Forest Ecology and Management 282 (2012) 10–22

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Review

Interactions between growth, demography and biotic interactions in determining species range limits in a warming world: The case of *Pinus sylvestris*

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A R T I C L E I N F O

Article history:
Received 13 May 2012
Received in revised form 27 June 2012
Accepted 28 June 2012

Keywords:
Biotic interactions
Climate change
Distribution limit
Scots pine
Tree line
Mortality

A B S T R A C T

Changes in climate are affecting the distribution and status of species on a global scale, through alteration of factors including their phenology, growth and ecological interactions. These alterations are often most apparent at species range edges, where changes to conditions previously limiting the species distribution can result in range shifts. In this paper, we review the rapid recent increase in our understanding of the factors limiting the distribution of a species to explore how the interaction of biotic and abiotic factors is likely to significantly alter its range edge behaviour beyond our current predictive capacity. We focus on Scots pine (*Pinus sylvestris* L.), one of the most abundant tree species on the globe. Glacial refugia and colonisation routes after last glacial maximum have strongly influenced the genetic diversity and local adaptation of this species. Over recent decades, increased reproduction and growth has been detected at the northern limit of *P. sylvestris* as a response to increased temperature, whereas at its southern limit, increased drought stress has resulted in decreased growth, low recruitment, and in some cases a massive mortality of this species. In addition, direct climatic effects on the species are acting together with indirect effects due to altered biotic interactions including outbreaks of insects, pathogens, and parasites, and increased herbivory linked to declining ecosystem productivity. However, whilst predictive studies forecast a gradual decline of the species at the southern range limit and expansion at higher latitudes, models do not commonly include biotic factors, which can significantly modify the response of the species to climatic changes. We conclude by discussing the early detection of imperilled areas and how their natural resistance and resilience to ongoing climatic changes might be increased.

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http://dx.doi.org/10.1016/j.foreco.2012.06.053

1. Introduction

Geographical distribution of plant species is restricted to those areas where historical factors permitted their colonisation and where the current suites of biotic and abiotic conditions allow them to grow and reproduce (Woodward, 1987). The rapid changes in climate and land use that are currently being recorded at a planetary scale (IPCC, 2007) are disrupting these conditions, inducing changes in phenology, growth and ecological interactions (see Parmesan (2006) for a recent review). These changes are often most apparent at species range edges, where ecological conditions are typically already at the species' limit of tolerance, and where the most dramatic effects are predicted to occur, ultimately resulting in an alteration of the species range (Hampe and Petit, 2005; Parmesan, 2006). However, conditions are altered range-wide such that changes in species' range optimum and range limits have been widely reported (Gross, 2005; Lenoir et al., 2008; Maggini et al., 2011; Parmesan et al., 1999). Limitations to the poleward and equatorial expansion of species are driven by different factors, usually cold stress in northern populations and a combination of drought and high temperature at the southern limit (Hampe and Petit, 2005), though interspecific competition also plays a key role (Woodward, 1987). Species with a wide latitudinal distribution will, therefore, be subjected to strongly contrasted environmental conditions at the limits of their distribution, such that demographic and growth responses to altered climate are unlikely to be equivalent at range edges (Fig. 1).

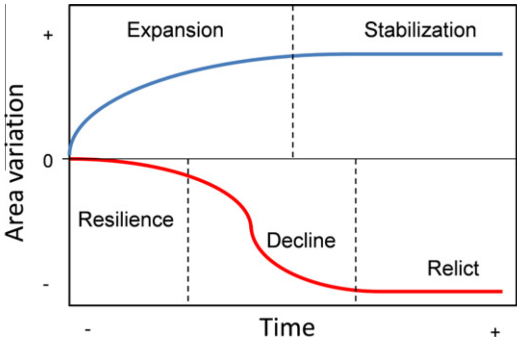

Fig. 1. Hypothesised changes in area occupied by woody species at the northern (blue line) and southern (red line) range limits under a global-change scenario. The zero line represents a stable distribution (no change). Positive values are range expansions and negative values are range contractions. At the northern limit we distinguish two main phases: (a) rapid expansion phase as a response to higher growth and establishment due to temperature increase; and (b) stabilization phase when species' optimum conditions are reached or maximum area available is occupied. At the southern limit we distinguish: (a) resilience phase, where species' range is maintained due to high individual longevity despite adverse conditions; (b) rapid decline phase characterised by a massive individual mortality when survival thresholds are exceeded; and (c) maintenance of relict populations in those small areas where topographic and microclimatic conditions allow species' persistence. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Changes in demographic dynamics are firstly determined by a modification of the survival probabilities as a response to environmental variations (Matías et al., 2011a; Allen et al., 2010). However, the ability of plant species to tolerate changing conditions is also influenced by levels of genetic variability within different populations, which can facilitate local adaptation, or allow a plastic response to new conditions (Jump and Peñuelas, 2005; Savolainen et al., 2011). This variability is in turn shaped by the species' demographic and biogeographic history and adaptation in response to past climatic changes (Cheddadi et al., 2006; Floran et al., 2011), necessitating that predictions of future dynamics should take past distributional shifts into account.

Understanding impacts on physiology and demography is essential for predicting responses of plant species to climate change, but understanding changes in biotic interactions is no less important (Carpenter et al., 1993). Climate and land-use changes may affect ecosystem dynamics by the introduction or extinction of species or by changes in phenology, physiology or demography of many different species (Parmesan, 2006). Existing mutualistic and antagonistic biotic interactions are likely to be altered, or new ones may emerge (Kearns et al., 1998; Hódar and Zamora, 2004; Stireman et al., 2005; Hódar et al., 2009). The alteration of biotic interactions might modify the response of plants to climatic changes, generating non-additive effects that could substantially alter ecosystem dynamics (Bigler et al., 2006; Allen et al., 2010). However, despite the importance of understanding biotic interactions, most predictive studies do not take them into account, and their inclusion into forecasting models still remains in debate (Araújo and Luoto, 2007).

Significant disciplinary increases in our understanding of range dynamics and limits have been made over past decades such that we are now in a position to take a more integrated approach to assessing the likely response of species to climatic changes from their biology to biogeography. Here we demonstrate this possibility focusing on Scots pine (*Pinus sylvestris* L.). This species has the largest geographical distribution of any pine species, is one of the most abundant trees in Europe and one of the most widespread conifer species on earth. It has a wide distribution that extends among almost all the width of Eurasia (Carlisle and Brown, 1968; Fig. 2). Its presence in Europe is known from the Tertiary (Molotkov and Patlaj, 1991), and its distribution area has undergone continuous latitudinal and altitudinal changes during glacial-interglacial cycles of the Pleistocene (Bennett et al., 1991; Bennett, 1997; Willis et al., 1998) and it is still changing (Kullman, 2002a; Benito Garzón et al., 2008a; Holtmeier and Broll, 2011). At an altitudinal scale, *P. sylvestris* occurs from sea level to 1000 m a.s.l. in the north of its range, whereas it occurs from 1200 to 2600 m a.s.l. in the south (Steven and Carlisle, 1959). This wide distribution range encompasses the broad range of climatic conditions that Scots pine is able to tolerate, from the severe cold winters of northern Siberia to the Mediterranean climate of southern Spain; and from the wet, oceanic climate of the west coast of Scotland to the dry continental climate of central Europe and Asia (Carlisle and Brown, 1968). The distribution of Scots pine is primarily limited by low temperatures at its northern range limit and by a

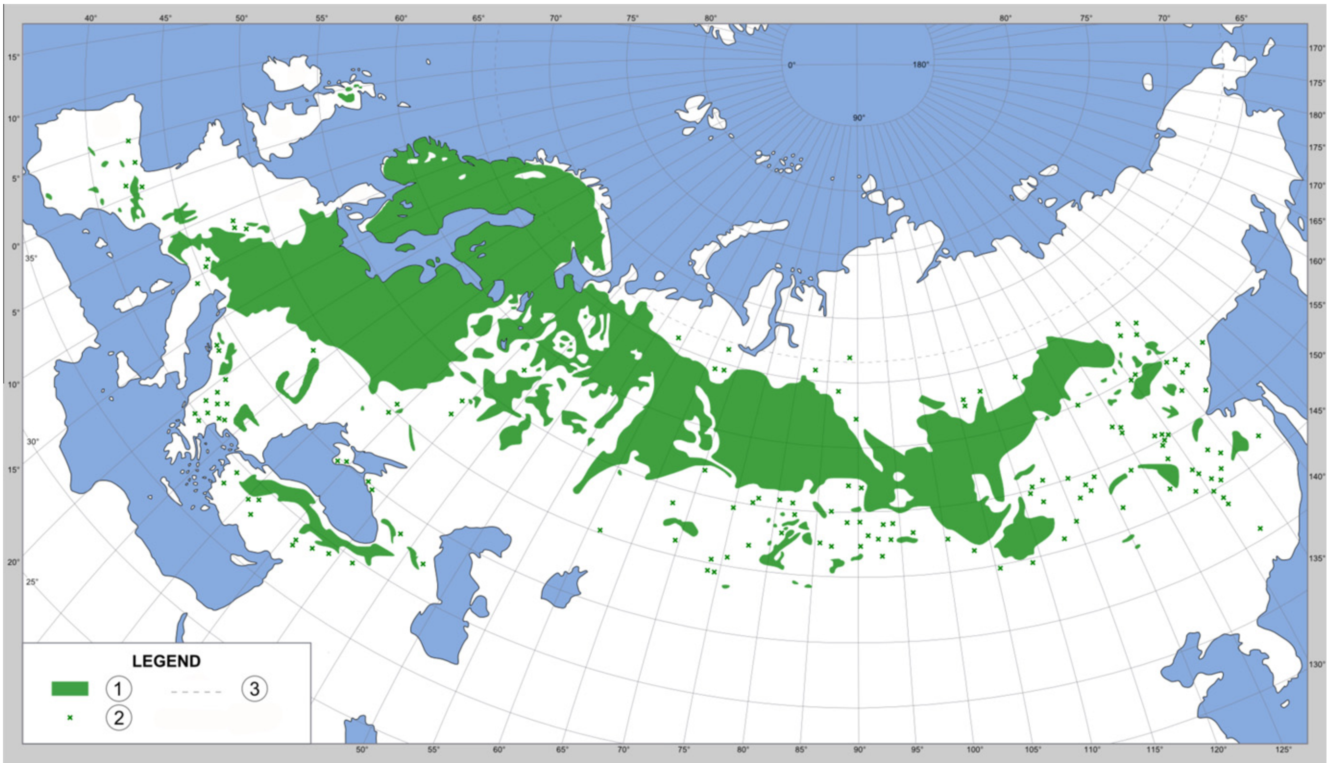

Fig. 2. Scots Pine (*Pinus sylvestris* L.) present distribution range. Legend: (1) Main range of the species. (2) Isolated occurrences. (3) Arctic Circle. Modified from B. Navez under Creative Commons license.

combination of high temperature and summer drought at its southern limit (Carlisle and Brown, 1968; Castro et al., 2004a; Mendoza et al., 2009a). Consequently, it is reasonable to predict that increased temperatures linked to global climate may cause significant alterations to the performance of current range-edge populations.

Scots pine is a very valuable species both from ecological and economic perspectives (Giertich and Mátyás, 1991; Kuper, 1994; Archibold, 1995). From an ecological standpoint, it is the only native pine in northern Europe, it is a keystone species for many ecosystems such as the Caledonian forest, taiga or Mediterranean mountain forests and supports many species of lichens, mosses, fungus and insects (Carlisle and Brown, 1968). The importance of Scots pine forests for conservation is reflected in their inclusion in at least 64 habitat types under Natura 2000 (EUNIS, 2012). From an economic point of view, this species is found in all member states of the EU, where it constitutes approximately 20% of the commercial forest area, and it is of considerable importance as a timber producing species, particularly in Nordic countries (Masón and Alía, 2000).

Based the very wide importance of Scots pine from the perspective of biodiversity to economics and from conservation management to forestry, this species has become one of the best studied tree species, with more than 12,000 published papers during the last decade (Web of Knowledge search topic: ''*Pinus sylvestris*'' for years 2002–2011). However, much of this work has been on specific aspects of this species biology, ecology or biotic interactions and an overview of how these aspects are likely to interact in modifying the distribution of this species under future climates is lacking. Consequently, we sought to review current knowledge of the history, ecology and biogeography of this species focussing on (1) the historical context for this species response to environmental change by focussing on past distribution changes during glacial periods; (2) current trends in the population dynamics at the rage limits of the species, with special interest in biotic and abiotic interactions as a response to recent alterations in climate; and (3) the forecast distribution for the present century under a climate-change scenario. We finish with a discussion of the prospects of populations at the retreating range edge of this species from a local rather than regional perspective and highlight management interventions that might be used to reduce immediate risks in priority populations.

2. Past distribution

The earliest known species of the *Pinus* genus dated from the Early Cretaceous (130 million years ago). From late Mesozoic to the middle Tertiary pine distribution shifted latitudinally and expanded and contracted their altitudinal extent several times (Millar, 1998), but it was after the last glacial maximum when pine species reached their present distribution ranges (Willis et al., 1998). For Scots pine, refugial areas during the last glacial maximum and the pattern of recolonisation during the Holocene have played a highly important role in the determination of its current natural distribution limits.

2.1. Historical minimum distribution: the role of glacial refugia

Climate in Europe has experienced substantial changes during the last 20,000 years, with the last glacial maximum (LGM around 18,000 years before present (BP)), being characterised by extreme values of ice volume, sea level, temperature and precipitation (Walker, 1995). These conditions restricted the range of tree species to small discontinuous glacial refugia (Bennett et al., 1991). During this period the distribution of Scots pine was restricted to several southern refugia, mainly in the Iberian Peninsula, around the Alps, the Balkans, the Hungarian plain and the Danube region

(Bennett et al., 1991; Willis et al., 1998; Willis and van Andel, 2004; Cheddadi et al., 2006; Faurdean et al., 2011), although a recent study suggest a possible ice-free refugia in Scandinavia during LGM (Parducci et al., 2012). Additional endemic refugia in Scotland and Norway still remain in debate (Ennos et al., 1997; Kullman, 2002a; Birks et al., 2005; Kullman, 2008). However, based on climatic simulations, many other areas throughout southern Europe (approximately between 40°N and 50°N) had the potential to act as glacial refugia for Scots pine (Cheddadi et al., 2006), though direct evidence for more widespread refugia is lacking.

2.2. Recolonisation patterns and genetic diversity

From the glacial refugia during the LGM, Scots pine started the northward recolonisation process when climate conditions were becoming more favourable, reaching the western Alps and south of France before 14,000 years BP (calibrated carbon years; Walker, 1995; Cheddadi et al., 2006.). As temperature rose, pine migrated northwards, covering Central Europe between 14,000 and 12,500 years BP, the south of the Scandinavian Peninsula from 11,700 to 10,000 years BP, and Scotland 9900 years BP (Birks et al., 2005; Eide et al., 2005; Froyd and Bennett, 2006; Cheddadi et al., 2006; Kullman, 2008). The species completed its maximal distribution 8000 years BP, with a tree line located at higher altitude and northern than the present limit (Barnekow and Sandgren, 2001; Gervais et al., 2002; Kullman and Kjälgren, 2006). Beyond this broad overview, the spread of Scots pine was more complex than a progressive range expansion from the southern refugia. For example, different centres of early occurrence have been detected in the British Isles between 10,000 and 6000 years BP (Birks, 1989), and differences in allozyme and monoterpene frequencies of current UK populations suggest an origin from multiple refugia (Forrest, 1980; Bennett, 1984; Kinloch et al., 1986; Sinclair et al., 1998). Likewise, several migration routes have been proposed in Fennonscandia (Seppä, 1996; Willis et al., 1998; Savolainen et al., 2011).

Around 7000 years BP Scots pine started to retreat from southern Iberian and Italian peninsulas, remaining only in some relict populations until present, while in northern Scandinavia, Scots pine retreated from its maximum distribution to its present position between 5700 and 3200 years BP (Willis et al., 1998). In the northern and western parts of the British Isles, there was also an abrupt decline in Scots pine population between 4800 and 4200 years BP. These changes in distribution have been related to a combination of changes in climate and anthropogenic impacts (Bennett, 1984; Bridge, 1990; Kullman, 1995; Willis et al., 1998). For example, in southern Europe Scots pine started a secondary recolonisation about 6000 years ago to areas previously covered by deciduous trees as a consequence of the widespread clearance using fire, heavy grazing pressure and depletion of the soil through intensive agriculture during Bronze and Iron Age (Willis et al., 1998). Thus, both climatic and anthropogenic factors have interacted in the determination of the present distribution of this species.

Several studies based on palynological records, macrofossil remains and DNA analyses have identified strong evidence for at least three principal origins of the current Scots pine populations: the Iberian Peninsula, Italy and central Europe from east Alps to the Danube region (Ennos et al., 1997; Sinclair et al., 1999; Soranzo et al., 2000; Cheddadi et al., 2006). The relative importance of each region in shaping the current distribution of intraspecific diversity remains uncertain (Sinclair et al., 1999; Cheddadi et al., 2006; Labra et al., 2006; Floran et al., 2011). However, the legacy of postglacial colonisation is that contemporary Scots pine populations often demonstrate strong differentiation in adaptive traits, with generally better performance of local vs. non-native populations providing evidence of frequent local adaptation in this species (Giertich and Mátyás, 1991; Cheddadi et al., 2006; Øyen et al., 2006; Richter et al., 2012; but see Helama et al. (2008) for contrasted results).

3. Present distribution

The present distribution of Scots pine continues to change as a consequence of current changes in climate and land use that are being recorded across the species' distribution (IPCC, 2007). Global warming is expected to cause temperature changes comparable to those during the late glacial-Holocene-transition, i.e. 2–6 °C increase within the next 90 years in the Northern Hemisphere. However, the rapidity of such changes will require a far faster rate of biotic response than that following the last ice age. For example, whereas Scots pine migrated ~400 m per year after last glaciations (Savolainen et al., 2011), Malcolm et al. (2002) have indicated that trees will have to be able to migrate at a rate of over 1000 m per year to be able to keep pace with human-induced environmental change. Consequently, forest habitats are expected to undergo major changes in composition, diversity, and structure (Thuiller et al., 2008).

Since the bioclimatic zones in Europe and Asia differ in their limitations for forest productivity (e.g. temperature, precipitation, substrate), increased temperature will have different effects in different locations depending on the principal limitations to growth in that region. For example, where low temperature currently limits, future climate will diminish this limitation, whereas those areas already limited by drought will be even more stressed (see Sections 3.1 and 3.2 for further details). Although changes in population dynamics across the whole distribution area of Scots pine might occur (Rehfeldt et al., 2002; Reich and Oleksyn, 2008; Allen et al., 2010), those changes at the range limits (both northern and southern) are expected to be the most evident and those that would have greater consequences for the species' distribution range. In addition, changes in climate are likely to affect the distribution and dynamics of many other interacting species, varying the intensity and the final outcome of biotic interactions, favouring the appearance of new interactions, and in turn modulating the consequences of climatic changes (Hódar et al., 2009). Despite the key importance of biotic interactions for the prediction of future species dynamics under a global change scenario, they are little considered. In this section, we analyse the changes that are currently being detected at the northern and southern limits of Scots pine and highlight some of the biotic interactions that are likely to modify its population dynamics.

3.1. Changes in the northern limit

Scots pine forms the northern conifer stands in northern Norway and Finland and the western Kola Peninsula, Russia. During the last century, this region has experienced an overall increase in temperatures that is larger than the European average (Moberg et al., 2005), with mean values ranging from 0.8 to 2.5 °C, both during summer and winter periods, and being especially important during the last 25 years (Moberg et al., 2005; Kullman and Öberg, 2009; Mathisen and Hofgaard, 2011). In fact, northern Scandinavia has registered higher temperatures during 20th century than any time in the past 4000–5000 years (Kullman and Kjälgren, 2000). This temperature increase has lead to a retreat of mountain glaciers, earlier snowmelt and a decrease of permafrost (Kullman, 2003, 2007a; Moberg et al., 2005). In addition, precipitation has increased by 5-10% over the past century, with the largest rise during the last 25 years (Kullman and Öberg, 2009; Lehman et al., 2011; Mathisen and Hofgaard, 2011). These changes in climatic conditions have lead to changes in the performance of Scots pine both at individual and population scales. In the short term, changes in the climate cause shifts or alterations in seed production, recruitment success, tree growth rate, stand structure and forest cover, and over the long term, displacement of the forest-tundra boundary in altitude and in latitude (Stöcklin and Körner, 1999; Kullman, 2001, 2002b; Juntunen and Neuvonen, 2006; Mathisen and Hofgaard, 2011). In the following section, we outline the main processes that are being altered at the northern limit of Scots pine. As the usage of 'tree line' and 'timberline' is rather confused in the literature, we use 'tree line' in a general sense for the entire border zone from closed forest-stands to the upper limit for trees (cf. Körner, 1998).

3.1.1. Seed production

Seed maturation in Scots pine is directly influenced by summer temperature, with a range of 790–950 degree days (with a threshold value +5 °C) required to mature the 50% of the seeds (Pohtila, 1980; Henttonen et al., 1986; Harju et al., 1996; Almqvist et al., 1998; Juntunen and Neuvonen, 2006; Kullman, 2007b). A high seed production and germination rate (over 50%) has been recorded at the northern tree-line of the species in northern Finland as a consequence of recent temperature rise, although inter-annual variability remains high (Juntunen and Neuvonen, 2006). Given high seed production and evidence for a viable seed bank extending above the tree limit (Kullman, 1993, 2007b; Molau and Larsson, 2000), it is likely that seed availability is not a major limiting factor for tree-line advance at the current northern limit of Scots pine. In addition, and as a consequence of predicted rising temperatures, seed production is expected to increase even in those individuals that are establishing beyond current tree-line (Holtmeier and Broll, 2011), thereby acting as a seed source for further tree-line advance (Slot et al., 2005; Kullman, 2007b).

3.1.2. Recruitment

Recruitment is considered the controlling factor driving population dynamics at the tree line (Rickebusch et al., 2007). Although Scots pine recruitment was minimal close to the treeline in the Swedish Scandes during the 1970s and 1980s (Kullman, 1991), a period of intensified reproduction prevailed from the 1990s (Stöcklin and Körner, 1999; Kullman, 2001, 2002b). Similarly, periodically high pine establishment has been recorded in northern Finland from the1970s to date at the tree-line, although this has not resulted in distributional changes so far (Juntunen et al., 2002; Juntunen and Neuvonen, 2006; Holtmeier and Broll, 2011). However, recruitment patterns differ substantially between neighbouring localities, as a consequence of local modification of site suitability by a range of biotic and abiotic factors such that seedling establishment may not be so tightly linked to macroclimate on the local scale (Kullman, 2000; Juntunen and Neuvonen, 2006). However, despite high spatial and temporal variability, a period of increased recruitment seems to be general at the northern altitudinal and latitudinal limit of this species.

3.1.3. Growth

Summer temperature is the primary determinant of height and diameter growth in boreal trees (Mäkinen et al., 2000). While radial growth is determined by temperature of current year, height growth is established during the bud formation in the previous summer, and thus depends on previous year temperature (Lanner, 1976; Junttila and Heide, 1981). However, non-growing season climate factors have been also reported to influence Scots pine growth (Mathisen and Hofgaard, 2011). The resource limitation hypothesis claims that tree growth at the tree line is limited by the uptake of carbon or nutrients. This hypothesis is in contrast to that of growth limitation (Körner, 1999), which states that growth is limited by low temperatures. Low temperature was identified as the major limiting factor for Scots pine growth in recent work of Rickebusch et al. (2007), Salminen and Jalkanen (2007) and Mathisen and Hofgaard (2011) although nutrient addition experiments conducted by Susiluoto et al. (2010), also found evidence for nitrogen limitation. During recent decades, however, increased growth has been recorded at the tree line of this species (Salminen and Jalkanen, 2007; Mathisen and Hofgaard, 2011), providing evidence that the predicted rise in temperature for this region in the coming years is likely to diminish the cold limitation and result in increased growth of Scots pine at its northern limit (Reich and Oleksyn, 2008).

3.1.4. Damage and mortality

At the tree line, winter frost, herbivory and pathogens are the main mortality causes in Scots pine. Overall, mortality declines with seedling height (Persson, 1998; Juntunen and Neuvonen, 2006), but increased mortality has been suggested to occur at the interval of 80–150 cm, when Scots pine seedlings project above the maximum wintertime snow-cover (Kullman, 1981). Winter desiccation is one of the main mortality causes in saplings, although its damaging effect has been reduced during the last decades (Kullman, 2007b; Kullman and Öberg, 2009). Herbivory also has the potential to control population dynamics at the tree line (Stöcklin and Körner, 1999; Cairns and Mohen, 2004). Reindeer (*Rangifer tarandus*) and moose (*Alces alces*) are the most important herbivores in the northern limit of the species, and may affect a high proportion of the seedlings and saplings (up to 80%; Helle and Moilanen, 1993; Stöcklin and Körner, 1999; Holtmeier and Broll, 2011), thus reducing the natural tree-line expansion process. In addition, the combination of increased temperatures and precipitation expected for the northern limit during the coming decades has the potential to induce the spread of fungal pathogens such as snow blight (*Phacidium infestans*) and Scleroderris canker (*Gremmeniella abietina*) (Stöcklin and Körner, 1999; Juntunen and Neuvonen, 2006; Sikström et al., 2011). Thus, in contrast to positive changes in seed production, recruitment and growth which should increase the growth rate of Scots pine populations, sporadic damage by frost, pests and herbivory may persist or even be intensified over the coming decades (Cairns and Mohen, 2004; Slot et al., 2005), potentially reducing rates of population expansion predicted based solely on direct effects of climatic changes on this species.

3.1.5. Tree-line advance

As a consequence of changes outlined above, increasing evidence of changes along the altitudinal and latitudinal limits of Scots pine have been recorded during the past two decades (Kullman, 2001, 2002b; Juntunen et al., 2002; Kullman and Öberg, 2009; Holtmeier and Broll, 2011). According only to environmental factors, the predicted increase of temperature for the end of this century in this region (A2 scenario, IPCC, 2007) will imply a 500 m uphill tree-line shift (Kullman and Öberg, 2009). This may be locally possible given that a tree-line rise of 100–525 m has been already registered in some areas (Kullman, 2002b; Kullman and Öberg, 2009). However, Kullman (2010) notes that this scenario is unrealistic from a landscape perspective, since the reported rapid tree-line advances are geographically limited to specific areas with favourable topographic or microclimatic conditions. Furthermore, latitudinal range shifts will need to occur over distances some one thousand times larger than altitudinal range shifts and are, therefore, highly likely to be dispersal limited (Jump et al., 2009). However, in forecasting treeline advance, it is important to take into account that in addition to predictions made from changes in climate and mean treeline position, other factors will modify the realised rate of advance. Outpost trees (old trees beyond the closed forest limit) can act as a seed source, as can existing anthropogenic plantings of the species beyond its natural range limits in some areas. Furthermore, facilitation processes by microtopography or existing vegetation can ameliorate stress factors such as winter frost or herbivory, whilst the competition with other vegetation types such as the birch belt (Stöcklin and Körner, 1999; Slot et al., 2005; Kullman, 2007b, 2010) are crucial factors that can modify Scots pine regeneration on the local scale. When acting together, and in combination with anthropogenic modification of landscapes and land use (Jump et al., 2009), these factors are likely to result in highly heterogeneous local responses to climate change which pose a major challenge for the detailed forecasting of tree-line advance.

3.2. Changes at the southern limit

The southern limit of the Scots pine is reached in the Mediterranean basin, distributed in mountain areas from Spain to Turkey (Fig. 2). Throughout the 20th Century, but especially from the mid 1970s, the Mediterranean region has recorded an increase in the mean temperature (IPCC, 2007). A decreasing trend in precipitation has also been identified, although its high variability makes it difficult to determine the magnitude of precipitation changes over the last century (Moreno, 2005). The Mediterranean region has been identified as one of the most prominent "hot-spots" in future climate change projections (Giorgi, 2006). Surface temperature increases in the region are predicted to rise during this century, being maximum in summer (~1.2 in 2001–2020 to 4.6 in 2081–2100) and minimum in winter (~0.7 to 3.1 °C). A progressive decrease in precipitation is expected in all seasons during the 21st Century, but especially during summer where a reduction of about 28% has been predicted by 2100 (Giorgi and Lionello, 2008). These changes in climate are likely to substantially alter population dynamics of many plant species, with those reaching a range edge in the region, such as Scots pine being especially vulnerable. As at its northern limit several indicators of population dynamics of Scots pine can already allow us to predict the ecological consequences of the predicted environmental changes.

3.2.1. Recruitment

Seed availability is the first step in determining the success of Scots pine recruitment (Boulant et al., 2008; Mendoza et al., 2009b) yet despite high inter-annual variability as a consequence climatic fluctuations (Thabeet et al., 2009), seed production and dispersal seem not to be limiting recruitment of this species at its southern limit (Debain et al., 2003; Mendoza et al., 2009b; Zamora et al., 2010). However, seed predation (pre- and post-dispersal) is hypothesised to be a major limitation to regeneration and expansion of Scots pine at Spanish tree lines (Castro et al., 1999), being especially intense in the shrubby areas adjacent to pine forest (Matías et al., 2009). Furthermore, the reduction in precipitation predicted over the coming decades has been shown to have no significant effect on seed germination of this species in southern Spain (Castro et al., 2005; Matías et al., 2012), although a positive effect of increased precipitation on emergence rate has been described in the Alps (Richter et al., 2012). Critically, it is during the seedling stage when precipitation deficit plays a major role by preventing seedling growth and elevating mortality. Contrary to the situation in the northern distribution of the species, the main abiotic factor constraining establishment of Scots pine in Mediterranean-type ecosystems is usually summer drought (Castro et al., 2004a; Matías et al., 2011b). Drought can prevent recruitment completely, and only some years with above average precipitation values are suitable for recruitment (Castro et al., 2005; Mendoza et al., 2009a; Matías et al., 2012). Thus, the already low current natural regeneration of Scots pine at its southern distribution limit in Mediterranean mountains (Mendoza et al., 2009b; Galiano et al., 2010) is predicted to be even more limited during the coming decades.

3.2.2. Growth

At the southern limit of the distribution, Scots pine growth is mainly determined by precipitation. Positive relationships between precipitation and height and radial growth have been widely documented in the Mediterranean region (Martínez-Alonso et al., 2007; Bogino et al., 2009; Dobbertin et al., 2010; Lebourgeois et al., 2010), as well as a decrease of radial growth as a consequence of dry periods (Tessier, 1989; Eilmann et al., 2006; Bigler et al., 2006; Thabeet et al., 2009). By contrast, the effect of temperature is not as clear as that of precipitation. Whereas winter and spring temperature has a positive impact on growth (Richter et al., 1991; Tardif et al., 2002; Thabeet et al., 2009), summer and autumn temperature is negatively related (Bogino et al., 2009; Thabeet et al., 2009). However, these correlations are highly variable among different populations, elevations or orientations (Rigling et al., 2002; Vila et al., 2008; Thabeet et al., 2009). This is consistent with the general pattern of the annual growth of conifers at low latitudes or altitudes, which identifies spring and summer water balance as critical factors in determining radial growth rates (Lebourgeois, 2007). However, the combined negative effect of higher summer and autumn temperatures and increased drought severity is unlikely to be cancelled out by any potential growth increase in response to increased winter and spring temperatures. Consequently, predicted climate conditions are expected to significantly reduce Scots pine growth during the coming decades (Reich and Oleksyn, 2008).

In addition to more gradual reductions in growth due to increasingly unfavourable mean climatic conditions, extreme drought have profound impacts on tree growth (Bigler et al., 2006; Thabeet et al., 2009) and also interact with previous growth reductions. Martínez-Vilalta et al. (2012) determined that those trees with slower growth (as a consequence of progressive drought increase for example) also recover slower after extreme drought events than trees with a previous faster growth. In addition, juvenile growth may be slowed down by other interacting factors as herbivory or pathogen attack (Section 3.3). A consecutive reduction in growth during several years induces a general weakening of trees, which may have stronger consequences at population level, as we outline in the following section.

3.2.3. Mortality (die-back)

The recent changes in precipitation and temperature are increasing the already limiting conditions of dry and warm summers for Scots pine at its southernmost limit (Castro et al., 2004a). This water stress during summer has induced a high mortality rate in Scots pine stands throughout the Mediterranean region and inner Alpine valleys (Vertui and Tagliaferro, 1997; Martínez-Vilalta and Piñol, 2002; Rebetez and Dobbertin, 2004; Dieguez-Aranda et al., 2005; Dobbertin et al., 2005a; Galiano et al., 2010). A single strong drought event is able to induce mortality in adult trees by cavitation or carbon starvation (McDowell et al., 2008; Martínez-Vilalta et al., 2009). But, even if mortality is not reached, water stress can increase the tree sensitivity to other stress factors as future drought events or pathogen attack, which could contribute to tree death (Dobbertin et al., 2005a; Allen et al., 2010; Galiano et al., 2010; Giuggiola et al., 2010). Thus, drought is considered both as an inciting and as a predisposing factor for the observed mortality (Bigler et al., 2006). For the coming decades, it is very likely that massive mortality events such as those reviewed by Allen et al. (2010) will increase in frequency throughout the southern portion of range of this species. As recruitment is also hampered by drought (Section 3.2.1), it is highly likely that rather than resulting in regrowth of Scots pine, mortality events are likely to result in a replacement by other species more tolerant to drought, such as *Quercus* ssp. (Zweifel et al., 2007; Galiano et al., 2010; Matías et al., 2012) and, consequently, in a progressive reduction of the area occupied by Scots pine in the Mediterranean region.

3.3. Changes in biotic interactions

Changes in climate and landscape structure have an impact at the ecosystem level. Such changes can directly affect individual species independently, but also their interspecific and environmental interactions, including the development of novel interactions and the establishment of new species within the ecosystem.

3.3.1. Insects and pathogens

Changes in climate, especially in temperature, have the potential to alter the life cycle, growth, movement, and population dynamics of phytophagous and xylophagous insects, nematodes and fungal pathogens (Neuvonen et al., 1999; Bale et al., 2002; Sikström et al., 2011). Overall, an increase in pathogen attack is expected as a consequence of temperature rise by means of population outbreaks and enhanced infection capacity (Juntunen and Neuvonen, 2006; Dobbertin et al., 2007; Fabre et al., 2011), as well as greater consequences of an attack due to the weakening of trees induced by drought in some areas (Croisé and Lieutier, 1993; Dobbertin et al., 2007; Wermelinger et al., 2008; Heiniger et al., 2011). In addition, warmer winters are currently triggering an uphill or northern displacement of pests limited by low temperatures (Ayres, 1993; Bale et al., 2002), allowing in some cases the establishment of biological interactions that are new for Scots pine. One of the best examples of these new interactions is the pine processionary caterpillar *Thaumetopoea pityocampa*. The incidence of this species is strongly related to climate conditions (Hódar and Zamora, 2004; Hódar et al., 2011), and the rising temperatures of the last decades have enabled *T. pityocampa* outbreaks at higher altitudes than the past limits in southern Spain, thus coinciding with the distribution of relict Scots pine populations which were previously out of the range of *T. pityocampa*. This has resulted in a reduction of the growth and reproductive capacity of defoliated pines by 50% (Hódar et al., 2003, 2004), which is likely to have serious negative consequences for these southernmost populations, given their already strongly climatically limited growth and reproduction that we outline above. There is broad agreement that negative impacts of pests and pathogens will increase throughout the entire distribution of the Scots pine over the coming decades (Dobbertin et al., 2007; Sikström et al., 2011; Stöcklin and Körner, 1999).

3.3.2. Browsing

Ungulate herbivores have the potential to affect the birth, death, immigration or dispersal rates of plant populations (Danell et al., 1991, 2003; Cairns and Mohen, 2004). Scots pine respond to browsing at different levels, from variations in the content of nutrients and chemical defences to changes in their biomass allocation pattern (Danell et al., 1994, 2003; Persson et al., 2005; Hódar et al., 2008; Baraza et al., 2009). However, one of the most important effects from a population dynamic perspective is the reduction in growth of saplings. At the tree line, the intensity of herbivory by ungulates is stronger than in woodland areas (Gill, 1992; Gómez et al., 2001; Zamora et al., 2001), and the impact of ungulates on saplings is much higher than the impact of insect herbivores (Herrero et al., 2012). The effect of browsers on Scots pine is especially important at the sapling stage, when the lost of the apical leader shoot can considerably delay the time taken to reach maturity. As a consequence, whereas an unbrowsed sapling growing at the southernmost limit of its distribution needs 21 years to reach 150 cm in height, a browsed sapling takes around 30 years (Zamora et al., 2001). This pattern of retarded growth seems to be common both at the northern and southern tree-line limits of the species (Danell et al., 1991; Gómez et al., 2001; Edenius et al., 2002; Persson et al., 2005; Herrero et al., 2012). Browsing may also have an interacting effect with environmental conditions. In this way, saplings that already experience growth limitation due to abiotic conditions (e.g. poor soils, low temperature or drought) are exposed to browsing for longer periods because they take longer to grow out of reach of browsers (Danell et al., 1991; Zamora et al., 2001; Herrero et al., 2012), and also because the low pasture production during dry years induces a higher consumption of pines (Zamora et al., 2001). Additionally, browsers may alter the relative distribution of tree species through selectively feeding on particular species (Baraza et al., 2006). If the ungulate density is too high, they may even completely arrest Scots pine succession in some areas (DeSoto et al., 2010), causing dramatic long-term and cascading changes in the ecosystem function. It is important to note, therefore, that changes in ungulate population sizes as a consequence of human management for both wild and livestock species, can have a significant impact on Scots pine dynamics.

3.3.3. Mistletoe

Pine mistletoe (*Viscum album* subsp. *austriacum)* is a subspecies of common mistletoe that occurs predominantly on pine species, and is of special importance for the Scots pine at its southern range edge. Hemiparasitic plants can impact on the water balance of host plants as a result of their high rates of transpiration, and their need to take up water, nutrients and carbohydrates from host trees. During drought, when the host tree closes its stomata to reduce transpiration, the mistletoe continues to transpire, increasing the drought stress of the tree and inducing mortality in some cases (Fischer, 1983; Dobbertin and Rigling, 2006; Galiano et al., 2010). In addition, mistletoe infestation has also been related to changes in crown architecture, loss of photosynthetic capacity, reduced leaf nitrogen, altered resource allocation, slower growth and reduction of reproductive capacity (Dobbertin and Rigling, 2006; Rigling et al., 2010; Galiano et al., 2011). The distribution of mistletoe is strongly determined by low temperatures (Iversen, 1944; Skre, 1979), but the rising temperatures registered during the past century have induced an upward movement of mistletoe limits between 150 and 200 m in Switzerland (Dobbertin et al., 2005b). The dispersal mechanism of mistletoe, mediated by frugivorous birds, allows rapid movement of the species, which is thus expected to migrate faster in altitude than Scots pine and to reach the upper altitudinal pine distribution limit over coming decades (Dobbertin et al., 2005b). Although the implications of changing climate for pine/mistletoe interactions have been best characterised in Switzerland, the implications of the reported range shifts in this parasitic species are likely to be relevant to many other areas of the distribution of Scots pine given the general temperature increase in the northern hemisphere and its strong importance in the control of mistletoe distribution.

In short, changes in climate and the increase of herbivory pressure by human practices are favouring a cocktail of negative interactions with synergistic effects that may drastically reduce the performance of Scots pine. In addition, biotic stressors will interact with other stress factors as drought, which can impair the natural resistance of Scots pine to these antagonistic biotic interactions. At the northern limit, insects and herbivores might slow down the growth increase and the tree-line advance induced by temperature rise. At the southern limit, the expected negative effects of summer drought on Scots pine recruitment, growth and survival, may combine with negative biotic interactions to result in recruitment failure, growth decline, and/or massive mortality (Bigler et al., 2006).

3.4. Ecological disturbances

Among the different ecological disturbances affecting Scots pine forests such as flooding, windstorms or insect outbreaks, fire is the most important and extensive one (Moreno et al., 1998). Although fire is a natural disturbance and pine species have evolved with this factor adapting their ecological dynamics to it (Agee, 1998), fire is considered as a global change driver and its frequency and intensity have risen during the last century beyond natural regimes (Moreno et al., 1998). In addition, the global temperature rise together with precipitation reduction experienced in some areas has lead to the forecast of further increases in fire frequency for the next century (Giorgi and Lionello, 2008; IPCC, 2007). Thus, fire is an important factor to be taken into account in the analysis and forecasting of Scots pine dynamics.

Fire has profound implications on Scots pine forests both at the northern and southern range limits, and its effects depend on several factors: grouped on site factors, i.e. understory vegetation, slope, elevation, time of the day, year; stand composition, i.e. tree species composition, age structure, basal area, stand structure, and fire behaviour, i.e. fuel moisture, rate of spread, and intensity (Angelstam, 1998). However, ecological consequences of fire on Scots pine forests are drastically different from the northern to southern limits. At the northern range, fire frequency in Scots pine stands is highly variable, from almost null at the tree line (Kullman, 1986) to every 40–60 years (Engelmark, 1987; Zackrisson, 1977). However, tree mortality in this region is frequently low due to the low fire intensity and the relatively low sensitivity of old Scots pines to fire conferred by the thick bark (Sannikov and Goldammer, 1996). This usually results in an increase of vertical heterogeneity of the forest (Angelstam, 1998) and in an increase of seedling emergence due to the burning of the humus layer exposing mineral soil (Sannikov, 1983). By contrast, at the southern range of the species, high intensity crown fires are more frequent and have increased during the last decades of the 20th Century (Pausas et al., 2008). Regeneration frequently falls dramatically after strong fires due to the lack of serotinous cones in this species, and Scots pine almost disappears from burned areas, often being replaced by *Quercus* species or shrubs (Retana et al., 2002; Vilà-Cabrera et al., 2012).

Fire has also an important role in the nutrient functioning of pine ecosystems. It may affect key ecosystem processes and properties such as the capacity for carbon sequestration, nutrient availability and cycling, soil texture and structure, cationic interchange capacity or water retention (Cerini, 2005; Wan et al., 2001). These changes are determined by fire intensity and duration, the compartment in which nutrients are stored in the ecosystem (foliage or soil) and by the capacity of the system to retain nutrients after the fire (Agee, 1998). Low intensity fires might only induce a water loss whereas, at higher temperatures, components of the forest crown begin to volatilise, and the alteration of soil nutrients and biota is then critical in determining the chemical and biological impact of fire (Agee, 1998). In addition, soil nutrient availability and dynamics can also be affected by changes in climate conditions (mainly temperature and precipitation), habitat structure or vegetation cover (Jensen et al., 2003; Matías et al., 2011c; Sardans and Peñuelas, 2007), inducing a complex network of interactions that strongly might affect Scots pine growth and regeneration, especially in nutrient-limited areas.

4. Future trends

Although a large amount of work has focussed on understanding factors limiting the growth, reproduction and mortality of Scots pine at the edges of its geographical range, relatively few studies have analysed future dynamics of Scots pine populations from a predictive standpoint. In a field study in southern Spain, Matías et al. (2012) showed that the predicted reduction in spring and summer precipitation for the end of present century in the area has the potential to completely prevent recruitment, leading to local extinction. This conclusion is in concordance with the results of several modelling studies, which predict a strong reduction of the distribution of conditions suitable for Scots pine in Spain by 2100 with only some remnant populations persisting in the northern mountain ranges (Benito Garzón et al., 2008a,b; Keenan et al., 2011). Similarly to the Iberian Peninsula, a strong reduction in area is expected in Italy, where Scots pine is only expected to survive in mountain regions of the Alps (Attorre et al., 2011; Di Traglia et al., 2011). However, even in many areas of the Alps a reduction in growth and survival has also been predicted under future simulated conditions due to drought stress (Richter et al., 2012). At the northern distributional limits of this species, predictive models foresee an expansion of the range of Scots pine northward and to higher elevations (in agreement with the currently observed trends outlined above). However, this species is also likely to decline in abundance in favour of broadleaved trees, which are expected to outcompete it in coastal areas and below 60°N (Sykes and Prentice, 1995; Koca et al., 2006).

Despite their utility for forecasting future dynamics, species distribution models must necessarily generalise and are, therefore, unable to represent the full complexity of the species (Hampe and Jump, 2011; Jump et al., 2010). Thuiller et al. (2008) comment that models commonly overlook biotic interactions, and fail to adequately account, amongst other factors, for local-scale processes during migration and range retraction. However, intraspecific variability in the climate response of species is also overlooked and is so poorly characterised for most species that its inclusion in models is not yet possible. Moreover, intraspecific phenotypic variation and local adaptation is a key factor in determining how individual populations will respond to altered conditions and in Scots pine is frequently substantial. For example, patterns of photochemical capacity and spring phenology were found to vary between common garden populations of Scots pine derived from geographically proximate but climatically divergent populations within the Scottish Highlands (Salmela et al., 2011). Provenance trials have also shown that populations in more arid sites, such as those at the southern range edge, often show local adaptation to these more stressful environments but less phenotypic plasticity than populations elsewhere. Furthermore, differential susceptibility to pests and pathogens has also been detected between Scots pine populations (Giertich and Mátyás, 1991; Mátyás et al., 2004). Local adaptation and phenotypic plasticity is, therefore, likely to alter the response of individual populations even if challenged with the same environmental changes. Such individualistic responses at the population level will increase uncertainty in model predictions and need to be taken into account if future population trends are to be better predicted (Benito Garzón et al., 2011; Savolainen et al., 2011), although data availability remains a barrier in this respect.

A major challenge in forecasting the future distribution of this and other species is that factors other than macroclimate, such as facilitation processes or microtopographic conditions, have the potential to alter the predicted distribution patterns for the coming decades at the local scale (Thuiller et al., 2008). The longevity of individual Scots pines might act together with the persistence of locally favourable microclimates to maintain relictual populations of this species under otherwise unfavourable future climatic conditions (Hampe and Jump, 2011). The persistence of such populations has already been documented for a wide variety of other species (Hampe and Jump, 2011), and whilst it would not prevent a substantial decrease in the abundance of the species on a regional basis (Jump et al., 2009), it might slow down range retraction and maintain a propagule source during infrequent climatic periods suitable for establishment (Castro et al., 2004b; Gómez-Aparicio et al., 2004; Gómez-Aparicio, 2009; Hampe and Jump, 2011).

5. Management implications in a changing climate

Given the ecological and economical importance of Scots pine, and the potential for rapid changes in the distribution of this species, the identification of those areas most at risk and the adequate management of high priority populations will become progressively more important over coming years, necessitating the development of appropriate monitoring and management strategies. Distribution models can give a first approximation of the most imperilled regions of the species' distribution (Benito Garzón et al., 2008a,b; Keenan et al., 2011). Subsequently, locally targeted monitoring will be needed to enable early detection of stand decline in order to provide the best opportunities for remedial management interventions. Foliar parameters such as crown transparency or leaf area index have been suggested as good indicators of tree health (Dobbertin et al., 2010) and could be assessed from remotely sensed indices at broad scales. However, these data should to be combined with detailed remote assessment of target regions and/or ground-based assessments of tree condition in sensitive populations to provide a detailed assessment of tree health and reproduction in at-risk areas (Jump et al., 2010). The combination of these approaches would identify areas where management interventions to slow decline might be employed, but any change of management must also be guided by the prioritising populations by conservation importance. Such prioritisation might be based on factors including, cultural, historical, or biogeographical value in addition to their value for genetic and species diversity. Prioritisation must recognise that as global temperatures continue to rise, the intensive management of large areas of forest at a landscape scale is unlikely to be viable, such that management efforts should be concentrated in most valuable and vulnerable populations where management objectives are achievable. The identification of local climatic refugia or patches of core habitat on the local scale even in regionally unfavourable areas represents an additional option to focus management resources, since their potential to maintain relict populations of the species will also enable conservation of seed sources from local provenances into the future (Hampe and Jump, 2011).

Once priority populations have been identified, natural resistance and resilience should be improved by adapting management plans to the specific source of perturbation (Millar et al., 2007; Jump et al., 2010). Among others, some risks and management practices include: (1) Inter-specific competition: since a changing climate may favour competitors, either native or alien species (Zweifel et al., 2007; Kullman, 2010; Matías et al., 2012). A selective thinning (if native) or complete removal (if alien) at an early stage may considerably diminish the decline risk. (2) Intra-specific competition: Scots pine plantations with high tree densities cover thousands of hectares in most countries of the Mediterranean Basin, where they have been widely used for reforestation after millennia of human impacts on native forests (Pausas et al., 2004; FAO, 2006). In these areas, there is an increasing pressure to convert them into more natural forests with active regeneration, high biodiversity levels, and high resilience to disturbances (Gómez-Aparicio et al., 2009; Zamora et al., 2010). In this case, a selective thinning of unhealthy trees will reduce competition for water and create a heterogeneous structure with small gaps that can improve natural regeneration when conditions allow. The higher tree vigour of remnant trees may also increase the population resistance to die-back (Bigler et al., 2006; Gómez-Aparicio et al., 2009). (3) Arrested recruitment: in those areas with hampered natural recruitment, sapling plantations are commonly used to improve regeneration, as in Mediterranean mountains. However, summer drought and ungulate browsing usually induce strong mortality that hinders reforestation efforts (Mesón and Montoya, 1993). Castro et al. (2004b) demonstrated by an experimental plantation in different microhabitats that the use of shrubs as nurse plants for plantations can increase sapling growth and survival by the reduction of drought stress and by the protection from herbivory. Thus, plant facilitation can be employed to enhance plantation success (Gómez-Aparicio et al., 2004). (4) Pests: insect outbreaks easily spread through dense populations, as is the case with pine plantations in some areas. Whilst pest outbreaks are sometimes controlled by the use of pesticides (Battisti et al., 1998), the fumigation of large forest areas once pest outbreaks establish has been shown to be of only limited effect for pest control (Grodzki et al., 2006; Cayuela et al., 2011), and is neither practical nor socially acceptable in most cases. Instead, the promotion of spatial heterogeneity at the landscape level and increasing tree health and biodiversity in converted plantations would increase the resilience of Scots pine forests to pest outbreaks (Jactel and Brockerhoff, 2007). (5) Browsing: in areas where ungulate herbivores are limiting sapling growth (Section 3.3.2), fencing of high priority populations to exclude herbivores or a strict control of wild and domestic ungulate densities may help to boost natural regeneration, though monitoring of interspecific competition will subsequently be necessary to ensure that grazing reduction does not lead to pine seedlings being outcompeted by other species (Zamora et al., 2001; Herrero et al., 2012). Whatever the source of stress, however, ongoing monitoring will be required and management plans must be flexible enough to respond to unexpected changes.

6. Conclusions and future research

Current distribution of Scots pine is changing, and the predicted conditions are expected to deeply alter population dynamics at the limits of its distribution and hence the distribution of the species. Both at the northern and southern limits, Scots pine is currently subjected to 'windows of opportunity' to recruit. The main difference is that whereas the limiting factor in north (temperature) is expected to be less stressful under future climate scenarios, in the south the limiting factor (drought) will be more severe. As a consequence, a reduction in Scots pine cover and an increase in the dominance of more drought tolerant species (such as *Quercus* ssp.) is predicted at the southern limit of the species over the coming decades, but potentially also an increase of competition with broadleaved trees in lowland areas near to the northern limit. Although the retraction of the southern portion of this species distribution seems inevitable as the climate warms, some factors have the potential to modify the rate of decline, by both accelerating it (e.g. extreme drought events, negative interactions) or by slowing it down (e.g. extremely rainy years, facilitation, microtopographical effects). Field and modelling studies at the scale of the species geographical distribution, but also with detailed fine scale local investigations are necessary to accurately predict the fate of this species as the global climate changes. Such work should take into account not only patterns of land use and climate predictions, but also patterns of local adaptation and the role of future relict populations for a more accurate forecasting of species' dynamics and the identification of imperilled areas. In addition, given the major, and potentially increasing importance of biotic interactions at the range limits, these must be integrated into future modelling approaches.

Acknowledgements

This work was supported by Universidad de Granada (Plan Propio de Investigación 2010) and EU Marie Curie (FP7-2011-IEF-300825) Fellowships to L.M. and by Natural Environment Research Council Grant NE/G002118/1 to A.S.J.

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