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Big game or big loss? High deer densities are threatening woody plant diversity and vegetation dynamics

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Abstract Land-use change and current game management have favored an increasing population of wild ungulates (especially deer) in many regions of the Northern Hemisphere. Here, we assess the impact of high deer densities (>30 ind km^{-2}) on the highly diverse woody vegetation of Mediterranean ecosystems, where big game have been favored for the last decades. We examine whether prolonged deer browsing (over 30 years) affected plant composition, diversity and dynamics of the original (non-browsed) vegetation. Deer browsing led to an average decrease of 30.4 % in woody plant diversity (species richness), due to a lack of regeneration for the most preferred plant species. Species belonging to early stages of succession (mostly Labiatae and Cistaceae) were non-preferred by deer. Conversely, the most preferred species belonged mainly to late stages of plant succession. Deer impact on Mediterranean shrublands is causing biotic homogenization of plant communities and is threatening vegetation dynamics by forcing it to return to earlier succession stages. Strict deer population control favouring larger trophies but lower offspring numbers together with an adequate habitat management (increasing grass and acorn availability) would be the most efficient measures to reverse this diversity loss. Restoration work seems only appropriate for the most vulnerable species. We highlight the need of sampling deer-free areas with low or null historical browsing to assess the real impact of deer on woody plant diversity and vegetation dynamics.

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Introduction

In most developed countries, the economic and environmental impact of hunting has increased considerably during the last decades (San Miguel et al. 1999; Fuller and Gill 2001; Gordon et al. 2004; Díaz et al. 2008; Martínez-Jáuregui et al. 2011). Hunting and game observation have become important outdoor activities for the increasingly urban societies (Hrubes et al. 2001; Gordon et al. 2004; Milner et al. 2006), who are willing to pay large sums of money. Consequently, game animal populations, and especially big game species, have started to render important economic benefits (Torres-Porras et al. 2009). As a result of this, current managers aim to increase, maintain or even introduce populations of big game species to guarantee a large number of captures (kills) or tourist visits year after year. Hunting of deer (Cervidae) is amongst the most popular choices for hunters due to a long established tradition, eye-catching trophies, meat quality and their widespread distribution all over the world (Hurtado-Gonzales and Bodmer 2004; Martínez et al. 2005; Milner et al. 2006). As well as being favored by hunting management practices, deer are increasing in their abundance and distribution because of widespread land-use changes (Gill 1990; Porter 1994; Kuiters et al. 1996; Côté et al. 2004; Gordon et al. 2004; San Miguel et al. 2010), such as the reduction of the extensive livestock grazing and the increase of forest land (MacDonald et al. 2000; Pineda 2001; Poyatos et al. 2003; Busch 2006; Rey-Benayas et al. 2007). According to Porter (1994) temperate ecosystems are currently supporting the highest densities of ungulates ever recorded. We, however, have a limited understanding of the ecological consequences of favoring wild ungulate populations (e.g., through intense hunting management).

Although the impact of deer browsing in plant regeneration (especially in trees) has been extensively studied (e.g. Marquis 1974; Anderson and Loucks 1979; Tilghman 1989; Gill 1992a, b; Putman 1994; Putman and Moore 1998; Gill and Beardall 2001; Horsley et al. 2003; Rooney and Waller 2003; Côté et al. 2004; White 2012), there is very little information on the long-term impacts of deer browsing on highly diverse shrublands, but see Stockton et al. (2005), Martin et al. (2010) and references therein. It is well known that browsers influence composition, structure, production and ecosystem processes in temperate forests by selectively foraging on preferred plant species (Alverson et al. 1988; McInnes et al. 1992; Pastor et al. 1993; Rooney and Waller 2003; Côté et al. 2004; Stockton et al. 2005; Martin et al. 2010; Miranda et al. 2011; White 2012). Some studies have shown that prolonged browsing of deer limits the recruitment of the most preferred plant species which are eventually replaced by less preferred woody species (White 2012). This selective foraging can also contribute to the biotic homogenization of understory communities (Olden 2006; Rooney 2009). However, most studies focusing on the impact of deer browsing are based on exclosures with low number of replicates (Horsley et al. 2003) and, have not compared the original vegetation (before deer densities started to rise) with the current vegetation (under high levels of deer browsing). Nevertheless, the use of these exclosures usually provides relevant information about the recovery of those ecosystems that have been subjected to deer browsing for long periods. Although there is evidence that this recent type of deer-based management (ungulate increase) for hunting

purposes is economically and socially sustainable (Martin and Gum 1978; Baker 1997; Knoche and Lupi 2012) there is no evidence on the ecological impacts of high levels of deer browsing on Mediterranean species and communities.

Over the last decades there has been an impressive emphasis on biodiversity research (Ghilarov 2000; Loreau et al. 2001) and many countries have developed national and international strategies for the conservation and sustainable use of diversity. Studies in search of a relationship between biodiversity and environmental factors have provided important advances to understand under what ecological conditions species diversity decreases or increases. However, the relative importance of each environmental factor or human-induced disturbance (e.g., browsing degree) as a determinant of species diversity and distribution is still poorly known. In this study, we assess the impact of high big game densities (deer) on the highly diverse woody vegetation of Mediterranean shrublands in Southern Spain. These areas have been intensely managed (e.g., properties perimeter fenced or supplementary feeding) for the last 30–40 years with the main aim of favoring big game hunting. We used paired samples inside the fenced hunting properties (with deer) and outside (without deer) to specifically address: (1) woody plant cover and composition inside an outside the fenced areas; (2) deer browsing damage on woody plants, and (3) deer preference for woody plant species. Then, we compared woody plant community (composition) of the sampled sites with and without deer to examine whether this intense management, promoting deer populations, is threatening woody plant diversity and vegetation dynamics. We predict a higher diversity and a greater abundance of late-successional species in the absence of deer browsing. Finally, to address the possible degree of ecosystem alteration due to this hunting management we analyze whether this prolonged deer browsing is causing biotic homogenization of Mediterranean shrubland communities. The analysis of the effect of these long term exclosures would allow for a better understanding of the ecological impact of high deer browsing on the highly diverse Mediterranean ecosystems and whether this intense management favoring high deer populations is ecologically sustainable.

Materials and methods

Study area

The study area is located in the East part of the mountain range "Montes de Toledo", South-central Spain (39°27′15″N; 4°3′51″W) at 700–1,300 m a.s.l. Our study area covers approximately 710 km^2. The climate is Mediterranean with a highly variable precipitation (mean annual rainfall of 541 mm) and 3–4 months of summer drought (June–September). Temperatures are high in summer (July mean temperature 25.1 °C) and relatively low in winter (January mean temperature 4.8 °C), with frequent frosts from November to March. Mean annual temperature is 13.4 °C. Soils are poor in nutrients and acid (pH 5.2) with a lithological substrate of quartzites and slates (Perea and Perea 2008).

Vegetation is dominated by sclerophyllous and semideciduous oak forests and woodlands (*Quercus ilex*, *Quercus faginea*, *Quercus pyrenaica*) with patches of evergreen shrubland (*Cistus*, *Rosmarinus*, *Erica*, *Phillyrea*). These evergreen shrubs constitute an important and permanent source of low-medium food quality for herbivores, of lower nutritional quality than green grass but higher than dried grass (San Miguel et al. 1999). Deer were very scarce in the area until the late seventies when managers started to favour ungulates for hunting purposes. The ownership is mostly private with large country estates

(usually over 1,000 ha each) that were fenced in their perimeters 30–40 years ago to keep the big game species inside and manage them independently from other properties. Fences are 2 m high made of strong wire that prevents medium and large mammals from moving freely from one side to the other. Fences, by law, are placed within the estate limits leaving some free space (usually 3–5 m) between the fence and the real property limits. Red deer (*Cervus elaphus*) is the main game species in this area although some managers introduced fallow deer (*Dama dama*). Roe-deer (*Capreolus capreolus*) are scarce in the area. Current densities of red deer are 30–60 individuals per km^2 (data obtained from land owners and the Regional Government) and deer hunting has become the main profit and the primary goal of management, usually with human intervention (supplementary feeding and concentrates, watering, etc.). Most of the wooded landscape is covered by these large fenced properties, not only in the study area but also in other parts of Southern Spain (e.g. Extremadura and Andalucia). Only some areas within the public domain (forests, roads, trails, rivers, etc.) or small private properties (<500 ha) have no large browsers because fences excluded their entry. Red deer have been described as mixed feeders that feed on grasses (grazer) but also on forbs and woody vegetation (browser; Bugalho and Milne 2003). The species browses more intensely in winter (December–March) and summer (July–September) when no alternative high-quality food is available (green grass or acorns). Currently, deer, in this area, have no natural predators (they went extinct) and their populations are regulated mainly by hunting.

Sampling design

Sampling was carried out through 82 field surveys (41 pairs, hereafter sites). All sampling sites comprised shrubland patches where deer could reach most part of the browse biomass. For each pair, one survey was performed where red deer are present (hereafter deer-present surveys) and the other survey was carried out where red deer are absent since approximately 30–40 years (hereafter deer-absent surveys). Surveys of each pair were separated by a game fence of 2 m high (see above) and less than 10 m from each other but farther than 2–3 m from the fence in the deer-present surveys to avoid the possible boundary effect because of the fence line. The two surveys of each site were chosen in that way they showed homogeneous ecological conditions (slope direction, soil, topography) to avoid confounding factors that could affect plant species composition and cover. Sites always belonged to different hunting properties to ensure statistical independence and were distributed the most homogeneously possible across the study area (approximately one site per 17 km^2) but could not be selected systematically because in some areas there were no excluded parts or were too small. The area sampled by each field survey was 78.5 m^2 corresponding to a circle of 10 m diameter.

For each deer-present survey we examined the effect of deer browsing on woody vegetation by estimating the degree of browsing (i.e., utilization at species level) of each woody species and their preference for foraging on them. The degree of browsing was estimated by using a 6-rank (0–5) method (Table 1). Preferences were studied by comparing the utilization of every woody species with their availability through a forage ratio index (Savage 1931; Jacobs 1974; Krebs 1999; Fernández-Olalla et al. 2006; see Fernández-Olalla and San Miguel 2008 for a complete review). The availability of each species was estimated with the Braun-Blanquet (1951) abundance scale, using the ground cover percentage of each plant species (Table 1). We, then, assigned these abundance degrees to the mid-point of each degree range (Table 1). The preference was evaluated by the next forage ratio index (Krebs 1999; Fernández-Olalla et al. 2006):

Table 1 Criteria used to collect woody plant utilization and availability in the surveys

Value	Utilization (browsing degrees)	Availability: Braun-Blanquet's (1951) abundance degrees	Mean ground cover (%) derived from Braun-Blanquet's degrees
0	No browsing evidence	0< Ground cover <5 % occasional presence	2
1	Slight browsing evidences: only few twigs browsed	5< ground cover <10 % non occasional presence	7
2	Low browsing intensity: plenty of twigs browsed but clearly under 50 % of browsable biomass. Flowering occurs only in those inaccessible twigs	10< ground cover <25 %	17
3	Intense, although sustainable, browsing: plenty of twigs browsed, around 50 % of browsable biomass. Successful flowering occurs very rarely	25< ground cover <50 %	37
4	High browsing intensity: consumption over 50 % of browsable biomass and clear shaping of the original plant form. No flowering	50< ground cover <75 %	62
5	Maximum browsing intensity: no or almost no browsable twig available	Ground cover >75 %	87

$$w_{ij} = \frac{o_{ij} * p_{ij} / \sum_{i=1}^{n} o_{ij} * p_{ij}}{p_{ij} / \sum_{i=1}^{n} p_{ij}} = \frac{o_{ij} \sum_{i=1}^{n} p_{ij}}{\sum_{i=1}^{n} o_{ij} * p_{ij}},$$

where w_{ij} is the *forage ratio* or preference (selection) index for the species i in the j site; o_{ij} is the browsing degree of the species i in the j site (value scaled from 0 to 5; Table 1); p_{ij} is the ground cover percentage of the species i in the j site (mean value; Table 1), and n is the number of woody species present in the j site. The final preference index for each species was the average of those calculated for every site (deer-present surveys) where the species occurred. In the deer-absent surveys we only recorded Braun-Blanquet cover for each plant species since we found no deer signs (excrements, footprints or damage to plants). Field sampling was carried out in March 2006 and 2008, since late winter is considered the best season for quantifying browsing damage in Mediterranean woody species.

Finally, to analyze possible changes in the vegetation dynamics we used the Map of Potential Vegetation of Spain (Rivas-Martínez 2011) to discriminate among the different stages of plant succession within the most common vegetation series in the study area (*Pyro bourgaeanae-Querco rotundifoliaea* S.). We, then, classify each woody plant species within three successional stages: (1) Early, when the plant species is more frequent in the *Scillo-Lavanduletum* or *Genisto-Cistetum* association (*Cisto-Lavanduletea* phytosocio-logical class, comprised mostly by dwarf and short shrubs); (2) Medium, when the plant species is more frequent in the *Retamo-Cytisetum* association (*Cytisetea scopario-striati* class, comprised mostly by medium-sized shrubs) and (3) Late, when the plant belongs to the association *Phillyreo-Arbutetum* (dominated by tall shrubs or small trees) or to the last stage community, the forest *Pyro-Quercetum* association, both within the *Quercetea ilicis* class.

Data analysis

To test for a difference in species composition between the deer-present and deer-absent surveys in each site, we used two matrices containing the species cover data for the areas with and without deer, respectively. For each matrix we performed a PCA (Principal Component Analysis). We then used Procrustes and ProTest analyses (Peres-Neto and Jackson 2001) to compare the first two axes of the two PCAs. Procrustes analysis works by scaling, rotating, and dilating one ordination solution and then superimposing it on a second ordination, maximizing the fit between corresponding observations of the two ordination configurations. The most frequently used method for Procrustean fitting is based on the least-squares criterion that minimizes the sum of the squared residuals (m^2) between the two configurations; the m^2 statistic is thus a measure of association (i.e., concordance) between the two configurations. This is a significance test for Procrustes analysis to verify whether multivariate configurations do match (Peres-Neto and Jackson 2001). ProTest extends Procrustes analysis by providing a permutation procedure to assess the statistical significance of the Procrustean fit (Peres-Neto and Jackson 2001). ProTest randomly permutes the original observations of one matrix so that each site can be assigned any of the values attributed to other sites (Jackson 1995). The m^2 statistic is then recalculated for each permutation, and the proportion of the statistics smaller than or equal to the observed value provides the significance level of the test.

We used a linear mixed effect model (LME) (Pinheiro and Bates 2000) to investigate the difference in species richness between the surveys with and without deer. Species richness was log transformed to achieve normality and site was entered as a random effect. All the analyses were performed using the R programming environment (R development core team

2012, http://www.r-project.org/). The mixed effect model analyses were carried out using the nlme package (Pinheiro et al. 2012), whereas for the Procrustes analyses we used vegan package (Oksanen et al. 2012). Chi square tests were performed for the comparison in plant abundance (cover), first between the early and late-successional plant species and, second, between the highly preferred and non-preferred plant species. Since the highest preference index was 3.0 (see "Results" Section) we considered that a species was highly preferred when preference index >1.5 and non-preferred when preference index = 0. Those species with a 0<preference index<1.5 were considered intermediately-preferred. To analyze the statistical validity of this categorization we performed a one-way ANOVA with a log-transformed response [y = log (preference index + 1)] to achieve normality. A Tukey's HSD test was used for multiple comparisons between the three categories.

Finally, to measure more intuitively the change in species composition (communities) between the areas with and without deer within each site we calculated a beta diversity index for presence-absence data (Koleff et al. 2003). We used the Jaccard similarity index (Jaccard 1912; Southwood and Henderson 2000; Koleff et al. 2003), which has a minimum value of zero (completely different communities) and a maximum of 1 (identical communities in terms of species presence/absence). We, then, calculated beta diversity for all possible combinations (pairs) of the deer-absent surveys (Total = 820 combinations) to compare whether there is a higher similarity in species composition among deer-absent surveys than between deer-present and deer-absent surveys within the same site. Similarly, we also compared Jaccard indexes obtained between all deer-present surveys (820 combinations) with those obtained between the deer-present and deer-absent areas to see if there is higher similarity across the deer-present surveys (homogenization of plant communities). To statistically validate these comparisons we performed Exact Permutation Tests estimated by Monte Carlo (9,999 replications), using the library "perm" and the function "permTS" of the R software.

Results

A total of 49 woody species were sampled in the 82 surveys (Fig. 1). We found 39 woody plant species that were present in, at least, three surveys (Table 2). Ten out of these 39 species (25.6 %) were only present in the deer-absent surveys (Table 2). There were five species with unsustainable browsing (browsing degree >3; Table 2). We found 10 highly preferred species (preference index between 1.5 and 3.0), 10 non-preferred species (preference index = 0) and 9 with intermediate values (Table 2). These 3 categories were significantly different across all surveys when analyzing the preference index ($F_{2, 393} = 76.23$; $P < 0.001$; $P < 0.002$ for all possible multiple comparisons by Tukey's HSD). Abundance (cover) for the highly preferred species was higher in the deer-absent surveys than in the deer-present surveys (mean $\pm$ SE cover increase of 43.0 $\pm$ 8.1 %). Contrarily, non-preferred species showed higher or equal abundance in the deer-present surveys (Mean $\pm$ SE increase of 46.7 $\pm$ 26.1 %), obtaining significant differences between both categories ($\chi_1^2 = 21.37$; $P < 0.001$).

The graphical description of the Procrustes analyses provides an indication of a clear difference in species composition between samples with and without deer (Fig. 2). Thus, the PROTEST analysis confirmed that species composition was different between deer-present and deer-absent surveys ($m^2 = 0.34$, $P < 0.05$). In addition, deer-absent surveys showed a mean of 9.2 woody plant species per survey whereas deer-present surveys showed a mean of
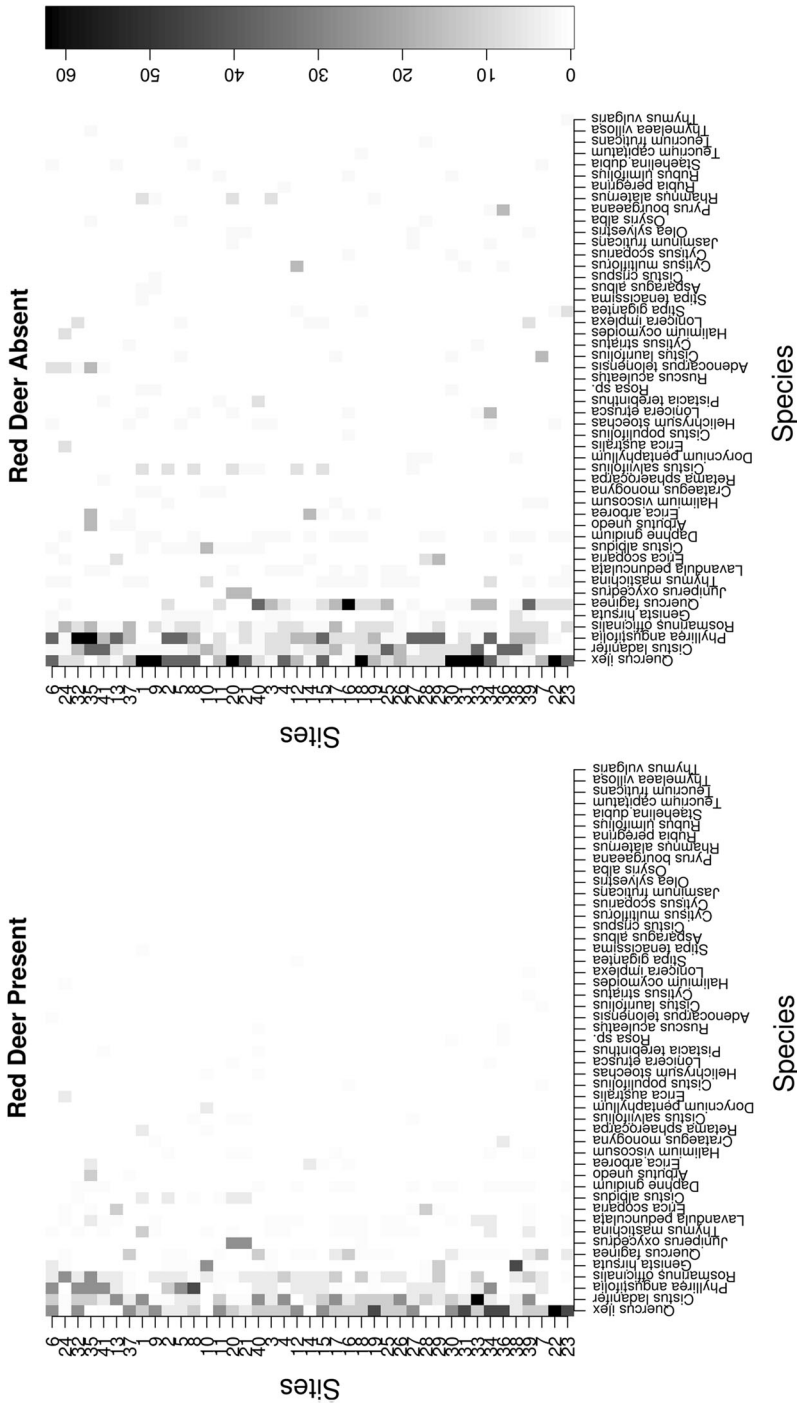
Fig. 1 Percentage of species abundance (cover) for the deer-present and the deer-absent surveys across the 41 paired samples. Species are shown in a decreasing order of cover for the deer-present surveys

Table 2 Summary of the values (mean ± SD) for abundance (cover in %), browsing degree and preference index for the plant species that were present in, at least, three surveys

Plant species	Deer-absent areas		Deer-present areas		Browsing degree (0–5)	Preference index	Successional stage
	N	Cover (%)	N	Cover (%)			
Adenocarpus telonensis	5	7.0 ± 6.1	1	2.0 ± 0.0	4.00	2.26	2
Asparagus albus	3	2.0 ± 0.0	0	–	–	–	2
Arbutus unedo	3	9.5 ± 10.6	2	7.0 ± 8.6	4.00 ± 0.00	2.33 ± 0.60	3
Cistus albidus	10	3.5 ± 4.7	7	4.9 ± 2.7	0.00 ± 0.00	0.00 ± 0.00	1
Cistus ladanifer	37	11.2 ± 12.3	36	17.0 ± 17.1	0.69 ± 0.78	0.82 ± 0.58	1
Cistus laurifolius	4	5.8 ± 7.5	1	2.0	1.00	0.48	1
Cistus populifolius	2	2.0 ± 0.0	1	2.0	2.00	2.41	2
Cistus salviifolius	8	5.3 ± 2.5	4	2.0 ± 0.0	2.00 ± 1.41	1.77 ± 1.17	1
Crataegus monogyna	4	2.0 ± 0.0	2	4.5 ± 3.5	1.5 ± 0.7	1.41 ± 1.57	2
Cytisus multiflorus	3	7.0 ± 8.7	0	–	–	–	2
Cytisus striatus	2	2.0 ± 0.0	1	2.0	0.00	0.00	2
Daphne gnidium	18	2.0 ± 0.0	15	2.0 ± 0.0	0.00	0.00	2
Dorycnium pentaphyllum	3	2.0 ± 0.0	1	7.0	0.00	0.00	1
Erica arborea	6	7.0 ± 7.7	4	4.5 ± 2.9	1.00 ± 0.82	0.72 ± 0.62	3
Erica scoparia	6	6.2 ± 5.8	7	6.3 ± 7.3	2.00 ± 0.82	1.80 ± 0.98	3
Genista hirsuta	12	2.4 ± 1.4	11	12.4 ± 19.7	0.18 ± 0.40	0.13 ± 0.30	2
Halimium umbellatum	4	2.0 ± 0.0	6	2.0 ± 0.0	0.00 ± 0.00	0.00 ± 0.00	1
Helichrysum stoechas	7	2.0 ± 0.0	2	2.0 ± 0.0	0.00 ± 0.00	0.00 ± 0.00	1
Jasminum fruticans	3	2.0 ± 0.0	0	–	–	–	2
Juniperus oxycedrus	2	17.0 ± 0.0	3	25.3 ± 20.2	1.0 ± 0.0	0.62 ± 0.54	3
Lavandula pedunculata	11	2.0 ± 0.0	18	2.8 ± 1.9	0.00 ± 0.00	0.00 ± 0.00	1
Lonicera etrusca	6	4.5 ± 6.1	2	2.0 ± 0.0	4.50 ± 0.72	2.67 ± 2.17	3
Lonicera implexa	5	4.0 ± 2.7	1	2.0	2.0	2.93	3
Olea sylvestris	4	2.0 ± 0.0	0	–	–	–	3

Table 2 continued

Plant species	Deer-absent areas		Deer-present areas		Browsing degree (0–5)	Preference index	Successional stage
	N	Cover (%)	N	Cover (%)			
Osyris alba	3	2.0 ± 0.0	0	–	–	–	1
Phillyrea angustifolia	34	19.6 ± 17.1	28	14.1 ± 16.5	3.25 ± 1.68	2.99 ± 3.18	3
Pistacia terebinthus	3	3.7 ± 2.9	2	2.0 ± 0.0	0.50 ± 0.70	0.39 ± 0.55	3
Pyrus bourgaeana	4	9.5 ± 0.47	0	–	–	–	3
Quercus faginea	24	12.4 ± 14.4	22	5.6 ± 5.8	2.36 ± 1.33	1.82 ± 1.75	3
Quercus ilex	37	27.1 ± 22.4	37	27.1 ± 21.1	2.68 ± 1.22	1.87 ± 1.31	3
Retama sphaerocarpa	1	2.0	2	4.5 ± 3.5	0.00 ± 0.00	0.00 ± 0.00	2
Rhamnus alaternus	5	2.7 ± 0.1	0	–	–	–	3
Rosa sp.	3	2.0 ± 0.0	2	2.0 ± 0.0	4.5 ± 0.71	1.23 ± 0.09	2
Rosmarinus officinalis	34	5.9 ± 4.7	34	9.4 ± 8.6	0.00 ± 0.00	0.00 ± 0.00	1
Rubus ulmifolius	3	2.0 ± 0.0	0	–	–	–	2
Ruscus aculeatus	2	2.0 ± 0.0	2	2.0 ± 0.0	1.5 ± 1.4	0.44 ± 0.61	2
Staehelina dubia	4	2.0 ± 0.0	0	–	–	–	1
Teucrium fruticans	4	2.0 ± 0.0	0	–	–	–	1
Thymus mastichina	18	2.6 ± 1.7	16	3.4 ± 3.7	0.00 ± 0.00	0.00 ± 0.00	1

N indicates the number of surveys. Successional stages indicate whether the plant species belongs mainly to early (1), medium (2) or late (3) stages of plant succession

Fig. 2 Procrustean superimposition plot generated from the ordinal results of the PCAs. The *circle* represents site scores for plots without deer and the point of the arrow for plots with deer. The distance between the two is the Procrustean residual. *Longer arrows* indicate residuals with higher values (i.e., a larger difference in species composition between a pair of samples)
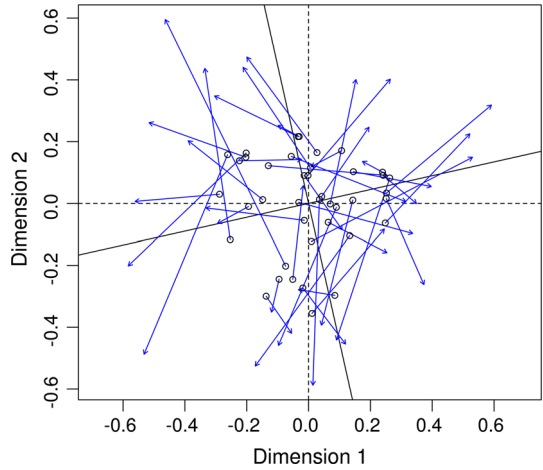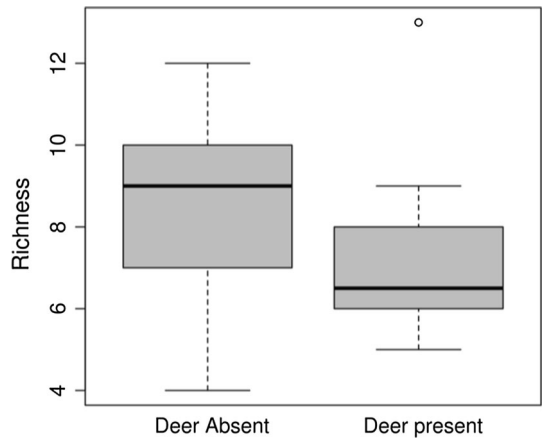

Fig. 3 Boxplot of woody plant diversity (species richness) for deer-absent and deer-present surveys. $F_{1,40} = 24.52$, $P < 0.001$. Each *box* shows the median (band in the middle of the box) and the first and third quartiles (edges). *Whiskers* represent the lowest and highest datum within the 1.5 interquartile range of the lower and upper quartile

6.4 species (Fig. 3). Therefore, we found an average of 30.4 % decrease in woody plant diversity (species richness) for the surveys with deer in comparison to those without deer. Results from the Linear Mixed Effect Model confirmed this strong difference in species richness between the surveys with and without deer (LME, $F_{1,40} = 24.52$, $P < 0.001$).

Pioneer species belonging to early stages of plant succession increased their abundance in areas where deer were present (Table 2). Thus, only 11 % of the early-successional species decreased their abundance when deer were present (67 % increased their abundance). Conversely, 70 % of the late-successional species decreased their abundance in those areas where deer were present (10 % increased their abundance), obtaining significant differences between both groups ($\chi_1^2 = 42.97$; $P < 0.001$).

Jaccard similarity index between the community with and without deer of each site was a mean ± SE of 0.57 ± 0.02 ($N = 41$ sites). However, Jaccard similarity index between all possible pairs of deer-absent surveys was 0.72 ± 0.01 ($N = 820$ combinations), obtaining significant differences ($P = 0.0062$ estimated by 9,999 Monte Carlo replications). This means that a higher similarity in plant species composition was found between deer-absent surveys across all sites (at different ecological conditions) than the two surveys (with and without deer)

within the same site (similar ecological conditions such as slope direction, climate and topography). Finally, Jaccard similarity index between all possible pairs of deer-present surveys was 0.90 ± 0.01 ($N = 820$ combinations), which indicates larger similarity between deer-present areas than between deer-absent areas ($P = 0.0004$ estimated by 9,999 Monte Carlo replications). Likewise, we found larger similarity between deer-present areas than between deer present-absent areas ($P = 0.0060$ estimated by 9,999 Monte Carlo replications).

Discussion

This study reveals a strong difference between the areas with and without deer in woody plant composition and diversity after 30–40 years of deer browsing. Results show that some plant species were highly preferred and became absent in the areas where deer were present at great densities (>30 ind km^{-2}) for a long period of time. By comparing surveys where deer were present with those where deer were absent, we were able to demonstrate that those plant species that are more vulnerable to deer browsing are failing to regenerate (browsing degree >3) and are even becoming locally extinct under high levels of browsing. The extinction or reduced presence of such species has caused a decrease in plant diversity as we found in our analyses (Fig. 3). In only 30-40 years this hunting management favouring high deer densities led to a 30.4 % decrease in species diversity (richness). This is compelling evidence that such intense deer-based management is ecologically unsustainable. Our results are concordant with other studies (Anderson and Katz 1993; De Calesta 1997; Stockton et al. 2005; Martin et al. 2010) that have also shown a decrease in plant diversity at high deer densities. Stockton et al. (2005) pointed out a decrease in species richness at the plot scale by 20–50 % in islands with deer in comparison with those without deer. Despite the unique value of this comparison between islands at different deer densities, in this study we selected close areas (side by side) within the same ecological conditions (soil, topography, climate, human intervention) except for the presence/absence of deer for the last 30–40 years. This allowed us to carry out an accurate analysis of the long-term effect of deer at both the species and the community levels. Here, we highlight the need for sampling deer-absent areas with low or null historical browsing in order to assess the real impact of deer on woody plant diversity since most studies only address the impact of deer browsing in areas with deer (by sampling existing and common plant species) or, at the most through exclosures (analyzing plant recovery), but neglect the impact on those species that are becoming rare or even extinct due to chronic browsing (see Rooney and Waller 2003 for a detailed review).

Surprisingly, we found higher similarity in plant species composition between deer-absent surveys across all sites (at different ecological conditions) than the two surveys (with and without deer) within the same site (similar ecological conditions such as slope direction, climate and topography). These results suggest that the legacy of high deer browsing should be considered as an important ecological factor which strongly determines plant species composition and diversity. Additionally, deer-present areas showed the largest similarity in woody plant composition, with an average similarity value of 0.90, which reflects that high populations of red deer are contributing to the biotic homogenization of Mediterranean shrubland communities, something that has been already highlighted in some North American forests (Stromayer and Warren 1997; Rooney 2009). Understanding the factors that affect species diversity across multiple scales is crucial in conservation biology and current ecology (Maestre 2004). In this study we already found that high levels of disturbance caused by deer browsing have an important effect on the local diversity of

Mediterranean shrublands (approximately one third of the whole woody plant diversity is locally threatened in the study area because of deer browsing). This was also observed in the species cover-abundance, which showed strong differences between samples with and without deer (Fig. 2). The abundance of the most preferred species (*Phillyrea angustifolia*, *Arbutus unedo*, *Adenocarpus telonensis*, *Lonicera implexa* and *Lonicera etrusca*), whose natural regeneration is highly compromised (no flowering), are likely to decline and could probably become extinct under the current deer densities. These species, together with those already missing (Table 2), are mostly part of the late successional communities towards the sclerophyllous oak forests, the potential vegetation type in this area under the current ecological conditions (Rivas-Martínez 2011). Conversely, pioneer species belonging to early stages of plant succession are increasing their cover-abundance (e.g., *Lavandula pedunculata*, *Thymus mastichina*, *Rosmarinus officinalis*, *Cistus* sp.) as a consequence of being less preferred by deer, probably due to their high content of essential oils (Oh et al. 1968; Gülz et al. 1984; Robles and Garzino 2000), which inhibit the microbial activity in the deer digestive tract (Dietz et al. 1962; Gershenzon and Croteau 1991). This lack of plant species belonging to later succession stages could compromise the fulfilment of the whole ecological succession (Tremblay et al. 2006) and the system dynamics would be stopped or, even, returned to early stage communities. Deer browsing could therefore have serious implications not only for species diversity but also for the ecosystem dynamics.

Conservation implications

Restoration work (e.g., planting, fencing extensive areas or protecting the most vulnerable plant species individually) could be useful measures to stop the current diversity loss. Managers could also favour plant diversity by using the non-preferred species as nurse plants of the highly preferred species, encouraging the facilitation process (Callaway 1995; Harmer et al. 2010). In that way, data about deer preferences for woody plants as those obtained in this study (Table 2) would be essential. However, all these measures are highly expensive and should not be implemented without a strong control (reduction) of deer population densities, which seems to be the most efficient and inexpensive strategy to preserve woody plant diversity in the long term. In that way, population density should reach values below the ecological carrying capacity (maximum sustainable density), which can be highly variable depending on the habitat management. For guidance on deer management, carrying capacity has been estimated in 20–25 ind/km^2 for a Public Property "Quintos de Mora" (unpublished data), whereas in the nearby "Cabañeros National Park" (with no crops and less intense habitat management), carrying capacity has been estimated in 10–15 ind/km^2 (Fernández-Ortiz 2007), very far from the current 30–60 ind/km^2 of most hunting properties. An additional step would be the increase of the population sex ratio towards males since most deer populations are currently biased towards females to obtain higher numbers of deer killed. The increase of sex ratio towards males would favour lower offspring numbers, lower competition for food and higher mating competition among males. Moreover, an increase in trophy size could compensate the economic loss for the decline in the total number of captures (kills) since hunters pay more for larger trophies (Festa-Bianchet 2003). Policies aimed at facilitating deer control (e.g., increase in the number of hunting days, allowance of different hunting strategies), together with the implementation of appropriate habitat management plans to create less available browse and more nutritious food (e.g., by favouring grasslands, crops or acorn production), would rapidly enhance the natural restoration of the highly degraded shrublands. Silviculture could also increase browse availability by offering the non-accessible browse (e.g. tree

branches) to the browsers after selective pruning. This would help the tree to develop a better crown and increase fruit production (especially acorns which are highly palatable and nutritious), while reducing the impact of deer browsing on woody plants. In areas with a strong legacy of deer browsing, population control and habitat management should come along with active restoration work, at least for the most vulnerable species.

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