Large-scale assessment of the defoliation and demography of Spanish forests along climatic gradients

Phd Tesis

Tesis Doctoral

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Chapter 1: Introduction

Introducció general

Actualment hi ha importants evidències de les ràpides i profundes modificacions que estan patint gran part dels ecosistemes terrestres com a conseqüència del canvi global (IPCC, 2007). En aquest context de canvi, diferents estudis apunten als boscos mediterranis com un dels ecosistemes més vulnerables als efectes del canvi global en les pròximes dècades (Lindner et al., 2010). De fet, durant els últims anys, diferents estudis han observat impactes del canvi global sobre la demografia d'aquests boscos (Andreu et al 2007, Sarris et al 2007). Recentment s'han descrit episodis de declivi i mortalitat forestal, disminucions de productivitat, migració d'espècies, o alteracions en els patrons de reclutament i creixement dels arbres (Ciais et al 2005, Breshears et al 2005, Andreu et al 2007). Els canvis en la demografia i els processos de declivi forestal s'han relacionat amb multiples factors, incloent variacions en el clima i els usos humans del territori.

Primerament, i com a conseqüència del canvi climàtic, els boscos mediterranis podrien estar sotmesos a un augment de les condicions d'estrès hídric. A aquestes observacions empíriques cal afegir que les projeccions climàtiques prediuen un increment generalitzat de la temperatura (IPCC 2013), i un augment de la freqüència i la intensitat de les sequeres i les precipitacions intenses a tot l'hemisferi nord, però especialment a la conca mediterrània durant les pròximes dècades (IPCC 2013). D'altra banda, el canvi d'usos del sòl i de gestió forestal que s'ha succeït a aquestes regions durant les últimes dècades situa els boscos Mediterranis en unes condicions completament noves. Durant les últimes dècades l'Europa Mediterrània ha experimentat canvis socioeconòmics a gran escala que han implicat una important disminució de la gestió forestal. Aquesta reducció de la gestió dels boscos ha afavorit l'evolució de boscos densos, un augment de biomassa, i un avanç dels processos successionals.

Tot i el gran interès que desperta conèixer les respostes dels boscos davant d'aquests canvis, encara queden grans incerteses. Gran part dels estudis que s'han fet a la conca Mediterrània són estudis locals, basats en un nombre reduït d'especies i sovint focalitzats a parametritzar una o poques variables demogràfiques (mortalitat, creixement, reclutament o altres). Cal tenir en compte que les respostes dels boscos davant el canvi global vénen profundament modificades per factors de variabilitat intraespecífica, interespecífica, interaccions biòtiques o altres factors. La naturalesa d'aquests estudis, i l'elevada variabilitat que inclouen provoca que tinguem una gran varietat d'enfocs, de resultats i de tendències, que sovint poden ser difícils d'interpretar, combinar i extrapolar per definir patrons a gran escala. Entendre i predir les conseqüències del canvi global sobre els boscos a escala macroecològica és encara un repte científic a assolir. La informació recollida en inventaris forestals s'ha revelat com una interessant i potent eina per descriure patrons i processos a gran escala i explorar els efectes del canvi global sobre diferents sistemes terrestres.

Dins d'aquest context, aquesta tesi té com a objectiu proporcionar una visió general dels factors que afecten a la defoliació i als processos demogràfics dels boscos Mediterranis utilitzant la informació extreta de bases de dades forestals. L'àrea d'estudi és la regió forestal espanyola, que ens ofereixen una molt bona oportunitat per avaluar l'impacte del canvi global sobre els boscos, ja que compren des dels boscos mediterranis semiàrids, limitats per l'aigua, a boscos subalpins o d'influència Atlàntica amb un règim de precipitacions totalment diferent.

En el primer capítol hem explorat els efectes de la sequera sobre la defoliació en els boscos Ibèrics. Hem utilitzat la base de dades del ICP forests, concebuda inicialment com una xarxa de seguiment dels efectes de la contaminació sobre la defoliació dels boscos europeus. En el segon capítol, utilitzant dades de l'inventari forestal espanyol (IFN), hem avaluat quina és la importància de diferents factors sobre els processos demogràfics, estudiant reclutament, mortalitat i creixement. Per últim, en el tercer capítol, i utilitzant també dades del IFN, ens hem focalitzat en els processos de reclutament i tots aquells factors que els determinen.

Chapter 2: Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought.

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2.1. Abstract

Climate change is progressively increasing severe drought events in the Northern Hemisphere, causing regional tree die-off events and contributing to the global reduction of the carbon sink efficiency of forests. There is a critical lack of integrated communitywide assessments of drought-induced responses in forests at the macroecological scale, including defoliation, mortality, and food web responses. Here we report a generalized increase in crown defoliation in southern European forests occurring during 1987–2007. Forest tree species have consistently and significantly altered their crown leaf structures, with increased percentages of defoliation in the drier parts of their distributions in response to increased water deficit. We assessed the demographic responses of trees associated with increased defoliation in southern European forests, specifically in the Iberian Peninsula region. We found that defoliation trends are paralleled by significant increases in tree mortality rates in drier areas that are related to tree density and temperature effects. Furthermore, we show that severe drought impacts are associated with sudden changes in insect and fungal defoliation dynamics, creating long-term disruptive effects of drought on food webs. Our results reveal a complex geographical mosaic of species specific responses to climate change–driven drought pressures on the Iberian Peninsula, with an overwhelmingly predominant trend toward increased drought damage.

2.2. Introduction

Global climate change is expected to cause progressively increased frequency and severity of drought events and heat waves in the Northern Hemisphere (Meehl and Tebaldi 2004, IPCC 2007). Globally, increased drought impacts have already been recorded over the last several decades, with anthropogenic forcing widely accepted as the most plausible cause (IPCC 2007, Hoerling and Kumar 2003, Yeh et al. 2009, Zeng and Qian 2005, Della_Marta et al. 2007, Zhao and Running 2010). These drought impacts have presumably altered carbon cycling dynamics over extensive areas, possibly contributing to the progressive global reduction in the efficiency of terrestrial sinks (Zeng and Qian 2005, Zhao and Running 2010, Canadell et al. 2007). Major drought impacts on vegetation are to be expected in arid and semiarid biomes, which usually respond to increased water deficit with greater reductions in productivity, although drought-induced tree mortality occurs across a broad range of forest types and mean climate conditions (Allent et al. 2010). In semiarid and Mediterranean systems, several studies have recently reported increased plant mortality rates and die-off events, reduced seedling recruitment, long-term shifts in vegetation composition, reduced radial growth, and increased crown defoliation responses (Allen et al. 2010, Mueller et al. 2005, Breshears et al. 2005, Andreu et al. 2007, Van Mantgem et al. 2009). Severe droughts also modify forest biogeochemical cycles by increasing nutrient loss through premature leaf fall without complete nutrient translocation (Martínez-Alonso et al. 2007). In addition, several studies have suggested the existence of important drought-induced cascading effects at higher trophic levels, affecting vertebrate, invertebrate, and fungal consumer populations; promoting insect outbreaks; and altering fundamental mutualistic processes, such as seed dispersal and pollination (Mueller et al. 2005, Breshears et al. 2005, Swaty et al. 2004). Overall, the long-term effects of climate change–type droughts may alter forest physiological responses over extensive areas (Mueller et al. 2005, Breshears et al. 2005, Swaty et al. 2004), potentially leading to extensive tree mortality and associated consequences for earth system processes (Allen et al. 2010, Adams et al. 2010).

In the Mediterranean basin and meridional Europe, long-term climatic series and multiproxy studies have demonstrated an unprecedented and significant increase in heat waves and drought impacts over the last several decades (Della-Marta et al. 2007, Andreu et al. 2007, Luterbacher et al. 2004, Luterbacher et al. 2006, Sarris et al. 2007, Briffa et al. 2009). In line with these findings, the significant increase in the frequency of positive phases of the North Atlantic Oscillation during winter over the last several decades has promoted a northward shift of the Atlantic storm track and possibly triggered droughts and heat waves in southern Europe (López-Moreno and Vicente-Serrano 2008, Rodríguez-Puebla and Nieto 2010). Comparisons of observational data over the last several decades and regional climate change simulations have identified the Mediterranean basin as a hot spot of hydrological cycle changes, and several regional and global models have consistently predicted increased drought impacts and heat waves in this area in the subsequent decades (Giorgi and Lionello 2008, Mariotti 2010). Droughts produce heterogeneous spatial and temporal impacts, however, and local studies have reported a wide variety of sitedependent and species-specific trends, including both positive and negative physiological responses in forest tree species (Martínez-Alonso et al. 2007). These differing findings preclude making generalizations based on available data at the local scale, and highlight the need for extensive community-wide assessments of the impacts of drought (Breshears et al. 2005). We currently lack large-scale, integrative, community-wide assessments of drought-induced forest responses, such as tree crown defoliation, mortality, and food web responses.

European national crown condition inventories derived from the International Cooperative Program on Assessment and Monitoring of Air Pollution Effects on Forests (hereinafter the ICP Forest Inventory) provide yearly species-specific measures of the percentage of defoliation of tree crowns over a wide geographic area (ICP 2006). During drought periods, a reduction in total leaf-transpiration area is a basic response of temperate and Mediterranean forests (Bréda et al. 2006). Forests affected by drought reduce overall tree transpiration through adjustments in total leaf area, allowing improved tree water balance and restoring leaf-specific hydraulic conductivity (Bréda et al. 2006). In the present study, we gathered crown defoliation data from the ICP Forest Inventories (ICP 2006) to assess the macroecological impacts of drought on water-limited southern European forests over the 20-y period of 1987–2006.

2.3. Material and methods

2.3.1. Data.

Defoliation data 1987–2007 were gathered fromthe ICP Forests program (ICP 2006), mortality data were provided by the Second and Third Spanish National Inventory (IFN3), and climatic data were derived from records of the Spanish National Institute of Meteorology (SI Appendix, Materials and Methods).

2.3.2. Climatic and Crown Defoliation Maps.

Interpolated climatic and crown defoliationmapswere derived by applying mixed spatial interpolationmethods that combine global and local interpolations (SI Appendix, Materials and Methods).

2.3.3. Statistical Analyses.

For defoliation analyses, we contrasted a battery of modeling approaches including ordinary least squares, generalized linear models, spatial simultaneous autoregressive models, generalized estimating equations, and generalized linear mixed models. First-order autocorrelative terms were introduced to account for temporal autocorrelation in the models, using the CorAR1 function in the R package. Spatial autocorrelation was assessed by applying Moran’s I correlograms and plotting spatial maps of the distributions of residuals. Mortality models were based on generalized linear models with a binomial error distribution (SI Appendix, Materials and Methods). Times series analyses were applied to assess the significance of temperature and rainfall trends during 1950–2006 (SI Appendix, Materials and Methods).

2.4. Results

We first contrasted the defoliation patterns of southern waterlimited forests relative to central and northern European forests. According to Fluxnet studies, the gross primary production and terrestrial ecosystemic respiration of European forests is limited by water deficit at latitudes below 52°N, whereas temperature effects predominate at latitudes above 52°N (Reichstein et al 2007). Our analysis of temporal defoliation dynamics across latitudinal bands demonstrated a significant increase in crown defoliation rates over the last two decades only in southern European forests, in contrast to the stable and moderate to high defoliation levels seen in northern and central European forests (Fig. 1). From the mid- 2000s to 2007, the highest defoliation levels were found in southern Europe.

To quantitatively assess the factors associated with this recent doubling of crown defoliation rates in southern European forests, we modeled crown defoliation and drought impacts in the Iberian Peninsula during 1987–2006. To study drought dynamics, we applied geographic information system–based interpolation techniques to obtain a monthly sequence of climatic maps for temperature, rainfall, and water deficit during 1951–2006. We then modeled defoliation responses using a battery of modeling approaches (Materials and Methods). We assessed the relative effect on defoliation of (i) climatic and topographic variables (i.e., temperature, rainfall, Emberger water deficit index, solar global radiation, and altitude); (ii) biological interactions (i.e., levels of vertebrate and insect herbivory, and fungal damage); (iii) soil structure (i.e., soil type and humus layer depth); (iv) forest management and fire damage; and (v) interactions between all of the independent variables explored (SI Appendix, Tables S1–S6). We also assessed the existence of drought-induced demographic responses by gathering tree mortality data from the Spanish National Forest Inventory (Materials and Methods).

We observed a significant tendency for increased mean annual temperatures and decreased annual rainfall ($P < 0.0001$) in 1951– 2006, coinciding with recently published meteorological studies of the study area (De Luis et al 2009). We studied drought dynamics in the Iberian Peninsula during 1951–2006 and used time series analysis to identify trends (SI Appendix, Figs. S1 and S2). We found that severe droughts occurred in 2005–2006 and during a long period of drought from 1990 to 1995 that coincided with an anomalous general circulation situation (Yeh et al. 2009, Rodriguez-Puebla & Nieto 2010). Coinciding with this long drought in 1990–1995, we found a strong and generalized crown defoliation response in all of the tree species examined (Fig. 2). The increase in crown defoliation during 1987–2006 was statistically significant for all tree species examined (ordinary least squares fits, $P < 0.001$) (SI Appendix, Fig. S3).

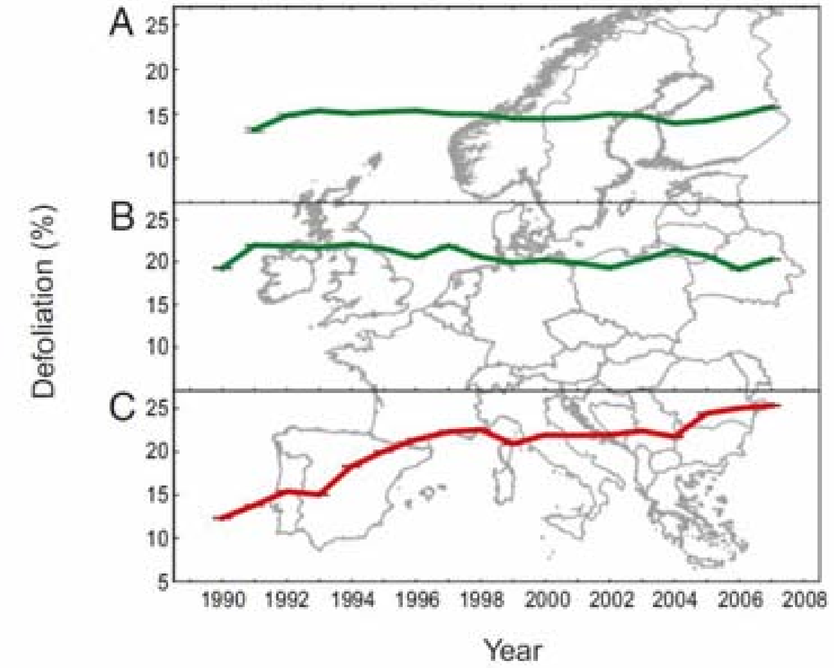

***Figure 1**. A comparison of crown defoliation trends in northern, central, and southern European forests during 1990–2007. Annual trends in averaged defoliation per plot (for all species grouped) are plotted for three latitudinal bands: (A) northern European forests (>58°N of latitude); (B) central European forests (46°N < latitude < 58°N); and (C) southern European forests (<46°N of latitude).*

The models indicated that drought damage was consistently the most important factor associated with the generalized increase in defoliation occurring during 1987–2006 (SI Appendix, Table S4). Associations with drought-related variables were significant and strongest in species distributed in more xeric areas (Fig. 3A). To more precisely assess how drought constrained the heterogeneity of tree physiological responses along climatic gradients, we divided the dataset for each species into quartiles of annual rainfall and independently modeled the defoliation and mortality responses to water deficit and temperature in each quartile (SI Appendix, Materials and Methods). We found close associations between water deficit and defoliation in the drier parts of the species' ranges (Fig. 3A), although each species demonstrated an idiosyncratic response pattern (SI Appendix, Fig. S4). The trends for increasing defoliation were consistent with mortality responses (Fig. 3 C–F). We found a significant and generalized increase of tree mortality rates between 1989–1996 and 1997–2007 by comparing the Second and Third Spanish National Forest Inventories (SI Appendix, Figs. S5 and S6). In turn, this increase in mortality was significantly associated with increased tree density and temperature effects in the 1997–2007 survey (SI Appendix, Fig. S7).

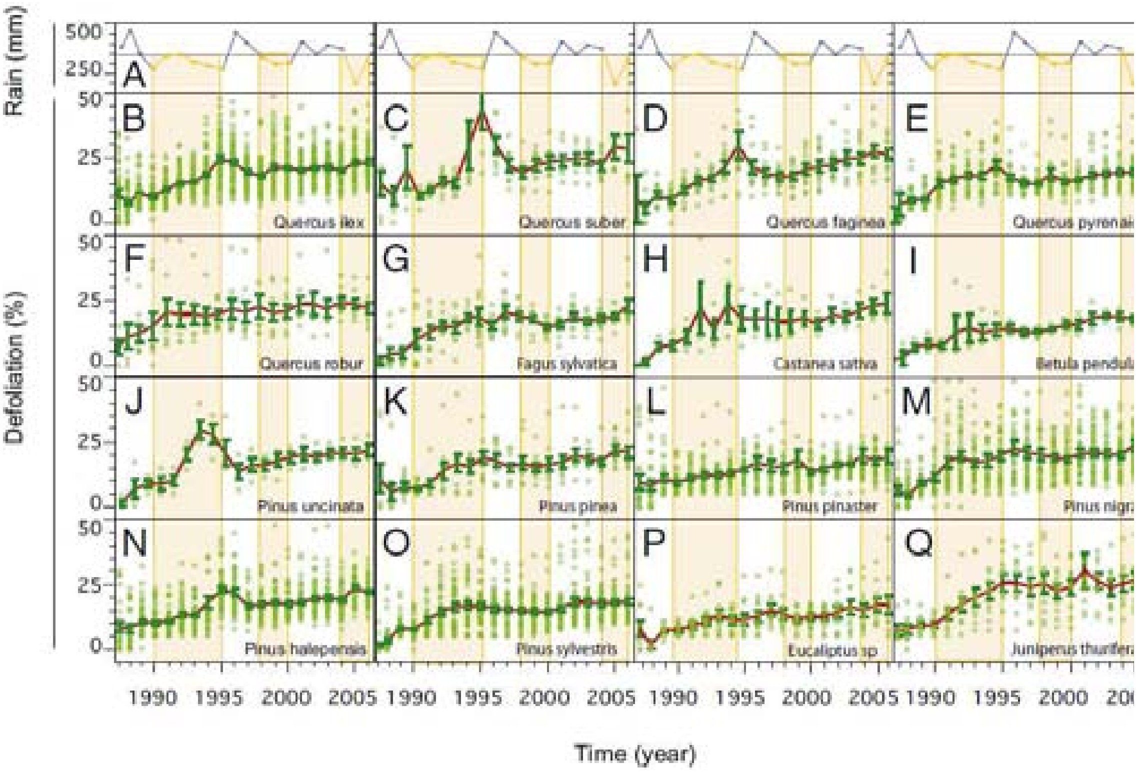

Figure 2. *Trends in crown defoliation for tree species in the Iberian Peninsula. (Upper) Spring–summer rainfall trends during 1987–2006. Orange bands indicate drought periods with spring–summer rainfall of <400 mm (1990–1995, 1999–2000, and 2005–2006). (B–Q) Crown defoliation trends for 16 main forest tree species (labelled in each panel).*

These results illustrate a complex geographical mosaic of species-specific responses to increased water deficit pressures. Our results show that most of the species studied experienced only partial recovery of crown condition after the 1990–1995 drought (Fig. 2), suggesting long-lasting chronic effects of drought on crown structure. This reduced capacity for recovery after drought is possibly due to a combination of limited investment in leaf production due to chronic stress and the presence of defoliated or dead modules in the crown that remain as nonfunctional units for several years (Bréda et al. 2006).

The trophic cascade impacts of climate change–related droughts at the macroecological scale remain largely unexplored, although several previous studies have suggested the existence of important drought-induced cascading effects at higher trophic levels (Mueller et al. 2005, Breshears et al. 2005, Swaty et al 2004, Shure et al 1998, Trotter et al 2010, Stone et al 2010). Forest drought usually results in reduced shoot growth, reduced nitrogen and water foliar concentrations, and increased allocation to secondary defensive metabolites, such as tannins. The combined effect of these factors can severely increase the mortality rates of insect herbivores during severe drought periods (Shure et al 1998) and even truncate multiyear insect outbreak dynamics (Esper et al 2007). Similarly, drought can significantly reduce the rate of fungal infection and sporulation capacity (Harvell et al 2002). We explored the existence of higher trophic-level effects by mapping insect- and fungal-related defoliation trends for each tree species, and compared the temporal dynamics of drought-induced defoliation, fungal damage, and insect herbivory damage. In the most widespread tree species, Quercus ilex, we found a sudden decrease in the impact of insect and fungal defoliation coincident with the abrupt increase of drought effects on trees in 1994–1995 (Fig. 4). We noted similar significant trends in insect defoliation in the less common, closely related species Q. suber (SI Appendix, Figs. S8 and S9). For all other tree species, fungal and insect defoliation patterns were unrelated or only weakly associated with drought dynamics. These results suggest the existence of species-specific drought-induced cascading effects at broad scales in the Iberian Peninsula.

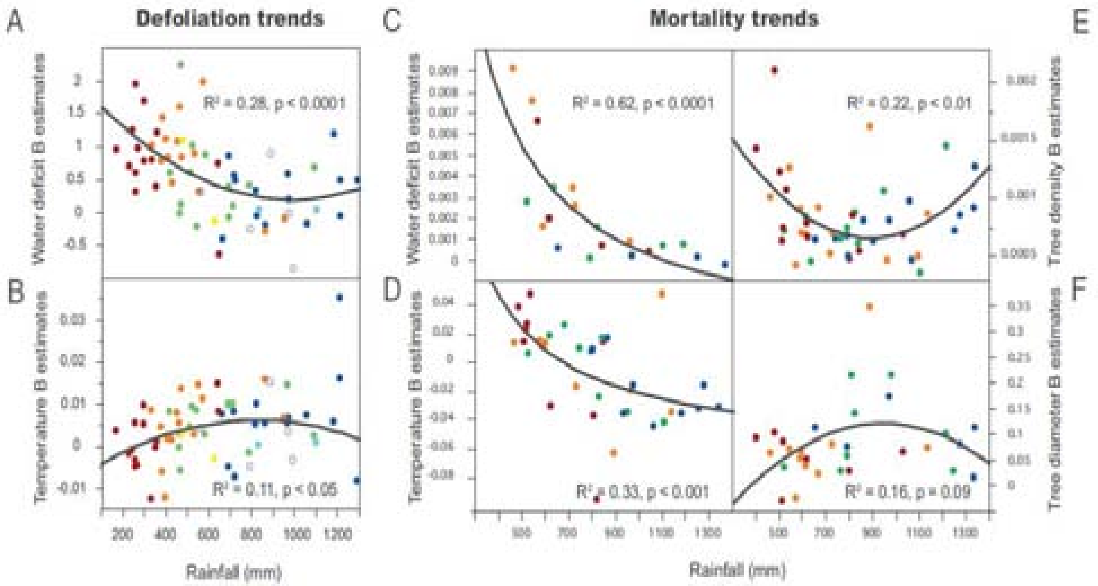

Figure 3 *Geographical variation in the effects of water deficit and temperature on crown defoliation and mortality. Defoliation is modeled as a function of Emberger water deficit and temperature in generalized linear mixed first-order autocorrelative models for each species and each rainfall quartile. Similarly, mortality is modeled as a function of temperature, water deficit, tree density, and tree diameter using generalized linear models for each species and quartile. Significant β estimates for all tree species are plotted. (A) Changes in Emberger water deficit β coefficient values with increased rainfall for defoliation models. (B) Changes in temperature β coefficient values with increased rainfall for defoliation models. (C) Changes in Emberger water deficit β coefficient values with increased rainfall for mortality models. Note that the water deficit variable was square-transformed to account for hump-shaped responses detected in exploratory graphical analyses. (D) Changes in temperature β coefficient values with increased rainfall for mortality models. (E) Changes in plot tree density β coefficient values with increased rainfall for mortality models. (F) Changes in tree diameter β coefficient values with increased rainfall for mortality models. The red dots represent 0–25 quantiles; orange dots, 25–50 quantiles; yellow dots, 0–50 quantiles; green dots, 50–75 quantiles; dark-blue dots, 75–100 quantiles; light-blue dots, 50–100 quantiles; white dots, species of restricted geographical distribution.*

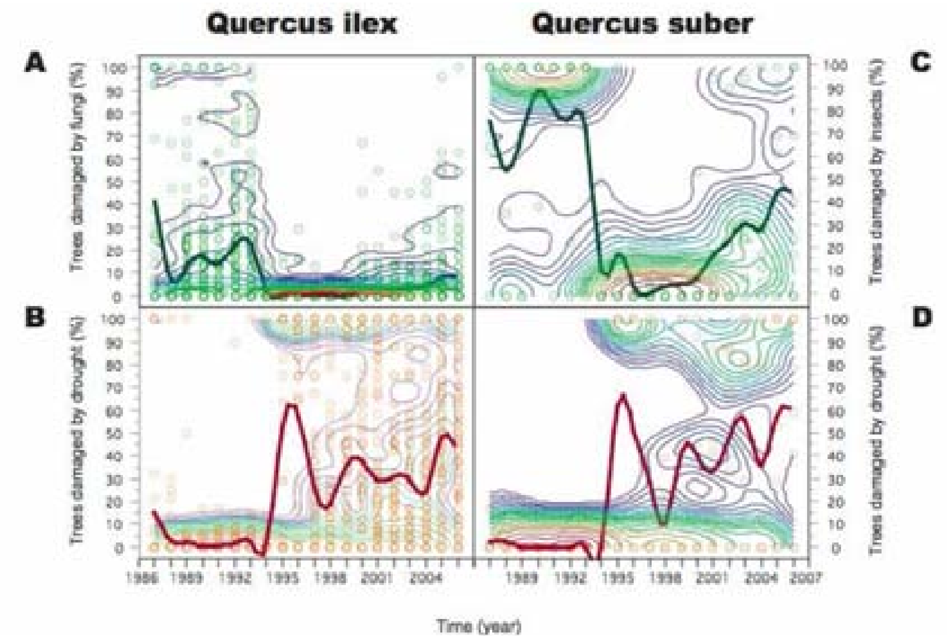

Figure 4. *Shifts in fungal damage and insect damage dynamics associated to drought impacts in Quercus ilex and Quercus suber; (A) Temporal trends in the percentage of Quercus ilex trees affected by fungal defoliation in the Iberian Peninsula; (B) Temporal trends in the percentage of Quercus ilex trees affected by drought; (C) Temporal trends in the percentage of Quercus suber trees affected by insects; (D) Temporal trends in the percentage of Quercus suber trees affected by drought. Dots represent sampled plots. A smooth surface showing the density of sampled plots is provided. Red contour lines indicate maximum point density. Spline fits describing the temporal variation in the percentage of trees affected by insect damage and drought are shown.*

2.5. Discussion

All of the forest tree species that we examined in the Iberian Peninsula have experienced a significant increase in crown defoliation over the last two decades, attributable mainly to the impacts of drought. The observed defoliation trends are consistent with increased tree mortality rates in drier areas and with sudden dynamic changes at higher trophic levels. Our results show that Iberian forests are experiencing long-term chronic effects due to severe climate change–related droughts, and that these effects are progressively more pronounced in more xeric localities.

The reported trends toward increasing defoliation and mortality in southern European forests may have positive and negative effects on the climate system through diverse paths that remain to be quantified more precisely (Bonan 2008, Chapin et al. 2008). For instance, increased crown defoliation in more xeric forested areas might elevate the albedo of defoliated forests and increase sensible heat flux to the atmosphere (Bonan 2008, Rotenberg & Yakir 2010). Widespread crown decline also might reduce the effects of forest evaporative cooling (Bonan 2008), thereby possibly contributing to the reported declining trend of global land evapotranspiration (Jung et al 2010). Notably, the increase in crown defoliation might reduce the evaporative cooling capacity of forests during hot periods and thus have a positive effect on extreme summer heat waves and long-lasting summer drought events (Teuling et al 2010). Moreover, widespread crown condition declines over large areas potentially could alter local or regional convective uplift dynamics and surface roughness effects (Bonan 2008,Rotenberg & Yakir 2010), as well as the production of volatile organic compounds and derived aerosols by forests, thereby possibly affecting the solar radiation balance and cloud formation processes (Peñuelas & Staud 2010).

In terms of chemical cycling dynamics, the trend of increasing defoliation (Fig. 2) suggests that the effects of drought are likely reducing the carbon sink efficiency of southern European forests, thereby contributing to the global reduction in carbon sink efficiency observed in the Northern Hemisphere and at the global scale (Zeng & Qian 2005, Canadell et al. 2007, Ciais et al 2005). These results are in line with the recently reported global reduction in terrestrial net primary production over the last decade (Zhao & Running 2010) and suggest that recurrent severe droughts may directly translate into generalized changes in carbon and nutrient cycling dynamics at the macroecological scale in more xeric Mediterranean areas. Indeed, previous empirical studies assert that severe defoliation events are also associated with increased nutrient cycling through leaf fall losses (Martínez-Alongso et al. 2007). Similarly, water availability has recently been described as a major determinant of terrestrial gross carbon dioxide uptake in Mediterranean and temperate regions (Beer et al 2010). In line with this assertion, European carbon flux anomalies are correlated with water deficit anomalies (Reichstein et al. 2006), terrestrial ecosystems seem to respond to droughts with increased carbon flux to the atmosphere (Reichstein et al. 2007), and dendrochronological studies at the local scale suggest that important geographic areas in the Mediterranean basin are already experiencing chronic drought-induced effects on tree radial growth, growth variability, and crown condition (Andreu et al 2007, Sarris et al 2007). In the same vein, several empirical studies have reported significant associations between crown condition decline and fine root mortality, reduced radial growth, and tree mortality (Dobberting & Brang 2001, Dobryshev et al 2007, Eckmuller & Sterba 2000).

Our present findings add to the increasing number of reports of drought-induced tree mortality responses, regional forest dieoffs, and vegetation shifts around the globe (Allen et al 2010). All of this empirical evidence highlights the need for improved long-term networks devoted to monitoring the impacts of climate change on forest health, functional trait variation, genetic variation, and forest demography (Allen et al 2010). Critically, the diverse physiological mechanisms implicated in the reported defoliation and mortality responses also remain to be elucidated. These may include longdistance phloem transport effects, carbon reserve dynamics, metabolic unbalances, and/or hydraulic failure processes (Sala et al 2010).

Finally, our results demonstrate that extreme droughts can substantially disrupt insect and fungi communities across extensive areas and induce long-term changes in community structure. These findings are consistent with previous studies that have reported 10-fold reductions in arthropod richness and abundance after long-lasting severe droughts and have identified foliage quantity and quality as important drivers of community structure (Trotter et al 2010, Stone et al 2010). Severe persistent droughts produce parallel disruptions in different groups, affecting ecto-mycorrizal fungi (Swaty et al 2004), defoliating fungi, herbivore and predator canopy insects, and parasitoids (Trotter et al 2010, Stone et al 2010). Bottom-up effects on vertebrate trophic chains have been poorly quantified but might occur, given the structural importance of insect resource channels in vertebrate networks in the Mediterranean basin (Carnicer et al 2009, Carnicer et al 2008). Whether large-scale food web disruptions produced by drought can influence the extinction risk of vulnerable insect species and secondary consumers is an open question that warrants further research. This topic may emerge as a relevant concern related to the conservation of currently endangered biotic communities in the Mediterranean basin (Stefanescu et al 2010).

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2.6. Supporting information: Material and methods

2.6.1. Data.

To study defoliation responses in the Iberian Peninsula and Europe we gathered data from ICP-Forests Level 1 network for 1987-2008 (ICP, 2006). European Level 1 network covers most of European forested areas with 6000 monitoring plots. In each Level 1 plot, 24 trees were annually sampled according to standardized procedures (ICP, 2006). Selected trees were predominant, dominant and co-dominant individuals with a minimum height of 60 cm and without significant mechanical damage (ICP, 2006). Annually, a visual evaluation of the defoliation and discoloration of each tree crown was performed. Defoliation was defined as the percentage of needle/leaf loss in the assessable crown as compared to a reference tree, using a sliding scale of 5%. To quantify defoliation, local reference trees were defined as the best tree with full foliage that could grow at this particular site (ICP, 2006). Each sampled tree was visually examined in the field and factors associated with the observed defoliation (vertebrate herbivory, insect herbivory, fungal damage, drought impacts, management impacts and fire damage) were recorded using a code of binary variables (0- damage type absence, 1-damage type presence; Table S1). Additionally, plot information on soil type and humus layer depth was recorded by means of ordinal variables (ICP, 2006). Similarly, tree diameter and density per plot were estimated. Tree density was estimated as the averaged spatial distance of the 24 sampled trees in each plot (ICP, 2006). A list of the tree species analyzed is provided in Table S2.

Mortality data were gathered from the Second and Third Spanish National Forest Inventory (IFN2 and 3), which respectively comprise an extensive network of 51.958 and 81.179 plots of 25 m of radius distributed across all types of forests in Spain. IFN2 field sampling plots were surveyed between 1989 and 1996. IFN3 plots were surveyed between 1997 and 2007. For each plot and species, three mortality measures were quantified: a binomial variable recording mortality presence or absence in a plot, the number of dead trees per hectare, and the percentage of dead trees relative to the total number of trees of the same species. In each IFN plot we also assessed the density of trees (number of trees per hectare with diameter > 7.5 cm) and the mean diameter at breast height in each plot. These variables were calculated both by grouping all species and for each species. Meteorological data for 1951-2006 in Spain were obtained from the Spanish Meteorological Agency (Ninyerola et al 2006, Ninyerola et al 2007). We gathered mean air temperature, minimum air temperature, mean maximum air temperature and rainfall data for each month. The number of meteorological stations increased progressively with time during 1951-2006, ranging from 212 to 1675 stations for temperature variables, and from 620 to 4515 stations for rainfall. Elevation data were obtained from a digital elevation model of 200 m of spatial resolution. Solar global radiation grids were derived from a physical computational model based on relief and the position of the Sun (Pons and Ninyerola 2008).

2.6.2. Climatic maps.

Interpolated climatic maps were derived applying a mixed spatial interpolation method that combines sequentially two interpolation techniques (Ninyerola et al 2006, Ninyerola et al 2007) (Fig. S1). Firstly the method applies a global statistical interpolation (multiple regression) using geographical variables, and subsequently calculates a local interpolation (inverse distance weighted) that uses the residuals of the regression fitting to generate a local anomalies corrector (Ninyerola et al 2006, Ninyerola et al 2007). Altitude, latitude, distance to the coast, solar global radiation and terrain curvature were introduced in the regression models (Ninyerola et al 2006, Ninyerola et al 2007). For each year, we randomly excluded 40% of the stations in order to cross-validate the model fit. To test the fitting we assessed the RMS (root mean square error) obtained for each map (Ninyerola et al 2008, Pons & Ninyerola 2008). The mean RMS for monthly temperature maps (mean, maximum and minimum) was 1.27, 1.72 and 1.73 ℃ respectively, while the mean RMS for monthly rainfall maps was 19 mm.

From 1951 to 2006, we obtained a set of monthly climatic maps for mean air temperature, mean maximum air temperature and rainfall with 200 m of spatial resolution. Monthly rainfall maps were accumulated to obtain annual rainfall maps. Likewise, annual temperature maps were averaged from monthly temperature maps. Using rainfall and temperature data, we calculated the Emberger water deficit index (Gavilán 2005) and mapped their distribution. Emberger water deficit was calculated simply changing the sign of the Pluviometric Quotient of Emberger (Gavilán 2005). Emberger index is considered a useful and suitable index because it accounts for irregular hydrothermic conditions in the Mediterranean basin (Gavilán 2005, Dufour-Dror 2004). We used MiraMon GIS software for all these calculations (Pons, 2009).

2.6.3. Crown defoliation maps.

To describe the spatiotemporal variation of crown defoliation in the Iberian Peninsula and Europe we built crown defoliation maps interpolating data from the Spanish and the European ICP Forests inventories (Fig. S3). The geographical range occupied by each tree species in Spain was derived from the Spanish National Forest Inventory (IFN), which has greater spatial resolution than the ICP-Forests Inventory. Similarly, European ICP-Forests datasets were used to explore latitudinal gradients in averaged defoliation for all species combined. In this case, we used Corine Land Cover 2000 map to define the spatial range of the forested areas in Europe. Crown defoliation maps were interpolated using the same methodologies as in climate data (see previous section). The variables included in the multiple regression models were altitude, latitude, distance to the coast, solar global radiation, terrain curvature, Emberger water deficit index and annual rainfall. The spatial resolution was 200 m and the temporal resolution ranged from 1987 to 2008. Using the same methodology, maps of the percentage of trees affected by different damage types were obtained for each species and year (Figs. S3 and S5).

2.6.4. Hypothesis testing: Crown defoliation.

To assess which ecological and climatic factors were consistently associated with crown defoliation trends we applied a model selection approach (Johnson & Omland, 2004). The statistical analysis was restricted to the 1987-2006 period. The response variable analyzed was the observed percentage of crown defoliation for each sampled tree. To perform the models, we crossed defoliation data with climatic data extracted from interpolated maps for each plot and year (temperature, rainfall and Emberger water deficit). In addition, we introduced in the models plot-specific measures of soil type, humus layer depth, altitude and solar global radiation and field measures of the impact of vertebrate grazing, insect herbivory, fungal damage, drought damage, management and fire (binomial variables recorded for each tree and year) (Table S1).

Many studies report lagged and cumulative effects of climatic factors on drought-induced physiological responses (e.g. defoliation, growth, mortality) during time-periods ranging from several weeks to few years (Vaganov et al 2009, Seidling 2007, Granier et al 2007). Furthermore, some empirical studies suggest that relative climatic variables (i.e. measures of the relative difference between a local climatic record and the long-term average in this locality) might in some cases perform as better predictor variables (Klap et al 2000, Piao et al 2009), presumably because trees are acclimated or adapted to specific local conditions. To screen the relative importance of cumulated and lagged climatic effects, we correlated defoliation with climatic lagged variables (with a lag of 1, 2 and 3 years) and with cumulated climatic variables (averaging for 1, 2 and 3 years). These correlations were calculated for maximum, minimum and mean annual and summer temperatures, annual rainfall, cumulated winter-summer rainfall (January- August) and Emberger water deficit. To account for local responses associated with deviations from long-term local climatic conditions, we calculated a relative Emberger index (REMB), defined as the relative difference of the Emberger index (for year i and census plot j) respect to the long-term mean value of the Emberger index in each plot (57 years mean, 1951-2006):

$$REMB_{i,j} = \frac{emb_{i,j} - mean(emb)_{1951\text{-}2006,j}}{mean(emb)_{1951\text{-}2006,j}}$$

Mean and lagged REMB values for 1, 2 and 3 years were also correlated with crown defoliation. After analyzing all these variables and correlates, we observed that averaged two-year mean summer temperature (June-July-August), and averaged two-year REMB (REMBi,2) presented the highest correlations with crown defoliation. Consequently, these climatic variables were finally selected and introduced in the models as independent variables.

Step function in R package (R Development Core Team 2007) was used to rank the independent variables for each model (according to AIC criteria). We contrasted a battery of modeling approaches (Ordinary Least Squares (OLS), Generalized Linear Models (GLM), Spatial simultaneous autoregressive models (SAR), Generalized Estimating Equations (GEE) and Generalized Linear Mixed Models (GLMM)) using R package (R Development Core Team 2007, Dormann et al 2007). GlmmPQL and lme4 packages in R were applied for the GLMM models, using respectively penalized likelihood (PQL) and Laplace parameter estimation techniques. In GLMM models, plot was introduced as a random factor. Quasipoisson and quasibinomial distributions (for count and proportion data respectively) were applied when significant overdispersion was detected. The degree of spatial autocorrelation in the residuals of the models was assessed both using Moran's I correlograms and plotting spatial maps of the distribution of residuals, following Dormann et al. (Dormann et al 2007). To account for the effects of temporal autocorrelation, GLMM and GEE models with a first order autocorrelative term were applied using corAR1 function in R package (Dormann et al 2007, van Mantgem & Stephenson 2007). Significant spatial and temporal autocorrelation was detected, suggesting the need for accounting for these effects. Cross comparisons of the modeling approaches (with or without spatial or temporal autocorrelation corrections) asserted that the results were robust to the autocorrelative effects (Table S4).

Several empirical studies assert that interactions between the predictor variables examined are likely to occur and may play an important role. For instance, climatic factors (water deficit, temperature, rainfall) can influence insect- and fungus-plant defoliation interactions via effects on the pathogen, the host or both (Havell et al 2002). Similarly, many studies assert that rising drought impacts also increase the recurrence and severity of fires (Schelhaas et al 2003, Pausas 2004), enhance vertebrate herbivory on trees (Zamora et al 2001) and interact with insect herbivory (Trotter et al 2002). To quantitatively assess the importance of these interactions, a supplementary modeling approach was performed accounting for these interactions (Table S5). Species-specific divergent responses to drought have been observed in previous studies (Peñuelas et al 2001, Peñuelas et al 2007). To assess how species differentially responded to temperature and drought impacts in dry and humid localities we divided the dataset in rainfall quantiles and performed an independent modeling analysis in each quartile. The datasets of species with larger number of plots available (N>15 plots) were divided in four quartiles. For species with smaller number of plots (10-15 plots) the dataset was divided in two quantiles. The datasets of species with less than 10 plots were not subdivided (Supplementary Table 2). In each quantile, we performed a GLMM-AR1 model with REMBi,2 and averaged two year summer temperature as independent variables.

2.6.5. Hypothesis testing: Tree mortality

Tree mortality responses were modeled applying generalized linear models with a binomial error distribution, and using mortality presence at the plot level per each species as the response variable. Supplementary analyses were performed using the percentage and the number of dead trees per hectare. Consecutive IFN field surveys were separated by a time lag of ten years, and the date (year) of sampling was variable depending on the plot. Therefore, mortality events in each plot survey cumulatively occurred during the10 year-period separating two consecutive IFN field surveys. Consequently, to assess the effects of climatic variables on mortality during this time period, we calculated for each plot a ten-year average of the climatic variables (Emberger water deficit, temperature and rainfall), using the date of survey to define the 10-year climatic temporal sequence considered. Finally, Emberger water deficit, temperature, plot tree density, and mean plot tree diameter were introduced in the generalized linear models as independent predictor variables. Exploratory graphical analyses showed that mortality and water deficit presented a hump-shaped relationship in many of the species, and therefore a quadratic term for water deficit was introduced in the model selectionprocedure, to fully account for these non-linear relationships. Mortality analyses were first performed for all the dataset (IFN2 & IFN3 grouped). Subsequently, we repeated the analyses for each survey (i.e. IFN2 [1989-1996] and IFN3 [1997-2007]), restricting the analysis to the plots that were surveyed in both inventories (42.230 plots).

2.7. Supplementary tables

Damage type	Description
Vertebrate herbivory	Cervidae, Suidae, Rodentia, birds, domestic animals and other vertebrates.
Insect herbivory	Defoliating insects. Stem, branch, twig, bud and fruit borer insects. Sucking insects, mining insects and gall-makers
Fungi	Needle cast and needle-rust fungi, stem and shoot rusts, dieback and canker fungi, root rot and decay fungi, leaf spot fungi, anthracnose, powdery mildew. Virus damages were also included
Drought and abiotic stress	Drought damage. Also includes secondary stresses derived from frost, hail,snow and wind impacts.
Management	Forest and land management.
Fire	Fire damage

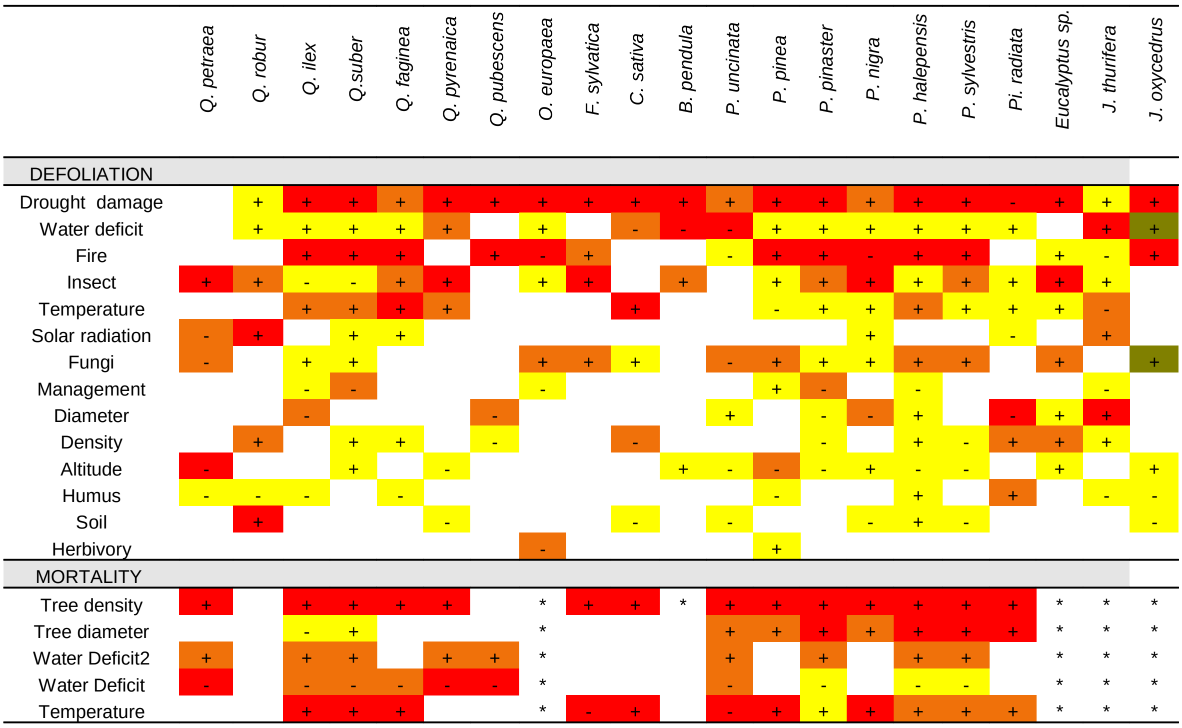
Table S1. *Damage type*

Species	Crown Defoliation and Damage type Maps	GLMM-AR1 Model (All_predictors)	GLMM-AR1 (REMB, Temp) Four Quartiles	GLMM-AR1 (REMB, Temp) Two Quantiles	GLMM-AR1 (REMB, Temp) Without Subgroups	Number of Plots
Abies alba	X					2
Acer campestre	X					4
Betula pendula	X	X			X	7
Castanea sativa	X	X	X			18
Eucalyptus sp	X	X	X			23
Fagus sylvatica	X	X		X		15
Juniperus oxycedrus	X	X	X			19
Juniperus thurifera	X	X	X			20
Olea europaea	X	X			X	5
Pinus halepensis	X	X	X			68
Pinus nigra	X	X	X			59
Pinus pinaster	X	X	X			56
Pinus pinea	X	X	X			19
Pinus radiata	X	X			X	6
Pinus sylvestris	X	X	X			67
Pinus uncinata	X	X			X	9
Quercus faginea	X	X	X			37
Quercus ilex	X	X	X			137
Quercus petraea	X	X			X	6
Quercus pubescens	X	X		X		13
Quercus pyrenaica	X	X	X			35
Quercus robur	X	X	X			24
Quercus suber	X	X	X			25

Table S2. *A summary of the crown defoliation analyses and maps performed for each species. GLMM-AR1: Generalized Linear Mixed model with a first order autocorrelative term (corAR1 function); REMBi2: Two-year averaged relative Emberger water deficit; Temp: averaged two year mean summer temperature.*

Factors Tested	Independent variables	Data source
Drought damage	Damage type binary variable	ICP Forests Inventory
Landscape water deficit	Averaged two-year relative Emberger index (REMBi2)	Spanish National Institute ofMeteorology
Insect damage	Damage type binary variable	ICP Forests Inventory
Fungal damage	Damage type binary variable	ICP Forests Inventory
Fire	Damage type binary variable	ICP Forests Inventory
Forest management	Damage type binary variable	ICP Forests Inventory
Vertebrate herbivory	Damage type binary variable	ICP Forests Inventory
Soil quality	Humus layer depth	ICP Forests Inventory
Soil type	FAO soil type	ICP Forests Inventory
Topography	Altitude Solar radiation	Pons and Ninyerola 2008 (S5)
Temperature	Averaged two-year mean summer temperature	Spanish National Institute of Meteorology
Tree density	Tree density	ICP Forests Inventory
Tree diameter	Mean tree	diameter ICP Forests Inventory

***Table S3**. Independent variables examined in the defoliation modeling analyses.*



	Q. petraea	*Q. robur*	*Q. ilex*	*Q.suber*	*Q. faginea*	*Q. pyrenaica*	*Q. pubescens*	*O. europaea*	*F. sylvatica*	*C. sativa*	*B. pendula*	*P. uncinata*	*P. pinea*	*P. pinaster*	*P. nigra*	*P. halepensis*	*P. sylvestris*	*Pi. radiata*	*Eucalyptus sp.*	*J. thurifera*	*J. oxycedrus*
DEFOLIATION																					
Drought damage		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+
Water deficit		+	+	+	+	+		+		-	-	-	+	+	+	+	+	+		+	+
Fire			+	+	+		+	-	+			-	+	+	-	+	+		+	-	+
Insect	+	+	-	-	+	+		+	+		+		+	+	+	+	+	+	+	+	
Temperature			+	+	+	+				+			-	+	+	+	+	+	+	-	
Solar radiation	-	+		+	+										+			-		+	
Fungi	-		+	+				+	+	+		-	+	+	+	+	+		+		+
Management			-	-				-					+	-		-				-	
Diameter			-				-					+		-	-	+		-	+	+	
Density		+		+	+		-			-				-		+	-	+	+	+	
Altitude	-			+		-					+	-	-	-	+	-	-		+		+
Humus	-	-	-		-								-			+		+		-	-
Soil		+				-				-		-			-	+	-				-
Herbivory								-					+								
MORTALITY																					
Tree density	+		+	+	+	+		*	+	+	*	+	+	+	+	+	+	+	*	*	*
Tree diameter			-	+				*				+	+	+	+	+	+	+	*	*	*
Water Deficit2	+		+	+		+	+	*				+		+		+	+		*	*	*
Water Deficit	-		-	-	-	-	-	*				-		-		-	-		*	*	*
Temperature			+	+	+			*	-	+		-	+	+	+	+	+	+	*	*	*

***Table S4** Effect tests for GLMM-AR1 crown defoliation models and for Generalized Linear Models of mortality. The sign (+/-) and significance (color code) of the test estimates is shown. For illustrative purposes, a different color code has been used to highlight the relative explanatory power of each significant factor. Red=first and second predictors (p<0.0001); orange= third and fourth predictors (p<0.05); yellow= all other significant predictors (p<0.05). GLMM-AR1: Generalized Linear Mixed model with a first order autocorrelative term. To fully account for the observed hump-shaped relationships between mortality and water deficit, a quadratic term was included in the models (Water deficit2). * Species with insufficient or no available mortality data.*

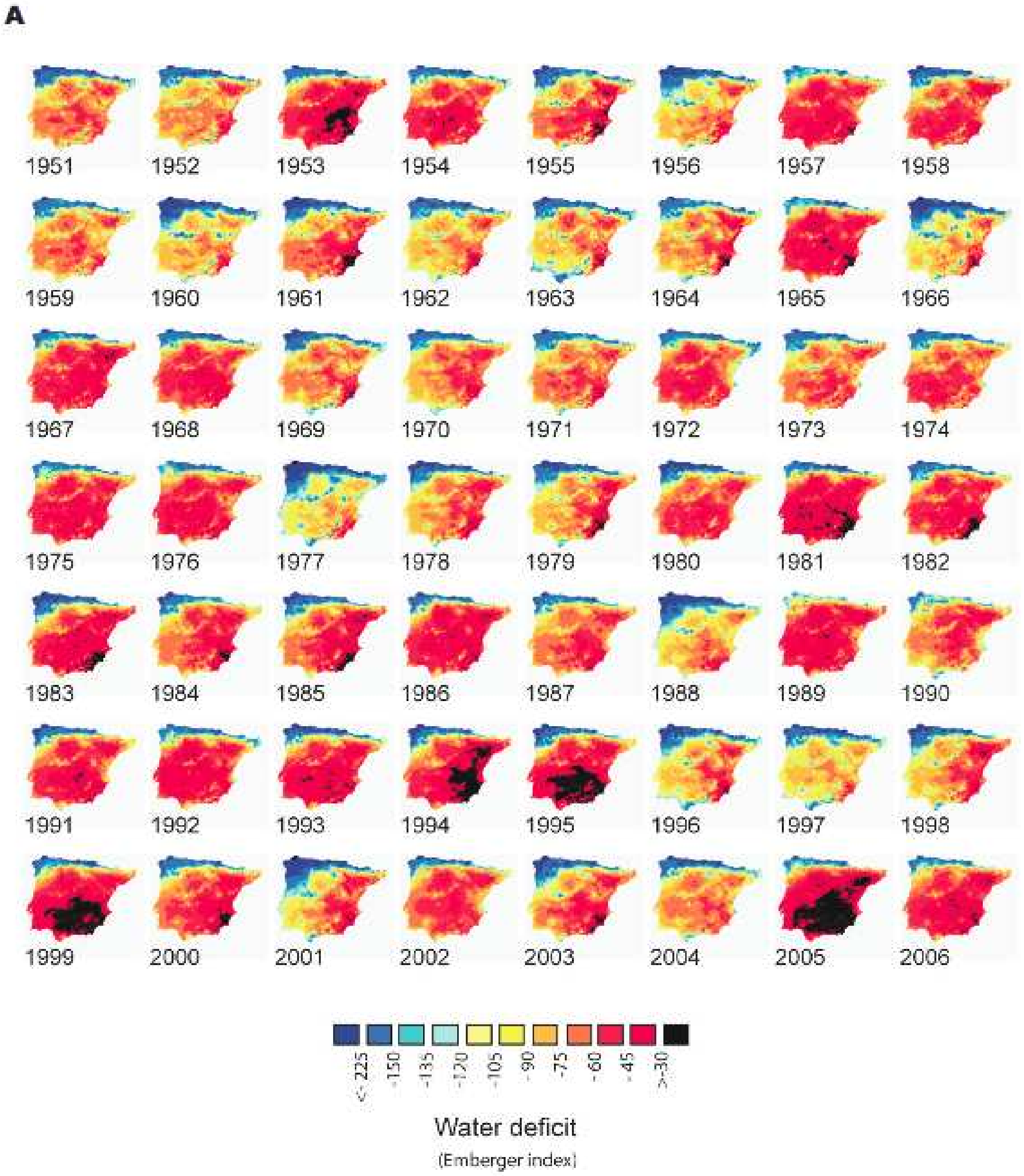
Species	Independent Variables	OLS	GLM	GLMM pql	GLMM Laplace	Spatial SAR	GEE AR1	GLMM AR1
Quercus ilex	Drought damage	+***	+***	+***	+***	+***	+***	+***
	Water deficit	+***	+*	+***	+*	+***	+***	+***
	Fire	+***	+***	+***	+***	+***	+***	+***
	Insect	-***	-***	-***	-***	-***	-***	-***
	Temperature	+***	+**	+***	+**	+*	+***	+***
	Radiation	+*						
	Fungi	+***	+*	+*	+*		+***	+***
	Management	-***	-***	-***	-***		-***	-***
	Diameter	-***	-***	-***	-***	-*	-***	-***
	Density	+*		+*				
	Altitude	-***				-*	-***	
	Herbivory	+**		+***			+**	
	Humus	-***	-*	-***	-*		-***	-***
	Soil	+**					+**	

Table S5. *A comparison of the estimates of the different modeling approaches applied for Quercus ilex defoliation. The sign (+/-) and significance (* p<0.05, ** p<0.01, *** p<0.001) of the test estimates are contrasted. Note that the sign and significance of main predictor variables (Drought, Fire, Landscape water deficit, Insect damage and Tree diameter) is robustly maintained across all modeling approaches.*

	Q. petraea	*Q. robur*	*Q. ilex*	*Q.suber*	*Q. faginea*	*Q. pyrenaica*	*Q. pubescens*	*O. europaea*	*F. sylvatica*	*C. sativa*	*B. pendula*	*P. uncinata*	*P. pinea*	*P. pinaster*	*P. nigra*	*P. halepensis*	*P. sylvestris*	*Pi. radiata*	*Eucalyptus sp.*	*J. thurifera*	*J. oxycedrus*
Water deficit * Herbivory			-	-																+	
Water deficit *Insect	+	-	+		-			+	-	-		-	-	+	-		-	+	-		
Water deficit *Fungi			-	+	-		-	-			+			-	-	-	+	-	+		-
Water deficit *Management		-	+	+		+					+		-	+			-				
Water deficit *Fire			-	+	-	+	+		+				+	-	+	-	+		-		
Water deficit *Diameter	+			-	-	-	-			+		+		-		-	-	-		-	
Water deficit *Density	+	+						+	+				-	+	+	-		+			-
Water deficit *Humus		+	-	+		-	+				+				+	-		-	+		
Water deficit *Soil		-	+						+		+	+		+	+	+				-	
Insect*Temperature		+	+		-	-	-				-	+	-			-		-		-	-
Insect*Diameter	-		+	-		-	+		+		+				-		-	+			
Insect*Density	-	+		-			+		+	+	+		+		+	-	-	-		+	+
Fungi*Temperature		-	+	-		+				-		-	+		-				-	-	
Fungi*Diameter	+		+		-				-							+	+				
Fungi*Density	+				-	-	-		-		-	+			+		-				

Table S6. *Test effects for the GLMM-AR1 crown defoliation models with interactions. The sign (+/-) and significance of the test estimates are shown. Yellow color indicates significant effects with p<0.05. Estimates for single predictors were also included in the model.*

2.8. Supplementary figures



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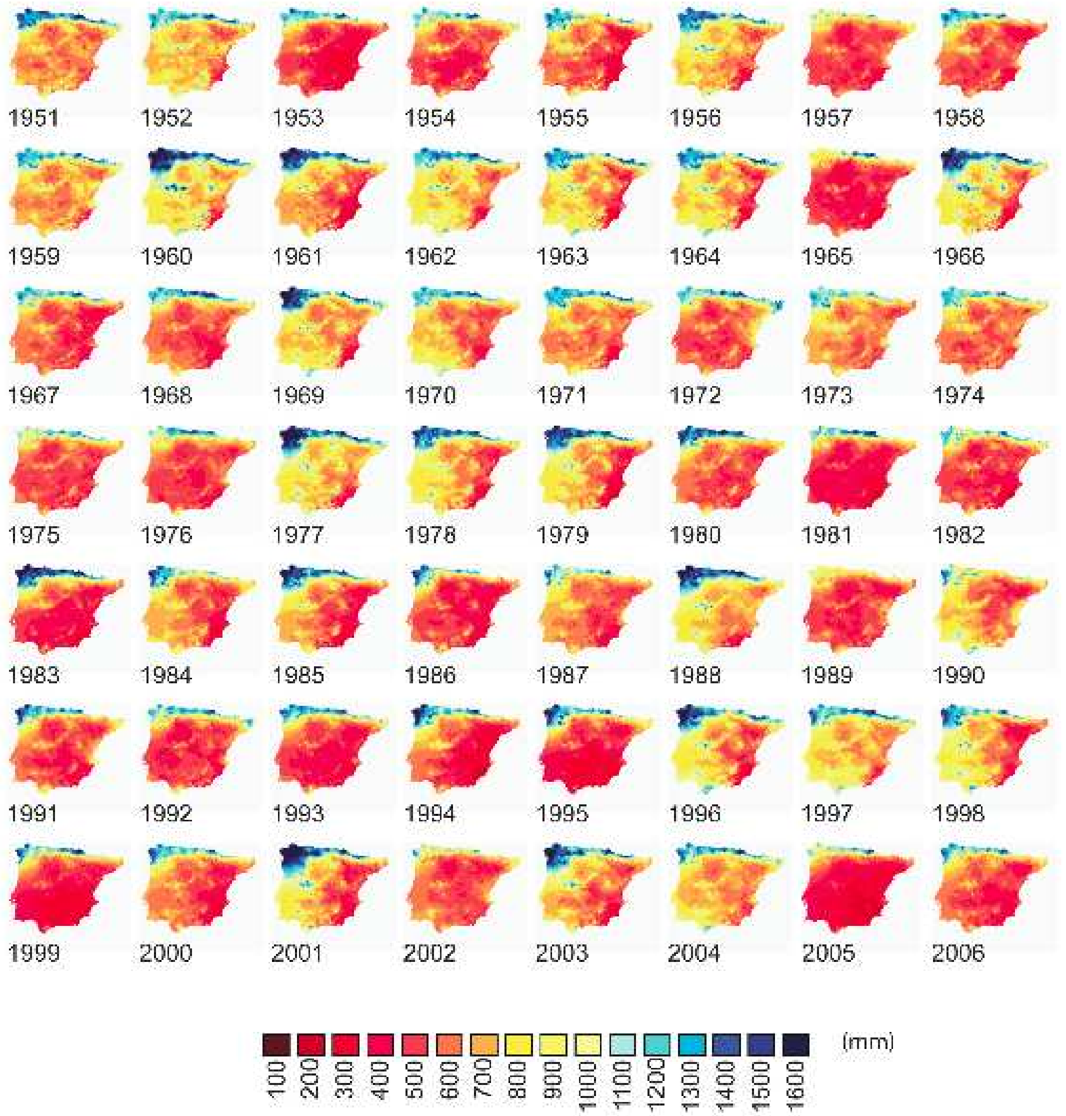
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1999
2000
2001
2002
2003
2004
2005
2006
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
1600
(mm)

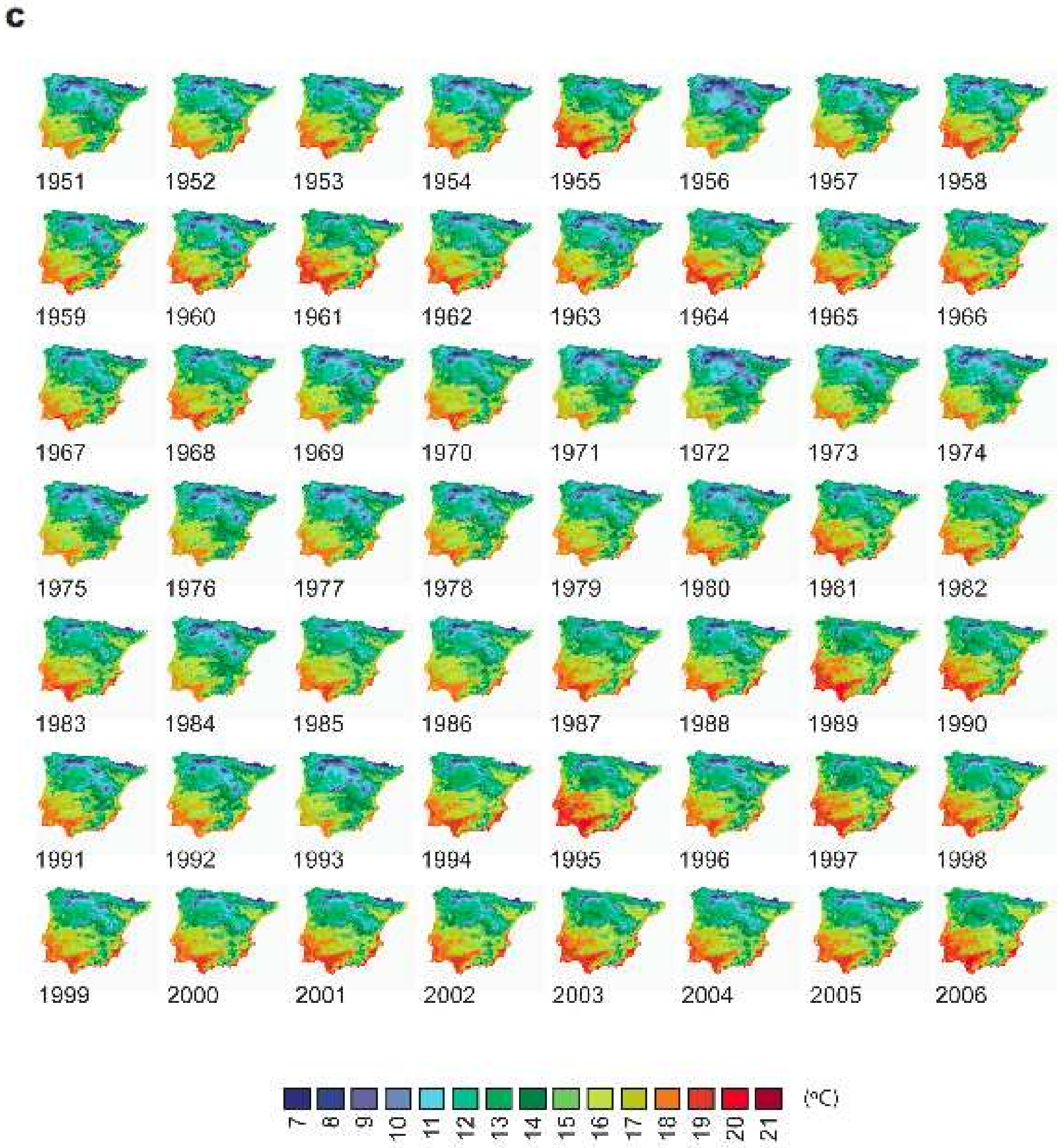


Figure S1. *Annual variation in Emberger water deficit index (A); annual rainfall (B); and annual temperature (C) during 1951-2006 in the Iberian Peninsula.*

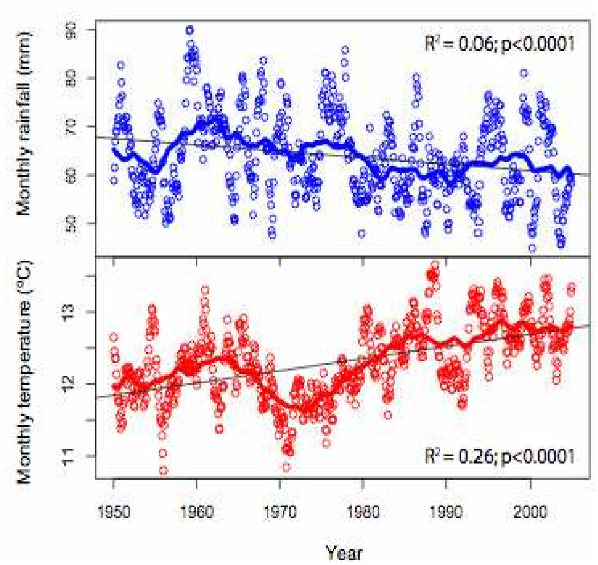
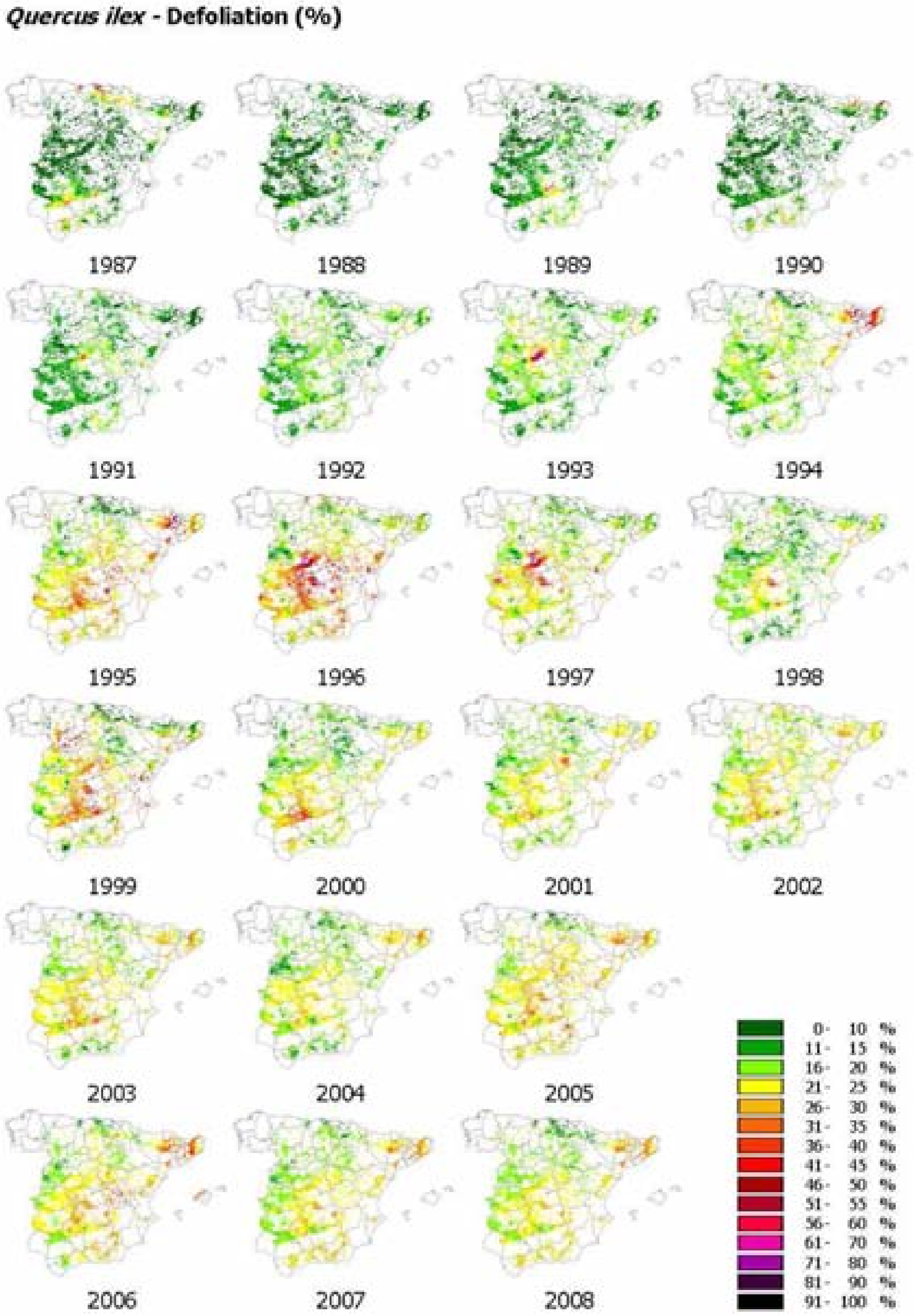
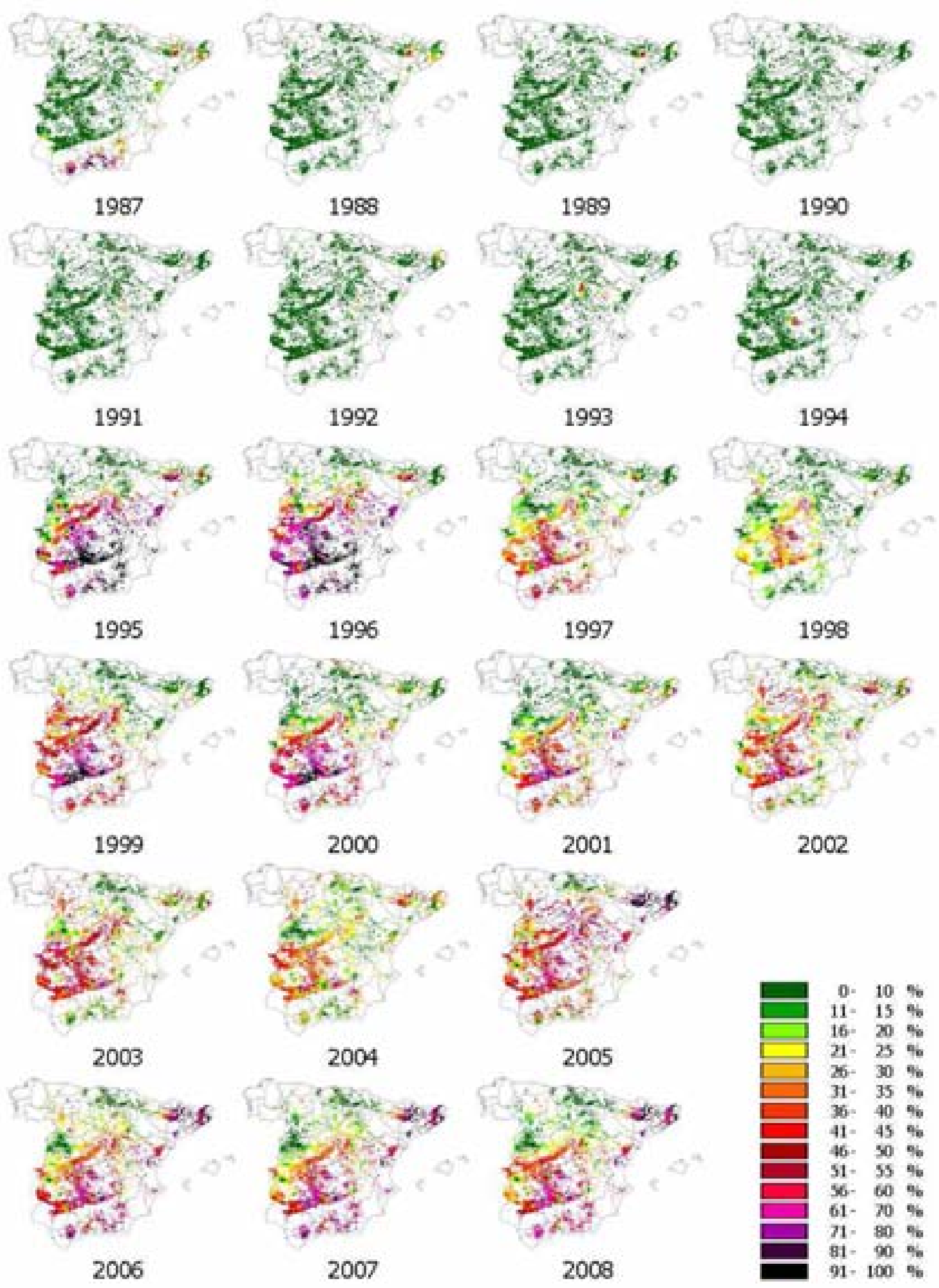


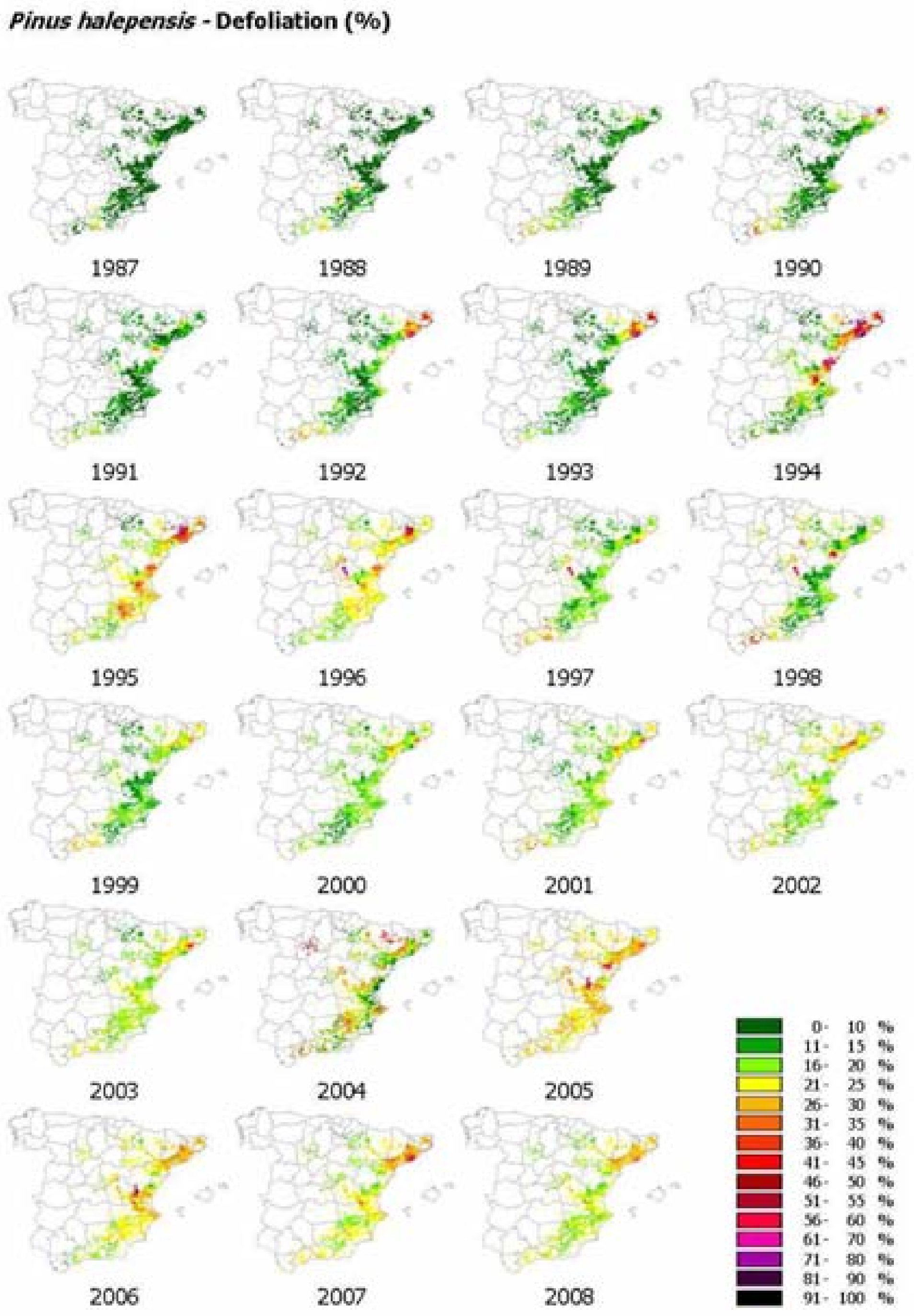
Figure S2. *Linear regression fits (black lines) and kernel smoothing functions (color lines) for one-year smoothed monthly temperature and monthly rainfall data in the sampled plots. The temporal increase of temperature and the decrease in rainfall for 1951-2006 were statistically significant (p<0.0001). Time series analyses (24) indicated a significant trend of increased temperature and reduced rainfall (Rainfall trend estimate (annual decrease of monthly rainfall): -0.13±0.02; t=-6.32; p<0.0001; Temperature trend estimate (annual increase of monthly temperature): 0.017±0.001; t=15.13; p<0.0001)*



Quercus ilex - Defoliation (%)

Quercus ilex **-** Drought (% damaged trees)




Pinus halepensis - Defoliation (%)
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
0- 10 %
11- 15 %
16- 20 %
21- 25 %
26- 30 %
31- 35 %
36- 40 %
41- 45 %
46- 50 %
51- 55 %
56- 60 %
61- 70 %
71- 80 %
81- 90 %
91- 100 %

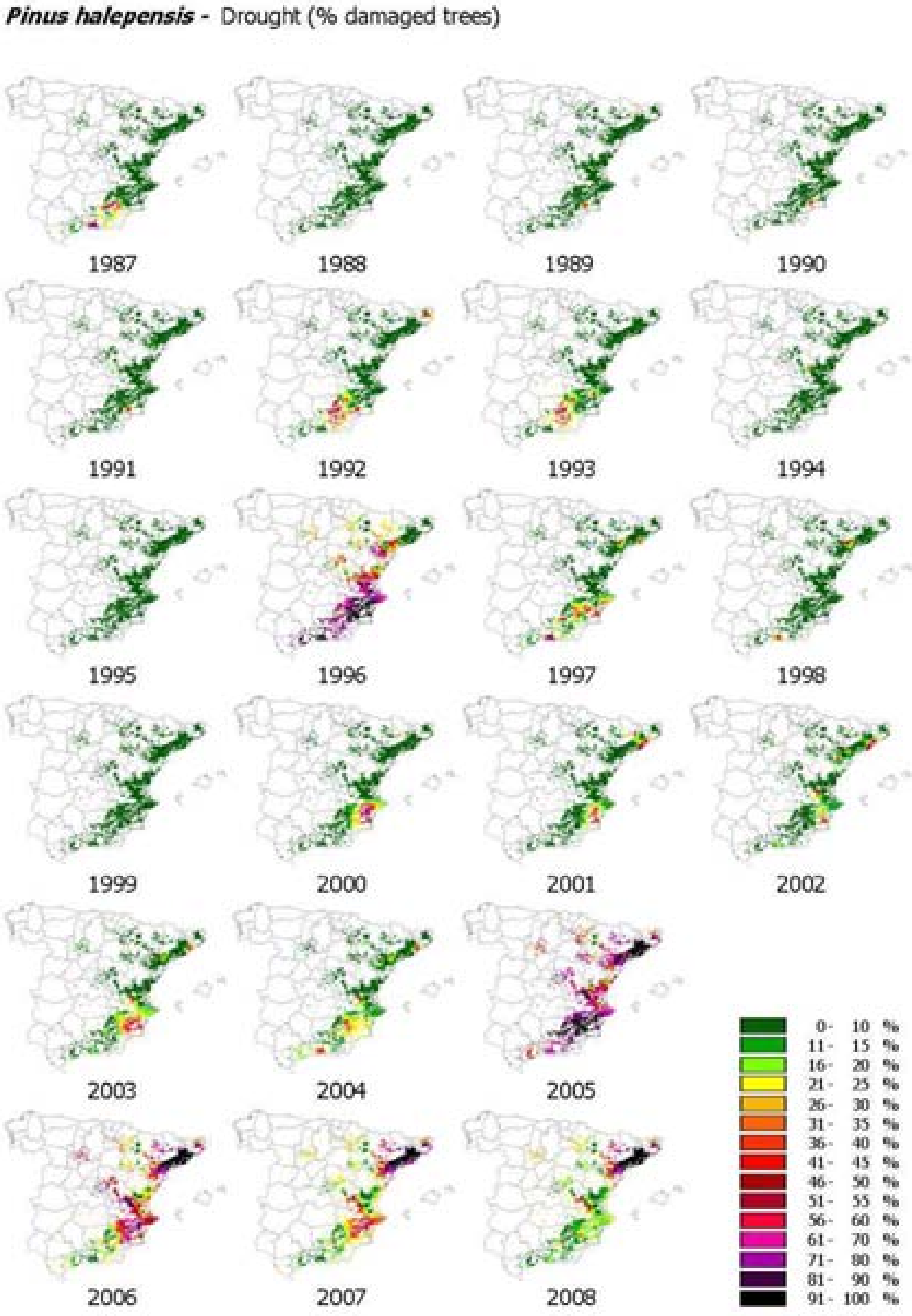


Figure S3. *Maps of the percentage of crown defoliation and drought impacts (percentage of trees affected by drought per plot) for each tree species. Quercus ilex and Pinus halepensis maps are shown as illustrative examples.*

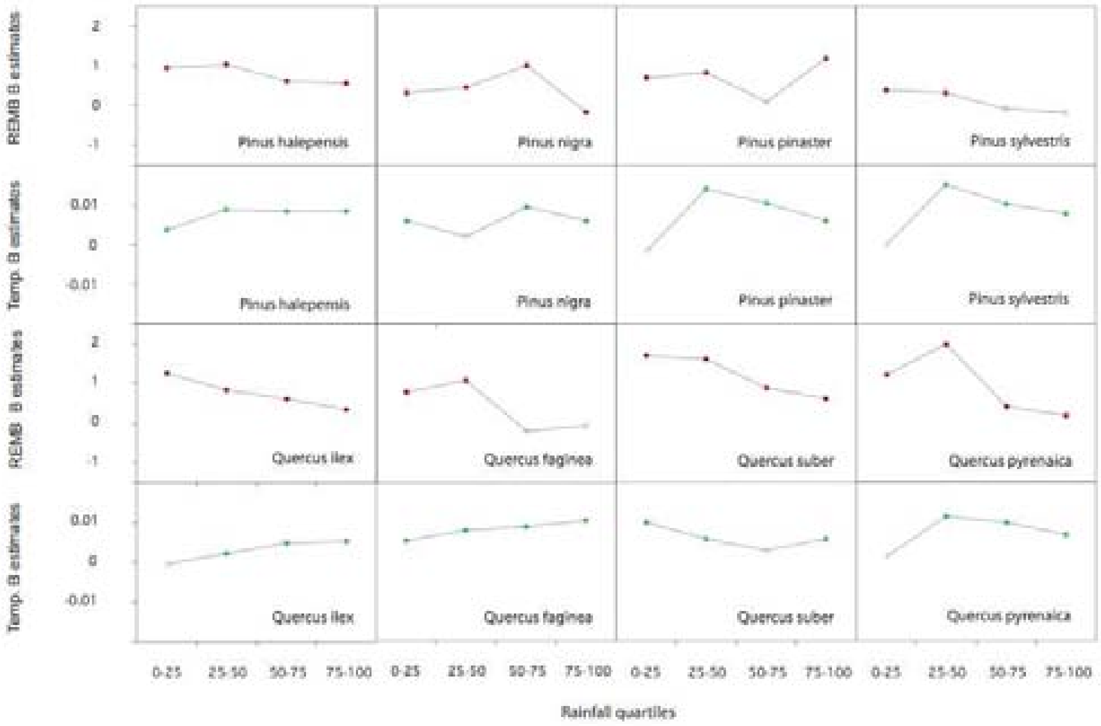


Figure S4. *Observed variation in beta coefficients of GLMM-AR1 models in each rainfall quartile for tree species with large sample size (N plots ≥ 25) (Model: Crown Defoliation = b1 REMBi2 + b2 Temperature). Red dots: Averaged two-year relative Emberger water deficit (REMBi2) beta coefficients; Green dots: averaged two-year summer temperature beta coefficients. Filled dots: significant coefficients. Empty dots: non-significant coefficients.*

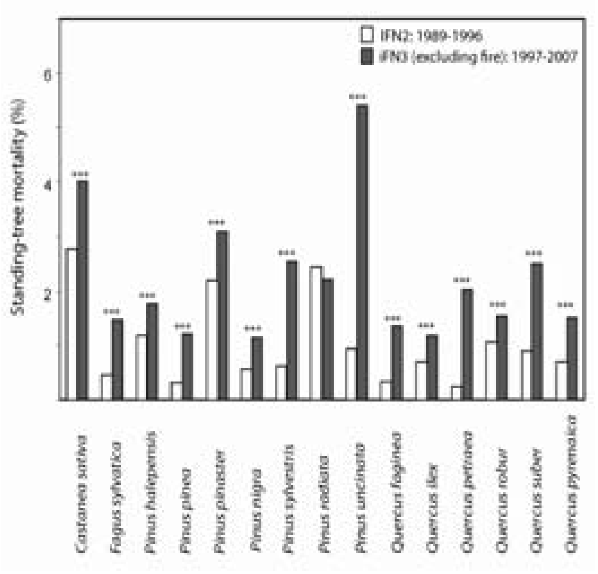


Figure S6. *Observed changes in the mortality rates between the second and third Spanish National Forest Inventories (IFN2 and IFN3). Mortality rates significantly increased in all species with the exception of Pinus radiata (F test, ***p<0.001).*

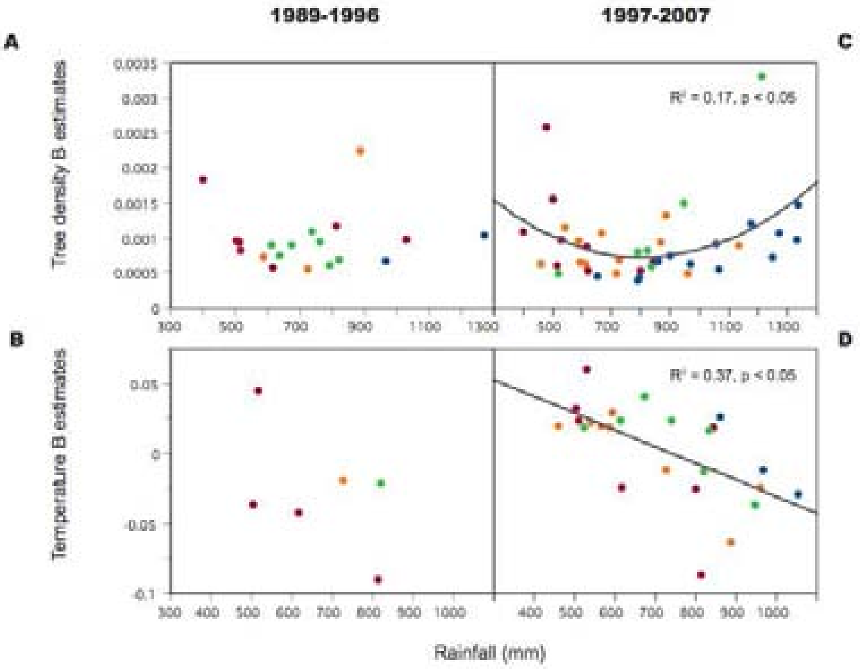
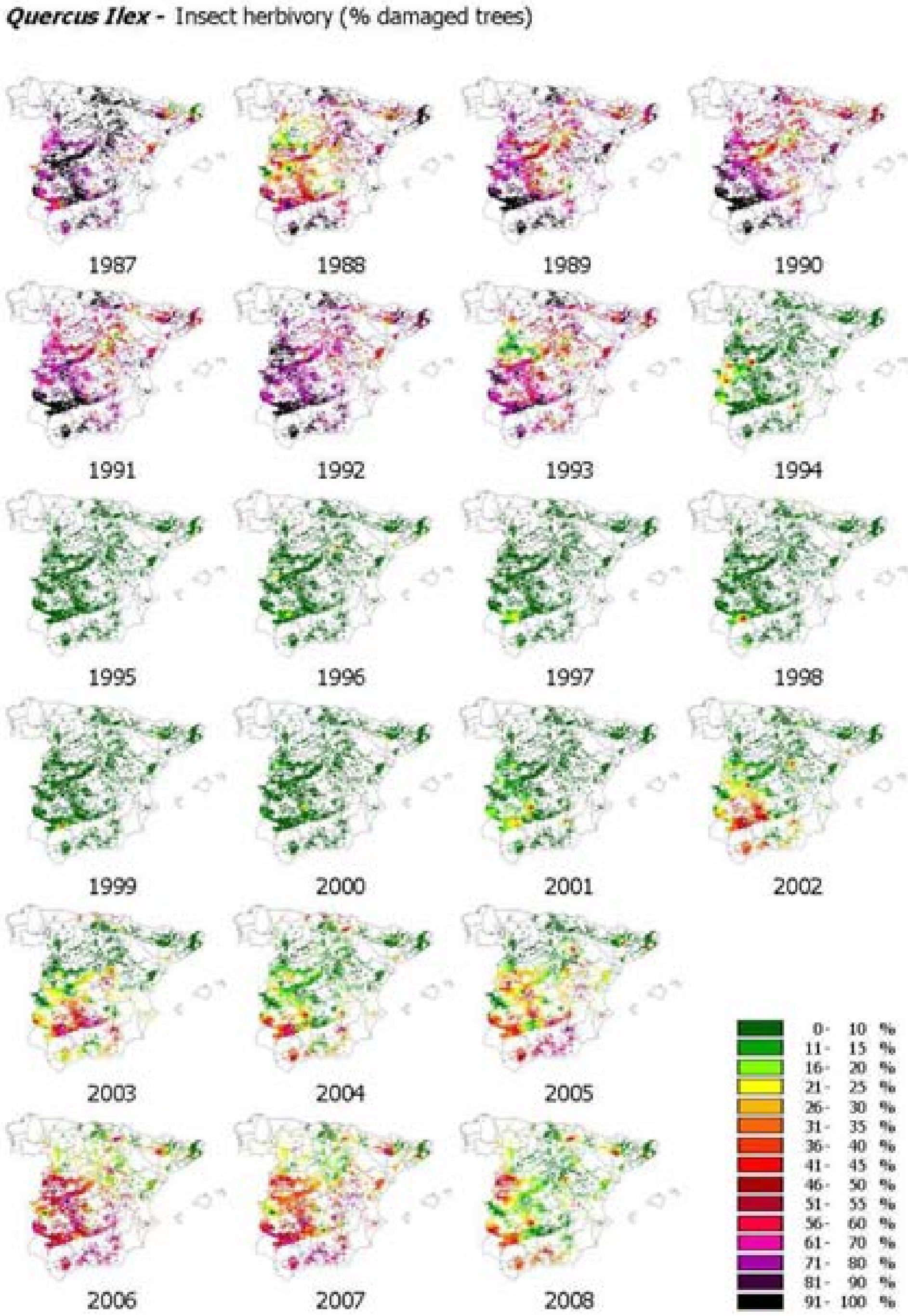


Figure S7. *A comparison of tree density and temperature effects on mortality between the Second Spanish Forest National Inventory (1989-1996, IFN2) and the Third Spanish Forest National Inventory (1997-2007; IFN3). We compared 42.230 plots that were surveyed in both inventories, with a time lag of 10 years between the two consecutive surveys. Mortality was modeled as a function of temperature, water deficit, tree density and tree diameter using Generalized Linear Models per each species and rainfall quartile. (A) Changes in plot tree density beta coefficient values with increased rainfall for mortality models for IFN2; (B) Changes in temperature beta coefficient values with increased rainfall for mortality models for IFN2; (C) Changes in plot tree density beta coefficient values with increased rainfall for mortality models for IFN3; (D) changes in temperature beta coefficient values with increased rainfall for mortality models for IFN3. Red dots: 0-25 quantiles; Orange dots: 25-50 quantiles; Yellow dots: 0-50 quantiles; Green dots: 50-75 quantiles; Dark blue dots: 75-100 quantiles.*


Quercus Ilex - Insect herbivory (% damaged trees)
1987
1988
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1990
1991
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1997
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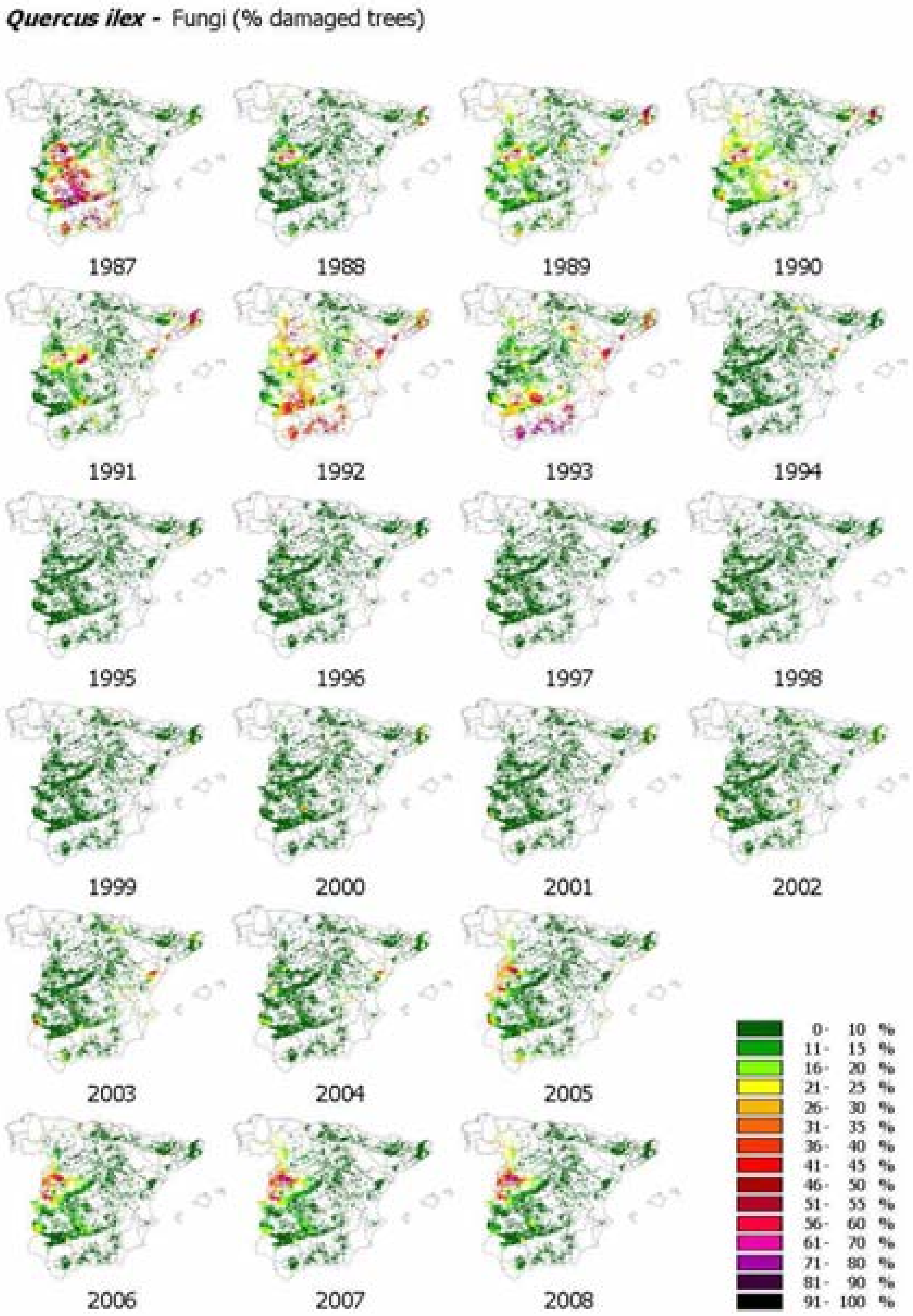
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
0- 10 %
11- 15 %
16- 20 %
21- 25 %
26- 30 %
31- 35 %
36- 40 %
41- 45 %
46- 50 %
51- 55 %
56- 60 %
61- 70 %
71- 80 %
81- 90 %
91- 100 %


Quercus ilex **-** Fungi (% damaged trees)
1987
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1990
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1995
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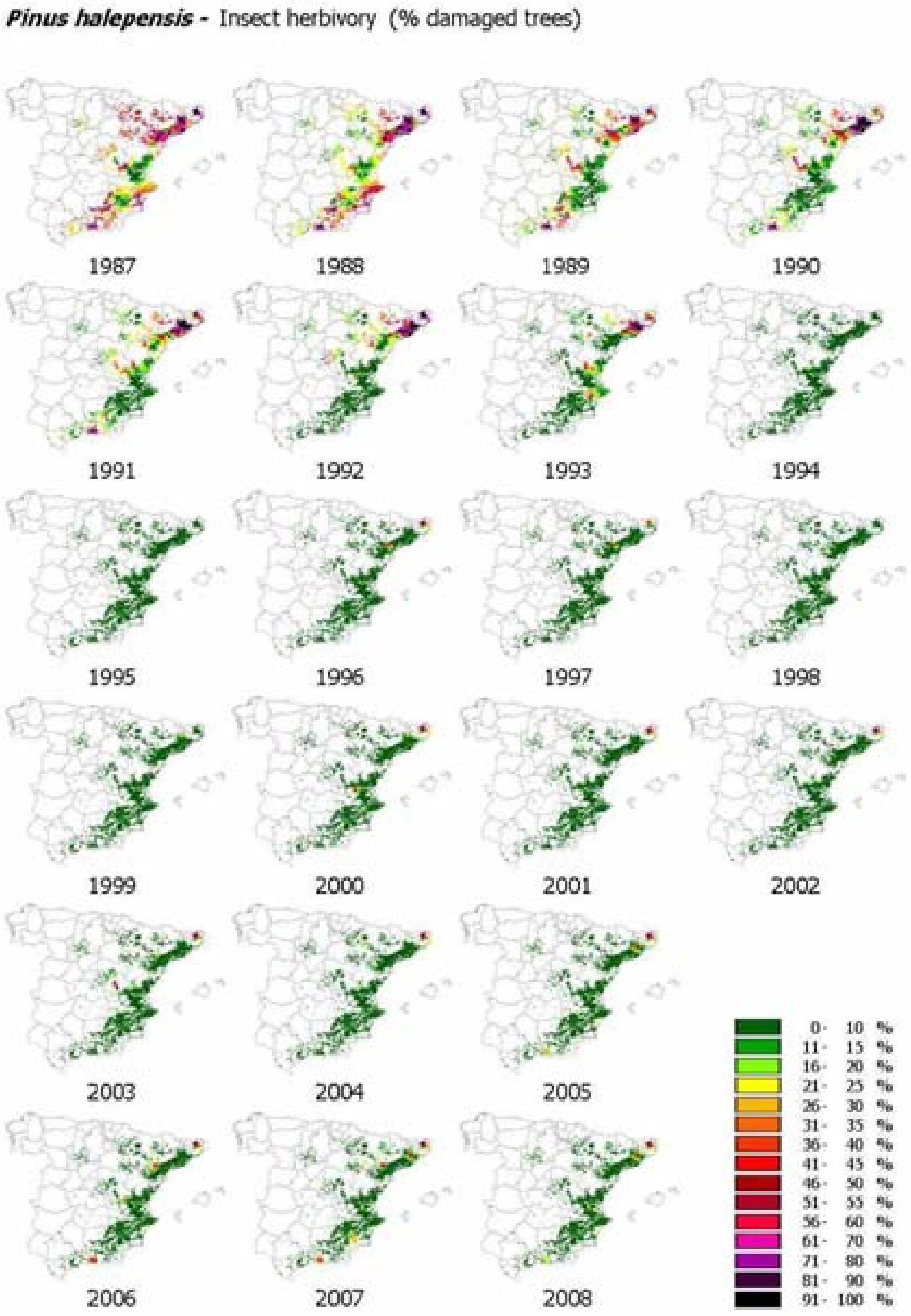
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
0- 10 %
11- 15 %
16- 20 %
21- 25 %
26- 30 %
31- 35 %
36- 40 %
41- 45 %
46- 50 %
51- 55 %
56- 60 %
61- 70 %
71- 80 %
81- 90 %
91- 100 %


Pinus halepensis - Insect herbivory (% damaged trees)
1987
1988
1989
1990
1991
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1996
1997
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1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
0- 10 %
11- 15 %
16- 20 %
21- 25 %
26- 30 %
31- 35 %
36- 40 %
41- 45 %
46- 50 %
51- 55 %
56- 60 %
61- 70 %
71- 80 %
81- 90 %
91- 100 %

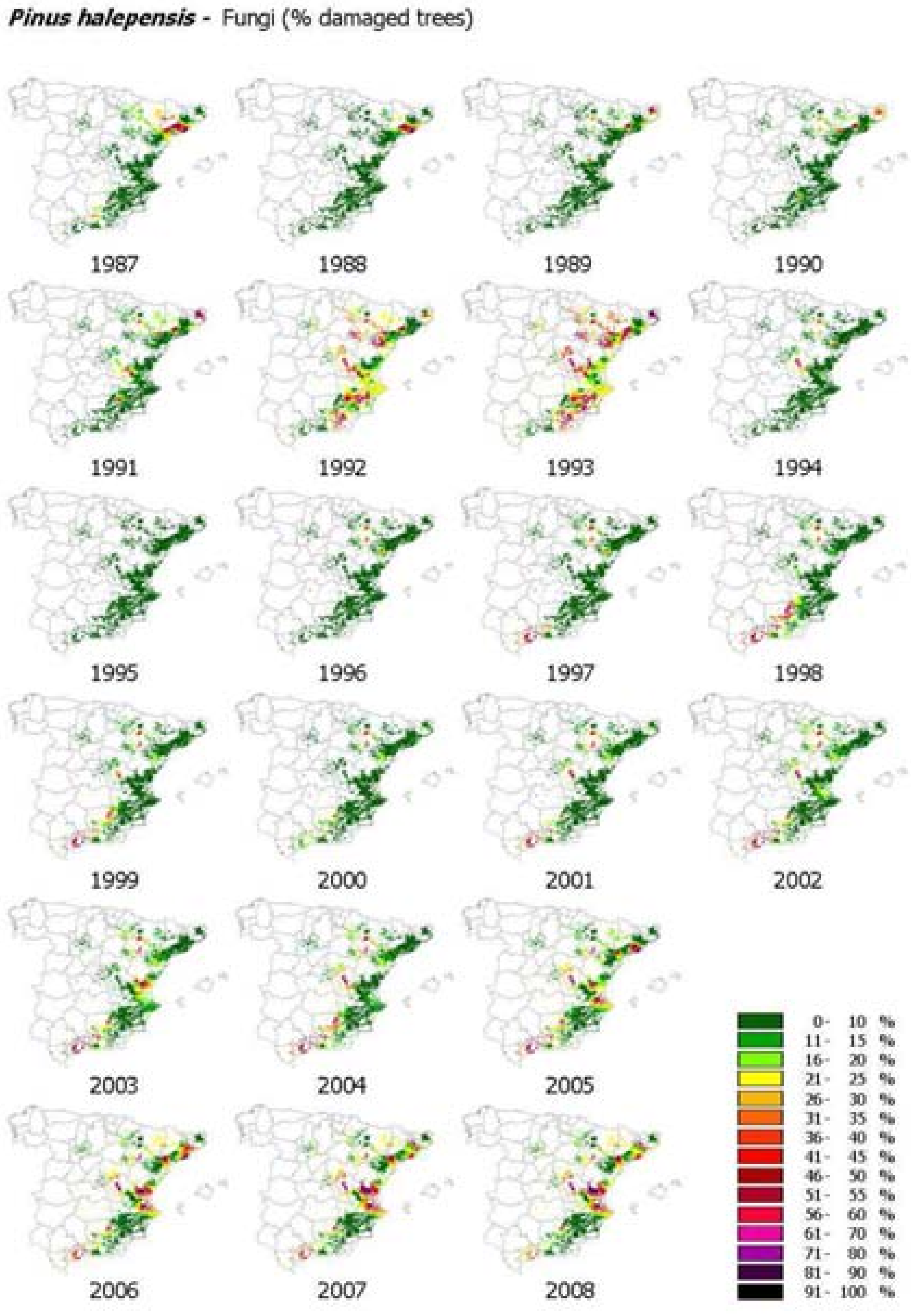

Figure S8. *Maps of the percentage of trees affected by insect and fungal damages for each tree species. Quercus ilex and Pinus halepensis maps are shown as illustrative examples.*

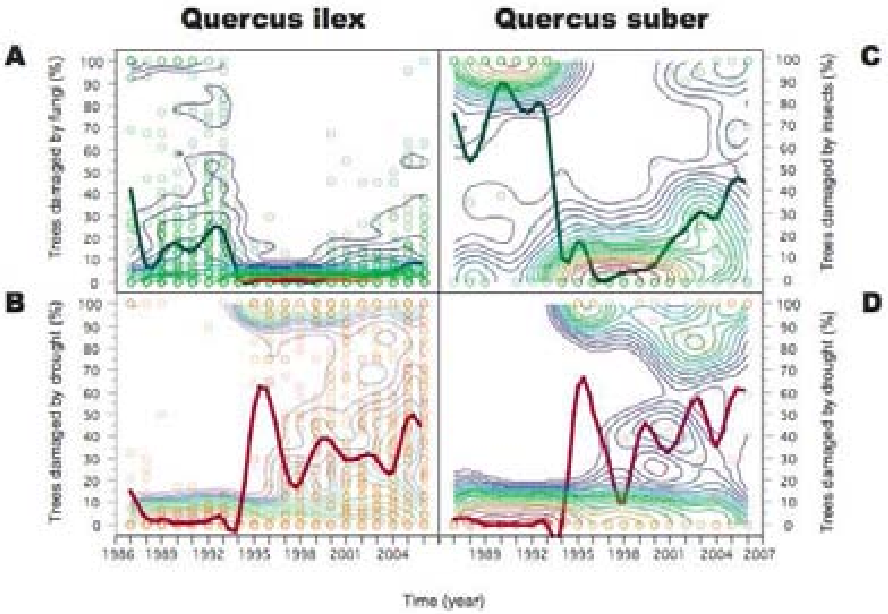

Figure S9. *Shifts in fungal damage and insect damage dynamics associated to drought impacts in Quercus ilex and Quercus suber; (A) Temporal trends in the percentage of Quercus ilex trees affected by fungal defoliation in the Iberian Peninsula; (B) Temporal trends in the percentage of Quercus ilex trees affected by drought; (C) Temporal trends in the percentage of Quercus suber trees affected by insects; (D) Temporal trends in the percentage of Quercus suber trees affected by drought. Dots represent sampled plots. A smooth surface showing the density of sampled plots is provided. Red contour lines indicate maximum point density. Spline fits describing the temporal variation in the percentage of trees affected by insect damage and drought are shown.*

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Chapter 3: Multivariate effect gradients driving forest demographic responses in the Iberian Peninsula

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Coll M., Peñuelas J., Ninyerola M., Pons X., Carnicer J. 2013. Multivariate effect gradients driving forest demographic responses in the Iberian Peninsula. Forest Ecology and Management 303: 195-209.

3.1. Abstract

A precise knowledge of forest demographic gradients in the Mediterranean area is essential to assess future impacts of climate change and extreme drought events. Here we studied the geographical patterns of forest demography variables (tree recruitment, growth and mortality) of the main species in Spain and assessed their multiple ecological drivers (climate, topography, soil, forest stand attributes and tree-specific traits) as well as the geographical variability of their effects and interactions. Quantile modeling analyses allowed a synthetic description of the gradients of multiple covariates influencing forest demography in this area. These multivariate effect gradients showed significantly stronger interactions at the extremes of the rainfall gradient. Remarkably, in all demographic variables, qualitatively different levels of effects and interactions were observed across tree-size classes. In addition, significant differences in demographic responses and effect gradients were also evident between the dominant genus Quercus and Pinus. Quercus species presented significantly higher percentage of plots colonized by new recruits, whereas in Pinus recruitment limitation was significantly higher. Contrasting positive and negative growth responses to temperature were also observed in Quercus and Pinus, respectively. Overall, our results synthesize forest demographic responses across climatic gradients in Spain, and unveil the interactions between driving factors operating in the drier and wetter edges.

3.2. Introduction

During the last decades, climate observations prove the existence of a global warming trend and an increase in the intensity and frequency of drought events in the Northern hemisphere (IPCC, 2007). In the Mediterranean Basin, unprecedented warming and extreme drought events have been reported over the last decades (Xoplaki et al., 2004; Lana et al., 2008). Moreover, future model projections predict the Mediterranean Basin to be largely affected by climate change (IPCC, 2007). By 2100 annual rainfall is expected to drop by up to 20% (up to 50% less in summer), and mean temperatures are expected to increase by 3–4 ºC (Giorgi and Lionello, 2008). Since many Mediterranean ecosystems are already water limited (Boisvenue and Running, 2006), several studies suggest that Mediterranean forests could be highly vulnerable to these future climate changes (Lindner et al., 2010).

Forest responses to climate change will ultimately depend on demographic processes, like recruitment, growth and mortality, which drive plant community dynamics (Clark et al., 2011a,b). Those forest demographical processes depend on local water availability and temperature conditions (Gerten et al., 2008), interacting with species-specific functional traits, phenotypically plastic responses and site-specific conditions (e.g. soil, slope and forest stand attributes) (Linares and Tíscar, 2010; Martínez-Vilalta et al., 2010; Lloret et al., 2012; Carnicer et al., 2011). Several types of interactions among these driving factors may determine future demographic responses in drier areas (Clark et al., 2011b). Firstly, even for forests growing under similar climatic conditions, demographic responses can greatly differ depending on site-specific forest stand attributes, which are often closely linked to both local competition intensity and to management practices (Linares et al., 2009). For instance, in dry environments, competition for water increases with increasing tree density (Linares et al., 2010; Fensham and Fairfax, 2007; Martín-Benito et al., 2007), producing spatial gradients in drought severity that may often not correspond to local climatic gradients (Maestre et al., 2005; Greenwood and Weisberg, 2008; Linares et al., 2010). Secondly, water availability and demographic responses in dry environments are also significantly influenced by local soil and topography (Guarín and Taylor, 2005; Worrall et al., 2008). Thirdly, since tree requirements, functional traits and competitive ability change across different tree life stages, demographic responses to climate are expected to significantly depend on tree age, size and height (He et al., 2005; Ryan et al., 2006; Nabeshima et al., 2010). Fourthly, inter- and intra-specific variability in functional traits can interact with climate factors and significantly affect demographic responses (Martínez-Vilalta et al., 2010). For instance, interspecific differences in ecophysiological strategies to cope with water deficit (e.g. Maherali et al., 2004; Breda et al., 2006; McDowell, 2011) can influence demographic responses to drought and temperature (e.g. Mueller et al., 2005; Allen et al., 2010; McDowell, 2011). Fifthly, within species, functional genetic variation, local adaptation and phenotypically plastic responses may influence tree demographical responses (Limousin et al., 2010; Grivet et al., 2011; Benito-Garzón et al., 2011). Sixthly, insect outbreak dynamics, tree diseases and diverse secondary consumers continuously interact with forest trees, affect their demographic responses, and can significantly interact with drought events (Carnicer et al., 2011; McDowell, 2011). Finally, the western Mediterranean basin has experienced a long history of different land uses, including deforestation and extensive pine afforestation plans (reviewed in Pausas et al. (2004), Blondel et al. (2010) and Ruiz-Benito et al. (2012)). All these historical and recent land uses can largely affect the observed demographic trends (Blondel et al., 2010).

Overall, disentangling and describing the relative contribution to forest demography of this complex network of interacting factors is essential to properly assess future demographic responses to climate change impacts. Indeed, there is a broad consensus that improved large-scale, multi-specific studies assessing all these contributing factors are warranted (Allen et al., 2010; Carnicer et al., 2011). Previous studies showed that quantile modeling analyses can provide synthetic descriptions of the multivariate gradients affecting forest demography at the large scale (e.g. Carnicer et al., 2011). In this direction, we propose to study the spatial patterns of three forest demographic variables (recruitment, tree growth and mortality) in peninsular Spain. Our objectives are: (1) to map and quantify the geographical variation of tree recruitment, growth and mortality of Iberian forests, (2) to apply quantile modeling techniques and synthetically describe the diverse ecological covariates significantly affecting forest demography in the most abundant forest tree species. Specifically, we want to assess the effect of these explanatory variables: (i) climatic and topographic variables (water deficit, temperature, terrain slope); (ii) forest stand attributes (tree density, basal area); (iii) soil properties (organic layer depth); and (iv) individual tree traits (tree diameter, tree height and relative social position in the forest stand). For twenty main forest tree species, we apply quantile modeling techniques (Carnicer et al., 2011), test the significance of these contributing variables, and examine how their effects on demography vary across environmental gradients. Overall, our main aim is to provide a synthetic quantitative description of the complex gradients of interacting covariates that affect forest demographic responses in the Spanish Iberian peninsula.

3.3. Materials and methods

3.3.1. Forest inventory data

The study system comprises all Spanish forested areas which are highly diverse, ranging from semiarid Mediterranean forests, which are strongly limited by water, to more mesic temperate and sub-alpine forests mainly distributed along mountain ranges and Northern localities with increased Atlantic influences.

The forest data were obtained from the Spanish National Forest Inventory (IFN) consisting of a regular grid of circular plots at a density of 1 plot/km^2 (Villaescusa and Diaz, 1998). We gathered data from IFN2 (surveys conducted from 1986 to 1996) and IFN3 (surveys conducted from 1997 to 2007). In each stand, four concentric circular plots (5, 10, 15 and 25 m radius) were designed to survey trees of four different size classes (see Villaescusa and Diaz, 1998). These categories were defined with the diameter at breast height (DBH) as follows: DBH > 7.5 cm (size class 1 [SC1]), DBH > 12.5 (SC2), DBH > 22.5 (SC3) and DBH > 42.5 (SC4). Dead trees were also identified and censused. Recruitment was measured in the IFN3 survey, counting all individuals with DBH < 7.5 cmlocated in the smallest circular plots (5 m). Following IFN methodology, four different recruitment stages were counted: height < 30 cm(recruitment class 1 [R1]), height between 30 and 130 cm (R2), height > 130 cm and DBH < 2.5 cm (R3) and height > 130 cm and DBH > 2.5 cm (R4) (Villaescusa and Diaz, 1998). Among all the tree species growing in the study area, we selected the 20 most abundant species (Abies alba, Castanea sativa, Eucalyptus camaldulensis, Eucalyptus globulus, Juniperus thurifera, Fagus sylvatica, Pinus halepensis, Pinus pinea, Pinus pinaster, Pinus nigra, Pinus sylvestris, Pinus radiata, Pinus uncinata, Quercus faginea, Quercus humilis, Quercus ilex, Quercus petraea, Quercus pyrenaica, Quercus robur, Quercus suber; see Table A1 for further details). Castanea sativa, E. camaldulensis, E. globulus and P. radiata are non-native trees.

3.3.2. Climatic data

The climatic data were obtained from the Climatic Atlas of the Iberian Peninsula (Ninyerola et al., 2007a,b). From 1951 to 2006, we obtained a set of monthly climatic maps for mean air temperature, mean minimum and maximum air temperature and rainfall with 200 m spatial resolution. Climatic maps were obtained applying a mixed spatial interpolation method that combines sequentially two interpolation techniques. Firstly, the method applies a global statistical interpolation (multiple regression) using geographical variables. Subsequently, this method calculates a local interpolation (inverse distance weighted or splines) that uses the residuals of the regression fitting to generate a local anomalies corrector (Ninyerola et al., 2000). Monthly rainfall maps were accumulated to obtain annual and summer rainfall maps (June– August). Likewise, annual and summer temperature maps were averaged from monthly temperature maps. Finally, we derived the Emberger water deficit index (WD; see Carnicer et al., 2011 for a detailed description) from rainfall and temperature maps. Emberger index is considered a useful and suitable index because it accounts for irregular hydrothermic conditions in the Mediterranean basin (Gavilán, 2005).

In each plot consecutive IFN2 and IFN3 surveys were separated by a time lag of 10 years. To obtain a plot-specific measure of the average climatic conditions experienced during this time lag, we calculated a 10-year average for all climatic variables, using plot survey dates to define the time period averaged. Plot-specific averaged 10-year climatic means were calculated for the following variables: Emberger water deficit index, mean annual temperature, mean summer temperature, mean annual rainfall and mean summer rainfall (June–August).

3.3.3. Dependent variables: recruitment, growth and mortality

For the 20 tree species listed on Table 1, recruitment presence was quantified defining a binomial variable (species' absence-presence of recruitment in each plot) for each of the four recruitment classes (R1-R4). Tree growth (G_i) was calculated for each individual tree *i* present at both surveys, using IFN2 and IFN3 data, following Klos *et al.* (2009):

$$G_i = \log\left\lfloor\left(\frac{BA_{i,IFN3} - BA_{i,IFN2}}{DBH_{i,IFN2}}\right) * \frac{1}{T_{lag}}\right\rfloor$$

where BA $_i$ is basal area of tree *i*, and T_{lag} is the time lag (years) between IFN2 and IFN3 measures. Similarly, mortality was evaluated at individual level defining a binomial variable (0/1 for alive and dead individuals, respectively). We considered those individuals that were alive during IFN2 and identified as dead during IFN3. Dead trees due to fire or management were identified and specifically classified using categorical variables.

3.3.4. Independent variables: climatic, topographic, soil, forest stand variables, tree-specific traits

Using IFN data, we quantified soil condition (organic layer depth) and forest stand variables [i.e. total tree density (number of trees/ha) and stand basal area (BAk, summation of the basal area of all trees in the plot k, accounting for sampling area differences between circular plots)] (e.g. Klos et al., 2009). In addition, we also calculated tree density and basal area (BA) for each species and plot (Klos et al., 2009). To account for individual tree specific traits and differences among different life-stages, we gathered data on tree size and tree height (Villaescusa and Diaz, 1998). We also estimated for each individual tree its social position relative to other trees in the stand. Following previous works (Bravo-Oviedo et al., 2006) tree social position (SPi) of a focal tree i was estimated as:

$$SP_i = \frac{DBH_i}{D\bar{B}H_k}$$

where DBHk is the mean diameter at breast height in the k plot. Individual tree traits (tree size, tree height, and tree diameter) were also obtained from IFN data. Finally, a binary variable to account for plantations and dehesa forests (0-forest; 1-plantation or dehesa forest) was defined using IFN data (Villaescusa and Diaz, 1998). Dehesas are agroforestry systems with scattered oak trees defining a savannah-like open tree layer (Joffre et al., 1999). These ecosystems are mainly located in the South Western part of the Iberian Peninsula, covering an area of about 3.5 million ha, and are mainly dominated by Mediterranean evergreen oaks, i.e. holm oak (Q. ilex) and cork oak (Q. suber) (Joffre et al., 1999).

3.3.5. Analyses

3.3.5.a. Geographical patterns of recruitment, growth and mortality

We used descriptive statistics and GIS mapping techniques (Pons, 2009) to describe the geographical variability of recruitment,growth and mortality measures along climatic gradients of rainfall, temperature, water deficit and forest structure gradients (i.e. basal area per plot, tree density, basal area of the species). Due to the key importance of water availability in this area (e.g.Carnicer et al., 2011), we opted to focus on the case study of the rainfall gradient in Section 4. Nevertheless, the analyses for all the other gradients (temperature, water deficit and forest structure gradients) were also implemented and are provided as additional materials (see Supplementary results). To analyze the variation of mean recruitment, growth and mortality across gradients, we divided the environmental variable in 10 quantiles. For each quantile, the mean and standard error of recruitment, growth and mortality was plotted. All these bi-plots were realized for: (1) all species grouped; (2) each tree species; (3) diameter and recruitment classes (all species grouped) and (4) each species and grouping by the four diameters (i.e. SC1–4) and recruitment classes (R1– R4).

3.3.5.b. Statistical analyses

To quantitatively assess the factors significantly associated with recruitment, growth and mortality, we applied a model selection approach, testing a battery of models (see Table 1 for a summary of dependent and independent variables). Firstly, we applied generalized linear models (GLMs) to model recruitment. Presence/absence of recruitment at the plot level was modeled taking a binomial error distribution and logit link function. Secondly, growth and mortality were modeled using individual tree data and including plot as a random covariate in generalized linear mixed models (GLMMs). More precisely, growth was modeled using a normal error distribution and identity link function. Mortality was modeled applying a binomial error distribution and logit link function.

Exploratory statistical analyses for recruitment revealed stronger correlations with summer rainfall and mean annual temperature, while those for growth and mortality revealed stronger correlations with Emberger water deficit index and mean annual temperature. Consequently, for recruitment models we tested the following variables: (i) climate and topography (summer rainfall, mean annual temperature, terrain slope), (ii) forest stand structure (tree density, basal area), (iii) soil (organic layer depth), (iv) species- specific tree density and (v) plantation/dehesa forest. According to Plieninger et al. (2010), species-specific tree density provides an indirect proxy for seed potential input from maternal trees in each plot. In the case of growth and mortality models we assessed these explanatory variables: (i) climate and topography (Emberger water deficit index, mean annual temperature, terrain slope), (ii) forest stand structure (tree density, basal area), (iii) soil (organic layer depth), (iv) individual tree traits (tree height, size (DBHi) and social position) and (v) plantation/dehesa forest. Mortality was expected to decrease with increasing tree-size, and increase again for senescence effects at the oldest tree cohorts (Monserund and Sterba, 1999). To capture this U-shaped pattern, following Monserund and Sterba (1999), we introduced both the inverse tree diameter (DBH1 i) and the squared diameter (DBH2i). Similarly, growth was expected to increase non-linearly with tree size. Following Wykoff (1990) for tree growth models (Gi), we introduced DBH, log(DBHi) and (DBH2i) as independent variables to account for non-linear effects of tree size. Exploratory statistical analyses also highlighted that the relationships between demographic variables and climatic factors were non-linear for many species. Thus, we included in the model selection quadratic effects for climatic variables.

To avoid collinearity effects, pairs of independent variables correlated with r2 values greater than 0.4 were not included together in any model. To account for spatial correlation effects, we performed a supplementary battery of models assessing spatial autocorrelation in the residuals of the statistical models. The degree of spatial autocorrelation in the residuals of the models was assessed using Moran’s I correlograms and plotting spatial maps of the distribution of residuals, following Dormann et al. (2007). To assess the level of significance at each distance class in the Moran’s I correlograms, we computed 1000 permutations using resamp argument in the correlog function (ncf package, R package). When significant autocorrelation in the residuals was detected, we applied spatial statistical modeling methods (spatial GLM and GLMM models) to remove or at least reduce the spatial autocorrelation in the residuals of the models (see Carnicer et al., 2011 for further details).

Dependent Variable	Factors tested	Independent variables
Recruitment	Forest stand structure	Density (Dens) Stand basal area (BA_k)
	Water deficit	Summer rainfall (SR)
	Temperature	Mean annual temperature (T)
	Soil	Humus layer depth
	Topography	Terrain slope
	Species-specific tree density	Tree density (DensSP)
Tree Growth and Mortality	Forest stand structure	Density (Dens) Stand basal area (BA) Basal area of larger trees (BAL_i)
	Water deficit	Emberger water deficit (WD)
	Temperature	Mean annual temperature (T)
	Social positionl	Social position (SP_i)
	Soil condition	Humus layer depth
	Topography	Terrain slope
	Individual tree traits	DBH_i Tree height (HT)

***Table 1**. Ecological factors and independent variables tested*

3.4. Results

3.4.1. Geographical variation of demographic variables, stand forest structure variables and individual tree traits across climatic gradients.

Maps of the geographical variability of recruitment, growth and mortality are shown in Figure 1,2. Spatial gradients on recruitment, growth and mortality along the rainfall gradient are summarized in Figure 3. These results describe significant large-scale gradients in the measured variables across the Iberian Peninsula.

3.4.1.a. Recruitment

A gradient in recruitment success was observed for all species grouped, with significantly increased recruitment success with increasing summer rainfall (Fig. 1a and f; Fig. 2g). The gradient in recruitment success was more marked in large saplings (R3–R4 diameter classes) than in small saplings (R1–R2 diameter classes) (Figs. 2g and B3a). Species-specific trends on recruitment success along climatic gradients were statistically significant in 16 out of 20 species but each species presented an idiosyncratic pattern. For most of the species with significant trends, recruitment success increased with increasing summer rainfall, following positive decelerating functions and hump-shaped functions (Fig. B4). Recruitment gradients significantly differed between the dominant genus Quercus and Pinus, with significantly higher proportion of new recruitment areas in Quercus, and significantly higher proportion of inhabited areas with absence of successful recruitment in Pinus (Fig. B5).

3.4.1.b. Growth

Tree growth per plot (accounting for all tree species) decreased in areas of low water availability, and this pattern was especially notorious in forest stands below 500 mm of mean annual rainfall (Figs. 2e and B3b). Similar and consistent results were obtained in species-specific trends, and reduced growth with increased dryness was also significant in most of the species (Fig. B6). However, species-specific responses of tree growth along climatic gradients (water deficit and temperature) were quite variable, and positive, negative and quadratic relationships were observed (Fig. B6).

3.4.1.c. Mortality

Higher mortalities were observed in more xeric localities (Figs. 2f and B7). Fire-related mortality accounted for an important fraction of the mortality events in the driest edge but showing similar qualitative patterns than when excluded (Fig. 2f, gray and dark line).

3.4.1.d. Forest stand attributes and individual-tree traits

Recruitment, growth and mortality gradients were paralleled by gradients in stand basal area, tree density, tree size (DBH) and tree height. Tree density showed a peak at intermediate rainfall values (Figs. 2 and B8–B9). Basal area, tree height and tree size increased monotonically with rainfall (Figs. 2 and B10). Remarkably, all these gradients emerged by the integration of several species-specific geographically divergent trends (described in detail in Figs. B6 and B11). Finally, a clear geographical gradient was detected also for individual tree traits (tree diameter and height) (Figs. B10 and B11). We observed an increasing height/diameter ratio along the rainfall gradient (Fig. B10). For each tree species, mean values of recruitment, tree density, basal area and growth are provided in Supplementary Tables A2 and A3.

In summary, across the examined rainfall gradient, we observed qualitatively different spatial gradients in all three measured demographic variables. These gradients were in turn paralleled by significant gradients in forest stand density and basal area, tree height and size.

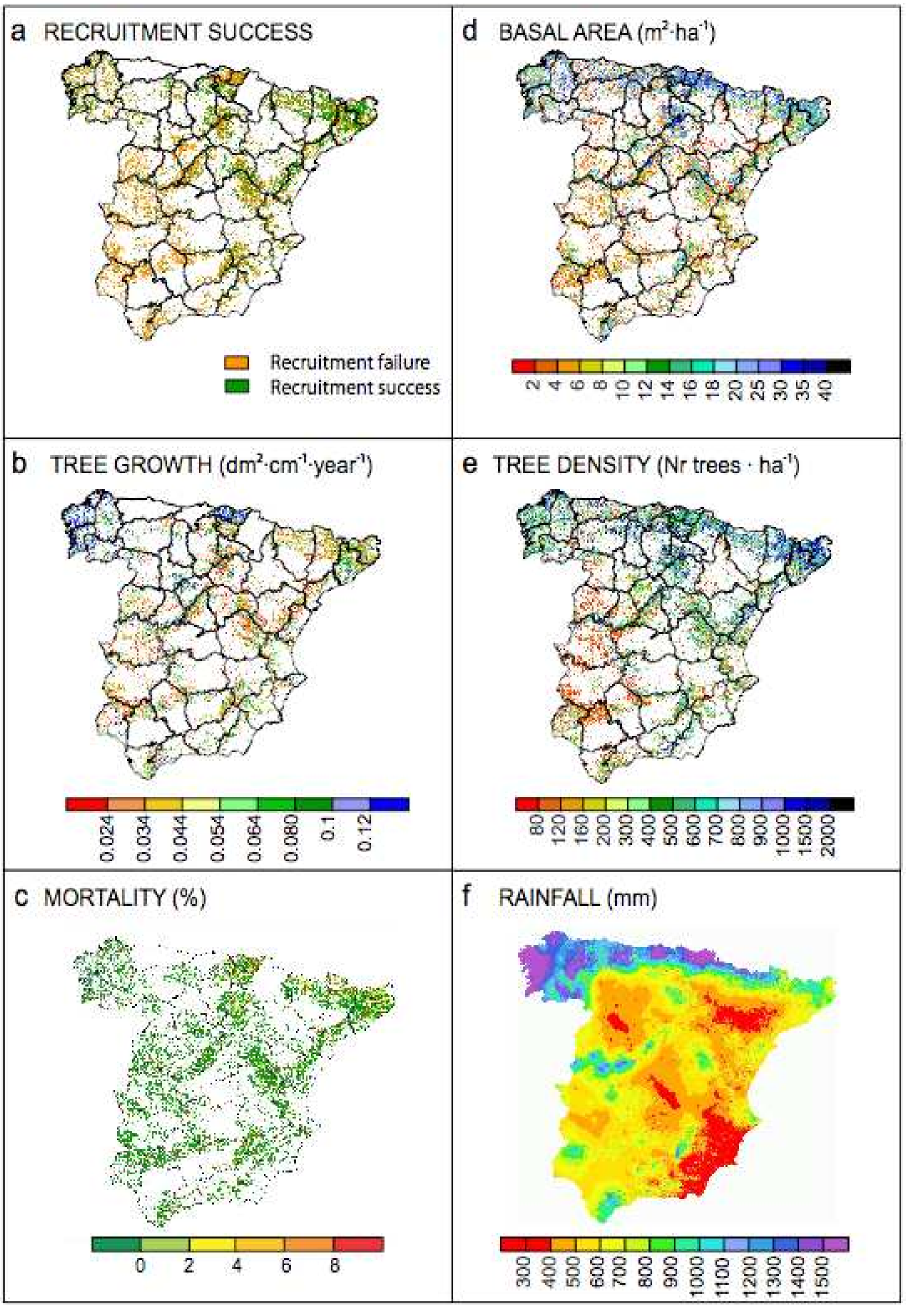


Figure 1. *Geographical variability of recruitment, growth, mortality, tree basal area, tree density and mean annual rainfall in the Iberian peninsula. (a) Geographical variability of recruitment. Recruitment class R4 (Height >130 cm and DBH>2.5 cm) is shown. Green areas show plots were recruitment success was observed for at least one species. Orange areas describe plots were no recruitment was observed for the analyzed species. (b) Geographical variability of mean tree growth. (dm^{2}•cm^{-1}•year^{-1}).. (c) Geographical variability of percentage of dead trees. In this map dead trees due to fire and management are excluded. Calculations are restricted to those trees that died between IFN2 and IFN3 inventories. (d) Geographical variability of Tree basal area (m^{2}·ha^{-1}) in the IFN3 inventory. (e) Geographical variability of Tree density in the IFN3 inventory. (Nr. trees·ha^{-1}) (f) Mean annual rainfall (1950-2006). White areas in panels a, b and c represent missing data*

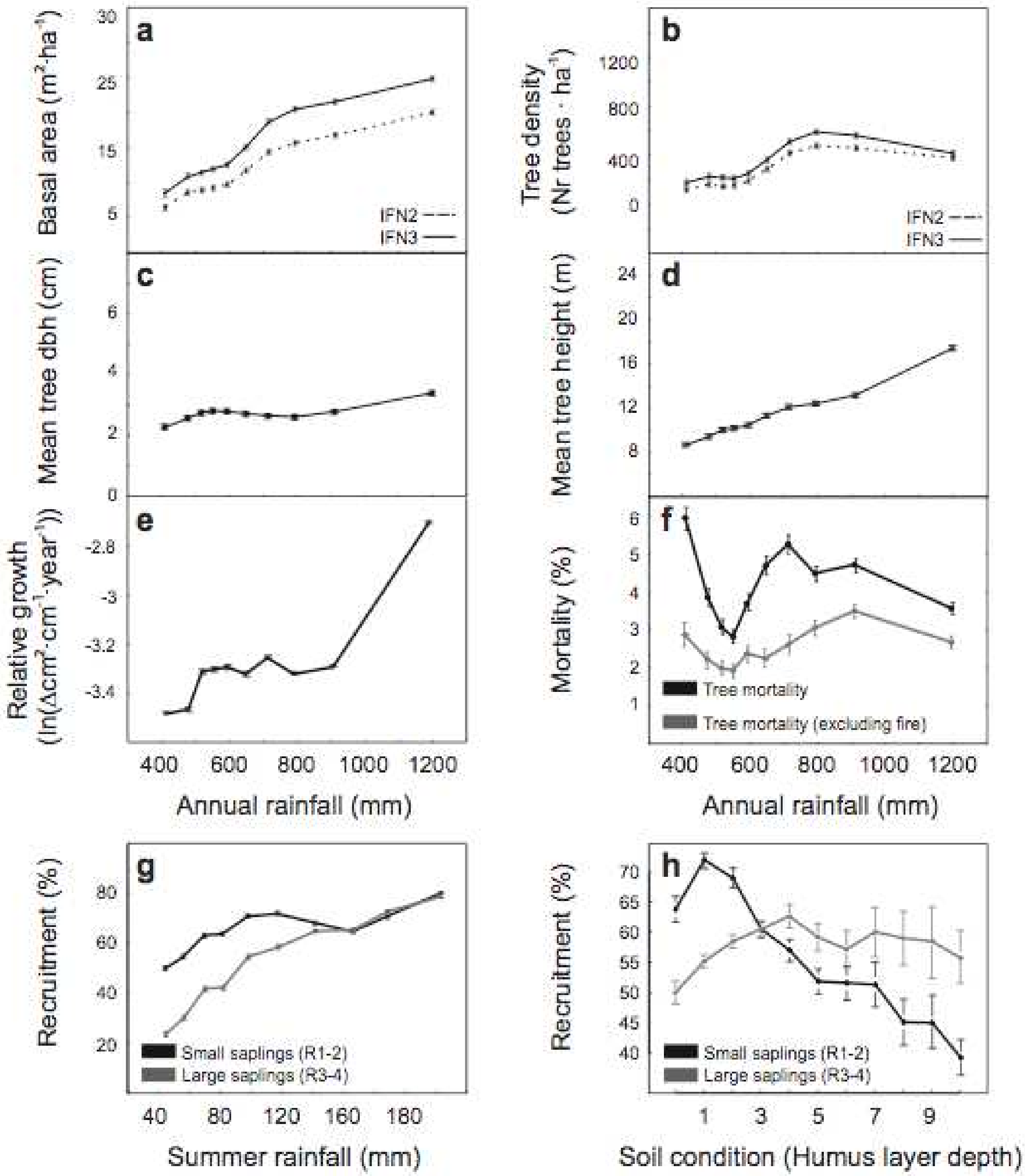
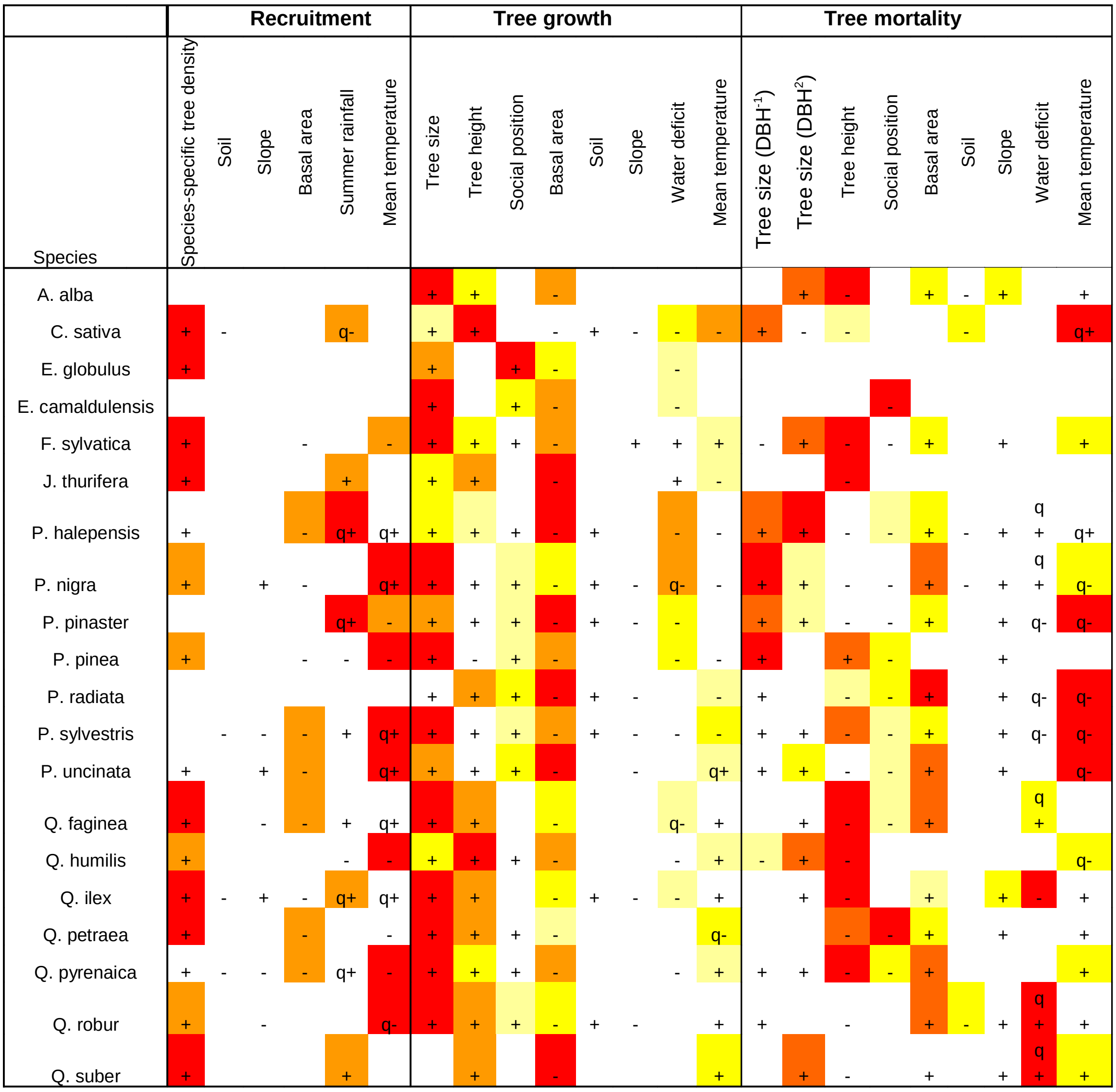


***Figure 2**. Geographic variability of forest stand basal area (a), tree density (b), mean tree DBH (c), mean tree height (d), relative growth (e), percentage of standing mortality (f), recruitment success across the rainfall gradient (g), and recruitment success across the humus layer depth gradient (h). Averages in these variables for all species grouped were calculated for 10 annual rainfall quantiles and represented along the gradient. Standard errors illustrate the observed variation in each quantile.*

3.4.2. Statistical analyses

Table 2 summarizes the model test effects for recruitment, growth and mortality for each species. Below we synthesize the results observed for each dependent variable. Detailed parameter estimates and standard errors for Table 2 are provided in Supplementary Table A8.



	Recruitment						**Tree growth**								**Tree mortality**								
Species	Species-specific tree density	Soil	Slope	Basal area	Summer rainfall	Mean temperature	Tree size	Tree height	Social position	Basal area	Soil	Slope	Water deficit	Mean temperature	Tree size (DBH^{-1})	Tree size (DBH^{2})	Tree height	Social position	Basal area	Soil	Slope	Water deficit	Mean temperature
A. alba							+	+		-						+	-		+	-	+		+
C. sativa	+	-			q-		+	+		-	+	-	-	-	+	-	-			-			q+
E. globulus	+						+		+	-			-										
E. camaldulensis							+		+	-			-					-					
F. sylvatica	+			-		-	+	+	+	-		+	+	+	-	+	-	-	+		+		+
J. thurifera	+				+		+	+		-			+	-			-						
P. halepensis	+			-	q+	q+	+	+	+	-	+		-	-	+	+	-	-	+	-	+	q+	q+
P. nigra	+		+	-		q+	+	+	+	-	+	-	q-	-	+	+	-	-	+	-	+	q+	q-
P. pinaster					q+	-	+	+	+	-	+	-	-		+	+	-	-	+		+	q-	q-
P. pinea	+			-	-	-	+	-	+	-			-	-	+		+	-			+		
P. radiata							+	+	+	-	+	-		-	+		-	-	+		+	q-	q-
P. sylvestris		-	-	-	+	q+	+	+	+	-	+	-	-	-	+	+	-	-	+		+	q-	q-
P. uncinata	+		+	-		q+	+	+	+	-		-		q+	+	+	-	-	+		+		q-
Q. faginea	+		-	-	+	q+	+	+		-			q-	+		+	-	-	+			q+	
Q. humilis	+				-	-	+	+	+	-			-	+	-	+	-						q-
Q. ilex	+	-	+	-	q+	q+	+	+		-	+	-	-	+		+	-		+		+	-	+
Q. petraea	+			-		-	+	+	+	-				q-			-	-	+		+		+
Q. pyrenaica	+	-	-	-	q+	-	+	+	+	-			-	+	+	+	-	-	+				+
Q. robur	+		-			q-	+	+	+	-	+	-		+	+		-		+	-	+	q+	+
Q. suber	+				+			+		-				+		+	-		+		+	q+	+

Table 2. *Summary of the effects tests observed for recruitment, growth and mortality models for each tree species. The sign (+/-) and significance (color code) of the test estimates is shown. For illustrative purposes, a different color code has been used to highlight the relative explanatory power of each significant factor. Red=first and second predictors (p<0.0001); orange= third and fourth predictors (p<0.05); yellow= all other significant predictors (p<0.05). q+ indicates positive, hump-shaped relationships in temperature effects. q- indicate negative, U-shaped relationships in temperature effects.*

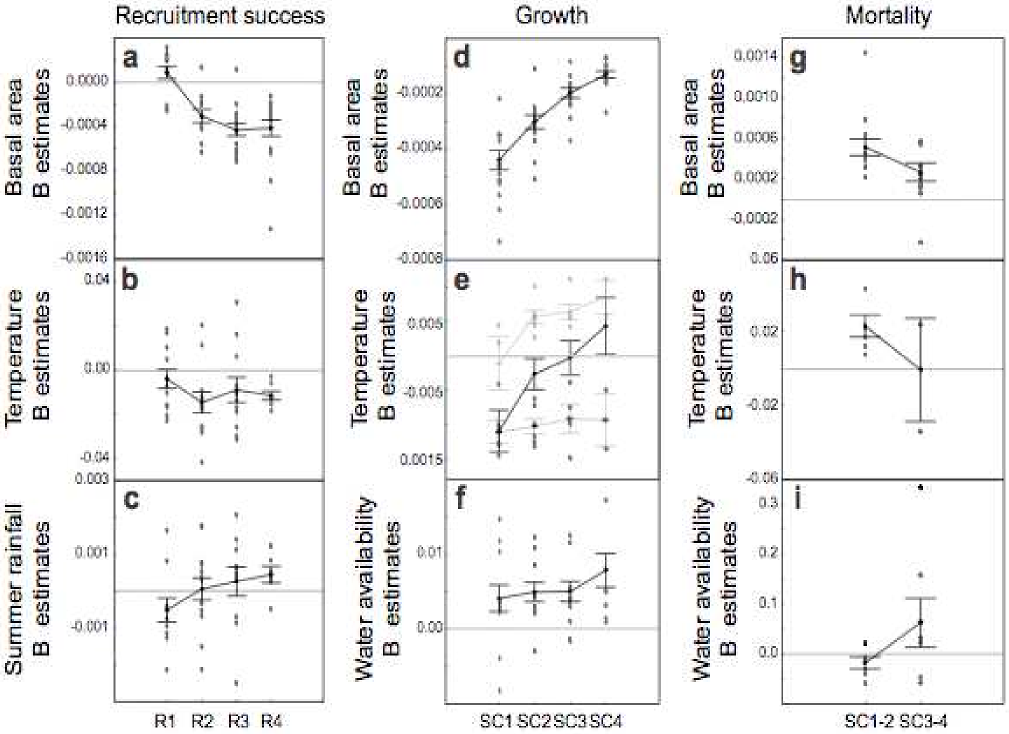


Figure 3. *Variation of Beta estimates for the size-specific models of recruitment, growth and mortality. Independent variables tested are labelled in the Y axis. In panel e, dark grey lines indicate the observed estimates calculated for the subgroup of Pinus species and light grey lines indicates the observed trends in the subgroup of Quercus species. For illustrative purposes and to facilitate interpretation Emberger water deficit is plotted as water availability (i.e. the negative transformation of Emberger; - WD).*

3.4.2.a. Recruitment

Adult tree density of the recruiting species, i.e. ‘‘species-specific tree density’’, was the most important determinant of local recruitment variation (Table 2). In addition, climatic variables (water deficit and temperature) and negative effects of forest basal area performed as complementary explanatory variables. Grouping by recruitment size classes, clear differences were observed in the effects tests: negative effects of stand basal area increased significantly and progressively from small (R1 [<30 cm height]) to big saplings (R4 [>130 cm height]) (Fig. 3a). In addition, positive effects of summer rainfall were more pronounced in larger saplings [>130 cm height; R3 and R4] (Fig. 3c).

Quantile modeling allowed us to disentangle the geographic variation of effect tests along rainfall gradients. Although we observed a variety of species-specific idiosyncratic responses, we found populations growing in the most xeric parts to be positively affected by summer rainfall, in all recruitment size classes (Figs. 4A and B12). Moreover, in the smaller recruits, we observed significant geographic gradients in the negative effects of organic layer depth and in the positive effects species-specific tree density (Fig. 4c and e). In line with these findings, a significant gradient of recruitment success was observed with increased organic layer depth (Fig. 2h), characterized by qualitatively different responses in different sapling size classes. In addition, remarkable significant differences between small (R1–R2) and large saplings (R3–R4) were observed in the effect-gradients of basal area, soil, speciesspecific tree density and summer rain (Figs. 3 and 4).

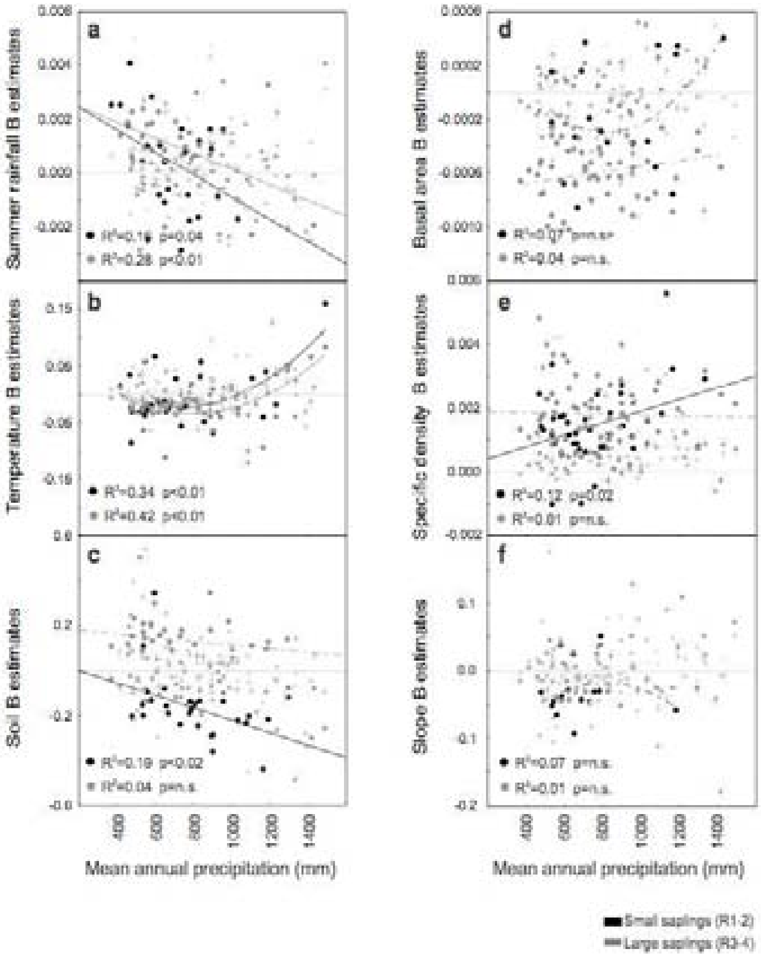


Figure 4. *Geographical variability in the effects (β coefficient values) on recruitment of summer rainfall (a), temperature (b), humus layer depth (c), basal area (d), species-specific density (e) and terrain slope (f) (quantile modelling, Q20). We divided each species in five rainfall quantiles and recruitment was independently modelled for each one. Small (R1-R2) and large (R3-R4) saplings were independently modeled. β estimates for all tree species and quantiles were plotted.*

3.4.2.b. Growth

Tree size, tree height, forest stand basal area and social position appeared as the best predictors of tree growth variation, and significant effects of climatic variables (water deficit and temperature), soil and terrain slope were also detected (Table 2). Quantile modeling results indicated significant geographical gradients in the effects of the examined variables. Hence, we

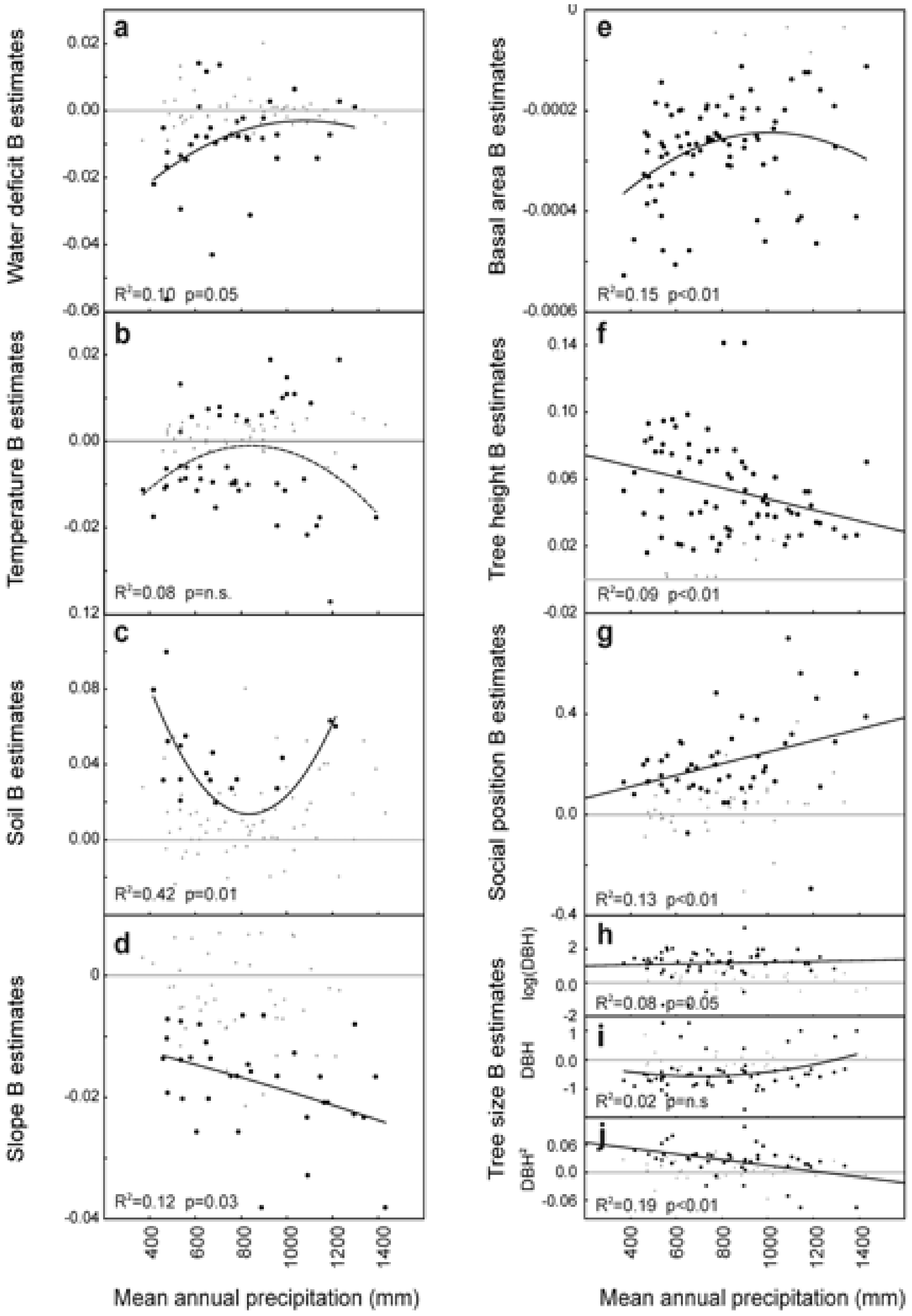


Figure 5. Geographical variability in the effects (β coefficient values) on tree growth of water deficit (a), temperature (b), soil quality (c), terrain slope (d), stand basal area (e), tree height (f), social position (g) and size (h-j) (quantile modelling, Q20). We divided each species in five rainfall quantiles and growth was independently modelled for each one. Solid dots represent significant β coefficient values and non-solid dots represent non-significant β coefficient values.

observed a significant geographical variation in the effects water deficit, organic layer depth, terrain slope, stand basal area, tree height and social position (Figs. 5 and B13). After grouping for size classes, the effects of climatic variables, tree height and stand basal area became more evident. The observed gradients were consistent across tree-size classes, but some differences emerged. Hence, we observed increased negative effects of total stand basal area in smaller size classes. In contrast in bigger trees we observed increased positive effects of tree height and more negative effects of terrain slope in larger trees (Table A4 and Fig. B14). Interestingly, the size-specific effects of climatic variables on growth were qualitatively different in the two most dominant genus (Quercus and Pinus) (Table A4 and Fig. B15). Positive effects of temperature predominated in the genus Quercus and negative effects were predominant in Pinus. Plot (included as random covariate) absorbed a considerable percentage of the explained variation in growth models (29% on average)

3.4.2.c. Mortality

Tree height, tree size, social position, stand basal area and climatic variables emerged as the most significant drivers of tree mortality (Table 2). Quantile modeling revealed significant gradients in the effects of water deficit, slope, tree height and social position (Figs. 6 and B16). Moreover, size-specific models highlighted qualitatively different effects across size classes (Table A6 and Fig. B17). Hence, negative effects of forest stand basal area were more pronounced in small size categories (Figs. 3g and B17) and stronger effects of climatic variables were observed on bigger saplings (Fig. 3i). In mortality models, plot (included as random covariate) absorbed smaller percentage of the explained variation (9% on average).

3.4.3. Interactions among the examined explanatory variables

The results of the models accounting for interactions among the explanatory variables are summarized in Table A7. Significant interactions were detected in recruitment, growth and mortality models between climatic variables, topographic variables, forest stand attributes, and individual traits (height and size). Moreover, quantile modeling highlighted the existence of significant geographic gradients in these diverse interactions, which are summarized in Fig. 7 (and see Figs. B18–23). Below, we briefly explain the observed gradients in the interactions for recruitment, growth and mortality; focusing specially on the interactions detected in the driest edge of the gradient.

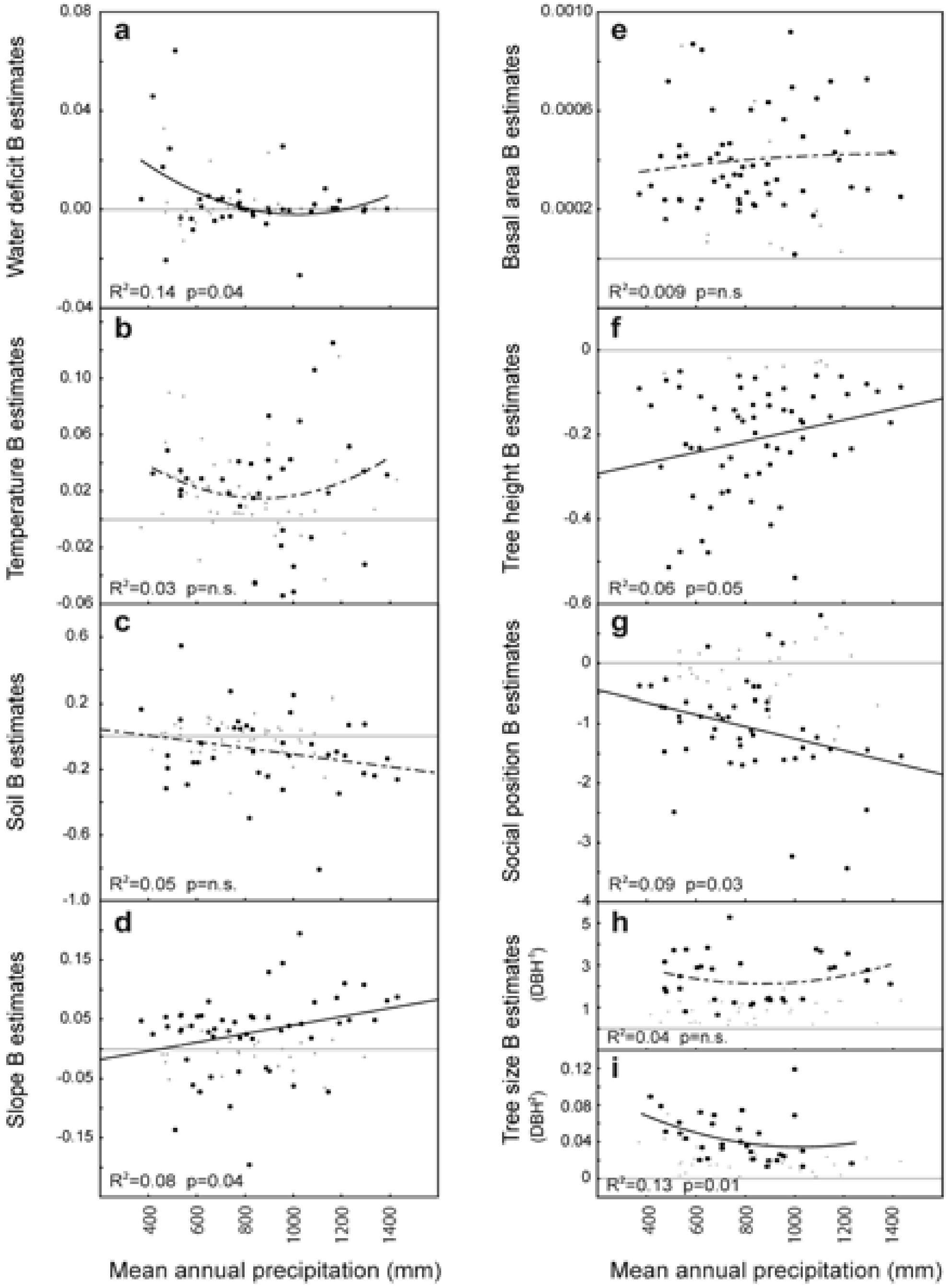


Figure 6. *Geographical variability in the effects (β coefficient values) on mortality of water deficit (a), temperature (b), soil quality (c), terrain slope (d), stand basal area (e), tree height (f), social position (g) and size (h-i) (quantile modelling, Q20). We divided each species in five rainfall quantiles and growth was independently modeled for each one. Solid dots representsignificant β coefficient values and non-solid dots represent non-significant β coefficient values.*

3.4.3.a. Recruitment

For recruitment, in the driest edge of the rainfall gradient increased positive effects of summer rainfall were highly significant. These positive effects were associated with significant interactions with temperature, soil and forest stand basal area. For example, recruitment was facilitated in areas of elevated temperature by relatively higher summer rain, leading to positive interactions between both variables in the driest edge (Fig. 7). Moreover, also in the driest edge of the gradient, positive interactions were observed between summer rainfall and soil in small saplings (R1–R2), indicating increased recruitment success in areas characterized by greater organic layer and relatively higher summer rainfall. Finally, note that in dry areas recruitment was also affected by negative interactions of rainfall and basal area, indicating increased recruitment in humid areas of relatively reduced basal area (Figs. 7 and B18–19). However, at the species-specific level, we observed significant positive as well as negative interactions for basal area. Positive interactions in Mediterranean lowland areas were observed in several species of the genus Quercus (e.g. Q. ilex, Q. suber, Q. Pyrenaica). These positive interactions indicated increased recruitment success in relatively more humid areas with elevated forest basal area. In contrast, in several species of the genus Pinus we observed negative interactions between basal area and summer rainfall, describing improved recruitment in either more humid localities with relatively low basal area or alternatively in dry areas with elevated basal area (e.g. P. halepensis, P. nigra, P. pinaster, P. sylvestris) (Figs. 7 and B18–19). Similar complex mosaics of positive and negative interactions were observed for the interactions of summer rainfall with organic layer depth, soil and temperature (summarized in Figs. 7 and B18–19).

3.4.3.b. Growth

For tree growth, water deficit effects on growth significantly interacted with forest stand basal area, soil, tree height and size. In the drier edge of the rainfall gradient, we observed increased negative effects of water deficit and basal area, and significantly higher positive effects of organic layer depth, tree height and size (Figs. 7 and B20–21). Moreover, these trends were paralleled by qualitatively stronger interactions also in the drier edge. Therefore effects on growth in the driest edge were modulated by complex interactions. For instance, in several species of the genus Pinus, and very significantly in P. halepensis, we observed highly positive interactions between tree size and basal area in the driest edge, due to reduced growth of smaller-sized trees in areas of relatively higher basal area.

3.4.3.c. Mortality

For mortality, like in recruitment and tree growth patterns, we observed significant spatial gradients in the interactions between explanatory covariates. In more xeric areas several types of interactions were detected. Firstly, water deficit (WD) interacted with forest stand basal area (BA) showing both positive and negative interactions. Positive interactions described a significant increase of tree mortality in areas with both elevated water deficit and high basal area, presumably due to reduced local water availability for the coupled effect of drought and competence (WD+, BA+; Figs. 7 and B22–23). These positive interactions were observed in typically Mediterranean species (P. halepensis, P. pinea, Q. ilex). These significant increases of mortality due to water deficit and positive interactions with basal area (WD BA) were mainly concentrated in the driest edge of the rainfall gradient.

In contrast, negative interactions between water deficit and basal area occurred in both dry and relatively wet sites but significantly tend to increase in strength and significance in relatively wetter localities, and were stronger in typically temperate and sub-alpine species (e.g. Q. petraea, A. alba). Negative interactions between water deficit (WD) and stand basal area (BA) contained two qualitatively different cases ([BA+, WD] and [BA, WD+]). Most of the species showed increased mortality in areas of elevated basal area and reduced water deficit (BA+, WD), showing an increase of mortality due to increased competitive effects in relatively more humid areas. A few species showed the opposite case (BA, WD+) showing increased mortality in areas of reduced basal area located in relatively dry areas (e.g. P. nigra, P pinea, Q. Petraea). The later case suggests that in some particular cases increased forest stand structure may reduce mortality impacts associated with hydric stress. Overall these results suggested that depending on complex local interactions, forest stand structure can act as either an enhancer or a mitigating factor of tree mortality.

In addition, also in more xeric areas along the rainfall gradient, tree-specific traits (height and size) showed significantly stronger interactions with both forest stand properties and water deficit, and these interactions were qualitatively different from those observed in more humid parts of the rainfall gradient. In the driest edge of the gradient, increased mortality of small trees was highlysignificant (Figs. B22 and B23). This effect was closely paralleled by increased positive interactions between tree height and forest stand basal area (Fig. 7), and increased negative interactions between water deficit and tree height (Figs. B22 and B23). Detailed analyses indicated that these interactions described increased mortality of small trees in dry areas characterized by reduced forest stand basal area. In a subset of the species of the genus Pinus (P. halepensis, P. pinea. P. pinaster, P radiata and P. nigra), these interactions also described increased mortality of large and thin trees inhabiting denser stands situated in relatively more humid sites. For these species, increased mortality of small trees in drier sites with low stand basal area was also significant. In wetter areas of the rainfall gradient, these interactions completely shifted their sign, describing increased mortality of small trees in more denser and relatively wetter stands (Figs. B22 and B23).

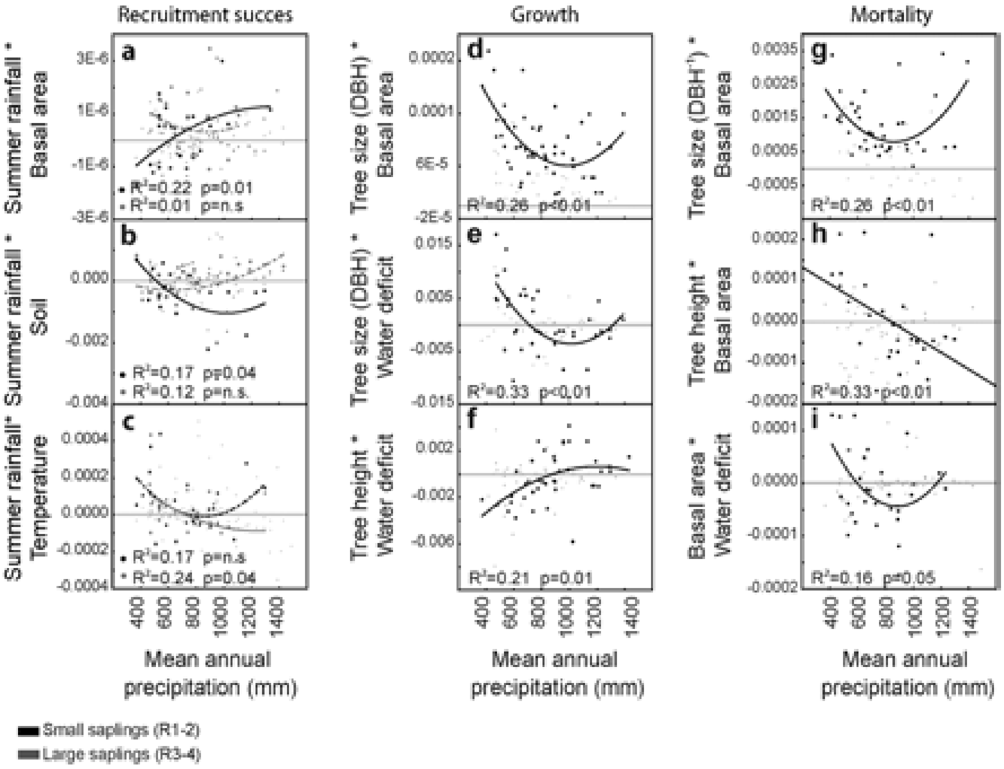


***Figure 7**. Geographical variability in the effects of interactions between explanatory factors in recruitment, growth and mortality models (quantile modelling, Q20). For recruitment models, black dots and lines indicate small saplings trends (R1-2). Grey lines illustrate large saplings trends (R3-4). (a) Changes in summer rainfall*basal area β coefficient values with increased rainfall in recruitment models. (b) Changes in summer rainfall*soil β coefficient values with increased rainfall in recruitment models (c) Changes in summer rainfall*temperature β coefficient values with increased rainfall in recruitment models. (d) Changes in tree size*basal area β coefficient values with increased rainfall in growth models. (e) Changes in tree size*water deficit β coefficient values with increased rainfall in growth models. (f) Changes in tree height*water deficit β coefficient values with increased rainfall in growth models. (g) Changes in tree size*basal area β coefficient values with increased rainfall in mortality models. (h) Changes in tree height*basal area β coefficient values with increased rainfall in mortality models. (i) Changes in basal area*water deficit β coefficient values with increased rainfall in mortality models. Solid dots represent significant β coefficient values and non-solid dots represent non-significant β coefficient values.*

3.5. Discussion

Our results synthetically describe how gradients in the effects of multiple contributing covariates influence forest demographic variables. These multivariate effect-gradients often show significantly stronger interactions at the extremes of the analyzed climatic gradients. The reported gradients of multiple interacting variables suggest that, even in the drier edge of the rainfall gradient, a heterogeneous mosaic of site- and species-specific responses may be the most likely scenario in the face of increased impacts of extreme droughts due to ongoing climate change. Interestingly, for each demographic variable we observed an idiosyncratic set of multiple interacting variables and qualitatively different geographic gradients. The observed variety of responses supports that different demographic processes (e.g. recruitment, growth, and mortality) respond differently to biotic and abiotic factors, suggesting that integrative whole-plant performance studies are required (Lichstein et al., 2010; Doak and Morris, 2010; Clark et al., 2011a).Moreover, the reported variety of demographic responses may provide stabilizing processes reinforcing population resilience (Doak and Morris, 2010; Lloret et al., 2012).

On the other hand, some shared effects and qualitatively similar trends were observed across all the examined demographic variables. Firstly, for all demographic variables water deficit effects were maximum at the driest edge of the rainfall gradient, and highly significant interactions were observed in this area with forest basal area, soil, slope and phenotypically plastic traits of individual trees (size and height). Secondly, in all the examined demographic variables we observed significant effects of forest stand variables presumably associated with tree competition effects. Forest stand effects were consistently observed across the whole rainfall gradient examined. However, interactions of forest stand and tree attributes with water deficit were mainly concentrated in dry localities (Fig. 7). The reported trends suggest that negative impacts of extreme climatic events on recruitment, growth and mortality are to be expected in more xeric Mediterranean areas.

Tree growth and young tree survival were increasingly limited by forest stand variables in drier sites, suggesting increased competition in these areas (Linares et al., 2010; Gómez-Aparicio et al., 2011; Ruiz-Benito et al., 2013). Furthermore, asymmetric competition effects between tree size classes were especially notorious in drier areas, suggesting that in many cases smaller, thinner and less competitive trees were specially affected by reduced water availability. This pattern was not supporting a general prediction of the stress gradient hypothesis (i.e. increased facilitative interactions in more stressful environments, Callaway, 2007), and it is consistent with previous studies in which the environmental stress gradient is induced by a resource for which plants compete (Callaway, 2007; Holmgren et al., 2012). The contrasting effects observed in size-specific models highlight the need to explicitly account for this factor (Dietze and Moorcroft, 2011; Clark et al., 2011b).

Acclimatory differences in whole-tree hydraulic architecture may contribute to explain the complex interactions between climate and forest stand variables and their varying effects observed across the rainfall gradient. For instance, in tree saplings located in shaded sites, a trade-off between shade and drought tolerance has received empirical support in eco-physiological studies (reviewed in Holmgren et al. (2012)). Briefly, increased investment in aerial parts of the sapling relative to the roots occurs in shaded sites, but this preferential allocation can produce higher susceptibility to drought events. This type of trade-offs could partially explain the reported positive interactions between water deficit and basal area in mortality trends (Fig. 7). Similarly, in adult trees, studies report higher growth rates, stature and leaf area index at the wettest sites (StPaul et al., 2012). However, these traits have been in turn significantly associated with greater sensitivity to drought, presumably due to a trade-off between growth rate and tolerance to water stress (StPaul et al., 2012; Voltas et al., in press). This type of trade-offs could also be associated with the reported interactions, for instance promoting increased effects of water deficit on tree mortality in stands with high basal area (Fig. 7).

The reported increased effects of rainfall and water deficit in the drier sites are also consistent with the ‘‘water-energy dynamics hypothesis’’ (O’Brien, 1998). Briefly, this macroecological rule states that water deficit and rainfall effects predominate in drier sites of climatic gradients and are progressively replaced by temperature effects in wetter localities. Stronger water deficit and rainfall effects were consistently observed in the three analyzed demographic variables (recruitment, growth, and mortality) (Figs. 4–6). In line with these findings, similar geographical shifts in the effects of water and energy variables have been reported in other taxa in the study region (e.g. Stefanescu et al., 2011; Carnicer et al., 2012, 2013).

Among the examined interacting covariates, it is well known that stand basal area, tree size and height structures are largely influenced by either forest abandonment and subsequent succession or by forest managing practices. In Spain there have been increased abandonment of both agricultural fields and forest management practices over the last decades, leading to tree density increases and competition intensification in extensive areas (e.g. Linares et al., 2009, Martín-Benito et al., 2011, Vayreda et al., 2012). Our results suggest that management and forest succession can largely determine future demographic responses to climatic events, in line with similar conclusions of several previous studies (Plieninger et al., 2010; Linares et al., 2010, Martín-Benito et al., 2011, Vayreda et al., 2012; Gómez-Aparicio et al., 2011; Candel-Pérez et al., 2012). For example, we observed consistent largescale differences in recruitment patterns between managed Dehesa forests and successional, unmanaged, Q. ilex forests (Figs. B4 and B5). Similarly, plantations significantly reduced recruitment and mortality, and improved tree growth in several species (Table 2). Overall, we suggest that future studies dealing with climatic effects in the driest edge should consider the intervention of multiple spatially correlated interacting covariates (soil, slope, basal area, and tree-specific phenotypic traits) and the human-related processes that largely affect these contributing variables (in particular land abandonment and succession, and forest management effects).

We also reported notorious differences in the demographic responses of the two dominant genus Quercus and Pinus. In the case of recruitment, Quercus species presented a significantly higher proportion of areas of new recruitment, probably determined by extensive ongoing forest abandonment and succession processes (Figs. B4 and B5). Similarly, we suggest that land abandonment and forest succession largely contributes to the observed reduced recruitment in extensive inhabited areas in several species of the genus Pinus (Figs. B4 and B5). When compared with Quercus, Pinus experienced much higher negative effects of forest stand basal area on growth pattern in both extremes of the rainfall gradient, and these trends were paralleled by higher effects of basal area on small-tree mortality observed in Pinus. These results coincide with studies revealing oaks less sensitive to competition than pines, suggesting that pines are in general less shade-tolerant than oaks and consequently more sensitive to competition from neighbors (Sánchez-Gómez et al., 2008; Gómez-Aparicio et al., 2011).

Negative effects of temperature on growth throughout the gradient in Pinus were in striking contrast with positive effects of temperature in the case of Quercus. Several hypotheses have been suggested to explain these contrasting growth responses to temperature between conifers and evergreens. Some authors have suggested a key role of the extension of the phenology to explain the observed positive relationships between growth and ambient temperature (extended phenology hypothesis; Gómez-Aparicio et al., 2011, and see Menzel and Fabian, 1999; Peñuelas et al., 2002; Gordo and Sanz, 2009; Way and Oren, 2010). However, experimental studies effectively controlling for phenological differences also report diverging growth responses to temperature (Way and Oren, 2010), suggesting that other plant traits could also be involved. For instance, deciduous angiosperms show significantly stronger growth responses to increased temperature when compared with conifers and evergreens (Way and Oren, 2010). Different plant traits could affect tree growth responses to temperature, including biochemical traits associated with photosynthesis and respiration, and a variety of leaf, root, stem, xylem and other vascular tissue traits. Consistent with this argument, constitutive differences between Quercus and Pinus have been described for leaf traits, xylem morphology, wood density, hydraulic safety margins, growth rates and allometric growth responses (Martínez-Ferri et al., 2000; Lusk et al., 2003; Martínez-Vilalta et al., 2010; Gómez-Aparicio et al., 2011; Flexas et al., 2012; Choat et al., 2012; Poorter et al., 2012, Lines et al., 2012). All these constitutive trait differences could to some extent underlie the contrasting growth responses to temperature observed between Quercus and Pinus species (Figs. 3e and B15). Way and Oren (2010) recently suggested a key role of photosynthetic and respiration traits, highlighting that photosynthesis and respiration differently respond to increased temperature, thus often allowing increased carbon fixation in warmer environments. However, more detailed studies are yet warranted to certify whether photosynthesis and respiration responses to temperature effectively differ between conifers and angiosperms (Way and Oren, 2010). Other studies suggest that leaf traits could also play a role in generating positive and negative growth responses to temperature. Leaf traits significantly differ between conifers and angiosperms, i.e. Evergreen Pinus typically have longer leaf lifespan, reduced mesophyll CO2 conductance, lower photosynthetic capacity and lower stomatal density when compared to angiosperms (Lusk et al., 2003; Niinemets et al., 2011; Flexas et al., 2012). As a result, Pinus and other evergreens trees usually show significantly different physiological responses to environmental factors like CO2 and climatic factors (Way and Oren, 2010; Niinemets et al., 2011). Moreover, according to Martínez-Ferri et al. (2000), leaf physiological responses to drought of Pinus and Quercus are qualitatively different. Pinus species prevent drought damage by early stomatal closure before any change in leaf water status occurs. In contrast, Quercus species maintain significant rates of assimilation even at low leaf and stem water potentials during drought. In Quercus species, drought-induced stomatal closure does not preclude carbon assimilation, whereas carbon assimilation is strongly inhibited in Pinus. In line with this, detailed eco-physiological studies at the local scale have reported a greater capacity to cope with drought effects in broadleaf Quercus species than in evergreen Pinus that coexist in the same stands (e.g. Pubescent oak relative to Scots pine; see Gimmi et al., 2010 and cites there in). All this evidence suggests that the reported negative effects of temperature on Pinus growth (Fig. 3e) could be related to their drought-avoidance strategy that precludes carbon assimilation due to early stomatal closure (Martínez-Ferri et al., 2000). Pinus and Quercus species also show significant differences in growth and allometrical responses to increased temperature (Way and Oren, 2010; Poorter et al., 2012, Lines et al., 2012). During the juvenile phase, maximum growth rates of conifers are usually slower than those of angiosperms (Lusk et al., 2003; but see Gómez-Aparicio et al., 2011 and Poorter et al., 2012). Similarly, Pinus and Angiosperms significantly differ in their xylem tissues. Pinus xylem typically has a lower specific conductivity than angiosperm xylem, as a result of greater hydraulic resistance in narrow-diameter tracheids than in vessels (Lusk et al., 2003). Some authors have suggested that increased growth rates in warmer areas could be associated with changing vessel structure and flow properties. Since warmer water is less viscous, this could lead to higher flow rates within vessels causing a higher mass concentration of dry matter (Lines et al., 2012 and cites there in). Likewise, Way and Oren (2010) suggested that tree growth responses to temperature are frequently not optimal in temperate and alpine species in native environments, presumably due to the operation of a trade-off between growth potential and cold-tolerance. This could also explain the positive growth responses to temperature observed in broadleaf temperate and alpine species. Finally, some authors have suggested that pine traits imply a water and nutrient-use conservative strategy (lower photosynthetic capacities, lower hydraulic capacity of vessels, lower stomatal conductances, reduced sapling light interception (Lusk et al., 2003, 2012; and see Sánchez-Gómez et al. 2006). These conservative traits could explain their preferential distribution in less productive and infertile sites (Bond, 1989; Coomes et al., 2005; Lusk et al., 2012) and a more conservative growth response to the variation of temperature (Way and Oren, 2010). Overall, a review of the literature highlights that positive and negative growth responses to temperature in Quercus and Pinus have been associated with a variety of different ecological hypotheses. Clearly, improved eco-physiological studies are yet warranted to test the relative importance of the different traits and ecological hypotheses.

Several methodological issues may be limiting the results of this study. Firstly, the reported patterns of recruitment presence and absence are influenced by the sampling effort applied (Villaescusa and Diaz, 1998). Increasing the surveyed area in each plot or the temporal sampling effort may provide different patterns. Recruitment was evaluated surveying, in each plot, an area of 78 m2. Secondly, this study considered mean annual temperature, summer rainfall and Emberger water deficit as climatic predictors. However, the inclusion of more detailed climatic variables (i.e. monthly and seasonal climatic variables) could unveil unreported patterns. For instance, spring rainfall has been significantly related to tree growth in several studies in Spain (Candel-Pérez et al., 2012). Thirdly, the precision of the classification of harvested and dead trees in the Spanish National Inventory is uncertain and is a putative source of bias (Villaescusa and Diaz, 1998). Fourthly, the two inventories are separated by a time span of 10 years. This is a limited period of time when compared with the life span of a typical tree. Therefore, improved studies covering a longer time period are warranted. In summary, these results provided a preliminary synthetic description of the observed gradients in forest recruitment, growth and mortality in Spain. Our results unveil a complex scenario of multiple interacting covariates with gradually varying effects across climatic gradients. The reported multifactorial gradients remain not previously described, and provide a general macroecologica framework for trait-based transect studies at the local scale in a study region affected by extreme drought events (e.g. Carnicer et al., 2011). In the light of these multifactorial gradients, we suggest that diverse, heterogeneous local responses to future extreme climatic events are likely, specially in the drier edge, where reported interactions with climatic variables are stronger.

3.5. References

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3.6. Supplementary tables

Species	Number of plots (Recruitment analysis)	Number of plots (growth and mortality analysis)	Number of trees	Number of dead trees	Percentage of plantations (%)
Abies alba	184	175	2214	134	0.54
Castanea sativa	902	800	4653	524	11.97
Eucalyptus camaldulensis	271	247	1390	106	76.01
Eucalyptus globulus	605	553	3515	12	31.24
Fagus sylvatica	1610	1561	20571	554	3.23
Juniperus thurifera	1339	1267	6153	77	2.14
Pinus halepensis	7032	6501	46691	2860	7.85
Pinus nigra	5220	4856	45580	1834	16.84
Pinus pinaster	7053	6567	75344	4131	18.33
Pinus pinea	2243	2099	14272	337	12.71
Pinus radiata	760	701	10186	518	73.25
Pinus sylvestris	6642	6358	88335	3227	16.23
Pinus uncinata	707	686	10496	791	2.40
Quercus faginea	2639	2248	11173	359	4.13
Quercus humilis	1160	1122	5432	116	2.37
Quercus ilex	10798	10376	50221	1133	1.88
Quercus petraea	564	532	4125	93	1.06
Quercus pyrenaica	2818	2711	21721	730	7.52
Quercus robur	1361	1263	7732	277	10.96
Quercus suber	2334	2176	13868	580	3.51

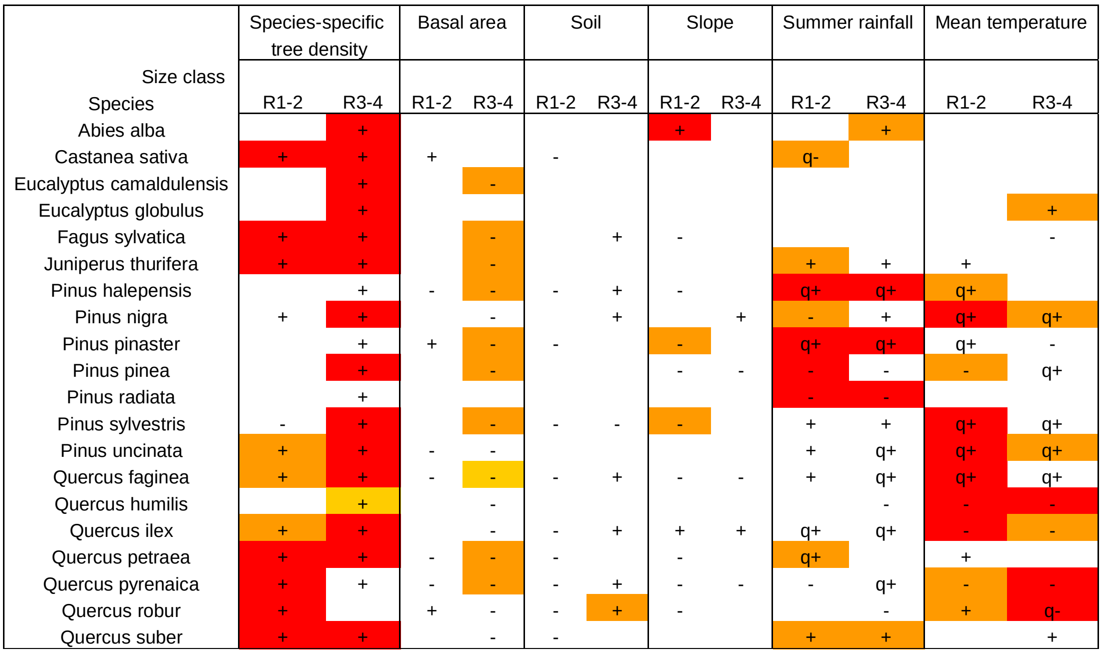
Table A1. *Number of plots and trees available for each species.*

Species	Recruitment succes (%)				
	Species-specific	Species- size class specific			
		R1	R2	R3	R4
Abies alba	0.80	0.55	0.64	0.46	0.53
Castanea sativa	0.69	0.34	0.43	0.40	0.35
Eucalyptus camaldulensis	0.55	0.08	0.20	0.28	0.44
Eucalyptus globulus	0.73	0.10	0.24	0.51	0.57
Fagus sylvatica	0.83	0.53	0.58	0.50	0.50
Juniperus thurifera	0.81	0.47	0.62	0.47	0.47
Pinus halepensis	0.72	0.38	0.37	0.38	0.43
Pinus nigra	0.60	0.26	0.35	0.30	0.38
Pinus pinaster	0.59	0.39	0.27	0.20	0.22
Pinus pinea	0.49	0.36	0.22	0.10	0.11
Pinus radiata	0.13	0.06	0.03	0.02	0.06
Pinus sylvestris	0.56	0.24	0.29	0.26	0.37
Pinus uncinata	0.68	0.28	0.45	0.40	0.51
Quercus faginea	0.81	0.65	0.61	0.43	0.49
Quercus humilis	0.55	0.44	0.43	0.26	0.29
Quercus ilex	0.82	0.70	0.72	0.56	0.51
Quercus petraea	0.70	0.56	0.49	0.25	0.33
Quercus pyrenaica	0.83	0.66	0.70	0.48	0.52
Quercus robur	0.82	0.46	0.47	0.36	0.33
Quercus suber	0.59	0.45	0.35	0.16	0.16

Table A2. *Percentage of recruitment success for each species and recruitment class. (R1) Surveyed recruitment class 1 (<30 cm height). (R2) Surveyed recruitment class 2 (30-130 cm height). (R3) Surveyed recruitment class 3 >130 cm heigh <2.5 cm dbh. (R4) Surveyed recruitment class 4 >130 cm heigh <7.5 cm dbh.*

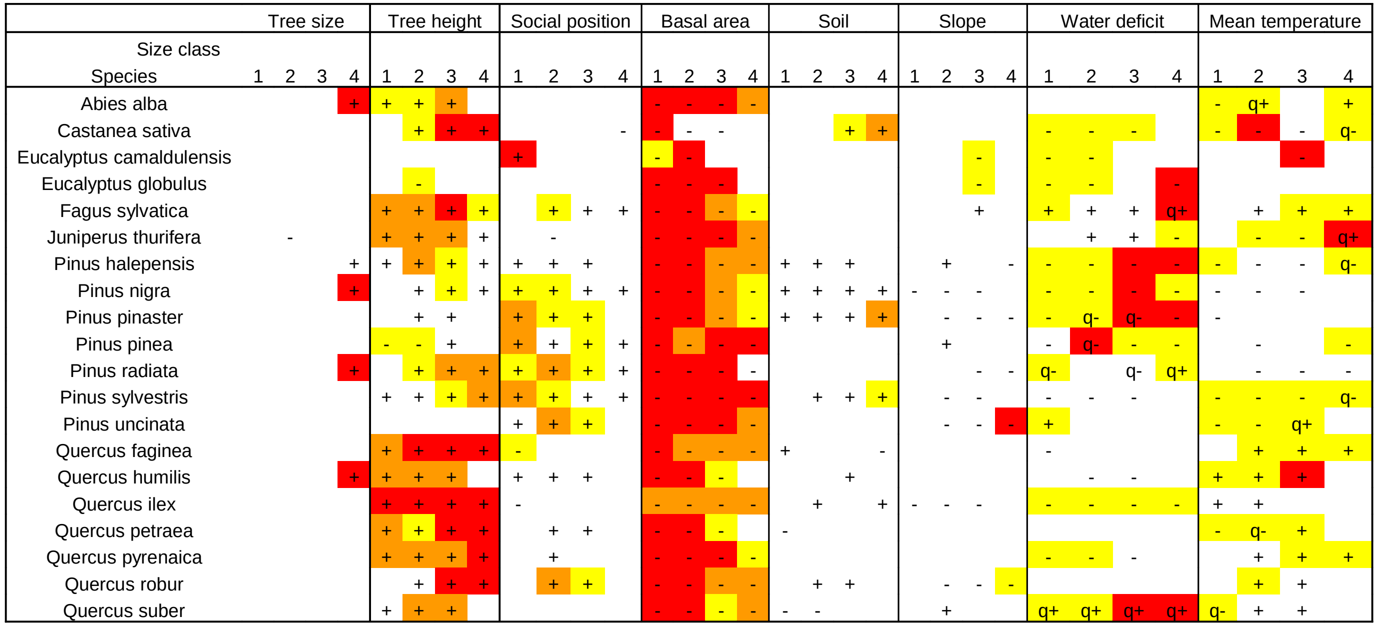
Species	Mean tree density IFN3 (trees·ha^{-1})	Mean basal area IFN3 (m^2·ha^{-1})	Mean growth (dm^2·cm^{-1}·year^{-1})
Abies alba	400.61 ± 28.38	18.61 ±1.24	0.0620±1.11E-03
Castanea sativa	251.72 ±13.39	12.15 ±0.50	0.0905±1.63E-03
Eucalyptus camaldulensis	381.51 ±17.51	7.64 ±0.33	0.0673±1.95E-03
Eucalyptus globulus	454.06 ±20.64	14.93 ±0.46	0.2587±3.28E-03
Fagus sylvatica	462.38 ±13.28	16.85 ±0.33	0.0464±3.11E-04
Juniperus thurifera	225.36 ±6.05	5.17 ±0.13	0.0246±2.96E-04
Pinus halepensis	342.46 ±4.05	8.85 ±0.08	0.0585±2.04E-04
Pinus nigra	422.68 ±6.63	11.08 ±0.14	0.0485±1.83E-04
Pinus pinaster	365.49 ±4.82	16.21 ±0.16	0.0858±2.47E-04
Pinus pinea	196.35 ±5.96	8.89 ±0.16	0.0663±3.75E-04
Pinus radiata	335.61±12.10	25.58 ±0.60	0.1684±1.10E-03
Pinus sylvestris	518.99 ± 6.31	17.39 ±0.17	0.0556±1.48E-04
Pinus uncinata	590.35 ± 20.64	18.97 ±0.55	0.0384±3.22E-04
Quercus faginea	331.25 ± 8.64	5.32 ±0.11	0.0316±2.52E-04
Quercus humilis	353.38 ± 4.81	6.03 ±0.05	0.0308±1.21E-04
Quercus ilex	324.78 ± 17.93	9.83 ±0.42	0.0413±5.16E-04
Quercus petraea	516.80 ± 11.25	9.86 ±0.17	0.0407±2.54E-04
Quercus pyrenaica	201.20 ± 7.41	8.77 ±0.23	0.0781±7.80E-04
Quercus robur	201.69 ± 5.83	8.40 ±0.15	0.0424±3.41E-04

Table A3. *Species-specific mean tree growth and forest stand attributes. Mean species-specific stand basal area and tree density were calculated from third forest inventory (IFN3). Growth was calculated from trees surveyed in both inventories.*



	Species-specific tree density		Basal area		Soil		Slope		Summer rainfall		Mean temperature	
Size class Species	R1-2	R3-4	R1-2	R3-4	R1-2	R3-4	R1-2	R3-4	R1-2	R3-4	R1-2	R3-4
Abies alba		🟥 +					🟥 +			🟧 +		
Castanea sativa	🟥 +	🟥 +	+		-				🟧 q-			
Eucalyptus camaldulensis		🟥 +		🟧 -								
Eucalyptus globulus		🟥 +										🟧 +
Fagus sylvatica	🟥 +	🟥 +		🟧 -		+	-					-
Juniperus thurifera	🟥 +	🟥 +		🟧 -					🟧 +	+	+	
Pinus halepensis		+	-	🟧 -	-	+	-		🟥 q+	🟥 q+	🟧 q+	
Pinus nigra	+	🟥 +		-		+		+	🟧 -	+	🟥 q+	🟧 q+
Pinus pinaster		+	+	🟧 -	-		🟧 -		🟥 q+	🟥 q+	q+	-
Pinus pinea		🟥 +		🟧 -			-	-	🟥 -	-	🟧 -	q+
Pinus radiata		+							🟥 -	🟥 -		
Pinus sylvestris	-	🟥 +		🟧 -	-	-	🟧 -		+	+	🟥 q+	q+
Pinus uncinata	🟧 +	🟥 +	-	-					+	q+	🟥 q+	🟧 q+
Quercus faginea	🟧 +	🟥 +	-	🟨 -	-	+	-	-	+	q+	🟥 q+	q+
Quercus humilis		🟨 +		-						-	🟥 -	🟥 -
Quercus ilex	🟧 +	🟥 +		-	-	+	+	+	q+	q+	🟥 -	🟧 -
Quercus petraea	🟥 +	🟥 +	-	🟧 -	-		-		🟧 q+		+	
Quercus pyrenaica	🟥 +	+	-	🟧 -	-	+	-	-	-	q+	🟧 -	🟥 -
Quercus robur	🟥 +		+	-	-	🟧 +	-			-	🟧 +	🟥 q-
Quercus suber	🟥 +	🟥 +		-	-				🟧 +	🟧 +		+

***Table A4**. Summary of observed estimates in size-specific recruitment models (R1-2 and R3-4). The sign (+/-) and significance (color code) of the test estimates is shown. For illustrative purposes, a different color code has been used to highlight the relative explanatory power of each significant factor. Red=first and second predictors (p<0.0001); orange= third and fourth predictors (p<0.05); yellow= all other significant predictors (p<0.05).*

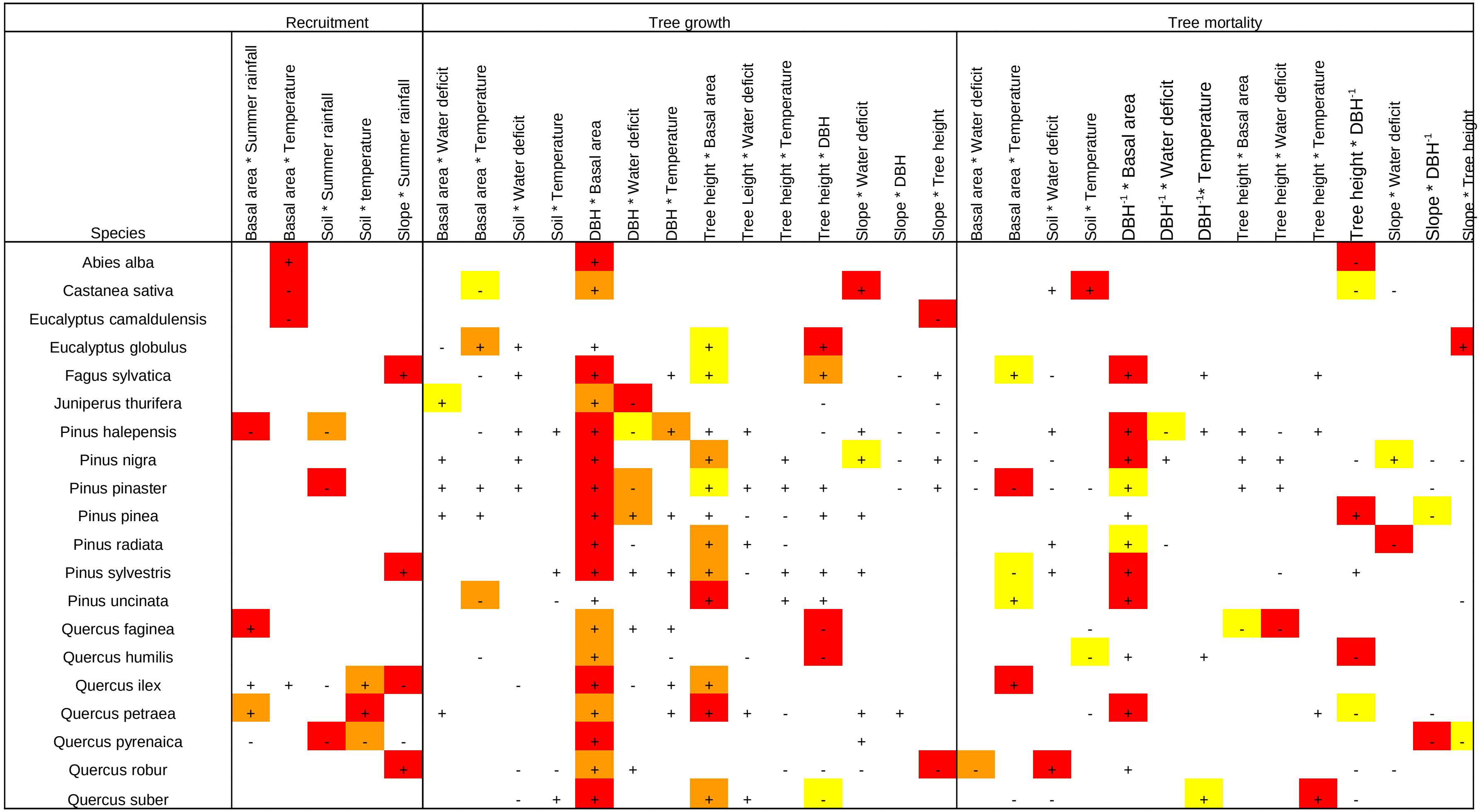


Size class	Tree size				Tree height				Social position				Basal area				Soil				Slope				Water deficit				Mean temperature			
Species	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Abies alba				+	+	+	+						-	-	-	-													-	q+		+
Castanea sativa						+	+	+				-	-	-	-				+	+					-	-	-		-	-	-	q-
Eucalyptus camaldulensis									+				-	-									-		-	-					-	
Eucalyptus globulus						-							-	-	-								-		-	-		-				
Fagus sylvatica					+	+	+	+		+	+	+	-	-	-	-							+		+	+	+	q+		+	+	+
Juniperus thurifera		-			+	+	+	+		-			-	-	-	-										+	+	-		-	-	q+
Pinus halepensis				+	+	+	+	+	+	+	+		-	-	-	-	+	+	+			+		-	-	-	-	-	-	-	-	q-
Pinus nigra				+		+	+	+	+	+	+	+	-	-	-	-	+	+	+	+	-	-	-		-	-	-	-	-	-	-	
Pinus pinaster						+	+		+	+	+		-	-	-	-	+	+	+	+		-	-	-	-	q-	q-	-	-			
Pinus pinea					-	-	+		+	+	+	+	-	-	-	-						+			-	q-	-	-		-		-
Pinus radiata				+		+	+	+	+	+	+	+	-	-	-	-							-	-	q-		q-	q+		-	-	-
Pinus sylvestris					+	+	+	+	+	+	+	+	-	-	-	-		+	+	+		-	-		-	-	-		-	-	-	q-
Pinus uncinata									+	+	+		-	-	-	-						-	-	-	+				-	-	q+	
Quercus faginea					+	+	+	+	-				-	-	-	-	+			-					-					+	+	+
Quercus humilis				+	+	+	+		+	+	+		-	-	-				+							-	-		+	+	+	
Quercus ilex					+	+	+	+	-				-	-	-	-		+		+	-	-	-		-	-	-	-	+	+		
Quercus petraea					+	+	+	+		+	+		-	-	-		-												-	q-	+	
Quercus pyrenaica					+	+	+	+		+			-	-	-	-									-	-	-			+	+	+
Quercus robur						+	+	+		+	+		-	-	-	-		+	+			-	-	-						+	+	
Quercus suber					+	+	+						-	-	-	-	-	-				+			q+	q+	q+	q+	q-	+	+	

Table A5. *Effect tests for size-specific growth models (SC1-SC2-SC3-SC4). The sign (+/-) and significance (color code) of the test estimates is shown. For illustrative purposes, a different color code has been used to highlight the relative explanatory power of each significant factor. Red=first and second predictors (p<0.0001); orange= third and fourth predictors (p<0.05); yellow= all other significant predictors (p<0.05)*

	Tree size (DBH^{-1})		Tree size (DBH^{2})		Tree height		Social position		Basal area		Soil		Slope		Water deficit		Mean temperature	
Size class Species	1-2	3-4	1-2	3-4	1-2	3-4	1-2	3-4	1-2	3-4	1-2	3-4	1-2	3-4	1-2	3-4	1-2	3-4
Abies alba		-	+			🟧 -			+	+	🟧 -		🟥 +	+		🟥 q-		+
Castanea sativa	+				🟧 -						-	🟧 -					🟥 +	🟥 q+
Eucalyptus camaldulensis					🟥 -		🟧 -											
Eucalyptus globulus																		
Fagus sylvatica		-		+	🟧 -	🟥 -	-		🟥 +	+			+	+			+	🟧 q-
Juniperus thurifera						🟥 -			🟥 +									
Pinus halepensis	🟧 +			+	-	-	🟥 -		+	🟧 +	-		+		-		+	🟥 q+
Pinus nigra	+				-		🟧 -		🟥 +			-	+	🟧 +	+		q-	🟥 q-
Pinus pinaster	+			+	-	-	🟧 -		+	+			+	+	q-	🟥 q-	🟥 q-	🟧 q-
Pinus pinea	+				🟧 -	+	🟥 -			-				🟧 +				
Pinus radiata		+		+	🟧 -	🟧 -	-	-	🟥 +	🟥 +				+			q-	q-
Pinus sylvestris	+				-	🟥 -	🟥 -		🟧 +	+			+		q-	q-	q-	🟧 q-
Pinus uncinata					-		-		🟥 +				🟧 +			🟥 q+	+	🟧 -
Quercus faginea					🟥 -	🟥 -	-		+	🟧 +					🟧 q+		+	
Quercus humilis		🟧 -			🟥 -	🟥 -	🟧 -											
Quercus ilex		-			🟥 -	🟥 -	-	+	+				🟧 +	🟧 +				
Quercus petraea					-		-		🟧 +					🟥 +			🟥 q-	
Quercus pyrenaica	+				🟥 -	🟥 -	-		🟧 +	🟧 +								
Quercus robur							-			🟥 +	🟧 -	-	+	🟧 +	🟥 q+	q+		
Quercus suber	+	-	+		🟧 -	🟥 -			🟥 +					🟧 +	-			

***Table A6**. Effect tests for size-specific mortality models (SC12-SC34). The sign (+/-) and significance (color code) of the test estimates is shown. For illustrative purposes, a different color code has been used to highlight the relative explanatory power of each significant factor. Red=first and second predictors ($p<0.0001$); orange= third and fourth predictors ($p<0.05$); yellow= all other significant predictors ($p<0.05$).*



	Recruitment					Tree growth														Tree mortality													
Species	Basal area * Summer rainfall	Basal area * Temperature	Soil * Summer rainfall	Soil * temperature	Slope * Summer rainfall	Basal area * Water deficit	Basal area * Temperature	Soil * Water deficit	Soil * Temperature	DBH * Basal area	DBH * Water deficit	DBH * Temperature	Tree height * Basal area	Tree Leight * Water deficit	Tree height * Temperature	Tree height * DBH	Slope * Water deficit	Slope * DBH	Slope * Tree height	Basal area * Water deficit	Basal area * Temperature	Soil * Water deficit	Soil * Temperature	DBH^{-1} * Basal area	DBH^{-1} * Water deficit	DBH^{-1}* Temperature	Tree height * Basal area	Tree height * Water deficit	Tree height * Temperature	Tree height * DBH^{-1}	Slope * Water deficit	Slope * DBH^{-1}	Slope * Tree height
Abies alba		+								+																				-			
Castanea sativa		-					-			+							+					+	+							-	-		
Eucalyptus camaldulensis		-																	-														
Eucalyptus globulus						-	+	+		+			+			+																	+
Fagus sylvatica					+		-	+		+		+	+			+		-	+		+	-		+		+			+				
Juniperus thurifera						+				+	-					-			-														
Pinus halepensis	-		-				-	+	+	+	-	+	+	+		-	+	-	-	-		+		+	-	+	+	-	+				
Pinus nigra						+		+		+			+		+		+	-	+	-		-		+	+		+	+		-	+	-	-
Pinus pinaster			-			+	+	+		+	-		+	+	+	+		-	+	-	-	-	-	+			+	+				-	
Pinus pinea						+	+			+	+	+	+	-	-	+	+							+						+		-	
Pinus radiata										+	-		+	+	-							+		+	-						-		
Pinus sylvestris					+				+	+	+	+	+	-	+	+	+				-	+		+				-		+			
Pinus uncinata							-		-	+			+		+	+					+			+									-
Quercus faginea	+									+	+	+				-							-				-	-					
Quercus humilis							-			+		-		-		-							-	+		+				-			
Quercus ilex	+	+	-	+	-			-		+	-	+	+								+												
Quercus petraea	+			+		+				+		+	+	+	-		+	+					-	+					+	-		-	
Quercus pyrenaica	-		-	-	-					+							+															-	-
Quercus robur					+			-	-	+	+				-	-	-		-	-		+		+						-	-		
Quercus suber								-	+	+			+	+		-					-	-				+			+	-			

***Table A7**. Effect tests for recruitment, growth and mortality models with interactions. For practical purposes, only the effect tests of interactions are shown. The sign (+/-) and significance (color code) of the test estimates is provided. For illustrative purposes, a different color code has been used to highlight the relative explanatory power of each significant factor. Red=first and second predictors (p<0.0001); orange= third and fourth predictors (p<0.05); yellow= all other significant predictors (p<0.05).*

Species		Species-specific tree density	Organic layer depth	Slope	Basal area	Plantation	Summer rainfall	**Sumer rainfall ²**	Mean temperature	**Mean temperature²**
Abies alba	Estimate	0.001								
	Error	0.001								
Castanea sativa	Estimate	0.001	-0.129		1.96E-04		-0.001		-0.016	
	Error	2.17E-04	0.030		5.27E-05		1.65E-04		0.007	
Eucalyptus camaldulensis	Estimate					2.265	0.013			
	Error					1.152	0.007			
Eucalyptus globulus	Estimate			-0.164						
	Error			0.065						
Fagus sylvatica	Estimate	3.63E-04		-0.017	2.62E-04	-0.907	-3.31E-04		0.009	
	Error	1.21E-04		0.007	4.87E-05	0.313	1.22E-04		0.004	
Juniperus thurifera	Estimate	0.001					0.002			
	Error	3.08E-04					0.001			
Pinus halepensis	Estimate	0.001			-0.015	-0.187	0.005	-2.43E-06	0.131	-4.51E-04
	Error	1.02E-04			0.005	0.098	3.94E-04	1.74E-07	0.035	1.18E-04
Pinus nigra	Estimate	0.001				-1.275	-4.40E-04		0.221	-0.001
	Error	8.65E-05				0.113	7.77E-05		0.052	2.22E-04
Pinus pinaster	Estimate	0.001	-2.34E-04	-0.068	0.032	-0.162	-0.001		0.148	-0.001
	Error	7.85E-05	2.88E-05	0.014	0.005	0.072	7.70E-05		0.022	8.34E-05
Pinus pinea	Estimate	0.001			1.98E-04	-0.409	-0.001		-0.016	
	Error	2.06E-04			6.89E-05	0.150	1.13E-04		0.003	
Pinus radiata	Estimate	0.001	-0.245				-0.002			
	Error	2.80E-04	0.090				0.001			
Pinus sylvestris	Estimate	1.59E-04	-2.65E-04	-0.057		-0.983			0.138	-0.001
	Error	6.97E-05	8.47E-05	0.016		0.102			0.021	1.07E-04
Pinus uncinata	Estimate	0.001			-0.032				0.226	-0.002
	Error	2.10E-04			0.005				0.069	0.001
Quercus faginea	Estimate	0.001		-0.103		-0.825			0.086	-3.60E-04
	Error	1.48E-04		0.025		0.142			0.030	1.13E-04
Quercus humilis	Estimate				2.925E-05				-0.015	
	Error				8.256E-06				0.004	
Quercus ilex	Estimate	0.001	-0.220		1.832E-04	-1.266	-3.667E-04		-0.015	
	Error	9.281E-05	0.016		4.223E-05	0.058	6.258E-05		0.001	
Quercus petraea	Estimate	0.002	-2.059E-04	-0.117	-0.035		0.005		0.012	
	Error	3.139E-04	9.442E-05	0.045	0.014		0.002		0.005	
Quercus pyrenaica	Estimate	0.001	-0.175	-0.017		-0.776	-0.001		-0.016	
	Error	1.178E-04	0.022	0.007		0.117	1.675E-04		0.003	
Quercus robur	Estimate	0.001	-0.079	-0.025	2.629E-04					
	Error	2.382E-04	0.021	0.010	5.118E-05					
Quercus suber	Estimate	0.002	-0.078		2.968E-04	-0.437	-2.702E-04		0.017	
	Error	2.311E-04	0.026		6.099E-05	0.125	1.051E-04		0.004	

***Table A8**. Tree recruitment. Estimates and standard errors for Table 2.*

Species		DBH	DBH^2	Tree height	Social position	Basal area	Organic layer depth	Slope	Plantation	Water deficit	Water deficit ^{2}	Mean temperature
Abies alba	Estimate	-0.666	0.027	0.028		-2.687E-04						
	Error	0.123	0.007	0.006		2.830E-05						
Castanea sativa	Estimate	-0.096		0.041		-4.670E-05	0.037	-0.009		-0.002		-0.011
	Error	0.042		0.005		1.860E-05	0.009	0.004		0.001		0.002
E. camaldulensis	Estimate	0.884	-0.076		0.325	-4.520E-04				-0.009		
	Error	0.386	0.032		0.067	1.117E-04				0.003		
E. globulus	Estimate	-0.753	0.033		0.274	-2.242E-04				-0.004		
	Error	0.134	0.010		0.046	2.530E-05				0.001		
Fagus sylvatica	Estimate	-0.466	0.019	0.037	0.046	-2.370E-04		0.005	0.817	0.002		0.009
	Error	0.043	0.003	0.002	0.020	1.444E-05		0.002	0.123	4.354E-04		0.001
J. thurifera	Estimate	0.405	-0.035	0.093		-4.312E-04			0.390	0.006		-0.012
	Error	0.115	0.009	0.009		2.880E-05			0.153	0.002		0.002
P. halepensis	Estimate	-0.624	0.021	0.058	0.104	-4.215E-04	0.043		0.323	-0.012		-0.011
	Error	0.075	0.007	0.002	0.011	1.281E-05	0.005		0.030	4.821E-04		0.001
Pinus nigra	Estimate	-0.763	0.026	0.021	0.110	-3.018E-04	0.060	-0.006	0.551	-0.026	6.800E-05	-0.005
	Error	0.055	0.005	0.002	0.012	9.760E-06	0.005	0.001	0.028	0.001	5.200E-06	0.001
Pinus pinaster	Estimate	-0.492	0.014	0.006	0.229	-2.468E-04	0.044	-0.008	0.316	-0.004		
	Error	0.056	0.005	0.002	0.015	7.380E-06	0.004	0.001	0.021	1.498E-04		
Pinus pinea	Estimate	-0.496	0.020	-0.009	0.096	-2.556E-04			0.356	-0.006		-0.005
	Error	0.068	0.005	0.004	0.021	1.777E-05			0.043	0.001		0.001
Pinus radiata	Estimate			0.036	0.528	-4.098E-04	0.024	-0.017				-0.014
	Error			0.002	0.038	1.970E-05	0.010	0.003				0.002
Pinus sylvestris	Estimate	-0.881	0.043	0.018	0.115	-2.682E-04	0.023	-0.004	0.571	-0.004		-0.008
	Error	0.042	0.004	0.001	0.012	6.280E-06	0.003	0.001	0.020	3.079E-04		0.001
Pinus uncinata	Estimate	-0.506	0.032	0.011	0.313	-2.072E-04		-0.007	0.635			0.040
	Error	0.125	0.010	0.004	0.047	1.474E-05		0.003	0.140			0.011

Quercus faginea	Estimate	-0.488	0.023	0.081		-2.659E-04			0.204	-0.010	4.800E-05	0.020
	Error	0.051	0.003	0.004		1.550E-05			0.046	0.003	1.560E-05	0.009
Quercus humilis	Estimate											
	Error											
Quercus ilex	Estimate	-0.482	0.023	0.081		-2.690E-04	0.020	-0.006	0.205	-0.003		
	Error	0.051	0.003	0.004		1.554E-05	0.005	0.002	0.046	0.001		
Quercus petraea	Estimate	-0.397	0.012	0.056	0.087	-2.070E-04						-0.046
	Error	0.064	0.003	0.005	0.039	2.548E-05						0.011
Q. pyrenaica	Estimate	-0.689	0.035	0.059	0.066	-2.800E-04				-0.002		0.005
	Error	0.043	0.003	0.003	0.012	1.183E-05				4.018E-04		0.001
Quercus robur	Estimate	-0.452	0.024	0.051	0.211	-2.130E-04	0.024	-0.015	0.196			0.005
	Error	0.095	0.006	0.004	0.035	1.833E-05	0.006	0.003	0.072			0.002
Quercus suber	Estimate			0.070		-2.440E-04			0.334			0.003
	Error			0.005		1.754E-05			0.043			0.001

Table A8. *Tree growth. Estimates and standard errors for Table 2.*

Species		DBH^2	Tree height	Social position	Basal area	Organic layer depth	Slope	Plantation	Water deficit	Water deficit ^{2}	Mean temperature	Mean temperature^2
Abies alba	Estimate	0.020	-0.076		2.069E-04	-0.091	0.054	2.768			0.020	
	Error	0.005	0.021		7.102E-05	0.041	0.016	1.081			0.009	
C. sativa	Estimate	-0.007	-0.044			-0.093	0.019	-0.682			0.582	-0.002
	Error	0.004	0.018			0.028	0.010	0.191			0.126	4.729E-04
E. camaldulensis	Estimate			-0.641								
	Error			0.277								
E. globulus	Estimate											
	Error											
F. sylvatica	Estimate	0.021	-0.210	-0.460	2.534E-04		0.038		0.003		0.023	
	Error	0.002	0.013	0.139	4.350E-05		0.007		0.001		0.004	
J. thurifera	Estimate		-0.798									
	Error		0.240									
P. halepensis	Estimate	0.068	-0.067	-0.648	4.021E-04	-0.062	0.019	-0.310	0.024	-2.280E-04	0.108	-3.320E-04
	Error	0.007	0.015	0.087	4.871E-05	0.021	0.005	0.123	0.010	6.509E-05	0.048	1.616E-04
P. nigra	Estimate	0.052	-0.089	-0.818	3.070E-04	-0.062	0.030		0.015	-5.432E-05	-0.186	0.001
	Error	0.008	0.022	0.157	4.702E-05	0.027	0.007		0.006	2.305E-05	0.060	2.581E-04
P. pinaster	Estimate	0.050	-0.096	-0.622	2.339E-04		0.021	-0.324	-0.012	4.549E-05	-0.160	0.001
	Error	0.005	0.010	0.079	2.009E-05		0.004	0.057	0.002	8.395E-06	0.016	6.210E-05
P. pinea	Estimate		0.179	-0.693			0.047	-0.534				
	Error		0.039	0.256			0.016	0.207				
P. radiata	Estimate		-0.106	-1.953	4.725E-04		0.019		-0.034	6.329E-05	-0.490	0.002
	Error		0.014	0.251	4.378E-05		0.008		0.009	1.996E-05	0.112	4.361E-04
P. sylvestris	Estimate	0.015	-0.149	-0.729	3.356E-04		0.008	-0.743	-0.023	1.027E-04	-0.098	0.001
	Error	0.005	0.009	0.076	1.988E-05		0.003	0.069	0.005	2.474E-05	0.013	6.832E-05
P. uncinata	Estimate	0.022	-0.044	-0.669	1.399E-04		0.017	0.923			-0.073	
	Error	0.006	0.016	0.177	3.422E-05		0.006	0.335			0.031	
Q. faginea	Estimate	0.013	-0.276	-0.368	4.609E-04				0.042	-2.452E-04	4.033E-04	
	Error	0.005	0.041	0.140	9.080E-05				0.020	9.538E-05	2.110E-04	
Q. humilis	Estimate	0.044	-0.380					2.830			-0.131	0.001
	Error	0.007	0.034					0.366			0.051	2.131E-04
Quercus ilex	Estimate	0.019	-0.498				0.041	-0.525	-0.011		0.030	
	Error	0.00	0.043				0.013	0.251	0.004		0.005	

		7										
Q. petraea	Estimate		-0.170	-1.972	4.457E-04		0.044				0.148	
	Error		0.043	0.492	1.338E-04		0.017				0.066	
Q. pyrenaica	Estimate	0.013	-0.312	-0.751	3.750E-04						0.015	
	Error	0.004	0.022	0.102	4.986E-05						0.003	
Q. robur	Estimate		-0.045		4.465E-04	-0.202	0.068		0.063	-1.526E-04	0.033	
	Error		0.021		7.486E-05	0.035	0.012		0.014	3.541E-05	0.007	
Q. suber	Estimate	0.018	-0.114		2.722E-04		0.031		0.022	-1.325E-04	0.034	
	Error	0.004	0.028		7.512E-05		0.012		0.009	3.853E-05	0.010	

Table A8. *Tree mortality. Estimates and standard errors for Table 2.*

3.7. Supplementary figures

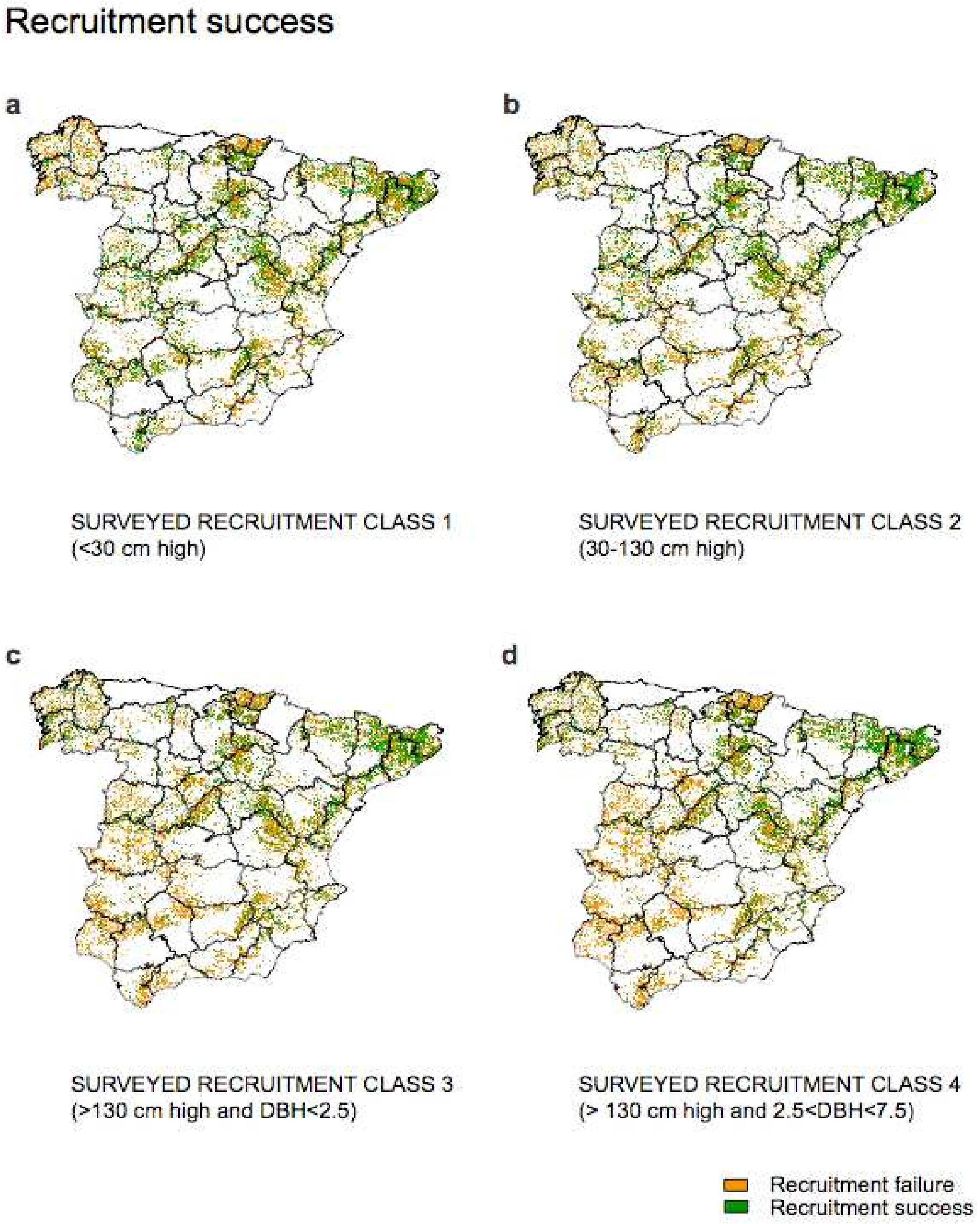


Figure B1. *Maps of recruitment success for each size class (R1-R2-R3-R4) for all species grouped and for each species. Note that white areas in Northern provinces represent missing data.*

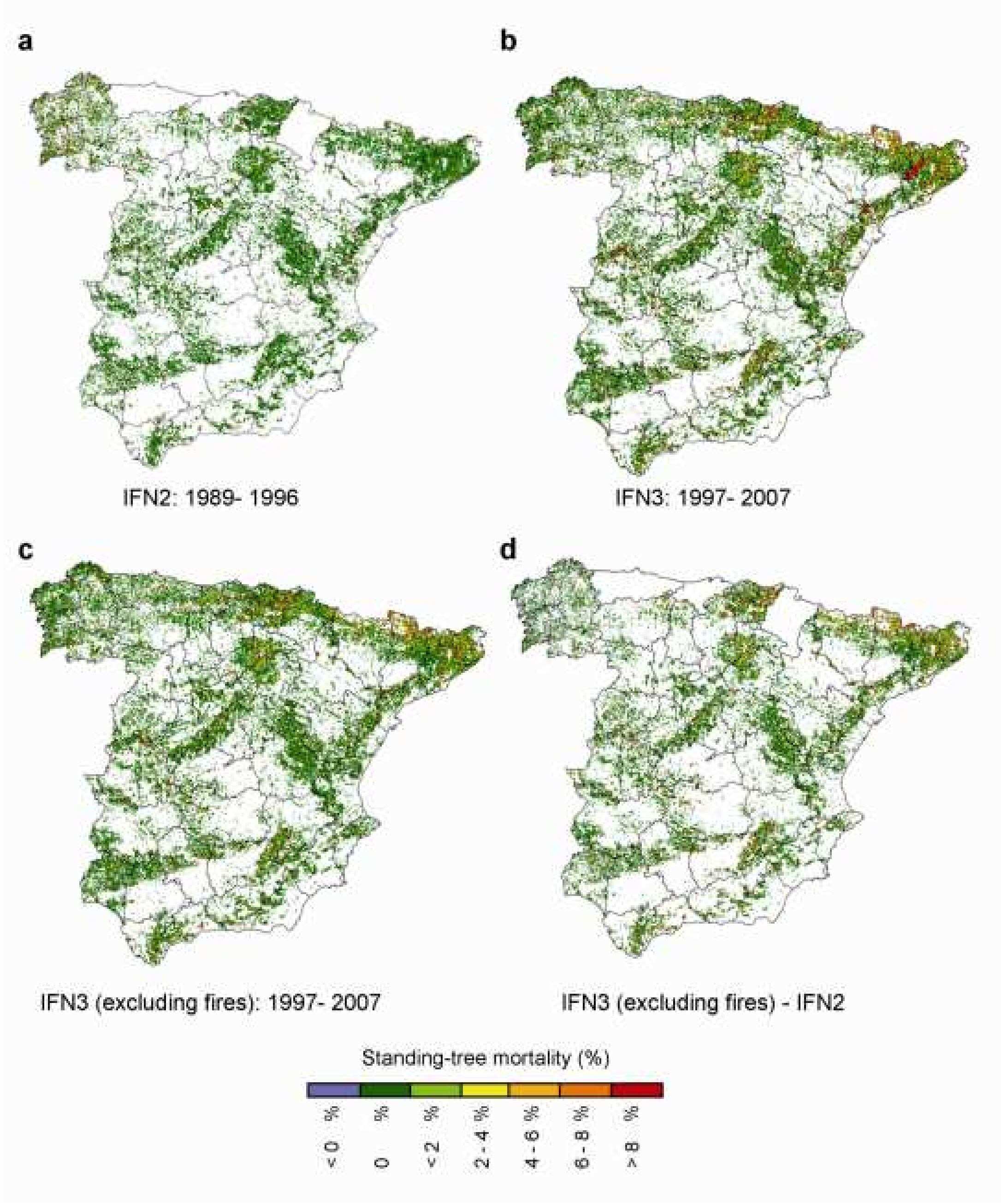


***Figure B2**. Maps of standing mortality (percentage of dead trees) for all species grouped in IFN2 and IFN3 (a-d). (c-d) Maps of mortality excluding fire events. Note that white areas in Northern provinces represent missing data.*

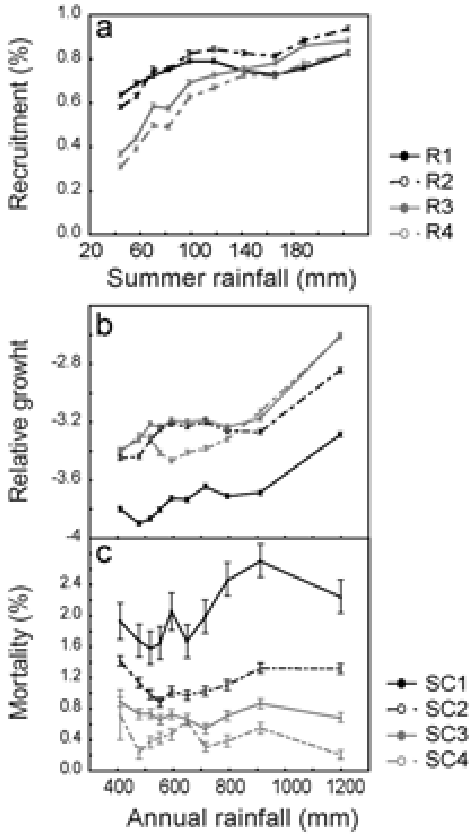


Figure B3. *Geographic variation across the rainfall gradient of recruitment, relative growth and mortality by size-classes. Averages in these variables were calculated for 10 annual rainfall quantiles for all species grouped. Standard errors illustrate the observed variation in each quantile.*

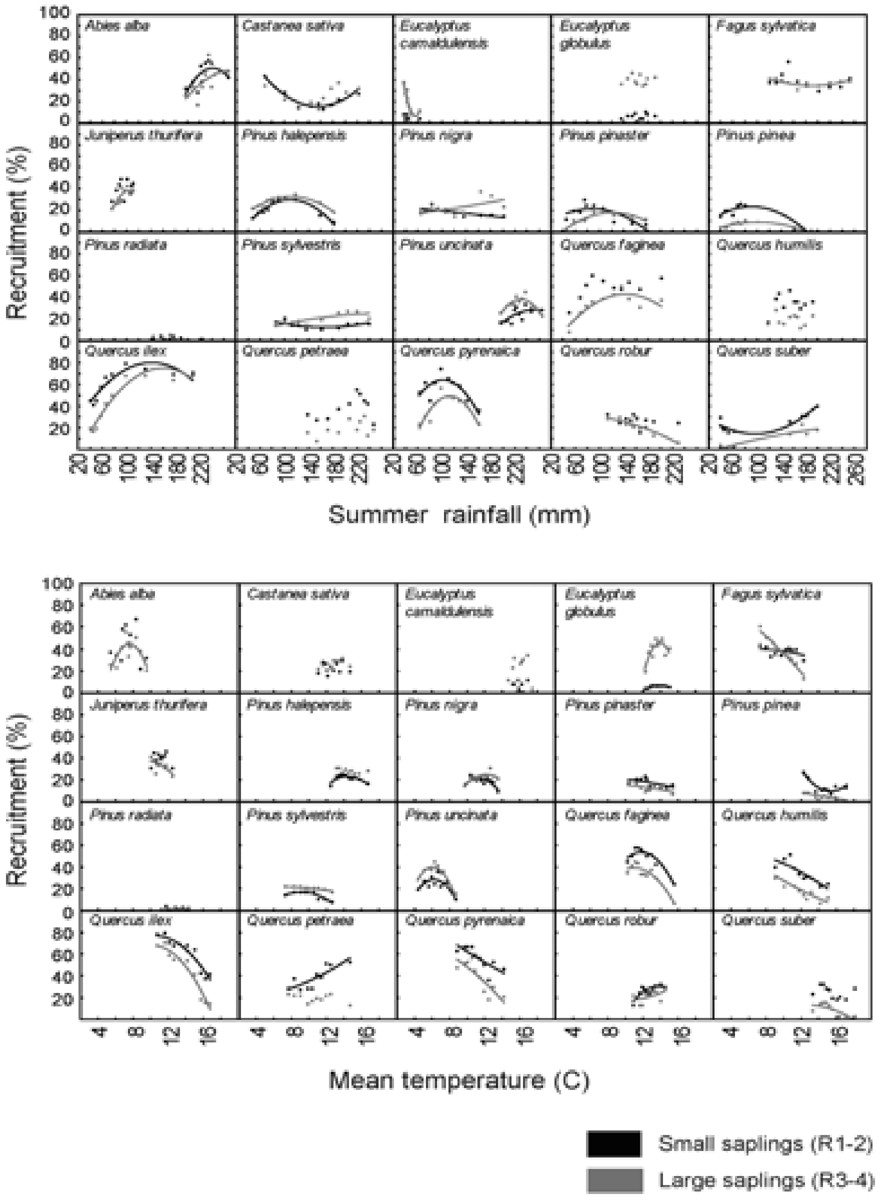


Figure B4. *Species-specific trends in recruitment success along the rainfall gradient for small saplings (R1-2; black dots and lines) and large saplings (R3-4, grey dots and lines). When significant, linear and polynomial fits are provided*

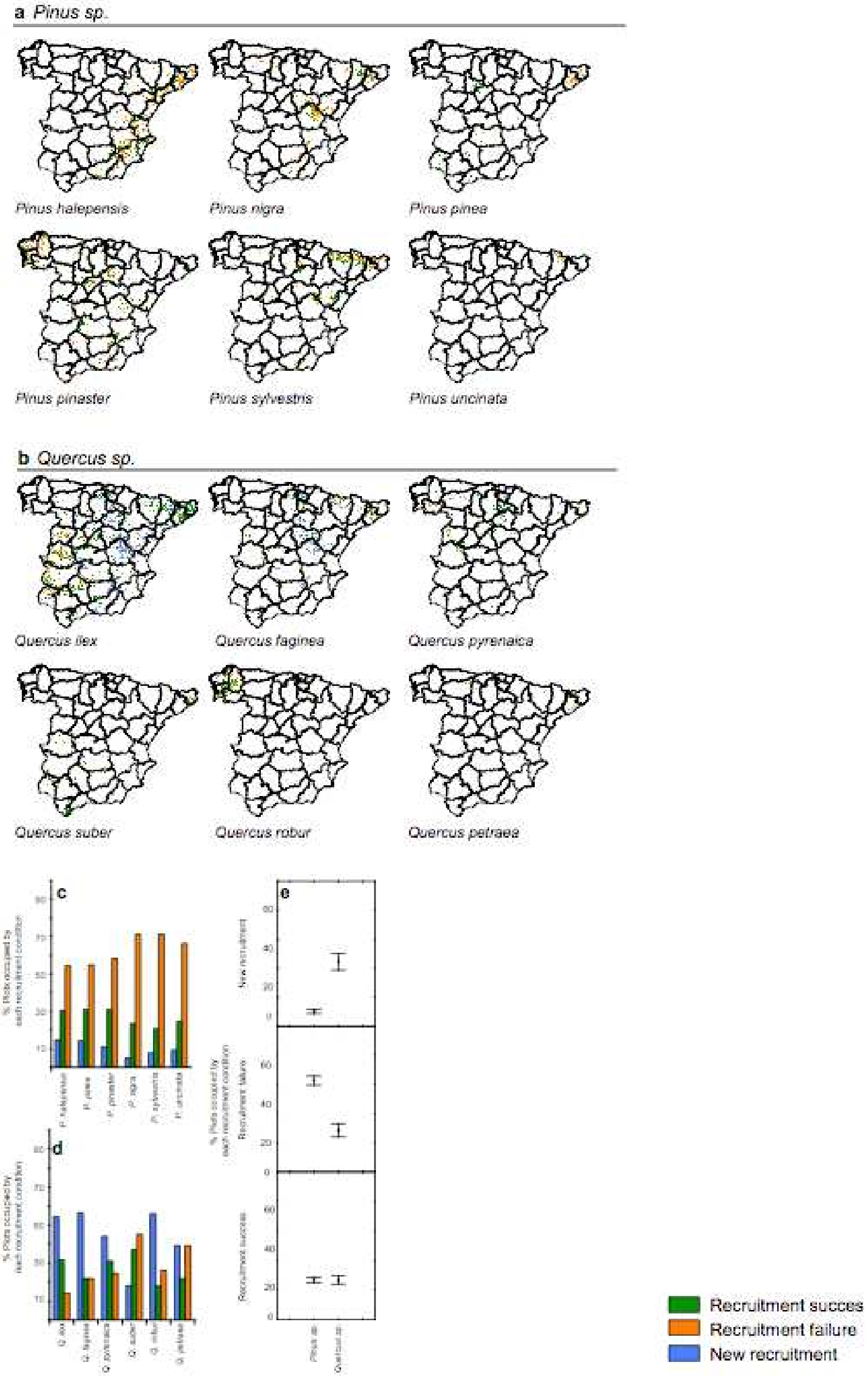


Figure B5. *Comparison of recruitment patterns between the dominant genus Pinus and Quercus. a) Recruitment succes maps in the size-class R1 for 6 Pinus species. b) Recruitment succes maps in the size-class R1 for six Quercus species. (c) Percentage of grids with new recruitment (blue), recruitment succes (green) and recruitment failure (orange)) for each Pinus species. (d) Percentage of grids with new recruitment (blue), recruitment succes (green) and recruitment failure (orange)) for each Quercus species. e) Comparison of the percentage of grids of new recruitment, recruitment succes and failure between Pinus and Quercus.*

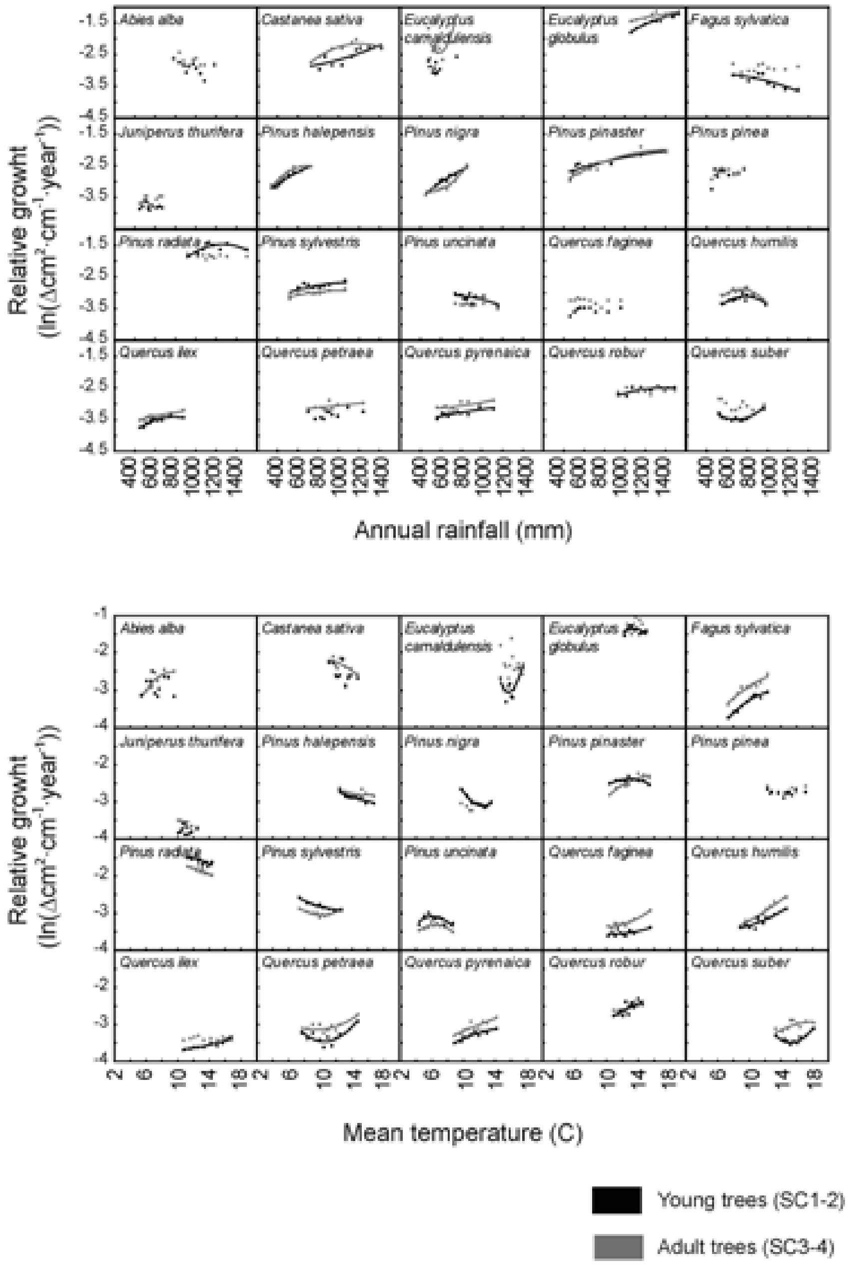


***Figure B6**. Species-specific trends in relative growth along the rainfall gradient for small (SC1-2, black dots and lines) and large trees (SC3-4, grey dots and lines). When significant, linear and polynomial fits are provided.*

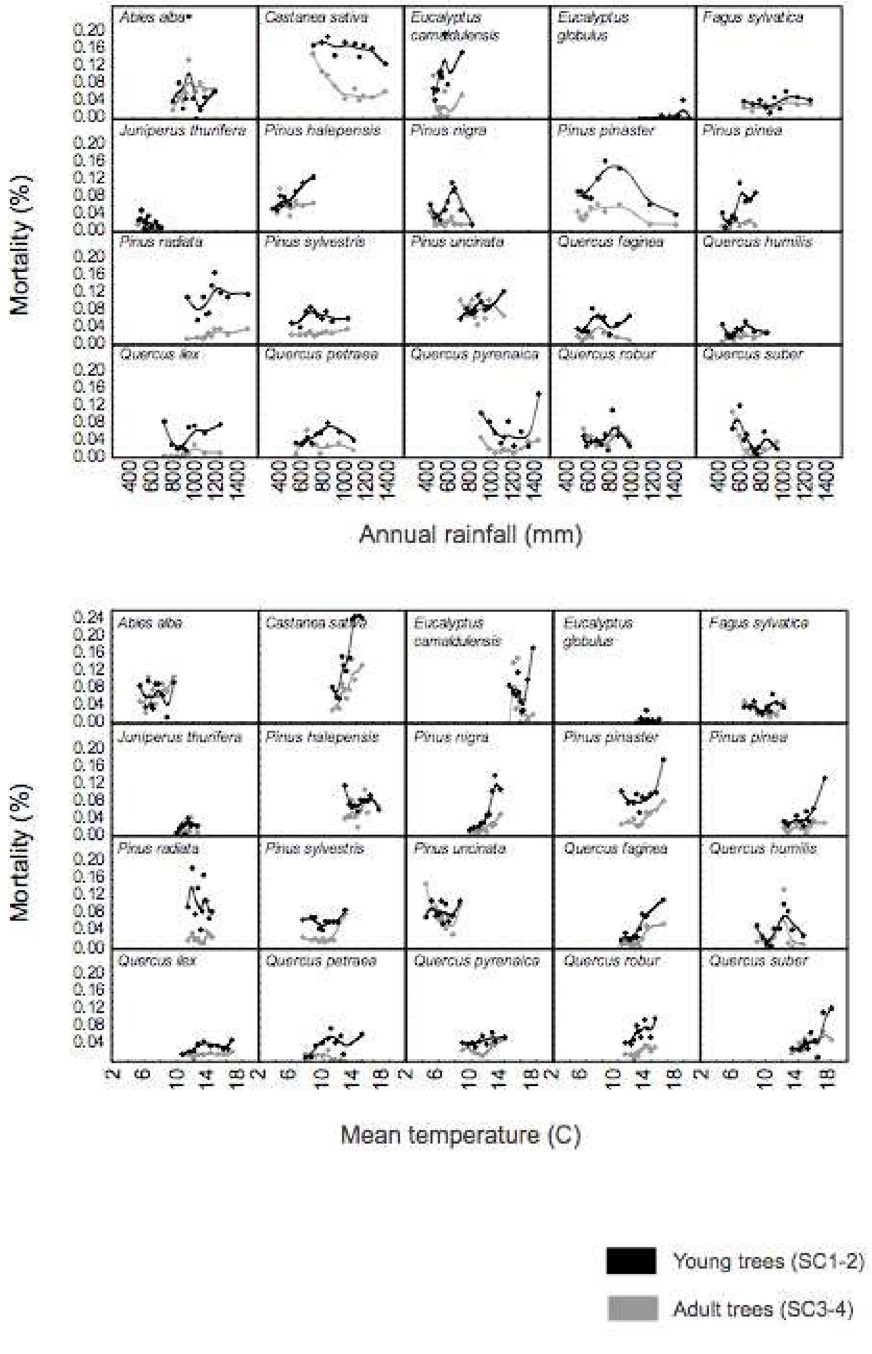


__Figure B7.__ Species-specific trends in percentage of standing mortality along the rainfall gradient for small (SC1-2, black dots and lines) and large trees (SC3-4, grey dots and lines). Distance-weighted fits are plotted (black and grey lines).

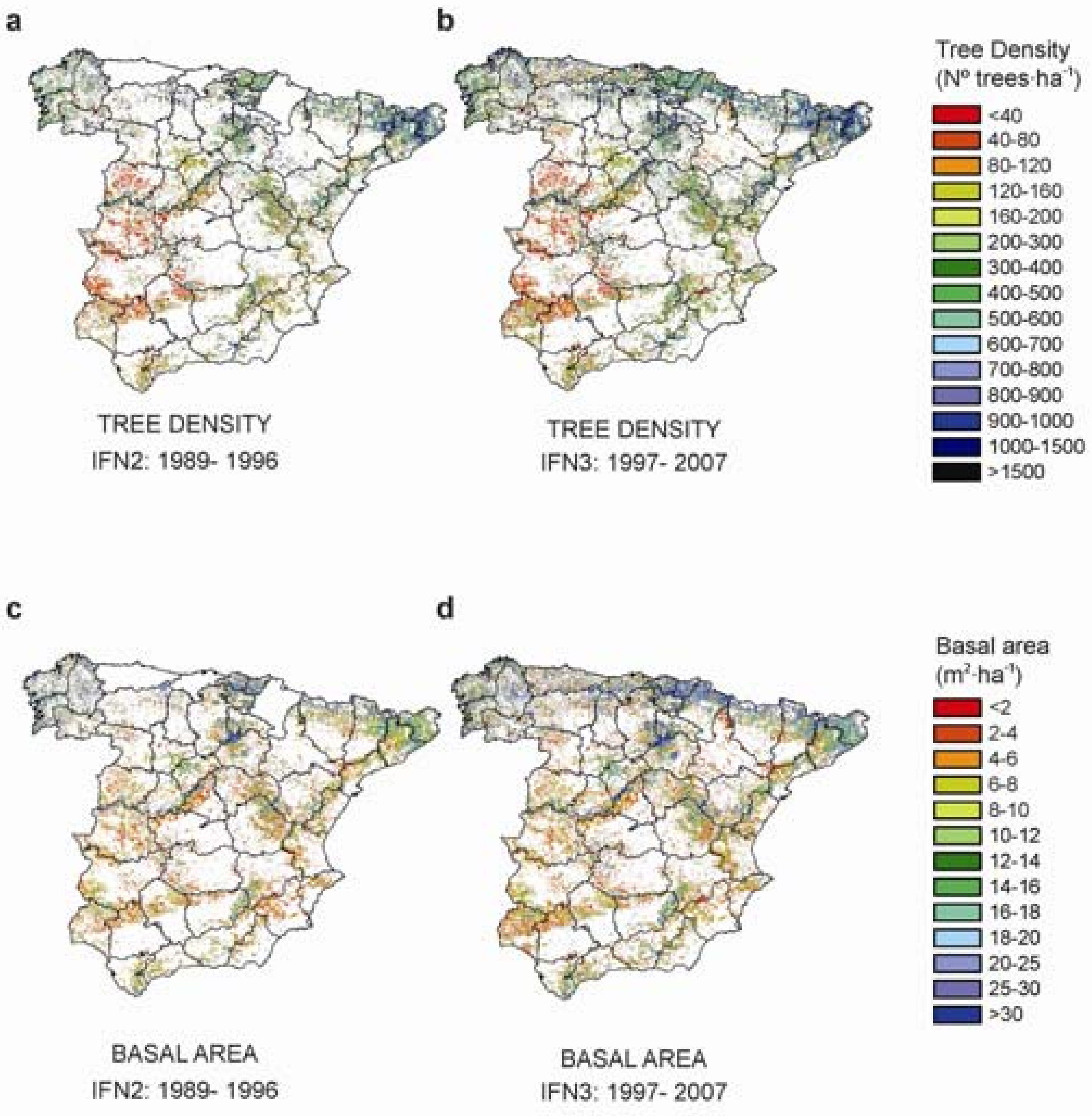


Figure B8. *Maps of tree density and basal area in IFN2 and IFN3.*

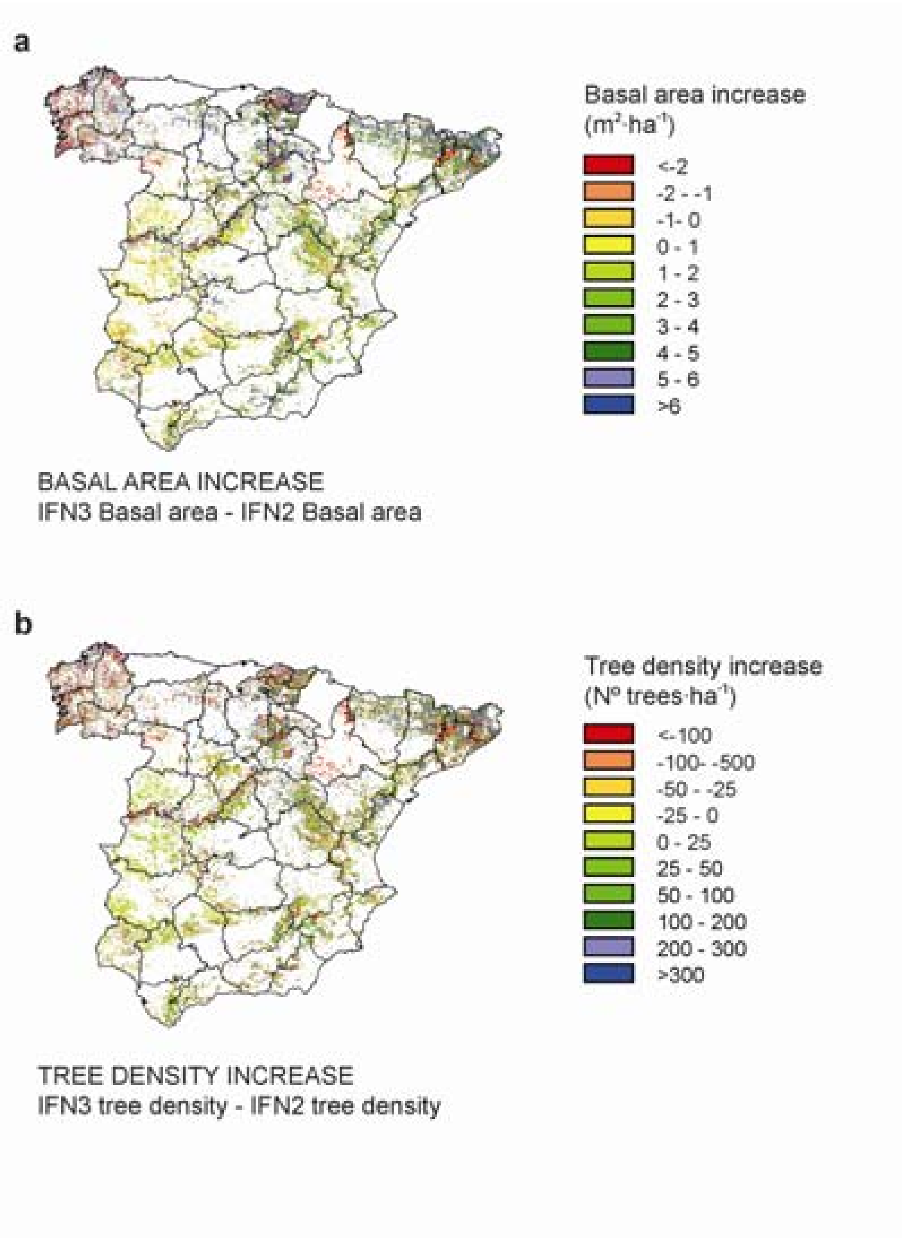


Figure B9. *Maps of basal area increase and tree density increase between IFN2 and IFN3 inventories.*

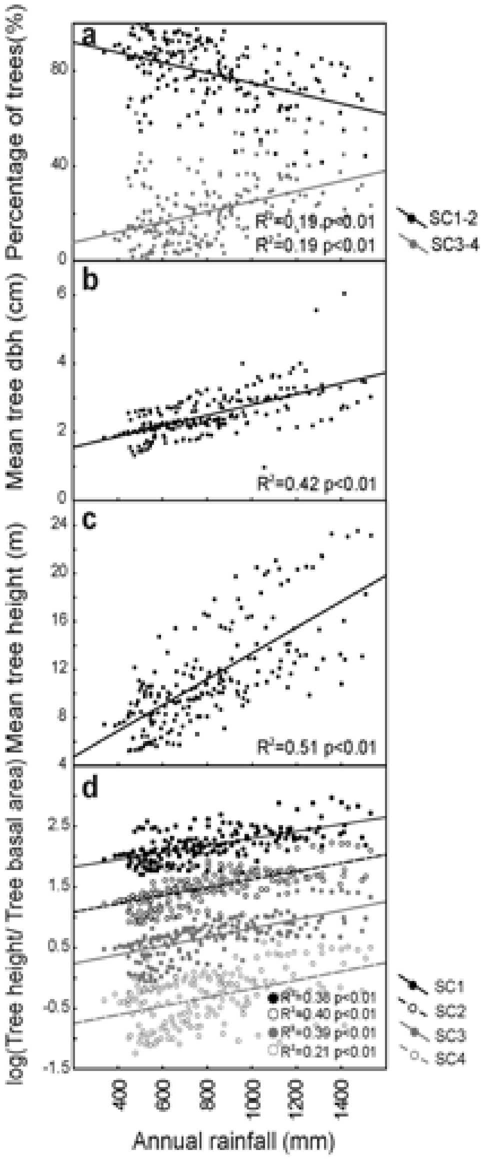


Figure B10. *Geographical variation for all species grouped of (a) percentage of trees by size classes (SC1-2; SC3-4), (b) Mean tree DBH, (c) mean tree height, and (d) tree height/DBH ratio by size classes (SC1-SC4) across the rainfall gradient.*

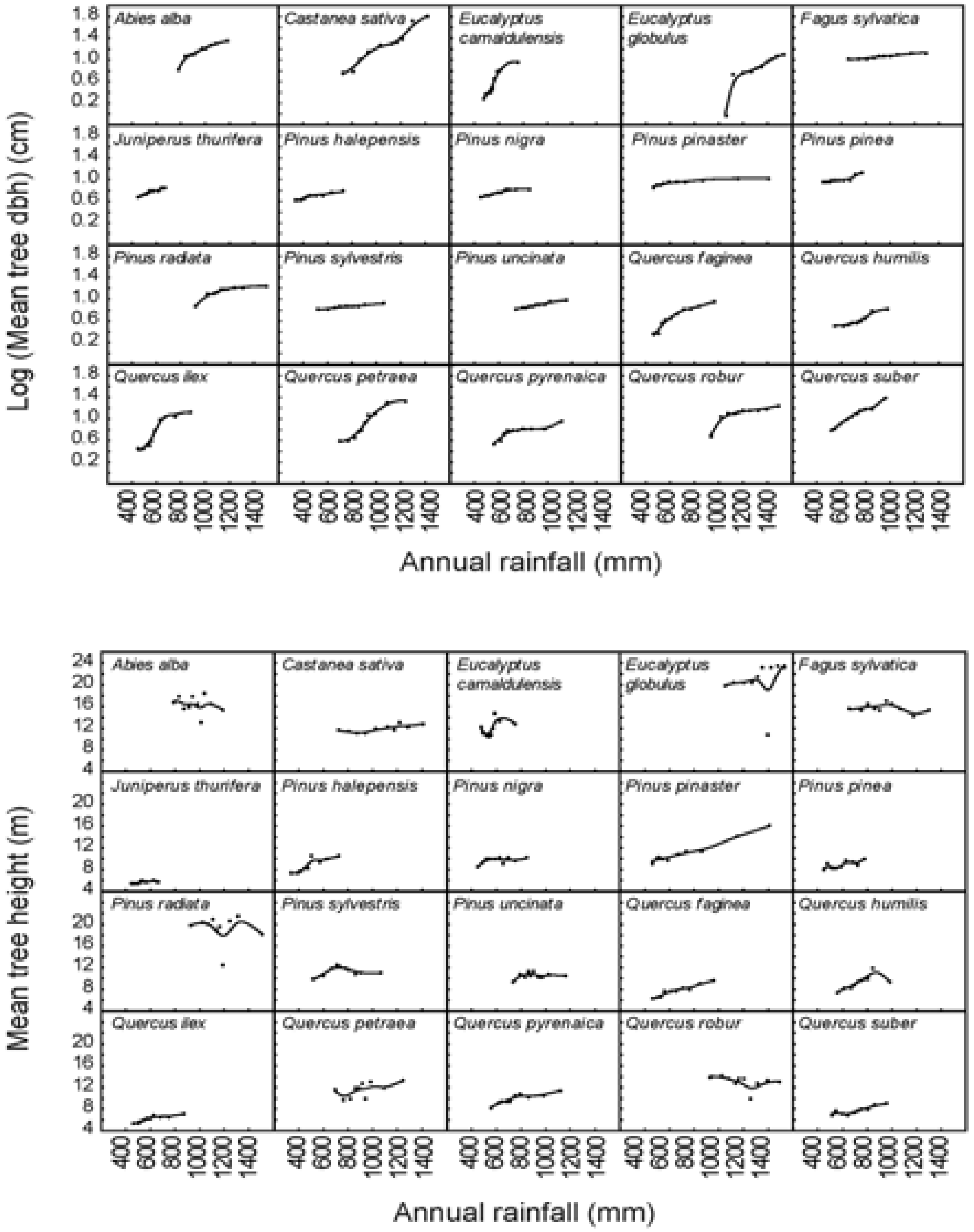
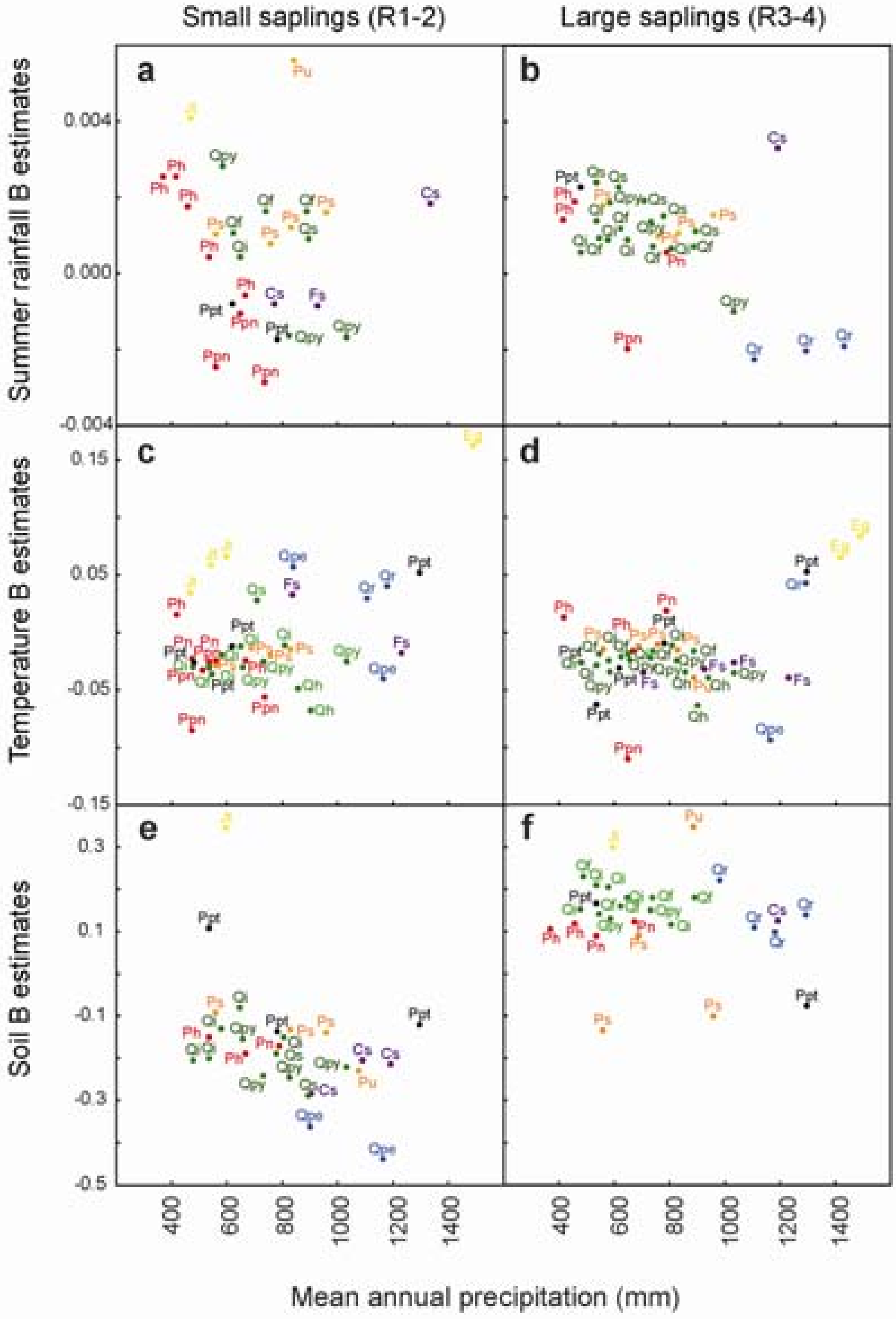


Figure B11. Species-specific patterns of variation of mean tree DBH and height across the rainfall gradient.


Small saplings (R1-2)
Large saplings (R3-4)
a
b
c
d
e
f
Summer rainfall B estimates
0.004
0.000
-0.004
Temperature B estimates
0.15
0.05
-0.05
-0.15
Soil B estimates
0.3
0.1
-0.1
-0.3
-0.5
400
600
800
1000
1200
1400
Mean annual precipitation (mm)

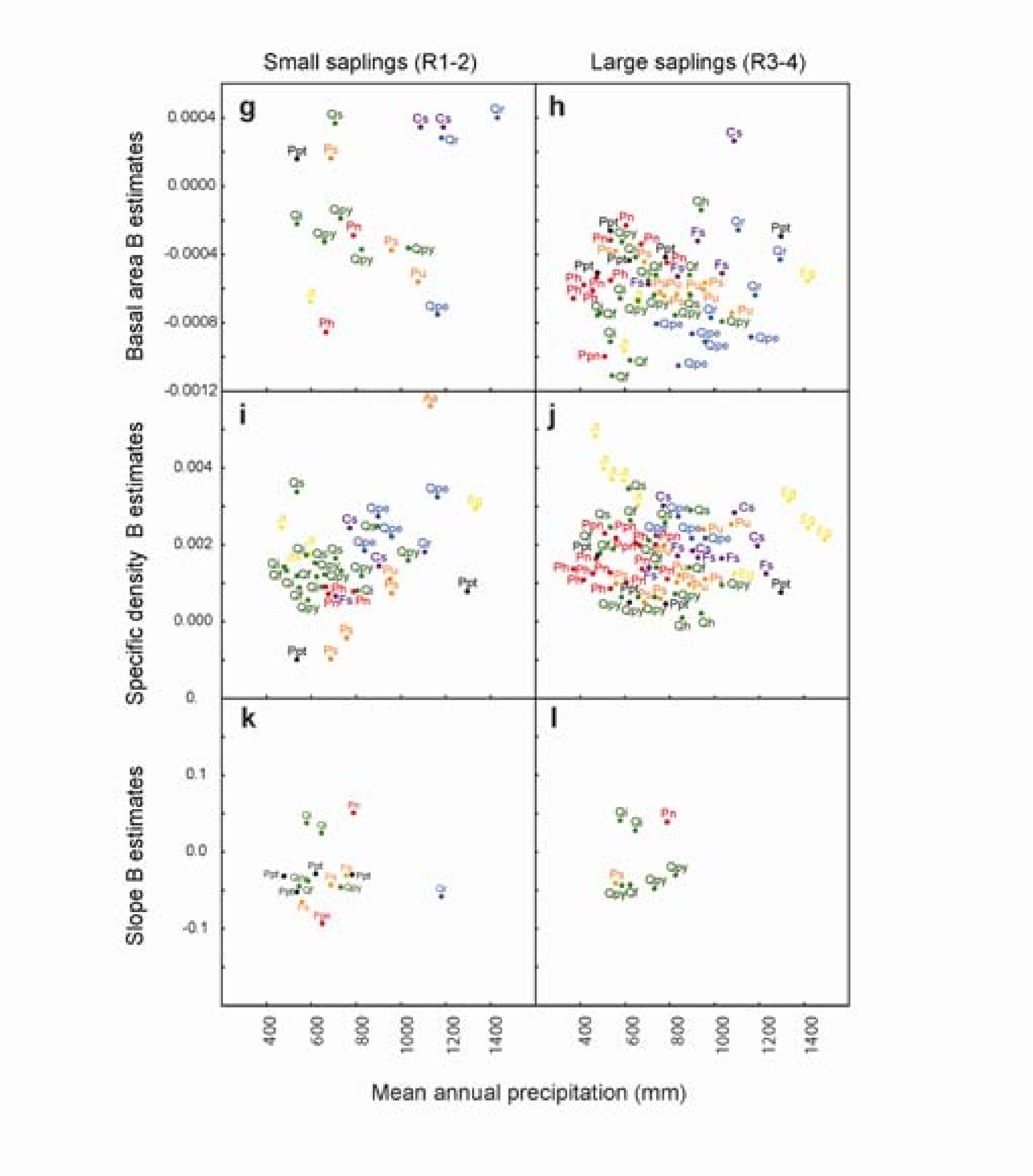


Figure B12. *Geographical variation in the effects (β coefficient values) of summer rainfall (a-b), temperature (c-d), organic layer depth (e-f), basal area (g-h), species-specific density (i-j) and terrain slope (k-l) on recruitment (quantile modelling, Q20). We divided each species in five rainfall quantiles and recruitment was independently modelled for each one. Small (R1-R2) and large (R3-R4) saplings were independently modelled. β estimates for all tree species and quantiles were plotted.*

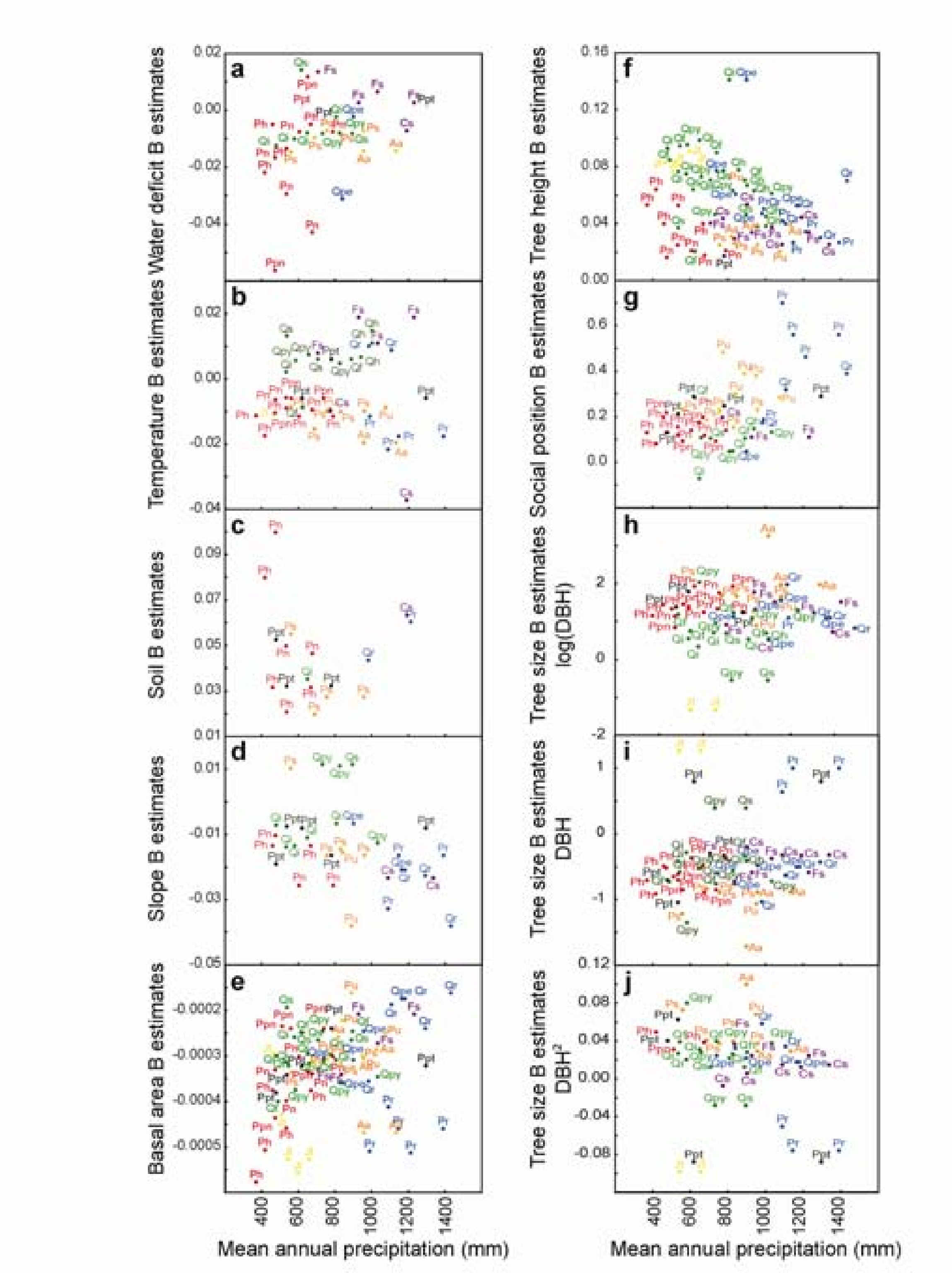


Figure B13. *Geographical variation in the effects (β coefficient values) of water deficit (a), temperature (b), organic layer depth (c), slope (d), basal area (e), height (f), social position (g) and size (h-j) on growth (quantile modelling, Q20). β estimates for all tree species and quantiles were plotted.*

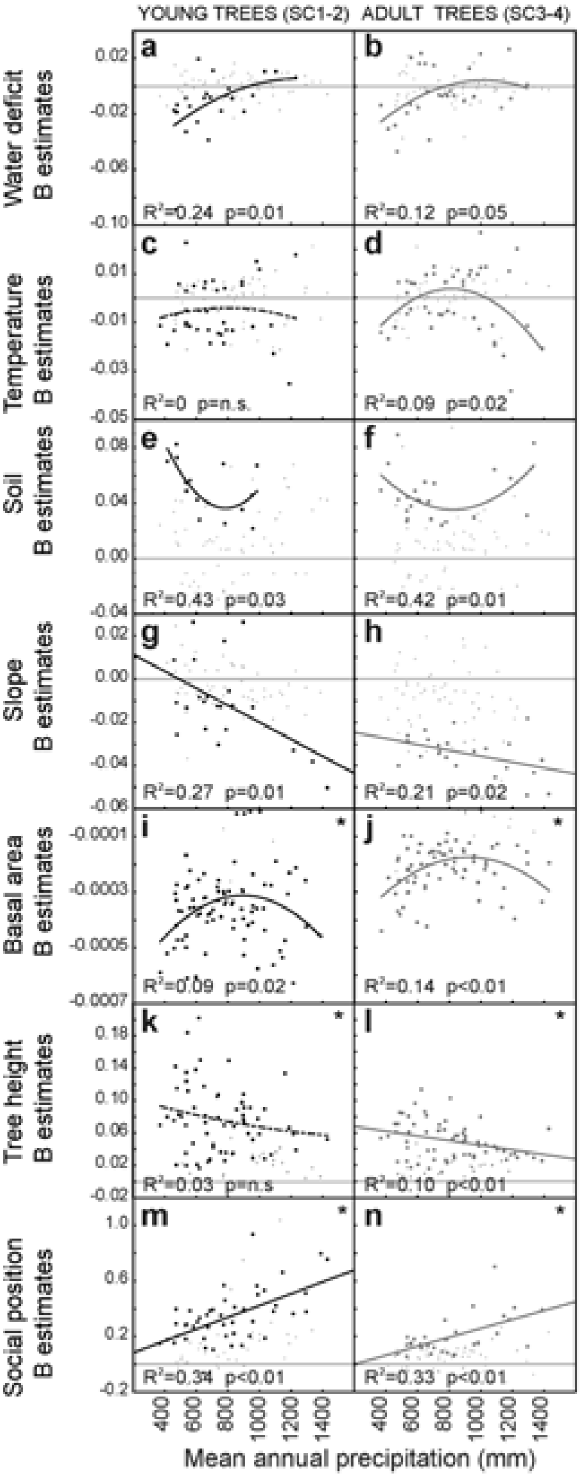


Figure B14. *Geographical variation in the effects (β coefficient values) of water deficit (a-b), temperature (c-d), organic layer depth (e-f), slope (g-h), basal area (i-j), height (k-l), and social position (m-n) on size-specific growth models (quantile modelling, Q20).*

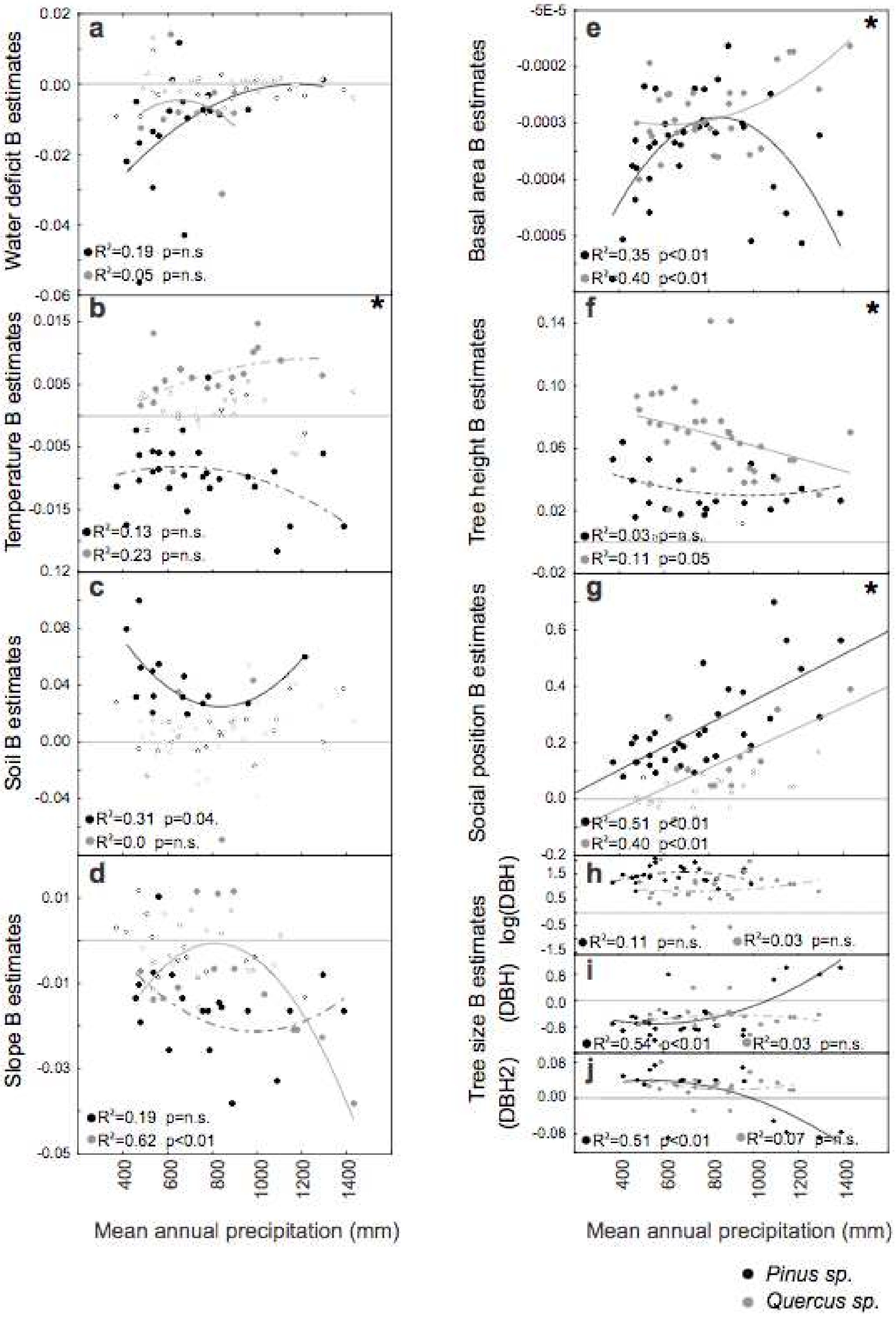


***Figure B15**. Geographical variation in the effects (β coefficient values) for Pinus (black dots and lines) and Quercus species (grey dots and lines) of water deficit (a), temperature (b), organic layer depth (c), slope (d), basal area (e), height (f), social position (g) and size (h-j) on growth (quantile modelling, Q20).*

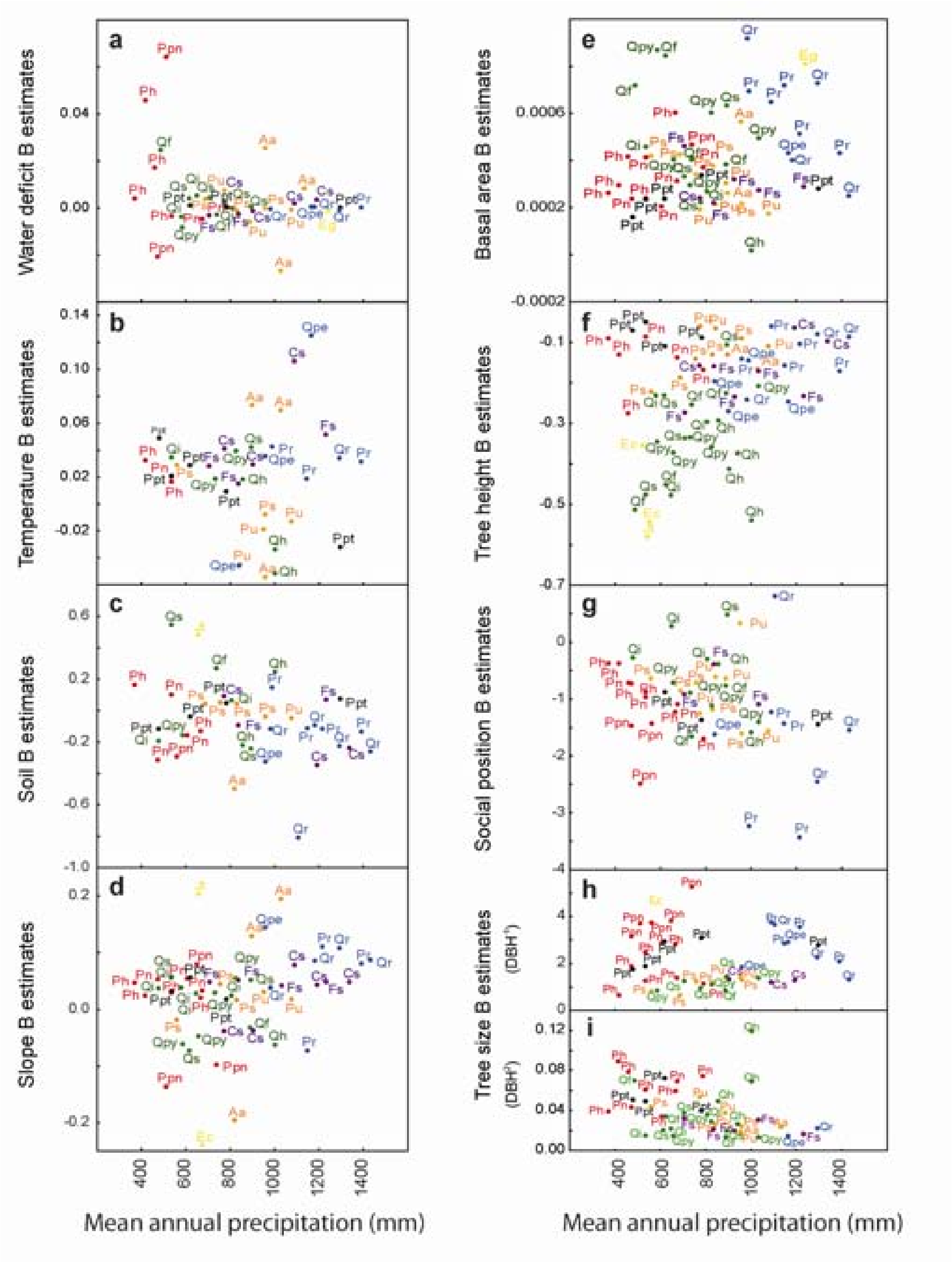


***Figure B16**. Geographical variation in the effects (β coefficient values) of water deficit (a), temperature (b), organic layer depth (c), slope (d), basal area (e), height (f), social position (g) and size (h-i) on mortality (quantile modelling, Q20).*

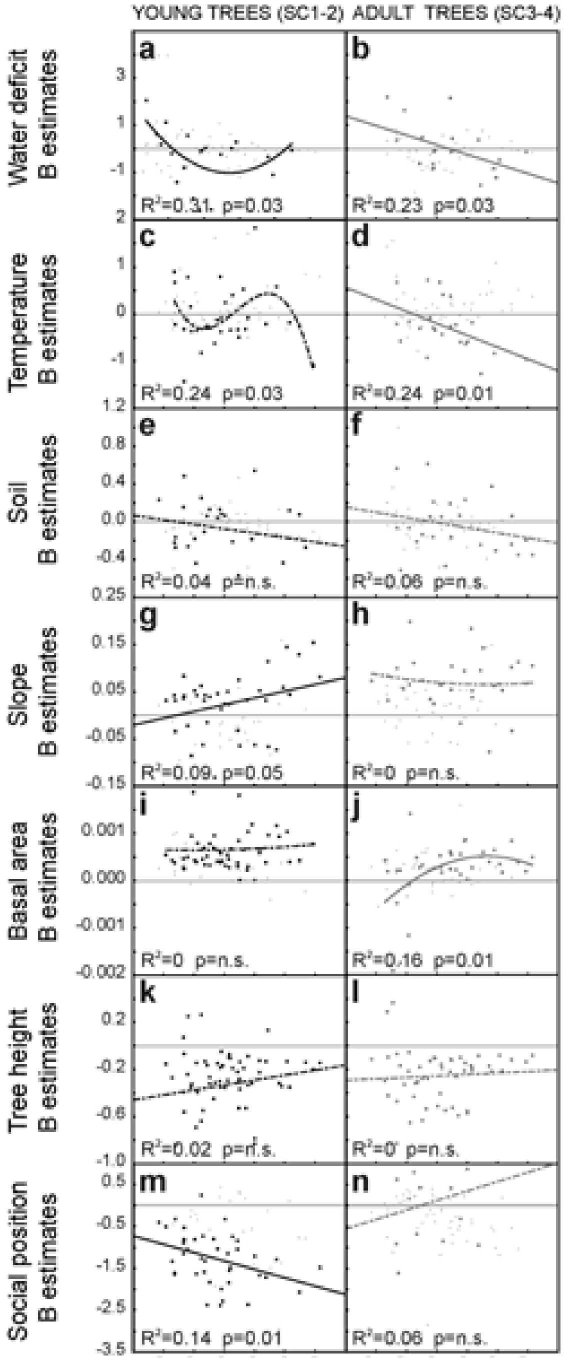


***Figure B17**. Geographical variation in the effects (β coefficient values) of water deficit (a-b), temperature (c-d), organic layer depth (e-f), slope (g-h), basal area (i-j), height (k-l), and social position (m-n) on size-specific mortality models (quantile modelling, Q20).*

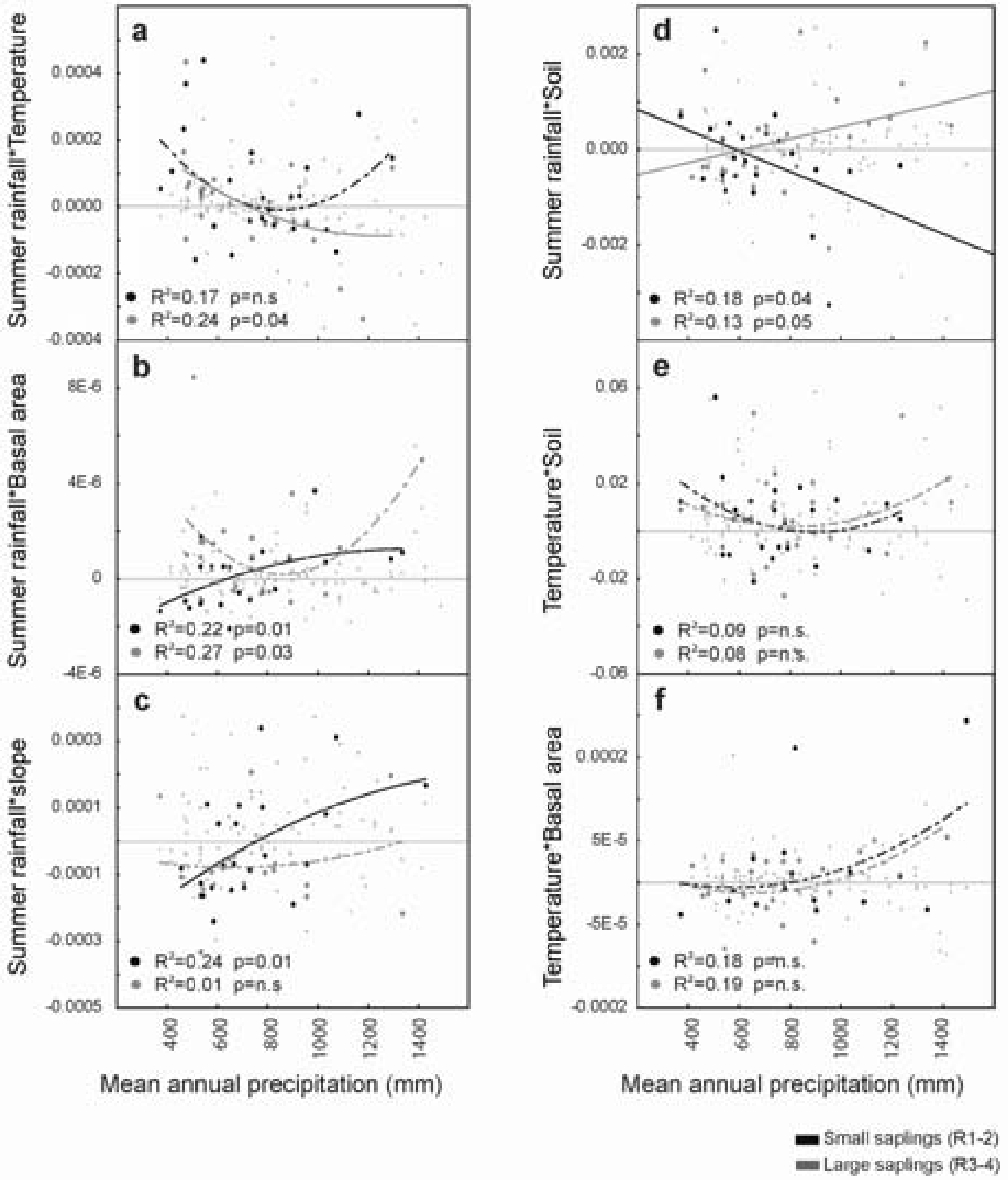


Figure B18. *Geographical variation in the effects of interactions between explanatory factors in recruitment models (quantile modelling, Q20). Black dots and lines indicate small saplings trends (R1-2). Grey lines illustrate large saplings trends (R3-4). Dotted lines indicate non-significant trends.*

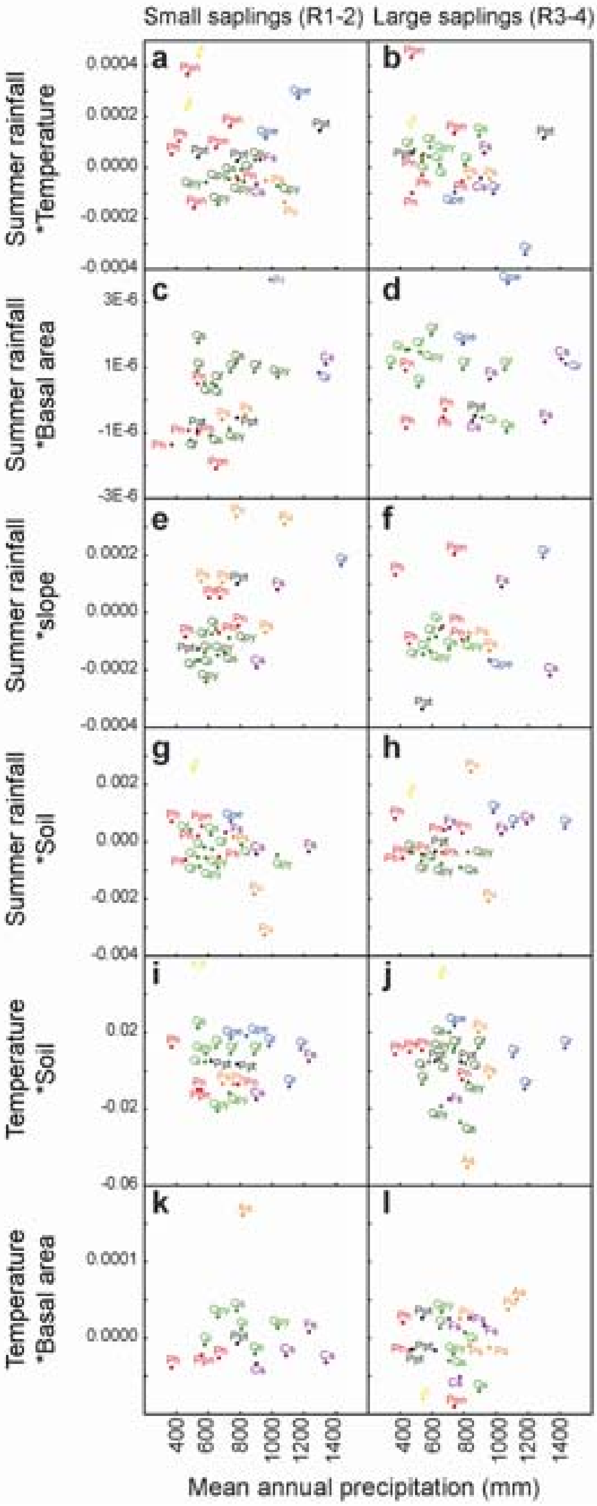


***Figure B19**. Geographical variation in the effects of interactions between explanatory factors in recruitment models (quantile modelling, Q20). The name of each species is labelled.*

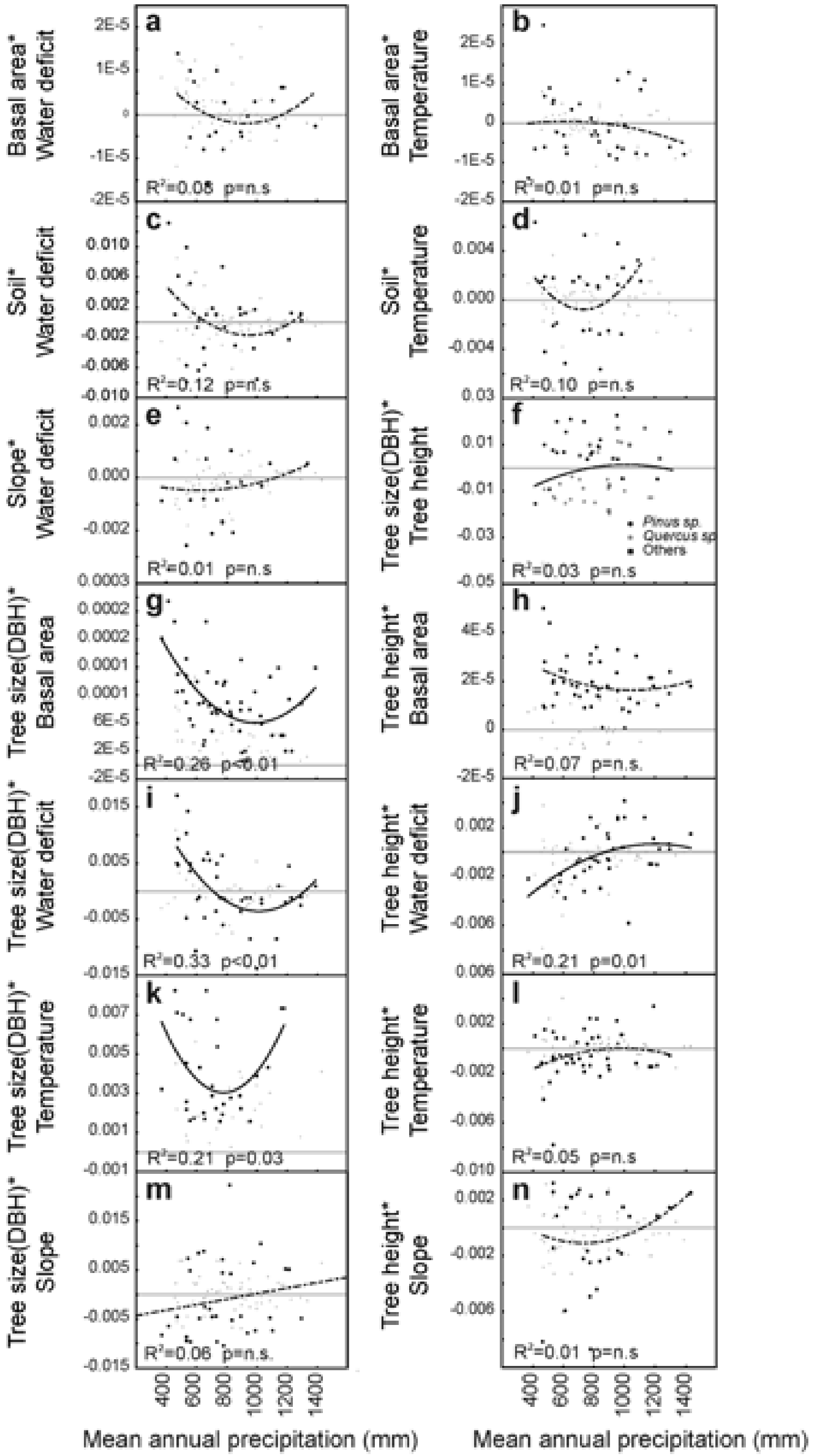
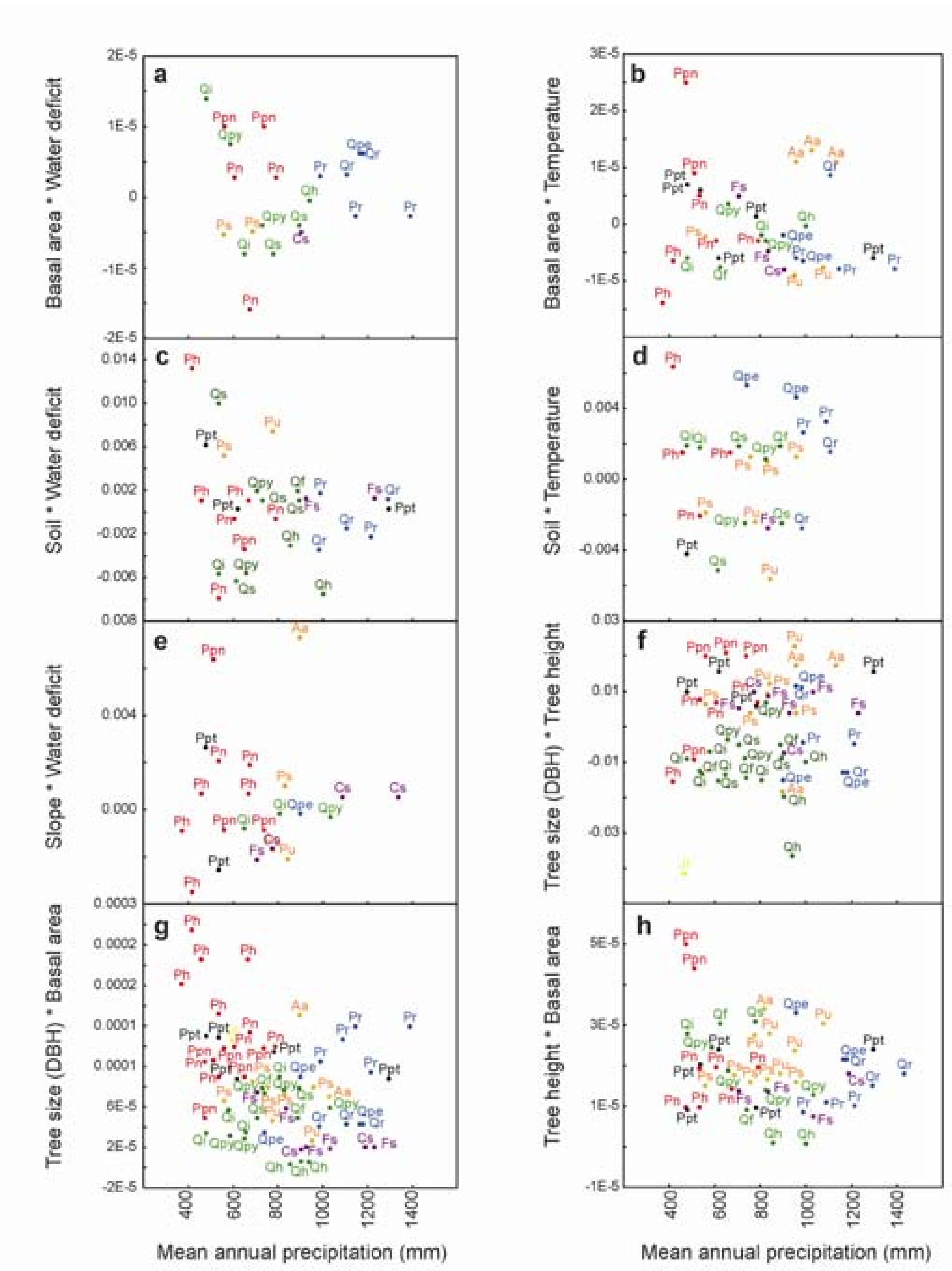


Figure B20. *Geographical variation in the effects of interactions between explanatory factors in growth models (quantile modelling, Q20).*


a
Basal area * Water deficit
2E-5
1E-5
0
-1E-5
-2E-5
b
Basal area * Temperature
3E-5
2E-5
1E-5
0
-1E-5
c
Soil * Water deficit
0.014
0.010
0.006
0.002
-0.002
-0.006
0.008
d
Soil * Temperature
0.004
0.000
-0.004
0.03
e
Slope * Water deficit
0.004
0.000
0.0003
f
Tree size (DBH) * Tree height
0.01
-0.01
-0.03
g
Tree size (DBH) * Basal area
0.0002
0.0002
0.0001
0.0001
6E-5
2E-5
-2E-5
h
Tree height * Basal area
5E-5
3E-5
1E-5
-1E-5
400
600
800
1000
1200
1400
Mean annual precipitation (mm)
Mean annual precipitation (mm)

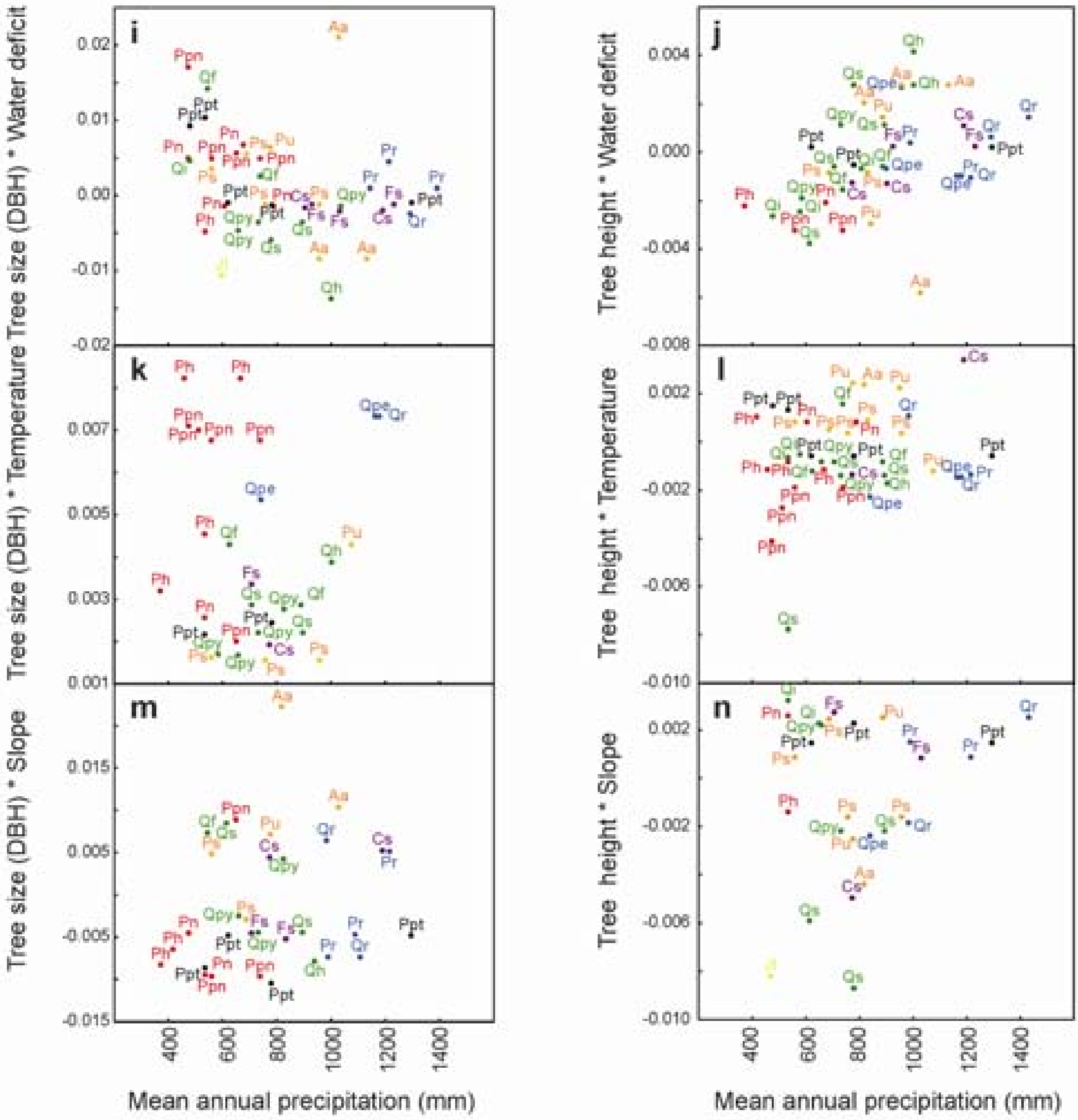


Figure B21. *Geographical variation in the effects of interactions between explanatory factors in growth models (quantile modelling, Q20) with the name of each species labelled*

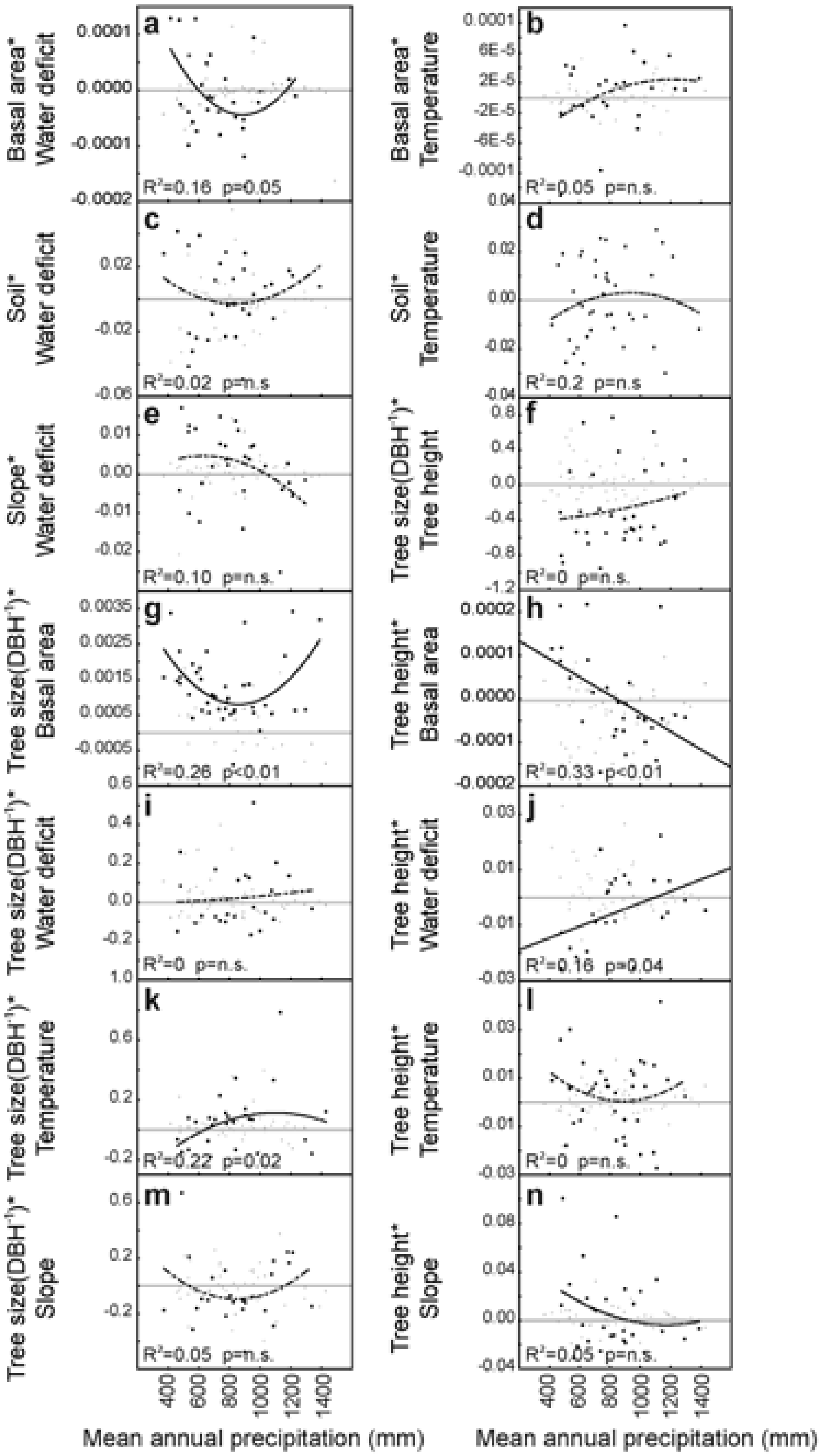
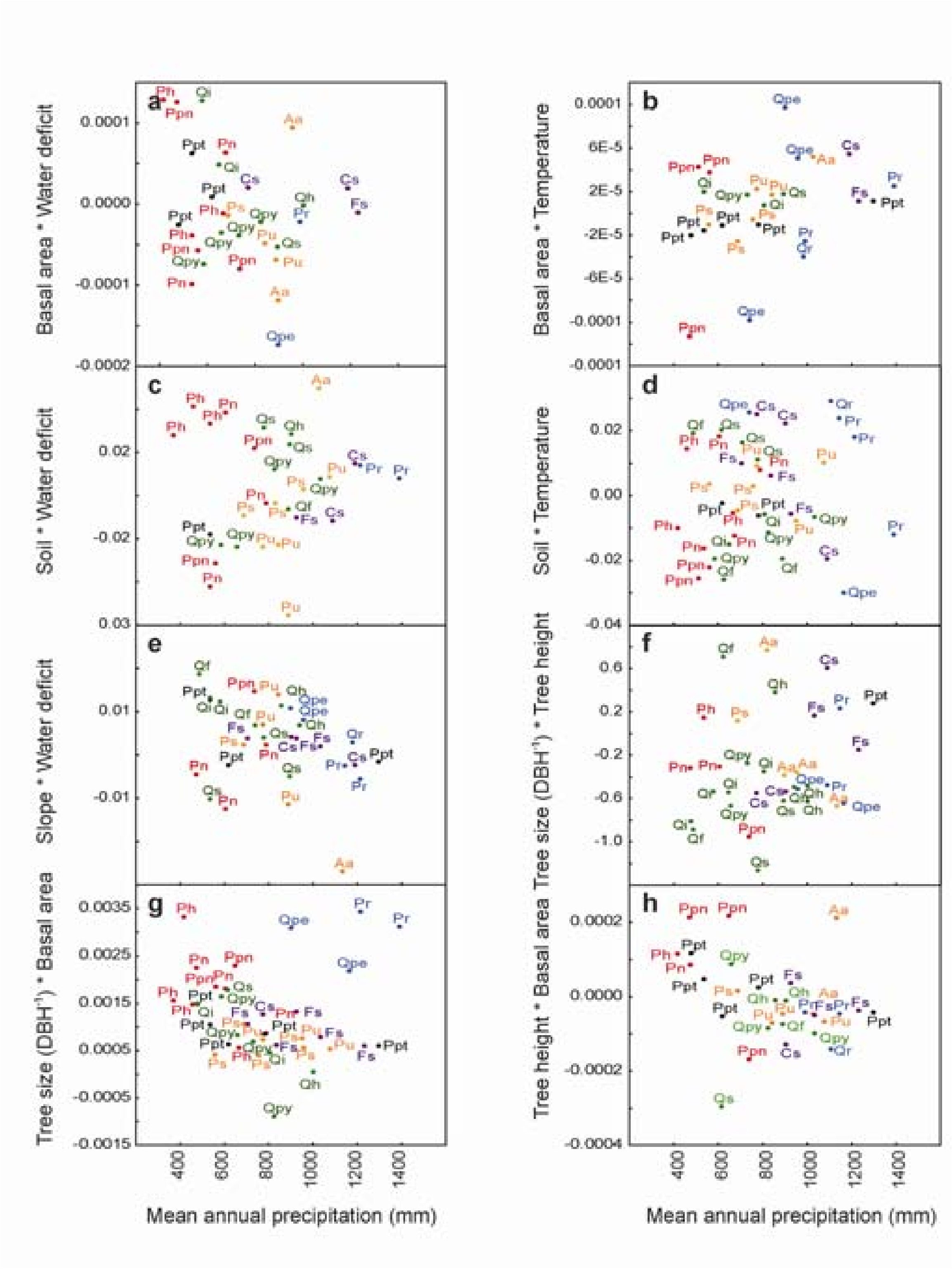


***Figure B22**. Geographical variation in the effects of interactions between explanatory factors in mortality models (quantile modelling, Q20).*


a
Basal area * Water deficit
0.0001
0.0000
-0.0001
-0.0002
b
Basal area * Temperature
0.0001
6E-5
2E-5
-2E-5
-6E-5
-0.0001
-0.0001
c
Soil * Water deficit
0.02
-0.02
0.03
d
Soil * Temperature
0.02
0.00
-0.02
-0.04
e
Slope * Water deficit
0.01
-0.01
f
Tree size (DBH^{-1}) * Tree height
0.6
0.2
-0.2
-0.6
-1.0
g
Tree size (DBH^{-1}) * Basal area
0.0035
0.0025
0.0015
0.0005
-0.0005
-0.0015
h
Tree height * Basal area
0.0002
0.0000
-0.0002
-0.0004
400
600
800
1000
1200
1400
Mean annual precipitation (mm)
Mean annual precipitation (mm)

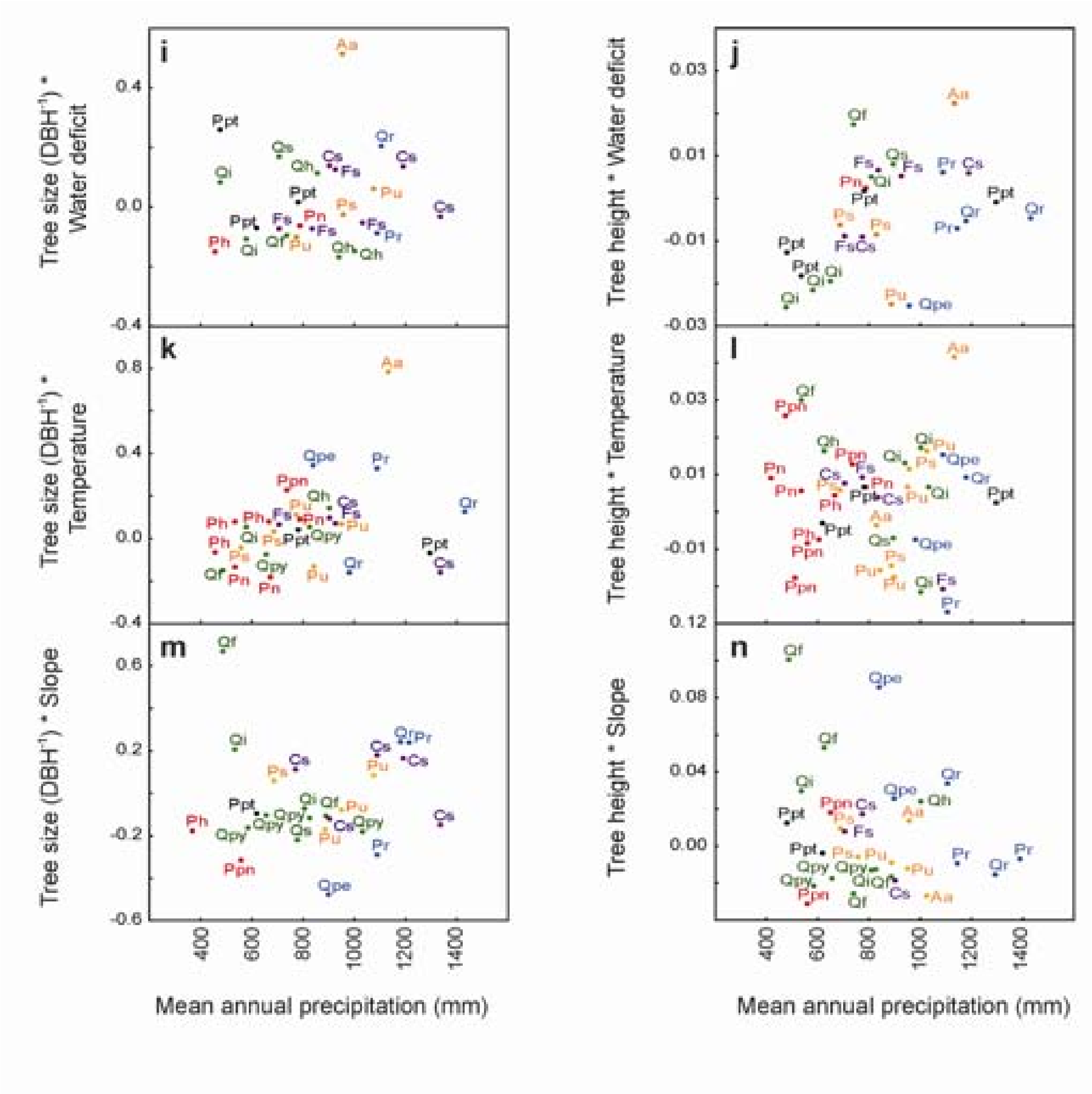


Figure B23. *Geographical variation in the effects of interactions between explanatory factors in mortality models (quantile modelling, Q20) with the name of each species labelled.*

3.8. Supplementary text

This appendix provides a brief summary of the main species-specific responses observed in the recruitment, growth and mortality models. We highlight the more important effects detected and list the species that followed the reported patterns.

3.8.1. Recruitment models

1.1-Summer rainfall effects:

Positive effects (in the drier edge): *J. thurifera, Q. ilex, Q. faginea, Q. suber, P. halepensis*

Negative effects: *P. nigra, P. pinaster, Q. robur.*

Variable effects (+/-): *Q. pyrenaica* (ranging from positive in dry sites to negative in wet sites)

1.2- Negative effects of organic layer depth in small recruits:

P. halepensis, P. sylvestris, Q. ilex, Q. pyrenaica, Q. suber, Q. petraea

1.3- Positive effects of organic layer depth in large recruits:

P. halepensis, P. nigra, Q. ilex, Q. faginea, Q. pyrenaica, Q. robur

1.4- Negative effects of temperature on recruitment*:*

P. pinaster, P. sylvestris, Q. ilex, Q. faginea, Q.pyrenaica, Q. humilis, Q. pyrenaica, F. sylvatica.

1.5- Negative effects of basal area on recruitment:

P. halepensis, P. nigra, P. pinaster, P. sylvestris, P. uncinata, Q. ilex, Q. suber, Q. pyrenaica, Q. faginea, Q. robar, Q. petraea, F. sylvatica.

1.6- Slope effects on recruitment:

Positive: *P. nigra, Q. ilex.*

Negative: *P. pinaster, P sylvestris, Q. pyrenaica*.

Interactions among driving factors in recruitment models:

*1.7- Temperature*summer rain*: greater recruitment in warm areas facilitated by summer rain

J. thurifera, P. halepensis, P. pinea

*1.8- Summer rain*soil:* higher recruitment success in areas of higher organic layer depth and increased summer rain.

J. thurifera, P. halepensis, P. pinea, Q. suber, Q. faginea.

1.9- *Rainfall*basal area*

· Negative interaction: increased recruitment in humid areas with reduced basal area and/or increased recruitment in dry areas with elevated basal area.

P. halepensis, P. pinea, P. pinaster, P. nigra, P. sylvestris, Q. faginea.

· Positive interaction: increased recruitment in humid areas with elevated basal area.

Q. ilex, Q. suber, Q. faginea, Q. pyrenaica.

3.8.2. Growth models

2.1- Water deficit on growth:

Negative: *P. halepensis, P. pinea, P. sylvestris, A. alba, Q. ilex, Q. humilis, Q. pyrenaica, Q. robur.*

Positive and negative: *P. pinaster; P. nigra* (mainly negative), *Q. suber*;

Positive: *J. thurifera, F. sylvatica*.

2.2- Temperature effects on growth:

Positive: *Q. ilex* (weak), *Q. humilis, Q. suber, Q. pyrenaica, Q. robur, F. sylvatica*,

Negative: *J. thurifera, P. halepensis, P. pinea, P. pinaster, P. nigra, P. sylvestris, P. uncinata, A. alba, C. sativa*

Positive and negative: *Q. faginea*.

2.3-Positive soil effects on growth

Mainlyobserved in *Pinus* (*P. halepensis, P. nigra, P. sylvestris, P. pinaster, P. radiata*)

Also reported in *Q. ilex, C. sativa, Q. robur*.

2.4- Slope effects on growth (observed mainly in *Pinus*):

Negative: P. halepensis, P. Pinaster, P. nigra, P. sylvestris, P. radiata, P uncinata, Q. ilex, Q. robur, Q. petraea, C. sativa.

Positive and negative: Q. pyrenaica.

2.5- Widespread negative basal area effects on growth:

J. thurifera, P. halepensis, P. pinea, P. nigra, P. pinaster, P. sylvestris, P. radiata, P. uncinata, A. alba. Q. ilex, Q. suber. Q. pyrenaica, Q. faginea, Q. humilis, Q. robur, Q. petraea,

C. sativa.

2.6- Widespread positive effects of tree height on growth:

J. thurifera, P. halepensis, P. pinaster, P. nigra, P.sylvestris, P. radiata, P. uncinata, Q. ilex, Q. suber, Q. pyrenaica, Q. faginea, Q. humilis, Q. robur, Q. petraea, F. sylvestris, C. sativa.

3.8.3. Mortality models

3.1- Widespread strong positive effects of basal area on mortality

P. halepensis, P. pinea, P. pinaster, P. nigra, P. sylvestris, P. radiata, P. uncinata, A. alba, E. globulus, Q. ilex, Q. suber, Q. pyrenaica, Q. faginea, Q. robur, Q. petraea, C.sativa, F. sylvatica.

3.2- Strong positive effects of temperature on mortality in *Pinus* relative to *Quercus*

P. nigra, P. pinaster, P. sylvestris, P. radiata, P. uncinata

3.3- Stronger negative effects of tree height on mortality in Quercus relative to Pinus species

Q. ilex, Q. faginea, Q. pyrenaica, Q. humilis.

3.4- Stronger effects of tree DBH on *Pinus* mortality than in *Quercus* species

P. halepensis, P. pinea, P. pinaster, P nigra.

Interactions among mortality driving factors:

3.5- Stronger effects of the interaction “DBH*stand basal area” on *Pinus* mortality than in *Quercus.*

P. halepensis, P. pinea, P. pinaster, P. nigra, P. sylvestris, P. radiata, P. uncinata.

Chapter 4: Large-scale recruitment limitation in Mediterranean pines: the role of *Quercus ilex* and forest successional advance as key regional drivers.

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Carnicer, J., Coll, M., Pons, X., Ninyerola, M., Vayreda, J. and Peñuelas, J. (2014), Large-scale recruitment limitation in Mediterranean pines: the role of *Quercus ilex* and forest successional advance as key regional drivers. Global Ecology and Biogeography, 23: 371–384.

4.1. Abstract

Aim: Large-scale patterns of limitations in tree recruitment remain poorly described in the Mediterranean Basin, and this information is required to assess the impacts of global warming on forests. Here we unveil the existence of opposite trends of recruitment limitation between the dominant genera *Quercus* and *Pinus* on a large scale and identify the key ecological drivers of these diverging trends.

Location: Spain.

Methods: We gathered data from the Spanish National Forest inventory to assess recruitment trends for the dominant species (*Pinus halepensis*, *P. pinea*, *P. pinaster*, *P. nigra*, *P. sylvestris*, *P. uncinata*, *Quercus suber*, *Q. ilex*, *Q. petraea*, *Q. robur*, *Q. faginea* and *Q. pyrenaica)*. We assessed the direct and indirect drivers of recruitment by applying Bayesian structural equation modeling techniques.

Results: Severe limitations in recruitment were observed across extensive areas in all *Pinus* species studied, with recruitment failure affecting 54-71% of the surveyed plots. In striking contrast, *Quercus* species expanded into 41% of the plots surveyed versus only 10% for *Pinus* and had a lower local recruitment failure (29% of *Quercus* localities compared to 63% for *Pinus* species). Bayesian structural equation models highlighted the key role of the presence of *Q. ilex* saplings and the increase in the basal area of *Q. ilex* in limiting *Pinus* recruitment in five *Pinus* species*.* The recruitment of *P. sylvestris* and *P. nigra* showed the most negative trends and was negatively associated with the impacts of fire.

Main conclusions: This study identified *Q. ilex*, the most widespread species in this area, as a key driver of recruitment shifts on a large scale, negatively affecting most pine species with the advance of forest succession. These results highlight that the future expansion/contraction of *Q. ilex* stands with ongoing climate change will be a key process indirectly controlling the demographic responses of *Pinus* species in the Mediterranean Basin.

Keywords: Forest succession, recruitment, *Quercus*, *Pinus*, global change, Mediterranean biome, forest management.

4.2. Introduction

The recruitment of trees is a critical process in the population dynamics of forests and significantly influences the composition of forest communities. Consequently, assessing the status of tree recruitment on several spatial scales is essential for evaluating potential future responses of forests in the face of ongoing global change (Pons & Pausas, 2006). The study of recruitment and its ecological drivers in the Mediterranean Basin have been mainly restricted to local or regional scales (e.g. Plieninger *et al.*, 2010; Urbieta *et al*., 2011), so the macroecological assessment of trends in forest recruitment is critically lacking. Notably, local-scale studies have frequently reported severe limitations in tree recruitment, which is often especially acute for pine species (Castro *et al*., 2004; Urbieta *et al.*, 2011; Galiano *et al.*, 2013). The macroecological extent of the observed recruitment limitations, however, remains poorly assessed, as is the geographic variability of the main ecological drivers of recruitment limitation on a large scale (Ruiz-Benito *et al*., 2012; Coll *et al*., 2013; Vayreda *et al*., 2013). This information is essential for assessing future scenarios of global change in the forests of the Mediterranean Basin. Here we attempt to fill this gap in our knowledge and provide an integrative assessment of the patterns of tree recruitment and their main drivers in Spain.

The ecological drivers of recruitment in the Mediterranean Basin are diverse, and a variety of species-specific responses have been reported. For example, recruitment limitation in Mediterranean forests has been associated with drought stress (Castro *et al*., 2004), forest succession and disturbance (Zavala & Zea, 2004) and changes in land uses and practices of forest management (Kouba *et al*., 2012). Drought and seasonal rains produce large interannual variations in the success of tree recruitment in Mediterranean forests (Gómez-Aparicio *et al*., 2005; Kouba *et al*., 2012). Succession also significantly determines the process of recruitment, because as forest succession advances, the ecological conditions in the understory that determine recruitment success are progressively modified (Zavala & Zea, 2004; Zavala *et al*., 2011). During succession, the saplings of shade-intolerant species are generally suppressed by adult trees of late-successional species, such as several species of oaks (Zavala *et al*., 2011). Finally, forest management, fire and changes in land use are also tightly related to observed recruitment responses. Indeed, forest management and fire in the Mediterranean Basin have historically delayed and modified successional paths and have altered patterns of tree recruitment and forest composition (Broncano *et al*., 2005; Kouba *et al*., 2012).

Widespread abandonment of land, fire suppression and reduced management, however, now favor forest succession in many areas, thus potentially constraining the recruitment of early-successional species on a large scale. Other important drivers of recruitment in the Mediterranean region include gradients of light and nutrients, soil properties, seed rain and seed dispersal, seed masting, seed predation, nursery and inhibitory effects of shrubs, herbaceous-layer effects and grazing pressure (Castro *et al*., 2004; Gómez-Aparicio *et* *al.*, 2005; Puerta-Piñero *et al.*, 2007; Urbieta *et al.*, 2011). The large-scale geographic variation in many of these drivers of recruitment remains poorly assessed. This lack of precise knowledge in recruitment patterns sharply contrasts with the available model predictions of global change for the Mediterranean Basin (Keenan *et al*., 2011; Ruiz-Labourdette *et al*., 2012; Loepfe *et al.*, 2012). These studies suggest that forests may be critically endangered by future impacts of climate change such as extreme drought events, more intense fires and increased temperatures (Keenan *et al*., 2011; Ruiz-Labourdette *et al*., 2012; Loepfe *et al.*, 2012). A detailed assessment of large-scale trends and driving factors in recruitment is urgently needed to properly assess the future responses of forests to global change.

Here we attempt to fill this gap in our knowledge and provide the first integrative assessment of the patterns of tree recruitment and its main drivers in the Iberian Peninsula of Spain. We began by assessing the macroecological trends in the recruitment of saplings of all species in the dominant genera *Pinus* and *Quercus*. These two genera have coexisted in the Mediterranean Basin over the last 2.3-3.5 million years (Scheffer, 2012) and are characterized by contrasting functional traits, reproductive phenologies and ecological strategies (reviewed in Supplementary text T1). Interestingly, we found striking differences in the observed patterns of recruitment between *Quercus* and *Pinus* species, showing limited recruitment of *Pinus*. We thus subsequently evaluated the putative ecological drivers of this limited recruitment of *Pinus*. The main objectives of this study were: (1) to contrast the large-scale geographic patterns of recruitment in the dominant *Pinus* and *Quercus* species, (2) to identify and quantify the main driving factors (climate, soil, topography, forest succession, fire and management) determining the observed large-scale patterns of recruitment, (3) to examine the structure of the causal relationships (direct and indirect) among the explanatory factors modulating *Pinus* recruitment and (4) to assess the geographic variation in the effects of recruitment drivers (climate, soil, topography, succession, fire and management) across climatic gradients.

4.3. Material and methods

4.3.1. Study area and species

We focused on the following target species: *P. halepensis* (Aleppo pine), *P. pinea* (Stone pine), *P. nigra* (Black pine), *P. pinaster* (Maritime pine), *P. sylvestris* (Scots pine), *P. uncinata* (Mountain pine), Q. *suber* (Cork Oak), *Q. ilex* (Holm oak), *Q. faginea* (Portuguese Oak), *Q. pyrenaica* (Pyrenean Oak), *Q. robur* (English oak) and *Q. petraea* (Sessile Oak). A brief description of the distribution of these species in the Iberian Peninsula is provided in Supplementary text T1.

4.3.2. Data

4.3.2.a. Forest inventory data

The forest data were obtained from the National Forest Inventory (IFN) and were collected from a regular grid of circular plots at a density of 1 plot/km^2 (Villaescusa & Díaz, 1998; Table S1). IFN surveys include information on composition, forest structure and demography. We gathered data from IFN2 (surveys conducted from 1986 to 1996) and IFN3 (surveys conducted from 1997 to 2008). In each plot, four circular subplots were defined (radii of 5, 10, 15 and 25 m) and served to assess trees with a diameter at breast height (DBH) >7.5, >12.5, >22.5 and >42.5 cm in the respective circles. A recruitment survey had been performed during IFN3 (1997-2008). All individuals with DBH<7.5 cm growing in the subplots of 5 m radius (78.5 m^2) were identified as recruits. Four recruitment stages were defined: height<30 cm (recruitment class 1 (R1)), height 30-130 cm (R2), height>130 cm and DBH<2.5 cm (R3) and height>130 cm and DBH>2.5 cm (R4).

4.3.2.b.Climatic and topographic data.

Climatic data were gathered from the Climatic Atlas of the Iberian Peninsula (Ninyerola *et al*., 2007ab). We obtained climatic maps by applying a global statistical interpolation with a corrector for local anomalies (Ninyerola *et al*., 2007ab, see further details in Supplementary text T2).

	Independent variables	Description
Forest stand attributes	Total stand basal area (BA)	Summation of basal area of all trees in the plot
	Stand tree density (Dens)	Numbers of trees per ha
	Species-specific basal area (BAsp)	Basal area calculated for each *Pinus* species
	Species-specific tree density (Denssp)	Tree density calculated for each *Pinus* species
Forest	*Quercus* sp. R4 sapling presence (Sap *Quercus*)	Presence/absence of *Quercus* sp. R4 saplings

Succession		Calculated for each species
	Quercus species basal-area increase (BAI*Quercus*)	BAsp IFN3- BAsp IFN2 (species-specific)
	Quercus species recruitment (QR)	Presence/absence of *Quercus* sp. R1 recruits for each species
	Pinus species sapling presence (Sap*Pinus*)	Presence/absence of *Pinus* R4 saplings, calculated for each species
	Pinus species basal-area increase (BAI*Pinus*)	BAspIFN3-BAspIFN2 (species-specific)
Climate	Mean annual temperature (MAT)	
	Mean annual rainfall (Rain)	
	Summer rainfall (SR)	
	Mean summer temperature (MST)	
	Mean Emberger water deficit index (EMB)	
	Mean minimum temperature (MMinT)	
	Mean maximum temperature (MMaxT)	
	Absolute minimum temperature (MinT)	
	Absolute maximum temperature (MaxT)	
	Absolute maximum Emberger water deficit index value (MaxEmb)	
Topography	Altitude	
	Slope	
	Aspect	
Soil	Soil condition	Organic-layer depth
Management	Stand management	Binary variable: managed (plots managed during the last 10 years (1)) / unmanaged (0)
Fire	Fire occurrence	Binary variable: burned(1) / non-burned (0)

Table 1. *List of independent variables examined in the study.*

4.3.2.c. Dependent and independent variables

The response variables were the recruitments of *Pinus and Quercus* saplings, defined as binary variables (presence-absence of R1 in the 5-m subplot for each species). Supplementary analyses were also performed on the R2, R3 and R4 classes of sapling size. We examined 25 independent predictor variables describing local climate (temperature, rainfall and water deficit), topography (altitude, slope and aspect), depth of organic layer, management practices (binary variable), fire occurrence (binary variable), attributes of forest stand (basal area and tree density) and variables of forest succession (presence of *Quercus* and *Pinus* saplings and species-specific increases of basal area). A detailed list and description of each variable are provided in Table 1.

4.3.3. Data analyses

4.3.3.a. Geographic patterns of recruitment

Geographic patterns of sapling recruitment in all recruitment classes (R1-R4) of *Pinus* and *Quercus* were first investigated by GIS (geographic information system) mapping. We subsequently explored recruitment trends along environmental gradients. Species-specific recruitment trends across gradients of climate (mean annual temperature (MAT), mean annual rainfall and summer rainfall), topography (slope and altitude) and attributes of forest stand

(stand basal area and species-specific basal area) were assessed. For the specific case of *Q. ilex*, geographic patterns of recruitment were separately mapped in forests and managed *dehesa* stands. Dehesas are agroforestry systems with scattered oak trees defining a savannah-like open tree layer. Dehesas cover an area of about 3.5 million ha, are mainly located in the southwestern part of Spain and Portugal and are usually dominated by *Q. ilex* and *Q. suber*.

4.3.3.b. Models

To identify the main factors limiting recruitment, we applied three basic modeling approaches. Firstly, we performed structural equation modeling (SEM) to precisely assess the putative causal relationships between the analyzed explanatory factors and recruitment. Secondly, we also modeled recruitment responses for each species using generalized linear models (GLM). Finally, to capture the geographic variation in the effects of the driving factors on recruitment, we divided the data set into climatic subsets and independently modeled recruitment responses in each climatic zone, following quantile modeling techniques used in a previous study (Carnicer *et al.*, 2011). Below we provide detailed information on each of these three modeling approaches.

4.3.3.c. Structural equation models

We used SEM to explore the structure of the causal relationships (direct and indirect effects) between the variables. More specifically, we applied SEM models to test whether the reduced recruitment found in *Pinus* species was significantly associated with the expansion of *Quercus* species, after accounting for other contributing factors such as climate, management, fire, soil or slope. All modeling was thus restricted to *Pinus* stands (i.e. stands with adult pines, Villaescusa & Díaz, 1998). Fig. 1 illustrates the set of relationships that were examined in the SEM models. More complex models and variants of the proposed scheme (Fig. 1) were also tested (results not shown). The SEM analyses were performed in each of the four categories of recruitment size (R1-R4). All tables and figures in the results section refer to SEM analyses of the R1 size class. The results obtained for R2-R4 size classes are located in the supplementary materials. SEM analyses were developed using AMOS software (Arbuckle, 2006); see Supplementary text T3 for further methodological details.

4.3.3.d. Generalized Linear Models

We used generalized linear models with a binomial distribution error and a logit link function. Recruitment presence-absence was selected as the dependent response variable. We tested the following independent variables: MAT, annual rainfall, summer rainfall, terrain slope, stand basal area, depth of organic layer, fire occurrence and variables of management and forest succession (i.e. increase in basal area of *Pinus* and *Quercus* species and presence/absence of saplings of *Pinus* and *Quercus* species; see below for a more detailed explanation). All GLM modeling was restricted to *Pinus* stands and considered only the R1 size class. *Pinus* stands were defined by the presence of adults of the focal species. We introduced both linear and quadratic terms because we observed some non-linear responses of recruitment to climatic variables. Highly correlated variables (i.e. $r>0.7$) were not included in the same models (Table S2) to avoid problems of collinearity. During model-selection analyses, we used the Akaike Information Criterion to evaluate the competing models. Our preliminary analyses indicated strong recruitment limitation in *Pinus* stands and significantly higher recruitment success in *Quercus* species. To evaluate if successful *Quercus* recruitment could be effectively limiting *Pinus* recruitment in pine stands, we introduced two variables as independent negative predictors of *Pinus* recruitment: 1) the presence of R4 saplings of *Quercus* (Sap*Quercus*) and 2) the increase in basal area of *Quercus* species (BAI*Quercus*). As shown in Table S2, for all pine species except *P. uncinata*, *Q. ilex* was the most abundant *Quercus* species recruiting in the understory. In the case of *P. uncinata*, however, *Q. humilis* was the most abundant species recruiting in the understory. Consequently, these two *Quercus* species were used in the *Pinus* recruitment analyses to calculate the independent variables Sap*Quercus* and BAI*Quercus*. We also examined whether *Pinus* recruitment in the same pine stands could be affecting *Quercus* recruitment, introducing Sap*Pinus* and BAI*Pinus* in the *Quercus* recruitment models.

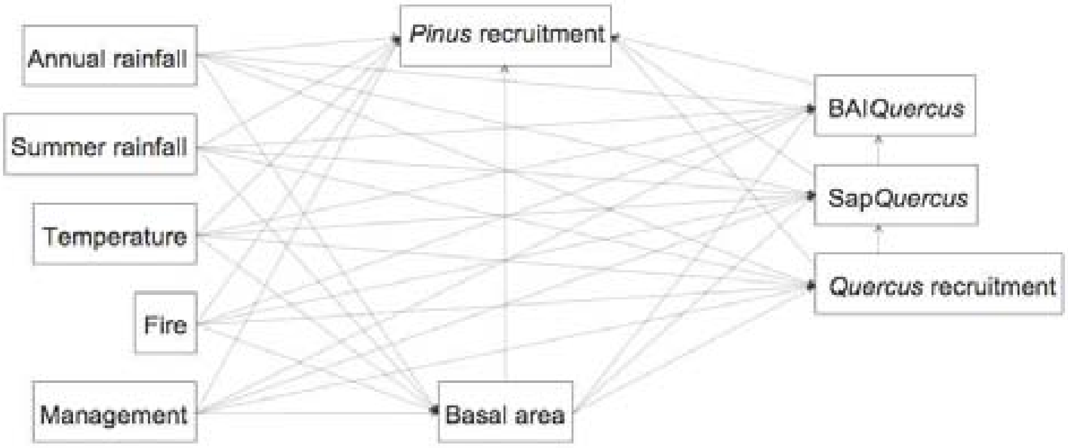


Figure 1. *An illustrative scheme of the relationships analyzed in the structural equation models (SEM). We tested the effects on Pinus recruitment (R1) of climatic variables, stand properties, management, fire and forest-succession variables (SapQuercus and BAIQuercus). SapQuercus: presence of Q. ilex saplings (R4 class). BAIQuercus: Q. ilex biomass increase between IFN2 and IFN3 in a given stand. Quercus recruitment: presence of Q. ilex recruits (R1 class). Note that in the case of P. uncinata, Q. humilis was the most abundant Quercus species in the understory and was used for the calculation of Quercus recruitment, SapQuercus and BAIQuercus.*

4.3.3.e. Geographic variation in the effects of recruitment drivers

To capture the geographic variation in the effects on recruitment of the independent variables, we independently modeled recruitment grouping by climatic subsets, using both GLM and SEM models. For the GLM analyses, we divided each species-specific data set into four climatic subgroups (quantile 25), exploring MAT, rainfall and summer rainfall quantile groups (Carnicer *et al.*, 2011). An independent quantile GLM analysis was performed for these three climatic variables. We fit *Pinus* and *Quercus* recruitment models (GLM) in each climatic quantile. The resulting significant β coefficients were compared across climatic gradients (Carnicer *et al*., 2011). For the SEM analyses, we divided the data set for each species into two groups (warm/cold or dry/wet) according to the median value of the climatic variable (MAT, rainfall and summer rainfall). We performed independent SEM analyses on each climatic subset. The parameter credibility intervals of each path were compared between the two climatic subsets to detect significant geographic shifts. The analyses of the geographic variation in the effects of predictors focused on the R1 size class. Complementary results for R2-R4 size classes are located in the supplementary materials.

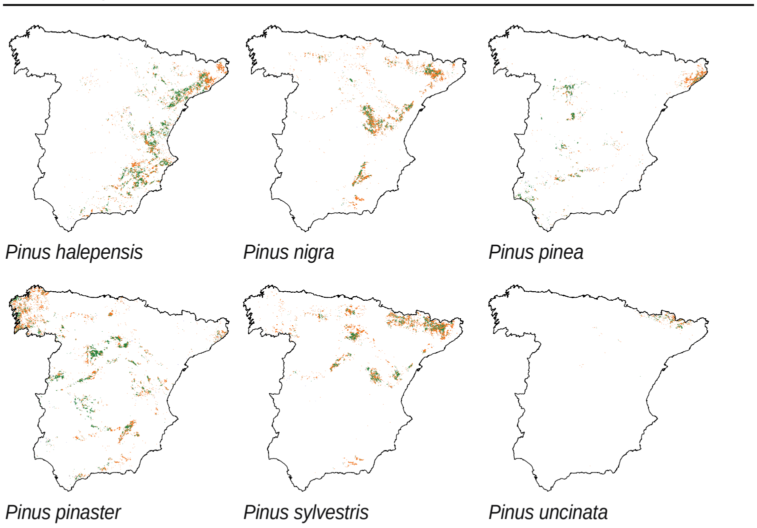
4.4. Results

4.4.1. Geographic patterns of recruitment

Observed trends in recruitment of *Pinus* and *Quercus* species in the R1 size class are summarized in Fig. 2. Trends for the R2-R4 size classes are described in the supplementary materials (Figs. S1 and S2). Plots were mapped in three categories for each species: 1) *areas of recruitment success*, i.e. plots in which we observed both saplings and adult trees of the focal species; 2) *areas of recruitment failure*, i.e. plots characterized by the presence of adult trees and the absence of saplings of the focal species and 3) *areas of new recruitment*, i.e. areas without adult trees but where saplings of the analyzed species were observed.

Quercus and *Pinus* species had strikingly divergent macroecological patterns in these three categories (Figs. 2, 3, S1 and S2). A large fraction of plots were characterized by R1 recruitment failure in all pine species (54-71% of the plots, depending on the species; see Table S3 for details). Pines also consistently showed a small proportion of areas of new R1 recruitment (5-15 % of the plots; Table S3). In contrast, *Quercus* species were characterized by reduced R1 recruitment failure (14-45% of the plots) and a much larger fraction of areas of new R1 recruitment (18-57% of the plots; Fig. 3, Table S3). *Pinus* species had a significantly higher average proportion of plots with R1 recruitment failure and reduced areas of new recruitment than did *Quercus* species (Fig. 3c, F=16.64, p=0.002; Fig. 3d, F=35.04, p=0.0001). Stands of *P. nigra*, *P. sylvestris* and, to a lesser extent, *P. uncinata* had the highest values of recruitment failure. The proportion of recruitment failure progressively increased from large (R4) to small (R1) saplings in these three species (Table S4; Figs. S1 and S2). Northeastern (Catalonia) populations of *P. pinea* had strong limitations in recruitment in all size classes (R1-R4; Table S4; Figs. S1 and S2), in contrast to the higher recruitment success in the R1 and R2 size classes in southwestern populations (Fig. S2). *P. halepensis* and *P. pinaster* had similar proportions of recruitment in all size classes (R1-R4; Table S4; Figs. S1 and S2). In contrast with these trends in *Pinus*, a progressive decrease in the proportion of recruitment failures from large (R4) to small (R1) saplings was observed in *Q. ilex*, *Q. faginea*, *Q. robur, Q. petraea* and *Q. pyrenaica* (Figs. S1 and S2).

a *Pinus* sp.



b *Quercus* sp.

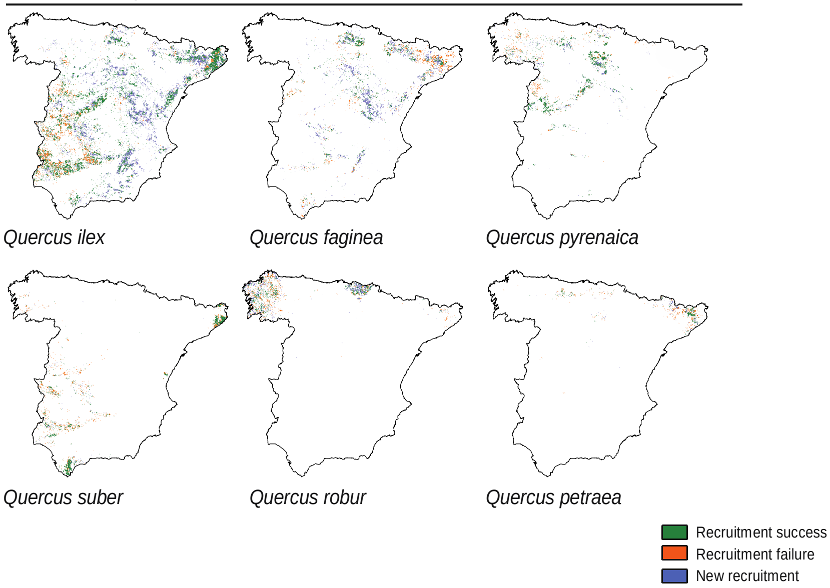


Figure 2. *Geographic variation in the trends of Pinus species R1 recruitment (a) and Quercus species R1 recruitment (b). For each species, surveyed plots were mapped in three categories: 1) green: areas of recruitment success (i.e. plots in which we observed both saplings and adult trees of the focal species), 2) orange: areas of recruitment failure (i.e. plots characterized by the presence of adult trees and the absence of saplings of the focal species) and 3) blue: areas of new recruitment (i.e. areas without adult trees in which saplings of the analyzed species were observed)*

Q. ilex was, by far, the most abundant non-pine species recruited in the stands of *P. halepensis*, *P. nigra*, *P. pinea*, *P. pinaster* and *P. sylvestris*, as illustrated by the high percentages of plots in which small (R1 size class) and large (R4 size class) saplings of *Q. ilex* were detected (Tables 2 S5 and S6). In line with these findings, 54% of the plots of *Q. ilex* were identified as "new R1 recruitment areas", i.e. plots without adult *Quercus* trees in which *Q. ilex* R1 saplings or recruits were observed. In contrast, extensive areas of recruitment failure in *Q. ilex* were mainly concentrated in southwestern dehesa-type stands (Fig. 4a,b). A clear general pattern emerged; *Quercus* species considerably extended their recruitment ranges across the Iberian Peninsula (Fig. 2, Figs. S1 and S2) and colonized large fractions of the pine stands (Table S3).

To explore whether the expansion of *Quercus* species across the peninsula was significantly associated with the observed reduced recruitment of *Pinus*, we compared the percentage of plots with recruitment success between pure pine stands and mixed pine stands for all recruitment categories (R1-R4). Results for the R1 size class are summarized in Fig. 4, and Table S7 presents the results for all recruit size classes (R1-R4). The recruitment of pines was significantly lower in mixed stands than in pure stands in all size classes (R1-R4) and for all *Pinus* species analyzed (Wald chi square=340.53, $p<0.01$; Fig. 4c (R1) and Table S7a (R1-R4)). Significant differences were also observed between unmanaged and managed pine stands (Wald chi square=198.56, $p<0.01$; Fig. 4d (R1 trends) and Table S7b (R1-R4)). Recruitment in the small size class (R1) was positively associated with managed forests in all analyzed *Pinus* species except *P. nigra* (Table S7b). In contrast, recruitment was significantly reduced by management practices in larger saplings (R3-R4) in *P. halepensis*, *P. nigra*, *P. pinea* and *P. sylvestris* (Table S7b).

4.4.2. The role of *Quercus* in pine recruitment

The structural equation models identified the presence of *Quercus* saplings and the increase in basal area of *Quercus* species as key negative factors precluding the success of *Pinus* recruitment. For example, the direct negative effects of both *sapling presence* and *basal-area increase* in *Q. ilex* emerged as strong direct predictors of recruitment in *P. halepensis*, *P. pinea*, *P. pinaster*, *P. nigra* and *P. sylvestris* (Table 3, Fig. S3). These trends were consistently observed in all recruitment size classes (Tables S8 and S9). Interestingly, these results confirmed a statistically significant relationship between the previously reported diverging trends observed in *Quercus* and *Pinus* species, i.e. the expansion of *Quercus* recruitment in many areas and the reduced recruitment success of *Pinus* (Figs. 2-4). The SEM and GLM analyses also confirmed that several contributing factors (climate, fire, management, forest basal area and soil) significantly shaped the patterns of recruitment (Tables 3 and S8-S10).

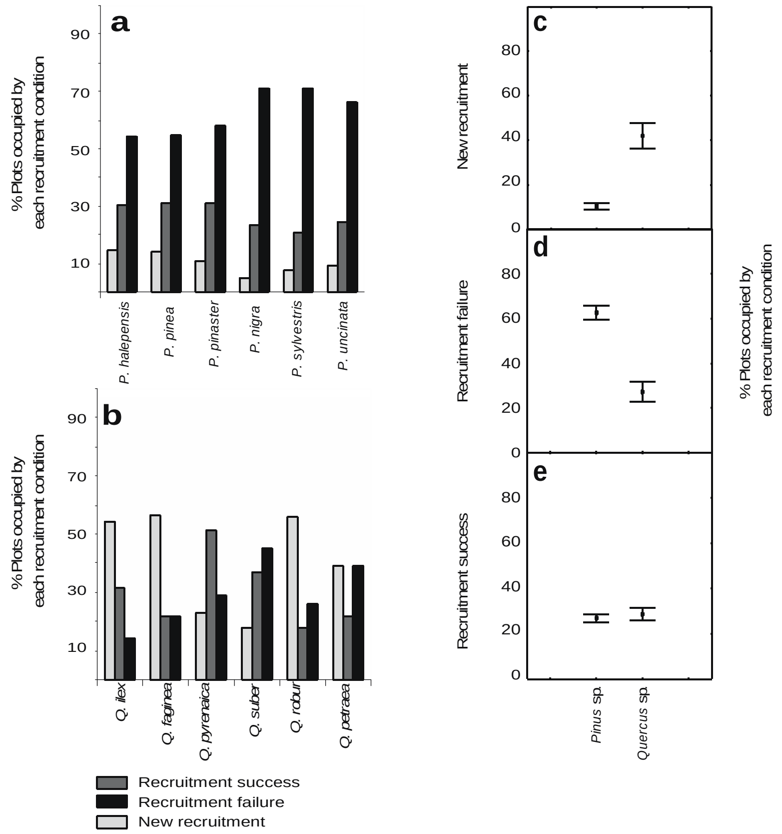


Figure 3. *A comparison of the diverging trends observed in recruitment (R1 size class) between Pinus and Quercus species on a large scale. (a) Percentage of plots with recruitment success (dark gray bars), recruitment failure (black bars) and new recruitment (light gray bars) for each Pinus species. (b) Percentage of plots with recruitment success (dark gray bars), recruitment failure (black bars) and new recruitment (light gray bars) for each Quercus species. (c-e) Differences between the genera Pinus and Quercus in the percentage of plots with recruitment failure, recruitment success and areas of new recruitment.*

Species	*Pinus* recruitment success (% of plots with R1 recruits)	*Quercus* sp. recruitment success in *Pinus* stands (% of plots with R1 recruits)		Mean annual temperature MAT(ºC)	Annual rainfall (mm)	Number of plots
		Q. ilex	Q. humilis			
P. halepensis	37.6	40.0	07/02/14	14.4	491	7028
P. pinea	36.1	60.2	13.2	14.3	586	2241
P. pinaster	38.7	38.7	1.6	12.8	746	7040
P. nigra	26.6	60.0	13.7	11.6	619	5201
P. sylvestris	23.9	29.8	18	10.0	765	6631
P. uncinata	28.5	5	11.9	6.4	909	706

Table 2. *A synthetic description of the plots of Pinus sp. stands analyzed in this study. We provide a summary of the R1 class recruitment observed in these stands for Pinus species, Q. ilex and Q. humilis. The conditions of mean temperature and rainfall for each pine species in the study area and the available number of plots are summarized. Pine R1 recruitment success in the first and second columns strictly refers to mature pine stands (i.e. stands without adult pine individuals were excluded from the calculation).*

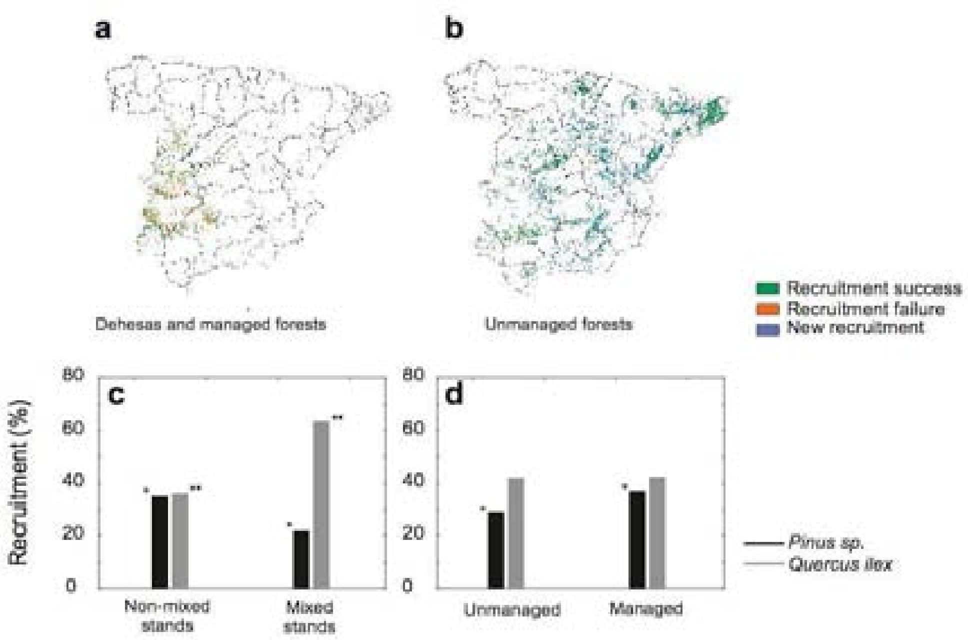


Figure 4. (a-b) *Observed recruitment trends in Q. ilex forests (R1 size class). (c-d) Observed variation in Pinus recruitment success with management and stand composition. The percentage of plots with recruitment success (R1 class) was calculated for each Pinus species and for the most abundant non-Pinus species recruiting in pine-forest understories (Q. ilex in all pines except Q. humilis in the case of P. uncinata). c) Observed variation in recruitment success with stand composition (monospecific stands/mixed forests). d) Observed variation in recruitment success with management condition (managed/unmanaged stands). An average for all Pinus and Quercus species is shown. Detailed species-specific trends for all recruit size classes (R1-R4) are provided in Table S6. Asterisks (*) indicate significant differences in Pinus recruitment between categories (Wald chi square test; p<0.01). Double asterisks (**) indicate significant differences in Quercus recruitment between categories (Wald chi square test; p<0.01).*

4.4.3. Ontogenetic shifts in SEM models across recruitment size classes (R1-R4)

SEM models for different size classes revealed ontogenetic shifts in the effects of some predictor variables. For example, the effects of fire shifted from positive (in R1-R2 size classes) to negative in larger saplings (R3-R4) of *P. halepensis*. A shift from positive effects of summer rain (in R1-R2) to negative (R3-R4) also occurred in this species. In contrast, fire affected the serotinous species *P. pinaster* negatively in R1, positively in R2 and R3 and non-significantly in R4. Finally, fire consistently affected all size classes (R1-R4) negatively in *P. nigra* and *P. sylvestris* (Tables 3 and S9).

	Summer rainfall	Annual rainfall	Temperature (MAT)	Fire	Management	Stand basal area	*Q. ilex/Q. humilis** sapling presence (R4)	*Q. ilex/Q. humilis** Basal-area increase	*Q. ilex/Q. humilis** recruit presence (R1)
P. halepensis	0.03	-0.20	-0.07	0.17	0.10	0.03	-0.22	-0.01	0.14
Dry sites	0.20	-0.04	0.07	0.21	0.14	0.05	-0.44	0.08	0.47
Wet sites	-0.03	-0.24	-0.04	0.12	0.11	-0.06	-0.31	-0.01	0.23
P. pinea		-0.11	-0.11	-0.14	0.08	0.06	-0.52	-0.06	0.36
Dry sites		0.14	-0.21	0.05	0.08	0.14	-0.44	-0.04	0.42
Wet sites		-0.10	0.08	-0.09	0.11	0.03	-0.47	-0.03	0.24
P. pinaster		-0.31	0.15	-0.02	0.08	0.20	-0.23	-0.08	0.12
Dry sites		0.15	0.04	-0.23	0.02	0.23	-0.12	-0.12	0.03
Wet sites		-0.02	0.19	0.00	0.20	0.15	-0.96	-0.05	0.89
P. nigra		-0.07	-0.06	-0.26	0.03	0.06	-0.53	-0.12	0.59
Warm sites		-0.01	-0.12	-0.32	0.08	0.00	-0.53	-0.10	0.61
Cold sites		-0.12	0.02	-0.02	-0.01	0.12	-0.06	-0.06	0.10
P. sylvestris		-0.10	-0.08	-0.05	0.12	0.00	-0.44	-0.06	0.47
Warm sites		-0.03	-0.16	-0.10	0.17	-0.07	-0.39	-0.06	0.42
Cold sites		-0.13	0.03	0.12	0.04	0.05	-0.77	-0.18	0.79
P. uncinata		0.05	-0.20		0.29	-0.12	0.22*		-0.14*

Table 3. *Summary of Bayesian structural equation models (SEM). Standardized parameter estimates of direct effects on Pinus recruitment are summarized (see Supplementary text T3 for details on the significance tests applied in Bayesian SEM analyses). Extended results reporting all direct and indirect effects are provided in Fig. S1 and Table S7. Results of SEM analysis for each species and for each species-specific climatic subset are presented. Significant parameter estimates are in bold. Asterisks (*) indicate the use of Q. humilis data in P. uncinata analyses. Summer rainfall was selected only in P. halepensis models.*

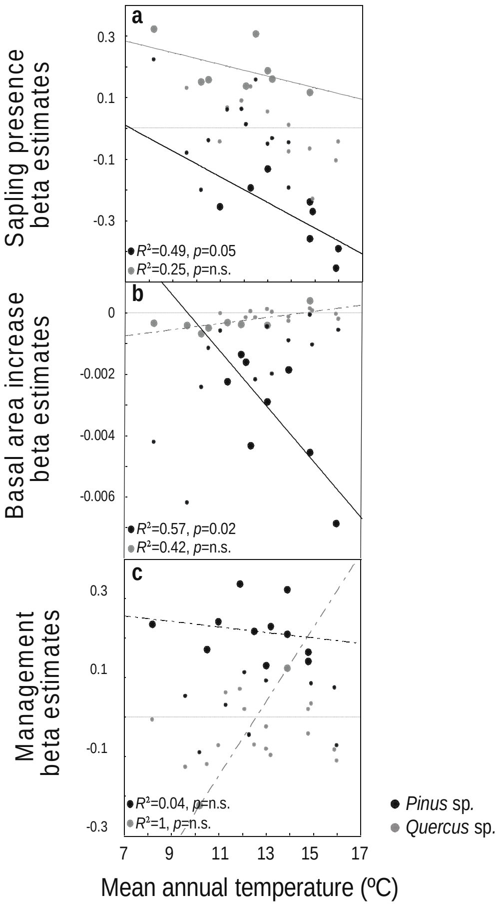


Figure 5. *GLM quantile modeling results. Geographic variation in the effects on Pinus and Quercus recruitment (R1) of forest succession and management variables across a temperature gradient. (a) Observed geographic variation in the effects (β estimates) of Quercus/Pinus R4 sapling presence (i.e. effects of Q. ilex/humilis R4 saplings on Pinus R1 recruits and effects of Pinus R4 saplings on Q. ilex/humilis R1 recruits), (b) observed geographic variation in the effects of basal-area increase (i.e. effects of Q. ilex/humilis biomass increase on Pinus R1 recruits and effects of Pinus biomass increase on Quercus R1 recruits) and (c) geographic variation in the effects of management on Pinus and Quercus R1 recruitment. Gray dots: β coefficients of Quercus recruitment models. Black dots: β coefficients of Pinus recruitment models. Large dots represent significant β coefficients, and small dots represent non-significant β coefficients. Dashed lines indicate non-significant fits.*

Ontogenetic shifts in the effects of management were also observed. Management positively affected R1 recruitment in both *P. halepensis* and *P. sylvestris* but negatively affected R2-R4. Similarly, management had no effect on *P. nigra* in R1 but consistently negative effects in R2-R4. Positive effects of management were observed in both *P. pinaster* and *P. uncinata* in R1 but shifted to non-significant effects in R2-R4. Finally, positive effects of management on *P. pinea* in R2 recruitment shifted to negative effects in R3-R4 (Tables 3 and S9). A general trend was observed in managed *Pinus* stands: positive effects in small saplings (R1-R2) tended to progressively shift to negative effects in larger saplings (R3-R4).

4.4.4. Geographic variation on the effects of recruitment predictors

The observed gradients of recruitment for all recruitment size classes are summarized in Figs. S4-S8. The significant predictors of recruitment showed strong geographic variation in their effects in quantile GLM modeling. Quantile GLM modeling revealed contrasting responses between *Quercus* and *Pinus* in the effects of forest structure and variables of forest succession (Fig. 5). Negative effects of forest succession on R1 recruitment were only observed in *Pinus* (i.e. the presence of *Q. ilex* saplings (R4) and the increase in *Q. ilex* basal area was negatively associated with *Pinus* recruitment). Stronger negative effects of forest succession in *Pinus* were observed in warmer localities (Fig. 5a,b). In contrast, *Quercus* R1 recruitment was positively associated with the presence of *Pinus* saplings (R4) (Fig. 5a), and strong, negative effects of the increase of *Pinus* basal area on *Quercus* recruitment were not observed. In line with these trends, management was a positive factor for R1 recruitment only in *Pinus* species, but significant geographic gradients were not observed for these effects (Fig. 5c).

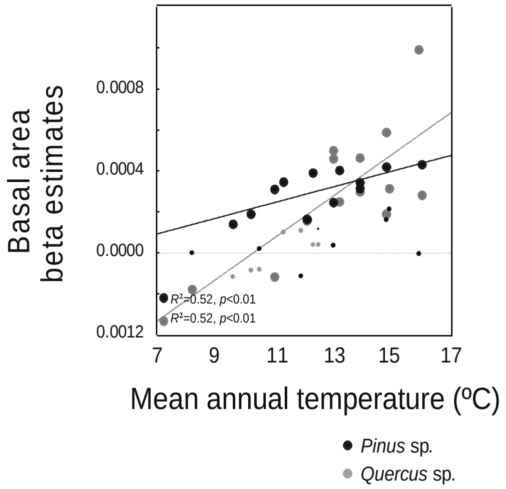


Figure 6. *Effects of stand basal area on Pinus and Quercus recruitment in GLM models. Geographic variation in the effects of stand basal area on Pinus and Quercus recruitment (R1 class) along a gradient of temperature. Gray dots: β coefficients of Quercus recruitment models. Black dots: β coefficients of Pinus recruitment models. Large dots represent significant β coefficients, and small dots represent non-significant β coefficients.*

Both *Pinus* and *Quercus* consistently showed significant geographic variation in the effects of stand basal area on recruitment (Fig. 6), with larger positive effects of stand basal area in warmer localities. These positive effects of stand basal area on R1 recruitment shifted to negative effects in supplementary models of the larger size classes (R2-R4; Fig. S9).

Climatic effects on R1 recruitment were highly variable (Fig. 7a,b), following a typical “water-energy dynamics” shift (i.e. increased positive effects of temperature in cold localities and negative effects of temperature and drought in warm localities). The observed geographic variation in the effects of climate, however, was only significant in *Quercus* species. We observed increased recruitment of *Quercus ilex* in cold-, high -altitude pine stands where adult *Q. ilex* were absent or had very small basal areas (MAT ≤7 ºC; Figs. S7b and S8). Similarly, we also observed increased recruitment of *Q. ilex* in dry pine stands where adult *Q. ilex* were absent or had small basal areas (mean annual rainfall ≤400 mm; Fig. S7a).

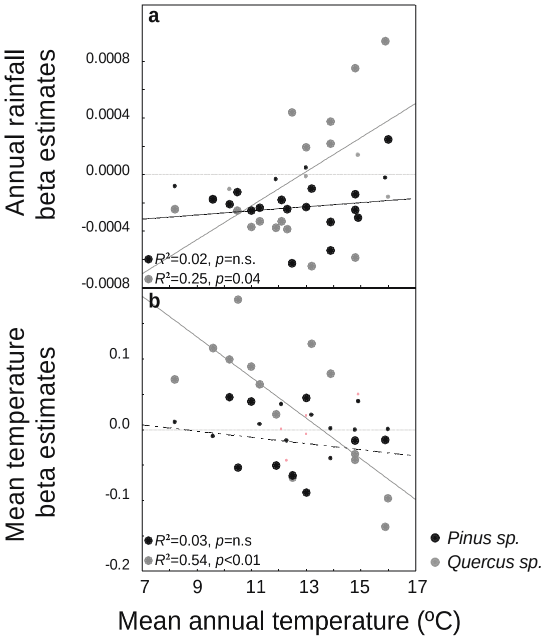


Figure 7. *Geographic variation in the effects of rainfall and temperature on Pinus and Quercus recruitment (R1) in GLM models. a) Observed variation in the effects of rainfall. b) Observed variation in the effects of temperature. Gray dots: β coefficients of Quercus recruitment models. Black dots: β coefficients of Pinus recruitment models (R1). Large dots represent significant β coefficients, and small dots represent non-significant β coefficients.*

4.5. Discussion

4.5.1.Generalized regeneration failure in *Pinus*

Our large-scale survey suggests that limited recruitment is common for all pine species across extensive areas (Fig. 2). A comparison of regeneration trends among *Pinus* and *Quercus* species indicated that the success of *Quercus* recruitment was clearly higher than that of *Pinus* species (Fig. 3). Furthermore, *Quercus* species had high recruitment rates under pine canopies (Table 2). Our modeling highlighted the existence of factors oppositely affecting *Pinus* and *Quercus* recruitment (Figs. 5-7) and identified forest succession, climatic limitations, management and fire as the main factors affecting the patterns of recruitment.

4.5.2. The roles of forest succession and biotic interactions along gradients

The limited *Pinus* recruitment, together with the spread of *Quercus* in some regions, could be partly due to the processes of succession and to biotic interactions. One late-successional species (*Q. ilex*) hampered the recruitment of five *Pinus* species (Table 3). These results agree with those of other studies that identified the presence of treelets of *Quercus* species as a limitation to the recruitment of *Pinus* (Rouget *et al*., 2001; Urbieta *et al*., 2011). Pine-oak secondary succession is generally associated with increased canopy cover, which in turn decreases the availability of light, buffers temperatures and often alleviates drought stress in the understory (Zavala & Zea, 2004). Consistent with these associations, several studies have reported improved performance of *Q. ilex* seedlings under shade (Espelta, 1995; Zavala *et al*., 2011; Poorter *et al*., 2012; Sheffer, 2012).

Q. ilex dominated in mesic areas along climatic gradients (i.e. sites with approximately 800 mm of annual rainfall and a MAT of 14 ºC; Figs. S4, S6 and S7). Our results suggest that the successional advance of *Q. ilex* is occurring across a wide range of climatic conditions including into drier *Pinus* stands (250-500 mm of annual rainfall and small basal area; Fig. S7) and colder and higher *Pinus* stands (MAT<6-10 ºC; Figs. S4 and S7). These results are consistent with recent trends observed on local and regional scales (e.g. Vilà-Cabrera *et al*., 2012b; Galiano *et al*., 2013; Rabasa *et al.*, 2013; Urli *et al.*, 2013).

Remarkably, *P. sylvestris*, *P. nigra* and *P. uncinata* showed a higher proportion of plots with recruitment failure in smaller size classes (R1) than in larger saplings (R4) (Table S4; Figs. 3 and S1), suggesting negative trends in recruitment dynamics for these species. Recruitment of *Q. ilex* was much more successful than recruitment of *P. nigra* across the entire distribution of this species (Fig. S6), and SEM analyses indicated significant negative effects of *Q. ilex* on *P. nigra* recruitment in both dry and wet localities (Table 3). *P. nigra* forests are on the list of endangered habitats in Europe requiring specific conservation measures (Resolution 4/1996 by the Convention on the Conservation of European Wildlife and Natural Habitats), so we suggest that these negative trends deserve further study and may have implications for forest conservation.

The advance of *Q. ilex* into *P. sylvestris* stands was concentrated in warm localities (MAT>10 ºC; Fig. S6), and improved recruitment of *P. sylvestris* was observed at cold sites (MAT<10 ºC) and at higher altitudes (Figs. S4-S6). These results are consistent with those of recent studies on local scales (e.g. Gómez-Aparicio *et al*., 2009; Benavides *et al*., 2013). Overall, in mid-altitude mountain pine forests, we observed a higher percentage of plots with recruitment of *Q. ilex* than of any pine species (Fig. S4-S6; Table S6a,b) and positive trends in *Q ilex* recruitment in pine stands with absent or very low basal area of adult *Q. ilex* trees (Figs. S7-S8). These trends suggest that these forests follow successional trajectories toward oak or mixed pine-oak forests (Gómez-Aparicio *et al*., 2009; Urbieta *et al*., 2011; Vilà-Cabrera *et al*., 2012b; Galiano *et al*., 2013). Higher success of *P. sylvestris* recruitment above 1600 m.a.s.l., however, contrasted with progressively lower and scant *Q. ilex* recruitment, suggesting autosuccessional trajectories at high altitudes (Fig. S4). Low temperatures and high radiation levels in these areas may limit the establishment of *Q. ilex* (Gómez-Aparicio *et al*., 2009). These trends are consistent with the higher positive effects of temperature on *Q. ilex* recruitment observed at low temperatures (Fig. 7).

Higher recruitment success in stands of *P. halepensis* relative to *Q. ilex* was only observed at very warm sites (MAT>15 ºC) with low stand basal areas and low rainfall (<600 mm; Figs. S4-S6). Recruitment success of *Q. ilex* progressively increased at more mesic sites, with a concomitant strong reduction in pine recruitment (Figs. S4-S6). *P. halepensis* is highly drought tolerant and is able to establish under dry conditions (e.g. Espelta, 1995; Osem, 2009). Previous studies have suggested that Aleppo pines may follow autosuccessional dynamics in arid, disturbed regions (Zavala & Zea, 2004; Osem *et al*., 2009; Sheffer 2012). The trends observed in *P. pinea* and *P. pinaster* are briefly discussed in Supplementary text T4. The reported trends can be applied to forest conservation and practices for adapting to climate change. For example, the recruitment maps (Figs. 2 and S2) may facilitate the identification of priority populations with positive recruitment trends (Hampe & Jump, 2011).

4.5.3. Management and fire and their effects on successional pathways

The effects of forest management on different ontogenetic stages of *Pinus* saplings varied from positive in small R1 recruits (*P. halepensis*, *P. pinaster*, *P. sylvestris* and *P. uncinata;* Figs. 4 and 5; Tables S7 and S8) to negative in larger R3-R4 saplings (*P. halepensis*, *P. nigra*, *P. pinea* and *P. sylvestris*). These trends are consistent with recent reports of limited recruitment in pine plantations in Spain (Ruiz-Benito *et al.*, 2013; Coll *et al.*, 2013). Other studies have reported limited pine recruitment and more expansion of *Quercus* oaks after the cessation of logging, grazing and management (Gimmi *et al*., 2010, Kouba *et al*., 2012, Vilà-Cabrera *et al*., 2012b).

Fire consistently had a negative effect on the recruitment of *P. nigra* and *P. sylvestris* at all sapling stages (R1-R4). In line with this, previous studies at smaller spatial scales have reported a null or very limited capacity of recruitment of *P. nigra* and *P. sylvestris* after fire and have predicted higher fire impacts in these species with ongoing climate change (Vilà-Cabrera *et al*., 2012a, Puerta-Piñero *et al.,* 2012). In contrast, we observed both positive and negative effects of fire on recruitment in *P. halepensis* and *P. pinaster*, which are consistent with the successional trajectories reported in mixed *P. halepensis*-*Q. ilex* stands after fire (Broncano *et al*., 2005, Puerta-Piñero *et al*., 2012 and citations therein). For example, Broncano *et al.* (2005) observed altitudinal differences in the successional pathways in mixed *P. halepensis*-*Q. ilex* stands after fires. At higher altitudes, *P. halepensis* forests often changed to mixed stands or *Q. ilex* forests after fire events. In contrast, at lowland sites, mixed *Q. ilex*-*P. halapensis* stands and *Q. ilex* plots more frequently changed to *P. halepensis* forests. Fire generally facilitated *Quercus* dominance at mesic sites with large *Q. ilex* basal areas and also allowed the recruitment and persistence of serotinous pines in dry localities with small basal areas of *Q. ilex*.

4.5.4. Climate change and forest conservation

We turn now to briefly discuss how future climate change may interact with the reported generalized limitation of recruitment in *Pinus* and the concomitant expansion of *Quercus* species. Predicted forest responses in the face of climate change in the Iberian Peninsula remain largely uncertain. The available model predictions vary from important range contractions to range maintenance to substantial range expansions (Benito-Garzón *et al*., 2011; Keenan *et al*., 2011; Ruiz-Labourdette *et al*., 2012; García-Valdés *et al*., 2013). Mapping and modeling consecutive ontogenetic tree stages provides complementary tools with some predictive capacity and enhance the assessment of ongoing demographic and distributional changes on large scales. For example, our results clearly highlight the need to explicitly account for successional advance and negative interspecific interactions in models. Our results describe a scenario of global change dominated by the widespread expansion of *Q. ilex* (and other broadleaved trees), increased suppression of pine recruitment (and growth) by *Q. ilex* and negative demographic trends in *P. sylvestris* and *P. nigra*. Furthermore, we suggest that negative synergistic effects of both forest succession and climate change are expected in *P. nigra* and *P. sylvestris.* For example, a higher frequency and intensity of fires due to climate change is expected to impact mesic sites in this area, negatively affecting recruitment and persistence in *P. sylvestris* and *P. nigra* (Loepfe *et al.*, 2012; Vilà-Cabrera *et al*., 2012a). Recent studies similarly show that fires can promote shifts in vegetation, from stands dominated by *P. sylvestris* and *P. nigra* to stands dominated by *Quercus* species (e.g. Puerta-Piñero *et al*., 2012). Moreover, extreme droughts increase mortality in *P. sylvestris* and reduce recruitment success and could therefore synergistically accelerate the ongoing succession to broadleaved forests (e.g. Galiano *et al*., 2010; Gimmi *et al*., 2010; Vilà-Cabrera *et al*., 2012b). Finally, temperatures have significantly increased in the study area during recent decades, and larger increases have been recorded at high altitudes (Carnicer *et al*., 2011 and citations therein). Higher temperatures could negatively influence the demographic responses of *P. sylvestris* and *P. nigra* at lowland sites and in turn promote the altitudinal advance of *Q. ilex*. Our results also highlight that selective thinning of *Q. ilex* treelets may be a useful measure to preserve contracting stands of *P. nigra* and *P. sylvestris*. Thinning is a common and well-studied practice, but more detailed experimental tests of this specific measure in *P. sylvestris* and *P. nigra* stands are likely needed.

The generalized advance of forest succession and the expansion of *Quercus* species substantially alter the distribution of forest fuel over extensive areas and may change fire-climate relationships. In line with this, recent studies suggest that fire activity in more arid conditions could be more sensitive to increased fuel loads and connectivity than to warming itself (Pausas & Paula, 2012; Loepfe *et al.*, 2012). Moreover, the combination of ongoing practices of fire suppression and the reported increased fuel load and connectivity may facilitate uncontrollable large fires under extreme meteorological conditions. The future dynamics of fire, however, are very difficult to predict and may include non-linear changes in fire frequency and intensity (Loepfe *et al*., 2012). On the other hand, several studies report decreased fire incidence from pine to evergreen broadleaved to deciduous broadleaved forests in this area (reviewed in Fernandes et al. 2013), suggesting that the reported advance of broadleaved species could reduce fire risk in some areas..

Beyond the basic trends reported, a proper assessment of the complex impacts of global change in this area will likely require the consideration of predictions from different approaches (Peñuelas *et al*., 2013), including the analysis of provenance trials, phenotypically plastic responses, genetic variation and evolutionary adaptation of local populations (Soto *et al*., 2010; Carnicer *et al*., 2012; Alberto *et al.*, 2013; García-Valdés *et al*., 2013); the study of gene flow over geographic ranges (Kremer *et al.*, 2012); the consideration of individual predispositions to drought-induced mortality (Voltas *et al*., 2013); the study of fuel loads, vegetation types and changing climate-fire relationships (Loepfe *et al*., 2012; Pauses & Paula, 2012); improved forest demographic analyses on large scales (e.g. Carnicer *et al*., 2011; Ruiz-Benito *et al*., 2012; Coll *et al*., 2013; Vayreda *et al*., 2013); the consideration of future changes in land use induced by shifts in global energy policies and the increased use of forests as a local energy source (Peñuelas & Carnicer, 2010; Carnicer & Peñuelas, 2012).

4.5.5. Concluding remarks

Our results implicate forest succession as a major determinant of patterns of recruitment limitation in *Pinus* species on a macroecological scale in the Iberian Peninsula. Other factors also clearly operate on these macroecological scales. For example, trends of recruitment limitation are also modulated by climatic effects, especially at the extremes of environmental gradients (Fig. 7). We conclude that *Q. ilex* acts as a key driver of large-scale shifts in recruitment trends in this region, negatively affecting most pine species with the advance of forest succession. Of the species studied, *P. nigra* and *P. sylvestris* showed the strongest negative trends. Droughts and fires triggered by climate change and the successional advance of *Q. ilex* could synergistically reduce the recruitment of these two species over extensive areas.

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4.7. Supplementary tables

Species	Number of plots	Percentage of plantations (%)
Pinus halepensis	7032	7.85
Pinus nigra	5220	16.84
Pinus pinaster	7053	18.33
Pinus pinea	2243	12.71
Pinus sylvestris	6642	16.23
Pinus uncinata	707	2.40
Quercus faginea	2639	4.13
Quercus ilex	10798	1.88
Quercus petraea	564	1.06
Quercus pyrenaica	2818	7.52
Quercus robur	1361	10.96
Quercus suber	2334	3.51

Table S1. *Number of plots examined in each species.*

	Altitude	Slope	Radiation	Mean annual rainfall	Summer rainfall	Mean annual temperature	Mean summer temperature	Mean maximum temperature	Mean minimum temperature	Water deficit	Absolute minimum rainfall	Absolute maximum temperature	Maximum water deficit
Altitude	1.00												
Slope	0.33	1.00											
Radiacio	-0.12	-0.32	1.00										
Mean annual rainfall	-0.05	0.19	-0.10	1.00									
Summer rainfall	0.05	0.31	-0.15	0.63	1.00								
Mean annual temperature	-0.84	-0.30	0.13	-0.33	-0.45	1.00							
Mean summer temperature	-0.60	-0.25	0.13	-0.59	-0.60	0.92	1.00						
Mean maximum temperature	-0.76	-0.32	0.12	-0.43	-0.55	0.98	0.96	1.00					
Mean minimum temperature	-0.88	-0.27	0.12	-0.24	-0.35	0.99	0.86	0.93	1.00				
Water deficit	-0.20	0.10	-0.07	0.96	0.56	-0.19	-0.51	-0.32	-0.09	1.00			
Absolute minimum rainfall	-0.08	0.11	-0.09	0.97	0.63	-0.35	-0.63	-0.46	-0.26	0.95	1.00		
Absolute maximum temperature	-0.85	-0.30	0.12	-0.31	-0.45	1.00	0.91	0.98	0.98	-0.17	-0.33	1.00	
Maximum water deficit	-0.18	0.07	-0.06	0.93	0.61	-0.26	-0.57	-0.38	-0.15	0.97	0.97	-0.24	1.00

Table S2. *Observed correlations (r) between climatic and topographic variables*

Species	New recruitment (%)	Recruitment failure (%)	Recruitment success (%)
P. halepensis	14.94	54.46	30.60
P. pinea	14.29	54.67	31.04
P. pinaster	11.08	57.95	30.98
P. nigra	5.11	71.45	23.44
P. sylvestris	7.87	71.46	20.67
P. uncinta	9.22	66.19	24.59
Q. ilex	54.27	14.20	31.54
Q. faginea	56.61	21.73	21.66
Q. pyrenaica	22.50	27.50	50.00
Q. suber	17.78	45.32	36.90
Q. robur	55.96	26.20	17.85
Q. petraea	38.93	39.13	21.94
Pinus sp.	10.41±3.79	62.69 ±8.01	26.88± 4.55
Quercus sp.	41.0±17.48	29.00±11.41	29.98±12.01

***Table S3**. Percentage of area of R1 new recruitment, R1 recruitment success and R1 recruitment failure in the Pinus and Quercus species analyzed. Table S3 provides somplementary trends for these two groups, for R2-R4 size classes.*

		Recruitment success	Recruitment failure	New recruitment
Pinus halepensis	R1	30.60	54.46	14.94
	R2	27.99	52.86	19.15
	R3	28.65	52.66	18.68
	R4	32.05	49.18	18.76
Pinus nigra	R1	23.44	71.45	5.11
	R2	29.38	62.12	8.50
	R3	24.63	67.22	8.16
	R4	30.90	57.20	11.90
Pinus pinaster	R1	30.98	57.95	11.08
	R2	22.47	66.08	11.45
	R3	17.03	71.24	11.72
	R4	17.85	68.56	13.58
Pinus pinea	R1	31.04	54.67	14.29
	R2	18.77	70.00	11.24
	R3	8.30	84.64	7.06
	R4	9.17	82.26	8.58
Pinus sylvestris	R1	20.67	71.46	7.87
	R2	24.36	63.29	12.34
	R3	21.87	66.93	11.19
	R4	29.45	55.69	14.86
Pinus uncinata	R1	24.59	66.19	9.22
	R2	36.54	48.50	14.95
	R3	33.18	53.50	13.32
	R4	40.35	42.50	17.15

Table S4. *Percentage of area of new recruitment, recruitment success and recruitment failure in the Pinus species analyzed in the four size categories (R1, R2, R3 and R4).*

	Abies alba	Castanea sativa	Fagus sylvatica	Juniperus thurifera	Pinus halepensis	Pinus nigra	Pinus pinaster	Pinus pinea	Pinus radiata	Pinus sylvestris	Pinus uncinata	Quercus faginea	Quercus humilis	Quercus ilex	Quercus petraea	Quercus pyrenaica	Quercus robur	Quercus suber
P.halepensis	0.0	0.0	0.0	0.3	100	7.5	4.8	4.4	0.0	1.9	0.0	2.6	2.4	12.4	0.3	0.0	0.0	1.1
P.nigra	0.0	0.2	0.2	5.3	10.2	100	9.4	0.9	0.2	24.3	0.1	8.7	4.5	15.1	0.1	1.3	0.2	0.2
P.pinaster	0.0	2.0	0.0	1.2	4.8	6.9	100	6.4	1.6	6.3	0.0	2.2	0.5	6.2	0.1	3.2	5.6	4.2
P.pinea	0.0	0.6	0.0	0.2	13.7	2.0	20.2	100	0.4	1.7	0.0	2.1	4.4	24.3	0.4	0.0	0.2	16.1
P.sylvestris	1.1	0.3	4.8	1.1	2.0	19.0	6.8	0.6	0.2	100	4.6	5.7	6.0	9.0	1.8	4.2	0.3	0.2
P.uncinata	9.1	0.1	4.5	0.0	0.0	0.6	0.1	0.0	0.0	43.6	100	0.0	7.5	0.1	0.6	0.0	0.0	0.0

Table S5. *Percentage of Pinus sp. plots in which one or more adult individuals of other tree species were detected in the surveys (i.e. percentage of non pure stands or mixed forests).*

a)	Abies alba	Castanea sativa	Fagus sylvatica	Juniperus thurifera	Pinus halepensis	Pinus nigra	Pinus pinaster	Pinus pinea	Pinus radiata	Pinus sylvestris	Pinus uncinata	Quercus faginea	Quercus humilis	Quercus ilex	Quercus petraea	Quercus pyrenaica	Quercus robur	Quercus suber
P.halepensis	0.0	0.0	0.0	0.7	37.6	2.8	2.1	1.1	0.0	0.9	0.0	10.9	7.2	40.0	0.8	0.0	0.0	1.1
P.nigra	0.0	0.7	1.0	5.7	2.8	26.6	4.2	0.4	0.0	10.7	0.1	32.9	13.7	60.0	0.6	4.4	0.8	0.3
P.pinaster	0.0	3.7	0.0	3.2	2.0	3.0	38.7	6.5	0.3	3.2	0.0	14.2	1.6	38.7	0.3	10.7	11.1	5.5
P.pinea	0.0	0.9	0.0	1.6	2.7	0.4	13.7	36.1	0.3	0.4	0.0	10.0	13.3	60.2	2.6	0.6	0.4	14.0
P.sylvestris	2.3	0.7	8.1	1.6	0.9	7.7	3.8	0.2	0.1	23.9	2.7	19.8	18.0	29.8	5.1	13.6	1.6	0.2
P.uncinata	16.9	0.4	5.9	0.0	0.1	0.3	0.0	0.0	0.0	18.6	28.5	1.3	11.9	5.0	5.0	0.6	0.6	0.0

b)	Abies alba	Castanea sativa	Fagus sylvatica	Juniperus thurifera	Pinus halepensis	Pinus nigra	Pinus pinaster	Pinus pinea	Pinus radiata	Pinus sylvestris	Pinus uncinata	Quercus faginea	Quercus humilis	Quercus ilex	Quercus petraea	Quercus pyrenaica	Quercus robur	Quercus suber
P.halepensis	0.0	0.1	0.0	0.6	43.5	6.4	2.0	0.9	0.0	1.9	0.0	5.6	4.2	26.0	0.6	0.0	0.0	1.0
P.nigra	0.0	0.6	0.7	5.1	3.8	38.5	3.5	0.2	0.1	15.8	0.2	14.2	8.9	33.0	0.2	3.2	0.2	0.2
P.pinaster	0.0	3.8	0.2	2.3	2.3	3.8	22.0	2.1	0.9	3.2	0.0	5.0	0.6	16.9	0.1	6.9	9.0	2.5
P.pinea	0.0	1.2	0.0	1.0	3.0	1.4	5.4	10.8	0.2	1.4	0.0	3.6	6.0	40.5	1.2	0.2	0.3	10.8
P.sylvestris	1.9	0.8	8.4	1.2	1.1	11.8	2.9	0.2	0.1	36.7	4.8	9,6	13.3	20.4	3.4	9.9	0.4	0.1
P.uncinata	15.7	0.4	6.1	0.0	0.2	0.3	0.0	0.0	0.0	35.0	51.3	1.0	5.4	2.1	2.8	0.0	0.4	0.0

__Table S6.__ a) Percentage of Pinus sp. plots in which small recruits (R1 size class) of other tree species (columns) were detected. (b) Percentage of Pinus sp. plots in which the presence of sapling presence (R4 size class) was observed.

a)	R1		R2		R3		R4		N plots	
Species	MIX	MONO	MIX	MONO	MIX	MONO	MIX	MONO	MIX	MONO
Pinus halepensis	0.29	0.41	0.3	0.39	0.28	0.42	0.3	0.48	2105	4923
Pinus nigra	0.23	0.31	0.31	0.42	0.26	0.35	0.35	0.43	3296	1905
Pinus pinaster	0.25	0.49	0.19	0.33	0.16	0.23	0.17	0.25	3201	3839
Pinus pinea	0.3	0.45	0.17	0.3	0.07	0.15	0.08	0.14	1438	803
Pinus sylvestris	0.2	0.28	0.26	0.33	0.23	0.3	0.33	0.4	3742	2889
Pinus uncinata	0.22	0.35	0.37	0.54	0.34	0.46	0.44	0.6	386	320
b)	R1		R2		R3		R4		N plots	
Species	UNM	M	UNM	M	UNM	M	UNM	M	UNM	M
All Groups	28.97	37.21	32.82	29.07	30.52	22.99	37.21	27.75	18075	9861
Pinus halepensis	35.75	42.14	37.92	33.80	40.25	33.70	45.53	38.64	4942	2086
Pinus nigra	25.76	28.14	37.82	30.15	32.52	23.81	41.64	31.66	3564	1592
Pinus pinaster	32.31	41.93	24.62	27.61	19.98	21.29	21.87	22.86	3383	3053
Pinus pinea	30.73	41.36	20.09	24.66	11.16	8.93	12.02	9.13	1165	1030
Pinus sylvestris	21.40	29.66	31.14	26.65	29.86	19.96	40.77	28.94	4457	1959
Pinus uncinata	25.89	39.01	45.39	44.68	41.13	36.88	52.30	47.52	564	141

__Table S7.__ a) A comparison of the percentage of plots characterized with Pinus recruitment success between unmanaged stands (UNM) and managed stands (M) for the four recruit size classes (R1-R4) and for each Pinus species (rows). b) A comparison of the percentage of plots in which recruitment success was observed for each recruit size class (R1-R4) and for each pine species (rows). Significant differences are highlighted in bold (Wald chi square tests; p<0.01).

Species	Subset		Direct effects									Indirect effects								
			Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	Quercus ilex R1 recruitment	Quercus ilex R4 sapling	Quercus ilex biomass increase	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	Quercus ilex R1 recruitment	Quercus ilex R4 sapling	Quercus ilex biomass incr.
P.halepensis	Species	Basal area	0.02	0.29	-0.08	-0.05	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R	0.07	0.21	-0.21	-0.04	0.01	0.17	0.00	0.00	0.00	0.00	0.05	-0.01	-0.01	0.04	0.00	0.00	0.00	0
		Quercus saplings	0.19	0.13	-0.12	-0.20	0.00	0.03	0.48	0.00	0.00	0.04	0.13	-0.11	-0.02	0.03	0.08	0.00	0.00	0
		Quercus BAI	0.07	0.07	0.08	-0.11	-0.07	0.04	-0.08	0.35	0.00	0.07	0.08	-0.06	-0.08	0.02	0.03	0.17	0.00	0
		Pinus recruitment	0.03	-0.20	-0.07	0.17	0.10	0.03	0.14	-0.22	-0.01	-0.04	-0.01	0.01	0.04	0.01	0.00	-0.11	0.00	0
P.halepensis	Dry	Basal area	0.15	0.00	-0.22	-0.03	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R	0.11	0.05	-0.47	-0.08	0.01	0.11	0.00	0.00	0.00	0.02	0.00	-0.02	0.00	0.03	0.00	0.00	0.00	0
		Quercus saplings	-0.04	-0.05	-0.06	0.05	0.02	-0.05	0.87	0.00	0.00	0.10	0.05	-0.42	-0.07	0.02	0.09	0.00	0.00	0
		Quercus BAI	0.04	0.01	-0.03	-0.26	-0.13	0.06	-0.27	0.38	0.00	0.00	-0.02	-0.06	0.02	0.02	-0.01	0.33	0.00	0
		Pinus recruitment	0.20	-0.04	0.07	0.21	0.14	0.05	0.47	-0.44	0.08	0.04	0.03	-0.04	-0.06	0.00	0.04	-0.38	0.03	0
P.halepensis	Wet	Basal area	0.01	0.18	0.02	-0.08	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R	0.11	0.15	-0.15	-0.05	-0.01	0.25	0.00	0.00	0.00	0.00	0.04	0.01	-0.02	0.06	0.00	0.00	0.00	0
		Quercus saplings	0.22	0.08	-0.05	-0.28	-0.02	0.00	0.62	0.00	0.00	0.07	0.12	-0.09	-0.04	0.03	0.15	0.00	0.00	0
		Quercus BAI	0.00	0.06	0.05	-0.04	-0.08	0.04	-0.13	0.48	0.00	0.13	0.08	-0.05	-0.15	0.01	0.04	0.30	0.00	0
		Pinus recruitment	-0.03	-0.24	-0.04	0.12	0.11	-0.06	0.23	-0.31	-0.01	-0.07	-0.03	0.01	0.09	0.00	0.01	-0.20	0.00	0

Species	Subset		Direct effects									Indirect effects								
			Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	Quercus ilex R1 recruitment	Quercus ilex R4 sapling	Quercus ilex biomass increase	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	Quercus ilex R1 recruitment	Quercus ilex R4 sapling	Quercus ilex biomass increase
P.pinea	Species	Basal area		0.21	-0.09	-0.07	0.13	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R		0.17	0.02	0.10	-0.02	0.17	0.00	0.00	0.00		0.03	-0.02	-0.01	0.02	0.00	0.00	0.00	0
		Quercus saplings		0.26	-0.16	-0.15	-0.05	-0.05	0.77	0.00	0.00		0.15	0.01	0.08	-0.01	0.13	0.00	0.00	0
		Quercus BAI		0.10	-0.02	-0.10	-0.16	0.00	-0.07	0.27	0.00		0.10	-0.04	-0.02	-0.02	0.01	0.21	0.00	0
		Pinus recruitment		-0.11	-0.11	-0.14	0.08	0.06	0.36	-0.52	-0.06		-0.14	0.08	0.08	0.05	0.02	-0.41	-0.02	0
P.pinea	Dry	Basal area		0.00	-0.06	0.08	0.08	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R		0.23	0.19	-0.10	-0.01	0.06	0.00	0.00	0.00		0.00	0.00	0.01	0.00	0.00	0.00	0.00	0

		Quercus saplings	0.00	-0.05	0.41	-0.02	-0.13	0.92	0.00	0.00	0.21	0.18	-0.10	-0.02	0.05	0.00	0.00	0
		Quercus BAI	0.08	0.04	-0.45	-0.08	0.07	-0.95	1.04	0.00	0.01	-0.04	0.43	-0.04	-0.14	0.97	0.00	0
		Pinus recruitment	0.14	-0.21	0.05	0.08	0.14	0.42	-0.44	-0.04	0.01	0.01	-0.16	0.02	0.05	-0.39	-0.04	0
P.pinea	Wet	Basal area	0.13	-0.14	-0.10	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R	-0.12	-0.22	0.27	0.00	0.30	0.00	0.00	0.00	0.04	-0.04	-0.03	0.06	0.00	0.00	0.00	0
		Quercus saplings	0.21	-0.25	-0.53	-0.02	-0.11	0.80	0.00	0.00	-0.08	-0.20	0.22	0.02	0.24	0.00	0.00	0
		Quercus BAI	0.11	0.00	-0.23	-0.19	-0.03	0.20	0.09	0.00	-0.01	-0.09	0.06	0.00	0.07	0.05	0.00	0
		Pinus recruitment	-0.10	0.08	-0.09	0.11	0.03	0.24	-0.47	-0.03	-0.08	0.14	0.21	0.02	0.01	-0.38	0.00	0

			Direct effects									Indirect effects								
Species	Subset		Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	Quercus ilex R1 recruitment	Quercus ilex R4 sapling	Quercus ilex biomass increase	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	Quercus ilex R1 recruitment	Quercus ilex R4 sapling	Quercus ilex biomass incr.
P.pinaster	Species	Basal area		0.15	-0.17	-0.02	0.25	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R		-0.43	0.18	-0.03	0.02	0.02	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus saplings		-0.08	0.03	-0.05	-0.01	-0.07	0.68	0.00	0.00		-0.30	0.13	-0.02	0.00	0.01	0.00	0.00	0
		Quercus BAI		0.02	-0.01	-0.05	-0.05	-0.02	-0.02	0.19	0.00		-0.07	0.03	-0.01	-0.01	-0.01	0.13	0.00	0
		Pinus recruitment		-0.31	0.15	-0.02	0.08	0.20	0.12	-0.23	-0.08		0.07	-0.05	0.01	0.06	0.02	-0.17	-0.02	0
P.pinaster	Dry	Basal area		0.10	-0.10	-0.03	0.20	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R		0.08	0.22	0.03	0.10	0.05	0.00	0.00	0.00		0.00	-0.01	0.00	0.01	0.00	0.00	0.00	0
		Quercus saplings		-0.05	-0.04	0.06	-0.02	-0.11	0.86	0.00	0.00		0.06	0.20	0.03	0.07	0.04	0.00	0.00	0
		Quercus BAI		0.04	-0.01	-0.05	-0.02	-0.02	-0.21	0.35	0.00		-0.02	0.01	0.03	-0.01	-0.03	0.30	0.00	0
		Pinus recruitment		0.15	0.04	-0.23	0.02	0.23	0.03	-0.12	-0.12		0.02	-0.04	-0.01	0.05	0.02	-0.12	-0.04	0
P.pinaster	Wet	Basal area		0.03	-0.20	-0.02	0.30	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R		-0.82	0.14	-0.05	-0.05	-0.01	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus saplings		0.21	-0.02	-0.12	-0.02	-0.03	0.92	0.00	0.00		-0.88	0.16	-0.05	-0.06	-0.01	0.00	0.00	0
		Quercus BAI		0.07	0.01	-0.09	-0.06	-0.01	0.11	0.11	0.00		-0.16	0.03	-0.02	-0.02	-0.01	0.12	0.00	0
		Pinus recruitment		-0.02	0.19	0.00	0.20	0.15	0.89	-0.96	-0.05		-0.22	-0.01	0.13	0.08	0.03	-0.89	-0.01	0

			Direct effects									Indirect effects								
Species	Subset		Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	Quercus ilex R1 recruitment	Quercus ilex R4 sapling	Quercus ilex biomass increase	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	Quercus ilex R1 recruitment	Quercus ilex R4 sapling	Quercus ilex biomass incr.
P.nigra	Species	Basal area		0.17	-0.09	-0.06	0.24	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R1		-0.18	0.33	0.00	-0.04	0.08	0.00	0.00	0.00		0.01	-0.01	-0.01	0.02	0.00	0.00	0.00	0
		Quercus saplings		0.11	0.11	-0.27	-0.01	-0.07	0.74	0.00	0.00		-0.13	0.24	0.00	-0.04	0.06	0.00	0.00	0
		Quercus BAI		0.02	0.05	-0.14	-0.09	0.00	-0.11	0.36	0.00		0.01	0.09	-0.10	-0.01	-0.01	0.27	0.00	0
		Pinus recruitment		-0.07	-0.06	-0.26	0.03	0.06	0.59	-0.53	-0.12		-0.08	-0.02	0.17	0.04	0.06	-0.42	-0.04	0
P.nigra	Warm	Basal area		0.19	-0.05	-0.07	0.24	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R		-0.16	0.04	0.08	-0.02	0.14	0.00	0.00	0.00		0.03	-0.01	-0.01	0.03	0.00	0.00	0.00	0
		Quercus saplings		0.10	0.08	-0.37	0.00	-0.09	0.70	0.00	0.00		-0.11	0.03	0.06	-0.01	0.10	0.00	0.00	0
		Quercus BAI		0.02	0.03	-0.01	-0.12	0.02	-0.17	0.46	0.00		0.02	0.04	-0.16	0.00	-0.02	0.32	0.00	0
		Pinus recruitment		-0.01	-0.12	-0.32	0.08	0.00	0.61	-0.53	-0.10		-0.08	-0.04	0.23	0.02	0.08	-0.38	-0.04	0
P.nigra	Cold	Basal area		0.15	-0.08	0.00	0.19	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R		-0.11	0.29	-0.04	-0.04	0.03	0.00	0.00	0.00		0.01	0.00	0.00	0.01	0.00	0.00	0.00	0
		Quercus saplings		0.06	0.02	0.01	-0.02	-0.03	0.50	0.00	0.00		-0.06	0.15	-0.02	-0.02	0.02	0.00	0.00	0
		Quercus BAI		0.00	0.03	-0.01	-0.04	-0.03	0.02	0.20	0.00		-0.01	0.04	0.00	-0.01	0.00	0.10	0.00	0
		Pinus recruitment		-0.12	0.02	-0.02	-0.01	0.12	0.10	-0.06	-0.06		0.01	0.01	0.00	0.03	0.01	-0.04	-0.01	0

			Direct effects									Indirect effects								
Species	Subset		Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	Quercus ilex R1 recruitment	Quercus ilex R4 sapling	Quercus ilex biomass increase	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	Quercus ilex R1 recruitment	Quercus ilex R4 sapling	Quercus ilex biomass increase
P.sylvestris	Species	Basal area		0.06	-0.22	-0.04	0.21	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R		-0.10	0.55	0.13	-0.01	-0.04	0.00	0.00	0.00		0.00	0.01	0.00	-0.01	0.00	0.00	0.00	0
		Quercus saplings		0.08	0.11	-0.22	-0.05	-0.07	0.85	0.00	0.00		-0.09	0.49	0.11	-0.03	-0.03	0.00	0.00	0
		Quercus BAI		0.01	0.00	0.04	-0.08	0.04	-0.28	0.62	0.00		0.02	0.20	-0.11	-0.04	-0.05	0.53	0.00	0
		Pinus recruitment		-0.10	-0.08	-0.05	0.12	0.00	0.47	-0.44	-0.06		-0.05	-0.01	0.12	0.03	0.03	-0.39	-0.04	0
P.sylvestris	Warm	Basal area		0.07	-0.17	-0.02	0.22	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R		-0.19	0.31	0.15	-0.01	-0.01	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0

		Quercus saplings	0.11	0.17	-0.32	-0.06	-0.07	0.80	0.00	0.00	-0.16	0.26	0.13	-0.02	0.00	0.00	0.00	0
		Quercus BAI	0.01	-0.02	0.07	-0.11	0.04	-0.25	0.64	0.00	0.02	0.19	-0.16	-0.04	-0.05	0.52	0.00	0
		Pinus recruitment	-0.03	-0.16	-0.10	0.17	-0.07	0.42	-0.39	-0.06	-0.07	-0.04	0.15	0.02	0.03	-0.33	-0.04	0
P.sylvestris	Cold	Basal area	0.06	-0.06	-0.14	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0
		Quercus R	0.00	0.23	0.11	-0.07	-0.09	0.00	0.00	0.00	-0.01	0.01	0.01	-0.02	0.00	0.00	0.00	0
		Quercus saplings	0.02	-0.03	-0.05	-0.05	-0.05	0.95	0.00	0.00	-0.01	0.23	0.12	-0.10	-0.08	0.00	0.00	0
		Quercus BAI	0.02	-0.07	-0.11	-0.04	-0.02	0.89	-0.49	0.00	-0.01	0.11	0.09	-0.01	-0.01	-0.47	0.00	0
		Pinus recruitment	-0.13	0.03	0.12	0.04	0.05	0.79	-0.77	-0.18	-0.02	0.02	0.05	0.06	0.04	-0.80	0.10	0

			Direct effects									Indirect effects								
Species	Subset		Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	Quercus humilis R1 recruitment	Quercus humilis R4 saplings	Quercus humilis biomass increase	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	Quercus humilis R1 recruitment	Quercus humilis R4 saplings	Quercus humilis biomass increase
P.uncinata	Species	Basal area		0.09	-0.03		0.21	0	0	0			0	0		0	0	0	0	
		Quercus R		0.054	0.57		-0.01	-0.024	0	0			-0	0.001		-0.01	0	0	0	
		Quercus saplings		-0.04	0.182		-0.09	0.016	0.71	0			0.038	0.402		-0.01	-0.016	0	0	
		Pinus recruitment		0.054	-0.2		0.29	-0.13	-0.143	0.22			-0.02	0.056		-0.05	0.011	0.155	0	

Table S8. *Extended results of the Bayesian SEM models for recruitment class R1. Standardized parameter estimates for direct and indirect effects are reported. The effect factors are placed in columns and response factors are distributed in rows. Significant parameter estimates are in bold. A effect is considered significant when its 95% credibility interval does not overlap 0. The table reports the results of SEM analyses for each species and for each species-specific climatic subset (dry/wet; cold/warm).*

	Direct effects									Indirect effects								
Pinus halepensis	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	*Quercus ilex* R1 recruitment	*Quercus ilex* R4 saplings	*Quercus ilex* biomass increase	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	*Quercus ilex* R1 recruitment	*Quercus ilex* R4 saplings	*Quercus ilex* biomass increase
R2																		
Basal area	0.01	-0.02	0.02	0.01	-0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quercus R	-0.19	0.18	-0.09	-0.01	0.04	-0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quercus saplings	-0.13	0.08	-0.02	-0.05	-0.01	-0.01	0.50	0.00	0.00	-0.09	0.09	-0.04	-0.01	0.02	-0.01	0.00	0.00	0.00
Quercus BAI	-0.06	0.05	-0.01	-0.02	-0.05	-0.03	0.00	0.25	0.00	-0.06	0.04	-0.02	-0.02	0.01	-0.01	0.13	0.00	0.00
Pinus recruitment (R2)	0.03	-0.07	-0.02	0.11	-0.04	0.04	0.04	-0.06	-0.04	0.01	-0.01	0.00	0.01	0.00	0.00	-0.03	-0.01	0.00
R3																		
Basal area	0.01	-0.02	0.02	0.01	-0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quercus R	-0.19	0.18	-0.09	-0.01	0.04	-0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quercus saplings	-0.13	0.08	-0.02	-0.05	-0.01	-0.01	0.50	0.00	0.00	-0.09	0.09	-0.04	0.00	0.02	-0.01	0.00	0.00	0.00
Quercus BAI	-0.06	0.05	-0.01	-0.02	-0.04	-0.03	0.00	0.25	0.00	-0.06	0.04	-0.02	-0.02	0.01	-0.01	0.13	0.00	0.00
Pinus recruitment (R3)	-0.02	-0.06	0.00	-0.07	-0.06	0.05	0.01	-0.09	-0.05	0.02	-0.02	0.01	0.01	0.00	0.00	-0.05	-0.01	0.00
R4																		
Basal area	0.01	-0.02	0.02	0.01	-0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quercus R	-0.19	0.18	-0.09	-0.01	0.04	-0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quercus saplings	-0.13	0.08	-0.02	-0.05	-0.01	-0.01	0.51	0.00	0.00	-0.09	0.09	-0.04	-0.01	0.02	-0.01	0.00	0.00	0.00
Quercus BAI	-0.06	0.05	-0.01	-0.02	-0.04	-0.03	0.00	0.25	0.00	-0.06	0.04	-0.02	-0.02	0.01	-0.01	0.13	0.00	0.00
Pinus recruitment (R4)	-0.04	-0.06	0.00	-0.16	-0.07	0.03	0.02	-0.06	-0.08	0.02	-0.01	0.00	0.01	0.00	0.00	-0.04	-0.02	0.

Pinus nigra	Direct effects									Indirect effects								
	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	*Quercus ilex* R1 recruitment	*Quercus ilex* R4 saplings	*Quercus ilex* biomass increase	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	*Quercus ilex* R1 recruitment	*Quercus ilex* R4 saplings	*Quercus ilex* biomass increase
R2																		
Basal area		-0.03	-0.015	0.002	-0.069	0	0	0	0		0	0	0	0	0	0	0	0
Quercus R		-0.007	-0.193	0.051	-0.008	-0.024	0	0	0		0.001	0	0	0.002	0	0	0	0
Quercus saplings		0.031	-0.014	-0.08	-0.007	0.002	0.468	0	0		-0.003	-0.09	0.024	-0.003	-0.011	0	0	0
Quercus BAI		0.002	-0.034	-0.018	-0.067	0.006	0	0.196	0		0.005	-0.021	-0.011	-0.002	-0.002	0.092	0	0
Pinus recruitment (R2)		0.01	-0.059	-0.101	-0.063	-0.04	0.121	-0.046	-0.066		-0.001	-0.014	0.011	0.007	-0.003	-0.028	-0.013	0
R3																		
Basal area		-0.03	-0.015	0.002	-0.069	0	0	0	0		0	0	0	0	0	0	0	0
Quercus R		-0.007	-0.193	0.051	-0.007	-0.024	0	0	0		0.001	0	0	0.002	0	0	0	0
Quercus saplings		0.031	-0.014	-0.079	-0.007	0.002	0.468	0	0		-0.003	-0.09	0.024	-0.003	-0.011	0	0	0
Quercus BAI		0.002	-0.034	-0.017	-0.066	0.006	0	0.196	0		0.005	-0.02	-0.011	-0.002	-0.002	0.092	0	0
Pinus recruitment (R3)		0.025	-0.05	-0.124	-0.073	-0.021	0.107	-0.034	-0.06		-0.001	-0.013	0.009	0.005	-0.002	-0.021	-0.012	0
R4																		
Basal area		-0.029	-0.015	0.003	-0.069	0	0	0	0		0	0	0	0	0	0	0	0
Quercus R		-0.007	-0.193	0.052	-0.007	-0.024	0	0	0		0.001	0	0	0.002	0	0	0	0
Quercus saplings		0.031	-0.014	-0.08	-0.006	0.002	0.468	0	0		-0.003	-0.09	0.024	-0.002	-0.011	0	0	0
Quercus BAI		0.002	-0.034	-0.018	-0.066	0.006	0	0.195	0		0.005	-0.02	-0.011	-0.002	-0.002	0.091	0	0
Pinus recruitment (R4)		0.044	-0.055	-0.149	-0.078	-0.026	0.088	-0.026	-0.066		-0.001	-0.01	0.008	0.006	-0.002	-0.018	-0.013	0

	Direct effects									Indirect effects								
Pinus pinaster	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	*Quercus ilex* R1 recruitment	*Quercus ilex* R4 saplings	*Quercus ilex* biomass increase	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	*Quercus ilex* R1 recruitment	*Quercus ilex* R4 saplings	*Quercus ilex* biomass increase
R2																		
Basal area		0.02	0.001	0.008	-0.052	0	0	0	0		0	0	0	0	0	0	0	0
Quercus R		0.252	-0.125	-0.023	-0.031	-0.003	0	0	0		0	0	0	0	0	0	0	0
Quercus saplings		0.011	-0.014	-0.01	-0.017	0.006	0.529	0	0		-0.016	-0.012	-0.066	0.133	-0.001	0	0	0
Quercus BAI		0.014	-0.008	0.009	-0.035	0.013	0	0.155	0		-0.006	-0.003	-0.012	0.023	0.001	0.082	0	0
Pinus recruitment (R2)		0.05	-0.031	0.04	0.009	0.006	-0.009	-0.042	-0.041		0.003	0.001	0.005	-0.01	-0.001	-0.025	-0.006	0
R3																		
Basal area		0.02	0.001	0.008	-0.052	0	0	0	0		0	0	0	0	0	0	0	0
Quercus R		0.252	-0.124	-0.023	-0.031	-0.003	0	0	0		0	0	0	0	0	0	0	0
Quercus saplings		0.011	-0.014	-0.01	-0.017	0.006	0.53	0	0		0.134	-0.066	-0.012	-0.016	-0.001	0	0	0
Quercus BAI		0.014	-0.009	0.009	-0.034	0.013	0	0.155	0		0.023	-0.012	-0.003	-0.006	0.001	0.082	0	0
Pinus recruitment (R3)		-0.013	-0.012	0.025	0.016	0.006	0.005	-0.009	-0.026		-0.001	0.001	0	0.001	0	-0.007	-0.004	0
R4																		
Basal area		0.02	0.001	0.009	-0.052	0	0	0	0		0	0	0	0	0	0	0	0
Quercus R		0.252	-0.124	-0.023	-0.03	-0.003	0	0	0		0	0	0	0	0	0	0	0
Quercus saplings		0.011	-0.014	-0.01	-0.017	0.006	0.53	0	0		0.134	-0.066	-0.012	-0.016	-0.001	0	0	0
Quercus BAI		0.014	-0.009	0.009	-0.035	0.013	0	0.155	0		0.023	-0.012	-0.003	-0.006	0.001	0.082	0	0
Pinus recruitment (R4)		-0.044	-0.019	-0.021	0.011	-0.011	-0.033	0.009	-0.013		-0.008	0.004	0	0.002	0	0.004	-0.002	0

	Direct effects									Indirect effects								
Pinus pinea	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	*Quercus ilex* R1 recruitment	*Quercus ilex* R4 saplings	*Quercus ilex* biomass increase	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	*Quercus ilex* R1 recruitment	*Quercus ilex* R4 saplings	*Quercus ilex* biomass increase
R2																		
Basal area		-0.047	0.036	-0.001	-0.046	0	0	0	0		0	0	0	0	0	0	0	0
Quercus R		0.061	0.017	0.032	-0.01	-0.059	0	0	0		0.003	-0.002	0	0.003	0	0	0	0
Quercus saplings		0.109	-0.043	-0.006	-0.036	-0.023	0.508	0	0		0.034	0.007	0.016	-0.003	-0.03	0	0	0
Quercus BAI		0.035	0.006	0.002	-0.038	0.015	0	0.158	0		0.022	-0.005	0.002	-0.007	-0.008	0.08	0	0
Pinus recruitment (R2)		-0.087	-0.087	-0.018	0.044	0.046	-0.012	-0.134	-0.014		-0.023	0.006	-0.002	0.004	0.008	-0.069	-0.002	0
R3																		
Basal area		-0.048	0.037	-0.001	-0.045	0	0	0	0		0	0	0	0	0	0	0	0
Quercus R		0.061	0.017	0.033	-0.01	-0.059	0	0	0		0.003	-0.002	0	0.003	0	0	0	0
Quercus saplings		0.11	-0.043	-0.006	-0.036	-0.023	0.507	0	0		0.034	0.007	0.017	-0.003	-0.03	0	0	0
Quercus BAI		0.035	0.005	0.001	-0.039	0.015	0	0.157	0		0.022	-0.005	0.002	-0.007	-0.008	0.08	0	0
Pinus recruitment (R3)		-0.043	-0.087	-0.01	-0.043	0.063	-0.024	-0.094	-0.008		-0.018	0.005	-0.002	0.001	0.006	-0.049	-0.001	0
R4																		
Basal area		-0.049	0.036	0	-0.046	0	0	0	0		0	0	0	0	0	0	0	0
Quercus R		0.061	0.017	0.033	-0.01	-0.059	0	0	0		0.003	-0.002	0	0.003	0	0	0	0
Quercus saplings		0.11	-0.043	-0.007	-0.037	-0.023	0.507	0	0		0.034	0.007	0.017	-0.003	-0.03	0	0	0
Quercus BAI		0.034	0.005	0.001	-0.039	0.015	0	0.158	0		0.022	-0.005	0.002	-0.007	-0.008	0.08	0	0
Pinus recruitment (R4)		-0.005	-0.048	-0.039	-0.048	0.059	0.033	-0.102	0.011		-0.015	0.006	0	0.001	0.003	-0.051	0.002	0

	Direct effects									Indirect effects								
Pinus sylvestris	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	*Quercus ilex* R1 recruitment	*Quercus ilex* R4 saplings	*Quercus ilex* biomass increase	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	*Quercus ilex* R1 recruitment	*Quercus ilex* R4 saplings	*Quercus ilex* biomass increase
R2																		
Basal area		-0.004	0.004	-0.002	-0.028	0	0	0	0		0	0	0	0	0	0	0	0
Quercus R		0.054	-0.359	0.058	-0.007	-0.006	0	0	0		0	0	0	0	0	0	0	0
Quercus saplings		0.029	-0.093	-0.032	-0.033	0.01	0.6	0	0		0.032	-0.215	0.035	-0.004	-0.003	0	0	0
Quercus BAI		0.016	-0.053	-0.014	-0.053	0.01	0	0.276	0		0.017	-0.085	0.001	-0.011	0.002	0.166	0	0
Pinus recruitment (R2)		0.015	0.043	-0.025	-0.043	0.004	0.035	-0.036	-0.046		-0.002	0.005	0.003	0.004	-0.001	-0.03	-0.013	0
R3																		
Basal area		-0.004	0.004	-0.003	-0.027	0	0	0	0		0	0	0	0	0	0	0	0
Quercus R		0.054	-0.358	0.057	-0.007	-0.006	0	0	0		0	0	0	0	0	0	0	0
Quercus saplings		0.029	-0.093	-0.031	-0.034	0.01	0.6	0	0		0.032	-0.215	0.034	-0.004	-0.003	0	0	0
Quercus BAI		0.017	-0.054	-0.015	-0.051	0.01	0	0.274	0		0.017	-0.085	0.001	-0.011	0.002	0.165	0	0
Pinus recruitment (R3)		0.017	0.019	-0.061	-0.099	0.001	0.076	-0.025	-0.057		0.001	-0.012	0.005	0.004	-0.001	-0.024	-0.016	0
R4																		
Basal area		-0.004	0.004	-0.004	-0.027	0	0	0	0		0	0	0	0	0	0	0	0
Quercus R		0.054	-0.359	0.057	-0.007	-0.006	0	0	0		0	0	0	0	0	0	0	0
Quercus saplings		0.029	-0.093	-0.031	-0.033	0.01	0.601	0	0		0.032	-0.215	0.034	-0.005	-0.003	0	0	0
Quercus BAI		0.016	-0.052	-0.014	-0.052	0.01	0	0.277	0		0.017	-0.085	0.001	-0.011	0.002	0.166	0	0
Pinus recruitment (R4)		0.028	0.012	-0.07	-0.106	-0.018	0.058	-0.004	-0.037		0.002	-0.014	0.004	0.003	-0.001	-0.009	-0.01	0

	Direct effects									Indirect effects								
Pinus uncinata	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	*Quercus humilis* R1 recruitment	*Quercus humilis* R4 saplings	*Quercus humilis* biomass increase	Summer rainfall	Annual rainfall	Mean annual temperature	Fire	Management	Total basal area	*Quercus humilis* R1 recruitment	*Quercus humilis* R4 saplings	*Quercus humilis* biomass increase
R2																		
Basal area		-0.105	-0.066		-0.015	0	0	0	0		0	0		0	0	0	0	0
Quercus R		-0.107	0.203		0.001	0.045	0	0	0		-0.005	-0.003		-0.001	0	0	0	0
Quercus saplings		-0.019	0.041		-0.006	-0.04	0.463	0	0		-0.048	0.095		0.001	0.021	0	0	0
Quercus BAI		-0.055	-0.065		-0.028	0.004	0	0.217	0		-0.015	0.029		-0.001	-0.004	0.101	0	0
Pinus recruitment (R2)		0.032	-0.067		-0.002	-0.081	-0.055	0.008	-0.052		0.018	-0.003		0.003	-0.003	-0.002	-0.011	0
R3																		
Basal area		-0.106	-0.068		-0.015	0	0	0	0		0	0		0	0	0	0	0
Quercus R		-0.107	0.203		0	0.045	0	0	0		-0.005	-0.003		-0.001	0	0	0	0
Quercus saplings		-0.019	0.041		-0.004	-0.04	0.465	0	0		-0.048	0.096		0	0.021	0	0	0
Quercus BAI		-0.057	-0.063		-0.029	0.004	0	0.216	0		-0.015	0.029		-0.001	-0.004	0.1	0	0
Pinus recruitment (R3)		0.051	-0.033		-0.034	-0.07	-0.007	-0.048	-0.039		0.014	-0.002		0.002	0.001	-0.026	-0.008	0
R4																		
Basal area		-0.106	-0.067		-0.014	0	0	0	0		0	0		0	0	0	0	0
Quercus R		-0.107	0.203		0.002	0.045	0	0	0		-0.005	-0.003		-0.001	0	0	0	0
Quercus saplings		-0.019	0.041		-0.005	-0.04	0.465	0	0		-0.048	0.096		0.001	0.021	0	0	0
Quercus BAI		-0.057	-0.065		-0.027	0.004	0	0.217	0		-0.015	0.029		-0.001	-0.004	0.101	0	0
Pinus recruitment (R4)		0.056	-0.026		-0.037	-0.048	-0.044	-0.069	-0.043		0.018	-0.014		0.002	-0.001	-0.037	-0.009	0

Table S9. *Extended results of the Bayesian SEM models for recruitment class R2, R3 and R4. Standardized parameter estimates for direct and indirect effects are reported. The effect factors are placed in columns and response factors are distributed in rows. Significant parameter estimates are in bold. A effect is considered significant when its 95% credibility interval does not overlap 0.*

	Pinus halepensis stands						*Pinus pinea* stands						*Pinus pinaster* stands					
	Pinus R			*Q.ilex* R			*Pinus* R			*Q.ilex* R			*Pinus* R			*Q.ilex* R		
	Coeff	Std,error	W std	Coeff	Std,error	W std	Coeff	Std,error	W std	Coeff	Std,error	W std	Coeff	Std,error	W std	Coeff	Std,error	W std
Sapling presence	-1.6 E-01	**3.4 E-02**	22.2	3.7 E-02	2.9 E-02	1.6	-2.5 E-01	**5.2 E-02**	22.9	6.4 E-03	7.7 E-02	0.0	-1.8 E-01	**3.8 E-02**	22.9	3.5 E-02	3.7 E-02	0.9
BAI	-9.2 E-04	**3.8 E-04**	5.9	-5.3 E-05	8.6 E-05	0.4	-1.1 E-03	**4.8 E-04**	5.5	-7.7 E-05	1.4 E-04	0.3	-2.5 E-03	**6.6 E-04**	15.0	1.1 E-04	**4.5 E-05**	5.6
Annual rainfall (1)	2.8 E-04	2.1 E-04	1.9	4.3 E-04	**3.6 E-05**	141.6	2.3 E-03	**5.3 E-04**	18.8	2.1 E-04	**5.2 E-05**	16.6	-1.4 E-04	**1.1 E-05**	183.4	-4.8 E-04	**1.8 E-05**	739.2
(2)	-3.4 E-08	2.0 E-08	2.9				-2.1 E-07	**4.4 E-08**	23.1									
Summer rainfall (1)	4.9 E-03	**4.7 E-04**	111.4	4.5 E-04	**1.0 E-04**	19.8												
(2)	-2.3 E-06	**2.2 E-07**	116.0															
Annual temperature (1)	1.6 E-01	**3.5 E-02**	20.0	-4.4 E-02	**2.5 E-03**	323.9	-5.2 E-03	3.4 E-03	2.4	7.1 E-01	**5.5 E-02**	162.0	1.2 E-01	**2.2 E-02**	31.1	2.4 E-02	**1.8 E-03**	164.1
(2)	-5.3 E-04	**1.2 E-04**	20.2							-2.4 E-03	**1.9 E-04**	160.1	-4.0 E-04	**8.5 E-05**	22.9			
Basal area	7.6 E-05	4.4 E-05	3.0	6.6 E-04	**4.7 E-05**	200.0	2.6 E-04	**6.1 E-05**	18.4	2.4 E-04	**6.6 E-05**	13.7	3.8 E-04	**2.5 E-05**	229.2	7.1 E-05	**2.8 E-05**	6.6
Management	1.8 E-01	**2.9 E-02**	37.9	1.5 E-02	3.1 E-02	0.2	1.5 E-01	**4.8 E-02**	9.3	-1.9 E-02	4.9 E-02	0.1	1.6 E-01	**2.8 E-02**	31.2	-2.0 E-02	3.2 E-02	0.4
Fire	3.6 E-01	**5.9 E-02**	36.9	-1.0 E-01	6.7 E-02	2.3	-9.7 E-02	2.2 E-01	0.2	2.7 E-01	2.3 E-01	1.3	-6.1 E-03	7.9 E-02	0.0	-1.7 E-01	**9.0 E-02**	3.8
Soil condition	-2.7 E-04	1.9 E-02	0.0	-5.4 E-02	**1.9 E-02**	7.7	-5.7 E-02	3.1 E-02	3.4	-7.3 E-03	3.0 E-02	0.1	-7.1 E-02	**1.4 E-02**	25.7	-1.2 E-02	1.6 E-02	0.5
Slope	-1.6 E-02	**4.8 E-03**	11.0	1.9 E-02	**5.1 E-03**	13.8	-2.8 E-02	**1.2 E-02**	5.9	1.9 E-02	**1.2 E-02**	2.8	-1.3 E-02	**4.6 E-03**	8.4	4.7 E-02	**4.8 E-03**	94.3

	Pinus nigra stands						*Pinus sylvestris* stands						*Pinus uncinata* stands					
	Pinus R			*Q.ilex* R			*Pinus* R			*Q.ilex* R			*Pinus* R			*Q.humilis* R		
	Coeff	Std,error	W std	Coeff	Std,error	W std	Coeff	Std,error	W std	Coeff	Std,error	W std	Coeff	Std,error	W std	Coeff	Std,error	W std
Sapling presence	-2.1 E-02	3.7 E-02	0.3	1.6 E-01	**3.3 E-02**	22.2	1.5 E-02	4.4 E-02	0.1	1.6 E-01	**3.4 E-02**	22.7	2.2 E-02	2.4 E-01	0.0	-6.3 E-02	1.4 E-01	0.2
BAI	-2.3 E-03	**4.7 E-04**	22.8	-2.3 E-04	**7.5 E-05**	9.9	-1.5 E-03	**4.4 E-04**	11.8	-3.9 E-04	**6.5 E-05**	37.2	-3.0 E-06		0.0	2.0 E-04	3.4 E-04	0.4
Annual rainfall (1)	1.3 E-03	**2.5 E-04**	29.6	-2.5 E-04	**2.5 E-05**	101.1	-1.1 E-04	**2.1 E-05**	27.2	-2.5 E-04	**2.3 E-05**	124.5	4.9 E-05	7.3 E-05	0.4	1.4 E-05	9.5 E-05	0.0
(2)	-1.2 E-07	**1.9 E-08**	35.8															
Summer rainfall (1)																		
(2)																		
Annual temperature (1)	2.9 E-01	**5.2 E-02**	30.5	5.2 E-02	2.9 E-03	325.0	1.1 E-01	2.1 E-02	29.5	8.2 E-02	2.7 E-03	939.0	2.4 E-01	**7.3 E-02**	11.0	-1.1 E-01	**1.3 E-02**	66.9
-2	-1.3 E-03	**2.2 E-04**	31.9				-6.1 E-04	**1.0 E-04**	33.8				-2.0 E-03	**5.7 E-04**	12.2			
Basal area	2.4 E-04	**3.4 E-05**	47.8	1.1 E-04	**3.4 E-05**	11.1	3.4 E-05	2.5 E-05	1.8	-5.8 E-05	3.0 E-05	3.8	-1.6 E-04	**7.1 E-05**	4.8	-1.9 E-05	1.1 E-04	0.0
Management	5.2 E-02	3.6 E-02	2.1	-2.2 E-02	3.5 E-02	0.4	1.8 E-01		33.1	-2.1 E-02	3.7 E-02	0.3	4.0 E-01	**1.1 E-01**	14.0	-3.9 E-02	1.7 E-01	0.1
Fire	-3.2 E-01	**9.6 E-02**	11.5	9.6 E-02	8.4 E-02	1.3	1.3 E-01		0.9	3.2 E-01	**1.4 E-01**	5.6						
Soil condition	-2.4 E-02	2.0 E-02	1.5	-2.3 E-02	1.8 E-02	1.6	-4.4 E-02		7.7	5.6 E-02	**1.5 E-02**	13.1	-2.5 E-02	3.6 E-02	0.5	-3.9 E-02	6.2 E-02	0.4
Slope	-1.8 E-03	5.2 E-03	0.1	6.4 E-02	**5.1 E-03**	155.0	-1.1 E-02		6.1	7.8 E-02	**4.9 E-03**	250.7	1.6 E-02	1.3 E-02	1.6	3.8 E-02	**1.8 E-02**	4.6

Table S10. *Summary of test effects for GLM models. Note that all models are restricted to Pinus sp. stands. In each class of pine stand, we performed independent models (GLM) for Pinus and Quercus species recruitment. Estimated coefficients, standard errors and Wald chi-square statistics are given for each variable. (2) indicates quadratic effects for climatic variables.*

4.8. Supplementary figures

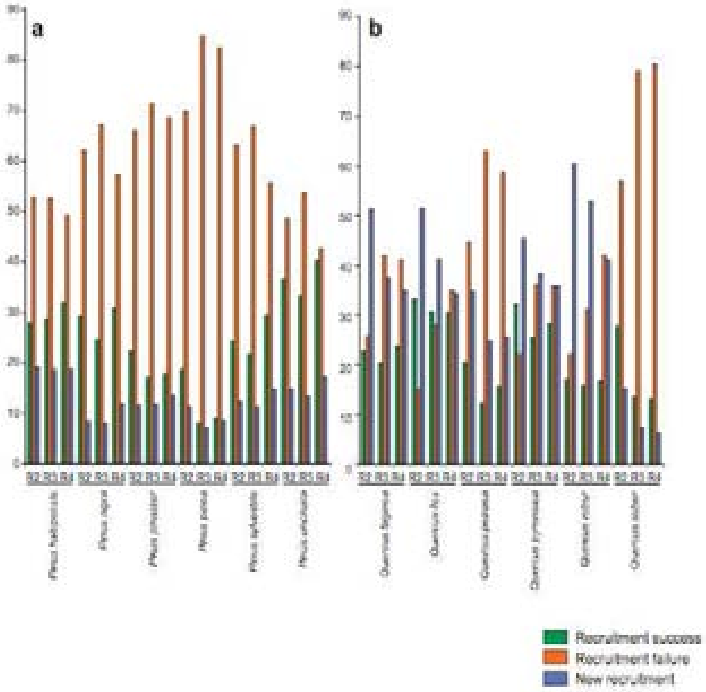
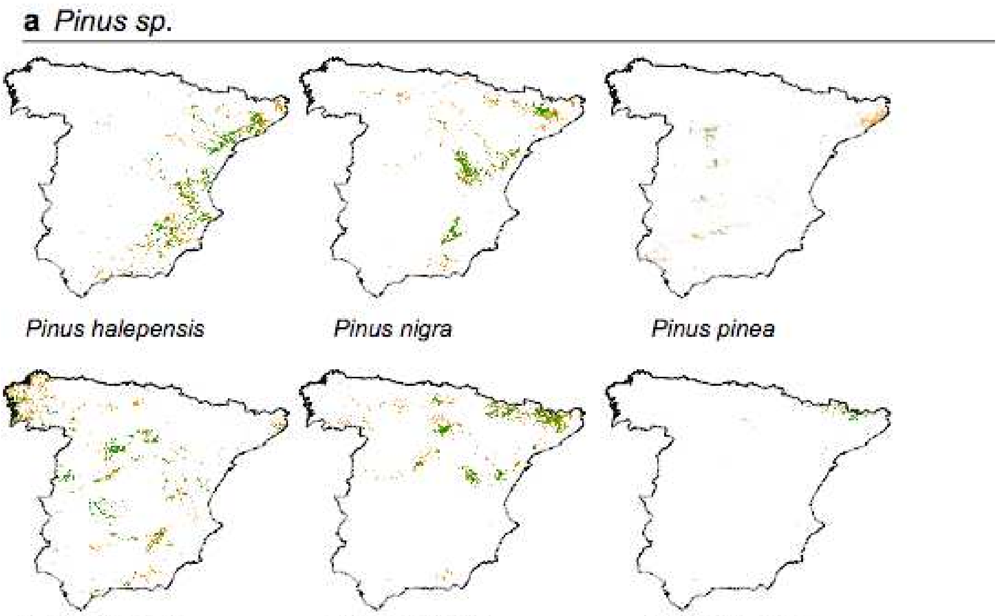


Figure S1. *A comparison of the diverging trends observed in recruitment (for R2, R3 and R4 size classes) between Pinus and Quercus species at the large scale. We first list the recruitment trends for Pinus (a) and subsequently provide the trends for Quercus (b) (in consonance with Table S3, that follows the same order). (a) Percentage of plots with recruitment success (green bars), recruitment failure (orange bars) and new recruitment (blue bars) for each Pinus species. (b) Percentage of plots with recruitment success (green bars), recruitment failure (orange bars) and new recruitment (blue bars) for each Quercus species.*

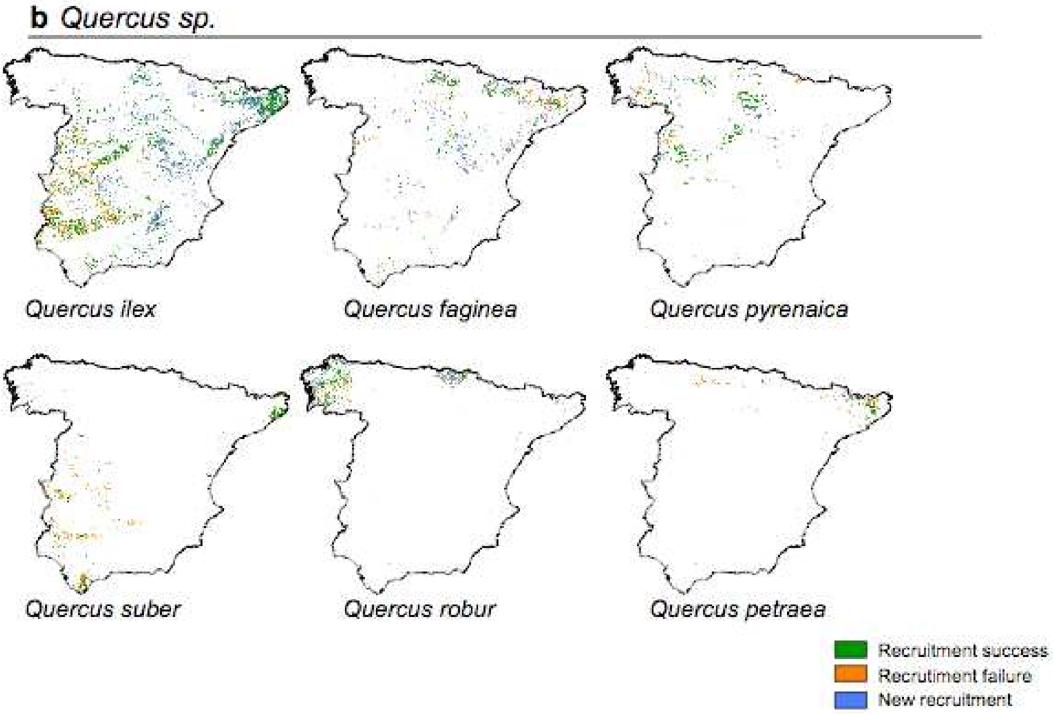
1. Recruitment class R2:



a *Pinus sp.*

Pinus halepensis *Pinus nigra* *Pinus pinea*

Pinus pinaster *Pinus sylvestris* *Pinus uncinata*

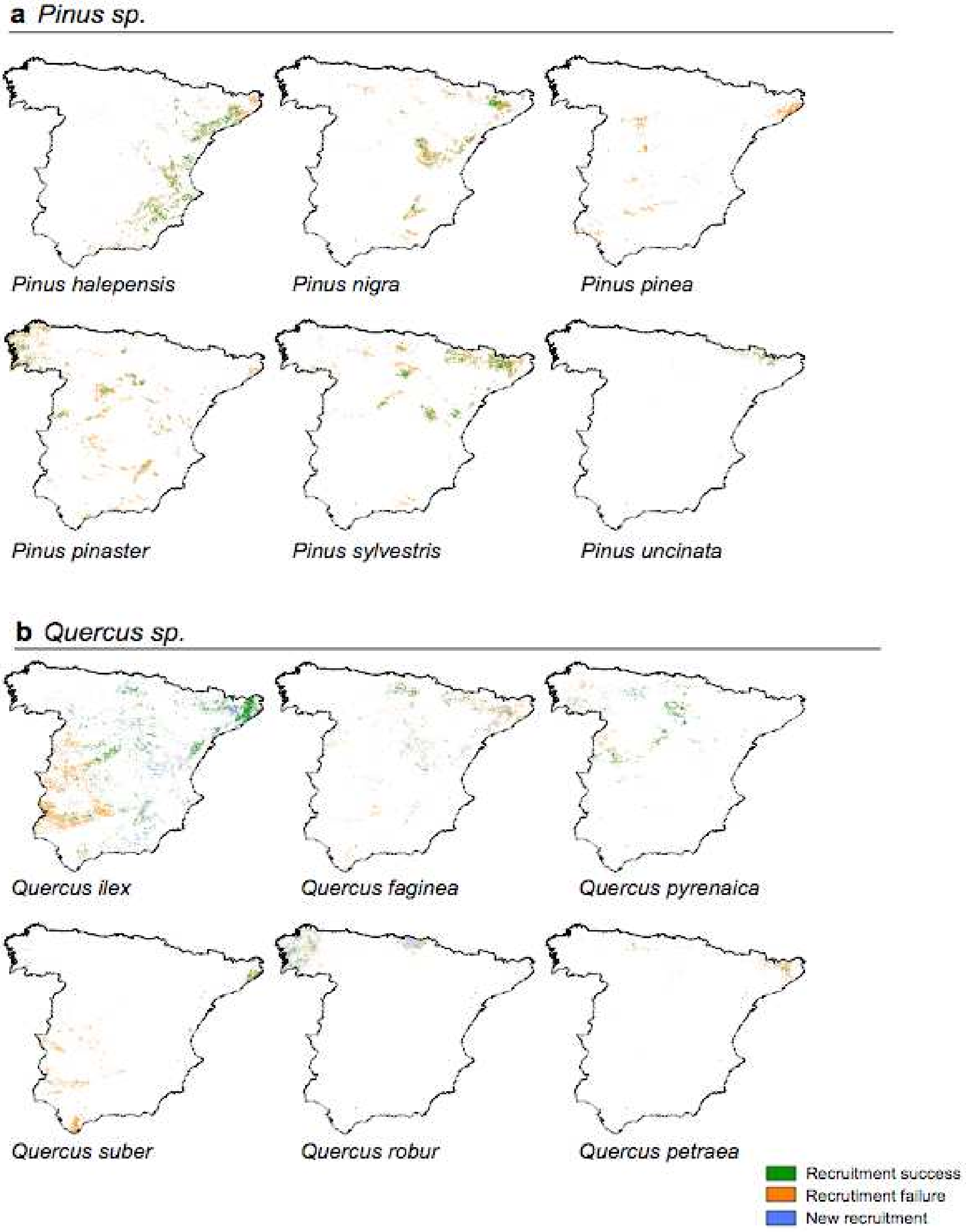


b *Quercus sp.*

Quercus ilex *Quercus faginea* *Quercus pyrenaica*

Quercus suber *Quercus robur* *Quercus petraea*

1. Recruitment class R3



1. Recruitment class R4

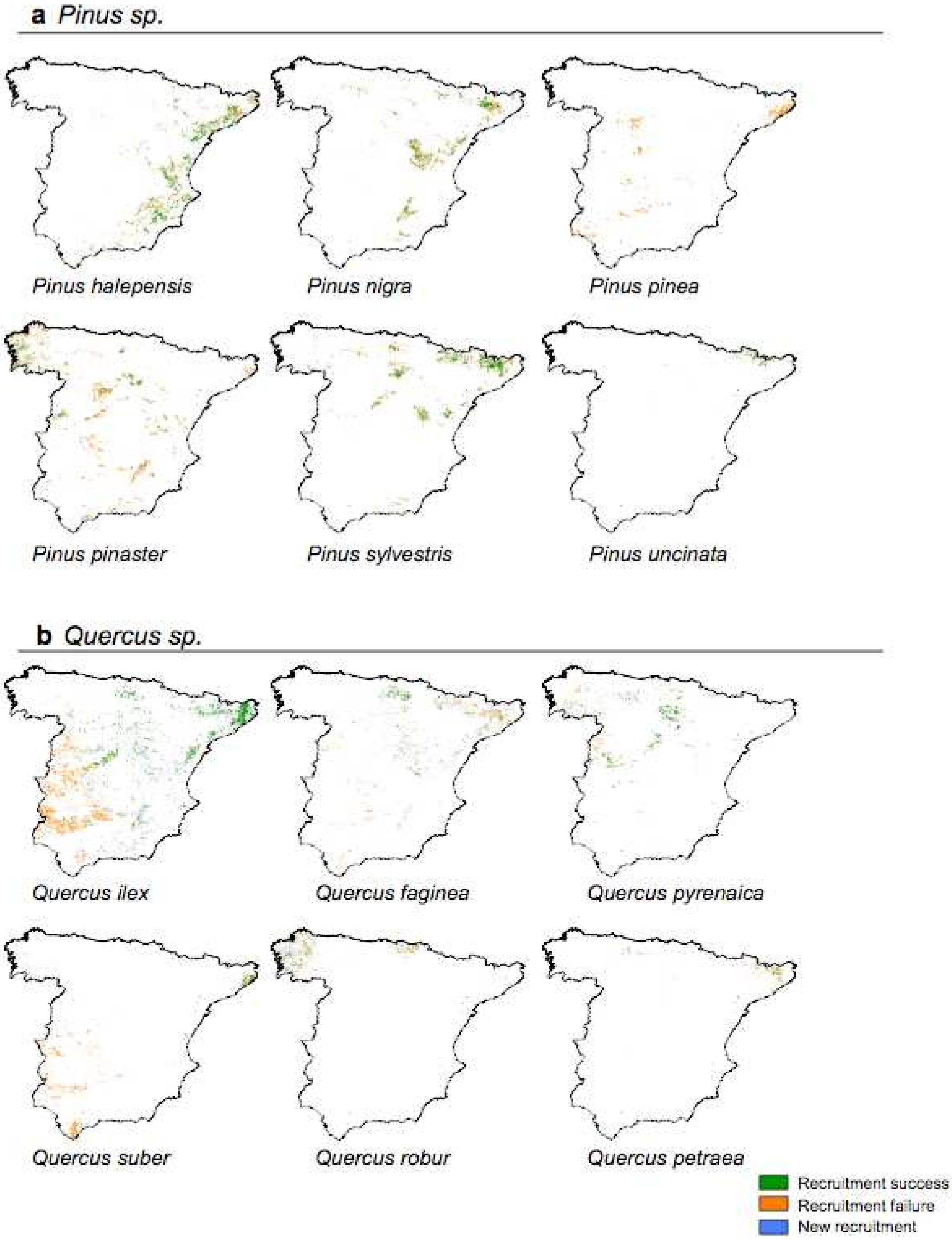
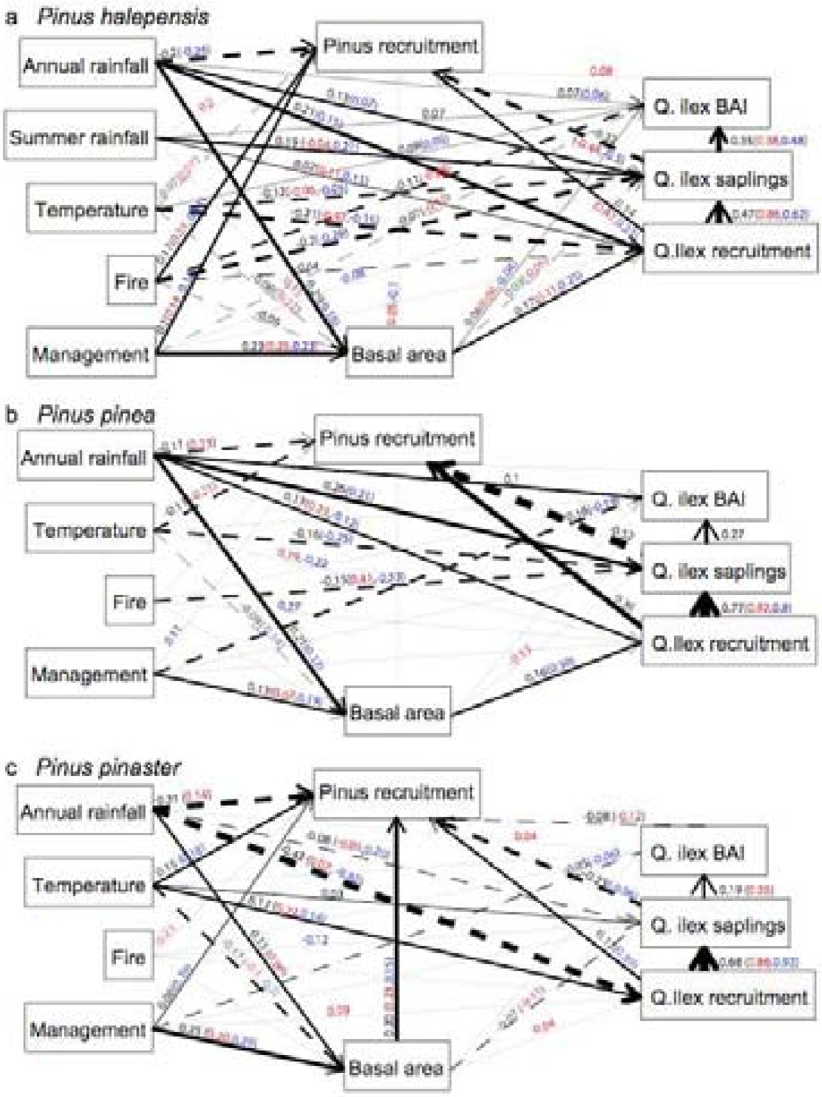


Figure S2 *Geographical variation of Pinus and Quercus species recruitment for R2, R3 and R4 size classes. For each species, surveyed plots were mapped in three categories: 1) Green areas: areas of recruitment success (i.e. plots in which we observed both saplings and adult trees of the focal species); 2) Orange areas: areas of recruitment failure (i.e. plots characterized by the presence of adult trees and the absence of tree saplings of the focal species) and 3) Blue areas: areas of new recruitment (i.e. areas without adult trees in which tree saplings of the analyzed species were observed).*



a *Pinus halepensis*

b *Pinus pinea*

c *Pinus pinaster*

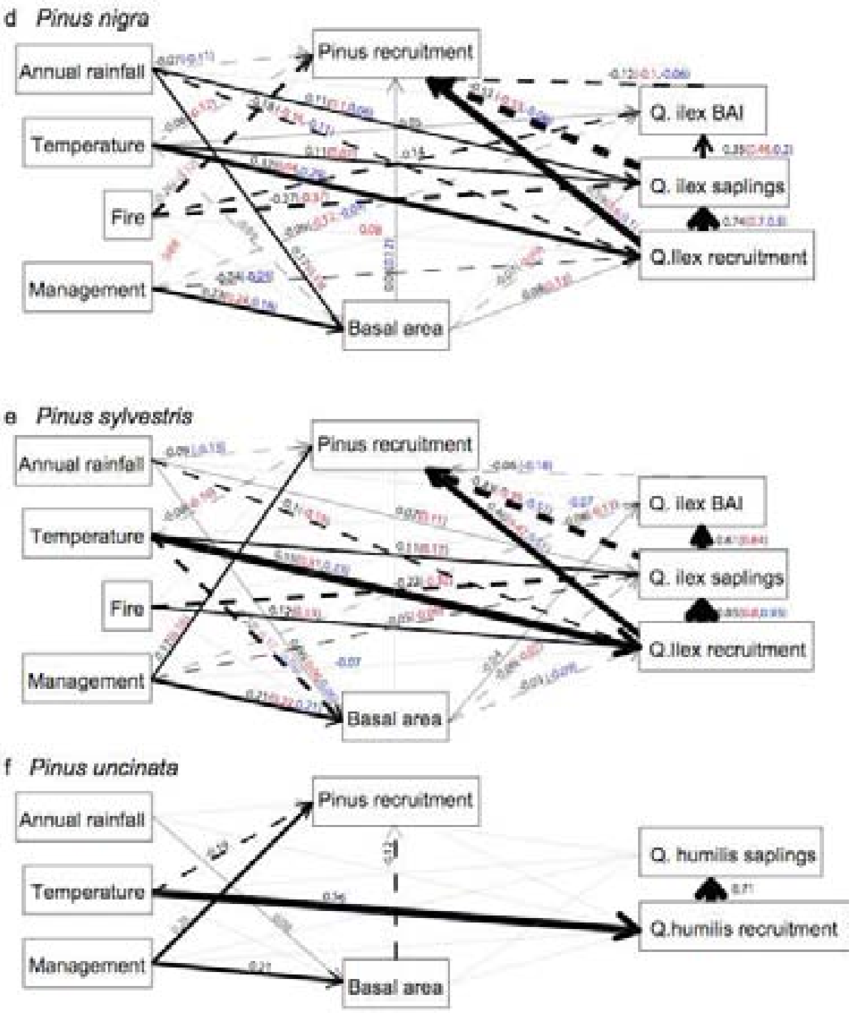


Figure S3. *Detailed results of the SEM models for Pinus species. Only significant coefficients are reported. Black coefficients correspond to the standard SEM models (i.e. using the whole dataset). Blue coefficients correspond to the SEM model restricted to the wet distribution subset. Red coefficients correspond to the SEM model for the dry distribution subset. Species: a) Pinus halepensis b) Pinus pinea c) Pinus pinaster d) Pinus nigra e) Pinus sylvestris f) Pinus uncinata.*

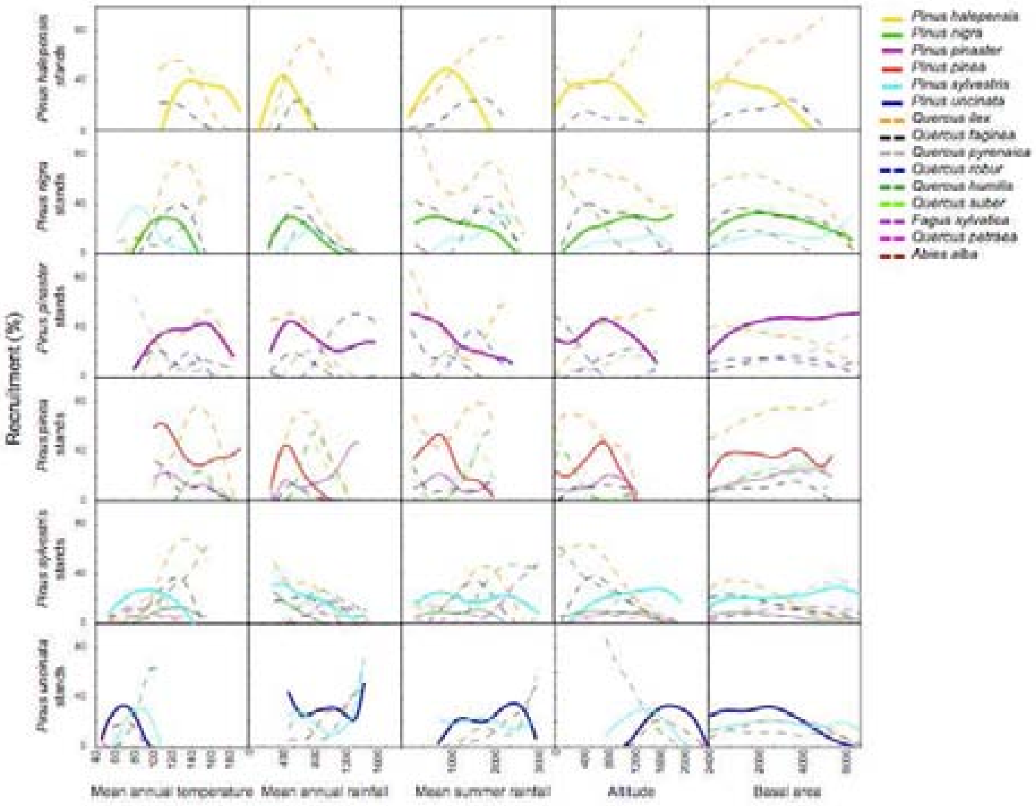


Figure S4. *Variation of the proportion of plots with R1 Pinus recruitment success along several environmental gradients (i.e. mean annual temperature, mean annual rainfall, mean summer rainfall, altitude, and stand basal area). A distance weighted squared procedure was used to fit the curves. Pinus species and non-Pinus species recruiting in more than 10% of plots (R1 size class) were represented.*

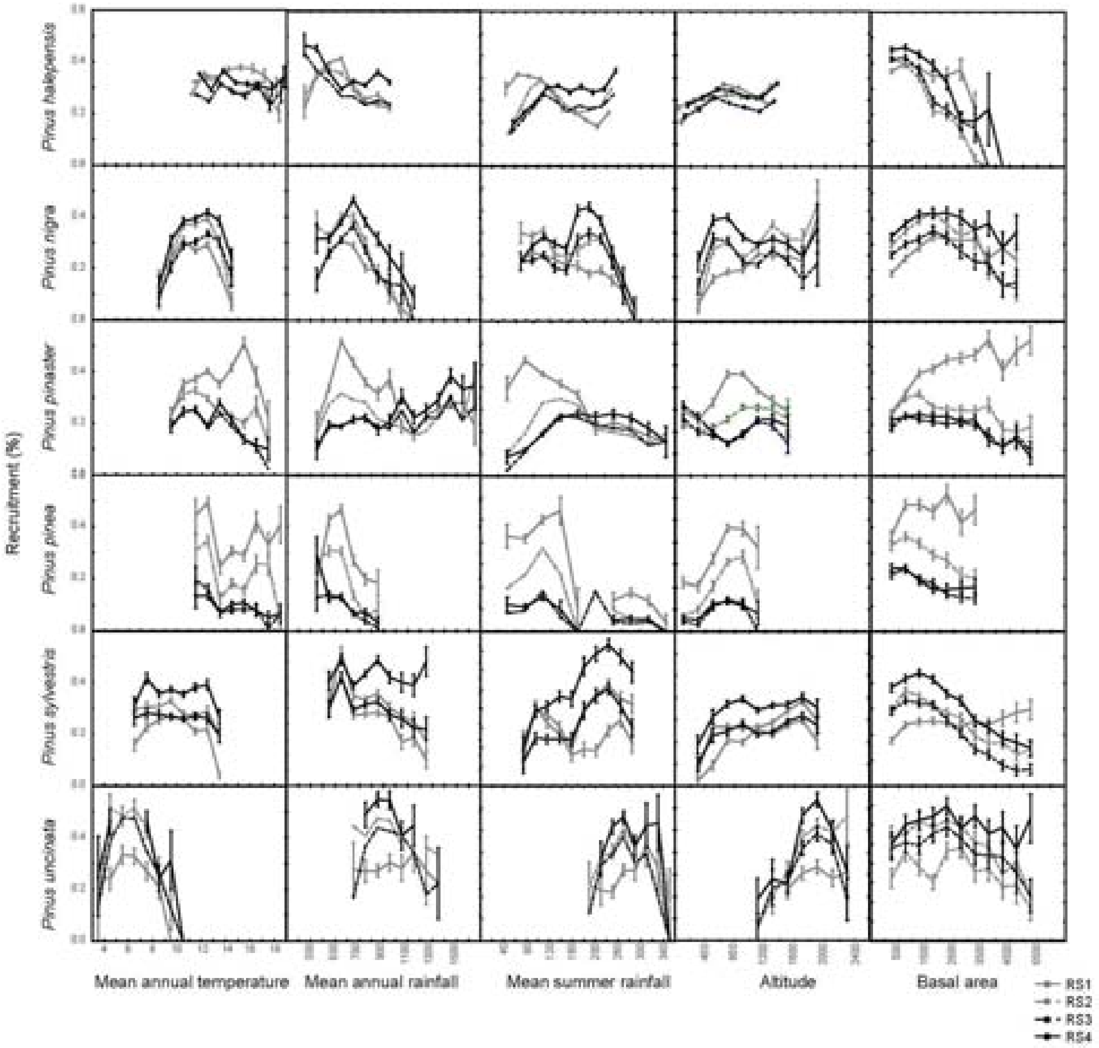


Figure S5. *Variation of the proportion of plots in which recruitment success (R1-R4 size classes) was observed, for each Pinus species and across diverse environmental gradients (rainfall, temperature, altitude and stand basal area gradients). Pinus species-specific datasets were divided in 10 quantiles, for each of the abovementioned environmental variables. For each quantile mean percentage and standard error are represented.*

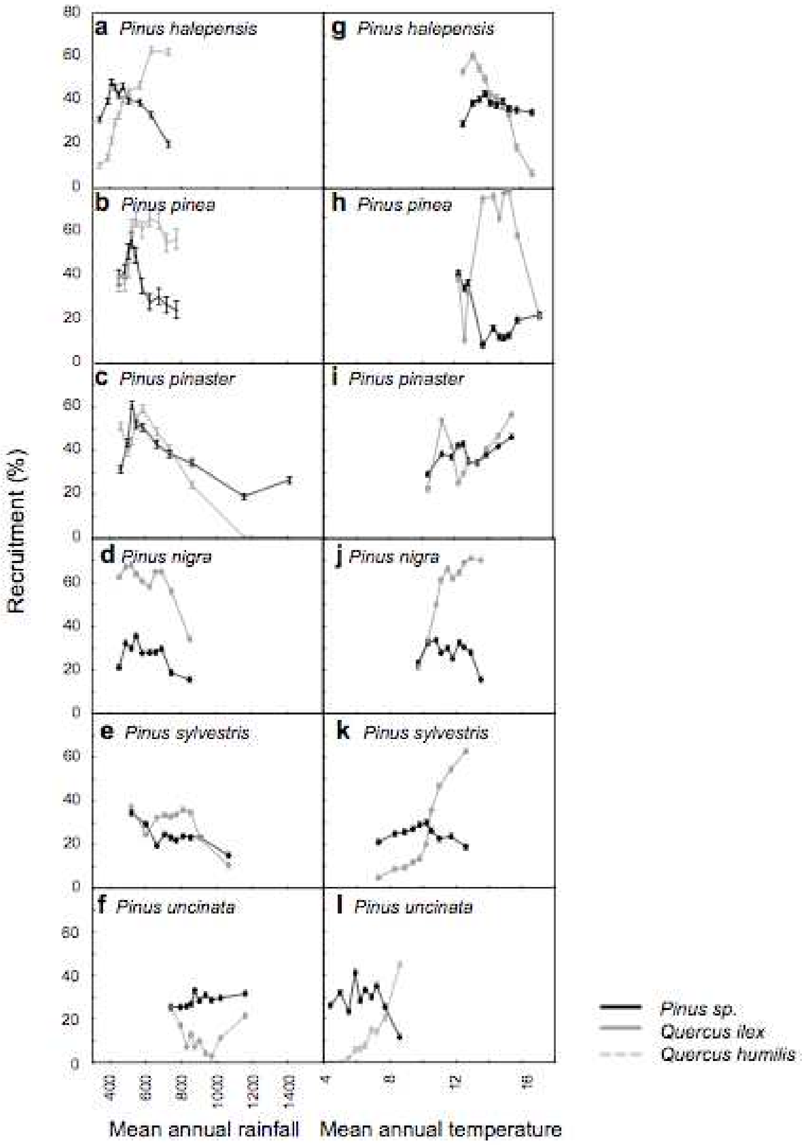


***Figure S6**. A comparison of the variation in the percentage of plots showing recruitment (R1 class) in Pinus species (black lines) and Quercus ilex (grey lines) across climatic gradients (rainfall and temperature).*

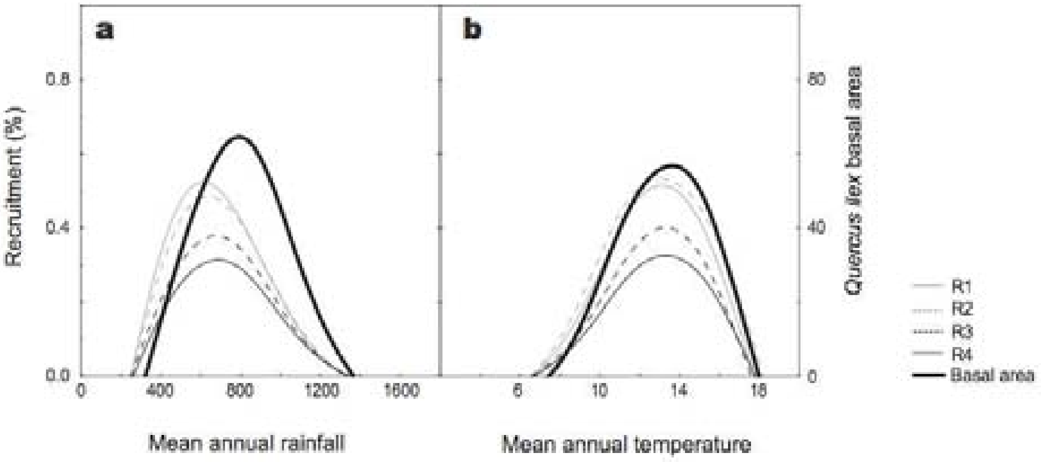


Figure S7. *Geographical variation of the percentage of plots with recruitment success in Quercus ilex in R1-R4 size classes in Pinus stands along temperature and rainfall gradients. Geographical variation of Q.ilex stand basal area is also plotted. Distance weighted squared procedure in Statistica 10, Statsoft Software, was used to fit the curves.*

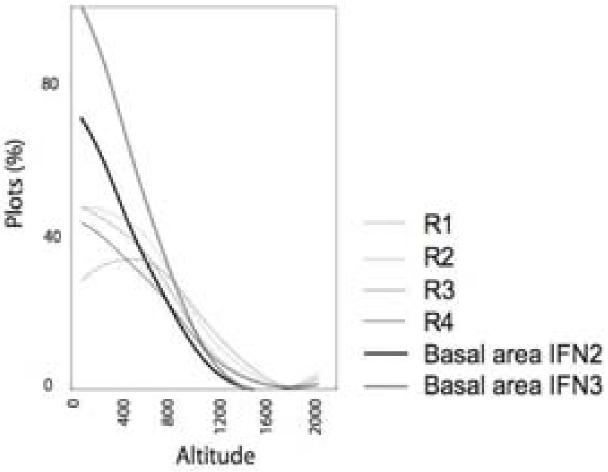


Figure S8. *Altitudinal variation of the percentage of plots with recruitment success in Quercus ilex in R1-R4 size classes in Pinus stands (IFN3). Geographical variation of Q.ilex stand basal area (IFN2 and IFN3) is also plotted. Distance weighted squared procedure in Statistica 10, Statsoft Software, was used to fit the curves.*

4.9. Supplementary text

Supplementary text T1. Traits differences between Pinus ad Quercus. Distribution in the Iberian peninsula.

Quercus are resprouter trees with large seeds dispersed by animals, and have distinctive traits associated with light acquisition and persistence in shaded environments (i.e. denser wood, higher shade tolerance, slow growth and reduced plasticity, saplings with wider crowns, adults with larger maximal crown size but smaller maximal height) (Poorter et al., 2012). In Quercus species, the Eurasian jay (Garrulus glandarius) plays a key role in facilitating long-distance seed dispersal in pine stands. Mediterranean Pinus species, in contrast, are non-resprouting, wind-dispersed trees with small seeds and have the opposite traits (low-density wood, higher growth rates and phenotypic plasticity, increased allocation to the formation of the central trunk rather than to branches, higher maximum height) (Poorter et al., 2012). Some Mediterranean pine species (P. halepensis, P. pinaster) show cone serotiny, early-age of first cone bearing and a high post-fire colonization capacity by wind-dispersed seeds. Noteworthy, small treelets and saplings of Pinus species are significantly more sensitive to growth suppression than Quercus in stands with large basal area (Zabala et al., 2011; Coll et al., 2013). In both Quercus and Pinus phylogenetic clades, a significant inter-specific trade-off has been described between shade and drought tolerance (Niinemets & Valladares, 2006). All these contrasting trait differences are associated with different demographic responses to climate, disturbance and fire and may have allowed the stable coexistence of Quercus and Pinus in the Mediterranean basin (Zabala & Zea, 2004; Zabala et al., 2011; Sheffer, 2012; Coll et al., 2013).

Iberian pine forests are distributed across broad geographic gradients, covering a great variety of climatic conditions, from arid Mediterranean to cool temperate climates (Soto et al., 2010). Thermophilous species (P. halepensis, P. pinea and P. pinaster) mainly occur in the Mediterranean lowlands. However, P. pinaster also extends its distribution over Atlantic climatic regions. In contrast, cold enduring mountain pines (P. nigra, P. sylvestris and P. uncinata) are mainly distributed over mountain ranges and cold continental areas. P. nigra and P. sylvestris grow in a wide range of temperate climatic conditions. In contrast, P. uncinata is mainly restricted to cold environments at high altitudes.

Quercus robur and Quercus petraea are temperate deciduous species distributed along the northern fringe of the Iberian peninsula, under the influence of mild Atlantic climates. Sub-Mediterranean species (Quercus pyrenaica, Q. humilis and Q. faginea) are distributed along drier and moderately colder continental areas. Finally, Mediterranean thermophilic species (Q. ilex and Q. suber) are mainly distributed over Mediterranean dry and warm lowlands. However, Q. ilex occurs in a wider range of conditions and soil types, inhabiting most of the Mediterranean dry and mesic areas.

Supplementary text T2. Climatic variables (methods).

We generated monthly maps for rainfall, mean temperature, mean minimum temperature, and mean maximum temperature, from 1951 to 2006. Monthly maps were combined to obtain annual maps (mean annual and summer rainfall (June-August), mean annual temperature (MAT) and mean summer temperature). Using IFN2 and IFN3 survey dates, we obtained plot-specific measures of the averaged climatic conditions occurred during the time lag between both surveys (Carnicer et al., 2011). Additionally, elevation, slope and aspect information were obtained from a digital elevation model.

Supplementary text T3. SEM methods.

Parameter estimation was performed using Bayesian methods, which allowed us to use non-normal data. Recruitment success is a binomial variable with a non-normal error distribution, so it violates least-square methods assumptions of normal error distribution. Bayesian approaches treat the unknown model parameters as random variables and assign probabilities to the subsets of the parameter space. Bayesian methods start assuming prior distributions for model parameters (regression coefficients and residual variances) and then use Bayes' theorem to derive the posterior distributions of parameters. Prior distributions describe the probability assigned to a parameter in advance of any empirical evidence. Numerical methods based on Markov Chain Monte Carlo (MCMC) simulations are used to derive posterior distributions. We used a MCMC algorithm to generate a marginal posterior distribution (Arbuckle, 2006) and therefore the reported parameters are means of marginal posterior distributions generated from MCMC algorithms. To judge model adequacy, Posterior Predictive *p* and Convergence Statistic (CS) values were examined. Posterior Predictive *p* is recommended to be close to 0.5. CS should be close to 1 and values below 1.1 are considered acceptable (Gelman *et al*., 2004). The conservative default convergence criterion threshold provided by AMOS software is 1.002, but this might be too stringent if the number of parameters is large (Gelman *et al.,* 2004). Therefore, we used the 1.1 acceptance threshold to judge the model adequacy. Furthermore, we examined the significance of each path using 95% Bayesian credibility intervals, because a coefficient can be considered significant when its 95% credibility intervals do not overlap zero (Arbuckle, 2006).

Supplementary text T4. Extended discussion of the recruitment trends of P. pinea, P. pinaster, Q.ilex and Q.suber.

In some species like *Q. ilex, Q. suber, P pinea and P. pinaster,* we observed large geographic zones with contrasting recruitment trends (Fig 2 and S2; fig. 4). In P. pinea, we observed contrasting recruitment trends in South-Western and North-Eastern populations (Fig 2, Fig. S2). North-Eastern populations (Catalonia) showed extensive recruitment failure whereas Western populations experienced more positive recruitment trends in small saplings (R1-R2) (Fig. 2, Fig. S2). In addition, Q. ilex showed higher recruitment success in mesic sites across the whole distribution of P. pinea (Figs S4-S6). These trends suggest that two separate geographic units may be considered for this species in terms of management and conservation practices associated with recruitment and unveil also a possible range retraction in Catalonia in the near future. Finally, extensive recruitment failure was observed in P. pinaster North-Western and North-Eastern plantations (Galicia and Catalonia; see also Ruiz-Benito et al., 2013). These diverging trends highlight the need of region-specific conservation practices, for instance in South-Western *Dehesa* systems and non managed *Quercus* stands.

Chapter 5:Conclusions

Chapter 2: Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought

1) Periodes de sequeres multi-anuals (1990-1995) han comportat un augment significatiu de les respostes de defoliació en els boscos del sud d'Europa, en contrast amb nivells estables i elevats de defoliació observats en boscos Centre- i Nord Europeus.

2) La sequera és un factor significatiu en les respostes de defoliació a gran escala en els boscos del sud d'europa.

3) Els patrons de defoliació suggereixen que els boscos ibèrics pateixen efectes crònics a llarg termini degut als llargs períodes de sequera observats.

4) Les sequeres extremes poden produir alteracions brusques en la dinàmica de les comunitats d' insectes i de fongs defoliadors, alterant els processos d'aquestes comunitats a gran escala després de sequeres extremes.

Chapter 3: Multivariate effect gradients driving forest demographic responses in the Iberian Peninsula

1) Les variables forestals demogràfiques (Reclutament, Creixement i Mortalitat) venen determinades per múltiples factors. Al llarg dels gradients climàtics cada un d'aquests factors pren una importància variable.

2) Les respostes de les variables demogràfiques descriuen un complex mosaic, on les variabiltats interespecífica, intraespecífica juguen un important paper.

3) Les diferents variables demogràfiques responen de manera diferent I independent davant dels factors biòtics I abiòtics. Això resalta la importància dels estudis que contemplen els cicles sencers de les plantes

4) Existeixen importants interaccions entre els factors estudiats. Les interaccions més fortes observades es troben als extrems dels gradients climàtics.

5) Els efectes del deficit hídric sobre les variables demografiques són màxims a les regions més àrides del gradient de precipitació.

6) Les variables associades a estructura del bosc, I per tan a efectes de la competència, tenen un important efecte sobre totes les variables demogràfiques. El creixement I la supervivència dels arbres està especialment limitat pels efectes de la competència a les zones més seques, suggerint un augment de la competència en regions àrides.

7) Existeixen importants diferències en els patrons de reclutament en zones gestionades I no gestionades.

8) S'observen importants diferències en les respostes demogràfiques dels dos gèneres dominants Quercus i Pinus.

> (a) Les espècies de Quercus presenten una proporció significativament major d'àrees amb presència de reclutament que les espècies de Pinus, probablement determinat per processos d'abandonament forestal.
>
> (b) La competència té efectes més negatius sobre les taxes de creixement I supervivència de Pinus que les de Quercus.
>
> (c) La temperatura té efectes negatius sobre el creixement de Pinus I efectes positius sobre el creixement de Quercus.

Chapter 4: Large-scale recruitment limitation in Mediterranean pines: the role of Quercus ilex and forest successional advance as key regional drivers.

1) Les espècies de pi presenten baixes taxes de reclutament, mentre que les taxes de reclutament de Quercus es mantenen signficativament més altes.

2) Els models que hem desenvolupat mostren que la limitació del reclutament de Pinus està lligada a processos successionals, al clima, a canvis de gestió i als incendis.

3) Els resultats impliquen que la successió és el major determinant de la disminució del reclutament dels pins a gran escala. Els models indiquen que la successió afecta positivament el reclutament de *Quercus* I negativament el reclutament de *Pinus*.

4) Els individus de *Quercus ilex* actuen com a factor clau en els canvis a gran escala dels patrons de reclutament. La presència de *Quercus ilex* afecta directament I negativament el reclutament de les espècies de pi.

5) Les condicions climàtiques són també un gran determinant dels patrons de reclutament. Els pins mediterranis tenen limitat el seu reclutament a causa del dèficit hídric a les regions més àrides de la seva distribució. *Pinus nigra I Pinus sylvestris* tenen els problemes de reclutament més greus. La reducció més important de les taxes de reclutament és a les zones més càlides de la seva distribució, on també s'observa un important augment del reclutament de *Quercus ilex*, afavorit per les altes temperatures. L'avanç del *Quercus ilex* i el canvi climàtic, poden reduïr dràsticament el reclutament d'ambdues espècies.

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