Ecol Res
DOI 10.1007/s11284-007-0343-6

ORIGINAL ARTICLE

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Patterns and ecological consequences of abiotic heterogeneity in managed cork oak forests of Southern Spain

Received: 5 October 2006 / Accepted: 11 January 2007

Abstract Spatial heterogeneity of abiotic factors influences the structure and function of forests and must be taken into account for their conservation and sustainable management. In this study, we evaluate the heterogeneity of abiotic environmental variables in managed cork oak (*Quercus suber* L.) forests in southern Spain at patch, site and regional scales. The extent of spatial heterogeneity depended on the environmental variable examined and the scale considered. For example, soil Mn and P and light availability in the understorey were very heterogeneous at the regional scale, while soil N had low regional heterogeneity, but high spatial variability, at patch scale, attributed to open overstorey and grazing disturbance. There was a general trend of increasing heterogeneity with spatial scale. We also study the effects of a silvicultural practice—shrub clearing on the forest environment and its consequence for spatial heterogeneity. Shrub clearing increased understorey light and decreased its spatial heterogeneity with idiosyncratic effects on soil properties and their spatial heterogeneity at each site. Finally, we compare the heterogeneity (estimated by the coefficient of variation) obtained in these cork oak forests with a database compiled from published studies on other forest environments. The comparison revealed a remarkable extent of abiotic heterogeneity in the cork oak forests studied, suggesting that a sustainable management of these forests should combine intrinsic and human induced abiotic heterogeneity to preserve crucial ecological processes and to maintain high levels of biodiversity.

Keywords Forest soil · Light availability · Mediterranean forest · *Quercus suber* · Shrub clearing

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Introduction

Heterogeneity in the forested landscape is produced by the interplay of the geophysical template, physical processes, disturbances and the activities of organisms (Pickett and White 1985; Wiens 2000). The sources of heterogeneity can be abiotic or biogenic (Wilson 2000). In forests, large-scale organisms (trees) impose a high biogenic heterogeneity for smaller organisms living at ground level, including tree seedlings and saplings: trees originate a variability in the intensity and quality of radiation reaching the ground (Canham et al. 1994; Breshears et al. 1997), the variation in the litter amount and quality determines differences in nutrient mineralization (Gallardo and Merino 1993; Finzi et al. 1998a, b; Saetre and Bååth 2000), and soil moisture is affected by evapotranspiration (Joffre and Rambal 1993) and by hydraulic lift (Caldwell and Richards 1989). At landscape level, a forest can be considered a shifting mosaic of patches of different ages and developmental stages (Spies and Turner 1999).

The spatial heterogeneity of abiotic factors influences the spatial patterning of plants, which in turn affects the spatial structure of these factors and, in particular, of soil properties. In fact, there is a close and bidirectional relationship between soil and vegetation (Schlesinger and Pilmanis 1998; Ettema and Wardle 2002; Maltez-Mouro et al. 2005). Soil heterogeneity can occur as a random process and the intrinsic heterogeneity of soil resources can be further altered by stochastic disturbances (Ettema and Wardle 2002). Spatial heterogeneity

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of soils can be observed at different spatial scales along the landscape (from a few millimetres to regional distances), and it is the result of both stochastic variation, explained in part by changes of soil-forming factors (Rossi et al. 1992), and management practices and land use (Kleb and Wilson 1997; Schmitz et al. 1998).

There are a few cases of studies documenting environmental heterogeneity in Mediterranean forest ecosystems. For example, Joffre et al. (1996) analysed the spatial variability of leaf area index (LAI), leaf litterfall and litter decomposition in a *Quercus ilex* stand; Balaguer et al. (2001) compared the light availability in the understorey of several *Quercus coccifera* stands and discussed the implications of spatial heterogeneity; Logli and Joffre (2001) related the individual local variability of *Quercus pubescens* with soil heterogeneity and competition. More recently, Valladares and Guzman (2006) have related canopy structure with spatial patterns of understorey light in abandoned Holm oak woodlands. In general, though, there is a scarcity of information on spatial scales of environmental heterogeneity and the relationships with forest structure and function in Mediterranean ecosystems despite their important influence in the maintenance of biodiversity and in many other ecological processes (Valladares 2003).

In this study, we evaluate the heterogeneity of abiotic environmental variables in three cork oak forests located in southern Spain. In particular, we study spatial changes in (1) light availability at ground (seedling) level in the forest understorey, (2) water content of the soil during different seasons, (3) soil texture, (4) content of soil organic matter and (5) concentration of macronutrients (N, P, Ca, Mg and K) and micronutrients (Fe, Mn and Cu). We investigate the heterogeneity of these variables at patch scale (transects of 20 m), at site scale (plots of 1 ha) and at regional scale (three forest sites 40 km apart from each other). We also study the effects of a silvicultural practice—shrub clearing on the forest environment and its consequence for spatial heterogeneity. Additionally, we compare the obtained pattern and extent of heterogeneity for the variables measured in these cork oak forests with a database compiled from published studies on other forest environments.

Methods

Study area

The study was carried out in the forested region at the southern tip of the Iberian Peninsula, near the Strait of Gibraltar. This region has a rough topography, the highest elevation being 1,091 m at Aljibe peak. Bedrock is dominated by Oligo-Miocene sandstone, which produces acidic, sandy, nutrient-poor soils, although frequently there are interspersed layers of marl sediments, yielding soils richer in clay. In the lowlands fringing the mountains, non-acid, loamy or marly soils are dominant.

The climate is subhumid Mediterranean-type with cool, humid winters and warm, dry summers. The total annual rainfall ranges from 701 mm in the lowlands to 1,331 mm in the mountains (mean of 1,056 mm for 15 weather stations). The mean temperature is mild: 15–18°C, with a monthly maximum mean of 36°C (July), and monthly minimum mean of 2°C (January). The mean number of frost days ranges from 10 to 20 days per year at the highest altitude, to 1 day per year in the vicinity of the coast. Mountains in this area intercept moist, SE-prevailing winds coming directly from the Mediterranean Sea, which reduce to some extent the severity of drought, especially during the summer (see general descriptions in Ojeda et al. 2000; Mejías et al. 2007).

The evergreen tree *Quercus suber* (cork oak) dominates most forests in this area, with the semi-deciduous *Q. canariensis* being locally abundant in valley bottoms. Riparian forests are more diverse in the tree and arborescent-shrub overstorey, harbouring temperate-climate tree species such as *Alnus glutinosa*. The sandstone ridges and hilltops are covered by open heathlands (with *Erica australis*, *Cistus populifolius* and others), while the marly and loamy lowlands are dominated by garrigue-type shrublands (with *Pistacia lentiscus* and *Olea europaea* as dominant) (Ojeda et al. 2000).

This area was protected in 1989 as *Los Alcornocales* Natural Park; it covers about 1,680 km^2 and is aimed at promoting the sustainable management of forest resources and maintaining its biodiversity (Anonymous 2005). The main forest enterprises are cork extraction from *Q. suber* trees (their bark is stripped off every 9 years), free-range livestock (mainly cattle) and game hunting (red deer and roe deer).

Experimental and sampling design

Three forest sites were selected in the Natural Park: a closed unmanaged 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, and two woodlands managed for cork extraction, one (hereafter called *Woodland*) at *Buenas Noches* site (36°22′56″N 5°34′57″W), 410–450 m a.s.l. on a NE slope, and another of lower tree density (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.

At each forest site, one experimental plot of about 1 ha was selected. Half of the plot (0.5 ha) was shrub-cleared and thinned, following the practice commonly used to manage cork oak forests in the region (Torres and Montero 2000). The other half of the plot had not been shrub-cleared for at least the last 20 years and was selected as the undisturbed forest control. Treatments were carried out during winter (January–March) 2000, and the resulting debris was burned outside the plot. After finishing the silvicultural practices, the complete experimental plot (1 ha) was fenced to exclude disturbance by large herbivores.

In each plot, eight permanent transects of 20 m were marked: four in the cleared half and four in the undisturbed forest. Overstorey composition and abundance were measured as the cover of each woody species intercepted by the 20-m line. In each transect, five permanent quadrats of 1 m^2 were marked (about 4–5 m apart along the transect). Thus, there were a total of 40 quadrats per plot and a grand total of 120 sampling points. Abiotic environmental variables were measured at the quadrat level. Density of woody species seedlings and presence of herbaceous species were also measured in each quadrat (results are presented elsewhere).

Light environment

Light availability at each sampling point was quantified by hemispherical photography. Photographs were taken at 0.4–0.6 m above ground level using a horizontally levelled digital camera (CoolPix 995, Nikon, Tokyo, Japan) with a fish-eye lens of 180° field of view (F8, Nikon). All photographs were taken on 30 April–1 May 2001, before dawn, after sunset, or at other times of the day when the sun was blocked by clouds, thereby ensuring homogeneous illumination of the overstorey canopy and a correct contrast between canopy and sky. Photographs were taken at the speed indicated by the camera exposure meter with an f-stop ≥7 to ensure sharpness of the image. The resulting images were downloaded to a computer and analysed for canopy openness using Hemiview canopy analysis software version 2.1 (1999, Delta-T Devices Ltd., UK). The direct site factor (DSF), indirect site factor (ISF) and global site factor (GSF) were computed by Hemiview, accounting for the geographical data of the site. These factors are estimates of the fraction of direct, daily and total radiation, respectively, expected to reach the site of the photograph (Anderson 1964). The effective leaf area index (referred here simply as LAI) was estimated with Hemiview as half of the total leaf area per unit ground surface area (Chen and Black 1992). More information on analyses of hemispherical photographs can be found in Valladares and Guzman (2006). Solar radiation at ground level (about 10 cm high) was measured in each quadrat with a quantum radiometer (Li-Cor, LI-185B). Four readings were taken, spatially dispersed within each 1 m^2 quadrat. Measurements were made during the central hours of the day (12 a.m.–2 p.m.) on clear days.

Soil and litter features

Soil water content was measured by Hydrosense (Campbell Sci.) with 12-cm-depth rods. This system uses a soil physical property—dielectric permittivity to make a quick estimate of the volumetric water content. Rods were inserted at four different points around each quadrat, totalling 480 readings for the three forest sites (4 × 120 quadrats). Soil moisture was measured on four occasions: autumn (October) 2000, winter (February) 2001, late spring (May–June) 2001 and late summer (September) 2001. Soil water potential was additionally measured in 72 quadrats (12 per plot) during late July 2000 using the filter-paper method (Deka et al. 1995).

One sample of superficial soil (0–10-cm depth) was taken near each of the 120 quadrats in summer (July 2000) 5 to 7 months after the shrub-clearing treatment. The samples were transported to the laboratory for analyses; once there, they were oven-dried (40°C, for at least 2 days) and crushed to pass a 2-mm sieve. Size-particle distribution was measured using a Boyoucos hydrometer.

Acidity (pH) was determined potentiometrically in a 1:2.5 soil–water suspension. Organic matter was determined using a modified Walkley and Black method. Nitrogen was determined using a Kjeldahl digestion and distillation–titration of the produced ammonium. Available phosphorus was extracted using ammonium fluoride and hydrochloric acid, and measured by spectrophotometry.

Available calcium, magnesium, potassium and sodium were extracted using ammonium acetate: K was measured by flame photometry, and Ca and Mg were determined by atomic absorption spectroscopy. Available micronutrients (Fe, Mn, Cu and Zn) and aluminium were extracted using a 0.05-M EDTA solution and analysed by ICP-OES (see methodological details in Page et al. 1982). Concentrations of the elements are given on a dry weight basis.

Litter fall was collected by traps (29-cm diameter) near each permanent quadrat. The content was removed bimonthly from February 2002 until January 2003, and the leaves were separated, dried and weighed. The cumulative year production of leaves for each sampling point is expressed as g m^{-2}.

Numerical analysis

The coefficient of variation (CV) was used as an estimate of the heterogeneity in the environmental variables, as done in many previous studies (e.g., Wiens 2000). CV was calculated as (100 × SD)/mean, where SD is the standard deviation, and was expressed as percentage. This index is used to compare the amount of variation where direct comparisons of the standard deviations are confounded by differences in scales. Because it is widely used, it also allows comparison of our results with previous studies by other scientists.

The spatial heterogeneity of the environmental variables was evaluated by grouping the data at three scales: (1) patch scale, data were grouped by transect (five quadrats each) and CV was calculated; the mean CV of the 24 transects represents the variability at patch scale;

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(2) site scale, data were grouped by forest site (40 quadrats each) and CV was calculated; the mean CV of the three sites represents the variability at site scale; (3) regional scale, all data (120 quadrats) were analysed together, and the overall CV represents the variability at regional scale. To illustrate graphically the changes of heterogeneity with the spatial scale, we plotted the ratios between CVs. For example, high values in the ratio between CV-by-site and CV-by-patch would mean that the heterogeneity is due mainly to differences between patches and within the forest site, while high values in the CV-by-region and CV-by-site ratio would mean that the heterogeneity is due to differences between the forest sites at regional scale.

To compare the internal heterogeneity between the three studied forest sites, we analysed their CV values (median of eight transects in each site) using the non-parametric Kruskal–Wallis test.

The effects of shrub-clearing treatment on the forest heterogeneity were evaluated separately for each forest site. We compared the CV values (median of four transects) of the two subplots (treated vs. undisturbed) in each forest site, using the non-parametric Mann–Whitney test. Then, we examined whether the trend was consistent for the different variables and for the three sites. In addition, we carried out a multivariate principal component analysis (PCA) of the environmental variables for the 40 plots in each forest site and compared the coordinates of the shrub-cleared and non-managed subplots. The dispersion of the scores for each axis (measured as CV) reflects the heterogeneity in the multivariate space.

Statistical analyses were carried out with STATISTICA (v. 5.1 StatSoft 1997). The normality of the distribution was tested by the Kolmogorov–Smirnov test; when normality failed, the data were transformed by logarithmic, square root or inverse functions and tested again. The program PC-ORD (MjM Software Design, v.4, 1999) was used for PCA analysis.

Results

Variability of the canopy overstorey and light environment in the forest understorey

The overstorey canopy was dominated by the evergreen cork oak (*Q. suber*), although mixed with different proportions of semi-deciduous oak (*Q. canariensis*) and a few species of arborescent shrubs and lianas (Table 1). *Forest* was the densest site, with 74% cover of *Q. suber*, total multistorey cover of 136% and only 7.1% open (gaps). *Woodland* site was codominated by *Q. suber* (44%) and the arborescent shrub *Arbutus unedo* (53%) and had 11.5%gaps. In contrast, the *Open woodland* site had 37.6%gaps and was codominated by *Q. suber* (21%) and *Q. canariensis* (27%). In general, the species overstorey cover was very heterogeneous (CV values higher than 100%). Some exceptions were *Q. suber* in the closed *Forest* (CV = 40), and the same *Q. suber* (CV = 50) and *A. unedo* (CV = 23) in *Woodland* site (Table 1).

The proportion of global (direct and diffuse) radiation under the forest canopy relative to that in the open (global site factor, GSF) had a mean value of 0.24, ranging from 0.11 up to 0.75; the CV was 56% (Table 2). The unmanaged subplot of the *Forest* site was the darkest (mean GSF of 0.14) and most homogeneous (CV of 14%), while the shrub-cleared subplot of the *Open woodland* site was the brightest (mean GSF of 0.36) and the most heterogeneous (CV of 56%). Absolute

Table 1 Composition of the forest overstorey in the three studied sites

Species	*Forest*		*Woodland*		*Open woodland*	
	Mean	CV	Mean	CV	Mean	CV
Trees						
Quercus suber	74.3	40	43.8	50	20.7	97
Quercus canariensis	37.6	106			27.1	140
Laurus nobilis	1.9	283				
Arborescent shrubs						
Phillyrea latifolia	5.4	141	0.8	283	11.4	146
Viburnum tinus	5.0	185				
Rhamnus alaternus	2.6	163	1.4	182		
Myrtus communis	1.3	283				
Arbutus unedo	0.6	283	52.8	23		
Phillyrea angustifolia			4.1	176	1.1	283
Pistacia lentiscus			1.1	283	3.9	194
Erica scoparia			4.5	147	0.5	283
Teline linifolia					9.3	205
Erica arborea					0.7	283
Lianas						
Hedera helix	4.3	128				
Smilax aspera	2.8	172	2.0	228	0.8	192
Lonicera implexa			0.3	283	1.8	283
Rosa sp.					0.1	283
Gaps	7.1	191	11.5	111	37.6	79

Mean and coefficient of variation (CV) of cover percentage, from eight transects. Gaps are estimated as open cover percentage

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Table 2 Heterogeneity of light availability and soil moisture variables in three Mediterranean forest sites

Environmental ariable	*Forest*		*Woodland*		*Open woodland*		Global	
	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Light availability								
Global site factor	0.17	29.5	0.25	52.1	0.30	53.7	0.24	55.7
Radiation (μmol m^{-2} s^{-1})	108	154.3	170	157.0	185	172.2	155	168.5
Leaf area index (m^2 m^{-2})	2.26	26.3	1.64	34.1	1.84	35.7	1.92	34.1
Leaf litter (g m^{-2})	482	22.3	404	26.3	266	51.5	384	38.4
Soil moisture								
Water content (%)								
October 2000	15.6	13.2	14.9	16.0	22.6	35.4	17.7	34.1
March 2001	26.9	10.4	34.6	17.7	42.9	43.0	34.8	37.4
June 2001	9.6	10.7	14.0	17.4	12.4	38.2	12.0	30.1
September 2001	14.3	15.7	7.4	22.4	12.8	50.7	11.5	43.4
Water potential (MPa)								
July 2000	−3.62	22.5	−7.97	54.5	−11.33	54.6	−7.64	70.0

Mean and coefficient of variation (CV) for each site (n = 40, with exception of radiation, n = 160, and soil water potential, n = 16) and for the global forested region (n = 120, except n = 480 for radiation and n = 48 for soil water potential)

values of solar radiation, measured at ground level, had a global mean value of 155 μmol m^{-2} s^{-1} and CV of 169% (Table 2).

Effective leaf area index (LAI) had a mean value of 1.92 m^2 m^{-2} and a CV of 34%. Comparing shrub-cleared versus unmanaged subplots, LAI was consistently lower in the treated subplots of the three sites; relative reductions were 18% in *Forest*, 44% in *Woodland* and 28% in *Open woodland*. Consequently, the understorey light availability (estimated by GSF) had higher mean values in those cleared subplots: 0.20 versus 0.14 (control) at *Forest*, 0.34 versus 0.16 at *Woodland* and 0.36 versus 0.25 at *Open woodland* site. Accumulated leaf litter during 1 year was higher in the *Forest* site (mean of 482 g m^{-2}), while smallest (266 g m^{-2}) and very heterogeneous (CV of 51.5%) at *Open woodland* site. Total mean value was 384 g m^{-2} with a CV of 38%.

Soil moisture and physical and chemical properties

The soil water content was highest in late winter (mean of 35% in March 2001) and lowest in late summer (mean of 11% in September 2001). The coefficient of variation ranged from 30% in late spring to 43% in late summer (Table 2). There were significant differences in soil moisture between forest sites. During late winter, soil at *Open woodland* site had higher water content (mean of 43%) than at *Woodland* (35%) and *Forest* (27%) sites; during the summer, the soil water content at the three sites decreased to 13, 7 and 14%, respectively. Soil water potential, measured during the summer drought, averaged −7.6 MPa, with CV of 70%. The driest site was *Open woodland* (mean of −11.3 MPa), followed by *Woodland* (−8.0 MPa) and *Forest* (−3.6 MPa).

The values of the soil texture and chemical properties presented in general a wide range of variation (Table 3). The global CV was exceptionally low for the pH (9%); for particle size fractions CV varied from 23% (sand) to 49% (clay). Chemical variables had a higher dispersion, with global CV ranging from 32% (total nitrogen) to 101% (available manganese). There was a variation among forest sites in soil chemistry (Table 3). For example, soils in *Open woodland* had the highest pH and concentration of Ca, Mg, K, Mn and Cu. The W*oodland* site had soils with the highest organic matter, P and Fe, but the lowest Na, while soils in the *Forest* site had the lowest organic matter, Ca and Mg.

Heterogeneity and spatial scale

The spatial heterogeneity of the soil variables (measured by calculating CV values with nested group of samples) increased from the patch scale (5–20 m) up to the regional scale (about 40 km) (Table 4). However, the pattern and magnitude of increasing heterogeneity were different among variables; some of them responded mainly at the macro (regional) scale, while others did so at the meso (site) scale. The step from site to region markedly increased (>1.5 times) the CV for the variables pH, Cu, Mn and Na, while the heterogeneity of light availability (measured as GSF) and soil moisture in winter increased mainly in the step from patch to site (Fig. 1). A third group of variables, such as soil N, K and texture (silt %), had similar CV values at the different spatial scales. There were significant differences between sites in terms of internal heterogeneity (mean CV values) of four soil variables—N, P, Mn and Al (Table 5). In all these cases, the *Woodland* site showed the highest internal heterogeneity.

Heterogeneity and forest management

Forest heterogeneity in this study combines the nested spatial pattern of patch (20-m scale), site (1-ha scale) and

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Table 3 Heterogeneity of soil texture and chemical variables in three Mediterranean forest sites

Variable	*Forest*		*Woodland*		*Open woodland*		Global	
	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Soil texture								
Gravel (%)	19.7	34.5	16.1	46.6	24.2	36.2	20.0	41.8
Sand (%)	55.2	15.7	65.2	15.4	46.3	26.2	55.6	23.1
Silt (%)	24.5	20.0	20.8	22.0	26.7	21.8	24.0	23.4
Clay (%)	20.1	35.9	14.0	54.7	26.6	39.3	20.2	49.1
Soil chemistry								
pH	5.6	6.3	5.2	4.0	6.2	3.5	5.7	8.9
Organic matter (%)	5.9	42.2	9.3	43.3	7.4	45.1	7.5	47.7
Total N (%)	0.37	25.6	0.37	34.7	0.37	36.0	0.37	32.1
C/N	9.3	37.6	14.3	22.4	11.8	33.1	11.8	34.5
P (mg kg^{-1})	4.9	33.1	6.3	72.1	4.7	84.2	5.3	68.7
Ca (mg kg^{-1})	1473	40.8	1923	44.7	2631	59.3	2009	58.6
Mg (mg kg^{-1})	219	33.4	266	35.9	314	33.2	266	37.2
K (mg kg^{-1})	139	34.3	136	37.0	179	38.0	151	38.9
Na (mg kg^{-1})	475	32.3	163	29.7	572	41.0	403	59.3
Fe (mg kg^{-1})	271	40.3	386	44.7	211	25.6	289	48.8
Mn (mg kg^{-1})	163	58.5	60	80.0	623	36.5	282	101.0
Cu (mg kg^{-1})	1.6	34.7	1.4	40.7	4.3	71.8	2.4	92.5
Zn (mg kg^{-1})	6.6	74.8	6.7	61.0	7.0	76.3	6.8	70.7
Al (mg kg^{-1})	563	26.3	261	51.4	341	43.2	388	49.3

Available values are given for P, Ca, Mg, K and Na, while EDTA-extracted values are for Fe, Mn, Cu, Zn and Al

Table 4 Heterogeneity of light and soil variables at different spatial scales, calculated as coefficients of variation (%) of nested group of samples

Variable	Patch (transects of five quadrats)			Site (plots of 40 quadrats)			Region (total of 120 quadrats)
	Mean (n = 24)	Max	Min	Mean (n = 3)	Max	Min	(n = 1)
Light (GSF)	21.3	47.2	4.0	45.1	53.7	29.5	55.7
Soil moisture (%)	14.7	49.8	5.1	34.9	44.0	17.7	37.4
Gravel (%)	36.2	77.8	17.3	39.1	46.6	34.5	41.8
Sand (%)	14.2	40.9	4.2	19.1	26.2	15.4	23.1
Silt (%)	18.8	31.1	8.2	21.3	22.0	20.0	23.4
Clay (%)	33.0	61.1	15.2	43.3	54.7	35.9	49.1
pH	3.3	11.4	0.7	4.6	6.3	3.5	8.9
Organic matter (%)	31.7	96.8	10.0	43.5	45.1	42.2	47.7
Total N (%)	28.8	60.7	13.2	32.1	36.0	25.6	32.1
C/N	19.0	44.7	3.9	31.1	37.6	22.4	34.5
P (mg kg^{-1})	48.9	94.8	21.3	63.1	84.2	33.1	68.7
Ca (mg kg^{-1})	32.5	69.5	11.3	42.9	44.7	40.8	58.6
Mg (mg kg^{-1})	26.0	59.1	8.3	31.1	34.4	25.6	37.2
K (mg kg^{-1})	31.4	55.6	9.3	36.4	38.0	34.3	38.9
Na (mg kg^{-1})	25.6	69.9	6.4	34.3	41.0	29.7	59.3
Fe (mg kg^{-1})	30.5	52.0	13.5	36.9	44.7	25.6	48.8
Mn (mg kg^{-1})	50.8	103.4	12.4	58.0	80.0	35.7	101.0
Cu (mg kg^{-1})	37.9	75.4	13.9	49.4	72.9	34.7	92.5
Zn (mg kg^{-1})	42.4	114.3	16.6	62.7	74.8	52.3	70.7
Al (mg kg^{-1})	31.0	61.3	7.8	40.3	51.4	26.3	49.3

Soil moisture values are for winter 2001. Sample size for regional heterogeneity is n = 120

region (40-km scale), together with the silvicultural treatment (two half plots per site). In Fig. 2 we have schematised the sequential variation of CV values for two representative variables—light and soil N. The heterogeneity of light environment at the layer of herbs and seedlings (measured as GSF) increased from 14% at patch scale (in the unmanaged half of the closed *Forest* site) to 56% at regional scale for the whole set of samples. The pattern of increasing heterogeneity differed between sites and scales (Fig. 2). *Forest* site (a dense forest of tall trees) was relatively homogeneous; *Woodland* site had a higher heterogeneity between transects than between treatments; *Open woodland* site showed a significant increase of heterogeneity in light availability associated with the shrub-clearing treatment (see also Table 6). Overall, shrub clearing significantly reduced overstorey LAI, increasing the understorey light availability, but this light increase was not uniform: the heterogeneity of light was higher in the shrub-cleared subplots than in controls. For example, calculating the CV values for 20 measurements (pooling four transects) in treated versus non-treated subplots resulted in 38 versus 15% for *Woodland* site, 30 versus 14% in *Forest* and 56 versus 34% in *Open woodland*. However, at the

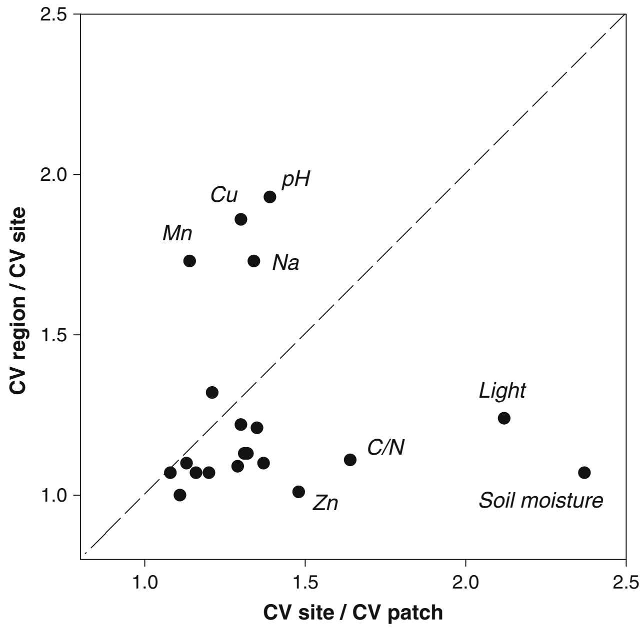

Fig. 1 Comparison between the heterogeneity of environmental variables at different spatial scales. Plot of the ratio between coefficient of variation at region and site scales, against the CV ratio between site and patch scales (see details in the text)

Table 5 Comparison between forest sites according to their internal heterogeneity

Soil variable	*Forest*	Forest site		Kruskal–Wallis test	
		Woodland	*Open woodland*	*K*	*P*
N	21.0^{b}	35.0^{a}	29.7^{a}	7.00	0.030*
P	32.0^{b}	57.9^{a}	51.4^{ab}	12.00	0.002**
Mn	55.9^{ab}	67.1^{a}	27.5^{b}	7.00	0.030*
Al	18.1^{b}	42.4^{a}	29.7^{ab}	9.00	0.011*

Only variables having significant differences (by Kruskal–Wallis test) in the values of coefficients of variation are shown. Same letter in the same row indicates no significant difference. Median values (for $n = 8$ transects) of CV are indicated
Significance level is * $P < 0.05$, ** $P < 0.01$

patch (5–20 m) scale, and for the mean CV values from the four transects within each subplot, the difference in light heterogeneity, associated to shrub-clearing remained significant only for *Woodland* site (Table 6).

The pattern of heterogeneity of soil N did not exhibit significant differences between sites, but significantly varied between treatments (Tables 5, 6). *Forest* site had a relatively homogeneous concentration of N in soil; *Woodland* and *Open woodland* sites had a relatively high heterogeneity within patch (20-m scale) and within site (1-ha scale) (see Fig. 2). In *Woodland* site, heterogeneity in soil N was higher in the shrub-cleared subplot (CV = 40%) than in the managed half (CV = 24%). Other soil variables showing a significantly higher heterogeneity in the shrub-cleared subplots in at least one

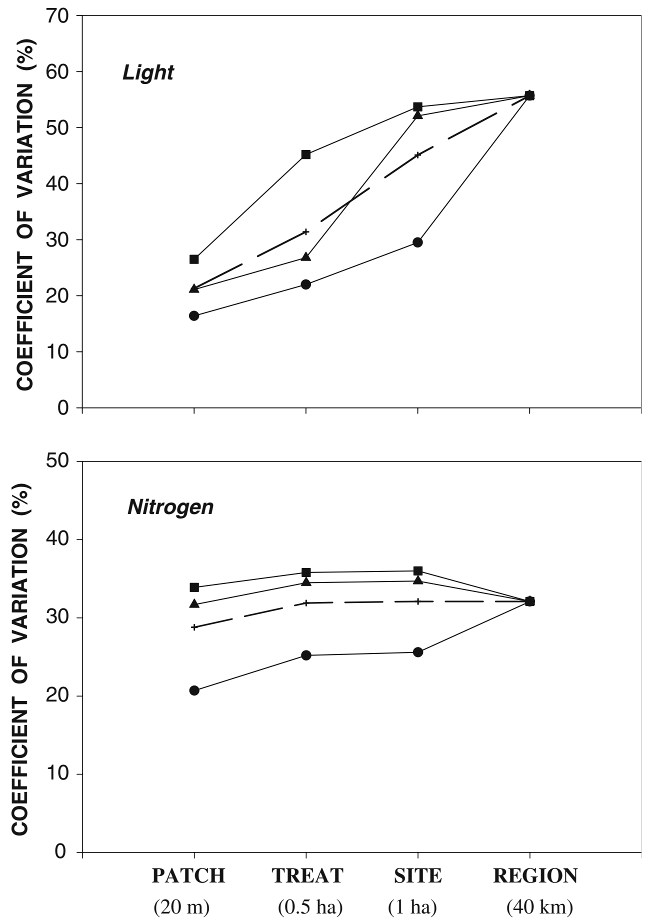

Fig. 2 Spatial scale changes in the CV values for light availability (*above*) and soil nitrogen (*below*). Graphs are represented separately by site: *Forest* (*filled circle*), *Woodland* (*filled triangle*) and *Open woodland* (*filled square*), and altogether (*dashed line*, *cross*). Mean of CV values is calculated for patch (from 48 transects), treatment (from 6 half-plots), site (from 3 plots) and region (from 1 regional pool)

forest site were soil moisture, texture (sand), organic matter (in two sites), C/N, K and Cu (in two sites) (Table 6).

The PCA analysis ordered the soil samples across two main trends or principal components (Table 7, Fig. 3). The first axis explained 30% variance and was defined by soil Cu and Ca, clay, moisture in winter and light availability (at the positive extreme) and leaf litter (negative extreme), while the second axis explained 16% variance and was associated with increasing soil P and organic matter (positive extreme) and decreasing soil Al (negative extreme) (Table 7). Unmanaged subplots of the three forest sites were relatively similar and overlapped in the PCA graph (Fig. 3). Shrub-clearing had little effect on the score variability of samples of *Forest* site within the multivariate space (Fig. 3); the CV of scores for axis 1 increased from 32 to 43%, while it decreased for axis 2 (from 36 to 25%). In contrast, in *Open woodland* site, shrub-cleared samples had a higher variability within the PCA space (Fig. 3), increasing the

Table 6 Comparison between shrub-cleared and control subplots with regards to heterogeneity of soil variables in the three cork oak forest sites

Soil variable	*Forest*		*Woodland*		*Open woodland*	
	U	*P*	*U*	*P*	*U*	*P*
Light (GSF)	5.00	0.386	0.00	0.021*	6.00	0.563
Soil moisture (%)	7.00	0.772	6.00	0.563	0.00	0.021*
Texture (% sand)	7.00	0.772	3.00	0.148	1.00	0.043*
Soil organic matter (%)	0.00	0.021*	0.00	0.021*	2.00	0.083
Total N (%)	3.00	0.149	0.00	0.021*	4.00	0.248
C/N	0.00	0.021*	7.00	0.772	2.00	0.083
K (mg kg^{-1})	6.00	0.563	6.00	0.563	1.00	0.043*
Cu (mg kg^{-1})	1.00	0.043*	2.00	0.083	0.00	0.021*

For simplicity, only *U* and *P* values from the Mann–Whitney test in the CV comparison are shown. In all the cases of significant difference, CV was higher in the shrub-cleared subplot
Significance level is * $P < 0.05$

Table 7 Comparison between shrub-cleared and control subplots with regards to heterogeneity of environmental variables in the three cork oak forest sites

	Axis 1	Axis 2
Variance extracted (%)	29.6	15.7
Variables scores		
Soil Cu	2.23	−0.16
Soil Ca	1.19	0.54
Clay	0.87	−0.42
Light (GSF)	0.85	−0.05
Soil moisture winter	0.78	−0.03
Leaf litter	−0.50	0.07
Soil P	0.40	0.94
Soil organic matter	0.06	0.69
Soil Al	−0.41	−0.44
Coefficient of variation (%)		
Forest		
Unmanaged	32.15	35.67
Shrub-cleared	43.13	25.09
Woodland		
Unmanaged	44.65	28.03
Shrub-cleared	41.73	39.58
Open woodland		
Unmanaged	19.96	32.13
Shrub-cleared	44.47	64.18

Results of the PCA analysis, significance (explained variance) of the two first axes, main variables defining the axes (with highest scores by weighted averaging) and the coefficient of variations of the scores of samples, separating shrub-cleared from unmanaged subplots, are shown

CV of both principal multivariate trends (from 20 to 44% for axis 1 and from 32 to 64% for axis 2).

Discussion

Heterogeneity of light and water availabilities

Forest environments are remarkably heterogeneous in space and time for the main abiotic factors. In a review of 22 datasets (Table 8), the mean coefficient of variation for 12 environmental variables was 36%. Light reaching ground level (CV = 51%) and concentration of Mn in soil (CV = 57%) were highly heterogeneous variables, while soil pH (CV = 11%) and organic matter (CV = 23%) showed the lowest heterogeneity.

Light is crucial for plant performance and forest dynamics, so the literature on spatial heterogeneity in forest understorey light associated with treefall gaps, and its role in tree species regeneration, is ample (e.g., Brown 1996; Denslow 1987; Schnitzer and Carson 2001). Other sources of understorey light heterogeneity operate at finer spatial scales and are related to the small impairments caused in the tree canopy by herbivores or by diseases, the temporal changes in sun angle and the interspecific variation in light transmission by the canopy trees (Canham et al. 1994; Valladares 2003). Two of the Mediterranean forests studied here (control plots) had mean GSF values of 0.14–0.16, and they were relatively homogeneous in light availability (CVs of about 15%). However, considering the whole dataset of forest sampled points, including those in plots recently treated with shrub-clearing practices, the overall median light availability (GSF) was 0.19, and they were highly heterogeneous (CV of 56%), which agrees with similar studies on Mediterranean oak forest (Valladares and Guzman 2006). Considering data from the very few detailed studies of the understorey light conditions of Mediterranean ecosystems, it can be concluded that in mature *Q. ilex* forests with minor water restrictions that reach LAI values around 4 m^2 m^{-2}, understorey PAR ranges from 2 to 7% (Gratani 1997; Gracia 1984). Mean values of understorey PAR estimated here for the cork oak forests are about twice the upper value of this range, presumably as a consequence of intense human intervention.

Soil texture affects water-holding capacity, aeration and organic matter retention, and thus—strongly—the growth and distribution of forest plants (Fisher and Binkley 2000). The heterogeneity of the clay fraction found in the cork oak forest soils (CV of 49%) was the highest within the five datasets reviewed (Table 8). This high variability in soil texture has to be, at least partly,

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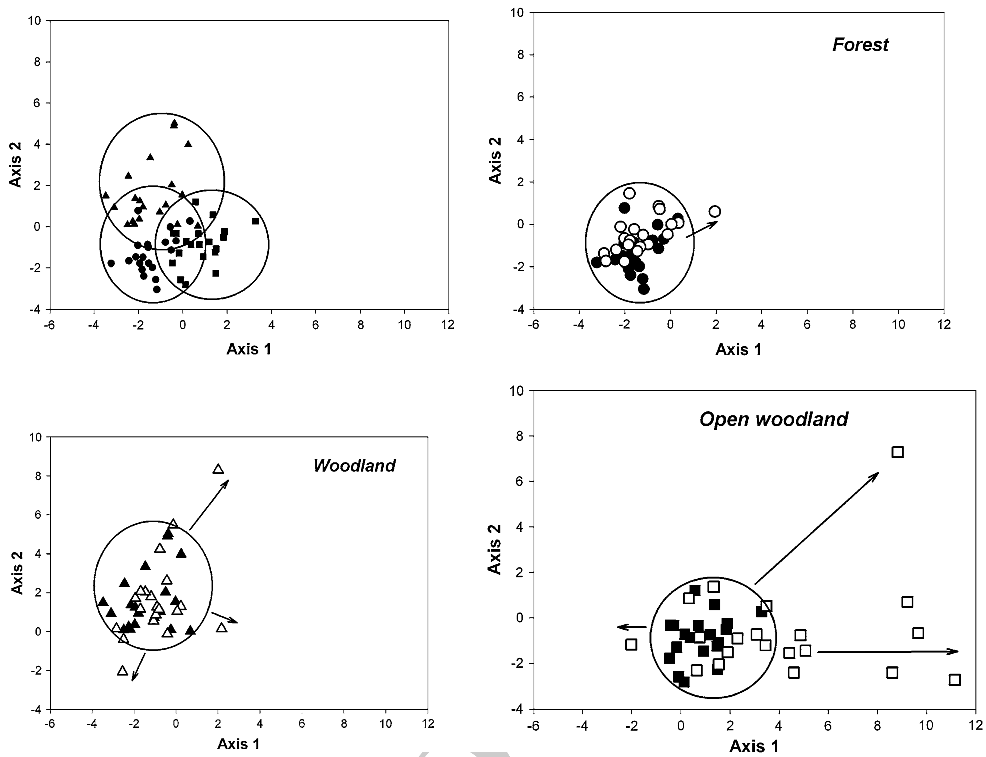

Fig. 3 Ordination by PCA analysis of the samples from unmanaged subplots of the three forest sites (graph *above left*), with ellipses enveloping each site; symbols are *Forest* (*filled circle*), *Woodland* (*filled triangle*) and *Open woodland* (*filled square*). In the same multivariate space, the changes with samples from shrub-cleared subplots (same *symbol*, but in *white*) are represented separately for each forest site. *Arrows* indicate the change trends

responsible for the broad range of water availability found in these forests (Table 2).

The interacting stress of drought and shade is critical for plants living in the understorey of Mediterranean forests (Sack et al. 2003; Quero et al. 2006; Sánchez-Gómez et al. 2006). Valladares and Pearcy (2002) found that drought was more severe for a Californian shrub during the dry summer in the shaded oak understorey than in the open habitat, despite the higher evaporative demand in the sun. Sack et al. (2003) have suggested that Mediterranean forest species tolerating both drought and shade have a combination of reduced resource demand (e.g., by high below-ground allocation and water storage ability, and SLA that decreases with age) and specialised resource capture (e.g., by plasticity in SLA and chlorophyll per unit mass, high root mass fraction and fine and dissected roots). Plant species can specialise within a broad range of light/water combinations with many possibilities for niche differentiation (Sack and Grubb 2002). In consequence, species diversity is expected to be favoured in heterogeneous forest environments.

Heterogeneity of soil chemistry

Heterogeneity of soil pH (CV of 9%) in the studied cork oak forests was similar to the mean (11%) calculated for the reviewed datasets (Table 8). In spite of the low CV value (attributable to the logarithmic nature of the parameter), there were significant differences between sites (regional heterogeneity) and within site (patch scale heterogeneity) in soil pH. These differences have important ecological consequences: soil pH affects the weathering of minerals, the distribution of cations in the exchange complex and the solubility of aluminium (Fisher and Binkley 2000). Soil pH has been detected as a major environmental factor affecting woody species composition and abundance in the forests and shrublands of the Aljibe Mountains (Ojeda et al. 2000), partly explained by the differential species tolerance to aluminium toxicity.

The studied cork oak forests were very heterogeneous in their soil organic matter (SOM); the coefficient of variation (48%) was twofold the mean of the reviewed database (Table 8). The spatial differences found in forest SOM will have consequences for the supply of soil nutrients, the soil structure, bulk density and hydraulic conductivity. SOM is the energy source for the soil fauna and flora (Fisher and Binkley 2000). Litter decomposition rates depend greatly on the source of the leaves (Gallardo and Merino 1993).

Total nitrogen content in the studied forest soils had a CV (32%) similar to the mean of the reviewed dataset (29%, Table 8). The mean value for soil N did not differ significantly between the three forest sites (Fig. 2), but the intra-site heterogeneity was lower in *Forest* than in the other two sites (Fig. 4). In a *Q. ilex* forest of NE Spain, Escarré et al. (1999) measured nutrient fluxes in litterfall; the spatial variation of N (CV of 19% for 18 plots) was similar to that for the litterfall mass, but lower in comparison with K and Mg (CV = 30–33%). Most of the N was found to be stored in the mineral soil

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Table 8 Comparative values of coefficient of variation for forest environmental variables from selected reports in the literature

Forest type (location)	*n*	Light	Soil moisture	Clay	pH	OM	Environmental variables							Reference
							N	Ca	Mg	K	P	Fe	Mn	
Mixed oak (USA)	27	70		17	19						52			Hutchinson et al. (1999)
Aspen forest (Canada)														Kleb and Wilson (1997)
Spring	10	45–120*	10–30*											
Summer	10	45–165*	8–22*											
Pinus silvestris (Finland)	181	28			8	5	13							Möttönen et al. (1999)
Acer rubrum (USA)	65		42		4	34								Görres et al. (1998)
Red oak (USA)	50		0.2		4	23								Morris (1999)
Mixed oak (Spain)	40			30	9	29	28	83		117	45			Leirós et al. (2000)
Pinus pinaster (Spain)	35			12	5	24	24				46			Paz-González and Taboada Castro (2000)
Castanea sativa (Spain)	30			31	8	52	60			73	106			Rubio et al. (1999)
Mixed conifer and hardwood forests (USA)	30				7		28	28	56	21				Grigal et al. (1991)
Pinus plantations (USA)	72				4	16		75	58	40	35			Haines and Cleveland (1981)
Fagus sylvatica (Germany)	38				56	12	123							Joergensen et al. (1995)
Temperate forest (USA)	82				4	20	17	28	28	33	38			Mollitor et al. (1980)
Q. pyrenaica (Spain)	96				3	21	18	64	47	27	21	34	53	Quilchano (1993)
Mixed forest (Spain)														
Fagus-Quercus	60				11	6	3	15	21	6	14			Schmitz et al. (1998)
Pinus plantation	53				10	7	4	17	18	7	13			
Mixed forest (USA)														Finzi et al. (1998b)
Fagus	12					21	23							
Quercus	12					15	15							
Pinus taeda (USA)	239					31	30							Ruark and Zarnoch (1992)
Pinus contorta (USA)	50						15	30	33	19	43	> 100*	16	Entry et al. (1987)
Acer saccharum (Canada)	15							35	51	75				Foster et al. (1989)
Mixed oak (Spain)	120	56	37	49	9	48	32	59	37	39	69	49	101	Present study
Mean CV values		51.4	24.1	27.8	10.7	22.8	28.9	43.4	38.8	41.5	43.8	41.5	56.7	
(Dataset size)		3	3	5	15	16	15	10	9	11	11	2	3	

Values marked with asterisks were not computed for the calculation of mean CV values

(90% of the total forest N), while a small portion (6%) was in the forest floor.

Soil nutrients (Ca, Mg and K) in the Aljibe forest sites had similar overall heterogeneity (CVs of 37–59%) to the corresponding averages in the reviewed database (Table 8). However, soil P was more heterogeneous in these forests (CV of 69%) than the average of the database (CV of 44%). Soil micronutrients had a relatively high spatial heterogeneity in these forests, following the increasing rank order: Fe (CV of 49%), Zn (71%) and Cu (93%) up to Mn (101%). There is a lack of knowledge on the differential response of Mediterranean forest plants to these micronutrients, but we can hypothesise that the high spatial heterogeneity of the forest soil will affect plant growth and distribution. Aluminium is a mineral element of particular relevance in acidic soils, because its solubility is strongly dependent on the pH level (it is more soluble as pH decreases), and it is highly toxic to most plant species (Woolhouse 1981). The availability of Al in the Aljibe soils (after extraction with EDTA) was spatially heterogeneous (CV of 49%), and it was shown that it affected the differential distribution of Al-tolerant versus Al-sensitive plant species (Ojeda et al. 2000).

Spatial scales of heterogeneity

Scaling is an essential feature of heterogeneity. The ecological meaning of the spatial scale of environmental heterogeneity is determined by the scales of response of the organism under study (Levin 1992; Wiens 2000). The environmental variables of the cork oak forests had different spatial heterogeneity patterns at the three scales studied. There was a general trend of increasing heterogeneity with spatial scale (Table 4); some soil variables, such as pH and concentration of Mn and Cu, had the highest heterogeneity increment from site to regional scales, while others, such as light availability in the understorey, increased heterogeneity mostly from patch to site scales (see Table 4, Fig. 1). In general, the variance of soil properties increases with the size of the sampled area. In other words, the coefficient of variation based on the pooled standard deviation over all soil types for each source of variation increases with spatial scale (Beckett and Webster 1971). This is shown, for example, by the CV values of soil pH, Mn and Cu in Table 4. However, some variables, such as total soil N, had similar or even smaller CV values at higher spatial scales (Fig. 2).

The quality and quantity of litterfall vary between tree species and create a heterogeneous chemical environment in the forest soil at patch scale (e.g., Dijkstra 2003). Finzi et al. (1998a, b) found differences in soil pH and exchangeable cations in the forest floor and mineral soil beneath the canopies of six different tree species in North America. Two main processes were involved in generating this spatial pattern: firstly, decomposing litter of different tree species varied in the production of organic acids, which in turn changed the relative quantities of exchangeable cations in the soil; secondly, tree species differed in cation uptake and allocation to biomass pools that had different turnover rates.

Forest management and heterogeneity

In general, shrub-clearing treatment induced a significant reduction of canopy LAI, and in consequence a higher light availability at ground level. The heterogeneity of light availability in a recently managed, shrub-cleared forest where there were contrasted shaded and exposed microsites was higher than in a non-managed adjacent forest where a dense multilayer canopy of trees and shrubs castmore uniform shade. However, there is a fine-scale variation in the quality (e.g., by inter-species difference in light transmission) and the quantity (by sunflecks) of the light reaching the understorey of a closed forest.

The ecological consequences of shrub-clearing management will depend on the spatial and temporal scales. At one extreme, a continuous and extensive elimination of shrubs will transform the forest into a savanna-like landscape, favouring the colonisation of light-demanding herbaceous plants. In fact, for centuries this process has been shaping large areas in the west of the Iberian Peninsula, where a sylvo-pastoral system today occupies more than 55,000 km^2 (Marañón 1988). At the other extreme, traditional shrub-slashing practices that are restricted in space (only around the cork oak trunks) and in time (every 9 years, before the cork extraction) should have little impact on the forest biodiversity.

Shrub clearing involves a disturbance in the forest nutrient cycling. Part of the nutrient pool is removed from the site. The usual practice is to pile and burn the debris, producing local accumulation of ashes and minerals (although in this experiment, burning was done outside the plot of 1 ha). Treated subplots had higher heterogeneity of soil organic matter, nitrogen content and C/N ratio (although significance depended on the site; see Table 6). Soil biological activity was also affected; thus, dehydrogenase activity was lower in the disturbed subplots than in the non-treated ones (a reduction observed in summer, but not in autumn). This reveals that the microclimatic changes associated with the disturbance could be detrimental to microbial activity, in particular during the drought (Quilchano and Marañón 2002). In a mosaic of native beech/oak forests and pine plantations in northern Spain the heterogeneity of SOM was lower in native forests (CV of 6% for 60 plots) than in disturbed, plantation clear-cuts (CV of 13% for 17 plots) and young pine plantations (CV of 14% for 17 plots). Disturbed soils associated with plantation practices suffered acidification, and had less ability to mobilise necromass and to recycle nutrients, showing a higher C/N ratio (Schmitz et al. 1998).

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Conclusions

There was a general trend of increasing heterogeneity with spatial scale, but the extent of variation depended on the environmental variable. Silvicultural practices, such as shrub clearing associated with cork oak trees, can induce an increased environmental heterogeneity (depending on the site characteristics), eventually promoting higher levels of plant diversity. However, extensive clearing of shrubs can induce light homogenisation and/or colonisation by generalist, weedy species to the detriment of shade-tolerant, forest species. The management of cork oak forests, traditionally oriented towards maximising cork production, should now takeinto account its impact on abiotic heterogeneity. This heterogeneity affects crucial biological processes such as regeneration, competition and plant–animal interaction, and thereby the structure and function of forests. A sustainable management of cork oak forests should combine intrinsic and human-induced heterogeneity of abiotic factors to maintain or even increase their biodiversity.

Acknowledgments This study was supported by the projects 1FD97-0743-C03-03, Heteromed (REN2002-04041-C02-02/GLO) and Dinamed (CGL2005-05830-C03-01), funded by the Spanish CICYT. We thank Luis V. García, Eduardo Gutiérrez and Malole Díaz-Villa for their field assistance and Juan Arroyo for advice on the experimental design. We also thank Felipe Oliveros (Director) and the staff of Los Alcornocales Natural Park for their support and co-operation in setting up the experimental plots. Personnel of TRAGSA conducted the silvicultural practices. Rafael López and the staff in the Soil Lab of the IRNAS made chemical analyses of soil samples. Co-operative work and discussion of the manuscript was facilitated by the Spanish Network GLOBIMED and PLASTOFOR, AGL2004-00536/FOR to FV.

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