Capítulo 5

Los efectos ingenieros del conejo (*Oryctolagus cuniculus*) sobre una comunidad de plantas mediterránea

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

Lucía Gálvez Bravo, Antonio López-Pintor, Salvador Rebollo & Antonio Gómez-Sal. (*Enviado a Plant Ecology*). Rabbit (*Oryctolagus cuniculus*) engineering effects on a Mediterranean plant community.

Parte de los resultados de este capítulo han sido publicados en:

Lucía Gálvez, Antonio López-Pintor, José M. de Miguel, Germán Alonso, Marta Rueda, Salvador Rebollo and Antonio Gómez-Sal (2008) Ecosystem engineering effects of European rabbits in a Mediterranean habitat. pp. 125-140 En: Lagomorph Biology: Evolution, Ecology and Conservation. Paulo C. Alves, Nuno Ferrand and Klaus Hackländer (Eds), Springer-Verlag, Heidelberg-Berlin

Resumen

Los mamíferos herbívoros pueden ejercer efectos muy significativos sobre la vegetación a través de varios mecanismos, incluyendo la herbivoría, pisoteo, escarbaduras, defecación, excavación, etc. En ocasiones, estas actividades pueden modificar la distribución de los recursos o crear hábitats para otras especies. A los organismos que tienen este tipo de efectos se les suele clasificar como ingenieros de ecosistemas. El conejo europeo (*Oryctolagus cuniculus*) es un herbívoro semi-subterráneo originario de la Península Ibérica, y una pieza clave de las redes tróficas mediterráneas. Las actividades de los conejos tienen lugar alrededor del vivar, pero existe poca información acerca de sus efectos sobre la comunidad herbácea dentro de su dominio vital. En el presente capítulo se estudia el papel de los conejos como ingenieros de ecosistemas en los pastizales mediterráneos del centro de la Península Ibérica. Se comparó la comunidad herbácea de los elementos creados por los conejos dentro de sus dominio vital (vivar, zona de influencia del vivar y letrinas) con la comunidad herbácea de parcelas de exclusión de conejos. Se estudiaron también las diferencias internas de cada elemento creado por los conejos en términos de composición de la comunidad y se cuantificó la contribución de los conejos a la diversidad Beta de estos pastizales. Los conejos propiciaron la existencia de diferentes comunidades herbáceas a través de varios mecanismos e incrementan la diversidad con respecto a las parcelas de exclusión. La composición de especies de cada elemento fue muy diferente a la de las parcelas de exclusión de conejos, y varias especies aparecieron claramente asociadas con distintas actividades de los conejos. Los vivares, letrinas y la zona de influencia del vivar mostraron diferencias internas con respecto a los parámetros de la vegetación herbácea. Los resultados de este estudio demuestran que todos los elementos dentro del dominio vital del conejo aumentaron significativamente la heterogeneidad en estos pastizales. Por lo tanto, los conejos pueden actuar como ingenieros de ecosistemas en los pastizales mediterráneos. Esto contrasta con los efectos potencialmente nocivos que pueden tener en lugares donde los conejos han sido introducidos, y resalta la importancia de distinguir entre los efectos de los ingenieros de ecosistemas dentro y fuera de sus lugares de origen.

Rabbit (*Oryctolagus cuniculus)* engineering effects on a Mediterranean plant community.

Gálvez Bravo, L.[1], López-Pintor, A.[2], Rebollo, S.[1] & Gómez-Sal, A.[1]

[1]Departamento de Ecología, Edificio de Ciencias, Universidad de Alcalá, E-28871 Alcalá de Henares. Madrid. Spain. Phone: +34 918856406; Fax: +34 918854929,

[2]Departamento de Ecología, Universidad Complutense. Facultad de Ciencias Biológicas, c/ José Antonio Novais 2, Ciudad Universitaria. 28040-Madrid, Spain.

E-mail: lucia.galvez@uah.es

Abstract

Mammalian herbivores can have dramatic effects on the vegetation through different mechanisms, including herbivory, trampling, scraping, dunging, burrowing, etc. Sometimes, these activities can modify resource distribution or create habitat for other species; and organisms that cause such changes are often classified as ecosystem engineers. The European rabbit (*Oryctolagus cuniculus*) is a semi-fossorial mammal native to the Iberian Peninsula and a keystone element in Mediterranean foodwebs. Rabbit activities usually take place around a central warren, but there is little information about their impacts on the herbaceous community within their home range. In this study, we explored the role of rabbits as ecosystem engineers on Mediterranean pastures in Central Spain. We compared the herbaceous community of elements created by rabbits within their home range (warrens, the warren influence area, and latrines) with the herbaceous community of rabbit exclusion plots. We studied the internal differences in community composition within each rabbit element and quantified the contribution of rabbits to Beta diversity in these pastures. Rabbits induced distinct herbaceous communities through several mechanisms, and increased diversity with respect to rabbit exclosures. Species composition in each rabbit element was very different from rabbit exclusion plots, and several species were clearly associated with rabbit activities. Warrens, latrines and the warren influence area also showed internal differences in herbaceous community parameters. Our results demonstrate that all elements within the rabbit home range, especially warrens, significantly increased heterogeneity in these pastures. Therefore, rabbits can act as allogenic ecosystem engineers in Mediterranean pastures. This is in contrast with the potentially detrimental effects of rabbits in places where they have been introduced, and highlights the importance of distinguishing between the effects of ecosystem engineers inside and outside their native range.

Keywords: burrowing mammals, Mediterranean pastures, diversity, floristic composition, latrines, warrens

1. Introduction

Mammalian herbivores can reach high densities and have dramatic effects on the vegetation (see Huntly 1995 and Crawley 1997 for reviews). Although most research has focused on effects through herbivory (mainly plant consumption and its consequences), some attention has also been given to non-trophic effects, which act through different mechanisms (e.g. foraging pits, trampling, scraping, dunging, foraging tunnels and burrows, etc.). These activities can modify resource distribution or create habitat for other species, and organisms that cause such changes are often classified as ecosystem engineers (Jones *et al.* 1994). Autogenic engineers change the environment through their own physical structures (e.g. corals), whilst allogenic engineers change the environment by transforming living or non-living materials from one physical state to another (e.g. beavers). Allogenic ecosystem engineers modulate the supply of certain resources for other species, for example by creating habitat patches where environmental conditions and resource availability are very different from the unmodified habitat (Jones *et al.* 1994, 1997). The relevance of patch creation has long been recognised (e.g. Paine 1969), since patches increase habitat heterogeneity and number of available niches, and therefore augment species diversity (e.g. Bazzaz 1975).

Some studies have looked at herbivore effects as allogenic ecosystem engineers, but they have often focused on physical aspects and effects on soil properties (see review in Gutierrez & Jones 2006). However burrowing herbivores may also influence vegetation to varying degrees, both spatially and temporally, and through several mechanisms (Whitford & Kay 1999). Patches with a different floristic community composition with respect to the surrounding matrix may be created, both through grazing and temporary disturbances such as pits and mounds (Gutterman 1997). Longer - term effects may be exerted via open burrow

systems, which are usually created by semi-fossorial mammals, i.e. those which use burrows mainly as refuge and breeding quarters, but feed on above-ground vegetation. These structures may be used for several generations, or even taken over by a different species. When abandoned, they may still remain as significant elements in the landscape, and continue serving as seed and litter traps (Whitford & Kay 1999). Burrow systems can also house a community of associated organisms (from microbes to insects, reptiles, birds, mammals...) that benefit from various advantages provided by burrows (protection, access to food and/or mates, a distinct microclimate, etc.), including "obligate commensals" (e.g. the gopher tortoise robber fly, see review by Eisenberg & Kinlaw 1999).

Although the ecosystem role of burrowing mammals such as pocket gophers and prairie dogs has been given some attention (e.g. Reichman & Seabloom 2002; Bangert & Slobodchikoff 2000, respectively), there are still many potential interactions between semi-fossorial herbivores and the vegetation that are yet to be discovered in different ecosystems around the world. This study aims to contribute to this knowledge by studying the effects of a burrowing ecosystem engineer on the herbaceous community within its home range.

European rabbits (*Oryctolagus cuniculus* L.) dig large, complex open burrow systems called warrens. Rabbits have been classified as allogenic ecosystem engineers, mainly because their burrows can be used as refuge by other species (Jones *et al.* 1994). Rabbits, however, may have ecosystem engineering effects through other mechanisms (herbivory, trampling, scraping, latrine generation, excavation, etc.). Rabbits are central place foragers, and a gradient of influence on the plant community surrounding their warrens was reported as early as 1917 by Farrow (1917). Effects on

vegetation composition, cover and standing crop were studied in the Pembrokeshire islands (Gillham 1955), and digging by rabbits has been shown to alter soil condition and affect erosion rates (Rutin 1992) and soil moisture (Gillham 1956).

The semi-arid grasslands of the Iberian Peninsula support a very high diversity of annual plants (Naveh & Whittaker 1980; Rey Benayas & Scheiner 2002), which have coexisted with rabbits since the Pleistocene (Corbet 1986). Existing research has been focused on the effects of rabbit herbivory on vegetation composition (Soriguer 1983; Petterson 2001) and architecture (Gómez-Sal *et al.* 1999); and some attention has been given to rabbit latrines. These are relatively small areas of faecal pellet accumulation that act as places of information exchange and territorial beacons (Cowan 1987a; Sneddon 1991). In the semi-arid southeastern Iberian Peninsula, rabbit latrines are important contributors to soil fertility (Willot *et al.* 2000) and may increase plant diversity and biomass (Petterson 2001).

Therefore, it is surprising that the influence of rabbit activities (e.g. warren building) on vegetation and soils has only been studied in Australia (Eldridge & Myers 2001; Eldridge & Simpson 2002; Eldridge *et al.* 2006; and Leigh *et al.* 1989), where they can have dramatic effects and are considered a pest. There are very few studies that investigate the relationship between rabbit activities and the plant community in the Mediterranean Basin, where rabbits originated (Monnerot *et al.* 1994), and where they play a crucial role as keystone prey (Delibes & Hiraldo 1981; Villafuerte *et al.* 1998).

This investigation aimed to explore the effects of allogenic ecosystem engineering by European rabbits on herbaceous communities within their native range. This was addressed by considering the effect of rabbit activities within their home range on a Mediterranean annual plant community, and comparing them with the community inside rabbit exclusion plots. Three main elements were identified inside rabbit home ranges: warrens, latrines and the influence area around each warren. We hypothesised that 1) overall, rabbit engineering activities will create distinct patches that promote heterogeneity in plant species composition and increase diversity in annual Mediterranean pastures with respect to pastures where rabbits have been excluded; 2) these effects would differ depending on the mechanisms promoting the internal patchiness of each element.

2. Materials and methods

Study area

The study was carried out in a 300 ha "dehesa" near Madrid, central Spain (40º 23´ N, 4º 12´ W). Mean altitude is 670 m and climate is Mediterranean-continental, with mean annual temperature and precipitation of 12ºC and 432.6 mm. Dehesas are savannah-like landscapes characterised by cleared holm oak woodlands with an annual grass understorey, and they usually support high rabbit densities (Blanco 1998). In the study area, the substrate is sandy, and lays upon fractured granite bedrock. The dominant tree species is *Quercus ilex* L. subsp. *rotundifolia* (Lam.). The main vertebrate herbivores are an abundant rabbit population (8.27 warrens/ha) and a herd of about 600 transhumant sheep. The area is still under traditional management practices, with periodic ploughing, mowing of the most productive grasslands, and small game hunting.

Sampling design

In order to study plant community changes induced by rabbit activities, a rabbit "home range" was considered as a roughly circular area of imprecise outer limits surrounding a warren, and containing the highest proportion of latrines. Ten of these home range units were selected for vegetation surveys, ensuring that the warrens were large (mean no. entrances/warren: 89.4±38.9; mean no. active entrances/warren: 38±20.5; total no. warrens in
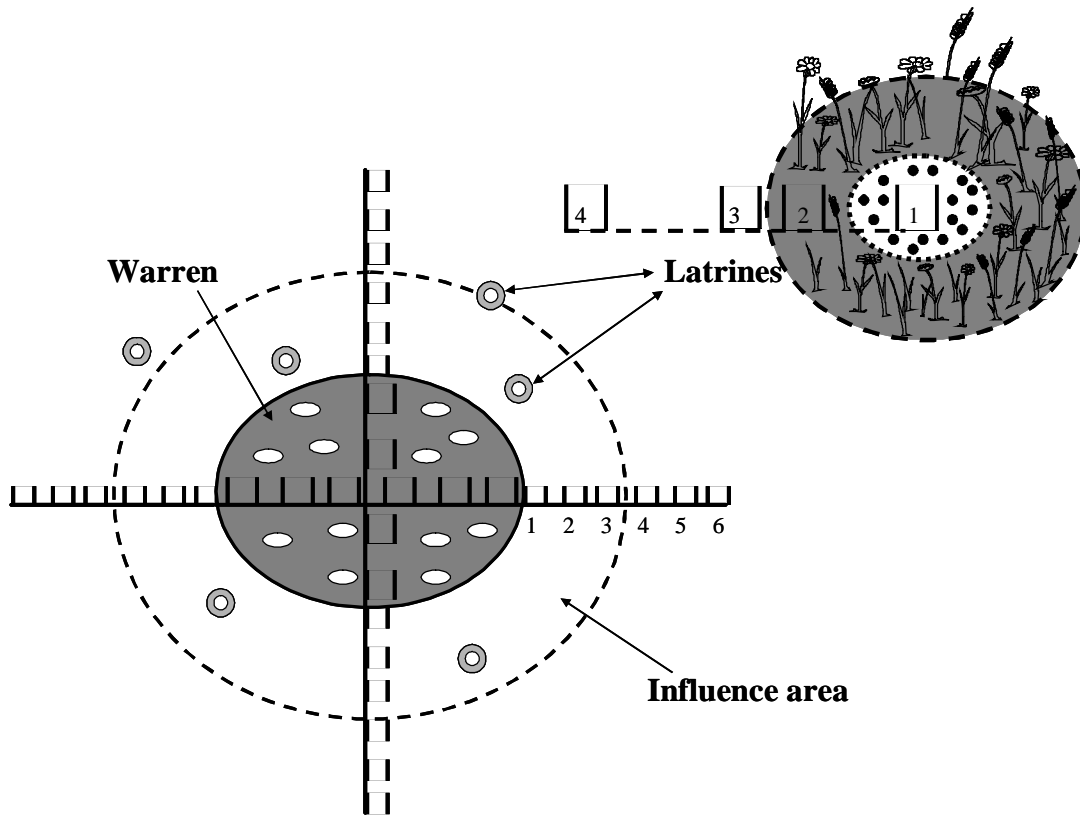
Figure 1. Sampling scheme for elements within the rabbit home range. Distance from the warren edge of quadrats on transects of the warren influence area: 1 = 0 m; 2 = 0.5 m; 3 = 1.5 m; 4 = 3.5 m; 5 = 7.5 m and 6 = 15.5 m. At latrines, quadrat number 4 was placed 1 m away from the central latrine area (quadrat 1).

the study area: 2415, mean size: 7.0 entrances/warren, range: 1-184 entrances/warren). Large warrens were chosen because rabbit numbers correlate strongly with number of entrances (Cowan 1987b; Palomares 2001), and a relatively high number of resident rabbits was desirable in order to observe their effects more easily. The vegetation was surveyed 1) inside the warren, 2) in the surrounding "influence area", 3) on latrines, 4) and at five rabbit exclusion plots, in the spring of 2002 and 2003. In all cases, individual species and total vegetation cover (canopy cover), mean and maximum vegetation height, and bare soil and litter cover were estimated at each sampling quadrat. Herbaceous species nomenclature follows (Tutin *et al.* 1964-1981).

1) Warrens: Inside the warren, two perpendicular transects were laid out, covering the entire extent of the warren (**Figure 1**). Along each transect, 50×50 cm quadrats were laid. Vegetation data were recorded in a minimum of 15 quadrats per warren (mean: 18.3±2.7 quadrats). In every quadrat, the percentage of the soil surface that was covered by different microtopographic structures was measured (called "structures" hereafter). These structures were identified as 1- entrances, 2- hollows, 3- scrapes, 4- mounds, and 5- flats. Entrances are the holes or burrows through which rabbits gain access into the warren. Hollows are relatively large concave areas, usually the result of the collapsing of flat areas between entrances due to excessive digging, or the "caving-in" of entrances. Scrapes are concave pits (usually not more than a few cm deep) produced by rab-

bits by scratching with their forepaws. Mounds are soil accumulations produced by rabbits when burrowing a new entrance. Flats are areas with no specific relief, interspersed among the other structures and forming the main "matrix" within the warren.

2) Warren influence area: Four transects were laid from the edge of each warren in order to observe differences in community parameters along the rabbits´ activity gradient (**Fig.1**). Six 25×25 cm quadrats were laid along each transect at increasing distances from the warren: 0, 0.5 m, 1.5 m, 3.5 m, 7.5 m and 15.5 m. Given the variation in warren size, maximum transect length was always maintained within 25 m from the warren centre to ensure data were recorded within the area where rabbit grazing intensity is greatest (Leigh *et al.* 1989). The total number of rabbit pellets in each quadrat was recorded in order to confirm the gradient of rabbit pressure, and as an overall indicator of rabbit activity throughout the year (Wood 1988; Palomares 2001). In the study area, rabbit pellets can persist between 12 and 20 months (Rueda 2006).

3) Latrines: A total of 48 latrines were selected in the vicinity of eight of the warrens surveyed. Vegetation data were collected in 10×10 cm quadrats following the scheme shown in Fig. 1. The outside quadrat was placed at approximately 1 m away from the external vegetation ring. Preliminary analyses of latrine data indicated that these quadrats were under the influence of latrine conditions (Gálvez *et al.* 2008).

4) Rabbit exclusion plots: Data from five 6 × 6 m rabbit exclusion plots set up in the study area in summer 2001 were included in the data analyses for comparison purposes. Exclosures were situated in locations with similar topography and vegetation to warren sites, and rabbits had been excluded for at least 9 months before data collection. Therefore, they were considered as comparable situations with no rabbit influence. Seven 25 × 25 cm quadrats were randomly distributed inside each plot for vegetation surveys.

Data analyses

Plant community parameters

*S*ix parameters were selected to characterise the herbaceous community: floristic composition, total vegetation cover, mean vegetation height, species richness, diversity H' (Shannon-Weaver diversity index, Shannon & Weaver 1949) and Pielou' s evenness index (Pielou 1966). Floristic composition was a synthetic variable obtained by applying a Non-Metric Multidimensional Scaling ordination (NMS) (Clarke 1993) to plant species data. The scores of the one-dimensional solution obtained were used as values representing the composition of each quadrat in further analyses. The distance matrix was calculated using the Sørensen (Bray-Curtis) index, more sensitive in heterogeneous data sets such as the one considered, and giving less weight to outliers than Euclidean distances (Roberts 1986).

To answer the essential questions in this study, a comparison of the herbaceous community of each element within the rabbit home range *versus* rabbit exclusion plots was required. Unfortunately, the size of sampling quadrats had to differ between elements, due to differences in size and soil surface heterogeneity within each element (**Appendix 1a**). For this reason, data from the smaller quadrats were added and scaled to the size of the largest quadrat (i.e. 50 × 50 cm quadrats used to sample warrens = 2500 cm^2). Total and individual species cover (cm^2) in each of the smaller quadrats were added up as appropriate (for example, data from the four quadrats of each position of the influence area were added: 4 x 625 cm^2 = 2500 cm^2), and community parameters were calculated using this new data matrix for general analyses. These data will be referred to as "summarised data" hereafter. ANCOVA tests, with quadrat size as a covariate, were performed to make sure that there was no influence of quadrat size on community parameters (Wilk´s Lambda = 0.779, $F_{6,23}$ = 1.085, p = 0.400, **Appendix 1b**).

Multivariate Analyses of Variance

Four Multivariate analyses of variance (MANOVAs) were computed. 1) Warrens, Influence area and Latrines vs. exclosures: to test differences in the herbaceous community between warrens, the warren influence area, latrines and rabbit exclusion plots (using the summarised data matrix). 2) Warren: tested differences between microtopographic structures inside warrens; 3) Influence area: analysed distance effects along transects in the influence area; and 4) Latrines: analysed distance effects along latrine transects. Only five parameters were considered for the warren MANOVA (2) since vegetation height data had not been recorded per structure.

Differences in rabbit use (pellet counts) between transect positions in the warren influence area were assessed using ANOVA. As each home range was considered a unit, mean values per warren were used, and warren identity was included as a block factor for all analyses. MANOVAs were followed up by simple ANOVAs and Tukey´s post hoc tests to explore the trends observed for each tested parameter individually. In all cases, normality of data and homogeneity of variances were tested and data transformed if necessary.

Indicator taxa

The presence of indicator taxa, both for general (Warrens, Influence area and Latrines vs. exclosures) and internal comparisons (Warren, Influence area and Latrines), was assessed using Indicator Species Analysis (*INDVAL*) (Dufrêne & Legendre 1997). This method takes into account whether a species is both abundant and faithful to a given group of quadrats. It produces an indicator value (*I*), which ranges from 0 (no indication) to 100 (perfect indication). Statistical significance was evaluated by means of Monte Carlo tests with 10000 permutations, which ensure precision for a-levels below 0.01 (Manly 1997). Only species with total cover above 5% were included in the analyses.

Therefore, 79 species were considered for warrens, 72 for the influence area, and 59 for latrines. In the analysis including all home range elements vs. exclusion plots, a total of 44 species were considered. In all cases, Holm´s correction for multiple hypotheses testing was applied (Holm 1979).

Beta diversity

The relevance of rabbit contributions to heterogeneity in species composition was evaluated by calculating Beta diversity. This was assessed as dissimilarity in community composition, using the Bray-Curtis coefficient (Bray & Curtis 1957). D values were calculated for the summarised home range data and rabbit exclusion plots, carrying out a subsequent T-test. Additionally, the dissimilarity between each rabbit element (warren, influence area and latrines), and rabbit exclosures was calculated, in order to test which rabbit element was introducing the most heterogeneity in Mediterranean pastures. Differences between these D values were analysed using ANOVA.

Statistical analyses were performed using PCORD 4.25 (McCune & Mefford. 1999); SPSS 13.0 (SPSS 13.0 2004) and R environment-2.2.1 (R Development Core Team 2005).

3. Results

1) Warrens, Influence area and Latrines *vs.* exclosures: The MANOVA revealed overall significant differences in herbaceous community parameters between warrens, the influence area, latrines and rabbit exclosures ($F_{12,22} = 5.990$, $p < 0.000$; block effect $F_{78,66} = 3.139$, $p < 0.000$). Subsequent ANOVAs and post hoc tests showed that the main differences were between rabbit elements and exclosures (**Table 1a** and **Table 2**). Rabbit exclosures had a different floristic composition to any of the rabbit elements, and were less diverse. Warrens were the most diverse rabbit element, with the tallest community, despite having lower vegetation cover than the warren influence area or

Table 1. a) ANOVA results for each community parameter included in MANOVA nº 1 (Warrens, Influence area and Latrines vs. exclosures). ´Floristic composition` refers to coordenates of the 1st axis of the NMS ordination (see Fig. 2a). S = species richness; E = Pielou´s Evenness; H´ = Shannon´s diversity index. * p = 0.05; ** = p = 0.01; *** = p = 0.001. b) ANOVA results for each community parameter included in the internal MANOVAs for each rabbit home range element: nº 2 (Warrens) nº3 (Warren Influence area) nº4 (Latrines). ´Floristic composition` refers to coordenates of the 1st axis of the NMS ordination in each case. S = species richness; E = Pielou´s Evenness; H´ = Shannon´s diversity index. * p = 0.05; ** = p = 0.01; *** = p = 0.001.* p = 0.05; ** = p = 0.01; *** = p = 0.001.

a)

	Df	Floristic Composition	S	E	H´	Veg. cover	Veg. Height
		F	F	F	F	F	F
1. Warrens, Influence area and Latrines vs. exclosures	3	31.27***	2.67[NS]	11.00***	11.88***	4.89*	26.23***

b)

	Df	Floristic composition	S	E	H´	Veg. cover	Veg. height
		F	F	F	F	F	F
2. Warren (Microtopographic structures)	4	1.30[NS]	36.22***	2.23[NS]	13.35***	10.99***	-
3. Warren Influence area	5	31.32***	2.28[NS]	0.99[NS]	1.14[NS]	1.25[NS]	7.27***
4. Latrines	3	0.91[NS]	21.19***	9.73***	24.12***	79.20***	15.0***

latrines (**Table 2**). Reinforcing the general trend observed for floristic composition (**Figure 2a**), Indicator Species Analysis showed that the central warren area is characterised by species such as *Carduus* sp., *Myosotis intermedia* and *Stellaria media*; the influence area by *Spergularia rubra*; latrines by *Vulpia myuros* and rabbit exclosures by *Ornithopus compressus* and *Leontodon longirrostris* (**Appendix 2a**).

2) Warren: There were significant differences in the herbaceous community of the different structures found within rabbit warrens (entrances, hollows, scrapes, mounds, and flats) (MANOVA: $F_{20,97} = 7.638$, p < 0.000; block effect: $F_{45,132} = 1.409$, p = 0.07). ANOVA results confirmed these differences for most community parameters (**Table 1b**). Flat areas were the predominant structure inside the warren (**Table 3**), and they had the highest species richness, diversity and vegetation cover. Despite their different nature, community parameters of concave structures such as hollows and scrapes were very similar to those of mounds, although mounds were significantly less vegetated (**Figure 3**). Although the ANOVA did not show differences in floristic composition between structures (**Table 1b**), the Indicator Species Analysis highlighted several taxa as indicators of hollows (*Carduus* sp., *Arenaria sepillyfolia*) and others as specific of flat areas (*Crepis capillaris*, *Spergularia rubra*) (**Appendix 2b**).

3) Warren influence area: Pellet counts confirmed a significant gradient of increasing rabbit use towards the warren (ANOVA: $F_{5,45} = 4.555$; p = 0.002, **Figure 4a**). There were overall differences in community parameters along this gradient (MANOVA: $F_{30,162} = 4.577$, p < 0.001; block effect: $F_{54,208} = 5.661$, p < 0.001). Both vegetation height and cover were slightly higher further away from the warren, although this trend was only significant for vegetation height. Floristic composition also varied along the transect positions of the warren influence area (**Table 1b**, **Figure 4b**). This variation is depicted in axis I of the NMS ordination in **Figure 2b**, where the arrow shows how floristic composition follows a parallel trend to rabbit use. Indicator Species values mainly discriminate between positions adjacent to the warren and

Table 2. Means ± S.D. for each community parameter at warrens, the influence area, latrines and rabbit exclosures. ´Floristic composition` refers to the coordenate of the 1st axis of the NMS ordination (see Fig. 2a). S = species richness; E = Pielou´s Evenness; H´ = Shannon´s diversity index. Different letters indicate statistically significant differences (p > 0.05), as revealed by Tukey´s post hoc tests.

	Warren	Influence area	Latrines	Rabbit exclosures
Floristic Composition	0.82±0.33**a**	0.15±0.25**b**	-0.11±0.33**b**	-1.75±0.15**c**
S	44.60±6.5**a**	42.90±2.64**a**	40.00±7.33**a**	25.20±2.28**a**
E	0.77±0.03**a**	0.75±0.04**a**	0.71±0.03**b**	0.73±0.099**b**
H´	2.93±0.04**a**	2.83±0.13**a**	2.61±0.24**b**	2.36±0.37**c**
Vegetation cover (%)	54.54±11.06**ab**	62.96±14.13**b**	59.48±6.07**b**	48.50±5.73**a**
Vegetation height (cm)	11.67±4.16**a**	3.99±2.03**b**	3.24±1.49**b**	3.50±1.51**b**

those furthest away. *Arenaria serpyllifolia* and *Carduus* sp., already identified as distinct "warren species", appear near the warren, whilst other species such as *Hypochoeris glabra* and *Trifolium arvense* are indicators of communities relatively far away from the warren (**Appendix 1b**).

4) Latrines: The herbaceous community was also significantly different along latrine transects (MANOVA: $F_{18,45}$ = 7.037, p < 0.001; block effect: $F_{42,78}$ = 1.875, p = 0.008). The central position of latrines was an area of pellet accumulation and hardly any vegetation (only a few species had a mean cover greater than 1% in this position). Vegetation height never exceeded 4cm due to constant mechanical disturbance by rabbits. In contrast, herbaceous vegetation in the surrounding vegetation ring was taller and significantly denser than at both the inside and outside positions of the latrine (**Table 1b**, **Figure 5**). Species such as *Vulpia ciliata* and *Andryala integrifolia* appear as indicators of the vegetation ring surrounding the latrine, and *Urtica urens* is an indicator of the central pellet accumulation area (**Appendix 1b**).

Beta diversity: Bray-Curtis dissimilarity (*D*) for summarised home range data and exclusion plots were 0.75±0.02 s.e. and 0.389±0.02 s.e. respectively, and these means were signifi-

cantly different (T-test = 9.826, p < 0.001). When elements within the rabbit home range were considered individually, ANOVA results revealed that warrens introduce the most heterogeneity in plant species composition (*D*: 0.82±0.2 s.e.) followed by the influence area (*D*: 0.73±0.26 s.e.) and latrines (*D*: 0.68±0.43 s.e.) (F = 13.973, p < 0.001).

4. Discussion

Our results show that rabbit engineering activities within their home range give rise to patches with an array of distinct herbaceous communities, different from rabbit exclusion plots. They promote floristic changes which in turn augment heterogeneity in herbaceous community composition and increase beta-diversity in the ecosystem. Rabbit activities are spatially segregated and, therefore, the predominant influence will be different in each element within their home range.

Internal differences in community parameters within each rabbit element

Inside the warren, locus of rabbit habitation and social interactions, there is a mosaic of different structures which have a complex spatial distribution and represent varying degrees and frequencies of pedturbation by rabbits (flats,
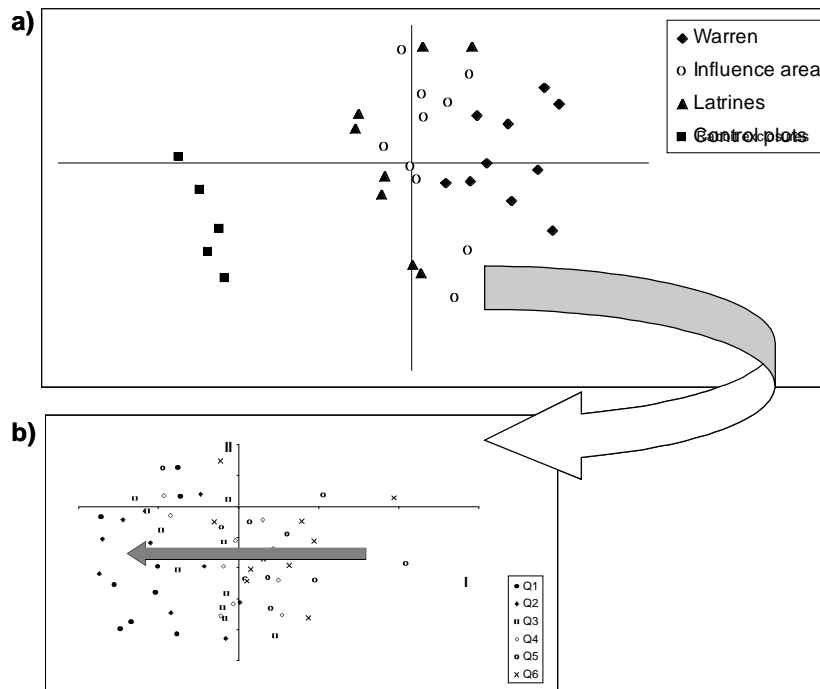
Figure 2. a) NMS ordination representing the floristic composition of summarised data for warrens, influence area, latrines and rabbit exclusion plots; ♦ = Warren; ○= Influence area; Δ = Latrines; ■ = Rabbit exclosures, b) NMS ordination representing floristic composition along the transect positions of the warren influence area. The arrow indicates the gradient captured by the first axis, which also reflects rabbit use measured as number of rabbit faecal pellets found in each quadrat. ●Q1 = position 1 (near the warren); ♦Q2 = position 2; ⊓ Q3 = position 3; ᴴQ4 = position 4; ○ Q5 = position 5; ✕Q6 = position 6 (furthest away from the warren).

scrapes, hollows, entrances and mounds). Excavating activities are mainly concentrated in this area of the home range, which cause alterations in edaphic properties with respect to adjacent control sites (Eldridge & Myers 2001). The spatial distribution of these effects promotes physical heterogeneity inside the warren (**Table 3**). Our results confirm that this disturbance, in addition to trampling, is probably the most important mechanism through which rabbits induce compositional changes within their home range, as Myers & Poole 1963) have already suggested.

Flats areas within the warren are characterised by a herbaceous community subjected mainly to trampling, and some urination, defecation and grazing. Several indicator species of flat areas are dispersed by rabbits in dung (e.g.

Sagina apetala, *Crepis capillaris* (Malo *et al.* 1995; Malo & Suarez 1995; see **Appendix 2b**). Others are characterised by their small size (e.g. *Crassula tillaea*), rosette or creeping growth forms (e.g. *Spergularia rubra*), and hairs

Table 3. Mean ± S.D. proportion and estimated mean surface area occupied by each microtopographic structure within warrens.

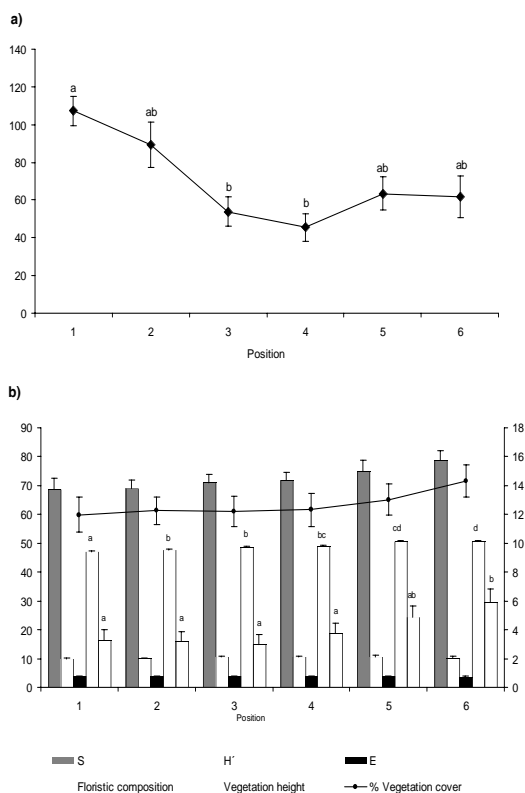|	Mean % cover per warren	Estimated mean total surface per warren (m^2)
Entrance	12.12 ± 2.19	35.81 ± 24.67
Hollow	3.22 ± 4.31	9.51 ± 6.55
Scrape	6.06 ±1.38	17.90 ± 12.33
Mound	4.29 ± 1.71	12.67 ± 8.74
Flat	73.88 ± 5.49	218.26 ± 150.44
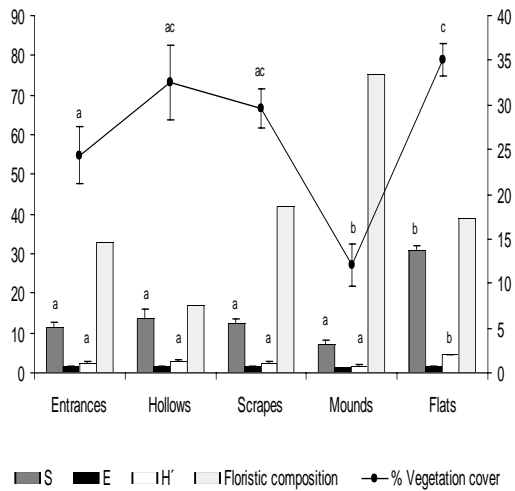
Figure 3. Differences in mean community parameters of each microtopographic structure within warrens. Mean % vegetation cover is represented on the left hand axis; floristic composition (transformed to aid graphic representation, NMS coordinate+10) and species richness (S); Shannon´s Diversity index (H´);and Pielou´s evenness index (E), are represented on the right hand axis. Error bars correspond to S.E of the mean. Significant differences between warren structures were investigated using Tukey´s post hoc test. Bars with equal letters are not significantly different (p > 0.05).

or other herbivore deterrents (e.g. *Andryala ragusina*, *Logfia minima*), all of them adaptations to herbivory avoidance/resistance and trampling (Lavorel *et al.* 1999; McIntyre *et al.* 1999). Scrapes and hollows are concave structures of different sizes and ages. They are analogous to pits and diggings produced by other animals that have been reported to be areas of moisture and nutrient accumulation (ibex diggings, Gutterman 1997; porcupine digs, Alkon 1999), as well as potential seed traps (Boeken *et al.* 1995). They represent excellent colonisation sites for plants that are benefited by such an accumulation of resources. This is the case of *Carduus* spp., a nitrophillous genus which stands out as an indicator of hollows within the warren and of the warren as a whole (**Appendix 2 a,b**). These processes would explain the relatively high vegetation cover of hollows and scrapes. Vegetation parameters in burrow entrances vary widely because they can
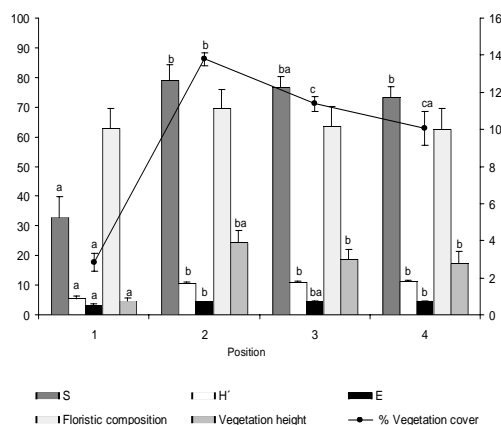
be active or inactive, and this condition changes throughout the year. Vegetation cover will vary with age and entrance activity, always remaining lower than in hollows and scrapes due to more frequent trampling and increased soil compaction. Mounds are the least vegetated structures because they are relatively young, originated from the accumulation of deep soil brought to the surface. They often smother former vegetation (only some creeping species can survive) and have a poor soil seed bank (Rebollo *et al.* 2003), which would account for the lowest values of vegetation cover and diversity.

The warren influence area receives the spill-off of intense rabbit activities inside the warren; but in this area herbivory and trampling are likely to have the strongest effects on the vegetation. These processes operate in a clear gradient from the warren edge outwards, in parallel with rabbit use (as shown by pellet counts). Along this gradient of rabbit activity, floristic composition changes are evident, but they are not coupled with remarkable changes in species richness, evenness or diversity. This suggests a replacement of species from the vicinity of warrens towards areas with relatively low rabbit activity, based on their functional traits and plasticity. Species with characteristics that enable them to cope with herbivory or disturbance tend to be less competitive in the absence of rabbit pressure, decreasing in abundance or disappearing as rabbit activity decreases (e.g. *Torilis arvensis*, *Arenaria serpyllifolia*). In contrast, species sensitive to rabbit pressure appear or increase in abundance in the community as this pressure diminishes (e.g. *Ornithopus compressus*, *Leontodon longirrostris*). Other species can change their growth form in response to herbivory, and therefore only their abundance is modified, not their presence. Indicator Species Analyses provide some examples, with *Carduus* sp., *Arenaria serpyllifolia* and V*ulpia ciliata* associated with the innermost position, in contact with the extremely disturbed and nitrophillous area of the warren; and

Tuberaria guttata, *Galium parisiense*, *Vulpia myuros*, *Hypochoeris glabra*, *Trifolium arvense* or *Logfia gallica* associated with the farthest positions. As expected in a community dominated by species adapted to herbivory, vegetation height followed an increasing trend as rabbit use decreases. Parallel to this trend, vegetation cover increased slightly from the warren outwards. This gradient of plant species substitution and changes in vegetation height and cover with distance from a warren or burrow has been observed for European rabbits in other regions

Figure 5. Differences in community parameters along the latrine transects (1 = central area, 2 = vegetation ring, 3 = just outside vegetation ring, 4 = 1 m away from vegetation ring). Floristic composition data have been transformed (NMS coordinate+10) to aid graphical representation. S = species richness; E = Pielou´s Evenness; H´ = Shannon´s diversity index. Means for all variables are represented on the left hand axis, except for Vegetation cover, which is represented on the right hand axis. Error bars correspond to S.E of the mean. Significant differences between transect positions were investigated using Tukey´s post hoc test. Bars with equal letters are not significantly different (p > 0.05).

of the world (e.g. United Kingdom, Gillham 1955; Chile, Holmgren *et al.* 2000; Australia, Eldridge & Myers 2001, Eldridge & Simpson 2002, and Eldridge *et al.* 2006), and other fossorial mammals (e.g. pikas, Huntly 1987; prairie dogs, Whicker & Detling 1998; vizcachas, Arias *et al.* 2003). This supports the idea of a niche creation role by rabbits, and the promotion of different "successional" stages by rabbit activities, already proposed by Gillham (1955) and Leigh *et al.* (1989).

Rabbits use latrines as territorial beacons and thus distribute them throughout the influence area around warrens. Latrines concentrate urine and faecal pellets, and a slight gradient effect can also be observed from the internal pellet accumulation area outwards, with highest vegetation height and cover in the surrounding vegetation ring, as well as slightly higher species richness. This high nutrient input may give some species a competitive advantage, especially nitrophillous species such as *Vulpia ciliata*

Figure 4. Effects of distance from warrens (warren influence area: 1 = near ; 6 = furthest away) on a) mean rabbit pellet abundance and b)community parameters (floristic composition data have been transformed (NMS coordinate + 50) to aid graphical presentation). Species richness (S); Shannon´s diversity index (H ´); Pielou´s Evenness (E), mean vegetation height (cm), and floristic composition are represented on the right hand axis; mean % vegetation cover is represented on the left hand axis. Significant differences between transect positions were investigated using Tukey´s post hoc test. Bars with equal letters are not significantly different (p > 0.05). Error bars correspond to S.E of the mean.

and *Veronica arvense*. This is in agreement with studies that have depicted rabbit latrines as important loci of nutrients (Willot *et al.* 2000), resulting in higher biomass and specific chemical and physical soil characteristics that alter the composition, density and biomass of the surrounding vegetation (Petterson 2001). In addition to nutrient enrichment, the central pellet accumulation area is affected by physical rabbit disturbance in the form of scrapes, which dramatically reduce vegetation cover. On average, scrapes covered up to 50% of the latrine surface area in this study, and only an extremely nitrophillous and resistant species, *Urtica urens*, was abundant enough to be considered an indicator of this area.

We have shown that rabbits can act as motors of change and diversity in dehesa pastures through different activities, either spatially concentrated or diffused in a gradient of intensity. But to what extent are these communities different from the surrounding vegetation? Answering this question in full would demand a comparison with similar pastures with a history of long-term rabbit absence, a situation difficult to find in the Iberian Peninsula given their historical coexistence with the vegetation. However, our results show that 9 months of rabbit activity exclusion are sufficient to observe significant changes in the herbaceous community, and these effects become stronger with time (unpublished data). Rabbits promote large differences in floristic composition within their home range, and diversity parameters were significantly higher inside the rabbit home range than in rabbit exclosures, being greatest inside the warren. In total, forty-two species found in elements within the rabbit home range were absent from rabbit exclusion plots, and only three were found exclusively in these plots (*Erophila verna*, *Diplotaxis tenuifloru*s and *Calendula arvensis*). In addition to this strong effect on floristic composition, all elements within the rabbit home range induced heterogeneity in species composition with respect to rabbit exclosures, and were important contributors to Beta diversity in this ecosystem. Moreover, vegetation cover is maintained, and a taller plant community is found inside warrens than in rabbit exclosures, thus promoting further heterogeneity in the physiognomy of the vegetation. The evidence presented from analyses of community parameters of the different microtopographic structures inside the warren explains the relatively high diversity, vegetation height and cover, and suggests that the patchy internal structure of warrens enhances heterogeneity at both the horizontal and vertical planes.

Evidence from the current study confirms that European rabbits act as allogenic ecosystem engineers for annual plants in this ecosystem, and suggests that they act mainly through patch creation. Rabbit activities promote both spatial (as explained above) and temporal heterogeneity in resources, since the various types of disturbances will change with time (e.g. scrapes fill up with soil, burrows collapse and give rise to hollows, latrine pellets degrade at different rates depending on productivity of the area and time of year, etc.). This heterogeneity in turn affects species coexistence and competitive interactions, and facilitates niches for plants which otherwise would not be able to establish. This is then translated into a more heterogeneous community, with higher alpha and beta diversity, as suggested by Tilman (1997).

Similar findings have been reported for other small burrowing mammals, species which are often in conflict with humans because they are considered "destructive" for crops and/or cattle pastures. However, within their native areas, burrowing mammals are often precursors of species diversity and heterogeneity: plateau zokors in the Himalayas increase diversity and often promote higher biomass around their dens (Zhang *et al.* 2003); different grazing intensities by vizcachas in Argentina did not reduce species richness (Branch *et al.* 1999); and diversity inside pika colonies in the Himalayas can actually be higher than at off-colony sites, whilst vegetation cover is maintained (Bagchi *et al.* 2006).

Contrary to other small mammals, rabbits have been transported out of their natural habitats, with dramatic consequences. Although similar results with regards to vegetation height and cover have been obtained in studies outside the Iberian Peninsula (e.g. Chile, Holmgren *et al.* 2000; and Australia, Eldridge & Simpson, 2002), the implications of species composition results are very different, since in these countries the local vegetation and soils may not be able to withstand rabbit activities and this may favour the establishment of "exotic" species that decrease the diversity of native communities. The exotic "weeds" associated with rabbit warrens in Australia, are common in Mediterranean pastures (eg. *C.melitensis*, *V.myuros*, *E.plantagineum*, *H.radicata*, Eldridge & Myers 2001, Eldridge *et al.* 2006).

This highlights the importance of distinguishing between the effects of ecosystem engineers in their native areas, and effects in those places where they have been introduced. In Australia, rabbits have coexisted with the vegetation for little over 80 years (Myers *et al.* 1994), so it is very unlikely that native plants could have adapted to rabbit activities. However, in areas where rabbits are not native, but have been established for centuries, for example the Pembrokeshire islands, Gillham (1955) reported the occurrence of species replacement in connection with rabbit warrens, but not necessarily a decrease in diversity; and species richness was occasionally higher in warrens. The results of this study support the idea that the detrimental effects of rabbits on plant diversity occur mainly in places where the plant community has not been given time to adapt to their influence.

Summarising, this study illustrates the significant contribution of an allogenic ecosystem engineer, the European rabbit, to niche creation; their ability to alter environmental conditions for plant species within their native Mediterranean ecosystems; and that their relevance for local biodiversity goes beyond their role as prey.

References

Alkon, P.U. (1999) Microhabitat to landscape impacts: crested porcupine digs in the Negev Desert highlands. Journal of Arid Environments 41: 183-202.

Arias, S.M., Madanes, N., & Quintana, R.D. (2003) Estructura y composición de la vegetación en vizcacheras activas e inactivas en el delta del Paraná. Mastozoología Neotropical 10: 9-20.

Bagchi, S., Namgail, T., & Ritchie, M.E. (2006) Small mammalian herbivores as mediators of plant community dynamics in the high altitude arid rangelands of Trans-Himalaya. Biological Conservation 127: 438-442.

Bangert, R.K. & Slobodchikoff (2000) The Gunnison´s prairie dog structures a high desert grassland landscape as a keystone engineer. Journal of Arid Environments 46: 357-369.

Bazzaz, F.A. (1975) Plant species diversity in old-field successional ecosystems in southern Illinois. Ecology 56(2): 485-488

Blanco, J.C. (1998) Mamíferos de España II Editorial Planeta, Barcelona.

Boeken, B., Shachak, M., Gutterman, Y., & Brand, S. (1995) Patchiness and disturbance: plant community responses to porcupine diggings in the central Negev. Ecography 18: 410 - 422.

Branch, L.C., Hierro, J.L., & Villareal, D. (1999) Patterns of plant species diversity following local extinctions of the plains vizcacha in semi-arid scrub. Journal of Arid Environments 41: 173-182.

Bray, J.R. & Curtis, J.T. (1957) An ordination of the upland forest of the southern Winsconsin. . Ecological Monographs 27: 325-349.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143.

Corbet, G.B. (1986) Relationships and origins of the European lagomorphs. Mammal Review 16: 105-110.

Cowan, D.P. (1987a) Aspects of the social organisation of the european wild rabbit (*Oryctolagus cuniculus*). Ethology 75: 197-210.

Cowan, D.P. (1987b) Group living in the European rabbit (Oryctolagus cuniculus): mutual benefit or resource localization? Journal of Animal Ecology 56: 779-795.

Crawley, M.J. (1997). Plant-herbivore dynamics. In Plant Ecology (ed M.J. Crawley), pp. 401-474. Blackwell Science, Oxford.

Delibes, M. & Hiraldo, F. (1981). The rabbit as prey in the Iberian Mediterranean ecosystem. In Proceedings of the World Lagomorph Conference, August 1979 (eds K. Myers & C.D. MacInnes), pp. 614-622. Guelph University Press, Guelph, Ontario.

Dufrêne, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345-366.

Eisenberg, J.F. & Kinlaw, A. (1999) Introduction to the Special Issue: ecological significance of open burrow systems. Journal of Arid Environments 1999: 123-125.

Eldridge, D.J., Costantinides, C., & Vine, A. (2006) Short-term vegetation and soil responses to mechanical destruction of rabbit (*Oryctolagus cuniculus* L.) warrens in an Australian Box woodland. Restoration Ecology 14: 50-59.

Eldridge, D.J. & Myers, C.A. (2001) The impact of warrens of the European rabbit (*Oryctolagus cuniculus* L..) on soil and ecological processes in a semi-arid Australian woodland. Journal of Arid Environments 47: 325-337.

Eldridge, D.J. & Simpson, R. (2002) Rabbit (Oryctolagus cuniculus L.) impacts on vegetation and soils, and implications for management of wooded rangelands. Basic and Applied Ecology 3: 19-29.

Gálvez, L., López-Pintor, A., De Miguel, J.M., Alonso, G., Rueda, M., Rebollo, S., & Gómez-Sal, A. (2008). Ecosystem engineering effects of European rabbits in a Mediterranean habitat. In Lagomorph Biology. Evolution, Ecology and Conservation (eds P.C. Alves, N. Ferrand & K. Hackländer), pp. 125-140. Springer-Verlag. Heidelberg-Berlin

Gillham, M.E. (1955) Ecology of the Pembrokeshire islands. III. The effects of grazing on the vegetation. Journal of Ecology 43: 172-206.

Gillham, M.E. (1955) Ecology of the Pembrokeshire islands. V. Manuring by the colonial seabirds and mammals, with a note on seed distribution by gulls. Journal of Ecology 44 (2): 429-454.

Gómez-Sal, A., Rey Benayas, J.M., López-Pintor, A., & Rebollo, S. (1999) Role of disturbance in maintaining a savanna-like pattern in Mediterranean *Retama sphaerocarpa* shrubland. Journal of Vegetation Science 10: 365-370.

Gutiérrez, J.L. & Jones, C.G. (2006) Physical ecosystem engineers as agents of biogeochemical heterogeneity. BioScience 56: 227-236.

Gutterman, Y. (1997) Ibex diggings in the Negev Desert Highlands of Israel as microhabitats for annual plants. Soil salinity, location and digging depth affecting variety and density of plant species. Journal of Arid Environments 37: 665-681.

Holm, S. (1979) A simple sequentially rejective multiple tests procedure. Scandinavian Journal of Statistics 6: 65-70.

Holmgren, M., Avilés, R., Sierralta, L., Segura, A.M., & Fuentes, E.R. (2000) Why have european herbs so succesfully invaded the Chilean matorral? Effects of herviory, soil nutrients and fire. Journal of Arid Environments 44: 197-211.

Huntly, N.J. (1987) Influence of refuging consumers (Pikas: Ochontona princeps) on subalpine meadow vegetation. Ecology 68: 274-283.

Huntly, N.J. (1995). How important are consumer species to ecosystem functioning? In Linking species and ecosystems (eds C.G. Jones & J.H. Lawton), pp. 72-83. Chapman and Hall, New York.

Jones, C.G., Lawton, J.H., & Shachak, M. (1994) Organisms as ecosystem engineers. Oikos 69: 373-386.

Jones, C.G., Lawton, J.H., & Shachak, M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78: 1946-1957.

Lavorel, S., McIntyre, S., & Grigulis, K. (1999) Plant response to disturbance in a Mediterranean grassland: How many functional groups? Journal of Vegetation Science 10: 661-672.

Leigh, J.H., Wood, D.H., Holgate, M.D., Slee, A., & Stanger, M.G. (1989) Effects of rabbits and kangaroo grazing on two semi-arid grassland communities in central-western New south Wales. Australian Journal of Botany 37: 375-96.

Malo, J.E., Jiménez, B., & Suarez, F. (1995) Seed bank build -up in small disturbances in a Mediterranean pasture: the contribution of endozoochorous dispersal by rabbits. Ecography 18: 73-82.

Malo, J.E. & Suarez, F. (1995) Establishment of pasture species on cattle dung: the role of endozoochorous seeds. Journal of Vegetation Science 6: 169-174.

Manly, B.F.J. (1997) A method for the estimation of parameters for natural stage-structured populations Researches on Population Ecology 39: 101-111.

McIntyre, S., Lavorel, S., Landsberg, J., & Forbes, T.D.A. (1999) Disturbance response in vegetation - towards a global perspective on functional traits. Journal of Vegetation Science 10: 621-630.

Monnerot, M., Vigne, J. D., Biju-Duval, C., Casane, D., Callou, C., Hardy, C., Mougel, F., Soriguer, R.C., Dennebouy, N., Mounolou, J:C., 1994. Rabbit and man: genetic and historic approach. Genetics Selection Evolution 26: 167-182.

Myers, K., Parer, I., Wood, D., & Cooke, B.D. (1994). The rabbit in Australia. In The European Rabbit. The history and biology of a successful colonizer (eds K. Thompson & C.M. King), pp. 108-157. Oxford University Press, Oxford.

Myers, K. & Poole, W.E. (1963) A study of the biology of the wild rabbit, Oryctolagus cuniculus (L.), in confined populations. IV.The effects of rabbit grazing on sown pastures. Journal of Ecology 51: 435-451.

Naveh, Z. & Whittaker, R.H. (1980) Structural and floristic diversity of shrublands and woodlands in northern Israel and other Mediterranean Areas Vegetatio 41: 171-190.

Palomares, F. (2001) Comparison of 3 methods to estimate rabbit abundance in a Mediterranean environment. Wildlife Society Bulletin 29: 578-585.

Petterson, D. (2001) The effects of the wild rabbit (Oryctolagus cuniculus) on soils and vegetation in semi-arid, south-eastern Spain. PhD Thesis. University of Leeds, Leeds.

Pielou, E.C. (1966) The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13: 131-144.

Rebollo, S., Pérez-Camacho, L., Valencia, J., & Gómez-Sal, A. (2003) Vole mound effects and disturbance rate in a mediterranean plant community under different grazing and irrigation regimes. Plant Ecology 169: 227-243.

Reichman, O.J. & Seabloom, E.W. (2002) The role of pocket gophers as subterranean ecosystem engineers. Trends in Ecology and Evolution 17: 44 - 49.

Rey Benayas, J.M. & Scheiner, S.M. (2002) Plant diversity, biogeography and environment in Iberia: Patterns and possible causal factors Journal of Vegetation Science 13: 245-258.

Roberts, D.W. (1986) Ordination and the basis of fuzzy set theory. Vegetatio 66: 123-131.

Rutin, J. (1992) Geomorphic activity of rabbits on a coastal sand dune, De Blink dunes, The Netherlands. Earth Surface Processes and Landforms 17: 85-94.

Rueda, M. (2006) Selección de hábitat por herbívoros de diferente tamaño y sus efectos sobre la vegetación. El papel del conejo (Oryctolagus cuniculus) en ecosistemas de dehesa. Tesis Doctoral. Universidad de Alcalá, Alcalá de Henares.

Shannon, C.E. & Weaver, W. (1949) The Mathematical Theory of Communication University of Illinois Press, Urbana, Illinois.

Sneddon, I.A. (1991) Latrine use by the european rabbit (Oryctolagus cuniculus). Journal of Mammalogy 72: 769-775.

Soriguer, R.C. (1983) Consideraciones sobre el efecto de los conejos y los grandes herbívoros en los pastizales de la Vera de Doñana. Doñana Acta Vertebrata 10: 155-168.

Tilman, D. (1997) Distinguishing between the effects of species diversity and species composition. Oikos 80(1): 185-185

Tutin, T.G., Heywood, V.H., Burguess, N.A., Moore, D.M., Valentine, D.H., Walters, S.M., & Webb, D.A. (1964-1981) Flora Europaea Cambridge University Press, Cambridge.

Villafuerte, R., Viñuela, J., & Blanco, J.C. (1998) Extensive predator persecution caused by population crash in a game species: the case of red kites and rabbits in Spain Biological Conservation 84: 181-188.

Whicker, A.D. & Detling, J.K. (1998) Ecological Consequences of Prairie Dog Disturbances. BioScience 38: 778-785.

Whitford, W.G. & Kay, F.R. (1999) Biopedturbation by mammals in deserts : a review. Journal of Arid Environments 41: 203-230.

Willot, S.J., Miller, A.J., Incoll, L.D., & Compton, S.G. (2000) The contribution of rabbits (Oryctolagus cuniculus L.) to soil fertility in semi-arid Spain. Biology, Fertility and Soils 31: 379-384.

Wood, D.H. (1988) Estimating Rabbit Density by Counting Dung Pellets. Australian Wildlife Research 15: 665-671.

Zhang, Y., Zhang, Z., & Liu, J. (2003) Burrowing rodents as ecosystem engineers: the ecology and management of plateau zokors Myospalax fontanierii in alpine meadow ecosystems on the Tibetan Plateau. Mammal Review 33: 284-294.

Appendix 1 (a and b)

a) Mean ± S.D. size of rabbit elements, soil surface characteristics and final sampling quadrat size chosen in each case.

	Mean size (m^2)	Soil surface characteristics	Quadrat size (cm)
Warren	295.40 ± 203.6	Heterogeneous	50 x 50
Influence area	2055 ± 487.7	Homogeneous	25 x 25
Latrines	0.26 ± 0.16	Heterogeneous	10 x 10
Rabbit exclosures	36 ± 0.0	Homogeneous	25 x 25

b) Results of ANCOVAs to test the influence of quadrat size on community parameters. Floristic composition` refers to coordenates of the 1st axis of the NMS ordination in each case. S = species richness; E = Pielou´s Evenness; H´ = Shannon´s diversity index.

	Df	*F*	p
Floristic composition	1	0.126	0.489
S	1	13.953	0.497
E	1	0.001	0.472
H´	1	0.009	0.660
% Vegetation cover	1	296.669	0.194
Vegetation height	1	12.008	0.202

Appendix 2a

Indicator values (*IV*) for species present in elements within the rabbit home range and rabbit exclusion plots. Figures in bold indicate significance after taking into account Holm´s correction for multiple hypothesis testing. All species are annuals. Families: B = Boraginaceae; C = Compositae; Ca = Caryophyllaceae; Cr = Cruciferae; G = Graminoids; L = Leguminosae; U = Urticaceae. * Hairs/thorns/spikes; **Creeping or rosette growth form; [H] Seeds dispersed in rabbit dung (Malo *et al.*1995, Malo & Suarez 1995); ■: Nitrophillous.

	Warren		Warren Influence Area		Latrines		Rabbit exclosures	
Species	*IV*	p	*IV*	p	*IV*	p	*IV*	p
Carduus spp. (C)*'■	**95.3**	**0.0001**	-	-	-	-	-	-
Stellaria media (Ca)*, **, [H]	**94.5**	**0.0001**	-	-	-	-	-	-
Myosotis intermedia (B)*	**79.7**	**0.0007**	-	-	-	-	-	-
Urtica urens (U)*'■	69.3	0.0039	-	-	-	-	-	-
Senecio jacobea (C)	46.1	0.0296	-	-	-	-	-	-
Andryala integrifolia (C)*	39.8	0.0503	-	-	-	-	-	-
Spergularia rubra (Ca)**	-	-	**42.8**	**0.001**	-	-	-	-
Sagina apetala (Ca)'[H]	-	-	43	0.014	-	-	-	-
Polycarpon tetraphyllum (Ca)[H]	-	-	50.5	0.030	-	-	-	-
Logfia minima (C)*	-	-	40.7	0.033	-	-	-	-
Herniaria hirsuta (Ca)*, **, [H]	-	-	49.7	0.044	-	-	-	-
Myosotis discolor (B)*,'[H]	-	-	44.7	0.047	-	-	-	-
Vulpia myuros (G)	-	-	-	-	46.4	0.0153	-	-
Poa bulbosa (G)	-	-	-	-	51.1	0.0416	-	-
Ornitopus compressus (L)	-	-	-	-	-	-	**89.1**	**0.0001**
Leontodon longirrostris (C)**	-	-	-	-	-	-	**78.9**	**0.0011**
Trifolium arvense (L)*	-	-	-	-	-	-	**75.7**	**0.0007**
Diplotaxis catholica (Cr)	-	-	-	-	-	-	60	0.0022
Hypochoeris glabra (C)**	-	-	-	-	-	-	53.2	0.002

Appendix 2b

Indicator values (*IV*) for species present in the microtopographic structures and gradients within each element.
Structure: microtopographic structure inside the warren for which the species is an indicator. Position: position along the transects of the warren influence area (1 = near the warren ; 6 = furthest away) and latrines (1 = central area, 2 = vegetation ring, 3 = just outside vegetation ring, 4 = 1 m away from vegetation ring) for which the species is an indicator. Figures in bold indicate significance after taking into account Holm´s correction for multiple hypothesis testing.
Families: B = Boraginaceae; C = Compositae; Ca = Caryophyllaceae; Ci = Cistaceae; Cr = Cruciferae; Cra = Crassulaceae; G = Graminoids; Ge = Geraniaceae; L = Leguminosae; Ro = Rosaceae; Ru = Rubiaceae; Sc = Scrophulariaceae; U = Urticaceae; Um = Umbelliferae. * Hairs/horns/spikes; **Creeping or rosette growth form; ■: Nitrophillous; [H]: Dispersed in rabbit dung (Malo *et al.*1995, Malo & Suarez 1995).

Species	Warren			Warren Influence area			Latrines
	Structure	*I V*	*p*	*Position*	*I V*	*p*	*Position*
Sagina apetala (Ca) [H]	Flat	**37.5**	**0.0002**	-	-	-	-
*Cerastium glutinosum** (Ca)	Flat	**33.1**	**0.0002**	-	-	-	-
Crepis capillaris (C)** [H]	Flat	**33.7**	**0.0003**	-	-	-	-
Vulpia bromoides (G)	Flat	**31.3**	**0.0002**	-	-	-	-
Vulpia membranacea (G)	Flat	27.6	0.0026	-	-	-	-
Mibora minima (G)	Flat	25.1	0.0008	-	-	-	-
Erodium cicutarium (Ge)**	Flat	24.3	0.003	-	-	-	-
Herniaria hirsuta (Ca)*,**, [H]	Flat	18.2	0.0035	-	-	-	-
Trifolium suffocatum (L)**, [H]	Flat	16.4	0.0145	-	-	-	-
Myosotis internedia (B)*	Flat	15	0.0405	-	-	-	-
Torilis arvensis (Um) ■	Hollow	7	0.0334	-	-	-	-
Carduus spp. (C) * ■	Hollow	32.4	0.0022	1	**22.5**	**0.0003**	-
Arenaria serpyllifolia (Ca)*	Hollow	**14.1**	**0.0007**	1	7.3	0.0412	-
Galium parisiense (Ru)**	Hollow	28.8	0.001	6	18.8	0.0136	-
Vulpia myuros (G)	Flat	28.2	0.0011	6	31.4	0.0244	2
Hypochoeris glabra (C)**	Flat	28.2	0.0004	6	21.8	0.0055	2
Vulpia ciliata (G)´[H] ■	Flat	21.6	0.0126	1	19.4	0.025	2
Tuberaria guttata (Ci)*[H]	Flat	10.7	0.0443	5	19.2	0.005	3
Logfia gallica (C)*	-	-	-	5	12	0.0476	4
Trifolium arvense (L)*	-	-	-	6	14.4	0.0236	-
Veronica arvense (Sc) [H] ■	Hollow	20.6	0.0017	-	-	-	2
Andryala integrifolia (C)*	Flat	**36.7**	**0.0003**	-	-	-	**2**
Aphanes microcarpa (Ro) [H]	Flat	19.4	0.046	-	-	-	2
Bisserula pelecinus (L)	Flat	16.1	0.0095	-	-	-	2
Crassula tillaea (Cra) [H]	Flat	**36.5**	**0.0002**	-	-	-	**3**
Spergularia rubra (Ca)**	Flat	**52**	**0.0001**	-	-	-	**3**
Logfia minima (C)*	Flat	**36.6**	**0.0002**	-	-	-	**4**
Urtica urens (U)*´■	-	-	-	-	-	-	1
Sedum caespitosum (Cra)	-	-	-	-	-	-	2