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# The use of shrub cover to preserve Mediterranean oak dehesas: a comparison between sheep, cattle and wild ungulate management

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*Cervus elaphus*; Deer; Extensive livestock; Facilitation; Herbivory; Oak savannas; Palatability; *Quercus ilex*; Seedlings; Stocking rates

**Nomenclature**
Castroviejo et al. (1986–2012)

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## Abstract

**Questions:** Oak savanna-like systems (dehesas) are highly valuable and protected systems that are strongly compromised by a continuous failure of oak recruitment. Our question is whether different long-term management types involving cattle, sheep and wild ungulates affect the abundance and diversity of safe microsites (shrubs) for oak recruitment. We also assess microsite location and species-specific differences among the nurse shrubs in order to provide management guidance.

**Location:** Dehesas of holm oak (*Quercus ilex*) in central Spain.

**Methods:** We examined oak regeneration in four different microsites (tree canopy, shrub cover, open and tree–shrub) and across three distinctive and representative management types for a period of, at least, 30 yr: (1) traditional management (i.e. extensive sheep rearing); (2) high commercially competitive management (extensive cattle); and (3) wildlife management (wild ungulate grazing, mostly deer).

**Results:** Wildlife management showed higher abundance and diversity of shrubs. Predicted seedling density under wildlife management was three-fold higher than sheep, and almost nine-fold higher than under cattle management. Highest oak density was found under shrubs that grew beneath trees, twice as high than under trees, ten-fold higher than under shrubs outside the tree canopy, and almost 40-fold higher than in open microsites. However, the proportional facilitative effect of shrubs was higher in open areas than under trees. Three shrub species (*Erica australis*, *Genista hirsuta* and *Rosmarinus officinalis*) showed significantly higher probability of facilitating oak seedlings in comparison to other shrub species, indicating species-specific differences in plant facilitation. Most young oak trees (saplings and juveniles) exceeded the average shrub height, suggesting that facilitation occurs mostly at the seedling stage.

**Conclusions:** Only dehesas under reasonable wildlife management showed a clear three-layered structure with a significant representation of the shrub layer, which increased seedling density. Current cattle management was the least sustainable in terms of oak regeneration. Even though shrub cover, in general, facilitated oak seedlings, not all species were equivalent facilitators. Only three low-palatable and large-sized shrub species were keystone facilitators that should be especially considered in restoration and management practices. Further agriculture policies should promote reduction of cattle densities, rotational grazing and mixed species management to enhance the regeneration of these systems.


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## Introduction

Open woodlands are usually the result of clearing and simplifying the structure of woody communities that were formerly part of forests, shrublands and close woodlands (Plieninger 2007; Rolo & Moreno 2011). The Mediterranean open woodlands, dominated by oak species (*Quercus* spp.), are systems that have been created and sustained by traditional management over a long period of time (Manning et al. 2006; Moreno & Pulido 2009). They have been named oak savannas or rangelands (e.g. in California), resembling a savanna landscape that yields a remarkable biodiversity and provides important ecosystem services (Eichhorn et al. 2006; Tyler et al. 2008; Campos et al. 2013). In southwest Europe these systems are known as 'dehesas' (Spanish name) and are included in the European Union Habitats Directive due to their high conservation value (Ramírez & Díaz 2008; Díaz & Pulido 2009). However, many open woodlands throughout the world, including most oak dehesas, are facing an important tree regeneration failure that threatens their long-term persistence (Pulido et al. 2001, 2010; Plieninger 2006; Tyler et al. 2006; Campos et al. 2013).

Traditionally, many Mediterranean dehesas were maintained through traditional extensive sheep grazing, with cattle restricted to more humid areas (Peco et al. 2006; Moreno & Pulido 2009; Carmona et al. 2013). However, over the last decades, management of most oak ranchlands and dehesas has changed towards a more commercially competitive approach, mainly involving extensive cattle rearing, usually with very high stocking rates (Joffre et al. 1988; Hartel & Plieninger 2014; López-Sánchez et al. 2014). On the other hand, a more recreational approach, focusing on wildlife management, is increasingly appealing to more managers that rely on alternative economic resources, such as hunting or ecotourism (San Miguel et al. 1999; Olea & San Miguel 2006; Herruzo & Martínez-Jáuregui 2013). Such a strong shift in management practices is expected to affect tree recruitment and plant composition of the currently threatened Mediterranean dehesas.

Several studies have argued that tree recruitment in Mediterranean environments is associated with 'safe microsites', mostly related to the presence and nurse effects of shrubs (Pugnaire et al. 1996; Castro et al. 2004; Gómez-Aparicio et al. 2004; Pulido & Díaz 2005; Smit et al. 2008; Perea & Gil 2014a,b). Consequently, favouring shrub cover, also known as 'shrub encroachment', has been recommended to ensure tree recruitment and the long-term conservation of the Mediterranean oak woodlands and dehesas (Ramírez & Díaz 2008; Moreno & Pulido 2009; Plieninger et al. 2010; Pulido et al. 2010). However, other studies showed that the effect of the shrub cover can be species-specific (Rolo & Moreno 2011; Rivest et al. 2011) and may strongly depend on the palatability of the shrub (Perea & Gil 2014a). Thus, further research is needed to clarify the facilitative vs competitive nature of tree–shrub interactions in order to establish appropriate management practices. The question that first arises is whether different management approaches, including wild ungulates, affect the abundance and diversity of the suggested safe microsites (i.e. shrubs). This is especially important because the abundance and diversity of the shrub cover as well as its location (e.g. in open or beneath the tree canopy) may lead to important differences in the distribution, abundance and performance of the tree recruitment. An additional question is whether all shrub species play similar tree-facilitative roles. A differential species-specific ability to facilitate seedling establishment will provide crucial information on the use of different shrubs to maximize tree recruitment.

This study aims to examine the recruitment of a foundation oak species (*Quercus ilex*) across different microsites and under three representative management types of the oak Mediterranean dehesas. We specifically analyse the abundance and diversity of safe microsites (shrubs) as well as the abundance of oak recruitment (seedlings, saplings and juveniles) under: (1) traditional management (i.e. extensive sheep rearing); (2) high commercially competitive management (extensive cattle); and (3) alternative management approaches that include only wildlife (wild ungulate grazing). We hypothesize that management involving wild ungulates may favour oak regeneration in comparison to livestock management, either sheep or cattle (extensive rearing). Particularly, we predict that shrub cover and diversity would be lower in the cattle-grazed areas than under both traditional sheep and wildlife management. However, we expect no differences in the microsite location of the current oak recruitment among the three management schemes. Thus, we predict higher abundance of oak recruitment in the so-called safe microsites (under shrub and shrub–tree cover) across the three management types. We also hypothesize that not all shrub species will be equivalent nurse plants for oak seedlings. We posit that, given the importance of safe microsites in the regeneration and conservation of the currently threatened oak dehesas, our findings can be of broad significance not only to better understand the role of different management schemes in providing safe microsites for seedlings, but also in assessing the species-specific differences among the nurse microsites that may lead to important restoration and management practices.

## Methods

### Study area

The study was conducted in oak dehesa systems in central Spain (39–40° N, 5° W), western Toledo province. The topography is fairly flat, with an elevation range of 300–400 m a.s.l. The climate is Mediterranean, with a mean annual temperature of 15.7 °C, and an average annual rainfall of 571 mm (weather station in Talavera de la Reina), with a 3–4-mo summer drought. Rainfall occurs mostly in winter (40%) although there is high intra- and inter-annual variation in precipitation. Mean temperature in Jan and Jul (coldest and hottest month, respectively) are 6.2 and 26.0 °C, respectively, although temperatures in summer can reach values over 40 °C. In winter frosts are common from Nov to Mar (temperatures can reach −10.8 °C). The whole study area covered 10 800 ha, with homogeneous characteristics. Soils are sandy (>80% sand) and acidic, and the topsoil has low organic matter content (<1% organic matter). The overstorey is dominated by holm oaks (*Quercus ilex* subsp. *ballota* (Desf.) Samp.), with some scattered cork oaks (*Quercus suber* L.). The understorey is dominated by herbaceous species, mainly comprising sub-nitrophilous Mediterranean annual communities (*Thero-Brometalia*), therophytic oligotrophic communities (*Tuberarietalia guttatae*) and therophytic oligotrophic communities on sandy soils (*Malcolmietalia*). Evergreen shrubs (usually <90-cm high) can also be found in the understorey at low densities (*Cistus ladanifer* L., *Lavandula stoechas* Lam., *Cistus salvifolius* L, *Halimium ocymoides* (Lam.) Willk., *Genista hirsuta* Vahl and *Rosmarinus officinalis* L.; Perea 2006). Dehesa systems are protected by the European Union Habitat Directive (92/43/EEC) under the habitat code 6310 (Díaz & Pulido 2009).

### Study sites

Three sites were selected within the study area. Each site had a distinct management, at least for the last 30 yr. None of the three sites were subjected to ploughing, shrub clearing or fire during the last 30 yr, and thus, the main management difference was the grazing regime. The first site, hereafter 'Cattle', has been supporting cattle (breed Avileña Negra Ibérica) year-round, with stocking rates of 0.33 $cow{\cdot}ha^{-1}$. This study site comprises 142 ha with multiple fences to control cattle movements and prevent wildlife and human access. Wild ungulates (mainly red deer *Cervus elaphus* L.) enter occasionally at low densities (<0.05 $ind{\cdot}ha^{-1}$, equivalent to 0.007 $cow{\cdot}ha^{-1}$), when they jump over fences or go through them. The second one, hereafter 'Sheep', supports sheep all year through (breed Talaverana), with stocking rates of 1.67 $sheep{\cdot}ha^{-1}$ (equivalent to 0.25 $cow{\cdot}ha^{-1}$ – using metabolic weight; 24% lower stocking rate than the previous site), representing the typical extensive sheep management (Plieninger et al. 2004). This study site comprises 140 ha, and is also fenced to control sheep movements and prevent wild ungulates and human access. Red deer have also been seen, but very rarely (A. Cobisa, pers. com.) since fences were stronger and better maintained than in the previous site (R. Perea and A. López-Sánchez, pers. obs.). Finally, the third site has not supported livestock since 1985. However, its management has been devoted to recreational big game hunting, mostly red deer but also some wild boar (*Sus scrofa* L.) for the past 50 yr. Stocking rates are 0.37 $deer{\cdot}ha^{-1}$ (equivalent to 0.11 $cow{\cdot}ha^{-1}$ – using metabolic weight; 67% and 56% lower stocking rates than cattle and sheep sites, respectively). This study site comprises 150 ha, and represents the typical deer management (densities) of Mediterranean hunting properties in oak-dominated woodlands and dehesas (Acevedo et al. 2008; Perea et al. 2014). Two of the sites (cattle and sheep) were adjacent and the other one (wildlife) was separate, approximately 5–7 km from the cattle and sheep sites.

### Data collection

We only examined *Q. ilex* regeneration since it is by far the dominant and most representative tree species of the dehesas (Díaz & Pulido 2009). For each study site we selected three different plots (5 ha each). The nine plots were selected in a way that contained a similar density of holm oak trees (Mean ± SD = 42.15 ± 11.44 $trees{\cdot}ha^{-1}$), with similar DBH (40.4 ± 16.23 cm). Then, eighteen 4 × 35 m belt transects (separated 40 m among them) were established within each plot (total $n$ = 162 transects). In each plot we recorded the four possible different microsites: under the tree canopy (hereafter tree), under the shrub canopy (hereafter shrub), under the tree and shrub canopy (hereafter tree–shrub) and in open grasslands (hereafter open). For each transect we recorded the relative abundance of each microsite by measuring the length of each microsite intercepting the transect tape. We then counted all oak seedlings (plants with one shoot and basal diameter <1 cm) that were found in each transect. We recorded the microsite where seedlings occurred and the height of each seedling. Shrubs were always identified to species level. Surveys were conducted in March–April 2014. Palatability of each shrub (preference by deer) was obtained from the literature (Fernández-Olalla et al. 2006; Perea et al. 2014).

In addition, we also recorded the abundance of oak saplings (one shoot and basal diameter of 1–5 cm) and juveniles (basal diameter ≥5 cm and ≤10 cm) in each transect to assess the whole oak regeneration structure and evaluate the proportion of seedlings reaching the next


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ontogenetic stage (young trees). However, in most cases, it was impossible to determine whether saplings and juveniles were facilitated by shrubs and, if so, what shrub species facilitated the oak juvenile, because young oak trees usually exceeded the height of the shrubs and outcompete them through the process of plant succession (Zavaleta & Kettley 2006). Additionally, juveniles may be older than 30 yr (holm oak is a slow-growing species; Crescente et al. 2002; Rey-Benayas & Camacho-Cruz 2004) and thus juveniles might have established under different management regimes. Hence, shrub facilitation could only be analysed for oak seedlings.

### Data analysis

Data processing and statistics were performed using R 3.1.1 (R Foundation for Statistical Computing, Vienna, AT) with the modules 'lme4', 'car' (Fox & Weisberg 2011), 'MuMIn' and 'nnet' (Venables & Ripley 2002).

To analyse whether there were any statistical differences in the abundance of each microsite across the three management types we developed four generalized linear mixed models (GLMMs; Zuur et al. 2009), one for each microsite. All models include the proportion of microsite in each transect as the response variable and management type (cattle, sheep and wildlife) as predictor. The random structure was plot-nested within each management type. The four models were fitted to a binomial error distribution with a logit link function.

To analyse oak recruitment density as a function of management regime and microsite, we developed zero-inflated generalized linear mixed models (ZIGLMMs; Zuur et al. 2012), with number of seedlings as the response variable. The random structure was plot-nested within each management type. The models included management (cattle, sheep and wildlife) and microsite (tree, shrub, tree–shrub, open) as predictors. Since the abundance of each microsite differed among sites and plots, we included a new predictor in the model to correct this uneven abundance of microsites. The new variable was the abundance of each microsite in each transect (i.e. number of meters of each microsite contacting the transect tape). For this variable we used the command 'offset', which allows us to correct the microsite effect without obtaining estimates for the model. The response variable (number of seedlings) was fitted to a negative binomial error distribution with a log-link function. We did the same with the number of saplings and juveniles. To analyse seedling height in relation to management type and microsite location we built another GLMM, where seedling height was fitted to a $\gamma$-error distribution, with a power $\lambda$ 0.70 link function. The random structure was the same as the models above.

For all models, we used the model averaging approach (Burnham & Anderson 2002; Anderson 2008) to obtain the importance of each predictor (from 0 to 1) using the 'model.avg' function of 'MuMIn'. We first fitted the maximal model, containing all the explanatory variables, then we performed model comparison of all possible models using the AIC weights. For model comparison we used the 'dredge' function within the 'MuMIn' package of R. Finally, to determine the actual facilitation of each shrub species on oak recruitment (species-specific effect) we used Chi-square tests ($\chi^2$ test). Thus, we compared the expected and observed abundance of oak seedlings under each shrub species and for each particular management.

## Results

Wildlife management showed significantly higher shrub cover than both cattle and sheep management (Table 1, Fig. 1). This was confirmed for both shrub cover beneath trees and shrub cover in open areas (Table 1, Fig. 1). Under wildlife management, overall shrub cover (including tree–shrub cover) was 38.0%, whereas under cattle and sheep management shrub cover only represented 0.2% and 0.6%, respectively (Fig. 1). No differences were

**Table 1.** Summary of the generalized linear mixed models (GLMM) to analyse the proportion of each microsite under the three distinct management types.

| Microsite | Predictor | Levels (Against cattle) | Coeff. | SE | *z*-Value | *P* |
|---|---|---|---|---|---|---|
| Tree | Management | Sheep | −1.352 | 0.690 | −1.960 | 0.061 |
| | | Wildlife | −0.801 | 0.586 | −1.367 | 0.172 |
| Tree–Shrub | Management | Sheep | 1.516 | 6.968 | 0.218 | 0.828 |
| | | **Wildlife** | 5.041 | 6.331 | 0.796 | **0.042** |
| Shrub | Management | Sheep | 0.588 | 3.842 | 0.153 | 0.878 |
| | | **Wildlife** | 5.535 | 3.092 | 1.790 | **0.034** |
| Open | Management | **Sheep** | 1.470 | 0.683 | 2.151 | **0.032** |
| | | **Wildlife** | −2.319 | 0.454 | −5.103 | **<0.001** |

Bold type indicates statistical significance ($P < 0.05$).

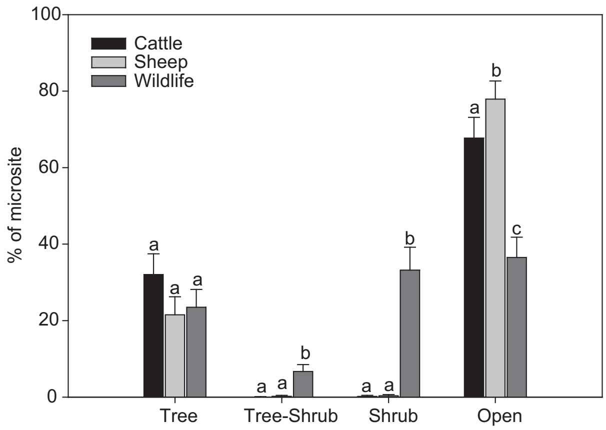


**Fig. 1.** Proportion of each microhabitat for the three management schemes. Error lines are 95% confidence intervals. Different letters indicate significant differences ($P < 0.05$).

found in tree canopy cover across the three management schemes (Table 1, Fig. 1). Only one and three shrub species were found in the cattle and sheep management, respectively, whereas 15 shrub species were found under wildlife management (Table 2).

Density of oak seedlings significantly differed across the three management types (Table 3). We found significantly higher density of seedlings under the wildlife management, followed by sheep and cattle management (Table 3, Fig. 2a). Predicted seedling density under wildlife management was 0.18 seedling·m$^{-1}$, three-fold higher than sheep, and almost nine-fold higher than cattle (Fig. 2a).

Microsite also had a significant effect on the density of seedlings (Table 3). Highest density was found under shrubs that grew below trees (tree–shrub microsite; Fig. 2b), with predicted density of 0.39 seedling·m$^{-1}$, twice higher than under trees, ten-fold higher than under shrubs outside the tree canopy and almost 40-fold higher than in open microsites (Fig. 2b). If we compare the effect of shrubs under trees and in open areas separately, we found that the proportional facilitative effect of shrubs was higher in open areas (four-fold higher predicted density under shrubs) than under the tree canopy (twofold higher predicted density under shrubs). Only three shrub species (*Erica australis*, *Genista hirsuta* and *Rosmarinus officinalis*) showed significantly higher probability of nursing seedlings beneath in comparison to the rest of the shrub species (Table 2), indicating species-specific differences in shrub facilitation.

Microsite location had an important effect on the height of seedlings (Table 4). Seedlings under shrub cover were significantly taller whereas seedlings in open areas were significantly shorter (Table 4, Fig. 3). Seedlings under trees or under shrub–tree cover had intermediate height, with no significant differences between the microsites (Table 4, Fig. 3). Management type had little effect on the height of seedlings (importance of 0.25; Table 4) and thus no significant differences were found in seedling height across the three management regimes (Table 4, Fig. 3).

Finally, saplings were also significantly more abundant in wildlife ($z = 3.536$, $P < 0.001$) and sheep ($z = 3.691$, $P < 0.001$) areas than in cattle areas (Fig. 4). However,

**Table 2.** Shrub palatability, relative abundance of each shrub species and proportion of seedlings growing beneath them for the three management types.

| Shrub species | Palatability* | Cattle | | Sheep | | Wildlife | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Abundance (%) | Seedlings (%) | Abundance (%) | Seedlings (%) | Abundance (%) | Seedlings (%) | $\chi^2$ | *P*-Value |
| *Arbutus unedo* | H | – | – | – | – | 0.04 | 0.00 | 0.20 | 0.657 |
| *Cistus ladanifer* | M | – | – | – | – | 53.83 | 55.10 | 0.75 | 0.386 |
| *Cistus salviifolius* | M | – | – | 34.90 | 0.00 | 3.66 | 6.13 | 0.84 | 0.358 |
| *Crataegus monogyna* | M | 100.00 | 100.00 | – | – | – | – | | |
| *Daphne gnidium* | L | – | – | – | – | 0.98 | 0.00 | 0.48 | 0.486 |
| *Dorycnium pentaphyllum* | L | – | – | – | – | 0.34 | 0.00 | 0.17 | 0.683 |
| ***Erica australis*** | **M** | **–** | **–** | **–** | **–** | **0.84** | **6.12** | **16.41** | **<0.001** |
| *Erica scoparia* | H | – | – | – | – | 0.31 | 0.00 | 0.15 | 0.696 |
| *Erica umbellata* | M | – | – | – | – | 0.77 | 0.00 | 0.38 | 0.537 |
| ***Genista hirsuta*** | **L** | **–** | **–** | **–** | **–** | **2.03** | **6.13** | **4.13** | **0.042** |
| *Halimium ocymoides* | L | – | – | 52.00 | 0.00 | 2.04 | 2.04 | 0.00 | 0.999 |
| *Halimium umbellatum* | L | – | – | – | – | 2.95 | 0.00 | 1.49 | 0.222 |
| *Lavandula stoechas* | L | – | – | 13.09 | 0.00 | 27.50 | 16.32 | 3.07 | 0.079 |
| *Osyris alba* | H | – | – | – | – | 0.05 | 0.00 | 0.02 | 0.876 |
| *Phillyrea angustifolia* | H | – | – | – | – | 2.26 | 0.00 | 1.13 | 0.287 |
| ***Rosmarinus officinalis*** | **L** | **–** | **–** | **–** | **–** | **2.40** | **8.16** | **6.95** | **0.008** |

*H = High; M = Medium; L = Low; Data obtained from Fernández-Olalla et al. (2006) and Perea et al. (2014). Bold type indicates shrubs that significantly facilitate seedlings better than other shrubs ($P < 0.05$).


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**Table 3.** Summary of the zero-inflated GLMM model averaging to analyse the density of oak seedlings under different microhabitats and for the three different management schemes.

| Fixed effects | Relative importance* | Averaged estimate | SE | *z*-value | *P*-value |
|---|---|---|---|---|---|
| Microsite (Referred to Tree Canopy) | 1.00 | | | | |
| **Shrub** | | −2.532 | 0.535 | 4.720 | **<0.001** |
| **Tree–Shrub** | | 0.151 | 0.673 | 0.224 | **0.023** |
| **Open** | | −3.025 | 0.437 | 6.912 | **<0.001** |
| Mangement (Referred to Cattle) | 1.00 | | | | |
| **Sheep** | | 1.362 | 0.480 | 2.829 | **0.005** |
| **Wild Ungulates** | | 2.171 | 0.501 | 4.327 | **<0.001** |

*Relative importance represents the sum of the AIC weights across all the models where the fixed effect occurs, with values from 0 (minimum importance) to 1 (maximum importance).
Bold type indicates statistical significance ($P < 0.05$).

**Table 4.** Summary of the gamma GLMM model averaging to analyse the height of seedlings under different microsites and for the three different management schemes.

| Fixed effects | Relative importance* | Averaged estimate | SE | *z*-value | *P*-value |
|---|---|---|---|---|---|
| Microsite (Referred to Tree Canopy) | 1.00 | | | | |
| **Shrub** | | 3.107 | 1.055 | 2.944 | **0.003** |
| Tree–Shrub | | 0.161 | 0.472 | 0.342 | 0.732 |
| **Open** | | −2.613 | 0.477 | 5.476 | **<0.001** |
| Mangement (Referred to Cattle) | 0.25 | | | | |
| Sheep | | 1.072 | 1.063 | 1.009 | 0.313 |
| Wild Ungulates | | −0.483 | 0.869 | 0.555 | 0.579 |

*Relative importance represents the sum of the AIC weights across all the models where the fixed effect occurs, with values from 0 (minimum importance) to 1 (maximum importance).
Bold type indicates statistical significance ($P < 0.05$).

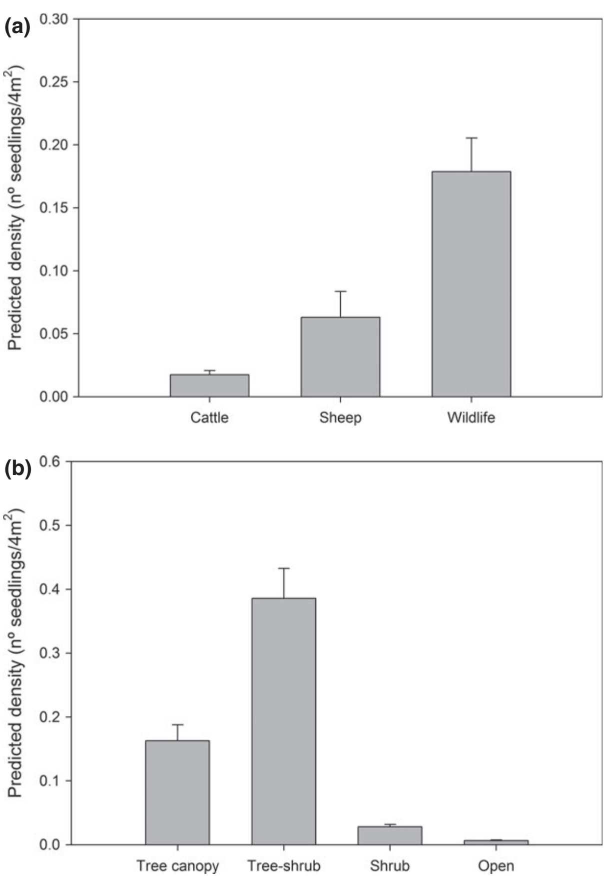


**Fig. 2.** Predicted density of seedlings for (**a**) the three management types and (**b**) the four different microsites. Error lines are 95% confidence intervals. All pair-wise comparisons were statistically significant ($P < 0.05$).

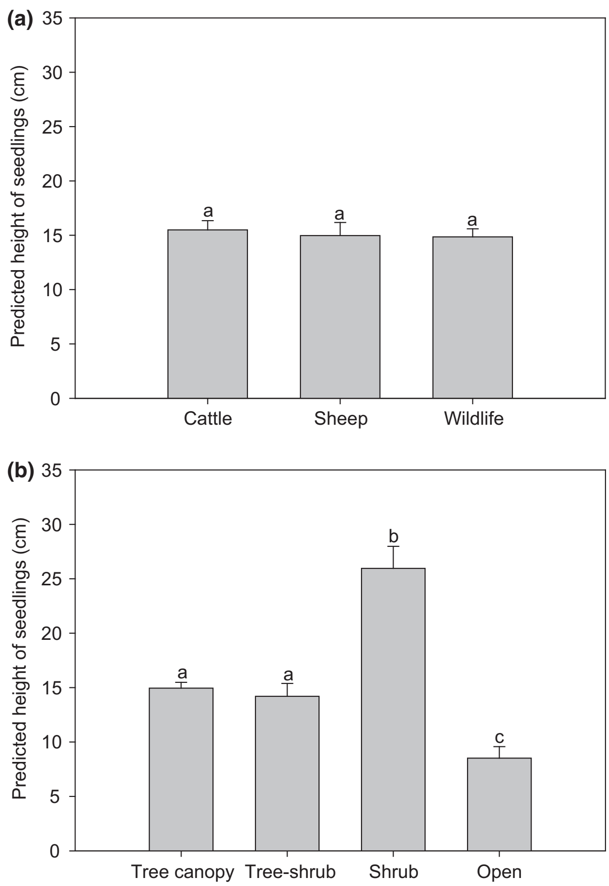


**Fig. 3.** Predicted height of seedlings for (**a**) the three management types and (**b**) across the four different microsites. Different letters indicate statistical significance ($P < 0.05$).

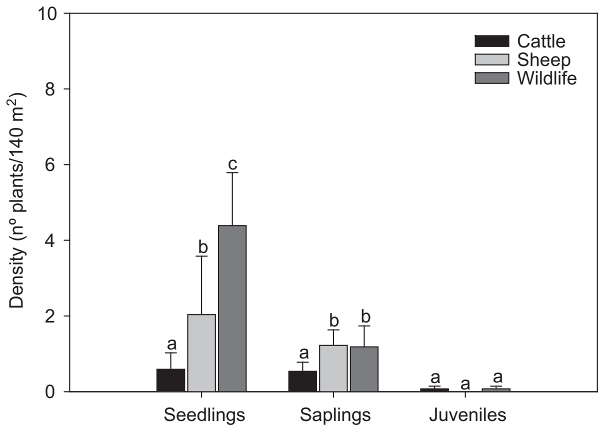


**Fig. 4.** Density of young oak trees (seedlings, saplings and juveniles) under each management regime. Values are mean ± SD. Different letters above the bars indicate significant differences ($P < 0.05$).

there were no differences in sapling density between sheep and wildlife areas ($z = -0.175$, $P = 0.983$; Fig. 4). Density of juveniles was very low for the three management regimes and showed no significant differences across the three management types ($P > 0.05$; Fig. 4). No young trees (saplings and juveniles) were found under shrub cover or under shrub–tree cover.

## Discussion

Our results show that long-term management (for periods longer than 30 yr), based on different grazing animals (cattle, sheep and wild ungulates) at their typical current stocking rates, led to a differential structure of the Mediterranean dehesas. This was mostly observed in areas under wildlife management, where dehesas showed a clear three-layered structure with a significant representation of the shrub layer (38% of total cover). However, dehesas under both sheep and cattle management showed a very similar structure, clearly dominated by two layers (tree and herbaceous; Fig. 1), with very little presence of shrub cover (<1%). This reveals that wildlife management, involving wild ungulates (mostly deer), even at relatively high densities (in this case 0.37 ind·km$^{-2}$) favours the co-existence of shrubs with herbaceous and tree species. This might be particularly relevant for the conservation and regeneration of these systems where shrub cover is considered a safe microsite that favours seedling establishment (Plieninger et al. 2004; Pulido & Díaz 2005; Smit et al. 2008; Gómez-Aparicio 2009). In fact, our results also showed that proportionally more seedlings were found under shrub cover (Fig. 2a), which confirms that shrubs are, indeed, safe microsites. However, here we add that the facilitative effect of shrubs is even higher in open areas, with four-fold higher predicted density of seedlings under shrubs than in open areas, whereas under the tree canopy, shrub cover only showed twofold higher predicted density. This seems to agree with the fact that under harsh and more exposed microsites (e.g. open) the facilitation effect might be stronger. In open areas shrubs can facilitate both biotically (reducing herbivory damage) and abiotically (mainly reduction of evapotranspiration by shading; Smit et al. 2008), whereas under the tree canopy biotic is probably the main, if not the only, mechanism of facilitation since shade is already provided by the tree canopy, and is usually stronger (denser shade). However, and probably related to the shorter distance to the mother trees, we found higher density of seedlings under the tree canopy, with an important and significant facilitative effect of shrubs under trees (Fig. 2b). Since the number of seedlings is always higher under the tree canopy it seems crucial to maintain or favour shrub cover not only in open areas but also under the trees.

Importantly, even though shrub cover clearly facilitates oak recruitment, we found that not all species act as equivalent facilitators, which is in line with previous studies that revealed a species-specific effect on seedling facilitation (Rolo & Moreno 2011; Perea & Gil 2014a), mostly based on their different palatability and preference by ungulates (Perea & Gil 2014a). In our study area three species showed significantly higher facilitative effects in comparison to the rest of the shrub species: *Genista hirsuta*, *Rosmarinus officinalis* and *Erica australis*. The first two species are known to be poorly palatable (Table 1), with long thorns (*Genista*) and plenty of aromatic compounds (*Rosmarinus*). Both physically and chemically defended shrubs have been shown to facilitate seedlings in other oak systems by reducing browsing damage (Perea & Gil 2014b) although some other mechanisms such as nutrient availability (Gómez-Aparicio et al. 2005) or shading (Smit et al. 2008) might also be involved. *Erica australis* is considered of intermediate palatability although it is also recognized as a low-preferred species by deer (Mesón & Montoya 1993; González-Hernández et al. 2002). Other non-preferred shrubs (e.g. *Lavandula*, *Halimium*, *Dorycnium*, *Daphne*) did not show such a significant facilitative effect, probably as a result of their smaller size and higher accessibility (less compact shrubs), which may reduce their protective effect against browsers or their ability to provide dense and extensive shade, the two main mechanisms of shrub facilitation in dry Mediterranean environments (Gómez-Aparicio et al. 2008; Smit et al. 2008; Soliveres et al. 2011; Perea & Gil 2014a).

### Specific applications to enhance oak regeneration

The differential effect of shrub species on oak facilitation has important implications for management practices


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since certain shrub species could be favoured over others to maximize oak recruitment. The three major nurse shrubs (*G. hirsuta*, *R. officinalis* and *E. australis*) seem to be key species in the regeneration of the studied Mediterranean dehesas and could be easily favoured since they are widely distributed and are important successional species in Mediterranean oak woodlands (Rivas-Martínez 2011). For instance, areas where these shrub species are dominant may become important source populations in the future and could be temporarily protected (fenced) or at least support lower instantaneous or permanent stocking rates (e.g. by promoting rotation among areas) in order to favour more rapid regeneration. Rotating the grazing species or establishing rotation per years according to the actual abundance and diversity of shrubs is highly recommended to reduce browsing pressure on woody plants. Additionally, the keystone shrubs can be planted or used in the reforestation programmes as natural protectors of seedlings. Shrubs might be a temporal solution to protect early stages of the oak recruitment (seedlings) since saplings and juveniles were mostly found above the height of most shrubs (>90-cm high). Oak saplings may still be highly vulnerable to browsing damage by large and medium-sized animals (cattle and deer) but not by small-sized grazers (sheep). Areas with sheep showed a proportionally higher number of saplings given the number of seedlings they had in comparison to wildlife areas (Fig. 4) and thus, sheep-rearing areas seem to favour the transition from seedlings to saplings. However, number of juveniles was very low across the three management regimes. This is probably related to the fact that oaks need more than 30 yr to reach the juvenile stage as they grow very slowly (Crescente et al. 2002; Rey-Benayas & Camacho-Cruz 2004). In addition, historic (and current) land management associated with many dehesas included tree and shrub clearing to promote pasture. Thus, shrub clearing, fire and ploughing were common management practices in the study sites >30–40 yr ago (A. Cobisa, L.F. Gómez, pers. com.) and are indeed still common in many other nearby dehesas. Therefore, we urge avoiding the use of these practices that reduce shrub cover for long periods and thus recommend shrub encroachment, particularly low palatable and large-sized shrub species, which favour the establishment and survival of the necessary seedlings to ensure regeneration of these systems.

Importantly, we found that seedling recruitment was higher under wildlife management, followed by sheep- and cattle-based management (Fig. 2a). Thus, traditional sheep management and alternative management based on recreational activities related to wildlife (e.g. ecotourism and hunting) seem to be more ecologically sustainable for these threatened ecosystems, at least under the current densities. Appropriate wildlife management provides higher abundance and diversity of safe microsites (shrub cover), whereas traditional sheep management implies lower stocking rates and higher movement (rotation) of the animals in different areas, which favours seedling survival (Carmona et al. 2013). Conversely, current cattle management involves high instantaneous stocking rates with low or null movement of the animals (López-Sánchez et al. 2014), reducing not only the abundance of seedlings but also the diversity and abundance of safe microsites (shrub cover). Therefore, it seems reasonable to reduce at least the permanent cattle stocking rate (0.33 cow·ha$^{-1}$) to values more sustainable such as those found in traditional sheep management (1.67 sheep·ha$^{-1}$), equivalent to 0.25 cow·ha$^{-1}$, which involves a 24% reduction in cattle density. Recommended management practices may also include an increase of cattle mobility (resembling sheep and deer management) by, for instance, promoting rotation among areas (non-continuous grazing management). Alternative management options may also include shifting or mixing grazing species within the ranch or establishing animal rotation per years according to the actual stage of shrub cover (or oak recruitment) across the different pasture areas. Therefore, further agriculture policies should consider reduction of the current stocking rates (especially for cattle-based management) and encouragement of rotational and mixed species grazing in order to foster the conservation of these highly valuable systems.

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## References

Acevedo, P., Ruiz-Fons, F., Vicente, J., Reyes-García, A.R., Alzaga, V. & Gortázar, C. 2008. Estimating red deer abundance in a wide range of management situations in Mediterranean habitats. *Journal of Zoology* 276: 37–47.

Anderson, D.R. 2008. *Model based inference in the life sciences: a primer on evidence*. Springer, New York, NY, US.

Burnham, K.P. & Anderson, D.R. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*, 2nd edn. Springer, New York, NY, US.

Campos, P., Huntsinger, L., Oviedo, J.L., Starrs, P.F., Díaz, M., Standiford, R.B. & Montero, G. 2013. *Mediterranean oak woodland working landscapes: Dehesas of Spain and Ranchlands of California*. Landscape Series, Springer, New York, NY, US.

Carmona, C.P., Azcárate, F.M., Oteros-Rozas, E., González, J.A. & Peco, B. 2013. Assessing the effects of seasonal grazing on holm oak regeneration: implications for the conservation of Mediterranean dehesas. *Biological Conservation* 159: 240–247.

Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M. & Gómez-Aparicio, L. 2004. Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: a 4-year study. *Restoration Ecology* 12: 352–358.

Crescente, M.F., Gratani, L. & Larcher, W. 2002. Shoot growth efficiency and production of *Quercus ilex* L. in different climates. *Flora* 197: 2–9.

Díaz, M. & Pulido, F.J. 2009. 6310 Dehesas perennifolias de *Quercus* spp. In: V.V.A.A. (ed.) *Bases ecológicas preliminares para la conservación de los tipos de hábitat de interés comunitario en España*, 69 pp. Ministerio de Medio Ambiente, y Medio Rural y Marino. Madrid, ES.

Eichhorn, M., Paris, P., Herzog, F., Incoll, L., Liagre, F., Mantzanas, K., Mayus, M., Moreno, G., Papanastasis, V., (...) & Dupraz, C. 2006. Sylvoarable systems in Europe: past, present and future prospects. *Agroforestry Systems* 67: 29–50.

Fernández-Olalla, M., Muñoz-Igualada, J., Martínez-Jáuregui, M., Rodríguez-Vigal, C. & San Miguel, A. 2006. Selección de especies y efecto del ciervo (*Cervus elaphus* L.) sobre arbustedos y matorrales de los Montes de Toledo, España central. *Forest Systems* 15: 329–338.

Fox, J. & Weisberg, S. 2011. *An R companion to applied regression*, 2nd edn. Sage, Thousand Oaks, CA, US.

Gómez-Aparicio, L. 2009. The role of plant interaction in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *Journal of Ecology* 97: 1202–1214.

Gómez-Aparicio, L., Zamora, R., Gómez, J., Castro, J. & Baraza, E. 2004. Appling plant facilitation to forest restoration: a meta-analysis for the use of shrubs as a nurse plant. *Ecological Applications* 14: 1128–1138.

Gómez-Aparicio, L., Valladares, F., Zamora, R. & Quero, J.L. 2005. Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: an experimental approach at different scales. *Ecography* 28: 757–768.

Gómez-Aparicio, L., Zamora, R., Castro, J. & Hódar, J.A. 2008. Facilitation of tree saplings by nurse plants: micro-habitat amelioration or protection against herbivores? *Journal of Vegetation Science* 19: 161–172.

González-Hernández, M.P., Meiriño, M. & Costa, L. 2002. Efectos de las altas densidades de ciervo sobre la vegetación del parque natural de O Invernadeiro (Ourense). Implicaciones en su manejo y conservación. *Cuadernos de la Sociedad Española de Ciencias Forestales* 14: 129–134.

Hartel, T. & Plieninger, T. 2014. *European wood-pastures in transition: a social-ecological approach*. Routledge/Taylor & Francis, London, UK.

Herruzo, A.C. & Martínez-Jáuregui, M. 2013. Trends in hunters, hunting grounds and big game harvest in Spain. *Forest Systems* 22: 114–122.

Joffre, R., Vacher, J., Llanos, C. & Long, G. 1988. The dehesa: an agrosilvopastoral system of the Mediterranean region with special reference to the Sierra Morena area of Spain. *Agroforestry Systems* 45: 57–79.

López-Sánchez, A., Schroeder, J., Roig, S., Sobral, M. & Dirzo, R. 2014. Effects of cattle management on oak regeneration in northern Californian Mediterranean oak woodlands. *PLoS ONE* 9: e105472.

Manning, A., Fischer, J. & Lindnmayer, D. 2006. Scattered trees are keystone structures – implications for conservation. *Biological Conservation* 132: 311–321.

Mesón, M. & Montoya, J.M. 1993. *Selvicultura Mediterránea*. Mundi-Prensa, Madrid, ES.

Moreno, G. & Pulido, F.J. 2009. The functioning, management and persistence of Dehesas. In: Rigueiro-Rodriguez, A., McAdam, J. & Mosquera-Losada, M.R. (eds.) *Agroforestry in Europe, current status and future prospects*, pp. 127–160. Springer, Dordrecht, NL.

Olea, L. & San Miguel, A. 2006. The Spanish dehesa. A Mediterranean silvopastoral system linking production and nature conservation. *Grassland Science in Europe* 11: 3–13.

Peco, B., Sánchez, A.M. & Azcárate, F.M. 2006. Abandonment in grazing systems: consequences for vegetation and soil. *Agriculture, Ecosystems and Environment* 113: 284–294.

Perea, R. 2006. *Estudio de la estructura de masa de una dehesa de encina con alcornoque en "El Deheson del Encinar"*. Master's thesis. Universidad Politecnica de Madrid, ES.

Perea, R. & Gil, L. 2014a. Shrubs facilitating seedling performance in ungulate-dominated systems: biotic versus abiotic mechanisms of plant facilitation. *European Journal of Forest Research* 133: 525–534.

Perea, R. & Gil, L. 2014b. Tree regeneration under high levels of wild ungulates: the use of chemically vs. physically defended shrubs. *Forest Ecology and Management* 312: 47–54.

Perea, R., Girardello, M. & San Miguel, A. 2014. Big game or big loss? High deer populations are threatening woody plant diversity and vegetation dynamics. *Biodiversity and Conservation* 23: 1303–1318.

Plieninger, T. 2006. Habitat loss, fragmentation and alteration – quantifying the impact of land-use changes on a Spanish dehesa landscape by use of aerial photography and GIS. *Landscape Ecology* 21: 91–105.

Plieninger, T. 2007. Compatibility of livestock grazing with stand regeneration in mediterranean holm oak parklands. *Journal for Nature Conservation* 15: 1–9.

Plieninger, T., Pulido, F.J. & Schaich, H. 2004. Effects of land-use and landscape structure on holm oak recruitment and


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regeneration at estate level in *Quercus ilex* L. dehesas. *Journal of Arid Environments* 57: 345–364.

Plieninger, T., Rolo, V. & Moreno, G. 2010. Large-scale patterns of *Quercus ilex*, *Quercus suber* and *Quercus pyrenaica* regeneration in Central-Western Spain. *Ecosystems* 13: 644–660.

Pugnaire, F.I., Haase, P. & Puigdefábregas, J. 1996. Facilitation between higher plant species in a semiarid environment. *Ecology* 77: 1420–1426.

Pulido, F. & Díaz, M. 2005. Regeneration of a Mediterranean oak: a whole cycle approach. *Ecoscience* 12: 92–102.

Pulido, F.J., Díaz, M. & Trucios, S.J.H. 2001. Size structure and regeneration of Spanish holm oak *Quercus ilex* forests and dehesas: effects of agroforestry use on their long-term sustainability. *Forest Ecology and Management* 146: 1–13.

Pulido, F., García, E., Obrador, J. & Moreno, G. 2010. Multiple pathways for tree regeneration in anthropogenic savannas: incorporating biotic and abiotic drivers into management schemes. *Journal of Applied Ecology* 47: 1272–1281.

Ramírez, J. & Díaz, M. 2008. The role of temporal shrub encroachment for the maintenance of Spanish holm oak *Quercus ilex* dehesas. *Forest Ecology and Management* 255: 1976–1983.

Rey-Benayas, J.M. & Camacho-Cruz, A. 2004. Performance of *Quercus ilex* saplings planted in abandoned Mediterranean cropland after long-term interruption. *Forest Ecology and Management* 194: 223–233.

Rivas-Martínez, S. 2011. Map of vegetation series, geoseries and geopermaseries from Spain. (Report on potential vegetation map of Spain). *Itinera Geobotanica* 18: 5–800.

Rivest, D., Rolo, V., López-Díaz, L. & Moreno, G. 2011. Shrub encroachment in Mediterranean silvopastoral systems: *Retama sphaerocarpa* and *Cistus ladanifer* induce contrasting effects on pasture and *Quercus ilex* production. *Agriculture, Ecosystems and Environment* 141: 447–454.

Rolo, V. & Moreno, G. 2011. Shrub species affect distinctively the functioning of scattered *Quercus ilex* trees in Mediterranean open woodlands. *Forest Ecology and Management* 261: 1750–1759.

San Miguel, A., Pérez-Carral, C. & Roig, S. 1999. Deer and traditional agrosilvopastoral systems of Mediterranean Spain. A new problem of sustainability for a new concept of land use. *Options Méditerranéennes* 39: 261–264.

Smit, C., den Ouden, J. & Díaz, M. 2008. Facilitation of holm oak recruitment by shrubs in Mediterranean open woodlands. *Journal of Vegetation Science* 19: 193–200.

Soliveres, S., García-Palacios, P., Castillo-Monroy, A.P., Maestre, F.T., Escudero, A. & Valladares, F. 2011. Temporal dynamics of herbivory and water availability interactively modulate the outcome of a grass–shrub interaction in a semi-arid ecosystem. *Oikos* 120: 710–719.

Tyler, C., Kuhn, B. & Davis, F. 2006. Demography and recruitment limitations of three oak species in California. *Quarterly Review of Biology* 81: 127–152.

Tyler, C., Davis, F.W. & Mahall, B.F. 2008. The relative importance of factors affecting age-specific seedling survival of two co-occurring oak species in southern California. *Forest Ecology and Management* 225: 3063–3074.

Venables, W.N. & Ripley, B.D. 2002. *Modern applied statistics with S-PLUS*. Springer, New York, NY, US.

Zavaleta, E.S. & Kettley, L.S. 2006. Ecosystem change along a woody invasion chronosequence in a California grassland. *Journal of Arid Environments* 66: 290–306.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. 2009. Mixed effects modelling for nested data. In: Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (eds.) *Mixed effects models and extensions in ecology with R*, pp. 101–142. Springer, New York, NY, US.

Zuur, A.F., Saveliev, A.A. & Ieno, E.N. 2012. *Zero Inflated Models and Generalized Linear Mixed Models with R*. Highland Statistics Limited Newburgh, Newburgh, UK.