

Capítulo 3

Factores ambientales y antrópicos como determinantes de la composición de los bosques del sur de la Península Ibérica: hacia un predominio del alcornoque debido al manejo forestal del siglo XX

Este capítulo reproduce el texto del siguiente manuscrito:

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Resumen

Tanto factores ambientales como factores humanos han configurado la estructura de los bosques mediterráneos durante milenios. Sin embargo, no se conoce con profundidad la influencia que las actividades humanas más recientes han ejercido en la composición actual de los bosques. En este estudio se han cuantificado los cambios ocurridos durante el último siglo en la composición de los bosques mixtos de *Quercus suber* L. (alcornoque) y *Q. canariensis* Willd. (quejigo moruno) de las sierras al norte del estrecho de Gibraltar. Se examinaron los efectos del manejo forestal y de los factores ambientales (clima, topografía) en la estructura de los bosques a diferentes escalas espaciales y temporales. En primer lugar, se analizaron los cambios en la composición de especies en nueve bosques mixtos (~ 40.000 ha) a partir de los datos de las series de inventarios forestales realizados a lo largo del último siglo, teniendo en cuenta los cambios en las condiciones ambientales y la gestión forestal de ese periodo. En segundo lugar, se analizó la estructura actual de las masas de *Q. suber*- *Q. canariensis* a lo largo de gradientes ambientales a dos escalas espaciales: (1) a escala de paisaje (~ 284 ha), combinando inventarios locales y variables topográficas derivadas de un modelo digital del terreno, y (2) a escala regional (~ 87.600 km²), combinando los datos del Segundo Inventario Forestal Nacional para Andalucía con estimaciones de variables climáticas. Los datos históricos mostraron cambios en la composición de los bosques debido a la influencia humana, con un rápido incremento en la densidad de alcornoques a lo largo del siglo pasado. La silvicultura ha favorecido al alcornoque (para la producción de corcho) a expensas del quejigo, lo que ha determinado en gran medida la estructura actual de los bosques mixtos. La abundancia de las dos especies es mayor a medida que aumenta la precipitación media anual, y coexisten a partir de los 800 mm (límite inferior para el quejigo). A pesar de que el alcornoque domina en la mayoría de los rodales, la red de drenaje condiciona la distribución diferencial de las dos especies en el paisaje, con los quejigares claramente asociados a los hábitats más húmedos cercanos a los cursos de agua. En lo relativo al papel de la gestión forestal, este estudio ilustra y cuantifica un ejemplo reciente de cambio en la composición de los bosques mediado por las actividades humanas. El nicho realizado del alcornoque ha sido ampliado a expensas del quejigo, lo que apoya las evidencias de que los seres humanos han inducido fuertes cambios en la composición de los bosques de *Quercus* en la cuenca mediterránea. No obstante, los recientes problemas de regeneración detectados en los rodales de alcornoque, la menor demanda de productos forestales, las nuevas políticas de conservación y el cambio climático auguran nuevos cambios en la composición de estos bosques.

Human and non-human determinants of forest composition in southern Iberian Peninsula: evidence of shifts toward cork oak dominance due to management over the past century

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Abstract

Both human and non-human determinants have shaped Mediterranean forest structure over millennia. The effects of recent human activities on forest composition, however, remains poorly understood. We quantified forest composition changes during the past century in the mixed forests of *Quercus suber* L. (cork oak) and *Q. canariensis* Willd. (Algerian oak) of the mountains north of the Strait of Gibraltar (S Spain), and explored the effects of forest management and environmental (climate, topography) factors on forest structure at different spatial and temporal scales. First, we quantified 20th century changes in species composition from a series of inventories in nine mixed forests (~ 40000 ha), and discussed them in terms of the management practices and environmental conditions. Second, we analysed present-day *Q. suber* and *Q. canariensis* stand structure along environmental gradients at two spatial scales: (1) that of the forest landscape (~ 284 ha), combining local inventories and topographic variables, using a digital elevation model, and (2) regional (~ 87600 km²), combining data from the Spanish Forest Inventory for the Andalusia region and estimates of climatic variables. Historical data indicate anthropogenic changes in stand composition, revealing a sharp increase in the density of cork oaks over the last century. Forest management has favoured this species (for cork production) at the expense of *Q. canariensis*. The impact of management is imprinted on the present-day forest structure. The abundance of both species increases with annual mean precipitation, and they coexist above 800 mm (the minimum threshold for *Q. canariensis*). *Q. suber* dominates in most of the stands, and species segregation in the landscape is associated with the drainage network, *Q. canariensis* being clearly associated with moister habitats near streams. Our study quantitatively exemplifies a recent human-mediated shift in forest composition. As a result of forest management, the realized niche of the cork oak has been enlarged at the expense of that of *Q. canariensis*, providing further evidence for humans as major drivers of oak forest composition across the Mediterranean. Recent regeneration problems detected in *Q. suber* stands, a lesser demand for wood products, conservation policies, and climate change augur new large-scale shifts in forest composition.

Keywords: Deciduous forest; environmental gradients; forest structure; human impact; land-use history; Mediterranean forest; *Quercus suber*; *Quercus canariensis*; sclerophyllous; Strait of Gibraltar.

Introduction

Contemporary vegetation patterns result from the combination of species' individual responses and interactions along environmental and disturbance gradients (Whittaker and Levin 1977). Furthermore, it is widely recognised that humans have played an important role in modifying and regulating the types and rates of ecosystem change at various spatio-temporal scales (Vitousek *et al.* 1997; Sanderson *et al.* 2002; Haberl *et al.* 2007). Thus, disentangling environmental versus human effects is critical for understanding current vegetation patterns and potential shifts under global change (e.g., Noble and Dirzo 1997; Levin 1999).

Humans have actively modified forest species distributions by deliberately introducing and harvesting selected species and genotypes, but also indirectly through forestry practices that have favoured certain species (e.g., Zobel *et al.* 1987; Crosby 1994; Richardson 1998; Le Maitre 1998; Gil *et al.* 2004). These effects have been particularly marked in regions such as the Mediterranean Basin, with a long history of human settlement, in which anthropogenic disturbances are considered key factors affecting forest structure and composition (Thirgood 1981; Quézel 1985; Blondel and Aronson 1995; Grove and Rackham 2001).

Palynological studies show that forest composition in the Mediterranean region has changed dramatically over the past millennia, including partial replacement of deciduous taxa by sclerophyllous species (Reille and Pons 1992; Blondel and Aronson 1999). For example, in the case of *Quercus* species, the evergreen *Q. ilex* L. and *Q. coccifera* L. appear to have replaced *Q. pubescens* Willd. in large areas of southern France during the last three millennia (Vernet 1973; Pons and Quézel 1985); *Q. ilex* and *Q. suber* L. may have replaced the deciduous *Q. canariensis* Willd. and *Q. pyrenaica* Willd. in northern Morocco (Reille 1977); and *Q. ilex* and *Q. suber* have generally become more abun-

dant at the expense of more mesic tree species in the Iberian Peninsula (Carrión *et al.* 2000). Post-glacial oak distribution changes were strongly correlated with large-scale shifts in the climatic conditions, and subsequently with interspecific competition and landscape topography (Brewer *et al.* 2002; Petit *et al.* 2002). Later changes during the last six millennia were more strongly controlled by human activities, such as the historical use of fire and livestock (Carrión *et al.* 2003). An increase in the impact of human activities would be expected to be seen with the approach of modern times (Hobbs *et al.* 2006), especially since forest management activities have intensified (e.g., Riera-Mora and Esteban-Amat 1994). The effects of more-recent (i.e., 20th century) human activities on forest composition remain, however, very poorly understood, and very few studies provide quantitative evidence of shifts in species composition due to forest management.

In this study, we focused on one of the largest oak forests within the Mediterranean Basin. It is located in the mountains north of the Strait of Gibraltar (Andalusia, southern Iberian Peninsula), and has experienced a long history of human impact. We tracked changes in forest composition over the last century, and analysed current forest structure along environmental (topographic and climatic) gradients. The forests are composed of the evergreen *Q. suber* (cork oak), which covers a wide range of coastal areas in the western Mediterranean, and the deciduous *Q. canariensis* (Algerian oak), which is mainly limited to the mountains on each side of the Strait of Gibraltar, and some patches in Catalonia (NE Iberian Peninsula) and the Algarve (S Portugal) (Costa *et al.* 2005). Palaeobotanical data of the study area -the Strait of Gibraltar- reveals human presence since the Palaeolithic, and a highly diversified landscape (including oak, pine, juniper and mixed woodlands), which suffered few changes during climatic fluctuations, and acted as a bio-

diversity refuge (Finlayson and Carrión 2007; Carrión *et al.* in press). More-recent palynological records show that deciduous oaks were dominant in northern Moroccan mountains from the end of the Boreal stage (about 7500 years B.P.) until a shift to the evergreens *Q. ilex* and *Q. suber*, associated with human colonisation and partial deforestation for agriculture (Reille 1977; Lamb *et al.* 1991). Modern forest management practices may have continued favouring species such as *Q. suber* (for agrosilvopastoral systems and cork harvesting) at the expense of other trees, particularly after the cork industry developed in the nineteenth century.

We followed a hierarchical approach to analyse patterns and factors operating at different scales (Willis and Whittaker 2002; Pearson and Dawson 2003) in order to disentangle the relative contribution of human and non-human determinants in shaping current forest structure. At a landscape scale, we analysed a sequence of forest inventories and historical records of temperature and precipitation to investigate the role that human management and recent changes in climatic conditions may have played in shaping mixed *Q. suber*-*Q. canariensis* forest composition over the past century. Furthermore, we targeted a mixed forest to examine present-day patterns of segregation and co-occurrence of the two species in relation to topography (aspect, drainage) and distance to roads (access-cost).

At a regional scale, we analysed the distribution of the two oak species along climatic gradients. Species-specific maximum-likelihood models relating species abundance to environmental variables (at both landscape and regional scales) were formulated to explore the main factors controlling stand structure. We addressed the following questions: (1) What are the main factors that have shaped current mixed *Q. suber* and *Q. canariensis* forest structure? (2) Has forest management over the past century driven major changes in stand composition -in particular, have silvicultural practices resulted in shif-

ting dominance of sclerophyllous cork oak versus deciduous *Q. canariensis* in mixed oak forests? (3) How does present-day stand structure vary along environmental and management gradients at landscape and regional scales? (4) Have historical factors left an imprint on current forest composition?

Material and methods

Study area

The study area is located in Andalusia (a region of 87600 km² in southern Iberian Peninsula), which is bordered by the Atlantic Ocean (on the south-west) and the Mediterranean Sea (on the south-east) (Fig. 3.1a). *Q. suber* is widely distributed in this region (Fig. 3.1b), where it is found in more than 15% (n=1983) of the Spanish Second Forest Inventory (SSFI) plots, showing a high proportion (42%) of monospecific stands. Its distribution area extends from west to east in the mountains north of the Guadalquivir fault, and in the southern mountains near the Strait of Gibraltar. It is not found in the most arid eastern areas and has been almost eliminated by agricultural transformation of the Guadalquivir river valley. In contrast, *Q. canariensis* has a smaller distribution area (Fig. 3.1c), and is found in just 2.3% (n=300) of SSFI plots in Andalusia, mainly in the elevations close to the Strait of Gibraltar. Within the distribution area of *Q. canariensis*, mixed stands of the two oaks are frequent; i.e., in 80% of *Q. canariensis* SSFI plots, it co-occurred with *Q. suber*.

The analysis of historical changes in forest composition and of species distribution at the landscape scale was focused on forests of the Aljibe Mountains (northern side of the Strait of Gibraltar), where the two oaks form a mixed woodland of about 1700 km², protected within Los Alcornocales (the Spanish term for: "cork oak woodland") Natural Park (see Figs. 3.1, 3.3). This area is part of the Betic-Riffian region, which has been identified as a hotspot of plant diversity within the Mediterranean Basin (Médail and Quézel 1997). The singularity and

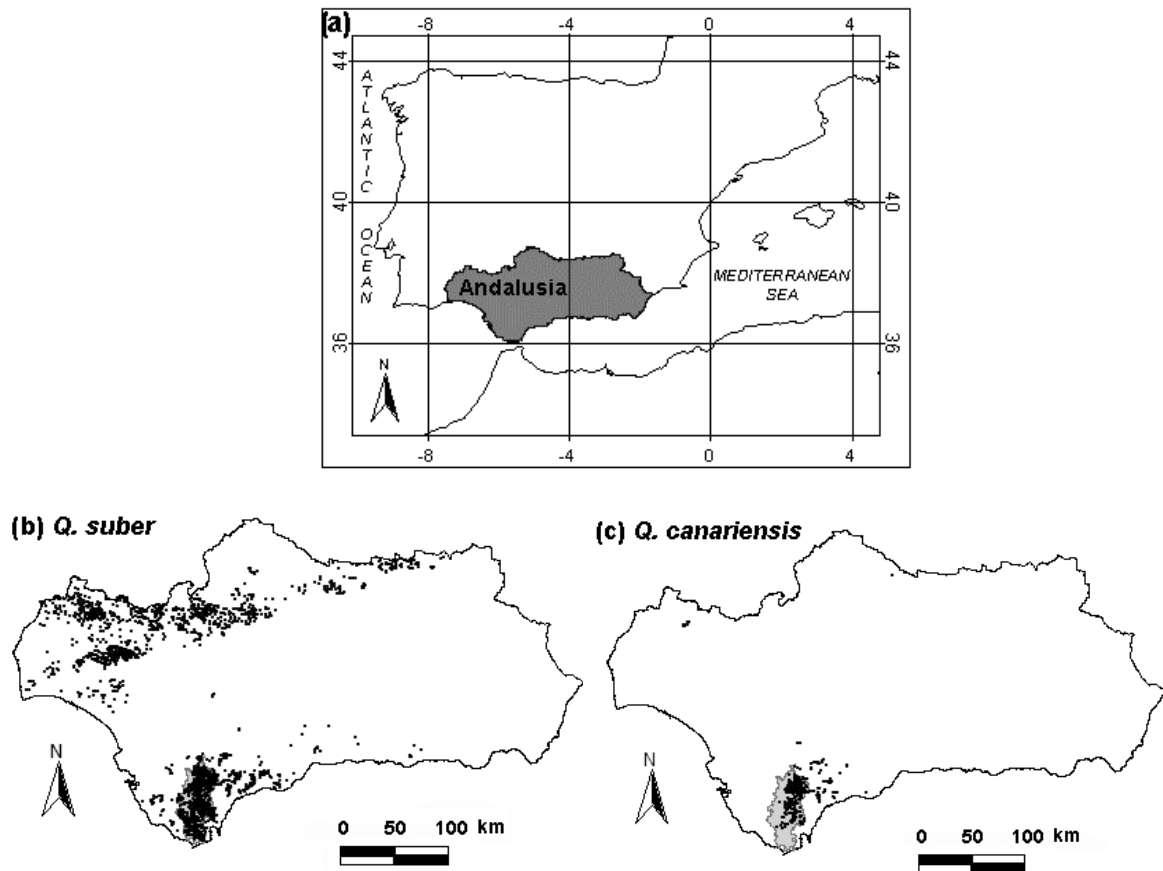


Figure 3.1 Study area in southern Iberian Peninsula (a). Distribution of *Q. suber* (n=1983) (b) and *Q. canariensis* (n=300) (c), based on presence data of the Spanish Second Forest Inventory (SSFI, total of 12572 plots in Andalusia). The grey area in the distribution map (c) corresponds to Los Alcornocales Natural Park's limits (~1700 km²).

high biodiversity value of this area, as a refuge for some taxa of Tertiary flora, has persisted in terms of both its ecological function and its genetic resources (see Mejías *et al.* 2007; Rodríguez-Sánchez *et al.* in press). The forests occur on acidic, nutrient-poor, sandy soils, derived from Oligo-Miocene sandstone, which harbour a rich endemic flora (Ojeda *et al.* 1996). The topography is mountainous, and maximum elevation is 1092 m a.s.l. The climate is sub-humid Mediterranean, with the heaviest rainfall in autumn, winter and spring, but with warm dry summers. Mean annual precipitation ranges from 800 mm near the coast to 1400 mm inland (exceeding 2000 mm in some years), and the mean annual temperature is 15-17 °C. A combination of ecological factors and favourable historical events may explain the exceptional sur-

vival of this wooded mountain landscape within the much deforested Mediterranean region (Marañón and Ojeda 1998).

Historical changes in oak forest composition

We compiled historical data from periodically inventoried public forest estates located in the area of Los Alcornocales Natural Park, in order to analyse changes in *Q. suber* and *Q. canariensis* stand composition during the last one hundred years. In particular, we analysed a sequence of historical management plans drawn up over the past century, which contained quantitative forest inventories and described management practices (see Appendix 3.1 for detailed information on the forest management plans consulted). We focused on nine

public forest estates covering a total area of approximately 40000 ha (see Fig. 3.3 for forest location). The first management plans dated from the end of the nineteenth century, when cork harvesting and manufacture started to intensify in the study area. Subsequently, every 10-15 years, forest inventories were updated and management plans revised. Inventories consisted of the individual counting of all trees with a diameter ≥ 10 cm in each of the blocks of about 20-30 ha delimited as management areas. Historical inventories did not include measurement of the diameter of individual trees, but rather an estimate of the number of individuals per diametric class (only for *Q. suber* and *Q. canariensis*). Thus, we annotated the total number of *Q. suber* and *Q. canariensis* individuals in each forest, and the rest of the tree species were grouped in a separate category as "other species".

Statistical analysis

We analysed changes in *Q. suber* and *Q. canariensis* density (individuals per total forest area in hectares) over the twentieth century in each of the nine forests targeted. The percentage of individuals per species was calculated at different periods, and changes in forest composition were examined, with emphasis on documented disturbances and forest management practices. We also explored and discussed the possible relationship between the general tendency of forest composition change and socio-economic indicators, such as the evolution of the cork trade from the second half of the nineteenth century onwards. Data were compiled by Parejo (2004), and homogenised to a unified currency and year (pesetas of year 2000), taking into account the fluctuations suffered in the price indexes in each historical period. We expressed the exported and imported values of raw cork (non-manufactured) in euros.

Finally, we explored and discussed the possible relationship between the general trend of forest composition change and the temporal trend in temperature and precipitation in the study area

from the beginning of the past century to date, and detected possible anomalies or fluctuations that could have affected the studied species. We analysed time series with moving averages (Štěpánek 2006), and calculated regression coefficients with time as independent variable. For this purpose, we selected historical records available from two meteorological stations: Grazalema (900 m a.s.l., series 1912-2000, provided by the Spanish Institute of Meteorology) and Gibraltar (5 m a.s.l., series 1840-2004, provided by GHCN, National Climatic Data Center, USA), located north-east and south of the study area respectively.

Present-day stand structure and environmental gradients

Landscape scale

At a landscape scale, we selected Los Arenales public forest estate, a 284 ha forest area where the two *Quercus* species co-occur, to analyse current forest structure along topographic gradients (see the forest marked with letter "e" in Fig. 3.3 for location). A detailed forest inventory (Egmasa 2003) was available, consisting of a grid of 129 circular (20 m radius) plots, one every 150 metres, defined by their spatial location (UTM coordinates). Sampling consisted of counting all trees and measuring (with a calliper) the trunk diameter at breast height (dbh; with breast height established as 1.3 m) of trees with a dbh >7.4 cm. We computed species basal area per plot, expressed in m²/ha, as a measurement of species abundance.

Additionally, each inventory plot was characterised with independent topographic data, using a Geographical Information System (GIS) (ArcView 3.2, ESRI Inc., Redlands, USA, 2000). We derived altitude (m), slope (%), and aspect (°) from a 20 m spatial resolution Digital Elevation Model (DEM), obtained from colour aerial photographs (scale 1:60000, provided by REDIAM -the Environmental Information Network of the Andalusian Government). The water flow accumulation map of the area

around the forest was created with HydroTools 1.0 for ArcView 3.2 (Schauble 2003), using a single-flow algorithm that computes the amount of water moving from water divides to valley floors. Pixels with the highest accumulation values were reclassified as part of the drainage network of the catchment area. We then calculated the distance of each inventory plot from the nearest stream bed. Finally, we constructed a map of access-cost, i.e. the cost or effort of reaching each plot from the main forest tracks/roads, which could be interpreted as an index of the socio-economic value of forest stands and human pressure (for example, as an approximate measurement of the cost of extracting cork in terms of accessibility). We digitised the tracks from maps and orthophotographs, and then used the cost-distance function of ArcView 3.2, including the distance from forest tracks to plots, and the slope map as a friction surface in the algorithm.

Regional scale

At a regional scale, data from the SSFI (Spanish Second Forest Inventory) were analysed in order to study current species distribution and forest composition in Andalusia along climatic gradients (see selected variables below). The SSFI inventory sampled wooded areas of the region in the period 1994-1996, based on a regular grid of survey plots with a density of approximately one circular plot per square kilometre (MMA 1996). Plots were circular, of various concentric radii (the minimum tree diameter measured varied with the radius of the plot), and were defined by their spatial location (UTM coordinates). The dbh of all trees with a dbh >7.4 cm was measured with a calliper. The inclusion of a tree in the sample was a function of its dbh and its distance from the centre of the plot.

Prior to the analyses, we checked the geographic position of all inventoried plots, superimposing them onto wooded areas of recent digital orthophotographs (JA 2003). Plots with georeferencing errors were rejected for the analyses.

Subsequently, we extracted a total of 12572 records containing the presence/absence of each species. In plots where *Q. suber* and/or *Q. canariensis* were present, we calculated their basal area, expressed in m²/ha. Additionally, each inventory plot was characterised with independent environmental data, using a GIS. Climatic data with 1 km spatial resolution were provided by the Spanish Institute of Meteorology as an interpolation (by kriging) of the information recorded from 1971 to 2000 in meteorological stations spread all over the Spanish territory (143 main stations, 1504 thermometric stations, and 4835 pluviometric stations) (INM unpublished).

We selected the following climatic variables: monthly and annual mean precipitation (P) (mm), annual mean radiation (RAD) (kW×h/m²), and monthly and annual mean temperature (T) in degrees centigrade (°C). We also derived the average temperature of the warmest month (TWM) (°C), average temperature of the coldest month (TCM) (°C), and thermal oscillation (TOSIC) (°C). Monthly and annual potential evapotranspiration (PET) (mm) were obtained as a function of mean temperature (Thornthwaite 1948). Computing monthly differences between P and PET, we calculated annual water surplus (WS) (mm) as the sum of positive differences between P and PET, annual water deficit (WD) (mm) as the sum of negative P-PET differences, and drought length (DL) as the number of months in which PET exceeded P. Finally, altitude (m) was derived from a DEM of 20 m spatial resolution.

Statistical analysis

We analysed whether present-day oak species abundance, i.e. basal area, was correlated with environmental gradients at landscape and regional scales. Because of the triangular and factor-ceiling distributions (sensu Thomson *et al.* 1996) found in the bivariate vegetation-environment relationships, we calibrated data-specific maximum-likelihood estimators, which are suitable for detecting biological signals within

heteroscedastic patterns (e.g., Floret *et al.* 1990; Zavala 2000). We selected those inventory plots where either one of the species or the sum of the two contributed to at least 95% of the total basal area of the stand. Based on exploratory analyses of potential distributions that best fitted our data, a gamma error distribution of species basal area was assumed, defined by a shape parameter n , which varies from exponential-like to bell-shaped but left-skewed forms. We specified the mean of the gamma distribution as a function of climatic or topographic variables, testing different functional forms that covered a wide range of possible responses: linear, exponential, power, and Michaelis-Menten-type.

All statistical models were parameterised with maximum likelihood (Edwards 1992), using a simulating annealing algorithm (Metropolis *et al.* 1953). Parameter 95% support limits were estimated by likelihood profile (Hilborn and Mangel 1997). In order to determine which variables were most strongly associated with species abundance, fitted models were compared with a null model of no factor effect through a Likelihood Ratio Test (LRT) (0.05 level), in which the degrees of freedom were equal to the difference in the number of parameters between models (Edwards 1992). Additionally, models were compared using Akaike's Information Criteria, specifically ΔAIC , which is defined for each Model_{*i*} as $AIC_i - AIC_{\text{minimum}}$ (Akaike 1992). Models with ΔAIC of 0-2 were considered to have equivalent and substantial empirical support, ΔAIC of 4-7 indicated less support, and models with $\Delta AIC > 10$ had very low empirical support (Burnham and Anderson 2002). All models and numerical algorithms were implemented in C (Borland C++ v.5.01, Borland International Inc., USA, 1996). Finally, we calculated Moran's I autocorrelation coefficient across distance classes for the raw species abundance data, and generated correlograms of model residuals using GS+ 5.1.1. (Gamma Design Software, Michigan, USA, 2001).

Results

Changes in mixed oak forest composition over the last century

A sharp increase in the number of cork oaks was observed in all studied forests (Fig. 3.2a-i), just after the first management plans started at the beginning of the twentieth century (with the exception of one forest, Fig. 3.2a). This trend slowed during the years following the Spanish civil war (1936-1939). Around the decade of the 1960s, there was another general increase in *Q. suber* density. In comparison, the density of *Q. canariensis* was higher than or very similar to that of *Q. suber* in some forests just before management plans started (Fig. 3.2a, b, d, and to a lesser extent, 3.2c). It remained constant, or even increased a little in some areas, during the first decades, but after 1940-50 generally decreased, due to selective logging of *Q. canariensis*, as documented. Species other than *Q. suber* and *Q. canariensis* (such as *Fraxinus angustifolia* Vahl., *Arbutus unedo* L., *Olea europaea* L. var. *sylvestris* Brot., *Pyrus bourgeana* Decne, and *Alnus glutinosa* (L.) Gaertn.) represented a small proportion of forest composition. The density of "other species" increased in some forests, primarily due to pine (*Pinus pinea* L., *P. halepensis* Mill., and *P. pinaster* Ait.) afforestation carried out from the middle of the century onwards (Fig. 3.2).

Overall, there was a shift to dominance by the sclerophyllous *Q. suber* in the study area in a few decades. Its relative density increased in all studied forests, as seen when forest composition at the beginning of the twentieth century was compared with that at the end of the century (Fig. 3.3). This trend was especially noticeable in the forest estates located in areas with higher annual mean precipitation (north of Los Alcornocales Park), where the proportion of deciduous species was greater than that of cork oak at the beginning of the century. Species other than *Quercus* showed an increased proportion in 1970-1980 as a result of pine afforestations.

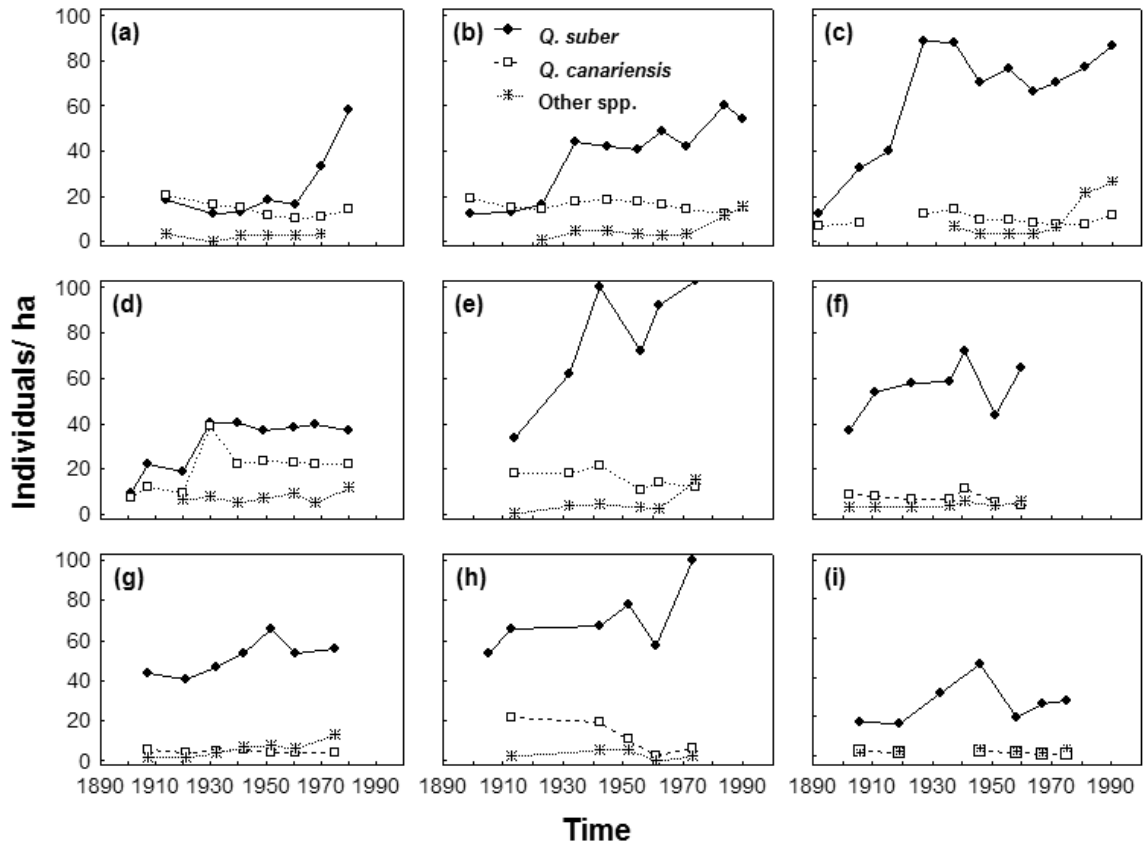


Figure 3.2 Changes in the number of individuals per hectare for *Q. suber*, *Q. canariensis*, and "other species", over the last century in each of the surveyed public forest estates (a-i). Other species inventoried included *Fraxinus angustifolia* Vahl., *Arbutus unedo* L., *Olea europaea* L. var. *sylvestris* Brot., *Pyrus bourgeana* Decne, *Alnus glutinosa* (L.) Gaertn, *Quercus ilex* L. (only in "a" and "d"), *Eucalyptus camaldulensis* Dehnh., and pines (*Pinus pinea* L., *P. halepensis* Mill., or *P. pinaster* Ait.) which were introduced from 1960 on. Note that species density (n° individuals) has been related to the total surface (ha) of each forest estate (including non-forested areas) for comparison among different inventories over time. See Fig. 3.3 for the geographic location of the forests (indicated with the same letters), and Appendix 3.1 for data sources.

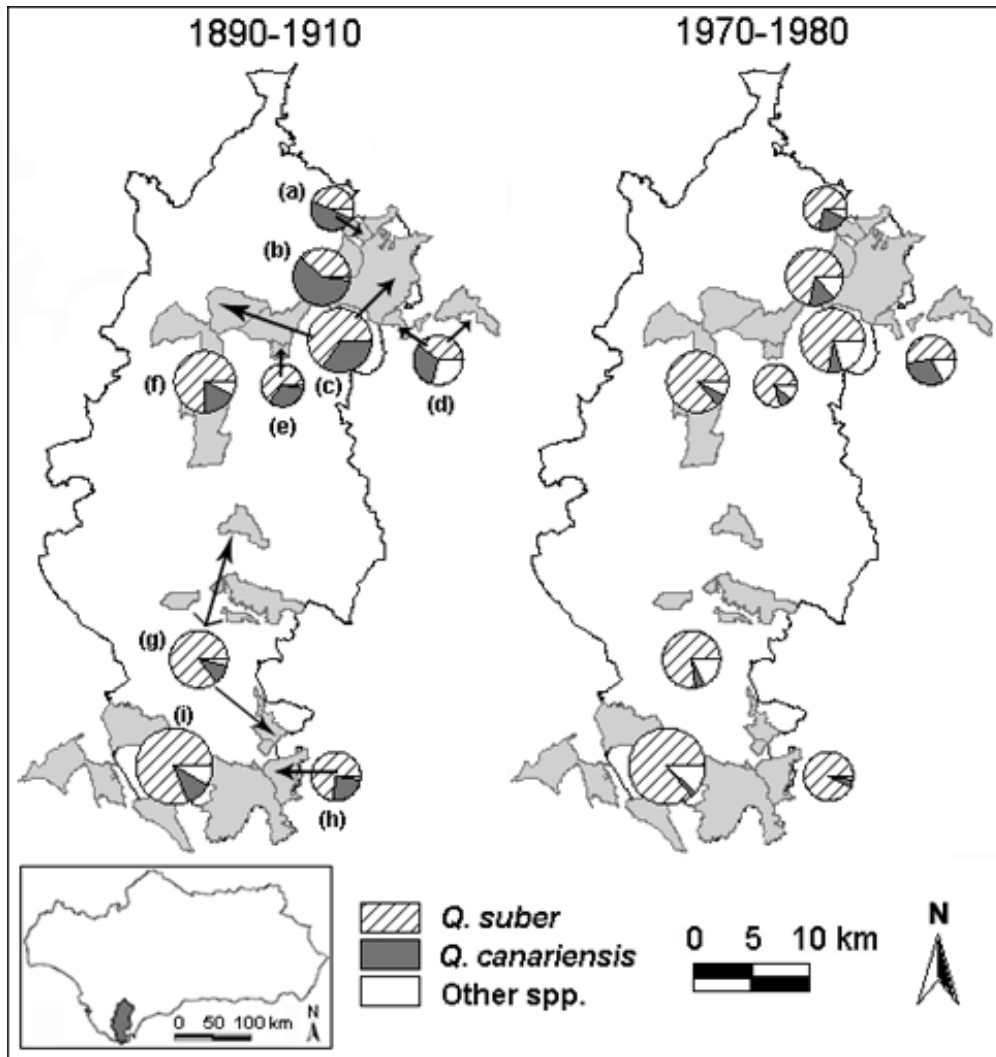


Figure 3.3 Changes in mixed *Q. suber*- *Q. canariensis* forest composition over the twentieth century in the area of Los Alcornocales Natural Park (limits in black line). Species percentage in each of the inventoried public forest estates (grey areas) at the beginning of the century (1890-1910) are compared to species relative abundance in the last shared historical inventories (1970-80). Charts are drawn on top of the corresponding forest and are proportional to the forest surface. Arrows indicate separated management areas of the same forest estate. An increase in cork oak proportion is observed at the expense of *Q. canariensis*, especially in northern areas with higher precipitation regimes.

Averaged over the nine forest estates, the number of cork oaks per hectare increased sharply through the twentieth century, especially during the first decades and the last quarter of the twentieth century, whereas *Q. canariensis* showed oscillations in its mean abundance (Fig. 3.4a). Over the same period, the Spanish export trade of cork generally increased (Fig. 3.4b), although it fluctuated. Decreases in the trade were linked to the periods of the two world wars and more significantly to the Spanish civil war, after which the commercial leadership significantly decreased, until the recent recovery. The abundance of imported cork was very low, even

zero, up until to the last few decades when it has since become a major crop plant (Fig. 3.4b).

Historical records of meteorological stations showed a gradient of decreasing rainfall from north (inland mountains) to south (coast) of the study area, with fluctuations between years. Mean yearly rainfall in the north (Grazalema, series 1912-2000) was 2097 mm \pm 774 mm standard deviation (SD) (range from 584 mm to 4000 mm in some years) (Fig. 3.4c). Whereas mean rainfall recorded in Gibraltar (series 1840-2004) was 822 mm \pm 270 mm SD in the south,

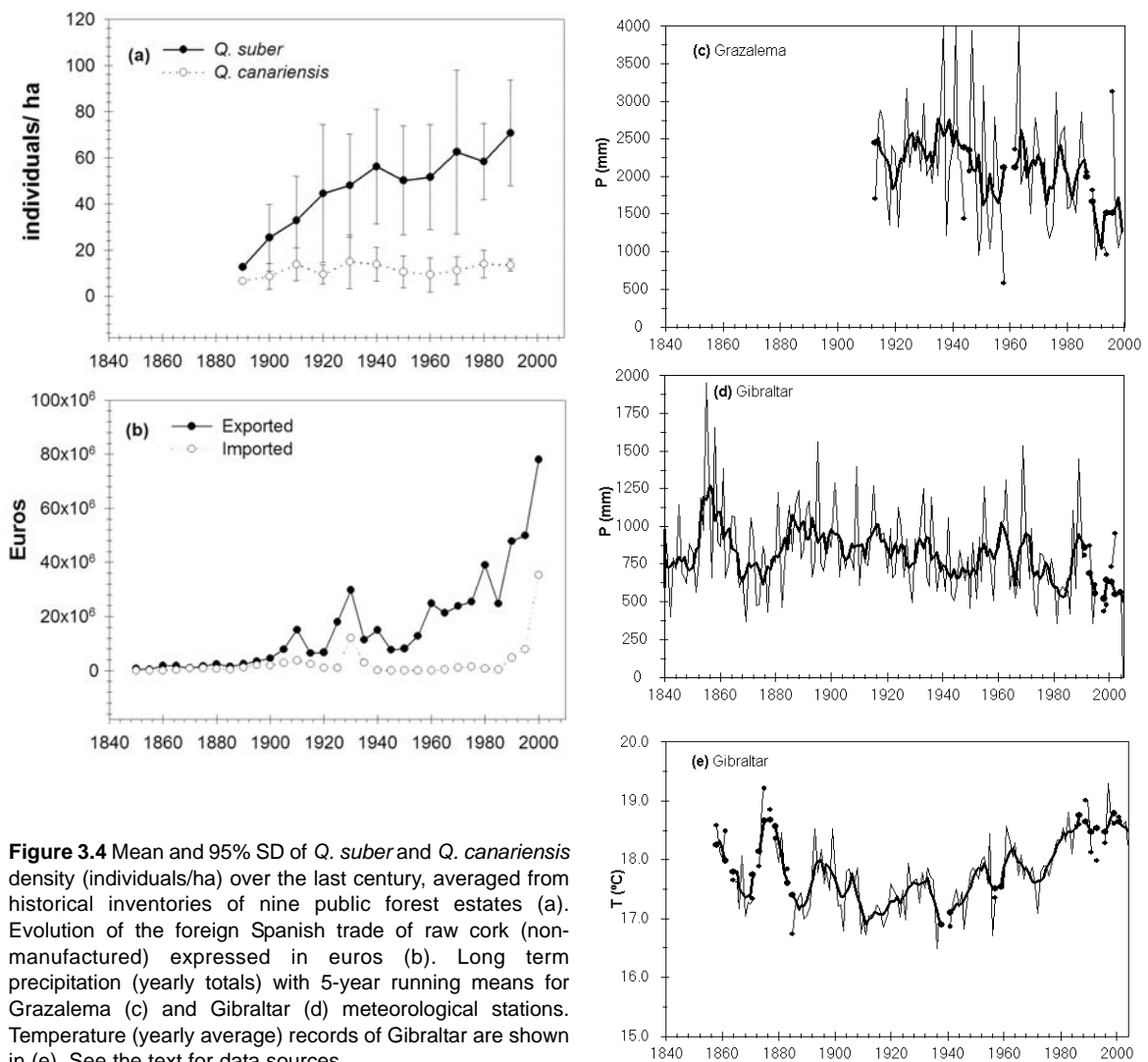


Figure 3.4 Mean and 95% SD of *Q. suber* and *Q. canariensis* density (individuals/ha) over the last century, averaged from historical inventories of nine public forest estates (a). Evolution of the foreign Spanish trade of raw cork (non-manufactured) expressed in euros (b). Long term precipitation (yearly totals) with 5-year running means for Grazalema (c) and Gibraltar (d) meteorological stations. Temperature (yearly average) records of Gibraltar are shown in (e). See the text for data sources.

reaching maximum values of 1955 mm and minimum of 356 mm (Fig. 3.4d). The regression model between mean rainfall and time had a significant negative slope, revealing a trend of a decrease in annual mean precipitation (with a trend/10years of -97.07 mm in the north and -12.62 mm in the south). Nonetheless, both climatic records showed runs of years well above or below the long-term mean, with alternate dry and wet periods. Temperature records showed fluctuations but without abrupt changes; nevertheless, as a general trend, mean temperature has progressively increased (trend/10 years of 0.05 °C) in the study area since the beginning of the twentieth century (Fig. 3.4e).

Landscape scale: patterns along topographic gradients

The local forest inventory revealed that Los Arenales forest estate is today mainly composed of *Q. suber* (found in 80% of the plots) and *Q. canariensis* (found in 52% of the plots). *Q. suber* occupies a high percentage of the stand basal area, and is found mixed with *Q. canariensis* in 59 out of 129 inventory plots. This pattern is in accord with the trend observed in the

historical time series analysed for this forest, where *Q. suber* had dramatically increased (see "e" in Figs. 3.2 and 3.3). Other tree species, such as *A. unedo*, *O. europaea* var. *sylv.*, *P. bourgeana*, and *A. glutinosa* are present but less abundant. Eucalyptus and pines have been planted at sites where oak forests were absent.

Parameter estimates that gave best fits relating species basal area with topographic factors are summarised in Table 3.1. As indicated by best-supported models ($\Delta AIC=0$; LRT, $p<0.001$), the distance from a watercourse best explained the two species' abundance in the landscape (Fig. 3.5a), although with contrasting direction (positive slope (p_2) for *Q. suber*, and negative for *Q. canariensis*, Table 3.1). That is, while mean basal area of *Q. suber* increased exponentially with distance from a watercourse, the opposite relationship was found for *Q. canariensis*, which was more abundant near stream beds (Fig. 3.5b). The model including drainage reduced spatial autocorrelation at short distances (150 m) for *Q. canariensis*, but did not account for the spatial pattern in *Q. suber* abundance (Appendix 3.2a, b). The altitude gave fits of

Table 3.1 Maximum likelihood parameter estimates for best-fit models relating *Q. suber* (n=94) and *Q. canariensis* (n=53) basal area (m²/ha) to topographic factors.

	<i>Q. suber</i>										
	Factor	Best fit	n	p ₁	p ₂	LogLike.	LRT (X ²)	p	AIC	ΔAIC	
	Distance from drainage	EXP	1.4	7.1	0.0049	-305.1	14.6	***	616.2	0.0	
	Access-cost	EXP	1.5	6.9	0.0001	-305.2	14.4	***	616.4	0.2	
	Altitude	LIN	1.5	-2.4	0.0528	-305.3	14.3	***	616.5	0.3	
	<i>Q. can</i>										
	Factor	Best fit	n	p ₁	p ₂	LogLike.	LRT (X ²)	p	AIC	ΔAIC	
	Distance from drainage	EXP	1.0	10.6	-0.0106	-148.8	12.1	***	303.6	0.0	
	Access-cost	EXP	0.9	8.9	-0.0001	-152.5	4.7	*	311.0	7.4	

Note: Best fits were found for the Exponential (EXP) response, where species' mean basal area = $p_1 e^{(p_2 \text{Factor}_i)}$; p_1 and p_2 are maximum likelihood parameter estimates, n is the shape parameter estimated for the gamma distribution of basal areas, where n ~1.5 indicates bell-shaped but left-skewed probability distribution, and n <1 exponential-like monotonically decreasing distribution.

LogLike. corresponds to the maximum log-likelihood: $\log(Lq|data, model)$. AIC (Akaike's Information Criteria) is calculated as: $AIC = -2\log(Lq|data, model) + 2K$, being K the number of parameters in the model. Factors' effects are evaluated through the loglikelihood ratio test (LRT, df=1, * $p<0.05$, ** $p<0.01$, *** $p<0.001$), and model fits through $\Delta AIC (AIC_i - AIC_{min})$.

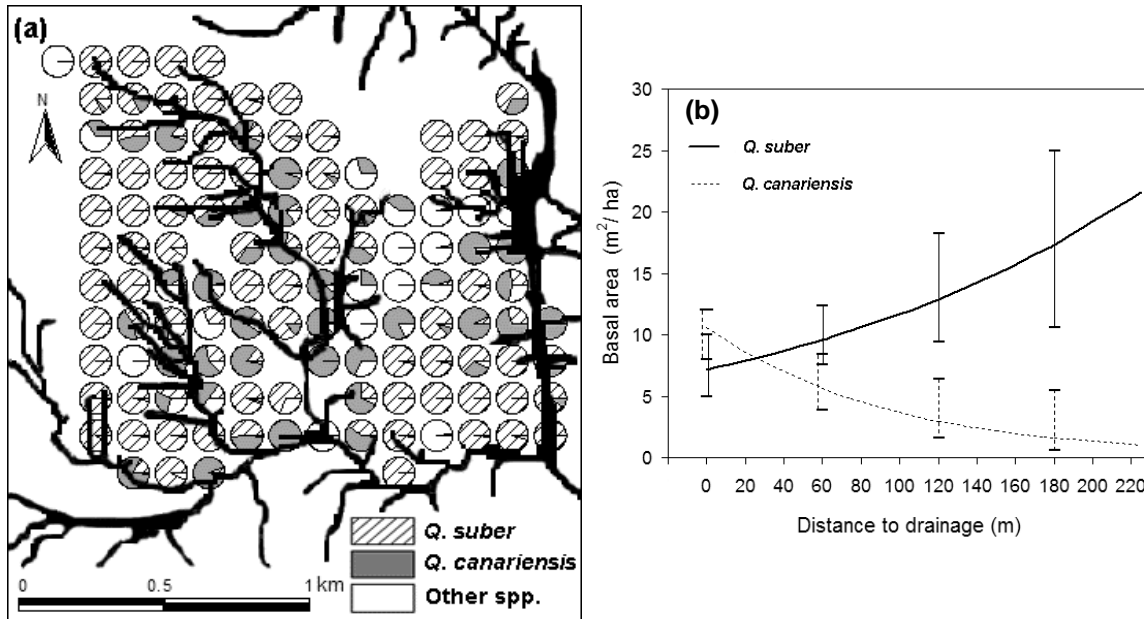


Figure 3.5 *Q. suber* and *Q. canariensis* distribution at landscape scale, in Los Arenales forest estate, along the drainage network (black line). See "e" in Fig. 3.3 for forest location. Sectors within charts are proportional to the percentage of species basal area in each inventory plot. "Other species" include mainly pines (*Pinus pinea*, *P. halepensis*, and *P. pinaster*), and to a lesser extent *Arbutus unedo*, *Olea europaea* var. *sylvestris*, *Pyrus bourgeana* and *Alnus glutinosa* (a). Differential response of *Quercus* species mean basal area (with 95% confidence intervals) along the gradient of distance to the drainage network, based on best model fits of local inventory data (b).

similar empirical support ($\Delta AIC < 2$) for *Q. suber*, with a positive relationship (i.e., its abundance increased with the altitude), but had negligible influence on *Q. canariensis* (Table 3.1). The variable quantifying the cost of reaching each inventory plot from the main forest tracks also had substantial support (within two AIC units of the best supported model) for *Q. suber*, but low support for *Q. canariensis*. Mean basal area of *Q. suber* increased along the access-cost gradient -i.e., its abundance was greatest in areas with low accessibility. Finally, models including altitude and cost reduced the level of spatial autocorrelation at the first distance class for *Q. suber* (Appendix 3.2a).

Regional scale: patterns along climatic gradients

Parameter estimates of models with the strongest empirical support relating present-day species mean basal area (m²/ha) with climatic factors at a regional scale are summarised in Table

3.2. The average temperature for the warmest month (TWM) was the best predictor ($\Delta AIC = 0$) of *Q. suber* abundance. As temperature increased, mean abundance decreased, following an approximately linear response. Other factors associated with water (i.e., annual precipitation, water surplus, water deficit) and energy (i.e., temperature oscillation) gave a significant fit (LRT, $p < 0.001$), but represented models with low empirical support based on ΔAIC s. Mean *Q. suber* abundance increased approximately linearly with annual mean precipitation (P) and water surplus (WS), while there was a negative effect of annual water deficit (WD) and temperature oscillation (TOSCI) (with negligible empirical support). For *Q. canariensis*, annual mean precipitation best explained its abundance (LRT, $p < 0.05$), following a positive and approximately linear relationship (Table 3.2). With similar empirical support ($\Delta AIC < 2$), basal area of the deciduous species increased with water surplus and mean radiation, whereas it decreased with water deficit.

Table 3.2 Maximum likelihood parameter estimates for best-fit models relating *Q. suber* (n=1983) and *Q. canariensis* (n=300) basal area (m²/ha) to climatic factors at the regional scale.

	Factor	n	p ₁	p ₂	LogLike.	LRT (X ²)	p	AIC	ΔAIC
Q. suber	T Warmest Month (TWM)	1.6	80.6	-2.8680	-2280.1	116.3	***	4566.1	0.0
	Annual P	1.6	-4.5	0.0155	-2286.6	103.2	***	4579.2	13.1
	Annual Water Surplus (WS)	1.6	0.5	0.0168	-2287.0	102.5	***	4580.0	13.9
	Annual Water Deficit (WD)	1.5	33.6	-0.0519	-2296.7	83.0	***	4599.4	33.3
	T Oscillation (TOSCI)	1.5	28.0	-1.2230	-2304.2	68.1	***	4614.4	48.3
	Factor	n	p ₁	p ₂	LogLike.	LRT (X ²)	p	AIC	ΔAIC
Q. can	Annual P	1.3	-12.5	0.0182	-355.0	8.1	**	716.1	0.0
	Annual Water Surplus (WS)	1.2	-5.8	0.0182	-355.6	7.0	**	717.2	1.1
	Annual Radiation (RAD)	1.2	-95.8	23.8900	-355.9	6.3	*	717.9	1.8
	Annual Water Deficit (WD)	1.2	31.6	-0.0570	-356.1	6.0	*	718.2	2.1

Note: Best fits were found for the linear response, where species' mean basal area = $p_1 + p_2 \text{Factor}_i$; p_1 and p_2 are maximum likelihood parameter estimates, n is the shape parameter estimated for the gamma distribution of basal areas, where $n \sim 1.5$ indicates bell-shaped but left-skewed probability distribution. Models are evaluated as in Table 3.1, through loglikelihood ratio tests (LRT, df=1, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$), and ΔAIC ($\text{AIC}_i - \text{AIC}_{\min}$).

To study interspecific differences, the abundance of each species was analysed along the annual mean precipitation gradient -i.e., the best predictor for *Q. canariensis* and the second best for *Q. suber*. Models had similar positive slopes, but species differed in the intercept parameter (p_1) (Table 3.2). *Q. suber* was present from 500 mm precipitation onwards, whereas the lower limit for *Q. canariensis* was 800 mm (Fig. 3.6a). The two species co-occurred at the wetter end of the gradient (800 mm onwards), where stand structure showed a greater variance. Examination of residuals indicated that models accounted for most of the spatial pattern in species abundance, except for *Q. suber* at short distances (Appendix 3.2c, d).

Discussion

Studying mixed oak forests by means of multi-scale focus (both temporal and spatial) enabled us to identify key environmental factors influen-

cing forest composition, as well as historical processes underlying present-day patterns. Results quantitatively highlight surprisingly rapid changes in forest composition over the past century in a Mediterranean landscape, reinforcing the evidence of human activities as the main drivers of recent forest dynamics.

Drivers of change in mixed oak forest composition in the last century

The analyses of historical forest inventory data revealed an increasing dominance of *Q. suber* during the twentieth century in all studied mixed forests, whereas *Q. canariensis* remained constant or even decreased in some periods. *Q. suber* expanded, and the number of individuals increased sharply, in a few decades in the most-productive areas (with higher annual precipitation, see Fig. 3.3), where *Q. canariensis* would find most-favourable conditions.

The first forest management plans, from the end of the nineteenth century, considered *Q. canariensis* a principal forest species together with *Q. suber*, particularly in those sites where the two species co-dominated (González *et al.* 1996). *Q. canariensis* wood was pollarded for charcoal production, and was used in railway construction (Jurado 2002). However, due to the increasing demand for cork as bottle stoppers, forest management restored plant cover by favouring the economically most valuable species, *Q. suber*, through seedling plantations and acorn sowing, and taking advantage of its extraordinary resprouting capacity from stem and basal buds. The traditional use of cork oak bark in leather tanning was progressively abandoned, and forests were divided into regular stands with trees of the same age in order to facilitate bark stripping approximately every decade. Conversely, *Q. canariensis* trees suffered selective clear-cuttings, as documented in some of the inventories, especially when alternative sources of energy (e.g., butane gas) replaced charcoal in the 1950-60s. Nevertheless, *Q. canariensis* stands were not completely substituted by cork oaks, given the complementary resources they provided, such as earlier seed production, which lengthened the period of acorn availability and improved animal feeding in mixed stands, and its nutrient-rich litter, which was believed to increase soil fertility and moisture.

On one hand, forest composition changes reported could be partly attributable to recent fluctuations in climate. A general decline in rainfall and a warming of up to 1 °C, most marked in winter, have been observed over the twentieth century in the study area (Wheeler and Martín-Vide 1992), but the magnitude of wet/dry year fluctuations seems similar in the past and present (Rodrigo *et al.* 2000). Inter-annual variations in climatic conditions most probably have had a differential influence on short-term processes such as fecundity, seedling survival, or tree growth (e.g., Costa *et al.* 2002), but were not intense enough (for example as episodic

droughts) to result in a significant adult tree mortality. Therefore, it is questionable whether the observed sharp changes in forest composition can be attributed to fluctuations in precipitation and temperature, given the long-term response of forests to those factors.

On the other hand, the impact of human activities may have modified the distribution of species outside the potential limit established by the environment (Thomson *et al.* 1996). This could be more likely for tree species such as oaks, which historically have been managed by human populations (Foster *et al.* 2002; Johnson *et al.* 2002). *Q. suber* has been artificially favoured and conserved in many parts of its natural range (Montoya 1988; Vieira Natividade 1991). Consequently, we support the inference that forest composition changes reported in the present study, which are reflected in present-day forest structure, are probably human-induced, due to their rate and magnitude.

Likewise, in holm oak (*Q. ilex*) stands (dehesas) of central and north-east Spain, land-use history and management have been found to be the most important factors determining current forest composition and structure (Gracia and Retana 1996; Joffre *et al.* 1999; Pulido *et al.* 2001; Plieninger *et al.* 2003). Other examples of the positive impact of human activities on certain tree species are, for example, olive tree (*Olea europaea* L.) domestication in the Mediterranean Basin (e.g., Terral *et al.* 2004), anthropogenic savannas with *Acacia caven* Mol. (espinales) in central Chile (e.g., Ovalle *et al.* 1996), increased dominance of *Acer rubrum* L. (red maple), *Betula* spp. (birch), and oak species following disturbances caused by post-settlement human activities in eastern North America (e.g., Abrams 1998; Bürgi *et al.* 2000), and *Pinus* and *Eucalyptus* genera widely planted outside their natural ranges in many zones for commercial forestry (e.g., Zobel *et al.* 1987; Richardson *et al.* 1994).

Influence of environmental factors on present-day mixed oak forest structure

Today, and partly as a consequence of reported historical changes in forest composition, the evergreen *Q. suber* is more abundant in a wider range of environmental conditions than is the deciduous *Q. canariensis*, which is restricted to areas with a high precipitation regime, lower water deficit, mild temperatures, and frequent mist in the mountains near the Strait of Gibraltar. Mean abundance of *Q. suber* and *Q. canariensis* increases with annual precipitation, and the two co-occur above 800 mm. However, accurate prediction of species basal area for a given point of the precipitation gradient is difficult, due to the effect of site factors, such as topographic variation and stand management history, which have influenced forest structure locally.

By reducing the scale of analysis to that of the landscape (Los Arenales forest, 1100 mm mean rainfall), where regional models would predict the co-occurrence of *Q. suber* and *Q. canariensis*, we observed that oak species were not randomly distributed in the landscape, but instead segregated along a gradient of water availability (i.e., distance from stream beds). The deciduous species, *Q. canariensis*, was found clearly associated with areas near streams, where microclimatic conditions (warm and moist) are in marked contrast with drier adjacent habitats, where *Q. suber* is more abundant, suggesting that *Q. canariensis* performs better than *Q. suber* under moister conditions. In Mediterranean ecosystems, factors associated with water availability are commonly found to have great influence on forest composition (Pigott and Pigott 1993; Zavala *et al.* 2000). Oak species' differential distribution patterns found along the water availability gradient might be partly determined by species' contrasting physiological and morphological features (Marañón *et al.* 2004; Quero *et al.* 2006). Under controlled greenhouse conditions, water treatments modified physiological traits of deciduous species (*Q. canariensis* and *Q. pyrenaica*),

increasing their stomatal conductance, photosynthesis, and respiration rate, but had little effect on *Q. suber* seedlings (Quero *et al.* 2006). Furthermore, in a field experiment, water addition during the dry period (simulating sporadic rains) reduced mortality of *Q. canariensis* seedlings, whereas *Q. suber* was not affected (see chapter 5).

On the basis of our results, we suggest that in the absence of human intervention, cork oak and *Q. canariensis* would have been more clearly segregated, with deciduous oaks dominating in the more humid areas (see Fig. 3.6b). Cork oak is currently a valuable species from the point of view of forest ecosystem conservation, and still has strong socio-economic implications for the cork industry. As revealed by the accessibility-cost analysis, *Q. suber* dominates in less accessible stands, despite the greater cost of reaching them, indicating that cork extraction and transport by mules has been a common practice in the whole forest area. Although the cork industry has suffered fluctuations over the century, with severe competition in recent years from synthetics (see Parsons 1962; Parejo 2004), the cork currently harvested in the area of Los Alcornocales Park represents approximately 30% of the Spanish and 8% of the world production (Anonymous 2004).

Future trends in forest composition and dynamics remain somewhat uncertain. A general decline and impaired regeneration has been detected in cork oak stands on both sides of the Strait of Gibraltar (Ajbilou *et al.* 2006), coupled with a reduction in cork production (Linares and Fariña 2002). Current management plans are implemented to reduce oak seedling mortality by large-scale fencing and exclusion of herbivores, as well as reforestations of *Q. suber* and other species. The Algerian oak (*Q. canariensis*), despite the historical reduction of its distribution area to favour cork oak, is expected to show an upward trend locally. *Q. canariensis* stands are currently protected as forest habitat (considered trees "of special interest" by regional laws), due to their rich understorey with high

taxonomic singularity (Ojeda *et al.* 1996). It would thus be reasonable to predict a trend of continuous replacement of old, injured (by periodic bark removal) cork oaks by young, vigorous deciduous oaks in those wetter and more-fertile areas where management has modified forest composition. At a longer time scale, both oak species will be severely affected

by the climate change prediction of warmer and drier conditions for this Mediterranean region (Schröter *et al.* 2005).

In conclusion, our study quantitatively exemplifies a human-mediated shift in forest composition. As a result of forest management, the realized niche of the cork oak has been enlarged at the expense of that of *Q. canariensis*, providing further evidence of humans as main drivers of oak forest composition and structure across the Mediterranean region. The present study supports palynological data which suggest that, in the absence of human influence, *Q. suber* would develop in mixed forests, sharing the arboreal stratum with other sclerophyllous species and with deciduous ones (Reille 1977; Carrión *et al.* 2000). Recent regeneration problems detected in *Q. suber* stands, a lesser demand for wood products, conservation policies, and climate change augur new large-scale shifts in forest composition.

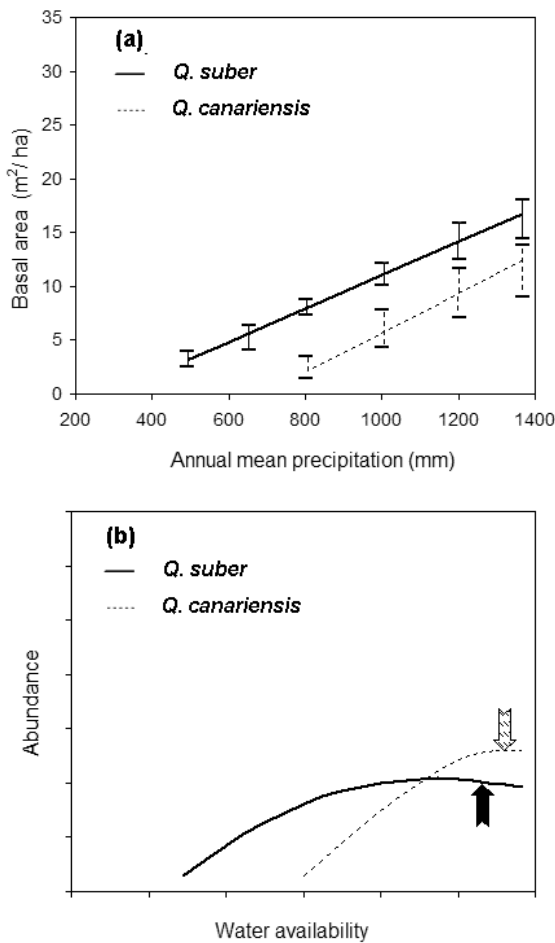


Figure 3.6 Species mean basal area (with 95% confidence intervals) along the gradient of annual mean precipitation (P), based on best model fits of SSFI data. Both species abundance (basal area) increases along the P gradient, and they co-occur 800 mm onwards (the lowest limit of *Q. canariensis*) (a). Representation of potential (without human intervention) distribution niches of evergreen and deciduous *Quercus* species, along a gradient of water availability (b). Arrows indicate the direction of human influence on each species. We suggest that in rainy areas humans have favoured *Q. suber* and reduced *Q. canariensis*' area. Panel (b) has been drawn to be compared to the current patterns observed in (a).

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Appendix 3.1

References of the management plans and forest inventories consulted for the analysis of historical changes in mixed oak forest composition (area of Los Alcornocales Natural Park, S Spain). Letters next to the name of the public forest estates correspond to their geographic position in the maps of Figure 3.3.

Forest	Surface (ha)	Author	Year	Forest Management Plan
La Cancha (a)	468	García, J.	1914	Proyecto de ordenación del monte "La Cancha". Propio de Villaluenga del Rosario.
		García, A.	1931	Proyecto de revisión ordinaria y segundo plan especial de aprovechamientos y mejoras correspondiente al monte "La Cancha".
		García, A.	1941	Proyecto de segunda revisión ordinaria y tercer plan especial de aprovechamientos y mejoras correspondiente al monte "La Cancha", nº 31 del catálogo y de la pertenencia de los Propios de Villaluenga del Rosario.
		García, L.	1951	Proyecto de tercera revisión ordinaria y cuarto plan especial de aprovechamientos y mejoras del monte "La Cancha", nº 31 del catálogo.
		García, L.	1961	Proyecto de cuarta revisión ordinaria y quinto plan especial de aprovechamientos y mejoras del monte "La Cancha", nº 31 del catálogo.
		Sánchez, P.	1970	Proyecto de quinta revisión ordinaria y sexto plan especial de aprovechamientos y mejoras del monte "La Cancha", nº 31 del catálogo.
		Lozano, A.	1980	Proyecto de sexta revisión ordinaria y séptimo plan de aprovechamientos y mejoras del monte "La Cancha" de Villaluenga del Rosario, nº 31 del catálogo. Término municipal de Cortes de la Frontera.
Las Majadas de Ronda (b)	4102	from González, A., Torres, E., Montero, G. & Vázquez, J. (1996) Resultados de cien años de aplicación de la selvicultura y la ordenación de montes alcornocales de Cortes de la Frontera (Málaga), 1890-1990. Revista Montes 43: 12-22.		
Grupo Cortes de la Frontera (c)	6895	from González, A., Torres, E., Montero, G. & Vázquez, J. (1996) Resultados de cien años de aplicación de la selvicultura y la ordenación de montes alcornocales de Cortes de la Frontera (Málaga), 1890-1990. Revista Montes 43: 12-22.		

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Grupo Gaucín y Algotocín (d)	1661	García, J.	1901	Plan de ordenación y plan de aprovechamientos y mejoras de los montes de Gaucín y Algotocín.
		Illegible	1907	Revisión del proyecto de ordenación del monte "Gaucín y Algotocín". Inventario, ordenación y planos.
		Illegible	1920	Proyecto de revisión ordinaria y tercer plan especial de aprovechamientos y mejoras, correspondientes al grupo denominado "Montes de Gaucín y Algotocín".
		Peña, A.	1930	Proyecto de revisión ordinaria y cuarto plan especial de aprovechamientos y mejoras, correspondientes al grupo denominado "Montes de Gaucín y Algotocín". nº 29 y 36 del catálogo.
		García, A.	1940	Proyecto de 4ª revisión y 5º plan especial de los "Montes de Gaucín".
		García, A.	1949	Proyecto de 5ª revisión y 6º plan especial de los "Montes de Gaucín".
		García, L.	1960	Proyecto de 6ª revisión ordinaria y 7º plan de aprovechamientos y mejoras del grupo de montes "Montes de Gaucín", nº 29 y 36 del catálogo. Términos municipales de Benarraba y Gaucín.
		Sánchez, P.	1968	Proyecto de séptima revisión ordinaria y octavo plan de aprovechamientos y mejoras del grupo de montes "Montes de Gaucín", nº 29 y 36 del catálogo. Términos municipales de Benarraba y Gaucín.
		Lozano, A.	1980	Proyecto de octava revisión y noveno plan especial de aprovechamientos y mejoras del grupo de montes "Montes de Gaucín", de Gaucín y Algotocín, nº 29 y 36 del catálogo de U.P. (Término municipal de Benarraba y Gaucín).
Los Arenales (e)	284	García, J.	1914	Proyecto de ordenación del Monte "Arenales" de Propios de Jimena de la Frontera (Cádiz).
		Avila, G.	1932	Revisión y proyecto del segundo plan especial del Monte "Los Arenales" de Jimena de la Frontera.
		Castro, M.	1942	Segunda revisión del proyecto del tercer plan especial del Monte "Los Arenales" de Jimena de la Frontera.
		Martín, E.	1956	Tercera revisión y cuarto plan especial, decenio 1951-52 al 1960-61, de proyecto de ordenación del monte "Los Arenales", nº 50 de Jimena de la Frontera.
		Robert, F.	1962	Cuarta revisión del proyecto de ordenación del Monte "Los Arenales", nº 50 del catálogo de U.P. y quinto plan especial (decenio 1961-62 al 1970-71). Memoria-Ordenación-Plan Especial.
		García, V.	1974	Quinta revisión del proyecto de ordenación del Monte "Los Arenales", nº 50 del catálogo de U.P. y sexto plan especial (decenio 1971-72 al 1980-81).
Grupo de Alcalá de los Gazules (f)	5899	Olazabal, S.	1902	Proyecto de ordenación de los Montes de "Alcalá de los Gazules". Apeo de rodales.
		Anonymous	1911	Montes de Alcalá de los Gazules. Proyecto de revisión. 2º plan especial de aprovechamientos.
		Quero, L.	1923	Revisión y proyecto del 3º plan especial en los montes de Alcalá de los Gazules de la provincia de Cádiz.
		Castro, M.	1941	Cuarta revisión del proyecto de ordenación de los montes de Alcalá de los Gazules y 5º plan especial. Texto.

Cambios en la composición de los bosques de *Q. suber- Q. canariensis*

		Castro, M.	1941	Cuarta revisión del proyecto de ordenación de los montes de Alcalá de los Gazules y 5º plan especial. Texto.
		Castro, M.	1951	Quinta revisión del proyecto de ordenación de los montes de Alcalá de los Gazules y sexto plan especial. Memoria.
		Robert, F.	1960	Sexta revisión del proyecto de ordenación del grupo de montes de Alcalá de los Gazules y séptimo plan especial (decenio 1961-62 a 1970-71). Memoria-ordenación-plan especial.
Grupo de Los Barrios (g)	4319	García, J.	1907	Proyecto de ordenación de los montes de propios de "Los Barrios" (Cádiz).
		Quero, L.	1921	Revisión y proyecto de 2º plan especial en los montes de "Los Barrios" de la provincia de Cádiz.
		Avila, G.	1932	Revisión y proyecto de tercer plan especial en los montes de "Los Barrios" de la provincia de Cádiz.
		(Illegible), M.	1942	Cuarta revisión del proyecto de ordenación de los montes de "Los Barrios".
		Castro, M.	1952	Cuarta revisión y quinto plan especial del proyecto de ordenación del Grupo montes de "Los Barrios".
		Gallego, L.A.	1961	Quinta revisión y sexto plan especial del proyecto de ordenación del Grupo montes de "Los Barrios" (decenio 1961-62 a 1970-71).
		Gallardo, J.	1975	Sexta revisión del proyecto de ordenación del Grupo de montes de "Los Barrios" nº 38 al 49 del catálogo de U.P. y séptimo plan especial (novenio 1971-72 a 1979-80).
Grupo de Montes de Algeciras (h)	1545	Illegible	1913	Revisión y proyecto de 2º plan especial en los "Montes de Algeciras" de la provincia de Cádiz.
		Castro, M.	1942	Segunda revisión del proyecto de ordenación del grupo de montes ordenados de los Propios de Algeciras y tercer plan especial.
		Castro, M.	1952	Tercera revisión y cuarto plan especial del proyecto de ordenación del Grupo de montes de Algeciras.
		Gallego, L.A.	1961	Cuarta revisión y quinto plan especial del proyecto de ordenación del Grupo de montes de Algeciras (decenio 1961-62 a 1970-71). Memoria Ordenación-Plan Especial.
		Junco, J.J.	1973	Quinta revisión del proyecto de ordenación del Grupo de montes de Algeciras, núms. 1 al 4 de catálogo de U. P. y 6º plan especial (convenio 1971-72 a 1979-1980).
Grupo de Montes de Tarifa (i)	14388	García, J.	1911	Proyecto de ordenación de los montes de Propios de Tarifa (Cádiz). Memoria.
		Atienza, F.	1919	Revisión reglamentaria del proyecto de ordenación del Grupo de Montes de Propios de Tarifa. Inventario, ordenación y segundo plan especial.
		Castro, M.	1946	Tercera revisión del proyecto de ordenación del Grupo de Montes de los Propios de Tarifa y cuarto plan especial.
		Rodenas, A.	1958	Cuarta revisión y quinto plan especial del proyecto de ordenación del Grupo de Montes del término y propios de Tarifa. Tomo 1º. Memoria.
		Junco, J.J.	1967	Quinta revisión del proyecto de ordenación del Grupo de Montes de Tarifa y sexto plan especial. Decenio 1964-65 a 1973-74. Memoria, ordenación y plan especial.
		Junco, J.J.	1976	Sexta revisión del proyecto de ordenación del Grupo de Montes de Tarifa nº 5 al 15 del catálogo de U.P. y séptimo plan especial. Novenio 1975 a 1983.

Appendix 3.2

Correlograms of *Q. suber's* and *Q. canariensis's* abundance (raw data) at a landscape scale, (a) and (b), and residuals adding different explanatory variables to models (see landscape models in Table 3.1 and Fig. 3.5b). For *Q. suber*, distance to drainage, access-cost and altitude equivalently explained its abundance pattern ($\Delta AIC < 2$), but access-cost and altitude reduced the level of spatial autocorrelation at short distances (a). Correlograms of Moran's I showing patterns of spatial autocorrelation of *Q. suber's* and *Q. canariensis's* abundance at a regional scale, (c) and (d), and residuals' autocorrelation after adding annual mean precipitation to models (see regional models in Table 3.2 and Fig. 3.6a).

