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Oak regeneration in heterogeneous landscapes: The case of fragmented *Quercus suber* forests in the eastern Iberian Peninsula

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Abstract

Quercus suber recruitment is quantified at local (in different vegetation types) and landscape level in three marginal populations (sites) ranging in size from 70 to 7000 ha and located in the eastern Iberian Peninsula (Spain). We hypothesised that: (1) recruitment of marginal *Q. suber* populations in eastern Iberia should be higher than in the core area of distribution, western Iberia, (2) within our study area, there should be a trend in the regeneration from north (the largest forest patch) to south (the smallest patch), and (3) within a site, recruitment should not be randomly distributed, but rather some vegetation types should show higher recruitment than other vegetation types. To test these hypotheses, a total of 61 plots measuring 12.5 m × 12.5 m were established on seven vegetation types in five previously selected 3 km × 3 km quadrats. On each plot all *Quercus* plants shorter than 3 m were labelled and tracked between 2003 and 2005. Results support the first and third hypotheses but not the second one. *Q. suber* recruitment densities ranged from 0 to 7200 plants per hectare. The complete regeneration process (from recruitment to growth) occurred on old fields; well-established seedling banks were abundant under forest canopies; recruitment in shrublands was practically null. To better understand *Q. suber* recruitment, both landscape configuration and interactions with other *Quercus* species should be considered.

Keywords: Cork oak; Evergreen oak; *Quercus suber*; Mediterranean ecosystems; Recruitment; Regeneration pattern; Seedling density

1. Introduction

Natural oak regeneration is the product of complex processes such as acorn production, predation, animal dispersion, germination and establishment in the habitat where the acorns were dispersed, and finally, growth to mature trees (Schupp, 1990). The combination of all these processes may determine the success or failure of oak regeneration and the final fitness of this species to a given set of conditions. Thus, evaluating natural regeneration is an integrative way to evaluate fitness and provides a first indication of the future of the populations under study.

Quercus suber (cork oak) is an evergreen tree species from the western part of the Mediterranean Basin (Tutin et al., 1964). In the Iberian Peninsula, most *Q. suber* occur in a highly managed savannah-like agrosystem (called *dehesa* or *montado*) on acidic soils (the core area). Nevertheless, several patches of cork oak (peripheral cork oak patches) also occur in the eastern part of the peninsula, where calcareous soils are dominant. There are some large *Q. suber* forests in the northern part of the eastern Iberian Peninsula (Catalonia, ca. 70,000 ha, Montero et al., 1994); however, patch size decreases towards the south by about three orders of magnitude. Thus, in the Valencia region (eastern Iberia), the main *Q. suber* forest patches range from ca. 70 to 7000 ha (Pausas et al., 2004) and are considered marginal and fragmented, and their future has been questioned. Even so, there is still some cork industry in the region. In fact, cork oak forests are protected by the European Union (Habitat directive 92/43/EEC), and the cork oak is considered an important species for the socio-economic development of some European regions due to its potential use in sustainable forestry (*Q. suber* products, cork and acorns, do not require the elimination of trees but rather their protection). Furthermore, *Q. suber* is a very good candidate for reforestation plans in the Mediterranean area due its efficient and rapid post-fire regeneration capacity (Pausas, 1997). All these aspects contribute to the importance of amassing knowledge on this species and its natural regeneration capacity in order to focus further

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restoration plans (Mosandl and Kleinert, 1998; Pausas et al., 2004). To date, however, very little research has been performed on the regeneration of *Q. suber* (Montero et al., 1994), and it has been carried out only in the core area of the species distribution. There is increasing evidence of the conservation and biodiversity value of peripheral populations (Lesica and Allendorf, 1995; Hampe and Petit, 2005), and specifically of *Q. suber*, due to the distinct genetic pools between central and peripheral populations (Jiménez et al., 1999).

Most current landscapes are highly heterogeneous at several spatial scales, and studies on oak dispersal and regeneration should account for this spatial variability in order to understand the future of this species. Thus our initial hypotheses are framed within different spatial scales: between eastern and western Iberian Peninsula, between different sites of the eastern Peninsula, and between different patch types within the landscape.

Regeneration problems have been described for a variety of *Quercus* species (e.g., Shaw, 1968; Mellanby, 1968; Loftis and McGee, 1993; Lorimer et al., 1994), but little is known about regeneration of Mediterranean species. Part of the research on Mediterranean *Quercus* has been performed in the *dehesa* agrosystems of SW Spain (Plieninget et al., 2004; Pulido and Díaz, 2005). In such *dehesas*, oak regeneration seems to be much lower than in forest ecosystems (Pulido and Díaz, 2005), probably because intense human impacts (Plieninget et al., 2004) have resulted in an unsuccessful acorn dispersal and a heavy grazing pressure (Pulido and Díaz, 2005). In eastern Iberia, these pressures (intense human impact and grazing) have decreased in recent last decades due to rural exodus and abandonment processes occurring on European Mediterranean coasts (Pausas, 2004). Thus, our first hypothesis is that *Q. suber* regeneration in eastern populations will be higher than *Quercus* regeneration in dehesas.

Our second hypothesis is that regeneration will decrease from northern (larger) to southern (smaller) populations (site–scale analysis) and that this may be due to different processes. It is well known that small populations may face both inbreeding effects and genetic erosion, which result in a reduction in their viable seed production and seed quality and make them more prone to extinction (Lawton, 1993; Vucetich and Waite, 2003). This would be reflected in the regeneration process. In this context, it has been demonstrated that marginal *Q. suber* populations have lower genetic diversity than central populations (Jiménez et al., 1999). Thus, we could expect a decreasing regeneration pattern that parallels the size of the different populations, especially with respect to the southernmost population (Pinet), which is considered small for a tree population (ca. 70 ha of low-density trees). Furthermore, the fact that forests are the main habitat for the oak-dispersal agent (the European jay *Garrulus glandarius*) and there is a decreasing abundance of forest stands from north to south in our study area (Pausas et al., 2004) could also contribute to reduced *Q. suber* regeneration. Finally, small populations have a higher edge effect, which may imply higher predation (Santos and Telleria, 1997) and disturbance sensitivity. All these processes would suggest that regeneration would decrease from northern to southern *Q. suber* populations in eastern Iberia.

Our third hypothesis is that, at landscape scale, regeneration will not be randomly distributed because environmental conditions and biotic factors (dispersal, predation, competition) affecting seed and seedling success vary in different landscape units (Grime and Hillier, 2000; Gómez et al., 2004). Thus, given the current heterogeneity of our landscapes we expect differential recruitment and regeneration processes for different spatial units.

To test these hypotheses we quantified the amount and variability of *Q. suber* recruitment and that of all other *Quercus* species appearing within the study area in different landscape units around the three main *Q. suber* patches in the Valencia region. We considered the following non-sequential stages of regeneration: recruitment, development of seedlings, formation of a seedling (sapling) bank and development to mature trees. The final objective was to understand to what extent these fragmented marginal cork oak populations are stable and would persist in the study area. Alternatively, other oak species may preferentially occupy the potential habitat of *Q. suber* and thus displace it.

2. Methods

2.1. Study area

The study area is located inside the Valencia region, which borders the Mediterranean coast in eastern Spain (Fig. 1). The climate is typically Mediterranean. The vegetation is a product of a long history of fire and land use, and many slopes were terraced and cultivated in the past, and then abandoned. In this region there are three main *Q. suber* patches (hereafter sites), from north to south: Espadà (Castelló, lat = 39°52′, ca. 7,000 ha), Calderona (València, lat = 39°44′, ca. 700 ha) and Pinet (València, lat = 38° 59′, ca. 70 ha). Soils in Calderona and Espadà are mainly acidic soils on sandstones. In Espadà soil pH ranges from 4.9 to 6.4 (mean: 5.7). In Pinet, cork oak occurs in non-carbonated soils on dolomites, with pH ranging from 5.5 to 7.5 (mean: 6.5). Average annual rainfall in these cork patches ranges from 500 to 800 mm, with a clear seasonal pattern showing two peaks, in spring and autumn. Espadà and Calderona are currently Natural Parks.

2.2. Sampling

In order to study a wide range of cork oak landscape conditions, we selected five 3 km × 3 km areas (hereafter quadrats) distributed on the three main sites: two quadrats on the Espadà site, two in Calderona and one in Pinet (Fig. 1). The quadrats include a variety of both vegetation types and environmental conditions (soils, aspect), but they mostly fall within the range of environmental conditions under which *Q. suber* is observed in the study area. For instance, soils are all non-carbonated, from acidic sandstones (mainly Espadà) to dolomitic soils (in Pinet). We mapped each quadrat into simple vegetation units during an intense field sampling; then the

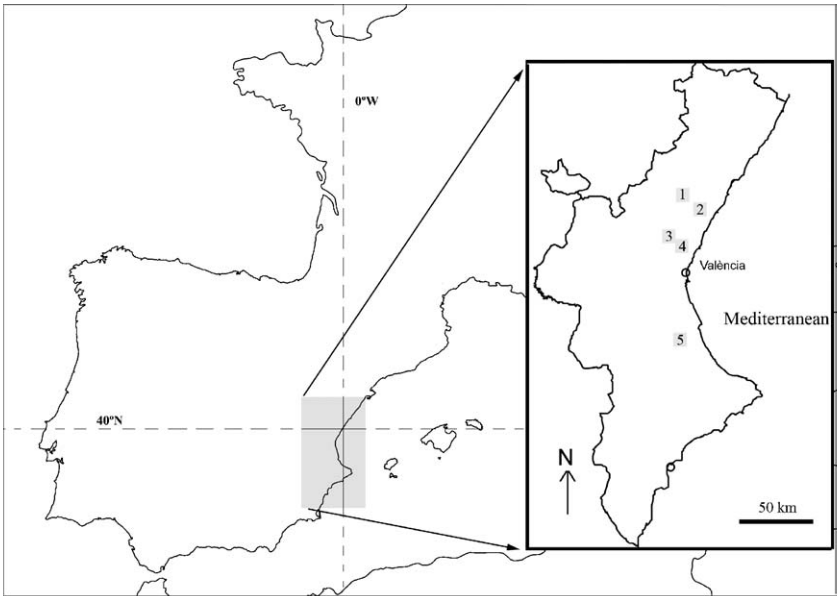

Fig. 1. Localisation of the five sampled quadrats. From north (top) to south (bottom), two quadrats in Espadà (1 and 2), two quadrats in Calderona (3 and 4) and one quadrat in Pinet (5).

information was translated to digital maps for subsequent landscape analysis. Vegetation units were aggregated into seven vegetation types (hereafter VTypes) for the regeneration sampling, as follows:

- *Yaf*: Recently abandoned (young) old fields, with grass-dominated vegetation.
- *Oaf*: Old fields abandoned long ago, currently dominated by woody plants.
- *Maf*: Old fields that apparently had an age between Yaf and Oaf due to the combination of grass and young woody plants.
- *Shrub*: Shrublands.
- *PineS*: Pine forest with shrubby understory.
- *PineC*: Pine forest with clear understory, that is, with low shrub cover or grassy understory.
- *Cork*: Cork oak forest.

In each vegetation unit, we sampled *Quercus* regeneration within 12.5 m × 12.5 m plots. In addition to *Q. suber*, other oak species found in the study area are two evergreen (*Q. ilex, Q. coccifera*) and one semi-deciduous (*Q. faginea*) species. The number of plots included in each site and Vegetation unit varied from 0 to 5 depending on the availability of the VTypes on each site (Table 1); for instance, the only old fields in the Pinet area were recently abandoned (Yaf), while Oaf and Maf were missing. All plots were located at a maximum of 150 m from adult *Q. suber* trees, as most dispersed acorns fall within this interval (Bossema, 1979; Pons and Pausas, unpublished). In June 2003, we counted and tagged all oak individuals regenerating on 36 plots. In June 2004 and 2005, we revisited all plots to quantify both the new recruitment and the aerial stem die-back of the individuals tagged in 2003. Additional plots were set in 2004 and 2005, reaching a total of 61 plots. Recruitment was classified in four categories: seedlings (with acorn or cotyledon scatters still attached), saplings (<50 cm without acorn and with a clear main stem), resprouting sapling (<50 cm with evidence of new shoots after top killing) and small trees (50–300 cm).

Table 1
Number of plots sampled in each VType and site

	Espadà	Calderona	Pinet	Total
Yaf	3	3	2	8
Maf	2	1	0	3
Oaf	3	3	0	6
Shrub	3	5	3	11
PineS	3	1	3	7
PineC	4	5	3	12
Cork	3	4	3	10
Others	2	1	1	4
Total	23	23	15	61

2.3. Data analysis

Landscape analysis was performed for each of the five quadrats using Fragstats (McGarigal and Marks, 1994). Regeneration density was expressed as the number of individuals in 100 m^2. Regeneration variability was tested against VType and site using ANOVA with Quadrat as the nested factor within site. Previous to analysis, regeneration density was square-root transformed. A one-way model with both VType and site was also performed to check the different amounts of variance explained by each of these two factors.

3. Results

3.1. Landscape analysis

Landscape pattern differs between different quadrats and sites (Table 2). The northern quadrats (Espadà) are more

Table 2
Composition and configuration attributes of the five landscape quadrats considered

	Espadà		Calderona		Pinet
	Q1	Q2	Q3	Q4	Q5
Landscape composition (% area)					
Fields	5.1	5.6	8.0	0.9	2.9
Old fields	2.0	**13.6**	4.1	0.3	1.4
Shrublands	29.1	22.3	43.7	**81.4**	**85.6**
Tree-shrublands	7.4	18.0	9.6	2.5	3.3
Pine forest	**31.5**	0.7	18.5	9.7	4.0
Oak forest	24.6	**38.4**	15.4	4.1	2.7
Urban	0.1	1.5	.6	0.1	0.0
Others	0.2	0.0	0.0	0.9	0.0
Landscape configuration					
Number of polygons	150	173	**194**	72	**58**
Mean polygon size (ha)	6.0	5.2	4.6	**12.5**	**15.5**
Polygon size S.D.	23.3	25.2	22.5	85.5	99.0
Total edge (km)	169	191	**209**	83	78
Shannon diversity index	1.747	1.741	1.757	1.495	1.552

In bold are relevant figures emphasising differences between quadrats (see main text and Fig. 1).

forested than the Calderona and Pinet quadrats. However, the type of forest differs between the two Espadà quadrats: Quadrat 1 includes a mixed forest with several oak and pine species, while Quadrat 2 is the result of several recent fires and the only dominant tree species is *Q. suber*. Quadrat 3 (Calderona) is the most patched quadrat, with both forests and shrublands. Quadrat 4 (Calderona) and Quadrat 5 (Pinet) are very homogeneous landscapes dominated by shrubs and result from fires during the 1990s. That is, forests decrease from Espadà to Pinet and from Quadrat 1 to Quadrat 5.

3.2. Recruitment

Table 3
Basic statistics for *Quercus* density values (individuals per 100 m^2) found in the study area in plots where at least one individual was present Qs: *Q. suber*; Others: other Quercus species

	n	%	Mean	S.D.	Max	p-Values
Qs year 2003	30		15.4	16.1	58.2	
Others year 2003	31		5.5	11.0	54.4	
Qs year 2004	48		16.1	18.7	67.8	
Others year 2004	48		6.1	10.7	58.9	
Qs year 2005	55		14.7	18.4	76.2	
Others year 2005	53		5.9	10.2	58.9	
Qs difference 2004–2003	29		+1.6	4.7	13.4	*
Others difference 2004–2003	30		+1.3	2.7	9.0	***
Qs difference 2005–2004	48		−0.4	3.6	9.0	**
Others difference 2005–2004	48		+0.2	1.9	5.8	***
Total Qs (n = 54)		100.0	15.0	17.7	67.8	
Seedlings		11.3	1.7	2.4	9.6	
Saplings		24.4	3.7	5.8	22.4	
Sprouting saplings		50.1	7.5	12.3	57.6	
Young trees		14.2	2.1	3.8	15.4	

[*] $p < 0.05$ (Shapiro test).
[**] $p < 0.01$ (Shapiro test).
[***] $p < 0.001$ (Shapiro test).

Recruitment of *Q. suber* is highly variable, ranging from 0 to 76.2 individuals/100 m^2 (Table 3), and shows a clearly skewed distribution (Fig. 2a). Most of the recruitment (50.1%) consisted of sprouting saplings, 24.4% were saplings, and the remaining were small trees (14.2%) and seedlings (11.3%). The distribution of each of these recruitment classes follows a similar pattern to the total regeneration. In 2005, 15 of the 55 plots showed no *Q. suber* regeneration. Changes in regeneration density follow a bell-shaped curve for both year pairs (Shapiro test, Table 3), with both gains and losses (Fig. 2b).

Overall, regeneration of other *Quercus* species represents 28% of the total *Quercus* regeneration, and ranged from 0 to

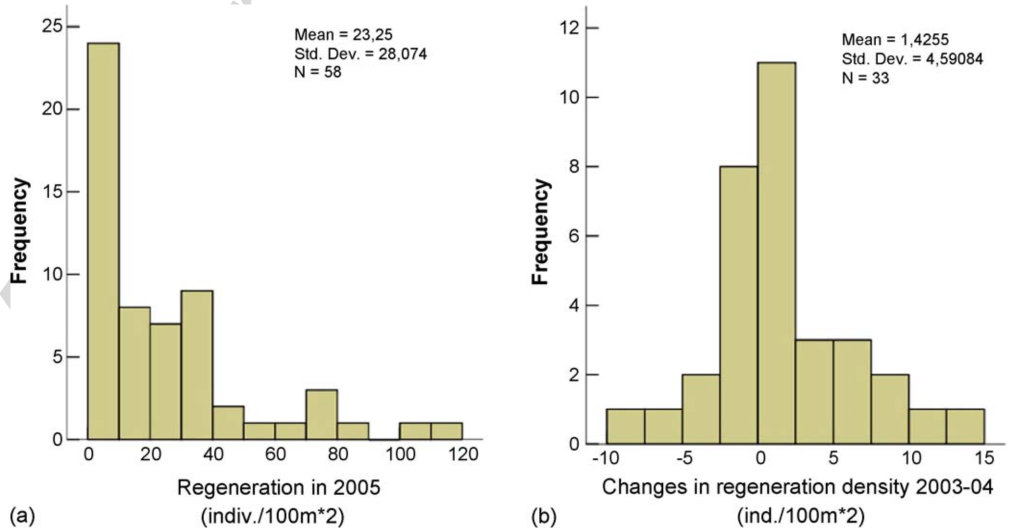

Fig. 2. (a) Frequency distribution of regeneration (individuals/100 m^2) in 2005 and (b) changes in regeneration density (individuals/100 m^2) between 2003 and 2004 (positive values are increases and negative values decreases).

Table 4
ANOVA results for *Q. suber* density and height

	p-Values					R^2		
	Model	V	S	Q(S)	VxS	V + S	V	S
Total density 2003	0.001	0.005	0.003	ns	ns	0.851	0.440	0.338
Total density 2004	0.000	0.000	0.002	ns	ns	0.783	0.484	0.237
Total density 2005	0.000	0.000	0.000	ns	ns	0.806	0.530	0.185
Difference 2003-04	0.082	ns	0.061	0.063	ns	0.683	0.424	0.278
Difference 2004-05	ns	ns	ns	ns	ns	0.250	0.072	0.068
Seedling density	0.002	0.023	0.001	ns	0.053	0.654	0.247	0.221
Sapling density	0.017	0.005	0.059	ns	ns	0.580	0.331	0.150
Sprout sap. density	0.000	0.000	0.006	ns	ns	0.789	0.582	0.121
Young tree density	0.000	0.008	0.000	ns	0.010	0.742	0.240	0.269

p-Values for the model with VType (V), site (S), quadrat nested within site (Q (S)), and the interaction (V × S); and R^2 of the model with only vegetation type, with only site and with both vegetation type and site (V + S). Density was square-root transformed previous to the analyses. ns indicates $p > 0.1$.

58.9 individuals/100 m^2 (mean for 2005 = 5.9 ± 10.2 S.D.), with a very strong skewed distribution: 30% of the plots had no regeneration of other *Quercus* species and 85% had less that 9 individuals/100 m^2. Changes in the regeneration density of these species are small and also follow a bell-shaped curve (Table 3). The species composition of this regeneration includes 54% of *Q. ilex*, 27% of *Q. coccifera* and 19% of *Q. faginea*.

Total *Q. suber* recruitment density for the 3 years of the study was significantly related to Vegetation Type (VType) and site, and most explained variance was due to VType (R^2 in Table 4). Similar trends were observed for each regeneration class (Table 4) with the exception of small trees, for which the site effect was more important than the VType effect. The highest recruitment was found in forest ecosystems, either pine (PineC) or cork oak forest (means for 2004 = 23 and 30.4 individuals/100 m^2, respectively), while the lowest was in shrublands (mean = 0.27 individuals/100 m^2). Old fields and shrubby pine forests (PineS) showed intermediate regeneration values (mean = 6.6–9.6 individuals/100m^2) (Table 5). Looking at the different recruitment classes (Fig. 3) a pattern emerges: (a) in old fields, there is a trend toward decreasing seedling and sapling density and increasing young trees with abandonment age, with very few levels of sprouting saplings in all old fields; (b) in the forests, the distribution of recruitment classes is similar, with increasing density from shrubby forest to cork forest; and (c) in shrublands, recruitment is almost negligible.

There is also some variation between sites, with Espadà presenting the highest plant density (22.35 ± 18 individuals/100 m^2), Calderona the lowest (6.7 ± 9.7 individuals/100 m^2), and Pinet an intermediate value close to that of Espadà (19.2 ± 20.46 individuals/100 m^2). These differences are due mostly to the number of sprouting saplings (Fig. 4).

Table 5
Summary of the significance between VTypes for each regeneration class (Fig. 3)

Regeneration classes	VTypes						
	Yaf	Maf	Oaf	Shrubs	PineS	PineC	Cork
Sprouting seedlings	bc	b	bc	bc	b	b	ab
Young trees	b	ab	a	b	ab	b	b

Regeneration densities in different VTypes with different letters are significantly different. Differences for seedlings, sapling and recruits are not significant. The mean density values decrease from a to c, within each regeneration class.

The changes observed in *Q. suber* recruitment density among the 3 years studied were not related exclusively to VType; some of the changes (for 2003–04) were related to quadrat or site (Table 4).

In general, the regeneration distribution pattern of the other *Quercus* species considered (*Q. ilex*, *Q. faginea* and *Q. coccifera*) was similar to that of *Q. suber*, when respective adults were nearby (not shown). Nevertheless, the relative abundance of other *Quercus* species (from 0.5% at Quadrat 2 to 54.9% in Quadrat 3) differs in each site and each Quadrat.

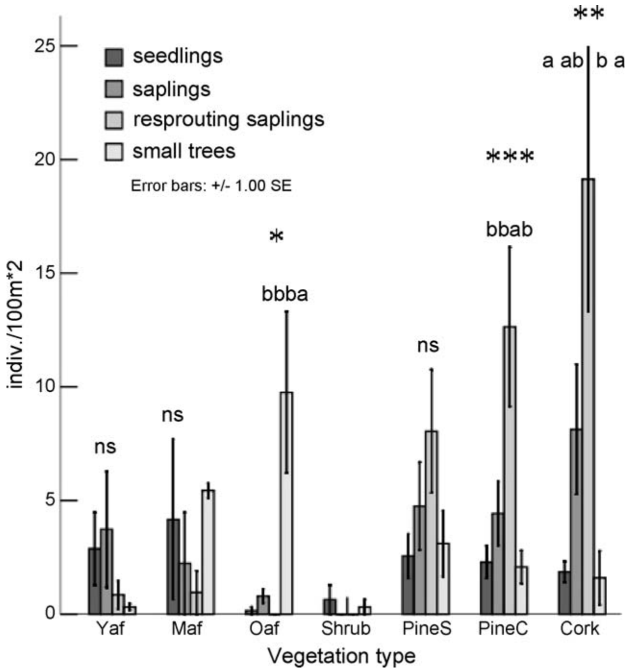

Fig. 3. Mean *Q. suber* regeneration density by VType and regeneration class. Non-different regeneration class density means (individuals/100 m^2) are identified by the same letters in each VType. Table 5 shows the significance of density differences between VTypes for each regeneration classes.

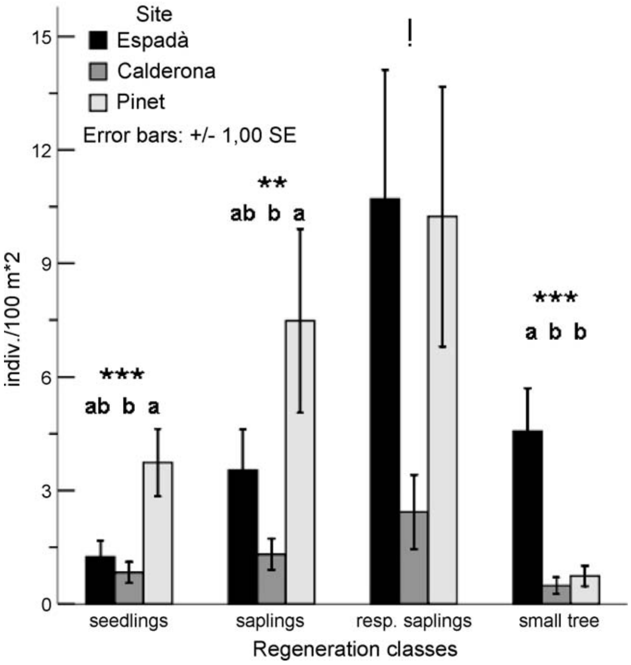

Fig. 4. Mean regeneration density on the three studied sites for each regeneration class of *Q. suber* recruits. Significant differences are coded by different letters. Symbols used for significant probability are: $^{!}p < 0.1$, $^{**}p < 0.01$, $^{***}p < 0.001$.

4. Discussion

4.1. Cork oak recruitment pattern

To our knowledge this is the first paper studying *Q. suber* recruitment at landscape level, and thus, most of the comparisons we make hereafter will be with other *Quercus* species, especially *Q. ilex*.

Overall *Q. suber* recruitment densities in marginal cork oak populations of the eastern Iberian Peninsula are highly variable depending on the vegetation type considered, and they fall within the broad range of density values available for *Quercus ilex* in nearby areas (see Table 6). In this region the habitat most similar to the western Iberian dehesa would probably be the old fields because both dehesas and old fields have non-continuous tree cover (absence of shaded microsites) with a large proportion of shrub-free soil. In our old fields, total densities are between five and nine times larger than in the dehesas. This may be due both to the current low grazing levels in our area and the dispersal limitation found in dehesas (Pulido and Díaz, 2005); a dispersal limitation has also been observed in North American forest–savannah ecotones (Weltzin and McPherson, 1999). Nevertheless, the maximum densities of *Q. ilex* seedlings under cospecifics reported in a study on mature Holm oak in Catalonia (NE Iberian Peninsula) were much greater than the maximum densities recorded in our study (Table 6).

The primary source of regeneration variation was found to be the vegetation type (habitat); moreover, the distribution of the regeneration between vegetation types was consistent (i.e., showing similar patterns) between sites, which suggests that similar processes were occurring on each site. These main processes are:

(a) There is very limited recruitment in shrublands (Fig. 3). Although we cannot yet pinpoint the causes, possible hypotheses are: limited seed arrival, high seed predation, germination failure or competitive exclusion. As all of these are sequentially connected, the first seems to be the limiting one since the jay's habit of directing dispersal to open soil and actively avoiding closed shrublands has been widely reported (Bossema, 1979; Darley-Hill and Johnson, 1981; Kollmann and Schill, 1996; Johnson et al., 1997; Frost and Rydin, 2000; Gómez, 2003). Furthermore, high acorn predator densities (mouse) are often found under shrublands (Wilson and Whelan, 1990; Alcantara, 2000; Hulme, 1994; Hulme, 1997). However, although limited, some recruitment occurred in shrublands composed mainly by *Erica* species under pines, and thus, a possible 'filtering' of recruits depending on shrub composition and structure (George and Bazzaz, 1999) deserves future attention in Mediterranean systems.

Table 6
Mean, S.D. and maximum recruitment values observed for different European *Quercus* species in relation to their habitat

Habitat	sp	Mean ± S.D.	Max density recruits (ha)	Study site	Reference
Dehesas[a]	Qi	136.4	>342	Extremadura (SW)	Plieninget et al. (2004)
Old fields	Qs	708 ± 805	2176	València (E)	This study
Pine forest	Qs	2309 ± 1698	5248	València (E)	This study
Pine forest	Qi	–	5461	València (E)	Own data (unpublished)
Pine forest[b]	Qi	1600	3800	Catalunya (NE)	Lookingbill and Zavala (2000)
Cork forest	Qs	806		Extremadura (SW)	Currás et al. (1995)
Cork forest	Qs	3040 ± 2103	6784	València (E)	This study
Holm oak forest	Qi		29000	Catalunya (NE)	Espelta et al. (1995)
Holm oak forest	Qi		40000	Catalunya (NE)	Gracia et al. (2001)
Holm oak forest[c]	Qi	1763–18024	–	Catalunya (NE)	Retana et al. (1999)
Pine forest (*P. sylvestris*)	Qp		4255	Saxony (Germany)	Mosandl and Kleinert (1998)

Species are *Quercus ilex* (Qi), *Q. suber* (Qs), *Q. petraea* (Qp). For the Iberian regions, cardinal locations within the Iberian Peninsula are given in brackets.

[a] Saplings.

[b] Seedlings (individuals under 25 cm in height without a well-developed lignotuber).

[c] Variability between two sites and three aspects.

(b) There is a clear dynamic process in old fields (Fig. 3 left): recruitment is observed at the beginning of abandonment; then, as the vegetation cover increases acorn inputs decrease and seedlings develop into saplings. Finally, shrubs and herbs cover ca. 100% of soil and no new seedlings appear (as in the shrublands), suggesting that the recruitment window closes when saplings develop into young trees. This emphasises the importance of the temporal regeneration window in old field succession (Kollmann, 1995). Although we do not have information on growth, the very low densities of sprouting saplings (i.e., low top killing) suggest very low stressful conditions in old fields, with the exception of eventual anthropogenic disturbances or grazing at the beginning of abandonment.

(c) In pine and oak forests, there is a high recruitment of new individuals; however, seedling desiccation and top killing is a very important process here, and many sprouting seedlings accumulate in a sprouting seedling bank without developing into trees (Fig. 3 right). Thus, under these conditions, *Q. suber* form a typical seedling bank (Kohyama, 1983; Marks and Gardesu, 1998; Antos et al., 2005), that is, a pool of suppressed slow-growing individuals waiting for improved growing conditions. *Quercus* seedling banks under conifers seem to be widely spread for different species and environments (Mosandl and Kleinert, 1998; Montero et al., 1994).

Variations at regional scale (between sites) occur primarily in the size of the seedling bank (Fig. 4) and are difficult to attribute to one unique cause. Our initial hypothesis that the recruitment density would decrease as the *Q. suber* population size decreased must be rejected because the northern and southern populations (Espadà and Pinet) showed similar recruitment levels while the central population (Calderona) showed lower recruitment levels. Alternative hypotheses may be related to (a) competition for dispersal, and (b) landscape structure. All *Quercus* species have the same dispersal agents and acorns of different species may compete to be dispersed. Thus, considering all *Quercus* species, the northern population (Espadà) has the densest *Quercus* recruitment. This would suggest that the future of *Q. suber* may interact with the dynamics of other *Quercus* species, including different degrees of asynchrony in the masting (Kelly and Sork, 2002). The landscape hypothesis suggests that the configuration and amount of suitable patches in relation to source patches may determine recruitment. For instance, it was expected that the Pinet population would have lower recruitment than the Calderona population both because Pinet is a small, marginal *Q. suber* population and because the amount of forest (jay habitat) in the area is very low (Table 2), but the opposite was true. Quadrat 4 in Calderona and Quadrat 5 in Pinet have a similar landscape composition (dominated by shrublands, Table 2), but the spatial configuration of the landscape is different (Fig. 5) in such a way that in Quadrat 5 the habitats with higher recruitment (pine forests and old fields) are surrounded by the source of acorns (cork oak forest), while in Quadrat 4 they are more spatially segregated. Thus, in Quadrat 5 shorter dispersal distances (jay flights) are required, which may explain the higher recruitment in Quadrat 5 than in Quadrat 4. Furthermore, the small amount of forest in the Pinet area, which we hypothesised to be negative because of the low jay habitat, may in fact be positive for regeneration because of the higher forest-to-jay pair ratio. Contrary to the results by Santos and Telleria (1997), overpressure by rodent populations on acorns in smaller forests does not seem to occur in our area as *A. sylvaticus* usually showed a lower preference for the forest habitat than for the surrounding matrix (shrubland), probably because of the higher predation risk in the forest (Díaz et al., 2005). A further difference between both sites is that red squirrels (*S. vulgaris*) were observed at Calderona (Q4) but not at Pinet (Q5); nevertheless, the role that this animal might have on recruitment is still unknown. All these hypotheses are at a smaller scale (quadrat) than the site, and they need further research.

Competitiveness from other *Quercus* at regeneration level seems to occur but our data are too limited to state general rules despite showing that some trends arise: in mesic forested areas with the absence of fires, *Q. ilex, Q. faginea* (and on more humid sites, *Q. pyrenaica*) seem to reduces *Q. suber* regeneration (Villamalur area, Quadrat 1). The same seems

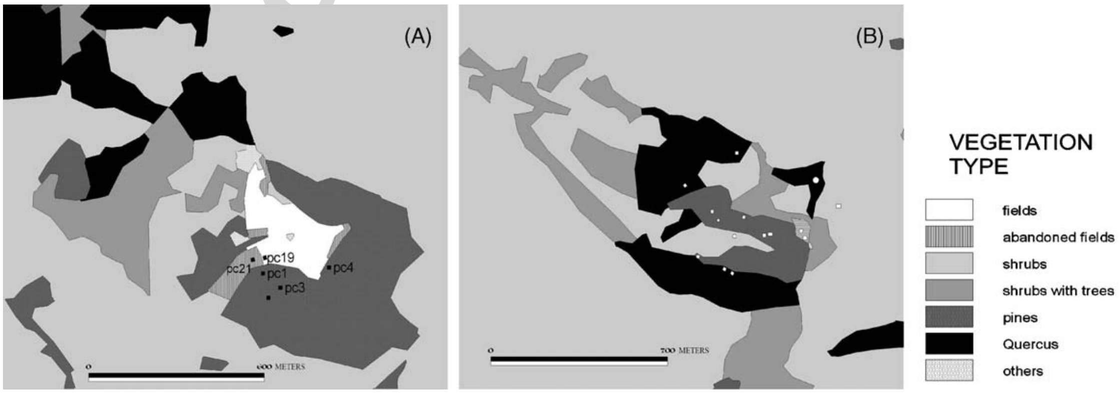

Fig. 5. Differences in spatial vegetation pattern at (A) Portacoeli (Quadrat 4) and (B) Pinet (Quadrate 5) in relation to the position of studied plot (black dots in A and white dots in B). In (A) the susceptible regeneration area (pine forests and fields) is aggregated to SW, at longer distances from acorn sources (black patches) than in B. In (B) *Q. suber* regeneration densities are greater, probably because the susceptible regeneration area is surrounded by acorn sources. Both areas are included in a shrubland matrix (pale grey).

true for *Q. ilex* and *Q. coccifera* in xeric areas (Calderona). However, the current and future fire regime seems to favour *Q. suber* due to its fire resistance mechanisms (Pausas, 1997).

4.2. Implications for cork oak regeneration

Our results indicate that good regeneration currently occurs on abandoned land. However, most of these fields were abandoned 25–40 years ago. As time passes, more fields will become incapacitated for new acorn arrival because of herb and shrub inhibition (Kollmann, 1995). The lack of wild herbivores and the abandonment of extensive livestock-breeding in Mediterranean dry areas have contributed to the homogenisation and loss of open areas in the region. Nevertheless, this loss of heterogeneity and continuity of fire fuels may increase the annual fire frequency and area burned (Pausas, 2004). And *Q. suber* will probably take advantage of this situation through three mechanisms:

(a) its strong fire resistance (Pausas, 1997) may give it a competitive advantage;
(b) fire may act as a grazer (Bond and Keeley, 2005) and re-open the regeneration window for *Q. suber* in old fields and shrublands; and
(c) despite the large amounts of recruitment in pine and oak forests (Fig. 3), regeneration does not occur, probably because the forest canopy reduces seedling growth. It has been proposed that close association with pines indicates a safe site for recruitment (Lookingbill and Zavala, 2000); however, in such conditions, tree development is difficult without a disturbance and, in fact, seedling banks under pine cover may be released after fire.

In general, *Q. suber* regeneration in the Valencia region seems to be in good condition, and some growth at the expense of old fields and pine forests (after the more-than-probable fires) will most likely occur. On the other hand, because of the reduced size and poor substrate conditions of the Pinet population, there is a need for some kind of sylvicultural intervention to increase the population here. On this site we observe a lack of regeneration outside the forest and especially in old fields >1.5 km away. We believe that the matrix of shrublands (88.9% of the area) has limited the populations and the dispersal activities of the jay. Since the acorns are not arriving naturally, the most economical alternative would be to substitute the dispersal vector by artificial means prior to regeneration-window closure.

5. Conclusions

Overall *Quercus* recruitment in the eastern Iberian peninsula is higher than in the western Iberian dehesas. *Q. suber* recruitment is relatively high in old fields and forest of the study area, at least in the range of distances from adult cork oak trees within the jay dispersal distances range; but recruitment is absent in shrublands. However, successful regeneration only occurs in old fields, while in forests (in both pine and oak forests), seedling development is suppressed by adult trees, and thus a seedling bank is generated in the understorey. These processes are similar for the three sites studied and there was no evidence of lower regeneration in the smallest oak patch. The process of regeneration inhibition may decrease with the current high rate of disturbances (wildfires) in the study area (Pausas, 2004) and together with the increase in land abandonment and old fields, it may facilitate the expansion of *Q. suber*.

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