



Patterns of plant species diversity following local extinction of the plains vizcacha in semi-arid scrub

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We examined changes in the diversity of herbaceous plant species at colony sites of the plains vizcacha (*Lagostomus maximus*) following local extinctions of this species in semi-arid scrub of central Argentina. These large rodents live in social groups, share a communal burrow system, and forage in a common home range around the burrow system. Through intense herbivory, vizcachas create large open patches in the understory of a landscape dominated by dense bunch grass and shrubs. In heavily grazed areas at the centers of vizcacha colonies, species richness of forbs was significantly higher than species richness of grasses. In lightly grazed areas at colony edges, both plant groups were equally common. Following local extinction of vizcachas, the number of forb species declined on colony sites as the cover of grasses increased, and within a year grass species were more numerous than forbs at the edges of colonies. Species richness of grasses increased slowly in the areas that had been heavily grazed by vizcachas. Five years after the population crash of vizcachas, species richness of grasses in centers of extinct colonies was less than 50% of the species richness in areas that had been lightly grazed at colony edges. In contrast, grass cover in areas that had been heavily grazed increased to levels similar to the ungrazed matrix within 2–3 years after extinction. Thus, the major transition in physical structure of the plant community occurred much more rapidly than the recovery of plant species richness.

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Introduction

Recently, there has been increasing recognition that herbivores play key roles in shaping the structure and function of ecosystems by altering the species composition of communities, controlling resource flows, and causing physical changes in the environment (Jones *et al.*, 1994; Chapin *et al.*, 1997). For example, herbivores may increase species diversity of plants by reducing the abundance of competitively dominant

species, induce shifts in relative abundance of species without changing species richness, or reduce species richness by causing local extinction of forage species (Waser & Price, 1981; Bowers, 1993; Heske *et al.*, 1993; Kelt & Valone, 1995). The outcome of plant–herbivore interactions depends on the density and distribution of herbivores and on biotic–abiotic interactions. Species such as colonial, burrowing mammals that occur in high densities and occupy the same site for many years are particularly likely to induce long-term changes in communities and ecosystems (Lawton, 1994). For example, studies of black-tailed prairie dog (*Cynomys ludovicianus*) colonies provide some of the strongest evidence for herbivore-mediated changes in community and ecosystem processes (Coppock *et al.*, 1983; Whicker & Detling, 1988).

Because animal populations are dynamic, their impacts vary through time and space. Ostfeld & Canham (1993) have suggested that the dynamics of herbivore populations can be viewed as a keystone process. Although the literature on herbivory is extensive, only a few studies have examined the long-term dynamics of changes induced by mammalian herbivores at a landscape scale (Norton-Griffiths, 1979; Whicker & Detling, 1988; Dublin *et al.*, 1990).

This study examined changes in plant species diversity at colony sites of the plains vizcacha (*Lagostomus maximus*) following local extinction of vizcachas. These large, herbivorous rodents (males 4.5–9.0 kg, females 2.5–4.5 kg), native to the grasslands and semi-arid scrub of Argentina, live in social groups (*c.* 10–30 animals) and share a communal burrow system (vizcachera; Llanos & Crespo, 1952; Branch, 1993*a*). All members of a social group forage in a common home range around the vizcachera (Branch, 1993*b*; Branch & Sosa, 1994). Vizcachas occupy the same burrow system for many generations and through their intense herbivory create large, discrete patches characterized by bare soil and low growing forbs imbedded in a matrix of dense bunch grass (Branch *et al.*, 1996; Campos, 1997).

Ecologically and behaviorally, the plains vizcacha is similar to the black-tailed prairie dog, a keystone species in the western prairies of the North America (King, 1955; Branch, 1993*a*; Hoogland, 1995). Vizcachas are likely to have equally profound effects in the grasslands and semi-arid scrub of Argentina, but have been much less studied. These two species also face many of the same threats. Through extermination programs and human-induced habitat change, black-tailed prairie dog populations have been reduced to less than 2% of their numbers several decades ago (Whicker & Detling, 1988). Similarly, the plains vizcacha has already disappeared from much of its original range and continues to be subjected to eradication programs because it is considered a competitor with domestic livestock. Understanding the ecological roles of such species is critical in developing compelling arguments for their conservation.

In a previous paper, we documented profound landscape-scale changes in vegetation structure associated with local extinctions of vizcachas, as more than 30% of the landscape shifted from open forb-dominated patches to bunch grass (Branch *et al.*, 1996). In this paper, we compare changes in plant species richness at the centers and edges of vizcacha home ranges (*i.e.* heavily grazed and lightly grazed areas) for 6 years following the same population extinction. The impact of vizcachas on plant species diversity has not been examined previously. We also ask the question: do changes in species diversity following local extinction of vizcachas exhibit the same temporal patterns as changes in vegetation structure?

Methods

Study area

Research was conducted in Lihue Calel National Park (8000 ha, 38°00' S, 65°35' W) in La Pampa Province, Argentina. This area of semi-arid scrub (300 m elevation) has hot

summers, cool winters, and low unpredictable rainfall (annual rainfall 1985–1995, mean \pm SE = 491 \pm 35 mm). Terrain is flat except for a large, isolated set of granitic outcrops (589 m elevation). Vegetation consists of creosote bush flats (*Larrea divaricata*, *L. cuneifolia*, *L. nitida*) and mixed shrub patches (e.g. *Condalia microphylla*, *Cercidium praecox*, and *Prosopis flexouosa* var. *depressa*) with an understory of grasses and forbs (Instituto Nacional de Tecnología Agropecuaria, 1980). The most common grasses are bunch grasses of the genus *Stipa*. Vegetation sampling was conducted at five vizcacha colonies that have formed part of a long-term study since 1985 (total area occupied by the colonies = 14 ha).

Vizcacha dynamics

Dynamics of vizcacha populations were monitored throughout this study by observation of marked animals and large-scale surveys of burrow activity. Details of population dynamics have been presented elsewhere and only will be summarized in this paper (Branch *et al.*, 1993, 1994 *a*, 1996). When the study began in 1985, vizcacha densities were very high in Lihue Calel National Park and on surrounding ranches, possibly because of higher than average rainfall and exceptional forage production from 1983–1985 (Branch *et al.*, 1994 *a*). No extinct colonies were observed prior to 1986. Vizcachas in the five study colonies were observed on 260 nights between March 1985 and August 1987 (Branch, 1993 *a*). The mean number of animals per vizcachera was 12 \pm 0.9 SE in March 1985 and peaked at 17 \pm 0.9 SE with summer recruitment in March 1986. The population then began declining. High animal density coupled with below average rainfall (343 mm) in 1986 resulted in insufficient food resources for maintenance of body weight in adults and growth of young (Branch *et al.*, 1994 *a*). Predation also was high. By mid 1987, four of the five study colonies were extinct, and no vizcachas were resident in the study colonies by 1988. Surveys of burrow activity in four areas of the park in 1991 indicated that the population crash was widespread with 86% of the vizcacheras ($N = 107$) extinct (Branch *et al.*, 1996).

Vegetation sampling

Vegetation was sampled in core areas used by five social groups of vizcachas (core area, mean \pm SE = 1.3 \pm 0.2 ha) and at the edges of the home ranges of three groups. Core areas and home range edges were defined with intensive observations of vizcacha behavior and by the distribution of fecal pellets (Branch, 1993 *b*). Core areas were heavily grazed when the study was initiated in November 1985. Plots at the edges of the home ranges were ungrazed when the study was initiated, but vizcachas occasionally foraged in these areas as they expanded their home ranges with the high population density in 1986. Exclosures were also established within each home range to compare grazed and ungrazed areas. However, following the crash in the vizcacha population early in the study, the exclosures lost their utility because grazing ceased on all plots. Therefore, only data from outside the exclosures are presented.

At quarterly intervals, vegetation was sampled in five plots (0.5 m \times 0.5 m) randomly located within each core area and in five plots located at 20-m intervals along the edges of each of three group home ranges. All plant species in each plot were recorded. Specimens that could not be identified in the field were collected and later identified at the Universidad Nacional de La Pampa. Sampling was conducted in the austral spring (November), late summer (March), autumn (May), and winter (late July or early August) from November 1985 to November 1995, except in November 1989 when no vegetation data were collected. Data are presented here through 1992; a lightning fire

burned the study area in February 1993 and potentially could confound interpretation of data collected after that date.

Analyses

For analyses of species richness, plants were grouped as follows: annual forbs (total of 16 species), perennial forbs (9 species), and perennial grasses (14 species). Annual grasses were rare and not included in analyses. To avoid pseudoreplication, the total number of species in the five quadrats in each area (a core area or home range edge) were summed and these areas, rather than individual plots, were used as replicates in all analyses of species richness. We assessed differences in species richness of perennial grasses and forbs within core areas and home range edges at particular sampling dates (e.g. the beginning of the study) using paired *t*-tests. Long-term trends in species richness following the extinction of vizcachas were analysed with a repeated measures model to account for lack of independence of samples through time. This approach allowed us to examine temporal trends in species richness while controlling for effects of annual rainfall within a repeated measures design (Branch *et al.*, 1996). Trends in species richness with time since extinction of vizcachas and with rainfall were examined by adding these two variables to the model as linear regressors. This analysis indicated whether there was a significant positive or negative trend in species richness with a particular regressor with the effects of the other regressor removed. Computations were performed using the mixed procedure in SAS (SAS Institute, 1992). All count data were subjected to a square root transformation before analysis (Sokal & Rohlf, 1995). Statistical analyses of long-term trends in species richness of perennials were conducted with samples from May to include all plants from the summer growing season. Annual plants are primarily winter species in our study area (Anchorena, 1988). Therefore, we examined trends in species richness of annual forbs using July samples. Trends in total species richness were examined for May and July samples.

The frequencies of occurrence of individual species (i.e. number of plots in which the species was present) were compared for the plots in three core areas ($N = 15$) and the edge plots adjacent to these core areas ($N = 15$ plots). A species was scored as present in a plot if it occurred in the plot during any May census (perennial forbs and grasses) or July census (annual forbs) from 1986–1992. Chi-square analyses were used to test for significant differences in frequencies between core and edge plots. Significance levels were adjusted for the error rate associated with multiple comparisons using Bonferroni's method (Sokal & Rohlf, 1995).

Results and discussion

Through intense herbivory, plains vizcachas significantly alter both the physical structure and species diversity of plants communities in the semi-arid scrub of central Argentina. Although vizcachas eat at least 58% of the forbs and grasses in our study area, they preferentially forage on grasses (Branch *et al.*, 1994b). When vizcachas were present in 1986, species richness of perennial grasses was significantly lower than species richness of perennial forbs in intensively grazed core areas ($t = 3.8$, $p < 0.02$, $df. = 4$; Fig. 1(a)). In contrast, species richness of perennial grasses and forbs were similar at the home range edges that were lightly grazed by vizcachas ($t = -1.0$, $p = 0.42$, $df. = 3$; Fig. 1(b)). The effects of vizcachas on species diversity parallel changes in plant cover induced by vizcachas. The most pronounced physical impact of vizcachas on vegetation was a reduction in perennial grass cover and associated impact of standing dead material near the burrows (Branch *et al.*, 1996).

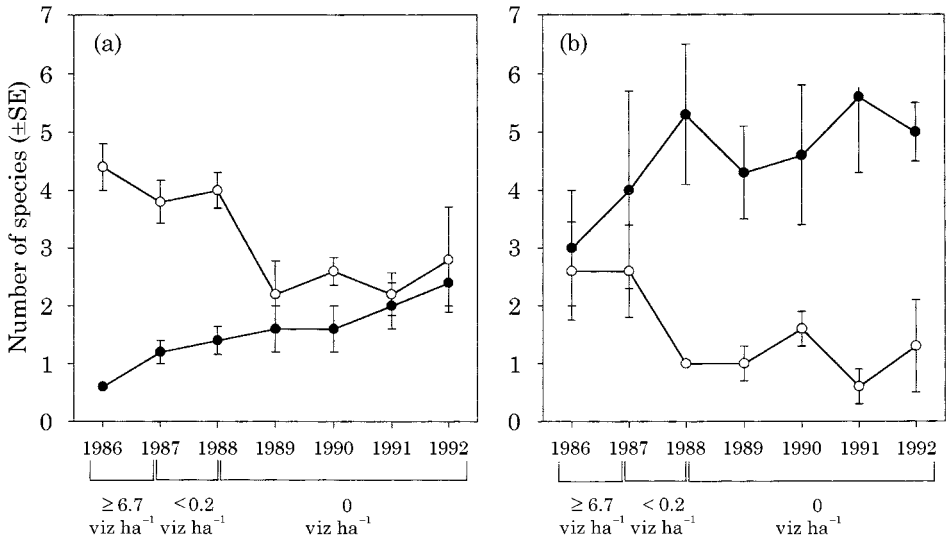


Figure 1. Species richness (mean ± SE) of perennial grasses (●) and perennial forbs (○) in (a) core areas (heavily grazed) and (b) edges (lightly grazed) of home ranges of five social groups of vizcachas. Data were collected each year in May from 1986–1992.

In a variety of ecosystems dominated by grasses, herbivory has been shown to increase the abundance of forbs through release of forbs from interspecific competition for resources (i.e. light, water, and nutrients) with removal of grasses (Coppock *et al.*, 1983; Heske *et al.*, 1993). In areas that had been heavily grazed by vizcachas, species richness of perennial grasses increased significantly over time following local extinction of the vizcacha population in late 1987, and species richness of forbs declined (Table 1;

Table 1. Summary statistics from analysis of repeated measures models for trends in species richness of herbaceous plants with rainfall and time as linear regressors after the population crash of vizcachas (1986–1992)

	Time after vizcacha crash		Rainfall	
	Trend	<i>p</i>	Trend	<i>p</i>
Core areas in the center of home ranges				
Annual forbs	0	0.09	+	0.001
Perennial forbs	–	0.009	0	0.20
Perennial grasses	+	0.004	0	0.51
All species (May)	0	0.56	0	0.57
All species (July)	0	0.07	+	0.002
Edges of home ranges				
Annual forbs	0	0.40	+	0.05
Perennial forbs	0	0.07	–	0.01
Perennial grasses	0	0.13	0	0.21
All species (May)	0	0.62	0	0.86
All species (July)	0	0.49	0	0.10

Analyses of perennial grasses and forbs were conducted with data from May. Analyses of annual forbs were conducted with July data. (See Methods).

Fig. 1(a)). The marked decrease in species richness of perennial forbs in core areas in late 1988 and early 1989 was concurrent with a dramatic increase in grass cover (Branch *et al.*, 1996), suggesting that this decline also may be related to competitive interactions with grasses.

At the edges of home ranges, the repeated measures analysis indicated no significant temporal trends in species richness of grasses (Table 1; Fig. 1(b)). Species richness of perennial forbs was related to rainfall but not time since extinction of vizcachas (Table 1). The apparent lack of a temporal trend in grasses at home range edges may have resulted from a rapid increase in species richness after extinction in these lightly grazed areas, followed by no additional increase through time (Fig. 1(b)). Also, the high variance in species number and small sample sizes provide low power to detect a trend. However, by 1988, species richness of perennial grasses was significantly higher than species richness of perennial forbs at colony edges ($t = 4.4$, $p < 0.05$, $df. = 2$; Fig. 1(b)).

The diversity of annual forbs was more clearly related to rainfall than to activity of vizcachas (Table 1; Fig. 2). The number of species of annual forbs generally tracked rainfall amounts except in 1987. Species richness in that year was higher than in 1988 and approximately equal to species richness in 1989 (Fig. 2), but annual rainfall in 1987 was lower (424 mm) than rainfall in either 1988 (487 mm) or 1989 (563 mm). The lack of concordance of species richness of annual forbs and rainfall in 1987 may have occurred because annual forbs respond to the timing of rainfall rather than annual totals (Pitt & Heady, 1978). However, it is also possible that this peak in species number is a temporary phenomenon related to 'a window of opportunity' between release from herbivory and lack of competition from grasses. At the time this peak

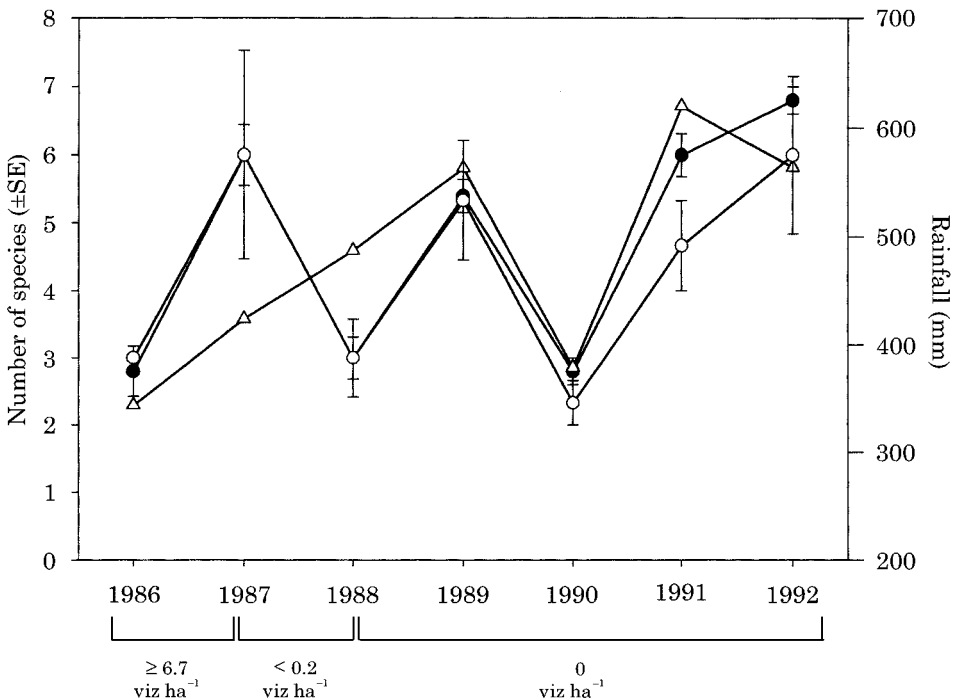


Figure 2. Annual rainfall (Δ), and species richness (mean \pm SE) of annual forbs in core areas (\bullet) (heavily grazed) and edges (\circ) (lightly grazed) of home ranges of five social groups of vizcachas from 1986–1992. Species richness data were collected in July of each year.

occurred, vizcacha populations had begun declining, but grass cover had not yet recovered. When annual forbs were released from intense herbivory by exclosures or the extinction of vizcachas, cover increased markedly within 6 months (Branch *et al.*, 1996). However, the abundance of some species, such as *Erodium cicutarium*, then declined as the large gaps created by vizcachas were recolonized by bunch grass. Thus, the short-term and long-term responses of annuals to the removal of vizcachas may differ in this landscape. Also, because precipitation is highly variable (temporally and spatially) in semi-arid areas and modulates annual plant abundance and diversity (Pitt & Heady, 1978; Samson *et al.*, 1992), the effects of herbivores on annual species often may be masked and difficult to detect without experimental manipulation.

Intermediate levels of grazing often increase species diversity in plant communities by reducing the abundance of dominant species and allowing competitively inferior species to persist; however, heavy grazing may reduce overall diversity (Waser & Price, 1981; Bowers, 1993). In this study, we detected no differences in total species richness between heavily and lightly grazed sites at the beginning of the study (mean number of species \pm SE in May 1986, colony cores = 6.6 ± 0.4 , colony edges = 9.0 ± 2.3), and there were no significant trends in total species number with time since extinction of vizcachas on either the core areas or edges of vizcacha home ranges (Table 1). Because of the strong preference of vizcachas for foraging on grasses, including a number of species that were relatively uncommon (e.g. *Pappophorum vaginatum*, *Setaria leucopila*; Branch *et al.*, 1994b), species richness of grasses was lower on grazed plots. Species that occurred in low abundance in the edge plots were absent from the core areas (Table 2). Three species of annual forbs and one perennial forb were more abundant in core areas than at the colony edges (Table 2). However, under the environmental conditions in this study, the diversity of forbs did not increase sufficiently to overcome the reduction in grasses.

The structural changes that occurred in the understory following the extinction of vizcachas (i.e. a shift from open patches of low growing forbs to dense bunch grass characteristic of the matrix; Branch *et al.*, 1996) were much more rapid than the responses in species composition. While vizcachas were present from 1986–1987, per cent cover of grasses was less than 5% during any sample period and composed only 5–25% of the perennial cover at any sample period. By 1990, cover of grasses (primarily *Stipa tenuis*) reached almost 25%, and throughout the remainder of the study grasses composed more than 70% of herbaceous perennial cover (Branch *et al.*, 1996). Thus the major transition in the physical structure of the plant community occurred within 2–3 years after extinction. These vegetation changes were similar to changes documented after removal of a guild of kangaroo rats (*Dipodomys* spp.) for 12 years in the Chihuahuan Desert (Brown & Heske, 1990). In contrast to the rapid increase in grass cover following the vizcacha extinction, species richness of grasses increased slowly at a rate of approximately 0.67 new species per year (all core areas combined from 1987–1995; Branch, Villarreal, & Hierro, unpub.). When vegetation sampling was terminated 8 years after the population crash, the structure of the landscape closely resembled an ungrazed landscape, but some species that typically occur in an ungrazed landscape were still absent.

Conclusion

With local extinction and colonization, vizcachas generate a dynamic mosaic of patches on the landscape. Our data indicate that the temporal patterns of change in species richness and vegetation structure following local extinctions differ greatly. Although vizcachas induce dramatic changes in the physical structure and species composition of semi-arid scrub, under the conditions of this study they altered species richness of

Table 2. Occurrence, by species, of annual forbs, perennial forbs, and perennial grasses in core areas of three social groups of vizcachas and in plots at the edges of these three core areas (N = total of 15 plots in each type of area). - = absent in all 15 plots; L = present in 1-5 plots; M = present in 5-10 plots; H = present in 11-15 plots. I = introduced species. ** p < 0.01; * p < 0.05 after correction by Bonferroni's method for multiple comparisons

Annual forbs		Core†		Perennial forbs		Core		Perennial grasses		Core		Edge	
<i>Carduus thoermeri</i> (I)	-	L		<i>Baccharis melanopotamica</i>	L	L		<i>Aristida spgazzini</i>	-	L			
<i>Centaurea solstitialis</i> (I)	-	L		<i>Boopis anthemoides</i>	L	-		<i>Aristida subulata</i>	-	L			
<i>Conyza bonariensis</i>	L	-		<i>Evolvulus sericeus</i>	L	-		<i>Aristida trachyantha</i>	-	M			
<i>Conyza floribunda</i>	-	L		<i>Glandularia parodii</i>	M*	L		<i>Hordeum stenostachys</i>	-	L			
<i>Daucus pusillus</i>	L	L		<i>Hoffmanseggia erecta</i>	H	H		<i>Melica bonariensis</i>	L	-			
<i>Draba australis</i>	M	M		<i>Nierembergia aristata</i>	L	L		<i>Pappophorum vaginatum</i>	-	L			
<i>Erodium cicutarium</i> (I)	H	H		<i>Sphaeralcea crispa</i>	L	-		<i>Poa lanuginosa</i>	L	M			
<i>Facelis retusa</i>	H**	L		<i>Thelesperma megapotamicum</i>	L	L		<i>Poa ligularis</i>	L	M			
<i>Gamochaeta argentina</i>	H**	L		<i>Thymophylla pentachaeta</i>	M	L		<i>Piptochaetium napostaense</i>	L	L			
<i>Herniaria cinerea</i> (I)	H**	L						<i>Setaria leucopila</i>	-	L			
<i>Medicago minima</i>	H	H						<i>Stipa ichu</i>	L	M			
<i>Pelletiera serpyllifolia</i>	H	M						<i>Stipa tenuis</i>	H	H			
<i>Plantago patagonica</i>	H	M						<i>Stipa tenuissima</i>	L	L			
<i>Solanum incisum</i>	-	L						<i>Stipa vaginata</i>	-	M*			
<i>Solanum tweedii</i>	-	L											
<i>Triodanis biflora</i>	L	-											

†The core and edge were tested for significant differences in frequencies for all species that differed in their abundance category (L, M, H) between these areas (see text).

particular growth forms but did not appear to affect total species richness of the plant community. Because the influence of biotic interactions may be contingent upon abiotic processes (Connell, 1961; Menge *et al.*, 1994; Guo & Brown, 1996), studies conducted under different conditions in semi-arid scrub (e.g. low-moderate densities of vizcachas and high rainfall) or in other habitats may reach different conclusions.

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