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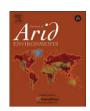
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Cattle grazing effects on annual plants assemblages in the Central Monte Desert, Argentina

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ABSTRACT

Plant assemblages' dynamics have been studied to evaluate the influence of different environmental factors. The aim of our work was to assess the effect of a disturbance in the form of livestock grazing on annual plants, in a South American desert. We tested the exclusion of cattle grazing by comparing the composition of annual plants in three major vegetation types within a MaB Reserve in the Monte Desert of Argentina, with those of an adjacent grazed field. Sampling was conducted in two consecutive years that differed in precipitation. We established three sampling sites within each vegetation type at the reserve and the grazed field. Transects were set to assess plant cover, abundance, and richness. Theoretically, changes in diversity are explained by changes in one of its components: species richness. Species richness of annual plants was not different between the grazed and ungrazed sites. However, plant cover and diversity were lower in grazed sites, whereas abundance increased. Owing to a strong species-specific effect, we propose that it is evenness the main parameter involved in diversity dynamics in the heterogeneous vegetation mosaic of the Monte desert. Finally, vegetation types (spatial heterogeneity) and rainfall regime (temporal heterogeneity) greatly interacted with grazing effects. We endorse the idea that rapid responses of annual plant assemblages to changes in rainfall conditions coupled with herbivore control, might result in a restoration pathway for degraded arid landscapes.

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1. Introduction

In desert environments, life forms have evolved mechanisms to respond to stress and capitalize on semi-predictable extreme events (Rundel and Gibson, 1996). One of these mechanisms is expressed through differences among reproductive strategies (e.g. annuals versus perennials). Annual plants, in general, exhibit short periods of active growth and long periods of seed dormancy (Philippi, 1993; Rundel and Gibson, 1996) and the trigger mechanism for these traits can be the beginning of rains (Keeley and Fotheringham, 2000). Annual plants are one of the characteristic elements in temperate deserts, like the Mojave Desert where they constitute up to 85% of the herbaceous species (Rundel and Gibson, 1996). Although perennials are usually dominant in terms of biomass, in certain years with favorable combinations of temperature, rainfall and light, annuals can make up an important proportion of biomass (Inouye, 1991).

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Previous results on the effects of livestock grazing on plant communities have been shown different responses (from positive to negative) depending on spatial and temporal scales (Olff and Ritchie, 1998), intensity and duration (Waser and Price, 1981), evolutionary history of grazing (Laurenroth, 1998; Milchunas et al., 1995), rainfall and soil nutrients (Meserve et al., 2003), herbivore body size (Olff and Ritchie, 1998), soil richness and moisture (Fahnestock and Knapp, 1994), and livestock density (Kelt and Valone, 1995) among the most important factors. In the Monte of Argentina plant establishment is strongly affected by the spatial variation in abiotic factors and by the interspersion of diverse vegetation types across a patchy landscape as reported for other arid ecosystems (Armas and Pugnaire, 2005). Particularly in Ñacuñán Reserve, heterogeneity of germination and growth conditions can enhance plant diversity (Rossi and Villagra, 2003). In this sense, it has been found that heavy grazing by cattle could reduce rangeland heterogeneity (Fuhlendorf and Engle, 2001).

This region is also characterized by a rainfall peak in spring which marks the beginning of the wet season (Ojeda et al., 1998), and triggers the growing of annual plants. Thus, once a year annual plants become an important, readily digestible food source for native and domestic herbivores, due to their high protein content

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and low level of secondary plant compounds. Furthermore, annual plants are especially sensitive to the effect of disturbances due to their structure and lack of quantitative and qualitative defences (Coley et al., 1985). Given all the exposed above, annual plants turn out a very useful model to assess the impact of livestock grazing on the vegetation structure of arid ecosystems.

Several studies have focused on the effect of disturbance on plants diversity and richness. The Intermediate Disturbance Hypothesis has proposed that, within a given patch, species richness and diversity should be highest at intermediate frequencies and intensities of damage (Connell, 1978; Petraitis et al., 1989). On the other hand, Waser and Price (1981) concluded that particularly in arid ecosystems diversity of annual plants is not enhanced by continuous cattle grazing and follows a negative curve.

The purpose of our research was to characterize the effect of a disturbance in the form of cattle grazing, on community parameters of the annual plant assemblage in the Monte Desert ecosystem. We postulated that cattle grazing effect would vary in space (i.e. across the mosaic of habitats) and time (between years).

2. Materials and methods

2.1. Study site

This study was carried out at the Nacuñán Man-and-Biosphere Reserve (34°0,2'S; 67°58'W) and a surrounding region of unprotected land in the central part of the Monte Desert, Mendoza province, Argentina (500 m a.s.l.), during October 2001 and October 2002.

The Nacuñán Reserve was established in 1961, and covers 12,800 ha. The characteristic vegetation is a shrubland that varies according to the latitude, topography and climate, resulting in a diverse matrix of plant and animal communities (Ojeda and Tabeni, 2009). Land use is dominated by cattle ranching throughout the region, but other important agents of land-cover change are fire, logging, and non-native species introductions. A fence was built around the reserve in 1970, protecting its ecosystems from grazing and logging, and promoting the recovery of vegetation following release from long-term grazing pressure. In the neighboring field, grazing is continuous with hotspots of grazing management and varying spatial grazing patterns. In this sense, Asner et al. (2003) demonstrated that in comparing Nacuñán Reserve and outside fields, long-term grazing accounts for significant differences such as woody vegetation encroachment, bare soil increase, lower C and N concentration in the soil, and changes in vegetation structure. Regarding the grazed field, Tabeni (2006) measured feces density in order to estimate livestock activity within vegetation types, and reported significant differences among all them. This author's estimations suggest that creosotebush is the most used vegetation type, followed by mesquite forest and finally sand dunes.

The climate is characterized by hot, wet summers, and dry, cold winters. Average annual precipitation is 326 mm and occurs in a unimodal fashion mainly in late spring and summer. Mean temperatures are lower than 10 °C in the winter and above 20 °C in the summer (Ojeda et al., 1998). The region is a diverse mosaic of vegetation types (Roig, 1971). Our study was performed at three distinct vegetation types or patches: the mesquite or "algarrobo" forest (*Prosopis*), sand dunes and creosotebush shrublands (*Larrea*), on both sides (e.g. the grazed and the nature reserve sites). The mesquite forest is the most complex and diverse vegetation type and is composed of three strata. The tree stratum is dominated by *Prosopis flexuosa* and *Geoffroea decorticans*, prevailing shrubs are *Larrea divaricata*, *Lycium* spp., *Condalia microphylla*, *Capparis atamisquea*, *Atriplex lampa* and *Verbena* spp., and the herb stratum is

rich in grass species such as *Pappophorum caespitosum*, *Digitaria californica*, *Setaria* sp., and in dicots like *Acantholippia seriphioides* or *Sphaeralcea miniata*. The creosotebush shrubland is characterized by the absence or low density of trees and a thick cover of *Larrea cunneifolia* and herbs (*Pitraea cuneato-ovata*, *Glandularia mendocina*, *Trichloris crinita*, and *Conyza apurensis*). Finally, sand dunes are characterized by sandy soils with an herbaceous stratum composed of *Panicum urvilleanum*, *Solanum eucanthum* and *Hyalis argentea*, and a shrub stratum including mainly *L. divaricata*, *L. cuneifolia* and *C. microphylla* (Roig, 1971).

2.2. Data collection

Data were collected from ungrazed (reserve) and grazed sites. In each vegetation type (creosotebush, mesquite forest and sand dunes) we established three sampling sites at least 100 m apart. At each site, two 50-m transects were set: one at the reserve and the other in the grazed field, each starting at 10 m from the boundary. Along each transect we placed 0.5-m \times 0.5-m (0.25-m²) sampling quadrats at 1.5-m intervals, i.e. a total of 25 quadrats per transect. Within each sampling quadrat we recorded at the herbaceous stratum number of species, plant cover, and number of individuals for each species.

The total number of samples was 900, 150 from each vegetation type, collected over both years.

2.3. Data analysis

Nested ANOVA were used to test for differences in plant cover and abundance of annual plants respectively, using year, vegetation type and grazing treatment as fixed factors and transect as a random factor. This analysis allows controlling for non-independence among data, since each transect is nested within the vegetation type where it was selected for measurements. Plant cover data were arc-sin transformed in order to meet the requirements of ANOVA. Post-ANOVA Tukey tests were used to assess differences between means (STATISTICA version 6). The Shannon index of diversity (H'), richness and evenness (J') were calculated using the abundance of individuals from each species. Richness and diversity were calculated and compared using INFOSTAT version 2008.6. Evenness was calculated by hand.

3. Results

Species richness did not differ between grazed (22 ± 1) and ungrazed (23 ± 1) treatments, it was significantly different between years: 2001 (23 ± 3) and 2002 (10 ± 3) , and regarding vegetation types, it was higher in sand dunes (21 ± 3) , intermediate in mesquite forest (17 ± 2) and lower in creosotebush (15 ± 3) . Particular effects of year and grazing treatments within vegetation types and among them are showed in Table 1.

Annual plant cover was significantly higher in 2001 (mean = 0.47) than in 2002 (mean = 0.22) (F = 398.01; P = 0.0001; df = 1). There were also significant differences between treatments (F = 53.52; P = 0.0001; df = 1) with high cover in the reserve (mean = 0.4) respect to the grazed field (mean = 0.3), and among all vegetation types (F = 13.35; P = 0.0061; df = 2) with the highest cover at creosotebush (mean = 0.41) followed by mesquite forest (mean = 0.35) and finally sand dunes (mean = 0.28). As regards interactions, there were significant interactions between year and treatment (F = 22.47; P = 0.0001; df = 1), year and vegetation type (F = 4.42; P = 0.0122; df = 2), treatment and vegetation type (F = 12.54; P = 0.0001; df = 2), and among year, treatment and vegetation type (F = 3.22; P = 0.0401; df = 2).

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Table 1 Synthesis of results for the variables considered: species richness, diversity, abundance, plant cover and evenness (mean \pm standard error) in each community, treatment and year. Different letters ('a' and 'b') were assigned to statistical differences between means and indexes within each vegetation type and year. The sample size was N = 75.

Variable	Treatment	Sand dunes		Creosotebush		Mesquite forest	Mesquite forest		
		2001	2002	2001	2002	2001	2002		
Richness	G	16 ± 2	6 ± 3	13 ± 1	6 ± 4	15 ± 4	3 ± 1		
	U	17 ± 4	8 ± 7	11 ± 3	1 ± 1	16 ± 3	3 ± 2		
Diversity (H')	G	$\textbf{1.74} \pm \textbf{0.43}$	$\textbf{0.71} \pm \textbf{0.27}$	0.82 ± 0.21 (a)	$\textbf{1.39} \pm \textbf{1.21}$	0.85 ± 0.18 (a)	1.01 ± 0.45		
	U	1.61 ± 0.4	0.69 ± 1.42	1.65 ± 0.78 (b)	0	1.34 ± 0.42 (b)	$\boldsymbol{0.67 \pm 0.93}$		
Abundance	G	10.48 ± 0.99 (a)	$\textbf{1.14} \pm \textbf{0.20}$	$95.86 \pm 8.89 (a)$	$\textbf{0.48} \pm \textbf{0.15}$	52.38 ± 5.31 (a)	$\boldsymbol{0.08 \pm 0.03}$		
	U	18.98 ± 1.40 (b)	3.00 ± 0.60	38.58 ± 3.98 (b)	0.05 ± 0.03	30.22 ± 2.96 (b)	$\textbf{0.32} \pm \textbf{0.09}$		
Plant cover	G	$\textbf{0.33} \pm \textbf{0.02}$	$\textbf{0.16} \pm \textbf{0.01}$	$0.43 \pm 0.02 (a)$	$0.22 \pm 0.01 (a)$	$0.43 \pm 0.02 (a)$	0.21 ± 0.009		
	U	$\textbf{0.42} \pm \textbf{0.02}$	$\textbf{0.19} \pm \textbf{0.01}$	0.64 ± 0.03 (b)	0.36 ± 0.02 (b)	0.59 ± 0.02 (b)	$\textbf{0.18} \pm \textbf{0.01}$		
Evenness (J')	G	0.43	0.27	0.22	0.53	0.21	0.63		
	U	0.39	0.23	0.47	-	0.33	0.42		

Regarding abundance, we found significant effects of year (F = 448.19; P = 0.0001; df = 1) with a higher abundance in 2001 (mean = 41.08) respect to 2002 (mean = 0.84). There were also significant effects of treatment (F = 36.88; P = 0.0001; df = 1) with a higher mean for the grazed field (mean = 26.74) than the reserve (mean = 15.19), and vegetation type (F = 8.25; P = 0.019; df = 2) with the highest abundance in creosotebush (mean = 33.74) followed by mesquite forest (mean = 20.75) and finally sand dunes (mean = 8.40). All interactions between effects were significant: year and treatment (F = 40.51; P = 0.0001; df = 1), year and vegetation type (F = 68.05; P = 0.0001; df = 2), treatment and vegetation type (F = 26.73; P = 0.0001; df = 2), year, treatment and vegetation type (F = 23.31: P = 0.0001: df = 2). These interactions reflect that the effect of considered factors on annuals abundance became less intense in the second sampling year, as well as tendencies among vegetation types were opposite (Table 1).

The diversity of annuals changed significantly between years resulting in higher annuals diversity in 2001 ($H'=1.5\pm0.57$) than in 2002 ($H'=0.97\pm0.93$). It was also significantly different between the grazed field ($H'=1.07\pm0.69$) and the reserve ($H'=1.79\pm0.56$). Regarding vegetation types, diversity was

significantly different between sand dunes ($H'=1.86\pm0.31$) and creosotebush ($H'=1.33\pm0.28$), between sand dunes and mesquite forest ($H'=1.3\pm0.18$), but not significantly different between mesquite forest and creosotebush. Nevertheless, under the ungrazed treatment differences among these vegetation types are not statistically significant (Table 1).

Evenness changed along with diversity: J' = 0.33 in 2001 and J' = 0.29 in 2002. It resulted higher in the reserve (J' = 0.39) with respect to the grazed field (J' = 0.23). Regarding vegetation types, evenness was higher in sand dunes (J' = 0.42), intermediate in creosotebush (J' = 0.34), and lower in mesquite forest (J' = 0.31). Means, standard errors, and indexes for each particular treatment are presented in Table 1.

Because of the massive differences regarding abundance and richness of annuals between years, the composition of annual plant assemblages (Table 2) was described using 2001 data only. There were five species exclusive in sand dunes, one species exclusive for mesquite forest and nine species shared by all vegetation types. There were three species occurring only under the grazed conditions, and conversely, there were five species that only occurred at the reserve (Table 2).

Table 2 Comparison of mean frequency (individuals/0.25 m²) and standard error of recorded species (2001). The Factorial ANOVA was used for comparing grazed and ungrazed areas (*p < 0.05; **p < 0.001).

	Sand dunes				Creosotebush			Mesquite forest					
	Grazed		Ungrazed		Grazed	Grazed		Ungrazed		Grazed		Ungrazed	
	Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.	
Stuckertiella peregrina		_	_	_	74.07	8.17	3.40	1.82*	40.11	5.22	2.87	1.28*	
Plantago patagonica	2.59	0.73	5.67	0.95	3.36	1.19	14.04	3.17*	2.00	0.50	9.99	1.30*	
Phacelia artemisoides	0.32	0.13	0.67	0.14	0.08	0.04	0.15	0.09	0.05	0.03	0.09	0.05	
Aristida mendocina	0.13	0.05	0.12	0.04	-	-	-	-	0.08	0.04	0.17	0.14	
Gamochaeta sp.	4.65	0.76	7.40	0.83	13.49	1.91	12.76	1.68	7.71	0.85	14.75	2.99*	
Conyza sp.	0.71	0.27	1.35	0.32	0.09	0.09	0.84	0.36	0.73	0.25	0.41	0.15	
Schismus barbatus	0.52	0.20	2.79	1.13*	0.16	0.06	0.00	_a*	0.03	0.02	0.04	0.04	
Mentzelia albescens	0.08	0.04	0.07	0.03	-	-	-	_	_	_	_	-	
Oenothera sp.	0.08	0.03	0.17	0.06	-	-	-	_	_	_	_	-	
Chenopodium papulosum	0.63	0.19	0.36	0.16	-	-	-	_	0.00	0.00	0.01	0.01 ^a	
Gnaphalium sp.	0.33	0.20	0.01	0.01	-	-	-	_	_	_	-	-	
Lappula redowskii	0.00	0.00	0.01	0.01 ^a	0.44	0.15	3.61	0.82*	_	_	-	-	
Ipamopsis gossypitera	0.20	0.20	0.11	0.06	-	-	-	-	-	-	-	-	
Glandularia mendocina	0.00	0.00	0.04	0.03	2.41	0.34	1.08	0.22*	0.56	0.15	0.43	0.11	
Descurainia argentina	0.03	0.02	0.00	_a	0.21	0.07	0.80	0.22*	0.00	_	0.13	0.05 ^a	
Parietaria sp.	0.01	0.01	0.00	_a	0.13	0.13	1.05	0.43*	0.12	0.05	0.12	0.05	
Bromus brevis	0.17	0.09	0.03	0.03	-	-	-	_	0.08	0.08	0.00	_a	
Lecanophora ecristata	0.00	_	0.05	0.04^{a}	-	-	-	_	_	_	-	-	
Sonchus sp.	_	_	_	_	0.05	0.03	0.15	0.06	0.01	0.01	0.04	0.02	
Crypthantha sp.	-	-	_	-	-	-	-	-	0.31	0.15	0.41	0.13	
Senecio goldsackii	0.01	0.01	0.11	0.05	0.01	0.01	0.00	_a	0.05	0.03	0.09	0.04	
Borraginaceae (unidentified)	-	-	-	-	1.35	0.19	0.71	0.23*	0.52	0.12	0.57	0.21	
Compositae (unidentified)	0.01	0.01	0.04	0.02	-	_	-	-	0.03	0.02	0.09	0.04	

^a A two-tailed *t* test was used to compare the abundance of a species between treatments (grazed or ungrazed) when one of the means was zero (0).

From a total of 23 annual plant species, *Plantago patagonica* and Stuckertiella peregrina were the most abundant, Particularly at creosotebush shrubland and mesquite forest, both species showed significant differences in abundance between the grazed field and the Reserve. P. patagonica was more abundant at the reserve while S. peregrina occurred more frequently at the grazed field. Particularly at sand dunes S. peregring was absent, and P. patagonica was present on both sides of the enclosure without a statistical difference. There was a second group of annual species that were more abundant at the grazed field such as G. mendocina, Bromus brevis and an undetermined Boraginaceae. Finally there was a more numerous group with higher abundance in the reserve that included Gamochaeta sp., Phacelia artemisoides, Aristida mendocina, Conyza sp., Lappula redowsky, Schismus barbatus and Senecio goldsackii. This tendency was statistically confirmed for several species as shown in Table 2.

4. Discussion and conclusions

Several studies have dealt with the relationship between livestock grazing and traits of the ecosystems, finding significant interactions (Bock et al., 1984; Waser and Price, 1981).

We found that grazing effects on species diversity components (e.g. richness and abundance) varied among vegetation types. Annual plant abundances were higher in the creosotebush and mesquite forest vegetation types under grazing treatment while in sand dunes the opposite occurred. Regarding species richness, there was a strong effect of year, but in general none of the vegetation types showed great changes in species richness between grazed and ungrazed treatments. Plant cover resulted higher in the reserve than in the grazed field, even though it was also differently affected by grazing among the different vegetation types. Diversity is not different among vegetation types in the reserve; however, under grazing treatment only at sand dunes this parameter remains constant, while it decreases in the creosotebush and mesquite forest. This could be related to differences in the activity of livestock among vegetation types as reported by Tabeni (2006) and explained above. Differential intensities of use by livestock should be added to the variation of responses also accounted for by variables such as soil, topography and complexity, which operate as sources of diversity (Kelt and Valone, 1995; Olff and Ritchie, 1998). We could consider that in the vegetation types under high level of use by cattle (cresotebush and mesquite forest) annual plants diversity decreases and under a lower level of disturbance (as in sand dunes) it remains stable, as expected from our theoretical framework.

Diversity is an attribute that depends on abundance and richness; therefore, it should increase along as one of these variables increase. Surprisingly, we found that diversity is significantly higher when abundance is lower, with no significant changes in richness. This particular response can be explained by taking into account evenness index. The effect of domestic livestock on diversity has been traditionally explained as a variation in the relative number of species (richness) and the change in their prevalence due to the disappearance of dominant species, which consequently would increase diversity (Connell, 1978; Petraitis et al., 1989). Other authors have reported little (Kelt and Valone, 1995) or negative effect of livestock on diversity owing to the lack of dispersion and germination (Waser and Price, 1981). Our results suggest that livestock grazing on the annual plant assemblages of the central Monte desert has a major effect in diversity through changes of evenness instead of richness. A feasible explanation for this is that as consequence of grazing, the settlement of uncommon species among resident ones occurs (Brooks, 1995; Collantes and Anchorena, 1993). Actually, some annual plants are opportunistic invaders that use free spaces and resources left by those affected by cattle. In our scenario, this seem to be the case of the small and flat herb *S. peregrina*. It is an uncommon species in the Monte Desert which became exceptionally abundant in the grazed mesquite and creosotebush habitats (Table 2), following a pattern that could be considered as a good biological indicator of grazing disturbance (Olff and Ritchie, 1998; Osem et al., 2002). This fact could explain the increase in abundance and the variations in evenness and diversity of annual plants.

As for temporal heterogeneity, we suggest that inter-annual variability of the assessed parameters was related to El Niño Southern Oscillation phenomenon (ENSO), which resulted in noticeable differences in the precipitation regime between 2001 and 2002. Interestingly, the effects of grazing on annual plants were only detectable during the ENSO year of 2001, when spring precipitation peak was at least three orders of magnitude higher than mean rainfall (Fig. 1). ENSO episodes are highly important for plant and animal dynamics as noted by Holmgren and Scheffer (2001, and references therein). Particularly, differences in the annual plants assemblage between both years could be because some seeds germinate only after some high rainfall threshold is reached, as previously reported by Marone et al. (2000). Furthermore, short term increases in cover and abundance of annual plants have been reported for a semiarid community in Chile and attributed to ENSO events (Meserve et al., 2003).

We endorse the idea that the ecological dynamics of annual plants in the Monte Desert reflect the interplay of landscape heterogeneity, disturbances (i.e. cattle grazing) and water availability, resulting in multiple "stable" states across a heterogeneous vegetational matrix. Despite the limited two-year evaluation, our preliminary results support the notion of considering ENSO episodes in disturbance assessments. In fact, our conclusions corroborate the idea that arid ecosystems undergo shifting control, with relatively greater importance of biotic interactions in wet years and of resource limitation in dry ones (Meserve et al., 2003). Thus, the rapid responses of annual plants assemblages to changes in rainfall conditions (i.e. water availability through ENSO episodes such as 2001) coupled with herbivore control (e.g. management of livestock density) might result in a restoration set of actions for degraded heterogeneous landscapes (Holmgren and Scheffer, 2001).

Summarizing, the heterogeneous vegetation matrix of the Monte desert represents different substrates for livestock effects, leading to diverse responses in some parameters which could be

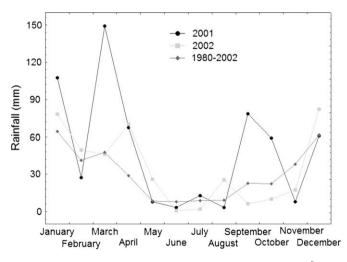


Fig. 1. Variation in monthly rainfall in the Man-and-Biosphere Reserve of Ñacuñán during 2001 (ENSO) and 2002, and mean annual rainfall from 1980 to 2002.

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due to different grazing intensities among other factors. Furthermore, there is an inter-annual variation in the properties of annual plants assemblages, and as a consequence, a differently sensitive substrate to grazing. We conclude that spatial-temporal heterogeneity promoted by different environmental factors, is determinant for the response to disturbance of desert communities. Our data on annual plants support that idea and confirm that these organisms are good models for this kind of assessment. We suggest, however, that long-term studies are necessary to fulfill the picture in our ecosystems, and finally accomplish the building of predictive models for the management of our resources.

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References

- Armas, C., Pugnaire, F.I., 2005. Plant interactions govern population dynamics in a semi-arid plant community. Journal of Ecology 93, 978–989.
- Asner, G., Borghi, C.E., Ojeda, R., 2003. Desertification in Central Argentina: changes in ecosystem carbon and nitrogen from imaging spectroscopy. Ecological Applications 13. 629–648.
- Bock, C.E., Bock, J.H., Kenney, W.R., Hawthorne, V.M., 1984. Responses of birds, rodents and vegetation to livestock exclosure in a semi desert grassland site. Journal of Range Management 37, 239–242.
- Brooks, M.L., 1995. Benefits of protective fencing to plant and rodent communities of the western Mojave Desert, California. Environmental Management 19, 65–74.
- Coley, P.D., Bryant, J.P., Chapin, F.S., 1985. Resource availability and plant antiherbivore defense. Science 230, 895–899.
- Collantes, M.B., Anchorena, J., 1993. Las malezas exóticas y plantas escapadas de cultivo en la región de estepa de Tierra del Fuego. Parodiana 8, 213–217.
- Connell, J.H., 1978. Diversity in tropical rainforests and coral reefs. Science 199, 1302–1310
- Fahnestock, J.T., Knapp, A.K., 1994. Responses of grasses to selective herbivory by bison: interactions between herbivory and water stress. Vegetatio 115, 123–131.

- Fuhlendorf, S.D., Engle, D.M., 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. Bioscience 51, 625–632.
- Holmgren, M., Scheffer, M., 2001. El Niño as a window of opportunity for the restoration of degraded arid ecosystems. Ecosystems 4, 151–159.
- Inouye, R.S., 1991. Population biology of desert annual plants. In: Polis, G. (Ed.), The Ecology of Desert Communities. The University of Arizona Press, Tucson, pp. 27–54.
- Keeley, J.E., Fotheringham, C.J., 2000. Role of Fire Regeneration from Seed. In: Fenner, M. (Ed.), The Ecology of Regeneration. CAB International, Oxon, UK, pp. 311–330. Seeds.
- Kelt, D.A., Valone, T.J., 1995. Effects of grazing on the abundance and diversity of annual plants in Chihuahuan desert scrub habitat. Oecologia 103, 191–195.
- Laurenroth, W.K., 1998. Guanacos, spiny shrubs and the evolutionary history of grazing in the Patagonian steppe. Ecología Austral 8, 211–215.
- Marone, L., Horno, M.E., Gonz lez del Solar, R., 2000. Post-dispersal fate of seeds in the Monte desert of Argentina: patterns of germination in successive wet and dry years. Journal of Ecology 88, 940–949.
- Meserve, P.L., Kelt, D.A., Milstead, W.B., Gutiérrez, J.R., 2003. Thirteen years of shifting top-down and bottom-up control. Bioscience 53, 633–646.
- Milchunas, D.G., Varnamkhasti, A.S., Laurenroth, W.K., 1995. Forage quality in relation to long-term grazing history, current-year defoliation, and water resource. Oecologia 101, 366–374.
- Ojeda, R.A., Campos, C.M., Gonnet, J.M., Borghi, C.E., Roig, V.G., 1998. The MAB Reserve of Ñacuñán, Argentina: its role in understanding the Monte Desert Biome. Journal of Arid Environments 39, 299–313.
- Ojeda, R.A., Tabeni, M.S., 2009. The mammals of the Monte Desert revisited. Journal of Arid Environments 73, 173–181.
- Olff, H., Ritchie, M.E., 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology and Evolution 13, 261–265.
- Osem, Y., Perevolotsky, A., Kigel, J., 2002. Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity. Journal of Ecology 90, 936–946.
- Petraitis, P.S., Latham, R.E., Niesenbaum, R.A., 1989. The maintenance of species diversity by disturbance. Quarterly Review of Biology 64, 393–418.
- Philippi, T., 1993. Bet-hedging germination of desert annuals: beyond the first year. American Naturalist 142, 474–487.
- Roig, F.A., 1971. Flora y vegetación de la Reserva Forestal de Ñacuñán. Deserta 1, 25–232.
- Rossi, B.E., Villagra, P.E., 2003. Effects of *Prosopis flexuosa* on soil properties and the spatial pattern of understorey species in arid Argentina. Journal of Vegetation Science 14, 543–550.
- Rundel, P.W., Gibson, A.C., 1996. Ecological Communities and Processes in a Mojave Desert Ecosystem: Rock Valley, Nevada. Cambridge University Press.
- Tabeni, M.S., 2006. Heterogeneidad espacio-temporal del ensamble de pequeños y medianos mamíferos del Desierto de Monte central. Doctoral Thesis. Universidad Nacional de Córdoba, Córdoba.
- Waser, N.M., Price, M.V., 1981. Effects of grazing on diversity of annual plants in the Sonoran desert. Oecologia 50, 407–411.