly affect these predictions (Table 2). The interaction between growth rate and initial composition was also highly significant, with the effect of the enhanced growth rate being greater for those situations where the initial percentage of *P. sylvestris* was lower (Table 2). For instance, the proportion of *P. sylvestris* in the stand after 100 years did not vary with enhanced growth when the initial proportion of this species was 90%, but it rose from 14.3% to 31.4% of the total basal area of the plot for the scenario in which the initial rate of *P. sylvestris* was 10% (Figure 6.4). For some scenarios, an enhanced growth rate of *P. sylvestris* resulted in a rank-reversal in species dominance. For instance, when the initial proportion of *P. uncinata* was 70%, an enhanced growth rate of 10%, 25% and 50% for *P. sylvestris* resulted in a final proportion of this species of 50.3%, 56.8% and 63.3%, respectively (Figure 6.4).

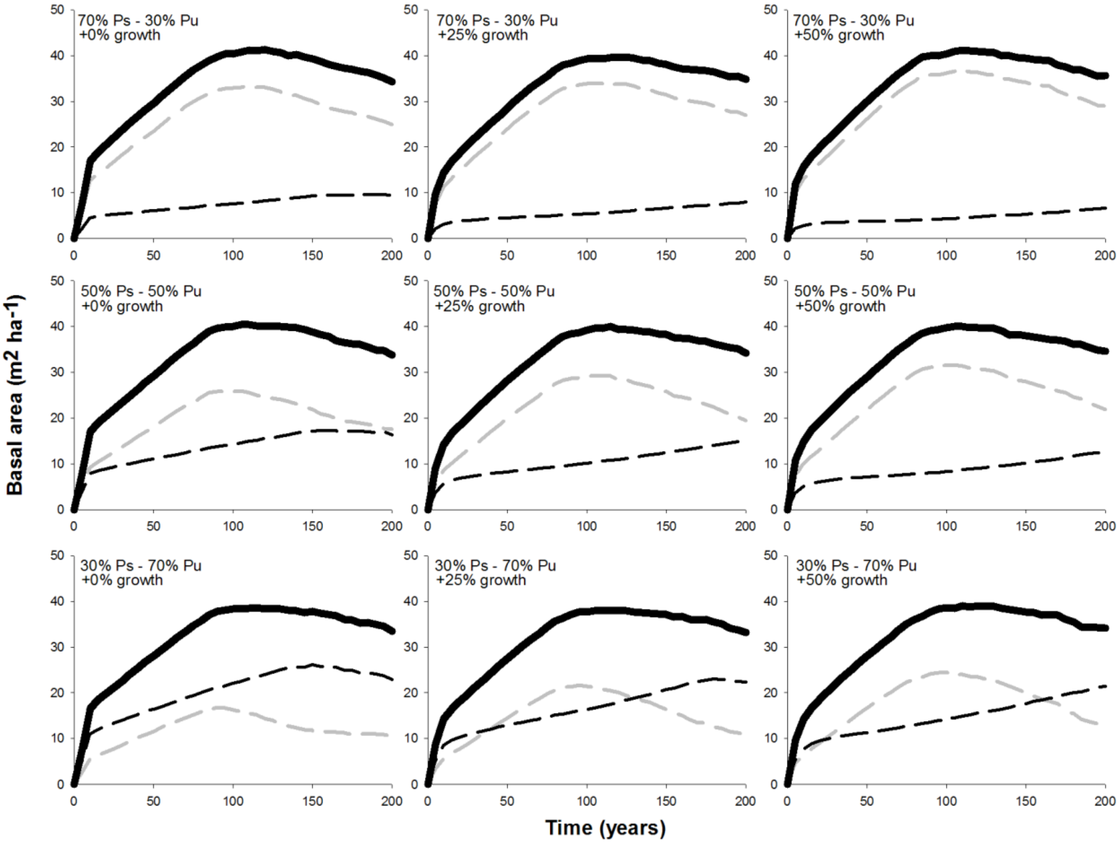


Figure 6.3. Output of the SORTIE-ND simulations for the pine mixed forest over a 200-year simulation period showing the basal area ($m^2 \cdot ha^{-1}$) of the adult trees (DBH > 7.5 cm) of *Pinus sylvestris* (grey dashed line), *Pinus uncinata* (black dashed line) and total (bold solid line). The legend in each figure indicates the different scenarios of initial stand composition and increase in juvenile growth rate for *P. sylvestris*. The values shown for each figure are the mean output for the ten repetitions run for each scenario.

The total basal area of the plot after 20 timesteps (*i.e.* 100 years) was not significantly affected by the initial conditions or the juvenile growth rate. The higher basal area obtained for *P. sylvestris* in some of the simulations was therefore not due to an increase in the productivity of the stand, but rather to a different repartition of the total basal area between species.Although increases of 50% in the growth of Scots pine due to temperature warming are not very likely to occur, our results show that, under certain conditions of initial composition, even small increments in *P. sylvestris* growth (of only 10%) may involve significant changes in the dynamics of these forests and an upward displacement of *P. sylvestris* into the *P. uncinata* domain. Nevertheless, some authors have suggested that recruitment ability may be the main factor limiting the ability of *P. sylvestris* to spread upwards. In a previous study, we observed high seedling mortality of this species when planted above its current elevational limit (Ameztegui and Coll, 2013), and Probst and Rouane (1984) suggested that faster germination of *P. sylvestris* compared to *P. uncinata* could make this species more susceptible to early frosts. On the other hand, Hättenschwiler & Körner (1995) pointed to canopy closure rather than climate as the most limiting factor for *P. sylvestris* establishment in a montane-subalpine ecotone in the Alps.

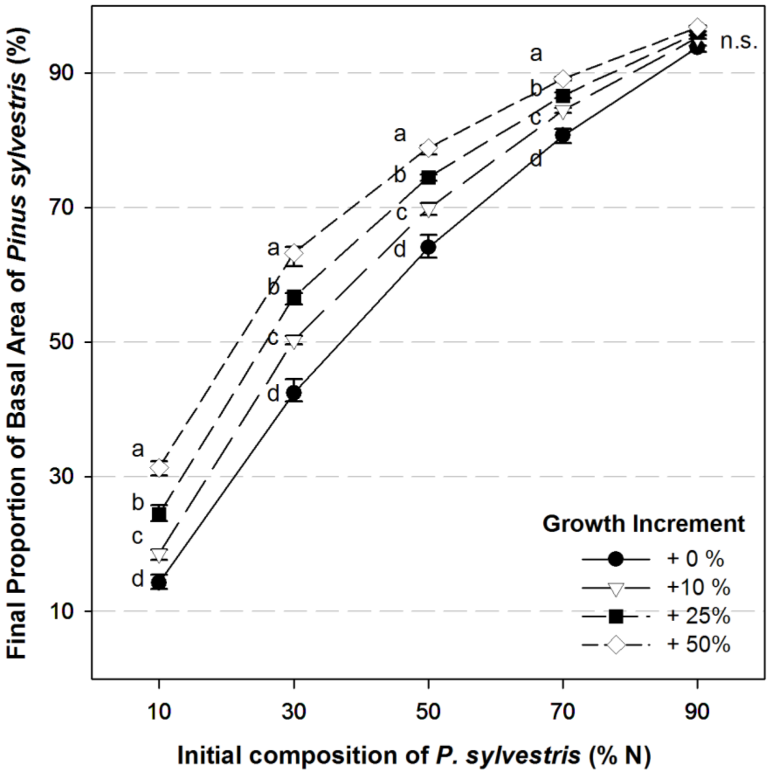


Figure 6.4. Predicted proportion of *P. sylvestris* at year 100 expressed as percentage of the total basal area of the plot (BA, $m^2 \cdot ha^{-1}$) for different scenarios combining different initial stand composition and growth rates for *P. sylvestris.* Legend indicates the simulated growth rate for juveniles of *P. sylvestris* as compared to current growth, whereas letters indicate significant differences for the outcome of different growth rates for a given initial composition. Symbols represent mean output for ten simulations run for each scenario and error bars are standard error of these repetitions.

6.3.2. Case study 2: *P. uncinata – A. alba* forests

In the case of the pine-fir forest, the baseline simulation (balanced composition of regeneration; current growth rate) showed a clear domination of pine during the first decades (associated to its higher growth rate), which reached a maximum basal area of 17 $m^2 \cdot ha^{-1}$ at year 70-80 (Figure 6.5). From this point, its dominance progressively weakened, being substituted by a second generation of firs, which started establishing in the understory from year 120, when the senescence of pines led to a drop in the total basal area of the stand below 20 $m^2 \cdot ha^{-1}$. Once this second generation of fir established, its slow growth rate and the progressive decline of pine (which virtually disappeared from the stand) made the total basal area of the plot fell to less than 12 $m^2 \cdot ha^{-1}$ at the end of the simulated period.

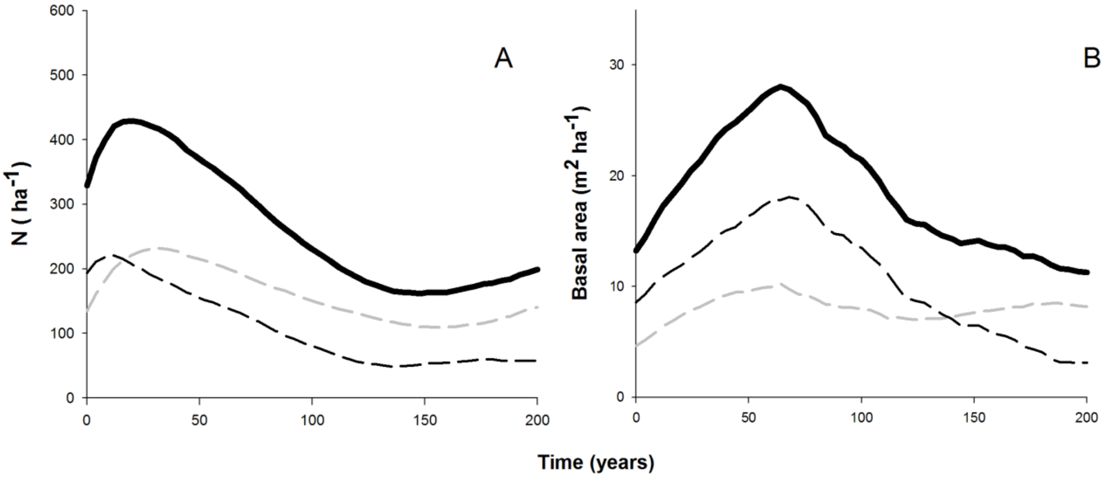


Figure 6.5 Output of the SORTIE-ND baseline simulations for the pine-fir mixed forest over a 200-year simulation period showing (a) the stem density (ha^{-1}) and (b) the basal area ($m^2 \cdot ha^{-1}$) of the adult trees (DBH > 7.5 cm). Species are represented as follows: *Abies alba* (grey dashed line), *Pinus uncinata* (black dashed line), and the total for the plot is represented by the black bold line. The baseline simulations represent the dynamics of a forest with a balanced initial composition of regeneration and no climatic constraints to juvenile growth. The values shown for each figure are the mean output for the ten repetitions run for each scenario.

The model predicted values of basal area at the end of the simulated period (12 $m^2 \cdot ha^{-1}$) that were below those currently observed for this type of forest in the Pyrenees (Figure 6.5B). The decrease in forest productivity predicted by the model (which mainly affected *A. alba),* could be associated to the high sensitivity of the adult radial growth of this species to climate change. According to the climatic predictions we used, rainfall expected in the plot by the end of the century would be 910 mm, a reduction of 13% that was sufficient to induce a decrease of 15% in the adult growth rate of fir (Appendix 6.I). The negative correlation between growth and precipitation in fir stands is well known and has been widely reported (Rolland *et al.*, 1999; Macias *et al.*, 2006; Toromani *et al.*, 2011).

In contrast to the results obtained for the pine-mixed forest, variations in the juvenile growth rate of fir did not induce significant differences in the output produced by the model (Figure 6.6). However, increases in the initial abundance of fir in the regeneration pool led to slight (although statistically significant) differences in the final abundance of this species. These results seem to indicate that an enhanced growth rate of silver fir associated to warming climate would not lead to significant improvements in the dominance of this species. More interestingly, they also suggest that a reduction in juvenile growth would not affect its performance either. This apparent lack of response of silver fir to variation in growth rates may be related to its shade-tolerant character. Silver fir has the capacity to remain suppressed in the understory for years due to its intrinsic ability to withstand low radial growth rates when growing in shade conditions (Ameztegui and Coll, 2011). At the same time, its growth rate is much lower than that of *P. uncinata* along almost the entire gradient of light availability, so even with an enhanced growth rate of 50% it would not reach that of pines.

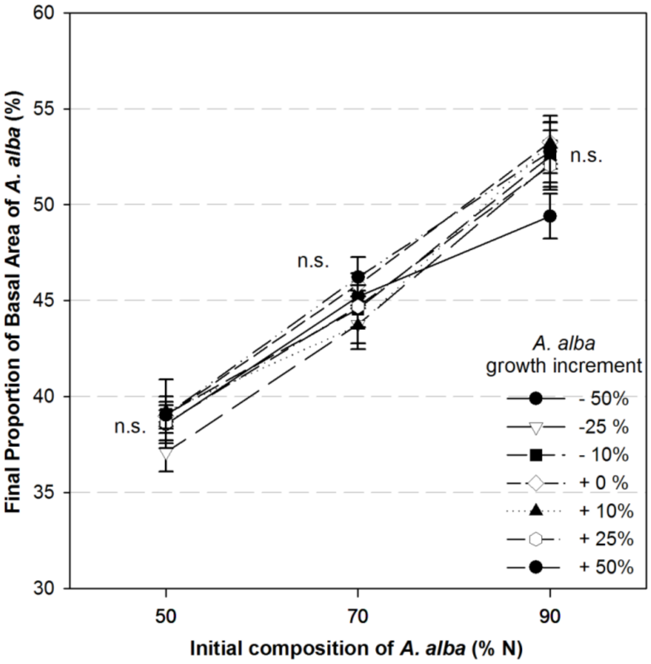


Figure 6.6 Predicted proportion of *A. alba* at year 100 expressed as percentage of the total basal area of the plot (BA, $m^2 \cdot ha^{-1}$) for different scenarios combining different initial stand composition and growth rates for *A.alba.* Legend indicates the simulated growth rate for juveniles of *A. alba* as compared to current growth, whereas n.s. indicates lack of significance for the values obtained between the outcome of different growth rates for a given initial composition.Symbols represent mean output for ten simulations run for each scenario and error bars are standard error of these repetitions.

There is a considerable amount of research that prove the drought-sensitivity of juveniles of *A. alba* (Pagès *et al.*, 2003; Robakowski *et al.*, 2003, 2005; Peguero-Pina *et al.*, 2007) and increases in the frequency, intensity and duration of drought periods are expected to lead important limitations in the performance of this species in particular when growing at its ecological xeric limit (Peguero-Pina *et al.*, 2007). Indeed, some authors have already reported signs of decline in the southernmost limit of *A. alba* distribution in the External Pyrenean ranges (Macias *et al.*, 2006; Camarero *et al.*, 2011) whereas it shows little signs of decline or problems to regenerate in the Main Range (Oliva and Colinas, 2007). In any case, whatever the response of *A. alba* juveniles to climate change, our results suggest that variations in juvenile growth rate or recruitment ability seem not to be sufficient to induce significant upslope retreat of this species in the mid-term in the montane-subalpine ecotone.

6.3.3. Conclusions

In this paper, we used the model SORTIE to evaluate the role of juvenile growth and initial stand composition on the future dynamics of two mixed-conifer forests in the montane-subalpine ecotone of the Pyrenees. For the ecologically similar species *P. sylvestris* and *P. uncinata* we observed that slight differences in initial composition of the stand and juvenile growth rate led to significant differences in their abundance in the mature stand. In the *P.uncinata – A. alba* forest, the ability of silver fir to remain suppressed in the understory seems to buffer the potential effect of changes in its juvenile growth rate. Other factors, such as constraint adult radial growth due to reduction in precipitation, may thus be more important in driving the dynamics of these forests.

The model of forest dynamics we used (SORTIE-ND) has proven to be adequate to simulate the dynamics of Pyrenean mixed forests. In effect, we were able to predict forest productivity and species composition under current conditions, and to detect the main bottlenecks in the future fate of these forests. However, it should be acknowledged that there are still many uncertainties in the growth response of these species to climate change (in particular at young stages). Further research should thus be devoted to improve our knowledge on these issues in order to have more realistic projections of the future dynamics of these forests under different climatic and management scenarios.

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Appendix 6.I. Effects of size, competition and climate on adult growth

To assess the effect of competition, tree size and climate on adult diameter growth we used the same approach as in Canham *et al*. (2006) and Gómez-Aparicio *et al*. (2011). Diameter growth of trees is estimated as:

$$\textit{Diam. Growth} = \textit{PDG} \cdot \textit{Size effect} \cdot \textit{Crowding effect} \cdot \textit{Temp. Effect} \cdot \textit{Prec. Effect} \qquad \text{(I.1)}$$

Where PDF is the average maximum potential diameter growth (in mm·yr^{-1}) whereas size effect, crowding effect, temperature effect and precipitation effect are all factors which act to reduce the maximum growth rate and will vary depending on the conditions a tree is in. Each of these effects is an scalar that ranges between 0 and 1, and which are formulated as follows:

$$Size\ efect = e^{-0.5\left[\frac{ln\left({DBH}/{X_0}\right)}{X_b}\right]^2} \qquad \textit{(I.2)}$$

where X_0 and X_b are estimated parameters, and DBH is of the target tree

$$Temperature\ effect = \ e^{-0.5\left(\frac{abs\ (T-To\ )}{T_b}\right)^{Tc}} \qquad \textit{(I.3)}$$

where T_0, T_b and T_c are estimated parameters, and T is annual rainfall, in mm

$$Precipitation\ effect = \ e^{-0.5\left(\frac{abs\ (P-Po\ )}{P_b}\right)^{Pc}} \qquad \textit{(I.4)}$$

where P_0, P_b and P_c are estimated parameters, and P is annual rainfall, in mm

$$Crowding\ effect = \ e^{-C \cdot DBH^{\gamma} \cdot ND^{D}} \qquad \textit{(I.5)}$$

where C, γ and D are estimated parameters, DBH is of the target tree and ND is the numer of neighbors with a DBH greater than the target tree's DBH.

For *Pinus sylvestris* and *Pinus uncinata*, parameter estimates for equations I.2, I.3 and I.4 were obtained from Gómez-Aparicio *et al*. (2011). The rest of the parameters were estimated using likelihood methods (i.e. we estimated those parameters that maximized the likelihood of observing the growth data measured in the field) and the Spanish Forest Inventory as data source.

Table 6.I.1. Parameter estimates for the equations I.2, I.3, I.4 and I.5. See text for a description of the parameters

Component	**Parameter**	***A. alba***	***P. sylvestris***	***P. uncinata***
Crowding effect	C	0.02988	0.05561	0.1671
	D	0.767	0.68	0.56
	γ	0.523	0.249	0.0026
Size effect	X_o	17.156	19.92	15.57
	X_b	1.137	1.11	1.44
Temperature effect	T_0	20.914	1.09	71.59
	T_b	26.53	11.75	230.38
	T_c	2	2	2
Precipitation effect	P_0	1818.95	2386.82	1369.72
	P_b	1021.637	2660.83	2999.98
	P_c	4.239	2	2

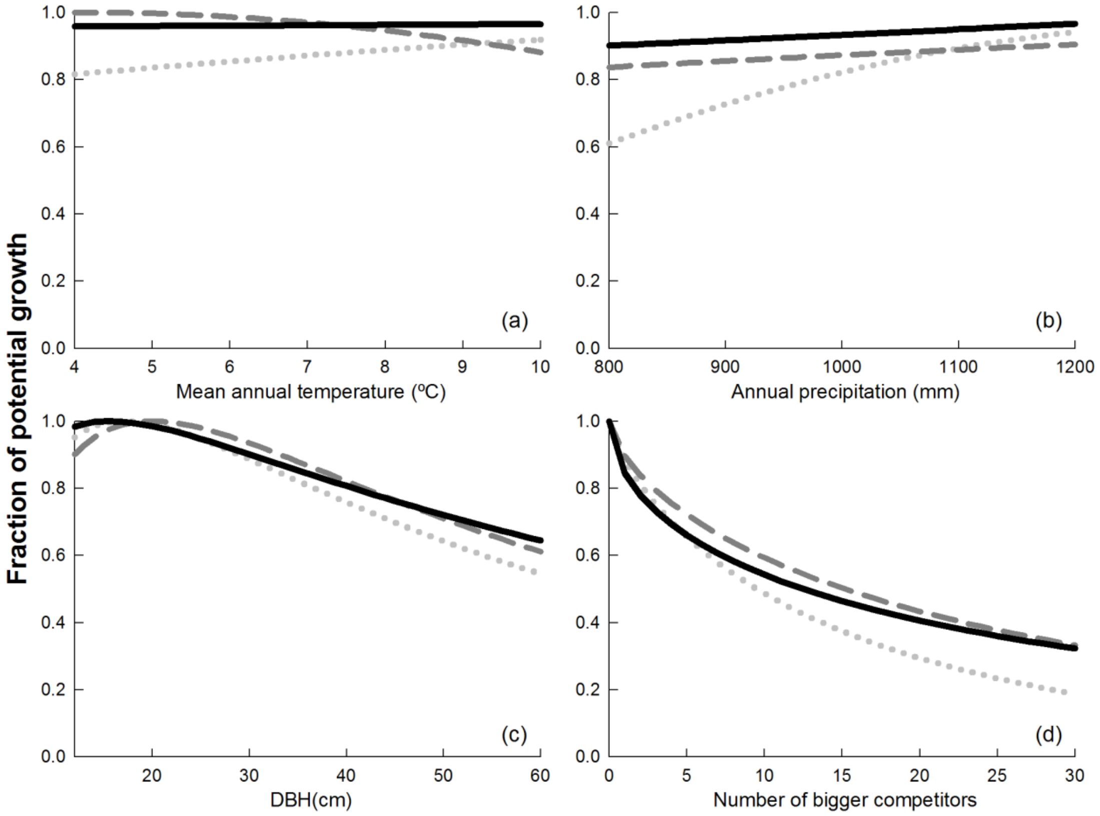

Figure 6.I.1 Predicted effect of (a) mean annual temperature, (b) annual precipitation, (c) target tree size, and (d) number of bigger competitors on adult radial growth for the three studied species: *Abies alba* (grey dotted line), *Pinus sylvestris* (grey dashed line) and *Pinus uncinata* (black solid line).

Appendix 6.II. Climatic predictions for the Pyrenees along the XXIst century

Table 6.II.1. Predicted variation in temperature and precipitation for the Pyrenees according to the B1 scenario of emissions

Period	Mean annual temperature	Mean annual precipitation
2011 – 2040	+ 0.9ºC	-5.0%
2041 – 2070	+ 1.4ºC	-6.4%
2071 – 2100	+2.6 ºC	-13.5%

Source: elaborated with data from Barrera-Escoda & Cunillera (2011). Data obtained from regionalized simulations based on the MM5 model. Reference period: 1971-2000.

7

General discussion

7. General discussion

The results of this doctoral thesis contributed to advance in the understanding of the role and effects of different drivers of change on the dynamics of mixed-conifer forests at the montane-subalpine ecotone in the Eastern Pyrenees. Furthermore, they also underline the importance of adequately defining the spatial and temporal scale to/in which these drivers are acting.

7.1. Drivers of forest dynamics at the landscape scale

Chapter 2 shows the critical role that land-use changes have played in the recent expansion and densification of mountain forests in the Eastern Pyrenees. We used as study case the forests of *Pinus uncinata*, which presents its lower boundary limiting with the highest ancient farmlands and the upper extreme with the subalpine grasslands. During the last five decades, mountain pine increased its surface coverage by more than 16% as the result of forest colonization of open lands. In addition, the mean canopy cover of mountain pine forests almost doubled in the same period. We found that forest encroachment and densification have not occurred homogeneously in space but matched the patterns of land-abandonment in the area at both the local and municipality scale (Figure 2.3). The match between the spatial patterns of forest expansion and those of land-use changes had already been observed at a more reduced spatial scale in several valleys of the Pyrenees (Fanlo *et al.*, 2004; Lasanta *et al.*, 2005; Vicente-Serrano *et al.*, 2005; Lasanta & Vicente-Serrano, 2007) but had never been analyzed at the regional scale. Our methodological approach, using a large set of aerial photographs (200 pairs of photographs covering more than 6,000 km^2, Figure 2.2) allowed us to work at a large spatial scale but retaining a relatively high resolution, so that we could capture the main potential processes operating at different spatial levels (regional, municipal, local).

The important role of land-use changes as drivers of forest dynamics does not mean in any way that climate change may not have modulated these processes. In our study, we found the rate of forest encroachment to be more important at low and medium elevations than at the treeline level. However, the influence of climate change should not be necessarily reflected as a displacement of the treeline position. In fact, the effects of climate warming have been reported to induce more important changes in the growth and recruitment rate of trees growing in the timberline ecotone than in those located at the treeline (Camarero & Gutiérrez, 2001, 2004; Ninot *et al.*, 2008). We also found a significant correlation between population decline, a proxy for livestock density, and forest expansion at the municipality level. These results suggest that variations in livestock pressure may have also played a significant role in driving forest expansion near the treeline as already demonstrated in Western European mountains (Cairns & Moen, 2004; Gehrig-Fasel *et al.*, 2007). In any case, the colonization rates observed near the treeline should be interpreted with caution, since changes in livestock pressure and climate have often occurred simultaneously, making it impossible to distinguish the role that each factor has played in the recent dynamics of the forest (Kupfer & Cairns, 1996; Gehrig-Fasel *et al.*, 2007).

Forest colonization of abandoned agricultural areas is not exclusive of the Pyrenees. All mountain ranges in western Europe have undergone through similar changes in land organization as a consequence of socioeconomic changes occurred during the first half of the twentieth century (MacDonald *et al.*, 2000). For example, forest expansion processes have been widely reported in the Alps (Dirnböck *et al.*, 2003; Gehrig-Fasel *et al.*, 2007; Gellrich *et al.*, 2007a, 2007b), the Apennines (Palombo *et al.*, 2013) and Mediterranean mountains in France (Chauchard *et al.*, 2007; Bodin *et al.*, 2013). In the Spanish Pyrenees, these socioeconomic changes occurred later due to the autarkic regime prevailing until the mid-twentieth century (Garcia-Ruiz & Lasanta, 1990; Domínguez, 2002).

In our study, we also detected a significant process of densification of existing sparse forests, which mean canopy cover rose from 31.0% to 55.6% in the last decades. This rise in canopy cover was especially important for previously sparse forests, which almost doubled their mean canopy cover in this period. This forest densification may reflect the decreasing use of fuelwood and timber due to population decline, the drop in timber profitability and the replacement of forest resources by other sources of energy (Poyatos *et al.*, 2003).

7.2. **Light as driver of mixed forest dynamics**

In the absence of large-scale disturbances, forest densification has led to a severe canopy closure that has affected not only *Pinus uncinata* but most Pyrenean forests (Burriel *et al.*, 2004; Piqué *et al.*, 2011). This may have profound implications for forest dynamics, since the absence of light in the understory limits the development of light-demanding species whereas shade-tolerants (e.g. *Abies alba)* are favoured (Aunós *et al.*, 2007). In **Chapters 3 and 4** we aim at advancing in the comprehension of the role of light as driver of mountain forest dynamics. Our results showed that variations in the abiotic environment affect the allometry, architecture and transparency of tree crowns and therefore the transmission of light through the canopy and the availability of light in the understory. We also determined the response of juveniles of the main species in the study area to variations in light availability in the understory and its potential implications on their future dynamics.

In **Chapter 3** we hypothesized that aspect would induce marked differences in the crown characteristics of individual trees of the three studied species (*P. sylvestris, P. uncinata* and *A. alba*). Tree and crown architecture are known to vary with some species-specific traits such as wood density, adult stature and shade tolerance, but also with some environmental factors such as competition and climate (Lopez-Serrano *et al.*, 2005; Poorter *et al.*, 2012). In the Pyrenees, as in many mountain ranges, aspect is one of the main sources of environmental variation. Solar photoperiod, evapotranspiration, hydrological regimes, forest productivity and species composition, among others, they all vary significantly with aspect (Verbyla & Fisher, 1989).

In our study we sampled 120 adult trees of each species growing at contrasting aspects. Our results showed that *P. uncinata* tended to develop narrower crowns than *P. sylvestris* for a given diameter, matching the results obtained by Poorter et al. (2012) from data of the Spanish Forest Inventory. Both pine species had longer and wider crowns in north-oriented slopes (Figure 3.3). This may reflect a strategy to optimize light interception (Purves *et al.*, 2007), but differences in soil quality and water availability may also be the underlying causes. Recently, Poorter et al. (2012) and Lines et al. (2012) found that trees had shorter stems and shallower crowns in areas with longer drought periods, so this factor may be the main cause at the origin of between-aspect differences in crown architecture. We also found that the most shade-tolerant species (*A. alba*) was the tallest species and produced the longest and widest crown for a given diameter (Figure 3.3). Interestingly, *A. alba* was the less responsive species, in terms of crown architecture, to environmental changes (Figure 3.3). These results suggest a relative low architectural plasticity of *A. alba* trees, a pattern that was also observed in another study conducted with juvenile individuals (Figure 4.7). In fact, juveniles of both pine species had higher apical growth than *A. alba* but presented narrower and slenderer morphologies (Figure 4.4 and 4.5). This growth pattern has commonly been reported for shade-intolerant species, which would favour height growth at the expense of less developed crowns (Givnish, 1988).

In addition to crown allometry, we found crown openness (CO) to also vary with aspect for the three studied species (Figure 3.6; Table 3.3). Within-species values of CO have been suggested to vary regionally with precipitation and water availability (Astrup & Larson, 2006) Lefrançois et al. (2008) for example showed enhanced CO values in plants growing in drier conditions. However, the species-specific patterns of variation in CO that we observed (increase in CO at southern aspects for *P. uncinata* and *A. alba* but the opposite for *P. sylvestris*) cannot be completely explained by a decrease in the amount of foliage supported by trees in dry conditions. Our data suggest that the increase in CO that *P. uncinata* and *A. alba* experience in sun-exposed slopes is probably related to a higher degree of leaf clumping. This trend has been described for trees developing at high elevation areas and has been associated to an strategy to avoid photo-damage caused by excessive radiation (Germino & Smith, 1999; Valladares *et al.*, 2005). The lower crown porosity of *P. sylvestris* in southern aspects may be explained by the increasing branchiness that this species is known to present in areas with a high evaporative demand, the increase in hydraulic segmentation representing a strategy to avoid cavitation in the tree (Berninger *et al.*, 1995; DeLucia *et al.*, 2000). However, it should be mentioned that our study did not allow confirming these hypotheses and accordingly, further research would be required to disentangle the role of these different factors.

We were able to correctly predict in our study the values of light transmitted in the understory for different mixed-forests of the Eastern Pyrenees (Figure 3.8). We noted that the methodology used for the determination of crown outline sharply affected estimated values of crown openness and in turn the predictions of understory light availability, as suggested by Boivin et al. (2011). Nevertheless, we found that differences in crown size, allometry and transparency associated to aspect caused even more variation in light transmission through the canopy of mixed Pyrenean forests than the ones associated to the delimitation of the crown outline. Light predictions in the understory sharply improved when crown parameters (crown radius, height and openness) were allowed to vary depending on the aspect of the plots (Figure 3.7). Consequently, we conclude that intra-specific differences in crown allometry and openness should be explicitly considered when studying and modeling the ecological processes and dynamics of these mixed-conifer forests.

Considering the process of canopy closure that has occurred in the Pyrenees in the last decades (see **chapter 2**), between-species differences in performance under low light conditions are likely to affect the fate of montane-subalpine forests of the Pyrenees. **Chapter 4** was devoted to the study of the response of the three main species constituting these ecotones (i.e. *P. sylvestris, P. uncinata* and *A. alba*) to contrasted light conditions. For these species, light availability was found to explain the major part of their variability in growth and mortality. *Abies alba* (the most tolerant of the three species) had the highest radial and apical growth in conditions of deep shade. However, it rapidly reached an asymptotic growth value, so both pine outgrew fir as light availability increased above 15% (Figure 4.1). *A. alba* also showed the lowest annual mortality rate for any given light level, confirming that its shade tolerance was not only due to its high radial growth in light-limiting environments but also to an intrinsic ability to withstand low radial growth rates (Figure 4.2). In fact, this capacity is considered as the ultimate factor determining the shade-tolerance of forest species (Pacala *et al.*, 1994; Kobe & Coates, 1997; Vieilledent *et al.*, 2010).

Despite its low annual mortality rate at any given light conditions (Figure 4.3a), the inability of *A. alba* to grow rapidly when in full-light resulted in a higher accumulated mortality rate over the period necessary to become an adult. Even in open areas, it took more than 25 years for a fir to become an adult (dbh > 7.5 cm). Accordingly, its accumulated survival rate never exceeded 60% and was surpassed by pines for light levels above 50% (Figure 4.3b). This results may explain the traditional observed inability of fir to colonize open areas (Ruiz de la Torre, 2006; Aunós *et al.*, 2007).

Both mountain and Scots pines showed similar behavior regarding light availability, with a slightly higher mortality rate for *Pinus sylvestris* in deep shade conditions (Figure 4.3). In any case, the inability of pines to restrain height growth when facing shade conditions (‘shade-escaping’ strategy (Givnish, 1988; Messier *et al.*, 1999; Claveau *et al.*, 2002)) resulted in an increasing mortality risk in such conditions, probably due to the higher respiration and maintenance costs associated to taller plants.

We found A. *Alba* to be the species showing the lowest architectural plasticity in response to different light conditions. This result is in conflict with what has been reported for other *Abies* species (see for example Kohyama, 1980; Takahashi, 1996; Aussenac, 2002; Gratzer *et al.*, 2004) but agrees previous findings for silver fir (Robakowski *et al.*, 2003, 2004). Conversely, *P. sylvestris* was the species showing the highest morphological and architectural plasticity, indicating a potential high capacity of responding and adapting to changes in environmental conditions. Finally, *P. uncinata* was found to be rather unresponsive, which could be related to its morphological and physiological adaptations to the harsh environments where it lives.

7.3. The role of abiotic and biotic factors at fine-scale

Despite the importance of temperature and light as main constraints to the growth of juvenile trees in mountain areas, ecological niches are multidimensional, and other factors acting at finer spatial and temporal scales can also be determinant for species performance, particularly at the boundaries of their current elevational range, where plants are developing at the limits of their physiological tolerance (Walther *et al.*, 2002; Dullinger *et al.*, 2004; Lenoir *et al.*, 2009). The experimental plantations described in **Chapter 5** aimed at a better understanding of the role of these fine-scale factors in the performance of the species constituting the montane-subalpine ecotone.

Our results showed that short events of extreme climatic conditions had a strong impact on juvenile tree mortality, mainly affecting the species growing further from their mean elevational range. Moreover, we found that positive plant-plant interactions were markedly species-specific and varied with elevation. They were in particular present in the subalpine sites, modulating the effects of unfavorable climatic conditions for species growing above their current limits. In contrast, we did not detect any positive nor negative effect of shrubs on the plants established at the low-elevation sites, suggesting that, in such conditions, the net effect of above- and belowground interactions is neutral. In these sites, the herbaceous cover was found to negatively affect *A. alba* survival, probably due to competition for water. Finally our results show a positive effect of canopy closure on silver fir survival. This may reflect an indirect facilitative effect of tree cover on *A. alba* seedlings by limiting the development of herbaceous plants (Pagès *et al.*, 2003; Saccone *et al.*, 2009).

In summary, our study underlined that plant-plant interactions and other factors driving at finer temporal and spatial scales can have a strong impact in the dynamics of montane-subalpine forests of the Pyrenees. These processes acting at microsite level should thus be explicitly considered when implementing management plans to contend the future impacts of climate change in these areas.

7.4. Future dynamics of the montane-subalpine ecotone

In **Chapter 6** we use all the information gathered on the three studied species in previous chapters to calibrate the individual-based, spatially explicit model of forest dynamics SORTIE-ND. This model is especially suited to simulate fine-scale spatial processes and mixed-forests dynamics and was used to assess the relative importance of climatic-induced changes in juvenile growth and initial composition in the future dynamics of the conifer montane-subalpine ecotone in the Pyrenees.

We chose the two most common ecotonal forests in the area as case studies: (i) pine-mixed forest (*P. uncinata* and *P. sylvestris*) and (ii) pine-fir mixed forest (*P. uncinata* and *A. alba*). The model was able to correctly predict the structure, species composition and dynamics of these mixed forests. The results of the simulations along 200 years showed that, for ecologically similar species (i.e. *P. sylvestris* and *P. uncinata*) slight differences in initial composition and juvenile growth rate can lead to significant differences in the future composition of the mature stand. In these forests, a potential increase of the growth rate of *P. sylvestris* due to climate change may induce a relative rapid upward displacement of *P. sylvestris* into forests currently dominated by *P. uncinata.*

In the case of the *P. uncinata – A. alba* forest, the low growth of the latter when growing in shade along with its capacity to remain suppressed in the understory for years without incurring higher mortality risk emerges as the main factor determining the future dynamics of these systems. The results of the simulations performed with SORTIE-ND showed that potential positive or negative climatic-induced variations in the growth rate of *A. alba* saplings had little or nil effect on the final composition of the stand. For all the tested scenarios, the model predicted a substitution of pine by the more shade-tolerant *A. alba*, a process that has already been reported in some areas of the Pyrenees (Aunós *et al.*, 2007; Oliva & Colinas, 2007). The model also predicted a relative decrease of the productivity of these stands in the future associated to the sensitivity of fir to the expected decreases in precipitation (Rolland *et al.*, 1999; Macias *et al.*, 2006). This issue is expected to be more important than juvenile performance in driving the dynamics of these mixed forests.

To sum up, we showed that SORTIE-ND was adequate to simulate the dynamics of Pyrenean mixed forests and to correctly estimate growth, productivity, structure and species composition for the two most common mixed forests in the area. Furthermore, the identification of the main bottlenecks in forest dynamics under global change will help to identify the future research needs and to improve our understanding of these systems and our ability to correctly simulate their fate under changing scenarios.

7.5. Perspectives and future research needs

In this doctoral thesis, we conducted works at different spatial scales that allowed us to identify the various factors that influence the dynamics of montane-subalpine forests. We have found land-use changes, climate, light availability, physiography and competitive and facilitative plant-plant interactions to be important actors in the fate of these forests. One of the main challenges when facing the study of forest dynamics is to integrate all this information in order to extract valuable insights for forest planning. Models can help to face and handle this complexity of scales, and the model of stand dynamics we used has proved to be adequate to infer the evolution of these forests in a global change context.

Nevertheless, there is always room for an improvement in predictions. In fact, the model itself is a helpful tool to identify the processes that deserve further interest from the scientific community. For example, the results of the model showed the importance of juvenile performance and recruitment ability in the future dynamics of forest systems. However the effects of the different components of change on these processes are far of being well understood. Moreover, even though our study area is currently not drought-limited, future climate change predictions forecast significant increases in the length and intensity of drought periods (IPCC, 2007). In this study we showed that this kind of short events of extreme climatic conditions can severely affect the dynamics of mountain forests. However this is still a relatively few explored issue that may undoubtedly require further attention from foresters and ecologists. Finally, a part of the research we have developed in this doctoral thesis has helped to identify the important role of factors acting at a microsite level (e.g. plant—plant interactions), on the dynamics of mountain ecosystems. The integration of these processes into the modeling procedure may also be a promising way to improve predictions of the evolution of these forests under changing climate.

However, it is important to note that in a modeling context *more* does not always mean *better*. In the last years it has become increasingly evident that higher complexity does not always lead to higher accuracy (Astrup *et al.*, 2008; Kimmins *et al.*, 2008). The inclusion of too much detail sometimes obscures understanding of the simulations and increases sensitivity and error propagation (Deutschman *et al.*, 1997) and thus careful assessment of the benefits of including more detailed processes should be previously made. Furthermore, adequately answering certain global questions sometimes requires working at larger spatial and temporal scales than stand-level, as observed in this own work. During the last years, considerable efforts have been made to simplify stand-level forest dynamics such as SORTIE-ND and to scale from the individual level to the forest-stand level in order to reduce parameterization and computational needs (Purves *et al.*, 2007, 2008; Purves & Pacala, 2008).

Although integration of models working at different spatial and temporal scales has long been one of the major goals in the field of forest modeling forest, experience shows that this integration is not easily implemented, and scaling issues must be considered (Deutschman *et al.*, 1997; Bugmann *et al.*, 2000). Therefore, further work should be done in identifying the appropriate spatial and temporal scale that is needed to adequately address different ecological and management issues.

7.6. References

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Concluding remarks

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8. Concluding remarks

1. *Pinus uncinata* increased its surface coverage by around 8,900 ha (more than 16%) in the last fifty years in the Catalan Pyrenees. During the same period, *P. uncinata* forests almost doubled their mean canopy cover. The patterns of encroachment and densification did not occur homogeneously in the space. Land-use changes, mainly farmland abandonment and reduction in livestock pressure, emerge as the main drivers of forest expansion and densification in the Pyrenees.

2. One of the main consequences of these socioeconomic changes that occurred in the Pyrenees during the last decades (in particular the decreasing use of fuelwood and timber) is the progressive increase in canopy cover of the existing forests. This process is expected to favour the development of more shade-tolerant, late-successional species.

3. In mountain areas, topographic factors such as slope aspect markedly affect the crown allometry and transparency of *P. uncinata*, *Pinus sylvestris* and *Abies alba* trees, modulating in turn the transmission of light through the forest canopy and the patterns of light availability in the understory.

4. Light availability explains the major part of the variability in growth and mortality for *P. uncinata, P. sylvestris* and *A. alba* at the montane-subalpine ecotone.

5. *A. alba* shows a conservative growth strategy and is able to reduce height growth in the shade increasing their survival chances. Pines, on the other hand, favour height growth in shade (*shade-escaping strategy*) but at the expense of higher mortality risks.

6. *P. sylvestris* presents a higher morphological plasticity to different growing conditions than *P. uncinata*. This could imply higher adaptive potential of Scots pine to the predicted changing environment.

7. Short periods of extreme climate can have a strong impact on seedling mortality of Pyrenean species growing above or below its current elevational range. Positive plant—plant interactions, i.e. facilitative processes, can mediate the effects of these unfavorable climatic periods and help montane species such as *P. sylvestris* to migrate upwards tracking predicted temperature increases.

8. In the montane areas, the canopy cover induces an indirect facilitative effect on *A. alba* seedlings by limiting the development of competitive herbaceous neighbors. This processes acting at microsite level are expected to gain in importance in the future context of increasing intensity and length of drought periods.

9. SORTIE-ND, an individual-based, spatially explicit model of forest dynamics proved to be a valuable tool to simulate the fate of mixed forests at the montane-subalpine ecotone of the Pyrenees under a global change context.

10. The model simulations showed that for ecologically similar species (e.g. Scots pine and mountain pine), slight differences in the response of sapling growth to climate can lead to significant changes in the future species composition of these mixed-stands.

11. In the absence of large-scale disturbances or active management, the future dynamics of the Pyrenean mixed-forests composed by species belonging to different successional stages seems to be rather irresponsive to potential climate-induced changes in sapling growth. In these stands, shade-tolerance emerges as more decisive than predicted temperature increases in driving the future composition of these forests in the short- and mid-term.