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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 (v). Sample units within patches have large values of v (v_i greater than 1.5) while units located within gaps have large but negative values of v (v_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 v_i, average $|v_j|$, and I_a (Xu and Madden, 2003). In our study, we use local v_i and $|v_j|$ 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 v 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

Thorectes' treatment, we placed three individuals of the *Thorectes* species that inhabits the study region (*Thorectes valencianus* Baraud) in the containers. Finally, in each container we evenly distributed 20 seeds of *E. praecox* separated by intervals of approximately 3 cm. As *Erodium* seeds have a hygroscopic behaviour, we simulated a total of eight wet/dry cycles. The duration of each cycle was 48 h. For each cycle, we counted the number of buried seeds. We consider a seed to be buried when the mericarp was buried. All containers were kept in a climatic chamber maintained at 25:20 °C (L:D), 70:85% RH (L:D), and a photoperiod of 15:9 (L:D). A non-parametric Kruskal–Wallis test with the Conover–Inman *post hoc* test for pair-wise comparisons was performed to estimate the statistical significance of treatment differences using StatsDirect software v.2.5.7 (StatsDirect Ltd., 2005).

3. Results

3.1. Spatial patterns and relationship between variables

The distributions of *E. praecox* individuals and rabbit dung heaps were highly aggregated in all latrines (Table 1). Spatial representations of the clustering index (v) show that the existence of patch clusters in rabbit dung heaps is partially associated with the centres of the respective *Erodium* patches (Fig. 1). The overall spatial association between *E. praecox* and dung heaps was positive and statistically significant in the four latrines ($X_{L1} = 0.51$, $P < 0.001$; $X_{L2} = 0.66$, $P < 0.001$; $X_{L3} = 0.49$, $P < 0.01$; $X_{L4} = 0.61$, $P < 0.001$). Local association analysis showed the sites with significant spatial association between rabbit dung heaps and *Erodium* plants (Fig. 1), highlighting the existence of a notable correspondence between significant positive clusters (with spatial association) and the centre of each latrine.

3.2. Rabbit latrines and the Erodium plants

The stem diameter of *Erodium* plants was negatively and significantly correlated with the distance to the centre of the rabbit latrines ($r = -0.68$, $P < 0.0001$). A polynomial regression shows that a quadratic function of the distance to the centre of the rabbit latrines accounts for 71% of plant size: *Erodium* diameter $= 59.22 - 1.10 \times$ distance $+ 0.01 \times$ distance^2 (b0: $t = 16.52$, $P < 0.0001$; b1: $t = -10.61$, $P < 0.0001$; b2: $t = 8.53$, $P < 0.0001$) (see Fig. 2).

3.3. Dung beetles as facilitators

Laboratory assays showed a clear and positive effect of dung beetle activity on the number of *Erodium* seeds buried (Fig. 3). The higher number of seeds buried was observed in the treatment in which dung beetles manage rabbit dung pellets (95% of seeds). However, an important number of seeds were also buried in latrines without dung beetles (50%). Surprisingly, in bare soil treatment, the final number of buried seeds was very low (12%). K–W test ($T = 10.05$, $P = 0.006$) and multiple comparisons showed significant differences among all treatments. Interestingly, the rate of buried seeds is especially quick during the first three wet/dry cycles when dung beetles are present (Fig. 3).

Table 1
Values for aggregation index (I_a), crowding index (J_a) and clustering indices (v_i and v_j) from SADIE analysis. For all discrete variables, the total number of counts is indicated (n).

	Latrine	I_a	J_a	$\|v_j\|$	v_i	n
E. praecox	L1	2.722*	1.168*	2.727*	2.442*	186
	L2	2.484*	1.120*	2.461*	2.089*	195
	L3	2.023*	1.455*	1.872*	2.241*	118
	L4	1.911*	1.438*	1.920*	1.809*	43
Rabbit pellets	L1	2.584*	1.225*	2.479*	2.139*	3362
	L2	2.308*	1.492*	2.062*	1.910*	2744
	L3	1.922*	1.610*	1.753*	1.724*	2623
	L4	1.825*	1.791*	1.695*	1.754*	1502

*$P < 0.001$.

4. Discussion

Facilitation occurs when one organism makes the local environment more favourable for another either directly or indirectly (Brooker et al., 2008; Bruno et al., 2003; Lortie, 2007). In arid and semi-arid environments of the Iberian Peninsula, Willot et al. (2000) clearly demonstrated that rabbit latrines generate significant but localised fertile soil patches; rabbit faecal pellets highly increase the concentrations of organic C, N, P and K as well as plant biomass when compared against control plots (Delibes-Mateos et al., 2008; Willot et al., 2000). Thus, rabbit latrines could be considered "islands of fertility" able to facilitate the development and colonization of some plant species. Furthermore, in the extreme conditions of semi-arid regions, vegetation with a high degree of patchiness is frequently seen (e.g. Armas and Pugnaire, 2005), and the heterogeneity generated by a species improves the environmental conditions for another species (Webster and Maestre, 2004). In our case, the micro-spatial heterogeneity due to the soil irregularities, which are caused by the aggregation of dung pellets, was sufficient to facilitate the burrowing of approximately 50% of *Erodium* seeds (see Fig. 3). However, our results also suggest that a positive interaction or facilitation process exists between a "nurse species" (the rabbit), which ameliorates the microhabitat conditions for the growing and reproduction of *Erodium* plants. Identifying the true causal process behind this increase in plant size would require additional research; the increase in fertility around rabbit latrines can reduce plant competition for soil nutrients or simply decrease the growth of plants without influencing their capacity to produce viable descendents.

Many *Erodium* species show aggregated spatial patterns (Angel and Wicklow, 1974; Coomes et al., 2002; Ernst, 1983; Stamp, 1984, 1989) as a consequence of soil characteristics (nutrients, surface irregularity, soil compacting and granulometry), but also due to their particular reproductive biology (Stamp, 1984, 1989) and the lack of relevance of both endozoochory and exozoochory seed dispersal strategies (Malo and Suárez, 1996). Although some species of *Erodium* have a relatively high capacity for colonization (Stamp, 1984; Young et al., 1981), such long distance dispersal may offer little advantage in semi-arid (Mediterranean) environments because, in general, suitable germination sites are generally more likely close to the maternal parent area. The patchiness of *Erodium* plants can be related both to its low seed dispersal capacity and the spatial aggregation of fertility conditions generated by rabbit latrines (Willot et al., 2000), as occurs among ant nests and *Erodium texanum* (see Whitford, 1988). In our case, this association was assessed at a fine-scale of only few meters but it would be more firmly established if the distribution of *Erodium* at wider scales also manifests a relationship with rabbit latrines. Provisional results on 60×60 m plots support the spatial patterns detected in our microscale study (Verdú, J.R., unpublished).

However, the most interesting and innovative result is that the joint influence of rabbits and the associated dung beetle fauna operate synergistically, jointly increasing the opportunities for the development of *Erodium* species. Rabbit latrines may be considered as potential maternal parent areas for this plant species due to the high spatial and temporal stability of rabbit latrines (Gibb, 1993). In this scenario, the role played by *Thorectes* dung beetle species

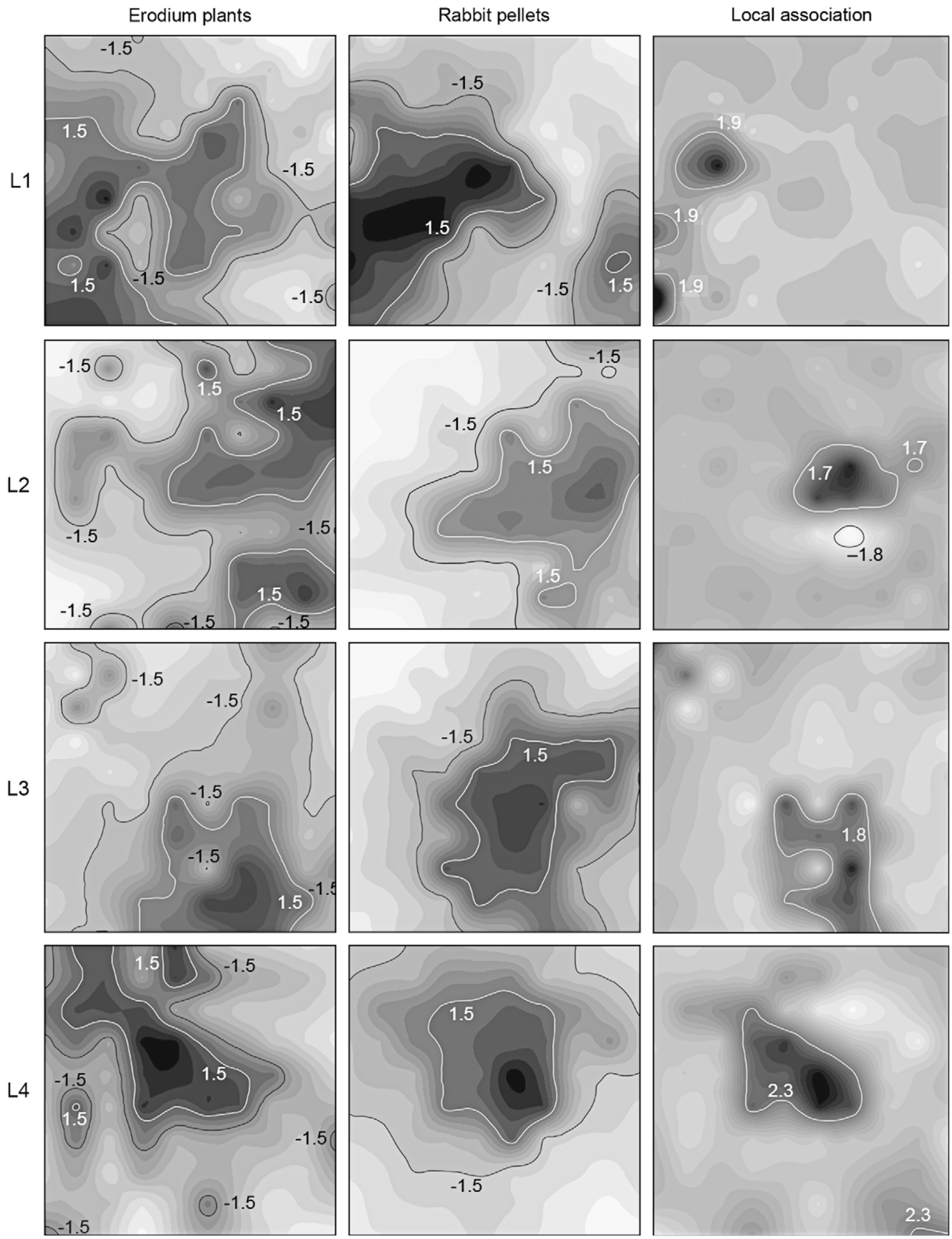

Fig. 1. Spatial representations of the clustering index for the number of rabbit dung heaps and *Erodium* individuals, and local association between them. Dark tones correspond to higher values. For clustering index maps, white isolines are contours enclosing patches of $v_i > 1.5$; and black isolines are contours enclosing gaps of $v_j < -1.5$. Contours were interpolated between sample units. Areas within white contours indicate significant patch clustering. By contrast, areas within black contours indicate significant gap clustering. For local association analysis, numbers indicate significant local association (positive values corresponding to the upper 95th percentile) and significant dissociation (negative values corresponding to the lower 5th percentile critical value). L1 through L4 are each of the studied 2×2 m plots in which there is a rabbit latrine.

seems to be crucial for the establishment of *Erodium* plants. Our results show that the latrines of the European rabbit affect *E. praecox* establishment but that their effect was higher when *T. valencianus* burrows exist.

Few data are available on the role of dung beetles associated with rabbit dung under Mediterranean conditions (Verdú and Galante, 2004). We suggest that *T. valencianus* play an important role as a facilitator by increasing the rate of nutrient cycling, soil

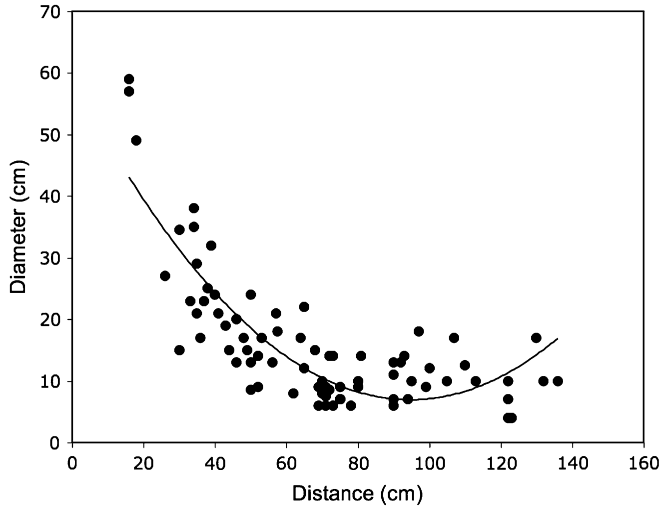

Fig. 2. Variation in the diameter of *E. praecox* basal rosettes (a surrogate of plant biomass) according to the distance against the centre of rabbit latrines.

fertilization, microbial activity, and soil aeration, which also occurs in other dung beetle species (Brussaard and Hijdra, 1986; Mittal, 1993; Nealis, 1977). In the study area, the burrows of *T. valencianus* increased nutrient availability in the soil due to the direct burial of rabbit pellets (e.g. we have counted a total of 80–125 rabbit pellets buried per pair of breeding beetles). In addition, *T. valencianus* increases the formation of small and low compacted bare soil areas (10–15 cm of diameter; personal observation). Thus, both physical (e.g. increasing surface irregularities and water infiltration but decreasing soil compaction) and soil chemistry changes (e.g. soil fertilization) can generate microsites capable of favouring the burrowing and germination of seeds of those *Erodium* species. Further studies are needed to estimate the possible role of the activity of this dung beetle species on other plant species as those of the genera *Poa*, *Festuca*, *Dactylis*, and *Trifolium*, as well as its potentially beneficial role for other insect species that are indirectly favoured by the increase in plant resources. Even if facilitation is not the consequence of a direct interaction with the plant, our results

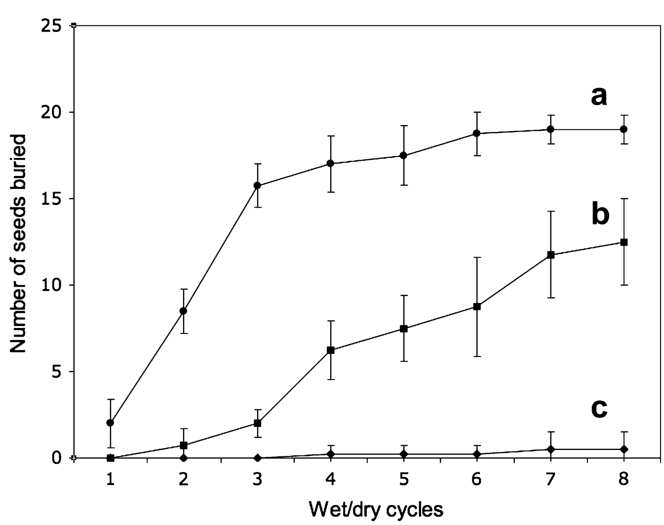

Fig. 3. Number of seeds (±SE) of *E. praecox* buried during eight wet/dry cycles in three different laboratory treatments: a) latrines with *Thorectes* (three individuals), b) latrines without *Thorectes*, and c) bare soil. Each treatment was replicated four times by placing 20 seeds of *Erodium praecox* at regularly separated intervals of approximately around 3 cm.

clearly show that the activity of *T. valencianus* has an indirect positive effect on the establishment and growth of a plant species. As with other ecological processes in which dung beetles are involved, this facilitation mechanism reflected that animals of this kind may also have an important role in the ecosystem functioning of arid environments (Nichols et al., 2007).

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