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Structural and climatic determinants of demographic rates of Scots pine forests across the Iberian Peninsula

Albert Vilà-Cabrera[1,2]*, Jordi Martínez-Vilalta[1,2,3], Jordi Vayreda[1] and Javier Retana[1,2]

[1]*CREAF, Centre for Ecological Research and Forestry Applications, Autonomous University of Barcelona, Bellaterra, Catalonia, E–08193, Spain*

[2]*Unit of Ecology, Autonomous University of Barcelona, Bellaterra, Catalonia, E-08193, Spain*

[3]*School of GeoSciences, University of Edinburgh, Edinburgh EH9 3JN, UK*

*Correspondence: Albert Vilà-Cabrera, CREAF, Centre for Ecological Research and Forestry Applications, Autonomous University of Barcelona, Bellaterra, Catalonia, E-08193, Spain. E-mail: a.vila@creaf.uab.es

ABSTRACT

The demographic rates of tree species typically show large spatial variation across their range. Understanding the environmental factors underlying this variation is a key topic in forest ecology, with far-reaching management implications. Scots pine (*Pinus sylvestris* L.) covers large areas of the Northern Hemisphere, being the Iberian Peninsula its south-western distribution limit. In recent decades, an increase of severe droughts and a densification of forests as a result of changes in forest uses have occurred in this region. Our aim was to use climate and stand structure data to explain mortality and growth patterns of Scots pine forests across the Iberian Peninsula. We used data from 2392 plots dominated by Scots pine, sampled for the National Forest Inventory of Spain. Plots were sampled from 1986 to 1996 (IFN2) and re-sampled from 1997 to 2007 (IFN3), allowing for the calculation of growth and mortality rates. We fitted linear models to assess the response of growth and mortality rates to the spatial variability of climate, climatic anomalies and forest structure. Over the period of approximately 10 years between the IFN2 and IFN3, the amount of standing dead trees increased eleven-fold. Higher mortality rates were related to dryness and growth was lower with increasing dryness and temperature, but results also suggested that effects of climatic stressors were not restricted only to dry sites. Forest structure was strongly related to demographic rates, suggesting that stand development and competition are the main factors associated with demography. In the case of mortality, forest structure interacted with climate, suggesting that competition for water resources induces tree mortality in dry sites. A slight negative relationship was found between mortality and growth, indicating that both rates are likely to be affected by the same stress factors. Additionally, regeneration tended to be lower at plots with higher mortality. Taken together, our results suggest a large-scale self-thinning related to the recent densification of Scots pine forests. This process appears to be enhanced by dry conditions and may lead to a mismatch in forest turnover. Forest management may be an essential adaptive tool under the drier conditions predicted by most climate models.

Keywords

Dryness, forest structure, growth, land use changes, mortality, National Forest Inventory of Spain, regeneration, *Pinus sylvestris*.

INTRODUCTION

Understanding the underlying processes driving forest demography is a central goal for forest research. This is becoming increasingly important in the face of global change and the many disturbances to which forests are being subjected, and the need to forecast how forests will change in the future (Bonan, 2008; Purves & Pacala, 2008). Given the long lifespan of trees, one of the main complications of this type of research is the need of extensive monitoring of relatively large populations over long periods of time.

Without disturbances, forest demography (survival, growth, recruitment) is determined by climate and by biotic interactions (Harper, 1977; Ibáñez *et al.*, 2007). During forest development, structural attributes modulate forest demography via competition and natural thinning processes, which favour the most vigorous trees and allow the emergence of new recruits (Peet & Christensen, 1987). In the face of disturbance, and depending on the climate conditions and competitive relations, the same type of forest community may respond differently and display different thresholds of change in demography patterns (Tessier, 1989). These two components, climate and forest structure, operate simultaneously and interactively, highlighting the need of taking them both into account in studies of forest dynamics (Linares *et al.*, 2009; 2010).

The ecological thresholds (cf., Anderesen *et al.*, 2008) of forest communities deserve special attention, as abrupt environmental changes could lead forests to exceed their adaptation capacity (Linares *et al.*, 2010). Changing environmental conditions may lead to alterations in the structure and dynamics of forests, as well as induce changes in species distributions (Hansen *et al.*, 2001). This is reflected by the recent episodes of forest dieback observed across a broad range of forest types around the globe (Allen *et al.*, 2010), as well as by the recent changes in tree growth and forest productivity observed worldwide, suggesting long-term alterations of forest-atmosphere interactions (Bonan, 2008).

The forests in the western Mediterranean have been managed for millennia, and current communities differ widely from those that would exist in the absence of humans (Blondel & Aronson, 1995). Forest expansions after agricultural abandonment and modifications in forest management have been particularly intense during the last century (Margaris *et al.*, 1996; Grove & Rackham, 2001), resulting in denser stands with increased competition for resources and potentially exacerbating the vulnerability of forests to drought periods (Linares *et al.*, 2009). This is critical if we consider that many Mediterranean forests are currently water-limited (Peñuelas *et al.*, 2001; Sarris et al., 2007) and that climate models predict that conditions will get drier in the future, with temperature increases of 3-4ºC during the next century and large reductions of annual precipitation, reaching 50% during the summer (EEA, 2008). The impact of climatic stressors on these forests could thus be dramatic (Aber *et al.*, 2001; Bréda *et al.*, 2006; Hartmann, 2010), particularly if we consider that many Mediterranean woodlands are in the low-latitude edge of their distribution and are likely to be particularly vulnerable to increased aridity (Hampe & Petit, 2005). In this context, understanding the regional patterns of forest demography in relation to the structural attributes and climate could be a relevant management tool to inform adaptation and mitigation strategies.

Human activities have affected the distribution, composition, and structure of pine forests for millennia (Richardson *et al.*, 2007). Scots pine (*Pinus sylvestris* L.) is the dominant tree species in large areas of the Northern Hemisphere, with the largest populations located in boreal regions. However, Scots pine also occupies large areas in the Mediterranean basin, with the Iberian Peninsula being the southwestern limit to its distribution. Scots pine forest dieback has been related to extreme drought episodes in European forests (Bigler *et al.*, 2006), including several populations in the Iberian Peninsula (Martínez-Vilalta & Piñol, 2002; Hódar *et al.*, 2003). At the same time, competition-induced mortality has also been documented for Scots pine (Bravo-Oviedo *et al.*, 2006), probably as a result of changes in land use and forest management. Regarding growth, several studies have documented that the relationship between water availability and demand during the summer is the main climatic factor limiting Scots pine (Martínez-Vilalta e*t al.,* 2008). Negative relationships have also been found between competition and growth of Scots pine in Mediterranean mountain areas (García-Abril *et al.*, 2007).

In this study we explore the recent dynamics of mortality and growth throughout the distribution of Scots pine in the Iberian Peninsula, using the extensive data base of the National Forest Inventory of Spain. This is one of the first times the intraspecific variation of demographic rates has been studied at such a large scale, and the first time these rates are studied extensively at the dry edge of the distribution of an important forest species such as Scots pine. Specifically, our main objective was to evaluate the response of mortality and growth rates to spatial variability of climate, climatic anomalies and forest structure during the last decades of the twentieth century. We addressed three main hypotheses: (1) Mortality rates would be relatively high and concentrated in more arid sites suffering higher climatic anomalies; (2) Given the recent increase in severe droughts we expect that the spatial variability in mortality and growth rates would be more related to climatic differences across sites and climatic anomalies than to differences in forest structure; (3) Mortality and growth would be negatively related across sites, indicating that the qualitative response of these rates to the major stress factors is similar. To evaluate the potential implications of the observed mortality patterns on forest dynamics, we also analyzed the relationship between mortality and potential regeneration of Scots pine.

MATERIAL AND METHODS

Study system

The studied area encompasses the forested territories of Spain (493720 km^2) located in the Iberian Peninsula (western Mediterranean basin, between 10º W and 3º E longitude, and between 43º N and 35º N latitude). This geographic location, together with the range of influences and the mountainous orography, produces a very heterogeneous climate. According to Capel Molina (2000), there are two major climatic domains: the temperate-oceanic, and the Mediterranean. The temperate-oceanic climate, with a dominant Atlantic influence, occurs in the north of the area, and has relatively wet and cold weather, with mean annual temperatures ranging from 9 to 15ºC, and annual precipitation ranging between 900 and 3000 mm. The rest of Spain falls within the Mediterranean domain, which is characterized by mild winters and hot and dry summers. Mean annual temperatures range from 15 to 19ºC, and annual precipitation ranges from 200 to 900 mm. There is also a continental gradient from the coast inland with increasing thermal amplitudes. This climate variability and the geographic location of the Iberian Peninsula are the main factors explaining the existence of a rich and varied flora. Vegetation types across the climatic-topographic gradients include: Atlantic, sub-Atlantic and sub-Mediterranean deciduous forests; montane, sub-alpine, and Mediterranean coniferous forests; sclerophyllous and evergreen shrublands and forests (Blanco *et al.*, 1997).

Scots pine (*Pinus sylvestris* L.) occupies large areas in the Spanish mountain forested areas, with a large phytogeographic region including sub-Mediterranean, Eurosiberian, and Boreoalpine chorologies (Rivas-Martínez, 1983). The distribution extends from the north to the Iberian and Central mountain ranges, with the most extensive populations located in the Pyrenees. According to Martínez-García (1999) Scots pine forests in Spain are distributed in eight major regions (Fig. 1). There have been important land use changes in the Iberian Peninsula during the last century, including the abandonment of agropastoral activities in mountain areas, the abandonment of forest exploitation (García-Ruíz *et al.*, 1996), and a large-scale afforestation starting in the 1940s that intensified during the 1950s and has continued albeit at lower rates until recent decades (Martínez-García, 1999). As a result, stand density has increased in many forests and the range of Scots Pine has expanded noticeably (Martínez-García, 1999; Poyatos *et al.*, 2003).

The data set: the National Forest Inventory of Spain (IFN)

The IFN is an extensive database of periodical forest surveys distributed systematically across the forested area of Spain (Villaescusa & Díaz, 1998). The IFN is based on a network of fixed circular plots at a density of 1 plot km^{-2}, which allows forest characterization and includes exhaustive information on the composition of canopy and understory woody species, as well as on forest structure and production. Within the plots, all trees ≥ 7.5 cm in diameter at breast height (DBH) were labelled, measured for DBH and height, identified to species and censused for mortality. Sampling followed a nested circular plot design. Thus, all trees with DBH > 7.5 cm were measured within 5 m of the centre of the plot, trees with DBH > 12.5 cm were also measured between 5 and 10 m around the centre of the plot, whereas trees with DBH > 22.5 cm and DBH > 42.5 cm were considered within 10-15 m and 15-25 m around the centre of the plots, respectively. Individuals with DBH between 2.5 and 7.5 cm were also counted (but not individually labelled) within the central 5 m plot. The first National Forest Inventory (IFN1) was conducted between 1965 and 1975, the second (IFN2) from 1986 to 1996, and the third (IFN3) from 1997 to 2007. The plots sampled during the IFN1 were different from those sampled during the IFN2 and IFN3, as the continuous character of the project started with the IFN2. We used data from the permanent plots surveyed in the IFN2 and revisited again in the IFN3.

For the present study we selected plots according to the following criteria:

a) Scots pine basal area ≥ 50% of the total plot basal area.

b) At least 10 Scots pine individuals were tracked through the two repeated censuses (IFN2 and IFN3). This criterion was introduced to reduce variation in plot–level demographic rates.

c) No evidence of forest management (cutting or thinning) nor recent disturbances (i.e., fires) was detected during the IFN3 survey. Forest management as detected in the IFN2 survey was used to study the influence of previous management in our results.

This filtering resulted in a total of 2392 plots with basal areas ranging from 5.6 to 80.8 m^2 ha^{-1} and densities between 305 and 3400 trees ha^{-1}.

Demographic rates

Mortality (MR) at the plot level was calculated as $N_{IFN2} – N_{IFN3}$, where N_{IFN2} is the number of living Scots pines at the IFN2 and N_{IFN3} the number of those that survived to the IFN3 survey. MR was averaged taking into account the unequal sampling effort across tree sizes (i.e. weighting the contributions of each size class by plot size), and was standardized for a period of 10 years to take into account differences among plots in the time interval (9-12 years) between the two censuses. Although annual mortality data were not available, we calculated the average annual mortality rate during the period between the two inventories (10 years) following Sheil *et al.* (1995). We also computed standing mortality (i.e., the percentage of dead trees per plot) as detected at the IFN2 and IFN3 surveys. It should be noted that in this case the period during which this mortality occurred is unknown, unlike what happens for MR as described above.

Mean annual basal area increment of surviving trees per plot, relative to mean tree size (mean DBH per plot, again taking into account the unequal sampling effort across tree sizes), was used as a measure of growth rate (GR, in $cm^2 \cdot cm^{-1} \cdot year^{-1}$). GR was calculated using the following equation:

$$GR = ([BA_{INF3} / N_{IFN3}] - [BA_{IFN2} / N_{IFN3}]) / (t * DBH_{IFN2})$$

where BA_{INF2} and BA_{IFN3} are the plot basal areas at the second and third national inventories, respectively, N_{IFN3} is the number of living pines per plot at the third national inventory, DBH_{IFN2} is the mean diameter at breast height at the IFN2 and t is the time interval between the two measurements (9-12 years). Basal area increment was normalized by the number of trees and by mean DBH to account for differences in forest development. This normalization was preferred over more conventional approaches using relative basal area increments because in our case dividing basal area increment by basal area over-corrected for size effects. Unequal sampling effort across tree sizes was also accounted for in the calculation of GR.

Finally, we used the number of Scots pine individuals with DBH between 2.5 and 7.5 cm detected at each plot during the IFN3 as an indicator of potential regeneration. It should be noted, however, that this count is not a measure of recruitment rate, as the age distribution of the counted saplings is unknown.

Climatic and forest structural data

Two climatic data sets were used, the first one to characterize the spatial variability of climate across the Iberian Peninsula, and the second to describe the climatic anomalies occurred during the time interval between the two surveys. Climatic variables associated with each individual plot were obtained from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola *et al.*, 2005), with a spatial resolution of 180 m. Two variables were used to characterize the climate at each plot (period 1950–1999): mean annual temperature (in ºC) and summer P/PET, defined as the average ratio of precipitation to potential evapotranspiration (the latter calculated following the Hargreaves-Samani method; Hargreaves & Samani, 1982) from June to August. Low values of summer P/PET correspond to dry sites, and high values to wet sites. The studied plots covered a wide climatic gradient, with mean annual temperatures ranging from 5 to 13.7ºC and mean summer P/PET from 0.04 to 1.12.

Climatic anomalies, defined as the difference between the value of a climate variable in a given period with respect to the mean value for a reference period, divided by the standard deviation, were obtained from the gridded 0.5x0.5º dataset produced by Willmott & Matsuura (http://climate.geog.udel.edu). Values of the positive (i.e., above average) and negative (below average) temperature and precipitation anomalies were computed for the period March-August of each year. We used cumulative anomalies of temperature and precipitation, calculated as the sum of the yearly anomalies with the same sign (either < 0 or ≥ 0) for the time interval between surveys for each study plot, resulting in four variables: negative anomaly of precipitation (NAP), positive anomaly of precipitation (PAP), negative anomaly of temperature (NAT), and positive anomaly of temperature (PAT). As periods between surveys varied between 9 and 12 years, all values were standardized to a period of 10 years. The absolute value of the anomalies was used in all analyses to facilitate the interpretation of the results.

To characterize the forest structure of each plot, we used total stand density (Density, in trees ha^{-1}) and mean Scots pine DBH (in cm) as measures of stand structure and competition intensity, both extracted from the IFN2 dataset and corrected for the unequal distribution of sampling effort across size classes (cf. above).

Statistical analyses

Statistical models to analyze MR and GR were constructed separately using the same predictor variables in both cases. We modelled demographic rates as a function of the following fixed factors: Density, DBH, mean annual temperature, summer P/PET, PAT, NAP, PAP, NAT and prior management (Management, dichotomic variable). The following interactions were also considered: Density x summer P/PET, DBH x summer P/PET, Density x NAP and DBH x NAP, as high competition may intensify the effect of water scarcity; and summer P/PET x NAP and summer P/PET x PAT to evaluate if there was a differential effect of anomalies along the climatic gradient. Region was introduced in the models as a random factor to account for spatial autocorrelation. Starting from the saturated model, we created the fully crossed set of models and ranked them from lowest to highest BIC (Bayesian Information Criterion). Models within 4 BIC units of the best model were considered equivalent in terms of fit and are all reported. Logarithmic transformations of GR, Density, and DBH were used to satisfy the normality assumption. The correlation among explanatory variables was always ≤ 0.4, suggesting that collinearity was not a problem in our models. Significance was accepted at $\alpha = 0.01$ given the large sample size. Statistical analyses were carried out with the R software (packages nlme and lme4, R 2.10.0, The R Foundation for Statistical Computing). Throughout the manuscript all values are given as mean ± standard error.

We used generalized linear mixed models (GLMM) to analyze the dependence of Scots pine mortality on climate and forest structure. Counts of demographic events (death) were modelled as a Poisson distribution with a log link function by using the Laplace approximation to estimate parameters. Since the variance of the counts was significantly greater than the mean, indicating overdispersion, we refitted the data with a quasi-Poisson model with Laplace approximation. An offset of ln[Scots pine population size] in the first census (IFN2) was included in the model to account for the different population size across plots. A mixed linear model was used to study the relationship between ln(GR) and the explanatory variables. Parameters were estimated by maximum likelihood.

To evaluate the relationship between growth or regeneration and mortality (the latter expressed as the percentage of individuals dying between the two censuses: MR%), as well as to check the effect of region and management on the previous relationships, we fitted linear models with GR (general linear model) or regeneration (negative binomial GLM) as dependent variables, Region and Management as factors, and MR% and the interactions Region x MR% and Management x MR% as covariates.

RESULTS

Mortality

The weighted percentage of dead Scots pines (standing mortality) increased from 0.39% in the IFN2 to 4.39% in the IFN3, and the number of plots with mortality also increased, from 89 (3.7% of the IFN2 plots) to 858 (35.8% of the IFN3 plots). The same pattern was observed at the plot level: mean mortality percentage per plot was 0.35 ± 0.05% in the IFN2, increasing to 3.99 ± 0.17% in the IFN3, implying that the amount of dead trees increased eleven-fold between the two surveys (Fig. 2). Prior management (before the IFN2) affected 27.3% of our plots but apparently did not bias our results, as the percentage of dead Scots pines increased dramatically between the two inventories both in unmanaged (from 0.45% to 4.57%) and in managed plots (0.18% to 3.86%).

Considering only the mortality occurred between the two censuses, mean annual mortality rate was 0.45 ± 0.02% per year for all plots, 0.48 ± 0.02% per year in unmanaged plots and 0.38 ± 0.03% per year in managed plots. Mortality rates showed a right-skewed distribution (Fig. 3), with most plots showing no mortality and a 14.5% of plots with mortality rates > 1% per year. Mortality rate was highest in small trees (7.5-12.5 cm size class), but values remained relatively high also in larger size classes (Appendix A).

Regarding the distribution of mortality occurred in the period between surveys (MR), there were 10 models within 4 BIC units that always incorporated the effect of Density, DBH, summer P/PET, NAP and the interactions DBH x summer P/PET and DBH x NAP (Appendix B; Table 1 for the model with lowest BIC). Denser stands showed higher levels of mortality (Appendix B; Table 1). The interaction between DBH and summer P/PET revealed that the effect of increasing DBH on MR was stronger at dry sites (Fig. 4a). Similarly, the effect of NAP (periods of low precipitation) on MR was more intense in stands with high DBH values (Fig. 4b). Regarding this last interaction, it should be noted that MR tended to increase at low NAP when DBH was large. All the other explanatory factors were either not retained in the best model set or had inconsistent effects across models.

Growth

Annual growth rate covered a range between 0.08 and 2.52 $cm^2 \cdot cm^{-1} \cdot year^{-1}$, with an average of 0.57 ± 0.01 $cm^2 \cdot cm^{-1} \cdot year^{-1}$ (Fig. 5). If the plots are split depending on whether they were recorded as managed during the IFN2, mean annual growth rate in unmanaged plots was 0.59 ± 0.01 $cm^2 \cdot cm^{-1} \cdot year^{-1}$, while in managed plots it was 0.50 ± 0.01 $cm^2 \cdot cm^{-1} \cdot year^{-1}$. Growth of individual trees in terms of basal area increment tended to increase with tree size (Appendix C).

Overall, the best model for GR included the effect of Density, DBH, annual temperature, summer P/PET, NAP and the interaction summer P/PET x NAP

(Table 2). There were no other models within 4 BIC units. Forest structure had a strong effect on Scots pine growth. GR was significantly lower with increasing Density and DBH (Table 2). Regarding the climatic variables, annual temperature had a significant negative effect on GR, indicating that GR was lower with increasing temperature (Table 2). Finally, the interaction between summer P/PET and NAP indicated that pines at dry sites tended to grow less and that the negative effect of NAP on GR was more intense at wet sites (Fig. 6).

Relationships between demographic rates

MR% and GR were negatively associated ($\beta = -0.022$, $P < 0.001$) indicating a lower growth of Scots pine in plots with high mortality levels. GR varied among regions ($P < 0.001$), but the interaction MR% x Region was only marginally significant ($P = 0.011$), indicating that the slope of the relationship between MR% and GR did not vary substantially across regions. GR did not vary as a function of prior management ($P = 0.738$), and the interaction term was marginally significant with a positive effect ($\beta = 0.012$, $P = 0.028$), suggesting a less marked relationship between GR and MR% in managed plots.

Only 46.3% of the IFN3 plots showed any Scots pine regeneration. Moreover, mortality was negatively related to regeneration, indicating low regeneration where mortalities were high ($\beta = -0.046$, $P < 0.001$). Additionally, regeneration also varied among regions ($P < 0.001$), but the interaction term was not significant ($P = 0.329$), i.e. that the slope of the regeneration–MR% relationship did not differ across regions. Regeneration did not vary as a function of management (P = 0.268) and the interaction term was not significant (P = 0.138).

DISCUSSION

Tree mortality between the two forest inventories considered in this study was 0.45 ± 0.02% per year on average. Unfortunately, annual mortality data were not available in our study and the previous figure masks year to year differences, which can be large. As a comparison, annual tree mortality in French coniferous forests has been around 0.2% since 1989, with some pulses of 0.4-0.5% (years 1991, 2005 and 2006), and only one pulse with higher mortality (around 1.2%) in 2004 (Bréda & Badeau, 2008). In a recent study, van Mantgem *et al.* (2009) have reported a rapid increase in pine mortality across Western USA, from a low value of around 0.25% per year in the mid 1950s to extremely high current values of around 2% per year. Although the overall mortality rates reported here are not as high, it should be noted that our mortality values correspond to an average over 10 years and across a very large area, and that there was a large number of plots with mortality rates far above the average (Fig. 3). This is consistent with some local observations of high mortality associated with drought episodes (Martínez-Vilalta & Piñol, 2002; Hódar *et al.*, 2003).

The amount of standing dead Scots pine trees increased dramatically (11-fold) over the 10 year period between IFN2 and IFN3. Although the difference between the two censuses is impressive, the interpretation of this result is limited by at least two facts. Firstly, as we only have data from two points in time it is impossible to draw strong conclusions about time trends. Secondly, the causes of this increase are likely to be multiple and complex. A large part of the difference between the two censuses could be due to changes in forest management and, in particular, in the way dead stems are dealt with, as they may have been more readily removed in the past, when forests were more intensively used. However, given the relatively low percentage of plots with management prior to the IFN2 (27%) and that the increase in standing mortality affected both managed and unmanaged stands in a similar manner, our results suggest that other factors besides management may have contributed to this recent increase in standing dead trees at such regional scale. Directional changes in climate and forest structure during the second half of the 20th century could have also contributed to the observed increase in standing dead trees. Regardless of the ultimate cause of the observed pattern, the observed increase in standing dead trees is large enough to have perceptible implications for the studied forests in terms of functioning and biotic interactions.

Mortality and growth in relation to forest structure and climate

In agreement with our first hypothesis, higher levels of Scots pine mortality were associated with climate dryness and climate anomalies characterized by low precipitation and high temperatures. The effect of recurrent and severe droughts on forest survival has been shown in other studies (Breshears *et al.*, 2005; van Mantgem *et al.*, 2009), including several studies on Scots pine forests (Martínez-Vilalta & Piñol, 2002; Bigler *et al.*, 2006). As expected, higher growth rates were associated with high water availability, both in space and time. Similar relationships have been observed for other species in Mediterranean regions (Sarris *et al.*, 2007) and for Scots pine populations at higher latitudes (Linderholm, 2001). Our results add to the evidence suggesting that the balance between water availability and demand during the summer (summer P/PET) is a key climatic factor controlling tree growth (as also observed by Bréda *et al*., 2006; Martínez-Vilalta *et al.*, 2008). Finally, our MR and GR models provided some evidence that the detrimental effects of climatic anomalies are not restricted to dry sites, suggesting that populations under relatively wet climates may be equally vulnerable to periods of drought stress.

However, forest structure explained a much larger % of the spatial variation in MR and GR than climate, contradicting our second hypothesis. These results were unexpected considering that we studied mostly populations at the dry limit of the distribution of a drought-sensitive species such as Scots pine. On the other hand, our findings are not surprising in the context of forest development theory, as many of the studied stands are relatively young and dense (see Appendix D) and could be at the “stem-exclusion stage” (Oliver & Larson, 1990). Thus, endogenous processes, such as self-thinning, could be the main driving force behind demographic rates (Lutz & Halpern, 2006), particularly considering the shade-intolerant nature of Scots pine (Ceballos & Ruiz de la Torre, 1971). The current structure of many Scots pine forests in Spain, associated with relatively homogenous and dense stands, is to a large extent the result of plantation policies and the abandonment of traditional agricultural and forest uses during the 20th century (Martínez-García, 1999; OSE, 2007).

Our study indicates that climatic effects interact with forest structure, particularly in older forests, and thus complements previous work showing that competition for resources might have a negative effect on tree survival (Bravo-Oviedo *et al.*, 2006) or could exacerbate the effects of strong and punctual periods of water deficit on forest dynamics (Klos *et al.*, 2009; Linares *et al.*, 2009). Overall, these studies suggest that forest structure may act as an intrinsic continuous stressor on trees through increased competition for resources, and that this condition could intensify under more extreme climatic conditions. Clearly, forest structure should be given a prominent role in the study of forest dynamics under environmental change, as structural attributes modulate the adaptation and vulnerability of forests to climate-induced stress (Linares *et al.*, 2010).

Finally, our results also show that mortality and growth rates were affected by similar environmental factors, so that conditions that were associated with high mortality (dense forests with high basal area, dry climates, periods of low precipitation) were also associated with low growth rates. In agreement with this, growth and mortality rates were negatively related at the plot level, in accordance with similar results obtained by previous studies relating low growth rates with increased mortality (Kobe, 1996; Bigler *et al.*, 2004; Das *et al.*, 2007).

Forest dynamics and management implications

Fewer than 50% of our study plots showed Scots pine regeneration. This result should be interpreted in the context of current stand development of the studied Scots pine forests (see previous section; Oliver & Larson, 1990). However, the fact that low regeneration was associated with high levels of tree mortality suggests that the interacting effects of structural and climatic stressors on Scots pine survival could be also acting negatively on its regeneration, indicating a potential mismatch in forest turnover, as already reported for other pine species (Gworek *et al.*, 2007).

Mitigation strategies such as thinning treatments and sustainable harvest activities to enhance structural diversity may release competition within denser stands (Bravo-Oviedo *et al.*, 2006), and could likely reduce vulnerability of forests to drought (Dale *et al.*, 2001). A release of competition for resources on the surviving trees can occur after mortality episodes (Martínez-Vilalta & Piñol, 2002), which could allow higher growth rates of surviving trees (Olano & Palmer, 2003). The key role of forest structure and structure-climate interactions observed in our study clearly shows the potential of forest management to modulate the demographic response of southern Scots pine forests to increased aridity.

Mediterranean forests have been in constant change for millennia, and especially during the last century, as a result of human impacts (Grove & Rackham, 2001). These changes are now accelerating in the context of global environmental change (Bonan, 2008). Our study indicates that forest management based on a sound understanding of how forests are responding to the different components of global change could be used to help forests accommodate to the expected new conditions (Millar *et al.*, 2007).

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Table 1 Summary of the mortality (MR) model with lowest BIC.

Effects	**Estimate**	**SE**	***T– value***
Intercept	– 22.6918	2.1464	– 10.572
DBH	4.3017	0.7116	4.301
Density	0.8739	0.0605	14.452
Summer P/PET	6.8993	1.7747	3.887
NAP	0.5952	0.1956	3.042
PAT	0.0551	0.0179	3.078
DBH x Summer P/PET	– 2.2172	0.6196	– 3.579
DBH x NAP	– 0.2066	0.0679	– 3.040

DBH, mean Scots pine diameter at breast height; NAP, negative anomaly of precipitation; PAT, positive anomaly of temperature; Summer P/PET, average ratio of precipitation to potential evapotranspiration from June to August.

Table 2 Summary of the growth (GR) model with lowest BIC. Growth was log-transformed.

Effects	**Estimate**	**SE**	**P–value**
Intercept	4.2554	0.2801	< 0.001
DBH	– 1.0210	0.0331	< 0.001
Density	– 0.4052	0.0176	< 0.001
Summer P/PET	2.2606	0.3862	< 0.001
Temperature	– 0.0263	0.0074	< 0.001
NAP	0.0777	0.0221	< 0.001
Summer P/PET x NAP	– 0.1845	0.0473	< 0.001

DBH, mean Scots pine diameter at breast height; NAP, negative anomaly of precipitation; Summer P/PET, average ratio of precipitation to potential evapotranspiration from June to August.

Figure legends

Figure 1 Map of the Iberian Peninsula showing the distribution of Scots pine (grey surface), and regions of provenance: R1: Pyrenees; R2: E Cantabrian mountain range-W Basque mountains; R3: N Iberian mountain range; R4: S Iberian mountain range; R5: SE Iberian mountain range-Catalan coastal mountain range; R6: Central mountain range; R7: Betic mountain range; R8: Cantabrian mountain range.

Figure 2 Average standing mortality (% ± SE) of Scots pine detected during the surveys.

Figure 3 Distribution of annual mortality rate of Scots pine (% year^{-1}) (± SE) in logarithmic scale. Only plots with mortality > 0 are shown (N = 858 out of a total of 2392 plots).

Figure 4 Surface plot showing the predicted effects on mortality of the interactions (a) DBH x Summer P/PET (b) DBH x NAP. Crosses represent each observation. DBH, mean Scots pine diameter at breast height; MR, mortality rate; NAP, negative anomaly of precipitation; Summer P/PET, average ratio of precipitation to potential evapotranspiration from June to August. Summer P/PET and NAP are variables dimensionless.

Figure 5 Annual growth rate of Scots pine (cm^{2} · cm^{-1} year^{-1}) (± SE) per range of densities (trees ha^{-1}).

Figure 6 Surface plot showing the predicted effects on growth of the interaction Summer P/PET x NAP. Crosses represent each observation. GR, growth rate; NAP, negative anomaly of precipitation; Summer P/PET, average ratio of precipitation to potential evapotranspiration from June to August. Summer P/PET and NAP are variables dimensionless.

Figure 1

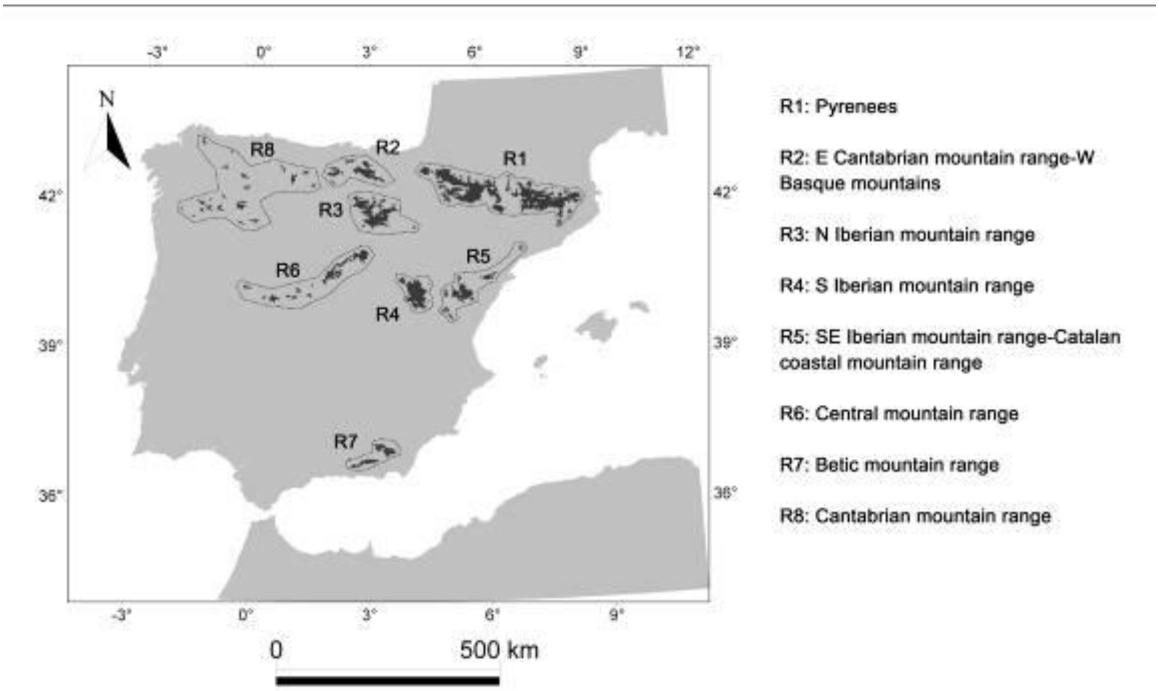
N
R1
R2
R3
R4
R5
R6
R7
R8
-3°
0°
3°
6°
9°
12°
42°
39°
36°
0
500 km
R1: Pyrenees
R2: E Cantabrian mountain range-W Basque mountains
R3: N Iberian mountain range
R4: S Iberian mountain range
R5: SE Iberian mountain range-Catalan coastal mountain range
R6: Central mountain range
R7: Betic mountain range
R8: Cantabrian mountain range

Figure 2

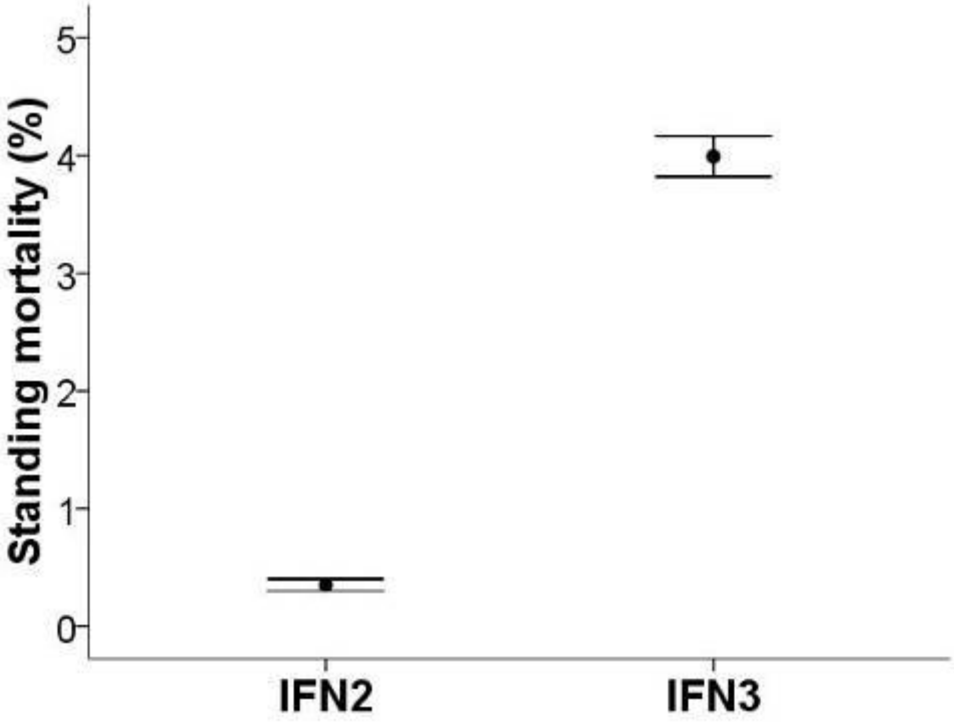

Figure 3

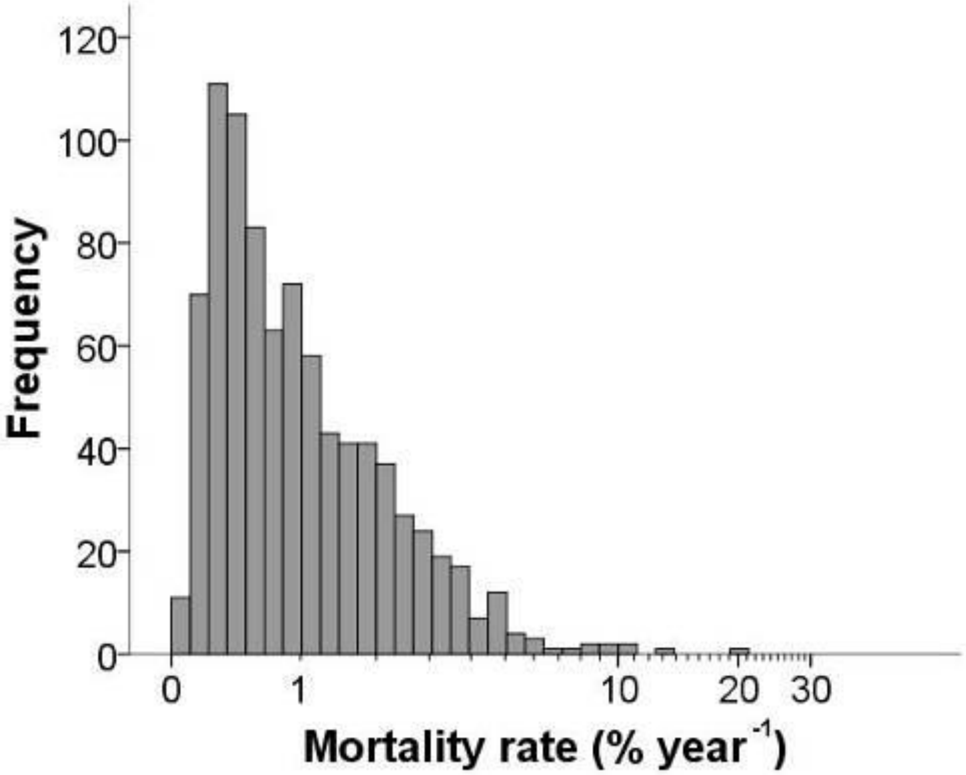
Frequency
120
100
80
60
40
20
0
0
1
10
20
30
Mortality rate (% year^{-1})

Figure 4

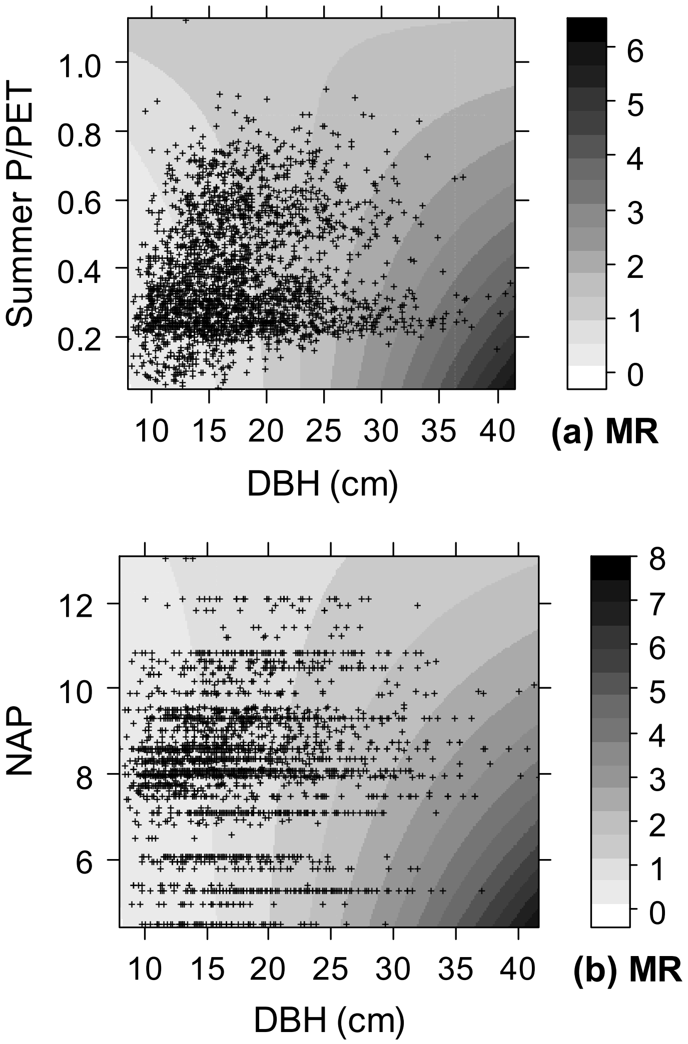
Summer P/PET
1.0
0.8
0.6
0.4
0.2
10 15 20 25 30 35 40
DBH (cm)
6
5
4
3
2
1
0
(a) MR
NAP
12
10
8
6
10 15 20 25 30 35 40
DBH (cm)
8
7
6
5
4
3
2
1
0
(b) MR

Figure 5

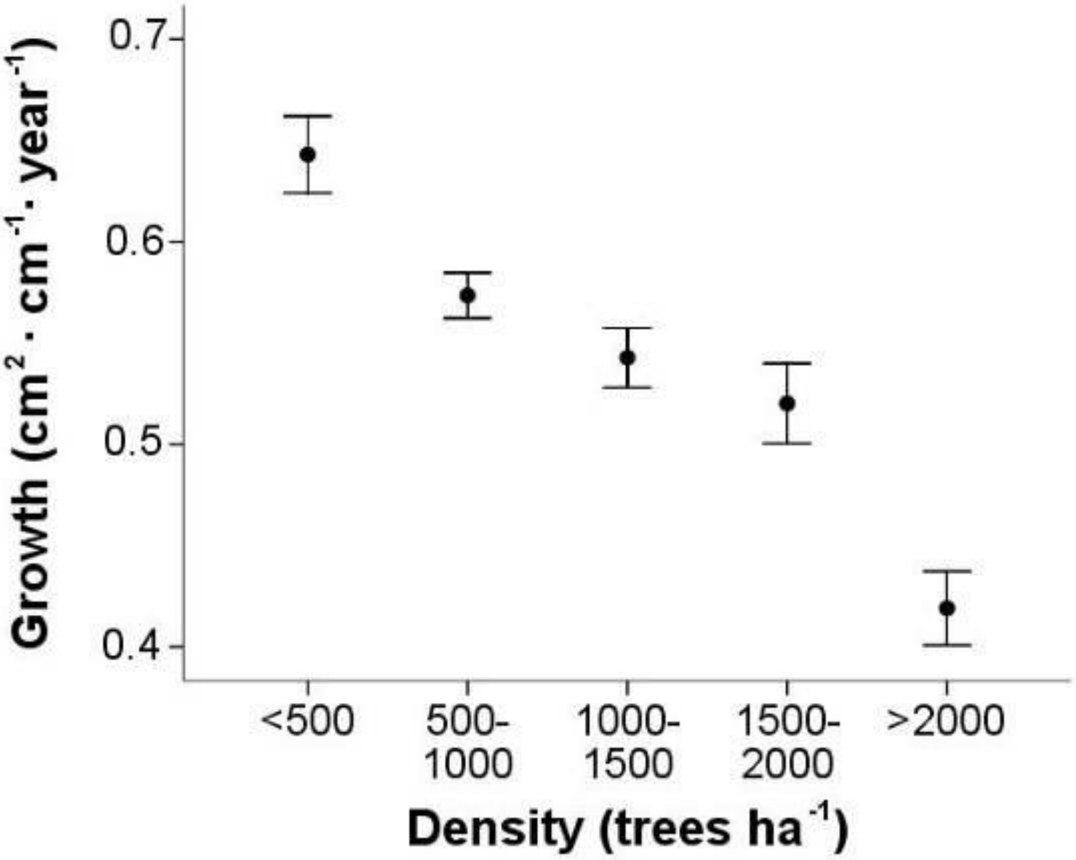
Growth (cm² · cm⁻¹ · year⁻¹)
0.7
0.6
0.5
0.4
<500
500-1000
1000-1500
1500-2000
>2000
Density (trees ha⁻¹)

Figure 6