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Forest structure and understory diversity in *Quercus pyrenaica* communities with different human uses and disturbances

Reyes Tárrega [a,*], Leonor Calvo [a], Elena Marcos [a], Angela Taboada [b]

[a] *Area de Ecología, Facultad de Ciencias Biológicas y Ambientales, Universidad de León, Campus Vegazana, 24071 León, Spain*
[b] *Departamento de Biología Animal, Facultad de Ciencias Biológicas y Ambientales, Universidad de León, 24071 León, Spain*

Abstract

The aim is to compare the diversity of the understory in *Quercus pyrenaica* communities according to the type of human intervention (grazing, obtaining wood or firewood, forest fires). This interaction results in a modification of the characteristics of the arboreal layer and shrub cover. Four types of oak communities were selected, each with five replicates: communities with a high density of shrubby oak (oak shrublands), open woodlands ("dehesas"), mature oak woods with abundant woody biomass in the understory and mature oak woods with little woody biomass in the understory. In each study site, we quantified the size of the trees (height, trunk perimeter and crown diameter) and their density, woody cover in the understory and species richness as well as diversity using the Shannon index, on both a small scale (per m^2) and for the total of each community. A clear difference was observed between the dehesas and the oak shrublands, the two community types with higher human intervention (the dehesas, with sustainable use for grazing and the oak shrublands, the most degraded due to repeated fires), in the principal components analysis carried out with these variables. The other two community types, considered more mature forests, presented an intermediate location on the principal components analysis. However, there was no clear relationship between the different community types and the diversity values. No differences were observed in total species richness, except that the number of annuals being significantly higher in the dehesas. Nor was it possible to detect any differences using the Shannon index, except for the oak shrublands which, although with a great variability among them, had a lower mean diversity than the other community types. The distance between trees was positively correlated to diversity, measured using the Shannon index, and to annual species richness and negatively correlated to woody cover in the understory. The variability in the distance between trees (associated with clumped distributions) was positively correlated to spatial heterogeneity, measured as S_β. The size of the trees had very little correlation to species diversity. As a whole, the results obtained show the difficulty involved in making generalised conclusions on the effects of disturbances on plant diversity.
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1. Introduction

The loss of diversity associated with exploitation by humans has been one of the main subjects of discussion in the last few decades and especially since the Rio declaration (United Nations Conference on Environment and Development, Río de Janeiro, 1992). However, the controversy among ecologists dates from much earlier and has produced different hypotheses. The first linked human use of resources with an almost automatic loss of biological diversity, which would then tend to increase in the course of succession. However, alternative hypotheses soon arose, such as that of intermediate disturbance, which proposes that maximum diversity will be attained with an intermediate level of disturbance (Connell, 1978; Huston, 1979). Although the controversy is classic, it has acquired new significance because of its implications for sustainable management (Pineda et al., 2002; Howard and Lee, 2003; Sheil and Burslem, 2003; Ishida et al., 2005). Some forms of traditional grazing management, like the dehesa systems, seemed to be linked to high plant diversity (Pineda and Montalvo, 1995), whilst a loss of woody or herbaceous species occurs in other cases because of grazing by domestic livestock or wild herbivores (González-Hernández and Silva-Pando, 1996; Marañón et al., 1999; Webster et al., 2005). Other forms of forest management, such as clearcutting, logging or fire, have been shown to affect plant diversity (Calvo et al., 1999; Kraft et al., 2004; Onaindía et al., 2004; Wardell-Johnson et al., 2004; Ishida et al., 2005), although this effect

is sometimes complex and more difficult to generalise than was originally thought.

Quercus pyrenaica oak forests are mainly distributed over the Iberian Peninsula, in a situation of transition between the typical Mediterranean sclerophyllous forests (dominated by *Quercus ilex*) and the clearly temperate deciduous forests (*Quercus petraea* or *Fagus sylvatica* forests). The current characteristics of these ecosystems are associated with their historic use for humans, by obtaining wood or firewood or for livestock use in dehesa systems, or with disturbances linked to these uses, like fire, which forms part of the traditional management of these areas by shepherds (Calvo et al., 1999; Luis-Calabuig et al., 2000). In the last few decades and linked to the decrease in the rural population, these traditional uses have been wholly or partially abandoned and this has brought about new changes, like the recovery of oak forests in old grazing or crop areas, or the proliferation of shrubby species in the understory as wood was no longer taken and livestock no longer passed through these forests.

The aim of this study is to determine whether the understory diversity in communities dominated by *Quercus pyrenaica* depends on the degree and type of human intervention. Given that in many cases there have been great variations in management and there is a lack of reliable quantitative data, we intend to relate the diversity of the low layer with the characteristics of the tree layer and the abundance of woody species, because both depend to a great extent on the way they are used and the superposition of impacts. Therefore, first we intend to carry out a comparative study of the density and dimensions of the oak trees in four types of oak forest communities: communities of shrubby oaks (oak shrublands, SL, result of secondary succession after abandoning grazing and halted by fire, or the progressive destruction of mature forests by felling and fires), dehesas (open woodland with few shrubs, DE, currently used as pasture), mature forests with practically no woody species in the understory (forests with open understory, FO, result of grazing or exploitation for firewood) and mature forests with abundant woody species in the understory (forests with shrubby understory, FS, where these uses have been abandoned). Secondly, we intend to compare diversity on a small scale (alpha diversity, per m^2), on a community scale (gamma diversity) and spatial or horizontal heterogeneity (beta diversity) in these communities and their relationship with the dimensions of the trees and their variability.

2. Materials and methods

Twenty *Quercus pyrenaica* study sites were selected, five of each type. To minimise the variability, geographically close study sites were selected (the total study area was 30 km × 25 km, situated in León province, NW of the Iberian Peninsula), with no slope or one of less than 10%, subhumid Mediterranean climate (mean annual temperature 10.9 °C, mean annual precipitation 927 mm, dry period in July and August, according to Ministerio de Agricultura, 1980) and humic cambisol type soil (Junta de Castilla y León, 1987). The

differences between study sites were intended to be minimal, except in the type and degree of human intervention. However, it must be taken into account that human intervention depends to a great extent on the characteristics of each community, which determines the type and intensity of use. On the other hand, within those included in the same type, there were also differences between the different study sites, as it was impossible for the intensity of use or disturbances to be of equal magnitude in all of them. Thus, the distinction between communities of shrubby oak (SL) and dehesa (DE) is clear, but between oak forests with open understory (FO) and oak forests with shrubby understory (FS), the differences in some cases are more quantitative than qualitative.

The shrubby oak communities (SL) were identified physiognomically by a great density of small size specimens deriving from vegetative resprout as a response to disturbances, generally fires. The selected study sites had not been burned for at least the previous 3 years. Their altitude is between 920 and 1220 m (Table 1). The dehesa communities (DE) are the result of a traditional livestock management method in which the forest is cleared, leaving a low density of trees, which are pruned to favour crown development at the expense of height growth. In contrast to the typical privately owned dehesas of Salamanca and Extremadura (Rodriguez, 2001), in the study sites they are used as communal pasture by livestock (generally, sheep, but sometimes cows too), so it is difficult to establish the livestock load, which is usually highly variable. In the selected dehesa communities, the altitude was between 975 and 1020 m. The other two forested community types represent a lesser degree of human intervention, the difference between them being the higher or lower abundance of woody species in the understory. Because of this, the former are called forests with shrubby understory (FS) and the latter

Table 1
Location of the study sites

	Locality	Altitude (m)	N exp.	W exp.
SL1	Herreros de Rueda	932	42°38′	5°10′
SL2	Llamas de Rueda	975	42°38′	5°05′
SL3	Valdavida	921	42°36′	4°59′
SL4	Canalejas	973	42°39′	4°59′
SL5	Guardo	1218	42°47′	4°52′
DE1	Canalejas	1002	42°39′	4°58′
DE2	Corcos	975	42°39′	5°05′
DE3	Valdavida	1004	42°37′	4°57′
DE4	Castromudarra	1002	42°37′	5°05′
DE5	Castromudarra	1020	42°36′	5°06′
FS1	Cebanico	991	42°44′	5°03′
FS2	Cebanico	990	42°44′	5°03′
FS3	Modino	1110	42°47′	5°02′
FS4	Modino	1182	42°47′	5°02′
FS5	Santa Olaja	994	42°45′	5°03′
FO1	San Pedro Cansoles	1035	42°44′	4°55′
FO2	Guardo	1255	42°48′	4°53′
FO3	Guardo	1230	42°47′	4°52′
FO4	Prado Guzpeña	1244	42°47′	5°01′
FO5	La Espina	1305	42°49′	4°54′

The closest locality, altitude and geographical coordinates are given. (SL, oak shrublands; DE, open woodlands "dehesas"; FS, forests with shrubby understory; FO, forests with open understory).

open forests or forests with open understory (FO). They were at an altitude of between 990 and 1300 m.

Since diversity is a parameter highly dependent on surface (Magurran, 1989), a systematic method was used for the low layer study so that the sampling area was similar in all the study sites. Two perpendicular transects of about 40 m were followed in each study site and 10 m × 1 m quadrats, each 3 m apart, were sampled in each transect. The firs quadrat of each transect was randomly selected. Therefore, data on 20 quadrats were available for each study site. All the species present in each quadrat were recorded, quantifying their abundance as a cover percentage (visually estimated). Sampling was carried out in June and July 2004.

The tree layer was sampled following the same transects as for the low layer. Five points 8 m apart were sampled in each transect. At each point the distance to the closest tree was measured in the four quadrants (Cottam and Curtis, 1956) in order to estimate the density based on mean distance (density = $1/(\text{mean distance})^2$). When in one point some of the trees had been already measured in the previous point, it was omitted and passed to the following point (another 8 m apart). The trunk perimeter (1 m above ground level) and two crown diameters (one in the transect direction and the other perpendicularly) were measured in the same trees. In addition the height (up to the top of the crown) was calculated as the mean of the visual estimation, always by the same researchers (so that the bias, if it existed, was similar in all the study sites). Therefore, 40 data were available for each study site, using their mean values for later analyses. In some sites, there was abundant vegetative oak regeneration, these shoots normally being less than 1 m high. Only the trees over 2 m high were considered for sampling. This criterion was used because the canopy exceeded this height in the five shrubby oak sites studied.

The measures of diversity were carried out with two indices, species richness (S) and the Shannon index ($H' = -\sum \text{pi} \ln \text{pi}$, where pi = abundance of i species/total abundance; Shannon and Weaver, 1949). They were calculated both on a small scale (per quadrat, or m^2), alpha diversity or microcosmic diversity (Whittaker, 1972; Magurran, 1989, 2004), and a community scale for each study site, gamma diversity or macrocosmic diversity (from the joint consideration of the 20 samples carried out in each study site). By using the comparison of both types of diversity, beta diversity or spatial heterogeneity was calculated. With the richness index, S_α was calculated as the mean of the number of species found per quadrat in each study site; S_γ as the total species number found in each study site; and S_β by the Whittaker formula (in Magurran, 1989): $S_\beta = (S_\gamma/S_\alpha) - 1$. With the Shannon index, H'_α was the average value of H' in the 20 quadrats from each study site; H'_γ the H' total value in each study site, and $H'_\beta = H'_\gamma - H'_\alpha$.

An analysis of variance was carried out to determine whether there were significant differences in tree density, trunk perimeter, crown diameter and height among community types. In addition to considering the mean values, the maximum and minimum values (the largest and smallest size tree in each study site) were also compared. The software used was Statistica 6.0. Analysis of variance was also used to compare

cover of woody species, cover of oak sprouts in the low layer (less than 1 m), the species richness (S) and diversity values (S_α, S_γ, S_β, H'_α, H'_γ and H'_β) for woody species, perennial and annual herbs. In all cases, five replicates were considered. The Scheffe test was applied for the post hoc comparisons when ANOVA was significant ($p < 0.05$). Sample normality had been checked beforehand using the Kolmogorov–Smirnov test and homogeneity of variances with the Cochran test.

For the joint comparison of all the results, a principal components analysis was carried out (using Statistica 6.0), considering 14 variables: distance between trees, mean height, mean perimeter and mean crown diameter of the oaks, woody species cover in the understory, number of woody species, number of perennial and of annual herbs and S_α, S_γ, S_β, H'_α, H'_γ and H'_β. The correlation among all of them was also analysed using the Pearson coefficient, including the coefficient of variation of the tree layer variables in the analysis, in order to determine whether the intra-stand variability in the dimensions and density of the trees affected understory diversity.

3. Results

The size structure diagrams showed that the dominant trees in most oak shrublands (SL) were between 2.5 and 5 m high (Fig. 1a), although there were some larger specimens in all the sites, even over 15 m in SL4. The stem perimeter almost never exceeded 50 cm and the crown diameter was usually below 2 m, although it was more than 4 m in some specimens. In the dehesas (DE), there was greater variability in the oak dimensions (Fig. 1b). The dominant height class was 15–17.5 m. The same can be said of the trunk perimeter, with some specimens less than 50 cm and others exceeding 2 m and even reaching 4 m in some study sites. The mean diameter of the crown varied from at least 2 m to over 18 m in some specimens. Nor did the group of oak forests with shrubby understory (FS) (Fig. 1c) present trees with a clear dominant height (15–17.5 m). The trunk perimeter was below 50 cm in most specimens and almost never exceeded 2 m, and the mean crown diameter was usually between 2 and 4 m. In the open forests (FO) (Fig. 1d), the dominant height was also between 15 and 17.5 m, with variable trunk perimeter and crown diameter.

The four community types differed in the mean (calculated as the mean for the 5 replicates of the mean values of the 40 measured trees in each study site) and maximum values (calculated as the mean values of the biggest tree in each site) (Fig. 2), but no differences were observed as regards the minimum values (calculated as the mean values of the lowest tree in each site), since some small specimens indicating regeneration appeared in all the study sites. The lowest mean height (Fig. 2a) was recorded in the oak shrublands (below 5 m), with statistically significant differences ($p < 0.05$) in comparison with the other three community types, among which no differences were detected. The same pattern was observed when comparing the highest trees in each study site. The values were higher in the oak forests (FO and FS) than in the dehesas, but it was not possible to detect this statistically. The trunk perimeter (Fig. 2b) was greater in the dehesas
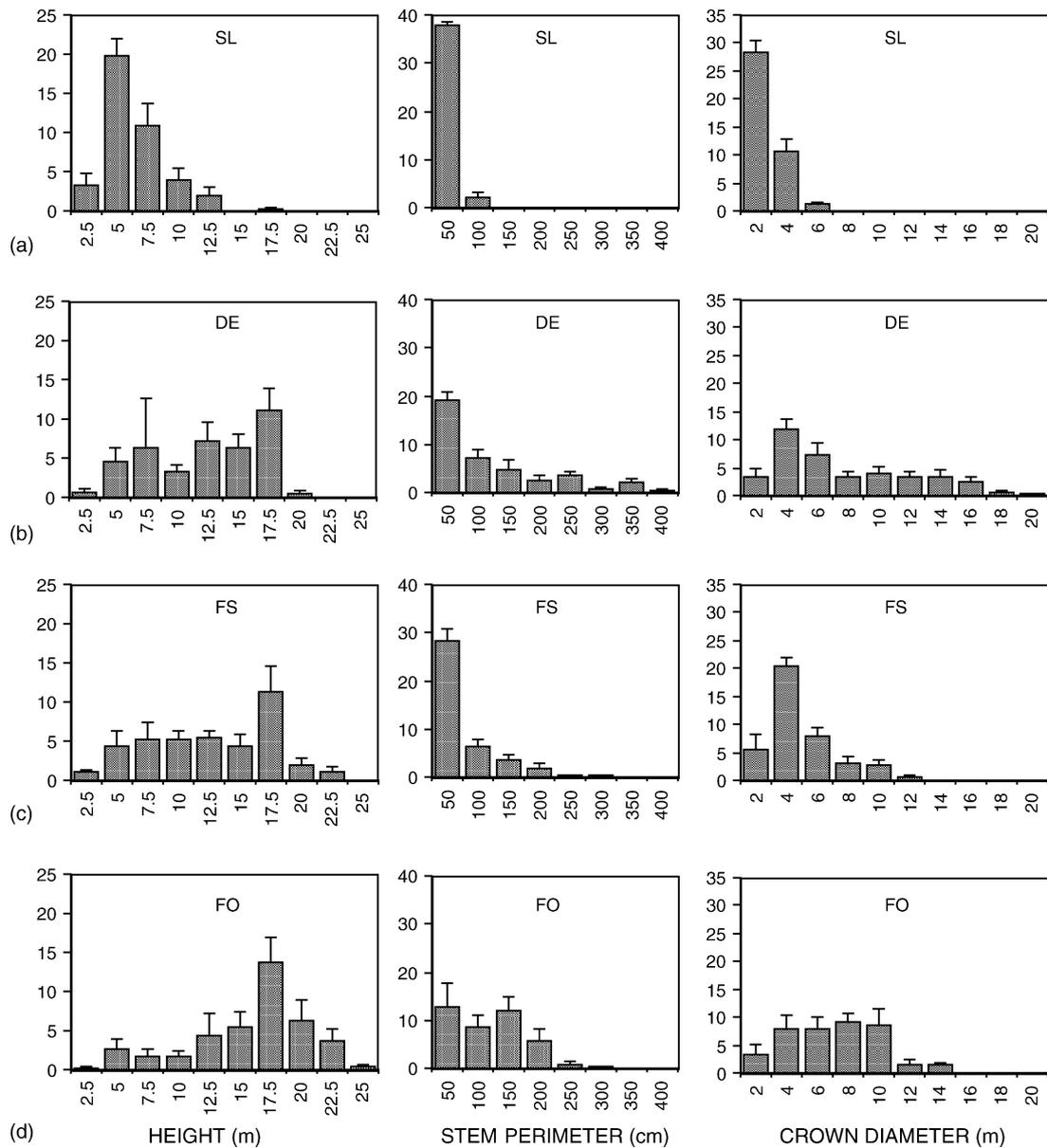
Fig. 1. Size structure diagrams of height (m), stem perimeter (cm) and crown diameter (m) of trees in the studied community types (mean values and standard error for the five replicates of each community type). (a) Oak shrublands (SL). (b) Dehesas (DE). (c) Oak forests with shrubby understory (FS). (d) Oak forests with open understory (FO).

and open forests but the differences were only significant ($p < 0.05$) in comparison with the oak shrublands; the forests with shrubby understory were of intermediate size. However, if the maximum values were compared, differences were detected ($p < 0.05$). The crowns reached maximum development in the dehesas (Fig. 2c), as was to be expected with this type of management, with statistically significant differences ($p < 0.05$) in relation to all the rest if the maximums are compared, but no differences in the mean values were observed between dehesas and open forests. The oak shrublands had a significantly smaller crown than the rest. Therefore, the smallest tree dimensions always corresponded to the oak shrublands; in the dehesas, the type of management determined greater trunk girth and crown cover at the expense of a lower height and the open forests presented intermediate

characteristics between the dehesas and the forests with shrubby understory, although they were more like the former except in height.

Density was expressed as number of stems per hectare, given the difficulty involved in identifying individual genetic specimens in a clonal species like *Quercus pyrenaica*, which has a great capacity for vegetative resprout. The highest densities were observed in the oak shrublands, with a mean of 2623 stem/ha (Fig. 3). However, there was great variability among them, as shown by the high standard error values. There were significant differences ($p < 0.05$) between the oak shrublands and all the other community types, except the forests with shrubby understory. The lowest density was observed in the dehesas, less than 200 stem/ha, but it was not possible to detect the differences in comparison with the open
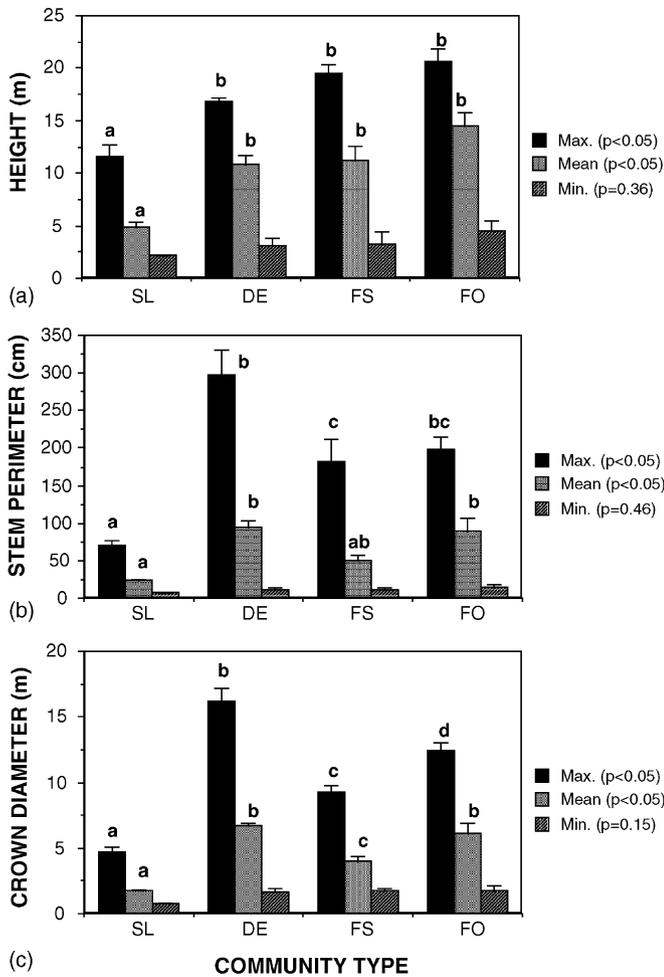
Fig. 2. Mean and standard error of maximum, mean and minimum values of (a) height (m), (b) stem perimeter (cm) and (c) crown diameter (m) of trees in the studied areas. Results of ANOVA are also included (when $p < 0.05$, different letters indicate significant differences by Scheffe test) (SL, oak shrublands; DE, dehesas; FS, oak forests with shrubby understory; FO, oak forests with open understory).
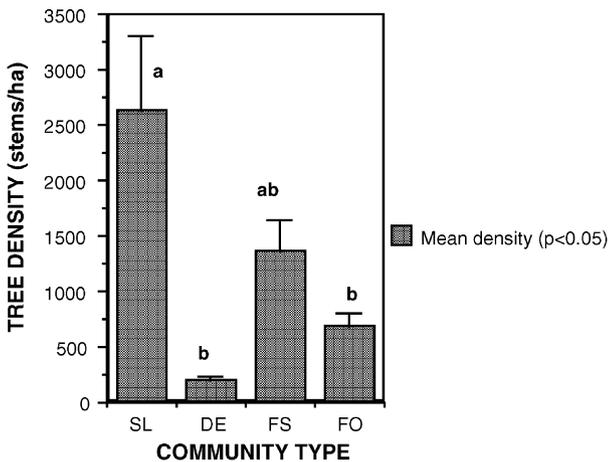

Fig. 3. Mean values and standard error of density (stem number/ha) of trees in the studied areas. Results of ANOVA are also included (when $p < 0.05$, different letters indicate significant differences by Scheffe test) (SL, oak shrublands; DE, dehesas; FS, oak forests with shrubby understory; FO, oak forests with open understory).
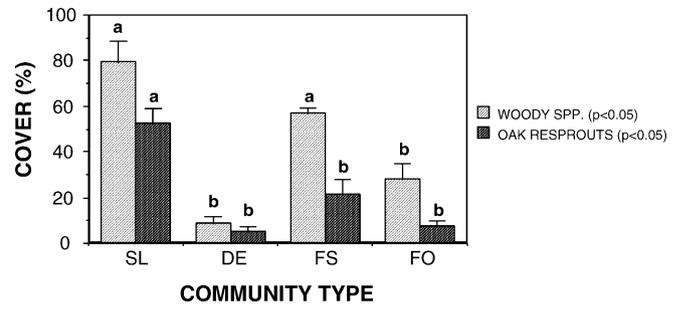

Fig. 4. Mean values and standard error of woody species cover and oak resprouts cover in the studied areas. Results of ANOVA are also included (when $p < 0.05$, different letters indicate significant differences by Scheffe test) (SL, oak shrublands; DE, dehesas; FS, oak forests with shrubby understory; FO, oak forests with open understory).

forests or the closed ones statistically. Woody species cover was at its maximum in the oak shrublands and its minimum in the dehesas (Fig. 4), with significant differences ($p < 0.05$) between oak shrublands and forests with shrubby understory on the one hand, versus dehesas and open forests, on the other. However, when considering the oak sprout cover, differences were only detected between the oak shrublands where regeneration is maximum, and the other community types.

The number of perennial species was similar in the four community types (Fig. 5) and, although the number of woody species was lower in the dehesas than in the other study sites, the differences do not reach levels of statistical significance ($p = 0.06$). However, the number of annuals was significantly higher ($p < 0.05$) in the dehesas, and there were no differences among the rest. The average of total richness on a small scale (S_α) varied between 13 and 16 species/m^2 in oak shrublands and dehesas, respectively (Fig. 6a). On a community scale (S_γ) the mean was 42 species, in both oak shrublands and forests with shrubby understory, and 56 in dehesas. There were no significant differences between the community types in the richness values or for S_α or S_γ. The values of the Shannon index, nevertheless, allowed differences between the values of H'_γ in oak shrublands in comparison with dehesas and forests with shrubby understory to be detected (Fig. 6b). The greatest spatial heterogeneity (Fig. 6c) corresponded to the dehesas and the lowest to the oak shrublands, but although the trend was the same using the two indices, it was much clearer using H'_β
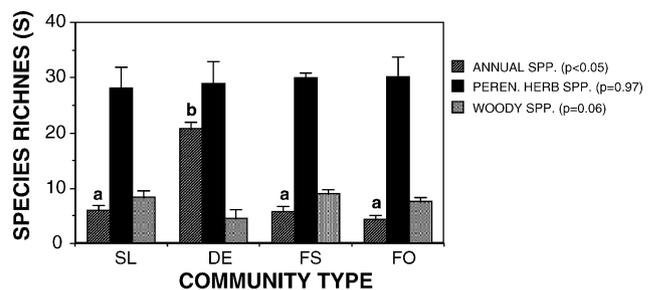

Fig. 5. Mean values and standard error of annual, perennial herbaceous and woody species richness in the studied areas. Results of ANOVA are also included (when $p < 0.05$, different letters indicate significant differences by Scheffe test) (SL, oak shrublands; DE, dehesas; FS, oak forests with shrubby understory; FO, oak forests with open understory).
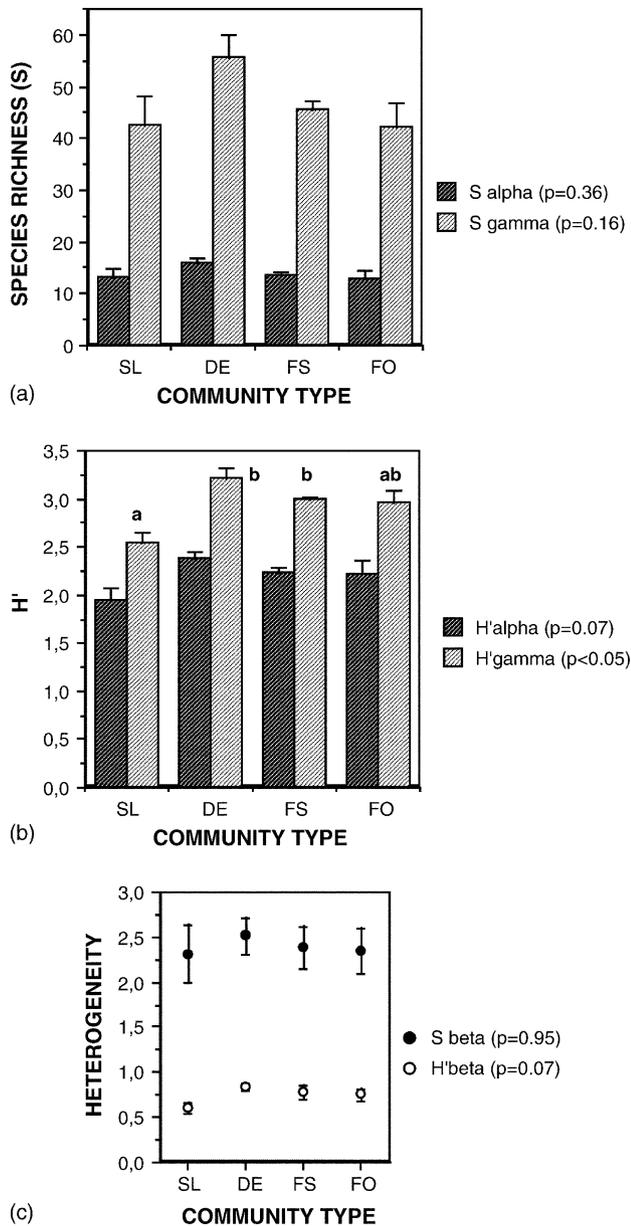
Fig. 6. Mean values and standard error of diversity values measured: (a) as S (species richness), (b) as H' (Shannon index) and (c) heterogeneity values. Results of ANOVA are also included (when $p < 0.05$, different letters indicate significant differences by Scheffe test) (SL, oak shrublands; DE, dehesas; FS, oak forests with shrubby understory; FO, oak forests with open understory).

Table 2
Factor loadings for variables in the firsts two axes in the principal components analysis

	Factor I	Factor II
Tree height	0.64	0.01
Stem perimeter	0.88[*]	0.02
Crown diameter	0.93[*]	0.11
Mean tree distance	0.86[*]	0.20
Understory woody cover	−0.86[*]	−0.27
Annual spp. number	0.60	0.43
Perennial herb spp. number	−0.28	0.88[*]
Woody spp. number	−0.69	0.29
S_α	0.06	0.84[*]
S_γ	0.07	0.95[*]
S_β	0.01	0.20
H'_α	0.35	0.72[*]
H'_γ	0.49	0.80[*]
H'_β	0.40	0.38

Explained variance—Factor I: 36%; Factor II: 29%.
[*] Marked loadings are 0.7 or higher.

with the oak forests (FO and FS) in intermediate positions, the forests with shrubby understory closer to the oak shrublands and the open forests closer to the dehesas (Fig. 7). However, this order was not associated with similar trends in each type of community as regards diversity values, which were explained to a large extent by the second axis. The variables with the highest loading factor for this second axis (explained variance 29%) were S_γ, S_α, number of perennial herb species, H_γ and H'_α, all of them situated towards the positive end. A great separation between communities of the same type was observed along axis II, except in the case of the forests with shrubby understory, with lower dispersion

($p = 0.07$). There was greater variability within the study sites included in the same community type using S_β, as can be seen from the high standard error values.

In the joint comparison of all these variables by a principal component analysis, axis I variables (explained variance 36%) with loading factors >0.7 (Table 2) were trunk perimeter, crown diameter and distance between trees (at the positive end) in contrast to the woody species cover (at the negative end). Therefore, the first axis ordered the study sites according to the size of the oaks with the largest dimensions associated with lower density (greater distance) and lower woody species cover. As a result, the dehesas were located at the positive end and the oak shrublands at the negative end,
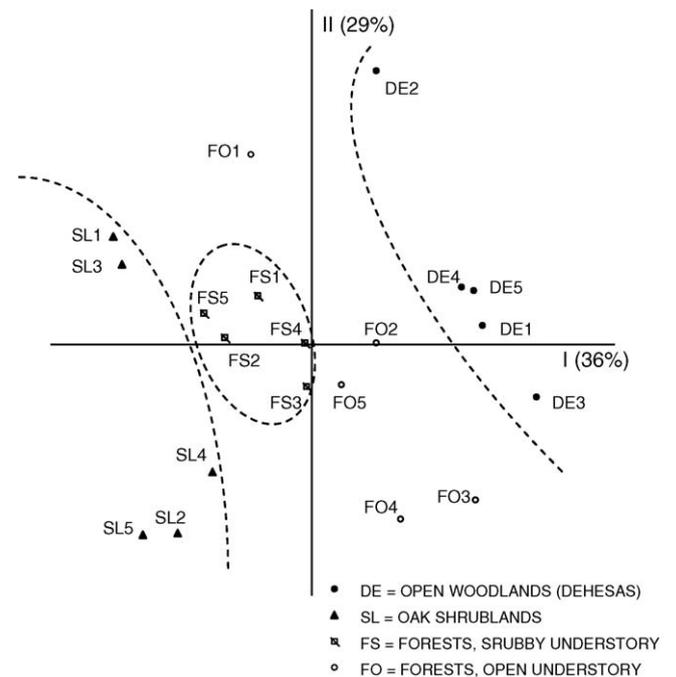

Fig. 7. Location of study sites in the plane defined by the first two axes in the principal components analysis. (SL, oak shrublands; DE, dehesas; FS, oak forests with shrubby understory; FO, oak forests with open understory).

Table 3
Pearson correlation analysis between the variables used in the principal components analysis

	TH	SP	CD	TD	UC	AN	PN	WN	S_α	S_γ	S_β	H'_α	H'_γ	H'_β	cvTH	cvSP	cvCD
SP	**0.79**[*]																
CD	**0.81**[*]	**0.97**[*]															
TD	0.31	**0.73**[*]	**0.77**[*]														
UC	**−0.48**[*]	**−0.68**[*]	**−0.77**[*]	**−0.74**[*]													
AN	−0.09	0.33	0.42	**0.81**[*]	**−0.65**[*]												
PN	−0.04	−0.15	−0.10	−0.17	−0.07	0.04											
WN	−0.03	−0.37	−0.41	**−0.60**[*]	**0.61**[*]	**−0.60**[*]	**0.54**[*]										
S_α	−0.02	0.10	0.15	0.32	−0.14	0.44	**0.61**[*]	0.16									
S_γ	−0.08	0.07	0.14	0.32	−0.35	**0.58**[*]	**0.82**[*]	0.19	**0.75**[*]								
S_β	−0.10	−0.06	−0.02	0.01	−0.28	0.20	0.33	0.11	−0.30	0.40							
H'_α	0.35	0.37	**0.45**[*]	0.39	−0.37	0.38	**0.46**[*]	−0.04	**0.84**[*]	**0.56**[*]	−0.40						
H'_γ	0.42	0.41	**0.55**[*]	**0.49**[*]	**−0.63**[*]	**0.53**[*]	**0.54**[*]	−0.10	**0.70**[*]	**0.70**[*]	0.02	**0.88**[*]					
H'_β	0.27	0.21	0.35	0.32	**−0.64**[*]	0.42	0.30	−0.13	−0.04	**0.46**[*]	**0.74**[*]	0.05	**0.52**[*]				
cvTH	**−0.78**[*]	**−0.55**[*]	**−0.54**[*]	−0.07	0.12	0.20	0.01	−0.13	−0.01	0.10	0.21	−0.24	−0.19	0.02			
cvSP	−0.14	−0.02	0.08	0.37	−0.37	**0.54**[*]	0.00	−0.40	0.29	0.29	0.03	0.34	0.44	0.30	**0.46**[*]		
cvCD	−0.26	0.03	0.11	**0.50**[*]	**−0.45**[*]	**0.65**[*]	0.13	−0.34	0.40	**0.45**[*]	0.15	0.28	0.37	0.26	**0.57**[*]	**0.84**[*]	
cvTD	**−0.46**[*]	−0.33	−0.39	−0.13	0.29	−0.01	0.06	0.32	−0.20	0.12	**0.54**[*]	**−0.54**[*]	−0.38	0.16	0.39	−0.18	0.03

$N = 20$; TH: tree height; SP: stem perimeter; CD: crown diameter; TD: mean tree distance; UC: understory woody cover; AN: annual spp. number; PN: perennial herb spp. number; WN: woody spp. number; cvTH: tree height coef. of variation; cvSP: stem perimeter coef. of variation; cvCD: crown diameter coef. of variation; cvTD: mean tree distance coef. of variation.

[*] Marked correlations are significant at $p < 0.05$.

and intermediate values. The most diverse communities were DE2, FO1, SL1 and SL3 and the least diverse FO3, FO4, SL2, SL5 and SL4.

In the analysis carried out to determine the relationship between the tree characteristics and the different diversity estimators (Table 3), a significant positive correlation was only observed between the crown size and H'_γ and H'_α, as well as between the distance between trees (lower density) and the number of annual species and H'_γ. The woody species cover in the understory, negatively correlated to the size of the trees, was positively correlated to woody species richness, and negatively to annual richness, H'_γ and H'_β. If instead of considering the correlation to the mean values of the tree characteristics, the correlation to its variability was analysed using its coefficient of variation, it was observed that the greater the perimeter variability, the greater the annual species richness. The same occurred with the coefficient of variation of the crown dimensions, which was also correlated to total richness (S_γ). On the other hand, the variability in the distance between trees (associated with clumped distributions) was positively correlated to the spatial heterogeneity, measured as S_β, and negatively to small scale diversity, quantified using the Shannon index (H'_α).

4. Discussion

In the studied zones, the great variability within community types means that it is not always possible to detect significant differences among communities in regard to the characteristics of the trees or the woody species cover in the understory. However, a joint comparison by PCA did show separation between them. In general, the most extreme values appeared in the two community types associated with greatest impact or human intervention, the shrubby oak communities and the dehesas. The fact that differences were not detected when

comparing the minimum values of the tree dimensions seemed to indicate the existence of regeneration in all the sites, although of different magnitudes. The number of small specimens was minimal in the dehesas and the open forests. Gómez et al. (2003) described the difficulty of *Quercus pyrenaica* in regenerating sexually, due to the action of acorn and seedling predators. Vegetative regeneration predominates, which makes colonization of the gaps between oak clumps difficult. In the oak shrublands regeneration was mostly vegetative, as shown by the great density of resprouts in the understory, and the same occurred in oak forests with shrubby understory. This is the most common way for *Quercus pyrenaica* to recover after disturbances (Luis-Calabuig et al., 2000). However, in the dehesas studied, although few small oaks appeared, they were sufficiently isolated to suspect that they came from acorns.

The lower number of woody species found in the dehesas in comparison with other community types, though not statistically significant, coincides with the results of Onaindía et al. (2004), who recorded the disappearance of some sensitive shrub species in grazed forests. The higher number of annual species in the same zones also coincides with the results of other authors, who associated grazing with a greater herb richness (Montalvo et al., 1993; Onaindía et al., 2004), although it is not a general trend, as an excessive grazing intensity by wild or domesticated herbivores can produce a drastic alteration in the herb community and the disappearance of sensitive species (Le Houérou, 1981; Webster et al., 2005). Crawley (1997) emphasizes the difficulty in generalising the effects of herbivorism on plant diversity, quoting various studies with contradictory results. In the studied zones it was not possible to detect differences in the total richness values and a lower diversity at community level was only found in the oak shrublands by using the Shannon index. The great variability in

the diversity values measured using different indices stands out when zones classed as the same type are compared (Fig. 7). This could be explained by the succession dynamic typical of these communities, with a tendency to recover by autosuccession (Hanes, 1971), due to the fact that vegetative regeneration predominates in many species and, in addition, seed dispersion occurs over short distances (Luis-Calabuig et al., 2000; Trabaud, 2000). Therefore, the species present in each zone when the level of use or disturbance stops or diminishes condition the recovery of the community. This is particularly important in zones where the presence of humans has created a significant level of fragmentation, as is the case in the whole Mediterranean basin and throughout Europe in general (Naveh, 1994), since there are no undisturbed *Quercus pyrenaica* forests nearby which could act as a seed source of the different species from these communities. Other authors have observed that when grazing by deer was excluded, recovery occurred from the herb species which had survived, but there was no recolonization of the most sensitive species which had been eliminated, attributing this to the unfavourable landscape context (Webster et al., 2005). Likewise, other authors explained the lack of some understory forest species in post-agricultural, secondary forests in North America by inherent limitations in their dispersal ability, even when environmental conditions were favourable (Donohue et al., 2000; Bellemare et al., 2002).

The greater annual species richness could be due to greater light availability, associated with lower tree density and lower woody species cover, which correlated with richness. The increase in the number of species in the understory associated with the presence of gaps has been observed by other authors (Schumann et al., 2003). In addition, the reduction in light availability has been used to explain the decrease in the number of species in mature succession stages (Howard and Lee, 2003). On the other hand, in many studies on recovery after disturbances an increase in species richness has been observed in the first years, but this is minimal in the intermediate successional stages, associated with greater shrub cover (Luis-Calabuig and Tárrega, 1993; Calvo et al., 1999, 2002; Onaindía et al., 2004; Wardell-Johnson et al., 2004). This diversity pattern coincides with the minimum diversity recorded in some of the oak shrublands studied, which can be assimilated to these intermediate recovery stages after a fire or after pasture or crops are abandoned.

An influence of the tree characteristics on total understory diversity is not very evident from the results obtained. Tree size is only correlated with diversity in the case of crown diameter. There is also a positive correlation between the distance between trees and diversity. However, interpretation of these results can be more complex than that of a simple direct effect, since there is a superposition in dehesas between livestock use, which affects the understory, and tree management system, which determines its growth and density. Nor does the variability in tree dimensions, quantified by the coefficient of variation, provide new information on the influence in the low layer. Other authors have also found only few and weak correlations between plant species diversity and heterogeneity of stand structure (Neumann and Starlinger, 2001).

In regard to beta diversity, the higher values associated with the dehesas can be explained by the individualized effect of each tree on the herb layer, which generates heterogeneneous mosaics (Puerto et al., 1977; Diez et al., 1991; Gómez-Gutierrez, 1991). There was also a clear relation between the greater variability in the distance between trees, associated with the clumped distribution, and the spatial heterogeneity at understory level (although only statistically significant when quantified as S_β). Contrary to the tree effect, woody species cover had a negative correlation with beta diversity (significant for H'_β). This is due to the fact that the presence of woody species in the understory of the study zones was either very small (in dehesas and open forests) or almost continuous (in oak shrublands and forests with shrubby understory), which determined conditions not of heterogeneity but rather of greater homogeneity.

In summary, the results obtained in this study confirm the difficulties involved in making general conclusions on the effects of disturbances and management systems on diversity, which have been stated by other authors. They attribute the contradictory results recorded to differences among the communities compared, the method used or the scale used to quantify diversity (Chiarucci et al., 2001; Rey Benayas, 2001; Sheil and Burslem, 2003). However, differences can appear in studies carried out with homogeneous methodology and scale, as in this study, even comparing very similar communities (belonging to the same community type). Small inherent prior differences in each study site (different species in the understory or in the soil seed bank, with different ability to survive or recovery after disturbances), can provoke the maintaining of these differences due to the recovery by autosuccession, or even an increase, if there are repeated disturbances, as fires, and the species massively resprouted (as *Quercus pyrenaica* do, determining a shrubby structure). This, combined with small changes in the intensity of use, even in communities classed as the same management type, can produce significant changes in understory diversity. For this reason, the proposed management systems for preserving diversity should be specific and preceded by a detailed study of each determined zone.

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