Species richness and similarity of vascular plants in the Spanish dehesas at two spatial scales

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Abstract

Aims of study: The goals of this paper are to summarize and to compare plant species richness and floristic similarity at two spatial scales; mesohabitat (normal, eutrophic, and oligotrophic dehesas) and dehesa habitat; and to establish guidelines for conserving species diversity in dehesas.

Area of study: We considered four dehesa sites in the western Peninsular Spain, located along a climatic and biogeographic gradient from north to south.

Main results: Average alpha richness for mesohabitats was 75.6 species, and average alpha richness for dehesa sites was 146.3. Gamma richness assessed for the overall dehesa habitat was 340.0 species. The species richness figures of normal dehesa mesohabitat were significantly lesser than of the eutrophic mesohabitat and lesser than the oligotrophic mesohabitat too. No significant differences were found for species richness among dehesa sites. We have found more dissimilarity at local scale (mesohabitat) than at regional scale (habitat). Finally, the results of the similarity assessment between dehesa sites reflected both climatic and biogeographic gradients.

Research highlights: An effective conservation of dehesas must take into account local and regional conditions all along their distribution range for ensuring the conservation of the main vascular plant species assemblages as well as the associated fauna.

Key words: agroforestry systems; mesohabitat; non-parametric estimators; alpha richness; gamma richness; floristic similarity; climatic and biogeographic range.

Introduction

Dehesa is probably the most widespread and well-known agroforestry system in Europe (San Miguel, 1994; Montero *et al.,* 1998; Papanastasis, 2004). This savanna-like landscape (Marañon, 1986; Joffre *et al.*, 1999; Marañon *et al.*, 2009) is a multipurpose agro-silvo-pastoral system mainly arising as a result of an ancient human activity which profoundly transformed the original structure of the stands through clearing evergreen woodlands, in order to optimize direct productions, and where trees, natural and managed grasslands, croplands and livestock interact under specific management practices (Campos, 1992; Montero *et al.*, 1998; Joffre *et al.*, 1999; Moreno and Pulido, 2008).

Dehesa landscapes are settled on flat or gently undulated topography, over poor or very poor soils not suitable for a permanent agricultural use. Presence of scattered trees (mainly species of genus *Quercus*) that produce fine branches, leaves and fruits to feed livestock, as well as long land use rotation between arable land, grassland and low scrubland, are the main characteristics of this management method applied to extensive territories. Dehesas cover large areas of western and south-western Iberian Peninsula. Nowadays, this agroforestry system comprises an area of 2.3 million hectares in Spain, across a north-south range of 500 km, and 400 km from west to east. In addition, the equivalent to the Spanish dehesas in Portugal, the "montados", cover 0.7 million hectares (MAPYA, 2004; Pereira *et al.,* 2004). This territorial amplitude includes different climate, topography and soil conditions resulting in diverse dehesa typologies – *i.e.* different tree dominant

species, density of trees, pasture composition, etc. In relation to tree species composition, Holm oak (*Quercus ilex*) is largely dominant in around 85% of the territory in pure dehesas or mixed with Cork oak (*Quercus suber*), Lusitanian oak (*Quercus faginea*) or Pyrenean oak (*Quercus pyrenaica*). These species are dominant in 15% of dehesa extension but Holm oak could be present as non dominant as well.

The dehesas have been mainly developed under Mediterranean climate conditions with three main climatic types (Sánchez de Ron *et al*., 2007). Heterogeneity in topography, soil and climate, interactions among species and the superimposed selective activity of herbivores, in addition to human activities, are main agents forging dehesa landscapes (Marañon *et al*., 2009). The interaction between abiotic conditions and the extensive regime of use at different scales is essential for high biodiversity of Spanish dehesa habitat (Díaz, 2008).

Several authors (Naveh and Whittaker, 1979; Pineda *et al*., 1981; Marañón, 1985; Marañón, 1986) have emphasized high values of vascular plant species richness (135 species/0.1 ha) and Shannon entropy (6 bits) and these values have been widely cited in the literature about dehesas. More recently, Díaz *et al.* (2003) reported values from 60 to 100 species/0.1 ha for *Quercus suber* woodlands, not strictly a dehesa, while Díaz *et al.* (1999) and Ojeda *et al.* (2000) provided figures of 67 species and 95 species/0.1 ha for vascular plants, respectively.

Most of the previous studies did not include questions about the scale of environmental heterogeneity that promotes species richness. Puerto *et al.* (1990) established that a typical slope used to reflect a transition of grassland communities from top to down conditioned by water availability, nutrient status and grazing intensity (oligotrophic, normal and eutrophic pastures, respectively). Other studies (see Montalvo *et al.*, 1993) relates species diversity to grazing intensity and soil treatments, that could also be related to degradation by land uses changes (Papanastasis, 2004) or management regime (Tárrega *et al.*, 2009). After grazing abandonment, it has been reported large changes in floristic composition (Peco *et al.*, 2005). Regulation of livestock pressure on a small scale in time and space will increases the local heterogeneity and therefore is a key factor for diversity of flora and fauna (Moreno and Pulido, 2008).
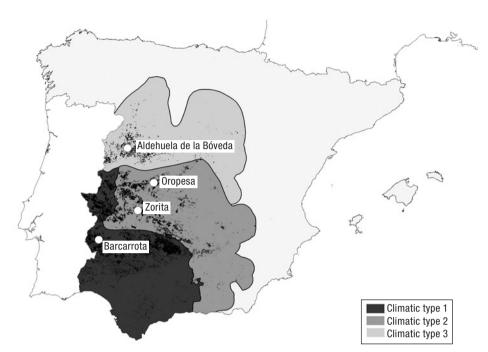
Moreover, one of the main challenging questions with increasing interest lies on the study of effects that changes in climate may have over the plant communities. Several studies in shrub and herbaceous communities under different environments have highlighted its influence on plant diversity's shifts (Jonas *et al.*, 2008; Matesanz *et al.*, 2009; Forrest *et al.*, 2010; Arnone *et al.*, 2011). In Mediterranean areas, where the climate is predicted to change severely, with a major temperature increase and a significant decline of precipitation and more irregular distribution (Christensen *et al.*, 2007), the study of variation in species richness and similarity along the entire distribution of the dehesa habitat, may help us to disentangle future responses to this global change driver.

There have not been studies to date, from a conservation point of view, covering the richness and floristic similarity in the dehesas along its climate and biogeographic range, and having into account the two scales of variation, local habitats conditions (hereafter mesohabitat level), and the dehesa habitat (hereafter dehesa site level). Thus, the objectives of this paper are: to summarize and to compare plant species richness and similarity at the two mentioned spatial scales, mesohabitat and dehesa habitat levels; and to establish guidelines for conserving species diversity across the geographic range where dehesas are distributed.

Methods

Study sites

The study was conducted in four sites (Fig. 1) that cover the entire climatic and biogeographic range of dehesas in Spain. Following the climatic typologies established in Sánchez de Ron *et al.*, (2007), we sampled one site belonging to Typology 1 or typical dehesas (Barcarrota), two sites belonging to Typology 2 or dry dehesas (Oropesa y Zorita) and one site belonging to Typology 3 or cold dehesas (Aldehuela de la Bóveda). The climate of the sampled sites ranges from the highest values in annual potential evapotranspiration, drought length and mean annual temperature in Barcarrota, on the south, to the lowest on the north, in Aldehuela de la Bóveda, henceforth referred to as Aldehuela. Between them, other two sites (Oropesa and Zorita) present intermediate climatic features. Main climatic, topographical and lithological, and stand variables, for each dehesa site are shown in Table 1. All sites are included in the Mediterráneo-Iberoatlántica biogeographic superprovince, mainly in the Luso-extremadurense province but also in the Carpetano-Ibérico-Leonesa province (Peinado Lorca and Rivas-Martínez, 1987).

Figure 1. Climatic typologies for dehesas in Spain (Sánchez de Ron *et al.,* 2007). Type 1 or typical dehesa, Type 2 or dry dehesa and Type 3 or cold dehesa. White dots indicated the four study sites.

Data collection

At each of the four dehesa sites, three mesohabitat typologies were selected for sampling, following a simplified gradient of oligotrophy and grazing pressure, described in Puerto *et al.* (1990), as representative of slope dynamics. The extension of mesohabitat patches was very variable ranging mainly from 1 to 10 ha. The

Table 1. Main climate, topography and lithology variables for each dehesa site. Climatic data derived from Gonzalo's model (2010)

Characteristic	Aldehuela	Oropesa	Zorita	Barcarrota
Longitude	6° 3' 7" W	5° 6' 33" W	5° 39' 10" W	6° 58' 47" W
Latitude	40° 51' 40" N	39° 59' 16" N	39° 17' 00" N	38° 28' 3" N
Altitude (m)	795	330	410	340
Annual mean temperature (°C)	12.2	16.0	16.4	16.7
Annual rainfall (mm)	521	694	648	608
Potential evapotranspiration (mm)	701	864	884	876
Length of drought (months)[1]	3.16	3.56	3.83	4.00
Intensity of drought (%)[1]	24.6	24.3	36.7	34.5
Moisture index[2]	−5.3 (subhumid dry)	7.5 (subhumid humid)	−7.1 (subhumid dry)	−2.0 (subhumid dry)
Soil texture	Sandy-loam	Sandy-loam	Sandy-loam	Sandy-loam
pH	Acidic	Acidic	Acidic	Acidic
Content of organic matter	Medium-low	Low	Medium-low	Low
Vegetation	Dehesa of holm oaks and annual sub-nitrophilous and other annual pastures	Dehesa of holm oaks and annual sub-nitrophilous pastures	Dehesa of holm oaks and annual sub-nitrophilous pastures	Dehesa of holm oaks and annual sub-nitrophilous pastures
Main tree species	*Quercus ilex*	*Quercus ilex* and *Quercus suber*	*Quercus ilex*	*Quercus ilex*
Stand age	Mature	Mature	Mature	Mature

[1] Walter and Lieth, 1960. [2] Thornthwaite, 1948.

extension of dehesa sites was variable too, ranging from 50 to 500 ha. The mesohabitat typologies were:

— Oligotrophic dehesas in upper slopes with low grazing pressure and three vegetation strata: trees, scattered low scrubs and herbaceous layer (hereafter oligotrophic dehesa).

— Normal dehesas in flat planes or medium slopes with increasing grazing pressure and two vegetation strata: trees and herbaceous layer (hereafter normal dehesa).

— Eutrophic dehesa in swamp or bottom zones related to non permanent water courses and three vegetation strata: trees, shrubs and herbaceous layer (hereafter eutrophic dehesa). These zones are used as shelter or summer pastures and are subjected to an intensive seasonal grazing pressure.

A 1,000 m² (50 m × 20 m) rectangular plot was established following Whittaker's multi-scale plot design, modified by Stohlgren *et al.*, (1995) and Ortega *et al.* (2004), for sampling the presence and abundance of vascular plant species in each mesohabitat. In the core of each mesohabitat, the plot is located at least 100 m far from the nearest edge, following the steepest slope in order to record a major environmental variability. Sampling within plots was nested as follows: (i) Ten subplots of 0.5 m × 2 m (1 m²) arranged equidistantly with the outer border of each subplot lying on the perimeter of the plot; (ii) two subplots of 2 m × 5 m (10 m²) in opposite corners of the plot, with their outer borders lying on the perimeter, and (iii) one subplot of 5 m × 20 m (100 m²) in the middle of the plot, without contact with any of the other subplots. In every 1 m² subplot the abundance of herbaceous and woody plants was estimated according to 5 cover categories: (1) < 5 % of the total subplot area, (2) between 5 and 12 %, (3) between 12.1 and 25 %, (4) between 25.1 and 50 % and (5) > 50 %. Subplots of 10 m² and 100 m² were sampled in the same way but for woody species only. The 1,000 m² plots were fully surveyed for species not found in the subplots of 1, 10 and 100 m², and an abundance rate of 0.01% was assigned to these species. Fieldwork was carried out in 2009 for Aldehuela and Barcarrota, 2008 for Oropesa, and 2005 for Zorita. Late spring (May-June) was considered to be the optimal phenological season (peak phenology *sensu* Stohlgren, 2007) for identifying the highest number of plant species. This methodology is useful for the comparison of plant diversity richness at different scales (see Stohlgren *et al.*, 1997; Wagner *et al.*, 2000; Ortega *et al.*, 2004). The use of 0.1 ha plots reduces the variability of total

species recorded as has been reported by Aronson and Shmida (1992) with five year series in Mediterranean environments of Israel, in order to compare samples from different years. Additionally, the use of richness estimators can extend the results of sampling (Hellmann and Fowler, 1999; Walther and Moore, 2005).

Data analysis

EstimateS 820 software (Colwell, 2005) was used for calculations of species richness (α and γ) at the two spatial levels, species-samples curve for each dehesas site and richness estimators (α and γ): Abundance-based Coverage Estimator —ACE— (Chazdon *et al.*, 1998) and Chao 1 (Chao, 1984). We compare the performance of two estimators of richness because when the number of samples is reduced, as is this case, figures of a single index could be in dissonance with figures of others that measure the same property of the sample. Also, two similarity indices were calculated, the Jaccard classic index (Jaccard, 1908) and the Chao-Jaccard abundance-based index (Chao *et al.*, 2005), a modification of the former that takes into account the abundance of the species in the samples. The comparison of the figures of the two indices is useful because although the lists of species could resemble little, the abundance-based index is able to detect trends in the proportion of the main species that implies similarities or dissimilarities on habitat's structure. Mesohabitats and dehesa sites β species richness were calculated by additive approximation (see Lande, 1996; Gering *et al.*, 2003, or Chandy *et al.*, 2006) where gamma diversity (DT or accumulated) per site or mesohabitat typology, minus alpha diversity (D_{within} or average per site or mesohabitat typology) is beta diversity (D_{among}).

$$DT = \overline{D_{within}} + D_{among} \; where \; \overline{D_{within}} = \sum_j q_j * D_j$$

Finally, hypothesis testing was performed in R (R Development Core Team, 2009) through the robust generalization of Welch's test (García Pérez, 2005) which is suitable for low number, non-normal samples.

Results

The results of species richness at 12 multi-scale plots in 4 dehesa sites are shown in Table 2. The minimum species richness per plot is 54 (normal dehesa, Aldehuela) and the maximum 102 (eutrophic dehesa,

Table 2. Species richness in four study sites (columns) and three mesohabitat types (rows). Alpha, beta, and gamma diversity were calculated using additive approximation for mesohabitat[1], site[2] and dehesa landscape[3]

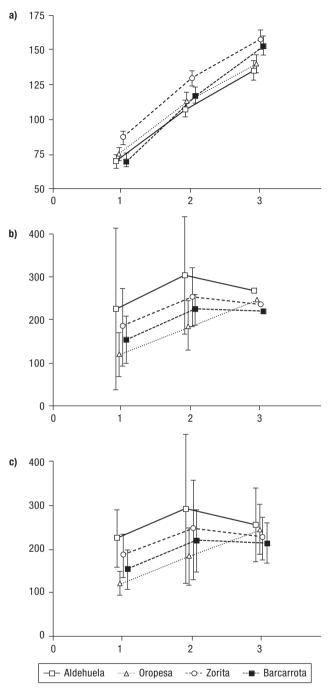| Dehesas	Aldehuela	Oropesa	Zorita	Barcarrota	Alpha	Gamma	Beta
Normal dehesa	54.0	67.0	69.0	55.0	61.3[1]	165.0[1]	103.7[1]
Eutrophic dehesa	93.0	75.0	102.0	80.0	87.5[1]	236.0[1]	148.5[1]
Oligotrophic dehesa	62.0	84.0	89.0	77.0	78.0[1]	216.0[1]	138.0[1]
Alpha	69.7[2]	75.3[2]	86.7[2]	70.7[2]	75.6[1,2,3]		
Gamma	135.0[2]	140.0[2]	157.0[2]	153.0[2]		340.0[3]	
Beta	65.3[2]	64.7[2]	70.3[2]	82.3[2]			264.4[3]

Zorita), with an average of 75.6 species per plot and standard deviation of 13.3. Alpha richness per dehesa site (average value for the three mesohabitats) ranges from 64.7 in Oropesa to 82.3 in Barcarrota. Gamma richness per dehesa site (average value for four dehesa sites) is 146.2 ± 10.4. No significantly differences were detected among dehesa sites ($p > 0.10$, Welch's test). Gamma richness for dehesa habitat is 340. The mesohabitat with highest alpha richness (average value for the four dehesas sites) is the eutrophic dehesa (87.5 species) while the lowest is the normal dehesa (61.3 species). Species richness in normal dehesas mesohabitat was significantly lower than in eutrophic dehesas ($p < 0.05$, Welch's test). Gamma richness per mesohabitat ranges from 165 species in normal dehesas to 236 in eutrophic dehesas. The cumulative curves for species richness and estimation of species richness per study site using ACE and Chao 1 classic non-parametric estimators are shown in Fig. 2. Zorita exhibits higher values of species richness than the other locations all along the curve (Fig. 2a). The estimation of species richness using ACE and Chao 1 classic non-parametric indices are highly coherent with each other (Fig. 2b y 2c), showing in both cases the maximum values in Aldehuela site, reaching 270 and 256 species, respectively, at the end of the curve. The minimum estimated values are for Barcarrota site (223 and 213 species). Nevertheless, a great variability has been detected, which prevents from significant differences among sites ($p > 0.10$, Welch's test) and makes us cautious about predicting what would be the most species-rich dehesa site.

Average similarity between plots of each dehesa site and average similarity between plots of each mesohabitat type, calculated by the Jaccard classic index and the Chao-Jaccard abundance-based index, are shown in Fig. 3. The two indices are consistent in their results because both indices reflect the same descending order of similarity, whether in the case of dehesa sites (Zorita, Oropesa, Aldehuela, and Barcarrota) or in the case of mesohabitats (normal, oligotrophic and eutrophic). Taking into account the abundance of species, the similarities and differences increase not only between dehesa sites (Fig. 3a) but also between mesohabitats (see normal mesohabitat in Fig. 3b). Pair-wise similarity among dehesa sites is shown in Table 3. In this case there are slight differences in the performance of the two similarity indices. While Jaccard's classic settles a stepped gradient where Oropesa and Zorita show the highest similarity (0.344), the similarity values of Aldehuela with Oropesa (0. 267) and Zorita (0.264) are located in a second step, and Barcarrota settles the third step reaching the lowest values in relation with the three others (0.25 with Zorita, 0.221 with Oropesa, and 0.215 with Aldehuela); Chao-Jaccard abundance-based index figures shows only two steps, the higher involving pair-wise similarity between Oropesa, Zorita and Aldehuela (ranging from 0.563 to 0.508), and the lower involving Barcarrota similarity with the three others (ranging from 0.357 to 0.364). Therefore, Barcarrota seems to be the most heterogeneous dehesa (Fig. 3a) and the most different from the other three (Table 3), mainly according to the normal dehesa and eutrophic dehesa mesohabitats. Additive approximation to β richness (Table 2) reinforces the idea that Barcarrota is more heterogeneous than the

Table 3. Pair-wise similarity index among dehesa sites

Site 1	Site 2	C_J	C_{CJ}
Aldehuela	Oropesa	0.267	0.508
Aldehuela	Zorita	0.264	0.563
Aldehuela	Barcarrota	0.215	0.362
Oropesa	Zorita	0.344	0.557
Oropesa	Barcarrota	0.221	0.357
Zorita	Barcarrota	0.250	0.364

C_J: Jaccard classic index. C_{CJ}: Chao-Jaccard abundance-based index.

Figure 2. Curves for species richness (a) and estimation of species richness per dehesa site using ACE (b) and Chao 1 (c) classic non-parametric estimator. Number of species in ordinates. Cumulative number of plots in abscissas. Error bars stand for one standard deviation.
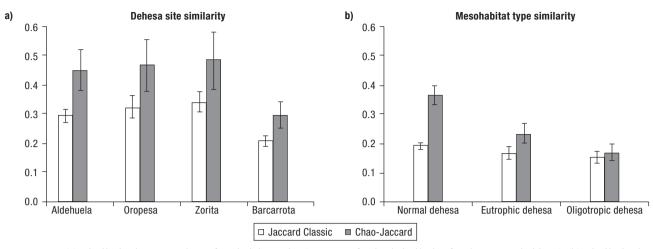
others. In opposition, Oropesa and Zorita are the most uniform and the most akin to each other (both of them belong to the same climatic typology and are geographically near). Aldehuela shows a greater similarity

with the two latter dehesas, but it is the most divergent in relation to the eutrophic mesohabitat. Finally, the mesohabitat types are not more similar among them than the dehesas themselves.

Discussion

Our results provide comparable vascular plant richness and similarity data in four dehesas ranging along different climatic and biogeographic conditions and the three main mesohabitats considered as representatives of each dehesa. We have found significant lower values of alpha richness (56 %) than those reported by Marañón (1985), though this can be due to his sampling strategy, in which the sites were visited three times in a year and subplots were subjectively distributed inside the 0.1-ha main plot. Nonetheless, our results are highly consistent with the values of 135 species reported, if we considered the three mesohabitat sampled (average species richness of four dehesas sites is 146.3). The three mesohabitats were not, in many cases, as far from each other than the larger side of the plot (100 m). This mean value of species shows low variation among sites (135 to 157). Furthermore, richness estimations (with both estimators used) are in accordance between them, as the average value of the four dehesas roughly fetches up 230 species. In any case, these figures are somewhat higher than other forest and agroforestry systems (Rice and Westoby, 1983; Díaz *et al.*, 1999; Ojeda *et al.*, 2000; Wagner *et al.*, 2000) in temperate climates.

The inclusion of three different mesohabitats inside each dehesa site has resulted in a largely positive contribution to understanding the scale where the diversity is supported. We have found indeed more dissimilarity at local scale (mesohabitats) than at regional scale (habitats): no significantly differences between dehesas sites could be detected (though the low number of samples can be hindering this detection), neither in species richness nor in similarity, but the normal dehesa mesohabitat resulted to be significant different (despite the small sample size) to the eutrophic dehesa mesohabitat. These facts highlight the importance of including such mesohabitats and not only the recurrent under canopy, canopy edge and open grasslands in diversity studies (García del Barrio *et al.*, 2006).

Interestingly, the higher values of richness in the oligotrophic dehesa mesohabitat versus the normal dehesa in all sampled sites suggest that current mana-

Figure 3. (a) Similarity between plots of each dehesa site (average of paired similarity for three mesohabitats) (b) Similarity between plots of each mesohabitat type (average of paired similarity for four dehesa sites). White, Jaccard classic index; light grey, Chao-Jaccard abundance-based estimator. Error bars indicates standard error.

gement practices, characterized by intensive techniques like free-range grazing at high stocking levels (Plieninger and Wilbrand, 2001), are not only hampering the natural regeneration of tree populations (Pulido *et al*., 2001; Pulido and Díaz, 2005) but also lessening species richness and diversity. Therefore, "oligotrophic dehesa" in a sense of lower grazing rates may retrieve species richness levels as well as endow with nurse plants for tree regeneration (Ramírez and Díaz, 2008). Moreover, since Spain has reinforced its commitment to the conservation of the dehesa as habitat of Community interest, stocking rate should be taken back to figures typical of the traditional management, in order to maintain this landscape in a favorable conservation status.

The use of estimators ACE and Chao 1 for calculating the species richness values that we could expect did not introduce great differences in relation with species richness sampled, but generated new richness relationships between dehesa sites. In this sense Aldehuela is the poorest species sampled but the richest species expected. This could be an artifact related not only to the low number of samples but also to the local climatic parameters of the sampling year, characterized by a long period of drought that brought about a meager average species cover (between a third and a half of the other three sites). In this case a few taxa were predominant over the rest and the estimation based on abun-dance is probably inflated (Fig. 2).

Similarity values provide support to the hypothesis that climatically and biogeographically close dehesas have comparable richness and species composition, and in this sense species richness and similarity could

be partly predicted as a function of a pool of variables including climatic ones (Laughlin and Grace, 2006; Stevens, 2006). Thus, Oropesa and Zorita, both located in the dehesa type dry, are the most akin, while Aldehuela and Barcarrota, situated at the opposite edges of the climatic gradient, have shown the highest figures in dissimilarity. C_J values calculated with qualitative data have shown Barcarrota as the most different from the other three sites. This dissimilarity was stressed when quantitative data was used for calculating C_{CJ}. Taking into account the high regional and interannual climatic variability, archetypal of the Mediterranean climate, and the fact that our samples were corresponded with an individual sampling year, it would not be rigorous to extend the conclusions of relationships between species composition and climate similarities without the knowledge of other main driving forces influencing vegetation, as could be recurrent disturbances like wildfires (see *e.g.* Pausas, 2004)

Dehesas and montados are extensive widespread land uses throughout western Iberian Peninsula, and the most representative savanna-like landscapes of Mediterranean region. Dehesa habitat includes a variety of mesohabitats related to local conditions and land use management intensity, which all together harbor high species richness, using vascular plants as reference group. Irrespective of the climatic and floristic gradient evidenced, the species richness of dehesas must be promoted and protected against eventual changes associated with global change, like climatic shifts and other land uses less conservative or not tested as sustainable as dehesa itself. To reach this goal, it

becomes necessary to consider the dehesas all along their ecological range to achieve a thorough conservation of their vascular plants as well as their associated fauna.

Acknowledgements

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