

# Native herbivore exerts contrasting effects on fire regime and vegetation structure

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**Abstract** Although native herbivores can alter fire regimes by consuming herbaceous vegetation that serves as fine fuel and, less commonly, accumulating fuel as nest material and other structures, simultaneous considerations of contrasting effects of herbivores on fire have scarcely been addressed. We proposed that a colonial rodent, vizcacha (*Lagostomus maximus*), reduces and increases fire intensity at different stages in its population cycle in the semiarid scrub of Argentina. Specifically, we hypothesized that, when colonies are active, vizcachas create natural fire-breaks through intense grazing, generating over time patches of large unburned shrubs in grazed zones. In contrast, when colonies are abandoned, recovery of fine fuels and

previous accumulation of coarse wood on colonies during territorial displays increases fire intensity, creating patches of high shrub mortality. To test these hypotheses, we estimated stem age of the dominant shrub (*Larrea divaricata*) and measured aboveground biomass in zones actively grazed by vizcachas and in ungrazed zones, and compared densities of live and dead shrubs on abandoned colonies and adjacent zones following fire. In active colonies, age and biomass of shrubs were much greater in grazed than ungrazed zones. In abandoned colonies that had been burnt, density of dead, burned shrubs was higher and density of live shrubs was lower than in adjacent zones. These results support our hypotheses and reveal a new interaction between native herbivores and fire, in which herbivores augment fire intensity by gathering fuel. Our findings indicate that, through opposing effects on fire, native herbivores enhance the heterogeneity of vegetation in woody-dominated ecosystems.

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## Introduction

The physical alteration of the environment by organisms can be so profound that it has been labeled as engineering (Jones et al. 1994). Many studies, embracing a broad range of taxa and habitat types, have shown that organismal engineering greatly influences the abundance and distribution of co-occurring species as well as the structure and dynamics of ecosystems (e.g., Stutzner et al. 2000; Reichman and Seabloom 2002; Badano et al. 2007; Troost 2010). Additionally, because some species-mediated modifications persist over geological time (e.g., Parris and

Casadío 2006), these changes have also been proposed to affect macroevolutionary patterns and diversity (Erwin 2008). Studying how organisms engineer their environments is thus intrinsically linked to understanding, managing, and restoring natural systems (Byers et al. 2006; Hastings et al. 2007).

Among the various ways ecosystem engineering is performed, modulating major abiotic agents has been suggested as inducing one of the strongest effects on communities and ecosystems (Jones et al. 1994). A prime example for this type of engineering is provided by grazing of large terrestrial mammals, which modify ecosystem structure and function by reducing fire intensity and frequency (Savage and Swetnam 1990; Hobbs et al. 1991; Knapp et al. 1999; Waldram et al. 2008; Holdo et al. 2009). Although less common, herbivores also have the potential to augment, rather than reduce, local fire intensity by gathering plant materials for food, nests, and other structures (e.g., Smith and Reichman 1984; Hansell 1993; Whitford and Kay 1999). Interactions between direct fuel accumulation by animals and fire, however, have received virtually no attention. Similarly, simultaneous considerations of contrasting effects of herbivores on fire regimes, and how they influence the structure and dynamic of ecosystems, have scarcely been addressed (see van Langevelde et al. 2003; Holdo et al. 2009, for modeling approaches).

The semiarid scrub (Monte) of central Argentina is characterized by patches composed of shrubs distinctly larger than surrounding vegetation. These patches coincide with occurrence of colonies of the plains vizacha (*Lagostomus maximus* Desmarest, Chinchillidae), a large burrowing herbivore (males, 4.5–9.0 kg; females, 2.5–4.5 kg) and ecosystem engineer (Branch et al. 1996; Machicote et al. 2004; Villarreal et al. 2008) native to grasslands and shrublands of southern South America (Jackson et al. 1996). Indeed, comprehensive quantifications of the effects of these rodents on ecosystem structure show that shrubs on and around active colonies are much larger than those in surrounding ungrazed sites (Villarreal et al. 2008); a pattern characterizing vizacha colony sites distributed across the entire width of the phytogeographic province of Monte in Argentina (i.e., >1,000 km; Campos 1997; Villarreal et al. 2008).

Preliminary field observations indicate that vizacha–fire interactions are likely to be important in shaping woody vegetation dynamics in Monte (Online Resource 1), and, here, we propose that the landscape-level pattern of larger shrubs in sites inhabited by vizachas is largely explained by modifications of the fire regime by these animals. Specifically, we hypothesize that grazing by vizachas reduces fine fuel loads around colonies (Branch et al. 1996; Villarreal et al. 2008), decreasing the probability that shrubs are burned, and producing in turn patches

of larger shrubs, “the cold spot hypothesis”. We examine this hypothesis by comparing stem age of the dominant shrub, creosotebush (*Larrea divaricata*), in grazed zones on and adjacent to vizacha colonies and in the ungrazed matrix. Older shrubs in grazed compared with ungrazed zones would indicate that shrubs in grazed zones burn less frequently or intensely than those in the ungrazed matrix.

Certainly, several alternative explanations for larger shrubs in vizachas sites can be proposed. First, vizachas may choose to place their burrow systems in patches of large shrubs. Contrary to this hypothesis, however, long-term field studies have shown that new vizacha colonies form in open areas following disturbances such as fire (Bucher 1987; Branch et al. 1994). Also, local extinction rates of vizacha colonies appear to be higher in areas with larger shrubs (Machicote 2001), which suggests that woody vegetation exerts a negative effect on vizacha populations. Second, vizachas could facilitate shrub growth through reducing competition from grasses and herbs; however, foliar nitrogen (N) and phosphorous (P) contents (Villarreal et al. 2008) and predawn xylem pressure potentials (Hierro 1999) in *L. divaricata* were similar in zones grazed by vizachas off burrow systems and in ungrazed zones. Thus, this mechanism is not substantiated by field data. Lastly, vizachas could increase resource availability to shrubs through burrowing and deposition of feces and urine belowground, as documented for other burrowing herbivores (Chew and Whitford 1992; Laundré 1993, 1998; Ayarbe and Kieft 2000). Consistent with this idea, predawn xylem pressure potentials (Hierro 1999) and foliar N and P levels (Villarreal et al. 2008) of *L. divaricata* were higher in individuals growing on burrow systems compared to those in surrounding grazed and ungrazed zones, and foliage of *L. divaricata* on burrow systems was depleted in  $^{15}\text{N}$ , indicating a link between belowground N deposition by vizachas, whose feces were relatively low in  $^{15}\text{N}$ , and N uptake by shrubs (Villarreal et al. 2008). Resource availability, however, is not enhanced in grazed zones adjacent to borrow systems (Hierro 1999; Villarreal et al. 2008), where shrubs are also larger than in the surrounding ungrazed matrix, suggesting that other mechanisms are involved.

In addition to reducing fire intensity through grazing, we propose that vizachas also exert the opposite effect on fire regime; that is, vizachas increase fire intensity by modifying the spatial distribution of coarse fuel. Male vizachas collect coarse woody debris from foraging areas and pile it on burrow systems during territorial displays (Online Resource 2; Branch 1993). Mass estimates of coarse wood on burrow systems exceed  $1,500 \text{ g m}^{-2}$ , compared to  $20\text{--}50 \text{ g m}^{-2}$  of coarse wood in the litter layer of the ungrazed matrix (Villarreal et al. 2008). If our hypothesis on reductions of fire intensity is correct, then coarse wood on

burrows is unlikely to burn while vizcachas are present because there is little fine fuel to carry a fire in grazed zones. Following local population extinction of vizcachas and subsequent recovery of fine fuels (Branch et al. 1994, 1996), however, fire intensity on abandoned burrow systems should be greater than in other parts of the landscape where coarse fuel loads are lower, thus increasing the probability of shrub mortality, “the hot spot hypothesis”. To examine this hypothesis, we compared densities of live and dead shrubs on abandoned burrow systems and surrounding zones in burned sites. Alternatively, increased shrub mortality on abandoned burrow systems may result from sources other than fire such as severe drought and/or competition with other shrubs and recovered herbaceous vegetation, because these processes could affect large shrubs on abandoned burrow systems more strongly than smaller shrubs in adjacent zones. Given the high resource concentration belowground in burrow systems (Hierro 1999; Villarreal et al. 2008), this alternative seems unlikely; regardless, we accounted for it by comparing shrub densities on abandoned burrow systems that have burned with those on abandoned burrow systems that have not burned. If both the cold spot and hot spot hypotheses are correct, then at different stages in their population dynamics, vizcachas promote persistence of shrubs over extensive areas, and then contribute to increased shrub mortality in small patches through a unique interaction with fire.

## Materials and methods

### Study area

Our research was conducted at Los Valles Ranch, a cattle ranch in southeastern La Pampa Province, Argentina (39°11'S, 63°42'W), Lihue Calel National Park (38°00'S, 65°35'W), and Los Ranqueles Ranch, a cattle ranch nearby Lihue Calel (37°56'S, 65°23'W). The national park and Los Ranqueles are located approximately 165 km northwest of Los Valles (Online Resource 3). Annual precipitation is similar across the area [ $480 \pm 35$  mm (mean  $\pm$  SE) for 1971–1998 at Río Colorado, 60 km W of Los Valles, and  $474 \pm 37$  mm for 1984–2000 at Lihue Calel National Park]. The topography consists of large flat valleys and low angle slopes. Vegetation is semiarid scrub dominated by *L. divaricata*, which comprises 67% of the individuals and 64% of the aboveground biomass of shrubs at our sites (J.L. Hierro, unpublished data). Less abundant shrubs include *Prosopis flexuosa* var. *depressa*, *Condalia microphylla*, *Geoffroea decorticans*, and *Prosopidastrum globosum*. The understory consists primarily of perennial bunchgrasses (e.g., *Nassella* spp.), subshrubs (e.g., *Senna aphylla*,

*Acantholippia seriphoides*), and herbs (e.g., *Conyza* spp., *Baccharis* spp.). Grazing by cattle is light to moderate at Los Valles Ranch and other ranches, and no livestock grazing occurs in Lihue Calel National Park. Previous work has documented the pattern of larger shrubs on sites impacted by vizcachas than in surrounding zones in locations with both cows (Hierro 1999; J.L. Hierro, unpublished data) and no cows (Villarreal et al. 2008). Lightning and human-induced fires are common in this region. For example, fires ignited by lightning have burned 30–40% of Lihue Calel National Park twice in the last 25 years, and numerous smaller fires have been recorded.

### Cold spots and vegetation structure on active vizcacha colonies

We assessed the effects of vizcachas on herbaceous and woody vegetation and tested the cold spot hypothesis on active colonies at Los Valles. Vegetation was measured inside 20 m  $\times$  20 m plots. One of these plots was located on the burrow system, another plot was placed within the first 25 m of the zone intensely grazed by vizcachas, in a random direction from the burrow system, and another one at 100–150 m from the burrow system in the ungrazed matrix, also in a random direction (Online Resource 4). Effects on herbaceous vegetation, which represents fine fuel loads, were examined by clipping aboveground mass (biomass + standing dead litter) inside 0.50 m  $\times$  0.50 m quadrats located at five random points within each 20 m  $\times$  20 m plot at five vizcacha colonies. Grasses and herbs were clipped to ground level during the period of peak standing mass near the end of the growing season. Samples were dried at 65° C until reaching constant weight. Mass values from the five quadrats inside 20 m  $\times$  20 m plots were averaged and the mean per plot was used in analyses. Assessments of woody vegetation included estimations of shrub aboveground biomass, density, and age. Aboveground biomass and density of shrubs were estimated in a 5 m  $\times$  5 m quadrat placed at the center of each burrow system, and in two 5 m  $\times$  5 m quadrats located randomly within each 20 m  $\times$  20 m plot in the adjacent grazed and ungrazed zones at ten colonies. The biomass of each shrub was estimated from field measurements and allometric equations developed for each species by destructive sampling of shrubs at nearby sites (Hierro et al. 2000), and the biomass of all individuals in a quadrat were summed to obtain total aboveground biomass. Data from the two quadrats in each 20 m  $\times$  20 m plot located in the adjacent grazed or ungrazed zone were averaged prior to analyses. Assessments of differences in shrub age to test the cold spot hypothesis focused on the dominant shrub *L. divaricata*. Age was estimated from ring counts from the largest stem of five individuals of *L. divaricata* in each

20 m × 20 m plot at the ten colonies. As in other members of the Zygophyllaceae, a thin line of parenchyma marks the limit between spring and summer wood in *L. divaricata*, and these “growth rings” should indicate the age of stems (Chew and Chew 1965; Vasek 1980; Fahn 1990). Growth rings have been used to age *L. tridentata* in North America (Chew and Chew 1965; Barbour 1969; Vasek 1980), and this technique has been used successfully to age stems of other species in shrub-dominated ecosystems (e.g., Keeley 1993; Flinn et al. 1994). To validate this technique, we examined the number of rings in *L. divaricata* stems at six locations with known fire history (range, 4.5–27.5 years since last fire) in Los Valles and Lihue Calel National Park. Unless a fire is intense enough to cause mortality, *L. divaricata* resprouts from the base soon after fire (Boó et al. 1997). Thus, stem age should correspond to the time since the last large fire. At each location, we cut the largest stem of five shrubs at 0.10 m above the ground. Cross-sections of stems were polished and growth rings were counted (three radii per stem) under a dissecting scope. Mean ring counts of the five shrubs from each location were regressed against time since last fire using a least-squares fit, and yielded the following relationship ( $r^2 = 0.98$ ,  $p < 0.001$ ):

$$\text{Estimated stem age (years)} = -2.776 + 0.911 \\ \times \text{ number of rings.}$$

Ring counts were higher than estimated ages, particularly in young stems, indicating that stems occasionally produce double rings (Chew and Chew 1965). Stem ages of *L. divaricata* on burrow systems, in the adjacent grazed zones, and in the ungrazed matrix were estimated using the methods and equation described above.

#### Hot spots and shrub mortality on abandoned vizcacha colonies

To examine the hot spot hypothesis, we measured the densities of live and dead shrubs, represented by live stems and charred stumps, on burrow systems and in adjacent zones at abandoned colonies that had burned in Lihue Calel National Park. The vizcacha population in the park crashed during a severe drought in 1987 (Branch et al. 1994), and within 4 years, understory vegetation in abandoned vizcacha colonies had recovered from grazing, resulting in fine fuel loads that resembled those in the ungrazed matrix (Branch et al. 1996; Online Resource 2). In 1993, about 30% of the park burned. Five years post-fire, we recorded shrub density in five abandoned colonies that had burned in this fire. At each colony, all live and dead shrubs were counted inside a 5 m × 5 m plot located at the center of the abandoned burrow system, and in three 25-m<sup>2</sup> plots located randomly within 30 m of this burrow system in a paired design (Online Resource 4). The numbers of live

and dead shrubs were averaged for the three random plots and these means were used in the analyses.

To evaluate the possibility that shrubs on abandoned burrow systems have high levels of mortality from sources other than fire, such as severe drought and/or competition with shrubs and recovered herbaceous vegetation, we compared the densities of live and dead shrubs on the five abandoned burrow systems that had burned in Lihue Calel with those on six abandoned burrow systems that had not burned in Los Ranqueles Ranch.

#### Statistical analyses

We tested for differences in herbaceous aboveground mass, shrub aboveground mass and density, and *L. divaricata* stem age among burrow systems, adjacent grazed zones, and ungrazed zones for the colonies sampled at Los Valles using mixed linear models that allow correlated error structure to account for lack of independence among zones at each colony site (Proc Mixed; SAS Institute 1996; Villarreal et al. 2008). In the model, colony and zones were introduced as random and fixed effects, respectively. Mean values of response variables for each zone at each colony were used as replicates ( $n = 5$  for non-woody vegetation,  $n = 10$  for shrub variables). Variables were log-transformed where necessary (herbaceous mass only) to meet assumptions of normality. The best model for each dataset was chosen based on Akaike's Information Criterion and Log Likelihood (Proc Mixed; SAS Institute 1996). Pairwise comparisons among zones were made with the Tukey method.

Differences in live and dead shrub densities between abandoned burrow systems and adjacent zones that had burned at Lihue Calel National Park were assessed with paired-sample *t* tests with abandoned colonies as replicates ( $n = 5$ ). In turn, the density of live and dead shrubs on burned ( $n = 5$ ) and unburned ( $n = 6$ ) abandoned burrow systems located at Lihue Calel and Los Ranqueles, respectively, was compared with *t* test. Density of live shrubs was square root-transformed to meet assumptions of normality.

## Results

#### Cold spots and vegetation structure on active vizcacha colonies

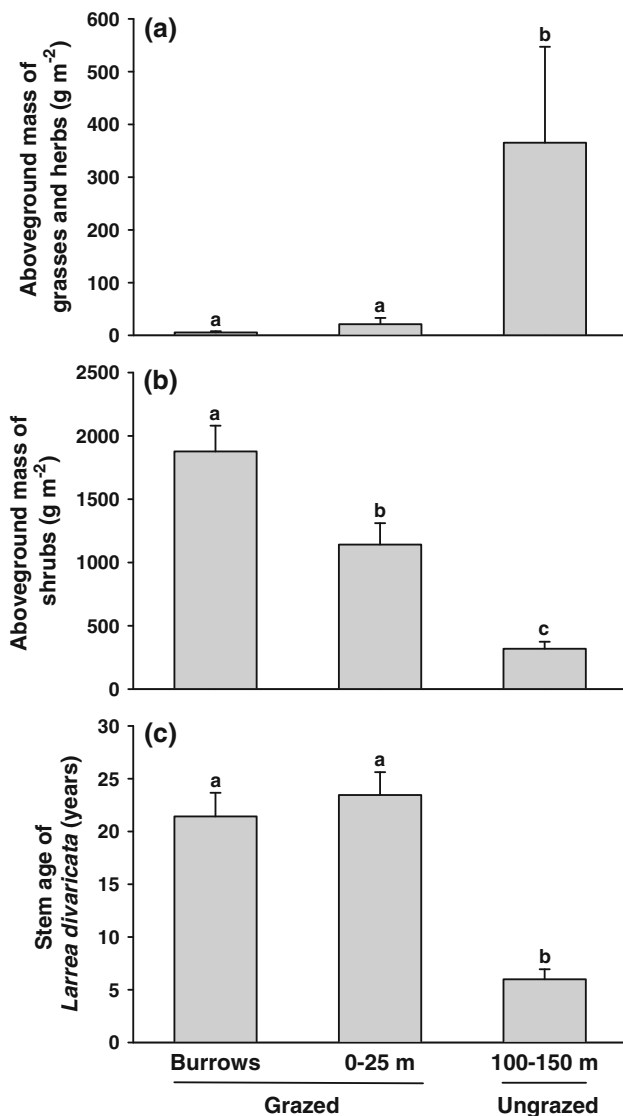
Vizcachas greatly reduced aboveground mass of herbaceous plants on burrow systems and in adjacent grazed zones, resulting in significant differences in fine fuel between these areas and the ungrazed matrix ( $F = 14.8$ ,  $df = 8$ ,  $p = 0.002$ ). Aboveground mass of herbaceous

plants did not differ between burrow systems and adjacent heavily grazed zones (Fig. 1). In sharp contrast, above-ground mass of woody vegetation was much greater in zones grazed by vizcachas than in the ungrazed matrix ( $F = 24.8$ ,  $df = 18$ ,  $p < 0.0001$ ). Shrub mass was higher on burrow systems than in any other zone and it was also greater in adjacent zones grazed by vizcachas than in the ungrazed matrix (Fig. 1). Shrub density did not differ significantly with vizcacha activity [ $F = 1.3$ ,  $df = 18$ ,

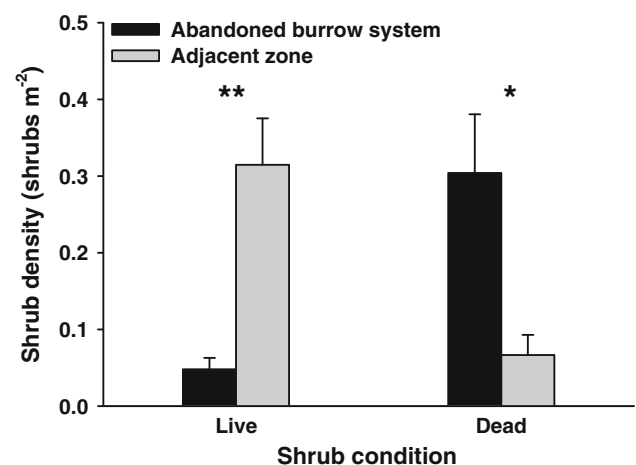
$p = 0.2$ ; mean shrub density (shrubs  $m^{-2} \pm SE$ ) on burrow systems =  $0.27 \pm 0.05$ , adjacent grazed areas =  $0.25 \pm 0.02$ , ungrazed matrix =  $0.37 \pm 0.07$ ]. Finally, supporting the cold spot hypothesis, estimated stem age of *L. divaricata* was similar between vizcacha burrow systems and adjacent grazed zones and more than three times greater in those locations than in ungrazed areas ( $F = 46.7$ ,  $df = 18$ ,  $p < 0.001$ ; Fig. 1).

Hot spots and shrub mortality on abandoned vizcacha colonies

Total density of shrubs (live + dead) was similar on abandoned burrow systems that had burned and in adjacent zones ( $t = 0.1$ ,  $df = 4$ ,  $p = 0.88$ ), but, consistent with the hot spot hypothesis, density of live shrubs was lower on abandoned burrow systems than in adjacent zones ( $t = -5.7$ ,  $df = 4$ ,  $p < 0.01$ ) and that of dead shrubs was higher on burrow systems than in adjacent zones ( $t = 3.1$ ,  $df = 4$ ,  $p = 0.04$ ; Fig. 2). Dead, burned shrubs comprised  $81.5 \pm 6.8\%$  of the shrubs on abandoned burrow system versus only  $11.5 \pm 3.8\%$  of the shrubs in the adjacent zones in burned sites. The stems of all dead shrubs were charred, indicating that they had burned. Further, no dead shrubs were encountered on unburned abandoned burrow systems. Total density of shrubs was almost identical for unburned burrow systems (live only,  $0.35 \pm 0.06$ ) and burned burrow systems (live + dead,  $0.35 \pm 0.07$ ;  $t = 0.02$ ,  $df = 9$ ,  $p = 0.98$ ), but density of live shrubs on abandoned burrow systems that had burned was much lower than that on abandoned burrow systems that had not burned ( $t = 5.9$ ,  $df = 9$ ,  $p < 0.001$ ).



**Fig. 1** Vegetation responses to grazing and related activity of vizcachas (*Lagostomus maximus*). **a** Aboveground mass (biomass + standing litter) of herbaceous vegetation, **b** aboveground mass of shrubs, and **c** estimated stem age of *Larrea divaricata* on active burrow systems, adjacent grazed zones (0–25 m from the burrow system), and ungrazed zones (100–150 m from the burrow system). Data are mean + 1SE for samples at five colonies for herbaceous vegetation and ten colonies for shrub variables. Different letters above bars indicate significant differences ( $p < 0.05$ ), as determined by Tukey test



**Fig. 2** Density of live and dead shrubs on burrow systems and in adjacent zones within 30-m of the burrow systems that were burned following local extinction of vizcachas. Data are mean + 1SE for paired samples at five colony sites. Significant differences between pairs of bars are indicated (\* $p < 0.05$ , \*\* $p < 0.01$ )

## Discussion

Modification of fire regimes associated with overgrazing by domestic livestock is one mechanism driving encroachment of woody vegetation in grasslands and woodlands worldwide (Savage and Swetnam 1990; Grover and Musick 1990; Roques et al. 2001). With the notable exception of well-studied African ecosystems, similar indirect facilitative effects of native herbivores on shrubs and trees are largely unknown (Laws 1970; Norton-Griffiths 1979; Dublin et al. 1990; van Langevelde et al. 2003; Holdo et al. 2009). Here, we found that a native burrowing herbivore, the plains vizcacha, reduces fine fuel loads and consequently fire frequency and/or intensity, increasing shrub persistence and generating over time sizeable patches (1–1.4 ha; Branch et al. 1996; Villarreal et al. 2008) of older and larger shrubs in the semiarid scrub of southern South America. Additionally, we found that vizcachas increase coarse fuel loads and, upon local extinction, fire intensity, increasing in turn shrub mortality in small patches ( $\sim 150 \text{ m}^2$ ). These results match our hypotheses, add to the direct and indirect mechanisms through which vizcachas engineer this semiarid scrub ecosystem (Branch et al. 1996; Machicote et al. 2004; Villarreal et al. 2008), and reveal a new interaction between native herbivores and fire, in which herbivores directly augment fire intensity. Our work thus indicates that negative and positive feedbacks between native herbivores and fire enhance the spatial heterogeneity of vegetation in woody-dominated ecosystems.

The presence of older shrubs on burrow colonies and adjacent grazed zones than in ungrazed zones provides strong support for the hypothesis that vizcachas facilitate shrubs by intense grazing and concomitant reductions in fire frequency and/or intensity. Increased shrub biomass on burrow systems compared to that in adjacent grazed zones suggests, however, that fire reduction is not the only mechanism through which vizcachas benefit woody plants. Previous studies have shown that vizcachas could also increase the biomass of shrubs on burrow systems by enhancing resource availability in these zones (Hierro 1999; Villarreal et al. 2008). Thus, our work indicates that both increased resource availability and reductions in fire intensity and/or frequency by vizcachas act in concert to generate larger shrubs on burrow systems than in adjacent grazed and ungrazed zones.

In grazed zones adjacent to burrow systems, on the other hand, resources are not enhanced (Hierro 1999; Villarreal et al. 2008), but shrubs are still much larger there than in the surrounding ungrazed matrix. Even though we took a descriptive approach to test our hypotheses, and thus alternative mechanisms cannot be completely ruled out, our finding that shrubs are also older in adjacent grazed zones than in ungrazed zones indicates that shrubs burn

less frequently and/or intensively in the former than the latter zones. The only explanation rivaling the proposition that older shrubs in sites inhabited by vizcachas results from the creation of fire-breaks by vizcacha grazing is that these animals choose to place their burrow systems in patches of older and (larger) shrubs. Long-term field data, however, offer no support for this possibility (Bucher 1987; Branch et al. 1994; Machicote 2001).

We have documented the engineering process through which vizcachas reduce fire frequency/intensity and create patches of unburned woody vegetation. Further work is needed, however, to unravel the ecological consequences of this phenomenon (Hastings et al. 2007), which likely include both community and ecosystem-level effects. Based on the mean densities of burrow systems from landscape-level surveys (0.3 colonies/ha; Branch et al. 1996), an estimated 30% (minimum) of the landscape in Lihue Calel National Park and surrounding ranches consisted of active colonies with reduced fine fuel loads during peak populations of vizcachas. Thus, potential effects of vizcachas on community and ecosystem processes can extend over large spatial scales (see also Branch et al. 1996; Villarreal et al. 2008). Possible variations in resource availability, predation levels, and competition intensity between patches of unburned vegetation created by vizcachas and surrounding burned sites could influence patterns of species diversity, as has recently been shown for alterations caused by other ecosystem engineers (Wright et al. 2002, 2006; Bartel et al. 2010). In addition, the increase in shrub age and biomass induced by vizcacha–fire interactions could impact the reproductive output and productivity of shrubs. Reproductive output in *L. tridentata* is low in young shrubs because proportionally more carbon is allocated to growth of stems, leaves, and roots (Chew and Chew 1965; Franco et al. 1994). However, beyond some threshold size and after attaining a maximum leaf area, older shrubs may also allocate fewer resources towards reproduction. As *L. divaricata* plants grow, the proportion of foliar mass decreases (Hierro et al. 2000), but the relationship between age and fruit production is unknown. By altering the aboveground age structure of shrubs, vizcachas could either increase or decrease reproductive output, depending upon the age at which flower and fruit production declines. Productivity of woody plants also increases with plant size up to a point, and then eventually declines (Ryan et al. 1997; Carey et al. 1998). By increasing shrub persistence in grazed areas and allowing shrubs to achieve relatively large leaf areas, vizcachas potentially increase rates of net assimilation and biomass accumulation by shrubs. Vizcachas, however, could also reduce shrub productivity by promoting their persistence beyond the most productive age. Lastly, unburned patches created by vizcachas could alter nutrient cycling in this system, as

reductions of fire frequency and/or intensity may result in the conservation of N in aboveground biomass and litter.

In contrast to reduced fire intensity and/or frequency on active colony sites, our data indicate that when local population extinctions of vizcachas and the recovery of grasses in previously impacted areas are followed by fire, shrub survival is reduced in “hot spots” associated with accumulated fuel loads on burrow systems resulting from piling of wood by male vizcachas during territorial displays. Because our sampling was conducted post-fire, we cannot be certain that dead shrubs had been alive prior to the fire. However, the absence of dead shrubs in unburned areas, and the low density of dead shrubs in burned areas off burrow sites, supports our conclusion. Fire appeared to have caused an average of 82% mortality of shrubs on burrow systems in extinct vizcacha colonies. This estimate exceeds the highest rate of mortality due to fire reported for *L. divaricata* (60%; Boó et al. 1997); and is much greater than our estimate of mortality for shrubs in areas adjacent to abandoned burrow systems that also burned (12%). By accumulating coarse woody debris on burrow systems, vizcachas greatly amplify the rates of fire-induced mortality of woody species in this ecosystem.

Hot spots in abandoned burrow systems potentially alter plant community structure in other ways in addition to reducing shrub density. By differentially affecting seedling production of shrubs and herbs, fire intensity in chaparral has been proposed as a major factor controlling species composition and diversity (Moreno and Oechel 1991). Through the formation of gaps, hot spots may provide colonization sites for plants that were excluded in pre-fire conditions (Myers 1990; Guevara et al. 1999). In addition, hot spots may alter nutrient cycling. Combustion of aboveground vegetation and litter results in N loss via volatilization (Hobbs et al. 1991), and fire also represents an important pathway for P mineralization (Moreno et al. 1994). If the accumulated fuel loads on burrow systems result in more complete combustion of vegetation and litter compared to sites without burrows, then nutrient availability and productivity may be affected in these patches (Weston and Attiwill 1990; Hobbs et al. 1991).

An important body of work now shows that, through direct perturbation and herbivory, burrowing mammals create mosaics of unique habitat across the landscape that cascade into community and ecosystem level processes in grasslands and woodlands around the world (North America: Huntly and Inouye 1988; Weltzin et al. 1997; Whitford and Kay 1999; Davidson and Lightfoot 2006; Eldridge et al. 2009; Ceballos et al. 2010; Davidson et al. 2010; South America: Branch et al. 1996, 1999, Machicote et al. 2004; Villarreal et al. 2008; Asia: Zhang et al. 2003; van Staaldin and Werger 2007). Our study adds to this literature by demonstrating that burrowing herbivores also

alter vegetation structure and increase heterogeneity in the landscape indirectly by modifying fire regimes. Among native herbivores, related indirect effects mediated by herbivory–fire interactions have been documented only for large herbivores in North American grasslands (Hobbs et al. 1991; Knapp et al. 1999; Joern 2005) and African savannas (Norton-Griffiths 1979; Dublin et al. 1990; van Langevelde et al. 2003; Waldram et al. 2008; Holdo et al. 2009). Because of the mobility and population fluctuations of herbivores, interactions between animals and fire are likely to generate more spatially and temporally dynamic patterns at the landscape scale than would be produced in their absence by other factors that control fire behavior such as fuel loads, topography, and microclimate (Whelan 1995; Bond et al. 2005). In the case of vizcachas, and probably other herbivores, these effects may be non-linear with population size because, beyond a threshold colony density, fire may not propagate across large portions of the landscape. Lack of recognition of these and other organismal engineering processes severely limits our understanding of ecological systems and consequently our abilities to successfully manage and restore them (Byers et al. 2006; Hastings et al. 2007).

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