

Contrasting effects of climate change along life stages of a dominant tree species: the importance of soil–climate interactions

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ABSTRACT

Aim For tree species, adult survival and seedling and sapling recruitment dynamics are the main processes that determine forest structure and composition. Thus, studying how these two life stages may be affected by climate change in the context of other abiotic and biotic variables is critical to understand future population trends. The aim of this study was to assess the sustainability of cork oak (*Quercus suber*) forests at the core of its distributional range under future climatic conditions.

Location Southern Spain.

Methods Using forest inventory data collected at two periods 10 years apart, we performed a comprehensive analysis to evaluate the role of different abiotic and biotic factors on adult survival and recruitment patterns.

Results We found that both life stages were influenced by climatic conditions, but in different ways. Adult tree survival was negatively impacted by warmer spring temperatures, while recruitment was positively affected by warmer winter temperatures. Our results also revealed the importance of soil texture as a modulator of winter precipitation effects on adult survival. With higher winter precipitation, adult survival increased in sandy soils and decreased in clayish soils. Therefore, under predicted future climate scenarios of wetter winters and warmer temperatures, the presence of cork oaks is more likely to occur in sandy soils vs. clayish soils. Biotic conditions also affected these life stages. We found a negative effect of heterospecific but not conspecific trees on both adult survival and seedling recruitment.

Main conclusions Overall, the sustainability of the studied forests will be highly dependent not only on future climatic trends, but also on their interaction with other key factors – soil properties in particular – that modulate the effects of climate on demographic rates.

Keywords

Bayesian analysis, declining forest, demographic rates, establishment, forest inventory data, Mediterranean region.

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INTRODUCTION

In forest ecosystems, mature tree survival and regeneration dynamics have long been recognized as the underlying processes determining forest structure and composition (Franklin *et al.*, 1987; Kobe, 1996; Lewis *et al.*, 2004) and hence, as the drivers of forest properties (Canham & Pacala, 1994;

Pacala *et al.*, 1996). Thus, changes in demographic rates at any of these stages could have great impact on the overall dynamics of forest ecosystems (Kobe, 1996). In the last decades, many forests have experienced a decrease in adult tree survival and/or recruitment because of global change-related events (Peñuelas *et al.*, 2007; Lloret *et al.*, 2009; Allen *et al.*, 2010). In particular, increasing temperatures and drought

events linked to climate change have been proposed as the likely drivers of recent tree decline in temperate ecosystems (van Mantgem *et al.*, 2009; Carnicer *et al.*, 2011; Vilà-Cabrera *et al.*, 2012). Tree seedling recruitment has also been shown to be negatively affected by drier conditions (Lloret *et al.*, 2004; Ibáñez *et al.*, 2007). As a species' response to environmental stressors may differ, in direction and magnitude, among its different life stages (Cavender-Bares & Bazzaz, 2000; He *et al.*, 2005; Niinemets, 2010), its persistence would depend on the net effect across all stages (Phillips & Gentry, 1994). Still, there is a surprising lack of studies exploring how a given global change driver (e.g. increase in temperature or reduced water availability) could simultaneously affect different life stages in the plant cycle, hampering our ability to predict the effects of future climate on forest ecosystems.

In an era of global change, with heavily modified landscapes and unprecedented rates of climate change, understanding how demographic rates of dominant species in forest systems could be affected by the future trends will be critical to successfully conserve and manage these ecosystems. Many forests world-wide have been highly modified by humans, giving rise to semi-natural forest types (Noble & Dirzo, 1997; Axelsson & Ostlund, 2001), frequently characterized by a dominant woody species (Bengtsson *et al.*, 2000) whose persistence will depend on human activities (Urbieto *et al.*, 2008; Brudvig & Damschen, 2011; Bugalho *et al.*, 2011). In the south-west of the Iberian Peninsula (Portugal and Spain), humans have highly impacted forest composition for centuries, increasing the dominance of sclerophyllous *Quercus* species (mainly *Q. suber*, cork oak) forming either agro-forestry systems known as 'montado' in Portugal or 'dehesa' in Spain (Olea & San Miguel-Ayanz, 2006) or closed forests in areas with higher precipitation (Urbieto *et al.*, 2008). In both ecosystems, dehesa and close canopy forest, the dominant woody species are a major structural element in these forests, frequently considered a 'keystone species'. Oak trees maintain ecosystem functions and services, such as protection from soil erosion, enhancement of plant and animal diversity (Marañón *et al.*, 1999; Reyes-López *et al.*, 2003; García *et al.*, 2011), provisioning resources (e.g. cork, livestock feed) and cultural services (e.g. hunting, recreation) (Olea & San Miguel-Ayanz, 2006; Marañón *et al.*, 2012). Although these forests have been managed and sustained for hundreds of years (Plieninger *et al.*, 2003; Bugalho *et al.*, 2011), their long-term viability could be threatened by the current decline in adult oak trees, arising from both abiotic (e.g. recurrent drought periods) and biotic (e.g. soil-borne pathogens) factors (Brasier, 1995; David *et al.*, 2004). This phenomenon, together with the lack of regeneration mainly due to seed predation (Pausas *et al.*, 2009; Pérez-Ramos & Marañón, 2012), massive seedling mortality during the summer (Gómez-Aparicio *et al.*, 2008) and seedling predation by domestic and wild herbivores (Pulido & Díaz, 2005; Pausas *et al.*, 2009), highlights the uncertainty of the sustainability of this ecosystem and the services it provides.

Cork oak is distributed along the Mediterranean Basin, this is a region expected to undergo substantial increases in temperature and aridity in the next decades (IPCC, 2007; Planton *et al.*, 2012), and it is considered one of the most vulnerable areas in the world under the predicted scenarios of climate change (Brunet *et al.*, 2007; Giorgi & Lionello, 2008). To assess the future of cork oak forests at the core of the species' distributional range, we carried out a comprehensive study that focused on the two main processes determining the future of this species: mature tree survival and regeneration patterns. Specifically, we used forest inventory data collected across Southern Spain to answer the following questions: (1) Are adult tree survival and recruitment dynamics equivalent along sites with different temperature and precipitation regimes? (2) How do other abiotic and biotic variables, and their interactions with climate, affect cork oak dynamics? (3) How will predicted changes in temperature and/or precipitation potentially affect adult tree survival and/or regeneration? By answering these questions, we aim to evaluate the specific life stage responses to environmental factors of *Q. suber* and to provide an overview of the current and likely future trends of this important declining species.

METHODS

Study area and tree species

The study area, Andalusia, is located in the West Mediterranean region, at the southern portion of Spain (7°31' W–1°39' W, 37°33' N–37°23' N, Fig. S1 in Supporting Information). It covers 87,268 km², and the climate is typical Mediterranean, with cool, humid winters and warm, dry summers. Forested areas in Andalusia cover near 40% of the total surface, *Quercus* being the predominant tree genus in these forests (Urbieto *et al.*, 2011).

Quercus suber, the study species, is a dominant tree in these landscapes. This is an evergreen species of great economic and ecological importance, present across 240,000 ha in the region. Cork oaks have low tolerance to extremely cold temperatures (frost) and severe droughts (they are rare in areas below 600 mm of annual rainfall), and they tend to prefer sandy soils (Aronson *et al.*, 2009). In Andalusia, *Q. suber* is distributed into two main subregions with varying precipitation: Alcornocales Natural Park (1031.8 ± 172.5 mm of annual precipitation, hereafter referred to as *wet region*) and Sierra Morena (767.3 ± 96.6 mm, hereafter *dry region*). In the *wet region*, forests have predominantly closed canopies (mean basal area ± SD 15.27 ± 8.84 m² ha⁻¹), while the *dry region* is mainly a savanna-like scrubland (10.21 ± 6.98 m² ha⁻¹; Table S1 for a summary of the main characteristics of the studied plots).

Cork oak can form mono-specific stands, but it is also frequently found intermingled with other species. *Olea europaea* var. *sylvestris* and *Quercus canariensis*, a winter deciduous oak, are the most common companion tree species in the

wet region, while *Quercus ilex* is dominant in the dry region. Cork oak trees are extensively managed for cork production, except in highly protected reserves (García *et al.*, 2011).

Forest inventory data

We used the Spanish National Forest Inventory (SNFI) dataset to investigate patterns in adult tree survival and natural regeneration of *Q. suber* in this region. We used the Second and Third SNFI censuses, where data were collected during the years 1995–1996 (SNFI2) and 2006–2008 (SNFI3). Stands were located on a grid of 1 × 1 km in forested areas and of 2 × 2 km in savanna-like scrublands (Villaescusa & Díaz, 1998). The stands are circular and composed of four concentric subcircles with radii 25, 15, 10 and 5 m each, defining four different areas where trees are sampled according to size [minimum diameter at breast height (dbh) threshold of 42.5, 22.5, 12.5 and 7.5 cm, respectively]. Trees within the stand were identified, measured (dbh) and mapped within the stand. The datasets contain information on recruitment as well (seedlings and saplings smaller than 1.30 m or dbh < 7.5 cm), measured within the 5-m-radii circle (Villaescusa & Díaz, 1998; Villanueva, 2004).

Stands were included in the analysis of adult tree survival if at least one mature cork oak tree (dbh > 7.5 cm) was measured. We discarded those stands with evidence of forest management (cutting or thinning) in the SNFI3 (accurately detailed in the database), resulting in a total of 755 stands used in the analysis. We then analysed changes in the number of trees present in each stand at time 1 (SNFI2), N_1 , and at time 2 (SNFI3), N_2 . As individuals were identified by their position within the concentric circles, we were able to discard in-growth trees, that is, those individuals with diameters growing above the 7.5 cm threshold during the two censuses.

For the analysis of natural regeneration, based on the SNFI3 census, we discarded the stands with reforestation activities. We worked with a total of 737 stands. The number of seedlings and saplings was recorded in ordinal categories: small seedlings (height < 0.30 m), large seedlings (height between 0.30 and 1.30 m), small saplings (height > 1.30 m and dbh < 2.5 cm) and large saplings (height > 1.30 m and 2.5 < dbh < 7.5 cm).

Abiotic and biotic predictors

The selected stands were characterized by 20 abiotic and two biotic variables. The abiotic factors included ten climatic, eight edaphic and two topographic variables. The ten climatic variables, calculated from Gonzalo's (2008) map with a 1-km² spatial resolution, were annual precipitation (mm) and seasonal precipitation (spring, summer, fall and winter), and mean annual and seasonal temperature (°C) (Table S2). We carried out a preliminary analysis and ran different models (see below for an in-depth description of the type of models used) that we parameterized with each one of the climatic variables. We compared those models to evaluate

the most influential temperature and precipitation measurements within the year, which were then selected for further analysis. The eight edaphic variables were estimated from different maps and models developed for the study area (De la Rosa *et al.*, 2002; De la Rosa & Monge, 2006; Monge *et al.*, 2008; see Table S2), calculated for the first 50 cm of soil and included pH, clay, sand and silt content (%), organic matter (%), soil water content at field capacity (g/100 g), soil bulk density (g/cc) and available water capacity (g/100 g). To avoid convergence problems during parameter estimation, we applied a principal component analysis (PCA) followed by a varimax rotation to discard those soil variables which were highly correlated (R Development Core Team, 2009). This approach was chosen to minimize the shared variance among the selected predictors. Given the results of the PCA (Table S3), we decided to include sand content (as representative of soil capacity to retain and percolate water), soil bulk density and organic matter content as variables representative of the edaphic conditions in each stand. The topographic variables were calculated from a SRTMv1 digital elevation model with a 1-km² spatial resolution (Shuttle Radar Topographic Mission, <http://www2.jpl.nasa.gov/srtm/>) and included slope (degrees) and a topographic radiation index. This last variable was calculated from the slope and aspect (degrees) as $\cos(\text{aspect}) \times \text{slope}/100$, with a value of zero for a flat surface, negative for a southern exposure and positive for a northern exposure (Dietze & Moorcroft, 2011).

The biotic variables considered were conspecific (*Q. suber*) and heterospecific (all other tree species) basal area in each stand (m² ha⁻¹). Correlation between all potential predictors was lower than 0.4. In an exploratory analysis, we found that the proportion of dead trees in the selected sites was similar across size classes, so we did not include size as a factor in the analysis. To improve model runs and to be able to make direct comparisons among parameter values, previous to the analysis, we standardized all the continuous explanatory variables by subtracting the mean and dividing by the standard deviation.

Data analysis

We tried several combinations of explanatory variables and of model structure (e.g. hierarchical estimation of the parameters, inclusion of spatial random effects). We first included climatic variables only, as temperature and precipitation are recognized as the main environmental variables associated with the decline processes (Carnicer *et al.*, 2011), and then included additional explanatory variables (edaphic, topographic and biotic) and their interactions with climate. We describe our final models below, and these were the model structures and combination of explanatory variables that best fitted the data based on predicted loss (D, Gelfand & Ghosh, 1998) which considers the goodness-of-fit of the model and a penalty term (the predictive variance). Models with the smallest D were a better fit to the data (for a list of other

alternative models and combination of explanatory variables we tried see Tables S4 and S5).

Analysis of tree survival

To analyse tree survival as a function of several environmental and biotic variables, we used adult census data for the two times, N_1 and N_2 in a binomial likelihood where trees survived between censuses with probability θ . We related θ to the explanatory variables using a logit link function (see Appendix S1 for further explanation).

Analysis of regeneration patterns

For the analysis of recruitment data (SFNI3), we split the data into two groups: seedlings less than 1.30 m height (*seedling group* hereafter; we considered together the two-first categories in SFNI3, see Table S6) and saplings, individuals higher than 1.30 and dbh smaller than 7.5 cm (*sapling group* hereafter, considering together categories three and four in SFNI3, see Table S6). We separated between seedlings and saplings, as plants within these two life stages can respond differently to environmental factors (Plieninger *et al.*, 2010). For the analysis of both seedling and sapling abundance, we considered that analysing the number of individuals at one time (i.e. SFNI3) for the two life stages was appropriate to get accurate insights on the success or failure of recruitment at these stages. This approach may have some limitations relating to saplings, whose differences between inventories could have been more precise to evaluate their performance. Nevertheless, due the nature of the data, we could not have discerned the reason of the differences in rates (i.e. sapling mortality rate or sapling recruitment rate, Vayreda *et al.*, 2013), and thus, a survival analysis between the two censuses and the abundance analysis for just one would be equivalent. As counts were recorded in ordinal categories, we used the average count for each of them: zero for plots without recruits, 2 for low (1–4), 10 for medium (5–15) and 20 for high (> 15), and the exact number of saplings in category 4 of the SFNI3. Models were fitted to each group separately. For the analysis of the *sapling group*, we considered as an additional explanatory variable the seedlings and saplings in category 1 in the first census (SFNI2, see Table S6). This is because it can influence sapling abundance by acting as a 'recruit bank' (Plieninger *et al.*, 2010).

In the analysis of the *seedling group*, we defined the likelihood using a zero-inflated Poisson (Zuur *et al.*, 2009) distribution with mean parameter μ . For the final model, the probability of a zero count was given by ω . We then related the parameter μ from the Poisson distribution to the explanatory variables using a log link function (see Appendix S2 for more detail).

For the analysis of the *sapling group*, we evaluated the abundance of saplings in those stands where they were present (71 stands in total). We used a Poisson likelihood (with parameter μ) to model the abundance of saplings recorded

in the second census (SFNI3). We related the parameter μ from the Poisson distribution to the explanatory variables using a log link function (see Appendix S3 for more detail).

We followed a Bayesian approach to estimate the parameters of the adult tree survival and recruitment models (see Appendix S4). Bayesian modelling allowed us to track the different sources of uncertainty inherent in the analysis, that is, the data, the process and the parameters (Clark, 2005). Parameters were estimated from non-informative prior distributions (see Appendix S4). Posterior densities of the parameters were obtained by Gibbs sampling (Geman & Geman, 1984) using OpenBUGS 3.1.2. (Thomas *et al.*, 2006). Models were run until convergence of the parameters was reached (*c.* 150,000 iterations), and parameters and their confidence intervals were estimated after discarding pre-converge 'burn-in' iterations (*c.* 10,000). Plots of predicted vs. observed values were also used to evaluate the fit of the model (unbiased model having a slope of unity). R^2 of observed vs. predicted values was used as a measure of goodness-of-fit. Fixed effects coefficients whose 95% credible intervals did not include zero were considered statistically significant.

Prediction of climate change effects

We also sought to forecast the most likely trends on the dynamics of this species under future conditions, in particular how the interaction between climate and other factors might affect cork oak dynamics. We used parameter values (mean, variances and covariances) from the model runs to predict changes in tree survival and recruitment under different climatic scenarios. To do this, we used a space-for-time substitution approach where variations in *Q. suber* demography along spatial climatic gradients reflected in our data were used to infer potential species responses to future changes in climate. Hence, to examine the potential effects of forecasted temperature increases (IPCC, 2007; Planton *et al.*, 2012), we used a mean predicted increase in 3 °C within each stand (mean of A2 and B2 regional predictions for 2070–2100) to predict survival and regeneration and compared these predicted values with current conditions.

RESULTS

Tree survival patterns

The fit of the best model predicting the data had an $R^2 = 0.54$ and a slope = 1.00 (Tables 1 and S4). The final model included the following: winter precipitation, spring temperature, slope, topographic radiation index, sand content, sand*winter precipitation and heterospecific basal area. In this model, temperature in spring and the interaction between winter precipitation and soil sand content were the most important variables affecting the survival of adult cork oak (Table 1, Fig. 1). In sandy soils, the effect of increased winter precipitation was positive, whereas in heavier soils,

the effect was the opposite (i.e. tree survival decreased for higher precipitation, Fig. 2). In flat areas, there was a tendency for higher survival, whereas steeper soils translated into lower probability of survival (Fig. 1). Similarly, there was a tendency of lower probability of survival at northern exposure compared with southern exposure (negative value of the parameter, Fig. 1). We also found that the presence and abundance of other species were associated with a decrease in the probability of cork oak survival (Table 1, Figs 1 and 3).

Regeneration patterns

In the analysis of the *seedling group*, the best model's R^2 between observed and predicted values was 0.18 and slope 0.92 (Tables 2 and S5). The final model included the following: winter precipitation, winter temperature, their interaction, slope and heterospecific basal area (Table 2).

Increasing winter temperatures had a positive effect on recruitment (Fig. 1), and there was a trend, although not significant, for higher precipitation favouring seedling

Table 1 Parameter estimates for the best model analysing mature tree survival. Values are posterior means \pm SD and 95% credible intervals. Bold values indicate coefficients that do not include zero in their credible intervals and denote a significant effect of the variable on survival. Letters indicate comparison: same letter indicates not differences between regions, and different letters indicate differences between regions

Parameter	Values
α_1 , wet region intercept	3.90 \pm 0.25 a 3.42, 4.42
α_2 , dry region intercept	3.65 \pm 0.37 a 2.94, 4.41
β_1 , winter precipitation	-0.09 \pm 0.39 -0.87, 0.61
β_2 , winter temperature	-0.89 \pm 0.30 -1.48, -0.26
β_3 , slope	-0.44 \pm 0.24 -0.91, 0.04
β_4 , topographic radiation index	-0.42 \pm 0.18 -0.79, -0.06
β_5 , sand content	0.02 \pm 0.24 -0.44, 0.49
β_6 , sand content * precipitation in winter	1.25 \pm 0.54 0.19, 2.30
β_7 , heterospecific basal area	-0.71 \pm 0.24 -1.16, -0.12
σ^2 , wet region	2.56 \pm 0.39 1.96, 3.57
σ^2 , dry region	2.08 \pm 0.57 1.38, 3.85
ρ , wet region	0.99 \pm 0.91 0.02, 3.51
ρ , dry region	0.99 \pm 1.01 0.03, 2.86

recruitment. However, the winter temperature \times precipitation interaction term was negative, meaning that recruitment would be favoured under warmer temperatures and drier conditions, diminishing the positive effect of warmer temperatures under wetter conditions (Figs 1 and 4). Given the parameter values and the credible intervals, the effect of the slope, although not statistically significant, was of biological relevance, showing less recruitment in steeper areas (Fig. 1). The presence of heterospecific trees had negative effect on this stage of recruitment (Fig. 3). Actual parameter values, standard deviation and 95% confidence interval are reported in Table 2.

From the analysis of the *sapling group* for which we had 74 plots, the value of predicted loss for all of the models did not improve the fit of the model when compared with the climate only model (see Table S7). However, the variables included in this model (mean annual temperature and spring precipitation) were not significant (i.e. the 95% confidence interval included zero, Table 2). Despite the findings on seedling patterns affected by different environmental factors, the scarcity of individuals found at the sapling stage could have hampered the detection of any effects at this stage.

Prediction of climate change effect

Based on the response of the studied variables along spatial environmental gradients, we predicted that under an intermediate scenario of 3 °C temperature increase, the probability of tree survival decreased compared with current conditions (Fig. 2), whereas recruitment abundance increased, especially noticeable under drier conditions (Fig. 4). Changes in precipitation would affect adult tree survival differently depending on the texture of soil, increasing in sandy soils and decreasing in heavier soils. Increase in precipitation would favour recruitment abundance, but this benefit would be less clear under higher temperatures.

DISCUSSION

There is the potential that future climatic trends will differently affect the life stages of organisms. It will be then the net effect along the life span of individuals that will determine the overall population response to future conditions. In this study, we investigated how climatic conditions influence *Q. suber* adult survival and seedling recruitment. Interestingly, our analysis showed contrasting responses of the two life stages studied (adult vs. seedling regeneration) to an increase in temperature, being detrimental for adult trees but beneficial for seedling recruitment. Furthermore, we found that soil conditions seem to modulate the effect of climate on adult tree survival by regulating the availability of water during the dry season. These results emphasize the need for simultaneously evaluating different life stages when studying plant population dynamics in response to varying environmental factors and highlight the importance of considering climate together with other interacting variables, in our case

Figure 1 Posterior mean parameter values for each of the variables included in the adult tree survival (black dots) and seedling recruitment (white diamonds) analyses. Symbols for each variable are shown only when the variable was included in the final model. Bars indicate the 95% credible interval. Coefficients that do not include zero in their credible intervals are considered statistically significant.

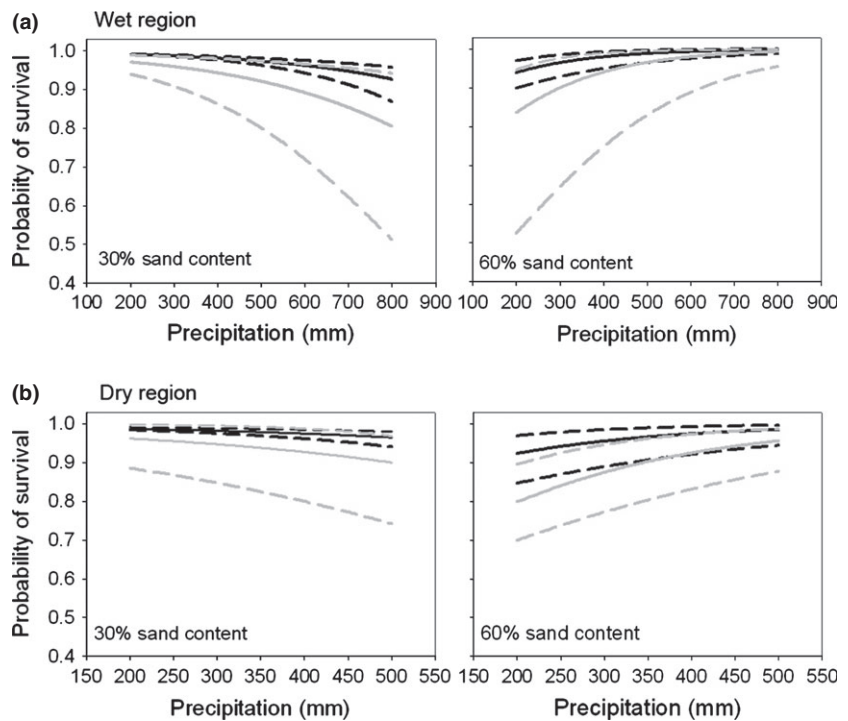
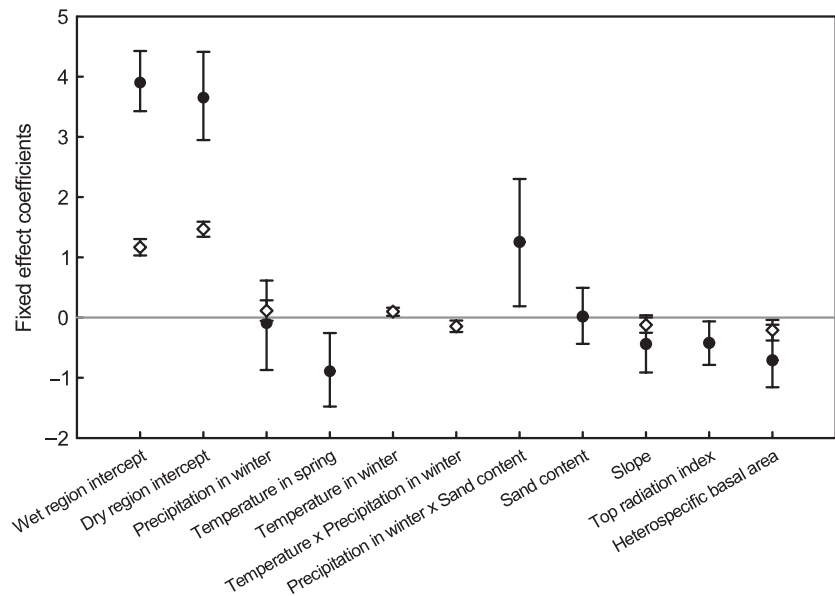


Figure 2 Predicted mean effect of precipitation on the probability of adult survival for soils with different sand content in the *wet region* (a) and the *dry region* (b). Effect under the mean temperature (black colour) and the effect of 3 °C temperature increase (grey colour) are shown. The solid line is the mean of the posterior predictions, and the broken lines represent the 95% predicted interval, for the two regions. Winter precipitation is limited to the range found for this variable in each region.

soil properties, when studying forest responses to future climates.

Tree survival patterns

Our results illustrate how adult tree survival was not only influenced by climate, in this case temperature in the spring having a negative effect, but also by the interaction between winter precipitation and soil texture. Spring is the season when mediterranean plants reach their maximum photosynthetic rates (Ogaya & Peñuelas, 2003); thus, plants in this region are especially sensitive to environmental conditions

during this season (Peñuelas *et al.*, 2002; Gordo & Sanz, 2010). Increased spring temperature may accelerate depletion of starch pools leading to carbon starvation and subsequent mortality during a drought year, according to the C-starvation hypothesis (McDowell & Sevanto, 2010).

One of the main results derived from our study is the important role played by soil texture as a modulator of winter precipitation effects on adult survival. Soil texture determines soil hydrological properties (water infiltration, retention and runoff) and, ultimately, soil water availability (Weltzin *et al.*, 2003). As expected, our results showed higher tree survival with higher winter precipitation, but

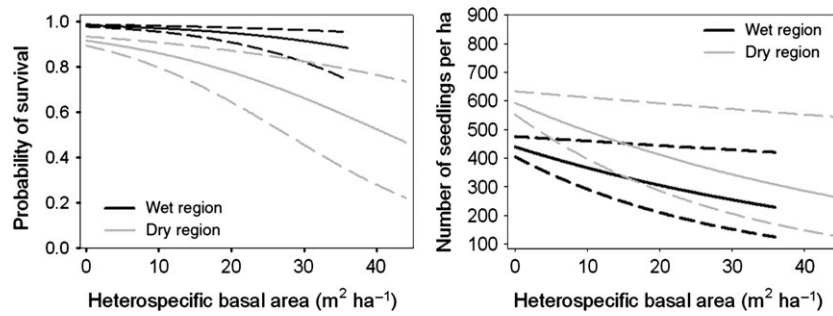


Figure 3 Mean effect of heterospecific abundance (basal area) on mature tree cork oak survival, left panel, and seedling recruitment, right panel, in the wet (black line) and dry (grey line) regions. The solid line is the mean of the posterior predictions, and the broken lines represent the 95% predicted interval. Heterospecific basal area is limited to the range found for this variable in each region.

Table 2 Parameter estimates for the best model analysing seedling and sapling abundance. Values are posterior means \pm SD and 95% credible intervals. Bold values indicate coefficients that do not include zero in their credible intervals and denote a significant effect of the variable on abundance. Letters indicate comparison: same letter indicates not differences between regions, and different letter indicates differences between regions

Parameter	Values
Seedling group	
γ_1 , wet region intercept	1.17 \pm 0.07 a 1.031, 1.303
γ_2 , dry region intercept	1.47 \pm 0.06 b 1.341, 1.591
ϕ_1 , winter precipitation	0.11 \pm 0.09 -0.05, 0.29
ϕ_2 , winter temperature	0.10 \pm 0.03 0.03, 0.16
ϕ_3 , winter temperature * winter precipitation	-0.14 \pm 0.05 -0.24, -0.05
ϕ_4 , slope	-0.12 \pm 0.06 -0.25, 0.00
ϕ_5 , heterospecific basal area	-0.21 \pm 0.09 -0.38, -0.04
σ^2 , wet region	0.05 \pm 0.01 0.03, 0.08
σ^2 , dry region	0.06 \pm 0.02 0.02, 0.13
ρ , wet region	1.025 \pm 0.99 0.02, 3.51
ρ , dry region	0.93 \pm 0.92 0.02, 3.31
Sapling group	
γ_1 , wet region intercept	1.44 \pm 0.18 a 1.09, 1.80
γ_2 , dry region intercept	1.50 \pm 0.19 a 1.12, 1.87
ϕ_1 , annual temperature	0.10 \pm 0.24 -0.37, 0.56
ϕ_2 , precipitation in spring	-0.20 \pm 0.30 -0.79, 0.41

surprisingly only in sandier soils. The positive effect of increase precipitation on sandy soils is probably due to the fact that rainfall percolates to deeper soil layers, ensuring the availability of water in the dry season (Brady & Weil, 1996). On the contrary, on clayish soils, characterized by poor drainage capacity, water tends to accumulate and produce temporal waterlogging conditions. Waterlogging negatively affects cork oak survival both directly due to lack of aeration (Gaertig *et al.*, 2002) and indirectly by favouring the accumulation of aggressive soil-borne pathogens (Gómez-Aparicio *et al.*, 2012), such as *Pythophthora cinnamomi*, the main soil-borne pathogen related to the decline of cork oak in the area (Tuset & Sánchez, 2004). Altogether, our results corroborate that soil texture is a key variable regulating the effects of varying climatic conditions on this species (Fernandez-Illescas *et al.*, 2001; Piedallu *et al.*, 2012). Consequently, although precipitation may be a good proxy for soil water availability to plants at very large scales, that is, regionally, soil hydrological properties have to be taken into account at smaller scales to fully describe the effects of changes on precipitation regime on plants.

In our analyses, we also found that biotic factors, in this case density of heterospecific species, had an effect on cork oak's adult survival. Unlike cool temperate forest systems where light is recognized as the major limiting factor for growth (e.g. Canham, 1988), in mediterranean climates, water availability is generally the most limiting resource (Carnicer *et al.*, 2011). The negative relationship between the abundance of heterospecifics and cork oak survival could then be related to competition for water resources. This result agrees with previous studies that have found an increase in the sensitivity of evergreen oaks to competition with decreasing precipitation (Gómez-Aparicio *et al.*, 2011). Nevertheless, we did not find any effect of conspecific trees on cork oak survival suggesting that interspecific competition for cork oak may be greater than intraspecific competition (Gómez-Aparicio *et al.*, 2011).

Recruitment patterns

Similar to what we found for adult survival, climatic variables had the most influence determining *Q. suber*

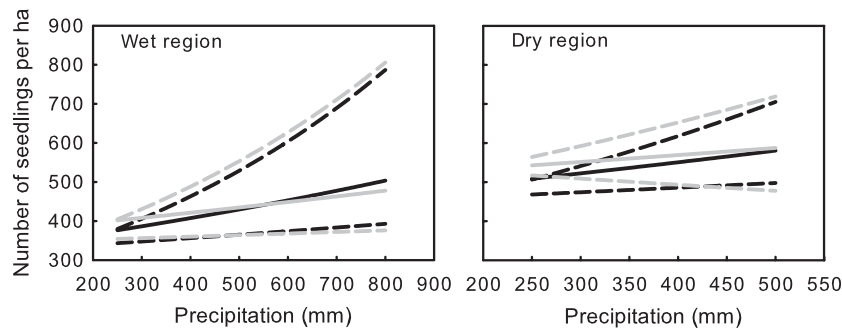


Figure 4 Predicted mean effect of precipitation on seedlings abundance (number of seedlings per hectare). Effects under the mean temperature (black colour) and under a 3 °C temperature increase (grey colour) are shown. The solid line is the mean of the posterior predictions, and the broken lines represent the 95% predicted interval, for the two regions. Winter precipitation is limited to the range found for each variable in each region.

regeneration dynamics. Nevertheless, the effects of climatic factors on recruitment of new individuals did not completely match with those from the adult trees analysis: seedling abundance was mainly affected by temperature in winter, with a positive response to warmer conditions, while adult tree survival responded negatively to spring temperatures. In addition, while our model provides very useful information for assessing recruitment, the R^2 obtained suggests that other factors are likely affecting the observed recruitment patterns.

The different response to seasonal temperatures between seedlings and adult trees may be due to the high sensitivity of cork oak seedlings to low winter temperatures (Aranda *et al.*, 2005). In fact, low temperatures have a more negative impact on the photochemistry of cork oak leaves than do low water availability and high temperatures in summer (Aranda *et al.*, 2005). Contrary to what we expected, the interaction between temperature and precipitation showed in our models could indicate that the positive effect of precipitation on the abundance of seedlings may be weaker under warmer temperatures. This surprising result seems to indicate that the effect of climate on cork oak recruitment could be largely mediated by indirect mechanisms related to the presence of soil-borne pathogens, whose abundance is favoured by soil moisture and warmer temperatures (Hendrix & Campbell, 1973; Sánchez *et al.*, 2002).

Here, again our models showed a negative effect of heterospecific trees on seedling recruitment. In the case of seedling recruitment, the negative effect that heterospecific trees seemed to have on recruitment may be due to competition for light. Some of the most common heterospecific species in our study sites (e.g. *Quercus canariensis*) create deep shade microsites under their canopy. Cork oak is a species of intermediate shade tolerance, and at low light levels, seedlings tend to allocate resources to leaves at the expense of the root system, preventing roots from reaching deeper water sources (e.g. Lloret *et al.*, 1999; Cardillo & Bernal, 2006). Still, the apparently lack of effect from conspecific adults on seedling abundance could be the result of several factors acting simultaneously with an overall neutral effect, a positive effect as

seed producers but a negative effect due to the accumulation of host-specific enemies like soil pathogens or herbivores according to the Janzen–Connell hypothesis (e.g. Clark & Clark, 1984).

Predictions under forecasted climate change scenarios

According to our model results, adult trees would respond negatively to warmer springs, and therefore, the predicted changes in climatic conditions could threaten the persistence of this species and the ecosystems it supports (see examples of other forest systems around the world in van Mantgem *et al.*, 2009; Allen *et al.*, 2010; Vilà-Cabrera *et al.*, 2012). Thus, our simulation forecasts illustrate how cork oak, a key species in the Mediterranean, would be affected by the predicted rise in temperature during the year (Brunet *et al.*, 2007). Global warming would affect both adult tree survival (influenced negatively by higher temperature in spring) and potentially recruitment patterns (influenced positively by higher temperature in winter), and it will be the net effect that will determine future dynamics. What is more, in these mediterranean forests, the inherent low abundance of seedlings and saplings resulting from their limiting climatic (e.g. high seedling mortality during summer) and management (e.g. overgrazing) characteristics makes the process of transition exceedingly slow, which highlights the important consequences that the increase in tree mortality and lack of recruitment may have on the continuity of these forests.

While there is a clear trend of increasing seasonal average temperature, the predicted seasonal changes in precipitation are more variable for the Mediterranean region. Although decreases are expected in the annual average and in average precipitation for most months, winter precipitation, our key variable, is expected to increase up to 30–40%, particularly in December and January (Brunet *et al.*, 2007; Planton *et al.*, 2012). Our results suggest that the predicted changes in precipitation could have very different effects on tree survival patterns depending on the characteristics of the soils, which

modulate the influence of climate. Therefore, under the predicted future climate scenarios, cork oak persistence is more likely to occur in sandy soils compared with clayey soils.

Most studies forecasting future plant distributions are based only on climate, neglecting the role of soils explaining distribution patterns. In our study, we have shown how soil characteristics are of crucial importance when determining the influence of climate on tree dynamics. Furthermore, for a more accurate assessment on plant dynamics, different life stages should be studied simultaneously as their different responses to environmental factors could determine the sign of the overall effect with great implications on the community.

Our models provided us with important information about underlying drivers of regeneration and mortality processes along large-scale climatic gradients, which shows contrasting trends at different life stages. However, other underlying drivers of these processes, such as herbivory in regeneration patterns (e.g. Pulido *et al.*, 2013) or biotic agents in mortality processes (e.g. Brasier *et al.*, 1993), could alter the observed trends. In addition, our approach, a space-for-time substitution, has several relevant limitations. Specifically, local adaptation of tree species and the interaction of climate with biotic factors might lead to departures from the forecasted results. Still, this approach is valuable and informative, as it provides us with realistic insights of the potential consequences of climate change on plant populations (e.g. Pearson & Dawson, 2003; Thomas *et al.*, 2004; Bradley *et al.*, 2009; Gómez-Aparicio *et al.*, 2011).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Map showing the location of the area of study within Spain.

Appendix S1 Analytical methods: Analysis of tree survival.

Appendix S2 Analytical methods: Analysis of the seedling group.

Appendix S3 Analytical methods: Analysis of the sapling group.

Appendix S4 Analytical methods: Parameter estimation.

Table S1 Summary of the data on the selected sites.

Table S2 Mean (\pm SD) and maximum and minimum values of the exploratory variables for each region.

Table S3 Factor loadings of varimax-rotated factors for the soil variables.

Table S4 Selected models used to evaluate the probability of mature tree survival.

Table S5 Selected models used to evaluate the number of seedlings less than 1.30 m high of cork oak.

Table S6 Classification of recruitment in the seedling and sapling groups.

Table S7 Predictive loss (D) for some of the models run in the analysis of saplings (> 1.30 m high).

BIOSKETCH

Beatriz Ibáñez is concluding her PhD under the supervision of T. Marañón, L. Gómez-Aparicio and L.V. García. She is studying the consequences of tree mortality and recruitment limitation in mediterranean forests affected by oak decline, aiming to gain knowledge on the functioning of these systems due to their ecological, economic and social importance.

Author contributions: B.I., T.M., L.G.A. and L.V.G. conceived this study; B.I. and I.I. analysed the data; P.R.B. adapted the database; all authors contributed to the writing of the manuscript.

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