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

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20 **Abstract** Spatial heterogeneity of abiotic factors influ-
21 ences the structure and function of forests and must be
22 taken into account for their conservation and sustain-
23 able management. In this study, we evaluate the hetero-
24 geneity of abiotic environmental variables in managed
25 cork oak (*Quercus suber* L.) forests in southern Spain at
26 patch, site and regional scales. The extent of spatial
27 heterogeneity depended on the environmental variable
28 examined and the scale considered. For example, soil
29 Mn and P and light availability in the understorey were
30 very heterogeneous at the regional scale, while soil N
31 had low regional heterogeneity, but high spatial
32 variability, at patch scale, attributed to open overstorey
33 and grazing disturbance. There was a general trend of
34 increasing heterogeneity with spatial scale. We also
35 study the effects of a silvicultural practice—shrub
36 clearing on the forest environment and its consequence
37 for spatial heterogeneity. Shrub clearing increased
38 understorey light and decreased its spatial heterogeneity
39 with idiosyncratic effects on soil properties and their
40 spatial heterogeneity at each site. Finally, we compare
41 the heterogeneity (estimated by the coefficient of varia-
42 tion) obtained in these cork oak forests with a database
43 compiled from published studies on other forest envi-
44 ronments. The comparison revealed a remarkable extent

of abiotic heterogeneity in the cork oak forests studied,
suggesting that a sustainable management of these for-
ests 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

Introduction

Heterogeneity in the forested landscape is produced by
the interplay of the geophysical template, physical pro-
cesses, 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 minerali-
zation (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 land-
scape 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 distur-
bances (Ettema and Wardle 2002). Spatial heterogeneity

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

88 There are a few cases of studies documenting
 89 environmental heterogeneity in Mediterranean forest
 90 ecosystems. For example, Joffre et al. (1996) analysed
 91 the spatial variability of leaf area index (LAI), leaf
 92 litterfall and litter decomposition in a *Quercus ilex*
 93 stand; Balaguer et al. (2001) compared the light
 94 availability in the understorey of several *Quercus*
 95 *coccifera* stands and discussed the implications of
 96 spatial heterogeneity; Logli and Joffre (2001) related
 97 the individual local variability of *Quercus pubescens*
 98 with soil heterogeneity and competition. More re-
 99 cently, Valladares and Guzman (2006) have related
 100 canopy structure with spatial patterns of understorey
 101 light in abandoned Holm oak woodlands. In general,
 102 though, there is a scarcity of information on spatial
 103 scales of environmental heterogeneity and the rela-
 104 tionships with forest structure and function in Medi-
 105 terranean ecosystems despite their important influence
 106 in the maintenance of biodiversity and in many other
 107 ecological processes (Valladares 2003).

108 In this study, we evaluate the heterogeneity of abiotic
 109 environmental variables in three cork oak forests located
 110 in southern Spain. In particular, we study spatial chan-
 111 ges in (1) light availability at ground (seedling) level in
 112 the forest understorey, (2) water content of the soil
 113 during different seasons, (3) soil texture, (4) content of
 114 soil organic matter and (5) concentration of macronu-
 115 trients (N, P, Ca, Mg and K) and micronutrients (Fe,
 116 Mn and Cu). We investigate the heterogeneity of these
 117 variables at patch scale (transects of 20 m), at site scale
 118 (plots of 1 ha) and at regional scale (three forest sites
 119 40 km apart from each other). We also study the effects
 120 of a silvicultural practice—shrub clearing on the forest
 121 environment and its consequence for spatial heteroge-
 122 neity. Additionally, we compare the obtained pattern
 123 and extent of heterogeneity for the variables measured in
 124 these cork oak forests with a database compiled from
 125 published studies on other forest environments.

126 Methods

127 Study area

128 The study was carried out in the forested region at the
 129 southern tip of the Iberian Peninsula, near the Strait of
 130 Gibraltar. This region has a rough topography, the
 131 highest elevation being 1,091 m at Aljibe peak. Bedrock
 132 is dominated by Oligo-Miocene sandstone, which pro-
 133 duces acidic, sandy, nutrient-poor soils, although fre-
 134 quently there are interspersed layers of marl sediments,
 135 yielding soils richer in clay. In the lowlands fringing the

mountains, non-acid, loamy or marly soils are domi- 136
 137

138 The climate is subhumid Mediterranean-type with
 139 cool, humid winters and warm, dry summers. The total
 140 annual rainfall ranges from 701 mm in the lowlands to
 141 1,331 mm in the mountains (mean of 1,056 mm for 15
 142 weather stations). The mean temperature is mild: 15–
 143 18°C, with a monthly maximum mean of 36°C (July),
 144 and monthly minimum mean of 2°C (January). The
 145 mean number of frost days ranges from 10 to 20 days
 146 per year at the highest altitude, to 1 day per year in the
 147 vicinity of the coast. Mountains in this area intercept
 148 moist, SE-prevailing winds coming directly from the
 149 Mediterranean Sea, which reduce to some extent the
 150 severity of drought, especially during the summer (see
 151 general descriptions in Ojeda et al. 2000; Mejías et al.
 152 2007).

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

164 This area was protected in 1989 as *Los Alcornocales*
 165 Natural Park; it covers about 1,680 km² and is aimed at
 166 promoting the sustainable management of forest re-
 167 sources and maintaining its biodiversity (Anonymous
 168 2005). The main forest enterprises are cork extraction
 169 from *Q. suber* trees (their bark is stripped off every
 170 9 years), free-range livestock (mainly cattle) and game
 171 hunting (red deer and roe deer).

172 Experimental and sampling design

173 Three forest sites were selected in the Natural Park: a
 174 closed unmanaged forest (hereafter called *Forest*) at
 175 *Tiradero* site (36°9'46"N 5°35'39"W), 335–360 m a.s.l.
 176 on a NE slope, and two woodlands managed for cork
 177 extraction, one (hereafter called *Woodland*) at *Buenas*
 178 *Noches* site (36°22'56"N 5°34'57"W), 410–450 m a.s.l.
 179 on a NE slope, and another of lower tree density
 180 (hereafter called *Open woodland*) at *Panera* site
 181 (36°31'54"N 5°34'29"W), 530–560 m a.s.l. on a NW
 182 slope.

183 At each forest site, one experimental plot of about
 184 1 ha was selected. Half of the plot (0.5 ha) was shrub-
 185 cleared and thinned, following the practice commonly
 186 used to manage cork oak forests in the region (Torres
 187 and Montero 2000). The other half of the plot had not
 188 been shrub-cleared for at least the last 20 years and was
 189 selected as the undisturbed forest control. Treatments
 190 were carried out during winter (January–March) 2000, 190

191	and the resulting debris was burned outside the plot.	a quick estimate of the volumetric water content.	244
192	After finishing the silvicultural practices, the complete	were inserted at four different points around each	245
193	experimental plot (1 ha) was fenced to exclude distur-	quadrat, totalling 480 readings for the three forest sites	246
194	bance by large herbivores.	(4 × 120 quadrats). Soil moisture was measured on four	247
195	In each plot, eight permanent transects of 20 m were	occasions: autumn (October) 2000, winter (February)	248
196	marked: four in the cleared half and four in the undis-	2001, late spring (May–June) 2001 and late summer	249
197	turbed forest. Overstorey composition and abundance	(September) 2001. Soil water potential was additionally	250
198	were measured as the cover of each woody species	measured in 72 quadrats (12 per plot) during late July	251
199	intercepted by the 20-m line. In each transect, five per-	2000 using the filter-paper method (Deka et al. 1995).	252
200	manent quadrats of 1 m ² were marked (about 4–5 m	One sample of superficial soil (0–10-cm depth) was	253
201	apart along the transect). Thus, there were a total of 40	taken near each of the 120 quadrats in summer (July	254
202	quadrats per plot and a grand total of 120 sampling	2000) 5 to 7 months after the shrub-clearing treatment.	255
203	points. Abiotic environmental variables were measured	The samples were transported to the laboratory for	256
204	at the quadrat level. Density of woody species seedlings	analyses; once there, they were oven-dried (40°C, for at	257
205	and presence of herbaceous species were also measured	least 2 days) and crushed to pass a 2-mm sieve. Size-	258
206	in each quadrat (results are presented elsewhere).	particle distribution was measured using a Boyoucos	259
206	Light environment	hydrometer.	260
208	Light availability at each sampling point was quantified	Acidity (pH) was determined potentiometrically in a	261
209	by hemispherical photography. Photographs were taken	1:2.5 soil–water suspension. Organic matter was deter-	262
210	at 0.4–0.6 m above ground level using a horizontally	mined using a modified Walkley and Black method.	263
211	levelled digital camera (CoolPix 995, Nikon, Tokyo,	Nitrogen was determined using a Kjeldahl digestion and	264
212	Japan) with a fish-eye lens of 180° field of view (F8,	distillation–titration of the produced ammonium.	265
213	Nikon). All photographs were taken on 30 April–1 May	Available phosphorus was extracted using ammonium	266
214	2001, before dawn, after sunset, or at other times of the	fluoride and hydrochloric acid, and measured by spec-	267
215	day when the sun was blocked by clouds, thereby	trophotometry.	268
216	ensuring homogeneous illumination of the overstorey	Available calcium, magnesium, potassium and so-	269
217	canopy and a correct contrast between canopy and sky.	dium were extracted using ammonium acetate: K was	270
218	Photographs were taken at the speed indicated by the	measured by flame photometry, and Ca and Mg were	271
219	camera exposure meter with an f-stop ≥7 to ensure	determined by atomic absorption spectroscopy. Avail-	272
220	sharpness of the image. The resulting images were	able micronutrients (Fe, Mn, Cu and Zn) and alumin-	273
221	downloaded to a computer and analysed for canopy	ium were extracted using a 0.05-M EDTA solution and	274
222	openness using Hemiview canopy analysis software	analysed by ICP-OES (see methodological details in	275
223	version 2.1 (1999, Delta-T Devices Ltd., UK). The direct	Page et al. 1982). Concentrations of the elements are	276
224	site factor (DSF), indirect site factor (ISF) and global	given on a dry weight basis.	277
225	site factor (GSF) were computed by Hemiview,	Litter fall was collected by traps (29-cm diameter)	278
226	accounting for the geographical data of the site. These	near each permanent quadrat. The content was removed	279
227	factors are estimates of the fraction of direct, daily and	bimonthly from February 2002 until January 2003, and	280
228	total radiation, respectively, expected to reach the site of	the leaves were separated, dried and weighed. The	281
229	the photograph (Anderson 1964). The effective leaf area	cumulative year production of leaves for each sampling	282
230	index (referred here simply as LAI) was estimated with	point is expressed as g m ⁻² .	283
231	Hemiview as half of the total leaf area per unit ground	Numerical analysis	284
232	surface area (Chen and Black 1992). More information	The coefficient of variation (CV) was used as an estimate	285
233	on analyses of hemispherical photographs can be found	of the heterogeneity in the environmental variables, as	286
234	in Valladares and Guzman (2006). Solar radiation at	done in many previous studies (e.g., Wiens 2000). CV	287
235	ground level (about 10 cm high) was measured in each	was calculated as (100 × SD)/mean, where SD is the	288
236	quadrat with a quantum radiometer (Li-Cor, LI-185B).	standard deviation, and was expressed as percentage.	289
237	Four readings were taken, spatially dispersed within	This index is used to compare the amount of variation	290
238	each 1 m ² quadrat. Measurements were made during the	where direct comparisons of the standard deviations are	291
239	central hours of the day (12 a.m.–2 p.m.) on clear days.	confounded by differences in scales. Because it is widely	292
240	Soil and litter features	used, it also allows comparison of our results with pre-	293
241	Soil water content was measured by Hydrosense	vious studies by other scientists.	294
242	(Campbell Sci.) with 12-cm-depth rods. This system uses	The spatial heterogeneity of the environmental vari-	295
243	a soil physical property—dielectric permittivity to make	ables was evaluated by grouping the data at three scales:	296
		(1) patch scale, data were grouped by transect (five	297
		quadrats each) and CV was calculated; the mean CV of	298
		the 24 transects represents the variability at patch scale;	299

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

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

Environmental variable	<i>Forest</i>		<i>Woodland</i>		<i>Open woodland</i>		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 ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	108	154.3	170	157.0	185	172.2	155	168.5
Leaf area index ($\text{m}^2 \text{m}^{-2}$)	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)

366 values of solar radiation, measured at ground level, had
367 a global mean value of $155 \mu\text{mol m}^{-2} \text{s}^{-1}$ and CV of
368 169% (Table 2).

369 Effective leaf area index (LAI) had a mean value of
370 $1.92 \text{ m}^2 \text{ m}^{-2}$ and a CV of 34%. Comparing shrub-
371 cleared versus unmanaged subplots, LAI was consis-
372 tently lower in the treated subplots of the three sites;
373 relative reductions were 18% in *Forest*, 44% in *Wood-*
374 *land* and 28% in *Open woodland*. Consequently, the
375 understorey light availability (estimated by GSF) had
376 higher mean values in those cleared subplots: 0.20 versus
377 0.14 (control) at *Forest*, 0.34 versus 0.16 at *Woodland*
378 and 0.36 versus 0.25 at *Open woodland* site. Accumulated
379 leaf litter during 1 year was higher in the *Forest*
380 site (mean of 482 g m^{-2}), while smallest (266 g m^{-2}) and
381 very heterogeneous (CV of 51.5%) at *Open woodland*
382 site. Total mean value was 384 g m^{-2} with a CV of 38%.

383 Soil moisture and physical and chemical properties

384 The soil water content was highest in late winter (mean
385 of 35% in March 2001) and lowest in late summer (mean
386 of 11% in September 2001). The coefficient of variation
387 ranged from 30% in late spring to 43% in late summer
388 (Table 2). There were significant differences in soil
389 moisture between forest sites. During late winter, soil at
390 *Open woodland* site had higher water content (mean of
391 43%) than at *Woodland* (35%) and *Forest* (27%) sites;
392 during the summer, the soil water content at the three
393 sites decreased to 13, 7 and 14%, respectively. Soil water
394 potential, measured during the summer drought, aver-
395 aged -7.6 MPa , with CV of 70%. The driest site was
396 *Open woodland* (mean of -11.3 MPa), followed by
397 *Woodland* (-8.0 MPa) and *Forest* (-3.6 MPa).

398 The values of the soil texture and chemical properties
399 presented in general a wide range of variation (Table 3).
400 The global CV was exceptionally low for the pH (9%);

401 for particle size fractions CV varied from 23% (sand) to
402 49% (clay). Chemical variables had a higher dispersion,
403 with global CV ranging from 32% (total nitrogen) to
404 101% (available manganese). There was a variation
405 among forest sites in soil chemistry (Table 3). For
406 example, soils in *Open woodland* had the highest pH and
407 concentration of Ca, Mg, K, Mn and Cu. The *Woodland*
408 site had soils with the highest organic matter, P and Fe,
409 but the lowest Na, while soils in the *Forest* site had the
410 lowest organic matter, Ca and Mg.

411 Heterogeneity and spatial scale

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

431 Heterogeneity and forest management

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

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) (n = 1)
	Mean (n = 24)	Max	Min	Mean (n = 3)	Max	Min	
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

434 region (40-km scale), together with the silvicultural
 435 treatment (two half plots per site). In Fig. 2 we have
 436 schematised the sequential variation of CV values for
 437 two representative variables—light and soil N. The
 438 heterogeneity of light environment at the layer of herbs
 439 and seedlings (measured as GSF) increased from 14% at
 440 patch scale (in the unmanaged half of the closed *Forest*
 441 site) to 56% at regional scale for the whole set of sam-
 442 ples. The pattern of increasing heterogeneity differed
 443 between sites and scales (Fig. 2). *Forest* site (a dense
 444 forest of tall trees) was relatively homogeneous; *Wood-*
 445 *land* 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 avail-
 ability, 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

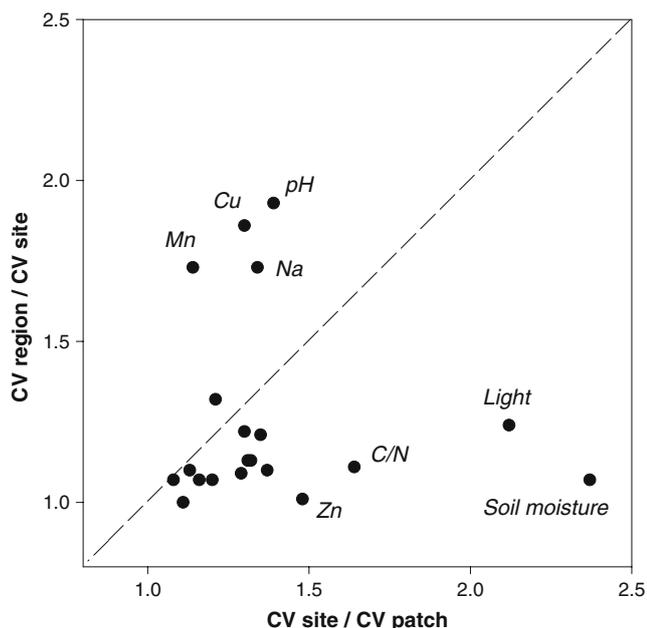


Fig. 1 Comparison between the heterogeneity of environmental variables at different spatial scales. Plot of the ratio between coefficient of variation at region and site scales, against the CV ratio between site and patch scales (see details in the text)

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 * $P < 0.05$, ** $P < 0.01$

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

462 The pattern of heterogeneity of soil N did not exhibit
 463 significant differences between sites, but significantly
 464 varied between treatments (Tables 5, 6). *Forest* site had
 465 a relatively homogeneous concentration of N in soil;
 466 *Woodland* and *Open woodland* sites had a relatively high
 467 heterogeneity within patch (20-m scale) and within site
 468 (1-ha scale) (see Fig. 2). In *Woodland* site, heterogeneity
 469 in soil N was higher in the shrub-cleared subplot
 470 (CV = 40%) than in the managed half (CV = 24%).
 471 Other soil variables showing a significantly higher hetero-
 472 geneity in the shrub-cleared subplots in at least one

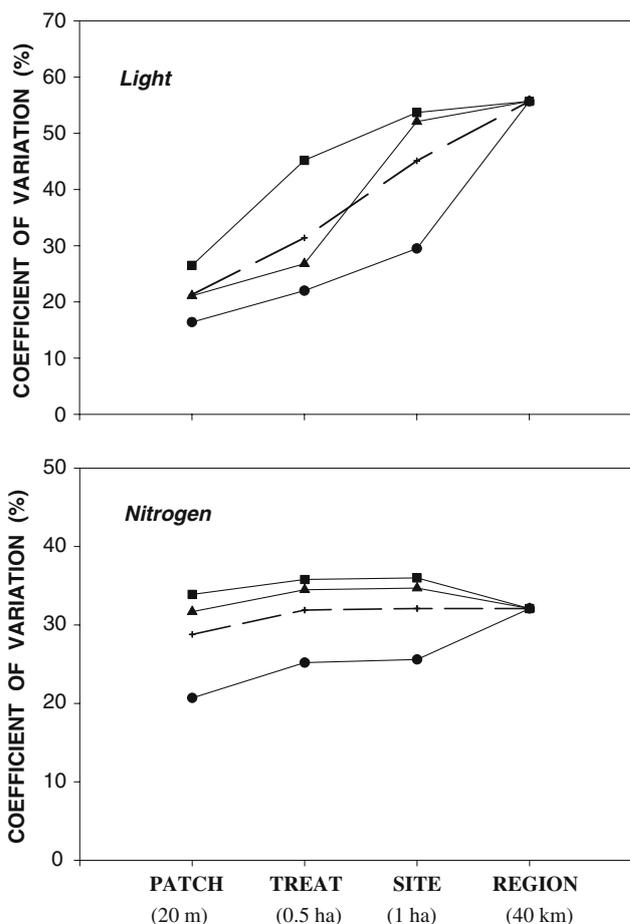


Fig. 2 Spatial scale changes in the CV values for light availability (above) and soil nitrogen (below). Graphs are represented separately by site: *Forest* (filled circle), *Woodland* (filled triangle) and *Open woodland* (filled square), and altogether (dashed line, cross). Mean of CV values is calculated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

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

476 The PCA analysis ordered the soil samples across two
 477 main trends or principal components (Table 7, Fig. 3).
 478 The first axis explained 30% variance and was defined
 479 by soil Cu and Ca, clay, moisture in winter and light
 480 availability (at the positive extreme) and leaf litter
 481 (negative extreme), while the second axis explained 16%
 482 variance and was associated with increasing soil P and
 483 organic matter (positive extreme) and decreasing soil Al
 484 (negative extreme) (Table 7). Unmanaged subplots of
 485 the three forest sites were relatively similar and over-
 486 lapped in the PCA graph (Fig. 3). Shrub-clearing had
 487 little effect on the score variability of samples of *Forest*
 488 site within the multivariate space (Fig. 3); the CV of
 489 scores for axis 1 increased from 32 to 43%, while it
 490 decreased for axis 2 (from 36 to 25%). In contrast, in
 491 *Open woodland* site, shrub-cleared samples had a higher
 492 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	
	<i>U</i>	<i>P</i>	<i>U</i>	<i>P</i>	<i>U</i>	<i>P</i>
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

493 CV of both principal multivariate trends (from 20 to
494 44% for axis 1 and from 32 to 64% for axis 2).

495 Discussion

496 Heterogeneity of light and water availabilities

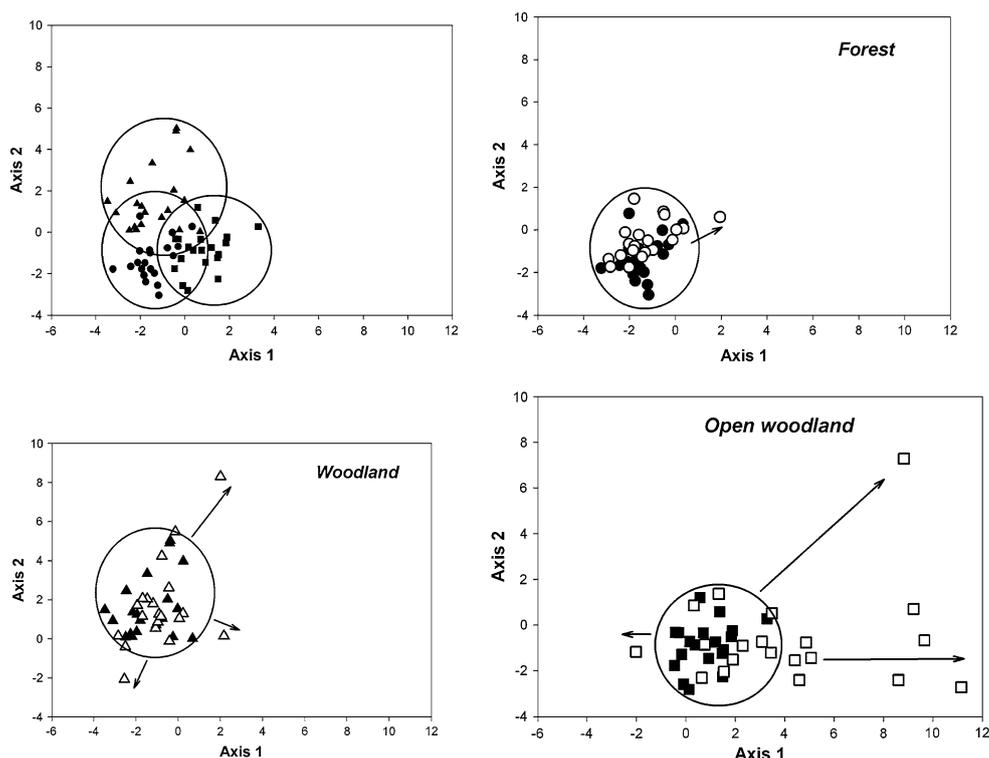
497 Forest environments are remarkably heterogeneous in
498 space and time for the main abiotic factors. In a review
499 of 22 datasets (Table 8), the mean coefficient of varia-

tion for 12 environmental variables was 36%. Light 500
reaching ground level (CV = 51%) and concentration 501
of Mn in soil (CV = 57%) were highly heterogeneous 502
variables, while soil pH (CV = 11%) and organic 503
matter (CV = 23%) showed the lowest heterogeneity. 504

Light is crucial for plant performance and forest 505
dynamics, so the literature on spatial heterogeneity in 506
forest understorey light associated with treefall gaps, 507
and its role in tree species regeneration, is ample (e.g., 508
Brown 1996; Denslow 1987; Schnitzer and Carson 509
2001). Other sources of understorey light heterogeneity 510
operate at finer spatial scales and are related to the small 511
impairments caused in the tree canopy by herbivores or 512
by diseases, the temporal changes in sun angle and the 513
interspecific variation in light transmission by the can- 514
opy trees (Canham et al. 1994; Valladares 2003). Two of 515
the Mediterranean forests studied here (control plots) 516
had mean GSF values of 0.14–0.16, and they were rela- 517
tively homogeneous in light availability (CVs of about 518
15%). However, considering the whole dataset of forest 519
sampled points, including those in plots recently treated 520
with shrub-clearing practices, the overall median light 521
availability (GSF) was 0.19, and they were highly het- 522
erogeneous (CV of 56%), which agrees with similar 523
studies on Mediterranean oak forest (Valladares and 524
Guzman 2006). Considering data from the very few 525
detailed studies of the understorey light conditions of 526
Mediterranean ecosystems, it can be concluded that in 527
mature *Q. ilex* forests with minor water restrictions that 528
reach LAI values around 4 m² m⁻², understorey PAR 529
ranges from 2 to 7% (Gratani 1997; Gracia 1984). Mean 530
values of understorey PAR estimated here for the cork 531
oak forests are about twice the upper value of this range, 532
presumably as a consequence of intense human inter- 533
vention. 534

Soil texture affects water-holding capacity, aeration 535
and organic matter retention, and thus—strongly—the 536
growth and distribution of forest plants (Fisher and 537
Binkley 2000). The heterogeneity of the clay fraction 538
found in the cork oak forest soils (CV of 49%) was the 539
highest within the five datasets reviewed (Table 8). This 540
high variability in soil texture has to be, at least partly, 541

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



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

544 The interacting stress of drought and shade is critical
545 for plants living in the understory of Mediterranean
546 forests (Sack et al. 2003; Quero et al. 2006; Sánchez-
547 Gómez et al. 2006). Valladares and Percy (2002) found
548 that drought was more severe for a Californian shrub
549 during the dry summer in the shaded oak understory
550 than in the open habitat, despite the higher evaporative
551 demand in the sun. Sack et al. (2003) have suggested
552 that Mediterranean forest species tolerating both
553 drought and shade have a combination of reduced re-
554 source demand (e.g., by high below-ground allocation
555 and water storage ability, and SLA that decreases with
556 age) and specialised resource capture (e.g., by plasticity
557 in SLA and chlorophyll per unit mass, high root mass
558 fraction and fine and dissected roots). Plant species can
559 specialise within a broad range of light/water combina-
560 tions with many possibilities for niche differentiation
561 (Sack and Grubb 2002). In consequence, species diver-
562 sity is expected to be favoured in heterogeneous forest
563 environments.

564 Heterogeneity of soil chemistry

565 Heterogeneity of soil pH (CV of 9%) in the studied cork
566 oak forests was similar to the mean (11%) calculated for
567 the reviewed datasets (Table 8). In spite of the low CV
568 value (attributable to the logarithmic nature of the
569 parameter), there were significant differences between
570 sites (regional heterogeneity) and within site (patch scale

heterogeneity) in soil pH. These differences have
571 important ecological consequences: soil pH affects the
572 weathering of minerals, the distribution of cations in the
573 exchange complex and the solubility of aluminium
574 (Fisher and Binkley 2000). Soil pH has been detected as
575 a major environmental factor affecting woody species
576 composition and abundance in the forests and shrub-
577 lands of the Aljibe Mountains (Ojeda et al. 2000), partly
578 explained by the differential species tolerance to alu-
579 minium toxicity.

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

590 Total nitrogen content in the studied forest soils had
591 a CV (32%) similar to the mean of the reviewed dataset
592 (29%, Table 8). The mean value for soil N did not differ
593 significantly between the three forest sites (Fig. 2), but
594 the intra-site heterogeneity was lower in *Forest* than in
595 the other two sites (Fig. 4). In a *Q. ilex* forest of NE
596 Spain, Escarré et al. (1999) measured nutrient fluxes in
597 litterfall; the spatial variation of N (CV of 19% for 18
598 plots) was similar to that for the litterfall mass, but
599 lower in comparison with K and Mg (CV = 30–33%).
600 Most of the N was found to be stored in the mineral soil
601

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											Hutchinson et al. (1999) Kleb and Wilson (1997)
Aspen forest (Canada)			10–30*													
Spring	10	45–120*	8–22*													
Summer	10	45–165*														
<i>Pinus silvestris</i> (Finland)	181	28			8	5	13									Möttönen et al. (1999)
<i>Acer rubrum</i> (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)
<i>Pinus pinaster</i> (Spain)	35			12	5	24	24					46				Paz-González and Taboada Castro (2000)
<i>Castanea sativa</i> (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)
<i>Pinus</i> plantations (USA)	72				4	16		75		58	40	35				Haines and Cleveland (1981)
<i>Fagus sylvatica</i> (Germany)	38				56	12	123									Joergensen et al. (1995)
Temperate forest (USA)	82				4	20	17	28		28	33	38				Mollitor et al. (1980)
<i>Q. pyrenaica</i> (Spain)	96				3	21	18	64		47	27	21	34	53		Quilehano (1993)
Mixed forest (Spain)																
<i>Fagus-Quercus</i>	60				11	6	3	15		21	6	14				Schmitz et al. (1998)
<i>Pinus</i> plantation	53				10	7	4	17		18	7	13				Finzi et al. (1998b)
Mixed forest (USA)																
<i>Fagus</i>	12					21	23									
<i>Quercus</i>	12					15	15									
<i>Pinus taeda</i> (USA)	239					31	30									
<i>Pinus contorta</i> (USA)	50						15	30		33	19	43				Ruark and Zarnoch (1992)
<i>Acer saccharum</i> (Canada)	15						32	59		37	39	69				Entry et al. (1987)
Mixed oak (Spain)	120	56	37	49	9	48	32	59		51	75	49	101			Foster et al. (1989)
Mean CV values (Dataset size)		51.4	24.1	27.8	10.7	22.8	28.9	43.4		38.8	41.5	43.8	41.5	56.7		Present study
		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

602 (90% of the total forest N), while a small portion (6%) 657
 603 was in the forest floor. 658
 604 Soil nutrients (Ca, Mg and K) in the Aljibe forest 659
 605 sites had similar overall heterogeneity (CVs of 37–59%) 660
 606 to the corresponding averages in the reviewed database 661
 607 (Table 8). However, soil P was more heterogeneous in 662
 608 these forests (CV of 69%) than the average of the 663
 609 database (CV of 44%). Soil micronutrients had a rela- 664
 610 tively high spatial heterogeneity in these forests, fol- 665
 611 lowing the increasing rank order: Fe (CV of 49%), Zn 666
 612 (71%) and Cu (93%) up to Mn (101%). There is a lack 667
 613 of knowledge on the differential response of Mediter- 668
 614 ranean forest plants to these micronutrients, but we can 669
 615 hypothesise that the high spatial heterogeneity of the 670
 616 forest soil will affect plant growth and distribution. 671
 617 Aluminium is a mineral element of particular relevance 672
 618 in acidic soils, because its solubility is strongly depen- 673
 619 dent on the pH level (it is more soluble as pH decreases), 674
 620 and it is highly toxic to most plant species (Woolhouse 675
 621 1981). The availability of Al in the Aljibe soils (after 676
 622 extraction with EDTA) was spatially heterogeneous (CV 677
 623 of 49%), and it was shown that it affected the differential 678
 624 distribution of Al-tolerant versus Al-sensitive plant 679
 625 species (Ojeda et al. 2000). 680

626 Spatial scales of heterogeneity 681

627 Scaling is an essential feature of heterogeneity. The 682
 628 ecological meaning of the spatial scale of environmental 683
 629 heterogeneity is determined by the scales of response of 684
 630 the organism under study (Levin 1992; Wiens 2000). The 685
 631 environmental variables of the cork oak forests had 686
 632 different spatial heterogeneity patterns at the three scales 687
 633 studied. There was a general trend of increasing hetero- 688
 634 geneity with spatial scale (Table 4); some soil variables, 689
 635 such as pH and concentration of Mn and Cu, had the 690
 636 highest heterogeneity increment from site to regional 691
 637 scales, while others, such as light availability in the un- 692
 638 derstorey, increased heterogeneity mostly from patch to 693
 639 site scales (see Table 4, Fig. 1). In general, the variance 694
 640 of soil properties increases with the size of the sampled 695
 641 area. In other words, the coefficient of variation based 696
 642 on the pooled standard deviation over all soil types for 697
 643 each source of variation increases with spatial scale 698
 644 (Beckett and Webster 1971). This is shown, for example, 699
 645 by the CV values of soil pH, Mn and Cu in Table 4. 700
 646 However, some variables, such as total soil N, had 701
 647 similar or even smaller CV values at higher spatial scales 702
 648 (Fig. 2). 703
 649 The quality and quantity of litterfall vary between 704
 650 tree species and create a heterogeneous chemical envi- 705
 651 ronment in the forest soil at patch scale (e.g., Dijkstra 706
 652 2003). Finzi et al. (1998a, b) found differences in soil pH 707
 653 and exchangeable cations in the forest floor and mineral 708
 654 soil beneath the canopies of six different tree species in 709
 655 North America. Two main processes were involved in 710
 656 generating this spatial pattern: firstly, decomposing litter 711

of different tree species varied in the production of or-
 ganic 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 signifi-
 cant reduction of canopy LAI, and in consequence a
 higher light availability at ground level. The heteroge-
 neity 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 cast more 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 man-
 agement 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-demand-
 ing 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 km² (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 af-
 fected; 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).

712 **Conclusions**

713 There was a general trend of increasing heterogeneity
 714 with spatial scale, but the extent of variation depended
 715 on the environmental variable. Silvicultural practices,
 716 such as shrub clearing associated with cork oak trees,
 717 can induce an increased environmental heterogeneity
 718 (depending on the site characteristics), eventually pro-
 719 moting higher levels of plant diversity. However,
 720 extensive clearing of shrubs can induce light homoge-
 721 nisation and/or colonisation by generalist, weedy species
 722 to the detriment of shade-tolerant, forest species. The
 723 management of cork oak forests, traditionally oriented
 724 towards maximising cork production, should now
 725 take into account its impact on abiotic heterogeneity.
 726 This heterogeneity affects crucial biological processes
 727 such as regeneration, competition and plant–animal
 728 interaction, and thereby the structure and function of
 729 forests. A sustainable management of cork oak forests
 730 should combine intrinsic and human-induced heteroge-
 731 neity of abiotic factors to maintain or even increase their
 732 biodiversity.

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746 **References**

747 Anderson MC (1964) Studies of the woodland light climate I. The
 748 photographic computation of light condition. *J Ecol* 52:27–41
 749 Anonymous (2005) PORN/PRUG/PDS Parque Natural Los Al-
 750 cornocales. Junta de Andalucía, Consejería de Medio Ambi-
 751 ente, Sevilla, Spain
 752 Balaguer L, Martínez-Ferri E, Valladares F, Pérez-Corona ME,
 753 Baquedano FJ, Castillo FJ, Manrique E (2001) Population
 754 divergence in the plasticity of the response of *Quercus coccifera*
 755 to the light environment. *Funct Ecol* 15:124–135
 756 Beckett PHT, Webster R (1971) Soil variability: a review. *Soils*
 757 *Fertil* 34:1–15
 758 Breshears DD, Rich PM, Barnes FJ, Campbell K (1997) Overstory-
 759 imposed heterogeneity in solar radiation and soil moisture in a
 760 semiarid woodland. *Ecol Appl* 7:1201–1215
 761 Brown N (1996) A gradient of seedling growth from the centre of a
 762 tropical rain forest canopy gap. *For Ecol Manage* 82:239–244
 763 Caldwell MM, Richards JH (1989) Hydraulic lift: water efflux from
 764 upper roots improves effectiveness of water uptake by deep
 765 roots. *Oecologia* 79:1–5
 766 Canham CD, Finzi AC, Pacala SW, Burbank DH (1994) Causes
 767 and consequences of resource heterogeneity in forests: inter-
 768 specific variation in light transmission by canopy trees. *Can J*
 769 *For Res* 24:337–349

Chen JM, Black TA (1992) Defining leaf area index for non-flat
 770 leaves. *Plant Cell Environ* 15:421–429
 771 Deka RN, Wairiu M, Mtakwa PW, Mullins CE, Veenendaal EM,
 772 Townend J (1995) Use and accuracy of the filter-paper tech-
 773 nique for measurement of soil matric potential. *Eur J Soil Sci*
 774 46:233–238
 775 Denslow JS (1987) Tropical rainforest gaps and tree species
 776 diversity. *Ann Rev Ecol Syst* 18:431–451
 777 Dijkstra FA (2003) Calcium mineralization in the forest floor and
 778 surface soil beneath different tree species in the northeastern
 779 US. *For Ecol Manage* 175:185–194
 780 Entry JA, Stark NM, Loewenstein H (1987) Effect of timber har-
 781 vesting on extractable nutrients in a Northern Rocky Moun-
 782 tains forest soil. *Can J For Res* 17:735–739
 783 Escarré A, Rodà F, Terradas J, Mayor X (1999) Nutrient distri-
 784 bution and cycling. In: Rodà F, Retana J, Gracia CA, Bellot J
 785 (eds) *Ecology of Mediterranean evergreen oak forests*. Springer,
 786 Berlin, pp 253–269
 787 Ettema CH, Wardle DA (2002) Spatial soil ecology. *Trends Ecol*
 788 *Evol* 17:177–183
 789 Finzi AC, Canham CD, Van Breemen N (1998a) Canopy tree–soil
 790 interactions within temperate forests: species effects on pH and
 791 cations. *Ecol Appl* 8:447–454
 792 Finzi AC, Van Breemen N, Canham CD (1998b) Canopy tree–soil
 793 interactions within temperate forests: species effects on soil
 794 carbon and nitrogen. *Ecol Appl* 8:440–446
 795 Fisher RF, Binkley D (2000) *Ecology and management of forest*
 796 *soils*, 3rd edn. Wiley, New York
 797 Foster NW, Nicolson JA, Hazlett PW (1989) Temporal variation in
 798 nitrate and nutrient cations in drainage waters from a decidu-
 799 ous forest. *J Environ Qual* 18:238–244
 800 Gallardo A, Merino J (1993) Leaf decomposition in two mediter-
 801 ranean ecosystems of southwest Spain: influence of substrate
 802 quality. *Ecology* 74:152–161
 803 Görres JH, Dichiaro MJ, Lyons JB, Amador JA (1998) Spatial and
 804 temporal patterns of soil biological activity in a forest and an
 805 old field. *Soil Biol Biochem* 30:219–230
 806 Gracia C (1984) Response of the evergreen oak to the incident
 807 radiation at the Montseny (Barcelona, Spain). *Bull Soc Bot Fr*
 808 131:595–597
 809 Gratani L (1997) Canopy structure, vertical radiation profile and
 810 photosynthetic function in a *Quercus ilex* evergreen forest.
 811 *Photosynthetica* 33:139–149
 812 Grigal DF, McRoberts RE, Ohmann LF (1991) Spatial variation in
 813 chemical properties of forest floor and surface mineral soil in
 814 the north central United States. *Soil Sci* 151:282–290
 815 Haines SG, Cleveland G (1981) Seasonal variation in properties of
 816 five forest soils in southwest Georgia. *Soil Sci Soc Am J* 45:139–
 817 143
 818 Hutchinson TF, Boerner REJ, Iverson LR, Sutherland S, Suther-
 819 land KS (1999) Landscape patterns of understory composition
 820 and richness across a moisture and nitrogen mineralization
 821 gradient in Ohio (USA) *Quercus* forests. *Plant Ecol* 144:177–
 822 189
 823 Joergensen RG, Anderson TH, Wolters V (1995) Carbon and
 824 nitrogen relationships in the microbial biomass of soils in beech
 825 (*Fagus sylvatica* L.) forests. *Biol Fertil Soils* 19:141–147
 826 Joffre R, Rambal S (1993) How tree cover influences the water
 827 balance of Mediterranean rangelands. *Ecology* 74:570–582
 828 Joffre R, Rambal S, Romane F (1996) Local variations of ecosys-
 829 tem functions in Mediterranean evergreen oak woodland. *Ann*
 830 *Sci For* 53:561–570
 831 Kleb HR, Wilson SD (1997) Vegetation effects on soil resource
 832 heterogeneity in prairie and forest. *Am Nat* 150:283–298
 833 Leirós MC, Trasar-Cepeda C, Seoane S, Gil-Sotres F (2000) Bio-
 834 chemical properties of acid soils under climax vegetation
 835 (Atlantic oakwood) in an area of the European temperate-hu-
 836 mid zone (Galicia, NW Spain): general parameters. *Soil Biol*
 837 *Biochem* 32:733–745
 838 Levin SA (1992) The problem of pattern and scale in ecology.
 839 *Ecology* 73:1943–1967
 840

- 841 Logli F, Joffre R (2001) Individual variability as related to stand
842 structure and soil condition in a Mediterranean oak coppice.
843 For Ecol Manage 142:53–63 894
- 844 Maltez-Mouro S, García LV, Marañón T, Freitas H (2005) The
845 combined role of topography and overstorey tree composition
846 in promoting edaphic and floristic variation in a Mediterranean
847 forest. Ecol Res 20:668–677 895
- 848 Marañón T (1988) Agro-sylvo-pastoral systems in the Iberian
849 Peninsula: *Dehesas* and *Montados*. Rangelands 10:255–258 896
- 850 Mejías JA, Arroyo J, Marañón T (2007) Ecology and biogeography
851 of plant communities associated with the post Plio-Pleistocene
852 relict *Rhododendron ponticum* subsp. *baeticum* in Southern
853 Spain. J Biogeogr (in press) 897
- 854 Mollitor AV, Leaf AL, Morris LA (1980) Forest soil variability on
855 Northeastern flood plains. Soil Sci Soc Am J 44:617–620 898
- 856 Morris SJ (1999) Spatial distribution of fungal and bacterial bio-
857 mass in southern Ohio hardwood forest soils: fine scale vari-
858 ability and microscale patterns. Soil Biol Biochem 31:1375–
859 1386 899
- 860 Möttönen M, Järvinen E, Hokkanen TJ, Kuuluvainen T, Ohtonen
861 R (1999) Spatial distribution of soil ergosterol in the organic
862 layer of a mature Scots pine (*Pinus sylvestris* L.) forest. Soil Biol
863 Biochem 31:503–516 900
- 864 Ojeda F, Marañón T, Arroyo J (2000) Plant diversity patterns in
865 the Aljibe Mountains (S. Spain): a comprehensive account.
866 Biodivers Conserv 9:1323–1343 901
- 867 Page AL, Miller RH, Keeney DR (1982) Methods of soil analysis.
868 Part 2. Chemical and microbiological properties, 2nd edn.
869 American Society of Agronomy, Madison 902
- 870 Paz-González Vieira SR, Taboada Castro MT (2000) The effect of
871 cultivation on the spatial variability of selected properties of an
872 umbric horizon. Geoderma 97:273–292 903
- 873 Pickett STA, White PS (eds) (1985) The ecology of natural distur-
874 bance and patch dynamics. Academic, San Diego 904
- 875 Quero JL, Villar R, Marañón T, Zamora R (2006) Interactions of
876 drought and shade effects on seedlings of four *Quercus* species:
877 physiological and structural leaf responses. New Phytol
878 170:819–834 905
- 879 Quilchano C (1993) Contribución al estudio de algunos parámetros
880 edáficos relacionados con los ciclos biogeoquímicos, en ecos-
881 sistemas forestales. Ph.D. Dissertation, University of Salam-
882 anca, Salamanca, Spain 906
- 883 Quilchano C, Marañón T (2002) Dehydrogenase activity in Med-
884 iterranean forest soils. Biol Fertil Soils 35:102–107 907
- 885 Rossi RE, Mulla DJ, Journel AG, Franz EH (1992) Geostatistical
886 tools for modeling and interpreting ecological spatial depen-
887 dence. Ecol Monogr 62:277–314 908
- 888 Ruark GA, Zarnoch SJ (1992) Soil carbon, nitrogen, and fine root
889 biomass sampling in a pine stand. Soil Sci Soc Am J 56:1945–
890 1950 909
- 891 Rubio A, Gavilán R, Escudero A (1999) Are soil characteristics
892 and understorey composition controlled by forest management?
893 For Ecol Manage 113:191–200 910
- Sack L, Grubb PJ (2002) The combined impacts of deep shade and
drought on the growth and biomass allocation of shade-tolerant
woody seedlings. Oecologia 131:175–185 897
- Sack L, Grubb PJ, Marañón T (2003) The functional morphology
of juvenile plants tolerant of strong summer drought in shaded
forest understories in southern Spain. Plant Ecol 168:139–163 898
- Saetre P, Bååth E (2000) Spatial variation and patterns of soil
microbial community structure in a mixed spruce-birch stand.
Soil Biol Biochem 32:909–917 900
- Sánchez-Gómez D, Valladares F, Zavala MA (2006) Performance
of seedlings of Mediterranean woody species under experi-
mental gradients of irradiance and water availability: trade-offs
and evidence for niche differentiation. New Phytol 170:795–806 901
- Schlesinger WH, Pilmanis AM (1998) Plant soil interactions in
deserts. Biogeochem 42:169–187 902
- Schmitz MF, Atauri JA, Pablo CL, Agar PM, Rescia AJ, Pineda
FD (1998) Changes in land use in Northern Spain: effects of
forestry management on soil conservation. For Ecol Manage
109:137–150 903
- Schnitzer SA, Carson WP (2001) Treefall gaps and the maintenance
of species diversity in a tropical forest. Ecology 82:913–919 904
- Spies TA, Turner MG (1999) Dynamic forests mosaics. In: Hunter
ML (ed) Maintaining biodiversity in forest ecosystems. Cam-
bridge University Press, Cambridge, pp 95–160 905
- Torres E, Montero G (2000) Los alcornoques del Macizo del Aljibe
y Sierras del Campo de Gibraltar. Clasificación ecológica y
caracterización selvícola y productiva. Ministerio de Agricul-
tura, Pesca y Alimentación, Madrid 906
- Valladares F (2003) Light heterogeneity and plants: from eco-
physiology to species coexistence and biodiversity. In: Esser K,
Lüttge U, Beyschlag W, Hellwig F (eds) Progress in botany.
Springer, Heidelberg, pp 439–471 907
- Valladares F, Percy RW (2002) Drought can be more critical in
the shade than in the sun: a field study of carbon gain and
photo-inhibition in a Californian shrub during a dry El Niño
year. Plant Cell Environ 25:749–759 908
- Valladares F, Guzmán B (2006) Canopy structure and spatial
heterogeneity of understory light in abandoned Holm oak
woodlands. Ann For Sci 63:1–13 909
- Wiens JA (2000) Ecological heterogeneity: an ontogeny of concepts
and approaches. In: Stewart AJA, John EA, Hutchings MJ
(eds) The ecological consequences of environmental heteroge-
neity. Blackwell, Oxford, pp 9–31 910
- Wilson SD (2000) Heterogeneity, diversity and scale in plant
communities. In: Stewart AJA, John EA, Hutchings MJ (eds)
The ecological consequences of environmental heterogeneity.
Blackwell, Oxford, pp 53–70 911
- Woolhouse HW (1981) Soil acidity, aluminium toxicity and related
problems in the nutrient environment of heathlands. In: Specht
RL (ed) Heathlands and related shrublands. Analytical studies.
Elsevier, Amsterdam, pp 215–224 912