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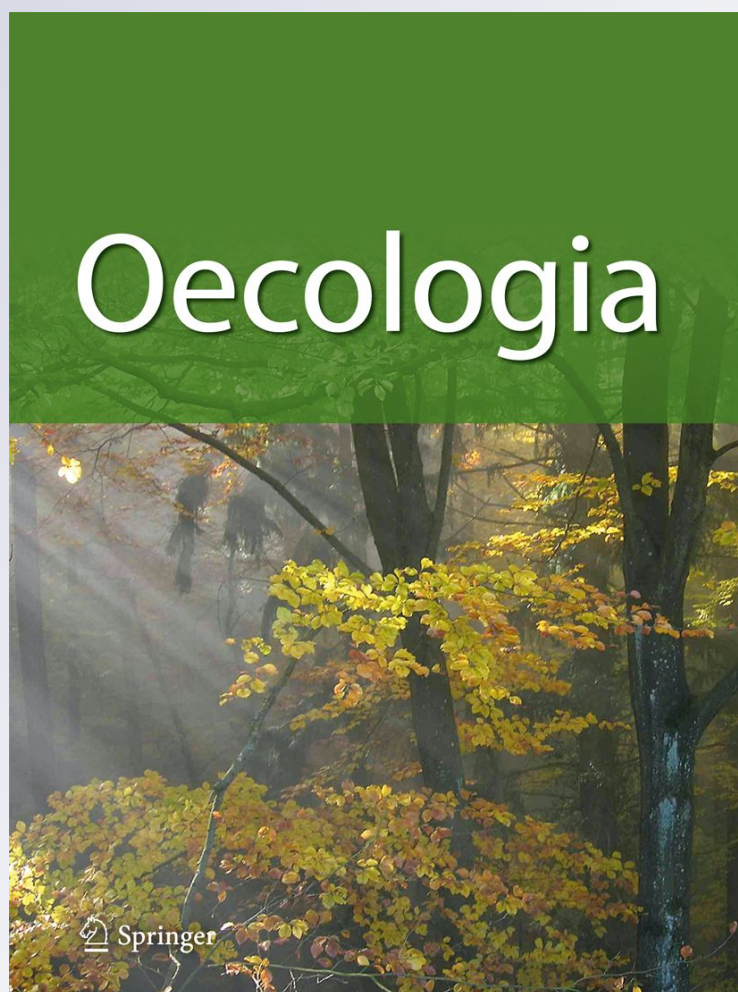
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# Small mammals cause non-trophic effects on habitat and associated snails in a native system

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**Abstract** Legacy effects occur when particular species or their interactions with others have long-lasting impacts, and they are increasingly recognized as important determinants of ecological processes. However, when such legacy effects have been explicitly explored, they most often involve the long-term direct effects of species on systems, as opposed to the indirect effects. Here, we explore how a legacy of small mammal exclusion on the abundance of a shrub, bush lupine (*Lupinus arboreus*), influences the abundance of a native land snail (*Helminthoglypta arrosa*) in coastal prairie and dune habitats in central California. The factors that limit populations of land snails are very poorly known despite the threats to the persistence of this group of species. In grasslands, prior vole (*Microtus californicus*) exclusion created long-lasting gains in bush lupine abundance, mediated through the seedbank, and was associated with increased snail numbers (10×) compared to control plots where mammals were never excluded. Similar plots in dune habitat showed no difference in snail numbers due to previous mammal exclusion. We tested whether increased competition for food, increased predation, and/or lower desiccation

explained the decline in snail numbers in plots with reduced lupine cover. Tethering experiments supported the hypothesis that voles can have long-lasting impacts as ecosystem engineers, reducing woody lupine habitat required for successful aestivation by snails. These results add to a growing list of studies that have found that non-trophic interactions can be limiting to invertebrate consumers.

**Keywords** Nontrophic interaction · Ecosystem engineer · Aestivation · Legacy effect · Mammal exclusion

## Introduction

Charles Elton revolutionized the field of community ecology by introducing the idea of food webs, diagrams that represent the feeding interactions between species (Elton 1927). It seems intuitive to seek relationships between producers, consumers and predators, and this led to the widespread acceptance of thinking about communities in terms of which organisms were eating which other ones. However, one limitation of a strictly food web perspective is that, while it highlights trophic relationships, it ignores other species interactions (Ohgushi 2005). We now have ample evidence that many important interactions are not restricted to feeding relationships but also include other mechanisms such as competition, facilitation and changes in the physical environment caused by one organism that affects others.

Not only can non-trophic interactions be important, but both trophic and non-trophic effects can combine in powerful ways to influence population and community structure. For example, strong top-down effects of plant consumers can alter fundamental features of the habitat,

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which can then indirectly influence species that rely on that habitat. These indirect effects of consumers have been best studied in forests and savannahs, where heavy ungulate herbivory can dramatically modify the abundance of dominant plants, which in turn can influence other animal populations (Keesing 1998; Berger et al. 2001; Smit et al. 2001). In these cases, consumption has strong indirect effects because of its “engineering” effect on the habitat structure (Jones et al. 1994, 1997).

Here, we examine how small mammal consumers, through their direct effects on the abundance of bush lupine (*Lupinus arboreus*), indirectly influence land snail (*Helminthoglypta arrosa*) populations. Species interactions of all sorts involving terrestrial land snails are particularly poorly studied, and we have little information about factors that limit their populations (Baur and Baur 1990; Foster and Stiven 1996; Speiser 2001; Kimura and Chiba 2010). Mollusks account for 20% of all threatened animal species and 37% of the known animal extinctions since 1600 (Dunk et al. 2004). Previous studies of mortality factors for land snails often found predation to be important (e.g., Pollard 1975) although other studies failed to find any evidence for predation (e.g., Heller and Dolev 1994). Trophic interactions are not the only important factors for terrestrial snails. For example, desiccation has also been identified as an important factor affecting snail distribution and abundance (e.g., Pollard 1975).

What makes this series of interactions particularly noteworthy is that long-term changes in the abundance of bush lupine shrubs appear to result from legacy effects of past rodent exclusion. Most often, legacy effects are examined in situations where preemption of space by one species has long-lasting impacts on the species that subsequently attempt to colonize that space. These effects often operate through long-term changes in soil conditions, for example, where one species enriches the soil, which has lasting impacts on subsequent interactions between species (Grman and Suding 2010). Experimental nutrient enrichment can also have long-lasting impacts on community structure (Milchunas and Lauenroth 1995). In our case, however, legacy effects of past rodent exclusion appear to be perpetuated through seed bank dynamics as opposed to soil conditions (Maron and Kauffman 2006).

We investigated the numbers of *H. arrosa* in plots that had been previously established to examine the impacts of rodent consumers on bush lupine abundance in grassland and dune habitats (Maron and Kauffman 2006). Rodent exclusion (and control) plots were established in 1998, cleared of dead lupine, and planted with two cohorts of lupine seedlings (in 1998 and 1999). We estimated percent cover of bush lupine in these plots that historically excluded or allowed rodent access but that have been open to these consumers since fall 2004. While the rodent

exclusion fences became permeable to small mammals after fall 2004, they continued to exclude larger animals such as rabbits, skunks, and deer. We examined how variation in lupine cover in turn influenced predation and desiccation of snails. We assessed whether snails were more likely to suffer predation and desiccate in plots open to small mammals compared to those that were closed. Our aim in this study was to evaluate the effects of mammal removal on snail populations and to determine the ecological mechanisms responsible for these effects.

## Materials and methods

### Experimental set up

We investigated the numbers of a native snail in plots that historically were either open or closed to small mammals. Plots were established during the spring of 1998 in three paired locations along a north–south gradient throughout the UC Bodega Marine Reserve in Sonoma County, California, USA (Maron and Kauffman 2006). At each location, eight plots measuring 9 × 9 m were established in the grassland habitat and an additional eight plots were established in the dune habitat. Four of the eight plots at each location were randomly assigned to have rodents excluded and four served as controls. Small mammals were excluded from experimental plots by using 90-cm-tall fences of PVC-coated welded wire (0.635-cm mesh), dug 30 cm into the ground and topped with 22.5 cm of aluminum flashing. Control plots that mammals could access were surrounded by welded wire fences without aluminum flashing with holes cut every 1.5 m. The enclosures were breached by mice and voles after fall 2004, when they were no longer actively maintained. Densities of rodents were not quantified although levels of vole activity within the enclosures following 2004 appeared as high as levels outside (personal observation).

### Natural history and effects of rodents on lupine cover

*Lupinus arboreus* is the dominant shrub in both the grassland and dune habitats where the plots were located (Barbour et al. 1973). *L. arboreus* grows very quickly but typically dies within 7 years of germinating (Davidson and Barbour 1977). Lupine seeds and seedlings suffer high levels of predation by mice and voles, respectively, but plants are seldom seriously damaged by deer. All plots were cleared of lupine in 1998, and 49 lupine seedlings were planted in each plot in January 1999; densities of lupine bushes became much higher (as much as 15-fold) by 2004 in plots with mammals excluded (Maron and Kauffman 2006). We estimated the percent area covered by

*L. arboreus* in March 2003, 2008, 2009, and 2010. This was accomplished by dividing plots into 81  $1 \times 1$  m quadrats and visually estimating percent cover in each quadrat. Cover estimates for 2008–2010 were highly correlated, so we calculated a mean cover value for these 3 years and used an arcsine transformation of all percent cover data to normalize them. We examined treatment effects of exclosures on lupine cover in 2008–2010 using an ANOVA model that included two habitats, three locations and their interactions (see below). Treatment effects on lupine cover prior to 2004 were published previously (Maron and Kauffman 2006).

*Helminthoglypta arrosa* is a native snail that lives for 2–3 years and feeds on the leaves of living and especially decaying forbs (van der Laan 1971, 1975a). Preferred food species at the study site include *Amsinckia* spp., *Phacelia distans*, *Claytonia perfoliata* and others. Several subspecies of *H. arrosa* are listed as being of special concern by the California Department of Fish and Game (<http://www.dfg.ca.gov/wildlife/wap/report.html>). In laboratory feeding trials, snails from this population rejected *L. arboreus* and all grasses as food. Snails are active during the rainy season (approximately December–April) and aestivate at other times by attaching themselves to the undersides of branches and other woody structures above ground and in the litter (Van der Laan 1971). They avoid exposure to sunlight or dry conditions and are active from late evening through morning, particularly on rainy days. Van der Laan (1971) noted that *H. arrosa* was attacked by carabid beetles and deer mice at the study site, but he concluded that voles, other mammals, birds, or reptiles were not potential predators and observed no parasites.

In both grasslands and dunes, the rodent community is composed of California voles (*Microtus californicus*), deer mice (*Peromyscus maniculatus*), harvest mice (*Rheithrodonomys megalotus*), and pocket gophers (*Thomomys bottae*). Voles can have strong impacts on lupine abundance due to their effects in killing seedlings (Maron and Kauffman 2006; Kauffman and Maron 2006), whereas mice (*P. maniculatus*) eat both lupine seeds (Maron and Simms 2001; Maron and Kauffman 2006) and arthropod prey. Species composition is strongly habitat dependent; voles are more abundant and have particularly strong impacts on lupine seedling survival in grassland habitat, and mice have large effects on seed survival and hence lupine recruitment in dunes (Maron and Kauffman 2006). Other species that are common at the study site and were excluded by the experimental fences include black-tailed deer (*Odocoileus hemionus columbianus*), black-tailed jackrabbits (*Lepus californicus*), brush rabbits (*Sylvilagus bachmani*) and striped skunks (*Mephitis mephitis*). Of this latter group, only skunks have the potential to feed on snails. Voles that entered the exclosures using gopher holes

were eliminated by trapping until 2004 (Maron and Kauffman 2006). After 2004, voles colonized all grassland plots.

#### Snail censuses and statistical analyses

We sampled snail densities in four pitfall traps per plot at three times during the winter of 2003. Pitfall traps were 170-ml yogurt containers filled with approximately 3 cm of beer placed with their tops at ground level on 21 February, 31 March, and 3 May, and left for 3 days. We analyzed the number of adult snails recovered in our pitfall traps using ANOVA (Fit Model command in JMP 7.0) with mammal treatment (exclusion or control), habitat (dunes and grassland) and location (north, middle or south) as fixed effects. Habitat and location were considered as fixed effects because there are two main terrestrial habitats at the Reserve and we sampled both; similarly, the locations of the plots along the north–south transect were restricted by the geography of the Reserve—the north and south blocks were at the two edges of the Reserve near the ocean and bay, respectively, and the middle block was just south of the cove, in the only possible site. In addition, the three blocks represent the three kinds of grassland at the Reserve with respect to colonization by the highly invasive annual grass (*Holcus lanatus*) (Bastow et al. 2008). The southern plots were heavily invaded, the middle block is close to the invasion front, and the northern block has not yet been invaded. We also ran the model with lupine cover, estimated during 2003, as a covariate (arcsine transformed) in our analyses to test the possibility of a relationship between lupine cover and snail abundance.

#### Snail survival and statistical analyses

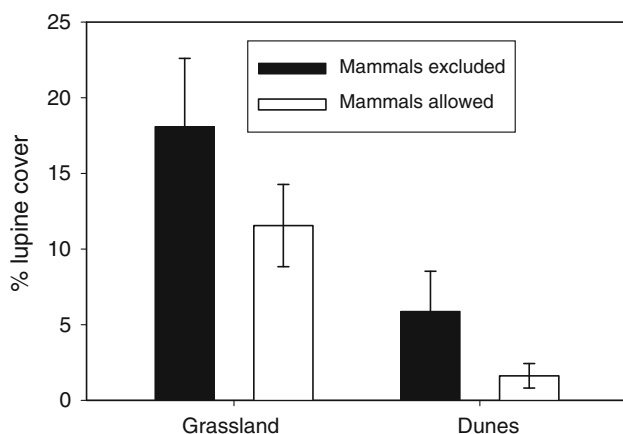
We conducted an experiment examining the fates of 48 aestivating adult *H. arrosa* snails tethered to 30-cm wooden pot labels stuck in the ground. We tethered a single snail in each of 24 plots with mammals excluded and 24 control plots in the grassland habitat. Each snail was attached to a 50-cm string with superglue, which was then tied around a pot label and placed in each of the 48 plots on 4 May 2003. We assessed the survival of each snail at weekly intervals and the cause of mortality for those individuals that were dead on 14 July. Snails with shells that were broken were assumed to have been killed by predators. Snails that dried up in their intact shells were assumed to have died as the result of desiccation. Associations between the various fates (alive, eaten, dried) and the presence of mammals (excluded, control) were examined using a *G* test of independence with William's correction for small sample sizes. Tethering snails is a well-established method although it can produce inflated

estimates of predation rates; it is considered a valuable technique to compare rates of mortality in different treatments (with and without mammals) since any potential artifacts of tethering should be similar in the two treatments (Aronson and Heck 1995; Rochette and Dill 2000).

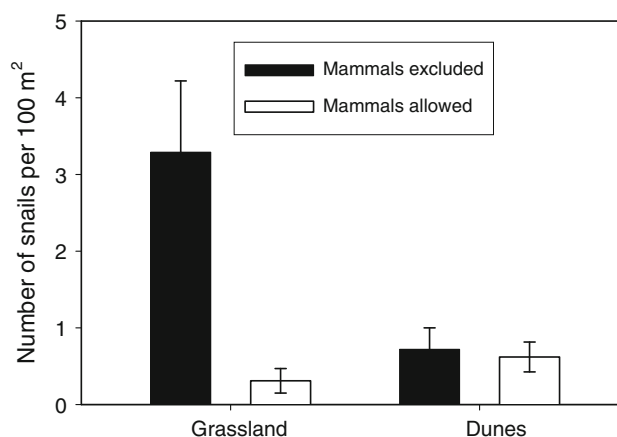
## Results

Each plot started in 1999 with 49 lupine seedlings. By 2004, plots without mammals had 15 times the number of lupine individuals as plots that mammals could access (Maron and Kauffman 2006). After 2004, rodents entered plots of both treatments as exclusion fences were breached. Despite this, lupine cover measured in 2008–2010 was reduced by 35% in grassland plots to which small mammals had had access and by 70% in dune plots to which small mammals had had access (Fig. 1). The effects of excluding small mammals were not different in the two habitats (interaction between treatment and habitat:  $F_{1,36} = 0.26$ ,  $P = 0.61$ ) so we analyzed mammal treatment effects in both habitats together to increase our statistical power. However, because of the limited number of exclosures, the effect of excluding mammals on overall lupine cover was not quite significant ( $F_{1,36} = 3.60$ ,  $P = 0.066$ ).

Adult snails were attracted to the pitfall traps filled with beer. The mammal exclosures had significantly different effects on numbers of snails in pitfall traps in the two habitats [ANOVA interaction between habitat (grassland vs. dune) and mammal treatment (excluded vs. control):  $F_{2,36} = 9.17$ ,  $P = 0.0006$ ]. As a result, we analyzed the results from each habitat separately. In the grassland habitat, plots from which mammals had been excluded had approximately 10 times the number of snails as plots with access by mammals (Fig. 2;  $F_{1,22} = 10.02$ ,  $P = 0.005$ ).



**Fig. 1** Cover of bush lupine (*Lupinus arboreus*) (mean  $\pm$  1SE) estimated in  $9 \times 9$  m plots in grassland and dune habitats during 2008–2010. Mammals were excluded from half of the plots by fences



**Fig. 2** Land snail (*Helminthoglypta arrosa*) abundance (mean  $\pm$  1SE) in plots in grassland and dune habitats with or without access by mammals

**Table 1** The fate of snails in grassland plots with mammals excluded or with access (controls)

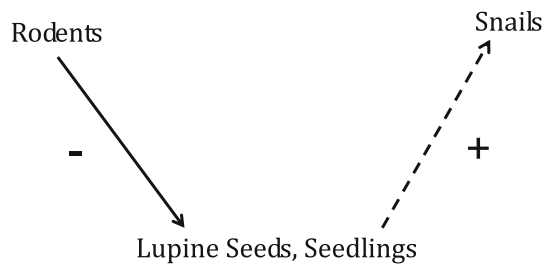
	Alive	Eaten	Dry	Total
Mammals present	4	5	9	18
Mammals absent	14	1	3	18
Total	18	6	12	36

The number of snails collected in the dunes did not differ for plots with access by mammals and those without mammals (Fig. 2;  $F_{1,22} = 0.09$ ,  $P = 0.76$ ). Lupine cover measured in 2003 was a significant covariate of snail abundance such that grassland and dune plots with more lupine had more snails ( $t = 2.07$ ,  $df = 43$ ,  $P = 0.04$ ).

In the grassland habitat, we followed the fate of 24 snails in plots with mammal access and with mammals excluded. Six snails were missing from each treatment and were not included in further analyses. Access by mammals affected the fates of tethered snails (Table 1;  $G = 11.16$ ,  $df = 2$ ,  $P = 0.004$ ). In plots with mammals excluded, snails were more likely to remain alive after 2 months, while in plots with mammals, snails were more likely to be eaten or to desiccate. Examining this result in more detail, predation was found to be 5 times more common in plots with access by mammals (Table 1;  $G = 7.76$ ,  $df = 1$ ,  $P = 0.005$ ). Predation was indicated by broken shells and we were not able to determine the identity of the predators responsible. Snails were also 3 times more likely to desiccate in plots with mammals (Table 1;  $G = 9.56$ ,  $df = 1$ ,  $P = 0.002$ ).

## Discussion

We found that the number of *H. arrosa* snails was greater in grassland habitat plots where small mammals had been



**Fig. 3** Rodents have an indirect, negative effect on snails that results from the two processes (arrows) represented in this path diagram. The solid line between rodents and lupine indicates an effect that is trophic and immediate. The dotted line between lupine and snails is non-trophic

excluded (Fig. 2). We observed no such increase in snail numbers in dune habitat plots. In addition, bush lupine abundance tended to be higher in plots where small mammals had been historically excluded even 4–6 years after fences failed to exclude rodents (Fig. 1). We infer that this legacy effect on vegetation may also have affected snail numbers. This finding is unusual in demonstrating an effect on snail numbers (Fig. 2) rather than on surrogates of performance such as growth rates or shell size reported in most of the few studies examining species interactions for land snails (see “Introduction”).

The two main results of this study were that rodents reduced lupine cover in both habitats and that lupine cover affected snail abundance in the grassland (Fig. 3). These results are unusual and surprising for two reasons. First, the processes can be described as a non-trophic indirect effect because, although the first link (rodents reducing lupine cover) is trophic, the second link (lupine cover affecting snail abundance) is non-trophic. Although community ecologists have traditionally focused solely on trophic interactions in food webs, this narrow perspective is likely to produce an inadequate understanding of the forces shaping communities (Ohgushi 2005). Second, the effect of the first link (rodents reducing lupine seed density) continued 4–6 years after the treatment was no longer maintained and rodents became abundant within the enclosures. Although most ecological studies are of short duration, many important ecological processes may take considerable time to manifest and become detectable (Brown et al. 2001). Legacy effects that reflect past, rather than current, conditions may indirectly shape populations long after their direct effects have disappeared. Two important ecological processes—exploitative competition for food and/or ecosystem engineering—could have contributed to the negative effect that mammals had on native snails in the grassland. Each of these processes will be discussed in turn.

Exploitative competition for food is unlikely to have caused these effects. Both voles and mice have been found

to reduce the abundance of bush lupine in grassland and dune habitats (Maron and Kauffman 2006; Fig. 1). This species is the dominant shrub at the study site and serves as an important food source for many herbivore species (Barbour et al. 1973). However, *H. arrosa* does not feed on living or dead leaves of *L. arboreus* (van der Laan 1975a), suggesting a mechanism other than food. Several of the preferred foods of *H. arrosa* are species that grow well in association with living and recently dead lupine bushes (personal observation) so that indirect effects associated with reduced lupine cover could also indirectly reduce food sources for these snails.

Changes in habitat structure, often identified as “ecosystem engineering” (sensu Jones et al. 1994, 1997), caused by excluding rodents may provide the best lead towards understanding the increase in snail density. Plots open to mid-sized mammals from 1998 to 2009 and rodents from 1998 to 2004 had lupine populations that were reduced by 15-fold in 2004 (Maron and Kauffman 2006) and by 35% in the grassland and by 70% in the dunes in 2008–2010 (Fig. 1). In the grassland habitat, voles killed lupine seedlings that were initially planted into plots in 1998 and 1999. This resulted in more adult shrubs in rodent exclusion plots, which in turn had large impacts on the size of the lupine seedbank in those plots (Maron and Kauffman 2006; Kauffman and Maron 2006). In the dune habitat, mice consumed seeds from 1998 to 2004. In both habitats, the large differences that these two rodents caused in the lupine seed bank (Maron and Kauffman 2006) were likely responsible for the difference in lupine cover that was still detectable from 2008 to 2010, 4–6 years after the treatments stopped being maintained (Fig. 1). This result is all the more remarkable since individual bushes do not live beyond 7 years (Davidson and Barbour 1977). Examination of high-resolution aerial photographs taken once every year at the Reserve revealed that most bushes in the grassland were visible for only 3 years and those in the dunes for up to 5 years. Most bushes that were visible in 2004 were gone by 2008–2010. This result suggests that the treatment that excluded rodents up to 2004 continued to affect subsequent generations of lupine by reducing the density of seeds that entered the seed bank.

Greater lupine cover could potentially increase snail numbers by providing protection from predation or desiccation. The results of the experiment in which aestivating snails were tethered to posts in the grassland (Table 1) indicate that more snails were eaten in plots that had mammals and therefore had much lower lupine cover. A likely explanation for this result is that lupine bushes may provide aestivation habitat, safe from predation. Van der Laan (1975b) found that mice and carabid beetles readily consume *H. arrosa*, and skunks may also be predators of snails at the study site (personal observation). *H. arrosa*

prefers to aestivate on the horizontal branches of lupine, and this behavior protected them from ground-foraging predators when they climbed 2–3 cm off the ground in laboratory experiments (van der Laan 1975b).

Snails were less likely to desiccate when they were tethered in plots with no mammal access and therefore greater lupine cover (Table 1). Van der Laan (1975b) noted that *H. arrosa* individuals that were able to completely seal their shell aperture during aestivation were better able to survive. Flat surfaces large enough to offer this microhabitat were rare; however, lupine branches provided this scarce resource.

Our results indicate that grassland plots without mammals supported both higher cover of lupine and more snails and that these differences in plant cover persisted for more than one lupine generation beyond the termination of mammal exclusion treatments. These results on snail populations in the grassland are unlikely to be caused by direct interspecific competition for food but may be caused by indirect facilitation of preferred food resources or by indirect protection from predation and desiccation. These findings may provide insights more generally into the factors that are important for land snails. In experiments that selectively excluded larger mammals in dune habitat on the California coast, we found that deer reduced the abundances of snails by 32% and jackrabbits reduced the abundances of snails by 44–75% (Huntzinger et al. 2008). Most of the snails in this study were introduced *Helix aspersa* with *Helminthoglypta arrosa* present but less common. Additional experiments with *H. aspersa* revealed that supplemental food (cabbage leaves) and structure (dead bushes) did not increase snail numbers, but plots with experimental shading had more than twice the number of snails compared to controls (Huntzinger et al. 2008). A study of the factors that affect abundances of *Helminthoglypta talmadgei* in forests of northern California found that tree basal area, downed woody debris, and summer precipitation were all positive predictors of snail presence (Dunk et al. 2004). We know little about the factors that are important to terrestrial mollusks, but existing information suggests that moisture and protection from desiccation deserve further examination, and the relative importance of food versus other factors remains unresolved.

In conclusion, this study provides rare information about the population dynamics of land snails. Surprisingly little is known about the ecology of land snails despite the conservation status of the group. This study also adds to our growing appreciation that non-trophic interactions between unrelated organisms at the same trophic level can be important and that habitat can be a limiting resource. In this case rodents serve as ecosystem engineers by reducing the availability of large woody stems that provide critical habitat for snails by reducing predation or desiccation risk.

These effects of rodents on the vegetation persisted for years and were probably mediated by changes in the lupine seed bank. If communities are held together by many different links such as those uncovered in this study, then it suggests that extirpating a native species may have important and unanticipated consequences in spatially and temporally distant parts of the interaction web.

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