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Interactions between rabbits and dung beetles influence the establishment of *Erodium praecox*

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ABSTRACT

We examine the potential for two species – the wild rabbit *Oryctolagus cuniculus* and the dung beetle *Thorectes valencianus* – to affect the establishment of *Erodium praecox*, an endemic plant of the Iberian Peninsula. Rabbit latrines may be considered potential maternal parent areas of *E. praecox*. The spatial and temporal stability for nutrients and surface irregularities caused by the activity of rabbits increases bare soil areas. A negative relation between diameter of the basal rosettes of *Erodium* and the distance to the centroid of latrines was observed. Rabbit latrines were important for *E. praecox* distribution but their effect was higher when *T. valencianus* burrows exist. In laboratory conditions, a higher number of seeds buried was observed in latrines with dung beetles, while a lower number of seeds buried was observed in bare soil. *T. valencianus* activity plays the role of a soil fertilizer, increasing the rate of nutrient cycling and microbial activity which could raise the rate of decomposition of pellets and result in the further release of nutrients. The excavation of the dung beetles increases the soil fertilization and the surface irregularities required for the seeds of *E. praecox* to be easily self-buried.

1. Introduction

Spatial distributions and diversity of plant communities are affected by interactions among different agents such as herbivores, seed dispersers, and predators (Dale, 1999; Deveny and Fox, 2006; Herrera and Pellmyr, 2002). At fine scales, the distribution of plant individuals within a micro-landscape (areas of a few square meters) will reflect the role played by processes such as seed dispersal, germination facilities, and survival to reproductive age (Tomita et al., 2002; Yamasaki et al., 2002). Although these processes are not necessarily the consequence of trophic interactions, they are major determinants of the distribution and abundance of plant species.

In Mediterranean ecosystems, wild rabbits (*Oryctolagus cuniculus*) have the potential to control the diversity in plant communities by mechanisms such as herbivory, seed dispersal, and resource availability (mainly water and nutrients) (Malo and Suárez, 1996; Malo et al., 1995). Several empirical studies (Sumption and Flowerdew, 1985; Thomas, 1960; Watt, 1981) have shown that rabbit grazing in a plant community produces notable changes in its composition, structure, and diversity (see review by Olff and Ritchie, 1998). In general, rabbits inhibit tree regeneration, favouring a mosaic of shrubland, grassland and small woodland patches, which corresponds with a landscape of high diversity and endemicity in Mediterranean ecosystems (Verdú et al., 2000). As endozoochorous seed dispersers, rabbits spread a considerable number of seeds from diverse types of plants over a wide area (Calviño-Cancela, 2002; Malo and Suárez, 1996; Malo et al., 1995; Pakeman et al., 1999; Zedler and Black, 1992). Moreover, rabbit latrines promote the creation of patches with a high concentration of nutrients (N, P and organic C), which contribute to local soil fertility and are relevant to establishing and maintaining plant cover and productivity (Willot et al., 2000). Since wild rabbits have a large impact on landscape structure (Delibes-Mateos et al., 2008; Lees and Bell, 2008), it is expected that they induce temporal and spatial patterns of disturbance that in turn may influence the establishment and micro-distribution of some coevolved plant species. This effect occurs especially in the original ancestral area from which this species successfully colonized all the World regions (Flux and Fullagar, 1992): the Iberian Peninsula.

Dung beetles play an important role in ecological processes, including dung recycling processes that contribute to topsoil fertilization and aeration (Brussaard and Hijdra, 1986; Mittal, 1993). In Mediterranean semi-arid ecosystems, the dung beetle community associated with rabbit dung heaps is complex and diverse in spite of the existence of adverse factors such as the low water and

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nutritional content of rabbit dung and environmental aridity (Verdú and Galante, 2002, 2004). Soil properties in semi-arid conditions are characterised by low concentrations of essential plant macronutrients (Puigdefábregas et al., 1996). Because of this, rabbit latrines may be considered "fertile islands" (Garner and Steinberger, 1989) that enhance plant growth (Willot et al., 2000). Dung beetles (*Thorectes* spp. *sensu lato*; see Martín-Piera and López-Colón, 2000; Verdú and Galante, 2004) contribute to soil fertility by decomposing and burying a high number of rabbit pellets. Dung beetles also have a role as secondary seed dispersers; they can bury faeces in the soil with seeds inside, thereby favouring the establishment of seedlings (Andresen, 2002; Sheperd and Chapman, 1998; Vander Wall and Longland, 2004; Vulinec, 2000).

Erodium praecox is nitrophilous (Ernst, 1983) and endemic to the Iberian Peninsula. Based on several field observations and literature (Guittonneau, 1972), it has been hypothesized that the establishment of *E. praecox* may be related to the concentration of nutrients from rabbit dung heap depositions (latrines). However, as the seeds of this plant species have hygroscopic self-burying dispersal mechanisms (Stamp, 1984, 1989), the possible relationship between *E. praecox* and dung beetle activities has never been suspected. In this paper, we report a study investigating the influence of rabbit latrines both on the spatial micro-distribution and on the establishment of *Erodium* plants, also examining the role played by the action of dung beetles on this facilitation process. We firstly examine the micro-distribution and degree of association between rabbit dung heaps and *Erodium* plants in a semi-arid Iberian environment, by analyzing the relationship between the diameter of *Erodium* plants (as a surrogate of plant growth) and the distance to latrines (as a variable positively related with the concentration of nutrients). Subsequently, the links between rabbit faeces and dung beetles on the burial of *Erodium* seeds were studied under laboratory conditions in order to assess, for the first time, the potential influence of dung beetle activities on the burying activity of this plant species.

2. Methods

2.1. Study area and sample design

The study was carried out in "Sierra de la Carrasqueta" Alicante Province, Spain (38°37′N–0°30′W) at 1100 m a.s.l. The climate is Mediterranean with a period of drought and high temperatures in summer. Precipitation ranges from 400 to 800 mm per annum with a strong rainfall peak in October. Vegetation types are (a) woodland, characterised by the Spanish holm-oak (*Quercus rotundifolia*); (b) shrubland (*Cistus albidus*, *Thymus vulgaris*, *Erinacea anthyllis*) resulting from fires, grazing by sheep, and small wild herbivores (such as rabbits); and (c) patches of grassland (*Stipa offneri*, *Brachypodium retusum*, *Brachypodium distachyon*, *Arrhenatherum album*, *Avenula bromoides*).

We selected two 60 × 60 m plots (local scale) within a landscape mosaic which alternates between grassland, shrubland, and woodland patches. In each of these plots, we marked, numbered, and geo-positioned all the available rabbit latrines that have a diameter higher than 30 cm and the presence of dung pellets of different ages with a conspicuous and recent pellet layer. To explore the micro-distribution and the possible spatial association between *E. praecox* and rabbit pellets, four rabbit latrines (L1–L4) were randomly selected among the plots with the formerly mentioned characteristics. In each latrine, a plot of 2 m × 2 m divided in 100 squares of 0.2 × 0.2 m (sampling units) was selected at random (fine-scale). The number of *E. praecox* plants (flowering or not) and the number of rabbit dung pellets were counted in each sampling unit. The study was conducted from April to June in 2004 and 2005, and from September to November in 2008.

2.2. Spatial analysis

We used Spatial Analysis by Distance Indices (SADIE; see Perry, 1995, 1998; Perry et al., 1999) to examine the spatial patterns of rabbit dung pellets and *Erodium* plants. After counting the number of dung pellets and plants in each sampling unit, we calculated (D) the minimum value of the total distance that the individuals would have to move in order to occupy a single sample unit (distance to crowding) or the total distance necessary to achieve the same number of individuals in each sample unit (distance to regularity). Permutations of the observed counts between sample units allow the calculation of the proportion of randomized samples with D values higher than observed one as well as the aggregation index I_a. An aggregated variable has an $I_a > 1$ (if $P < 0.05$), a spatially random variable has an $I_a = 1$, while a regularly distributed variable has an $I_a < 1$. We also used J_a as a supplementary index based on the distance of crowding. J_a detects aggregation of a single cluster more powerfully than I_a (Perry, 1995). As with I_a, values of $J_a > 1$ (if $P < 0.05$) indicate aggregation, $J_a = 1$ indicates randomized count data, and $J_a < 1$ (if $P < 0.05$) indicates a regular sample. The SADIE approach can also be used to find patches and gaps by means of the clustering index (ν). Sample units within patches have large values of ν (ν_i greater than 1.5) while units located within gaps have large but negative values of ν (ν_j below -1.5) (Perry et al., 1999). We used I_a and J_a as global descriptor statistics of the spatial structure (such as aggregation) because of the existence of a close correlation between the average ν_i, average $|\nu_j|$, and I_a (Xu and Madden, 2003). In our study, we use local ν_i and $|\nu_j|$ values calculated for each sample unit in order to represent the spatial configuration of patches and gaps. To test for associations between rabbit dung pellets and *Erodium* plants, we measured the overall spatial association (X) obtained from the measures of local association (χ_k). Results of ν and χ_k were mapped using interpolation techniques (kriging) implemented in the package MF-works 3.0 (Keygan Systems) for a more clear illustration of the obtained spatial patterns.

2.3. Rabbit latrines as fertile islands

We hypothesized that the concentration of nutrients due to rabbit dung heap depositions should be a key factor in explaining the growth of *Erodium* seedlings. Thus, we predicted a negative relationship between plant growth and distance from the centre of the latrine. To test this hypothesis, we randomly select five latrines within local scale plots and measured both the stem diameter of all *Erodium* plants (a surrogate of plant growth) found at a distance of 2 m from the latrine centre and the minimum distance of each plant from the centre of the latrine (a surrogate of the concentration of nutrients). In total, the data of 77 *Erodium* plants were analyzed by calculating Spearman's rank correlation coefficient values and polynomial regression analyses using the Statistica software package (StatSoft Inc., 1997).

2.4. Dung beetles as facilitators of seed burial

In order to test whether soil disturbance promoted by dung beetles altered the burial of *Erodium* seeds, we undertook a laboratory assay consisting of three treatments: a) latrines with *Thorectes*, b) latrines without *Thorectes*, and c) bare soil. Each treatment was replicated four times. Plastic containers (30 cm in diameter and 40 cm in height) were used for each treatment. In each one of the twelve containers, 7000 cm^3 of soil obtained from sampling site was introduced and slightly squashed with the hands so the soil in all containers was similar. Artificial latrines consisted in 250 cm^3 of rabbit pellets disposed in the centre of the arena. For 'latrines with