

**Large-scale patterns of *Quercus ilex*, *Quercus suber*, and *Quercus pyrenaica* regeneration  
in Central-Western Spain**

Shortened version for page headings:

Mediterranean oak regeneration

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## ABSTRACT

In Central-Western Spain, forests and woodlands composed of *Quercus* sp. support outstanding levels of biodiversity, but there is increasing concern about their long-term persistence due to a lack of regeneration. We hypothesize that this regenerative lack is operating on a large geographic scale; that there are differences in the abundance of regeneration between three oak species; that oak regeneration is governed mainly by forest management and structure; and that shrubs act as important physical protectors of seedlings and saplings. We analyzed whether densities of oak seedlings and saplings in several size classes were related to stand-structure, understorey and physiographic variables potentially affecting regeneration. Data collected at a regional level (1 km x 1 km grid) by the Spanish Forest Inventory were evaluated from 2,816 plots. Results revealed that regeneration failure was common for all size categories, from small seedlings to large saplings, and, for the three species studied, especially the evergreens. Of the *Quercus ilex*, *Q. suber* and *Q. pyrenaica* plots studied, 49%, 62%, and 20% were lacking any small seedlings, and 82%, 96%, and 56% did not have any large saplings, respectively. Regeneration was positively correlated with tree cover and density, especially of small and medium-sized trees, and negatively correlated with the presence of large trees, indicating that regeneration failure is mostly associated with more open, uniform and/or aged woodlands. Regeneration densities of *Q. ilex* and *Q. suber* were positively correlated with all understorey variables, suggesting that the presence of pioneer shrubs represent a major safe site for early tree recruitment, independent from specific shrub species.

**Key words:** dehesa; logistic regression; Mediterranean forest; regional survey; sapling recruitment; seedling establishment; shrub encroachment; shrub facilitation; stand dynamics; tree demography.

## INTRODUCTION

In the Mediterranean Basin, forests and woodlands are highly diverse in their architecture, appearance, and woody plant composition, a result of disparate ecological conditions and land use histories. Oaks are the predominant and most crucial forest species, especially in the meso- and supra-mediterranean life zones (Blondel and Aronson 1999). But in the past decades – as in other Mediterranean climate zones (Tyler and others 2006) – widespread concern about oak regeneration has emerged. Lack of recruitment seems a particular threat to forest sustainability in the savanna-like oak woodlands (‘dehesas’) in the lowlands of the Iberian Peninsula, where regeneration failure has been accompanied by a gradual dieback of existing forest stands. In consequence, a significant decrease in the extension and tree density of open oak woodlands has taken place locally (Pereira and others 2004; Plieninger 2006).

Concern for the long-term persistence of Mediterranean oak stands has led to a number of experimental studies or field surveys at small and medium scales. In Central-Western Spain, holm oak (*Quercus ilex*), cork oak (*Q. suber*), and Pyrenean oak (*Q. pyrenaica*) are the predominant oak species. Although regeneration failure potentially has a large spatial impact on all of these species, most studies have focused on *Q. ilex*, while few have included *Q. suber* and almost none have looked at *Q. pyrenaica* (Retana and others 1999; Pulido and Díaz 2005; Pausas and others 2009). Survival of acorns, seedlings, and saplings has been monitored, depending on various environmental and management factors (Lookingbill and Zavala 2000; Cierjacks and Hensen 2004; Plieninger and others 2004; Pulido and Díaz 2005; Bugalho and others 2006; Pausas and others 2006; Pons and Pausas 2006; Smit and others 2009). Regeneration failure varies widely among oak species (McCreary 2001), and in preliminary studies has been demonstrated for 72% of studied *Q. suber* woodlands and 87% of *Q. ilex* woodlands (Moreno and Pulido 2008). For closed *Q. ilex* stands, a recruitment bottleneck was found at the sapling stage which prevents population renewal (Espelta and others 1995). Significantly lower seedling numbers were found in small

*Q. ilex* woodlots than in unfragmented stands (Santos and Tellería 1997). Reports on missing regeneration have been confirmed by indirect measures (based on the observation of age or size structures of tree populations) that evaluated how regeneration failure translates into specific demographic structures of forest stands (Pulido and others 2001; Plieninger and others 2003, Barbour and others 2007; Ramírez and Díaz 2008). In most of the *Q. ilex* stands studied until now, an almost complete lack of juvenile age classes has been found in their demographic structures (Pulido and others 2001).

The lack of natural oak regeneration has been explained by differences in the success of seed dispersal to sites suitable for seedling establishment and in adequate conditions for seedling survival (Pulido and Díaz 2005). Specific associations of *Q. ilex* juveniles and saplings have been found with mature trees, shrubs, and rock outcrops: a result of directional dispersal, facilitation of seedling establishment and sheltering from livestock browsing (Plieninger and others 2004). These results point to a central insight of current research on Mediterranean oaks: Acorn and seedling survival is critically related to ‘safe sites’ offered by the presence of shrubs, a phenomenon known as ‘facilitation by nurse plants’ (Castro and others 2004; Gómez-Aparicio and others 2004; Gómez-Aparicio and others 2005; Pulido and Díaz 2005). The most prominent facilitative effects of shrubs on regeneration are protection against browsers and shading from direct radiation, which reduces water stress and increases soil water content (Pausas and others 2009; Smit and others 2008). Shrubs may also improve nutrient availability, reduce soil compaction, and support populations of seed-dispersing animals, such as rodents (Muñoz and others 2009). Yet shrubs can also contribute to increased seed removal (Smit and others 2008) and compete for soil nutrients and soil moisture with oak seedlings (Moreno and others 2007). All in all, however, the balance of positive and negative effects seems to result in a net facilitative effect for evergreen oaks (Pulido and Díaz 2005; Pulido and others 2009).

Despite a wealth of studies investigating singular determinants and processes of oak regeneration done at limited geographic scope, several gaps in knowledge about Mediterranean oaks remain. A review of regeneration studies of Mediterranean oaks in California revealed that the vast majority of studies have been of short duration (less than three years), focused on the acorn and early seedling life stages, and were conducted at only a few locations within each species' geographic range (e.g. in greenhouse pots or within field plots totaling <2 ha) (Tyler and others 2006). Most of the studies of Iberian oak woodlands cited above have equally derived their conclusions regarding the situation based on just one or a few estates. What have foremost been missing both in California and the Mediterranean Basin are studies on the variation of regeneration failure across geographic sites and over longer time spans, leading to problems of validity. For example, small-scale studies in California repeatedly claimed oak regeneration failure, but a statewide study showed that in some areas there were more favorable conditions for regeneration, seeming to stabilize oak population dynamics at the landscape level (McCreary 2001). Also unknown is how far the drivers of regeneration vary in function of larger site and climate factors and whether there are general determinants of poor regeneration. Among the drivers that have remained untested in California at the landscape scale are annual grasses competing for soil moisture, livestock grazing, rodent populations, fire, and climate change (McCreary 2001). In the Mediterranean Basin there have been few studies comparing the relative performance of regeneration between several oak species and age classes, growing under different site conditions. What remains unspecified with regard to nurse effects is whether they a) operate at large spatial scales, irrespective of site conditions; b) can be extended to any shrub species or are shrub species-specific; and c) act specifically upon a single oak species or operate similarly for a range of oaks in the Mediterranean Basin.

### **Aims and hypotheses**

The goal of the present study has been to perform a regionally extensive survey of *Q. ilex*, *Q. suber*, and *Q. pyrenaica* regeneration across the Extremadura region of Spain and to reveal the factors significantly associated to their variation. Our aim has been to explore the validity of processes learnt about through small-scale experiments at a larger, regional scale (compare Brudvig 2008). Based on the state of the art of research on Mediterranean oak regeneration, we developed and tested the following questions and hypotheses:

1. At what spatial scale does regeneration failure of the three investigated oak species act?  
Based on the finding of lacking regeneration of most small-scale studies, we hypothesize that regeneration failure is a general phenomenon operating on a large geographic scale (several 1,000 km<sup>2</sup>) and affecting the majority of oak stands.
2. Are there differences in the magnitude of oak regeneration failure? We hypothesize that the phenomenon is very serious for *Q. ilex* and *Q. suber*, as the land use systems they are part of experience intensive management pressures. Due to the specific ability of *Q. pyrenaica* to resprout and a generally lower land use pressure, we expect higher levels of regeneration for this species. Concluding from the insight of small-scale studies, we expect that the sapling stage will be more greatly affected than the seedling stage.
3. What ecological drivers govern the abundance of regeneration of the three oak species?  
As single-species studies of the three oaks consistently identified significant impacts of forest management and structure, (absence of) livestock grazing, and certain site conditions, we hypothesize that regeneration of the three oak species is associated with similar ecological and management parameters.
4. ‘Safe sites’ (especially shrubs) offer protection from abiotic stress and herbivory for oak regeneration. Is their protective role more physical or biological? If it is more physical, then overall shrub cover should exert a more influential nurse effect than cover of specific shrub species.

In the following, we first evaluate oak seedling and sapling abundance and stand size structure by customizing publicly available forest inventory data. Second, we explore regionally robust patterns of regeneration depending on stand-structure, understorey, and physiographic variables, interpreting these as gradients of abiotic stress and herbivory pressure. Third, we integrate these findings through development of six logistic regression models to predict the probability of oak regeneration based on a large set of variables.

## **METHODS**

### **Study area**

We surveyed oak regeneration in the Extremadura region, an area that occupies 41,000 km<sup>2</sup> in Central-Western Spain. The region was selected for several reasons: First, it represents the primary area for oak forests in Spain, with 15,590 km<sup>2</sup> dominated by oak forests and woodlands (MMARM 2006). Second, it includes gradients of altitude, temperature, precipitation, forest stand structure, and intensity of land management. Third, it represents the core area for *Q. ilex* (*Qi*) and includes a large proportion of Spain's *Q. suber* (*Qs*), and *Q. pyrenaica* (*Qp*) stands (which differ in resource requirements), with both open and closed oak woodlands coexisting intimately and in similar proportions. We preferred to focus on the core area rather than on populations at the edge of species distributions, as we were mostly interested in the impact of forest management and structure and intended to exclude other confounding factors prevailing in more extreme environmental conditions (regeneration at the borders of a range of oak populations, where climatic variables may act more strongly, has been studied e.g. by Pausas and others 2006). The landscapes of the region are flat or gently undulated lowlands (approx. 200 m in altitude), but low (<1,000 m altitude) and high mountains (maximum altitude 2,400 m) are also present. The climate is typically Mediterranean, with rainfall regularly concentrated in fall, winter and spring. Mean annual rainfall ranges between 400 and over 2,000 mm in the depressions of the main rivers and

around the high mountains, respectively. Mean annual temperature ranges between 18-19 °C (main depressions) and 4-5 °C (high mountains). Winters are moderately cold and summers very warm. Water deficit is intense and usually lasts for four months. Soils have developed over acid bedrocks and are shallow and poor in organic matter and nutrients.

### **The trees**

*Qi* grows in sites with a dry, continental climate, over a large range of altitudes (from 300-1,800 m), and does well in a wide range of soil chemistry and texture. Minimum annual rainfall for *Qi* forests is around 400-450 mm (Terradas 1999). Important life traits are evergreenness, sclerophylly, and widely branched and deeply reaching root systems. *Qs* occurs in regions with average annual precipitation above 600 mm and average temperatures near 15°C, usually at 800 m altitude. It is evergreen, has sclerophyllous leaves, a deep root system and a thick and rugged corky bark, protecting the tree from fire. *Qs* is less frost- and drought-tolerant than *Qi* (Aronson and others 2009). *Qp* is a deciduous tree common in the Mediterranean and Eurosiberian biogeographic regions of Spain. It is found in areas where the summer dry period is less marked, especially in mountain ranges of 400-1,600 m, receiving 400-1,200 mm of precipitation (Tárrega and others 2009).

In Spain, *Qi*, *Qs*, and *Qp* woodlands are commonly categorized into forests and dehesas, based on differences in the forms of human impact. Forests are formations of dense shrubland and woodland in which oaks are accompanied by a dense woody understorey. In most forests vegetation has not been formally managed (see Pulido and others 2001). Dehesas are non-equilibrium systems, wherein a grass layer is maintained through formalized and coordinated management practices comprised of a) regular thinning and pruning of trees for purposes such as enhancing herbage growth, ensuring maximum cork and acorn yields, and obtaining browse, firewood, and charcoal; b) livestock grazing for preventing shrub encroachment of pastures, improving pasture quality, and ameliorating soil quality; and c) periodical or



rotational clearance of shrubs for controlling shrub encroachment, avoiding soil compaction, and (sometimes) cultivating crops (Moreno and Pulido 2009).

### **Data base**

All data sets used for our analysis (except regarding climate and altitude) stem from the Spanish Forest Inventory and were used as a systematic, large-scale complement to localized experiments. This inventory sampled the forestry areas of Extremadura between 2000 and 2002, based on a regular grid of circular survey points with a density of approximately one point per square kilometer (total number of records in Extremadura: 4560). The inventory did not include cultivated dehesas or other very open woodlands. Survey points were defined by their spatial location (UTM coordinates). The three samples for this study – comprised of *Qi*, *Qs*, and *Qp* woodlands – were defined as any survey points of the Forest Inventory that included at least one adult tree (diameter at breast height [dbh]  $\geq 7.5$  cm) of *Qi* (2,157 plots), *Qs* (631 plots), or *Qp* (337 plots). The three types of oak were recorded as main species in the majority of the plots. Only in 1.2% (*Qi*), 15.1% (*Qs*), and 1.5% (*Qp*) of the plots, respectively, were they clearly subordinate species, representing <10% of sampled trees.

Three main weaknesses have been detected in the Spanish Forest Inventory, which were taken into account during data analysis and interpretation. First, regeneration has been classified by the Inventory according to plant size rather than age. This could be confounding in cases where local environmental or management effects suppress or enhance plant growth and, thus, change the age-size relationship (Mitchell-Olds 1994). Still, there are several reasons why size-based demographic approaches have been taken in most studies on oak regeneration (e.g. Lookingbill and Zavala 2000; Dufour-Dror 2007; Maltez-Mouro and others 2007; Kabrick and others 2008): Plant growth and mortality are often more size-dependent than age-dependent, and limiting abiotic and biotic factors change as plants grow larger, but not necessarily as they grow older. Moreover, size classes can be determined with more

precision, and it may be hard to justify destructive sampling procedures for plant age determination given the low number of seedlings at most sites (Rooney and Waller 1998; Rooney and others 2000; Plieninger and others 2004).

Second, the Inventory does not separate generative and vegetative origins of regeneration. Some smaller-scale studies have lumped generative and vegetative regeneration as well (e.g. Acacio and others 2007; Maltez-Mouro and others 2007), while others have explicitly recorded them separately (e.g. Pausas and others 2006; Santos and Tellería 1997) to quantify the importance of vegetative versus generative reproduction. To compound vegetative and generative reproduction together aggravates the interpretation of processes such as seed dispersal and nurse shrubs, as these apply to seedlings of sexual origin only. It also aggravates a direct comparison of species-specific strategies regarding sexual versus asexual regeneration between the three oak species. Especially in disturbed sites, a considerable part of oak regeneration may result from resprouting (Retana and others 1992; Tárrega and others 2009). To reduce the impact of such perturbations we excluded those plots of the Forest Inventory that had experienced important changes within the preceding 10 year period.

Third, forest and dehesa management have been distinguished visually, blending together both management and vegetation structures. According to the Inventory, plots were categorized as forest where the tree layer dominated and where ecosystem functioning seemed hardly or only moderately influenced by humans. Plots were grouped as dehesa if tree cover was low, combined with crops and pastures, and with the presence of livestock. Analysis of the data confirmed that forest and dehesa plots were actually different in terms of forest stand structure: Mean tree cover ( $Z=-13.84$ ,  $p<0.001$  for  $Qi$ ), *Quercus* density ( $Z=-14.18$ ,  $p<0.001$ ,  $Qi$ ), and shrub cover ( $Z=-20.68$ ,  $p<0.001$ ,  $Qi$ ) were significantly lower, and mean dbh ( $Z=-21.59$ ,  $p<0.001$ ,  $Qi$ ) was higher in dehesas compared to forests for all three oak types.

In addition to the data of the National Forest Inventory, each inventory plot was characterized through the use of climatic and altitude data, using a GIS. Data on mean annual temperature and precipitation (1971-2000) were derived from a set of meteorological stations of the Spanish National Institute of Meteorology and interpolated by kriging (resolution: 1 km). Altitude data were provided by the Spanish National Geographic Institute and fitted with a digital elevation model (resolution: 25 m).

### **Regeneration variables**

The survey measured four life stages of oak regeneration that were delimited by size: small seedlings (height <30 cm), large seedlings (height: 30-130 cm), small saplings (height >130 cm, dbh <2.5 cm), and large saplings (height >130 cm, dbh  $\geq$ 2.5 cm). In the following, ‘seedlings’ will be used as an indication of recent recruitment, while both seedlings and saplings together will be more generally referred to as ‘regeneration’. Seedlings are in a stage that is still affected by losses through herbivory, competition, or desiccation, so that recent recruitment does not guarantee successful regeneration of an existing stand (Tiver and Andrew 1997). Seedling and small sapling abundance was grouped in four categories: absent, 1-4 individuals within a circular plot of 5 m radius, 5-15 individuals, and >15 individuals. For large saplings, continuous density values were additionally calculated.

### **Stand structure, understorey, and physiographic variables**

We separately calculated total mature tree cover (in %) and mature stand densities (expressed in  $N\ ha^{-1}$ ) for the respective oak species (as a surrogate of local seed input) as well as for four different dbh classes of each oak species (Appendix 1). Stand density was recorded by counting and measuring adult trees of all forest species with a caliper. The inclusion of a tree in the sample was a function of its dbh and its distance from the plot center. Plot radius was 5 m for trees from 7.5-12.4 cm (‘small trees’), 10 m for trees from 12.5-22.4 cm (‘medium

trees'), 15 m for trees from 22.5-42.4 cm ('large trees'), and 25 m for trees  $\geq 42.5$  cm ('very large trees') dbh. As a measure of heterogeneity of tree diameters, we calculated Shannon diversity indices that consider both the number of different diameter classes (four classes maximum in our case) and the abundance of each diameter class as a proportion of total abundance of adult oaks. (This parameter, however, offers only a rough estimate of the heterogeneity of tree diameters, as the different diameter classes were recorded on concentric circles, so that mean abundance values entered into the Shannon index.) The categorical variable 'stand management' (dehesa/forest) acts as a synthesizing variable that subsumes several variables of forest structure. Additionally, we used more specific overstorey variables (e.g. DBH) for the study of stand structure variation within both dehesas and forests separately, as neither forests nor dehesas are uniform in their stand structure. The cover of shrub species was estimated visually on site within a circle of 10 m radius. The superposition of several shrub species resulted in cover values  $>100\%$  on some plots. We included both overall shrub cover and the cover of nine common shrub species in the analysis. Slope was measured in % using a clinometer, the prevailing aspect in centigrades with a compass. Soil variables were measured at 2 m distance from the plot center by excavating a vertical soil profile of at least 30 cm depth. Rock cover was estimated visually. Humus layer was measured as the height of the humus layer above the mineral soil. Soil texture was determined in the field by feel; soil organic matter was subdivided as a function of estimated Munsell values. An exact description of slope, aspect, rock cover, humus layer, soil texture, and soil organic matter measurements can be found in Tragsatec (without date).

### **Data analysis**

First, we summarized the variation of oak regeneration via histograms and by calculating means, standard errors, minima and maxima of large sapling abundance. Second, we calculated Spearman correlation coefficients to determine if  $Q_i$  regeneration abundance was

spatially associated with regeneration abundance of  $Q_s$ ; for this analysis, we included only those 280 plots where at least one adult tree of  $Q_i$  and of  $Q_s$  were present. Third, we used Spearman correlation analysis to test the relationship between consecutive size classes (both regeneration and tree), as we expected that, for example, the abundance of small saplings will be a function of the abundance of large seedlings at a specific site. Fourth, for each of the four size classes and each of the three oak species, we separately identified individual relationships between the predictor variables listed in Appendix 1 and the abundance of oak regeneration. We used Spearman correlation analysis to explore correlations with ordinal and continuous stand-structure, understorey, and physiographic parameters. Mann-Whitney and  $\chi^2$  tests were used to test if categorical variables (soil texture, stand management, habitat type) determine abundance of oak regeneration. To separate overarching effects of dehesa/forest management and stand structure variation within both dehesas and forests some associations of stand structure have been analyzed separately for dehesas and forests.

In a fifth step, we used multiple logistic regression to disentangle the effects of multiple factors influencing oak regeneration and in order to account for collinearities which may exist, especially between stand structure variables. We proposed that the probability of occurrence of oak regeneration would be influenced by a combination of the given explanatory variables. The goal was to explain variation in regeneration abundance using the fewest number of vegetation-structure and physiographic variables. Logistic regression allows the use of a binary dependent variable and several continuous, nominal or binary independent variables, which do not need to have a normal distribution. To reduce the number of models to be constructed, the four regeneration size classes were redefined into two categories (1: ‘seedlings’ – previously ‘small seedlings’ and ‘large seedlings’ and 2: ‘saplings’ – previously ‘small saplings’ and ‘large saplings’), the absence or presence of which was calculated for each plot. Thus, six models were developed:  $Q_i$  seedlings,  $Q_i$  saplings,  $Q_s$  seedlings,  $Q_s$  saplings,  $Q_p$  seedlings, and  $Q_p$  saplings. The presence on a plot of at least one seedling or

sapling (coded as 1) or their total absence (coded as 0) was used as dependent variable. The variables listed in Appendix 1 were included as influencing factors in the regression. Stand management, habitat type, and soil texture were entered as categorical covariates (repeated coding). We used a forward stepwise procedure (LR forward selection) to select the explanatory variables from the full list of measured variables. Only variables with a significance level of  $p < 0.05$  were included in the final models. Model fitting  $\chi^2$  statistics and Hosmer-Lemeshow goodness of fit statistics were used to determine a significant predictor set for oak seedlings and saplings (Peng and others 2002). Effect size of each model was assessed by Cox and Snell  $R^2$  and Nagelkerke  $R^2$ , subsequently validated by analyzing the proportion of cases that were classified correctly. PASW Statistics 17 was used for all statistical analyses.

## RESULTS

### Magnitude of regeneration failure

Oak regeneration was absent from a considerable proportion of the plots. Cork oak regeneration of all four size classes was completely lacking at 56.7% of all plots, Holm oak at 39.1%, and Pyrenean oak at 12.8% (small seedlings: 62.3% [ $Q_s$ ], 48.7% [ $Q_i$ ], 20.8% [ $Q_p$ ]). However, more than 15 small seedlings were found at 21.7% ( $Q_i$ ), 8.7% ( $Q_s$ ), and 53.4% ( $Q_p$ ) of the plots, indicating that oak regeneration exists under certain ecological circumstances. Figure 1 shows that densities strongly and continually decreased from small seedlings to large saplings. Density of large saplings varied strongly, but was generally marginal, with mean values ranging from 18.37 ( $\pm 6.16$  S.E.) trees  $\text{ha}^{-1}$  for  $Q_s$ , 110.26 ( $\pm 8.16$  S.E.) trees  $\text{ha}^{-1}$  for  $Q_i$ , to 432.60 ( $\pm 48.10$  S.E.) trees  $\text{ha}^{-1}$  for  $Q_p$ . The largest sapling densities found were 2,546 ind.  $\text{ha}^{-1}$  ( $Q_s$ ), 4,966 ind.  $\text{ha}^{-1}$  ( $Q_i$ ), and 6,239 ind.  $\text{ha}^{-1}$  ( $Q_p$ ). The mean number of large saplings relative to the number of mature trees on a plot was 0.26 ( $\pm 0.10$  S.E.) ( $Q_s$ ), 1.95 ( $\pm 0.30$  S.E.) ( $Q_i$ ), and 1.49 ( $\pm 0.31$  S.E.) ( $Q_p$ ). This ratio was below 1.00 in

97.3% ( $Q_s$ ), 84.6% ( $Q_i$ ), and 71.8% ( $Q_p$ ) of all plots, indicating a severe regeneration failure. Abundance of the size classes was positively correlated within all three species (Table 1), with the strongest correlations being found between small and large seedling abundances. For the very large tree class, correlations with the previous size class became insignificant or – at  $Q_i$  sites – turned negative. Regeneration of  $Q_i$  and  $Q_s$  was positively correlated over all size classes (Spearman  $r_s=0.163$ ,  $p<0.01$  [small seedlings];  $r_s=0.240$ ,  $p<0.001$  [large seedlings];  $r_s=0.246$ ,  $p<0.001$  [small saplings];  $r_s=0.175$ ,  $p<0.01$  [large saplings];  $n=280$ ). In contrast, there was no significant correlation between  $Q_i$  and  $Q_p$  ( $n=31$ ) or between  $Q_s$  and  $Q_p$  ( $n=15$ ) for any of the correspondent regeneration classes.

### **Effects of stand management and structure**

Presence of regeneration of all size classes was significantly higher in forests than in dehesas across all oak species. A comparison of sapling densities and sapling-to-mature tree ratios showed the same tendency. Significantly higher frequencies of plots with presence of all regeneration classes on forest sites were revealed through  $\chi^2$  tests (Table 2). Plots with seedling presence and those with seedling absence exhibited different diameter structures (Figure 2): At plots without seedlings, the diameter structure of adult trees was bell-shaped, the most frequent diameter classes being 22.5-42.5 cm for  $Q_i$  and  $Q_s$  and 12.5-22.5 cm for  $Q_p$ . Diameter structures of  $Q_i$  and  $Q_p$  at plots with seedlings present resembled an inverse J-shaped distribution, where frequency declines with increasing diameter class.

Both tree cover and the densities of adult trees of the respective oak species were positively related to the regeneration classes of  $Q_i$ ,  $Q_s$ , and  $Q_p$  (Table 3). The smaller diameter classes of the oak overstorey showed positive relationships, while for the larger diameter classes the relationship became weaker, not significant, or even negative. Consistent with that, abundances of all regeneration classes decreased with increasing mean dbh of the respective adult oak stands. Abundance of most seedlings and saplings was also related to the

heterogeneity of *Quercus* tree diameters: Plots with a relatively uniform dbh structure (indicating that trees are of the same age) showed significantly less regeneration than stands with a more heterogeneous dbh distribution. Associations with large *Qi* saplings were also tested for dehesa (n=1,635) and forest (n=522) plots separately to explore variation within these fundamentally different forest structures. In line with the overall results, large saplings in dehesa plots showed the same highly significant associations with stand variables, both positive (tree cover: Spearman's  $r_s=0.144$ ,  $p<0.001$ ; density of adult *Qi*:  $r_s=0.203$ ,  $p<0.001$ ; heterogeneity:  $r_s=0.113$ ,  $p<0.001$ ) and negative (*Qi* dbh:  $r_s=-0.241$ ,  $p<0.001$ ). Forest plots showed stronger correlations within the same direction (tree cover:  $r_s=0.196$ ,  $p<0.001$ ; density of adult *Qi*:  $r_s=0.356$ ,  $p<0.001$ ; *Qi* dbh:  $r_s=-0.388$ ,  $p<0.001$ ), but with one exception: Stand heterogeneity was not a significant variable.

A Mann-Whitney test revealed that the categorical habitat type was another significant variable for *Qp* and *Qs*: Monospecific stands had significantly higher abundances of all *Qp* regeneration classes ( $Z=-3.76$ ,  $p<0.001$  [small seedlings],  $Z=-4.75$ ,  $p<0.001$  [large seedlings],  $Z=-3.47$ ,  $p<0.01$  [small saplings],  $Z=-2.90$ ,  $p<0.01$  [large saplings]). The three minor *Qs* classes were also more abundant in pure than in mixed-species forests ( $Z=-6.19$ ,  $p<0.001$  [small seedlings],  $Z=-4.77$ ,  $p<0.001$  [large seedlings],  $Z=-2.51$ ,  $p<0.05$  [small saplings]). In contrast, small *Qi* seedlings were slightly more abundant in mixed-species forests ( $Z=-2.17$ ,  $p<0.05$ ).

### **Understorey effects**

The analysis of several variables characterizing the shrub layer revealed strong significances for *Qi* and *Qs* size classes, but hardly any with regard to *Qp* regeneration (Table 4). The strongest positive correlations were found between the regeneration variables and shrub cover as well as the number of shrub species. For *Qi*, all shrubs species but *Rubus* sp. showed a positive and significant correlation with three or four of the size classes of regeneration.



Among the prevailing shrub species in the region's woodlands, *Lavandula stoechas* showed the strongest positive correlation with regeneration of evergreen oaks. There were few significant relationships between understorey variables and large saplings of *Qs*, which may be due to the fact that only 23 plots had any large *Qs* saplings at all.

### **Physiographic effects**

Spearman rank correlation analysis revealed significant univariate relationships between the regeneration categories of the three oak species and several climatic, topographic, and edaphic variables (Table 5). Larger abundances of all size classes and all species were found on steeper slopes. Rock cover was significantly related to *Qi* regeneration, but not to *Qs* and *Qp*. Thickness of humus layer proved significantly related to three *Qi* size classes. Mean annual temperature was negatively and altitude was positively correlated with most *Qi* and *Qp* classes. Three *Qi* classes were less abundant with lower mean annual precipitation, while all *Qp* classes were more abundant with increasing precipitation. A Kruskal-Wallis test revealed no significant differences between any of the regeneration classes of *Qs* and *Qs* and soil texture categories. However, as a subsequent Mann-Whitney test showed ( $Z=-3.136$ ,  $p<0.002$ ,  $n=330$ ), small *Qp* saplings have a significantly higher abundance on sandy than on silty soils.

### **Logistic regression models**

Logistic regression analysis produced six models for seedling and sapling presence/absence of the three oak species. These models indicate the relative and combined importance of stand-structure, understorey, topographic, climate, and soil-predictor variables in accounting for variation in local oak presence. Hosmer-Lemeshow tests yielded results which were not significant for five of the six models (and one weak significance for the *Qi* seedling model), indicating that the models had a good fit. The strength of the relationship between dependent and explanatory variables (as expressed by Nagelkerke's  $R^2$ ) was greater for the sapling than

for the seedling models for all three oak species. Although most variables were significant in the univariate models, collinearities among some variables resulted in low partial correlations with oak presence; consequently, they were removed from the multivariate models. In the final model for *Qi* seedlings, tree cover, oak density, dbh, dehesa management, habitat type, shrub species richness, *Retama* cover, and *Arbutus* cover were a highly significant predictor set ( $p < 0.01$ ) of seedling presence (Table 6). The sapling model included seedling presence, tree cover, density of adult *Qi* and that of the smallest adult size class, dbh, dehesa management, habitat type, and shrub cover as highly significant predictors. For *Qs* seedlings, the highly significant predictor set comprised *Q.* density, *Q.* density of the largest size class, habitat type, and shrub species richness. For *Qs* saplings, seedling presence, *Q.* density, shrub cover, and precipitation showed highly significant (Table 7). In the case of *Qp* seedlings, only dbh was highly significant, whereas the following set was significant in the *Qp* sapling model: seedling presence, oak density 1, dbh, shrub cover, and soil texture (Table 8).

## DISCUSSION

### Generalized regeneration failure

The foregoing large survey upscaled insight obtained at plot level and revealed that regeneration failure was common for the four size categories, from small seedling to large saplings, throughout the core area of the three oak species. Most of the plots had fewer saplings than mature trees. Globally, these results confirmed our first hypothesis: Regeneration failure is a general phenomenon of oak woodlands in Central-Western Spain. However, our large-scale approach also revealed a high degree of variation, including large abundances of regeneration at some (albeit few) sites. In the face of increasing heterogeneity of Mediterranean landscapes, this underlines the need to account for the spatial variability of oak regeneration (Pons and Pausas 2006). Where present, regeneration densities decreased strongly and continuously from the small seedling to the large sapling stage (Figure 1, Table

1). This multistage bottleneck, at which point only some individuals of a size class reach the following size class – a gradual mortality – is a common characteristic of most tree species (Acacio and others 2007; Kobe 1996). Consequently, the abundance of one class is determined by the abundance of the previous one. This was confirmed in our study for all three species, but only for the first transitions (seedlings to saplings; see Table 1, and models 2 of Tables 6-8). By contrast, the transitions from large saplings to young trees and beyond were poorly or (in the case of *Q. ilex*) even negatively correlated (Table 1). Two coexistent circumstances may explain this finding: In one situation, probably common forests, an abundant regeneration would produce numerous saplings and small and medium trees. Large trees are rare because of strong interspecific competition, as Moreno and Cubera (2008) have demonstrated for *Q. ilex* stands of high density. In another situation, probably common in dehesas, excessive thinning has favored the development of large trees, but suppressed regeneration. Hence, sites with an absence of regeneration are associated with plots having a non-natural tree-size distribution that has shifted toward larger size classes (more managed systems), while sites with a presence of regeneration show a typical inverse J-shaped distribution (more natural systems) (Figure 2).

### **Relative abundance of oak regeneration**

Our survey was the first study that systematically compared the magnitude of regeneration failure among three dominant oak species. As expected in our second hypothesis, regeneration was generally scarce, but seedling and sapling abundances of *Q. pyrenaica* were clearly above those of *Q. ilex* and *Q. suber*. Unexpected, however, is that regeneration failure was considerably more pronounced for *Q. suber* than for *Q. ilex*: 49%, 62%, and 21% of the *Qi*, *Qs* and *Qp* plots, respectively, were lacking any small seedling, and 82%, 96%, and 56% did not have any large sapling (Figure 1). The relatively high percentage of regeneration for *Q. pyrenaica* is probably determined by the ability of this species to re-sprout (Tárrega and

others 2009). Where more than one *Quercus* species coexisted, there was a high correlation between the regeneration of *Q. ilex* and *Q. suber*, while there was no correlation with *Q. pyrenaica*. This supports our third hypothesis that regeneration of *Q. ilex* and *Q. suber* seems to be governed by similar factors, while that of *Q. pyrenaica* seems favored by other conditions.

### **Impact of forest structure and management**

A large number of significant explanatory variables describing forest structure indicates the existence of strong collinearities. Many of these variables, such as tree cover, oak density, dbh, and shrub cover, can be concentrated into one overarching determinant: which we called 'stand management' (open dehesa or closed forest) and which was one of the variables best correlated with regeneration. Forests generally had much higher values of regeneration than dehesas (Table 2). This confirms our third hypothesis: Forest management and structure are among the most influential drivers of oak regeneration; for the first time, this was confirmed consistently for all three oak species common to Central-Western Spain. In dehesas, acorns are profusely foraged by livestock and wild species (mostly rodents) (Muñoz and others 2009), but the abundance of seed dispersers of acorns decreases in dehesas when compared to forests (Gómez 2003; Pons and Pausas 2008). Besides, microhabitats facilitating seedling establishment and protection against dessication (Smit and others 2009) and browsers are lacking in dehesas, and most of the regeneration is browsed (Pausas and others 2009; Plieninger 2007). All in all, dehesas are unfavorable habitats for tree regeneration, similar to other heavily grazed savannas and open woodlands occurring in drier portions of their ranges in California, the Mediterranean basin, Asia, Britain, and Eastern North America (Manning and others 2006; Tyler and others 2006). But oak regeneration failure is not restricted to open forests. There is also evidence of oak recruitment failure under dense canopies (Brudvig 2008; Johnson and others 2002; McCreary 2001), such as when water shortage inhibits seedling

growth. Unfortunately, literature is sparse on regeneration in closed forests of the three oak species investigated here. Our study has shown that more than 50% of *Q. ilex* and *Q. pyrenaica* (and even more than 85% of *Q. suber*) forest plots did not have any sapling. Thus, regeneration failure is also common in forests, although with less intensity and with different ecological drivers than in dehesas. Both within dehesas and forests there was significant variation: Regeneration was positively associated with tree cover and density, especially of small and medium sized trees, while the presence of large trees was negatively correlated with regeneration (Table 3). Regeneration was also negatively correlated with the size of trees (dbh), and – for dehesa plots only – with the heterogeneity of tree species and tree size. These results again indicate that regeneration failure is mostly associated with more open, uniform and/or aged woodlands.

### **The role of shrubby understorey**

The data analyzed here have revealed that regeneration densities of *Q. ilex* and *Q. suber* were positively correlated with shrub species richness, cover of most of the shrub taxa, and with overall shrub cover (Table 4). Our results confirmed that shrubs represent a major safe site for oak recruitment during secondary succession. The finding that the positive effect of shrub cover is hardly shrub-species specific also answered our fourth question: The physical protection from browsers (which is relatively independent of shrub species) seems more influential than biological facilitation (which depends on the properties of a specific shrub species). This is in contrast to other findings within marginal *Q. suber* forests, which stress the importance of the configuration of landscapes. Pons and Pausas (2006), for example, found very limited recruitment in shrublands and assessed shrub composition and structure as highly influential. Our hypothesis was not confirmed for the deciduous oak, *Q. pyrenaica*, which grows in more the humid mountain areas of the region studied. Here, hardly any shrub variable was related to regeneration, probably because *Q. pyrenaica* is a more light- and

water-demanding species than others. Therefore the net effect of facilitation/competition may be insignificant. It is necessary to keep in mind that shrub-seedling interactions vary with the physical and biological environment (Gómez-Aparicio and others 2005).

### **Physiographic drivers of regeneration**

Our study contrasted regeneration of the three oaks under a broad gradient of site conditions. Occurrence of regeneration varied rather slightly over climatic, topographic, and edaphic site factors, as indicated by generally low Spearman's  $r$  values (Table 7). Multiple logistic regressions further confirmed that regeneration was mostly independent of these biophysical variables (Tables 6-8). However, bivariate associations showed remarkable differences between species. While *Q. pyrenaica* regeneration increases with annual rainfall, *Q. ilex* regeneration decreases, whereas it has a neutral effect on *Q. suber*. This differential association with rainfall agrees with the water-related performance of the three species, with *Q. ilex* being more water-deficit resistant, occupying the drier areas, and with *Q. pyrenaica* being at the other extreme (Corcuera and others 2002). The three species showed a negative trend of regeneration with temperature and, accordingly, a positive relation with altitude, but the dependence of *Q. pyrenaica* was stronger than the dependence of evergreen oaks. Finally, *Q. ilex* exhibited better regeneration with higher slope and rock cover, which could be related to management (see below), but could also be indicative of the strong resistance of this species to dry sites. Mixed stands with *Q. pyrenaica* (found in the driest extreme of *Q. pyrenaica* distribution) showed less regeneration than in pure stands, which are on average more humid.

### **The role of grazing intensity**

Grazing has been described as a main constraint on natural regeneration of trees species in extensive semi-natural silvopastoral systems in general (e.g. Cierjacks and Hensen 2004; Bugalho and others 2006; Dufour-Dror 2007) and in dehesas in particular (Plieninger 2007).

Unfortunately, the Spanish Forest Inventory did not explicitly include information related to grazing intensity. Notwithstanding these constraints, a number of results presented here indicate the role of grazing as an inhibitor of oak regeneration. The most outstanding is the net difference found in comparing dehesas with forest. While grazing intensity has recently decreased in forests, it has doubled in the last two decades in the dehesas of Extremadura (Moreno and Pulido 2008). The presence of shrubs seems generally linked to low rates or a complete absence of grazing (for *Q. ilex* and *Q. pyrenaica*, compare Ramírez and Díaz 2008; Tárrega and others 2009). This may be due to both direct impacts of livestock trampling and browsing and indirect effects of range management (e.g. shrub clearance for pasture improvement). Hence, shrubs protect against herbivores, but they encroach only in sites where grazing pressure is low or absent. This can be seen as reinforcing the nurse effect of shrubs for oak regeneration. Another indication that reveals the direct relationships among grazing intensity and tree regeneration is that oak regeneration increased with slope and rock cover (in the latter case only significant for *Q. ilex*). Under such conditions, soils are shallower, with lower water holding capacity, and consequently seedling recruitment probably will be more difficult. The only plausible advantage of these hard conditions is reduced grazing pressure. For example, Snow (1972) detected increased levels of *Q. agrifolia* regeneration around rock outcrops in California, which he attributed to protection from browsing. In these areas, practices for controlling encroachment (cultivation, shrub clearing) are also less frequently applied. Hence, livestock per se reduces the opportunities for regeneration, but, additionally, management practiced for livestock rearing may eliminate chances for any early regeneration. These direct and indirect impacts can generate patches of regeneration at different spatial scales (Bisigato and others 2005; Tasker and Bradstock 2006).

### **The importance of large-scale studies**

This study was performed in response to the frequent call for large-scale ecological studies, which are expected to generate insights missed at smaller scales (Carpenter 1990; Walters and Holling 1990). This seems to be especially relevant for the study of oak regeneration (Brudvig 2008; Tyler and others 2008). The use of the spatially extensive data of the Spanish Forest Inventory has allowed illustration of the state of regeneration of oak woodlands in Central-Western Spain and statistical analyses of its most important correlates. Our study demonstrates two potential uses of large-scale ecological studies. On the one hand, large-scale surveys can complement small-scale studies focusing on ecological mechanisms that operate over short time and space intervals (e.g. transition rates from acorn to emergent seedling or microsite effects on early survival and growth). Large-scale studies incorporate larger spatial and temporal scales and a broader range of environmental gradients (e.g. to describe stand level seedling recruitment or the relative importance of factors limiting seedling and, especially, sapling recruitment across sites) (Tyler and others 2008). Here, we have sought to advance existing knowledge on, for example, shrub-regeneration interactions, suggesting that facilitative effects may occur irrespective of shrub species, which implies that shrubs play more a protective role than does biological facilitation. We have also refined the role of dehesa management by showing that there are additional constraints to regeneration within dehesas. Some factors associated with regeneration failure operated similarly in both forest and dehesa stands. On the other hand, large-scale studies can confirm insights from smaller experimental studies and can extrapolate scientific knowledge to spatial scales at which conservation and management activities act. For example, our large-scale study identified that regeneration failure – previously analyzed only at the farm level – is acting over thousands of km<sup>2</sup> of oak woodlands and that therefore oak conservation requires coordinated policy efforts beyond single farms, i.e. at regional and national scales.

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## Tables

Table 1: Spearman rank correlation between the size classes of *Q. ilex*, *Q. suber*, and *Q. pyrenaica*

Table 2: Differences in vegetation structure between dehesas and forests (Mean  $\pm$  S.E.)

Table 3: Bivariate associations of *Q. ilex*, *Q. suber*, and *Q. pyrenaica* regeneration with stand structure variables

Table 4: Bivariate associations of *Q. ilex*, *Q. suber*, and *Q. pyrenaica* regeneration with understorey variables

Table 5: Bivariate associations of *Q. ilex*, *Q. suber*, and *Q. pyrenaica* regeneration with topographic, climate, and soil variables

Table 6: Vegetation and physiographic variables influencing presence and absence of *Q. ilex* seedlings (model 1) and saplings (model 2) on sampling plots (estimated logistic regression coefficient (B), standard error (S.E.), Wald-statistic, significance level (p), odds ratio (Exp (B)))

Table 7: Vegetation and physiographic variables influencing presence and absence of *Q. suber* seedlings (model 1) and saplings (model 2) on sampling plots (estimated logistic regression coefficient (B), standard error (S.E.), Wald-statistic, significance level (p), odds ratio (Exp (B)))

Table 8: Vegetation and physiographic variables influencing presence and absence of *Q. pyrenaica* seedlings (model 1) and saplings (model 2) on sampling plots (estimated logistic regression coefficient (B), standard error (S.E.), Wald-statistic, significance level (p), odds ratio (Exp (B)))



**Table 1:** Spearman rank correlation between the size classes *Q. ilex*, *Q. suber*, and *Q. pyrenaica*<sup>a</sup>

<b>Variables</b>	<b><i>Q. ilex</i></b>	<b><i>Q. suber</i></b>	<b><i>Q. pyrenaica</i></b>
Small seedlings – large seedlings	0.666***	0.575***	0.685***
Large seedlings – small saplings	0.593***	0.480***	0.524***
Small saplings – large saplings	0.649***	0.409***	0.586***
Large saplings – small trees	0.432***	0.302***	0.580***
Small trees – medium trees	0.238***	0.159***	0.489***
Medium trees – large trees	n.s.	0.243***	0.157**
Large trees – very large trees	-0.209***	n.s.	n.s.

<sup>a</sup> n=2157 for *Qi*, n=631 for *Qs*, and n=337 for *Qp*

\* Indicates a significance level of p<0.05, \*\* of p<0.01, \*\*\* of p<0.001, n.s.=not significant



**Table 2:** Differences in regeneration between dehesas and forests (Mean  $\pm$  S.E.)

Variables	<i>Q. ilex</i>			<i>Q. suber</i>			<i>Q. pyrenaica</i>		
	Dehesa (n=1635)	Forest (n=522)	X <sup>2</sup> /Z (p)	Dehesa (n=341)	Forest (n=290)	X <sup>2</sup> /Z (p)	Dehesa (n=27)	Forest (n=310)	X <sup>2</sup> /Z (p)
Large sapling density (N ha <sup>-1</sup> )	44.2 $\pm$ 5.0	317.2 $\pm$ 28.0	Z=-17.09 (<0.001)	5.6 $\pm$ 4.0	33.4 $\pm$ 12.5	Z=-4.00 (<0.001)	9.4 $\pm$ 9.4	469.5 $\pm$ 51.8	Z=-4.30 (<0.001)
Large sapling/mature tree ratio	1.2 $\pm$ 0.3	4.2 $\pm$ 0.8	Z=-16.35 (<0.001)	0.1 $\pm$ 0.0	0.5 $\pm$ 0.2	Z=-3.99 (<0.001)	1.9 $\pm$ 1.9	1.46 $\pm$ 0.29	Z=-4.03 (<0.001)
Presence of small seedlings	44.5%	72.4%	X <sup>2</sup> =123.17 (<0.001)	32.0%	44.5%	X <sup>2</sup> =10.45 (0.001)	55.6%	81.3%	X <sup>2</sup> =10.00 (0.002)
Presence of large seedlings	40.9%	74.9%	X <sup>2</sup> =182.87 (<0.001)	18.5%	34.5%	X <sup>2</sup> =20.96 (<0.001)	40.7%	77.7%	X <sup>2</sup> =18.03 (<0.001)
Presence of small saplings	17.4%	49.2%	X <sup>2</sup> =213.79 (<0.001)	3.8%	13.8%	X <sup>2</sup> =20.29 (<0.001)	14.8%	47.7%	X <sup>2</sup> =10.88 (0.001)
Presence of large saplings	10.0%	42.0%	X <sup>2</sup> =276.13 (<0.001)	0.9%	6.9%	X <sup>2</sup> =16.15 (<0.001)	3.7%	48.1%	X <sup>2</sup> =19.79 (<0.001)

**Table 3:** Bivariate associations of *Q. ilex*, *Q. suber*, and *Q. pyrenaica* regeneration with stand structure variables <sup>a</sup>

Variables <sup>b</sup>	<i>Q. ilex</i>				<i>Q. suber</i>				<i>Q. pyrenaica</i>			
	Small seedlings	Large seedlings	Small saplings	Large saplings	Small seedlings	Large seedlings	Small saplings	Large saplings	Small seedlings	Large seedlings	Small saplings	Large saplings
Tree cover	0.179***	0.274***	0.279***	0.241***	0.220***	0.154***	0.101*	n.s.	0.359***	0.366***	0.253***	0.385***
Q. sp. density	0.291***	0.309***	0.294***	0.328***	0.376***	0.341***	0.221***	0.160***	0.441***	0.463***	0.276***	0.523***
Q. sp. density 1	0.219***	0.269***	0.326***	0.432***	0.136**	0.245***	0.347***	0.302***	0.398***	0.425***	0.288***	0.580***
Q. sp. density 2	0.271***	0.265***	0.222***	0.236***	0.227***	0.210***	0.190***	0.139***	0.370***	0.371***	0.144**	0.304***
Q. sp. density 3	0.097***	0.084***	0.066**	n.s.	0.247***	0.245***	n.s.	n.s.	n.s.	n.s.	n.s.	-0.168**
Q. sp. density 4	-0.205***	-0.213***	-0.206***	-0.243***	0.127**	n.s.	n.s.	n.s.	-0.301***	-0.332***	-0.283***	-0.284***
dbh Q. sp.	-0.352***	-0.379***	-0.362***	-0.392***	-0.199***	-0.241***	-0.227***	-0.155***	-0.385***	-0.487***	-0.372***	-0.581***
Stand size heterogeneity	0.136***	0.139***	0.107***	0.078***	0.305***	0.305***	0.165***	0.094*	0.211***	0.196***	n.s.	0.135*

<sup>a</sup> n=2157 for *Qi*, n=631 for *Qs*, and n=337 for *Qp*

<sup>b</sup> for relationships between ordinal and continuous variables, Spearman's  $r_s$  is reported

\* Indicates a significance level of  $p < 0.05$ , \*\* of  $p < 0.01$ , \*\*\* of  $p < 0.001$ , n.s.=not significant

**Table 4:** Bivariate associations of *Q. ilex*, *Q. suber*, and *Q. pyrenaica* regeneration with understorey variables <sup>a</sup>

Variables <sup>b</sup>	<i>Q. ilex</i>			<i>Q. suber</i>			<i>Q. pyrenaica</i>					
	Small saplings	Large saplings	Small seedlings	Small saplings	Large saplings	Small seedlings	Small saplings	Large saplings	Small seedlings	Small saplings	Small saplings	Large saplings
Shrub cover	0.334***	0.362***	0.299***	0.283***	0.266***	0.284***	0.245***	0.142***	n.s.	n.s.	0.167**	n.s.
Shrub species richness	0.357***	0.369***	0.274***	0.268***	0.353***	0.335***	0.206***	0.099*	n.s.	n.s.	n.s.	n.s.
<i>Cistus</i> cover	0.210***	0.122***	0.094***	0.142***	0.197***	0.198***	0.120**	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Retama</i> cover	n.s.	0.139***	0.100***	0.061**	n.s.	0.082*	0.154***	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Lavandula</i> cover	0.263***	0.279***	0.225***	0.248***	0.231***	0.231***	0.158***	0.078*	n.s.	n.s.	n.s.	n.s.
<i>Erica</i> cover	0.108***	0.093***	0.113***	0.191***	0.144***	0.117**	n.s.	0.084*	n.s.	n.s.	n.s.	n.s.
<i>Phyllirea</i> cover	0.132***	0.130***	0.088***	0.209***	0.173***	0.134**	0.080*	n.s.	n.s.	-0.133*	n.s.	n.s.
<i>Arbutus</i> cover	0.050*	0.052*	0.049*	0.156***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Rubus</i> cover	0.041*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-0.117*	n.s.	n.s.	n.s.
<i>Genista</i> cover	0.044*	0.070**	0.073**	n.s.	n.s.	0.148***	0.173***	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Ulex</i> cover	0.132***	0.122***	0.065**	0.091***	0.203***	0.130**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

<sup>a</sup> n=2157 for *Qi*, n=631 for *Qs*, and n=337 for *Qp*

<sup>b</sup> Spearman's *r* is reported

\* Indicates a significance level of  $p < 0.05$ , \*\* of  $p < 0.01$ , \*\*\* of  $p < 0.001$ , n.s.=not significant

**Table 5:** Bivariate associations of *Q. ilex*, *Q. suber*, and *Q. pyrenaica* regeneration with topographic, climate, and soil variables <sup>a</sup>

Variables <sup>b</sup>	<i>Q. ilex</i>			<i>Q. suber</i>			<i>Q. pyrenaica</i>					
	Small saplings	Large saplings	Small seedlings	Small saplings	Large saplings	Small seedlings	Small saplings	Large saplings	Small seedlings	Small sapl.	Large sapl.	
Altitude	n.s.	0.073**	0.071**	0.085***	n.s.	0.116**	n.s.	n.s.	0.174**	0.224***	0.152**	0.201***
Slope	0.266***	0.263***	0.223***	0.257***	0.170***	0.193***	0.149***	n.s.	0.130*	0.135*	0.187**	n.s.
Northness	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Rock cover	0.101***	0.112***	0.114***	0.147***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Mean temperature	n.s.	-0.081***	-0.075***	-0.103***	n.s.	-0.102*	n.s.	n.s.	-0.178**	-0.202***	-0.165**	-0.202***
Mean precipitation	n.s.	-0.066**	-0.078***	-0.090***	n.s.	n.s.	n.s.	0.096*	0.178**	0.190***	0.112*	0.124*
Humus layer	n.s.	0.164***	0.130***	0.102***	0.078*	0.114**	0.139***	0.117**	n.s.	n.s.	n.s.	0.116*
Soil texture <sup>c</sup>	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Organic matter	n.s.	0.049*	0.054*	0.053*	n.s.	n.s.	n.s.	n.s.	-0.162**	-0.115*	n.s.	-0.147**

<sup>a</sup> n=2157 for *Qi*, n=631 for *Qs*, and n=337 for *Qp*

<sup>b</sup> for relationships between ordinal and continuous variables, Spearman's r is reported

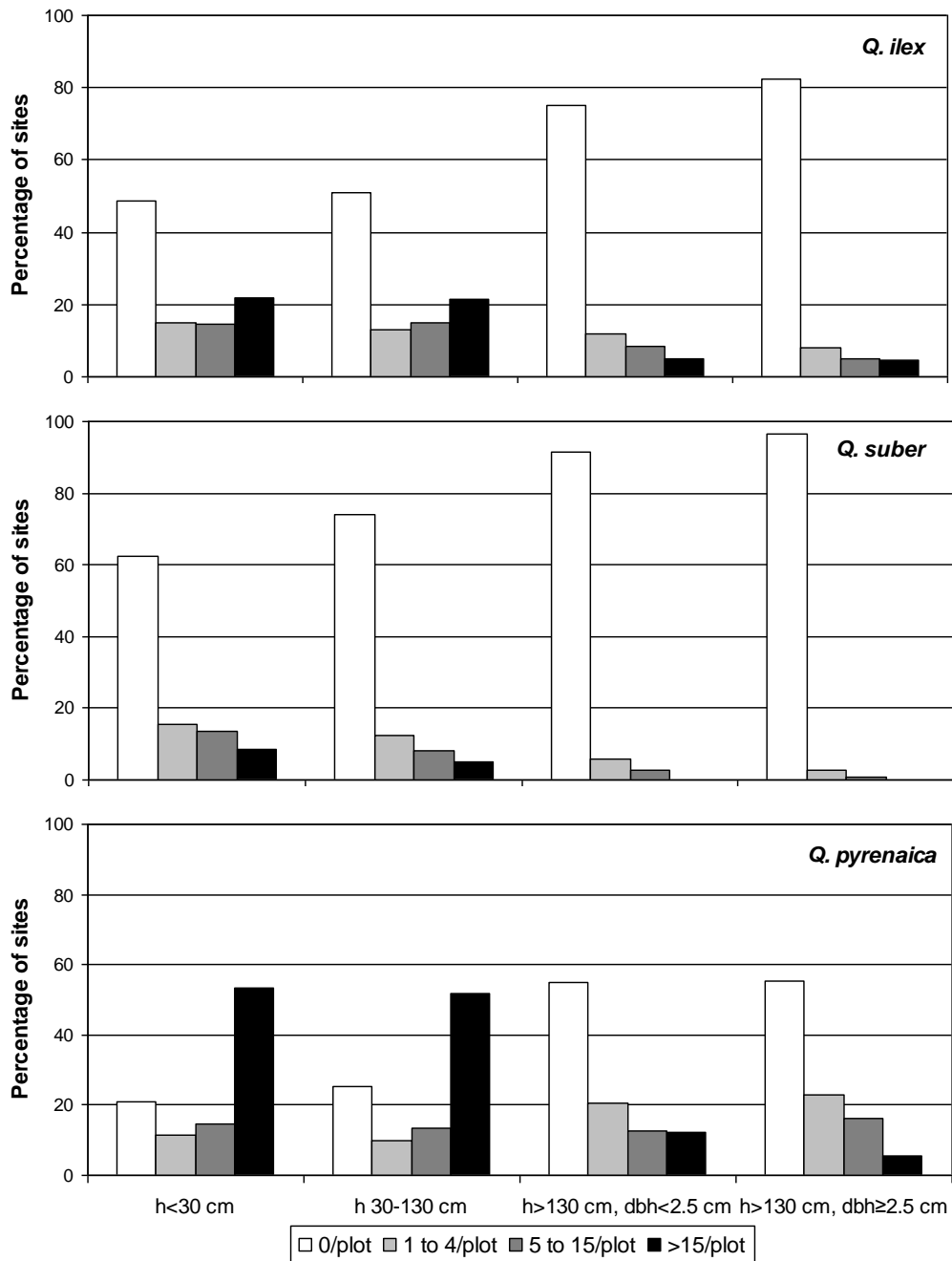
<sup>c</sup> Kruskal-Wallis test has been performed for this categorical variable

\* Indicates a significance level of p<0.05, \*\* of p<0.01, \*\*\* of p<0.001, n.s.=not significant

## Figures

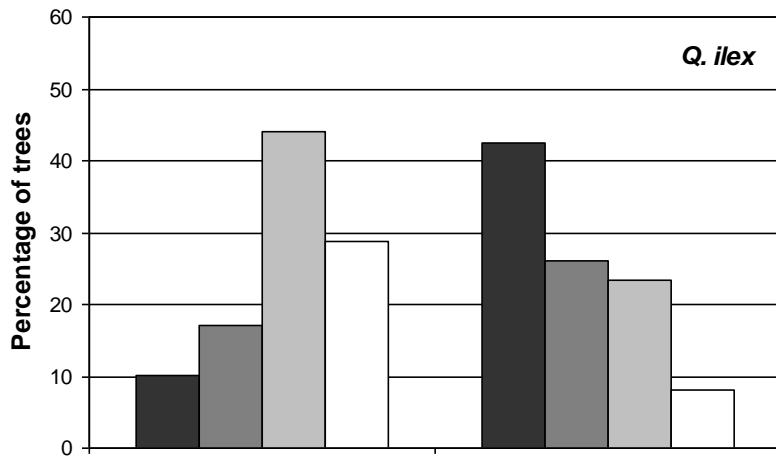
Figure 1: The percentage of sites containing 0 individuals, 1-4 individuals, 5-15 individuals, and >15 individuals in each of the four size classes. Percentages add up to 100% in each size class.

Figure 2: Diameter structure of adult oak populations at plots with presence and absence of seedlings.



**Figure 1:** The percentage of sites containing 0 individuals, 1-4 individuals, 5-15 individuals, and >15 individuals in each of the four regeneration classes. Percentages add up to 100% in each size class.





1  
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**Figure 2:** Diameter structure of adult *Qi*, *Qs* and *Qp* populations at plots with presence and absence of seedlings.

