Universitat de Lleida

Tree-species diversification in Sub-Mediterranean pine forests: drivers, consequences and management options

Santiago Martín Alcón

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Departament de Producció Vegetal i Ciència Forestal

Doctorat en Gestió Multifuncional de Superficies Forestals

Tree-species diversification in Sub-Mediterranean pine forests: drivers, consequences and management options

Diversificación de especies arbóreas en pinares Submediterráneos: agentes causales, consecuencias y opciones silvícolas

TESIS DOCTORAL

Autor: Santiago Martín Alcón

Director: Lluís Coll Mir

Tutor: Álvaro Aunós Gómez

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Tesi presentada per **Santiago Martín Alcón** per a optar al grau de Doctor per la Universitat de Lleida.

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Abstract

The sub-Mediterranean pinewoods in the eastern Pre-Pyrenees have undergone a long history of human alteration by means of a wide variety of human uses, which have led to a simplification of both their structural and compositional attributes. The recent land-use changes in the region have given place to generalized processes of forest densification and to the progressive development of the understory layer dominated by shrub and tree species previously less abundant or absent. These pinewoods, mostly dominated by black pine (*Pinus nigra* ssp. *salzmannii*) and Scots pine (*Pinus sylvestris*), develop in the bioclimatic transition between the genuinely Mediterranean territories and the temperate and alpine areas of the Pyrenees. Due to their transitional nature these areas are particularly threatened by climate change and thus the implementation of forest management practices aimed at enhancing their resilience and adaptive capacity to changing climate are more and more considered for their future persistence.

This doctoral thesis includes four studies aimed to deepen the knowledge on the main factors that drive the current natural dynamics of tree-species diversification in the Sub-Mediterranean pinewoods and the consequences of such processes with regards to their responses to forest fires. Ultimately, the doctoral thesis aimed to advance in the understanding of the main variables modulating the success of assisted migration practices to enhance or promote tree-species diversification and stand resilience.

Our results confirm that sub-Mediterranean pinewoods are currently undergoing a progressive and generalized process of spontaneous diversification by broadleaved tree species (especially evergreen and marcescent oaks). The establishment of *Quercus* seedlings under the pine canopy was favored by the current levels of both canopy closure and shrub cover. However, these conditions hamper pine recruitment and the established oaks (particularly *Q. ilex*) to reach more advanced developmental stages. We also show that the occurrence of large stand-replacing fires triggers important vegetation changes from pinewoods to other types of woody vegetation (shrublands or forests dominated by resprouting tree species). Transitions to grassland communities, in contrast, are rare and only occur at very specific site conditions (mountain ridges, hilltops and rocky sites, etc). At landscape level, the nature of these changes does not only depend on fire severity and topographic variables, but also on fire legacies (presence of unburned patches) and the characteristics of the pre-fire vegetation (e.g. land use history and tree canopy cover).

Finally, the results of this thesis support the feasibility of management interventions based on planting or sowing late-successional species for diversifying sub-Mediterranean pine forests when the process does not occur naturally. In this regard, our results advise assisted migration programs to manage risks by thoroughly considering species and provenances selection, thermal migration distances and the occurrence of extreme cold events in the planting site. We also show that negative responses associated to these events could be partially buffered by sowing and planting under relatively closed canopy.

Resumen

Los pinares Submediterráneos de los Pirineos orientales han experimentado una larga historia de alteración humana a través de una amplia variedad de usos antrópicos, los cuales han dado como resultado la simplificación de sus características estructurales y florísticas. El reciente cambio de usos acontecido en la región ha dado lugar a procesos generalizados de densificación de las masas forestales y al progresivo desarrollo del sotobosque dominado por especies arbustivas y arbóreas anteriormente menos abundantes o ausentes. Estos pinares, principalmente dominados por el pino laricio (*Pinus nigra* ssp. *salzmannii*) y el pino silvestre (*Pinus sylvestris*), se desarrollan en la transición bioclimática entre los territorios genuinamente Mediterráneos y las áreas templadas y alpinas de los Pirineos. Debido a su naturaleza de transición estos sistemas se encuentran particularmente amenazados por el cambio climático, y por ello la implementación de prácticas de gestión forestal dirigidas a mejorar su resiliencia y capacidad adaptativa frente a perturbaciones y al cambio climático son cada vez más tenidas en cuenta de cara a su futura persistencia.

La presente tesis doctoral incluye cuatro estudios dirigidos a profundizar en el conocimiento de los principales factores causales de la actual dinámica natural de diversificación de especies arbóreas en los pinares Submediterráneos y las consecuencias de estos procesos en relación a la su respuesta frente a los incendios forestales. Asimismo, la tesis pretende incrementar el conocimiento acerca de las principales variables que condicionan el éxito de prácticas de migración asistida para mejorar o fomentar la diversificación de especies arbóreas y la resiliencia de estos pinares.

Los resultados de esta tesis confirman que los pinares Submediterráneos están actualmente experimentando un progresivo y generalizado proceso de diversificación espontánea por especies frondosas (especialmente robles perennes y marcescentes). En nuestros estudios encontramos que los niveles actuales de espesura de las cubiertas arbórea y arbustiva favorecen el establecimiento de quercíneas bajo el dosel arbóreo. Sin embargo, estas condiciones dificultan la regeneración del pino así como el crecimiento de los robles hacia estadios más avanzados de desarrollo. También se muestra que la ocurrencia de grandes incendios forestales desencadena importantes cambios de vegetación desde pinares hacia otras comunidades leñosas (matorrales o bosques dominados por especies arbóreas rebrotadoras). Las transiciones hacia comunidades herbáceas, por contra, son raras y solo ocurren en condiciones estacionales muy específicas (crestas y cimas de montañas, sitios rocosos, etc.). A escala de paisaje, la naturaleza de estos cambios no solo depende de la severidad del fuego y factores topográficos, también de ciertas consecuencias del incendio (la presencia de islas no quemadas) y las características de la vegetación existente con anterioridad al incendio (e. g. la historia de usos y la cobertura arbórea).

Finalmente, los resultados de esta tesis sustentan la viabilidad de intervenciones de gestión consistentes en plantaciones o siembras de especies arbóreas para la diversificación de los pinares Submediterráneos cuando el proceso no ocurre naturalmente. En relación a esto, nuestros resultados aconsejan que los programas de migración asistida gestionen los riesgos considerando de manera rigurosa la selección de especies y procedencias, las distancias térmicas de migración y la ocurrencia de eventos de frío extremo, y muestran que las respuestas negativas asociadas a estos eventos podrían ser parcialmente mitigadas plantando o sembrando bajo condiciones de dosel relativamente cerrado.

Resum

Les pinedes Submediterrànies dels Pirineus orientals han experimentat una llarga historia d'alteració humana a través d'una àmplia varietat d'usos antròpics, els quals han donat com a resultat la simplificació de les seves característiques estructurals i florístiques. El recent canvi d'usos esdevingut a la regió ha donat lloc a processos generalitzats de densificació de les masses forestals i al progressiu desenvolupament del sotabosc dominat per espècies arbustives i arbòries anteriorment menys abundants o absents. Aquestes pinedes, principalment dominades per la pinassa (*Pinus nigra* ssp. *salzmannii*) i el pi roig (*Pinus sylvestris*), es desenvolupen en la transició bioclimàtica entre els territoris genuïnament Mediterranis i les àrees temperades i alpines dels Pirineus. A causa de la seva natura de transició aquests sistemes es troben particularment amenaçats pel canvi climàtic, i per això la implementació de pràctiques de gestió forestal dirigides a millorar la seva resiliència i capacitat adaptativa enfront de pertorbacions i al canvi climàtic són cada vegada més tingudes en compte de cara a la seva futura persistència.

La present tesi doctoral inclou quatre estudis dirigits a aprofundir en el coneixement dels principals factors causals de l'actual dinàmica natural de diversificació d'espècies arbòries en les pinedes Submediterrànies i les conseqüències d'aquests processos en relació a la la seva resposta enfront dels incendis forestals. Així mateix, la tesi pretén incrementar el coneixement sobre les principals variables que condicionen l'èxit de pràctiques de migració assistida per millorar o fomentar la diversificació d'espècies arbòries i la resiliència d'aquestes pinedes.

Els resultats d'aquesta tesi confirmen que les pinedes Submediterrànies estan actualment experimentant un progressiu i generalitzat procés de diversificació espontània per espècies frondoses (especialment roures perennes i marcescents). En els nostres estudis trobem que els nivells actuals d'espessor de les cobertes arbòria i arbustiva afavoreixen l'establiment de quercines sota el dosser arbori. No obstant això, aquestes condicions dificulten la regeneració del pi així com el creixement dels roures cap a estadis més avançats de desenvolupament. També es mostra que l'ocurrència de grans incendis forestals desencadena importants canvis de vegetació des de pinedes cap a altres comunitats llenyoses (matolls o boscos dominats per espècies arbòries rebrotadores). Les transicions cap a comunitats herbàcies, per contra, són rares i solament ocorren en condicions estacionals molt específiques (crestes i cims de muntanyes, llocs rocosos, etc). A escala de paisatge, la natura d'aquests canvis no solament depèn de la severitat del foc i factors topogràfics, també de certes conseqüències del incendi (la presència d'illes no cremades) i les característiques de la vegetació existent amb anterioritat al 'incendi (e. g. la història d'usos i la cobertura arbòria).

Finalment, els resultats d'aquesta tesi sustenten la viabilitat d'intervencions de gestió consistents en plantacions o sembres d'espècies arbòries per a la diversificació de les pinedes Submediterrànies quan el procés no ocorre naturalment. En relació a això, els nostres resultats aconsellen que els programes de migració assistida gestionin els riscos considerant de manera rigorosa la selecció d'espècies i procedències, les distàncies tèrmiques de migració i l'ocurrència d'esdeveniments de fred extrem, i mostren que les respostes negatives associades a aquests esdeveniments podrien ser parcialment mitigades plantant o sembrant sota condicions de dosser relativament tancat.

1

Introduction

1. Introduction

1.1. Long-term human alteration on the Iberian Mediterranean forests

The European Mediterranean forests have undergone a long history of human alteration by means of a wide variety of human uses, which have affected their structure, composition and dynamics from the beginning of the Neolithic period (Barbero et al. 1990; Williams 2000). Actually, the northern Mediterranean basin is one of the clearest examples in the world of a long-term human-modified landscape (Bengtsson et al. 2000; Blondel 2006; Carrión et al. 2001; Nilsson 1997). Impacts of human societies have already lasted for so long that practically no pristine forests (i.e. unaltered by human) are left in the region (Blondel and Médail 2009; Kaplan et al. 2009; Nilsson 1997; Valladares 2004). The disturbances varied in frequency and intensity throughout ages, but forest degradation was the most noticeable consequence of such long-term relation, as demonstrated by many paleobotanical, archaeological, and historical records (e. g., Debussche et al. 1999; Gil-Romera et al. 2009; Kaplan et al. 2009; Navarro and Pereira 2012; Thirgood 1981). The hunting of megaherbivores and predators, the grazing of domestic herbivores, the burning and clearing of forests for agriculture, firewood and industrial purposes, are examples of such human impacts. All together, they have created a vast array of cultural landscapes and agroecosystems reflecting the historical and cultural diversity of the region.

One of the main heritages of these long-term linkages has been the current dominance of strongly modified forests (Bengtsson et al. 2000; Vallejo et al. 2012a) with altered disturbances dynamics (Pausas et al. 2008). Humans have also actively impacted forest species distributions by deliberately introducing and harvesting selected species and genotypes, but also indirectly through forestry practices that have favored certain species (Urbieta et al. 2008). Palynological studies show that forest composition in the Mediterranean region has changed dramatically over the last few millennia. For instance, it has been observed a partial replacement of deciduous taxa by sclerophyllous broadleaves and *Pinus* species associated to historical repeated burning and overgrazing practices (Carrión et al. 2003). There is a general consensus that the intensive history of human-use during the last centuries (by overgrazing, wood harvesting, coppicing to produce firewood and charcoal, etc) has led to a simplification of both the structural and compositional attributes of Mediterranean forests (Nocentini and Coll 2013).

In the context of the Iberian Peninsula, this long history of intense human-use reached its peak during the end of the 19th and first half or the 20th century (Garcia-Ruiz et al. 1996). However, the second half of the 20th century brought major socioeconomic changes leading to generalized land abandonment processes in marginal areas −generally mountainous systems− and to land-use intensification in broad valleys and coastal regions (Chauchard et al. 2007; Garcia-Ruiz et al. 1996; Lasanta-Martinez et al. 2005; Vicente-Serrano et al. 2004). This, together with the development of the forest and agricultural sciences and the extensive implementation of reforestation programs, triggered extended encroachment and densification processes in forest stands (Améztegui et al. 2010; Navarro and Pereira 2012; Stellmes et al. 2013).

As a result of this process of forest encroachment, the forested area (i.e. forest area presenting tree canopy cover higher than 5%) in Spain has increased at an annual rate of 2.19% between 1990 and 2010, which is much higher than the average one in the European Union (0.51%) (European Commission 2011). Actually, Spain is the third European country in forested area, with a total of 18.2 million ha of forests, from which about one third corresponds to pure pine stands (MARM 2011). In parallel, the standing wood volume in Spain has increased in 62.6% during the period between 1990 and 2010, which also represents a much higher increase than the average in the UE-27 (24.4%). However, both the forested area and standing wood volume still have ample room for further growth since, on the one hand, Spain has more than 9 million ha of non-wooded forest land and, on the other hand, the average standing wood volume in forested areas is still very low (34.8 m^3/ha) (European Commission 2011).

The noticeable decrease of human pressure on the Iberian Mediterranean forests, and especially the dramatic decrease of forest grazing, has also triggered a remarkable reduction of the pressure on the forest understory and an increase of tree recruitment either by new cohorts of the dominant species or by new species (in most cases late-successional ones) (Carnicer et al. 2014; Urbieta et al. 2011; Vayreda et al. 2013). This has led to a gradual reduction of the area occupied by many semi-natural mono-stratified forest habitats in Mediterranean mountains, which were previously maintained by traditional practices (Chauchard et al. 2007; Debussche et al. 2001). A generalized growth of the shrub layer of these forests has also been reported (Moreira et al. 2011). Such shrub layer can compete for soil and light resources with the tree-species regeneration (Royo and Carson 2006), but in some particular conditions (e.g. in areas with high browsing pressure) it can facilitate the establishment of the regeneration (Brooker et al. 2008).

1.2. The case of Sub-Mediterranean pinewoods in the eastern Pre-Pyrenees

1.2.1. Sub-Mediterranean climate and forests

In the Iberian Peninsula, the transition zone between the genuinely Mediterranean and the temperate Eurosiberian regions forms a band where both regions become diluted and mix (Sánchez de Dios et al. 2009). Such areas are generally termed Sub-Mediterranean. There is no complete agreement on the boundaries of the Sub-Mediterranean territories, although there are some concordant definitions of their environmental characteristics. For instance, Rivas-Martínez et al. (2011) defined Sub-Mediterranean climate as a variant of the temperate climate, but in which monthly precipitation (in mm) of at least one month in summer is lower than 2.8 x T (average monthly temperature, in ºC). In general, areas with this climate are characterized by summer (and total) rainfall and mean temperature values between those found in the Mediterranean and temperate regions. However, they have the original feature of suffering cold winters (Sánchez de Dios et al. 2009). In the eastern Iberian Peninsula, these conditions are mostly found in the montane belt of the Pre-Pyrenees and the Iberian Mountain Range (Rivas-Martínez et al. 2011). Due to their transitional nature, Sub-Mediterranean forests are especially vulnerable to climate change (Lindner et al. 2010; Petit et al. 2005).

In general, forest communities distributing in the Sub-Mediterranean region are, in their mature stages, dominated by marcescent hardwoods (sometimes in mixture with sclerophyllous species) and some types of xerophytic coniferous forests. In the context of the Iberian Peninsula, these forests are commonly composed with marcescent oak species and/or black pine (*Pinus nigra* Arn. ssp. *salzmannii*) as well as with all their possible mixtures with sclerophyllous oak species and/or other xerophytic pines, including Scots pine (*P. sylvestris* L.). These communities occupy around 20% of all the Iberian forested land (Sánchez de Dios et al. 2009).

1.2.2. Sub-Mediterranean forests in the Pre-Pyrenees

The Pyrenees extends 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 temperate 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. Finally, the eastern area has a stronger Mediterranean influence particularly at lower elevations, where many valleys evidence different degrees of summer drought. The external ranges of the Spanish side of the Pyrenees are known as the Pre-Pyrenees.

As in every mountain system, the Pyrenees and the Pre-Pyrenees present climatic gradients associated to the abrupt terrain involving marked altitudinal zonation of the vegetation. In the central and eastern sectors of the Pre-Pyrenees, this altitudinal zonation clearly corresponds to the transition between the genuinely Mediterranean territories, and the temperate and alpine bioclimates that dominate the axial Pyrenees and inner ranges. According to Ninot et al. (2007), this transitional band corresponds to the Sub-Mediterranean floristic territory and it coincides mostly with the dominance of forests of marcescent oaks (*Quercus pubescens* Willd., *Q. faginea* Lam. and hybrids) and/or related pinewoods (of black and Scots pines). Its upper limit runs at 1100-1300 (1500) m above sea level (a.s.l.), depending on areas and exposures. In the lower part of this band, the landscape is usually formed by the typical Mediterranean mosaic-like landscape, with cultivated lands and scrublands interspersed with forest areas. However, as elevation increases forests become the most abundant land cover (Burriel et al. 2004). There is a great proportion of coniferous forests in the Pyrenean Sub-Mediterranean belt. They are mostly dominated by black pine, but frequently it also appears in mixed stands with Scots pine, which becomes the dominant species as elevation increases and climatic conditions match to the temperate and alpine bioclimates. These black pine-dominated pinewoods in the Pyrenean Sub-Mediterranean belt are the object of study of the present work.

1.2.3. Main species and characteristics

The dominant pines

European black pine (*P. nigra*) is widely distributed across the Mediterranean basin. The subspecies *P. nigra* Arn. ssp. *salzmannii* covers about half a million ha of mostly pure stands in eastern Spain and southern France. In the eastern calcareous mountains of Spain, the black pine dominates mid-altitude forests, where it has been traditionally favored over broadleaved tree species (different species of the genus *Quercus, Sorbus, Acer, Prunus*, etc), but especially over the marcescent oaks. In the northeastern part of Spain, and particularly in the Pre-Pyrenees, black pine grows mainly on relatively warm north-facing slopes, where it occupies around 140,000 ha (Figure 1). On the other hand, Scots pine is the most widely distributed conifer in the world, spreading through more than 14,000 km and covering around 30º in latitude and 130º in longitude between Europe and Asia. 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 heliophilous character has also contributed to the wide spread of this species, enabling it to outcompete other species and to colonize cleared lands to form second-growth forests (Cañellas et al. 2000). In the Pyrenees, Scots pine is the most common tree species and dominates the upper-montane belt (Figure 1). Black and Scots pine differ in their habitat preferences and thus have different geographical distribution patterns at the broad scale, but there is a significant overlap in their Sub-Mediterranean distribution area, with an important degree of coexistence at the local scale. It is estimated that around 20,000 ha of *P. nigra* - *P. sylvestris* mixed stands exist only in the Catalan Pre-Pyrenees (Vigo et al. 2006).

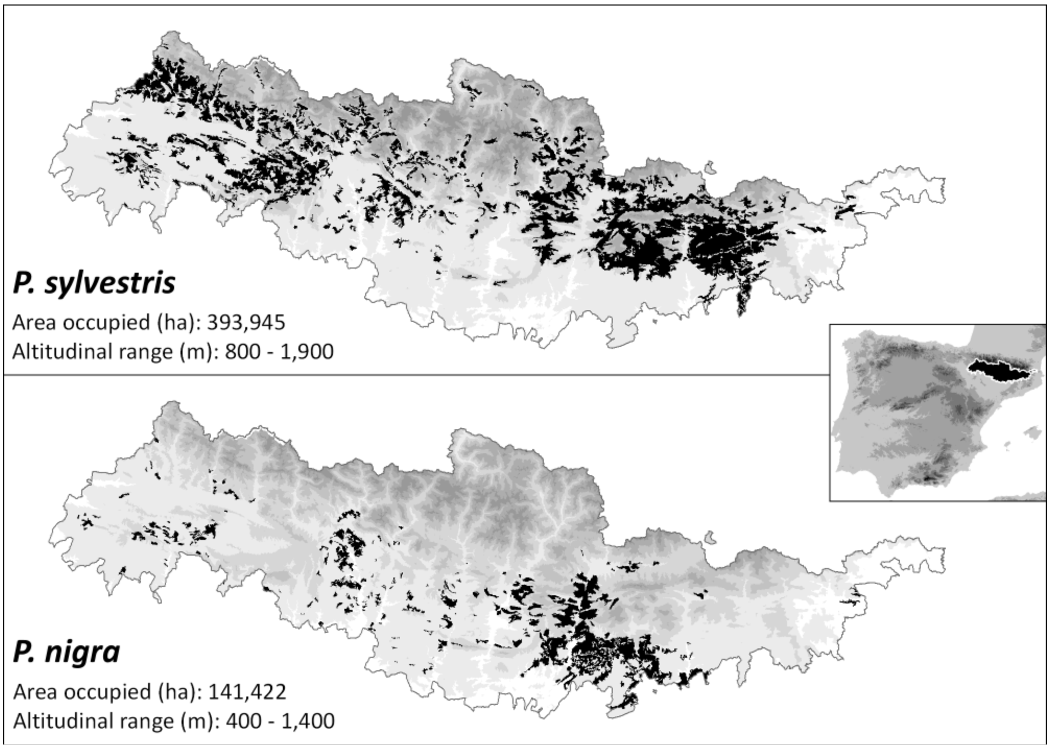

Figure 1: Distribution area of the forests dominated by Scots and black pines in the southern side of the Eastern Pyrenees, according to the 1:50,000 Spanish Forest Map (DGCN 2001).

In the Pre-Pyrenees, black pine forests are mostly located in private land. However, the proportion of public forests with pine species becomes greater as elevation increases, matching with the increasing importance of Scots pine in the stands. These pinewoods are in general more abundant on north-facing slopes, in part due to the more intensive and recent human use of south-facing slopes for grazing and agriculture. Due to the good quality of their wood, both species have traditionally been managed for production purposes (Ruiz de la Torre 2006). For even-aged stands (more common in public forests), uniform shelterwood regeneration cuts have mostly been applied, using rotation lengths of 100-120 years and regeneration periods of 20-30 years (Aunós et al. 2009; Bravo and Diaz-Balteiro 2004). For uneven-aged stands, the traditional management was based on periodic cuttings in which the most vigorous and well-shaped trees were extracted (with rotation period of around 15-20 years). These practices (a regressive way of individual-tree selection cuttings) allowed forest owners to get steady incomes from their small forest surfaces (as those common in private lands), but sometimes at the expenses of their long-term stability and vigor (Aunós et al. 2009; Trasobares and Pukkala 2004). In addition, these forests were usually grazed by domestic animals, which helped to control the development of the understory.

As described in the previous sections, a significant decrease of human pressure occurred during the last decades on these pinewoods (and particularly the strong decrease of silvicultural interventions and livestock grazing) allowing the establishment of new cohorts of the dominant pine species and causing a generalized densification of the stands and a progressive process of understory colonization by shrubs and late-successional tree species, mainly *Quercus* species (Carnicer et al. 2014; Urbieta et al. 2011; Vayreda et al. 2013). The analysis of the recent evolution of the overstory and understory structure and composition of the Pre-Pyrenean Sub-Mediterranean pinewoods confirms that these processes of densification and species diversification are still active (Table 1).

Table 1. Evolution of some key forest variables describing the overstory and understory structure and composition of the Pre-Pyrenean Sub-Mediterranean pinewoods (n = 527)[1], in the period between the 2nd and 3rd Spanish National Forest Inventories. Descriptive statistics are mean and standard deviation (in brackets).

Variable (units)	2nd SNFI (1990-1994)	3rd SNFI (2000-2004)
Tree layer		
Basal area (m^2/ha)	16.63 (7.86)	21.72 (8.33)
Tree density (stems/ha)	982.8 (558.6)	1089.6 (544.8)
Mean *dbh* (cm)	14.62 (3.5)	15.81 (3.59)
Basal area of oaks[2] (% of total)	2.39 (4.69)	3.25 (5.67)
Tree species regeneration		
Density of pine[3] saplings (stems/ha)	722.6 (822.5)	553.4 (691.3)
Density of oak[2] saplings (stems/ha)	177.3 (440.4)	186.2 (420.7)
Shrub layer		
Shurb cover (% of plot area)	34.6 (25.4)	43.7 (27.7)

The main late-successional hardwoods

The evergreen holm oak (*Q. ilex* L.) together with the marcescents gall oak (*Q. faginea* Lam.), pubescent oak (*Q. pubescens* Willd.) and their hybridization (also known as *Q. cerrioides* Wilk. & Costa) are the main broadleaved tree species sharing ecological requirements with black

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[1] SNFI re-measured plots in the Pyrenean provinces presenting tree canopy cover > 10%, in which the percentage of basal area corresponding to black pine was ≥ 80%; or ≥ 40% when the sum of the percentage of basal area corresponding to black pine and Scots pine was ≥ 80%.

[2] Black or Scots pine saplings

[3] Saplings of all *Quercus* tree species.

pine and Scots pine in the Sub-Mediterranean area (Figure 2). Other species of the genus *Sorbus*, *Acer*, *Prunus*, etc. are also present in these forests, but usually appear in a much more scattered way. *Q. ilex* is an evergreen, sclerophyllous and drought-adapted tree growing from cold, semiarid to temperate, humid bioclimates, but generally under climatic conditions marked by dry and hot summers. *Q. faginea* is a semi-deciduous (marcescent) species that is common in mesic Sub-Mediterranean or continental Mediterranean (not very extreme) locations. *Q. pubescens* is another Sub-Mediterranean marcescent broadleaved tree. It is less represented in sites with lower water availability (e.g., shallow soils, south-facing slopes) and tends to disappear in the drier part of the meso-Mediterranean climatic zone. Finally, *Q. cerrioides* presents intermediate characteristics between *Q. faginea* and *Q. pubescens.* These *Quercus* species are widely distributed in the western Mediterranean basin, growing on calcareous soils (Ruiz de la Torre 2006). All of them are considered as intolerant or intermediate shade -tolerant species and require certain shading during their establishment phase, especially when growing under stressing climatic conditions (Broncano et al. 1998; Caldeira et al. 2014; Gómez-Aparicio et al. 2008; Lookingbill and Zavala 2000; Quero et al. 2006; Retana et al. 1999). All these oaks are resprouting species (Pausas 1999; Pausas 2001). Although they exhibit different preferences in their habitat and thus different geographical distribution patterns at the regional scale, there is a significant overlap in their Sub-Mediterranean distribution areas, with an important degree of coexistence at the local scale (Figure 2).

According to the climatic characteristics of their current distribution areas, these species may be ordered regarding drought tolerance as *Q. ilex* > *Q. faginea* > *Q. cerrioides* > *Q. pubescens* (Figure 2). In relation to their thermal preferences, the same order may be deduced from the mean temperatures and elevation of the sites in which they grow, with *Q. ilex* being the one able to grow in warmer sites, and *Q. pubescens* in colder sites. However, the great overlap in their environmental requirements suggests that all of them could coexist in most of the Sub-Mediterranean areas dominated by *P.nigra* and *P. sylvestris*. The presence of these oaks in the current Sub-Mediterranean forest is much lower than in certain periods of the past (Carrión et al. 2010; Carrión et al. 2003; Gil-Romera et al. 2010). This is explained in part by the long-term history of human alteration suffered by these forests, that often favored pine species and sclerophyllous oaks (the later in some locations) against marcescent and deciduous hardwoods (Nocentini and Coll 2013; Urbieta et al. 2008).

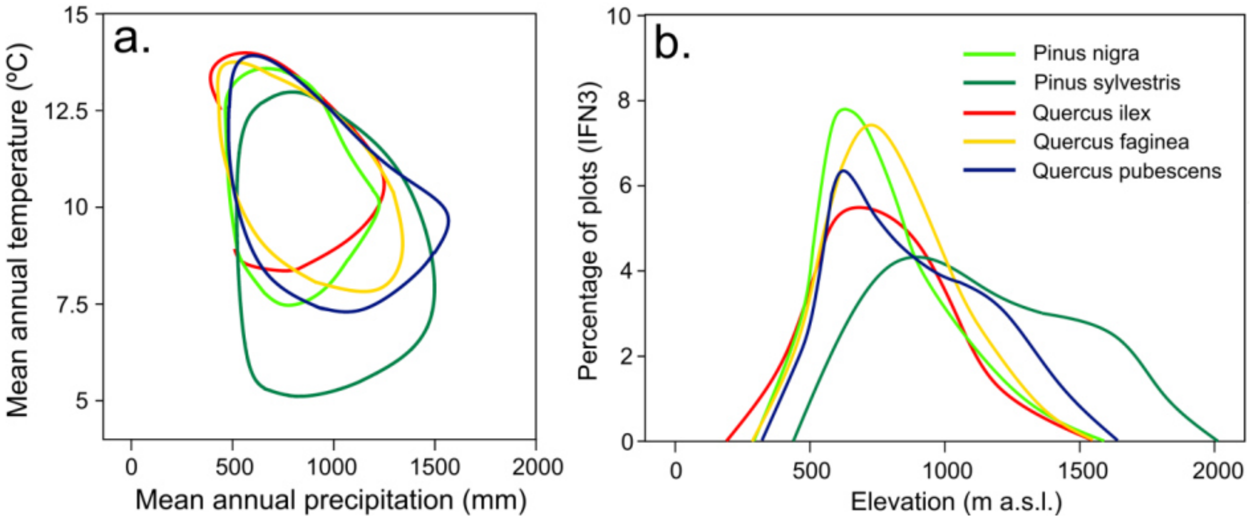

Figure 2: Temperature and precipitation requirements (a) and histogram of the altitudinal distribution (b) of *Pinus nigra* (light green), *P. sylvestris* (dark green), *Quercus ilex* (red), *Q. faginea* (yellow), and *Q. pubescens* (blue) based on their presence according to the 3rd Spanish National Forest Inventory (DGCN 2007) in the Pyrenean provinces. Climatic data was extracted from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola et al. 2005).

1.3. Main risks associated to Sub-Mediterranean pinewoods

1.3.1. Global warming

The European Mediterranean region is expected to be one of the most threatened regions in the world with regards to the different components of global change (Giorgi and Lionello 2008; IPCC 2007; Lindner et al. 2010). Climate change models predict increased aridity and higher temperatures across large areas of Europe in coming decades, the impact of which is expected to be particularly important in the Mediterranean region and mountain areas, as they are transitional climatic regions (Giorgi and Lionello 2008; Lavorel et al. 1998). Increasing atmospheric concentrations of greenhouse gases will also exacerbate the intensity and frequency of extreme weather events such as intense droughts and heat waves in these areas (Lindner et al. 2010; Resco de Dios et al. 2006).

The current context of changing climate is predicted to lead to major changes in Mediterranean forests structure and composition (Benito Garzón et al. 2011; Lindner et al. 2010). It is worth mentioning that the Mediterranean presents a large area of mountain forests with species distributing at the southernmost limit of their range. The Mediterranean does also hold a large number of endemic species as well as species whose gene pools differ from those of their European counterparts (Benito-Garzón et al. 2008). Climate change effects in this region can be aggravated in the Iberian Peninsula by the increasing density of its forests, which is expected to lead to high mortality rates (Ruiz-Benito et al. 2013; Vayreda et al. 2012) due to the inability of many species to tolerate deep shading (Niinemets and Valladares 2006; Zavala et al. 2011) or water shortage driven by competition (Vilà-Cabrera et al. 2011). Climate change-mediated geographical displacement of tree species has been estimated at different scales and in different regions, usually by the use of bioclimate envelope models, which have predicted notable displacements for all the future climate scenarios studied (Thuiller et al. 2005; Valladares et al. 2014). For the Iberian Peninsula, Benito-

Garzón et al. (2008) predicted most of Sub-Mediterranran forests (including forests dominated by black and Scots pine) to suffer a major decline in the second half of the 21th century under IPPC climatic change scenarios.

1.3.2. Forest disturbances

The prolonged droughts and hot spells predicted on most climatic change scenarios are expected to further aggravate both the frequency and severity of forest disturbances such as forest fires, pests and diseases, and to facilitate the establishment of invasive species (Lindner et al. 2010). Wildfires are considered the most important forest disturbance in the Mediterranean and can potentially trigger abrupt vegetation shifts. Although wildfires have been frequent in the Mediterranean forest since earlier than the late Quaternary (Gil-Romera et al. 2010; Pausas et al. 2008), large crown fires are relatively new in the recent history of these forests (Pausas et al. 2008). Its increment during the last decades has been attributed to a combination of factors related to both land-use and climatic changes (Loepfe et al. 2012; Pausas 2004). This type of wildfires is expected to be particularly destructive, among other cases, when they affect forest types that had not historically been subject to them (Gonzalez-Olabarria et al. 2008; Loepfe et al. 2012; Pausas et al. 2008).

Sub-Mediterranean black pine forests, as well as Scots pine forests in the upper-montane belt are clear examples of forest systems which have been increasingly affected by large crown fires during the last decades, leading in many cases to abrupt vegetation changes (Barbero et al. 2000; Ordóñez et al. 2006; Pausas et al. 2008; Retana et al. 2002; Rodrigo et al. 2004; Vacchiano et al. 2014). Recent models have predicted an overall decrease of the area occupied by these species (mainly of black pine and Scots pine) as a consequence, in part, of the increasing occurrence of this type of fires (Loepfe et al. 2012; Retana et al. 2002; Vilà-Cabrera et al. 2012). Only in the Catalonia region, where black pine occupies an area of around 134,000 ha, around 23% of the black pine dominated forests have been affected by fire during the last two decades, mostly by stand-replacing fires (Gonzalez-Olabarria et al. 2008; Gonzalez-Olabarria and Pukkala 2007).

The high sensitivity of these species to large crown fires is mainly associated to the lack of direct post-fire regeneration mechanisms, since they are not able to resprout, they do not produce serotinous cones and their seeds are not able to resist the high temperatures reached during their occurrence (Pausas et al. 2008; Retana et al. 2002). Moreover, the short dispersal distance of these species does not allow effective colonization from unburned edges to occur (Ordóñez et al. 2006; Vilà-Cabrera et al. 2012). In contrast, black pine and Scots pine can be defined as fire-tolerators (*sensu* Pausas 2015) since they present other traits (i.e. thick basal bark, self-pruning) which allow them to survive under frequent understory fires.

1.4. The importance of tree-species diversification in resilience of Sub-Mediterranean pinewoods

1.4.1. The role of diversity on forest resilience

In general, Mediterranean forests are considered to be highly resilient to disturbances due to its demonstrated ability to persist despite severe and very frequent human and natural disturbances (Blondel 2006; Di Castri and Mooney 1973). This high tolerance to changes has generally been explained by the phenotypic plasticity of most species, their capacity to adapt to new conditions though evolutionary processes –appearance of new species, subspecies or genotypes–, and their ability to quickly migrate to more suitable places, etc (Joffre et al. 2007; Pausas et al. 2004b; Ramirez-Valiente et al. 2010; Sánchez-Gómez et al. 2008; Valladares 2004).

Most of the mechanisms that confer forest stands with the natural capacity to adapt to changes are directly related with plant diversity (Elmqvist et al. 2003). At the stand level, diversity affects forest resilience through a series of attributes or processes such as (Thompson et al. 2009): *i*) niche selection or differentiation of the different species leads to more species adapted to survive in changed conditions; *ii*) functional complementarity among species favors the development of favorable combinations of species under changed conditions; *iii*) functional diversity increases the probability of favorable responses to changed conditions; *iv*) functional redundancy protects against effects of species loss; *v*) genetic diversity is the basis for the natural selection of genotypes within populations and species as they respond or adapt to environmental changes; and *vi*) phenotypic plasticity allows a greater range of permissible responses that are suited to the new conditions.

In the Mediterranean context, several studies have found a positive relationship between diversity and stand productivity (del Rio and Sterba 2009; Vilà et al. 2013; Vila et al. 2007), mostly explained by the occurrence of resource partitioning (species complementarity) or facilitation-like processes (Kunstler et al. 2007; Smit et al. 2008). High levels of species and structural diversity also have been proven to difficult the spreading of large diebacks, due to the diversity of resistances and responses that different species and stages of development present (Jactel et al. 2009). At a lower level, genetic diversity may enhance resistance and resilience through adaptation to these biotic menaces (Carnus et al. 2006). Similarly, diversity of species, ages or morphotypes can lead to better responses to episodes of extreme droughts (Choat et al. 2012; Galiano et al. 2010; Linares et al. 2010), and to a more variety of possible adaptive responses to cope with forest fires (Pausas et al. 2008; Retana et al. 2002). Finally, higher values of species and genetic diversity can also mitigate the consequences of rapid northward and upward displacements of the ecological niches due to global warming (Jump et al. 2006; Valladares et al. 2014). This would be mediated by the increasing probability of finding individuals, species or communities able to survive through plastic phenotypic responses, local adaptation, or successful migration.

In general, increasing forest diversity does not only provide more chances for the system to respond to future disturbances and environmental change, but also generates the complexity needed to sustain a wider range of ecosystem services (Campbell et al. 2009; Drever et al. 2006).

1.4.2. Factors driving natural diversification process and open questions

Natural diversification processes consist on the progressive colonization of the forest stand by tree species others than the ones occupying the dominant canopy. This process has been widely studied in the literature in the context of different forest systems, and is known to depend on a number of factors acting at different spatio-temporal levels (seed dispersion into the stands, establishment of the plants and growth to reproductive maturity) (Sheffer 2012; Zavala et al. 2011). Seed arrival, for example, is influenced by the abundance and spatial distribution of seed sources in the surrounding landscape (González-Moreno et al. 2011; Zamora et al. 2010), but also depends on other factors such as the abundance and behavior of seed dispersers and predators (Gómez 2003; Gonzalez-Rodriguez and Villar 2012; Pérez-Ramos and Marañón 2008). Once the seeds are dispersed into the stands, plant establishment and future growth is triggered by a combination of factors acting at micro-site level: the environmental conditions of the site (climate, soil, etc.), the characteristics of the stand (over- and understory structure and composition), the attributes of the overstory (gap shape, size) (e.g. Caldeira et al. 2014; Garcia-Barreda and Reyna 2013; Lookingbill and Zavala 2000; Smit et al. 2008), and the occurrence of browsing events (e.g. Ameztegui and Coll 2015).

The occurrence of natural or anthropogenic small-scale disturbances may also be a key element of this process, since they can alter many of the above-mentioned factors. For instance, small-scale disturbances causing the death of a few trees can lead to moderate canopy openings in the stands and generate enough heterogeneity in the understory to cause changes in micro-site environmental conditions (humidity, temperature) and allow the seedlings of the dominant species and those coming from adjacent stands to prosper (Ligot et al. 2014; Runkle 1981; Yamamoto 2000).

In the context of Mediterranean pinewoods, several studies have reported an ongoing recessive trend in pine regeneration in parallel to a noticeable increase of broadleaves recruitment and ingrowth (Urbieta et al. 2011; Tiscar and Linares 2014). In general, these studies have not found a direct relationship between this process and climate (or recent warming). Conversely, the increasing dominance of broadleaves in the understory of the pinewoods have usually been related the current trend of increased canopy closure (Vayreda et al. 2013; Carnicer et al. 2014).

Most of the factors driving colonization of pine stands by late-successional broadleaves show highly variable effects depending on the shade- and drought-tolerance of the different species involved, the different microsite conditions and the presence of land use legacies or large-scale climatic gradients (Sheffer 2012; Zavala et al. 2000). Due to this, fine-scale community-based studies are required to generate detailed knowledge and allow the adjustment of management practices oriented to promote diversification and enhance stand resilience.

1.4.3. The importance of pre-fire forest attributes on post-fire regeneration trajectories

Diversity of tree species with different functional traits is an essential feature for rapid post-fire recovery of Mediterranean pinewoods (Baeza et al. 2007; Broncano et al. 2005; Puerta-Piñero et al. 2012). In effect, post-fire vegetation after stand-replacing fires is known to depend, among other factors, on pre-fire vegetation characteristics (Arnan et al. 2007; Pausas 2001; Pausas et al. 2004b;

Retana et al. 2002). The presence of functional vegetative propagules (seeds, stems, roots, etc) after the fire will largely relate on attributes such as the species composition of the stands or the size of the trees prior to the fire (Arnan et al. 2007; Espelta et al. 2003; Ordoñez et al. 2005). In the Mediterranean context these attributes are strongly related to the land-use history of the stands (Martin-Alcon et al. 2012; Puerta-Piñero et al. 2012).

Other factors that have proven to strongly affect post-fire regeneration are those related to fire behavior and, in particular, to fire severity and disturbance legacies (i.e., residual canopy cover, type of post-fire seedbed, distance from the surviving seed trees, etc). All these factors represent a source of variation that may strongly influence both the type and success of regeneration at any particular area (Boiffin and Munson 2013; Bonnet et al. 2005; Broncano and Retana 2004; Lentile et al. 2007; Ordóñez et al. 2006; Pausas et al. 2002; Vacchiano et al. 2014). At the landscape level, climate and topography have also been shown to modulate regeneration patterns, mostly because they drive soil moisture distribution (e.g. Baeza et al. 2007; Buhk et al. 2006; Coop et al. 2010; Keeley and Keeley 1981; Pausas et al. 2004c). Ultimately, post-fire management practices have also great potential for influencing regeneration trajectories, especially in the context of erosion-prone and/or poor soil sites (e.g. Castro et al. 2011; Keyser et al. 2009; Martínez-Sánchez et al. 1999; Oliveira and Fernandes 2009; Vallejo et al. 2012b; Vega et al. 2008).

In the particular case of *P. nigra* or *P. sylvestris* pinewoods, all the abovementioned factors have been reported to modulate post-fire regeneration dynamics (Arnan et al. 2007; Puerta-Piñero et al. 2012; Retana et al. 2002; Rodrigo et al. 2004; Vacchiano et al. 2014). However, the relative importance of each of them has not been assessed yet. It is worth to mention that some of these factors (e.g. local topography, climate or land use history) can hardly be modified by silvicultural interventions, but others such as the pre-fire vegetation attributes can be at least partially modified by means of preventive silvicultural practices. Thus, advancing in the knowledge of the relative importance of the manageable factors, such as the role played by the structure and composition of the stands prior to the fire, is of great importance to develop strategies aimed to partially direct regeneration dynamics anticipating fire occurrence.

1.4.4. Assisted diversification and assisted migration as management actions enhancing forest resilience

As mentioned above, the implementation of forest management practices aimed at favoring tree-species diversification processes in Mediterranean pinewoods is of major interest under the current context of climate change. In the particular case of the Sub-Mediterranean *P. nigra* and *P. sylvestris* forests, natural tree-species diversification may still be far from being widespread at the landscape and regional scales. This would be due to different constraints such as seed dispersal limitations (González-Moreno et al. 2011; Zamora et al. 2010), the occurrence of unfavorable stand structures (i.e. over-stocked pine plantations in which no thinning operations have been realized) (Navarro-González et al. 2013) and to limitations related to site microclimatic conditions (Gomez-Aparicio et al. 2009) or derived from the current disturbance regimes (Pausas et al. 2004a; Rodrigo et al. 2004). With the aim of accelerating this process and/or coping with such limitations, assisted diversification measures based on planting or sowing late-successional species have been recently proposed (Gomez-Aparicio et al. 2009; González-Rodríguez et al. 2011; Palacios et al. 2009; Prévosto et al. 2011).

In the Mediterranean region, the climatic conditions to which tree populations are locally adapted are expected to change dramatically in response to future rapid global warming (Benito-Garzón et al. 2008; Keenan et al. 2011). In such context, assisted migration practices can be considered when implementing diversification actions in particularly vulnerable areas (Benito-Garzón et al. 2013; Frascaria-Lacoste and Fernández-Manjarrés 2012; Kreyling et al. 2011; Pedlar et al. 2012). Assisted migration –also known as assisted colonization, or population translocation– refers to the intentional movement of focal units (ecotypes, species, taxa, functional types, life forms) to recipient localities, where these focal units are currently absent, and where they cannot be expected to colonize by natural means within a short time frame (i.e. years or decades) (Kreyling et al. 2011). In forestry, assisted migration is generally focused on keystone tree species moved within (or modestly beyond) a species' current range (Frascaria-Lacoste and Fernández-Manjarrés 2012; Kreyling et al. 2011; Pedlar et al. 2012).

The implementation of assisted migration measures needs of previous research aimed at providing valuable information about, for example, recommend species and seed sources or adequate migration distances, in order to avoid possible maladaptation of translocated populations to the new environmental conditions in the recipient locality (Benito-Garzón et al. 2013). Common garden and field experiments are the most powerful tool for testing population translocations and generating this information (Matyas 1996), but these type of field experiments are still very scarce, at least in the Mediterranean Basin.

1.5. Objectives and structure of the doctoral thesis

The main objective of the doctoral thesis is to deepen the knowledge on the main factors driving the natural dynamics of tree species diversification in the Sub-Mediterranean pinewoods and on the consequences of such processes with regards to forest resilience to forest fires. Furthermore, the doctoral thesis aimed to gain deeper insight into the main variables modulating the success of assisted migration practices to enhance or promote tree-species diversification and stand resilience. The assessment of these objectives has required working at different scales, from micro-habitats to landscape level, and the use of different approaches and tools, from in-field monitoring of plant performance, to remote sensing-based vegetation characterization at the landscape level (Figure 3).

The thesis has been structured in chapters, written in the format of scientific articles that have been submitted for publication to international peer-reviewed scientific journals. The first study (Chapter 2) consisted in a stand-level analysis of the main drivers of tree-species diversification in Sub-Mediterranean black pine-dominated pinewoods, using a combination of field inventory and remote sensing data. More precisely, we sampled 155 plots distributed in 8 different stands and analyzed the role played by a number of site factors and stand attributes (including canopy openness characterized from remote sensing data) on the abundance of seedlings and saplings of the main tree-species in the area (i.e. black pine, evergreen oak and marcescent oaks).

The next two chapters were aimed to provide an integrative and spatially-continuous analysis of the main drivers determining post-fire regeneration trajectories in Sub-Mediterranean black pine-dominated pinewoods after a large crown fire. In Chapter 3, we used a combination of airborne LiDAR and multispectral imagery to assess post-fire regeneration types using a black pine forest that burned in 1998 as a case study. In Chapter 4 we carried out a multi-factorial analysis to determine the relative importance of the structure and composition of the pre-fire vegetation compared to topographical variables and fire behavior and legacies on the occurrence of the predefined vegetation types.

Finally, in Chapter 5, we present the findings of the initial 3-year monitoring period of a long-term field experiment designed to advance in the understanding of the main factors driving the success of assisted migration practices, and to assess how some of the species most suitable for diversifying sub-Mediterranean pine forests will respond to the changing climatic conditions derived from translocation. To do this, we sowed acorns and planted seedlings of four *Quercus* species from two contrasted provenances in the understory of sub-Mediterranean pinewoods, along gradients of elevation and microsite conditions (light availability and herbaceous and shrub cover). We evaluated seedling responses to translocation by assessing seedling emergence, seedling survival, and re-sprouting after dieback events according to seedling provenance, thermal migration distance, extreme cold events and microenvironment.

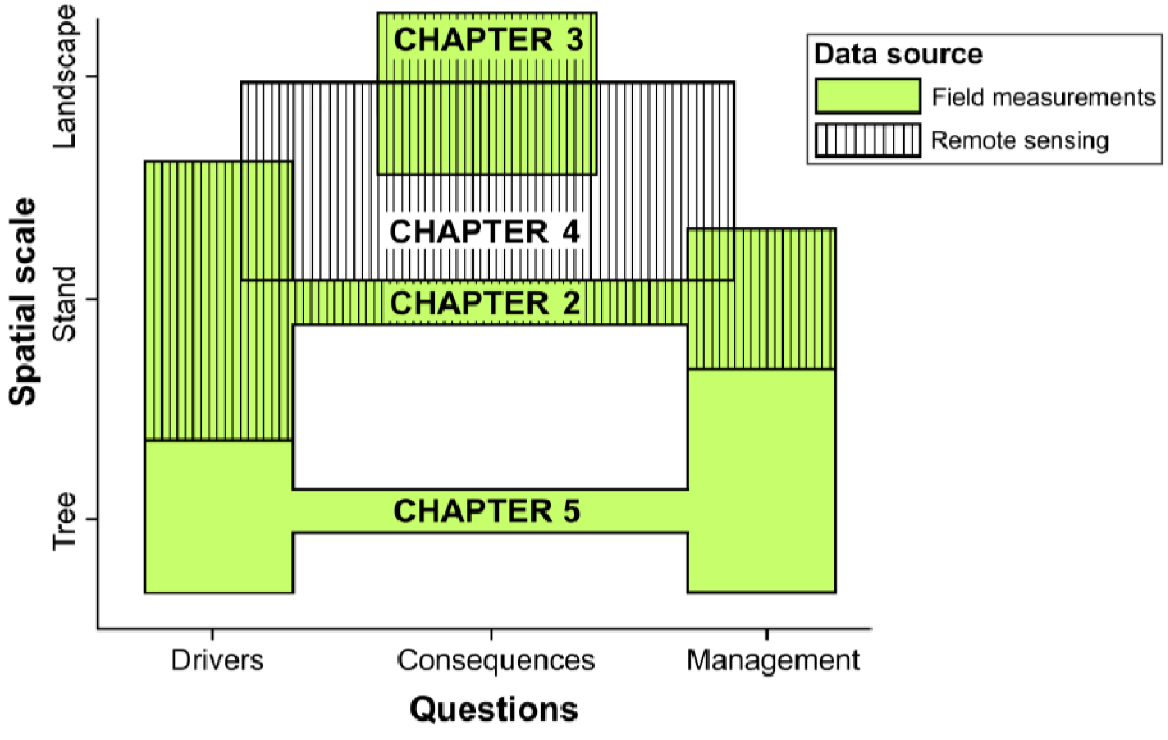

Figure 3: General structure of the thesis based on the data source, spatial scale and addressed questions of the different chapters regarding the process of tree-species diversification in the Pre-Pyrenean Sub-Mediterranean pine forests.

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2

Stand-level drivers of tree-species diversification in Mediterranean pine forests after abandonment of traditional practices

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Santiago Martín-Alcón, Lluís Coll and Serajis Salekin

2. Stand-level drivers of tree-species diversification in Mediterranean pine forests after abandonment of traditional practices

Abstract

The progressive abandonment of traditional forest management over the last few decades has led to significant densification processes in most Mediterranean pine stands. In parallel, some of these stands have also shown tree-species diversification processes, the occurrence of which is considered essential for future adaptability and resilience to change.

Here we aim to gain further understanding of the main factors driving these diversification processes via a case-study approach using the long-term-managed black pine (*Pinus nigra* Arn. ssp. *salzmannii*) forests of the Catalan Pre-Pyrenees (NE Spain). For this purpose, we sampled 155 plots distributed in 8 different stands and analyzed the role played by a number of microsite factors and stand attributes (including canopy openness and heterogeneity) on the abundance of seedlings ($h < 1.3$ m) and saplings ($h > 1.3$ m; $dbh < 7.5$ cm) of the main tree-species in the area (i.e. black pine, evergreen oak and marcescent oaks).

Results revealed ongoing black pine recruitment limitation processes mainly associated to the high canopy cover of the overstory and the increasing abundance of shrubs, which may compete with pines for light resources. In contrast, we found that current environmental and stand-level conditions favor the progressive advance of the recruitment of evergreen and marcescent oaks, which are able to establish successfully under the dominant pine canopy. However, in the absence of canopy openings, light levels may not allow the established oaks (in particular the evergreen *Quercus ilex*) to grow and progress to higher developmental stages.

Our findings bring deeper insight into the role of stand-level factors regulating species diversification, and can be used by forest managers to adjust their practices (e.g. by modifying the spatial and temporal patterns of silvicultural treatments such as thinnings or selection cuttings) in order to favor this natural process and increase stand resilience.

Keywords: *Pinus nigra*; regeneration; oak recruitment; mixed forests; canopy attributes

2.1. Introduction

The distribution, structure and composition of Mediterranean forests have been shaped over millennia by human practices (Debussche et al. 1999; Nocentini and Coll 2013; Vallejo 2005). Over time, this long history of human use has resulted in a significant reduction of the extent and inherent structural and compositional diversity of Mediterranean forests (Blondel 2006; Ciancio and Nocentini 2000). In the context of the Iberian Peninsula, this long history of intense human-use reached its peak at the end of the 19th century (Garcia-Ruiz et al. 1996; Linares et al. 2010; Pausas et al. 2004). However, the 20th century brought major socioeconomic changes leading to generalized land abandonment processes in marginal areas -generally mountainous systems- and to land-use intensification in broad valleys and coastal regions (Chauchard et al. 2007; Garcia-Ruiz et al. 1996; Lasanta-Martinez et al. 2005; Vicente-Serrano et al. 2004). This, together with extensive reforestation programs initiated with the aim of restoring the most heavily-degraded areas -most of which with pine species-, have triggered extended encroachment and densification processes in forest stands (Améztegui et al. 2010; Navarro and Pereira 2012; Ruiz-Benito et al. 2012).

Black pine-dominated forests (*Pinus nigra* Arn. ssp. *salzmannii*) in the Pre-Pyrenean range (NE Spain) are clear examples of forests undergoing such processes. These forests were intensively managed for timber harvesting and pasture grazing until the mid-20th century (Ruiz de la Torre 2006), but from that point onwards the intensity of human practices decreased significantly (Vicente-Serrano et al. 2004). During the past few decades, just a few individual-tree selection cuttings affecting only the most vigorous and well-shaped trees have been conducted on these forests (Aunós et al. 2009; Trasobares and Pukkala 2004). Such lessening of human pressure (particularly the strong decrease of silvicultural interventions and livestock grazing) has allowed the establishment of new cohorts of the dominant pine species, causing a generalized densification of the stands (DGCN 2007) and a progressive process of colonization by late-successional tree species, mainly *Quercus* species (Carnicer et al. 2014; Urbieta et al. 2011; Vayreda et al. 2013).

The promotion of diversified forests is gaining currency as an appropriate management strategy to improve stand adaptability to environmental variations, including changes in disturbance regimes (e.g. Campbell et al. 2009; Puettmann 2011; Thompson et al. 2009). Advancing knowledge of the ecological factors driving tree-species diversification in Mediterranean forest stands is of major interest, due to the particular vulnerability of this bioclimatic region to the effects of global change (Lindner et al. 2010). In the particular case of black pine-dominated forests, for example, the occurrence of natural diversification processes allowing resprouting species such as oaks to establish in the pine understory is reportedly essential for rapid vegetation recovery after the occurrence of large wildfires (Puerta-Piñero et al. 2011).

The progressive colonization of a given forest stand by tree species others than the ones occupying the dominant canopy is a complex process, the success of which depends on a number of factors acting at different spatio-temporal levels (seed dispersion into the stands, establishment of the plants and growth to reproductive maturity) (Sheffer 2012; Zavala et al. 2011). Seed arrival, for example, is influenced by the abundance and spatial distribution of seed sources in the surrounding landscape (González-Moreno et al. 2011; Zamora et al. 2010), but also depends on other factors such as the abundance and behavior of seed dispersers or predators (Gonzalez-Rodriguez and Villar 2012;

Pérez-Ramos and Marañón 2008). Once the seeds are dispersed into the stands, and in the absence of significant human disturbances and/or intensive browsing events, plant establishment and future growth will be triggered by a combination of factors acting at micro-site level: the environmental conditions of the site (climate, soil, etc.), the characteristics of the stand (over- and understory structure and composition) and the attributes of the canopy layer (gap shape, size) (Garcia-Barreda and Reyna 2013; Lookingbill and Zavala 2000; Smit et al. 2008).

The occurrence of natural or anthropogenic small-scale disturbances leading to moderate openings of the stands is a key element of the above mentioned process of tree-species diversification. These openings generate heterogeneity in the understory and lead to micro-site-level changes in environmental conditions (humidity, temperature) and resource availabilities (e.g. light, soil water) allowing the seedlings of the dominant species and those coming from adjacent stands to prosper (Ligot et al. 2014; Runkle 1981; Runkle and Yetter 1987; Yamamoto 2000).

This study aims to shed light on these processes which, contrary to other bioclimatic regions, have so far been little explored in the Mediterranean. More specifically, we aimed to answer the following questions: (*i*) have the sub-Mediterranean black pine forests undergone active regeneration and tree-species diversification processes during the last decades? (*ii*) Which are the main stand-level factors driving such processes? and (*iii*) Do the canopy openness and the gap attributes play a key role on them? For this purpose, we used the long-term-managed Sub-Mediterranean black pine forest of the Catalan Pre-Pyrenees (NE Spain) as case study. We selected a number of stands showing a large gradient of canopy openness and structural heterogeneity and analyzed the role played by different stand-level factors in the abundance of the different species at different life-history stages: seedlings and saplings. We expected stand structure and, particularly, canopy attributes to play a key role in driving stand-level species diversification allowing species other than pine to survive and prosper under the dominant pine canopy.

2.2. Materials and methods

2.2.1. Study area and stands selection

The study was conducted in the Catalan Pre-Pyrenees, Northeastern Iberian Peninsula, in a mountainous range limited at East and West by the basins of the rivers Segre and Cardener (between 1° 11′ 6″ and 1° 36′ 57″ E, and 41° 56′ 57″ and 42° 3′ 43″ N, DATUM WSG84) (Figure 1). These mountains are formed by folded structures of sedimentary carbonate rocks (mainly lutite, marlstone, limestone and conglomerate), characterized by vertical elevation ranging from 400 to 1000 m.a.s.l. Climate in the area is sub-humid from Mediterranean-continental to Mediterranean-montane, characterized by mean annual precipitation of around 700 mm and mean annual temperature around 12 °C (Ninyerola et al. 2005). Rainfall is usually concentrated in autumn and spring, and winter is the season with least precipitation. In summer, short convective storms also provide significant precipitation input (around 100–130 mm in average during the hottest months, July and August). However, due to the high inter-annual variability in the occurrence of this type of rainfall events, the occurrence of summer dry periods is not unusual. Within this general geographic context, the study focused on the forests dominated by black pine (*P. nigra* Arn. ssp. *salzmannii*) which are the most abundant in the study area.

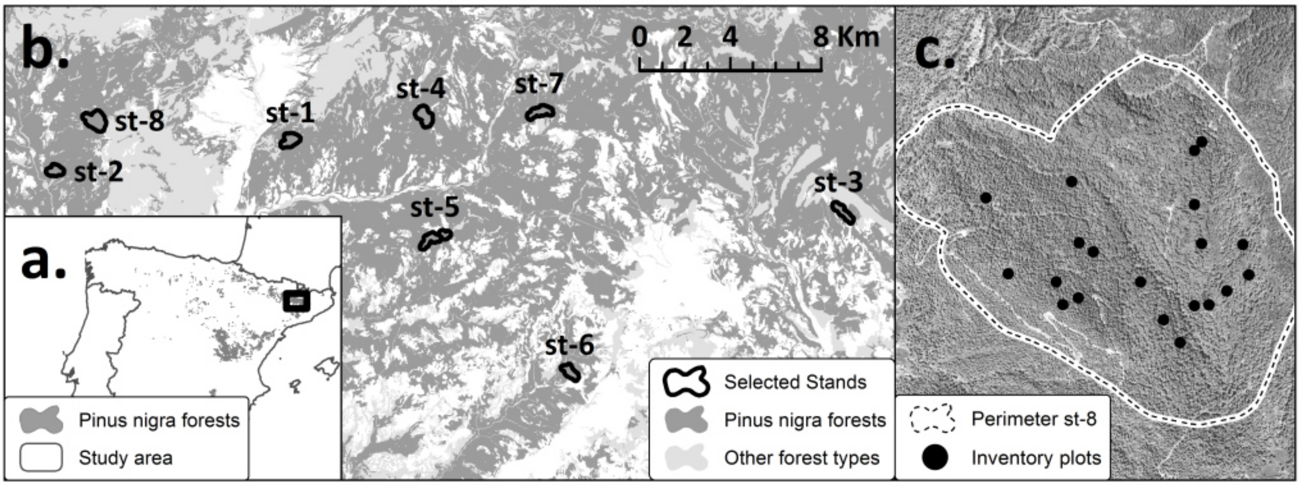

Figure 1. Location of the study area (a), the sampled stands (b), and the inventory plots within one of the stands (c).

A set of eight stands were selected along the study area (Figure 1) based on the following three criteria: (*i*) patches larger than 2 hectares and clearly dominated by black pine at the canopy level (i.e. with black pine occupancy > 90% of total basal area), (*ii*) not coming from recently abandoned open-areas (i.e. agricultural land, grassland, shrubland), and (*iii*) with absence of signs of any recent silvicultural interventions or grazing activity. The first criterion was checked with the help of the third Spanish National Forest Inventory plots (which provided information on current structure and composition) (DGCN 2007), the Spanish National Forest Map 1:50.000 (DGCN 2001), and the third version of the Land Cover Map of Catalonia (CREAF 2007). The second criterion was tested by visually comparing the most recent aerial photographs of the area (taken in 2012) and the most ancient ones (taken in 1956) and aimed at discarding from the study those young stands established in open-areas recently abandoned which due to their young age were much less susceptible of undergoing diversification processes by late-successional tree species (Puerta-Piñero et al. 2012). Twelve stands meeting the first two criteria were preselected and examined on-site in order to detect signs of recent silvicultural interventions or grazing activity. Four of the twelve preselected stands did not meet this criterion and were ultimately discarded from analysis.

2.2.2. Remote sensing data acquisition and pre-processing

Two different sources of remote sensing data were used to characterize the forest canopy: aerial Light Detection and Ranging (LiDAR) and multi-spectral aerial imagery (including red–green–blue (RGB) and near-infrared (IR) bands). The LiDAR-derived data consisted in a two-meter resolution DVM (Digital Vegetation Model) generated in the framework of the LiDARCAT project led by the Cartographic and Geological Institute of Catalonia (ICGC). Flight dates ranged from April 2009 to August 2009 and provided a minimum first-return density of 0.5 pulses m^{-2} and an overall quantity of four height bins per first return. The RGB and near-IR data were obtained from multi-spectral aerial photographs taken in the framework of the ICGC's annual coverage flights at 22 cm GSD (ground sample distance). The imagery was taken in the same time period as the LiDAR data, with DMC 26 and DMC 14 cameras.

The near-IR and the R bands from aerial images were used to calculate the NDVI (Normalized Difference Vegetation Index) (Tucker, 1979). Then, both the DVM from LiDAR and the calculated NDVI layers were clipped to the boundaries of the 8 selected stands, and used in an object-oriented semi-automatic image analysis (carried out with eCognition Developer 8.9) to classify the area within the stands into three classes: 'CLOSED CANOPY', i.e. area covered by the main pine canopy showing a continuity larger than 10,000 m^2; 'GAPS', i.e. area of less than 500 m^2 not covered by (but surrounded by) the main pine canopy (Messier et al. 2005; Schliemann and Bockheim 2011); 'OPEN AREA' for the rest of the area (which includes small canopy patches, isolated trees and open areas larger than 500 m^2). The accuracy of the semi-automatic classification was visually assessed on 120 observation points distributed in the study area following a stratified random sampling, one half (60) randomly located in the area automatically classified as 'GAPS', and the other half in the area automatically classified as 'CLOSED CANOPY'. About 97% and 95% of the points semi-automatically classified as 'GAPS' and 'CLOSED CANOPY', respectively, were visually confirmed as belonging to each class. The accuracy of the method in classifying 'OPEN AREA' was not tested because these areas were not the focus of this study.

2.2.3. Sampling design and field inventory

In order to cover a wide gradient of canopy openness and heterogeneity in the study area, we established the field inventory plots using a stratified random design. First, a 20 × 20 m mesh was created within each selected stand and the percentage of area covered by the 'GAPS' class in the area surrounding each point in the mesh was computed. For this purpose we used a 18-m diameter of the area of influence, equivalent to the mean dominant height for black pine in the selected stands. Then, four classes of gap abundance were created (0: gap percentage ranging from 0% to 5%; 1: gap percentage ranging from 5% to 15%; 2: gap percentage ranging from 15% to 30%; 3: gap percentage above 30%). Those plots located at less than 10 m from patches classified as 'OPEN AREA' (e.g. roads, agricultural field, harvested areas, etc.) were rejected. Second, 5 points in each class of gap abundance were randomly selected in each stand and used to locate the inventory plots (160 in total, 20 per stand). Inventory plots were circular, with a 6-m radius centered at the randomly selected points. In each plot, a set of site attributes including UTM central coordinates, slope and aspect were collected. The tree canopy layer was characterized by identifying the species and measuring the diameter at breast height (*dbh*) of all trees with *dbh* > 7.5 cm. Percentage of soil covered by woody shrubs was also estimated. The most frequent shrubby species in the understory was common box (*Buxus sempervirens* L.), followed by the two main juniper species in the area (*Juniperus communis* L. and *Juniperus oxycedrus* L.), and the kermes oak (*Quercus coccifera* L.). Other species of the genus *Crataegus*, *Rhamnus*, *Viburnum*, *Rubus*, *Lonicera*, etc. were also very frequently inventoried. Finally, the abundance of stones, herbs and moss were visually estimated and classified into three categories (*low*: less than 1/3 of the plot area; *medium*: between 1/3 and 2/3 of the plot area; and *high*: more than 2/3 of the plot area).

Finally, tree-species regeneration was assessed by counting the number of seedlings (plants shorter than 1.3 m) and saplings (plants taller than 1.3 m but with a *dbh* < 7.5 cm) of each species. We also took a digital hemispherical photograph from the center of each plot under overcast sky conditions using a Nikon CoolPix 4500 camera with an FC-E8 fish-eye lens. Five out of the 160 selected plots were rejected for subsequent analyses due to recent wild boar damage recorded when visited.

2.2.4. Data processing

Both field and remote sensing-derived data were processed and grouped for subsequent analysis into a number of response and explanatory variables. As response variables, we used the abundance of regeneration found in the understory, grouped by development stage (seedlings and saplings), and functional types: (1) pines, only represented by the pine species dominating the tree canopy (*P. nigra* Arn. ssp. salzmannii); (2) evergreen oaks, represented by the only one species appearing in the area (*Quercus ilex* L.); and (3) semi-deciduous (marcescent) oaks, represented by two species (*Quercus faginea* Lam. and *Quercus cerrioides* Willk & Costa). Although the field inventories also recorded the presence of other broadleaved species (e.g. *Sorbus*, *Acer*), we discarded them from the analysis due to the shortage of individuals.

The quantitative explanatory variables derived from the field surveys and remote-sensing data included environmental descriptors of the sites and different variables related to stand structure and composition, including the gap attributes (see Table 1).

Table 1. Descriptive statistics of the quantitative explanatory variables presenting significant effects in the models (n = 155).

Variable, unit	Min.	Max.	Mean	Std. Dev.
Site factors				
CURVATURE Index	-1.77	2.17	0.10	0.65
NORTHNESS Index	-0.38	0.60	0.22	0.18
MARTONNE Index	28.47	35.47	32.69	1.27
Stand structure & composition				
MATURITY Index	0.00	0.99	0.22	0.26
G (Basal Area), m^2/ha	5.81	75.76	37.36	14.10
SHRUBS (woody shrubs cover), %	1.00	95.00	48.67	24.81
Grel_BL (relative G of broadleaves), ppu	0.00	0.22	0.03	0.05
Grel_Qm (relative G of marcescent Q. spp.), ppu	0.00	0.22	0.02	0.04
Grel_Qi (relative G of evergreen *Q. ilex*), ppu	0.00	0.16	0.00	0.02
CO (Canopy Openness), %	12.72	38.54	21.16	4.82
GSI (Gap Shape Index)	0.00	4.05	1.98	0.34
MGS (Mean Gap Size), meters	0.00	141.60	14.97	18.35

In relation to the first group of variables, we computed three different indexes (NORTHENESS, CURVATURE and MARTONNE) with the aim of broadly characterizing the climatic and topographic conditions at each plot. The NORTHNESS Index was calculated as the product of the slope (%) and the cosine of the aspect (degrees) measured in the field inventory (Holden et al. 2009). This index was used as a proxy for solar radiation budget at the plot surface, and took higher positive values as aspect gets closer to North and slope increases, and lower negative values as aspect gets closer to South and slope also increases. As aspect gets closer to East or West and/or slope decreases, the NORTHNESS Index draws closer to 0. The CURVATURE Index was calculated as a proxy of local topography, which is considered to be highly related to soil water content distribution along a given slope (Gómez-Plaza et al. 2001). For this purpose, we used the equation proposed by Moore et al. (1991) on a 5-m-resolution digital elevation model. Higher positive values indicate convex terrain and lower negative values indicate concave terrain. Finally, the MARTONNE Index was calculated from the equation proposed by De Martonne (1926), as ,$M = P \times (T + 10)$ where M is the value of the index, P (mm) is annual precipitation, and T (°C) is annual mean temperature. P and T were obtained from the Climatic Atlas of the Iberian Peninsula (Ninyerola et al. 2005). The value of the MARTONNE index decreases with increasing aridity.

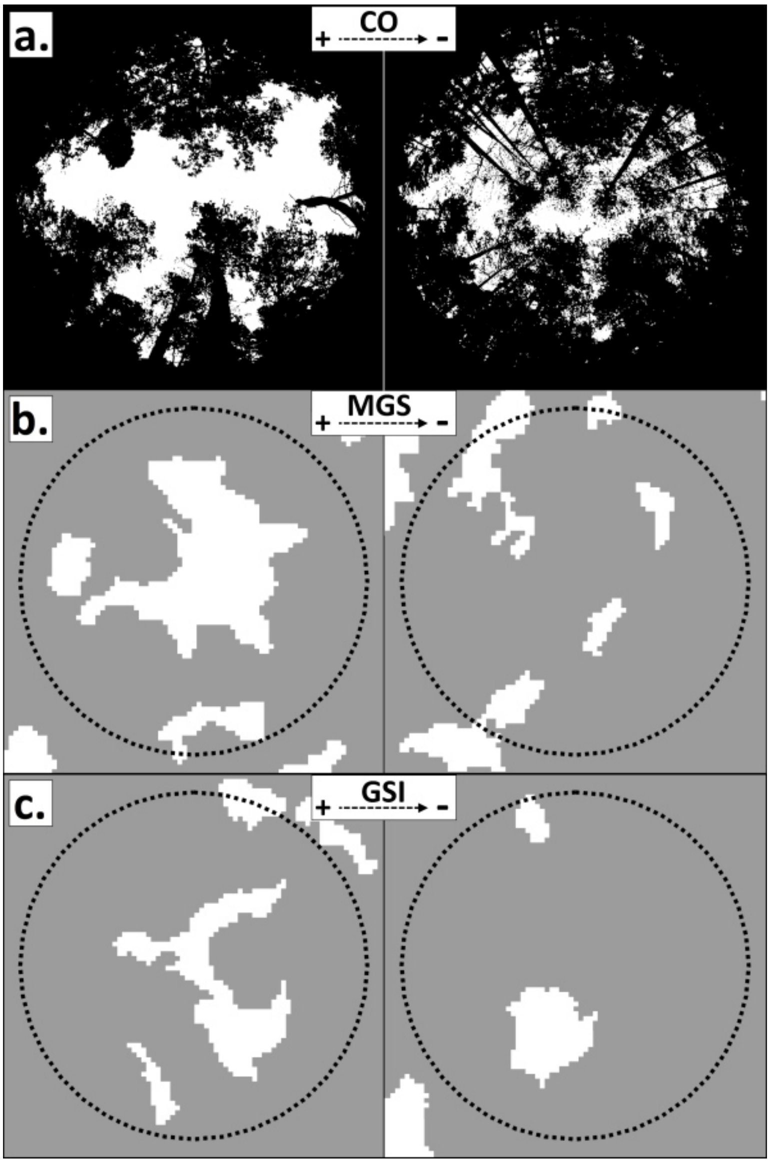

Figure 2. Examples of plots showing (a) high and low values of CO (Canopy Openness, calculated from hemispherical photographs); (b) high and low values of MGS (Mean Gap Size, calculated from the analysis of remote-sensing data); and (c) high and low values of GSI (Gap Shape Index, calculated from the analysis of remote sensing data).

The structure and composition of the tree layer were characterized by total basal area of the plot (*G*), contribution of non-dominant (i.e. non-black pine) species to total *G*, and a MATURITY Index, calculated as the ratio of thick wood (with *dbh* > 27.5 cm) to total basal area. Finally, the characteristics of the gaps were assessed by the Canopy Openness value (CO), calculated as the overall percentage of gap area in the digital hemispherical photographs (obtained with GLA software; Frazer et al. (1999)), and two variables reflecting size and shape of the gaps: MGS (Mean Gap Size, in m^2) and GSI (Gap Shape Index; see Figure 2). These two variables were calculated using the Patch Analysis extension for ArcGIS (Rempel et al. 2012) in a 9-m-radius circle set around the plot center (i.e. diameter of the area of influence = 18 m, equivalent to the mean dominant height for black pine in the selected stands). They complement the information given by the CO (e.g. a plot with a given CO could present many small gaps of a just a few large ones), yielding information on the mean size of the gaps (MGS) and their irregularity (GSI) within the area of influence around the plot, ranging from 1 when all gaps are circular to higher values when they are more irregular.

2.2.5. Data analyses

We first executed an exploratory analysis to check for potential colinearity problems between the candidate predictors. We only found significant correlation ($P < 0.001$) between MGS and CO (Pearson's correlation coefficient = 0.313,$n = 155$) but it was considered not high enough to cause colinearity problems. Later, the regeneration abundance of the different species and development stages in each ground inventory plot were regressed against the different micro-site explanatory variables and stand structural and compositional characteristics through Generalized Linear Mixed-effects Models (GLMM). Since the regeneration frequency data presented numerous 'zero' counts and a few very high counts, GLMMs were constructed assuming a Poisson distribution of errors with a log-link function. We used penalized quasilikelihood (PQL) with restricted maximum-likelihood (REML) method to estimate GLMMs parameters (Breslow and Clayton 1993). Because our data were unbalanced, we used Satterthwaite's method to determine the approximate denominator degrees-of-freedom for tests. Nesting of sample plots within the 8 surveyed stands was considered using STAND as a random effect in the mixed model. Selection of variables for inclusion in the final models was based on likelihood ratio tests comparing the full model (i.e. that including all the potential predictors) against reduced models in terms of the Bayesian information criterion (BIC). Information- theoretic methods such as BIC estimate statistics that quantify the magnitude of difference between models, with lower BIC values indicating stronger empirical support for a model (Hoeting et al. 1999). Quadratic terms for basal area, woody shrubs cover, canopy openness and mean gap size (e.g. $MGS^{0.5}$ and MGS) were tested in our models to account for nonlinear responses of species to these structural attributes as well as some interactions selected on a rational basis. The interaction between woody shrub cover and MGS (i.e. SHRUBS∗MGS) was included to test whether potential facilitative or competitive effects of shrubs on the regeneration were maintained or not in gaps of different sizes. We also considered the interaction between GSI and MGS (i.e. GSI∗MGS) to analyze the potential role of the shape of the gaps (GSI) in attenuating or amplifying the effect of the gap size on the different species regeneration.

Once the final models had been generated for the different species and development stages (i.e. seedlings and saplings), we performed linear regressions (with a zero intercept) between observed regeneration density and predicted regeneration density, and used their slope and their R^2 to measure the biases of the models (with an unbiased model having a slope of 1) and to estimate their goodness-of-fit. In order to estimate the relative importance of each group of factors (site *vs*. stand structure and composition), the final models were compared on the basis of BIC against models that ignored the effect of one of the two groups, with higher variations in BIC indicating stronger effect of the ignored group of factors. We also used the likelihood ratio test for model comparison, once the models re-estimated by the maximum-likelihood method. GLMMs were obtained using the GENLINMIXED command in IMB SPSS Statistics 22 software (IBM Corporation 2013), while model comparisons were performed using R 3.1.1 software (R Development Core Team 2014) and the 'lme4' v. 1.1-7 (Bates 2010) package.

2.3. Results

2.3.1. Effect of site factors

The exploratory analyses revealed more regeneration of *Quercus* species (in terms of number of plants per inventoried surface) than pines in the study area (Figure 3). Oak regeneration was basically present in the form of young seedlings, contrary to what was observed for pines where more advanced stages (saplings) dominated. Regeneration of other deciduous tree species (grouping species of the genus *Sorbus*, *Acer*, *Prunus*, etc.) was also found, but its abundance was very low both for seedlings ($\bar{X}$: 2.6, σ: 12.0) and for saplings ($\bar{X}$: 1.6, σ: 3.7).

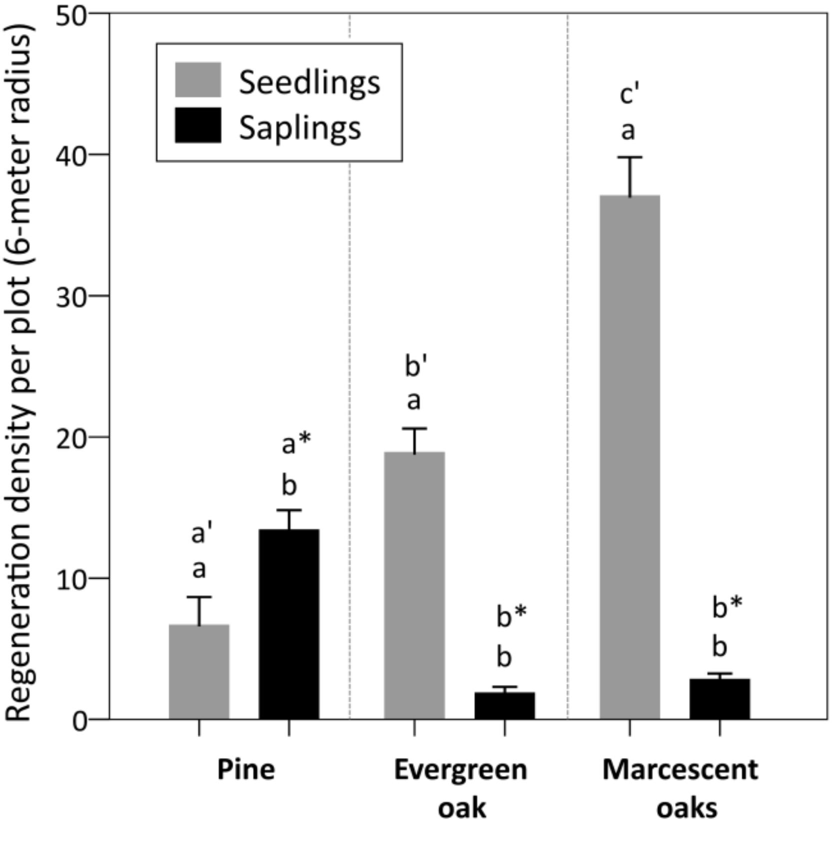

Figure 3. Bar-plot showing mean and standard error of the regeneration density of the main tree species in the 155 inventory plots, separated into functional groups of species (Pine: *P. nigra*; Evergreen oak: *Q. ilex*, Marcescent oaks: *Q. faginea* &*Q. cerrioides*) and development stage (seedlings when h≤1.3 m; saplings when h>1.3 m and *dbh* ≤ 7.5 cm). Plain letters indicate significant difference between seedlings and saplings of each species; letters with apostrophe (') indicate significant difference among seedlings of the different species; letters with asterisk (∗) indicate significant difference among saplings of the different species.

The different variables used here to characterize the environmental characteristics of the sites were found to significantly affect the abundance of the regeneration of the studied species (Table 2). The presence of *Q. ilex* seedlings, for example, was more important in convex (i.e. ridges, spurs, upper slopes, etc.) than concave areas (i.e. valley bottoms, mid- and lower slopes, etc.), whereas pines and marcescent oak seedlings followed the opposite trend. The abundance of seedlings of evergreen oaks also showed a clear pattern in relation to site exposure, being higher with decreasing northness (i.e. conditions closer to south-facing slopes). Climatic aridity was also found to modulate the abundance of pine seedlings, which prefer drier sites. The abundance of saplings of the different species showed similar responses to site factors as seedlings, although some small differences emerged (Table 3). In particular, the effect of northness shifted from non-significant in the case of pine seedlings to a positive effect on the abundance of pine saplings, and from non-significant (for seedlings) to negative (for saplings) in the case of marcescent oaks. Interestingly, climatic aridity emerged as one of the factors influencing the abundance of marcescent oaks saplings, which appeared to prefer drier sites.

Table 2. Coefficients for generalized linear mixed-effects models with log-link function of density of seedlings (per 6-m radius plot) of pine, evergreen oak, and marcescent oaks in 8 sampled black pine-dominated stands. See Table 1 for abbreviations.

Target	**Pine (*P. nigra*)**				**Evergreen oak (*Q. ilex*)**				**Marcescent oaks (*Q. faginea. Q. cerrioides*)**			
Fixed effects	**Est.**	**SE**	**t**	**Sig.**	**Est.**	**SE**	**t**	**Sig.**	**Est.**	**SE**	**t**	**Sig.**
Intercept	12.023	4.774	2.519	*	-12.720	1.880	-6.766	***	-4.787	1.412	-3.389	*
Site factors												
CURVATURE	-0.559	0.082	-6.849	***	0.369	0.038	9.643	***	-0.266	0.024	-10.924	***
NORTHNESS				NS	-1.673	0.154	-10.898	***				NS
MARTONNE	-1.075	0.082	-13.093	***				NS				NS
Stand structure & composition												
MATURITY	4.534	0.217	20.931	***				NS				NS
$G^{0.5}$	-0.354	0.043	-8.163	***	0.496	0.164	3.034	**	0.256	0.100	2.568	*
G				NS	-0.040	0.013	-2.960	**	-0.026	0.008	-3.209	**
$SHRUBS^{0.5}$				NS				NS	0.607	0.066	9.129	***
SHRUBS	-0.039	0.004	-10.756	***	0.004	0.001	3.011	**	-0.051	0.005	-10.193	***
SHRUBS *MGS	0.0012	0.0002	6.550	***				NS	0.00014	0.00007	2.223	*
$CO^{0.5}$	10.276	1.740	5.905	***	5.855	0.769	7.611	***	3.202	0.567	5.646	***
CO	-0.906	0.176	-5.157	***	-0.617	0.079	-7.784	***	-0.374	0.060	-6.279	***
GSI	-3.124	0.396	-7.895	***	-0.189	0.140	-1.353	NS	-0.802	0.094	-8.497	***
$MGS^{0.5}$	2.109	0.211	10.003	***	0.383	0.093	4.098	***	0.534	0.076	7.050	***
MGS	-0.528	0.052	-10.081	***	-0.077	0.017	-4.618	***	-0.135	0.019	-7.088	***
GSI*MGS	0.103	0.011	9.734	***	0.014	0.003	4.721	***	0.00015	0.00007	2.223	***
Random effects	**Est.**	**SE**	**Z**	**Sig.**	**Est.**	**SE**	**Z**	**Sig.**	**Est.**	**SE**	**Z**	**Sig.**
STAND Intercept	3.827	2.141	1.787	NS	0.315	0.176	1.795	NS	0.240	0.130	1.855	NS

Note: Est. = Estimate; SE = Standard Error; Sig. = Significance level (*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p \geq 0.05$).

Table 3. Coefficients for generalized linear mixed-effects models with a log-link function for sapling density (per 6-m radius plot) of pine, evergreen oak, and marcescent oaks in the 8 sampled black pine-dominated stands. See Table 1 for abbreviations.

Target	**Pine** **(*P. nigra*)**				**Evergreen oak** **(*Q. ilex*)**				**Marcescent oaks** **(*Q. faginea. Q. cerrioides*)**			
Fixed effects	**Est.**	**SE**	**t**	**Sig.**	**Est.**	**SE**	**t**	**Sig.**	**Est.**	**SE**	**t**	**Sig.**
Intercept	-1.777	2.651	-0.670	NS	-5.997	1.946	-3.081	**	-1.654	5.046	-0.328	NS
Site factors												
CURVATURE				NS	0.659	0.112	5.886	***				NS
NORTHNESS	0.974	0.176	5.535	***	-3.609	0.436	-8.272	***	-1.465	0.363	-4.030	***
MARTONNE	-0.193	0.040	-4.799	***				NS	-0.651	0.078	-8.299	***
Stand structure & composition												
MATURITY				NS				NS				NS
$G^{0.5}$	1.329	0.201	6.620	***	1.838	0.576	3.191	**				NS
G	-0.131	0.017	-7.734	***	-0.161	0.049	-3.290	***	-0.034	0.004	-7.801	***
$SHRUBS^{0.5}$	0.421	0.076	5.521	***				NS	1.517	0.298	5.097	***
SHRUBS	-0.049	0.006	-7.995	***				NS	-0.091	0.021	-4.389	***
SHRUBS*MGS				NS				NS				NS
Grel_BL	-2.065	0.644	-3.206	**				NS				NS
$CO^{0.5}$	3.360	0.993	3.385	***				NS	8.474	1.672	5.068	***
CO	-0.449	0.105	-4.258	***	0.097	0.015	6.327	***	-0.916	0.171	-5.355	***
GSI				NS				NS				NS
$MGS^{0.5}$	0.325	0.049	6.618	***	-0.229	0.059	-3.869	***				NS
MGS	-0.016	0.004	-3.688	***				NS				NS
GSI*MGS				NS				NS				NS
Random effects	**Est.**	**SE**	**Z**	**Sig.**	**Est.**	**SE**	**Z**	**Sig.**	**Est.**	**SE**	**Z**	**Sig.**
STAND Intercept	0.222	0.125	1.784	NS	0.769	0.441	1.745	NS	1.466	0.836	1.754	NS

Note: Est. = Estimate; SE = Standard Error; Sig. = Significance level (*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; NS = $p \geq 0.05$).

2.3.2. Effects of stand structure and composition

Total basal area of the plot and woody shrub cover were found to significantly affect the recruitment of all three species. Basal area exhibited a negative effect on abundance of pine seedlings but a quadratic effect (i.e. first positive, later negative) on abundance of evergreen and marcescent oak seedlings. Similarly, shrub cover showed a negative effect on the abundance of pine seedlings but a positive effect on oak seedlings (although the effect was quadratic for marcescent oaks). Interestingly, the effect of shrub cover on the density of pine seedlings was almost null in stands with large gaps, in which pine regeneration was always very low. Similarly, the negative effect of the shrub cover on the abundance of marcescent oaks seedlings was found to be attenuated in the case of large gaps, as shown by the significant interaction between shrub cover and gap size (Table 2, Figure 4). The regeneration models were not improved (in terms of BIC) by the inclusion of the visual estimates of the plot stoniness, the herbaceous or the moss cover for any of the species. Finally, MATURITY index was positively correlated to the density of pine seedlings but did not affect oak seedlings. Surprisingly, no compositional factors (i.e. relative abundance of evergreen oak, marcescent oaks or broadleaves in general in the overstory) were found to have a significant effect on abundance of seedlings of any of the species studied. Only the abundance of broadleaves in the dominant canopy emerged as a factor negatively affecting abundance of pine saplings.

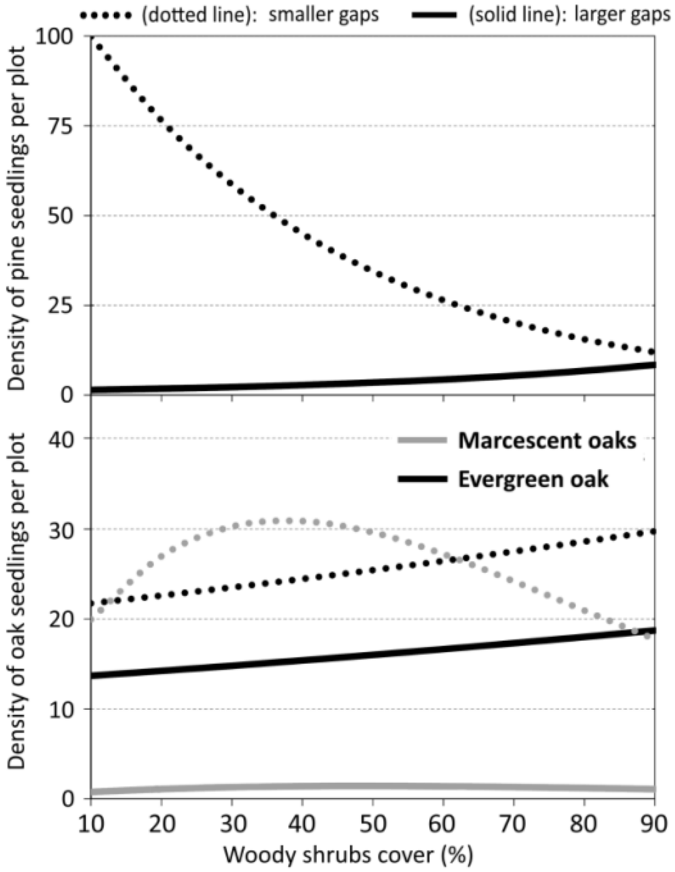

Figure 4. Expected density of seedlings as a function of woody shrub cover and mean gap size (MGS when smaller gaps = 10 m^2; MGS when larger gaps = 50 m^2), according to the models presented in Table 2. For variables other than SHRUBS and MGS, mean values are used (Table 1). Plots were 6-m radius.

All the gap attributes considered in the analysis showed significant effects on recruitment of all three species. Overall CO always showed a quadratic effect, revealing the existence of different optimal levels of CO depending on species. Gap attributes had wider effects on the abundance of young seedlings compared to saplings. In fact, only CO was found to modulate the abundance of the saplings of all three functional groups of species (Table 3). In the particular case of pines, CO values maximizing the abundance were significantly lower for saplings than for pine seedlings (Figure 6). Conversely, the effect of CO on abundance of evergreen oak saplings was positive and thus markedly different to its effect on the abundance of oak seedlings (Figure 6). Finally, the abundance of both young seedlings and saplings of marcescent oak showed a fairly similar quadratic response to CO. For a given CO, the density of seedlings of all the species was found to be higher under small canopy gaps, or large ones if irregularly shaped. Interestingly, the interaction between the mean shape and mean size of the gaps was found to be significant in all cases, with the most irregular gaps attenuating the general negative effect of large gaps on seedling recruitment (Figure 5). Overall, we found the marcescent oaks to be much more sensitive to large openings than the evergreen ones (Figure 5).

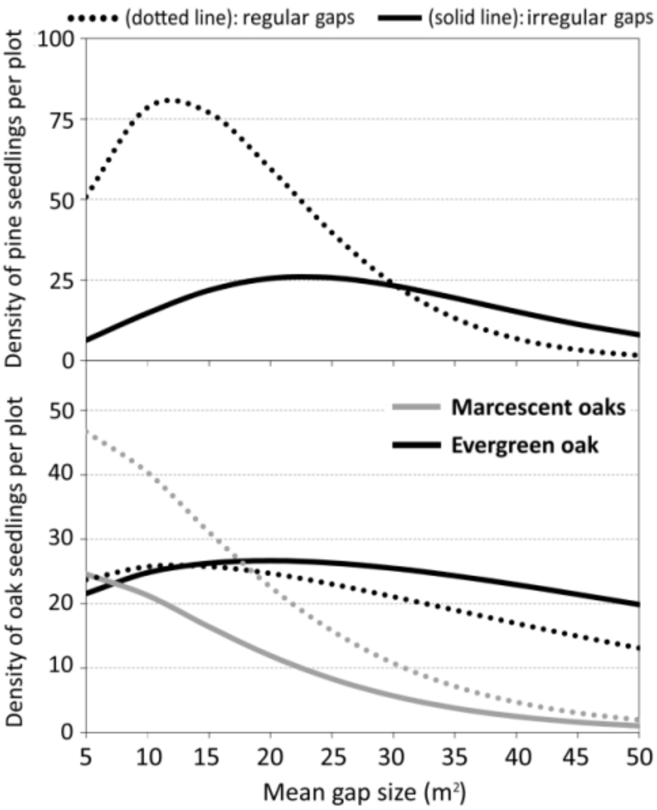

Figure 5. Expected seedling density as a function of mean gap size and mean gap shape (GSI when circular gaps = 1.6; GSI when irregular gaps = 2.4) according to the final models presented in Table 2. For variables other than MGS and GSI, mean values are used (Table 1). Plots were 6-m radius.

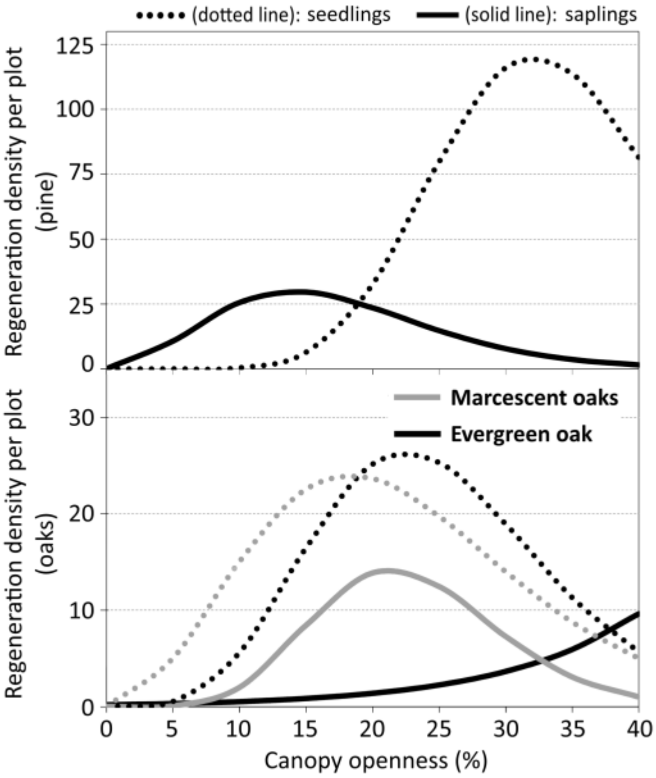

Figure 6. Expected regeneration density as a function of canopy openness (CO) according to the final models presented in Table 2 and Table 3. For variables other than CO, mean values are used (see Table 1).

2.3.3. Relative importance of site and stand structural attributes in driving tree-species regeneration

The final model for predicting the abundance of both seedlings and saplings of the studied functional groups included variables related to the environmental characteristics of the sites and to the structure and composition of the adult stands (Table 4). Most of the models produced unbiased estimates of regeneration density (i.e. slopes of predicted *vs*. observed density were all close to 1), with the exception of those related to pine seedlings and evergreen oak saplings which showed slope values of the predicted *vs* observed data of 0.92 and 1.22, respectively. The models predicting the abundance of oak regeneration (both seedlings and saplings) and pine saplings explained a percentage of variance in the data (i.e. adjusted-R^2) that was higher than 60%. However, our models did not adequately predict the presence of pine seedlings (adjusted-R^2 value of 0.25). The effect of stand structural variables was particularly important to explain pine and marcescent oaks regeneration (both seedlings and saplings), as indicated by the larger increase in BIC observed when the structural factors were dropped from the final models. In contrast, site factors explained the highest portion of the variance of evergreen oak abundance (Table 4).

Table 4. Comparison of the alternative models for the three target species using Bayesian Information Criterion (BIC). Final models are those presented in Tables 2 and 3; partial models are the same after extracting the variables of a given group; and null models only included the intercept in the fixed effects. Higher variation in BIC (ΔBIC) indicates stronger effect of the ignored group of factors. Final and partial models always fitted significantly better (P < 0.001) than the respective null models according to the likelihood ratio (LR) test.

Target		Final model			Null model	Partial models	
Group	Species	Slope (bias)	Adjusted R^2	BIC_{FM}	BIC_{NM}	ΔBIC_1 (no site)	ΔBIC_2 (no structure)
Seedlings	*Pine*	0.92	0.25	2,461.9	3,586.3	141.9.	1,117.3
	Evergreen oak	1.03	0.63	2,210.1	2,573.0	202.6	160.8
	Marcescent oaks	1.02	0.74	3,168.2	3,694.4	68.1	453.8
Saplings	*Pine*	1.04	0.67	2,132.1	2,694.3	34.8	546.3
	Evergreen oak	1.22	0.60	752.5	950.3	91.3	47.5
	Marcescent oaks	1.05	0.63	853.7	1,071.3	86.2	108.7

2.4. Discussion

2.4.1. Factors behind pine retreat

We found a scarcity of young *P. nigra* seedlings in the understory of the monitored stands, suggesting ongoing recruitment limitation processes in this species. The observed recessive trend in this species has already been reported for other areas of the Iberian Peninsula (e.g. Carnicer et al. 2014; Tiscar and Linares 2014; Urbieta et al. 2011) and has also been observed for other Mediterranean pines (Carnicer et al. 2014; Urbieta et al. 2011). One of the main factors likely triggering this regeneration decrease is the low light availability that characterizes the understory of most pine stands in the Mediterranean although other factors such as the presence of a competitive grass layer can also play an important role (Lucas-Borja et al. 2011; Prévosto et al. 2012). In the particular case of black pine, which is considered one of the most shade-tolerant European pine species (Niinemets and Valladares 2006), our models put the optimum CO for pine seedlings at around 30–35%, which is higher than the CO preferred by oak seedlings. Changes in land-use practices over the past few decades have notably affected the structure of most pine stands (Martin-Alcon et al. 2012; Montes et al. 2005) and may have worsened the conditions for their regeneration. In our study area, for example, we found higher density of pine seedlings in stands with a high presence of big trees (with *dbh* > 27.5 cm) but low basal area values. However, this type of mature moderately opened stand is fairly uncommon nowadays (Aunós et al. 2009) due to the generalized decrease of forest management that has led to active densification of the stands (Poyatos et al. 2003). These processes are relatively slow and have only recently reached density levels high enough to hinder pine recruitment, as indicated by the higher presence of pine saplings compared to young seedlings in the understory of the stands. Other factors, such as the increasing abundance of shrubs associated to a general decline in grazing by domestic livestock, may also act as an aggravating factor for black pine regeneration decrease (Tiscar and Linares 2014). Competition for light is probably at the origin of the observed negative effects of shrub cover on pine seedlings. Increasing abundance of the shrubby and herbaceous layer also contributes by creating an organic soil layer that acts as a physical barrier preventing fallen seeds from contacting the mineral soil, which is the most appropriate seedbed for pine germination (del Cerro Barja et al. 2009; Lucas-Borja et al. 2011). In this work we did not find a significant effect of the grass layer on pine and oaks regeneration, probably due the low variation found on this variable among the sample stands. Finally, we found a shift in both pine seedlings and saplings towards drier sites. This might be explained by the different temporal dynamics of the tree and shrub densification processes which occur more slowly in drier locations (Améztegui et al. 2010; Coop and Givnish 2007; Poyatos et al. 2003).

2.4.2. Factors driving tree-species diversification in black pine forests

Our analysis showed a progressive advance of broadleaved species recruitment (especially evergreen and marcescent oak species) under the pine canopy, consistently with trends observed by other authors (e.g. Carnicer et al. 2014; Coll et al. 2013; Urbieta et al. 2011; Vayreda et al. 2013). This process is mostly mediated by acorn dispersers such as jays which preferentially cache the acorns from neighboring seed sources in these formations (Gómez 2003). The very high abundance of young *Quercus* seedlings compared to saplings reveals the fairly recent origin of these processes and may be a response to two different drivers: (*i*) the relatively recent abandon of intensive grazing practices (Navarro-González et al. 2013; Zamora et al. 2010) and (*ii*) the ongoing densification of the forest stands and associated lack of light in the understory which prevents these shade-tolerant species (Niinemets and Valladares 2006) from thriving to more advanced developmental stages. Our results provide evidence of the important role that site factors play in the observed niche regeneration partitioning between evergreen and marcescent oaks, with evergreens being more competitive in harsher site conditions (i.e. south-facing slopes and shallower soils) while marcescents are more competitive in sites with higher soil moisture availability. In contrast, other variables related to stand structure and canopy attributes seem to very similarly affect regeneration rates of all oaks. Contrary to pines, shrubs were found to be a positive driver of oaks recruitment under the pine canopy. Oak recruitment largely depends on seed dispersers like jays and mice that cache acorns at suitable places, such as shrubs (Gómez 2003). Shrubs could also improve germination and emergence conditions and facilitate seedling survival by improving nutrient and water availability, reducing soil compaction, and offering protection against browsing by ungulates (Gómez-Aparicio et al. 2005;

Kunstler et al. 2007; Rousset and Lepart 1999; Smit et al. 2008). However, our results indicate that in some situations the shrubby layer can increase its development in terms of cover and biomass up to a point at which the positive effect on marcescent oak recruitment turns negative.

Despite their contrasting leaf habit, both evergreen and marcescent oak seedlings showed fairly similar preferences in terms of overall canopy openness, with maximum recruitment occurring at around 15–25% CO (which matches the average CO currently found in the monitored black pine-dominated stands; see Table 1). Several studies have described the relatively high moisture levels that *Q. ilex* requires to effectively germinate and establish (Broncano et al. 1998). These requirements are usually found under moderately-closed pine canopies, where the water status of the plants is generally improved through the protection provided by the overstory from direct exposure to light and high evaporative demands (Caldeira et al. 2014; Lookingbill and Zavala 2000; Retana et al. 1999). Interestingly, we found the evergreen and the marcescent oaks to have noticeable different preferences in terms of spatial distribution and morphology of gaps in the forest canopy. In the case of the marcescent oaks, seedling recruitment was found to be particularly important under small or irregularly shaped canopy gaps, confirming their high sensitivity to high light exposure found in stands with large and more regular (i.e. circular) openings (Gomez-Aparicio et al. 2008; Marañón et al. 2004). On the other hand, the evergreen oak's seedling bank was rather similar along the sampled gradient of gap sizes and shapes; which indicates its higher tolerance to direct light exposure, in agreement with what was previously reported in other mountain areas (Gomez-Aparicio et al. 2008).

Once the oak seedlings have established, the evergreen and marcescent oaks seem to have different environmental requirements in order to grow and reach more advanced developmental stages. Previous studies have shown higher height growth in young seedlings of evergreen oaks compared to marcescent ones under shade conditions (Gómez-Aparicio et al. 2006; Prévosto et al. 2011). However, the marcescents presented in general better performance suggesting that the stronger vertical growth of *Q. ilex* occurred at the expense of root growth and overall fitness. In our study, we found considerably higher density of saplings of the marcescent oaks (*Q. faginea*, *Q. cerrioides*) than the evergreen *Q. ilex* under the closed-canopy conditions that characterize most of the studied stands, which may suggest a higher capacity of the first for coping with low light levels (i.e. canopy openness). Under shade conditions, the established *Q. ilex* are nevertheless able to persist without significant net growth (Espelta et al. 1995; Garcia-Barreda and Reyna 2013), forming dense seedling banks and perpetuating through repeated shoot dieback and re-sprout until light conditions improve (Johnson 2009).

2.4.3. Management implications

Our study analyzes the factors driving the current tree-species diversification of long-term-managed *P. nigra* stands in the Catalan Pre-Pyrenees (NE Spain). These diversification processes are characterized by the gradual return of shade-tolerant broadleaved species, and are considered to enhance the capacity of these systems to adapt and respond to rapid environmental changes. In those areas where these processes do not occur naturally, forest managers could envisage practices designed to help generate a diversity of traits of responses to change (e.g. drought tolerance, seed mobility, resprouting ability) and promote functional redundancies (i.e. coexisting species with similar response traits, which would provide resilience in terms of maintaining productivity and other functions in the face of species loss). The results of our study bring insights into the role of a number of stand-level drivers that modulate these processes. This information can be used by forest managers to adjust their practices oriented to modify stand structure and canopy attributes in order to favor this natural diversification process and increase stand resilience to the various components of global change. In the particular case of Mediterranean *P. nigra* stands, we show current levels of both canopy closure and shrub cover are adequate to allow the establishment of *Quercus* seedlings but too high to permit pine regeneration. In addition, the low level of light reaching the understory hampers the growth of established oaks (particularly *Q. ilex*) which may prove unable to reach sapling and pole stages. If the densification of the pine canopy continues at the current rate, the light arriving at the understory will probably soon become too low to allow oak recruitment, in which case the currently active diversification process would likely slow until small-scale disturbances occur. According to our results, the application of frequent low-intensity selection cuttings could revert this process by helping to maintain an adequate amount of light for oaks seedlings to establish in the understory. If this type of management is applied in a heterogeneous way, with low to moderate variation of intensity along the stand, and it is accompanied by understory treatments such as partial shrub-layer removal, pine regeneration and growth and oak seedling development would be also favored and the future persistence of the mixed stand promoted.

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3

Combining aerial LiDAR and multispectral imagery to assess post-fire regeneration types in a Mediterranean forest

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Santiago Martín-Alcón, Lluís Coll, Miquel De Cáceres, Lídia Guitart, Mariló Cabré, Ariadna Just and José Ramón González-Olabarría

3. Combining aerial LiDAR and multispectral imagery to assess post-fire regeneration types in a Mediterranean forest

Abstract

Wildfires play a major role in driving vegetation changes and can cause important environmental and economic losses in Mediterranean forests, especially where the dominant species lacks efficient post-fire regeneration mechanisms. In these areas, post-disturbance vegetation management strategies need to be based on detailed, spatially continuous inventories of the burned area.

Here, we present a methodology in which we combine airborne LiDAR and multispectral imagery to assess post-fire regeneration types in a spatially continuous way, using a Mediterranean black pine (*Pinus nigra* Arn ssp. *salzmannii*) forest that burned in 1998 as a case study.

Five post-fire regeneration types were obtained by clustering field-plot data using Ward's method. Two of the five regeneration types presented high tree cover (one clearly dominated by hardwoods and the other dominated by pines), a third type presented low to moderate tree cover, being dominated by hardwoods, and the remaining two types matched to areas dominated by soil–herbaceous or shrub layers with very low or no tree cover (i.e., very low to no tree species regeneration). These five types of regeneration were used to conduct a supervised classification of remote sensing data using a nonparametric supervised classification technique. Compared with independent field validation points, the remote sensing based assessment method resulted in a global classification accuracy of 82.7%.

Proportions of regeneration types in the study area indicated a general shift from the former pine-dominated forest toward hardwood dominance and showed no serious problems of regeneration failure. Our methodological approach appears to be appropriate for informing post-disturbance vegetation management strategies over large areas.

Keywords: post-fire regeneration types, remote sensing data, wildfire effects, post-disturbance management, *Pinus nigra.*

3.1. Introduction

Wildfires have been the most important natural disturbance in Mediterranean ecosystems since at least the late Quaternary (Carrión et al. 2010; Pausas et al. 2008). In the Mediterranean region, humans have lived with fire and used it in their agricultural and rural activities for millennia. However, in the last midcentury, there has been an increase in the number of ignition sources, causing an increase in fire risk and in the frequency of uncontrolled fires (González-Olabarría and Pukkala 2007; San-Miguel-Ayanz et al. 2013; Schelhaas et al. 2003). This increase has been attributed to a combination of factors that are related to, among others, land abandonment, the increase in the number of days with extreme fire hazard weather, and the increasing number of human-related ignition sources (Loepfe et al. 2010). In the Iberian Peninsula, large wildfires (>500 ha) have hit almost every type of forest ecosystem over the last decades, representing almost one-half of the total burnt area during this period (Cubo María et al. 2012). This scenario of increased fire impacts may be further magnified in the future, as climate forecasts point to prolongation of droughts and hot spells, which are likely to further aggravate forest fire risk (Keenan et al. 2011; Lindner et al. 2010; Piñol et al. 1998; Resco de Dios et al. 2006).

In addition to changes in fire frequency and extent, some areas have suffered an increase in the occurrence of high-intensity crown fires, affecting forest types that had not historically been subject to fires such as the montane (sub-Mediterranean) forests dominated by Mediterranean black pine (*Pinus nigra* Arn ssp. *salzmannii*) or Scots pine (*Pinus sylvestris* L.) (Ordoñez and Retana 2004; Pausas et al. 2008; Vilà-Cabrera et al. 2012). These pine species lack direct postfire regeneration mechanisms and usually show almost no regeneration after crown fires (Pausas et al. 2008). In these areas, substitution of the pines by resprouting hardwoods (mostly *Quercus* species) is generally observed when the latter were present in the understory of the burnt stands (Puerta-Piñero et al. 2011; Rodrigo et al. 2004). In the particular case of *P. nigra* forests, the thick bark and high self-pruning ability of this species allow for the persistence of some surviving trees in the form of small islands interspersed across the burned landscape (Ordoñez et al. 2005). The existence of such islands, together with the moderate shade tolerance of this species (Niinemets and Valladares 2006), may lead to greater opportunities for its mid- to long-term colonization of the burned area. In contrast, in the areas without the presence of sprouting species or remaining trees, important problems of soil recovery by woody vegetation are likely to arise, leading to increased soil erosion and forest degradation and causing long term environmental and economic damage (Selkimäki et al. 2012).

Several factors inherent to forests in the Mediterranean basin such as the small size of forest ownership, slow growth rate due to limited water availability, or the dominance of mountainous terrain raise the cost of forestry operations and hamper the development of management actions (European Forest Institute (EFI) 2010; González-Olabarría et al. 2008), including post-fire restoration measures (Espelta et al. 2003a). These impediments may be, in part, tempered if detailed, spatially continuous assessments directed to classify the burned area by regeneration success, vegetation types, and (or) management are available (Vallejo et al. 2012). However, the extent of these types of disturbances makes these detailed, spatially continuous assessments often unattainable through field data gathering. Thus, the general approach that is used to run post-fire assessments usually involves implementing a statistical sampling design to decide the location of inventory plots

(Pausas et al. 2004; Proença et al. 2010; Puerta-Piñero et al. 2012; Shatford et al. 2007) and then applying modeling (i.e., extrapolation) techniques. The use of remote sensing (RS) data has recently emerged as an efficient alternative to provide adequate regeneration assessments over large areas that are affected by forest disturbances. In this line, some recent studies have used indicators like the normalized difference vegetation index (NDVI) (Tucker 1979), extracted from satellite imagery, to evaluate short term regeneration success and recovery rates in terms of the total plant cover (Belda and Meliá 2000; Diaz-Delgado et al. 2003; Gouveia et al. 2010; van Leeuwen et al. 2010; Viedma et al. 1997; Vila and Barbosa 2010), even distinguishing the cover of woody shrubs or tree species regeneration (Riaño et al. 2002; Vicente-Serrano et al. 2011).

From an operational point of view, the value of these post-disturbance regeneration assessments might significantly increase if they were complemented with data that described the structure of the vegetation (e.g., relative cover of the different strata or functional groups, etc.). In relation to this, light detection and ranging (LiDAR) has recently emerged as a powerful tool for characterizing such structural attributes (Lefsky et al. 2002; Wulder et al. 2012) and holds great potential for evaluating medium- to long-term post-disturbance regeneration (Debouk et al. 2013; Johnstone et al. 2004). Combining LiDAR data with multispectral images could further improve the assessment of post-fire vegetation by making it possible to accurately characterize low vegetation attributes (Erdody and Moskal 2010; Riaño et al. 2007) and to identify individual tree species (Hill et al. 2010; Holmgren et al. 2008; Waser et al. 2011). It also enables the identification of vegetation typologies (Bork and Su 2007; Goetz et al. 2010; Mutlu et al. 2008), which may be especially appropriate in the case of low-resolution data. Typological characterization of forest stands for management purposes has been widely used on adult forest stands (e.g., Aubury et al. 1990; Herbert and Rebeirot 1985; Martín-Alcón et al. 2012; Reque and Bravo 2008), providing detailed, objective classifications of the stands according to their structural and floristic attributes. In the case of regenerating forest stands, such attributes are expected to largely influence the long-term dynamics of the forest and its accompanying ecosystem services (Elmqvist et al. 2003).

The aim of this study was to develop and test a simple, cost-effective methodology for conducting a detailed, spatially continuous characterization of post-fire regeneration (i.e., recovery of vegetation cover) from widely available RS data, using a large forest fire in the Mediterranean basin as a case study. To this purpose, we defined and mapped the main post-fire regeneration types in the study area using a combination of low-resolution airborne LiDAR data (useful for characterizing the three-dimensional structure of plant canopies) and NDVI data, computed from multispectral data from aerial images, potentially suitable for differentiating between species groups with different spectral signatures. We applied this methodology to the particular case of a large wildfire in a Mediterranean zone, but we anticipate that it could be easily adapted to assess vegetation responses to other forest disturbances and a wide range of forest ecosystems such as large-scale disease outbreaks or wind-throw events.

3.2. Material and methods

The methodological approach adopted to assess post-fire regeneration types based on RS data can be summarized in the following steps: (*i*) RS data processing (raw LiDAR data and raw NDVI data), (*ii*) establishment and measurement of a set of field inventory plots located in two subsets of the study area (training areas), (*iii*) selection of the most informative RS variables to be used as candidate predictors, (*iv*) definition of alternative post-fire regeneration typologies based on training field data, (*v*) selection of a regeneration typology on the basis of the classification accuracy of a supervised classification model using RS variables, (*vi*) extrapolation of the regeneration typologies to the whole study area through the application of the corresponding supervised classification model, and (*vii*) validation of the resulting classification using a set of observation points randomly located across the study area (validation stands) (Figure 1).

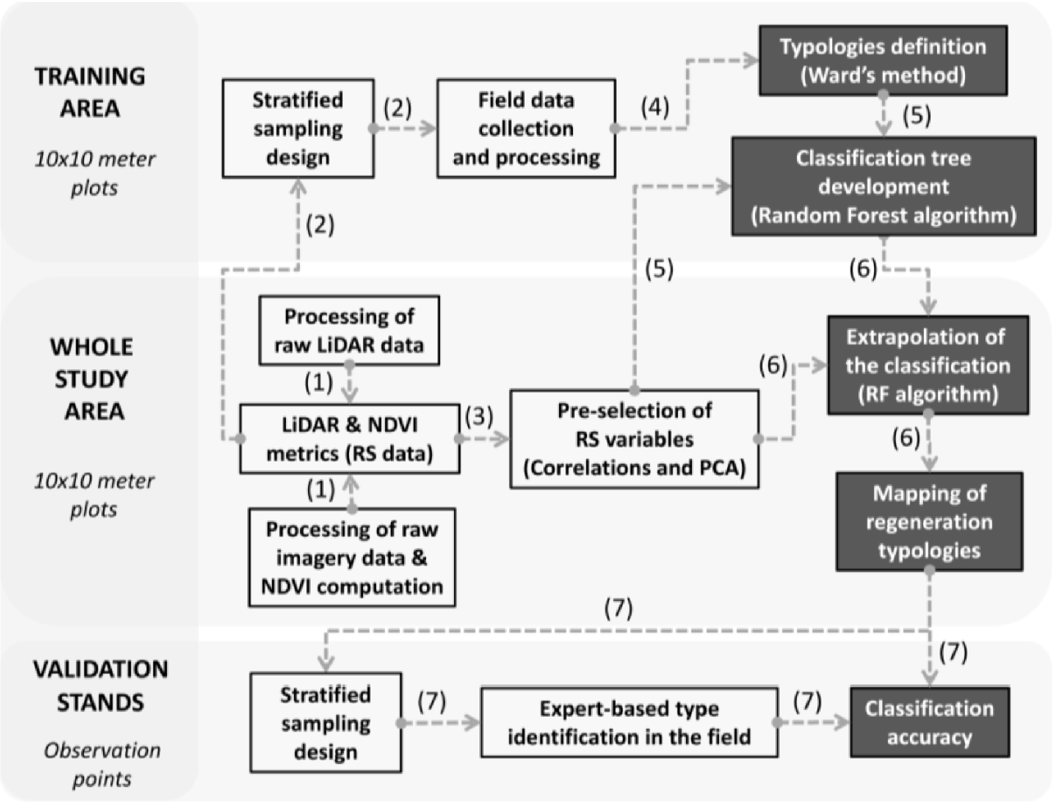

Figure 1. Flowchart depicting schematically the methodological approach. Numbers indicate the step order.

3.2.1. Study area

The study was conducted in an area affected by a large forest fire in the central region of Catalonia (northeastern Spain). This wildfire burned nearly 24 000 ha in 1998 (Figure 2), leading to almost complete loss of forest cover (Rodrigo et al. 2004). Prior to the wildfire, the area was composed of the typical Mediterranean mosaic-like landscape, with cultivated lands and scrublands (7700 ha and 2000 ha, respectively) interspersed with forest areas (14 000 ha). According to data in the Forest Ecological Inventory of Catalonia (Burriel et al. 2004), the dominant species before the wildfire was black pine, which covered 75% of the total forest surface. Aleppo pine (*Pinus halepensis* Mill.) was the second most abundant species, covering 15% of the forest surface. Both black pine and Aleppo pine forests appeared as pure stands or as two-layered stands in which pine dominated the overstory and resprouting hardwoods dominated the understory (Figure 2). The remaining forest surface was mainly covered by mixed hardwoods (mainly *Quercus ilex* L. and *Quercus cerrioides* Willk. & Costa) and *Pinus sylvestris* L. stands. The area presents a gentle relief with low hills ranging in elevation from 480 to 910 m above sea level (a.s.l.) and a dry–subhumid to subhumid Mediterranean climate, according to the Thornthwaite index.

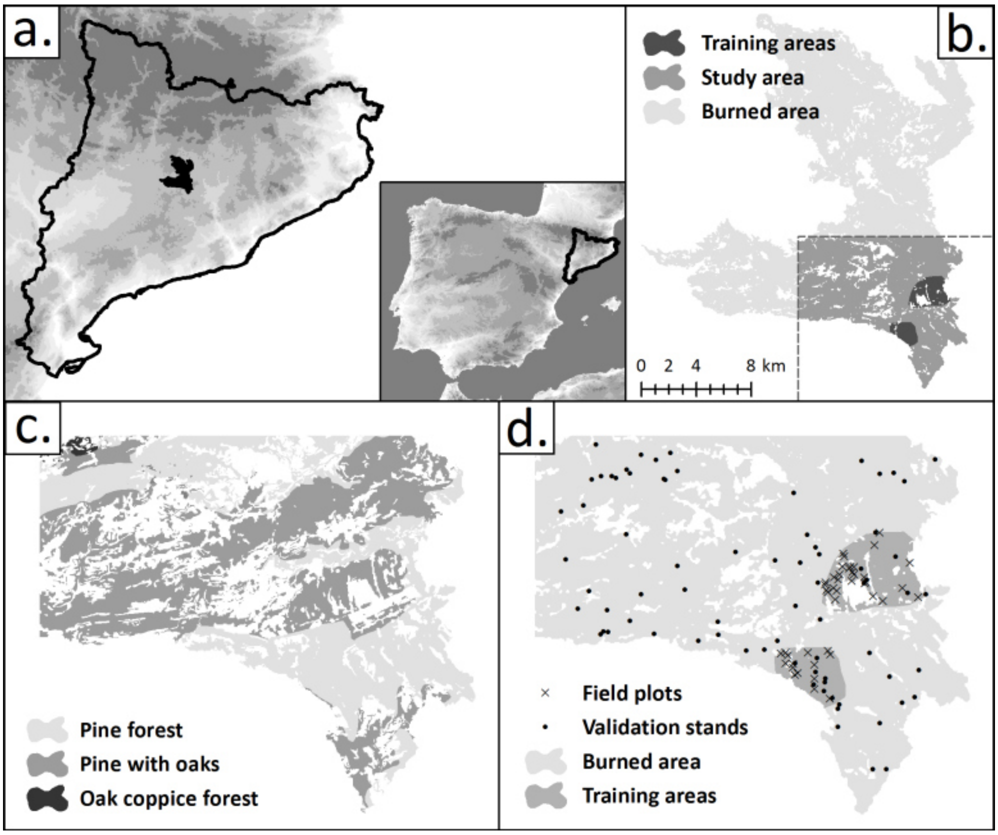

Figure 2. Location and boundaries of (a) the wildfire location in the Iberian Peninsula and Catalonia region, (b) the study area and the calibration areas within the wildfire zone, (c) the dominant forest types in the study area before the 1998 wildfire (Centre for Ecological Research and Forestry Applications (CREAF) 1993; Dirección General de Conservación de la Naturaleza (DGCN) 2001), and (d) the field plots and the validation stands within the study area.

From the total forest area that was affected by the 1998 wildfire, we selected a portion of 3,973 ha that had burned at high severity (i.e., with no remaining adult trees) (Figure 2). Areas affected by roads, agricultural fields, and other non-forest uses were excluded from the analysis, leaving a total of 3,192 ha to be used for the post-fire regeneration assessment. Additional criteria to determine the study area were the characteristics of the available RS data, as a minimum seasonal similarity in both LiDAR data and aerial images was required to avoid potential mismatches due to the use of data from different seasons (e.g., before and after budbreak in broadleaves). In our particular case, the LiDAR data were taken in the early summer of 2009 and the aerial photographs were taken in the early spring of 2011.

3.2.2. LiDAR data acquisition and processing

LiDAR data were acquired via the LidarCAT project (Cartographic and Geological Institute of Catalonia). The entire study area was covered by seven flight lines, and data were captured with an ALS50 II LiDAR sensor that was mounted on a Cessna Caravan 208B aircraft. The flight dates ranged from 30 May 2009 to 3 June 2009. The mean first-return point density of these LiDAR data was 0.5 pulses·m^{-2}, and each pulse captured up to four returns. LiDAR point coordinates were adjusted according to the methodology proposed by Kornus and Ruiz (2003). After filtering the clouds, low-intensity returns, and air points, LiDAR returns were automatically classified with the TerraScan ground classification routine (Terrasolid 2012) to differentiate ground from non-ground returns. Ground routine classified ground points by iteratively building a triangulated surface model. The routine started by selecting some local low points that are confident hits on the ground. It was assumed that any 40 m × 40 m area would have at least one hit on the ground and that the lowest point would be a ground hit. This routine built an initial model and started molding the model upwards by iteratively adding new laser points to it. Each added point made the model follow the ground surface more closely. Iteration parameters of angle (4°) and distance (1 m) determined how close a point must be to a triangle plane to be accepted as a ground point and added to the model. The remaining non-ground points were visually inspected and manually classified to extract wires and towers (as the low point density of the LiDAR data advised against the implementation of automatic algorithms for this purpose). Building roofs were extracted automatically using a new routine that classified non-ground points that formed a planar surface of at least 40 m^2. Finally, the remaining non-ground returns were classified as vegetation, and LiDAR height was replaced by its vertical distance to a triangular irregular network generated from ground returns.

The LiDAR vegetation point cloud was analyzed in a 10 m × 10 m regular grid with the FUSION software system (McGaughey and Carson 2003) to obtain structured statistical information on the laser returns. A height of 0.15 m, predefined from the vegetation field inventory, was used as a threshold to separate woody and shrubby vegetation from herbaceous vegetation and bare soil. Intensity data were normalized by the range normalization to a user-defined standard range (Donoghue et al. 2007; García et al. 2010):

$$(1) \qquad I' = I\frac{R^2}{R_S^2}$$

where I' is the normalized intensity, I is the raw intensity value, R is the range (LiDAR sensor–target distance), and R_S is the standard range (in this case, 2,225 m, which corresponds to the mean range in the study area). This method eliminated the effect of path length variations on the intensity recorded by the system, providing values equivalent to the intensity that would have been recorded if all points were at the same range. The exact value of the range was not available for each LiDAR point; therefore, it was approximated by the use of the difference between the mean altitude of the flight and the elevation of each point and the projected distance between the point and the flight line. This approach should cause smaller errors than the option of using the altitude difference instead of the actual range (Coren and Sterzai 2006; Kukko et al. 2008). Only the first echoes that were returned from the aboveground vegetation were used for computing a set of LiDAR height and intensity metrics suitable to characterize forest vegetation structure and floristic composition (e.g., Donoghue et al. 2007; García et al. 2010; Holmgren et al. 2008; Latifi et al. 2012; Morsdorf et al. 2006). These metrics were the following: (*i*) percentiles of pulse height (H_P05, H_P10, H_P20, …, H_P80, H_P90, and H_P95) and pulse intensity (Int_P05, Int_P10, Int_P20, …, Int_P80, Int_P90, and Int_P95); (*ii*) mean (H_MEAN and Int_MEAN), mode (H_MODE and Int_MODE), standard deviation (H_SD and Int_SD), coefficient of variation (H_CV and Int_CV), interquartile range (H_IQ and Int_IQ), skewness (H_Sk and Int_Sk), and kurtosis (H_Kur and Int_Kur) of both pulse height and pulse intensity values. In addition, the following three ratios were generated: percentage of vegetation points (height > 0.15 m) in relation to all first returns (FR_VEG), percentage of vegetation points in relation to all returns (AR_VEG), and percentage of first returns above the mean (FR_abMEAN) and the mode (FR_abMODE) height.

3.2.3. Multispectral image acquisition and processing

NDVI imagery were obtained from the Cartographic and Geological Institute of Catalonia annual coverage flights at a ground sample distance of 22 cm and were generated from aerial photos with RGB (red, green, and blue) and near-infrared bands. The aerial photos were taken between 2 April 2011 and 10 April 2011 with digital mapping cameras (DMCs) DMC-26 and DMC-14 and were later ortho-rectified without stitching. The implemented procedure to produce NDVI from DMC imagery used the original DMC LR4 series files (low-resolution multispectral bands) with absolute radiometric calibration and was based on the manufacturer's calibration of the DMC, following the methodology proposed by Martínez et al. (2012). Radiance values from the red and near-infrared bands and their respective reflectances (i.e., ratio between incoming energy from the sun and reflected energy modulated by some geometric factors such as location, date, and time of exposure during acquisition) were obtained for each pixel using the following equations:

$$(2) \qquad R = \frac{\pi\, L_R}{\mu\, E_O}$$

$$(3) \qquad NIR = \frac{\pi\, L_{NIR}}{\mu\, E_O}$$

where R and NIR correspond to the reflectance values of each pixel from the red and the near-infrared bands, respectively, L_R and L_{NIR} are radiance values from the red and the near-infrared bands, μ is a geometric factor, and E_0 is the extraterrestrial solar radiation. Then, NDVI was calculated using the following equation:

$$(4) \qquad NDVI = \frac{(NIR - R)}{(NIR + R)}$$

NDVI values were then aggregated to match the same 10 m × 10 m grid as used to aggregate the LiDAR data, and a set of NDVI statistics potentially suitable to describe regeneration structure and composition was calculated. For the NDVI distribution, the quartiles (NDVI_Q1, NDVI_Q2, and NDVI_Q3), interquartile range (NDVI_IQ), mean (NDVI_MEAN), coefficient of variation (NDVI_CV), and standard deviation (NDVI_SD) were obtained. NDVI values in the regenerating area generally ranged between 0 and 0.6. On this basis, the portion of each 10m× 10mcell presenting NDVI values within a variety of subranges were computed, using 0.05 increments (0.15–0.2, …, 0.55–0.6), 0.10 increments (0.15–0.25, …, 0.45–0.55), and 0.15 increments (0.15–0.3, 0.3–0.45, and 0.45–0.6) to maximize the chance of differentiating species or groups of species based on their different NDVI values.

3.2.4. Field data gathering

A field inventory was performed to define post-fire regeneration types. The inventory consisted of a set of forty-four 10 m × 10 m plots placed along two sub-areas that were considered to be representative of the overall study area (hereafter training areas) (Figure 2). Stratified random sampling was applied to capture the range of regeneration patterns in the training areas. For this purpose, LiDAR variables that were expected to describe plant height distribution and the distance to unburned patches were used to ensure that we covered both the structural (relative abundance of trees) and compositional (as pines are expected to be more abundant near the unburned patches) gradients characterizing the postfire vegetation. For each plot, a set of variables describing the floristic composition and aboveground biomass structure were measured. These were the percentage of the plot area covered by soil or herbs (%SOIL), low shrub species (0.15–0.5 m tall; %LOW SHRUBS), high shrub species (>0.5 m tall; %HIGH SHRUBS), pine regeneration (%PINES), and tree species regeneration (i.e., refers to all trees species, including pines; %TREES). Low and high shrub covers were later summed as %SHRUBS. We also measured mean height (cm) of all tree species (HTREES), pines (HPINES), and hardwoods (HHW). To improve the accuracy of the measured vegetation variables, each 10 m × 10 m plot was subdivided into 2.5 m × 2.5 m subplots. The variables were measured at the subplot level and converted into plot-level values by averaging the values of the measured subplots within each plot.

3.2.5. RS data reduction

A first preselection of the 64 LiDAR- and NDVI-derived variables that were initially considered was executed to avoid using redundant variables as candidate predictors. Principal component analysis with a Varimax rotation was executed on the whole set of RS data to identify groups of highly collinear variables. In parallel, we computed Pearson correlation coefficients to measure the associations between RS variables and the list of forest variables measured in the field plots. A total of 14 variables from the original 64 variables were finally preselected. These variables were the ones showing the highest correlation with field variables among each group of highly collinear variables (i.e., variables with very similar principal component analysis factor loadings). They comprised five height metrics (coefficient of variation, kurtosis, 10th and 95th percentile height, percentage of first returns of vegetation, and percentage of first returns above the mode of the height distribution), three LiDAR intensity metrics (standard deviation and 50th and 90th percentile intensities), and five NDVI-derived variables (1st quartile NDVI and percentage of plot with NDVI between 0.45 and 0.5, between 0.25 and 0.35, between 0.15 and 0.3, and between 0.45 and 0.6).

3.2.6. Definition of post-fire regeneration types

A subset of the variables measured in the field (%SOIL, %PINES, and %TREES) was deemed sufficient to define post-fire regeneration types, as they described the distribution of the plot cover among the main strata (soil–herbs, trees, and indirectly, shrubs) and the main floristic groups of the tree layer (pines and hardwoods). The 44 training plots were clustered according to their squared Euclidean distances using Ward's hierarchical method (Ward 1963) based on these variables. Several alternative partitions of the resulting dendrogram (i.e., those exhibiting high between-group distance (Hair et al. 2009) and strong ecological rationale) were saved.

3.2.7. Development of the classification model

We used preselected RS variables from the field plots and the Random Forest (RF) classification algorithm (Breiman 2001) to evaluate the different partition alternatives and to obtain a model for the classification of the whole study area. RF is a nonparametric, supervised classification technique that has shown good performance in classifying remotely sensed data (e.g., Falkowski et al. 2009; Hudak et al. 2012). The RF technique uses a bootstrap approach for achieving higher accuracies while simultaneously addressing over-fitting problems associated with traditional classification tree models. A large number of classification trees are produced from a random subset of training data (approximately 63% for a random subset), permutations are introduced at each node, and the most common classification result is selected. We ran each RF model with 5,000 bootstrap replicates (i.e., individual classification trees). With the goal of avoiding bias in the prediction caused by imbalanced classes, the number plots per class in bootstrap samples was equal to the number of plots of the less frequent class (Evans and Cushman 2009). Out-of-bag (OOB) error estimates were calculated for each tree by classifying the portion of training data not selected in the bootstrap sample, and overall accuracy was calculated by averaging error rates across all trees in the model; this is analogous to cross-validated accuracy estimates (Cutler et al. 2007).

A model-selection procedure (i.e., variable reduction) was employed to select the optimal RS variables to use in the classification of post-fire regeneration types. The procedure was formulated to develop the most parsimonious classification model while retaining the highest possible classification accuracy. We ran a RF model-selection function that uses model improvement ratio (MIR) standardized importance values (Evans et al. 2011; Evans and Cushman 2009) to objectively choose the most important RS variables for predicting the regeneration type of each plot. The MIR uses the permuted variable importance, represented by the mean decrease in OOB error, standardized from zero to one. The variables were subset using 0.10 threshold increments on the original model's variable importance, with all variables above the threshold retained for each model. Each subset model was compared, and the model that exhibited the lowest total OOB error and lowest maximum within-class error was selected. After selecting the best model for each one of the different alternative partitions, we determined the final regeneration typology as that whose classification model had obtained the highest classification accuracy. For this study, the RF algorithm was implemented using the RandomForest package (Liaw and Wiener 2002) in the R statistical program (R Development Core Team 2007).

3.2.8. Mapping of regeneration types and field-based validation

Each 10 m×10 m plot in the study area was classified into one of the regeneration types by applying the final classification model on the RS variables. Regeneration types were then mapped and a set of landscape metrics were generated for explaining the spatial configuration of the landscape according to the distribution of regeneration patches. These size- and shape-related metrics were the area and percentage covered by each regeneration type, the percentage of the type area by patch size classes, the mean patch size (PS_m) and its coefficient of variation (PS_{cv}), and the mean shape index (MSI), as defined by Rempel et al. (2012).

The validity of the final classification for the whole study area was evaluated by comparing the regeneration type assignations made from the supervised classification of RS data (using the classification model generated by RF) with visual assessments obtained in the field. For this purpose, 15 sampling points per regeneration type were distributed along the study area using stratified random sampling (Figure 2). An independent user was asked to assign each of these stands to one of the regeneration types, based on a visual examination of the stand characteristics, using the type descriptions in terms of forest variables (see Table 1 and Figure 3) as a guide. Measures of height and cover of the different vegetation strata were taken when visual estimation was not obvious. Finally, a confusion matrix was generated to estimate the accuracy of the RS-based assignations with respect to the visually based assignments.

3.3. Results

3.3.1. Post-fire regeneration typologies

The dendrogram resulting from the application of Ward's clustering method on the variables measured in the 44 field plots[4] led to three possible choices for the placement of the cut-off point of the hierarchical tree (i.e., three partition alternatives), creating a four-type, five-type and six-type partitions. By comparing the classification accuracy of the models developed using RF for the four-, five-, and six-type partitions, we found the five-type partition to be the best in terms of overall accuracy, with 79.55% of the plots being correctly classified (i.e., OOB error estimate rate, 20.45%) with the use of six RS variables as predictors. The four-type[5] and six-type[6] partitions presented accuracies of 75% and 71.45%, respectively, and neither of them selected less than six RS variables as predictors. Therefore, the five-type partition was selected as the basis for representing the regeneration types (Table 1). The characteristics of the five regeneration types were as follows: type 1, characterized by a very low vegetation cover; type 2, characterized by very low tree regeneration but remarkable shrubs abundance; type 3, included hardwoods in low to moderate cover mixed with shrubs; type 4, presented high cover of hardwood regeneration; type 5, consisting of stands dominated by pine regeneration in moderate to high cover (Table 1; Figure 3).

Table 1. Descriptive statistics (mean (standard deviation)) of the main field variables for each of the regeneration types obtained in the five-type classification generated by Ward's clustering method.

Type	n	%SOIL	%LOW SHRUBS	%HIGH SHRUBS	%TREES	%PINES	HHW (cm)	HPINES (cm)
1	5	54.11 (10.21)	39.11 (10.91)	3.21 (1.21)	3.61 (5.31)	0.41 (0.31)	84.31 (111.61)	55.91 (62.71)
2	5	28.71 (5.01)	39.91 (18.51)	24.41 (19.21)	7.01 (4.51)	1.91 (2.71)	125.61 (116.71)	130.91 (125.91)
3	11	26.61 (6.61)	28.41 (11.11)	10.11 (7.31)	34.91 (7.81)	7.71 (7.81)	272.41 (104.31)	122.61 (71.01)
4	10	14.81 (6.11)	17.41 (6.51)	14.71 (13.31)	53.11 (9.51)	6.61 (6.81)	361.61 (67.91)	119.81 (60.41)
5	13	13.71 (5.81)	20.91 (14.31)	8.51 (9.51)	57.01 (17.31)	45.41 (16.51)	215.51 (145.51)	206.11 (53.61)

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[4] Figure 1S in Supplementary material

[5] Table 1S in Supplementary material

[6] Table 2S in Supplementary material

The following six RS variables were selected to identify the five regeneration types: the 10th and 95th percentile height (H_P10 and H_P95, respectively), the percentage of first returns above the mode of the height distribution (H_abMODE), the coefficient of variation of the height distribution (H_CV), the 1st quartile NDVI (NDVI_Q1), and the percentage of plot with NDVI between 0.15 and 0.3 (NDVI_15_30) (Figure 4). OOB classification accuracies of the RF model by regeneration type were 80% for type 1, 100% for type 2, 81.8% for type 3, 70% for type 4, and 76.9% for type 5.

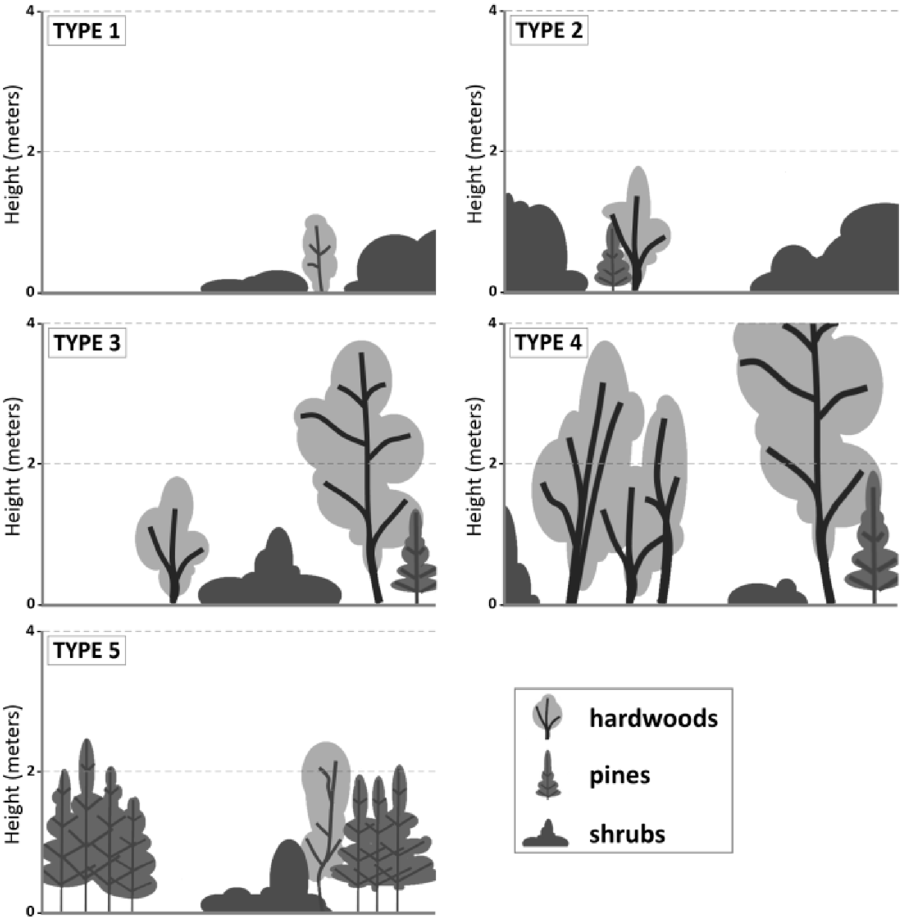

Figure 3. Schematic interpretation of the 56 post-fire regeneration types obtained from Ward's clustering method. Regeneration types are as follows: type 1, defective cover of woody vegetation; type 2, dominance of shrub cover; type 3, hardwoods, low–moderate cover; type 4, hardwoods, high cover; type 5, pines, moderate–high cover.

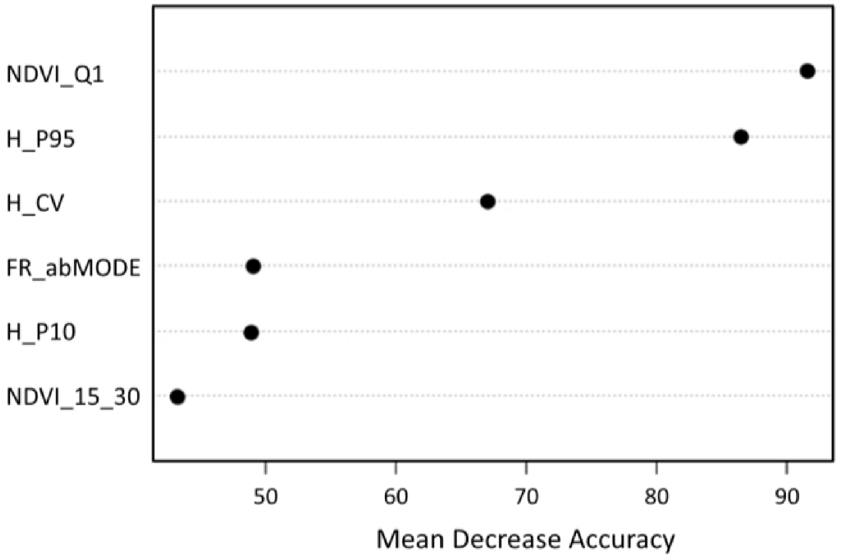

Figure 4. Variable importance plot for the for the five-type classification model of post-fire regeneration types. Higher values of mean decrease accuracy represent higher variable importance in the model. See Materials and methods for variable definitions.

3.3.2. Mapping post-fire regeneration types and validation with visual estimates

The whole study area (3191.8 ha) was classified into the five regeneration types (Figure 5). More than a decade after the wildfire, almost one-half of the area (42.6%) showed high tree cover, with a clear dominance of resprouting hardwoods (type 4). About 17% of the study area was still dominated by resprouting hardwoods but with low to moderate tree cover (type 3). Pine regeneration appeared in moderate to high cover in approximately 11% of the study area. Finally, the rest of the area showed sparse or no tree regeneration (type 2 and type 1, respectively) (Table 2). Patches of type 1 and type 3 were usually very small (i.e., with an area smaller than 0.1 ha), with type 1 showing the most regular patch shape (i.e., closer to a circular shape). In contrast, type 4 had the highest amount of area covered by large patches (0.1–1 ha, 1–5 ha, and >5 ha) and showed the most irregular shapes. Type 2 and type 5 were also present in a wide range of patch sizes, but in them, small patches were more common than in type 4.

The evaluation of classification accuracy compared with visual estimation resulted in 82.7% accurately classified plots (between 74.1% and 91.2% were accurately classified with a 95% confidence interval), being close to the OOB classification accuracy obtained for the training dataset. Type 1 and type 5 showed the highest classification accuracy, at 93.3% (95% confidence interval, 80.7%–100%) and approximately 92.3% (77.8%–100%), respectively. The classification of type 4 was also highly accurate, with 84.6% (65%–100%) of plots accurately classified. Finally, type 2 (shrub dominance with very low tree cover) and type 3 (low to moderate tree cover dominated by hardwoods) reported lower classification accuracies, with 72.2% (51.5%–92.9%) and 75% (53.8%–96.2%) of plots accurately classified, respectively.

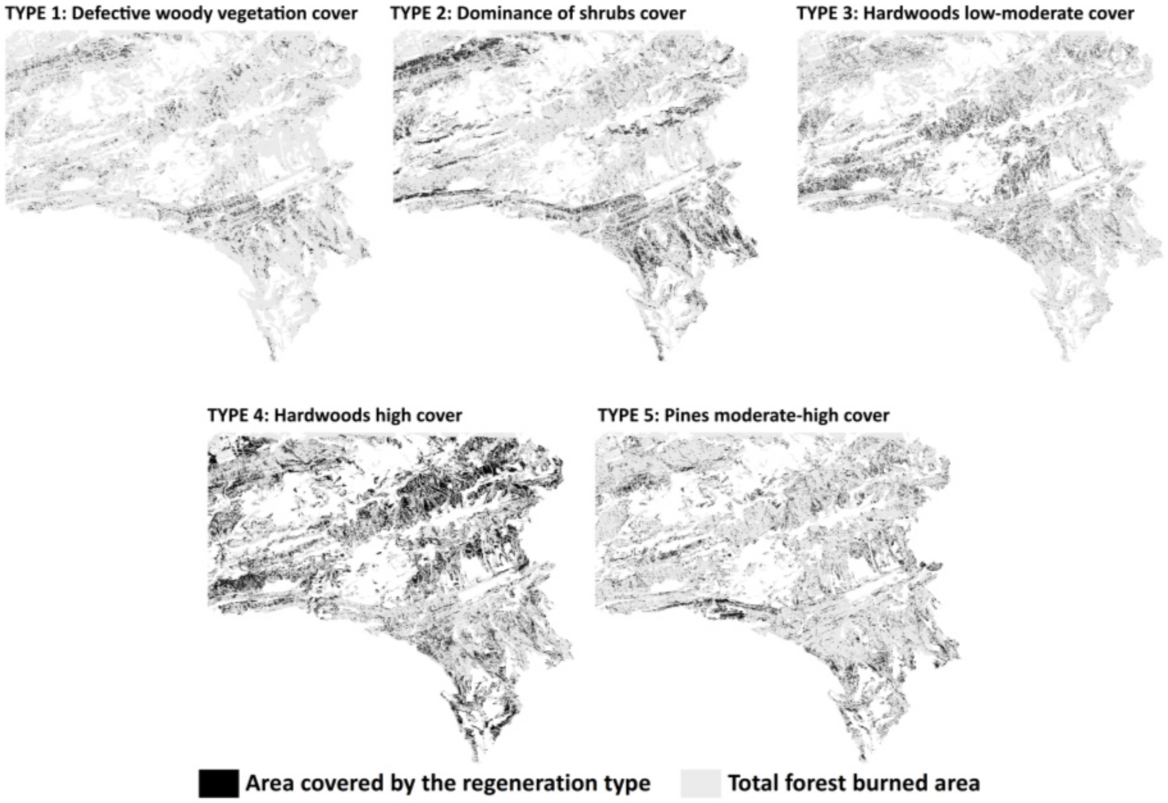

Figure 5. Spatial distribution of regeneration types in the study area.

Table 2. Basic patch size and shape characterization of the five regeneration types in the study area.

TYPE	Area (ha)	Area (% of total)	% of TYPE area by size classes				PSm (ha)	PScv (%)	MSI
			< 0.1 ha	0.1-1 ha	1-5 ha	> 5 ha			
1	298.3	9.35	79.16	20.84	0.00	0.00	0.0164	81.8	1.198
2	652.0	20.43	57.67	28.13	12.17	2.03	0.0177	83.1	1.232
3	532.3	16.68	80.26	19.55	0.20	0.00	0.0169	82.1	1.203
4	1359.0	42.58	32.63	36.32	25.15	5.90	0.0198	86.1	1.291
5	350.2	10.97	59.96	30.04	7.76	2.23	0.0177	85.0	1.223

Note: Total area was 3191.8 ha. PSm, patch size mean; PScv, patch size coefficient of variation; MSI, mean shape index.

3.4. Discussion

This study presents a methodological approach that combines airborne LiDAR data and single-date NDVI data, computed from aerial images, to provide precise, georeferenced, and spatially continuous information on post-fire regeneration over a large area. The presented methodology was not intended for short-term assessments — for which, the analysis of NDVI values extracted from satellite imagery may be enough (Diaz-Delgado et al. 2003; Gouveia et al. 2010; van Leeuwen et al. 2010; Vicente-Serrano et al. 2011; Vila and Barbosa 2010) — but for mid- to long-term assessments, which are crucial for appropriately designing and planning post-disturbance silvicultural treatments (Alloza and Vallejo 2006; Bauhus et al. 2013; Stephens et al. 2010). The information generated by this methodology provides forest stand structure and composition information that can be used to predict its potential evolution patterns, detect areas with persistent regeneration problems, and delimit forest stands for planning management operations. This ultimately enables management interventions to be prioritized and allocated.

There are some differences between our RS-based assessment and evaluations traditionally made from field-based inventories. On one hand, the level of detail in describing the postfire vegetation communities is, in general, higher in field-based inventories where measurements are conducted at individual-plant level (e.g., Curt et al. 2009; Proença et al. 2010). However, RS-based assessments entail less time and fewer spatial constraints than field inventories, as they are much less time consuming and less exposed to the uncertainties associated with inference and estimation from sample surveys in areas showing fine-scale heterogeneity. Assessments based on RS data also allow for the estimation of quantitative tree and forest attributes across large areas by using regression methods (e.g., Andersen et al. 2005; García et al. 2010; Latifi et al. 2012; Wulder et al. 2009). However, that approach requires working with high-resolution LiDAR data, especially when forest attributes are related to low vegetation. In our case, we aggregated RS metrics to the plot level (10 m × 10m) to make a community-based assessment instead of a plant-based assessment, and we estimated forest types instead of quantitative forest attributes, in concordance with the potential and limitations of the available low-resolution LiDAR data. Our approach permits the discernment between regeneration types by using height and intensity variables from LiDAR data and NDVI metrics, computed from single-date multispectral aerial imagery, thus providing forest managers with most of the information that they need for midterm operational planning of restoration activities and silvicultural operations (Vallejo et al. 2012). In addition, the provision of continuous, spatially explicit information at the landscape scale allows for easy implementation of relevant forestry applications such as the characterization and mapping of forest canopy fuels and fire risk (Erdody and Moskal 2010; García et al. 2011; González-Olabarria et al. 2012; Mutlu et al. 2008; Pierce et al. 2012; Riaño et al. 2007). The resulting maps of regeneration types also offer a starting point for the analysis of postdisturbance vegetation dynamics at large scales (Debouk et al. 2013; Goetz et al. 2010; Holmgren et al. 2008). Our methodology is appropriate for largescale assessment, as regional and national LiDAR coverages are often collected at low resolutions. The NDVI data that we used were derived from four-band aerial imagery, which are being used more and more frequently for national surveys. They have higher spatial resolution that the data derived from satellite imagery, although they are more limited for multitemporal analyses due to the generally low temporal resolution.

Our approach requires a prior categorization of the vegetation that is to be extrapolated using RS data. Such characterization can be achieved not only by generating vegetation typologies from the analysis of quantitative field data (as presented here), but also by using existing classifications when types of vegetation are previously known (Falkowski et al. 2009). Other areas may have different pre-fire forest composition and structure or be more or less severely impacted by fire and present different post-fire regeneration trajectories. Thus the number and characteristics of the regeneration types may change from one area to the other, and the RS variables selected for the classification model will be different in each particular case, as other types of vegetation may be better explained by a different combination of RS variables. In our case, the best fit was attained with just a combination of LiDAR height and NDVI variables. LiDAR-normalized intensity variables were not found to be essential in discerning our regeneration types, but they could be more important in other cases (Bork and Su 2007; Donoghue et al. 2007; García et al. 2010).

Our methodology is applicable as long as the input data (LiDAR and NDVI) are available and the chosen typologies can be accurately reproduced using supervised classification of RS data. Even so, to exploit the full potential of combining LiDAR and NDVI data for vegetation characterization, our approach calls for a certain period of time to pass between the occurrence of the disturbance and the acquisition of the RS data to allow for height differentiation between species and groups of species. Other aspects that must be considered when applying this methodology are the characteristics of the RS data available, particularly in terms of collection dates (year and season) and spatial resolution. In this regard, increasing the intensity of field sampling would be necessary for a disturbed area for which date and season of collection of the RS data are not comparable. Meanwhile, the spatial resolution of the RS data available may dictate how the level of detail in characterizing regeneration types needs to be adapted. Finally, the use of this methodology also requires good knowledge of the vegetation in the specific area under study and a decision about the desired level of detail when categorizing it to adequately design the field inventory, with more heterogeneous environments typically requiring a denser network of field plots.

The five regeneration types obtained in our study area adequately represent the wide range of postfire conditions described in previous field studies (Retana et al. 2002, 2012; Rodrigo et al. 2004). Furthermore, the results of the field validation revealed high (>80%) overall classification accuracy levels. For three of the five types, the field validation matched the classification implemented through RS variables in >80% of the cases. The types dominated by shrubs with very low tree cover (i.e., type 2) and by low to moderate tree cover dominated by hardwoods (i.e., type 3) showed sensibly lower accuracy levels (around 70%–75%). Most of the misclassified type 2 plots were assigned to type 3, meaning that the cover of hardwoods was overestimated in the classification model based on RS data. Misclassified type 3 plots were assigned to type 4 (very similar to type 3, as they are dominated by hardwoods regeneration but with higher hardwoods cover). Overall, misclassification problems could be considered relatively small and occurred among closely related regeneration types. Interestingly, two of the regeneration types of major interest for management purposes (type 1, with defective cover of woody vegetation, and type 5, with moderate to high tree cover of pine regeneration) were identified with high accuracy. In the case of type 5, this may indicate very good performance of NDVI-derived variables for species differentiation, as previously shown in other studies (Hill et al. 2010; Key et al. 2001).

Regarding the spatial distribution of the forest regeneration, we found resprouting hardwoods to be presently dominating almost 60% of the area that was formerly dominated by pines. These results demonstrate the important species-dominance shifts that crown fires may induce in Mediterranean black pine forests, as reported by Rodrigo et al. (2004). However, it should be stressed that the level of detail achieved in our study did not allow for proper identification of the presence of small pines on forest areas that were dominated by high shrubs or hardwoods, leading to certain underestimation of the pine regeneration. Interestingly, we also found <10% of the burned area to be in high risk of soil erosion due to a defective cover of woody vegetation. This lack of regeneration appeared in very small patches, which sometimes could be associated with the presence of small rocky outcrops. The information generated through our methodological approach should be useful for the definition of vegetation management and restoration strategies over large areas affected by disturbances, as it helps to identify areas where woody species are struggling to regenerate (thus potentially needing restoral actions) and to provide information on areas showing regeneration success and their current vegetation structure. For example, restoration actions designed to facilitate tree cover recovery could be envisaged areas of our case study where the predominant postfire regeneration pattern was identified as type 1 and type 2, especially in the larger patches (more frequently classed as type 2). In parallel, early thinning interventions designed to reduce competition, increase tree growth and vigor, and reduce the amount and continuity of fuels could be planned for patches classified as type 5 (Gonzalez-Olabarria et al. 2008; Moya et al. 2008; Verkaik and Espelta 2006), whereas coppice thinning could be proposed for stands classified as type 4 (Cotillas et al. 2009; Espelta et al. 2003*b*).

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Supplementary material

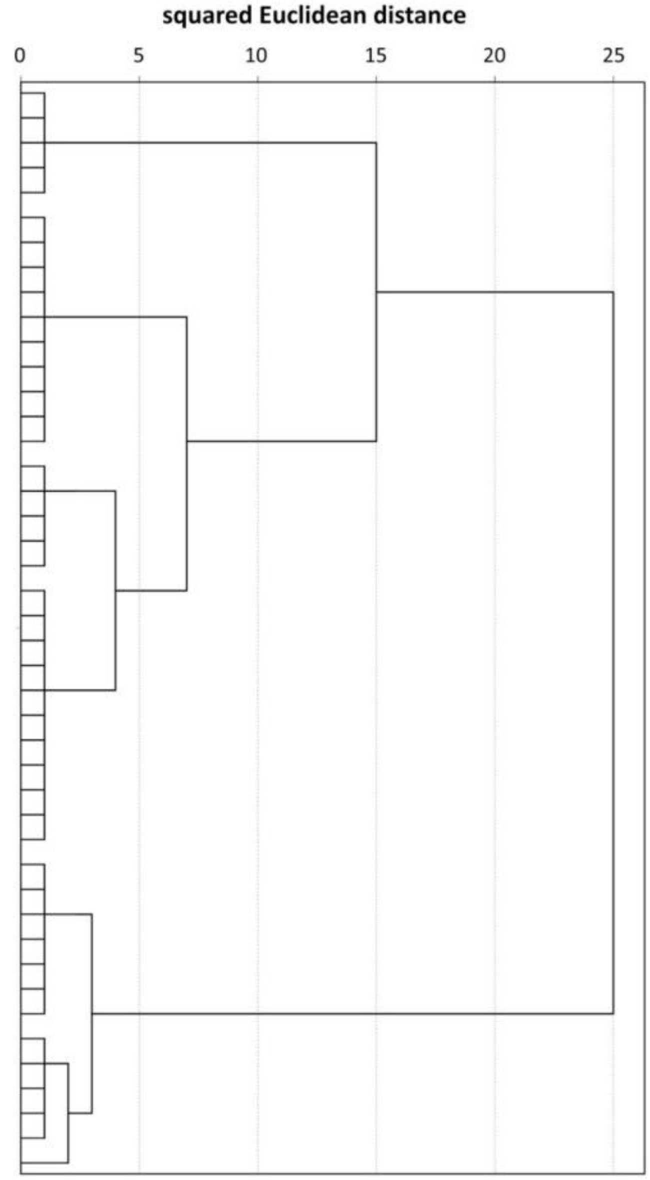

Figure 1S: Dendrogram illustrating the result of the cluster analysis using Ward's method applied on forest variables measured in the field plots (n = 44)

Table 1S: Descriptive statistics (mean and standard deviation) of the main field variables (see abbreviations in section 2. 2. 3) for each of the regeneration types obtained in the 4-type classification after Ward's method clustering.

TYPE	n	%SOIL	%LOW SHRUBS	%HIGH SHRUBS	%TREES	%PINES	H_HW	H_PINES
1	5	54.11 (10.21)	39.11 (10.91)	3.21 (1.21)	3.61 (5.31)	0.41 (0.31)	84.31 (111.61)	55.91 (62.71)
2	16	27.31 (6.01)	32.01 (14.31)	14.61 (13.51)	26.21 (15.01)	5.91 (7.11)	226.51 (125.81)	125.21 (87.21)
3	10	14.81 (6.11)	17.41 (6.51)	14.71 (13.31)	53.11 (9.51)	6.61 (6.81)	361.61 (67.91)	119.81 (60.41)
4	13	13.71 (5.81)	20.91 (14.31)	8.51 (9.51)	57.01 (17.31)	45.41 (16.51)	215.51 (145.51)	206.11 (53.61)

Table 2S: Descriptive statistics (mean and standard deviation) of the main field variables (see abbreviations in section 2. 2. 3) for each of the regeneration types obtained in the 6-type classification after Ward's method clustering.

TYPE	n	%SOIL	%LOW SHRUBS	%HIGH SHRUBS	%TREES	%PINES	H_HW	H_PINES
1	5	54.11 (10.21)	39.11 (10.91)	3.21 (1.21)	3.61 (5.31)	0.41 (0.31)	84.31 (111.61)	55.91 (62.71)
2	5	28.71 (5.01)	39.91 (18.51)	24.41 (19.21)	7.01 (4.51)	1.91 (2.71)	125.61 (116.71)	130.91 (125.91)
3	11	26.61 (6.61)	28.41 (11.11)	10.11 (7.31)	34.91 (7.81)	7.71 (7.81)	272.41 (104.31)	122.61 (71.01)
4	10	14.81 (6.11)	17.41 (6.51)	14.71 (13.31)	53.11 (9.51)	6.61 (6.81)	361.61 (67.91)	119.81 (60.41)
5	7	16.81 (6.11)	27.71 (15.51)	12.01 (11.71)	43.51 (7.31)	36.81 (10.11)	166.51 (129.91)	200.91 (48.11)
6	6	10.11 (2.91)	12.91 (7.91)	4.41 (3.81)	72.71 (10.31)	55.41 (17.41)	272.81 (152.41)	212.11 (63.51)

4

Unraveling the relative importance of factors driving post-fire regeneration trajectories in non-serotinous Mediterranean pinewoods

Santiago Martín-Alcón and Lluís Coll

4. Unraveling the relative importance of factors driving post-fire regeneration trajectories in non-serotinous Mediterranean pinewoods

Abstract

Sub-Mediterranean non-serotinous pinewoods of *Pinus nigra* Arn. ssp. *salzmannii* are suffering an increasing occurrence of high-severity crown fires that usually drive vegetation shifts to fire-adapted communities and a decrease in pine-dominated area. Here we used a case-study approach on a large area burned in 1998 to gain further understanding of the relative importance of different factors related to local topography (elevation, aspect, slope, curvature), pre-fire vegetation (land-use history, canopy cover) and fire behavior (burn severity, presence of unburned patches) as drivers of post-fire regeneration dynamics.

The results find that pine shows locally resilient responses driven mainly by factors related to fire legacies (presence of unburned patches) and the characteristics of the pre-fire vegetation (i.e. stable forest areas). When vegetation changes occurred, landscape 15 years post-fire was dominated by woody vegetation, with some rare grassland communities emerging under very specific conditions. Recessive conversion from forest to shrubland occurred mainly in the most xeric sites (south-facing areas, in some cases with steep slopes) and areas dominated by young pine stands prior to the fire. Preventive management strategies anticipating fire occurrence may help partially direct regeneration dynamics. At landscape level, managing forest fuels to favor the occurrence of unburned patches and modify their spatial distribution along the burned landscape will favor a more resilient pine response. At stand level, adjusting silvicultural interventions to favor the natural establishment of late-successional tree species will favor post-fire oak regeneration.

Keywords: *Pinus nigra*, *Quercus*, crown fires, resilience, vegetation shift, unburned patches, pre-fire vegetation.

4.1. Introduction

Since the last midcentury, the Mediterranean Basin has suffered an increase in the number of catastrophic forest wildfires (San-Miguel-Ayanz et al. 2013; Schelhaas et al. 2003) that has been attributed to a combination of factors related to changes in land-use (i.e. abandonment of traditional rural practices) and climate warming (Loepfe et al. 2010; Pausas 2004). The net effect has often led to deep socio-economic and environmental impacts (Pausas et al. 2008; Vallejo et al. 2012). In some areas, large crown fires have affected forest types that had not historically been subjected to them—a typical case is the Sub-Mediterranean montane pinewoods dominated by black pine (*Pinus nigra* Arn. ssp. *salzmannii*) or Scots pine *(P. sylvestris* L.) (Barbero et al. 2000; Pausas et al. 2008; Retana et al. 2002; Rodrigo et al. 2004; Vacchiano et al. 2014). These species present a number of traits (i.e. thick basal bark, self-pruning) that allow them to survive under frequent understory fires (Pausas 2015). However, they are very sensitive to crown fires due to a lack of direct post-fire regeneration mechanisms, i.e. they are unable to resprout or to produce serotinous cones or seeds able to resist the high temperatures reached during this type of fires (Pausas et al. 2008; Retana et al. 2002). These characteristics usually cause these pinewoods to shift toward different vegetation states post-fire (Rodrigo et al. 2004). In the Mediterranean, the increased drought and hot spells predicted for the coming decades by most climate models and the associated increase in fire risk are considered to put the future persistence of particular vulnerable populations of such pines (such as those distributed in the southern distributional edge) at high risk (Vilà-Cabrera et al. 2012).

In the absence of management practices, the nature of these fire-mediated vegetation changes, and particularly whether they move toward early-successional communities such as grasslands or shrublands or toward new forest types dominated by other tree species, will depend on a complex array of factors, including the characteristics of the fire event, the environmental conditions of the affected area and the pre-fire forest attributes. Fire behavior, especially fire severity and disturbance legacies (i.e. residual canopy cover, type of post-fire seedbed, distance from the surviving seed trees, etc) are known to strongly influence both the type and success of post-fire vegetation recovery in a given burnt area (e.g. Bonnet et al. 2005; Broncano and Retana 2004; Lentile et al. 2007; Vacchiano et al. 2014). Climate and topography have also been shown to significantly modulate regeneration patterns at landscape level, mostly because they drive soil moisture distribution (e.g. Buhk et al. 2006; Coop et al. 2010; Keeley and Keeley 1981; Pausas et al. 2004). Post-fire recovery after high-intensity crown fires is also largely dependent on the presence and abundance of available vegetative propagules (seeds, stems, roots, etc) in the burned stands. In the case of non-fire-adapted pinewoods, for example, the presence of vegetative propagules of resprouting tree species (e.g. *Quercus* ssp.) can prove essential for rapid post-fire forest recovery (Baeza et al. 2007; Puerta-Piñero et al. 2012).

The role of each of the abovementioned factors in driving post-fire regeneration trajectories has been investigated in a number of studies, but there are still very few large-scale integrative works assessing the relative importance of each of these individual factors. While some of these factors (e.g. local topography, climate or land-use history) cannot be modified by silvicultural interventions, others (e.g. fire behavior and pre-fire vegetation attributes) can be at least partially managed by means of preventive silvicultural practices. Consequently, further insight into the relative importance of the manageable factors would better inform the suitability of preventive management strategies to prevent regressive vegetation shifts. Here we address this issue using a large wildfire recorded in 1998 that burned a forest area dominated by Mediterranean black pine in the central region of Catalonia (NE Spain). For this purpose, we used a previous assessment of post-fire regeneration types in the area affected by this wildfire and we generated models for predicting the occurrence of each regeneration type from a set of topographic, fire behavior, and pre-fire forest cover attributes. The aim was to answer the following questions: (*i*) what is the relative importance of factors related to topography, fire behavior, and pre-fire forest cover in enabling direct (pine) post-fire regeneration in burned pinewoods dominated by non fire-adapted species?; (*ii*) which of these factors are the most important drivers of fire-induced change towards different alternative vegetation states? We hypothesized that apart from the presumably strong influence of topography, factors related to fire behavior such as burn severity or the abundance of unburned patches will largely drive direct pine regeneration, while the attributes of the pre-fire forest cover will chiefly shape the occurrence and success of regeneration of resprouting tree species ahead of shrublands or grassland communities.

4.2. Materials and Methods

4.2.1. Study area

The study was conducted in an area in the central region of Catalonia (NE Spain) affected by a large forest fire (Figure 1) in 1998 that burned nearly 24,000 ha, leading to almost complete loss of forest cover (Rodrigo et al. 2004). Inside the total burned forest area, our study focused on a roughly 2000-ha portion located in its southeastern part (between 1° 33' 48" and 1° 38' 39" E, and 41° 45' 4" and 41° 50' 2" N, DATUM WSG84) (Figure 1). Prior to the fire, the vegetation in the area was composed of the typical Mediterranean mosaic-like landscape, with cultivated land and scrubland interspersed with forest areas. The forest area was almost totally dominated by European black pine (*P. nigra*), although Aleppo pine (*P. halepensis* L.) was also frequent in some locations. Both black and Aleppo pine forests were either pure stands or two-layered stands with pine dominating the overstory and resprouting hardwoods (mostly oaks) appearing frequently in the understory (Burriel et al. 2004). The area presents gentle relief with low hills mostly oriented W-E ranging in elevation from 480–910 m above sea level (a.s.l.), and formed by folded structures of sedimentary carbonate rock (mainly lutite, marlstone and limestone) and gypsum sediments. Climate in the area is dry-sub-humid to sub-humid Mediterranean climate according to the Thornthwaite index, characterized by a mean annual precipitation of around 650 mm and a mean annual temperature of around 12ºC (Ninyerola et al. 2005). Rainfall is usually concentrated in autumn and spring. In summer, short convective storms also provide significant precipitation input (around 150 mm in average during the summer), but the occurrence of summer dry periods is not unusual.

A total of 1,915 ha of forest that totally burned (i. e. with no vegetation remaining after the fire) in 1998 were selected for the assessment of the factors driving post-fire regeneration trajectories (Figure 1). Areas affected by roads, agricultural fields and other non-forest uses had previously been excluded from the analysis. Some green islands (i.e. patches of adult trees that survived the fire) were found surrounding the study area. When implemented, post-fire management consisted of generalized salvage logging (cut and deadwood removal) that was mostly executed during the first winter after the fire.

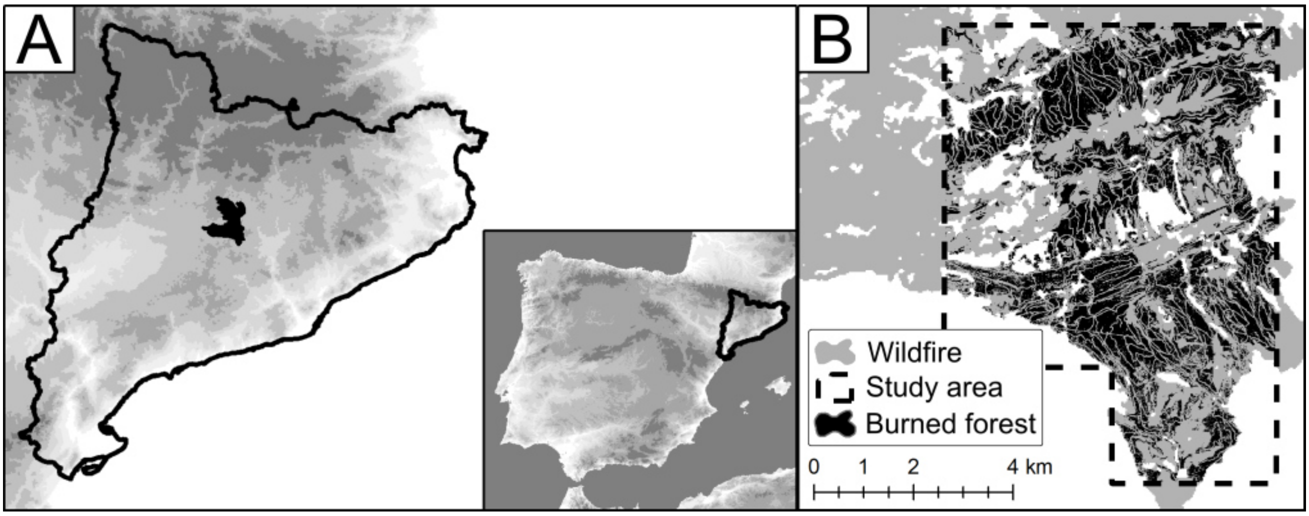

Figure 1. Location and boundaries of: A) the 1998 wildfire in the Iberian Peninsula and Catalonia region; B) the burned forest area within the study perimeter for which post-fire regeneration types were assessed by Martín-Alcón et al. (2015a).

4.2.2. Classification and characteristics of post-fire regeneration types

Martín-Alcón et al. (2015a) had previously classified post-fire regeneration in the burned forest area into five post-fire regeneration types. This classification was based on analysis of remote sensing data from airborne LiDAR and multi-spectral imagery calibrated with field data measurements. It was realized on the vegetation growing naturally in the burned area almost 15 years after the occurrence of the wildfire, at a time when all the species with regeneration potential in the area had likely been established (Gracia et al. 2002). The final classification algorithm classified each 10*x*10 portion of the burned area into the following post-fire regeneration types (Table 1): two types presenting high cover of tree species—one clearly dominated by hardwood regeneration (T4), the other dominated by pine regeneration (T5)—; a third type showing low-to-moderate tree cover, dominated by hardwood regeneration (T3); and the last two types matching to areas dominated by soil/herbaceous (T1) or shrub layers (T2) with very low or no tree-species regeneration. The hardwoods dominating tree-species regeneration in types T4 and T3 are marcescent oaks (*Quercus faginea* Lam. and *Q. cerrioides* Willk. & Costa) and the evergreen oak *Q. ilex* L. Other species of the genus *Sorbus*, *Acer*, *Prunus*, etc. are also present but only in scattered numbers. The main pine species dominating regeneration type T5 is black pine, although Aleppo pine may also be present in some locations. Finally, the shrub species appearing in all the regeneration types are mainly *Quercus coccifera*, *Crataegus monogyna*, *Viburnum lantana, Rubus ulmifolius* and *Buxus sempervirens* and less frequently (although locally abundantly) *Rosmarinus officinalis*, *Juniperus oxycedrus*, *Prunus spinosa*, *Cornus sanguinea, Genista scorpius* and *Rhamnus alaternus*. According to the post-fire regeneration assessment, regeneration type T4 is the most abundant in the study area, covering 43.6% of the burned area; types T3 and T2 cover 18.9% and 16.3%, respectively; and types T5 and T1 are the least abundant, at 11.5% and 9.7%, respectively (Table 1).

Our initial response variable was a categorical variable that classified each subject (i.e. each one of the 10*x*10 meter plots of burned forest area) into one of the five abovementioned regeneration types. As we suspected our response variable to feature significant spatial autocorrelation, we explored changes in the join-count statistic (Cliff and Ord 1981) as a function of the Euclidian distance between the plots classified in each one of the regeneration types. As this analysis showed high autocorrelation at low distance classes (up to 30-50 m), regular sub-sampling was applied (Munroe et al. 2004). Thus, one of each of the five points in both the *x*- and *y*-axes (of the 10*x*10-m grid) was sampled, thus yielding a total of 7,702 plots (Table 1). The new subset of plots no longer presented significant autocorrelation according to the join-count statistic. For this subset of plots, a series of explanatory variables were computed.

Table 1. Forest regeneration type with descriptions (from Martin-Alcon et al. 2015), and number of 10*x*10-meter plots corresponding to each type (i) in the entire study area and (ii) in the subsample used for the subsequent analyses.

Regeneration type	Description	Short name	Total number of plots in class	Number of plots after regular subsampling
T1	Very low vegetation cover; absence of tree species regeneration	Low woody	18,455	739
T2	Very low tree regeneration but remarkable shrub cover	Shrubby	36,263	1,523
T3	Dominance of hardwoods regeneration in low to moderate cover, mixed with shrubs	Oaks low	31,204	1,190
T4	Dominance of hardwoods regeneration in high cover	Oaks high	83,507	3,371
T5	Dominance of pine regeneration in moderate to high cover	Pines	22,059	879

4.2.3. Topographic attributes

Among the potential topographic drivers of post-fire regeneration trajectories, we selected four variables derived from remote-sensing data: elevation, aspect, slope and curvature. Elevation was extracted from a 5-m-resolution digital elevation model (DEM), and in the study area is directly related to plot position along the slope gradients, with lower values occurring in valley bottoms, higher values in mountain tops, and intermediate values on the slopes. Aspect was pre-transformed into a northness index to more adequately reflect the variation between north and south exposures. Northness index increased from -1 on south exposures to 1 on north exposures, with east and west aspects given a value of 0. This is a key gradient under Mediterranean climates, since the higher amount of radiation received in south-facing slopes significantly increases the evaporative demand to which plants are exposed. Finally, slope and curvature of the terrain were extracted from the 5-m-resolution DEM, and both were considered local topography attributes highly related to the soil water content distribution along a given slope (Gómez-Plaza et al. 2001). The terrain curvature was calculated following the equation proposed by Moore *et al.* (1991).

4.2.4. Estimation of land-use history and pre-fire forest cover

A second set of candidate variables to explain the distribution of post-fire regeneration trajectories was related to the pre-fire vegetation attributes and land-use history. First, we wanted to assess the relative importance of time since land-use abandonment on post-fire regeneration trajectories (addressed in Puerta-Piñero et al. 2012). For this purpose, we used an object-oriented semi-automatic image analysis on the most ancient aerial photographs in the area (taken in 1956 as grey-scale 1-m-resolution images). The analysis was based on patch-level segmentation and a later classification of land-cover objects according to their spectral signatures and texture attributes. The following land-cover classes were delimited and assigned to each 10*x*10 portion of burned land: (*i*) ‘cultivated land’, including agricultural fields and other highly altered areas (roads and paths, farms, etc.); (*ii*) ‘non-wooded land’, including areas of natural vegetation with no or only scattered trees; (*iii*) ‘open woodland’, for woodlands presenting low-to-moderate tree density; and (*iv*) ‘closed woodland’, for woodlands presenting moderate-to-high tree density (Figure 2). In addition, we wanted to assess the relative importance of pre-fire forest cover, which is known to highly affect the characteristics of the understory vegetation (Coll et al. 2011; Martín-Alcón et al. 2015b). To do this, a new object-oriented semi-automatic image analysis was executed on 50-cm-resolution grey-scale aerial photographs taken three years before the fire (in 1995). The analysis consisted in generating a rule-set based on fine-resolution segmentation and a classification of tree-cover objects according to their spectral signatures and their position with respect to other objects previously identified as tree shades. Both image analyses were performed in eCognition Developer 8.9 software.

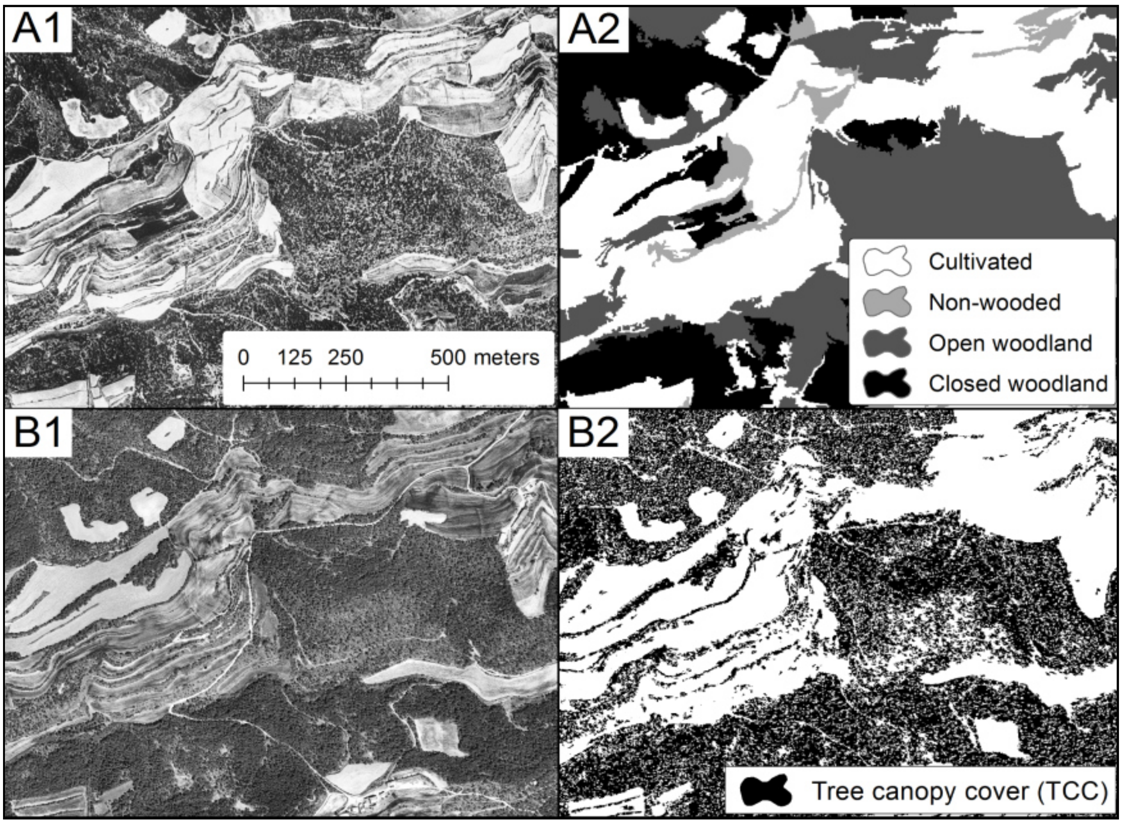

Figure 2. Example of aerial photographs from 1956 (A1, more than four decades before the wildfire) and 1995 (B1, three years before the wildfire), and the resulting information after object-oriented semi-automatic image analysis for 1956 land-use (A2) and 1995 tree canopy cover (B2).

4.2.5. Estimation of burn severity and influence of unburned areas

The last set of explanatory variables was related to the characteristics of the wildfire. First, we computed the Relative Differenced Normalized Burn Ratio (RdNBR) (Miller et al. 2009) to assess burn severity in the study area. The RdNBR is a variant of the Differenced Normalized Burn Ratio (dNBR) (Key and Benson 2006) that accounts for the relative amount of pre- to post-fire change by dividing dNBR by pre-fire NBR value. The Normalized Burn Ratio (NBR) was first computed from Landsat TM NIR and SWIR bands (4 and 7, respectively). The pre-fire image was taken in 1992, which was the closest available image to the wildfire date, and the post-fire image was taken in 1999 (the year after the fire). Both images were taken during the second half of July. Finally, we computed a variable related to the location of each plot in relation to unburned forest patches. It was calculated as the sum of unburned forest area at a radius of 150 meters from each plot, and was named as 'Area of unburned patches'.

Table 2. Descriptive statistics of the continuous explanatory variables in the subsample of plots used for the analyses (n = 7,702).

Variable (units)	Mean	Std. Dev.	25th percentile	75th percentile
(a) Topographic variables				
Elevation (m a.s.l.)	724.80	89.08	652.92	798.36
Northness	0.08	0.72	-0.64	0.83
Slope (°)	18.30	7.22	12.52	23.63
Curvature	0.10	3.26	-0.84	1.28
(b) Vegetation and land use				
1995 tree canopy cover (ppu)	0.57	0.22	0.45	0.73
(c) Fire effect				
RdNBR	691.84	173.50	598.16	812.59
Area of unburned patches (ares)	48.76	73.59	1.00	69.00

4.2.6. Statistical analysis

First, we examined Pearson's correlations among the continuous explanatory variables in order to check whether there was any pair of highly-correlated variables potentially affecting the interpretation of the subsequent analyses. The highest significant Pearson's coefficient found was between northness and the TCC in 1995 (Pearson's $r = 0.274$). All the other pairwise correlations gave a Pearson's r below 0.25. We then ran non-parametric Kruskal–Wallis tests in order to check whether there were statistically significant differences between two or more of our regeneration types in terms of our continuous explanatory variables. Kruskal–Wallis tests were used instead of one-way ANOVA because our variables were not normally distributed and variable transformations did not normalize the data. Post-hoc tests were also computed in order to see which pairs of types differed significantly on each one of the explanatory variables. For the only categorical explanatory variable (i.e. land use cover type in 1956), significant differences among groups were analyzed using chi-square tests.

Occurrence probabilities were modeled for each regeneration type and variable importance was computed using the Random Forests method (Breiman 2001). Random Forest (RF) is a nonparametric supervised classification technique that has shown good performance in modeling the occurrence of species or vegetation types (e.g. Evans et al. 2011; Evans and Cushman 2009; Falkowski et al. 2009). We ran one RF model for each regeneration type. To do this, the response variable for each model was defined as a binary response, i.e. presence (1) / absence (0) of a given regeneration type. The RF technique uses a bootstrap approach to achieve higher accuracies while simultaneously addressing over-fitting problems associated with traditional classification tree models. A large number of classification trees are produced from a random subset of training data (approximately 63% random subset), permutations are introduced at each node, and the most common classification result is selected. In an effort to avoid bias in the prediction caused by imbalanced classes, the number of plots per class in bootstrap samples was always equal to the number of plots of the less frequent class (i.e. n = 739 cases, which is the number of cases in regeneration type T1) (Evans and Cushman 2009). Bootstrap samples for class 0 ($y = 0$) were always constructed by stratified random sampling with equal proportions among the four regeneration types other than the type of interest (which corresponds to class $y = 1$). We ran each RF model with 10,000 bootstrap replicates (i.e. individual classification trees). Out-of-bag (OOB) error estimates and classification error for the class of interest ($y = 1$; presence of a given regeneration type) were calculated for each tree by classifying the portion of training data not selected in the bootstrap sample, and overall accuracies were calculated by averaging error rates across all trees in the model. No variable selection procedure was applied in any case, because we were more interested in inferring the relative importance of each explanatory variable on the occurrence of a given regeneration type than in developing a parsimonious classification model for each type. A Model Improvement Ratio (MIR) was calculated from standardized importance values for computing variable importance (Evans et al. 2011; Evans and Cushman 2009). As an output from RF, metrics are ranked in order of importance (I) based on the number of times a given metric decreased the mean squared error. However, unlike a raw I score, which can be influenced by the total number of metrics in the model, the MIR is comparable among models (Murphy et al. 2010). MIR values were calculated as $[I_n/I_{max}]$, where I_n is the importance of a given metric and I_{max} is the maximum model improvement score. A high positive MIR value (i.e. closer to 1) indicates high importance of the variable, whereas a low-positive or a negative value indicates that the variable is irrelevant.

Finally, in order to further deepen the understanding of the main factors driving the occurrence of the most abundant regeneration types (T2, T3 and T4, which account for nearly 80% of the burned area), we computed new RF models and recalculated variable importance for each pairwise combination. In all cases, the RF algorithm was implemented in R statistical software (R Development Core Team 2014) using the Random Forest package (Liaw and Wiener 2002).

4.3. Results

4.3.1. Effects of topography on post-fire regeneration trajectories

All the topographic attributes analyzed had effects on the occurrence of the different post-fire regeneration types (Table 3). Elevation and northness were the factors that most strongly differentiated the sites according to type of regeneration they presented (based on chi-square statistics), although slope also had a substantial effect. Post-hoc tests revealed that type T1 (presenting low cover of woody vegetation) occurred at higher altitudes than other types, whereas type T4 (presenting high-density oak regeneration) occurred at significantly lower elevation (Figure 3). On the other hand, two regeneration types dominated by re-sprouted oaks (T3 and T4) were found to be more frequent on north-facing slopes, whereas the shrub-dominated type (T2) was more frequent on south-facing slopes. Slope was slightly steeper in the sites that showed shrub or pine dominance (types T2 and T5, respectively) than in the rest of the cases. Finally, the regenerated sites dominated by shrubs (T2) appeared more frequently on convex terrain whereas sites presenting high density of oaks (T4) were found more frequently on concave terrain.

Table 3. Effects of topographic, pre-fire-vegetation, and fire-related variables on post-fire regeneration types (n=7,702).

Variable	Type	Test	Chi-Square statistic	Significance
(a) Topographic variables				
Elevation	Covariate	Kruskal-Wallis	558.71	<0.0001
Northness	Covariate	Kruskal-Wallis	327.98	<0.0001
Slope	Covariate	Kruskal-Wallis	192.73	<0.0001
Curvature	Covariate	Kruskal-Wallis	15.48	0.004
(b) Vegetation and land use				
1956 land-use cover type	Factor (4-level)	χ^2	262.32	<0.0001
1995 tree canopy cover	Covariate	Kruskal-Wallis	197.49	<0.0001
(c) Fire effect				
RdNBR	Covariate	Kruskal-Wallis	177.73	<0.0001
Area of unburned patches (r=150 m)	Covariate	Kruskal-Wallis	143.30	<0.0001

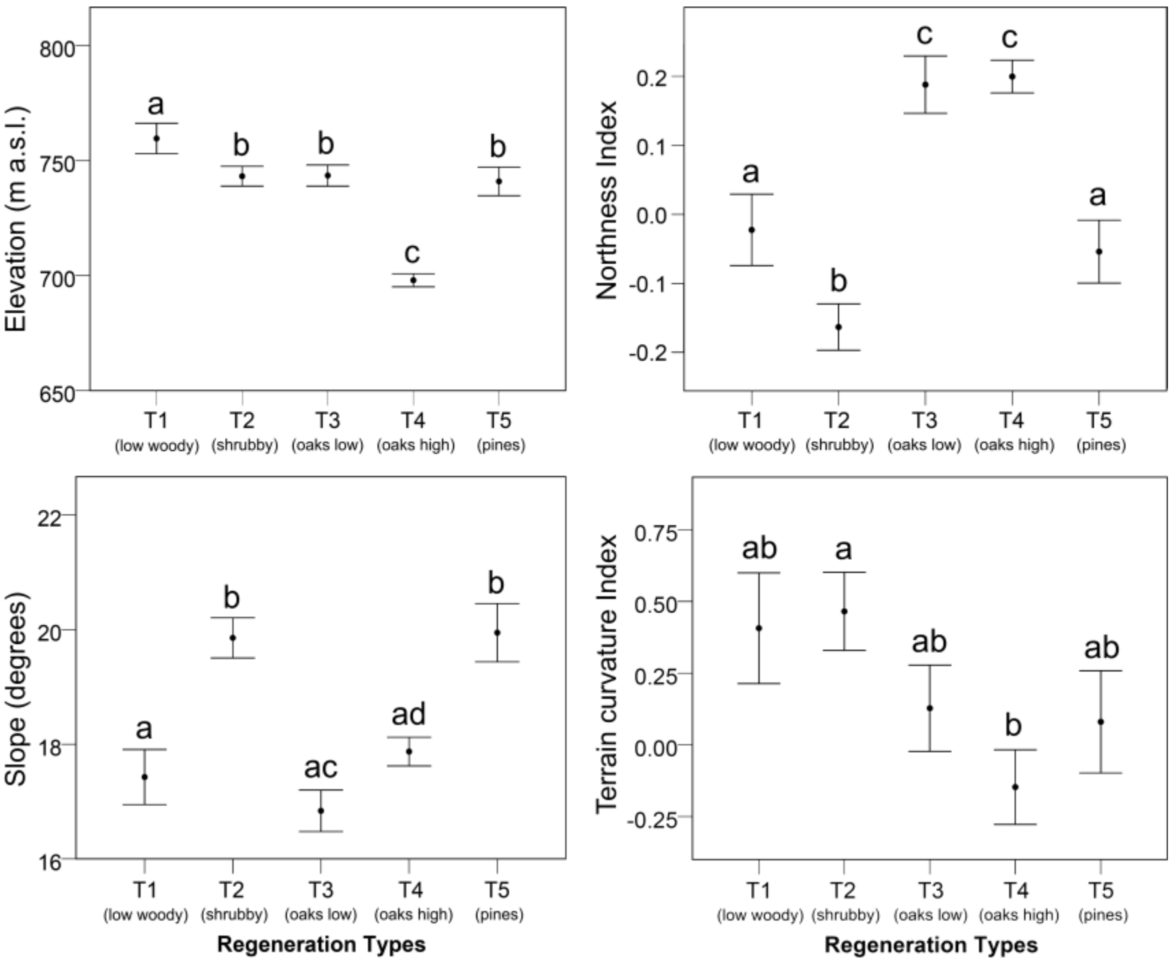

Figure 3. Mean (± S.E.) values of the four topographic covariates for the plots classified in each of the regeneration types. Different letters indicate significant differences among types according to the Kruskal–Wallis post-hoc tests for all pairwise comparisons.

4.3.2. Effects of land-use history and pre-fire forest cover

The land-use type in 1956 and the pre-fire TCC cover showed significant effects on post-fire regeneration (Table 3). The regeneration types with higher abundance of tree-species regeneration (T3, T4 and T5), and especially T4, occurred more frequently at sites with a longer history of dense tree cover (i.e. sites that had been dense woodlands from at least 1956) compared to sites characterized by very low or no tree-species regeneration (T1 and T2) (Figure 4). Pine regeneration (T5) occurred a little more frequently in sites classified as open woodlands in 1956 (i.e. woodlands with low-to-moderate tree cover) than oak regeneration (T3 and T4), although this difference was only significant with T4 (Figure 4). On pre-fire TCC, regeneration types without tree-species regeneration (T1 and T2) were found to occur in sites with significantly lower TCC values than sites with oak and pine regeneration. Between the two oak-dominated regeneration types, pre-fire TCC was slightly higher for T4 than for T3 (Figure 4).

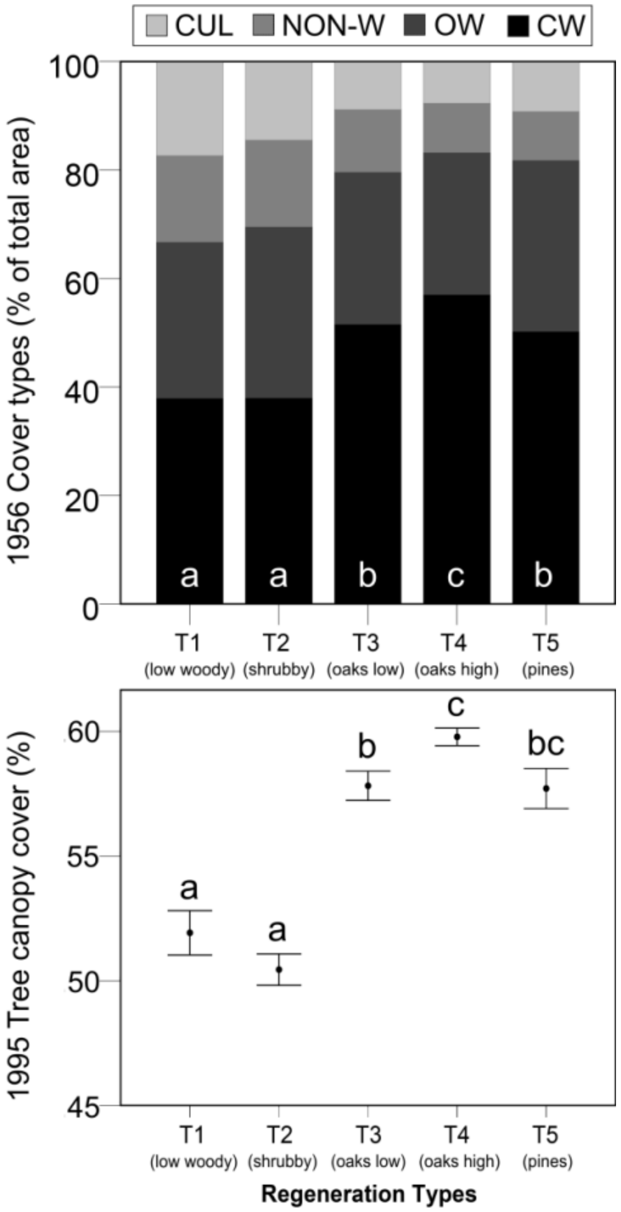

Figure 4. Differences among regeneration types for the pre-fire-vegetation attributes. (A) Frequency of each 1956 land-use-cover class for the plots classified in each of the regeneration types. Acronymed descriptions of land-use-cover classes (see text for extended descriptions) are: CUL, cultivated land; NON-W, non-woody vegetation; OW, open woodland; and DW, dense woodland. Different letters indicate significant differences among types according to the chi-square tests for all pairwise comparisons. (B) Mean (± S.E.) values of 1995 TCC for the plots in each of the regeneration types. Different letters indicate significant differences among types according to the Kruskal–Wallis post-hoc tests for all pairwise comparisons.

4.3.3. Effects of fire behavior

The two factors related to the characteristics of the wildfire (burn severity and presence of unburned patches close to the regenerating areas) played an important role in the occurrence of the different post-fire regeneration types (Table 3). The effect estimate (chi-square Statistic) associated to burn severity (as RdNBR) was slightly higher than the effect estimate related to abundance of unburned forest patches around each plot. The resulting RdNBR values (ranging around 500–900) confirmed that the study area was burned at moderate-high to high severity as based on the criteria established by Miller and Thode (2007). Post-hoc tests revealed that fire effects mostly affected the occurrence of pine regeneration (T5) (Figure 5). On one hand, pine regeneration tended to occur much more frequently in areas in which unburned forest patches were more abundant (Figure 5). On the other hand, burn severity was significantly lower in sites marked by pine regeneration than in sites presenting any other regeneration types. Between the two regeneration types dominated by oaks, burn severity was higher for T3 than for T4, and in both cases was significantly higher than in the areas currently dominated by shrubs (Figure 5).

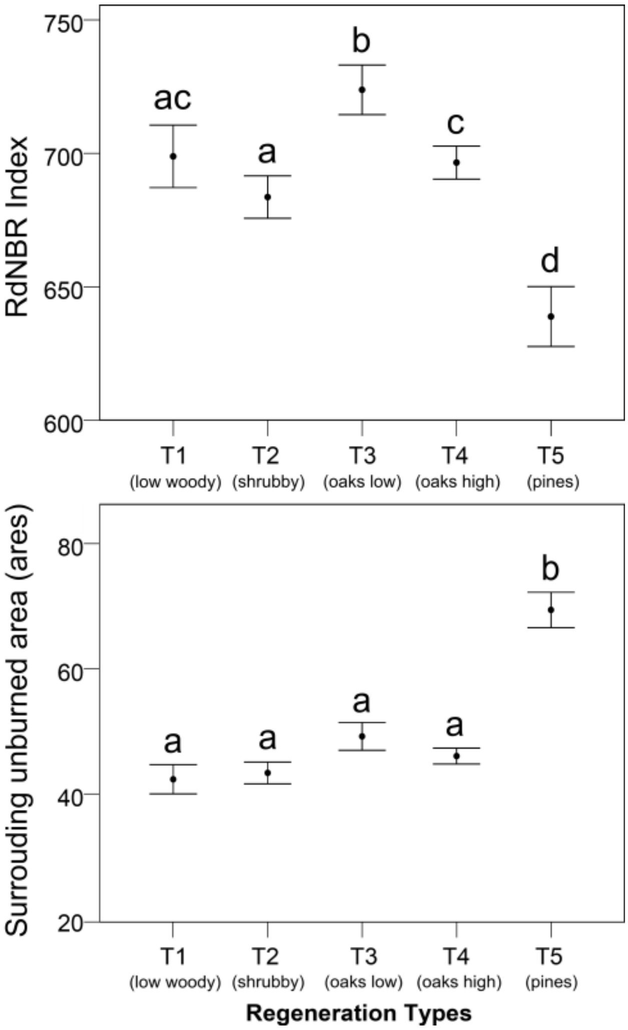

Figure 5. Mean (± S.E.) values of the two covariates related to fire effects for the plots classified in each of the regeneration types. Different letters indicate significant differences among types according to the Kruskal–Wallis post-hoc tests for all pairwise comparisons.

4.3.4. Relative importance of the different factors on the regeneration trajectories

Our models revealed that the occurrence of regeneration types presenting high cover of tree species (oaks in T4 and pines in T5) were the most accurately predicted by the set of topographic, pre-fire vegetation, and fire-related factors, at 50.7% (T4) and 47.5% (T5) of classification error. In contrast, the classification models for the post-fire types characterized by shrubby vegetation (T2) and low-to-moderate density of oak regeneration (T3) proved the least accurate (57.2% and 56.6% of classification error, respectively; Table 4). The most important variable differentiating the sites with low woody vegetation cover from the rest was elevation, which confirmed that this regeneration type is strongly bound to upper-slope sites, probably in mountain ridges or hilltops (which also meet the other important classification criteria, i.e. low slopes, convexity and absence of marked aspects). These areas also showed a high percentage of non-wooded and cultivated areas en 1956, and in general they burned at fairly high severity.

In relation to the other post-fire vegetation types, areas dominated by shrubby vegetation (T2) was strongly driven by topographic variables and was predominantly found at mid-to-high elevations on south-facing slopes. They also occurred in areas where the pre-fire TCC was low and in which the presence of neighboring unburned patches was scarce. Similarly to T1, land-use cover type in 1956 was also an important driver for this type, which very often occurred in areas showing non-wooded and cultivated land. Topographic factors were also highly relevant variables differentiating T3 (low-to-moderate cover of oak regeneration) from the rest, with T3 areas locating to mid-to-upper-slope sites, mostly north-facing and/or with gentle slope. Land-use cover type in 1956 (with high percentage of woodland) and burn severity (usually high) also appeared as decisive factors triggering the occurrence of T3. The occurrence of a high cover of oak regeneration (T4) was mostly driven by elevation but, contrary to T1, this regeneration type was bound to lower-slope sites and valley bottoms, mostly on north-facing slopes. Other important but less determinant characteristics of the sites regenerated as T4 were that they burnt at fairly high severity and presented a longer history of dense tree cover, higher pre-fire TCC and lower abundance of neighboring unburned patches than any other types. Finally, the occurrence of pine regeneration (T5) was fundamentally driven by attributes related to fire effects (Table 4). T5 appeared mostly in sites burned at lower severity and surrounded by substantial areas of unburned patches (Figure 5). Pre-fire vegetation factors were also very important for the occurrence of T5 which, similarly to T4, appeared in sites having a long history of tree cover and high pre-fire TCC. In terms of topographic factors, pine regeneration appeared preferentially in quite steep mid-to-upper-slope sites but not on pure north-facing or on marked south-facing sites.

Table 4. Computed variable importance in the Random Forest model for predicting the occurrence of each regeneration type according to Model Improvement Ratio (MIR). The overall out-of-bag (OOB) error estimates and classification errors in each model are also reported.

Regeneration type	T1	T2	T3	T4	T5
Model OBB estimate of error rate (%)	30.6	30.7	31.6	28.6	27.2
Classification error class 0 (%)	24.9	24.1	25.4	23.1	22.1
Classification error class 1 (%)	53.3	57.2	56.6	50.7	47.5
Variable importance (MIR)					
(a) Topographic variables					
Elevation	1.00	0.93	0.66	1.00	0.63
Northness	0.35	0.92	0.87	0.59	0.78
Slope	0.39	0.79	0.73	0.44	0.57
Curvature	0.23	0.36	-0.12	0.17	0.11
(b) Vegetation and land use					
1956 LU	0.55	0.63	0.99	0.32	0.67
1995 TCC	0.40	1.00	0.39	0.45	0.77
(c) Fire effect					
RdNBR	0.51	0.18	1.00	0.41	0.99
Area of unburned patches	0.15	0.93	0.30	0.29	1.00

Our analysis of the most important variables differentiating the occurrence of the three most abundant regeneration types (T2, T3 and T4) by pairwise combinations found that topography and burn severity mediate the occurrence of high cover of oak regeneration (T4) instead of low-to-moderate cover (T3). In this regard, elevation was the most important driver, with T4 mostly locating to lower-slope sites and valley bottoms (Figure 6). In contrast, the occurrence of oak regeneration in place of shrubby vegetation (T2) was mediated by a combination of factors, including topographic attributes (northness and slope), vegetation-related factors (i.e. 1956 land use and 1995 TCC), and burn severity (Figure 6).

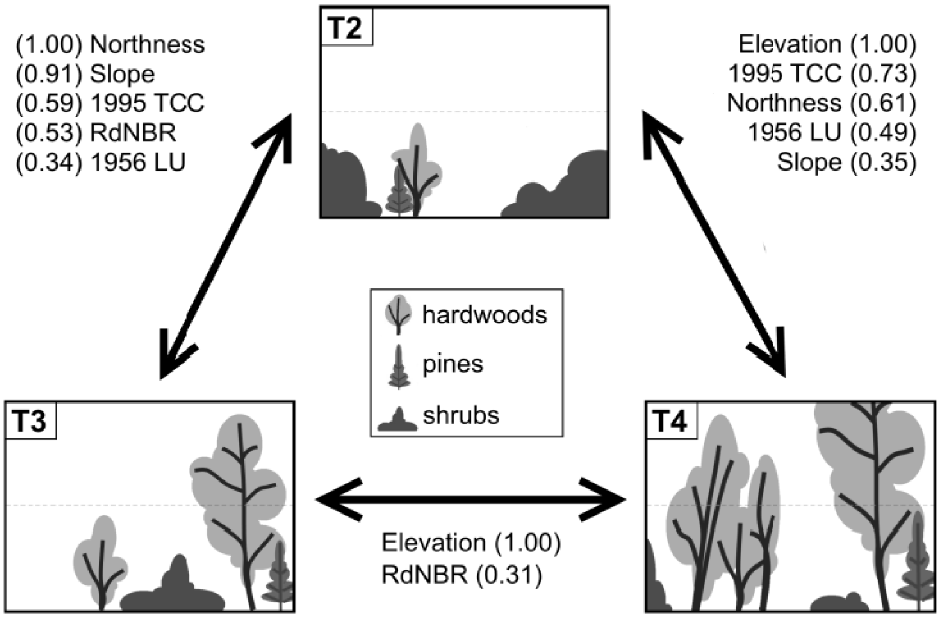

Figure 6. Diagram showing the main factors (i.e. with a relative importance of > 0.3 on Model Improvement Ratio) obtained in the Random Forest models predicting the occurrence of regeneration types for each pairwise combination of the three most abundant types in the burned area.

4.4. Discussion

4.4.1. Post-fire regeneration of black pine

Fifteen years after the wildfire, a relatively small proportion of the studied area showed black pine regeneration despite black pine having been the main tree species before the fire event. This corroborates the low ability of this species to efficiently respond to high-severity crown fires (Pausas et al. 2008; Retana et al. 2002). We nevertheless found some sites all along the study area where abundant pine regeneration occurred, mostly corresponding to zones that burnt at lower severity than the rest and that were close to unburned patches. The dependency of pine regeneration to the presence of unburned patches has already been reported in previous studies (Ordóñez et al. 2006; Vilà-Cabrera et al. 2011) and is explained by the relatively limited seed dispersal distance of this species. In some cases the surviving adult trees may also shield seedlings against direct sun exposure and thus favor their establishment and survival, according to their intermediate shade-tolerant character (Niinemets and Valladares 2006) and low ability to colonize very open spaces (Ordoñez et al. 2004; Tiscar and Linares 2014).

Our results show that patches presenting abundant pine regeneration also occurred in areas with low-to moderate presence of resprouting species and thus relatively free of competition from these resprouters in the early post-fire period (Gracia et al. 2002; Ordoñez and Retana 2004). Prior to the fire, these areas may have corresponded to pure pine stands with a poorly developed understory layer, which would partly explain why they burnt at lower severity than others (Broncano and Retana 2004). On the other hand, the higher occurrence of abundant pine regeneration in sites with a long history of forested cover might be related to the higher probability of presenting mature trees in the surrounding unburned patches. Mature trees are known to produce large amounts of cones when they remain in highly exposed conditions, such as in small isolated patches surrounded by burnt area (Ordoñez et al. 2005). Finally, we found an important effect of topographic factors on pine regeneration, but this effect seemed to be highly variable depending on local climate and microsite conditions. For instance, we found the highest occurrence of pine regeneration on neutral exposures (W and E), whereas Gracia et al. (2002) reported that the post-fire regeneration of black pine occurred almost exclusively in wet north-facing slopes. In our study area, regeneration in north-facing slopes was mostly dominated by fast-growing shrubs and oak sprouts, which may have exerted severe competition on the pine seedlings during the first years after the fire.

4.4.2. Vegetation shift and alternative regeneration trajectories

Post-fire regeneration trajectories dominated by woody vegetation types are prevalent in sites where pine regeneration was unable to establish. Grassland communities, in contrast, appear rarely and are usually restricted to very specific site conditions (mountain ridges or hilltops, mostly rocky sites, etc), mostly in areas that were not forested prior to the fire. In the expected scenario of an increasing occurrence of large crown fires in these systems, fire-mediated reversion of black pine stands into other types of woody vegetation (shrublands or forests dominated by resprouting tree species) is expected to happen more and more frequently, as already seen in other non-serotinous pine forests hit by fire in different temperate regions of the world (Keane et al. 2008; Strom and Fulé 2007; Trabaud and Campant 1991; Vacchiano et al. 2014). In our case, the recessive conversion from pinewood to shrubland is mostly mediated by the characteristics of the pre-fire vegetation and the topographic attributes of the burnt sites. This vegetation shift mainly occurred on young and relatively open pre-fire pine stands that have recently colonized old fields or open land and that, accordingly, were much less susceptible to diversification processes by resprouting tree species (Caldeira et al. 2014; Martín-Alcón et al. 2015b; Navarro-González et al. 2013; Puerta-Piñero et al. 2012). These areas also burned at the lower end of the severity range, likely indicating lower fuel amount and lower abundance of hardwoods in the pre-fire stand composition (Broncano and Retana 2004), and were far from unburned patches, which means pine seeds were scarce or absent after the fire (Ordóñez et al. 2006). Finally, these sites mostly occurred in south-facing areas (in some cases with steep slopes) generally showing the poorest site quality (and lowest water availability), which may have hampered the establishment and growth of sprouting trees (Gracia and Retana 2004; Gracia et al. 2002).

Around 60% of the burned area changed from pine to oak-dominated woods. This reflects the high availability of plant propagules of oaks and points to a fairly widespread presence of them in the pre-fire forest composition in the form of young recruits established under the pine canopy or adult individuals sharing the overstory with pines (Martín-Alcón et al. 2015b; Retana et al. 2002). Fire severity does appear to have little impact on the post-fire resprouting ability of these oaks (Broncano et al. 2005; Espelta et al. 2003; Pausas 1999). The dominance of oak regeneration in the burnt area should nevertheless be interpreted with caution, since the typologies developed in Martín-Alcón et al. (2015a) differentiated regeneration types based on the relative cover of the dominant species/layer but did not drill down to a full identification of the presence of small pines on forest areas dominated by shrubs or hardwoods. Indeed, young pines are actually relatively frequent in these areas (personal observation). The recruitment of these pines probably began some years after the fire (in particular in the most xeric sites) once the seedlings were able to benefit from a certain degree of protection from the oak canopy against direct exposure to sun (del Cerro Barja et al. 2009; Gracia et al. 2002; Martín-

Alcón et al. 2015b; Tiscar and Linares 2014). Some of these areas will likely evolve in the mid-term towards mixed pine-oak stands (Gracia et al. 2002).

4.4.3. Post-fire dynamics and management implications

This study provides an integrative landscape-level analysis of the main factors driving post-fire regeneration dynamics in the case of non-serotinous pinewoods. The analysis underlines key roles of a number of variables that have been under-explored to date, such as the role of land-use trajectories and pre-fire forest cover. Based on our results, important vegetation changes are to be expected in the near future in these Sub-Mediterranean pinewoods where the occurrence of catastrophic wildfires is predicted to further increase. These disturbances may lead to a mosaic of forest types (including shrublands, pinewoods, oak-dominated forests and pine-oak mixed forests) shaping a new forest landscape that may in some cases emerge as more heterogeneous and diverse than the pre-fire landscape (Lloret et al. 2002; Turner et al. 1998). We found that the nature of these changes will strongly depend on the pre-fire characteristics (structure and composition) of the vegetation, so preventive management strategies may help to partially direct regeneration dynamics and increase the resilience of these stands. On the one hand, modifying the spatial distribution of fuel types across the landscape by creating more fragmented landscapes and generating strategic areas with less vulnerable stand structures may increase the abundance of unburned patches and modify their spatial distribution along the burned landscape (Fulé et al. 2012; Ritchie et al. 2007; Strom and Fulé 2007), and thus consequently favor pine regeneration. At stand level, the natural establishment of late-successional tree species such as resprouting broadleaves could be favored by the implementation of silvicultural interventions designed to modify the overstory structure (Lookingbill and Zavala 2000; Martín-Alcón et al. 2015b; Navarro-González et al. 2013). Finally, post-fire restoration measures to promote soil protection in low-quality sites may also help achieve a faster and more generalized recovery of the forest cover, as certain topographic factors such as slope or aspect also play an important role (through their effects on soil moisture distribution) in driving the occurrence of shrublands or sites with low-density of tree regeneration.

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5

Diversifying sub-Mediterranean pinewoods with oak species in a context of assisted migration: responses to cold and microsite conditions

Santiago Martín-Alcón, Lluís Coll, Aitor Ameztegui

5. Diversifying sub-Mediterranean pinewoods with oak species in a context of assisted migration: responses to cold and microsite conditions

Abstract

Questions: How do thermal migration distance and extreme cold events affect seedling emergence and survival in assisted migration schemes in the Sub-Mediterranean context? What role does plant provenance play? Can biotic interactions such as nurse effect of the overstory and shrub layer buffer the negative responses to plant translocation? Are any of these effects species-specific?

Location: Three pinewoods in the Catalan Pre-Pyrenees, northeastern Iberian Peninsula.

Methods: We used a replicated field trial to test the early-years establishment of two contrasted provenances of four *Quercus* species (*Q. coccifera*, *Q. ilex*, *Q. faginea* and *Q. pubescens*) that were sown and planted along gradients of elevation and understory microsite conditions in sub-Mediterranean pine forests. Seedling responses to translocation were evaluated by assessing seedling emergence, seedling survival, and re-sprouting after dieback events according to seedling provenance, thermal migration distance, extreme cold events and microenvironment.

Results: The study reports high success of both the planting (with an overall 76.3% of initial 3-year survival) and sowing (with an overall 50% of seedling emergence) experiments. The results show that: *i*) both thermal distance and extreme cold events have strong effects on the responses of the translocated populations; *ii*) the forest overstory plays an important role in attenuating the negative effects of thermal distance and extreme cold events on seedling survival; and *iii*) these responses are species-specific. The evergreen *Quercus* species and to a lesser extent the marcescent *Q. pubescens* showed quite clear signs of high ecotypic differentiation in terms of cold tolerance, enabling local provenances to respond better to translocation. In contrast, marcescent species, especially *Q. faginea*, showed high phenotypic plasticity that led to a better overall establishment success.

Conclusion: The implementation of assisted migration is a feasible option to increase the diversity and resilience of the sub-Mediterranean pinewoods. Assisted migration programs should manage risks by thoroughly considering thermal migration distances and the occurrence of extreme cold events when selecting species and seed sources, since Mediterranean tree species show different strategies regarding adaptation to cold. Program managers should also consider the advantage of planting/sowing under relatively closed canopy to buffer some of the negative responses associated with translocation.

Keywords: Climate change; Forest management; Diversification; *Pinus*; *Quercus*; Germination; Survival; Resprouting; Local adaptation; Phenotypic plasticity

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5.1. Introduction

Across the northern shore of the Mediterranean Basin, generalized depopulation in rural areas over the second half of the twentieth century has led to the abandonment of once cultivated areas and pastures, and thus a strong decrease in human interventions on forests (Vicente-Serrano et al. 2004; Lasanta-Martinez et al. 2005; Chauchard et al. 2007). These land use changes together with extensive reforestation programs have triggered extended encroachment and densification processes in forests, mainly pinewoods (Améztegui et al. 2010; Navarro & Pereira 2012). More recently, the activity of seed dispersers like jays or mice (Gómez 2003) and the increasing cover of facilitating shrubs in the understory of pine forests —favored by the sharp decrease in grazing pressure by domestic animals— are enabling a gradual entry of late-successional broadleaved species in their understory (Gracia et al. 2007; Martin-Alcon et al. 2012), thus propitiating natural processes of tree-species diversification (Gómez 2003; Gómez-Aparicio et al. 2005; Navarro-González et al. 2013; Martín-Alcón et al. 2015b). An increase in tree species diversity is generally thought to enhance the forest resilience to environmental changes, including variations in disturbance regimes (e.g. Campbell et al. 2009; Thompson et al. 2009; Puettmann 2011). In the particular case of the sub-Mediterranean pine forests, the presence of resprouting species such as oaks in the understory of pinewoods dominated by black pine (*Pinus nigra* Arn. ssp. *salzmannii*) or Scots pine (*Pinus sylvestris* L.) is essential for rapid vegetation recovery after the occurrence of forest fires (Puerta-Piñero et al. 2011; Martín-Alcón et al. 2015a).

Natural tree-species diversification processes are still far from widespread at landscape and regional scales, due to limiting factors such as seed dispersal constraints (Zamora et al. 2010; González-Moreno et al. 2011), unfavorable stand structures —i.e. over-stocked pine plantations (Navarro-González et al. 2013; Martín-Alcón et al. 2015b)—; harsh microsite conditions (Gomez-Aparicio et al. 2009) or inadequate current disturbance regimes (Pausas et al. 2004; Rodrigo et al. 2004). To cope with such limitations and accelerate the natural process, forest managers are increasingly looking at assisted diversification measures based on planting or sowing late-successional species are being more and more considered (Gomez-Aparicio et al. 2009; Palacios et al. 2009; González-Rodríguez et al. 2011; Prévosto et al. 2011).

The climatic conditions to which Mediterranean tree populations have been locally adapted are expected to change dramatically in response to rapid ongoing global warming (Benito-Garzón et al. 2008; Keenan et al. 2011). In this context, assisted migration practices can be considered as a way to help implement diversification actions in particularly vulnerable areas (Kreyling et al. 2011; Frascaria-Lacoste & Fernández-Manjarrés 2012; Pedlar et al. 2012; Benito-Garzón et al. 2013). Assisted migration —also known as assisted colonization, or population translocation— is the intentional movement of focal units (i.e. ecotypes, species, taxa, functional types or life forms) to recipient localities where these focal units are currently absent and cannot be expected to colonize by natural means within a short timeframe (i.e. years or decades) (Kreyling et al. 2011). In forestry, assisted migration is generally focused on keystone tree species moved within, or modestly beyond, a species' current range (Kreyling et al. 2011; Frascaria-Lacoste & Fernández-Manjarrés 2012; Pedlar et al. 2012). The assertion that southern populations facing climate-induced risks can be safely translocated to colder regions still needs to be further explored, since southern populations may maladapt to extreme cold events in the north, which would result in significant economic loss (Benito-Garzón et al. 2013). Common garden and field experiments are the most powerful tools for testing population translocations (Matyas 1996), but these type of field experiments remain scarce, at least in the Mediterranean context.

Here, we present the findings of the initial 3-year monitoring period on a long-term field experiment in which we sowed acorns and planted seedlings from two contrasted provenances along gradients of elevation and microsite conditions (light availability and herbaceous and shrub cover). The study included the four most widespread *Quercus* species in the calcareous mountains of the Eastern Iberian Peninsula (*Q. coccifera* L., *Q. ilex* L., *Q. faginea* Lam. and *Q. pubescens* Wild.), which were planted and sown in the understory of sub-Mediterranean pinewoods. The aim was to gain deeper insight into the main factors driving the success of assisted migration practices, and to assess how some of the species most suitable for diversifying sub-Mediterranean pine forests will respond to translocation-induced change in climate conditions. To our knowledge, this is the first study designed to test assisted migration of the main broadleaf species in sub-Mediterranean pinewoods of the Iberian Peninsula. However, previous studies on the ecophysiologic responses of these species to extreme climatic events have observed broad inter- and intraspecific differences in phenotypic plasticity and local adaptation capacity (Martínez-Ferri et al. 2001; Gimeno et al. 2008; Andivia et al. 2011; Arend et al. 2011; Wellstein & Cianfaglione 2014). Consequently, we expected to find that: (*i*) climate, and particularly minimum temperatures, would play a determinant role in seedling emergence and mortality in the first few years, especially at high elevations; (*ii*) extreme cold events (if any) would accentuate seedling mortality; (*iii*) plant provenance would strongly affect emergence and survival, with southern provenances performing worse, especially at high elevations; (*iv*) biotic interactions, through the protection provided by the overstory and/or shrub cover, could partially buffer the signs of maladaptation to local conditions, especially those species and provenances established further from their current climatic range, and (*v*) responses to translocation distance and extreme cold events, as well as the effects of plant provenance and biotic interactions would be species-specific.

5.2. Materials and Methods

5.2.1. Study area

The experiment was conducted at three pine forests located in the Catalan Pre-Pyrenees (NE Iberian Peninsula), a mountain range extending from East to West, south from the main Pyrenean range (Figure 1). The three forests are located on northern slopes of the same valley but set 10-15 km apart from each other, in mountains dominated by limestone and calcareous soils, covering an altitudinal gradient from around 900 to 1,700 m asl. In the area, this gradient includes the transition from sub-Mediterranean to upper montane bioclimatic territories, and involves the *Pinus nigra–P. sylvestris* transition zone, with *P. nigra* clearly dominating the overstory up to 1,100 m and *P. sylvestris* dominating from 1,400 m upwards. Although forests in the area are clearly dominated by pines, some individuals or small groups of broadleaved tree species (*Quercus*, *Acer*, *Sorbus* or *Prunus)* can be found sparsely distributed along the slopes, more frequently at low elevations. The main understory species is common box (*Buxus sempervirens* L.), but other species of genera *Juniperus*, *Cotoneaster*, *Crataegus* or *Arctostaphylos* are also frequent.

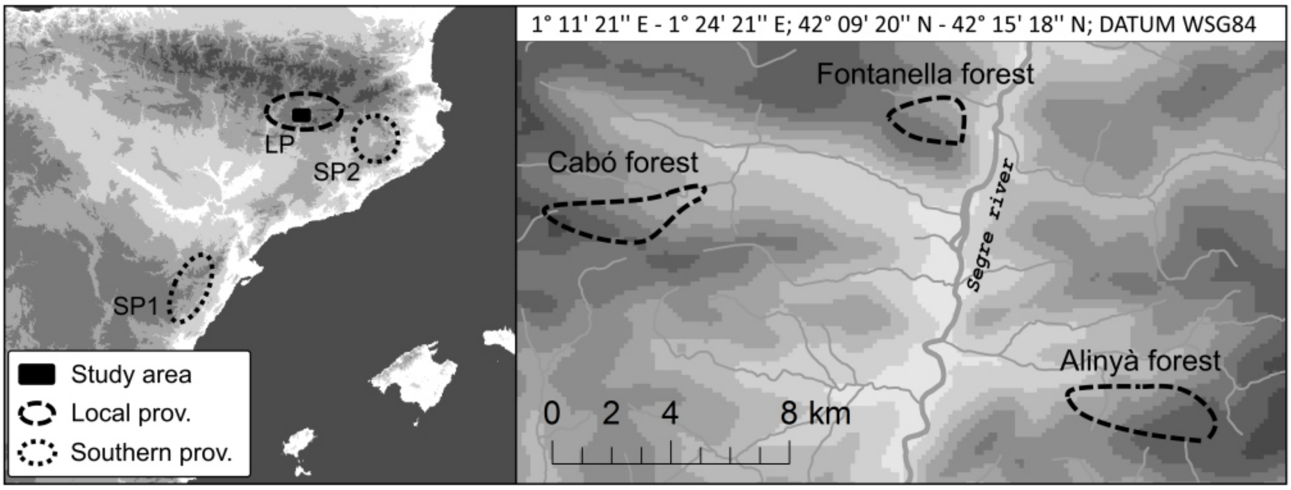

Figure 1. Location of (a) the study area in northeastern Iberian Peninsula and approximate zonation of local provenance (LP) of the vegetative material of all 4 species (*Q. coccifera*, *Q. ilex*, *Q. faginea* and *Q. pubescens*), southern provenance of *Q. ilex* and *Q. faginea* (SP1), southern provenance of *Q. pubescens* (SP2), and (b) the study area spanning the three forests hosting the experiment.

5.2.2. Species characteristics

We selected four *Quercus* species, each of which is widely distributed in the western Mediterranean Basin and part of the ongoing process of tree-species diversification in Mediterranean pine forests (Navarro-González et al. 2013; Vayreda et al. 2013; Martín-Alcón et al. 2015b). *Q. coccifera* L. and *Q. ilex* L. are common evergreen sclerophyllous oaks in Mediterranean areas of the Iberian Peninsula, whereas *Q. faginea* Lam. and *Q. pubescens* Wild. are semi-deciduous (marcescent) oaks commonly growing in sub-Mediterranean locations. All four species can be found growing naturally in the study sites, with the exception of *Q. coccifera* which is nevertheless common in the southern slopes of the same mountains. The four species can be ranked on drought tolerance as *Qc* > *Qi* > *Qf* > *Qp* (see ranges of Thornthwaite precipitation effectiveness index in their distribution areas in Figure 2) and rank in the opposite order for cold tolerance (see ranges of average minimum daily temperatures in Figure 2). All the species can be defined as intolerant to intermediate-tolerant to shade (Niinemets & Valladares 2006), although they are favored by moderate to high shading during the seedling establishment phase (Broncano et al. 1998; Retana et al. 1999; Lookingbill & Zavala 2000; Quero et al. 2006; Gómez-Aparicio et al. 2008; Caldeira et al. 2014). Moreover, all are resprouting species (Pausas 1999; Pausas 2001).

For three of the four species studied (*Q. ilex*, *Q. faginea* and *Q. pubescens*), we selected vegetative material (seeds and plants) from two provenance regions: (*i*) a local provenance (central Catalan Pre-Pyrenees) which corresponds to the study area, and (*ii*) a southern provenance which corresponds to more xeric sites, located in the mountainous area extending between the South Iberian range to the Mediterranean coast in the case of *Q. ilex* and *Q. faginea* and the Catalan Pre-Coastal range in the case of *Q. pubescens* (Figure 1). In the case of *Q. coccifera*, only the local provenance was tested. In order to get a proper idea of the suitability of the study locations for each of the species and provenances, we calculated the average climatic conditions of the sites in which they are currently distributed. Climatic variables considered were annual average minimum and maximum daily temperatures as indicators of thermal conditions, and average Thornthwaite's index of precipitation effectiveness (Thornthwaite 1931) calculated with the Hargreaves & Samani (1982) equation as an indicator of water availability. The different climatic variables were calculated separately for the entire distribution area of each species in Peninsular Spain and for the geographic area of each region of provenance (Figure 2). An approximation to species distribution areas was obtained by using the plots of the third Spanish National Forest Inventory (DGCN 2007) in which each of the species were present, and we crossed them with climatic data from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola et al. 2005). The geographical limits of the species provenance regions used were those identified by the Spanish Ministry of the Environment (Alía et al. 2005). In terms of the mean climatic attributes of the experimental sites, all of them may satisfy the water requirements of the different species but their thermal conditions are in the coldest range of the distribution area of all the species and provenances tested, or even modestly below these ranges in some cases (Figure 2).

5.2.3. Experimental design

We selected three altitudinal levels at each of the three forests studied to represent a range of thermal migration distances: low (around 1,000 m asl), intermediate (around 1,250 m asl), and high (around 1,500 m asl). The choice of elevation gradient was based on the observed gradient of mean minimum daily temperatures (*Tmin*) along the slopes, as this was thought to be one of the most important climatic attributes determining thermal migration distance. We thus chose our upper altitudinal level aiming to slightly surpass the range of *Tmin* observed along the current distribution area of the local provenance of all 4 species (Figure 2), and the lower altitudinal level to be within but in the lower end of the range of *Tmin* observed along the current distribution area of the southern provenances. At each elevation, two 12 × 12 meter plots were established: one plot was located under continuous pine overstory (canopy plots), and the other was placed under a small canopy gap with an extent that was equivalent to the area occupied by two to three adult trees (gap plots).

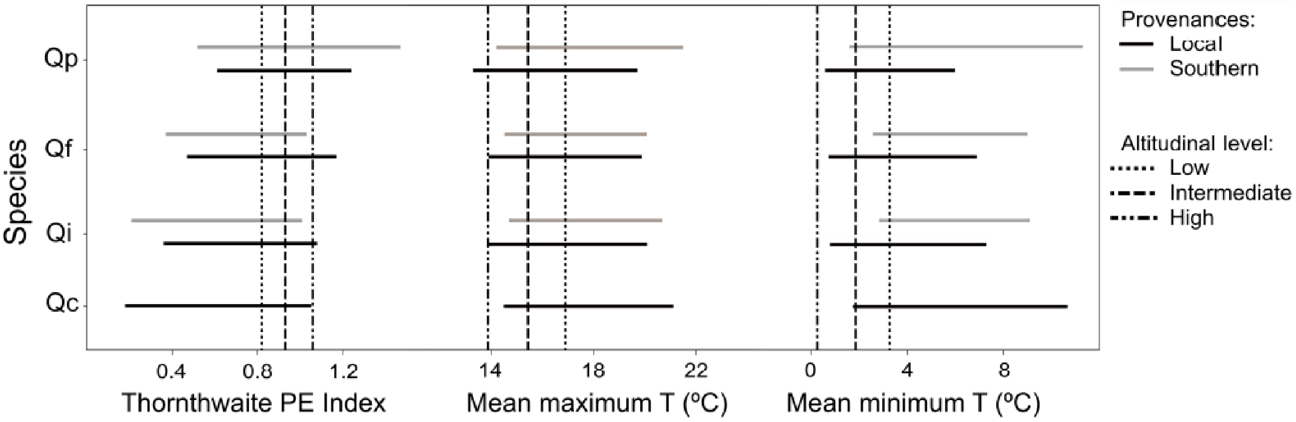

Figure 2. Mean climatic characteristics in the study plots (vertical lines) and ranges of the same climatic variables in the current distribution area of the studied species and provenance regions (horizontal lines). Species distribution areas were approximated from the third Spanish National Forest Inventory (DGCN 2007), and climatic data was extracted from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola et al. 2005). See text for details on data processing.

Seven two-year-old seedlings of each combination of species × provenance were planted in each plot in October-November 2011, for a total sample size of 882 seedlings (126 per species and provenance). Seedlings were planted at least one meter apart to avoid cross-interactions. The seedlings were randomly distributed across each plot and planted with care to minimize alteration of the microenvironment. The seedlings had been grown in nurseries located in the same region of provenance in which the seeds had been collected, i.e. the seed and the nursery were located inside the same region of provenance (Alía et al. 2005). Even though all plots were fenced off to prevent damages by wild or domestic animals, 29 seedlings (out of 882) had to be excluded from analyses due to damage by animals (probably small rodents).

One year after plant establishment, we selected 5 sowing points in each of the 18 plots (3 forests × 3 elevations × 3 light conditions). Three acorns of each species × provenance combination were sown at 4 cm depth in each sowing point in November 2012. Acorns were collected the same autumn from trees growing in the same region of provenance from which the seedlings had been acquired. Non-viable acorns were eliminated by floating and visual screening prior to sowing. Each sowing point was covered with a 80 cm × 80 cm wire mesh (0.6 cm mesh size) to avoid predation. Despite this protection, one of the plots had to be discarded due to severe damage by animals.

5.2.4. Monitoring

For the plantation experiment, seedling mortality was regularly monitored throughout the duration of the experiment. With the aim of disentangling the main factors driving mortality for each species at each location, we divided the observed mortality into either winter mortality (registered after each winter season) or summer mortality (registered after each summer season). 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 symptoms of disease) at the end of the previous one. All seedlings determined as dead during one of the field campaigns were re-visited during the next growing season. Those seedlings that were able to resprout were then reclassified as alive for the analysis of mortality, and thus coded as 'resprouted'.

The emerged seedlings were inspected and registered at different dates: June 2013, October 2013, June 2014 and October 2014. Every new seedling recorded was identified and its health status was monitored during the next visits. We stopped monitoring seedling emergence after October 2014 since only two new emergences had been registered in that visit. At that point, all the individuals were unearthed in order to check whether they were independent seedlings or different stems of the same individual. Seedlings that were qualified as multi-stemmed were then re-considered as a single individual. Seedling emergence was determined as number of emerged seedlings per plot (i.e. the sum of the 5 sowing points in each plot) during two growing seasons after the date of sowing.

5.2.5. Characterization of the environment and micro-site explanatory variables

To better characterize climatic differences across the elevation gradient, we continuously measured air temperature in all the plots using HOBO Pendant Temperature/Light Data Loggers (Onset, MA) (see Figure 2 and Table 1 for average temperatures registered in the experimental sites).

We also gathered meteorological data from the closest meteorological station to the study forests (EMA Organyà, Servei Meteorològic de Catalunya), located 5 km from Fontanella and Alinyà forests and 10 km from Cabó forest. These data revealed the occurrence of some extreme climatic events over the three years of the study, and in particular an extraordinarily dry and cold period the first winter after planting (from December 2011 to February 2012) (Figure 3) which exposed the vegetation to a significant risk of frost damage (aggravated by the low water content in the soil). In contrast, the winters of 2013 and 2014 were closer to the average climate of the area. During the first summer there was another rather dry period that extended over three months (from June to August 2012), accompanied by slightly above-average maximum temperatures. The next two summers registered short dry periods (June 2013, May-June 2014), but in both cases closer to the normal climatic variability in the area.

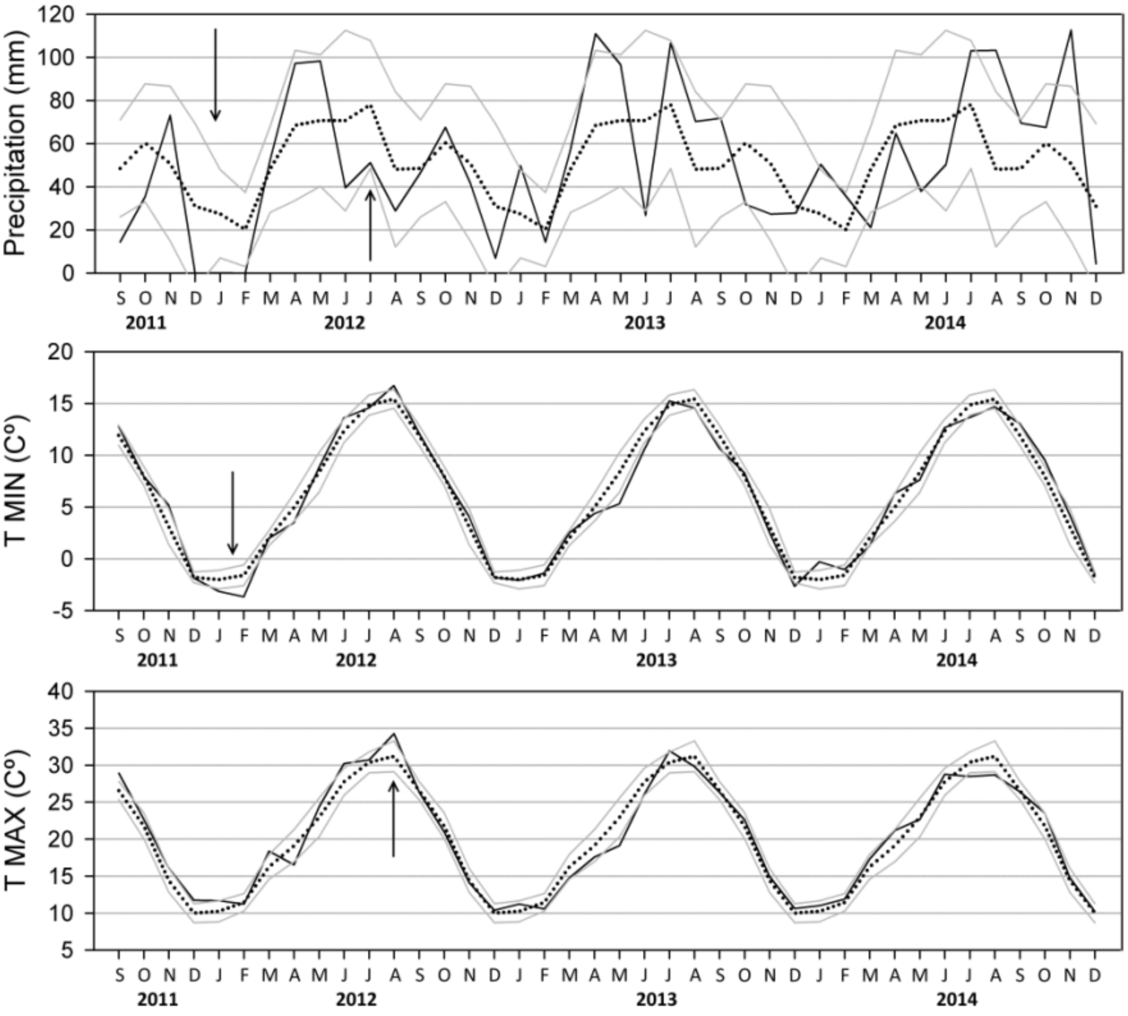

Figure 3. Time-course of precipitation and monthly averages of minimum (T MIN) and maximum (T MAX) temperatures in the study area over the 3-year study period (2012–2014). Dashed black lines indicate average values during the last 10 years. Solid grey lines indicate mean ± SD values during the last 10 years. Solid black lines indicate measured values. Data are from the Organyà meteorological station (566 m a.s.l.), located less than 10 km away from the three forests. Vertical arrows flag the extreme climatic events of winter 2012 and summer 2012 (see text for details).

To characterize the microsite conditions of the planted seedlings, light availability and percentage of herbaceous and shrub cover were measured for each seedling (Table 1). Light availability was measured using two Li-190SA quantum sensors (Li-COR, NE). 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). Percentage of herbaceous and shrub cover surrounding the seedlings was visually estimated to the nearest 5% using a 80 × 80 cm square centered on the plant. Finally, stand structure was characterized in each plot by determining basal area, stand density and quadratic mean diameter from forest inventories performed with relascope plots (as Piqué et al. 2011).

Table 1. Mean abiotic and biotic characteristics of the 18 plantation plots, stratified by altitudinal level and type of canopy cover. Values for light availability, herbaceous cover and shrub cover are means ± SD (n = 147).

	Low elevation		**Intermediate elev.**		**High elev.**	
Plot-level attributes	**Canopy**	**Gap**	**Canopy**	**Gap**	**Canopy**	**Gap**
Tm annual (ºC)	10.9		9.1		7.3	
Tm warmest month (ºC)	21.8		20.0		18.0	
Tm coldest month (ºC)	2.0		-0.1		-2.1	
Elevation (m asl)	967.7	970.3	1283.8	1251.4	1507.2	1545.0
Aspect	N/NE		N/NE		NW/NE	
Slope (%)	43.9	34.3	38.9	29.4	34.4	40.1
Bedrock	Limestone		Limestone		Limestone	
Dominant species	Pn		Pn, Ps		Ps	
Dg (cm)	18.7	18.9	23.4	26.7	21.8	23.8
G (m^2/ha)	33.7	17.8	34.0	14.5	33.0	18.3
N (stems/ha)	1257.6	630.8	820.8	268.3	906.3	416.9
Herbaceous cover (%)	37.9 ± 26	38.8 ± 22.1	39.9 ± 25.6	52.6 ± 27.3	36.9 ± 23.3	43.1 ± 22.7
Shrub cover (%)	11.6 ± 7.7	20.8 ± 15.9	31.5 ± 25.6	16.6 ± 12.9	22.1 ± 18.1	20.9 ± 14.9
Light availability (%PPFD)	17.9 ± 2.4	36.4 ± 7.2	19.6 ± 5.5	36.8 ± 10.3	13.3 ± 2.2	28.8 ± 6.9

5.2.6. Data analyses

Seedling emergence was analyzed using a log-linear mixed-effects Poisson model, with counts of emerged seedlings per plot (from 0 to 15) as the response variable. GLMMs parameters were estimated using Maximum-likelihood (ML) with Gauss-Hermite quadrature approximation (Pinheiro & Chao 2006). We fitted one model for each of the four species, and elevation (at three levels), canopy cover type (two levels) and provenance (two levels) were included as fixed effects in the model, whereas forest was considered a random factor. Selection of variables for inclusion in the final models was based on Akaike's information criterion (AIC), with lower AIC values indicating stronger empirical support for a model (Bolker et al. 2009). Once the best model was obtained, it was compared against the null model (containing only random intercept and fixed intercept) using the likelihood ratio (LR) test.

The effect of elevation, canopy cover type and region of provenance on survival of planted seedlings was assessed by developing survival function curves based on Kaplan-Meier estimates, and the Mantel-Cox log-rank test was used to determine the significance of the differences between factor levels. To test the effect of both categorical and continuous covariates on seedling survival, we used a mixed-effects Cox model (Therneau & Grambsch 2000), which is a modification of the commonly used Cox's Proportional Hazards (coxPH) model (Cox, 1972) that allows for inclusion of random effects. Summer and winter mortality were segregated as response variables, so we fitted a mixed-effects Cox model for each response variable and species. Elevation and provenance were introduced as fixed factors, and the three variables measured at microsite level (herbaceous cover, shrubs cover, and light availability) and initial seedling size were introduced as fixed covariates. Plot and forest were considered random factors. For the Cox model, the variables for inclusion in the final models were selected by comparing the full model against reduced models in terms of the log-likelihood (Loglik) value, with higher Loglik values indicating a better-fitting model (Huelsenbeck & Crandall 1997). The hazard ratio (HR) was computed for each significant predictor variable. For categorical variables, HR represents the quotient of the hazard functions for each of the factor levels compared to a reference level. For continuous variables, HR indicates the expected change in the risk of mortality with a one-unit increase in the explanatory variable.

Finally, to assess seedling resprouting after dieback, logistic mixed-effects models were fitted for each species using the ML method with Laplace approximation in the same model structure (i.e. candidate predictors and random factors) as in the mixed-effects Cox models. We created a response variable named 'resprouted' that takes value of '1' for seedlings that were able to resprout and survived, and '0' otherwise. The inclusion of variables in the logistic mixed-effects models was based on the AIC, and comparison of nested null and best models was assessed using the LR test. All analyses were performed using R 3.1.1 software (R Development Core Team 2014) and the 'lme4' v. 1.1-7 (Bates 2010), 'survival' v. 2.38–1 (Therneau & Lumley 2011) and 'coxme' v.2.2–4 (Therneau 2012) packages for R.

5.3. Results

5.3.1. Seedling emergence

The emergence of oak seedlings occurred in stages during the first two growing seasons. A total of 69 *Q. coccifera*, 249 *Q. ilex*, 267*Q. faginea* and 305 *Q. pubescens* seedlings emerged during this period, representing 27%, 49%, 52% and 60% of the sown acorns, respectively. *Q. coccifera* presented the most delayed emergence, with 43.5% occurring during the second growing season compared to around 23% for the other species. For all species, lag to emergence was related to altitudinal level, with plots at high elevations showing the most delayed emergence (40.8% during the second growing period) compared to intermediate (25.6%) and low elevation plots (16.6%). We found no noticeable differences in emergence date between the two levels of canopy cover type or between seed provenances. For all species except *Q. pubescens,* emergence was significantly lower at plots located at highest elevation but did not differ between low and intermediate plots (Table 2). Seed provenance only affected seedling emergence for *Q. ilex*, with the southern provenance presenting lower emergence rates across altitudinal levels. No differences in emergence were found between canopy and gap plots.

Table 2. Results of the log-linear mixed-effects Poisson models of seedling emergence. Significant fixed terms in the best model for each of the sown species are shown, along with the AIC of both the best model (AIC_{Best}, containing all the fixed terms that produced a significant effect) and the null model (AIC_{Null}, containing only the intercept), and the significance of the LR test realized for model comparison.

Species	Best model terms (Fixed)	Estimate	SE	Sig.	AIC_{Best}	AIC_{Null}	P (>Chisq)
Q. coccifera	Intercept	1.598	0.231	0.002	29.207	42.978	<0.001
	Elevation=H	-1.420	0.448	0.007			
Q. ilex	Intercept	1.877	0.144	<0.001	57.713	71.118	<0.001
	Elevation=H	-0.466	0.173	0.007			
	Provenance=L	0.402	0.130	0.002			
Q. faginea	Intercept	2.480	0.127	<0.001	35.626	39.271	0.022
	Elevation=H	-0.405	0.146	0.07			
Q. pubescens	Intercept	2.101	0.060	<0.001	-	41.100	-

5.3.2. Seedling survival

Seasonal patterns and altitudinal effects

Overall survival rate of planted seedlings after three growing seasons was significantly higher ($P < 0.001$) for marcescent species (*Q. faginea* and *Q. pubescens,* both showing 82.7% survival) than for evergreen oaks (*Q. coccifera* and *Q. ilex*, with 63.2% and 69.9% survival, respectively). Furthermore, these two groups showed different seasonal patterns of mortality: mortality for evergreen oaks occurred mostly during winter (93% and 90%, respectively), especially the first winter (80% and 73%), and mortality was significantly higher at the highest plots ($P < 0.001$ for both species). On the other hand, mortality for marcescent oaks was concentrated on the first two years after plantation, but was evenly distributed over seasons, and with much lower effect of elevation on survival.

When splitting the data into winter and summer mortality, mixed-effects Cox models showed that winter mortality rates were significantly higher at the highest altitudinal level compared to the lower levels for all four species (Table 3). This effect was stronger in the case of *Q. pubescens* (HR = 9.328) and *Q. coccifera* (HR = 8.070), followed by *Q. ilex* (HR = 5.75), and was weaker, but still significant, for *Q. faginea* (HR = 3.806). For *Q. ilex,* significantly higher winter mortality rates were also found in the intermediate altitudinal level (HR = 2.273) compared to the lower level. Both local and southern provenances of *Q. ilex* were negatively affected by elevation, although the effect was more pronounced for the southern-provenance seedlings (see Kaplan-Meier curves for the interaction between elevation and provenance in Figure 4). In fact, the significantly higher mortality rates of the southern-provenance *Q. ilex* compared to local provenance (HR = 2.408) were fundamentally linked to the winter mortality events (Table 3).

Microsite effects

In the case of *Q. coccifera,* the negative effect of elevation on seedling survival was accentuated under gap conditions. The Cox models for this species revealed a significant effect of plant exposure (as light ratio at each seedling location, %PPFD) for both winter (HR = 1.033) and summer (HR = 1.165) mortality events. In the case of *Q. pubescens*, the Kaplan-Meier curves for factor interactions (Figure 4) revealed that the negative effect of elevation was almost exclusively linked to southern-provenance seedlings planted under canopy gap conditions. Canopy cover type was found to significantly affect seedling mortality for the two marcescent species, both of which showed significantly higher mortality rates under gap conditions (P = 0.016 for *Q. faginea*, and P = 0.013 for *Q. pubescens*). Looking at the interaction between elevation and canopy cover type, we found that the significant reduction of *Q. faginea* mortality rates under continuous canopy occurred only in the lower and intermediate altitudinal levels, but not in the higher level. A similar effect was found by the summer mortality Cox model for *Q. pubescens*, which showed higher ratio of summer mortality of *Q. pubescens* with increasing light ratio (HR = 1.052). Grass or shrub cover surrounding the seedlings was not found to negatively affect their survival, with the exception of *Q. faginea* in the summer (Table 3). Similarly, size of the seedling at the time of plantation (represented by the seedling basal diameter, DO) had very little effect on seedling survival and only affected *Q. coccifera* plants that showed a significantly lower ratio of winter mortality with increasing DO.

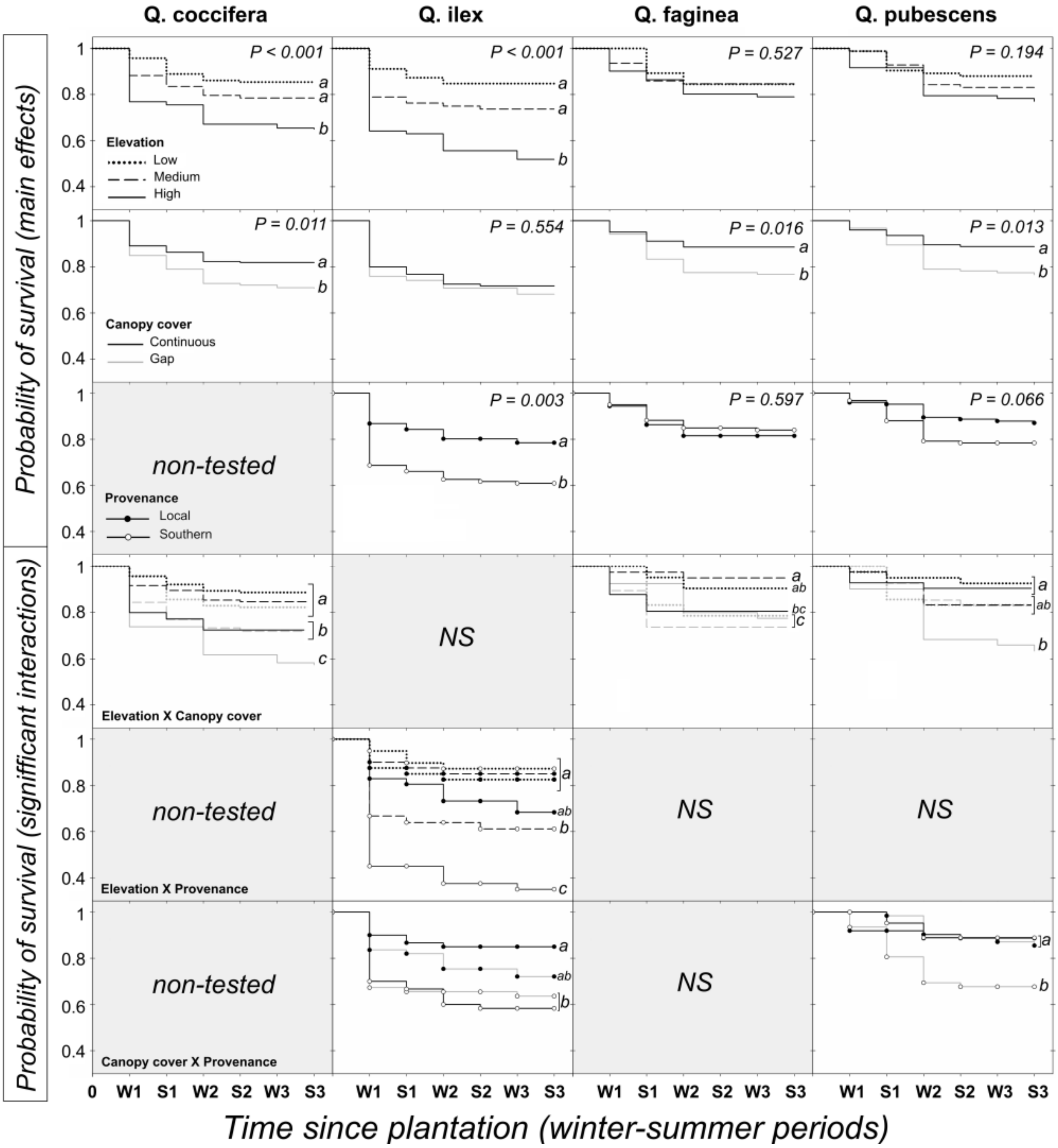

Figure 4. Survival curves for the panted seedlings of the four tree species over the course of the 3-year study period, based on Kaplan–Meier estimates. Rows represent the different main effects and interactions, and columns represent the different species. Legends for each row of the main effects are in the first plot of the row, and legends for each row of the interactions correspond to the union of the legends of the effects taking part in the interaction. P-values indicate significance of the log-rank test between factor levels for each species. W periods in the x-axis correspond to the 1st, 2nd and 3rd winter seasons after plantation, and S periods to the summer seasons.

Table 3. Mixed-effects Cox proportional-hazards model of 3-year winter and summer mortality of the planted seedlings of the 4 *Quercus* species. Significant fixed factors and covariates in the best model for each of the species are shown with their hazard ratio (HR) values, along with the log-likelihood (Loglik) values of both the best model (Loglik$_{BM}$, containing all the fixed terms that produced a significant effect) and the null model (Loglik$_{NM}$, containing only the intercept), and the significance of the LR test realized for model comparison.

Species	Model	Terms	Estimate	SE	HR[7]	Sig.	Loglik$_{BM}$	Loglik$_{NM}$	P (>Chi^2)
Q. coccifera	Winter mortality	Elevation=H	2.088	0.511	8.070	<0.001	-179.21	-194.72	<0.001
		Light ratio	0.033	0.013	1.033	0.012			
		D0	-0.827	0.279	0.437	0.003			
	Summer mortality	Light ratio	0.153	0.071	1.165	0.032	-9.74	-13.25	0.008
Q. ilex	Winter mortality	Elevation=IM	0.821	0.417	2.273	0.049	-331.08	-316.44	<0.001
		Elevation=H	1.749	0.378	5.750	<0.001			
		Provenance= S	0.879	0.262	2.408	<0.001			
	Summer mortality	-	-		-	-	-	-	-
Q. faginea	Winter mortality	Elevation=H	1.337	0.567	3.806	0.018	-126.08	-129.46	0.034
	Summer mortality	Shrub cover	0.024	0.010	1.024	0.020	-86.65	-88.82	0.037
Q. pubescens	Winter mortality	Elevation=H	2.233	0.778	9.328	0.004	-143.72	-148.9	0.006
	Summer mortality	Light ratio	0.050	0.018	1.052	0.006	-77.57	-81.13	0.008

5.3.3. Seedling resprouting after dieback

The ability to recover by resprouting after a dieback event was higher for *Q. faginea* than for the other species (70.4% of the 142 seedlings of this species suffering a dieback event were able to re-sprout during the next seasons). The percentages of re-sprouted seedlings for the other species were 59.7% for *Q. coccifera* (from 77 dieback events), 59.0% for *Q. pubescens* (from 105 dieback events), and 54.5% for *Q. ilex* (from 156 dieback events). Surprisingly, none of the candidate explanatory variables showed a significant effect on resprouting in *Q. faginea* seedlings. For *Q. pubescens* and *Q. coccifera*, the models found an effect of seedling size, with individuals presenting higher stem diameter being more able to resprout. Interestingly, the southern provenances of *Q. pubescens* and *Q. ilex* showed significantly lower resprouting ability than the local provenances.

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[7] For categorical predictor variables, the hazard ratio (HR) represents, the quotient of the hazard functions for each of the factor levels compared to a reference level (Low, for Elevation; Local, for Provenance). For continuous variables, HR indicates the expected change in risk of mortality with a one-unit increase in the parameter in question.

Table 4. Results of the logistic mixed-effects models of seedling re-sprout after dieback events. Significant fixed terms in the best model for each of the planted species are shown, along with the AIC of both the best model (AIC_{Best}, containing all the fixed terms that produced a significant effect) and the null model (AIC_{Null}, containing only the intercept), and the significance of the LR test realized for model comparison.

Species	Model term (Fixed effects)	Estimate	SE	AIC_{Best}	AIC_{Null}	P (>Chi²)
Q. coccifera	Intercept	-4.035	1.289	101.07	109.80	0.001
	DO	1.284	0.447			
Q. ilex	Intercept	0.707	0.452	207.74	213.93	0.004
	Provenance=M	-0.999	0.362			
Q. faginea	Intercept	0.943	0.298	-	176.02	-
Q. pubescens	Intercept	4.873	2.086	134.13	145.11	<0.001
	Provenance=M	-2.377	1.091			
	DO	0.362	0.181			

5.4. Discussion

5.4.1. Thermal distance and extreme cold events in assisted migration

The results of our study confirm that both the thermal distance between the current species' distribution range and the recipient locality and the occurrence of extreme cold events have strong effects on the performance of the translocated populations. Both these factors therefore warrant careful consideration when selecting species and seed sources for assisted migration programs (Vitt et al. 2010; Pedlar et al. 2013; Benito-Garzón & Fernández-Manjarrés 2015). Potential signs of having surpassed the prudential migration distance in some of the species used in this study include: (*i*) the overall lower germination rate of *Q. coccifera*, which is the species the most displaced from its ecological range; (*ii*) the lower germination rate of almost all the species (except *Q. pubescens*) at the highest altitudinal level; (*iii*) the mid-to-low survival of the evergreen *Q. coccifera* and *Q. ilex* seedlings planted at the highest elevation, and; (*iv*) the lower germination and survival of some of the southern provenances (especially of *Q. ilex*), for which the thermal migration distance was much higher than for the local provenances. The fact that most of the winter mortality of the species showing higher sensitivity to cold (*Q. coccifera* and *Q. ilex*) occurred during the extreme cold event in the first winter confirmed the decisive role of such events as a driver of seedling responses to translocation (Ameztegui & Coll 2013; Benito-Garzón et al. 2013). In contrast, the extraordinarily hot and dry summer periods did not lead to any substantial increase in mortality, which may indicate that seedlings are well adapted to cope with the more severe summer drought events surely occurring in their distribution areas.

5.4.2. The role of forest overstory in buffering negative responses to translocation

The fact that forest overstory plays an important role in maintaining a suitable microenvironment for the germination and early establishment of *Quercus* species has been widely reported and generally attributed to the fact that the canopy provides protection from direct exposure to light and high evaporative demands (Broncano et al. 1998; Lookingbill & Zavala 2000; Prévosto et al. 2011; Caldeira et al. 2014; Martín-Alcón et al. 2015b). In our study area, we found higher summer mortality in three of the four species (*Q. coccifera, Q. faginea* and *Q. pubescens*) when planted under gap conditions and at lower elevations, thus confirming the facilitative role of canopy cover. In addition, the pine overstory also played an important role in buffering the negative effects of thermal distance (represented by elevation) and extreme cold events on seedling survival, by reducing winter mortality at higher elevations. This result has important implications and suggests the advantage of planting/sowing under relatively closed canopy to buffer negative responses to cold in assisted migration programs. Previous studies had also demonstrated a facilitative effect of shrubs in the establishment of *Quercus* seedlings, especially in the context of very open habitats (Rousset & Lepart 1999; Gómez-Aparicio et al. 2005; Kunstler et al. 2007; Smit et al. 2008), but we did not find any such effect here. The relatively low abundance of shrubs in the understory of our study sites together with the lack of important differences in shrub cover between the canopy and the gap plots might be at the origin of this divergence.

5.4.3. Intra- and inter-specific differences in responses to plant translocation

This experiment found important inter- and intra-specific differences in responses to translocation in terms of germination, survival and resprouting. We expected a high sensitivity to translocation for *Q. coccifera*, which is the species with the highest thermal migration distance to all the study sites. However, *Q. coccifera* showed more than 50% survival after the 3 years, high resprouting rates after dieback, and delayed seedling emergence, which indicates a non-negligible plasticity to temperature. The plastic behavior of this species was also observed by Baquedano et al. (2008) who found that phenotypic plasticity in response to water stress explained around 75% of the variability of different physiological and structural parameters among individual plants.

The other evergreen species (*Q. ilex*) was expected to respond to translocation is much the same way as *Q. faginea*, since both species coexist in both southern and local provenance regions, where they occupy similar ecological niches (Espelta et al. 2005; Juárez-López et al. 2008). However, we found that *Q. ilex* was less able to cope with cold stress than *Q. faginea,* as shown by its higher mortality when growing at high elevations. This negative response was particularly important for *Q. ilex* plants from the southern populations, which points to the existence of high ecotypic specialization in this species (Gratani et al. 2003; Peguero-Pina et al. 2014). In contrast, provenance did not play a significant role in the survival of *Q. faginea* or *Q. pubescens* along the altitudinal gradient studied. Although previous studies have shown similar phenotypic plasticity to light and drought between evergreen and marcescent oaks (Espelta et al. 2005; Castro-Díez et al. 2006), our results would suggest higher plasticity of marcescent oaks in response to cold stress. This could be related to their higher capacity to adapt phenology in response to low temperatures (Morin et al. 2007; Vitasse et al. 2014), contrasting with the reported higher phenological plasticity of evergreen oasks in response to summer-drought (Montserrat-Martí et al. 2009).

5.4.4. Conclusions

This study serves as a first replicated field trial to evaluate the feasibility of management interventions based on planting or sowing late-successional species for diversifying sub-Mediterranean pine forests using an assisted migration approach. Initial establishment success was high in both the planting (with an overall 76.3% survival after the 3 years, reaching 82.7% for the species showing better performance) and sowing (with an overall 50% of seedling initial emergence, reaching 60% for the species showing better performance) experiments, in line with previous diversification experiments carried out in Mediterranean pine forests (Palacios et al. 2009; González-Rodríguez et al. 2011; Prévosto et al. 2011). However, the performance of the translocated populations was found to be highly dependent on the distance in thermal conditions from source locality to recipient locality and on the occurrence of extreme cold events. Our results also showed the important role of forest overstory in buffering the negative effects of thermal distance and extreme cold events on seedling survival. Finally, we found signs of high ecotypic differentiation in regard to cold tolerance among different oak species (in particular the evergreens). In contrast, the marcescent species, principally *Q. faginea*, showed high phenotypic plasticity to cold. These key intra- and inter-specific differences strongly underline the importance of managing risks in assisted migration programs by employing multiple seed sources, establishing field trials to guide seed movements, and exercising caution when calculating migration distances.

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6

General discussion

6. General discussion

The results of this doctoral thesis contributed to advance in the understanding of the current dynamics of the Sub-Mediterranean pinewoods in the eastern Pre-Pyrenees. Particularly they provide further information on: (*i*) the drivers of tree-species diversification processes, (*ii*) the main factors modulating post-fire regeneration dynamics and in particular on the role played by pre-fire vegetation attributes, and (iii) key elements to consider when applying diversification actions using different species in an assisted-migration approach. Our findings can be used by forest managers to design management actions oriented to enhance the resilience of these pinewoods to future environmental changes.

6.1. Drivers of natural tree-species diversification and fire-absent dynamics of Sub-Mediterranean pinewoods

The results presented in chapter 2 showed that Sub-Mediterranean pinewoods in the eastern Pre-Pyrenees are currently undergoing a progressive and generalized advance of broadleaved tree species (especially evergreen and marcescent oaks). This is consistent with trends observed by studies developed at broader scales (e.g. Carnicer et al. 2014; Urbieta et al. 2011; Vayreda et al. 2013). This process is known to be mostly mediated by acorn dispersers such as jays (*Garrulus glandarius* L.), which preferentially cache the acorns from neighboring seed sources under the pine canopies (Gómez 2003). In our sampled stands, we found very high abundance of young *Quercus* seedlings compared to saplings, which reveals the rather recent origin of these processes. Other broadleaved species (e.g. *Sorbus*, *Acer*, *Prunus*, etc) were found to be part of the new cohort of colonizing tree species, but their abundances were very low compared to the density of *Quercus* species.

The different studies of this thesis provide evidence of the important role that factors related to stand structure and canopy attributes play in the establishment and growth of oak recruitment. In chapter 2 we found that, despite their contrasting leaf habit, both evergreen (*Q. ilex*) and marcescent oak (*Q. faginea* and *Q. cerrioides*) seedlings showed similar preferences in terms of overall canopy openness, with maximum seedling recruitment occurring at around 15–25% (which matches the average values currently found in the studied stands). The effective germination and establishment of oaks in these moderately-closed pine canopies might be mediated by the protection provided by the overstory to the seedlings from direct exposure to light and high evaporative demands (Retana et al. 1999; Sheffer 2012). The results presented in chapter 4 supported these findings, since they reported higher success of post-fire oak regeneration in sites that were forested during the last decades and that presented a higher tree canopy cover prior to the fire. This corresponded to the conditions more favorable for undergoing diversification processes by resprouting tree species such as oaks (Navarro-González et al. 2013; Puerta-Piñero et al. 2012). Finally, the pine overstory was also found to facilitate oak seedling survival in the diversification experiment presented in chapter 5, particularly by buffering the negative effects of extreme climatic conditions derived from plant translocation to colder localities.

In chapter 2 we looked deeper into the role of canopy attributes on tree-diversification and we found the marcescent and the evergreen oaks to respond differently to them. In the case of the marcescent oaks, seedling recruitment was found to be particularly important under small or irregularly shaped canopy gaps, confirming their higher sensitivity to high light exposure during their early stages of development (Marañón et al. 2004). On the other hand, the evergreen oak's seedling bank was rather similar along the sampled gradient of gap sizes and shapes; which indicates higher tolerance of this species to direct light exposure, in agreement with what had been previously reported for other mountain areas (Gómez-Aparicio et al. 2008; Gómez-Aparicio et al. 2006).

The models presented in chapter 2 did also show an overall favorable effect of the shrub layer on the recruitment of oaks, which may in part be due to the behavior of seed dispersers like jays and mice, which tend to cache acorns below them (Gómez 2003). In addition, shrubs can also improve germination and emergence conditions and facilitate seedling survival by improving nutrient and water availability, reducing soil compaction, and offering protection against browsing by ungulates (Gómez-Aparicio et al. 2005; Kunstler et al. 2007; Rousset and Lepart 1999; Smit et al. 2008).

Once the oak seedlings have established, our models reported different environmental requirements for the evergreen and marcescent oaks to grow and reach more advanced developmental stages. We found considerably higher density of saplings of the marcescent oaks than the evergreen ones under the closed-canopy conditions that characterize most of the studied stands, which may suggest a higher capacity of the first for coping with low light levels (i.e. canopy closure). Under shade conditions, the established *Q. ilex* are nevertheless able to persist without significant net growth (Espelta et al. 1995; Garcia-Barreda and Reyna 2013) forming dense seedling banks and perpetuating through repeated shoot dieback and re-sprout until light conditions improve (Johnson 2009).

In summary, our results showed that current levels of both canopy closure and shrub cover are propitiating the establishment of *Quercus* seedlings under the pine canopy. However canopy closure seemed to be too high to allow the growth of established oaks to more advanced developmental stages (particularly *Q. ilex*). If the densification of the pine stands continues at the current rate, light levels at the understory will probably become in the next years too low to allow oak recruitment, in which case the currently active diversification processes would likely slow. Nevertheless, the occurrence of anthropogenic or natural small-scale disturbances generating small openings in the overstory of these stands would lead to a progressive colonization by oak species evolving at the mid-term toward mixed pine-oak and/or oak-dominated stands.

6.2. Post-fire regeneration dynamics and the role of pre-fire vegetation and tree-species diversity

The remarkable increase of fuel loads in the forest stands jointly with the predicted increase of droughts and hot spells are expected to severely increase the risk of the sub-Mediterranean pinewoods to suffer severe wildfires. Our results in chapters 3 and 4 confirm the important vegetation changes from non-serotinous pinewoods to other types of woody vegetation (shrublands or forests dominated by resprouting tree species) triggered by the occurrence of such large stand-replacing fires (Barbero et al. 2000; Pausas et al. 2008; Retana et al. 2002; Rodrigo et al. 2004). Such important fire-meditated vegetation shifts are not unique to the Mediterranean region but also common in other temperate regions of the world (Keane et al. 2008; Strom and Fulé 2007; Trabaud and Campant 1991; Vacchiano et al. 2014).

The methodological approach presented in chapter 3 proved the feasibility of combining airborne LiDAR data and single-date NDVI data from aerial images to provide precise, georeferenced, and spatially continuous information on post-fire regeneration over a large area. The information generated by this mid-term regeneration assessment provides forest stand structure and composition information that can be used to predict its potential evolution patterns, detect areas with persistent regeneration problems where interventions need to be prioritized, and delimit forest stands for planning management operations.

In chapter 4 we provide an integrative landscape-level analysis in which the relative importance of some of the main factors driving post-fire regeneration in forest systems is assessed. At the mid-term, we found regeneration trajectories dominated by woody vegetation types to dominated most of the burned area, while grassland communities appeared rarely and are usually restricted to very specific site conditions. In addition to the well-known effects of the fire behavior and topographical variables on post-fire recovery, our analysis stressed the important role played by land-use trajectories and the pre-fire forest cover in these processes. In particular, the characteristics of the pre-fire vegetation were found to determine in part the probability of reversion from pine dominated areas to shrublands, with these vegetation shifts mainly occurring on areas dominated by young forest prior to the fire, and thus much less susceptible of undergoing diversification processes by resprouting late-successional tree species (Navarro-González et al. 2013; Puerta-Piñero et al. 2012). Other factors such as the distance to unburned patches and the occurrence of poor site quality might have also contributed to such reversion by hampering the establishment and growth of sprouting trees (Gracia and Retana 2004; Gracia et al. 2002).

More than half of the burned area studied in chapter 4 changed from pine to oak-dominated woods, a forest type that is considered to maintain most of the goods and ecosystem services than the pinewoods provided before burning. Our results suggested that the pre-fire composition of the forest overstory and understory (inferred from fire severity, land-use trajectories and the pre-fire forest cover) were among the most important drivers of oak regeneration. However, we found the density and development of the oak sprouts to be almost totally driven by topographic factors, and linked to high-quality sites, as previously suggested by Espelta et al. (2003). The important cover of oak sprouts in the burnt area- reflects the high availability of plant propagules of these species prior to the fire, probably under the form of young recruits or adult individuals sharing the overstory with pines (Espelta et al. 2003; Retana et al. 2002). According to our findings, and matching with previous studies (Broncano et al. 2005; Espelta et al. 2003; Pausas et al. 1999), the severity of the fire seems to not affect much the post-fire resprouting ability of these oaks.

The apparently dominant fire-mediated conversion from pinewoods to oak woods should nevertheless be interpreted with caution, since some of these areas could evolve at mid- to long-term to mixed pine-oak stands (Gracia et al. 2002). Black pine presents a moderate shade-tolerant character that allows it to regenerate until some years after the fire (Gracia et al. 2002) and could benefit from a certain protection to direct sun exposure by the pre-established oak canopy (del Cerro Barja et al. 2009; Lucas-Borja et al. 2012a; Tiscar and Linares 2014).

6.3. Management implications

6.3.1. Adapting silvicultural treatments to promote natural diversification

In the previous chapters, we have constated that the presence of resprouting species under the pine canopy is of great importance for rapid recovery of the soil after the occurrence of wildfires and to the maintenance of the main ecosystem services after the disturbance. We have also shown that the characteristics of the overstory are key elements of the gradual colonization and development of different oak species in the pinewoods. Thus, under the present context of increasing vulnerability of the sub-Mediterranean pinewoods to the effects of climate change, the use of management practices oriented to modify such canopy attributes in order to favor diversity of tree species in forest stands might be more and more considered.

As reported above, we expect that the current rate of densification and closure of the pine canopy may cause in the short-term some problems to oak recruitment (and especially oak growth) due to critically low light levels. According to our results, the application of frequent low- to moderate-intensity selection cuttings could help to maintain an adequate amount of light for oaks seedlings to establish in the understory. In the case of evenaged stands, the compliance of a thinning program directed to avoid an excessive densification of the stand would favor the progressive establishment of oak seedlings at the same time that the vigor and growth of the remaining pines is enhanced (del Río et al. 2008; Gonzalez-Olabarria et al. 2008; Martin-Benito et al. 2010; Trasobares and Pukkala 2004). Moreover, if regeneration cuttings are executed according to the shelterwood system with a long regeneration period (i.e. around 30 years or more) and gradual opening of the stand by means of several regeneration fellings, the conditions for oak growth into sapling and pole stages may be favored (del Cerro Barja et al. 2009; Lucas-Borja et al. 2012b). More interestingly, if both selection cuttings in unevenaged stands and regeneration cuttings in evenaged stands are applied in a heterogeneous way, with variation from low to moderate intensity along the stand (i.e. from individual-tree to group selection cuttings in unevenaged, and from uniform shelterwood to group shelterwood in evenaged stands), the growth of oak seedlings into sapling and pole stages would be favored at the same time than pine regeneration (Ciancio et al. 2006; Garcia-Barreda and Reyna 2013). Then, these silvicultural interventions may ensure a certain rate of broadleaves occupancy into the stand (which can be variable according to the management objectives), that would enable the future persistence of the mixed stand.

In pine stands affected by crown fires, the development of mid-term regeneration assessments through methodological approaches such as the one presented in chapter 3 may generate useful information to be used for the definition of vegetation management and restoration strategies, as it would help to effectively identify areas where woody species are struggling to regenerate (thus potentially needing restoral actions). Our assessment also provided information on the main variables defining the structure of the post-fire vegetation. This information could be used, for example, to define early thinning interventions with the aim of reducing competition and the amount and continuity of fuels. These actions would also increase tree growth and vigor and may contribute to select species for enabling the future development of a healthy mixed stand (Cotillas et al. 2009; Espelta et al. 2003; Verkaik and Espelta 2006).

6.3.2. Managing for the persistence of Sub-Mediterranean non-serotinous pines under forest densification and the threat of large crown fires

Our results report an ongoing recruitment limitation of black pine in the Sub-Mediterranean pinewoods of the eastern Pre-Pyrenees (see chapter 2). The observed recessive trend in the recruitment of this species matches with the results of other large-scale studies conducted in the Iberian Peninsula (Carnicer et al. 2014; Tiscar and Linares 2014; Urbieta et al. 2011; Vayreda et al. 2013). In our context, this regeneration decrease was found to be mainly triggered by the low light availability that characterizes the understory of most pine stands. Although black pine is considered one of the most shade-tolerant European pine species (Niinemets and Valladares 2006), the models of pine recruitment presented in chapter 2 showed optimum canopy openness values for pine seedlings of around 30-35%, which are rather higher than the ones currently found in these stands (of around 15-25%). Changes in land-use practices over the past few decades have notably affected the structure of most pine stands (Martin-Alcon et al. 2012; Montes et al. 2005) and may have worsened the conditions for pine regeneration. For example, mature and moderately opened stands are known to favor the establishment of pine seedlings, but this type of stands is fairly uncommon nowadays (Aunós et al. 2009). The increasing abundance of shrubs, probably associated to a general decline in grazing by domestic livestock, could also act as an aggravating factor for black pine regeneration, in particular in closed stands where the shrub layer may exert high competition to the seedlings for light (Tiscar and Linares 2014). In these areas, promoting pine regeneration would require not only the application of silvicultural interventions aimed to create adequate levels of canopy openness (e.g. group selection cuttings in unevenaged stands, or group shelterwood cuttings in evenaged stands), but local understory treatments such as partial shrub layer removal.

On the other hand, our results in chapters 3 and 4 confirm the high sensitivity of black pine forests to crown fires (Pausas et al. 2008; Retana et al. 2012; Retana et al. 2002). However, we found a few sites presenting resilient responses of black pine (i.e. sites in which abundant pine regeneration occurred), with these responses being mostly mediated by the occurrence of unburned patches in the proximities, the higher presence of mature trees in these patches, and the low to moderate abundance of propagules of resprouting species after fire (Gracia et al. 2002; Ordoñez et al. 2004). These findings recommend keeping a number of mature trees uniformly distributed along the stands (both in evenaged and unevenaged stands) in order to maximize the chance of a sufficient number of them surviving to a hypothetic fire and enabling direct pine regeneration. At the landscape level, our findings point to modify the spatial distribution of fuel types across the landscape by creating more fragmented landscapes and generating strategic areas with less vulnerable stand structure, in order to increase the abundance of unburned patches uniformly distributed along the burned landscape, which would also contribute to increase the success of post-fire regeneration of these non-serotinous pines (Fulé et al. 2012; Ritchie et al. 2007; Shive et al. 2013; Strom and Fulé 2007).

6.3.3. Preparing Sub-Mediterranean pinewoods for climate change: diversification in the context of assisted migration

In chapter 5 we present the first results of a replicated field trial aimed to evaluate the feasibility of management interventions based on planting or sowing late-successional species for diversifying sub-Mediterranean pine forests using an assisted migration approach. Initial establishment success was relatively high in both the planting (with an overall 76.3% survival after the 3 years) and sowing (with an overall 50% of seedling initial emergence) experiments, in line with previous diversification experiments carried out in Mediterranean pine forests (González-Rodríguez et al. 2011; Palacios et al. 2009; Prévosto et al. 2011). These results encourage the use of this type of management actions, especially in those sites where natural tree-species diversification processes does not occur naturally.

Our results showed that the performance of the translocated populations is highly dependent on: (*i*) the distance in thermal conditions from source locality to recipient locality and (*ii*) the occurrence of extreme cold events. We also found the forest overstory to play an important role in buffering the negative effects of thermal distance and extreme cold events on seedling survival. This result has important management implications and suggests the advantage of planting/sowing under relatively closed canopy. We found signs of high ecotypic differentiation in regard to cold tolerance among different oak species (in particular the evergreens). In contrast, the marcescent species, principally *Q. faginea*, showed high phenotypic plasticity to cold. These key intra- and inter-specific differences strongly underline the importance of managing risks in assisted migration programs by employing multiple seed sources, establishing field trials to guide seed movements, and exercising caution when calculating migration distances (Benito-Garzón and Fernández-Manjarrés 2015; Pedlar et al. 2013).

6.4. Research needs and open questions

The research developed in this doctoral thesis provides a better understanding of the main factors driving the natural dynamics of sub-Mediterranean pinewoods and valuable information for its future management. However, further research is needed to fully understand how future climate change may interact with the processes studied. In particular, additional works would be needed to address the role of the predicted increases in drought frequency and severity (and its interaction with the light environment and the shrub layer) on such dynamics. In addition, it is necessary to deeply analyze the main factors driving the overall result of the interactive relationships between the *Quercus* species and black pine recruitment. This information would be of great value to gain knowledge about the suitability of mixed oak-pine stands as a management objective for these areas in the context of climate change.

Regarding the post-fire dynamics of this system, there is a need for further studies on the effect of different silvicultural interventions, such as thinning or treatments on the shrub layer, on the growth and vigor of the tree-species regeneration, and about the suitability and methods of planting or sowing actions in those sites in which trees did not regenerate naturally. It would also be of high interest to address in future research how climate change predicted effects (e.g. water limitation, recurrent fires, etc.) can affect the post-fire regeneration dynamics of the system.

Finally, more research is needed in order to properly design and execute potential assisted migration programs oriented to mitigate the consequences of rapid northward and upward displacements of the ecological niches due to global warming. Additional field trials need to be established under different environmental gradients to further study the role of seed sources and migration distances, and to better understand our main tree species in regard to their adaptation mechanisms.

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7

Concluding remarks

7. Concluding remarks

1. Sub-Mediterranean pinewoods in the eastern Pre-Pyrenees are currently undergoing progressive natural diversification processes by broadleaved tree species (especially evergreen and marcescent oaks) and a generalized decrease in pine recruitment.

2. Current levels of both canopy closure and shrub cover are propitiating the establishment of *Quercus* seedlings under the pine canopy. However, these conditions hamper pine recruitment and the established oaks (particularly *Q. ilex*) to reach more advanced developmental stages.

3. The evergreen and marcescent oaks show different preferences with regards to canopy openness levels and the spatial distribution and morphology of gaps in the pine canopy. The evergreen *Q. ilex* reports in general greater tolerance to higher light exposure.

4. The combination of airborne LiDAR data and NDVI data from aerial images can successfully be used to provide precise continuous information on regeneration vegetation types over large areas affected by forest disturbances.

5. The occurrence of large stand-replacing fires triggers important vegetation changes from pinewoods to other types of woody vegetation (shrublands or forests dominated by resprouting tree species). Grassland communities appeared rarely and are usually restricted to very specific site conditions.

6. The nature of fire-mediated vegetation changes in these systems strongly depends on some key attributes of the vegetation prior to the fire, such as the tree canopy cover and the history of land uses. Both factors affect the post-fire availability of vegetative propagules and seeds.

7. The use of diversification measures on the basis of assisted migration programs is a feasible management option to enhance the resilience of sub-Mediterranean pinewoods. These practices can be especially suitable for those sites in which natural tree-species diversification processes are absent or too slow due to different limiting factors.

8. Important intra- and inter-specific differences exist in the response of some of the most important oak species in the Mediterranean context to plant translocation. This underlines the importance of using multiple plant provenances, establishing field trials to guide seed movements, and exercising caution when calculating migration distances.

9. In assisted migration actions, the survival of the sowed and planted oak species is enhanced under the canopy of the pine stands which buffer the negative effects associated to translocation to colder localities.