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# Soil disturbance by a native rodent drives microhabitat expansion of an alien plant

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**Abstract** The "niche opportunity" hypothesis proposes that alien plant establishment is generally driven by the integrated effects of environmental conditions, changes in resource availability and reduced herbivory pressure, but there is yet little evidence supporting such a complex interaction in nature. We evaluated the interactive effects of soil disturbance by the native fossorial mammal *Spalacopus cyanus*, microhabitat (beneath shrubs and open areas), and introduced herbivores (rabbit, *Oryctolagus cuniculus*) on the

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establishment (seedling emergence, adult abundance, aboveground biomass, and reproductive effort) of the alien annual plant Fumaria capreolata in a coastal matorral of central Chile. In the absence of disturbance, seedling emergence and plant establishment of F. capreolata was largely restricted to understory microhabitats. Soil disturbance by S. cyanus significantly increased seedling emergence and establishment, both beneath shrubs and in open areas. There was no effect of herbivore exclusion on the abundance, biomass and reproductive effort of F. capreolata, although the biomass of other co-existing species was reduced. Overall, these results suggest that native fossorial mammals may favor the invasion of F. capreolata by allowing microhabitat expansion into open areas and by increasing its performance in those microhabitats already occupied. We show how the interplay between soil disturbance, microhabitat, and reduced herbivory may explain invasion patterns at the local scale in natural communities.

**Keywords** Habitat expansion · Exotic species · Mediterranean ecosystems · Microenvironment · Resource availability

# Introduction

In the context of classic niche theory (Hutchinson 1959) applied to invasion ecology, Shea and Cheeson

(2002) proposed that the lack of natural enemies, changes in resource availability and favorable environmental conditions interact with each other to generate a "niche opportunity" for invaders, thus increasing their probability of successful establishment. Although the "niche opportunity" hypothesis is widely accepted by invasion ecologists, few field experiments have shown habitat expansion of alien species by such a three-factor interaction (e.g. D'Antonio 1993).

Disturbance is a key driver of alien plant invasions (Davis et al. 2000; Lake and Leishman 2004; Hierro et al. 2005, 2006). Human-induced disturbances often generate a niche opportunity for alien plant species by disrupting native species interactions and changing resource availability (Davis et al. 2000; Byers 2002). In contrast, natural disturbances not always promote plant invasion, partly because native plant communities are somewhat adapted to this type of disturbance. For example, small-scale disturbances, such as mounding by native fossorial mammals, do not promote invasion if native species have the ability to rapidly colonize the mounds (Mazía et al. 2010) or if generalist native herbivores are attracted to the gaps and reduce the performance of the invasive plants (D'Antonio 1993). There are several cases, however, in which these natural disturbance agents facilitated the establishment and spread of alien plants (Hobbs and Mooney 1991; Schiffman 1994; Larson 2003). For instance, soil disturbance by pocket gophers had positive effects on the dynamics of native plant communities but also facilitated the invasion by the alien Bromus mollis in California grasslands (Hobbs and Mooney 1991). In the same ecosystem, giant kangaroo rats promoted the establishment of alien ruderals such as Erodium cicutarium and Bromus madritensis on their burrow precincts at the expense of native species (Schiffman 1994). Likewise, in a semiarid shrubland in central Chile the invasive succulent Mesembryanthemum crystallinum was significantly more abundant in sites with burrows of the fossorial rodent Spalacopus cyanus than in burrowfree adjacent sites (Contreras and Gutiérrez 1991). In these cases, the invasion of a microhabitat (mounds) previously occupied by native species might be explained by fitness advantages of alien species associated with herbivore release/resistance or a greater ability in resource exploitation (McDougall et al. 2009).

Herbivores can play an important role in the invasion process by alien species (Maron and Vilà 2001, Keane and Crawley 2002, Levine et al. 2004, Parker et al. 2006). It has been proposed that alien plants become invasive, in part, because their specialist herbivores are absent in the new range (Keane and Crawley 2002). In a meta-analysis, Parker et al. (2006) found that native herbivores tend to consume exotic plants, thus slowing the invasion process, while exotic herbivores tend to consume native plants, thus favoring exotic plants and promoting invasion. Another meta-analysis reported that vertebrate herbivores prefer to feed on native plants relative to exotic plants, while invertebrate herbivores prefer exotic plants over native plants (Oduor et al. 2010). In several ecosystems the introduction of exotic vertebrate herbivores, such as cattle and rabbits, has driven the dominance of alien plants because of their greater impact on native plants (e.g. Holmgren et al. 2000; Holmgren 2002).

Environmental conditions associated with native vegetation can also affect the successful establishment of alien plants (Newingham et al. 2007; Martin et al. 2009). In semiarid ecosystems, both microclimate and nutrients drastically differ between open areas and those beneath the canopy of shrubs. Areas under shrub canopies are characterized by lower irradiance and air temperature, and higher soil moisture (Del Pozo et al. 1989; Valiente-Banuet and Ezcurra 1991; Callaway 1992; Maestre et al. 2003). In addition, woody species can increase the availability of soil nutrients and organic matter because of the accumulation of litter beneath their canopies in comparison with open areas that are dominated by grasses and forbs (Aguiar and Sala 1994; Gómez-Aparicio et al. 2005). This difference is more marked in the case of Mediterranean-type ecosystems, where herbaceous cover is seasonal (Di Castri et al. 1981). Native woody vegetation can also be a refuge from herbivores for palatable plants (reviewed in Callaway 1995; but see Chaneton et al. 2010). In Chilean semiarid ecosystems, protection from herbivores explained the disproportionate abundance of herbs beneath shrub canopies (Jaksic and Fuentes 1980) and the association between a native perennial vine and both shrubs and cacti (González-Teuber and Gianoli 2008). Furthermore, this associational resistance may increase the probability of recruitment for some alien plants (Iponga et al. 2009).

We carried out a field experiment to evaluate whether microenvironmental conditions, disturbance-

mediated increased resource availability, and reduced herbivory interact to create a "niche opportunity" for invaders in nature. Specifically, in a coastal matorral of central Chile we evaluated the interactive effects of (1) soil disturbance by the native fossorial rodent S. cyanus (Octodontidae), (2) microhabitat determined by native vegetation (beneath shrubs and open areas), and (3) exotic herbivores (rabbits, Oryctolagus cuniculus), on the establishment (seedling emergence and adult abundance) and performance (aboveground biomass and reproductive effort) of the alien plant Fumaria capreolata (Fumariaceae). We expected two possible scenarios. First, the alien plant would take advantage of enhanced microhabitat conditions and reduced herbivory, and therefore would show better performance on rodent mounds beneath shrubs. Second, the alien plant would not depend on canopymediated amelioration of abiotic conditions and would not suffer significant herbivory, and thus would show increased performance on rodent mounds in open areas, with reduced competition from native plants. The latter scenario would imply a microhabitat expansion by F. capreolata, because this alien species it is mainly distributed beneath shrub canopies in the study area.

## Materials and methods

#### Study system

This study was conducted in a south-west facing slope at Los Molles (33°07'S; 71°21'W; 100 m a.s.l.), 20 km E of Viña del Mar, central Chile. The climate is Mediterranean with a mean annual precipitation of 370 mm, falling in the winter, severe summer drought (7–8 months), and the mean annual temperature in the study area is 15°C (Luebert and Pliscoff 2006). These climatic conditions favor the germination of herbs after the first rains and restrict their vegetative period to the months between June and February (Montenegro et al. 1978). The vegetation corresponds to a secondary-type matorral, the most common successional stage nowadays (Holmgren 2002). The main woody species are: Acacia caven, Colliguaja odorifera, Lithraea caustica, Peumus boldus, Quillaja saponaria, and Retanilla trinervia. In open areas, the prevailing herbs are exotics such as Avena barbata, Hypochaeris glabra, Lolium temulentum and Vulpia 1213

myuros; less abundant native grasses are Bromus berteroanus, Deschampsia caespitosa and Vulpia antucensis. Common herbs beneath shrub canopies are the alien species F. capreolata and Euphorbia peplus, while native species such as Olsynium junceum and Stellaria chilensis occur at lower densities (Gómez-González 2008).

The Chilean matorral is characterized by patches of shrubs and trees surrounded by an herbaceous layer dominated by alien species. Understory microhabitats are regarded as refuges for native plant species (Gulmon 1977; Jaksic and Fuentes 1980; Arroyo et al. 2000), because their establishment in open areas is limited by several factors such as competition with alien grasses, high irradiance, and human disturbance (Fuentes et al. 1984, 1986; Holmgren 2002). But the main cause for the scarcity of native herbs in open areas has been attributed to herbivory by the European rabbit (Oryctolagus cuniculus). The European rabbit is native to the Mediterranean Basin and was introduced into Chile in the late 19th century (Jaksic 1998). Rabbits have produced a significant impact on the landscape and structure of the matorral (Fuentes et al. 1983). This alien herbivore forages mainly in openings and causes more damage to native than alien plant species (Jaksic and Fuentes 1980; Fuentes et al. 1984; Holmgren 2002). In our study site, the occurrence of rabbits was evidenced by the presence of their feces. Some horses were sporadically present, but they foraged along downhill trails and not on the study plot, which was located uphill (horse dung was not found there).

Fumaria capreolata (Fumariaceae) is an annual herb native to Europe that is widely distributed along Chile (from 26°S to 44°S, Matthei 1995). Fumaria capreolata was unintentionally introduced into Chile over a century ago (Philippi 1875). Díaz et al. (1988) classified this species as nitrophilous, which explains its presence mainly in disturbed habitats such as road borders. However, it has begun to invade natural matorral communities by finding a favorable habitat beneath the canopies of shrubs and trees (Gómez-González 2008). A preliminary sampling performed across four coastal matorral sites in central Chile showed that F. capreolata distribution is largely restricted to shaded microhabitats beneath canopies, and that it invades the understory of 89% ( $\pm$ 8.1 SD) of the shrubs and trees sampled (Online Resource 1). In this microhabitat, F. capreolata is one of the most abundant species,

reaching up to 30% of total plant cover in some sites (C. Torres-Díaz et al., unpublished data).

Spalacopus cyanus (Octodontidae), commonly known as "cururo", is a small fossorial rodent endemic to Chile (Contreras 1986; Begall and Gallardo 2000). Cururos are social herbivores whose foraging activities and subterranean tunnel construction cause significant soil disturbances resulting in the deposition of soil mounds (Contreras 1986; Begall and Gallardo 2000). Spalacopus cyanus is very abundant both in the Coastal Range and in the Andes, and it is distributed along the coastal range between 27°S and 36°S (Contreras 1986; Contreras et al. 1987). Cururos preferentially consume geophyte bulbs and, to a lesser extent, shoots of herbs and forbs (Contreras and Gutiérrez 1991). They tend to forage beneath shrubs canopies, since bulbs of geophytes such as Leucocoryne ixioides are more abundant there. However, once L. ixioides bulbs have been depleted, S. cyanus starts foraging in open areas where bulbs of other geophytes such as Conanthera campanulata are more abundant (C. Torres-Díaz et al., unpublished data). Unlike most subterranean mammals, cururo is a social species and occurs in colonies of about 20 individuals (Begall and Gallardo 2000). In the coastal matorral of central Chile, cururos remove as much as 10-20 kg of soil (fresh weight) per mound, and up to 8-12 tons of soil per hectare (C. Torres-Díaz et al., unpublished data).

## Sampling

After the first fall rains of 2007 (early June), we counted the number of F. capreolata seedlings in plots located in the study site. Because rabbit browsing does not affect the process of emergence per se, at the seedling stage we only evaluated the effects of cururos' disturbance and microhabitat. Thus, seedling emergence was evaluated in the following conditions: (1) beneath canopy and on cururo mound, (2) beneath canopy without disturbance, (3) open area and on cururo mound, and (4) open area without disturbance. We randomly selected 34 independent shrub/tree clumps (blocks) at least 4 m apart from each other and having natural cururo mounds in their understory. Beneath each canopy, we established a sampling plot on a cururo mound and another one in the adjacent area without disturbance. Then, we selected an open area separated at least 2 m from the edge of the canopy projection and established the same paired plots (cururo mound and adjacent undisturbed area). Plot size  $(0.25 \times 0.50 \text{ m})$  was determined according to the

average area of cururo mounds in the study site. A similar field sampling was carried out later in the season (September 2007), during the flowering stage. This sampling aimed to determine the effects of soil disturbance, above-ground herbivory and microhabitat on: (1) the abundance of adult F. capreolata individuals, (2) their mean above-ground biomass, and (3) their reproductive effort. We randomly selected 7 independent shrub/tree clumps (blocks). Within each block, eight different treatments were established after a factorial array of two microhabitat conditions (beneath shrubs and open areas), two disturbance conditions (undisturbed soil and cururo mound) and two herbivory levels (with and without herbivore exclusions). Treatments were applied to plots with the dimensions described above. Herbivore exclusions were constructed using four steel corner bars (0.6 cm diameter) as posts and galvanized sheet (1.2 cm mesh) to wrap around the perimeter of the exclusion cages  $(50 \times 25 \times 40 \text{ cm high})$ . Cages were buried into the soil to prevent access via tunneling. For each plot, the abundance of F. capreolata was expressed as the number of individuals per square meter. Afterwards, 10 plants per plot were randomly selected to determine mean dry weight. These F. capreolata individuals were harvested and oven-dried for 48 h at 70°C. To evaluate the effects of the studied factors on the reproductive effort of F. capreolata, the total number of flowers per individual was counted in the same 10 plants. Additionally, the rest of plant species found on each plot was harvested and dried, and the total aboveground biomass was determined in order to be considered as covariate in the analyses. We also calculated the total above-ground biomass of both native and alien species, separately, to assess herbivory effects on them.

## Statistical analysis

The effects of cururo disturbance and microhabitat on seedling emergence were analyzed using a two-way mixed ANOVA, where these two factors were considered the main (fixed) effects and the plot was entered as random factor (with 34 levels). Seedling emergence data were square-root-transformed to achieve a normal distribution. The significance of differences between means for the effect of disturbance within microhabitat treatments was tested with paired t tests.

The effects of microhabitat, soil disturbance and herbivore exclusion on the abundance, above-ground biomass and reproductive effort of F. capreolata were tested using three-way mixed ANCOVAs, entering the total biomass of other coexisting species as covariate, and the plot as random factor (with 7 levels). Post hoc comparisons of means between treatments were made using paired t tests. In order to contrast the influence of herbivores on F. capreolata versus other co-existing species, we evaluated the effect of herbivory exclusion on the total above-ground biomass of both natives and alien species using paired t tests. Above-ground biomass data were square-root-transformed and data of plant density and reproductive effort were transformed using  $\log_{10} (x + 1)$ . All analyses were done using R 2.8.0 software (R Development Core Team 2008).

## Results

The emergence of *F. capreolata* seedlings was significantly affected by microhabitat, disturbance and the interaction of both factors (Table 1). Thus, soil disturbance by *S. cyanus* significantly affected the spatial pattern of seedling emergence. Considering undisturbed areas only, seedling emergence beneath shrubs was six times higher than in open areas (Fig. 1). Cururo mounds significantly increased seedling emergence in both microhabitats (3.5- and 24-times higher beneath canopies and in open areas, respectively), and the emergence of *F. capreolata* seedlings in cururo mounds was similar in open areas and beneath shrubs (Fig. 1).

**Table 1** Mixed two-way ANOVA evaluating the interactive effects of microhabitat (beneath shrubs and open areas) and soil disturbance (undisturbed sites and cururo mounds) on seedling emergence of the alien plant *Fumaria capreolata* 

Source of variation	df	M.S.	F	P value
Microhabitat	1	28.41	13.60	<0.001
Disturbance	1	408.13	195.36	<0.001
Microhabitat $\times$ disturbance	1	45.24	21.66	<0.001

In this model, block was entered as random factor (n = 34 blocks). Significant *P* values (<0.05) are highlighted in bold



**Fig. 1** Emergence of *Fumaria capreolata* seedlings growing on different soil substrates (undisturbed sites and cururo mounds) and in different microhabitats (*beneath shrubs* and *open areas*). Means  $\pm$  SE are shown (n = 34). *Bars* with *different lowercase letters* are significantly different (P < 0.05; paired *t* test)

There were no effects of herbivore exclusion on the density, biomass and reproductive effort of F. capreolata (Table 2). In contrast, all three variables were significantly affected by microhabitat and disturbance (Table 2; Fig. 2a-c). Beneath shrubs, the abundance of individuals per plot, above-ground biomass and the number of flowers per plant in cururo mounds were between two and threefold higher than in the adjacent undisturbed soil (Fig. 2a-c). In open areas, plant density, biomass and reproduction of F. capreolata in cururo mounds were 21-, 7-, and 8- times higher than in the adjacent undisturbed areas, respectively (Fig. 2a-c). The abundance of F. capreolata plants within cururo mounds from open areas was as high as that from mounds beneath canopies (Fig. 2a). Both individual above-ground biomass and the mean number of flowers per plant in cururo mounds reached similar values to those of plants grown in undisturbed soil sites beneath shrubs (Fig. 2b, c). The significant interaction between disturbance and microhabitat for plant density and reproductive effort (Table 2) indicates that the effect of S. cyanus soil disturbance on F. capreolata establishment and fitness was of greater magnitude in openings than in understories.

Unlike *F. capreolata*, the total above-ground biomass of coexisting species was significantly reduced by herbivory (Fig. 3). Such a negative effect of herbivory was mainly due to the biomass reduction of other alien species, since the total biomass of native species was not affected by herbivore exclusion (Fig. 3).

### Discussion

The establishment of the alien plant *F. capreolata* in the coastal matorral of central Chile is strongly affected by environmental conditions associated with the native vegetation, since it is mainly found beneath shrub canopies. However, when soil disturbances by the native fossorial mammal *S. cyanus* occur, this alien

Table 2 Mixed three-way ANCOVA evaluating the interactive effects of microhabitat (beneath shrubs and open areas), soil disturbance (undisturbed sites and cururo mounds) and

plant can thrive in open sites too. Furthermore, unlike other resident species, *F. capreolata* is not affected by herbivory, which surely enhances its establishment in both understory and open microhabitats. These fieldbased evidences illustrate the hypothesized interplay between environmental conditions, disturbance-mediated changes in resource availability and reduced herbivory in explaining plant invasion success (Shea and Cheeson 2002).

A number of studies have reported that soil disturbances by native mammals have beneficial effects on native plant species (e.g. Hobbs and Mooney 1991; Huntly and Reichman 1994; Hobbs

herbivory (herbivore exclusion and exposed plants) on the abundance, mean above-ground biomass and reproductive effort of the alien plant *Fumaria capreolata* 

Source of variation	df	M.S.	F	P value
Number of F. capreolata individuals per plot				
Total above-ground biomass of co-existing species (Covariate)	1	13.69	6.57	0.014
Microhabitat	1	23.10	11.09	0.002
Disturbance	1	203.3	97.65	<0.001
Herbivory	1	0.65	0.31	0.579
Microhabitat $\times$ disturbance	1	15.87	7.62	0.009
Microhabitat $\times$ herbivory	1	0.05	0.05	0.823
Disturbance × herbivory	1	0.48	0.23	0.633
Microhabitat $\times$ disturbance $\times$ herbivory	1	3.84	1.84	0.182
Above-ground biomass per F. capreolata plant				
Total above-ground biomass of co-existing species (Covariate)	1	0.01	1.13	0.294
Microhabitat	1	0.77	70.40	<0.001
Disturbance	1	0.36	33.22	<0.001
Herbivory	1	< 0.01	0.05	0.813
Microhabitat $\times$ disturbance	1	< 0.01	0.18	0.670
Microhabitat $\times$ herbivory	1	< 0.01	< 0.01	0.937
Disturbance × herbivory	1	< 0.01	0.23	0.633
Microhabitat $\times$ disturbance $\times$ herbivory	1	0.01	0.69	0.409
Number of flowers per F. capreolata plant				
Total above-ground biomass of co-existing species (Covariate)	1	1.84	5.43	0.025
Microhabitat	1	18.51	54.66	<0.001
Disturbance	1	22.94	67.73	<0.001
Herbivory	1	0.03	0.10	0.748
Microhabitat $\times$ disturbance	1	3.21	9.46	0.004
Microhabitat $\times$ herbivory	1	0.07	0.19	0.657
Disturbance $\times$ herbivory	1	0.24	0.71	0.404
Microhabitat $\times$ disturbance $\times$ herbivory	1	0.31	0.92	0.342

In these models, the total above-ground biomass of co-existing species was incorporated as covariate and block as random factor (n = 7 blocks). Significant *P* values (<0.05) are highlighted in bold



**Fig. 2** Plant density (**a**), shoot biomass (**b**), and reproductive effort (**c**) of the alien plant *Fumaria capreolata* growing on different soil substrates (undisturbed sites and cururo mounds) and in different microhabitats (*beneath shrubs* and *open areas*) in a coastal matorral of central Chile. Means  $\pm$  SE are shown (n = 14). *Bars* with *different lowercase letters* are significantly different (*P* < 0.05; paired *t* test)

and Mooney 1995; Karsten et al. 2007; El-Bana 2009), even preventing the establishment of alien plants (Mazía et al. 2010). This is likely given that native species have evolved with the presence of mounds in the landscape and are somewhat adapted to colonize them. Nevertheless, our results demonstrate that alien plant species can also be favored by these natural disturbances, as has been shown earlier for other systems. Hobbs and Mooney (1991) reported that



Fig. 3 Effect of herbivory exclusion on the total above-ground biomass per plot of species coexisting with the alien plant *Fumaria capreolata* (natives, aliens and all species). Means  $\pm$  SE are shown (n = 28). *Asterisks* indicate significant differences between treatments (P < 0.05) and n.s. means no significant effect (paired *t* test)

invasion by B. mollis in a serpentine annual grassland in northern California only took place on native gopher mounds. Likewise, mounds created by a native burrowing mammal in the Tibetan Plateau promoted the invasion of alpine meadows by the alien plant Descurainia sophia (Li et al. 2009). Fitness differences when occupying the same microhabitat might explain-at least in part-why either native or alien plants are favored by natural disturbances (McDougall et al. 2009). Thus, alien species could outcompete supposedly adapted native species when co-occurring in disturbed sites if the former accrue fitness benefits due to, for instance, a greater efficiency in resource use or reduced herbivore pressure (McDougall et al. 2009). Both of these factors seem to be involved in the observed advantages in performance of F. cap*reolata* when this alien plant, otherwise confined to shrub understories, successfully colonizes cururo mounds in open areas, thus expanding its microhabitat distribution. Niche expansion of alien plant species has been previously reported (e.g. Mandle et al. 2010). To our knowledge, the microhabitat expansion of an alien plant as a consequence of natural soil disturbance by native mammals has not been reported before.

The main positive effect of the shrub canopy on F. *capreolata* seedling recruitment in this Mediterranean-type ecosystem is probably the creation of a more favorable microclimate, where seedlings experience reduced water stress during the summer drought, thus increasing their survival (Fuentes et al. 1984, 1986). However, the fact that cururo mounds decrease the dependence of F. capreolata upon shaded microhabitats, suggests that the more benign microclimatic conditions beneath shrubs are not the only factor explaining the strong spatial association between F. capreolata and shrub understories. This association may also be explained by the higher nutrient availability beneath shrubs compared to openings (Aguiar and Sala 1994; Gómez-Aparicio et al. 2005). In view of our results, the latter idea is plausible, considering that a number of studies have documented that soil disturbances by small mammals increase nutrient availability (Hobbs and Mooney 1985; Huntly and Reichman 1994; Fields et al. 1999; Canals and Sebastià 2000; Canals et al. 2003; Karsten et al. 2007). For example, Canals et al. (2003) documented that plant removal by gophers caused an impact on N-cycling through both elimination of plant uptake of inorganic N and reduction of rootenhanced microbial immobilization of NO<sub>3</sub>-N. Because F. capreolata is a nitrophilous plant (Díaz et al. 1988), changes in nitrogen availability caused by soil plowing and by competition release probably explain its ability to colonize open areas. Another conceivable mechanism would be that cururo mounds act as seedtraps, thus increasing the emergence of F. capreolata compared to undisturbed areas, as has been observed in arid ecosystems (Reichman 1984; Guo et al. 1998). However, this is unlikely because there is profuse germination of F. capreolata on recently excavated mounds which do not overlap with seed dispersal, further suggesting that seedlings proceed from seedbank. Moreover, bare ground was not common in the study site. Instead, there was a dense litter of comparable height to cururo mounds. Consequently, it is hardly possible that cururo mounds would act as seed-traps in a better way than the surrounding matrix of litter.

Several studies in the Chilean matorral and in other ecosystems have shown that exotic herbivores tend to consume native plants, thus favoring exotic plants and promoting invasion (Parker et al. 2006; Jaksic and Fuentes 1980; Holmgren et al. 2000). In contrast, we have found that herbivores—presumably European rabbits—reduce the above-ground biomass of alien plant species but have no effects on native plants in this coastal matorral community. Interestingly, the former pattern does not hold for the study species because there was no effect of herbivore exclusions on its abundance, above-ground biomass and reproductive effort. This suggests that F. capreolata may be an unpalatable plant for rabbits; interestingly, another Fumaria species has shown spasmogenic activity on isolated rabbit intestine (Gilani et al. 2005). Alternatively, F. capreolata could be able to compensate the above-ground biomass lost to herbivores, as has been shown for other herbs in Central Chile (González-Teuber and Gianoli 2007; Gonzáles et al. 2008). Given that exotic herbivores produce strong, landscape-scale effects on the matorral (Holmgren 2002), herbivore resistance (or tolerance) could be a key factor for F. capreolata current and future success as invader in this ecosystem.

The Mediterranean region of central Chile is a global biodiversity hotspot (Myers et al. 2000), but habitat loss and biological invasions threaten its unique biodiversity (Arroyo et al. 2006). In the Andean matorral, Castro et al. (2010) recently showed that the presence of the alien annual Anthriscus caucalis reduces the diversity and survival of native species in refuge habitats beneath the woody vegetation. The abundance of F. capreolata in both the understory of the coastal matorral and cururo mounds in open areas could have similar negative effects on the native flora adapted to inhabit these microhabitats. Cururos are an old component of the Chilean matorral (Contreras and Gutiérrez 1991) and mounds have probably served as a safe site for the establishment of native plant species through evolutionary time. For instance, geophytes are frequently associated with mounds at the local scale and show overlapping distribution with cururos at the biogeographical scale (Contreras et al. 1987). Canals et al. (2005) showed that the identity of plant species that initially colonize gopher mounds can significantly alter N-dynamics, so F. capreolata could negatively affect native geophytes via changes in nutrient availability. Future studies on this coastal matorral should address the impact of F. capreolata on native plants both beneath shrubs and on cururo mounds in open areas. This will shed light on the ecological consequences of the observed habitat expansion of an alien plant species driven by the exploitation of soil disturbances by a native mammal.

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