

Capítulo 2

Desacoplamiento entre la distribución de los bosques de *Pinus* y *Quercus* mediterráneos y su regeneración a lo largo de gradientes ambientales: ¿Qué papel juega la facilitación?

Este capítulo reproduce el texto del siguiente manuscrito:

Urbietta, I.R., García, L.V., Zavala, M.A. and Marañón, T. Uncoupling of Mediterranean pine-oak forest distribution and regeneration along environmental gradients: does facilitation matter? (*In preparation*).

Resumen

Los factores ambientales, las perturbaciones y las interacciones entre especies determinan ensamblajes biológicos a diferentes escalas espaciales. Un mejor conocimiento de la estructura de los bosques y de los procesos de facilitación de las especies a lo largo de gradientes ambientales puede ayudar a anticipar la respuesta de las comunidades vegetales ante cambios ambientales y es de utilidad para el desarrollo de programas de restauración forestal. El objetivo de este estudio es describir de forma cuantitativa las relaciones vegetación-ambiente en cinco especies de pinos (*Pinus halepensis*, *P. pinaster*, *P. pinea*, *P. nigra*, *P. sylvestris*) y cinco especies de *Quercus* (*Q. ilex*, *Q. suber*, *Q. faginea*, *Q. canariensis*, *Q. pyrenaica*) del sur de la Península Ibérica, poniendo especial énfasis en el análisis de la distribución de los adultos y de la regeneración forestal (plántulas y juveniles) para comprobar si muestran diferentes requerimientos ambientales. Se caracterizaron 12.572 parcelas del segundo Inventario Forestal Nacional con información climática, edáfica, topográfica y de la frecuencia de incendios en un sistema de información geográfica. Se analizaron las diferencias en abundancia (área basal) entre adultos y regenerado a lo largo de los gradientes ambientales principales mediante un análisis canónico de correspondencias (CCA) y modelos lineales generalizados (GLZs). El gradiente térmico determinó la segregación de las especies de pinos, mientras que la precipitación de invierno explicó la distinta distribución de los *Quercus*, siendo el contenido de calcio en el suelo un factor determinante en la distribución de algunas especies. Aproximadamente un 45% de los rodales de pino mostraron una limitada regeneración, mientras que en los *Quercus* este porcentaje varió entre un 20% y un 60%, alcanzando los valores más altos en el alcornoque (*Q. suber*) y en el quejigo moruno (*Q. canariensis*). La regeneración de los pinos se encontró fundamentalmente bajo el propio dosel de los pinares y de forma importante en zonas abiertas sin cobertura arbórea, reflejando su capacidad colonizadora. En cambio, en algunos *Quercus* las condiciones ambientales en las que se encontraron los adultos y el regenerado divergieron. En el caso de la encina (*Q. ilex*) y el quejigo (*Q. faginea*), la abundancia de regeneración fue mayor bajo el dosel de los pinares, particularmente en las zonas con mayor limitación ambiental, es decir, en las zonas más frías y áridas, donde no se encontraban encinares ni quejigares, lo que sugiere que los pinares pueden estar ejerciendo un efecto de facilitación en el establecimiento de estas especies de *Quercus*, con el resultado de una expansión de sus nichos realizados. Los resultados de este estudio ponen de manifiesto la importancia de las interacciones entre los pinos y los *Quercus* en la estructura de los bosques mediterráneos, e identifican un problema global de falta de regeneración en los bosques que debe abordarse en los planes de conservación y restauración.

Uncoupling of Mediterranean pine-oak forest distribution and regeneration along environmental gradients: does facilitation matter?

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Abstract

Environmental drivers, disturbance processes, and species interactions determine biological assemblages at different spatial scales. Improved understanding of forest structure and facilitation processes along environmental gradients gives insights for the development of tools for ecosystem restoration, and for anticipating the response of plant species and communities to key environmental change drivers. The aim of this study was to quantitatively describe vegetation-environmental relationships of five pine species (*Pinus halepensis*, *P. pinaster*, *P. pinea*, *P. nigra*, *P. sylvestris*) and five oak species (*Quercus ilex*, *Q. suber*, *Q. faginea*, *Q. canariensis*, *Q. pyrenaica*) in southern Iberian Peninsula, with emphasis on the differences between adults' environmental requirements and those of seedlings and saplings (regeneration). 12572 forest inventory plots were characterized with climatic, edaphic, topographic and fire frequency data in a geographical information system. Differences in adult and regeneration abundance (basal area) along the main environmental gradients were analysed by canonical correspondence analysis (CCA) and generalized linear models (GLZs). Pine species segregated along a gradient of temperature, whereas oaks were associated with the winter precipitation gradient; with soil calcium content as a key factor for some species. Around 45% of pine forest stands showed a limited regeneration, whereas in oak stands this percentage varied from 20% up to 60% in some species, with highest proportion for *Q. suber* and *Q. canariensis*. Pines' regeneration occurred mainly under the canopy of pine forests, and significantly in areas without tree cover, reflecting their colonizer ability. Conversely, some oak species diverge substantially in the environmental conditions under which canopy trees and recruits were found. Oak regeneration was highest in pine-dominated stands (for *Q. ilex* and *Q. faginea*), particularly in areas with increasing environmental severity, i.e., in the coldest and more arid extremes of the environmental gradients explored; this suggests that a possible facilitative effect of pine forests on the establishment of oak species might be occurring, which provides an expansion of oaks' realized niches. Results show the importance of pine-oak interactions in driving Mediterranean forest structure, and identify a regeneration problem in most of the studied species that would need urgent action through conservation and restoration programmes.

Keywords: Gradient analysis; niche-based model; pines; oaks; Mediterranean forest; facilitation; forest regeneration.

Introduction

A fundamental issue to conservation biogeography is to interpret the manner in which broad environmental drivers, local sites factors and disturbance processes interact to control patterns and changes in biological assemblages at different spatial scales (Grime 1979; Huston 1994). Our ability to understand current ecosystem structure, composition and function is key to address conservation management and restoration ecology more effectively.

Ecosystems are dynamic as a consequence of disturbance and environmental change which interact with biological processes, including species ability to reproduce and disperse (i.e., colonization of adjacent habitats) and species positive and negative interactions (i.e., competition and facilitation). Main broad-scale vegetation controls appear to be climatic and historical constraints, such as geographical dispersal limitation, which have strongly conditioned current species distribution ranges (Montoya *et al.* 2007; Svenning and Skov 2007). At a more local scale, soil factors can determine plant species distribution in the landscape (Roberts and Wuest 1999; Coudun *et al.* 2006). Furthermore, there is a clear linkage between ecosystem history and current pattern and processes that makes increasingly necessary that long-term perspectives are integrated into plant species distribution studies (Foster *et al.* 2002).

Since distribution and abundance of many plant species are influenced by the presence of others, inter-specific interactions can be very important in determining species coexistence (Pacala *et al.* 1996; Callaway and Walker 1997). Community composition is regulated by plant-plant interactions, which can change along environmental gradients from facilitation to competition (Holmgren *et al.* 1997; Pugnaire and Luque 2001; Stultz *et al.* 2007). Net positive interactions (i.e., the beneficial impacts of neighbours) are likely to occur with increasing environmental severity as reported in recent

studies (e.g., Maestre *et al.* 2003; Gómez-Aparicio *et al.* 2004). Bruno *et al.* (2003) discussed a revision of the niche theory to include the potential for expansion of the realized niche of species by facilitation (as empirically demonstrated by Hacker and Gaines 1997; Choler *et al.* 2001). Thus, because positive interactions alleviate abiotic stress, the distribution of a species (realized niche) could be expanded by facilitative interaction with its neighbours. Studies looking at species interactions often examine one particular species pairing, but few have attempted to take a broader approach and examine patterns at the community level and across gradients.

Plant resources (i.e., light availability, nutrient supply, or water regime) can change significantly through the life of individuals. Tree seedlings have smaller and shallower root systems than mature trees, and occur in soil layers most susceptible to drying from soil surface evaporation and transpiration of neighbouring trees and herbaceous layer (Weltzin and McPherson 1997; Kolb and Stone 2000). Thus, there might be changes in carbon and water relations (e.g., drought response strategies and differences in photosynthetic capacity) with ontogeny, i.e., between seedlings, saplings and mature trees (Cavender-Bares and Bazzaz 2000; Mediavilla and Escudero 2004; Quero *et al.* 2007). Consequently, effective regeneration might be distant (under different resource conditions) from adults, associated with certain microhabitats within a forest or located in areas where the tree layer is absent.

Although, plant species' environmental limiters provide clues to reconstruct species past distribution and restore ecosystems (Arundel 2005), it is crucial to assess how populations, e.g. forest stand structure, vary along environmental gradients. Specially important in areas where natural regeneration is scarce or where species find constraints (environmental or disturbances)

for regeneration, and thus, persistence. Most tree species biogeography studies however, often focus on species presence/absence data, and overlook population structure behind and species interactions along environmental gradients.

This study analyses the relationship between the abundance of five oak (*Quercus* spp.) and five pine (*Pinus* spp.) species and several environmental factors (climatic, topographic, soil characteristics, and fire frequency) in Andalusia region (Southern Spain), based on forest inventory data linked to independent environmental information in a Geographical Information System (GIS). The aim was to study the relative contribution of the complex abiotic environment to explain species distribution and forest structure, in order to characterise species' environmental niches (i.e., realized niches), and to explore whether environmental requirements of adult canopy trees differed from those of saplings and seedlings (i.e., advance regeneration).

Pine and oak forests are major structural components of Mediterranean ecosystems (see Richardson 1998; Quézel 2000; Rouget *et al.* 2001; Purves *et al.* 2007). Both natural and anthropogenic disturbances (i.e., wildfires, forest management etc.) have governed pine and oaks dynamics at various spatio-temporal scales (Zavala *et al.* 2000; Carrión *et al.* 2003; Benito Garzón *et al.* 2007). In recent times, particularly over the twentieth century, forest management has traditionally encouraged land cover changes in Mediterranean landscapes. For example, forest restoration techniques relied on the establishment of tree cover for soil conservation purposes, mainly by means of extensive plantations of fast growing pioneer species such as pines, in natural or degraded ecosystems, assuming this species would facilitate the establishment (artificial or natural) of late-successional species such as oaks (Gil and Prada 1993; Pausas *et al.* 2004b). The fingerprint of such widespread management may still be reflected in present-day forest structure.

With this purpose, we analysed pine and oak forest regeneration and stand structure along environmental gradients, with emphasis on identifying those species with a limited regeneration, and evaluating if oaks regenerated under the canopy of pine forests. Specifically we address the following questions: (1) What are the main factors (climatic, topographic, edaphic, fire frequency) determining intra- and inter-genera differences between pine and oak species abundance distribution? (2) What is the proportion of stands with limited regeneration for oak and pine species? (3) What are the types of habitat in which pine and oak regeneration is present? (3) Does species regeneration niche differ from adult's environmental niche with respect to critical environmental factors? (4) Is oak regeneration effective under the canopy of pine forests?

Material and methods

Study region and species

The study area is located in Andalusia (southern Iberian Peninsula), region of ~ 87600 km² which encompasses a large altitudinal gradient (0-3480 m) (Fig. 2.1). Mountain systems surround the region and lie to both sides of the Guadalquivir Depression, with paleozoic materials and siliceous rocks to the north (i.e., Sierra Morena) and sedimentary materials (limestone) originated in the Alpine orogeny to the south (i.e., Betic mountain ranges); main soil types found in the region are summarized in Appendix 2.1. The climate is Mediterranean but quite variable, with mean annual precipitation ranging from 140 mm up to 1400 mm. Dry and warm summers (average July temperature: 15 °C to 27 °C) are followed by fairly cold winters (average January temperature: -2 °C to 12 °C). The landscape is a mosaic of semi-natural forests, dehesas (oak savannas), shrublands, grasslands, intensive agricultural fields, and urban areas. Forest areas are absent in the most arid south-eastern territory, and have been almost eliminated by agricultural transformation from the River Guadalquivir valley (Fig. 2.1).

For the purpose of this study, we focused on five oak (*Quercus*) species and five pine (*Pinus*) species representative of Mediterranean forests: evergreens *Quercus ilex* and *Q. suber*, and winter deciduous *Q. faginea*, *Q. canariensis* and *Q. pyrenaica*; *Pinus halepensis*, *P. pinaster*, *P. pinea*, and montane *P. nigra* and *P. sylvestris* (see species distribution in Fig. 2.1). Selected species are major structural components of forests and woodlands covering the greatest part of the forest surface in Andalusia (in approximately 70% of the SSFI plots pine and/or oak presence was found). Forests harbour a rich biodiversity; and provide valuable socio-economic resources (cork, timber, acorns, pine cones, resins, etc.). Furthermore, most of these species are used in forest restoration programs. We analysed all SSFI plots including stands with native trees but that might had been planted in the past, due to the difficulty to disentangle their true origin. Exotic pine species (*P. radiata* and *P. canariensis*), present in less than 1% of plots, were excluded for the analyses.

Data set

Permanent plots of the Spanish Second Forest Inventory (SSFI) were chosen as sampling/mapping units. Wooded areas in Andalusia were inventoried between 1994 and 1996, with an intensity of approximately one circular plot per square kilometer (MMA 1996). The information (provided by province) was first processed separately and then gathered all (8 provinces) in one single database. Previous to the analyses, we checked the geographic position of all inventoried plots, superimposing them onto forest areas of recent digital orthophotographs (JA 2003). Plots with georeferencing errors were discarded for the analyses, giving a total of 12572 plots. Each forest inventory plot was characterized with independent environmental data according to their relevance to tree survival and growth, including climatic, topographic, soil characteristics, and fire frequency (see below for selected variables). We combined raster maps and sampling locations (UTM

coordinates) for each species data to determine the values of each environmental variable in each SSFI plot using a GIS (ArcView 3.2, ESRI Inc., Redlands, USA, 2000).

Stand structure. - SSFI plots were circular of various concentric radii up to 25 metres, and were defined by their spatial location (UTM coordinates of the centre of the plot). Trunk diameter at breast height (dbh, 1.30 m) of all trees with a dbh greater than 7.4 cm was measured by two perpendicular measurements with a calliper. The minimum measured dbh varied with the radii of the plot: 7.5 cm dbh (5 m radius), 12.5 cm dbh (10 m), 22.5 cm dbh (15 m), 42.5 cm dbh or greater (25 m). For saplings (2.5-7.4 cm dbh) the number of individuals (density) was estimated within 5 m radius circle; we assumed a mean diameter of 5 cm per individual for basal area calculation. For seedlings (dbh < 2.5 cm) only their presence or absence was recorded within 5 m radius; if present, we assumed to be at least one seedling of 1.25 cm diameter in order to differentiate them from zero values (i.e., absences). Species basal area was calculated as the addition of the basal areas (m²) of all trees of the same species present in each plot (assuming a circular cross-section of the trunk), and then expressed on a unit area basis, i.e., in square meters per hectare (m²/ha). For the analyses, we first considered species abundance as the total basal area, i.e., the addition of all inventoried tree sizes. Then, we divided this value in two, as the sum of the basal areas of trees with a dbh > 7.4 cm, i.e., hereafter *adults* "a", and the basal areas of individuals with a diameter = 7.4 cm including saplings and seedlings, i.e., hereafter *regeneration* "r".

Climatic factors. - Climatic data with 1 km spatial resolution was provided by the Spanish Institute of Meteorology (INM) as an interpolation (kriging) of the information recorded from 1971 to 2000 in meteorological stations spread all over the Spanish territory (143 main stations, 1504 thermometric, and 4835 pluviometric stations) (INM unpublished). We assigned the

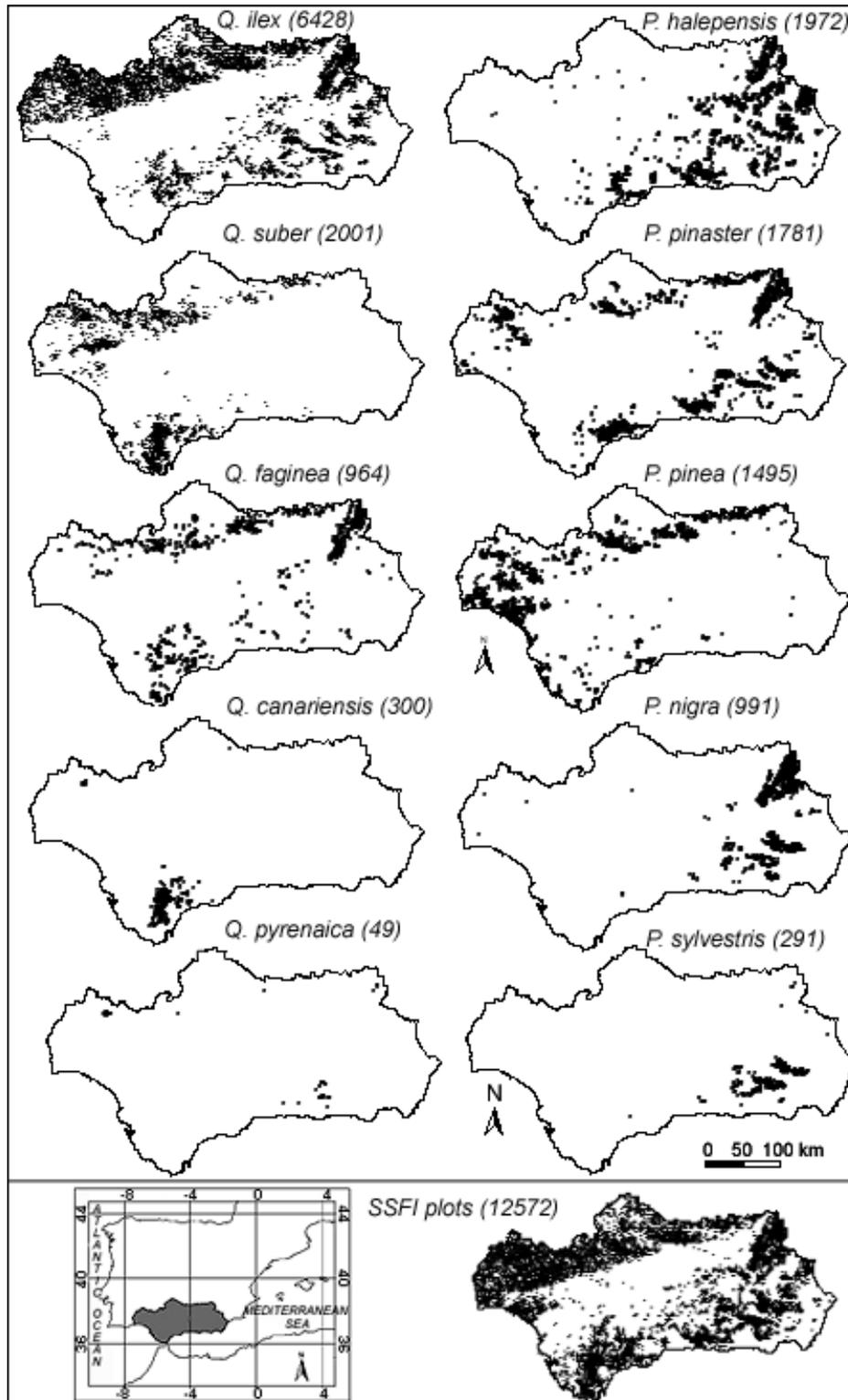


Figure 2.1 *Quercus* and *Pinus* species distribution in Andalusia (S Iberian Peninsula) based on SSFI plots (the number of plots per species is indicated in brackets).

following climatic variables to each SSFI plot: Monthly and annual mean precipitation (PANU) (mm), from which spring (PSPR), summer (PSUM), autumn (PAUT), and winter (PWIN) precipitation were calculated. Monthly and annual mean radiation (RADANU) (kwh/m²), from which radiation per season was derived (RADSPR, RADSUM, RADAUT, RADWIN). Monthly and annual mean temperature (TANU) (°C), from which the average temperature of the warmest month (TWM), average temperature of the coldest month (TCM), and thermal oscillation (TOSIC) were calculated. Monthly and annual potential evapotranspiration (TPET) (mm) were obtained as a function of mean temperature (Thorntwaite 1948). Computing monthly differences between P and PET we calculated annual water surplus (TSUP) as the sum of positive differences, annual water deficit (TDEF) as the sum of negative differences, and drought length (DL) as the number of months in which PET exceeded P.

Topographic factors. - Altitude (m) (ALT), slope (degrees) (SLOP), and aspect (degrees with respect to north) (ASP) of each SSFI plot were derived from a 20 m digital elevation model (DEM), obtained from colour aerial photographs (scale 1:60000, provided by REDIAM, the Environmental Information Network, Junta de Andalucía). Aspect directional data were subjected to inverse polar transformation, which produced two Cartesian variables accounting for slope orientation in the south-to-north (SN) and west-to-east (WE) directions.

Soil factors. - We assigned the dominant soil typological unit (named according to the FAO-UNESCO soil legend) to each SSFI plot, from the soil geographical database of Europe, scale 1/1000000, included in the European Soil Database v 1.0 (European Soil Bureau 1999) (Appendix 2.1). Using the FAO-UNESCO definition criteria for the different soil units, we derived ordinal categories for some relevant soil properties: soil depth (SDEPTH); soil base saturation (SBASE); presence of CaCO₃ (or in a few sites other calcium-rich materials as

gypsum) in the soil (SCALC). We also used other attributes included in the soil database and derived estimates for overall soil water capacity (SAWC, mm), using the estimates for topsoil and subsoil water capacity given in European Soil Database (European Soil Bureau 1999).

Fire frequency. - Cartographic layers of fire surface, with a cover of at least 10 hectares, were elaborated based on Landsat images of Andalusia at the end of each fire campaign. Fire occurrence (FIRE) between 1987 and 2002 expressed in frequency was assigned to each SSFI plot. This information was provided by REDIAM (Junta de Andalucía unpublished).

Statistical analysis

Species abundance patterns

A Canonical Correspondence Analysis (CCA, ter Braak 1986) was carried out to study the relationship between species abundance and environmental variables (climatic, soil, topographic factors, and fire frequency). Basal area data were log transformed (log x+1) to minimize bias. To avoid artefacts, results were checked for uni- and multivariate extreme values (ter Braak and Smilauer 2002). Manual selection and Monte-Carlo permutation test (p< 0.01), with 999 unrestricted permutations under full model, were used for the selection of the most significant variables from the explanatory set, as well as to evaluate the significance of extracted axes. The stepwise option was used to exclude highly redundant environmental variables and to accurately detect the best predictors in the model (Økland and Eilertsen 1994; Vandvik and Birks 2002), excluding those with VIF (variance inflation factor) greater than 20. Environmental variables and tree species abundance were plotted in the environmental space (CCA biplots). CANOCO software v. 4.5 was used for these statistical analyses (ter Braak and Smilauer 2002).

To account for the spatial component, variance partitioning was performed by using the canoni-

cal modelling developed by Borcard *et al.* (1992), and Borcard and Legendre (1994). The overall species variance was partitioned into four components: (1) a non-spatially-structured component which is explained by the environmental variables, (2) a spatially-structured component explained by the environmental variation, (3) a spatially-structured component which is not explained by the environmental variables, possibly related to community dynamics, and (4) a residual, non-explained fraction. The relative importance of the three first components provides further insights into community organization (Maltez-Mouro *et al.* 2005, 2007). Significance was fixed at the 0.05 level throughout the study. Since repeated tests were carried out, corrections to limit type I error inflation were performed according to García (2004).

We analysed *Quercus* and *Pinus* species responses along the main CCA axes and the most relevant environmental variables, and fitted GLZs (Generalized Linear Models) (see Guisan *et al.* 2002), which were selected following the Akaike's Information Criteria (AIC, Akaike 1992) using the Canodraw for Windows program (ter Braak and Smilauer 2002). We tested for a bell-shaped unimodal response of species along the underlying environmental gradients, which is the form usually assumed to describe vegetation-environment relationship (ter Braak 1985; Whittaker 1978; Retuerto and Carballeira 2004; but see Austin 2002; Oksanen and Minchin 2002). Because of the skewed distribution of species' abundance, the huge quantity of absence data (i.e., species basal area equal to zero), and the positive response values, we assumed a Poisson distribution, log-link option, according to Leps and Smilauer (2003).

Adults versus regeneration

We analysed inter-specific differences in species' realized niches (all the inventoried individuals included, see above), and furthermore, we also compared the distribution patterns between adults and regeneration intraspecifically.

First, adult/regeneration proportion found for each species in SSFI plots was analysed, with emphasis on describing the type of habitat (under canopy or in open-shrubby areas) in which species regenerate, and identifying species with a limited regeneration. Second, we compared 95% confidence intervals of adults and regeneration along CCA axes using the Canodraw for Windows program facilities. Finally, we analysed by means of GLZs if the abundance of canopy trees and recruits differed along the main environmental gradients.

Results

Species abundance along environmental gradients

The ranges of environmental conditions (for each of the initially selected abiotic factors, i.e., climatic, topographic and soil variables) for *Quercus* and *Pinus* species are summarized in the Appendix 2.2.

Distribution of oaks and pines was non-random and CCA results were highly significant. The global model (considering all extracted axes) explained nearly 23% of the overall species variance. The three main axes alone explained 18.4% of the overall species data, which means 86.6 % of the explained species variance (Table 2.1). The three first CCA axes were significant at $p < 0.001$ based on Monte Carlo 999 permutation tests. Axis 1 explained 9.5% of overall species variance, while Axis 2 a variance of 5.9 %, and Axis 3 accounted for 3%. In all cases, climatic variables entered first, followed by soil and topographic variables last, while fire frequency did not enter as a significant predictor. Those species with larger number of samples tend to have increased model success, except *Q. faginea* and *P. pinaster* which showed a low fitted variance. Species with more limited distribution such as *Q. pyrenaica* and *P. sylvestris* were difficult to analyse for the coarse scale data to capture, and thus had a low model success (Table 2.1).

CCA first two axes were interpreted by means of intra-set correlations and ordination biplots (Table 2.1, Fig. 2.2). Axis 1 was strongly and positively correlated with the temperature of the coldest ($r= 0.9$) and warmest ($r= 0.7$) months, and negatively with summer precipitation ($r= -0.7$) and radiation ($r= -0.56$). Altitude was not included in the model due to its strong negative correlation with temperature and positive correlation with summer precipitation, but indirectly defines Axis 1, increasing towards the negative extreme ($r= -0.9$). Edaphic and topographic factors such as soil calcium content ($r= -0.6$), soil depth ($r= 0.56$), soil base saturation ($r= -0.45$), and slope ($r > -0.3$), were also captured by Axis 1. Axis 2 was strongly correlated with water

availability conditions, positively with drought length ($r= 0.65$), and negatively with winter precipitation ($r= -0.70$). It also showed positive correlation with soil water storage capacity ($r > 0.45$), and temperature of the warmest month ($r= > 0.5$) (Table 2.1, Fig. 2.2).

Partial canonical correlation analysis (pCCA) showed that climatic variables had the highest unique contribution (53%) to the explained species variance, while topographic (slope) and soil related variables had a unique contribution of just 18%. The remained fraction (29%) of species' variance explained was a shared contribution of the two groups of factors. Therefore the climatic set alone accounted for 82% of the

Table 2.1 Explained variance for each of the first three CCA Axes, their correlation with the environmental variables, and fitted variance per species (see main text for abbreviations).

	CCA Axis 1	CCA Axis 2	CCA Axis 3
Eigenvalues :	0.58	0.35	0.18
Species-environment correlations :	0.82	0.65	0.48
Explained variance (% species data) :	9.50	5.90	3.00
Cumulative (%) of species data :	9.50	15.40	18.40
Cumulative (%) of species-envir. relation :	44.60	72.40	86.60
Weighted correlations			
SLOP	-0.32	-0.18	0.42
PSUM	-0.69	-0.33	-0.23
PWIN	0.54	-0.70	0.17
DL	0.22	0.67	0.27
RADSUM	-0.56	0.35	-0.56
TWM	0.70	0.52	-0.31
TCM	0.90	0.20	0.24
SBASE	-0.45	0.22	0.05
SCALC	-0.59	0.15	0.46
SDEPTH	0.56	0.32	0.00
SAWC	0.20	0.46	-0.19
Fitted variance (%)			
<i>Q. ilex</i>	0.97	4.00	20.20
<i>Q. suber</i>	29.82	41.12	44.81
<i>Q. faginea</i>	0.48	1.11	1.18
<i>Q. canariensis</i>	3.04	6.16	6.96
<i>Q. pyrenaica</i>	0.01	0.02	0.02
<i>P. halepensis</i>	11.88	23.09	32.58
<i>P. pinaster</i>	2.79	4.12	4.12
<i>P. pinea</i>	7.39	15.13	15.16
<i>P. nigra</i>	25.89	39.15	39.22
<i>P. sylvestris</i>	2.24	3.74	3.95

explained species variance, while topographic and soil-related variables alone were able to account for 47% of the explained species variance. Table 2.2 summarises the sequential analyses carried out for variance partitioning calculation, including: (1) unconstrained (CA); (2) stepwise CCA selecting the best, non-redundant, environmental predictors; (3) stepwise CCA selecting the best, non-redundant, spatial predictors; (4) stepwise partial CCA after adjusting

by the best spatial set obtained in step 3; and (5) stepwise partial CCA using only spatial predictors, after adjusting for the best environmental set obtained in step 2. According to results, nearly 23% of species variance may be explained using spatial and environmental predictors. However, most of the explained species variance (72%) was spatially structured, while only a 28% was independent of the space.

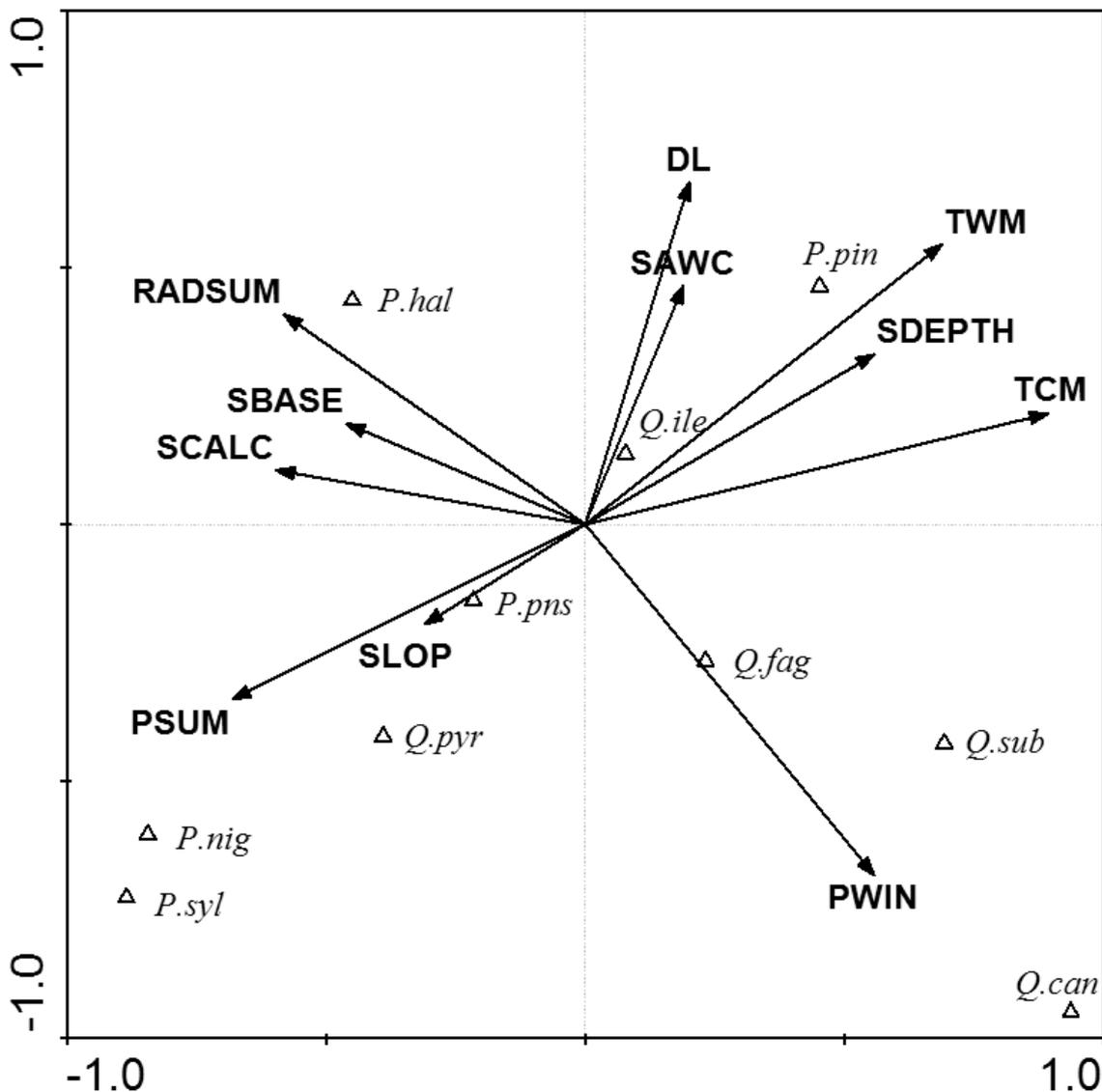


Figure 2.2 CCA biplot of environmental variables in relation to five *Quercus* and *Pinus* species distribution on Axes 1 and 2 (see main text for abbreviations).

Table 2.2 Sequential analyses carried out for variance partitioning calculation. The sum of all eigenvalues (trace), the percentage of the community variance explained and the model significance (by Monte Carlo test) are shown for each analysis.

Analysis (#)	Independent set	Covariable set	Trace	p (trace)	% variance
DCA (1)	-	-	7.95	-	100
CCA (2)	Environmental	-	1.35	< 0.001	17.0
CCA (3)	Spatial	-	1.31	< 0.001	16.5
pCCA (4)	Environmental	Spatial	0.50	< 0.001	6.3
pCCA (5)	Spatial	Environmental	0.46	< 0.001	5.7

According to GLZ models, which provided a description of the environmental (realized) distribution niche of tree species, *Pinus* and *Quercus* species segregated along Axis 1 (Fig. 2.2), with oaks located towards positives values of the gradient (with the exception of *Q. pyrenaica* and the extreme of *Q. ilex*'s niche) and pines towards the negative side (with the exception of *P. pinea*). This way, the species sequence found from negative to positive values of Axis 1, i.e., from high-steep cold areas, to lower areas with milder climatic conditions was: *Q. pyrenaica*, *Q. ilex*, *Q. faginea*, *Q. suber*, and *Q. canariensis* for oaks (Fig. 2.3a), and *P. sylvestris*, *P. nigra*, *P. halepensis*, *P. pinaster*, and *P. pinea* for pines (Fig. 2.3b). Axis 2 stressed the differences between certain species; *P. pinea* and *P. halepensis* were located at the driest part of the gradient, and *Q. ilex* differed from the rest of oaks reaching drier areas, with lower winter precipitation, longer drought period but under deeper soils with higher water retention capacity (Fig. 2.2).

P. nigra and *P. sylvestris* showed similarities and narrow niches, associated with high elevation, steep slopes, shallow soils, low temperatures, and high values of summer precipitation probably caused by the effect of the orography (Fig. 2.2). At high and steep habitats *Q. pyrenaica* was found, followed by *P. pinaster* and *Q. ilex*, which showed a broader niche amplitude at intermediate conditions. Conversely, *P. pinea*

was clearly associated to low elevation warmer areas and deeper soils, and *P. halepensis* in areas with high summer radiation and basic soils with high base saturation and calcium content. *Q. suber* and *Q. canariensis* were restricted to areas with high winter precipitation, mild temperature conditions, shorter drought length, and low calcium soil content. Towards more arid conditions (less winter rain, higher drought and summer radiation), and soils with higher calcium content and base saturation, *Q. faginea* and *Q. ilex* were found. All environmental variables that entered the CCA model provided a significant fit when tested singly to explain species abundance. Overall, environmental variables associated to Axis 1 such as the mean temperature of the warmest and coldest months, explained best the differences between pines (Fig. 2.3d); whereas variables correlated with Axis 2, such as winter precipitation, described oaks segregation at regional scale (Fig. 2.3c).

Quercus and Pinus forest regeneration

Adult/regeneration proportion found for each species in SSFI plots have been summarized in Figure 2.4. A high percentage of pine and oak forests showed a limited regeneration (i.e., lack of individuals with a diameter = 7.4 cm). For the five pine species, around 40-55 % of the SSFI plots (with presence of the species) were mature stands with adults (i.e., individuals with a dbh = 7.4 cm) but without saplings or seedlings (i.e., advance regeneration) in the understorey.

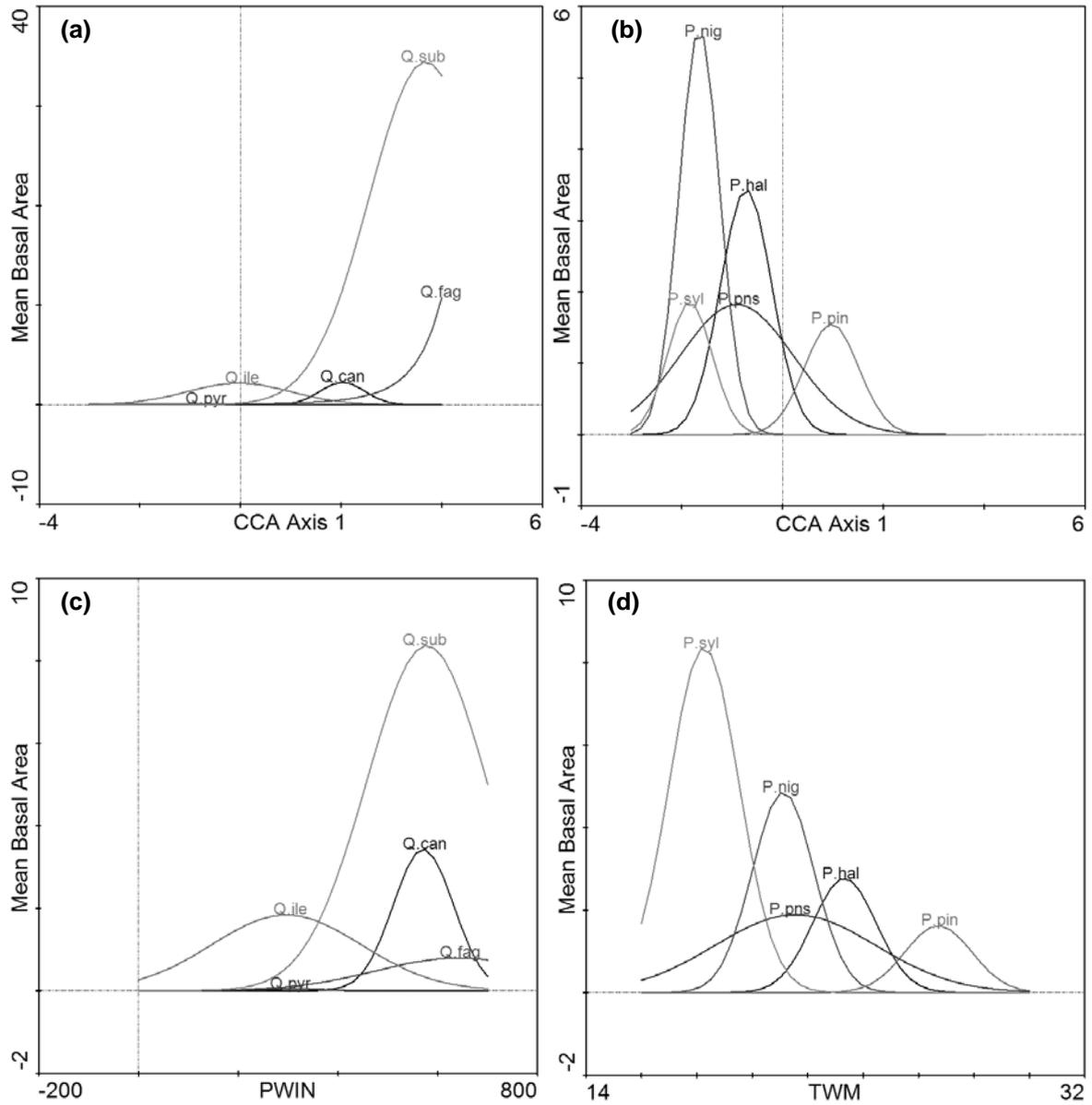


Figure 2.3 *Quercus* (a) and *Pinus* (b) species abundance (mean basal area, m²/ha) variation along the CCA Axis 1, which is positively correlated with the temperature of the coldest and warmest months, and soil depth; and negatively correlated with summer precipitation, radiation, slope, soil calcium content and soil base saturation. Distribution of *Quercus* (c) and *Pinus* (d) species along the gradients of the temperature of the warmest month (°C) and mean winter precipitation (mm), respectively.

Among oaks, the percentage of forest stands with limited regeneration varied between species, from 60-70 % of plots for *Q. suber* and *Q. canariensis*, followed by *Q. ilex* and *Q. faginea* (30-40 %) and *Q. pyrenaica* (approximately 25 %) (Fig. 2.4).

Pines' regeneration occurred mainly under the canopy of pine forests, with proportions (from total SSFI plots of species) ranging from 15-20 % for *P. pinea* and *P. pinaster*, to 30-40 % for *P. sylvestris*, *P. nigra*, and *P. halepensis*. Regeneration under the canopy of oak forests for all five pine species was scarce, with less than 10% of plots per species. The remaining plots included pine regeneration in areas with no canopy (i.e., sampled plots with no tree layer but potentially with shrubby vegetation, where pine "colonization" might be occurring), with *P. pinea* (25%), *P. halepensis* (20%), and *P. pinaster* (15%) showing a significant proportion (Fig. 2.4). On the contrary, oaks that showed some regeneration, such as *Q. faginea* and *Q. ilex*, had as much regeneration under their own canopy as under pine forests: (around 30% for *Q. faginea*), or even a greater proportion under pines (30%) than under oaks (15%) in the case of *Q. ilex* (Fig. 2.4). The scarce regeneration of *Q. canariensis* (30% in total) was found mainly under its own canopy. *Q. suber* showed simi-

larly low regeneration under its own canopy than in forest areas with no tree layer (approximately 10% in each). *Q. pyrenaica* and *Q. ilex* also showed a significant proportion (20-25 %) of plots in areas outside forest stands with no canopy.

Adults versus regeneration distribution patterns

The abundance of pine and oak regeneration and adults was plotted in the bi-dimensional environmental region defined by the first two CCA axes (Fig. 2.5). Highly significant unimodal models showed that pines had overall closely associated distribution areas between their adults and regeneration. Conversely, some oak species diverged in the environmental conditions under which both stages, adult trees and regeneration, were found as inferred from their non- overlapping 95% confidence intervals. Specifically, *Q. pyrenaica* tended to regenerate in areas slightly different from its adults, with lower summer precipitation, higher mean temperatures of the coldest and warmest months, and smoother relief (Fig. 2.5). *Q. faginea's* regeneration niche was characterized by conditions under lower winter precipitation, higher summer radiation and greater calcium soil content than those found for *Q. faginea* adult trees.

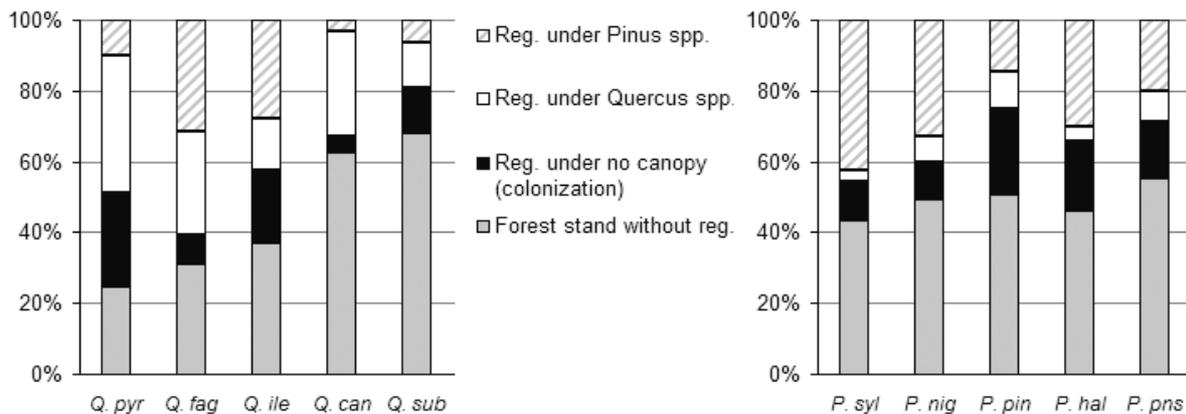


Figure 2.4 Adult and regeneration proportion found in SSFI plots for *Quercus* (left) and *Pinus* (right) species. The type of habitat in which species regeneration occurs is specified, i.e., under the canopy of *Pinus* or *Quercus*, or treeless forest areas. Percentages are referred to the total number of plots each species was found (see Fig 2.1).

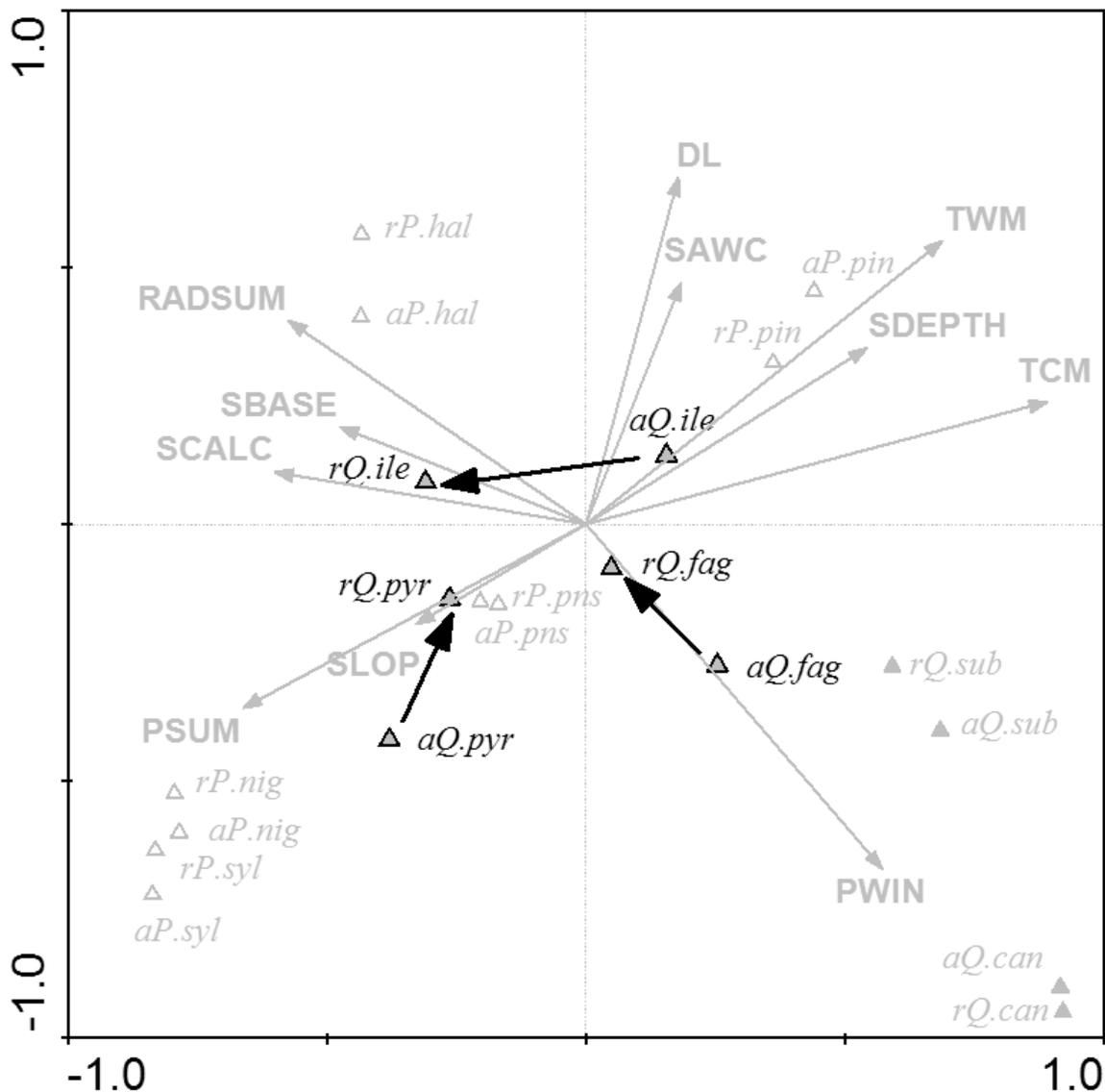


Figure 2.5 CCA biplot of environmental variables, analogous to Fig. 2.2, but showing the centroid for regeneration "r" and adults "a" of *Quercus* and *Pinus* species. For the three species highlighted, *Q. ilex*, *Q. faginea* and *Q. pyrenaica*, adult and regeneration distribution are far apart, with no overlap in their confidence intervals (not shown for better visualization). See the main text for abbreviations.

Similarly, *Q. ilex* regeneration was found in colder areas, with higher summer radiation, and clearly associated to high levels of base saturation and calcium content in the soil compared to adults (Fig. 2.5). Results of stepwise partial CCA (differentiating regeneration and adults) but constrained by environmental variables and using the best spatial predictors as covariables

(i.e., analysis labelled as (4) in Table 2.2) showed the same global distribution pattern of species. However, the differential distribution found between adults and regeneration got slightly reduced, especially for *Q. ilex*, in which the spatial structure of data might be exerting some influence in the distribution patterns described.

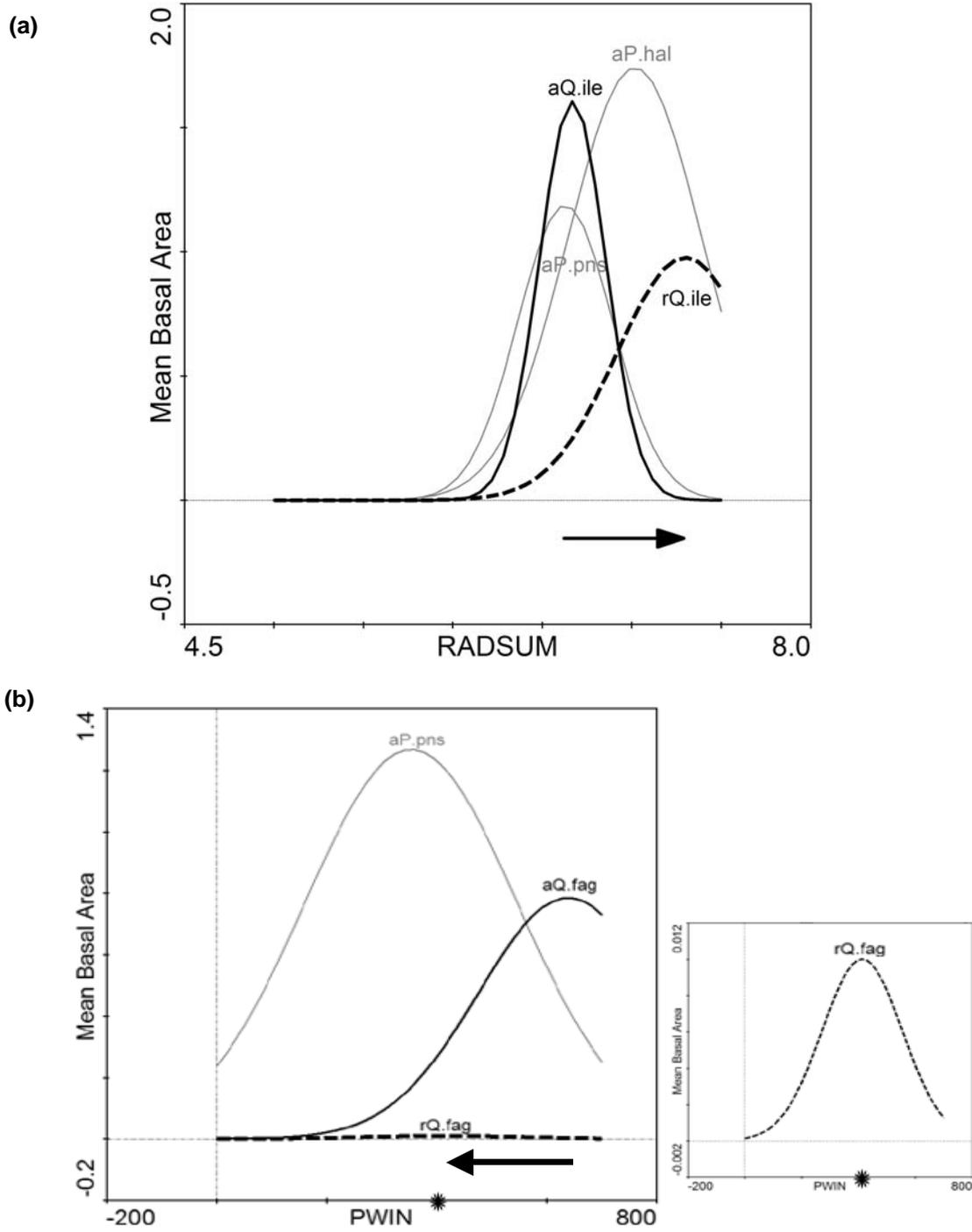


Figure 2.6 *Q. ilex* (a) and *Q. faginea* (b) adult's distribution (black line) and regeneration niche (dotted line) along the summer radiation (kwh/m^2) gradient and winter precipitation gradient (mm), respectively. *Pinus* species distribution along the gradients is represented in grey lines. Both *Quercus* species show the maximum of the regeneration curves displaced towards more arid areas under the canopy of pines. A zoom has been made in (b) to the regeneration curve of *Q. faginea* for a better visualization with the asterisk as reference for comparison (notice different scales).

Since *Q. ilex* and *Q. faginea* regeneration had been found to be substantial under pines' canopy (see Fig. 2.4), we explored possible interaction of both oak species with pines along the main environmental gradients. *Q. ilex* adults and regeneration distribution differed substantially along the summer radiation gradient. *Q. ilex* regeneration was displaced toward positive values of the gradient, reaching areas with higher radiation where *Q. ilex* forest stands (adult trees) were not present. More interestingly, *Q. ilex* regeneration occurred principally under the canopy of *P. pinaster* and *P. halepensis* (Fig. 2.6a). Likewise, the same pattern was found along the gradient of temperature of the coldest month, where *Q. ilex* regenerated in the coldest areas mainly under *P. halepensis* canopy (figure not shown). *Q. faginea* showed the same proportion of regeneration under pines than under its own canopy. Along the gradient of mean winter precipitation, regeneration niche was found at drier areas (with 400 mm mean rainfall) than *Q. faginea* adults (around 700 mm). Furthermore, at the driest part of the gradient *Q. faginea* regeneration occurred mainly under the canopy of *P. pinaster* (Fig. 2.6b).

Discussion

Broad scale vegetation controls: climate and soil influence

Results evidence a primary importance of climate in explaining pine and oak species abundance at regional scale in Andalusia, and a secondary (but key for some species) relevance of substrate (soil characteristics) and microclimate (topography). Low winter temperatures and water stress have been considered to exert influence on many features of the flora in the Mediterranean region (Mitrakos 1980). Pine and oak species segregate along altitudinal gradients that often correlate with the variability in resources (e.g., water availability) or environmental condition (e.g., temperature or radiation). Overall, pines were found in habitats with colder conditions and at highest altitudes than oaks. The abundance distribution of oaks was

explained by a water availability gradient, i.e. winter precipitation. Thus, we confirmed the importance of temperature (for pines) and precipitation regime (for oaks) in controlling species abundance patterns at a regional scale, as found in previous studies (Rouget *et al.* 2001; Thuiller *et al.* 2003). Soil factors were key for some species such as *Q. suber* and *Q. canariensis* which were associated to acidic, non-calcareous soils, and for *P. halepensis*, frequently located on calcareous soils.

Studied species exhibit quite different life history and ecophysiological strategies (see Sánchez-Gómez *et al.* 2006a; Valladares and Sánchez-Gómez 2006), which could partly explain their differential distribution. The temperature gradient exerts an important influence on pine species distribution (Morin *et al.* 2007). We found that a gradient from high-steep cold areas to lower areas with milder climatic conditions, explained the differential distribution between pines, with *P. sylvestris* and *P. nigra* in the coldest extreme (see Castro *et al.* 2004), followed by *P. halepensis* and *P. pinea* in milder environments, and *P. pinaster* tolerating a wider range of conditions.

Among Mediterranean oaks, different strategies in response to drought may contribute to explain species differences in productivity, competitive ability and distribution patterns along aridity gradients (Salleo and Lo Gullo 1990; Acherar and Rambal 1992), which appear to be controlled by their differential leaf habit and tissue water relationships (Villar-Salvador *et al.* 1997; Castro-Díez *et al.* 1998; Quero *et al.* 2006). Our results showed evergreens (especially *Q. ilex*) reaching drier conditions than deciduous oaks. Under water stress the low cell-wall elasticity of evergreens allow them a rapid recovery after a decrease in soil water content, whereas the elastic cell walls of the deciduous oaks would experience a greater water loss in leaves than those of evergreens (Corcuera *et al.* 2002). *Q. faginea* shows a higher stomatal conductance and requires higher water availability to simultaneously increase

growth and storage than *Q. ilex* (Sanz-Pérez *et al.* 2007); thus, the former could be classified as a water-spending species while the later as a drought-avoiding species (Mediavilla *et al.* 2004). Furthermore, under mild freezing conditions common in winter, the maintenance of both photosynthetic and vascular function allows the evergreen species to continue photosynthesis and gas exchange throughout the winter, providing an advantage over their deciduous congeners, which show a higher sensitivity to freezing in leaves and xylem (Cavender-Bares *et al.* 2005). *Q. ilex*, the species with the longest leaf lifespan and narrowest vessel diameters, shows the highest drought and freezing tolerance, which could explain its ability to inhabit a broader range of conditions in Andalusia.

Given the regional scale of the study, the spatial structure detected in species data is mainly related to the strong spatial structure of the main conditioning environmental factors, as the climatic ones. On the contrary, in small spatial scale studies we have found that most of the explained spatially structured variance is related to community-based processes, instead to spatially structured environmental variation (Maltez-Mouro *et al.* 2005, 2007). Furthermore, current distribution of some Mediterranean species is strongly influenced by land use history and current management. For example, *Pinus* and *Quercus* species distribution patterns in North-eastern Iberian Peninsula show a shifting mosaic in stand composition of pines and oaks along disturbance and aridity gradients (Retana *et al.* 1996; Zavala 1999). SSFI sampling favoured abundant species and scarce species are likely to have been under-sampled (e.g., *P. sylvestris*, *Q. pyrenaica*). Although fire frequency did not come to be a significant factor in the models, probably due to the type of variable used in the analyses, it also plays a crucial role in Mediterranean landscapes (Pausas *et al.* 2004a; Broncano *et al.* 2005), together with other factors not recorded here, such as dispersal limitation (Purves *et al.* 2007) or human disturbances (Pliening *et al.* 2003; Urbieta *et al.* in press), which can alter species-environment

correlation (see Pacala and Hurtt 1993; Purves *et al.* 2007).

Pine and oak forest regeneration and stand dynamics

Inventory data revealed that a high percentage of pine and oak forests showed limited regeneration, specially remarkable in the case of *Q. suber* and *Q. canariensis* stands, which emphasize the importance of these species to be included in restoration and conservation plans. Pines' regeneration occurred mainly under the canopy of pine forests, and significantly in forest areas with no tree canopy. Conversely, oaks showed as much regeneration under their own canopy as under pine forests (for *Q. faginea*), or even a greater proportion under the canopy of pines (for *Q. ilex*). These findings support other studies in different regions which reported evidence of pines regenerating mostly in pine-dominated fragments or open areas, and oaks showing highest regeneration in pine dominated stands (Galindo-Jaimes *et al.* 2002).

It is well established that many pine species can germinate and establish successfully in open areas (Broncano *et al.* 1998; González-Espinosa *et al.* 1991), due to their wind dispersed seeds, and their ability to survive and maintain high plant growth in open habitats (Valladares and Sánchez-Gómez 2006), which allow them to become successful invaders (Richardson and Bond 1991). Pines are likely to persist in frequently disturbed stands, thanks to their effective post-fire regeneration (Pausas *et al.* 2003; Broncano *et al.* 2005) or under stressful, i.e. xeric, conditions (Zavala and Zea 2004). Radiation intensity and water stress diminish and can facilitate subsequent oak establishment (Retana *et al.* 1999), which survive better under moderate radiation conditions (Espelta *et al.* 1995; Rey Benayas 1998), such as those found under the canopy of pine forests (Lookingbill and Zavala 2000). At the long run oak saplings might survive under pine canopy due to their greater tolerance to shade (Sánchez-Gómez *et al.* 2006b).

Niche expansion of oaks by facilitation

Many plants modify the local environment and facilitate neighbouring plants of different species simply through their presence, especially in areas with abiotic stress such as the Mediterranean (Bertness and Callaway 1994; Gómez-Aparicio *et al.* 2004). Facilitative interactions may lead to a species' realized niche being larger than its fundamental niche, and might promote the expansion of a species' range margin into more severe environmental conditions than would otherwise be tolerable (Bruno *et al.* 2003). Since high radiation levels lead to increased temperature and high water evaporation rates, germination of many Mediterranean species is expected to be favoured under some degree of canopy closure (Bran *et al.* 1990; Espelta *et al.* 1995). For example, high radiation levels exert a negative effect on oak seedlings as shown experimentally by Valladares *et al.* (2000).

Our results show that a high proportion of the forest regeneration for *Q. ilex* and *Q. faginea* occurs under the canopy of pines, particularly in areas with increasing environmental severity, i.e., in the coldest and more arid extremes of the environmental gradients explored. This suggests a possible facilitative effect of pines on the establishment of oak species. The consequences of the forest regeneration patterns described in this study for stand dynamics support the evidence that an eventual replacement of pines by oaks may occur as predicted in other areas (see Zavala and Zea 2004). The improvement in soil fertility and microclimate provided by *P. halepensis* canopy is known to facilitate the establishment of perennial grasses and shrubs (Maestre *et al.* 2004; Arrieta and Suárez 2006), but negative effects on species richness and plant establishment in the understory have also been reported (Bellot *et al.* 2004). Thus, the suitability of pine forests on spontaneous vegetation establishment is still an open debate (see Maestre *et al.* 2004). Improved understanding of forest structure and facilitation processes along environmental gra-

dients has direct relevance for the development of tools for ecosystem restoration, and for anticipating the response of plant species and communities to key environmental change drivers.

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Appendix 2.1

Principal dominant soil typological units in Andalusia, named according to the FAO-UNESCO soil legend, and derived from the soil geographical database of Europe (scale 1/1000000) (European Soil Bureau 1999). The number of SSFI plots found in each soil type are summarized.

F.A.O. (1974, act)	# SSFI plots
Eutric Planosol	23
Gypsic Xerosol	8
Gleyic Solonchak	0
Rhodo-Chromo-Calcic Luvisol	3
Pellic Vertisol	36
Calcic Xerosol	39
Dystric Lithosol	188
Calcaric Fluvisol	121
Gleyic Acrisol	51
Luvic Arenosol	506
Calcaric Lithosol	223
Rhoso-Chromic Luvisol	123
Chromic Vertisol	299
Eutric Cambisol	1297
Rendzina	1126
Humic Cambisol	605
Calcic Cambisol	3239
Dystric Regosol	1245
Eutric Regosol	3415
MISSING	25
TOTAL	12572

Appendix 2.2

Tables with environmental characteristics of *Quercus* and *Pinus* species distribution range in each of the originally selected environmental variables. See the main text for abbreviations and units.

Variable	<i>Q. ilex</i> (n=6428)				<i>Q. suber</i> (n=2001)				<i>Q. faginea</i> (n=964)			
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
UTMX			105,948	596,000			113,799	494,000			140,068	577,000
UTMY			4,036,000	4,287,000			3,994,000	4,255,000			3,996,000	4,262,000
ALTI	755	432	10	1938	408	222	4	1280	783	384	45	1780
SLOP	13	10	0	53	13	9	0	45	17	9	0	45
SN	0.0	0.7	-1.0	1.0	0.0	0.7	-1.0	1.0	0.2	0.7	-1.0	1.0
PANU	667	167	268	1366	838	182	489	1366	800	175	350	1315
PSPR	177	48	71	356	198	39	111	338	216	56	97	356
PSUM	39	15	13	90	29	9	14	53	45	19	16	85
PAUT	190	41	96	357	241	49	145	355	218	44	108	344
PWIN	262	83	83	655	373	98	186	655	323	88	99	596
TPET	781	79	525	938	827	41	677	929	767	67	557	901
TSUP	341	150	18	1039	484	167	172	1039	465	160	76	970
TDEF	454	70	277	634	471	48	371	601	430	68	289	567
DL	5.1	0.7	4	8	5.0	0.5	4	8	4.7	0.5	4	7
RADANU	4.5	0.1	4.2	4.7	4.4	0.1	4.1	4.6	4.4	0.1	4.1	4.7
RADSUM	6.7	0.1	6.1	7.1	6.5	0.2	5.4	6.9	6.6	0.1	6.2	7.0
TANU	14.8	2.1	7.6	18.3	16.4	1.0	12.3	18.3	14.5	1.9	8.4	18.0
TWM	24.6	1.9	17.9	28.4	25.1	1.1	21.4	27.3	24.4	1.6	18.8	27.3
TCM	6.9	2.1	0.2	11.6	9.3	1.6	5.0	12.5	6.7	2.2	0.9	12.3
TOSCI	17.7	1.4	13.7	20.5	15.8	2.0	12.2	20.4	17.7	1.9	12.2	20.5
SAWC	127.3	48.5	12.0	220.0	120.6	48.0	16.5	220.0	113.2	47.9	12.0	220.0
Variable (*)	Median	Quart.	Min.	Max.	Median	Quart.	Min.	Max.	Median	Quart.	Min.	Max.
SBASE	3	0	1	3	3	2	1	3	3	0	1	3
SCALC	1	2	1	3	1	0	1	3	2	2	1	3
SDEPTH	3	0	1	3	3	0	1	3	3	0	1	3
FIRE (**)	215 (3.3 %)				119 (6.0 %)				29 (3.0 %)			

(*) Median, Quartile range (Q3-Q1), Maximum, Minimum

(**) Number and percentage of SSFI plots that have suffered a fire between 1987-2002

Variable	<i>Q. canariensis</i> (n=300)				<i>Q. pyrenaica</i> (n=49)			
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
UTMX			172,293	366,000			175,418	538,000
UTMY			4,012,000	4,246,000			4,077,000	4,250,000
ALTI	431	206	34	1346	1246	415	538	1926
SLOP	16	8	0	45	18	10	0	45
SN	0.2	0.7	-1.0	1.0	0.0	0.7	-1.0	1.0
PANU	1073	111	628	1338	770	121	603	990
PSPR	249	30	140	332	198	33	148	283
PSUM	27	5	18	49	43	13	26	82
PAUT	304	28	170	352	218	30	165	278
PWIN	496	53	232	638	312	60	216	426
TPET	798	33	661	876	695	83	537	797
TSUP	703	107	298	1011	459	90	290	609
TDEF	424	27	351	520	384	48	303	462
DL	4.8	0.4	4	5	4.7	0.5	4	5
RADANU	4.3	0.1	4.1	4.5	4.5	0.1	4.3	4.6
RADSUM	6.3	0.1	6.2	6.7	6.7	0.1	6.5	6.8
TANU	16.0	0.9	11.7	18.0	12.4	2.5	7.9	15.6
TWM	24.1	0.6	20.8	25.8	22.3	2.3	18.3	25.8
TCM	9.6	1.2	5.2	12.3	4.9	2.5	0.4	8.2
TOSCI	14.5	0.9	12.7	19.1	17.4	1.1	15.4	20.4
SAWC	79.0	36.5	16.5	220.0	129.6	46.7	63.5	165.0
Variable (*)	Median	Quart.	Min.	Max.	Median	Quart.	Min.	Max.
SBASE	1	2	1	3	3	0	1	3
SCALC	1	0	1	3	1	2	1	3
SDEPTH	3	0	1	3	3	0	1	3
FIRE (**)	5 (1.6%)				1 (2.0%)			

Distribución y regeneración de los bosques de *Quercus* y *Pinus*

Variable	<i>P. halepensis</i> (n=1972)				<i>P. pinaster</i> (n=1781)				<i>P. pinea</i> (n=1495)			
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
UTMX			162,673	597,000			110,800	583,000			108,905	544,000
UTMY			4,008,000	4,261,000			4,002,000	4,262,000			3,995,000	4,261,000
ALTI	946	301	20	1666	918	416	5	1958	362	268	0	1426
SLOP	18	10	0	53	18	9	0	49	10	9	0	41
SN	0.0	0.7	-1.0	1.0	0.0	0.7	-1.0	1.0	-0.1	0.7	-1.0	1.0
PANU	557	187	212	1363	723	191	308	1361	633	96	350	1321
PSPR	154	57	57	355	193	56	82	356	156	26	96	333
PSUM	39	16	11	86	41	17	12	84	29	11	12	78
PAUT	161	43	71	357	203	50	90	356	183	28	116	345
PWIN	202	88	62	654	286	97	91	654	265	50	108	606
TPET	738	51	623	915	748	72	525	919	855	43	674	929
TSUP	248	167	0	1033	397	169	41	1033	301	87	76	980
TDEF	429	56	15	673	422	64	288	603	521	50	1	603
DL	5.6	1.2	1	11	4.9	0.7	4	8	5.6	1.1	1	8
RADANU	4.5	0.1	4.2	4.7	4.5	0.1	4.1	4.7	4.4	0.1	4.1	4.7
RADSUM	6.7	0.1	5.8	7.1	6.6	0.1	5.9	7.1	6.5	0.2	5.3	6.9
TANU	13.9	1.5	10.3	18.4	14.0	2.0	7.6	18.3	16.7	1.2	11.7	18.4
TWM	23.6	1.2	20.3	27.5	23.8	1.9	17.9	27.9	26.0	0.8	21.3	27.9
TCM	6.3	1.8	2.4	12.0	6.4	2.2	0.2	12.0	8.9	1.8	3.6	12.3
TOSCI	17.3	1.4	12.6	20.2	17.4	1.7	12.4	20.4	17.1	2.1	12.2	20.4
SAWC	122.4	52.6	12.0	220.0	113	50.6	12.0	220.0	132	41.9	63.5	220.0
Variable (*)	Median	Quart.	Min.	Max.	Median	Quart.	Min.	Max.	Median	Quart.	Min.	Max.
SBASE	3	0	1	3	3	0	1	3	3	1	1	3
SCALC	3	0	1	3	1	2	1	3	1	1	1	3
SDEPTH	3	0	1	3	3	0	1	3	3	0	1	3
FIRE*	96 (4.8%)				152 (8.5%)				63 (4.2 %)			

(*) Median, Quartile range (Q3-Q1), Maximum, Minimum

(**) Number and percentage of SSFI plots that have suffered a fire between 1987-2002

Variable	<i>P. nigra</i> (n=991)				<i>P. sylvestris</i> (n=291)			
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
UTMX			127,364	583,000			318,000	578,000
UTMY			4,061,000	4,249,000			4,063,000	4,239,000
ALTI	1492	256	41	2305	1807	215	1214	2309
SLOP	18	9	0	53	17	7	0	42
SN	0.1	0.7	-1.0	1.0	0.1	0.7	-1.0	1.0
PANU	715	211	347	1129	562	102	391	1066
PSPR	213	71	97	356	156	25	111	330
PSUM	59	19	15	90	42	7	25	78
PAUT	192	39	108	280	170	28	110	278
PWIN	252	89	88	437	195	54	106	417
TPET	656	32	525	896	625	33	523	715
TSUP	398	193	50	791	275	104	86	713
TDEF	338	30	277	565	336	27	276	415
DL	4.5	0.6	4	8	4.9	0.4	4	6
RADANU	4.5	0.1	4.3	4.7	4.6	0.1	4.3	4.6
RADSUM	6.7	0.1	6.4	6.9	6.7	0.0	6.5	6.8
TANU	11.3	1.0	7.6	18.0	10.3	1.1	7.3	13.5
TWM	21.6	1.1	17.9	26.3	20.1	1.1	17.4	23.2
TCM	3.6	1.0	0.2	10.9	3.2	1.0	-0.1	6.6
TOSCI	18.0	1.0	15.0	19.4	16.9	0.7	15.2	19.0
SAWC	76.2	44.6	12.0	165.0	64.5	46.4	12.0	165.0
Variable (*)	Median	Quart.	Min.	Max.	Median	Quart.	Min.	Max.
SBASE	3	0	1	3	3	0	1	3
SCALC	3	0	1	3	1	2	1	3
SDEPTH	2	1	1	3	3	2	1	3
FIRE*	11 (1.1%)				7 (2.4%)			