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LONG-TERM EFFECTS OF UNGULATES ON PERFORMANCE, ABUNDANCE, AND SPATIAL DISTRIBUTION OF TWO MONTANE HERBS

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Abstract. Herbivores highly reduce the performance of many plant species. However, little empirical information exists on the real effect that these organisms have on plant populations. With a long-term (seven-year) ungulate exclusion experiment in two areas of southeastern Spain, I demonstrated that these organisms can affect not only individual performance, but also the population dynamics and spatial structure of two short-lived monocarpic herbs, *Erysimum mediohispanicum* and *E. baeticum*. There was between-year and among-microhabitat variability in damage, with plants growing under shrubs being less damaged than those growing in open sites. Ungulates consumed flowers and fruits, severely decreasing plant reproductive output. The postdispersal seed predation rate increased after ungulates were excluded, presumably as a consequence of the relaxation of competition between seed predators and ungulates. The effect of ungulates on *Erysimum* early establishment was nonsignificant, although >50% of *Erysimum* seedlings died due to ungulate trampling. The exclusion experiment also revealed that, as a consequence of their impact on seed production, ungulates affected the population dynamics of their host plants; their removal produced a significant increase in the abundance of the two studied plant species. Furthermore, habitat distribution of plants was also influenced by the activity of ungulates. In control plots, most *Erysimum* individuals grew under the canopy of co-occurring shrubs. In contrast, a dramatic spatial redistribution of plants occurred in ungulate-excluded plots, where they started to colonize open sites. Consequently, the spatial structure of the plants excluded from ungulates significantly differed from that in control plots and became statistically similar to the structure expected according to the cover of every microhabitat. Finally, this experiment revealed that, for plants inhabiting heterogeneous landscapes, abundance and spatial structure are tightly related. Thus, I found that abundance increased in ungulate-excluded plots due not to a general and homogeneous increase, but to a significant increase in those microhabitats inaccessible to ungulates in control plots. These findings suggest that herbivory effects on plants are intricate, affecting not only their performance or population dynamics, but also their habitat distribution and niche structure.

Key words: Cruciferae; effect of microhabitat; Erysimum baeticum; Erysimum mediohispanicum; *habitat distribution; mammal herbivory; Mediterranean mountains; plant population dynamics; postdispersal seed predation; seedling survival; short-lived perennial herbs; spatial structure of plant populations.*

INTRODUCTION

The relationship between plants and herbivores is probably the most ubiquitous and relevant ecological interaction in terrestrial systems. Thus it is not strange that it has been given profound attention from ecologists working in diverse and disparate ecosystems (Crawley 1983, 1997, Marquis 1992, Zamora et al. 1999). It has been shown repeatedly that the performance (growth, reproductive output, and survival) of many plant species is negatively affected by the impact of vertebrate and invertebrate herbivores (Crawley 1983, 1992, 1997, 2000, Louda 1989, Marquis 1992, Guretzky and Louda 1997). This detrimental effect of herbivory is evident, irrespective of plant life history: significant negative effects on plant performance have been reported for a diverse array of plants including annuals, perennial herbs, shrubs, and trees (Marquis 1992, Crawley 1997, Zamora et al. 1999). Nevertheless, the existing information demonstrates that the severity of herbivore impact depends on several extrinsic and intrinsic factors, such as the availability of resources for the plants, plant age, plant compensation ability, the type of herbivores, or the kind of plant tissue consumed by the herbivores (Lehtilä and Strauss 1999, Mothershead and Marquis 2000, Gómez and Zamora 2000*a*, *b*, Hawkes and Sullivan 2001, Zamora et al. 2001, Hambäck and Beckerman 2003, Allcock and Hik 2004). For example, the effect of herbivory on plant performance may be disproportionate to the amount of biomass removed, especially if biomass is removed during sensitive stages of the life cycle, or from specific

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meristems like flowers or fruits (Louda and Potvin 1995, Maron 1998, Gómez and Zamora 2000*a*, *b*, Gómez 2003). In addition, although herbivory can decrease adult survival, it is at the seedling stage when herbivores have the most harmful effect (Louda 1982*b*, Hulme 1994, Bastrenta et al. 1995, Root 1996, Maron 1998, Edwards and Crawley 1999, Carson and Root 2000, Gómez et al. 2003). Furthermore, most studies considering the simultaneous activity of vertebrates and invertebrates have found that the former have a much stronger impact on plant performance (Hulme 1994, 1996, Gómez 1996, Palmisano and Fox 1997, Gómez and Zamora 2000*a*, *b*, Sessions and Kelly 2001, Shaw et al. 2002).

Contrasting with this copious literature concerning the effect of herbivores on individual plants, much less empirical information exists on the effect that these organisms have on the abundance and density of plants (Crawley 1997). Consequently, the importance of herbivory for plant populations remains a controversial issue (Hendrix 1988, Andersen 1989, Crawley 1989*a*, *b*, 1990, 1992, 2000, Eriksson and Ehrlén 1992, Marquis 1992, Osem et al. 2004). Although, in theory, herbivores can affect plant abundance by arresting recruitment, only a few studies have been able to demonstrate this effect experimentally. Carson and Root (2000) demonstrated that phytophagous insects control the abundance of the goldenrod *Solidago altissima*, whereas Maron and Simms (2001) showed that granivory by rodents affects *Lupinus arboreus* recruitment and thereby adult abundance. Unfortunately, the effect of herbivores on plant population dynamics is usually inferred from their effect on some demographic components, such as seed germination, seedling emergence, or juvenile recruitment (Louda 1982*a*, *b*, 1983, Crawley and Long 1995, Louda and Potvin 1995, Hulme 1996, 1997, Curran and Webb 2000, Maron and Gardner 2000, Wenny 2000, Ehrlén 2003, Gómez et al. 2003, Pearson et al. 2003). For example, the harmful impact of specialist flower- and seed-feeding mammals and invertebrates on seedling recruitment and juvenile abundance has been interpreted as evidence of significant effects of herbivory on the population dynamics of several host plants (e.g., Louda 1982*a*, *b*, 1983, Louda and Potvin 1995, Juenger and Bergelson 2000, Clarke and Kerrigan 2002, Maron et al. 2002).

However, it is not proper to infer any effect on populations from the effects on demographic components. First, individual components of the life cycle of plants, such as seed production or seedling survival, cannot be universally used as a surrogate for the total performance, because total performance in many plant species represents the integration of the effects occurring during different phases of the life cycle (Ehrlén 2002, 2003). As a consequence, it is not always possible to identify which component better explains the overall reproductive success and performance of plants. Second, a significant herbivore effect on host population dynamics only takes place when the number of propagules entering the adult stage is smaller than the number of deaths by herbivory (Harper 1977). Under field conditions, plant recruitment depends on the availability of seeds as well as on the availability of suitable microsites for seed germination and seedling survival (Eriksson and Ehrlén 1992, Clark et al. 1998, Edwards and Crawley 1999, Nathan and Müller-Landau 2000). When plant populations are limited by the availability of microsites rather than by the production of seeds, an increase in propagule production via release from herbivores does not automatically translate to an increase in plant abundance (Hulme 1998, Turnbull et al. 2000). Consequently, when no information exists on the extent to which density-dependent compensation counteracts the effect of seed and seedling reduction caused by herbivores, a common mistake is to assume that a strong herbivore effect on plant performance implies an equally intense effect on plant population dynamics (Andersen 1989, Louda 1989, Crawley 1992, Louda and Potvin 1995, Edwards and Crawley 1999, Hickman and Hartnett 2002). Any extrapolation from short-term experimental or demographic studies to explain herbivore effect on the dynamic and spatial structure of plant populations is highly inaccurate and risky.

Besides hampering the number of recruits, herbivores can also affect the spatial structure of plant populations (Crawley 1992, 2000, Müller-Landau et al. 2002, Passos and Oliveira 2002). This effect takes place mainly when the impact of herbivores varies spatially between microhabitats (Rey and Alcántara 2000, Gómez et al. 2001, 2003, Tomita et al. 2002), and it is further magnified when herbivores over-damage the recruits dispersed to or established in those high-quality microsites where recruitment would be most probable if herbivores were absent (Callaway 1992, Crawley and Long 1995, Rousset and Lepart 2000). The risk of attack by a generalist herbivore depends not only on plant traits such as chemistry, morphology, or phenology, but also on the spatial structure of the plant community and the quality and abundance of the neighbors (Holmes and Jepson-Innes 1989, Danell et al. 1991, Hjältén et al. 1993, Wahl and Hay 1995, Hjältén and Price 1997, WallisDeVries et al. 1999, Rebollo et al. 2002). Under these circumstances, the habitat distribution of plant species inhabiting heterogeneous landscapes can be a direct consequence of the activity of their major herbivores (Jordano and Herrera 1995, Schupp 1995, Schupp and Fuentes 1995, Louda and Rodman 1996, Cabin and Marshall 2000, Rey and Alcántara 2000, Sipura and Tahvanainen 2000). Despite its crucial importance, no study has experimentally demonstrated, as far as I know, the role that herbivores play in shaping the spatial distribution pattern of plant populations.

Objectives

The main objective of this study was to test the long-term effect of ungulates on the population dynamics

PLATE. 1. *Erysimum mediohispanicum*, photographed at 1900 meters above sea level in the Sierra Nevada (southeast Spain). Photo credit: J. Gómez.

and spatial structure of two short-lived monocarpic herbs, *Erysimum mediohispanicum* Polatschek (see Plate 1) and *E. baeticum* (Heywood) Polatschek (Cruciferae). To reach this goal, an ungulate exclusion experiment was done during seven years, in which the effects of these mammals on the abundance of adult reproductive plants, rather than on juveniles, were quantified. In addition, I explored the mechanisms by which ungulates influence plant populations, such as seed production, seedling survival to postdispersal seed predation, seed germination, and seedling recruitment. Finally, I used a spatially implicit approach to study the effect of ungulates on the habitat distribution of plants. Specifically, I quantified: (1) the intensity of herbivory undergone by the plants throughout the study period; (2) the effect of microhabitat on herbivory intensity; (3) the impact of herbivory on flower display, fruit set, and seed production; (4) the herbivore-mediated spatial, between-microhabitat differences in seed production; (5) the indirect effect of ungulates on postdispersal seed predation; (6) the effects of ungulates on seed germination and seedling early recruitment; (7) the role of shrubs in the early establishment of plants; and (8) the long-term effect of ungulate exclusion on the spatial distribution of plants and on the abundance of adults.

Plant natural history

The genus *Erysimum* comprises ~17 species in the Iberian Peninsula, ranging from annual to biannual and perennial, mono- and polycarpic (Nieto Feliner 1993). *Erysimum mediohispanicum* and *E. baeticum*, are biannual to perennial monocarpic herbs, the former found in many montane regions of southeastern Spain and the latter endemic to the Sierra de Baza and Sierra Nevada of Granada province, southeastern Spain (Blanca et al. 1992, Nieto Feliner 1992, 1993), although they do not coexist. They appear from 1100 to 2000 m a.s.l. (Blanca et al. 1992), inhabiting forests and scrublands. Plants usually grow for 2–3 years as vegetative rosettes, then die after producing 1–8 reproductive stalks, which can display between a few and several hundred hermaphroditic, slightly protandrous bright yellow (in *E. mediohispanicum*) or purple (in *E. baeticum*) flowers (Nieto Feliner 1993).

In southeastern Spain, reproductive individuals are consumed by many different species of herbivores. Several species of sap-suckers (primarily the bugs *Eurydema oleraceae*, *E. fieberi*, *E. ornata*, and *Corimeris denticulatus*) feed on the reproductive stalks during flowering and fruiting. In addition, stalks are bored into by a weevil species (presumably *Lixus ochraceus*), which consumes the inner tissues, whereas another weevil species (presumably *Ceutorhynchus chlorophanus* in *E. mediohispanicum*) develops inside the fruits, living on developing seeds. Some floral buds do not open because they are galled by flies (*Dasineura* sp.). However, the main herbivores in the study zones are the Spanish ibex (*Capra pyrenaica*, Bovidae) for *E. mediohispanicum* and domestic sheep for *E. baeticum*. These two ungulates consume flowers and green fruits by browsing on the reproductive stalks. There is no quantitative information about ungulate density or grazing regime in the study sites. Nevertheless, during the study period I observed in the Sierra Nevada study site a group of 7–15 ibex moving freely. In contrast, in the Sierra de Baza there was a herd composed of ~75–100 sheep that moved altitudinally and that grazed in the study plots during 15–20 days between late July and early August. Post dispersed seeds of both *Erysimum* species are consumed by woodmice (*Apodemus sylvaticus*, Muridae), several species of birds (*Fringilla coelebs*, *Serinus serinus*, and *Carduelis cannabina* [Frigillidae], among others), several species of medium-sized granivorous beetles (*Iberozabrus* sp. [Carabidae], among others), and ants (*Lasius niger*, *Tetramorium caespitum*, and probably *Cataglyphis velox* and *Leptothorax tristis*). These animals feed on the seeds from late August to early April. Seedlings and juveniles are injured by ibex, sheep, wild boars (*Sus scrofa*, Suidae), hares (*Lepus granatense*, Leporidae), and voles (*Pitimys* spp., Arvicolidae).

Study site

This study was conducted in two mountain ranges of southeastern Spain, Sierra Nevada (for *E. mediohispanicum*) and Sierra de Baza (for *E. baeticum*). In Sierra Nevada, the study was conducted in an area ranging between 1550 and 1900 m a.s.l. The landscape is a complex mosaic of small patches of mixed oak (*Quercus ilex*)–autochthonous pine (*Pinus sylvestris nevadensis*) woodlands coexisting with several to many pine afforestation stands, old pinewood stands, and scrublands where a diverse community of shrub species coexist. The climate in the zone is continental Mediterranean, with cold winters and hot summers, and severe summer drought (July–August). The mean minimum temperature (January) is −0.9°C, the mean maximum (July) is 29.0°C, and the mean annual temperature is 11.5°C. Rainfall is concentrated mainly in autumn and spring, with an annual rainfall of 825 mm. One main site, Loma de los Panaderos (37°5′ N, 3°28″ W, 1850 m a.s.l.), was selected for this study. It is a scrubland dominated by *Salvia lavandulifolia* (>90% of relative abundance; see Castro et al. [1999] for further details). In this site I established three blocks (each ~2000 m^2), where all experiments and observations were conducted. Blocks were located within a large *E. mediohispanicum* population, and were separated by >100 m.

In the Sierra de Baza, the study was conducted in an area located 80 km north of the Sierra Nevada study area at an altitude of 1700–1900 m. The landscape is well-preserved open pine woodland where dominant trees are autochtonous Scots and black pine (*P. nigra salzmanii*). The climate is also continental Mediterranean, with cold winters and hot summers, and severe summer drought (July–August). No temperature information exists for this area, although the mean minimum and maximum temperatures as well as the mean annual temperature are similar to those in the Sierra Nevada. Rainfall is concentrated mainly in autumn and spring, with an annual rainfall of 544 mm. One main site, Collado de Boleta (37°23′ N, 3°51″ W, 1900 m a.s.l.; see Castro et al. [1999] for further details) was selected for this study. It is an open pine woodland with *Juniperus communis*, *J. sabina*, and *Berberis hispanica* dominating the understory. As in Sierra Nevada, experiments were conducted in three blocks located in an *E. baeticum* population and separated by >200 m.

METHODS

General experimental design

Two plots (~1000 m^2) were marked per block, one being fenced in 1997 to exclude ungulates from the plants and the other left unfenced as a control. These resulted in three ungulate-excluded plots and three control plots per mountain range. Fencing was assigned at random in each study site. Although the fences excluded ungulates, they allowed the entrance of small animals such as wood mice, hares, and voles. During the first year of the experiment, I determined the spatial structure of the vegetation in all plots by means of 10 linear 25 × 2 m transects running the length of each plot (Bullock 1996). At each meter of the tape, the presence/absence and the identity of vegetation covering the ground were recorded at three points: the center and 1 m to each side and perpendicular to the transect (N = 1500 points per plot). I defined three types of microhabitats: (1) under shrubs, those places completely covered by any of the species of shrubs growing at the study sites; (2) shrub edge, those places located at the edge of the shrubs, where rosettes were under the shade of the shrubs but accessible to ungulate trampling; and (3) open, those places located in the open interspaces between the shrubs. I decided to pool all of the shrub species in one single functional microhabitat type because, in preliminary analyses, I did not find any difference among them in plant and plant herbivore traits ($P > 0.2$ in all cases, one-way ANOVAs). Furthermore, the vegetation spatial structure did not differ between ungulate-excluded and control plots when I began the experiment (for Sierra Nevada, $\chi^2 = 0.06$, $P = 0.97$; for Sierra de Baza, $\chi^2 = 2.80$, $P = 0.25$). In 2001, I repeated the transects, in order to check whether the structure of the woody vegetation had changed during the experimental period. No significant change was found ($P > 0.1$ for all comparisons, log-linear analyses). On average, the surface of the plots covered by shrubs ranged between 48% and 52% in Sierra de Baza and 41% and 42% in Sierra Nevada.

Plant labeling and ungulate effect on plant reproduction

Between 180 and 300 reproductive individuals of each species (30–50 individuals per plot) were labeled each study year with aluminium tags attached to the rosettes. Plants were labeled when they started to produce the flowering stalks, to assure that all of the studied plants were reproducing during the current year. When the first flower opened, I quantified the following traits for each plant: (1) microhabitat in which the plant was growing; (2) number of flowering stalks; (3) reproductive stalk height (measured to the nearest 0.5

cm), as the distance from the ground to the top of the tallest opened flower; (4) basal diameter of the stalk (in millimeters, by a digital caliper to the nearest 0.1 mm), as the diameter of the tallest stalk at the point where it joins the rosette; and (5) number of flowers. At the end of the flowering period, but before seed dispersal, I revisited the plants, quantifying (6) the occurrence of damage by ungulates; (7) the amount of flowers escaping herbivores; and (8) the number of ripe fruits produced per plant. After this, I collected from each plant a sample of fruits that were taken to the lab, where they were opened under a binocular glass (60×) to quantify (9) the number of ripe seeds produced per fruit. In total during the study, I examined 1555 plants and 4460 fruits of *Erysimum mediohispanicum* and 750 plants and 2250 fruits of *E. baeticum*.

The interaction between ungulates and plants was quantified by using the following estimates:

1) *Herbivory rate*, defined as the percentage of damaged plants, and determined by checking the labeled plants for presence of damage by ungulates. Ungulate damage was easy to differentiate from damage of other common herbivores such as seed predators or stem borers, because ungulates are the only animals at the study site that partially or completely remove flowering stalks.

2) *Damage intensity*, defined as the percentage of tissue consumed by ungulates per damaged plant, and estimated by determining the height at which the stalks were cut by ungulates and quantifying the difference in plant size before and after the damage.

3) *Flower loss*, defined as the percentage of flowers consumed by ungulates, considering both damaged and undamaged plants.

To estimate plant reproductive output, I used the following sequential estimates of the female reproductive success: (1) number of flowers; (2) number of fruits produced per plant, counting only those surviving ungulate damage; (3) percentage of flowers ripening to successful fruit (fruit set, hereafter); (4) number of seeds produced per plant (female fecundity), found by multiplying the number of fruits per plant × the number of seeds per fruit. Female fecundity represents an accurate estimate of the lifetime reproductive output of the individuals because the studied species are monocarpic, reproducing only once during their life.

Effect of ungulates and microhabitat on postdispersal seed predation

The effect of ungulates and microhabitat on the postdispersal seed predation rate was investigated in two independent experiments conducted in September of 1999 and 2002, respectively. The experiments were conducted during the period of seed dispersal of the studied plants.

1999 experiment.—The objective of this experiment was to determine the identity of the major postdispersal seed predators and the spatial pattern of predation on the two *Erysimum* species. Three factors were considered:

1) Block, with two levels, because the experiment was replicated in two blocks. The experiment was performed only in the ungulate-excluded plots, to avoid any disturbance by ungulate trampling to the experimental framework.

2) Microhabitat, with three levels: open, shrub edge, and under shrub.

3) Treatment, with four levels: (i) all predators, with the seeds being accesible to all predator species; (ii) only ants and beetles, with the seeds excluded from birds and wood mice by 10-mm mesh cages; (iii) only ants, with seeds excluded from the remaining predators by 2-mm mesh cages that precluded the passage of medium-sized granivorous beetles; and (iv) no predator, with seeds completely excluded from any predator type by using the previous cage and adding granular insecticide to the borders to preclude the passage of any insect.

The general design was the following: in each study site (Loma de Panaderos and Collado Boleta), I established 14 stations in each of two ungulate-excluded plots. In every experimental station, I marked one point per microhabitat, 42 points per plot. I located four small Petri dishes per point, assigning each one at random to a level (i–iv) of the factor predator identity. In every Petri dish I placed 10 seeds (40 seeds per point, 1680 seeds per block, 3360 seeds per study site, for 6720 seeds in total).

2002 experiment.—The objective of this experiment was to detemine the putative effect of ungulates on the postdispersal seed predation rate; it was performed only with *E. mediohispanicum*. Four factors were considered in this experiment:

1) Block, with two levels, because the experiment was replicated in two blocks.

2) Microhabitat, with two levels, because I decided to locate seeds only under shrubs and in open microsites.

3) Ungulate exclusion, with two levels: ungulate-excluded plots (to prevent access of these mammals to the seeds) and control plots.

4) Treatment, with two levels: no predator and all predators. I did not use the four treatments described for the 1999 experiment, because determining the identity of the predators was not the main goal of the 2002 experiment.

The design was the following: in each block I established 50 stations, half of them in the ungulate-excluded plots and the remaining in the control plots. At every experimental station, I marked one point in the open microhabitat and another point under shrub, for a total of 50 points per plot. At each point, I placed 10 seeds open to all predators in a small Petri dish (500 seeds per plot and 2000 seeds in total). In addition, I randomly selected 10 stations per plot, where I also placed 10 seeds excluded to all predators using the method described for the 1999 experiment (200 seeds per plot and 800 seeds in total).

In both experiments, I checked the points periodically every 3–5 days during the first month, every 15 days during the second and third months, and monthly until April. I noted the number of seeds still at the points, and the presence of seed-coat remains. In addition, I checked whether the insecticide was effective, and, when necessary, I reapplied it to ensure that insect exclusion worked during the whole experiment.

Effect of ungulate exclusion and microhabitat on seedling establishment

The effect of ungulates on seedling emergence and survival was observationally and experimentally determined in March of 1999. First, I quantified the number of seedlings naturally establishing per microhabitat in the ungulate-excluded and control plots for both *Erysimum* species. For this, in March–April I counted the number of seedlings appearing in 100–200 quadrats (10 × 30 cm) located at random in each microhabitat and ungulate exclusion level ($N = 830$ quadrats for *E. mediohispanicum*, $N = 634$ quadrats for *E. baeticum*). The number of quadrats located per microhabitat was proportional to the abundance of that microhabitat in the study plot.

During the first week of March 1999, I also experimentally determined the effect of ungulate exclusion and microhabitat on seedling emergence and survival. The experimental design for *E. baeticum* was the following: in each of two blocks, I located 20 planting stations per microhabitat, half of them in the ungulate-excluded plots and the remaining in the control plots (120 planting stations in total). The planting stations were separated by >1 m. For *E. mediohispanicum*, it was impossible to use two blocks; thus seeds were sown only in one block (60 planting stations). In each station, I sowed 20 seeds, for a total of 2400 seeds for *E. baeticum* and 1200 seeds for *E. mediohispanicum*.

To distinguish each experimental seed, I laid on each station a 20 × 4 cm grid composed of 10 × 2 4-cm^2 cells, and sowed one seed per cell. Seeds were thus separated by 2 cm and were buried at 0.5 cm to avoid removal by postdispersal seed predators. Prior to seeding, I removed the naturally occurring seedlings and the top layer of the soil to avoid the emergence of non-planted seedlings.

I checked the experiments every 10 days until June, noting the number of emerging seedlings and the time of emergence. In addition, I studied seedling survival during the first summer for *E. baeticum* by periodic surveys made throughout the entire summer (until October, when first rains came). During each census, I recorded seedling survival, any sign of damage to cotyledons or leaves, and cause of death when possible. I identified three causes of seedling mortality ($N = 340$ seedlings): trampling by ungulates, desiccation, and damage by invertebrates and rodents (vole tunnels). It was easy to differentiate among these mortality factors, because desiccated seedlings invariably appeared light-brown in color and with cotyledons shriveled, whereas invertebrates and rodents cut the stems and ungulates killed the seedlings by uprooting them without consuming them.

Adult abundance and spatial distribution pattern

The abundance of flowering plants was determined every year in each plot by means of 10 linear 25 × 2 m transects running the length of each plot (Bullock 1996). These transects covered between 17% and 25% of the surface of the plots. In each transect, I noted the number of plants flowering during the current year and the microhabitat in which they appeared. An individual was considered as being in shrub edge when its rossette was under the canopy of the shrub but the flowering stalk grew from one side of it; it was considered as being under shrubs when even the flowering stalk was growing intermingled with the shrub. Censuses were done during the flowering peak (early to mid-June), to ensure that all adult plants had flowered by the time of the census. Those plants with vegetative rosettes of a similar size or even larger than flowering plants, but not producing flowering stalks, were not included in the counts.

Data analysis

The spatiotemporal variability of ungulate damage was analyzed only for the plants located in the control plots, considering year, block, and microhabitat as main factors (Table 1). Only block was considered as random. I decided to consider year as fixed because it refers to the number of years from the start of the experiment (1997). Herbivory rate was analyzed with a log-linear model because it had a binomial distribution (Proc CATMOD; SAS Institute 1997), whereas damage intensity and flower loss were analyzed with a three-way mixed ANOVA using the recommended REML method (Proc MIXED; SAS Institute 1997). The effect of plant phenotypic traits on herbivory rate was analyzed by log-linear models (Proc GENMOD; SAS Institute 1997), whereas their effects on damage intensity and flower loss were analyzed by multiple regression (Proc GLM; SAS Institute 1997). In these models, I used the total number of plants marked during the seven years of study. Nevertheless, I introduced year and its interactions as covariates to control for annual variation on the effect of plant phenotype on herbivore damage.

The effect of ungulate exclusion on plant reproductive output was analyzed by three-way ANOVAs (Proc GLM; SAS), introducing year, ungulate exclusion, and microhabitat as main factors (Table 1). Block was removed from this analysis because it yielded a singular variance–covariance matrix. For this reason, because all of the main factors are fixed, I fitted the model using the traditional OLS method. Only six years were used

TABLE 1. Summary of the statistical models used in this study, indicating the nature of each dependent variable and the factors considered.

Dependent variable	Distribution	Link function	Model
Herbivory rate†	binomial	logit	$\mu + \beta + \tau + \beta\tau + \gamma + \beta\gamma + \tau\gamma + \beta\tau\gamma + \varepsilon$
Damage intensity†	normal	identity	$\mu + \beta + \tau + \beta\tau + \gamma + \beta\gamma + \tau\gamma + \beta\tau\gamma + \varepsilon$
Flower loss†	normal	identity	$\mu + \beta + \tau + \beta\tau + \gamma + \beta\gamma + \tau\gamma + \beta\tau\gamma + \varepsilon$
Plant reproductive output	normal	identity	$\mu + \alpha + \beta + \alpha\beta + \gamma + \alpha\gamma + \beta\gamma + \alpha\beta\gamma + \varepsilon$
Seed predation 1997‡	normal	identity	$\mu + \tau + \gamma + \tau\gamma + \rho + \tau\rho + \gamma\rho + \gamma\tau\rho + \varepsilon$
Seed predation 2002‡§	normal	identity	$\mu + \alpha + \tau + \alpha\tau + \gamma + \alpha\gamma + \tau\gamma + \alpha\tau\gamma + \varepsilon$
Seedling abundance‖	binomial	logit	$\mu + \alpha + \beta + \alpha\beta + \tau + \alpha\tau + \beta\tau + \alpha\beta\tau + \varepsilon$
Seedling emergence	binomial	logit	$\mu + \alpha + \tau + \alpha\tau + \gamma + \alpha\gamma + \tau\gamma + \alpha\tau\gamma + \upsilon(\gamma) + \varepsilon$
Seedling survival	binomial	logit	$\mu + \alpha + \tau + \alpha\tau + \gamma + \alpha\gamma + \tau\gamma + \alpha\tau\gamma + \upsilon(\gamma) + \varepsilon$
Plant spatial distribution	multinomial	logit	$\mu + \alpha + \beta + \alpha\beta + \tau + \alpha\tau + \beta\tau + \alpha\beta\tau + \varepsilon$
Plant abundance¶	Poisson	log	$\mu + \alpha + \beta + \alpha\beta + \tau + \alpha\tau + \boldsymbol{\beta\tau} + \boldsymbol{\alpha\beta\tau} + \varepsilon$

Note: Model terms are: α, Ungulate exclusion; β, Year; τ, Block; γ, Microhabitat; ρ, Treatment; υ, Seeding point; μ, overall mean; ε, error term.

† No ungulate-exclusion term was included in the models because they were fitted only for plants in the control plots.

‡ Seed predation was fitted to a normal distribution because the dependent variable was the percentage of seeds lost per seeding points (see *Methods: Data analysis*).

§ Treatment was not included because the dependent variable in this model was difference between no-predator and all-predators points (see *Method: Effect of ungulates and microhabitat on postdispersal seed predation*).

‖ Seedling abundance was fitted to a binomial distribution because it was considered as presence/absence of seedlings per quadrat (see *Methods: Data analysis*).

¶ Plant abundance is the number of adult plants per transect. In this model, the three blocks were pooled due to analytical problems (see *Methods: Data analysis*). Thus, the two interactions in boldface type cannot be resolved.

for *E. mediohispanicum*, because in one year (2002) there were no data on one microhabitat (shrub edge).

Seed predation rate was analyzed by mixed three-way ANOVAs (Proc MIXED; SAS) because the dependent variable considered in these analyses was the percentage of seeds lost per seeding point. In the 1997 experiment, the main factors were microhabitat, block, and predator identity, whereas the error terms were the experimental seeding points (Table 1). Ungulate exclusion was not introduced in the model because the experiment was set up in ungulate-excluded plots. The main factors in the 2002 experiment were ungulate exclusion, microhabitat, and block (Table 1). In this case, predator identity was removed from the model because the dependent variable used was the difference in seeds lost between control and predator-excluded points belonging to the same microhabitat × block × ungulate exclusion combination.

Seedling abundance, emergence, and survival probability were analyzed with log-linear models (Proc CATMOD; SAS), because all of them were fitted to binomial distributions (Table 1). Seedling abundance was also binomial because it was considered as presence/absence of seedlings per quadrat; in more than 97% of the quadrats there were zero or one seedling. In these models I introduced ungulate exclusion and microhabitat as main effects, and in the model testing experimental emergence and survival, the seedling points nested into microhabitat (Table 1). Block was removed from the models testing the experimental emergence because the *E. mediohispanicum* experiment was performed only in one block. Nevertheless, I performed the complete model including block for *E. baeticum* and there were no statistical differences (results not shown). Emergence time was analyzed by an accelerated failure-time model (Proc PHREG), using the maximum partial likelihood as the estimation method and the Weibull as the survival distribution (Allison 1995). To handle the ties in survival times occurring in the data sets, I used the EXACT method that assumes a true, but unknown, ordering for the tied event times (Allison 1995).

The effect of ungulate exclusion on plant spatial distribution was analyzed by a log-linear model (Proc CATMOD), considering as main factors the ungulate exclusion, year, and block, and fitting the dependent variable to a multinomial distribution with three levels, open, shrub edge, and under shrubs (Table 1). The effect of the experiment on plant abundance was analyzed by a generalized linear model (Proc GENMOD), using as main factors the ungulate exclusion, year, and block, but fitting the dependent variable to a Poisson distribution (Table 1). In this model I pooled all of the interactions involving block within the residuals because they provoked singularity in the variance–covariance matrix. In addition, I did not include microhabitat because I performed a separate analysis for plants occurring in each microhabitat.

The variables fitted to a normal distribution were transformed to approach normality and homoscedasticity when necessary. Ratio variables were arcsine-transformed whereas real variables were log-transformed (Zar 1996).

RESULTS

Ungulate damage

When feeding on a plant, ungulates damaged the inflorescences and infructescences, cutting them and

TABLE 2. Summary of the log-linear analysis (χ^2 values) testing the spatiotemporal variability in herbivory rate (percentage of plants damaged by ungulates) and the REML-ANOVA (F values) testing the damage intensity (percentage of tissue lost to herbivory).

	E. mediohispanicum			*E. baeticum*		
Source	df	χ^2/F	P	df	χ^2/F	P
Herbivory rate†						
Year	6	12.11	0.030	3	33.87	0.0001
Block	2	31.36	0.0001	1	0.52	0.471
Microhabitat	1	25.82	0.0001	2	51.89	0.0001
Year × Block	4	2.66	0.616	2	0.01	0.908
Year × Microhabitat	5	3.21	0.667	6	4.14	0.658
Microhabitat × Block	3	2.78	0.427	2	0.02	0.991
Year × Block × Microhabitat	4	1.38	0.848	2	0.89	0.640
Error	710			336		
Damage intensity‡						
Year	6	15.69	0.0001	3	18.10	0.0001
Block	2	4.63	0.0008	2	0.31	0.575
Microhabitat	2	17.17	0.0001	2	31.02	0.0007
Year × Block	12	3.38	0.009	6	0.88	0.349
Year × Microhabitat	12	2.20	0.020	6	2.88	0.010
Microhabitat × Block	4	0.60	0.731	4	4.24	0.015
Year × Block × Microhabitat	24	1.68	0.109	12	0.84	0.433
Error	298			163		

Notes: Only plants located in control plots were introduced in these analyses. Block was introduced as random.

† The whole model log-likelihood was 361.27 for *E. mediohispanicum* and 170.25 for *E. baeticum*.

‡ Only plants attacked by ungulates were computed to obtain damage intensity. The whole-model R^2 was 0.22 for *E. mediohispanicum* and 0.27 for *E. baeticum*.

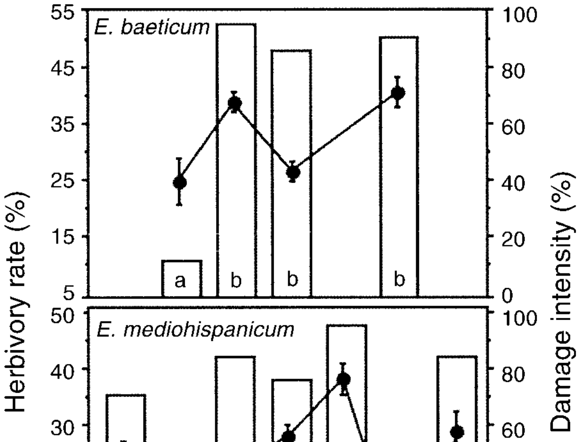

FIG. 1. Temporal variation in herbivory rate (histograms showing the percentage of plants damaged by ungulates) and damage intensity (circles and lines showing the percentage of plant tissue lost to herbivory of damaged plants; mean ± 1 SE) for the two species of *Erysimum* from 1997 to 2003. Histogram bars with different letters are statistically different at $\alpha < 0.05$.

consuming the flowers or fruits plus the stalks. By contrast, no mammal damage to basal rosettes was observed during any of the study years. Ungulates started to feed on the plants at the end of the flowering period or during the onset of the fruiting period (June–July), when other herbaceous species had already dried up at the study sites. For this reason, damage to plants occurred before they had dispersed their seeds.

Ungulates damaged 33.5% (N = 760 plants) of the *Erysimum mediohispanicum* plants and 43.6% (N = 337) of the *E. baeticum* plants marked outside the fences. When attacking plants, ungulates consumed, on average, 55.8% ± 2.2% (mean ± 1 SE; N = 212 damaged plants) of the tissue produced by *E mediohispanicum* individuals and 50.5% ± 2.1% (N = 147 damaged plants) produced by *E. baeticum* plants. Consequently, damaged plants lost to ungulates 50.3% ± 2.5% of initial flowers in *E. mediohispanicum* and 57.1% ± 2.4% in *E. baeticum*.

Spatiotemporal variability in herbivory.—There was significant spatiotemporal variability in the frequency of plants damaged by ungulates (Table 2). The percentage of individuals damaged varied among years for the two species (for *E. mediohispanicum*, $\chi^2 = 14.6$, df = 6, $P = 0.015$, $N = 760$ plants; for *E. baeticum*, $\chi^2 = 34.5$, df = 3, $P = 0.0001$, $N = 337$), ranging between 22% and 47% for *E. mediohispanicum*, and between 11% and 53% for *E. baeticum* (Fig. 1). I also found spatial, among-block differences in the rate of herbivory for *E. mediohispanicum*, but not for *E. baeticum* (Table 2). Thus, in the former species herbivory

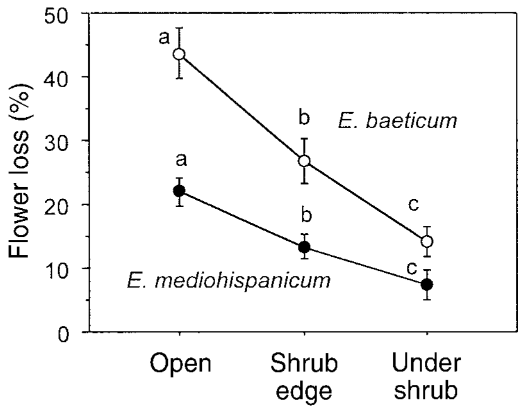

FIG. 2. Percentage of flowers of two *Erysimum* species lost to ungulate herbivory (mean ± 1 SE), depending on the microhabitat occupied by each plant. Both damaged and undamaged individuals are considered to compute these estimates. Means with different letters are statistically different at $\alpha < 0.05$.

rate ranged from <10% in some blocks to >75% in other blocks.

There was temporal variability in the damage intensity suffered by the two species (for *E. mediohispanicum*, $F = 17.8$, df = 6, 298, $P < 0.0001$; for *E. baeticum*, $F = 11.4$, df = 3, 163, $P < 0.0001$; one-way ANOVAs), ranging between 17% and 80% for *E. mediohispanicum* and 40% and 73% for *E. baeticum* (Fig. 1). Again, spatial variation in damage intensity only occurred for *E. mediohispanicum* (Table 2).

Variability at the microhabitat level.—The specific microhabitat location of the plants significantly affected the rate of herbivory for *E. mediohispanicum* ($\chi^2 = 51.2$, df = 2, $P < 0.0001$, $N = 760$ plants) as well as *E. baeticum* ($\chi^2 = 46.1$, df = 2, $P < 0.0001$, $N = 337$). For both species, the lowest probability of damage occurred when plants were growing under shrubs (11.2% in *E. mediohispanicum* and 24.3% in *E. baeticum*), whereas it was intermediate when they were at the edge of shrubs (31.5% and 45.9%, respectively) and highest when they were in the open interspaces (45.6% and 69.6%).

By contrast, once a plant was attacked by ungulates, its association to shrubs did not protect it against these mammals. Indeed, no effect of microhabitat was found on the percentage of tissue removed (for *E. mediohispanicum*, $F = 2.23$, df = 2, 154, $P = 0.11$; for *E. baeticum*, $F = 1.91$, df = 2, 138, $P = 0.15$).

The percentage of flowers lost to herbivory differed between microhabitats ($F = 14.55$, df = 2, 655, $P = 0.0001$ and $F = 20.73$, df = 2, 334, $P = 0.0001$ for *E. mediohispanicum* and *E. baeticum*, respectively). The best microhabitat for both species, that in which the amount of flowers lost to ungulates was lowest, was Under shrub, followed by Shrub edge, whereas Open was the worst microhabitat in which to circumvent ungulate damage (Fig. 2).

Effects of plant traits on damage probability

Damaged plants had wider (2.44 ± 0.06 vs. 2.04 ± 0.04 mm), taller (40.03 ± 0.91 vs. 34.81 ± 0.63 cm), and more stalks (1.58 ± 0.08 vs. 1.26 ± 0.06 stalks/plant) and flowers (53.80 ± 2.71 vs. 42.45 ± 1.86 flowers/plant) than undamaged ones in *E. mediohispanicum* (Table 3). The only traits significantly related to herbivory rate in *E. baeticum* were stalk height (Table 3), which was greater in damaged plants (49.52 ± 1.20 vs. 46.43 ± 1.33 cm), and number of flowers (Table 3), which was slightly lower in damaged plants (41.11 ± 20.85 vs. 41.72 ± 1.59 flowers/plant).

Damage intensity significantly increased in *E. mediohispanicum* with the number of stalks produced by the plants (Table 3). In *E. baeticum*, damage intensity increased with stalk diameter and the number of stalks, but decreased with the stalk height and the number of flowers displayed by the plants (Table 3). Flower loss was not related to any morphological trait in *E. mediohispanicum* (Table 3), whereas in *E. baeticum* it was related positively to the number of stalks and negatively to the number of flowers (Table 3).

Effect of ungulates on reproductive output

In both *Erysimum* species, the number of flowers was significantly affected by the year of study and the microhabitat (Table 4). Plants growing in open sites produced fewer flowers than plants growing in shrub edges or under shrubs (Fig. 3). This difference was temporally constant in *E. baeticum* (Fig. 3), as suggested by the nonsignificant interaction term between year and microhabitat (Table 4). By contrast, *E. mediohispanicum* flower production did not differ between microhabitats for some of the years (Fig. 3), which renders a significant Year × Microhabitat interaction term (Table 4). Ungulate exclusion affected flower production only for *E. baeticum* (Table 4), with plants located in ungulate-excluded plots producing significantly more flowers than plants located in control plots (Fig. 3). By contrast, *E. mediohispanicum* flower production was similar inside and outside the fences (Fig. 3).

The fruit set differed among years for both *Erysimum* species (Table 4), with 1999 also yielding the lowest value (Fig. 3). Fruit set also varied between treatments (Table 4), being higher for plants located inside the fences. Microhabitat affected fruit set only in *E. baeticum* (Table 4). However, according to the significant Microhabitat × Ungulate exclusion interaction term, the effect of the microhabitat on fruit set was not similar outside and inside the exclosures (Fig. 4). Whereas in ungulate-excluded plots the fruit set did not differ among microhabitats (nonsignificant according to a post hoc Bonferroni-Dunn test), in control plots fruit set was significantly lower in the open than in the shrub edge and under shrubs ($P < 0.001$ according to a post hoc Bonferroni-Dunn test). A similar pattern was found for *E. mediohispanicum*, according to the significant

TABLE 3. Effect of plant morphological traits on herbivory rate (log-linear model; χ^2 values), damage intensity (log-transformed, multiple regression; t values), and flower loss (arcsine-transformed, multiple regression; t values).

	E. mediohispanicum				*E. baeticum*			
Source of variation	df	χ^2/t	P	Coeff. ± 1 SE	df	χ^2/t	P	Coeff. ± 1 SE
Herbivory rate†								
Stalk diameter	1	17.40	0.0001	0.56 ± 0.10	1	0.62	0.433	0.17 ± 0.22
Stalk height	1	9.38	0.002	0.03 ± 0.01	1	3.92	0.048	0.02 ± 0.01
No. stalks	1	8.08	0.004	0.21 ± 0.07	1	1.68	0.194	0.29 ± 0.22
No. flowers	1	3.39	0.059	0.01 ± 0.002	1	4.65	0.031	−0.02 ± 0.01
Damage intensity‡								
Stalk diameter	1	−0.02	0.98	−0.15 ± 6.14	1	3.54	0.0005	44.41 ± 12.54
Stalk height	1	−0.90	0.37	−0.19 ± 0.21	1	−3.54	0.0005	−2.74 ± 0.77
No. stalks	1	3.42	0.0008	5.91 ± 1.73	1	2.22	0.028	7.20 ± 3.25
No. flowers	1	−0.49	0.62	−0.10 ± 0.20	1	−4.12	0.0001	−0.63 ± 0.15
Flower loss§								
Stalk diameter	1	0.91	0.36	4.25 ± 4.67	1	0.05	0.96	0.80 ± 15.36
Stalk height	1	−0.86	0.39	−0.18 ± 0.21	1	1.00	0.32	0.96 ± 0.96
No. stalks	1	−0.45	0.65	−0.96 ± 2.13	1	2.70	0.007	14.15 ± 5.24
No. flowers	1	−1.56	0.12	−0.22 ± 0.14	1	−4.61	0.0001	−1.29 ± 0.28

Notes: The three control plots have been pooled for this analysis. $N = 760$ plants for *E. mediohispanicum*, and $N = 337$ plants for *E. baeticum*. Year and its interactions were introduced in the models to control for temporal changes in ungulate preferences. Because results were not significant for these factors ($P > 0.1$ for all analyses), they were omitted from definitive models.

† The whole-model log-likelihood was 411.29 for *E. mediohispanicum* and 226.82 for *E. baeticum*.

‡ The whole-model R^2 was 0.10 for *E. mediohispanicum* and 0.22 for *E. baeticum*.

§ The whole-model R^2 was 0.02 for *E. mediohispanicum* and 0.19 for *E. baeticum*.

Microhabitat × Ungulate exclusion interaction term (Table 4). Plants located under shrubs had the lowest fruit set in ungulate-excluded plots, but the highest fruit set in control plots (Fig. 4).

The number of fruits produced by the plants also varied between years (Table 4, Fig. 3). Plants attacked by ungulates produced fewer fruits than those with ungulates excluded, for every study year ($P < 0.001$ in all years for both plant species, one-way ANOVAs; Fig. 5). As observed in Fig. 5, ungulate damage greatly decreased fruit production, with plants losing >75% of produced fruits to ungulate damage in some years. Consequently, fruit production was also affected by ungulate exclusion for the two studied species (Table 4), being significantly higher in ungulate-excluded (ex) than in control (c) plots when all years of study were pooled (Fig. 3). However, the magnitude of this benefit varied among years, according to the significant Ungulate exclusion × Year interaction term obtained for both species (Table 4). For *E. baeticum*, nevertheless, for every year there was a significant increase in fruit production inside relative to outside the exclosures ($P < 0.01$ in all cases; Bonferroni-Dunn intra-annual comparisons). In contrast, ungulate exclusion significantly increased *E. mediohispanicum* fruit production in five of the seven study years (Fig. 5). In every year, the magnitude of the difference in fruit production inside vs. outside the exclosure in *E. mediohispanicum* was significantly related to the intensity of herbivory suffered by the plants (number of $\text{fruits}_{\text{ex}} -$ number of $\text{fruits}_{\text{c}} = -41.49 + 12.51$ (log(herbivory rate)); $t = 3.04$, $P = 0.029$, $R^2 = 0.65$, $N = 7$ years).

Microhabitat did not affect *E. mediohispanicum* fruit production, but did affect *E. baeticum* fruit production (Table 4). According to the significant Microhabitat × Ungulate exclusion interaction term in the latter species (Table 4), this effect varied in ungulate-excluded vs. control plots (Fig. 4). There was also a marginally significant Microhabitat × Ungulate exclusion interaction term for *E. mediohispanicum* (Table 4). Indeed, fruit production inside the exclosures was similar in open sites, shrub edges, and under shrub (nonsignificant according to a post hoc Bonferroni-Dunn test). By contrast, outside the exclosures, fruit production of plants located in open sites was significantly lower than fruit production of those located under shrubs ($P < 0.05$ according to a post hoc Bonferroni-Dunn test), but not in shrub edges (Fig. 4).

E. mediohispanicum seed production also varied among years and between ungulate-exclusion treatments (Table 4, Fig. 3), being significantly higher inside the fences for all years of study pooled. However, there was a significant Year × Ungulate exclusion interaction, because fences significantly benefited seed production only during 2001 ($P < 0.0001$, one-way ANOVA). Seed production was not affected by the microhabitat, although there was a marginally significant Ungulate exclusion × Microhabitat interaction (Table 4). Thus, although seed production gradually increased in control plots from open sites to shrub edges to under shrubs, in ungulate-excluded plots the highest seed production was obtained by plants inhabiting open sites (Fig. 4). For every year, the magnitude of the difference in *E. mediohispanicum* seed production

TABLE 4. Summaries of the three-way ANOVAs testing the effect of the experiment on the estimate of the reproductive output considered for the two species of *Erysimum*.

	Erysimum mediohispanicum				*Erysimum baeticum*			
Source of variation	df	ss	*F*	*P*	df	ss	*F*	*P*
No. flowers								
Year (Y)	5	7.30	26.64	0.0001	3	2.94	23.15	0.0001
Ungulate exclusion (U)	1	0.03	0.43	0.511	1	1.25	29.51	0.0001
Microhabitat (M)	2	0.50	3.67	0.026	2	0.35	4.17	0.016
Y × U	5	0.58	2.12	0.076	3	0.56	4.40	0.004
Y × M	10	1.71	0.21	0.002	6	0.12	0.49	0.815
U × M	2	0.05	0.02	0.709	2	0.04	0.46	0.634
Y × U × M	10	2.04	0.25	0.0003	6	0.12	0.47	0.831
Residuals	1300	76.01			611	25.87		
No. fruits								
Year	5	23.97	34.82	0.0001	3	18.82	41.47	0.0001
Ungulate exclusion	1	4.38	25.44	0.0001	1	18.82	128.92	0.0001
Microhabitat	2	0.16	0.47	0.622	2	4.41	15.10	0.0001
Y × U	5	7.41	10.76	0.0001	3	6.39	14.60	0.0001
Y × M	10	5.31	3.85	0.0002	6	1.50	1.72	0.114
U × M	2	0.81	2.35	0.095	2	2.07	7.10	0.0009
Y × U × M	10	0.45	3.27	0.001	6	1.09	1.24	0.280
Residuals	1300	190.90			611	89.21		
Fruit set								
Year	5	6.79	21.07	0.0001	3	5.07	25.08	0.0001
Ungulate exclusion	1	2.40	29.85	0.0001	1	7.18	106.48	0.0001
Microhabitat	2	0.32	2.01	0.134	2	1.60	8.90	0.0001
Y × U	5	3.38	10.51	0.0001	3	1.80	11.83	0.0001
Y × M	10	3.34	5.19	0.048	6	0.82	2.02	0.061
U × M	2	0.49	3.05	0.0008	2	1.34	9.92	0.0001
Y × U × M	10	2.35	3.65	0.0007	6	0.70	1.65	0.130
Residuals	1300	89.21			611	41.07		
No. seeds†								
Year	5	38.91	17.49	0.0001				
Ungulate exclusion	1	23.34	41.97	0.0001				
Microhabitat	2	0.14	0.26	0.613				
Y × U	5	41.16	18.95	0.0001				
Y × M	10	19.03	8.55	0.0001				
U × M	2	1.81	3.24	0.072				
Y × U × M	10	8.30	3.73	0.005				
Residuals	1300	618.01						

Notes: All variables were log-transformed prior to analyses except Fruit set, which was arcsine-transformed. Only six years were used for *E. mediohispanicum*. Block was not introduced in this analysis because it generated singularity in the variance–covariance matrix. The whole-model R^2 values were as follows: for *E. mediohispanicum* no. flowers, $R^2 = 0.11$; for *E. baeticum* no. flowers, $R^2 = 0.09$; for *E. mediohispanicum* no. fruit, $R^2 = 0.18$; for *E. baeticum* no. fruit, $R^2 = 0.19$; for *E. mediohispanicum* fruit set, $R^2 = 0.16$; for *E. baeticum* fruit set, $R^2 = 0.21$; and for *E. mediohispanicum* no. seeds, $R^2 = 0.17$.

† No data for *E. baeticum* no. seeds are available.

between treatments was also significantly related to the rate of herbivory (number of seeds_{ex} − number of $\text{seeds}_{\text{c}} = -452\,574 + 16\,514(\log(\text{herbivory rate}))$; $t = 25.85$, $P = 0.01$, $R^2 = 0.90$, $N = 6$ years).

Effect of ungulate exclusion and microhabitat on postdispersal seed predation

1999 postdispersal seed predation experiment.—The postdispersal seed predation rate was low in the two species of *Erysimum* during the first experiment. Thus, 20.1% ± 2.8% of the *E. baeticum* seeds open to all predators were consumed at the end of the experiment (Fig. 6). Although in the most inclusive model no effect of treatment was found (Table 5), all treatments significantly differed from control groups (Fig. 6). In addition, it seems that the major seed predators of this species were ants and rodents, because 14.4% ± 2.6% of the seeds excluded only from vertebrates and thus open to beetles and ants and 15.8% ± 3.1% of the seeds open only to ants were consumed (Fig. 6). Similarly, 24.6% ± 3.3% of the *E. mediohispanicum* seeds open to all predators were consumed. In this case, 23.3% ± 3.2% of the seeds open to beetles and ants and 20.8% ± 3.2% of those open only to ants disappeared. These findings suggest that the most important predators of the two *Erysimum* species are ants, which consumed between 75% and 84% of the predated seeds, followed by rodents.

Although predation rate did not vary among microhabitats for any species (Table 5), it was highest under shrubs (21.3% ± 3.3% and 31.3% ± 3.5% for *E. baeticum* and *E. mediohispanicum*, respectively), inter-

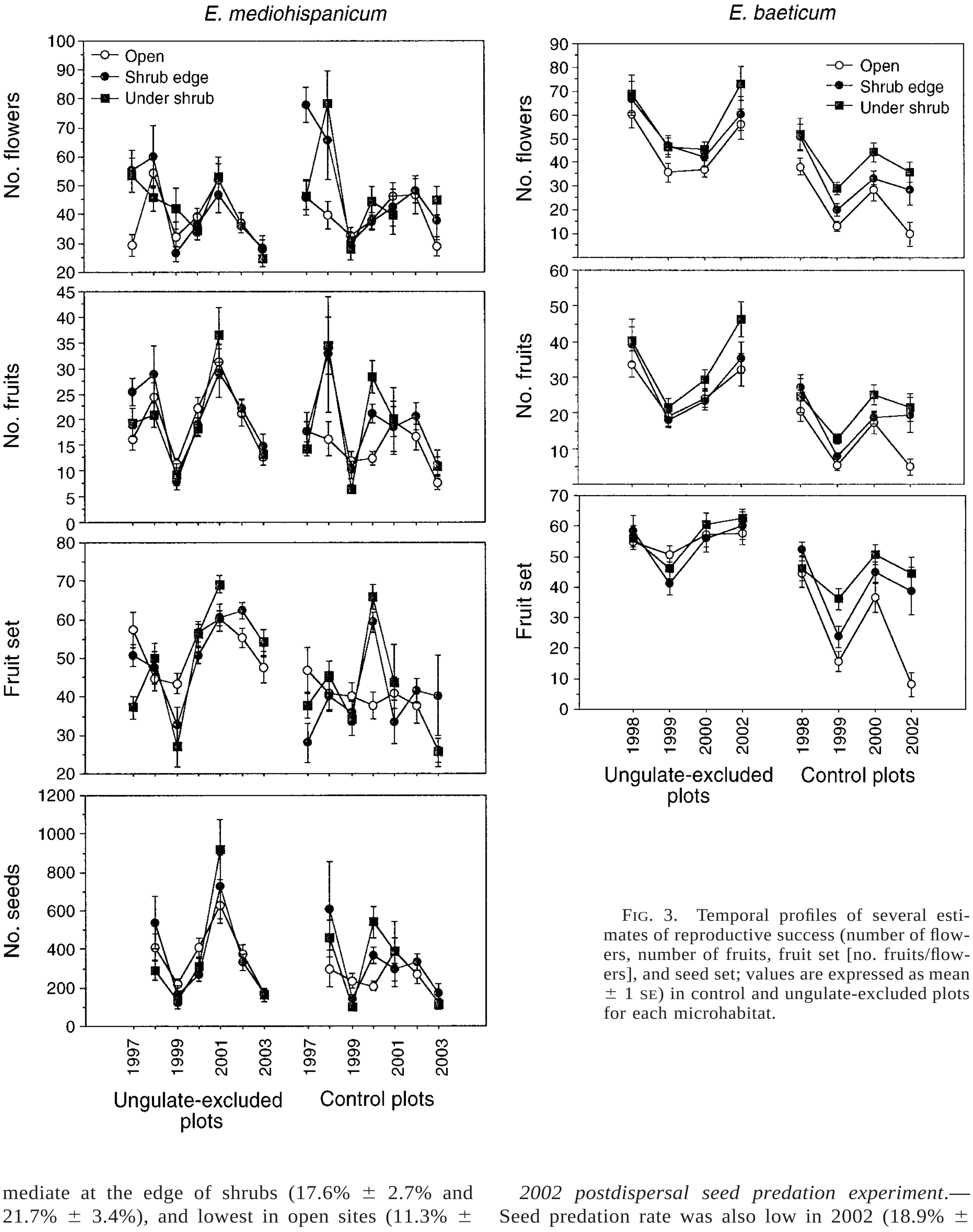

FIG. 3. Temporal profiles of several estimates of reproductive success (number of flowers, number of fruits, fruit set [no. fruits/flowers], and seed set; values are expressed as mean ± 1 SE) in control and ungulate-excluded plots for each microhabitat.

mediate at the edge of shrubs (17.6% ± 2.7% and 21.7% ± 3.4%), and lowest in open sites (11.3% ± 2.2% and 15.5% ± 2.3%; Fig. 6). The experiments also suggest that predation rate was spatially constant for both species, since no difference was found between blocks. Furthermore, the absence of any significant interaction term (Table 5) means that the relative intensity of predation rate by the different predators was similar in all microhabitats (Fig. 6).

2002 postdispersal seed predation experiment.—Seed predation rate was also low in 2002 (18.9% ± 1.2%; Fig. 7). It was affected by the ungulate exclusion (Table 5): predators consumed 15.5% ± 1.6% of the seeds in the control plots and 22.1% ± 1.7% in the ungulate-excluded plots. The significant Block × Ungulate exclusion interaction term indicates that this effect of ungulate exclusion was not similar in both blocks. In fact, as shown in Fig. 7, predation rate was

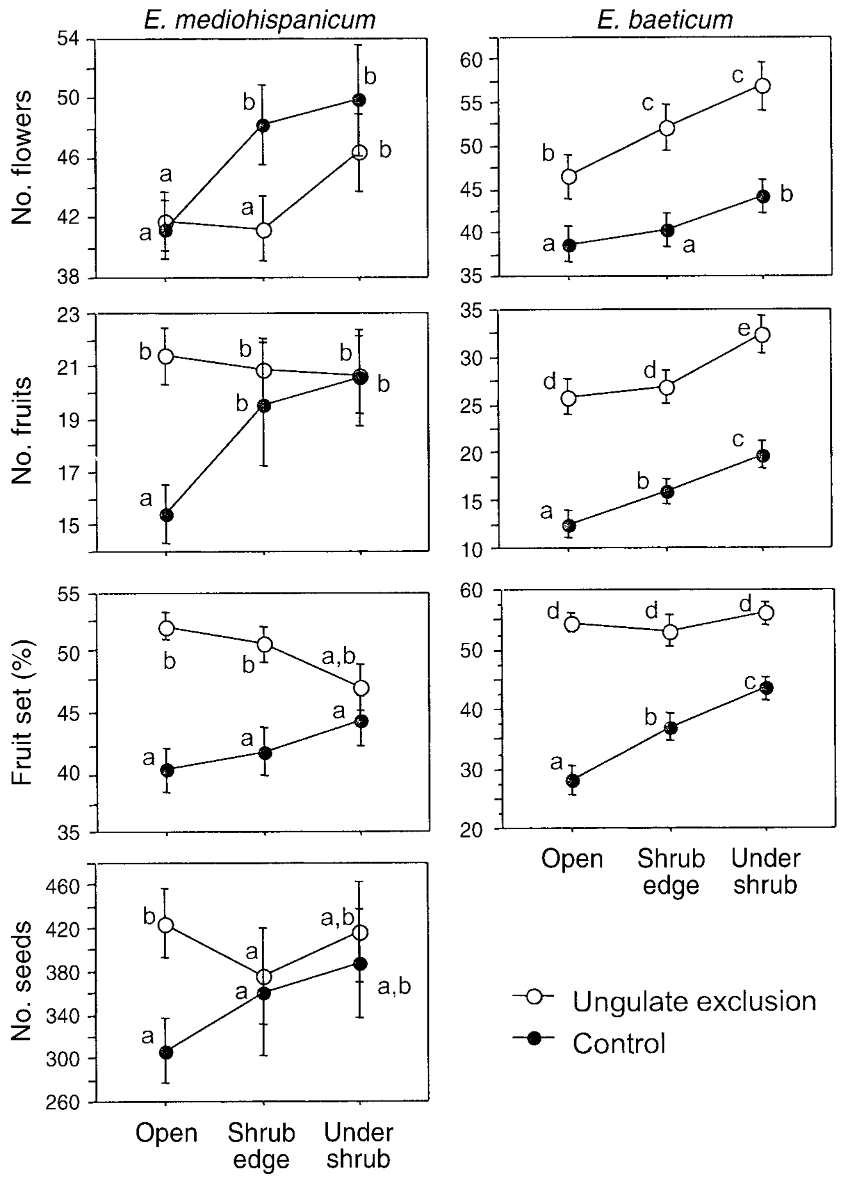

FIG. 4. Among-microhabitat differences in *Erysimum* reproductive success (mean ± 1 SE). Within each panel, figures with different letters are statistically different at $\alpha < 0.05$ after Bonferroni correction.

significantly higher inside the fences only in block II. No effect of microhabitat was found in this experiment (Table 5, Fig. 7).

Effect of ungulate exclusion and microhabitat on seedling establishment

The abundance of naturally established seedlings was extremely low for both *Erysimum* species, ranging, on average, between 2 and 5 seedlings/m^2 (Fig. 8). In addition, seedling abundance was not affected in either species by ungulate exclusion (for *E. mediohispanicum*, $\chi^2 = 0.02$, df = 1, $P = 0.88$; for *E. baeticum*, $\chi^2 = 1.87$, df = 1, $P = 0.17$) or microhabitat (for *E. mediohispanicum*, $\chi^2 = 0.52$, df = 2, $P = 0.77$; for *E. baeticum*, $\chi^2 = 0.41$, df = 2, $P = 0.82$). As observed in Fig. 8, no apparent difference in seedling abundance existed between ungulate-excluded and control plots. The Ungulate exclusion × Microhabitat interaction term was significant only for *E. baeticum* ($\chi^2 = 5.79$, df = 2, $P = 0.05$), not for *E. mediohispanicum* ($\chi^2 = 1.29$, df = 2, $P = 0.52$); the abundance of seedlings was higher in the open microhabitat outside than inside the exclosure (Fig. 8).

Seedling emergence rate (percentage of experimental seeds producing a seedling) was low for both species: 19.3% ± 1.4% for *E. baeticum* and 9.3% ± 1.6% for *E. mediohispanicum*. Similarly to natural abundance, seedling emergence was not affected by the microhab-

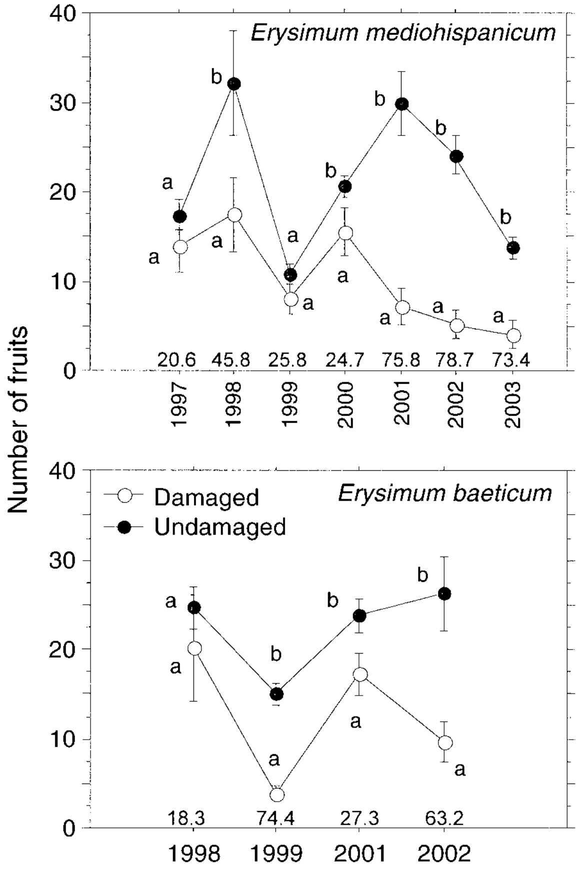

FIG. 5. Difference in fruit production (mean ± 1 SE) between ungulate-damaged and undamaged plants in control plots. The percentage differences are the values above the *x*-axes. Figures with a different letter for each year are statistically different at $\alpha < 0.05$ after Bonferroni correction.

itat (for *E. mediohispanicum*, $\chi^2 = 0.40$, df = 2, $P = 0.82$; for *E. baeticum*, $\chi^2 = 0.71$, df = 2, $P = 0.70$) for either of the two plant species, even though, in general, the emergence rate was slightly higher in open sites (Fig. 8). Ungulate exclusion affected seedling emergence in *E. mediohispanicum* ($\chi^2 = 4.33$, df = 1, $P = 0.04$) but not in *E. baeticum* ($\chi^2 = 2.36$, df = 1, $P = 0.12$), because it was slightly higher in control plots (Fig. 8). However, the Microhabitat × Ungulate exclusion interaction term was significant for both *Erysimum* species (for *E. mediohispanicum*, $\chi^2 = 23.22$, df = 2, $P = 0.0001$; for *E. baeticum*, $\chi^2 = 129.30$, df = 2, $P = 0.0001$), indicating that the effect of microhabitat differed in ungulate-excluded vs. control plots. Thus, in *E. mediohispanicum*, emergence rate was significantly higher in open sites only in control plots, whereas in ungulate-excluded plots it was similar across microhabitats. In *E. baeticum*, in contrast, emergence rate was significantly higher in open sites and shrub edges in the ungulate-excluded plots, being similar across microhabitats in the control plots (Fig. 8).

The time to seedling emergence differed greatly among microhabitats for *E. mediohispanicum* (likelihood ratio [LR], $\chi^2 = 8.72$, $P = 0.01$), being faster for seeds sown in open sites (median = 39 days) than for seeds located at shrub edges and under shrubs (median 46 days; Fig. 9). No effect of ungulate exclusion (LR, $\chi^2 = 2.08$, $P = 0.15$) or the interaction term (LR, $\chi^2 = 2.95$, $P = 0.23$) was found. For *E. baeticum* there were no effects of microhabitat (LR, $\chi^2 = 2.01$, $P = 0.37$), ungulate exclusion (LR, $\chi^2 = 2.23$, $P = 0.13$), or the interaction term (LR, $\chi^2 = 2.75$, $P = 0.25$) on the time to emergence (median = 27 days in all cases; Fig. 9).

Survival of *E. baeticum* seedlings during the first year, the only species for which I quantified this variable, was not affected by microhabitat (LR, $\chi^2 = 4.32$, $P = 0.11$), or ungulate exclusion (LR, $\chi^2 = 0.01$, $P = 0.95$), although in control plots there was a higher between-microhabitat difference in survival (76% for under shrubs, 74% for shrub edges, and 64% for open) than in ungulate-excluded plots (75%, 73%, and 67%, respectively). The most frequent mortality factors in control plots were trampling by ungulates (50% of the dying seedlings), desiccation (49%), and damage by unidentified invertebrates (<1%). In ungulate-excluded plots, >95% of the seedlings died due to drought; the remainder died due to invertebrate damage.

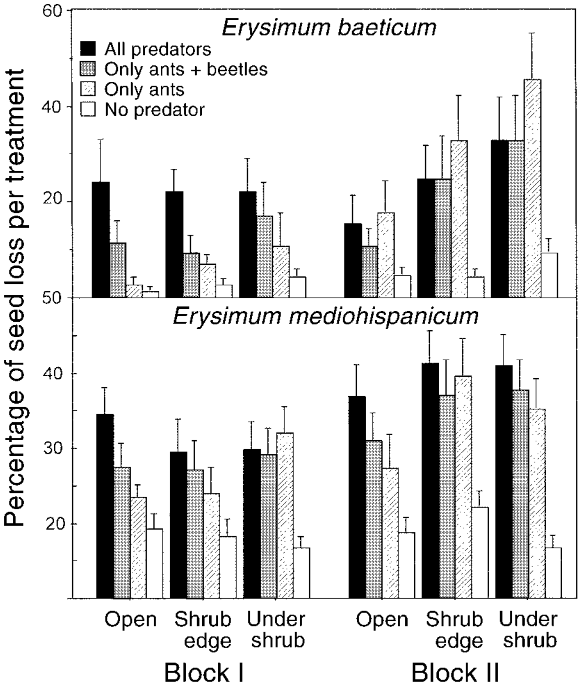

FIG. 6. Summary of the results of the 1996 experiment testing the effect of microhabitat and type of predator on *E. mediohispanicum* and *E. baeticum* postdispersal seed predation rate (mean ± 1 SE).

TABLE 5. Summary of the REML-ANOVAs testing the effect of microhabitat, the type of predators (1999 experiment), and the ungulate exclusion (2002 experiment) on the percentage of seeds lost per seeding point to postdispersal seed predation.

		Erysimum baeticum			*Erysimum mediohispanicum*		
Source of variation	df	SS	*F*	*P*	SS	*F*	*P*
1999 experiment							
Microhabitat (M)	2	0.77	3.23	0.24	0.14	0.52	0.66
Treatment (T)	3	0.94	2.61	0.23	7.69	18.87	0.01
Block (B)†	1	0.27	2.23	0.27	0.58	4.20	0.17
M × T	6	0.32	0.45	0.84	0.67	0.83	0.59
M × B	2	0.28	1.17	0.31	0.54	1.99	0.22
T × B	3	1.47	4.12	0.007	0.06	0.11	0.95
M × T × B	6	0.25	0.34	0.91	0.09	0.11	0.99
Residuals	312	37.21			42.39		
2002 experiment‡							
Microhabitat (M)	1				0.11	1.69	0.195
Ungulate exclusion (U)	1				0.52	8.05	0.005
Block (B)†	1				0.00	0.14	0.709
M × U	1				0.12	1.98	0.170
M × B	1				0.12	2.03	0.160
U × B	1				0.88	14.60	0.0001
M × U × B	1				0.00	0.01	0.970
Residuals	268				10.98		

Note: The dependent variable was arcsine-transformed prior to analysis.

† Block was included as random.

‡ The 2002 experiment was performed only with *Erysimum mediohispanicum* (see *Methods: Effects of ungulate exclusion and microhabitat on postdispersal seed predation*).

Effect of ungulate exclusion on Erysimum *spatial distribution*

At the onset of the experiment, most plants in both species were associated with shrubs; only 11% of *E. baeticum* individuals and 17% of *E. mediohispanicum* individuals were growing in open areas (Fig. 10). This spatial pattern was similar in control and ungulate-excluded plots, and was statistically different from the expected pattern according to the relative percentage of the plots covered by each microhabitat (Fig. 10). For *E. baeticum*, spatial distribution was affected by both the exclusion of ungulates and the year of study (Table 6). In control plots there were more plants associated with shrubs than expected according to a random distribution. This association was maintained during the entire study period (Fig. 10). In the ungulate-excluded plots, by contrast, the percentage of plants that colonized open sites increased throughout the experimental period (Fig. 10). As observed in Table 6, the spatial distribution of *E. mediohispanicum* was also affected by the exclusion of ungulates. In control plots, the plants were highly associated with shrubs, yet open sites were the most abundant microhabitat (Fig. 10). For this reason, the observed spatial distribution differed from the expected distribution in every year after the initial one (Fig. 10). In the ungulate-excluded plots, the plants began to colonize open areas one year after the start of the experiment and, consequently, their observed spatial distribution became statistically similar to the expected distribution (Fig. 10).

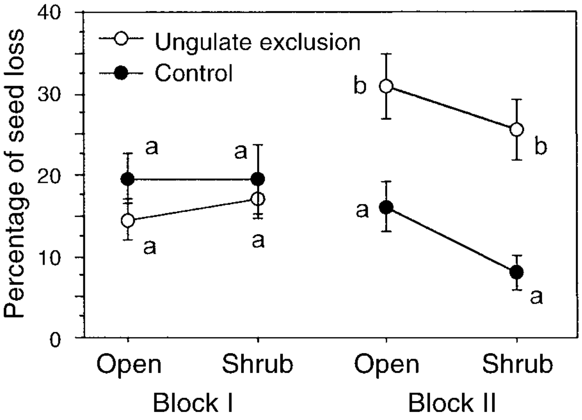

FIG. 7. Summary of the results of the 2002 experiment testing the effect of microhabitat and ungulate exclusion on *E. mediohispanicum* postdispersal seed predation rate. Symbols with different letters are statistically different at $\alpha < 0.05$ after Bonferroni correction; values are means ± 1 SE.

Effect of ungulates on plant abundance

The abundance of *Erysimum* species was affected by the ungulate exclusion. At the onset of the experiment, the abundance of the two species was similar between control and ungulate-excluded plots, about 5 flowering individuals/100 m^2 for *E. mediohispanicum* and 9 flowering individuals/100 m^2 for *E. baeticum* (Fig. 11). However, there was a significant increase in the abundance of flowering plants inside the fences, and the models built to test the change in plant abundance in relation to ungulate presence were significant for both *E. mediohispanicum* ($F_{14, 271}$ = 17.90, P = 0.0001, R^2

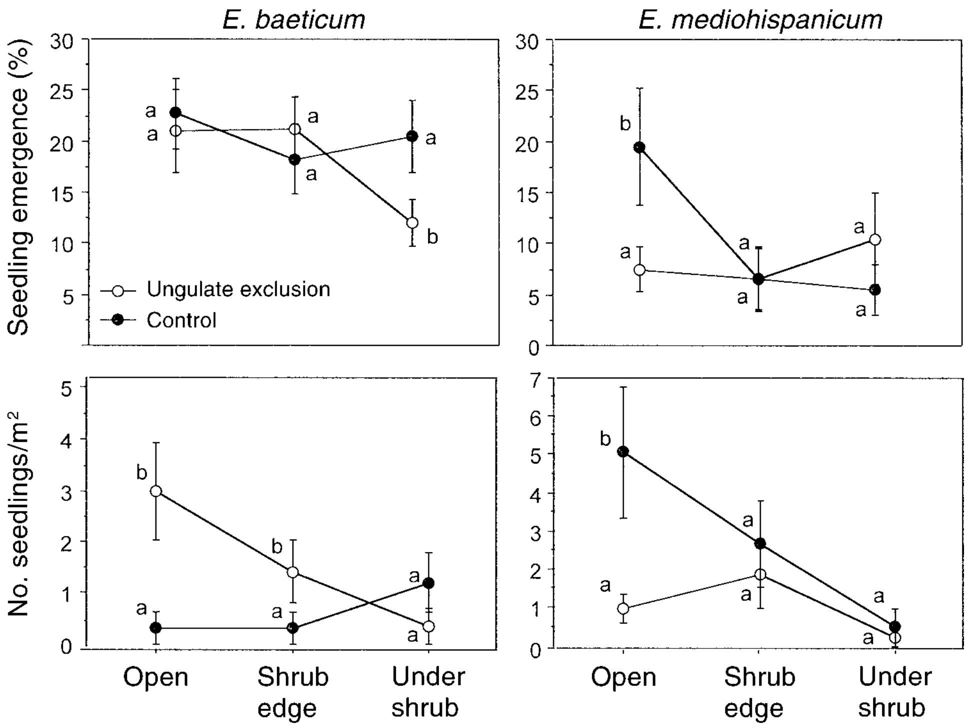

FIG. 8. Effect of ungulate exclusion and microhabitat on emergence rate (estimated as percentage of seeds producing seedlings) and seedling abundance (no. seedlings/m^2) in both *Erysimum* species during 1999. Within panels, different letters indicate statistically significant differences at $\alpha < 0.05$ after Bonferroni correction; values are means ± 1 SE.

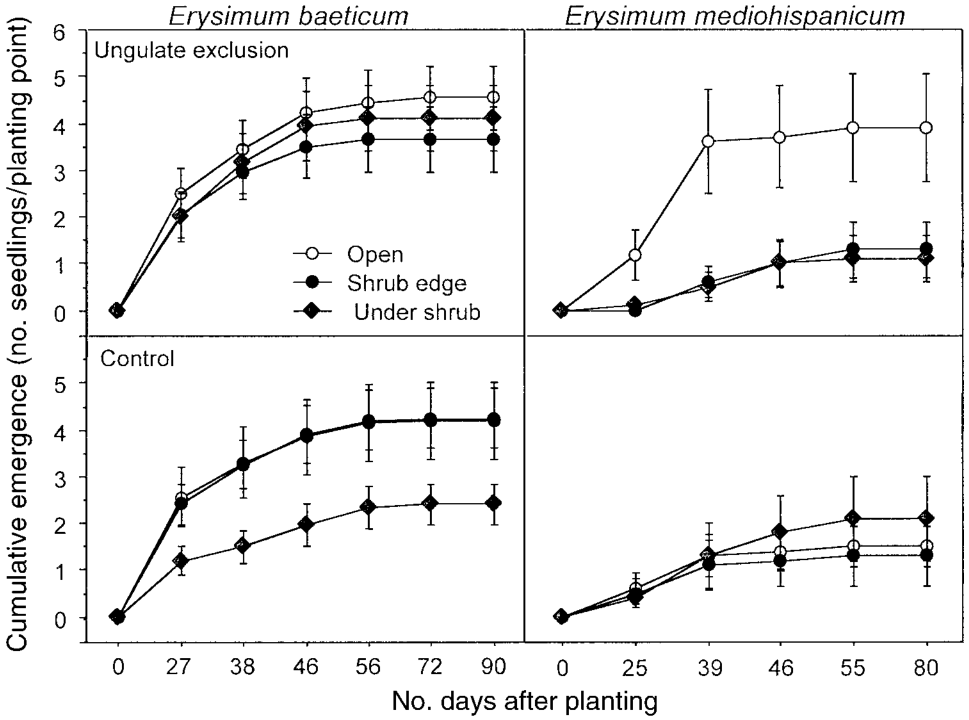

FIG. 9. Effect of ungulate exclusion and microhabitat on emergence timing, estimated by cumulative curves of emerged seedlings (mean ± 1 SE).

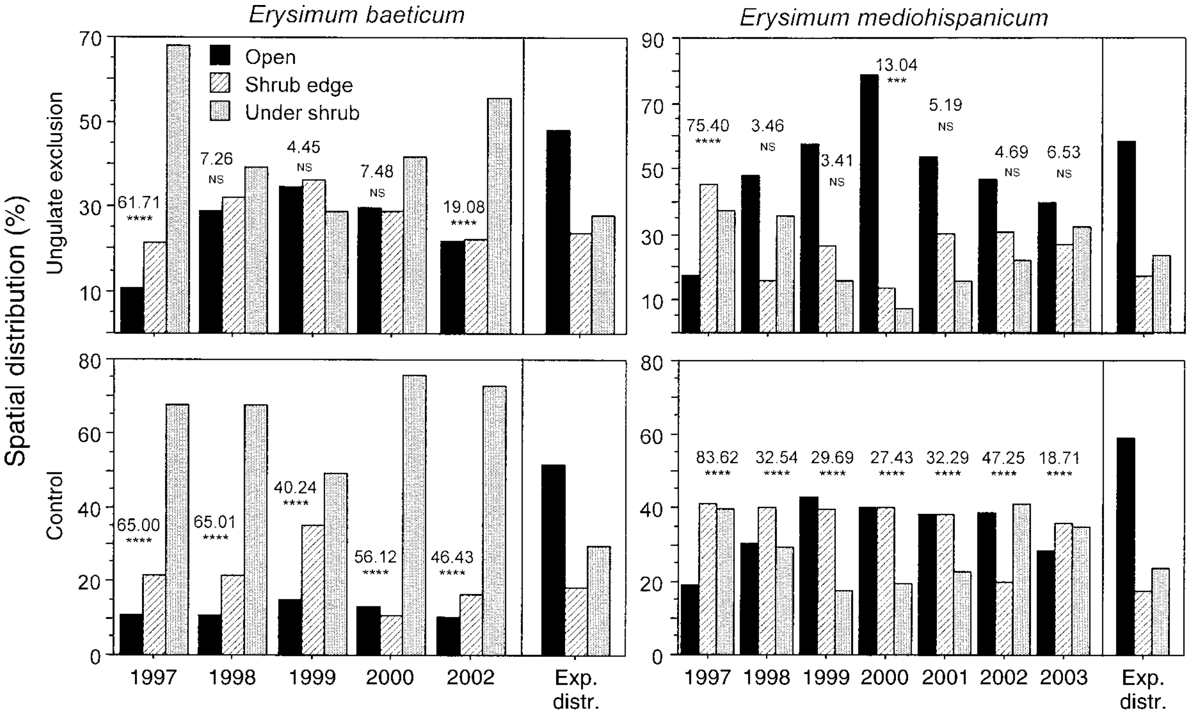

FIG. 10. Spatial distribution pattern of flowering individuals of *E. baeticum* and *E. mediohispanicum*. The figures show the percentage of plants located in each microhabitat every year in control and ungulate-excluded plots. Also shown on the right of each panel for each species is the percentage of the landscape covered by each microhabitat, used to find the expected spatial distribution pattern (Exp. distr.) of plants. The number appearing above each distribution refers to the Wald χ^2 testing the difference between observed and expected spatial distribution patterns (NS, nonsignificant; *** $P < 0.001$; **** $P < 0.0001$).

$= 0.48$) and *E. baeticum* ($F_{11,268} = 24.13$, $P = 0.0001$, $R^2 = 0.50$). As observed in Table 7, there was a significant effect of ungulate exclusion on the overall abundance of the two species. In fact, pooling all years of study, abundance was significantly higher in ungulate-excluded plots (for *E. mediohispanicum*, 11.30 ± 0.91 flowering individuals/100 m^2, $N = 152$ censuses; for *E. baeticum*, 10.63 ± 1.22, $N = 140$ censuses) than in control plots (for *E. mediohispanicum*, 6.86 ± 0.69 individuals/100 m^2, $N = 134$ censuses; for *E. baeticum*, 6.93 ± 0.89, $N = 140$ censuses). In addition, the significant Ungulate exclusion × Year interaction term suggests that the difference in abundance was not temporally consistent (Table 7). In fact, the abundance of plants was quite similar in both kinds of plots, fenced and unfenced, until 1999, the third experimental year (Fig. 11). After this year, the abundance of plants started to increase faster inside the fences (Fig. 11).

The increase of *Erysimum* abundance inside the fences was not similar for all microhabitats; the number of plants inhabiting open sites and shrub edges signifi-

TABLE 6. Summary of the log-linear analysis testing the effect of ungulate exclusion on *Erysimum mediohispanicum* and *E. baeticum* spatial pattern of distribution, quantified as the percentage of flowering plants appearing in each microhabitat.

	E. mediohispanicum			*E. baeticum*		
Source of variation	df	χ^2	*P*	df	χ^2	*P*
Ungulate exclusion (U)	6	18.72	0.0001	6	7.77	0.020
Year (Y)	2	58.10	0.0001	2	16.09	0.003
Block (B)	4	2.38	0.660	2	1.02	0.601
U × Y	6	17.93	0.006	6	2.95	0.565
U × B	4	1.28	0.860	2	0.42	0.811
Y × B	4	34.35	0.0000	2	1.75	0.417
U × Y × B	4	18.99	0.0000	2	1.63	0.440
No. Plants	1067			1037		

Note: The whole-model goodness of fit is as follows: for *E. mediohispanicum*, $R^2 = 0.16$, $\chi^2 = 370.73$, $P = 0.0001$; for *E. baeticum*, $R^2 = 0.10$, $\chi^2 = 77.04$, $P = 0.0001$.

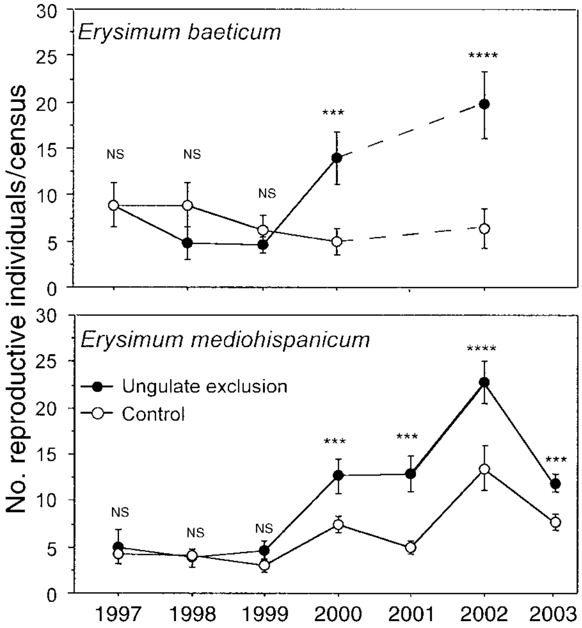

FIG. 11. Temporal variation in *E. baeticum* and *E. mediohispanicum* density (number of flowering plants per 100 m^2; mean ± 1 SE) in control and ungulate-excluded plots during the seven study years. Intra-annual between-treatment comparisons were performed by using one-way ANOVAs after data transformation (NS, nonsignificant; *** $P < 0.001$; **** $P < 0.0001$).

cantly increased inside the fences (Fig. 12). A significant effect of both ungulate exclusion and the interaction between ungulate exclusion and year on the abundance of both *Erysimum* species inhabiting these two microhabitats was observed (Table 7). By contrast, there was no effect of fencing on the number of *E. mediohispanicum* plants located under shrubs, whereas the effect on *E. baeticum* was temporally inconsistent; in some years the abundance of plants under shrubs was higher in control plots, whereas other years it was higher in ungulate-excluded plots (Fig. 12, Table 7).

DISCUSSION

Spatiotemporal variation in the interaction between ungulates and plants

Erysimum mediohispanicum and *E. baeticum* were damaged by ungulates in every year of the study, and observations suggest that herbivory by ungulates is frequent in both plant species in the Sierra Nevada and Sierra de Baza (J. M. Gómez, *personal observation*). However, this long-term study has shown the existence of spatial and, mainly, temporal variation in the intensity of the interaction occurring between ungulates and the two studied plant species. The intensity of herbivory was very low during some years, such as 1998 for *E. baeticum*, when only 11% of the labeled plants were damaged (Fig. 1). By contrast, in some other years, such as 1999 for *E. baeticum* or 2001 for *E. medio-*

TABLE 7. Summary of the generalized linear models testing the effect of ungulate exclusion on *Erysimum mediohispanicum* and *E. baeticum* abundance, quantified as the number of flowering plants per transect.

Source of variation, by microhabitat	*E. mediohispanicum* df	−LR†	χ^2	*P*	*E. baeticum* df	−LR†	χ^2	*P*
Ungulate exclusion (U)	1	1141.38	34.90	0.0001	1	862.63	15.18	0.0001
Year (Y)	5	1389.32	530.80	0.0001	4	886.00	61.93	0.0001
U × Y	5	1137.79	27.72	0.0001	4	912.72	115.37	0.0001
Block	3	1179.97	112.08	0.0001	2	1106.07	502.08	0.0001
Deviance‡	271	1167.55			268	865.90		
Open								
Ungulate exclusion	1	708.45	6.17	0.013	1	382.16	25.76	0.0001
Year	5	777.65	144.56	0.0001	4	371.66	4.76	0.190
U × Y	5	720.92	31.10	0.0001	4	375.03	11.50	0.009
Block	3	799.33	187.92	0.0001	2	382.25	25.97	0.0002
Deviance	248	583.61			268	222.11		
Shrub edge								
Ungulate exclusion	1	616.33	6.26	0.012	1	341.31	12.63	0.0004
Year	5	671.14	115.89	0.0001	4	335.61	1.23	0.750
U × Y	5	626.21	26.64	0.0001	4	346.99	23.99	0.0001
Block	3	653.22	80.04	0.0001	2	360.24	50.47	0.0001
Deviance	248	446.65			268	213.83		
Under shrub								
Ungulate exclusion	1	659.97	1.105	0.293	1	537.83	2.73	0.098
Year	5	764.09	209.34	0.0001	4	539.20	70.06	0.0001
U × Y	5	664.69	10.55	0.061	4	509.07	57.51	0.0001
Block	3	694.80	70.76	0.0001	2	574.22	181.59	0.0001
Deviance	251	581.10			268	455.57		

Notes: The interactions involving block cannot be resolved because the three blocks were pooled prior to analysis (see *Methods: Data analysis*).

† LR is the likelihood ratio.

‡ Goodness of fit of the models is shown by the deviance likelihood.

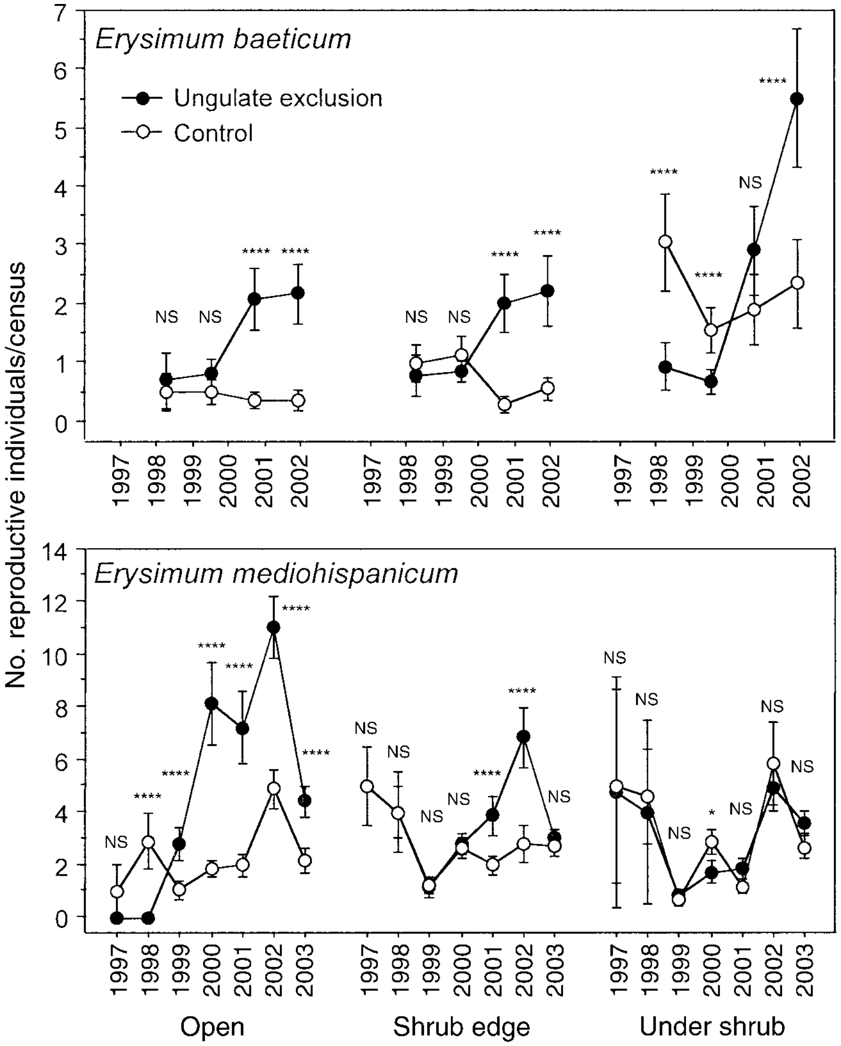

FIG. 12. Microhabitat and temporal variation in *E. baeticum* and *E. mediohispanicum* density (number of flowering plants per 100 m^2; mean ± 1 SE) in control and ungulate-excluded plots throughout the seven study years. Intra-annual between-treatment comparisons were performed by using one-way ANOVAs after data transformation (NS, nonsignificant; *** $P < 0.001$; **** $P < 0.0001$).

hispanicum, ungulates had a very strong impact on plants, damaging up to 50% of the labeled individuals and consuming >80% of the plant tissues (Fig. 1). Temporal variability in the intensity of the interaction between plants and herbivores has been shown for many different kind of herbivores, such as seed predators, nectar robbers, folivores, or floral herbivores (Traveset 1995, Ehrlén 1996, Root 1996, Sperens 1997, Thompson 1998, Piquera 1999, Gómez and Zamora 2000*a, b,* Utelli and Roy 2001, Leimu et al. 2002).

The causes provoking temporal variability in herbivory intensity can be very diverse, whether intrinsic (i.e., plant changes in the amount and quality of chemical compounds) or extrinsic (i.e., climatic variability leading to changes in herbivore load). I believe that, in my study systems, the major factors explaining temporal variability in the interaction between mammalian herbivores and plants were all extrinsic. Both domestic sheep and Spanish ibex are generalist herbivores that feed on *Erysimum* during midsummer, when most other plants are drying up. In years with high availability of alternative resources due to an increase in rainfall regimes, their incidence on *Erysimum* will surely decrease. In fact, I found a significant negative correlation ($r = -0.77$, $P = 0.04$, $n = 7$ years; Pearson correlation) between damage to *E. mediohispanicum* and the spring–early summer rainfall (May–July), indicating that herbivore damage increased in dry years when alternative resources are scarce (no data are available for *E. baeticum*). In this respect, Osem et al. (2004) have recently proposed that the yearly rainfall regime is a crucial factor determining the damage intensity and the magnitude of population response of plants to grazing in Mediterranean and semiarid environments. Nevertheless, other factors can also explain the temporal variability in the interaction reported in the current study. For example, yearly alterations in the grazing regimes of sheep in Sierra de Baza and in the altitudinal movements of both wild and domestic ungulates can also provoke temporal variability if ungulates feed during the ''wrong'' time of the year (i.e., when *Erisymum* plants have dispersed the seeds, or when there is still much alternative food). In a similar way, Piqueras (1999) reported that damage intensity to *Trientalis europaea* in Sweden varied between years due to concomitant temporal fluctuations in the population of voles, its major herbivore, rather than to changes in plant traits.

In addition to temporal variation, significant between-microhabitat variability in the interaction between plants and ungulates was also found. Plants were less damaged when growing under shrubs (Fig. 2). Protection by shrubs against herbivore damage, a phenomenon called ''associational plant refuge'' or ''associational resistance,'' has been shown repeatedly for other plant species (i.e., Callaway and D'Antonio 1991, Callaway et al. 1991, Huntly 1991, Hjälten et al. 1993, Callaway 1995, Wahl and Hay 1995, Hjälten and Price 1997, Callaway and Davis 1998, Rousset and Lepart 1999, 2000, Rebollo et al. 2002). More importantly, the benefit of growing where completely protected by shrubs has been shown for some trees co-occurring with *Erysimum*, such as *Taxus baccata*, *Acer opalus granatense*, *Quercus ilex*, *Quercus pyrenaica*, or *Pinus sylvestris* (García et al. 2000, Gómez et al. 2001, 2003, Gómez 2004, Gómez-Aparicio et al. 2005). The present study indicates that this spatial pattern of herbivory pressure occurs not only for woody species but also for herbaceous species. Associational resistance can result from several mechanisms. In some cases, a plant escapes damage by growing beneath a protective mechanical barrier produced by other species (Jaksic and Fuentes 1980, Herrera 1991, García et al. 2000). In other cases, herbivory can be avoided by associating with unpalatable or less preferred plants (Atsatt and O'Dowd 1976), because generalist herbivores usually seek the highest quality patches within the habitat (Danell et al. 1991, Hjältén et al. 1993, Hjältén and Price 1997, WallisDeVries et al. 1999, Palmer et al. 2003). I have no data to accurately infer the exact causes of this associational resistance. Nevertheless, the trophic generalism displayed by both sheep and Spanish ibex (e.g., Martínez 1988, 1990, 1995, Fandós 1991, García-González and Cuartas 1992*a*, *b*, Bartolomé et al. 1998) suggests that, as occurs with other plants in the same site, it is based not just on nutritional and chemical attributes of the neighboring plants, but also on the mechanical barriers produced by shrubs (Gómez et al. 2001, 2003, Baraza 2004).

Effect of ungulates on Erysimum *performance*

The effect of ungulates has been analyzed through four components of *Erysimum* perfomance: fecundity, seed survival to postdispersal seed predation, seedling emergence, and survival. I found that herbivorous mammals heavily affected the reproduction of the plants. Thus, damaged plants lost to herbivory >50% of the potential reproductive output; in some years these losses rose to 75% (Fig. 5). A severe effect of herbivores on plant seed production has been reported for other plant species (i.e., Root 1996, Ehrlén 1995*a*, *b*, 2003, Gómez and Zamora 2000*b* and references therein). In this study, nevertheless, the effect of ungulates on plant seed production is even more harmful because the two studied plants are monocarpic. This means that every time the ungulates damage a plant, they are affecting its lifetime production of seeds. Most theoretical and empirical approaches suggest that herbivore effect on plant performance is stronger when plants are annual or perennial monocarpic (Crawley 1997, Maron 1998).

A major factor accounting for this strong effect on plant reproductive output is the feeding style of the herbivores analyzed in this study. Because they fed on reproductive tissue, the percentage of tissue ingested by herbivores can be translated directly to herbivore effect on plant reproduction (Root 1996). In fact, a voluminous literature on plant–animal interactions indicates that herbivores feeding on reproductive structures tend to have a stronger impact on plant reproductive output than herbivores living in the vegetative parts of the plants (Crawley 1989*a*, 1997, Louda and Potvin 1995, Maron 1998, Gómez and Zamora 2000*a*, *b*). This harmful effect is particularly evident in those plant species, such as the two studied species, unable to fully compensate for herbivore damage (Gómez and Zamora 2000*b*). In fact, the compensation ability was low in both species, with only some additional production of flowers occurring in lateral stalks when the main flowering stalk was consumed. This result contrasts with that of Huhta et al. (2000*a*, *b*), who showed that *Erysimum strictum* can fully compensate (even overcompensate) after apical damage. I think that a main factor explaining the low ability of *E. mediohispanicum* and *E. baeticum* to compensate for ungulate damage is related to the timing of damage. *E. strictum* was experimentally clipped during the floral bud stage (Huhta et al. 2000*b*), whereas *E. mediohispanicum* and *E. baeticum* are consumed by ungulates during the fruiting stage. In fact, the compensation ability is highly dependent on the timing of damage (Vaughton 1993, Gómez and Fuentes 2001, Gómez and Zamora 2003).

Another factor affecting the severity of ungulate impact on seed production is related to their foraging behavior. Thus, the risk of being damaged depended on some plant traits for *E. mediohispanicum*. Spanish ibex preferred feeding on larger plants with more and taller flowering stalks and with more flowers (Table 3). Similar preference for high flower number has been reported in other plants, such as *Ipomopsis aggregata*, *Bartsia alpina*, *Daphne laureola*, *Lathyrus vernus*, or

Hormathophylla spinosa (Hainsworth et al. 1984, Molau et al. 1989, Alonso and Herrera 1996, Ehrlén 1997, Gómez and Zamora 2000*a*, *b*). This latter example is especially interesting, because it involves another crucifer species also used by the Spanish ibex in the high mountains of the Sierra Nevada (Gómez and Zamora 2000*b*). The findings reported in this study suggest that large size and the production of many flowers provide not only a benefit in potential reproduction but also a cost to *E. mediohispanicum* plants in the form of heightened risk of being damaged by Spanish ibex. Indeed, it has been shown elsewhere that there is a conflict in *E. mediohispanicum* with respect to the optimal height and number of flowers to produce, because large size and abundant flower production strengthens fitness via pollination but weakens fitness by attracting ungulates (Gómez 2003). In contrast with these results, it seems that sheep did not select *E. baeticum* plants based on morphological traits (Table 3). This outcome is even more paradoxical if we take into account the fact that sheep damaged almost the same percentage of plants in Sierra de Baza that Spanish ibex did in Sierra Nevada, ~40% of the labeled individuals. Nevertheless, the percentage of tissue consumed by sheep did depend on the plant morphological traits. Indeed, these mammals consumed proportionally more tissue in plants bearing wider, shorter, and more stalks and displaying fewer flowers (Table 3). Thus, it seems that sheep preference for plant traits did not manifest itself in the process of attraction to plants, but in the process of tissue consumption.

The exclusion experiments have demonstrated that the postdispersal seed predation is not strong in the two studied *Erysimum* species; it is $<$20% in all cases, and it is produced by a diverse assemblage of organisms, from ants to rodents (Fig. 6). However, it seems that ungulates have an indirect effect on the interaction between the seed predators and *E. mediohispanicum*, because the rate of seed removal by predators was significantly higher inside than outside the exclosures (Table 5 and Fig. 7). Several non-exclusive reasons can account for this result. First, it could be a consequence of exploitative competition occurring between seed predators and ungulates, which means that after ungulates are removed, seed-predator abundance could increase. Competition among ungulates, phytophagous insects, and granivorous rodents has been widely reported (Davidson et al. 1984, 1985, Baines et al. 1994, Tscharntke 1997, Gómez and González-Megías 2002). It may occur as a consequence of resource removal (flowers, fruits, and seeds) as well as of the negative effect of vegetative tissue removal on flower and fruit production (Meyer 1993, Meyer and Root 1993, Müller-Scharer and Brown 1995). In the studied systems, by consuming flowers and fruits, sheep and ibex surely deplete the resources used by granivorous mammals and invertebrates (not only *Erysimum*, but presumably also other plant species, because postdispersal seed predators are highly generalist). Furthermore, when herbivores differ in major traits, such as size, the outcome of competition between them is expected to be highly asymmetrical, with ungulates significantly affecting the populations of small herbivores but not vice versa (Christensen and Whitham 1993, Harrison et al. 1995, Lucas et al. 1998, Gómez and González-Megías 2002). In addition, ungulates can also affect seed predators by changing vegetation structure and thereby altering the shared habitat (Abensperg-Traun et al. 1996, Bestelmeyer and Wiens 1996, Dennis et al. 1997, Seymour and Dean 1999). Several studies have shown that grazing by ungulates indirectly affects ant communities in some disparate ecosystems such as deserts or high mountains (Bestelmeyer and Wiens 1996, González-Megías et al. 2004, and references therein). Nevertheless, irrespective of the reason provoking this increase in seed predation inside the fences, this finding strongly suggests that the removal of ungulates, in addition to having potential positive effects, can have indirect negative effects on plants due to an increase in the rate of seed consumption by animals. Similarly, Smit et al. (2001) have reported that the exclusion of ungulates greatly increased the intensity of predation by small rodents on beechnuts and acorns. These authors think that ungulates decrease seed predation by reducing the habitat quality for small rodents that prey upon those seeds.

The effect of ungulates on early establishment of *Erysimum* was less clear. *Erysimum* seedlings died due mainly to summer drought and trampling by ungulates, two factors widely reported as major mortality agents for many herbaceous and woody Mediterranean plants (Herrera et al. 1994, Castro et al. 1999, 2004, Escudero et al. 1999, Rey and Alcántara 2000, García 2001, Hampe and Arroyo 2002, Mejías et al. 2002, Gómez et al. 2003, Traveset et al. 2003, Gómez 2004). However, although $>$50% of the dying *Erysimum* seedlings in non-fenced plots were killed by trampling, my experimental results suggest that early recruitment of *Erysimum* is not affected by the presence of ungulates. Indeed, seedling emergence and survival were similar in the ungulate-excluded and control plots (Fig. 8). It seems that summer drought can compensate for the amount of seedlings surviving to ungulate trampling, indicating that these two mortality factors are not additive in the study systems.

Do shrubs facilitate Erysimum*?*

The existence of positive interactions between plants is common in environments characterized by strong abiotic and biotic stress, such as the Mediterranean (Bertness and Callaway 1994, Callaway 1995, Brooker and Callaghan 1998, Maestre et al. 2003, Gómez-Aparicio et al. 2004). The facilitative role of nurse plants occurs because they can modify the aboveground and belowground biotic and abiotic variables (protection against high irradiance and temperature, amelioration of drought, enhancement of nutrients in the rhizosphere, protection against herbivore damage, etc.; see Callaway 1992, Pugnaire et al. 1996, Wied and Galen 1998). As previously indicated, several components of *Erysimum* performance have been explored in this study. To know how the shrubs enhance some or all of these components is important in unraveling their protective role.

As a consequence of both the severe effect of ungulate damage on plant seed production and the protection exerted by shrubs against herbivores, the reproductive output of plants was highest under shrubs (Fig. 4). More important, this beneficial effect of shrubs on plant reproduction was only evident in control plots; reproductive success was similar in all microhabitats in the ungulate-excluded plots (see Fig. 4 and the significant U × M interaction terms in Table 4). Although facilitation has been studied intensively in recent years, few examples of plant reproduction improvement due to plant–plant interactions have been found (but see Callaway et al. 2002).

Contrasting with the previous result, shrubs did not have any effect on seed fate for surviving postdispersal predation. Indeed, seed predation was spatially homogeneous; it did not vary among microhabitats for either of the species studied (Tables 5 and 6). This exceptional result contrasts with that of many other studies showing that seeds escape predation in some specific microhabitats (e.g., Russell and Schupp 1998, Alcántara et al. 2000, García 2001, Jordano and Godoy 2002, Rey et al. 2002). A main reason explaining this spatial homogeneity in predation rate can be related to the fact that *Erysimum* seeds are simultaneously consumed by multiple taxa and/or species that may have contrasting microhabitat preferences. This diversity of predators could contribute to homogenize seed attack, because each predator can be more active in a different microhabitat (for similar results, see Castro et al. 1999, Gómez et al. 2003). Thus, rodents prefer to forage in the microhabitats heavily covered by vegetation (Díaz 1992, Wada 1993, Herrera 1995, Kollman and Schill 1996, Manson and Stiles 1998, Alcántara et al. 2000), whereas seed-harvesting ants forage preferentially in open areas (Hulme 1997, 1998, Wilby and Shachak 2000).

Seed germination and seedling emergence were also similar between microhabitats, always lower than 25%. *Erysimum* starts to germinate during late March or early April. During this period, soil water content is similar in open sites and under shrubs (Gómez 2004). This is presumably the main reason for similarity in the probability of seed emergence. In fact, spatial homogeneity in seed germination and emergence also has been shown for other species in the same sites (Castro et al. 2004, Gómez 2004).

In brief, by integrating the results obtained on the most important components of *Erysimum* performance, it seems that shrubs have a positive net effect on these herbs because they decrease herbivory and increase fecundity without affecting other postdispersal processes such as escape from predation, emergence, or seedling survival.

Ungulate effects on plant spatial patterns: the importance of herbivory as determinant of habitat distribution in Erysimum

This study has demonstrated that the spatial distribution of the two species studied is influenced by the activity of ungulates. Thus, under the natural intensity of ungulate pressure existing in both study sites, most *Erysimum* individuals grew under the canopy of co-occurring shrubs, and they were associated with shrubs more than expected according to the relative abundance of this microhabitat (Fig. 10). In contrast, the exclusion of ungulates produced a dramatic redistribution of plants among microhabitats, with the spatial pattern of both plant species changing promptly after ungulate exclusion (Fig. 10). Thus, the spatial pattern of *E. baeticum* became similar to random after two years of exclusion, whereas in *E. mediohispanicum* the percentage of plants growing in open sites was even higher than expected based on the surface covered by this microhabitat (Fig. 10). This modification in the spatial pattern is a rigorous demonstration of the facilitative effect of shrubs on *Erysimum* performance and establishment when ungulates are present. Furthermore, these findings suggest that the environmental conditions under which both species of *Erysimum* grow are only a fraction of the overall range of conditions. In fact, the several experiments done during this study and the outcomes obtained in the ungulate-excluded plots have shown that those parts of the landscape uninhabited by plants in the control plots (the open sites and, to a lesser extent, the shrub edges) actually represent suitable sites. This means that the action of ungulates directly determines the realized niche of both species of *Erysimum* in the study areas.

Several studies have suggested that some herbivores are able to shape the habitat distribution of their host plants (Bruelheide and Scheidel 1999, Kleijn and Steinger 2002, DeWalt et al. 2004). Two pieces of information have been used to support this proposal: the mere existence of habitat dependence in the activity of herbivores (Boyd 1988, C. M. Herrera 1990, 1993, J. Herrera 1991, Gómez 1996, Louda and Rodman 1996, Cabin and Marshall 2000, Sipura and Tahvanainen 2000), and the effect of herbivore release in the habitat expansion of invasive plants (*enemy-release hypothesis*; Keane and Crawley 2002, DeWalt et al. 2004). However, to my knowledge, this study is the first one to experimentally demonstrate a direct causal relationship between the exclusion of herbivores and a significant change in the habitat distribution of plants.

Effects of ungulates on Erysimum *population abundance*

This experimental study has also revealed a significant effect of ungulates in the population dynamics of both species of *Erysimum*. The removal of ungulates produced a significant increase in the abundance of the two species studied (Fig. 11). Furthermore, the increase in plant abundance in ungulate-excluded plots started two years after the onset of the experiment. This temporal delay in the populational response fully matches the life history of both species. Indeed, *E. mediohispanicum* and *E. baeticum* are both biannual species, indicating that any enhancement in plant performance during the years 1997 and 1998, when fences were set up, will translate into an increase in adult abundance two years later (1999 and 2000), as observed in this study (Fig. 11). My long-term experiment (seven years) even allows one to quantify the effect of ungulates on the observed population growth rate of the two species of *Erysimum*. I tentatively calculated the growth rate of the populations ($\log N_{t+i}/N_i$, according to McCallum [2000]) in the ungulate-excluded and control plots. This rate was 0.334 for *E. mediohispanicum* and 0.435 for *E. baeticum* inside the fences, indicating that *Erysimum* populations grew during the experimental period by $\sim$35% in the ungulate-excluded plots. However, the parameter was much lower for the populations located outside, 0.114 for *E. mediohispanicum* and −0.147 for *E. baeticum*, suggesting that population growth was much lower, or even negative, in control plots. Although the experiment has lasted only seven years, I think that the effect of excluding ungulates has produced a permanent increase in the population abundance of plants. Thus, as shown in Fig. 11, there was a decrease in *E. mediohispanicum* abundance in the last year of the study, driven mostly by climatic factors. Despite this, the difference between ungulate-excluded and control plots in plant abundance remained highly significant. I think that the exclusion of ungulates has allowed the plant populations to reach another density level in the study sites.

Because I quantified the abundance of reproductive adults, rather than the density of seedlings or pre-reproductive rosettes, these results prove that ungulates provoke a true effect on the populations of the two considered plant species, irrespective of the putative existence of density-dependent mortality during early-recruitment stages. Linking the effects of ungulates on plant performance and abundance, it seems that the benefit to plant populations of excluding ungulates is produced mainly by an increase in seed production and, to a lesser extent, seedling survival. This suggests that the abundance of *Erysimum* is mostly limited by availability of seeds and that the exclusion of ungulates relaxes this limitation (Müller-Landau et al. 2002, Schupp et al. 2002). Turnbull et al. (2000) have shown that, from a diverse collection of plant species, annual/biannual herbs comprise the highest percentage of species having seed-limited recruitment.

The two *Erysimum* species have many characteristics that facilitate a potential control of their populations by herbivores (Maron and Gardner 2000): (1) ungulates consume flowers and fruits, thus having a direct effect on the reproductive success by the removal of reproductive structures; (2) neither *Erysimum* species studied here can regenerate by vegetative means; (3) these species are short-lived, monocarpic, and do not have a persistent seed bank; (4) ungulates are extreme generalists in the study site. Indeed, according to Crawley (1989*a*) and Louda and Potvin (1995), populations of long-lived plant species having a high capacity for compensation after defoliation and/or large seed banks are less likely to be controlled by herbivores than those lacking any of these characteristics. Furthermore, the propensity of ungulates to feed on bigger plants, those displaying more flowers, may also magnify their detrimental effect, because they are selectively removing individual plants that potentially contribute more to the next year's seed pool.

This study goes one step further and proposes a novel mechanism by which herbivores can presumably affect the population abundance of plants: the colonization of new microhabitats. Thus, as observed in Fig. 12, the increase in plant numbers after excluding ungulates did not occur in all microhabitats with similar intensity, but only in open sites and shrub edges. The observed increase in plant abundance in ungulate-excluded plots was not produced by a homogeneous population increase in the whole landscape, but only by an increase in those parts of the landscape previously unoccupied by plants due to the detrimental effect of ungulates. This means that, although *Erysimum* abundance is probably seed limited, this limitation is not randomly distributed across the landscape but is spatially structured. That is, *Erysimum* seed limitation occurs mainly in some microsites, suggesting that, in heterogeneous environments, seed and establishment limitation are neither exclusive nor independent processes (Schupp et al. 2002). Although I believe that this is a crucial consequence of the interaction occurring between plants and herbivores that deserves much more attention, it has been completely ignored not only in empirical studies but also in most theoretical treatments (Marquis 1992, Crawley 1997, 2000, Olff et al. 1999, Zamora et al. 1999).

Conclusions

I have reported the results of a 7-year ungulate exclusion experiment, demonstrating that these mammalian herbivores had a strong long-term impact on the fecundity, establishment, interaction with postdispersal predators, population dynamics, and spatial population structure of two short-lived herbs. In addition, this study has also demonstrated that ungulates are a main factor determining the habitat distribution of *Erysimum mediohispanicum* and *E. baeticum* in the study sites. In natural conditions, plants are unable to exploit the entire environment because ungulates confine them to specific parts of the landscape. The experimental exclusion of ungulates has allowed the plants to colonize open interspaces. This expansion of the habitat distribution has had significant and unexpected consequences on the population dynamics of the plants, because it has allowed for the maintenance of more abundant populations in the whole study area. This long-term experiment has revealed that, for plants inhabiting heterogeneous landscapes, population abundance and spatial structure are tightly related. These findings suggest that the effect of herbivory on plants can be intricate, affecting not only their performance or population dynamics but also their habitat distribution and niche structure.

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