



Human and non-human determinants of forest composition in southern Spain: evidence of shifts towards cork oak dominance as a result of management over the past century

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ABSTRACT

Aims Both human and non-human determinants have shaped Mediterranean forest structure over the last few millennia. The effects of recent human activities on forest composition, however, remain poorly understood. We quantified changes in forest composition during the past century in the mixed forests of *Quercus suber* (cork oak) and *Q. canariensis* (Algerian oak), and explored the effects of forest management and environmental (climate, topography) factors on forest structure at various spatial and temporal scales.

Location Mountains north of the Strait of Gibraltar (southern Spain).

Methods First, we quantified 20th-century changes in species composition from a series of inventories in nine mixed forests (c. 40,000 ha), and examined 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 (c. 284 ha), combining local inventories and topographic variables and using a digital elevation model; and (2) regional (c. 87,600 km²), combining data from the Spanish Forest Inventory for the Andalusia region and estimates of climatic variables.

Results 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*). *Quercus 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.

Main conclusions 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 reduced 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 canariensis*, *Quercus suber*, sclerophyllous species, Strait of Gibraltar.

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INTRODUCTION

Contemporary vegetation patterns result from a combination of species' individual responses and their interactions along environmental and disturbance gradients (Whittaker & Levin, 1977). Furthermore, it is widely recognized 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 from human effects is critical for understanding current vegetation patterns and potential shifts under global change (e.g. Noble & Dirzo, 1997; Levin, 1999).

Humans have modified forest species distributions actively 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, 1986; Le Maitre, 1998; Richardson, 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 as key factors in forest structure and composition (Thirgood, 1981; Quézel, 1985; Blondel & Aronson, 1995; Grove & Rackham, 2001).

Palynological studies show that forest composition in the Mediterranean region has changed dramatically over the last few millennia, for instance in the partial replacement of deciduous taxa by sclerophyllous species (Reille & Pons, 1992; Blondel & 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 & 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 abundant at the expense of more mesic tree species in the Iberian Peninsula (Carrion *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 (Carrion *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 because forest management activities have intensified (e.g. Riera-Mora & 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 resulting from 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

Spain), 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 limited mainly to the mountains on each side of the Strait of Gibraltar, and to some patches in Catalonia (north-east Spain) and the Algarve (south Portugal) (Costa *et al.*, 2005). Palaeobotanical data on the study area – the Strait of Gibraltar – reveal 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 biodiversity refuge (Finlayson & Carrion, 2007; Carrion *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 yr BP) until a recent shift to the evergreens *Q. ilex* and *Q. suber*, associated with human colonization 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 19th century.

We followed a hierarchical approach for analysing patterns and factors operating at various scales (Willis & Whittaker, 2002; Pearson & 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 last century driven major changes in stand composition – in particular, have silvicultural practices resulted in a shifting dominance of sclerophyllous cork oak over 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?

METHODS

Study area

The study area is located in Andalusia (a region of 87,600 km² in southern Spain), and is bordered by the Atlantic Ocean (to the south-west) and the Mediterranean Sea (to the south-east) (Fig. 1a). *Quercus suber* is widely distributed in this region (Fig. 1b), where it is found in more than 15% ($n = 1983$) of

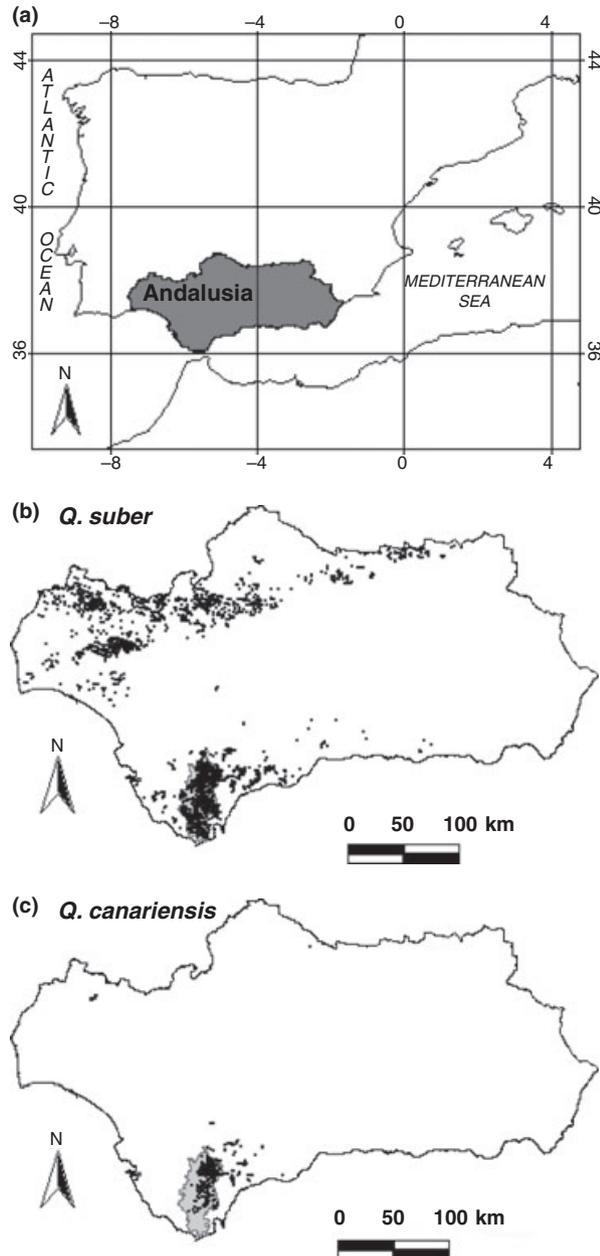


Figure 1 (a) Study area in southern Spain. Distribution of (b) *Quercus suber* ($n = 1983$) and (c) *Q. canariensis* ($n = 300$), based on presence data of the Spanish Second Forest Inventory (SSFI, total of 12,572 plots in Andalusia). The grey area in the distribution map (c) corresponds to the Los Alcornocales Natural Park limits (c. 1700 km²).

the Spanish Second Forest Inventory (SSFI) plots, with a high proportion (42%) of monospecific stands. Its distribution area extends from west to east in the mountains north of the Guadalquivir fault, and includes the southern mountains near the Strait of Gibraltar. It is not found in the most arid eastern areas, and has been almost eliminated by the agricultural transformation of the Guadalquivir river valley. In contrast, *Q. canariensis* has a smaller distribution area (Fig. 1c), and is found in just 2.3% ($n = 300$) of SSFI plots in Andalusia, mainly in the mountains close to the Strait of Gibraltar. Within the distribution area of *Q. canariensis*, mixed stands of the two oaks are frequent: 80% of *Q. canariensis* SSFI plots contain *Q. suber*.

The analysis of historical changes in forest composition and of species distribution at the landscape scale 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 1 & 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 & Quézel, 1997). The uniqueness and high biodiversity value of this area, as a refuge for some taxa of the Tertiary flora, have 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, that harbour a rich endemic flora (Ojeda *et al.*, 1996). The topography is mountainous, and the 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 survival of this wooded mountain landscape within the much deforested Mediterranean region (Marañón & 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 100 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 S1 in Supplementary Material for detailed information on the forest management plans consulted). We focused on nine public forest estates covering a total area of approximately 40,000 ha (see Fig. 3 for forest location). The first management plans date from the end of the 19th century, when cork harvesting and manufacture started to intensify in the study area. Subsequently, forest inventories were updated and management plans revised every

10–15 years. 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 analyses

We analysed changes in *Q. suber* and *Q. canariensis* density (individuals per total forest area in hectares) over the 20th century in each of the nine forests targeted. The percentage of individuals per species was calculated for various periods, and changes in forest composition were examined, with emphasis on documented disturbances and forest management practices. In addition, 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 last century to the present day, detecting possible anomalies or fluctuations that could have affected the studied species. We analysed time series of temperature and precipitation with ten-year moving averages (Štěpánek, 2006), and calculated regression coefficients with time as the 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 the 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 the letter ‘e’ in Fig. 3 for the location). A detailed forest inventory (Egmasa, 2003) was available, consisting of a grid of 129 circular (20-m radius) plots, one every 150 m, defined by their spatial location (UTM coordinates). Sampling consisted of counting all trees and measuring (with a calliper) the trunk diameter at breast height (d.b.h.; with breast height established as 1.3 m) of trees with a d.b.h. > 7.4 cm. We computed species basal area per plot, expressed in $\text{m}^2 \text{ha}^{-1}$, as a measurement of species abundance. In addition, each inventory plot was characterized 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 ($^\circ$) from

a 20-m spatial resolution digital elevation model (DEM), obtained from colour aerial photographs (scale 1 : 60,000, 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. (Schäuble, 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, that is, 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 digitized 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 the 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 1994–96, 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 d.b.h. of all trees with a d.b.h. > 7.4 cm was measured with a calliper. The inclusion of a tree in the sample was a function of its d.b.h. 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 from the analyses. Subsequently, we extracted a total of 12,572 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 $\text{m}^2 \text{ha}^{-1}$. In addition, each inventory plot was characterized 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 m^{-2}), and monthly and annual mean temperature (T) ($^\circ\text{C}$). We also derived the average temperature of the warmest

month (TWM) (°C), the 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). Regarding 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 differences between P and PET, 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 analyses

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 for which either one of the species or the sum of the two contributed 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 various functional forms that covered a wide range of possible responses: linear, exponential, power, and Michaelis-Menten-type.

All statistical models were parameterized with maximum likelihood (Edwards, 1992), using a simulating annealing algorithm (Metropolis *et al.*, 1953). Parameter 95% support limits were estimated by likelihood profile (Hilborn & 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). In addition, models were compared using Akaike's information criterion, specifically ΔAIC , which is defined for each Model_{*i*} as $\text{AIC}_i - \text{AIC}_{\text{minimum}}$ (Akaike, 1992). Models with a ΔAIC of 0–2 were considered to have equivalent and substantial empirical support, a ΔAIC of 4–7 indicated less support, and models with a $\Delta\text{AIC} > 10$ had very low empirical support (Burnham & Anderson, 2002). All models and numerical algorithms were implemented in C (Borland C++ v.5.01, Borland International Inc., Austin, TX, 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, Plainwell, MI, 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. 2a–i), just after the first management plans started at the beginning of the 20th century (with the exception of one forest, Fig. 2a). This trend slowed during the years following the Spanish civil war (1936–39). 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. 2a,b,d, and, to a lesser extent, Fig. 2c). It remained constant, or even increased slightly in some areas, during the first decades, but after 1940–50 generally decreased, as a result of 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 as a result of the pine (*Pinus pinea* L., *P. halepensis* Mill., and *P. pinaster* Ait.) afforestation carried out from the middle of the century onwards (Fig. 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 20th century is compared with that at the end of the century (Fig. 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 afforestation.

Historical records of meteorological stations showed a gradient of decreasing rainfall from north (inland mountains) to south (coast) in the study area, with fluctuations between years. The linear 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/10 years of –97.07 mm in the north and –12.62 mm in the south). However, 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; however, 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 20th century.

Landscape scale: patterns along topographic gradients

The local forest inventory revealed that the Los Arenales forest estate is today composed mainly of *Q. suber* (found in 80% of the plots) and *Q. canariensis* (found in 52% of the plots).

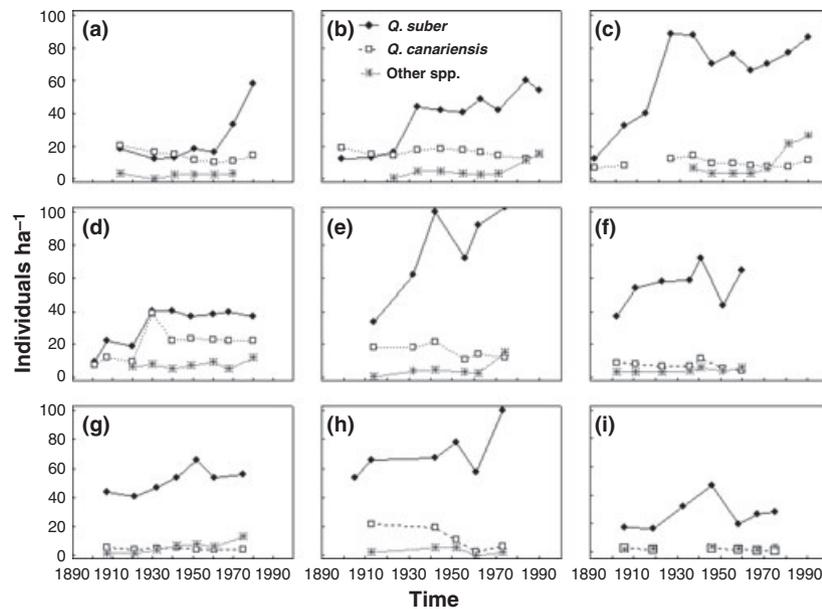


Figure 2 Changes in the number of individuals per hectare for *Quercus suber*, *Q. canariensis*, and ‘other species’ over the last century in each of the surveyed public forest estates (a–i). Other species inventoried included *Fraxinus angustifolia* Vahl., *Arbutus unedo* L., *Olea europaea* L. var. *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 onwards. Note that species density (no. individuals) has been related to the total surface (ha) of each forest estate (including non-forested areas) to enable comparison among different inventories over time. See Fig. 3 for the geographic location of the forests (indicated with the same letters), and Appendix S1 for data sources.

Quercus 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, in which *Q. suber* dramatically increased (see (e) in Figs 2 & 3). Other tree species, such as *Arbutus unedo*, *Olea europaea* var. *sylvestris*, *Pyrus bourgeana*, and *Alnus glutinosa* are present but less abundant. Eucalyptus and pines have been planted at sites where oak forests were absent.

The parameter estimates that gave the best fits relating species basal area with topographic factors are summarized in Table 1. The 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. 4a, Table 1). The altitude and access-cost gradient gave fits of similar empirical support for *Q. suber*, but had negligible influence on *Q. canariensis* (Table 1). The mean basal area of *Q. suber* increased with altitude, and its abundance was greatest in areas with low accessibility. 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. Finally, models including altitude and cost reduced the level of spatial autocorrelation at the first distance class for *Q. suber* (Appendix S2a,b).

Regional scale: patterns along climatic gradients

Parameter estimates of models with the strongest empirical support relating present-day species’ mean basal area

($\text{m}^2 \text{ha}^{-1}$) with climatic factors at a regional scale are summarized in Table 2. The average temperature for the warmest month (TWM) was the best predictor of *Q. suber* abundance. As temperature increased, mean abundance decreased, following an approximately linear response. Other factors associated with water (annual precipitation, water surplus, water deficit) and energy (temperature oscillation) gave a significant fit (LRT, $P < 0.001$), but represented models with low empirical support based on ΔAICc . Mean *Q. suber* abundance increased approximately linearly with annual mean precipitation (P) and water surplus (WS), whereas 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, following a positive and approximately linear relationship (Table 2). With similar empirical support, basal area of the deciduous species increased with water surplus and mean radiation, whereas it decreased with water deficit.

To study interspecific differences, the abundance of each species was analysed along the annual mean precipitation gradient; that is, 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 2). *Quercus suber* was present from 500 mm precipitation onwards, whereas the lower limit for *Q. canariensis* was 800 mm (Fig. 4b). 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

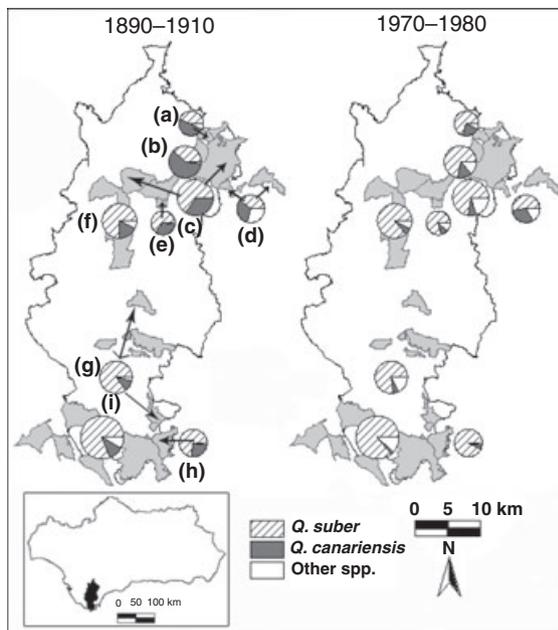


Figure 3 Changes in mixed *Quercus suber*–*Q. canariensis* forest composition over the 20th century in the area of Los Alcornocales Natural Park (limits in black line). Species relative abundance in each of the inventoried public forest estates (grey areas) at the beginning of the century (1890–1910) are compared with 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.

that models accounted for most of the spatial pattern in species abundance, except for *Q. suber* at short distances (Appendix S2c,d).

DISCUSSION

Studying mixed oak forests by means of multi-scale focus (both temporal and spatial) enabled us to identify key environmental factors influencing 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 for 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 20th century in southern Spain in all studied mixed forests, whereas *Q. canariensis* remained constant or even decreased in some periods. *Quercus 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), where *Q. canariensis* would find the most favourable conditions.

The first forest management plans, from the end of the 19th 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). *Quercus canariensis* wood was pollarded for charcoal production, and was used in railway construction (Jurado, 2002). However, as a result of 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 by 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

Table 1 Maximum likelihood parameter estimates for best-fit models relating *Quercus suber* ($n = 94$) and *Q. canariensis* ($n = 53$) basal area ($\text{m}^2 \text{ha}^{-1}$) to topographic factors.

| Factor | Best fit | n | p_1 | p_2 | LogLike. | LRT (X^2) | P -value | AIC | ΔAIC |
|---------------------------|----------|-----|-------|----------|----------|---------------|------------|-------|--------------------|
| <i>Q. suber</i> | | | | | | | | | |
| Distance from stream beds | 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. canariensis</i> | | | | | | | | | |
| Distance from stream beds | 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 |

Best fits were found for the exponential (EXP) response, where species' mean basal area = $p_1 \exp(p_2 \text{Factor})$; 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 $n < 1$ indicates an exponential-like monotonically decreasing distribution.

LogLike. corresponds to the maximum log-likelihood: $\log(L|\text{data}, \text{model})$. AIC (Akaike's information criterion) is calculated as $\text{AIC} = -2\log(L|\text{data}, \text{model}) + 2K$, where K is the number of parameters in the model. Factor effects are evaluated through the log-likelihood ratio test (LRT, d.f. = 1, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$), and model fits through ΔAIC ($\text{AIC}_i - \text{AIC}_{\min}$).

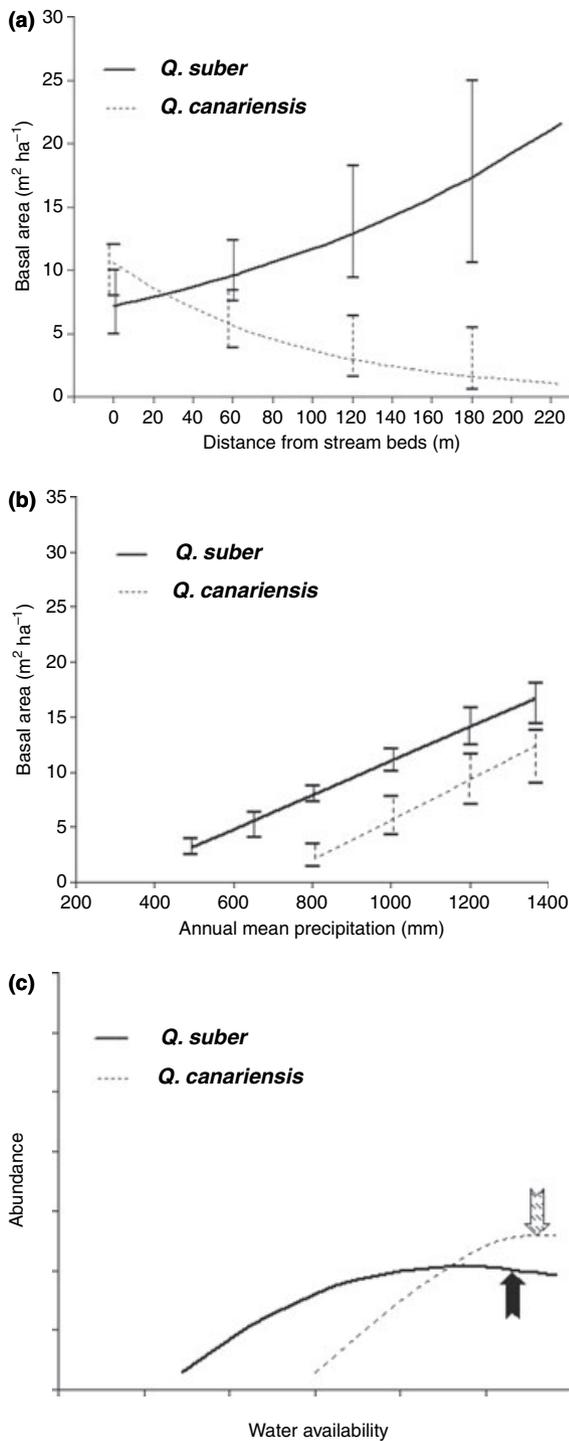


Figure 4 (a) Differential response of species mean basal area, with 95% confidence intervals (CIs), as a function of the distance from the drainage network. (b) Species mean basal area (with 95% CIs) along the gradient of annual mean precipitation, based on best model fits of Spanish Second Forest Inventory data. (c) Representation of potential (without human intervention) distribution of *Quercus* species, along a gradient of water availability. Arrows indicate the direction of human influence on each species. We suggest that in rainy areas humans have favoured *Q. suber* and reduced the distribution area of *Q. canariensis*. Panel (c) has been drawn to be compared with the current patterns observed in (b).

order to facilitate bark stripping approximately every decade. By contrast, *Q. canariensis* trees suffered selective clear-cuttings, as documented in some of the inventories, especially when alternative sources of energy (for example butane gas) replaced charcoal in the 1950–60s. However, *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-richer litter, which was believed to increase soil fertility and moisture.

On one hand, the reported forest composition changes could be partly attributable to the observed significant trends in climate over the last century. A general decline in rainfall and a warming of up to 1°C, most marked in winter, have been observed over the 20th century in the study area (Wheeler & 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 probably have had an influence on short-term processes such as fecundity, seedling survival, and 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). *Quercus 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 the forest composition changes reported in the present study, which are reflected in present-day forest structure, are probably human-induced, owing to their rate and magnitude.

Likewise, in the holm oak (*Q. ilex*) stands 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 & 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* species being widely planted outside their natural ranges in many zones for commercial forestry (e.g. Zobel *et al.*, 1987; Richardson *et al.*, 1994).

Table 2 Maximum likelihood parameter estimates for best-fit models relating *Quercus suber* ($n = 1983$) and *Q. canariensis* ($n = 300$) basal area ($\text{m}^2 \text{ha}^{-1}$) to climatic factors at the regional scale.

| Factor | n | p_1 | p_2 | LogLike | LRT (X^2) | P -value | AIC | ΔAIC |
|---------------------------|-----|-------|---------|---------|---------------|------------|--------|--------------------|
| <i>Q. suber</i> | | | | | | | | |
| Temp. warmest month (TWM) | 1.6 | 80.6 | -2.8680 | -2280.1 | 116.3 | *** | 4566.1 | 0.0 |
| Annual precipitation (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 |
| Temp. oscillation (TOSCI) | 1.5 | 28.0 | -1.2230 | -2304.2 | 68.1 | *** | 4614.4 | 48.3 |
| <i>Q. canariensis</i> | | | | | | | | |
| Annual precipitation (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 |

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

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. The 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, owing 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 to be clearly associated with areas near streams, where microclimatic conditions (warm and moist) are in marked contrast to those of 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 a great influence on forest composition (Pigott & Pigott, 1993; Zavala *et al.*, 2000). The differential distribution patterns of oak species found along the water availability gradient might be partly determined by the contrasting physiological and morphological features of the different species (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 the mortality of *Q. canariensis* seedlings, whereas *Q. suber* was not affected (Pérez-Ramos, 2007).

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. 4c). 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 (Consejería de Medio Ambiente, 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 & Fariña, 2002). Current management plans aim to reduce oak seedling mortality by large-scale fencing and exclusion of herbivores, and to encourage the reforestation 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. *Quercus canariensis* stands are currently protected as forest habitat (considered

trees 'of special interest' by regional laws), because of their rich understory with high taxonomic uniqueness (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. On a longer timescale, 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).

CONCLUSIONS

Our study quantitatively demonstrates 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 the main drivers of oak forest composition and structure across the Mediterranean region. The present study supports palynological data that 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 reduced demand for wood products, conservation policies, and climate change augur new large-scale shifts in forest composition.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 List of references of the historical management plans consulted, which included quantitative inventories and management practices in the mixed oak state forests (area of Los Alcornocales Natural Park, southern Spain).

Appendix S2 Correlograms of best-fit models for *Quercus suber* and *Q. canariensis* abundance at landscape and regional scales.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01886.x> (This link will take you to the article abstract).

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