



Dynamics of understorey herbaceous plant diversity following shrub clearing of cork oak forests: A five-year study

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Abstract

Cork oak forest management has been traditionally oriented towards optimization of cork production. Shrub clearing is a traditional silvicultural practice aimed to: (1) facilitate cork extraction (conducted every nine years); (2) increase cork yield by reducing competition from neighbouring shrubs; and (3) reduce fire risk by decreasing fuel load. These silvicultural practices, however, may interfere with current objectives of conservation and sustainable use of biodiversity. The effects of shrub clearing on different diversity components were assessed in three structurally contrasting forest sites, located in Southern Spain. A fenced experimental plot (1 ha) was established at each forest site. Half of each plot was shrub-cleared and the other half was left unmanaged (control stand). Afterwards, the presence of herbaceous species was monitored during five consecutive years in a total of 120 permanent quadrats (1 m²). Species richness (α - and γ -diversity) increased with the clearing, mainly by expansion of open grassland species, while β -diversity declined due to the homogenizing process associated with this expansion. Thus, the herbaceous species composition was modified by these silvicultural practices, especially the second year following treatment application. Effects differed across forest stands, being more marked in the *Open Woodland*, while there was no significant effect observed in the closed *Forest*. Understorey herbaceous communities were resilient to shrub clearing and initial diversity values were approximately restored after five years. The high resprouting potential of shrubs contributed to this resilience. Based on the results of this study, we propose several low costs strategies to be incorporated in forest management plans to reconcile cork oak extraction with the maintenance of biodiversity.

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1. Introduction

Mediterranean plant communities exhibit a remarkable biodiversity, which is in part maintained by a certain level of anthropogenic exploitation derived from ancient land use practices (Pons and Quézel, 1985; Blondel and Aronson, 1999; Grove and Rackham, 2001). Current forest policy is concerned with the development of sustainable forest management practices that allow simultaneous exploitation of goods and services, and preservation of structural and functional attributes of forest ecosystems (Riley, 1995; Brown et al., 2001; Thomas

et al., 2006). Understanding how silvicultural practices impact plant community structure (e.g., biodiversity) and function is thus a critical goal of current applied ecology (Franklin, 1993; Roberts and Gilliam, 1995; Pimentel et al., 1997; Decocq et al., 2004; Young et al., 2005).

The management of cork oak forests in the Mediterranean Basin has been mainly oriented towards maximization of annual yield in cork production. For this purpose, the forest is typically divided into various management units which are periodically managed (roughly every nine years, depending on the locality) for cork extraction. Shrub clearing is a common silvicultural practice associated with cork extraction, which consists of cutting of shrubby cover and damaged trees every nine years, with the following objectives: (1) to facilitate the extraction of oak tree bark to obtain cork; (2) to increase cork production by reducing competition from neighbouring shrubs; and (3) to reduce the risk of fires by decreasing the amount of

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fuel. Traditionally, shrub clearing was carried out manually and only around productive cork oaks, saving money and energy, and indirectly minimizing the damaged area. Today, due to both public subsidies to forestry and availability of motor powered machinery, shrub clearing is far more intensive and extensive, producing a more homogeneous and intense perturbation in managed forests. Shrub clearing could negatively impact herbaceous plant species diversity in the forest understorey.

In general, forest management has been identified as one of the main causes of plant diversity loss (Gilliam and Roberts, 1995); however, an increasing number of studies show that silvicultural practices can have a positive or neutral effect on understorey plant species richness (e.g., North et al., 1996; Gale et al., 1998; Jenkins and Parkers, 1999; Battles et al., 2001). Nevertheless, the number of plant species (species richness) is only one component of biological diversity; the understorey species composition, the spatial scale (β - and γ -diversity), as well as other components, such as number of endemic species and taxonomic singularity of the elements (Ojeda et al., 1995), must be also taken into consideration (Zavala and Oria, 1995). In addition, the effects of silvicultural practices should be evaluated over a temporal sequence. This long-term perspective is critical for the design of sustainable and conservation-oriented management practices (Scarascia-Mugnozza et al., 2000; Rees et al., 2001).

In this study, we investigated the effects of shrub clearing on various components of understorey herbaceous biodiversity, and their temporal trends along a period of five years. Using cross-comparisons between shrub-cleared and paired unmanaged stands, we examined whether initial biodiversity values (previous to treatment application) were restored before completion of the cork extraction cycle. The study was conducted in three stands located within one of the largest cork oak forests in Europe, “Los Alcornocales” Natural Park (South Spain). The selected stands varied structurally, representing a wide range of cork oak forests in this region: an open woodland with nearby grasslands, a woodland with small trees and intermediate tree density, and a closed forest.

Specifically, we sought to answer the following questions: (i) What are the effects of shrub clearing on the different diversity components (α -, β - and γ - diversity) of the herbaceous understorey?; (ii) Is there any temporal change in herbaceous composition after shrub clearing?; (iii) What is the balance between local colonization and extinction rates?; (iv) Are these changes, if any, consistent across forest stands?; and (v) How persistent are these effects over a five-year period?

2. Methods

2.1. Study area and forest sites

The study area is located in the oak forests of Aljibe Mountains, near the Strait of Gibraltar, in Southern Spain. Bedrock is dominated by Oligo-Miocenic sandstone, with a rough relief and a highest peak of 1092 m a.s.l. Climate is subhumid mediterranean-type, with cool and wet winters,

alternating with warm and dry summers. Mean annual temperature ranges from 14.6 to 18.4 °C, with a mean monthly maximum of 36 °C (July) and mean monthly minimum of 2 °C (January). Mean annual rainfall varies from 701 to 1331 mm (mean of 1056 for 15 weather stations), depending on the effects of the local orographic relief. The mean number of frost days ranges from 10 to 20 days per year at the highest altitude, to one day per year in the vicinity of the coast (see climate description in Mejías et al., 2007).

Vegetation is dominated by evergreen cork oak (*Q. suber*) forests, mixed with winter deciduous oaks (*Q. canariensis*), which are more abundant near streams (Urbietta et al., in press). The shrubby understorey is diverse and rich in endemic taxa (see general vegetation description in Ojeda et al., 2000). The area is located in the Baetic-Riffian diversity hot spot, which extends across South Spain and North Morocco, and is rich in endemic plant species, but also is threatened by human intervention (Medáil and Quézel, 1997). Most of the forested area was protected in 1989 as *Los Alcornocales* (meaning “cork oak forests”) Natural Park, covering about 1680 km².

The main forest enterprises are cork extraction from *Q. suber* trees (their bark is stripped off every nine years), free-range livestock (mainly cattle), and game hunting (especially of red deer and roe deer) (see a description of the Park management in CMA, 2005).

Three structurally different forest sites were selected within this protected study area (Fig. 1): a closed forest (hereafter called *Forest*) at “Tiradero” site (36° 9' 46" N, 5° 35' 39" W), 335–360 m a.s.l. on a NE slope; a woodland located at “Buenas Noches” (hereafter called *Woodland*, 36° 22' 56" N 5° 34' 57" W), 410–450 m a.s.l. on a NE slope; and an open woodland (hereafter called *Open Woodland*), at “Panera” site (36° 31' 54" N, 5° 34' 29" W), 530–560 m a.s.l. on a NW slope. Values of stand tree density, basal area and woody species composition of the three forest sites are shown in Table 1 (see also Quilchano et al., 2008 for description of study sites). Differences in overstorey canopy cover (leaf area index, LAI) and light availability at ground level (GSF) are also shown in Table 1. Both parameters were quantified by hemispherical photographs, a widely accepted technique for exploring forest structure and understorey light conditions (see details in Valladares and Guzmán, 2006). Photographs were taken in the centre of each of 120 sampling quadrats (see sampling design below) in spring (April–May) of 2001, at 0.5 m above ground level, using a horizontally-levelled digital camera (Coolpix 4500, Nikon, Tokio, Japan) with a fish-eye lens of 180° field of view (FCE8, Nikon). Images were analysed using Hemiview Canopy Analysis software version 2.1 (1999, Delta-T Devices Ltd, Cambridge, UK).

The forest stand (*Forest*) exhibited the highest basal area and the lowest light availability at ground level. The overstorey consisted of a well-developed mixed *Q. suber*–*Q. canariensis* stands and the shrub layer was dominated by *Phillyrea latifolia* and *Viburnum tinus*. The woodland stand (*Woodland*) had the highest tree density, though with a lower total basal area in comparison with the *Forest* site. Leaf area index (LAI) and light availability values (GSF) were intermediate between the other

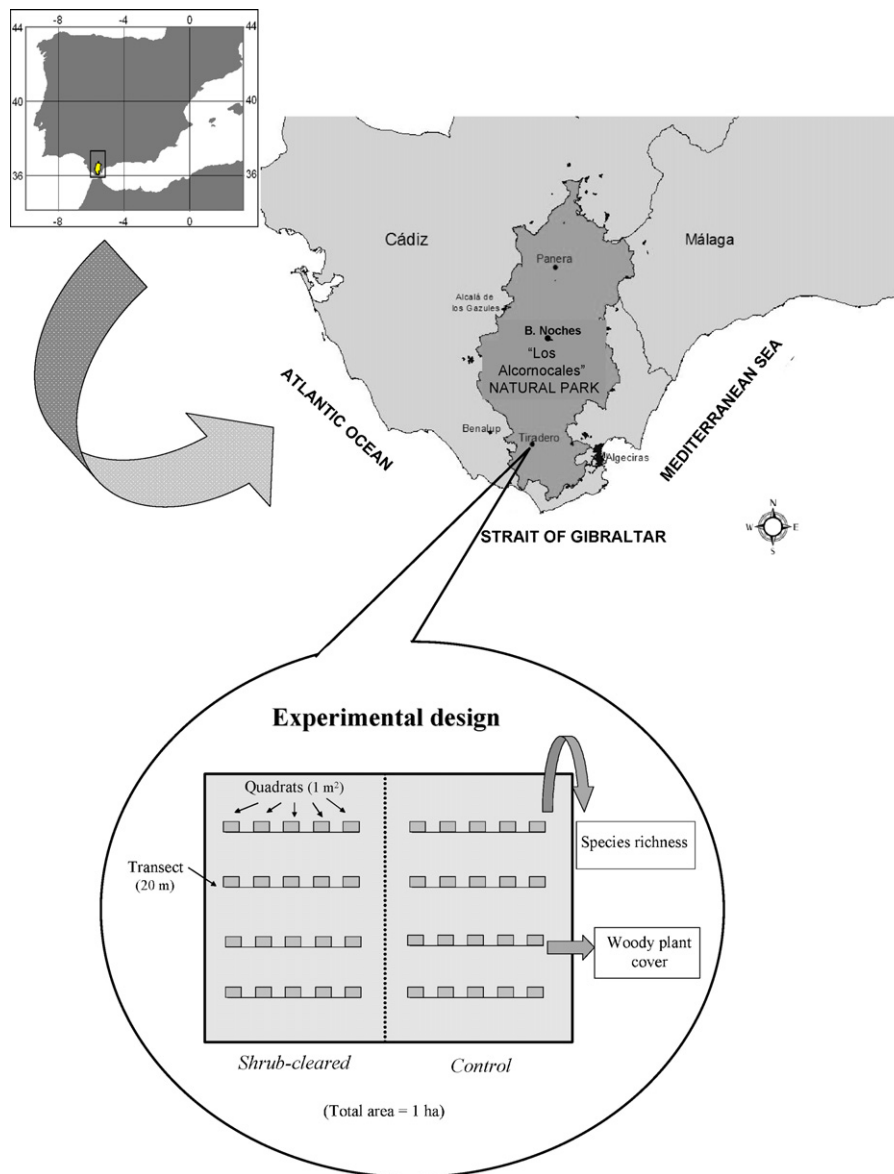


Fig. 1. Localization of study area and forest sites with illustration of experimental design.

two sites. The overstorey was dominated by small trees of *Q. suber* and *Arbutus unedo*, but no *Q. canariensis* trees were found in this stand. Shrub layer was dominated by *Erica scoparia* and *P. latifolia*. The *Open woodland* stand exhibited the lowest density of trees (although some of them had an enormous size, up to 134 cm dbh) and the highest mean light (GSF) values. Oaks (*Q. suber* and *Q. canariensis*) shared the overstorey while the shrub layer was dominated by *P. latifolia*, *Genista linifolia* and *E. arborea*. Nomenclature of species follows Valdés et al. (1987).

2.2. Experimental and sampling design

At each forest site, one experimental plot of about 1 ha was selected. On half of each plot (0.5 ha), shrub clearing was applied according to the traditional practice commonly used to manage cork oak forests in this region (Torres and Montero, 2000). The other half of each plot, that had not been shrub-

cleared for at least the last 20 years, was selected as the undisturbed control stand. Before treatment application, understorey herbaceous composition was similar in the two sides of each plot (per. obs.). Treatments were carried out during winter 1999–2000, and the resulting debris was burned outside the plot. After finishing the silvicultural practices, the three complete experimental plots were fenced to exclude disturbances by large herbivores (mainly deer and cattle).

In each plot, eight permanent 20 m transects were set up: four in the shrub-cleared half and four in the control stand (Fig. 1). The minimum distance between different transects was 20 m. Understorey woody composition and abundance were measured periodically as the cover of each woody species intercepted by the 20-m line. Density and basal area of overstorey woody species were also measured (in autumn 2004) in 20 m × 10 m rectangular samples (eight per forest site), using the permanent transects as the midline of each sample. All individuals inside the sample were counted and their

Table 1
Density (S.D., in stems ha⁻¹) and basal area (BA, in m² ha⁻¹) of tree and arborescent shrub species in the three studied forest sites

Species	Forest		Woodland		Open woodland	
	S.D.	BA	S.D.	BA	S.D.	BA
<i>Arbutus unedo</i>	6.3	0.34	731.3	9.9	–	–
<i>Cistus ladanifer</i>	–	–	6.3	0.01	–	–
<i>Crataegus monogyna</i>	18.8	0.12	–	–	6.3	0.002
<i>Erica arborea</i>	37.5	0.18	25	0.24	87.5	0.11
<i>Erica scoparia</i>	–	–	243.8	1.16	–	–
<i>Frangula alnus</i>	–	–	6.3	0.01	–	–
<i>Genista linifolia</i>	–	–	–	–	125	0.19
<i>Laurus nobilis</i>	6.3	0.06	–	–	–	–
<i>Myrtus communis</i>	12.5	0.03	–	–	–	–
<i>Olea europaea</i>	6.3	0.02	–	–	18.8	0.4
<i>Phillyrea angustifolia</i>	–	–	37.5	0.3	–	–
<i>Phillyrea latifolia</i>	75	0.27	68.8	0.51	137.5	0.9
<i>Pistacia lentiscus</i>	–	–	12.5	0.04	62.5	0.31
<i>Quercus canariensis</i>	387.5	10.38	–	–	87.5	8.84
<i>Quercus suber</i>	381.3	36.57	400	15.26	131.3	13.22
<i>Rhamnus alaternus</i>	31.3	0.1	25	0.15	6.3	0.02
<i>Teucrium fruticans</i>	–	–	–	–	6.3	0.02
<i>Viburnum tinus</i>	62.5	0.28	–	–	–	–
Total	1025	48.3	1556.3	27.6	668.8	24.01
Light at ground level	0.17 ± 0.008		0.25 ± 0.02		0.30 ± 0.03	
Effective LAI	2.26 ± 0.09		1.64 ± 0.09		1.84 ± 0.10	

Mean and S.E. of light availability at ground level (GSF) and leaf area index (LAI) of the overstorey canopy (for $n = 40$) are also indicated for each site.

diameters at breast height (dbh) were measured (only individuals with a dbh ≥ 2 cm were included in the study).

Along each transect, five 1 m² permanent quadrats were marked (separated about 4–5 m along the transect) and herbaceous species richness was quantified inside each of them by periodic presence-absence inventories. The 120 quadrats were periodically monitored during five consecutive years after shrub clearing (since spring 2000 until autumn 2004); censuses were carried out at two-month intervals during the first three years and every six months (in spring and after summer) during the last two years. All herbaceous species detected in the different censuses of each year were added together in order to obtain measures of cumulative annual species richness. Autumnal herbaceous species (a relatively small fraction of species richness) was not included in this study. For diversity components calculations, we restricted to the herbaceous community (excluding woody species) because of its high species turnover in response to treatments.

2.3. Data analyses

The effects of shrub clearing on the understorey herbaceous community were evaluated by using three diversity components: local species richness (α -diversity), total species richness (γ -diversity, estimated by means of randomised curves extrapolation) and spatial heterogeneity in herbaceous species composition (β -diversity).

First, the temporal variation of local species richness or α -diversity (defined as the number of species in a particular area; Magurran, 1988) was calculated for each 1 m² quadrat, during the five sampled years. To evaluate the “quality” of herbaceous

species composition in each treatment, plant species were also grouped according to its habitat preference in “grassland” versus “forest” species, following the information provided by a local flora (Valdés et al., 1987).

Second, since it is well known that plant species richness depends on the size of the sampled area (Palmer, 1990), species randomised curves were extrapolated from sequential re-sampling in each treatment (Supplementary data; see Colwell and Coddington, 1994). The cumulative number of species encountered within a given area was calculated as a function of the estimated effort to find them (i.e., number of sampled quadrats) (Battles et al., 2001). Because the order in which plots are added to the total affects the shape of the curve, average richness was calculated for all possible permutations of the order of entry. The curves traced in this way were adjusted to parametric functions (linear, exponential and Clench function), as proposed by several authors (Clench, 1979; Soberón and Llorente, 1993) for the estimation of total species richness (γ -diversity). The function which provided the best fitting (highest R^2) was selected in each case to calculate the asymptote value, which can be used as a good estimate of the total species richness (see Colwell and Coddington, 1994).

Third, herbaceous vegetation heterogeneity was calculated from the β -component of diversity, which was estimated by using the Sørensen similarity index between all pairs of 1 m² quadrats. This index ranges from zero (when the two compared sets are dissimilar and have not species in common) to one (in cases of complete similarity). In consequence, the higher this similarity coefficient, the lower the β -diversity or the species composition heterogeneity of the forest stand. Similarity in species composition was evaluated at three spatial scales: (1)

Patch scale, averaging Sørensen indices between all pairs of quadrats belonging to the same 20-m transect; (2) Site scale, for all pairs of quadrats belonging to different transects, but within the same 1-ha plot; and (3) Regional scale, for all pairs of quadrats belonging to different sites. Quadrats were also separated according to treatment application into shrub clearing and control stands.

The changes through time and by effect of shrub clearing treatment in these three diversity components, as well as in the plant woody cover, were analysed using a repeated measures ANOVA. Differences between treated and control stands for each forest site and year were tested using one-way ANOVAs.

To understand the process of diversity changes, we also explored species turnover for each quadrat. Local species colonization and extinction rates were calculated as the average number of new or disappeared species, respectively, by m² and year. Specifically, we showed the results of turnover rates between 2000 and 2001 years, where the most marked differences appeared. In this case, differences between treatments were also determined using one-way ANOVAs.

Finally, Non-metric multidimensional scaling (NMS) was used to ordinate the community composition and to evaluate differences among treatments and forest sites. This approach was selected because it assumes only a monotonic (not a linear)

Table 2

Results of repeated measures ANOVA analysis for woody plant cover, similarity (expressed as Sørensen index) and herbaceous species richness (both local and separating “grassland” and “true forest” species) during the five sampled years

	Forest				Woodland				Open woodland			
	SS	d.f.	MS	<i>p</i>	SS	d.f.	MS	<i>p</i>	SS	d.f.	MS	<i>p</i>
Woody plant cover (%)												
Between												
Treatment	829.8	1	829.8	0.345	140.00	1	140.00	0.523	3423.9	1	3423.9	0.011
Error	4750.4	6	791.7	1831.48	6	305.25	1558.4	6	259.7			
Within												
Time	626.7	3	208.9	0.001	1254.12	3	418.04	0.006	3090.8	3	1030.3	0.000
Time × treatment	1159.3	3	386.4	0.000	3356.24	3	1118.75	0.000	2270.6	3	756.9	0.000
Error	422.9	18	23.5	1321.80	18	73.43	754.6	18	41.9			
Local species richness (no. spp/m ²)												
Between												
Treatment	0.07	1	0.07	0.431	1.23	1	1.23	0.002	0.18	1	0.18	0.272
Error	4.08	38	0.11	4.27	38	0.11	5.49	38	0.14			
Within												
Time	0.95	4	0.24	0.000	0.51	4	0.13	0.000	1.55	4	0.39	0.000
Time × treatment	0.15	4	0.04	0.000	0.11	4	0.03	0.000	0.15	4	0.04	0.000
Error	0.97	152	0.01	0.75	152	0.00	0.73	152	0.00			
Grassland species richness (no. spp/m ²)												
Between												
Treatment	13.01	1	13.01	0.128	16.82	1	16.82	0.150	165.62	1	165.62	0.022
Error	203.59	38	5.36	295.90	38	7.79	1100.6	38	28.96			
Within												
Time	22.72	4	5.68	0.000	110.52	4	27.63	0.000	204.67	4	51.17	0.000
Time × treatment	7.72	4	1.93	0.012	2.88	4	0.72	0.526	163.73	4	40.93	0.000
Error	87.56	152	0.58	136.60	152	0.90	412.80	152	2.72			
Forest species richness (no. spp/m ²)												
Between												
Treatment	0.25	1	0.25	0.610	16.82	1	16.82	0.076	6.84	1	6.84	0.215
Error	35.11	38	0.92	192.20	38	5.06	163.63	38	4.31			
Within												
Time	25.73	4	6.43	0.000	15.37	4	3.84	0.001	44.75	4	11.19	0.000
Time × treatment	0.73	4	0.18	0.802	5.83	4	1.46	0.127	4.33	4	1.08	0.443
Error	67.94	152	0.45	121.60	152	0.80	175.32	152	1.15			
Similarity (Sorensen index)												
Between												
Treatment	0.00	1	0.00	0.463	0.05	1	0.05	0.013	0.01	1	0.01	0.053
Error	2.41	378	0.01	2.77	378	0.01	0.27	78	0.00			
Within												
Time	0.11	4	0.03	0.000	0.07	4	0.02	0.000	0.05	4	0.01	0.000
Time × treatment	0.01	4	0.00	0.033	0.04	4	0.01	0.000	0.01	4	0.00	0.000
Error	1.75	1512	0.00	1.58	1512	0.00	0.18	312	0.00			

relationship between ordination distance and compositional dissimilarity.

Before the analyses, those variables not normally distributed were log-transformed and tested with the Kolmogorov–Smirnov test. EstimateS version 7.0 software (Colwell, 2005) was used for similarity coefficients and species randomised curves, PC-ORD v5 (MjM Software 2006) for NMS, and the STATISTICA 6.0 program (Stat Soft Inc. 2001) for other statistical analyses.

3. Results

In general, shrub-clearing treatment altered the different diversity components of the herbaceous community, though the effects were not persistent through time and varied as function of the forest site. In fact, effects associated with shrub clearing were most marked in the *Open Woodland*, while almost all were non-significant in the closed *Forest* site (Table 2 and Fig. 2). As expected, the percentage of woody plant cover in the shrub

layer just after treatment application (2000) was much lower in shrub-cleared treatments than in unmanaged stands, appearing significant differences both in the *Woodland* ($F = 60.47$; $p < 0.001$) and in the *Open Woodland* sites ($F = 37.2$; $p < 0.001$) but not in the closed *Forest* ($F = 1.54$; $p = 0.26$). However, the woody plant layer of the treated plots grew quickly during the study period, eliminating initial differences and even reaching, in some cases, slightly higher mean percentage cover values than in control stands (Fig. 2, top).

3.1. Species richness and turnover rates

For estimation of total species richness (γ -diversity), the Clench function provided the best adjustments in all data sets, explaining over 97% of the variance (Table 3). Total species richness (asymptote values) was greater for the *Open Woodland* (up to 119 species/20 m² on 2001) and lower in the closed *Forest* site (minimum of 26 species/20 m² on 2004). The *Woodland* site had intermediate values of total species richness,

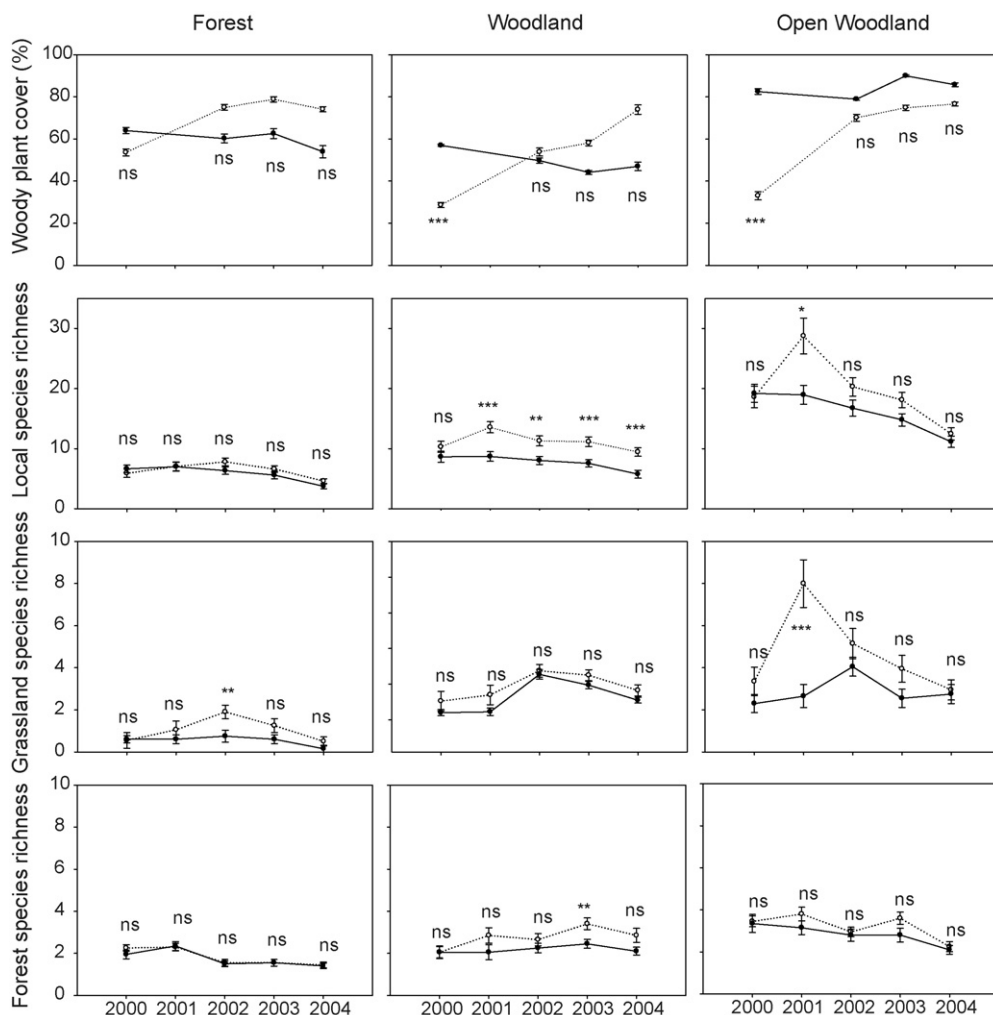


Fig. 2. Temporal dynamics during the five sampled years in: woody plant cover (with the exception of 2001 because there are not available data) (top row graphs); local species richness at quadrat scale (second row graphs); “grassland” species richness at quadrat scale (third row graphs); and “forest” species richness at quadrat scale (bottom row graphs). Mean and S.E. (error bars) values have been represented, separating shrub-cleared (white symbols and dotted line) and unmanaged (black symbols and solid line) treatments, for the three forest sites. The effect of shrub clearing practices has been evaluated for each sampled year, and significance level is expressed as follows: ns, not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 3
Estimated asymptote values (γ -diversity) by fittings of species randomised curves to the Clench function, for each sampled year and forest site (separating shrub-cleared and control treatments)

Year	Forest						Woodland						Open woodland					
	Shrub-cleared			Control			Shrub-cleared			Control			Shrub-cleared			Control		
	Explained variance (%)	Asymptote (γ -diversity)	Final residuals	Explained variance (%)	Asymptote (γ -diversity)	Final residuals	Explained variance (%)	Asymptote (γ -diversity)	Final residuals	Explained variance (%)	Asymptote (γ -diversity)	Final residuals	Explained variance (%)	Asymptote (γ -diversity)	Final residuals	Explained variance (%)	Asymptote (γ -diversity)	Final residuals
2000	97.6	33	14.8	98.5	39	13.3	97.7	43	18.3	98.4	38	12.8	99.5	108	21.1	99.4	108	21.3
2001	99.6	30	4.9	99.2	32	8.2	99.0	52	14.8	99.5	38	7.6	99.3	119	28.3	99.4	119	21.0
2002	99.8	27	3.5	99.1	36	8.8	98.3	44	16.3	99.1	33	9.1	99.2	80	19.5	99.4	80	16.2
2003	99.0	30	8.5	99.5	31	5.1	98.9	40	12.6	99.4	31	6.4	99.6	67	12.5	98.5	67	25.2
2004	98.9	27	7.8	99.3	26	6.1	99.3	39	9.0	99.2	27	6.9	99.6	73	13.9	99.3	73	15.0

with a maximum value of 52 species/20 m² and a minimum value of 27 species/20 m² (Table 3).

Local species richness was affected by the shrub clearing treatment, but changes through time were site-specific (Fig. 2, second row). The largest differences appeared in *Woodland* and *Open Woodland* sites; however, in the latter site, the effect was only significant in the second monitored year. In general, silvicultural practices increased the number of herbaceous species (α -diversity) in the understorey; although in the closed *Forest* site these effects were not significant. During the first year of monitoring (just a few months after shrub clearing) there was almost no effect, while effect was more marked in the second year after treatment application. At the *Open woodland* site, these differences narrowed after 2002 until similar species richness values were reached on both treatments. In contrast, at the *Woodland* site, species richness gain kept nearly constant until the fifth year (Fig. 2b). On the three forest sites, local species richness decreased along the time, though the trend was lightly different in both treatments, as “Time-Treatment” interactions were statistically significant (Table 2).

In some cases, the increase in local species richness associated with shrub clearing occurred mainly due to the expansion of grassland species (e.g., pioneers with a good colonizing ability) that could take advantage of open conditions newly encountered in managed microhabitats. At the *Open Woodland* site, shrub clearing increased species richness in the second year after treatment (2001), particularly ruderal species, while the number of herbaceous species typical of forest habitats was relatively similar across treatments (Fig. 2, third and bottom rows). Even at the *Forest* site, with only small differences between treatments in the total α -diversity, the number of grassland species was significantly higher in the treated stand, for the third-year census.

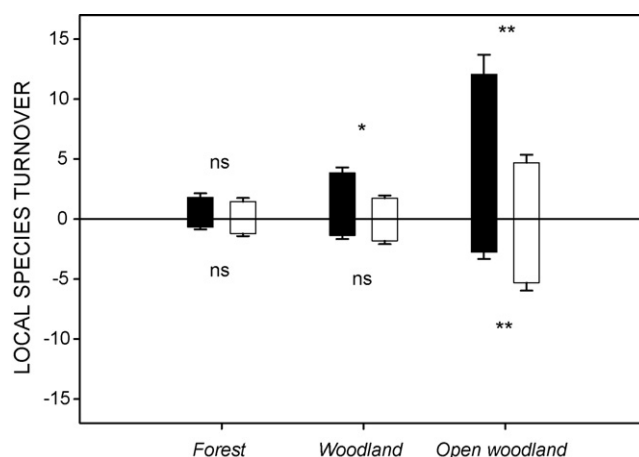


Fig. 3. Turnover of herbaceous species per quadrat (1 m²) between the first (2000) and second (2001) census after shrub clearing; mean and S.E. (error bars) values are indicated. Positive values indicate local colonization (new species in the quadrat) while negative values indicate local extinction (existing species not present in the next year). For each forest site, the treated (black bar) and unmanaged (white bar) quadrats are compared, and the significance level is expressed as follows: ns, not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Differences in species turnover (from year 2000 to 2001) associated with shrub clearing were highest in the *Open woodland*, while they were not significant in the closed *Forest* site (Fig. 3). The local colonization rate increased ($F = 17.15$; $p < 0.001$) in the shrub-cleared treatment of *Open woodland*, while the local extinction rate decreased ($F = 8.24$; $p = 0.007$). At the *Woodland* site, there was also an increase in the local colonization rate ($F = 17.05$; $p < 0.001$), but no significant

difference in the extinction rate. In contrast, both colonization and extinction rates were not significantly affected by shrub clearing in the closed *Forest* site.

3.2. Similarity (β -diversity)

In general, there was a higher among-quadrats similarity for herbaceous species composition in shrub-cleared compared to control treatments, which reflects a reduction in β -diversity (Fig. 4). Changes were site-specific: at the *Woodland* and *Open woodland* sites, the highest increase in similarity (lower β -diversity) was found during the third and fourth years after shrub clearing, but converged with control values for the fifth year. In contrast, at the closed *Forest* site, there was no significant change between both treatments in the similarity of understorey herbaceous composition.

Similarity among quadrats decreased with increasing distance between them. Thus, maximum values of Sørensen index were found at patch scale (less than 20 m), followed by site (about 100 m) and regional (20–40 km) scales (Fig. 5). Differences across treatments were statistically significant only at the two higher spatial scales, varying also through time. At site scale, differences between treatments initiated in 2001 reached the maximum in 2003 and then decreased in 2004. At the regional scale, there were differences in 2002 and 2003.

3.3. Understorey herbaceous composition

The ordination analysis detected marked differences in community herbaceous composition among the three forest sites. Within each forest, control quadrats were only clearly segregated from those in the shrub-cleared zone at the *Open Woodland* site and during the second-year census (Fig. 6).

The three forest sites differed substantially in the most-common herbaceous species. At the closed *Forest* site, the most

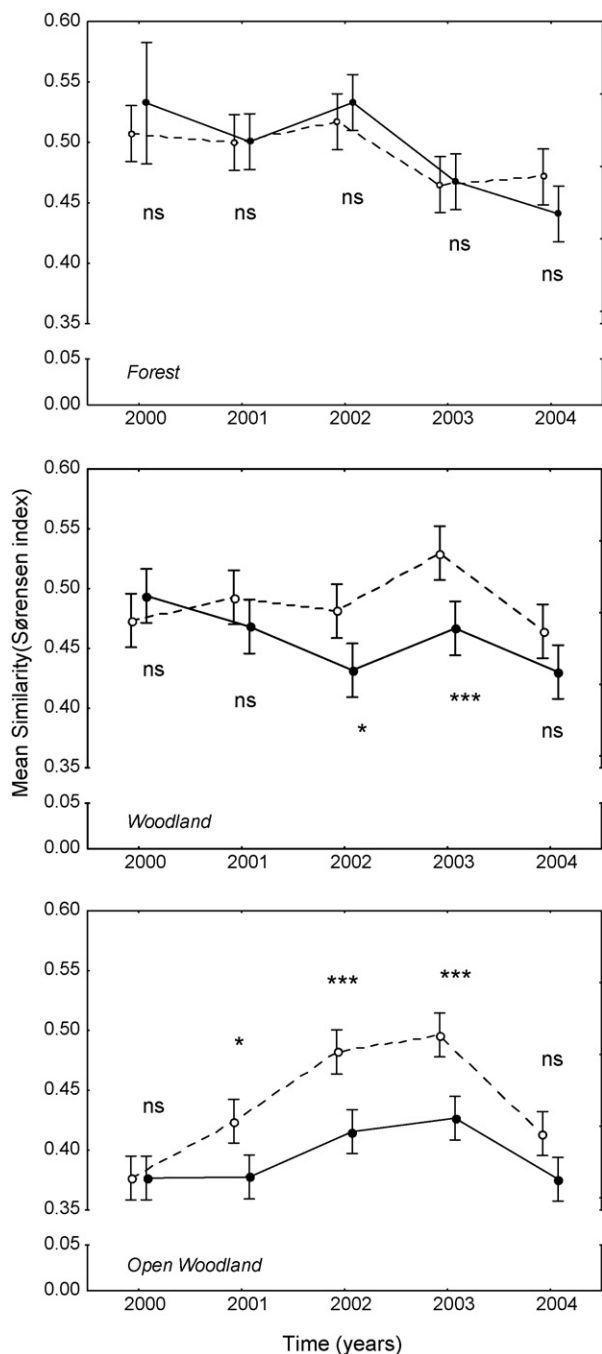


Fig. 4. Similarity between shrub-cleared (white dots and dashed lines) and control (black dots and solid lines) treatments, separating the three forest sites. Mean and S. E. bars ($n = 190$ combinations of pairs of quadrats) of Sørensen values have been indicated. Higher similarity values mean higher homogenization and lower β -diversity. The significance level is expressed as follows: ns, not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

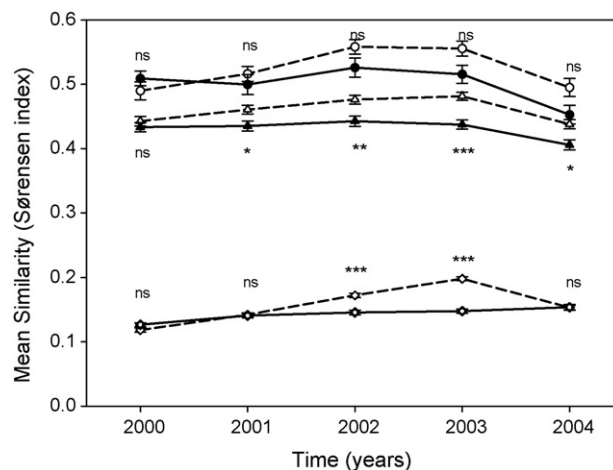


Fig. 5. Changes with time in mean similarity values (expressed as Sørensen index) in shrub-cleared (symbol in white and dashed line) and control (symbol in black and solid line) treatments, at three spatial scales: patch (20 m, circles), plot (100 m, triangles), and region (40 km, diamonds). Vertical bars denote standard error values. The effect of shrub clearing practices has been evaluated for each sampled year and spatial scale, and significance level is expressed as follows: ns, not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

abundant species were *Arisarum proboscideum*, *Rubia peregrina*, *Tamus communis* and *Ruscus hypophyllum*, being the last three ones typical of shaded forest sites. At the *Woodland* stand, the understorey of the two treatments was dominated by *Galium aparine*, *Holcus grandiflorus*, and the Liliaceae *Scilla monophyllos* and *Simethis planifolia*. In the case of the *Open Woodland* site, the most common species in the two treatments were *Allium triquetrum*, *Bellis sylvestris*, *Carex* sp., *Ranunculus paludosus*, *Rubia peregrina* and *Vinca difformis* (Supplementary data).

At the three forest sites, there was a certain difference in relative abundance of herbaceous species between shrub-cleared and control treatments, that was more marked in the *Open Woodland* site. In this plot, the species with the greatest relative abundance in shrub-cleared stands were those typical of open grasslands, such as *Brachypodium distachyon*, *Euphorbia pterococca*, *Scorpiurus muricatus* and *Torilis nodosa*. In contrast, the species more abundant in control stands were those typical of shaded forests, such as *Conopodium capilifolium*, *Avenula sulcata* subsp. *albinervis* or *B. gaditanum* (Supplementary data).

4. Discussion

4.1. Diversity components and turnover rates

The different diversity components were modified by the effect of shrub clearing practices, probably as a consequence of

the new abiotic conditions resulting from structural changes in the shrub layer. In a parallel study (Quilchano et al., 2008), we demonstrated that shrub clearing reduced effective cover (LAI) of cork oak forests and, consequently, resulted in a higher light availability at ground level. In addition, the elimination of shrubs, which are piled and burned during these silvicultural practices, also decreased the amount of litterfall in shrub-cleared treatments (Quilchano et al., 2008). On one hand, the higher radiation at the soil surface could favour the colonization of new herbaceous species (mainly ruderal), either through seed dispersal from nearby grassland patches or by stimulating germination of persistent soil seed banks (Díaz-Villa et al., 2003). This trend of higher species richness with increasing light availability at the forest floor has been documented in other studies (e.g., Suding, 2001; Kraft et al., 2004). On the other hand, the thicker litter layer found in unmanaged stands might reduce colonization rates of herbaceous plants, likely through inhibition of seedling establishment by shading and physical obstruction (e.g., Clark and Clark, 1989; Marañón and Bartolome, 1993). Moreover, the reduced litter accumulation also could affect soil nutrient availability and interactions with soil micro-organisms (mycorrhizae, pathogens, etc.), thus influencing the floristic composition of the forest understorey (e.g., Maltez-Mouro et al., 2005). In the studied forest sites, shrub-clearing practices increased local colonization rates of new herbaceous species, and reduced local extinction rates (in the most open woodland site). Since species richness is the

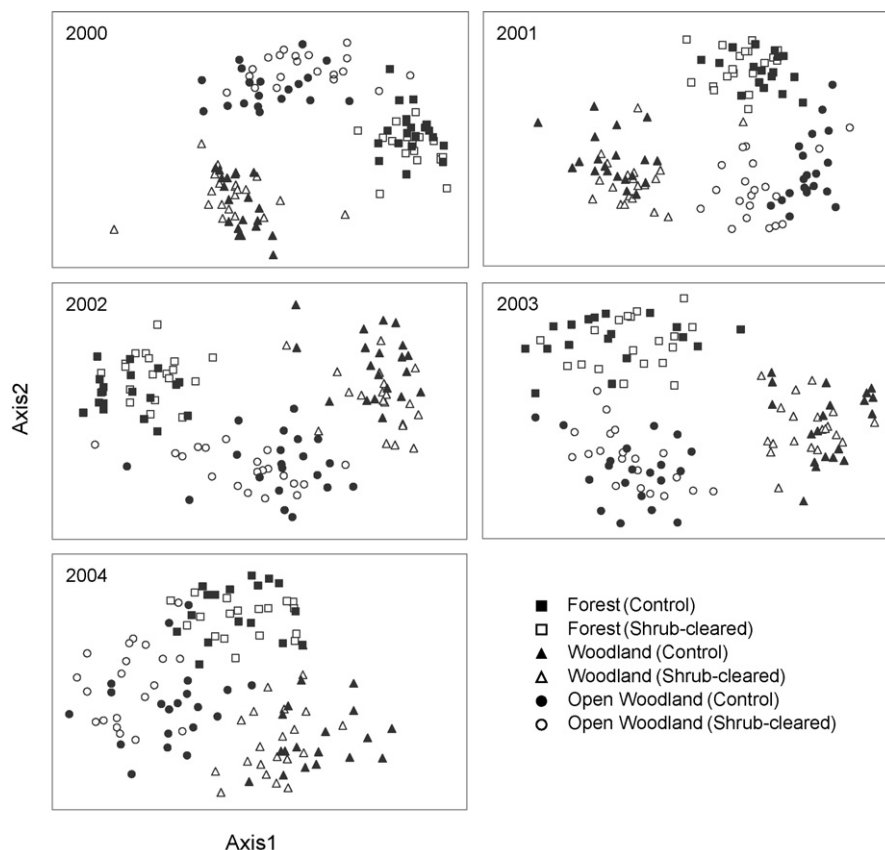


Fig. 6. Ordination (by non-metric multidimensional scaling) of herbaceous community composition for 120 quadrats of the three forest sites, separating shrub-cleared (white symbols) and unmanaged (black symbols) treatments. Data of the five sampled years have been represented (see symbol types in the figure).

result of the balance between local extinction and colonization (Mac Arthur and Wilson, 1967), these results translated into a higher number of herbaceous species (local and total diversity) in those stands subjected to shrub clearing.

In contrast, shrub clearing decreased the spatial heterogeneity in understorey herbaceous composition and, thereby, the β -diversity of the studied cork oak forests. This homogenizing process (reflected in a higher among-quadrats similarity) was likely associated with the colonization and expansion of common herbaceous species, usually typical of disturbed and open sites (see below), which thrived in the new understorey conditions. However, this effect of homogenization in herbaceous composition was only statistically significant at higher spatial scales (both site and regional level), but not at patch scale, probably because of the high internal variability at this scale. Changing the spatial scale, similarity values decreased as the quadrats were more separated in distance, probably due to the lower homogeneity among them in environmental conditions and the existence of short-range dispersal (Janzen, 1970; Hubbell, 1980).

It is important to remark that the impact of shrub clearing on diversity components (α -, β - and γ - diversity) was site-specific and depended on the forest structure. At the *Open woodland* site, understorey changes associated with shrub clearing – a higher species richness and a lower β -diversity – were highly significant compared to control stands. However, at the closed *Forest* site, the effects of shrub clearing on understorey diversity components were negligible. The pool of herbaceous species in each site is determined by the set of available species in the surrounding landscape and the environmental sieve filtering species by abiotic factors (e.g., light and soil chemistry) and biotic interactions (e.g., competition and herbivory) (Zobel, 1997; Díaz-Villa et al., 2003). At the *Forest* site, due to the more shaded conditions generated by the dense tree canopy, the shrub layer was less abundant and shrub clearing caused only a small change in light availability at ground level. In this closed forest site, the mean GSF of the shrub-cleared treatment was 36% higher than control, while in the *Woodland* stand the increment reached 131% (Quilchano et al., 2008). Thus, even after shrub clearing, light availability (reduced by the tree layer) was still relatively low (with GSF mean values below 20%) at the *Forest* site, which probably precluded the massive colonization of light-demanding species. Moreover, the soil seed bank of herbaceous species in these shaded conditions was relatively low (unpublished data) and their propagules probably scarce in the surroundings.

4.2. Understorey herbaceous composition

The three studied oak forest sites showed substantial differences in understorey herbaceous composition, probably as a consequence of differences in habitat affinity – with underlying gradients in light levels, soil physical properties, fertility or management history (Reich et al., 2001). Differences associated with shrub clearing practices in herbaceous community composition were most evident at the *Open Woodland* site (especially on the second year after treatment),

mainly by expansion of grassland species. Thus, those herbaceous species mostly ruderal and typical of open sites had higher relative abundance in the disturbed, shrub-cleared stands than in unmanaged control ones; similar patterns have been documented in other studies (Roberts and Gilliam, 1995; Fredericksen et al., 1999; Nagaike et al., 1999; Battles et al., 2001).

Disturbances may increase species richness by lowering the dominance of a few species, freeing resources for early successional plants and providing opportunities for aggressive ruderal species to spread rapidly (Beese and Bryant, 1999; Decocq et al., 2004). Although in this study the richness of “typical of forests” species was similar in both types of stands (treated and non-treated), the relative abundance of some forest species, such as *Conopodium capilifolium*, *Avenula sulcata* subsp. *albinervis* or *Brachypodium gaditanum*, decreased in shrub-cleared stands. Similarly, Decocq et al. (2004) found a negative impact of silvicultural practices on true forest species in a temperate deciduous woodland. Therefore, simple increases in species richness may not always be indicative of success in reaching conservation goals.

4.3. Resilience after shrub clearing

This study shows that the herbaceous community of cork oak forests may be highly resilient to shrub clearing, with “resilience” defined as the ability of an ecosystem or community to return to pre-disturbance conditions (e.g., Lavorel, 1999). We found that, within a five-year period, shrub-cleared stands reached very similar diversity values to the unmanaged treatments (assumed to be similar to initial pre-treatment stage). At the *Open woodland* site, maximum between-treatments differences in α -diversity were found the year after shrub clearing and then differences decreased to reach similar values by the fifth year. Differences in among-quadrats similarity for community composition also had also a short-term increase and then diminished over time to be non-significant by the last year. At the *Woodland* site, species richness gain kept nearly constantly during the sampled years, but similarity values (β -diversity) also converged five years after shrub clearing. Remarkably, this high resilience implies a return to a lower herbaceous species richness, mainly by decreasing the number of grassland species (which can be considered less important from a conservation point of view). Our results are in accordance with previous studies focusing on diversity dynamics through silvicultural cycles, where species richness peaks shortly after disturbances and then declines to pre-managed levels (Metzger and Schultz, 1984; Peet and Christensen, 1988; Decocq et al., 2004).

The high resilience exhibited by the understorey herbaceous community in shrub-cleared oak forests may be the result of a combination of processes. At first, there is a rapid colonization process by herbaceous (mostly annuals) plants from the soil persistent seed bank (Díaz-Villa et al., 2003) and by dispersal (mainly by wind) from nearby unmanaged patches. On the other hand, cleared shrubs have a high resprouting ability, typical of Mediterranean woody plants in response to fire and

other disturbances (Pate et al., 1990; Canadell and López-Soria, 1998); they grow rapidly, restoring shrub-layer cover. Shady conditions probably limit the colonization of light-demanding species, while alleviating the competition pressure on shade-tolerant forest herbs, thus restoring initial values of species richness and β -diversity for the whole community.

The recovery rate was probably accelerated owing to the favourable conditions of excluding large herbivores (deer and cattle) in the experimental plots. In fact, species richness and similarity not only decreased through time in the shrub-cleared stands, but also in unmanaged treatments. Browsing affects the composition and structure of forests through the direct effects of physical damage to plants as well as by the indirect effects related to changing environmental conditions and competitive interactions among surviving plants (e.g., Augustine and Frelich, 1998; Horsley et al., 2003; Kraft et al., 2004). Therefore, it would also be interesting to evaluate the impact of shrub clearing on understorey diversity dynamics but without excluding large herbivores.

4.4. Management applications

In the Mediterranean region, biodiversity conservation is a key component of sustainable regional development (Blondel and Aronson, 1999). A promising example is found in the Management Plan of “Los Alcornocales” Natural Park that proposes: “forestry practices will be conditioned to the improvement and conservation of the forest, and the maintenance of the ecosystem diversity and stability” (CMA, 2005). On the basis of our study, we propose some realistic and low-costs strategies to be incorporated in forest management plans to reconcile cork oak extraction with that maintenance of biodiversity. These proposals are more adequate for oak woodlands with low or intermediate tree density, where the impact of shrub clearing is more marked.

(1) Given the negative effects of shrub clearing on some diversity components, we propose to reduce the intensity and extension of those perturbations; for example, concentrating operations around cork oak trees, as was done traditionally, and leaving some undisturbed patches within each forest stand. (2) To maintain the current nine-year frequency between successive shrub clearings and even increasing them to 10-year cycles, whenever possible, as recommended in protected cork oak forests. Although the traditional recurrence of shrub clearings seems to be enough to allow for the recovery of herbaceous communities, a longer buffer period would compensate the possible reverse trends during dry years (expected to become more frequent under the current climate change scenario) and the interference of large herbivores, which are known to slow down the regeneration of plant biodiversity after perturbation (and were excluded in this experiment). (3) To avoid indiscriminate cutting of understorey plants during shrub clearing operations, with special attention to minimise disturbance of shade-tolerant and true forest herbs. (4) To increase the area devoted to unmanaged forest, embedded into the current array of rotation stands, favouring a mosaic of micro-reserves that will preserve the

typical species composition in the understorey of old-growth forests.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2008.01.069.

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