



The fencing paradigm in woodland conservation: consequences for recruitment of a semi-arid tree

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Keywords

Habitat protection; Monte Desert; Population structure; *Prosopis flexuosa*; Recruitment limitation

Nomenclature

Roig (1987) for tree species, and Morello (1958) for vegetation

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Introduction

Fencing is a common, almost paradigmatic, conservation strategy that relies on the idea that ecological communities require protection from some external influences, particularly anthropogenic activities, if they are to be assured for future generations. Therefore, exclusion fences have been

Abstract

Question: How does long-term fencing against large domestic herbivores affect regeneration of the dominant tree, *Prosopis flexuosa*, and hence the structure of semi-arid woodlands?

Location: Woodlands in the Central Monte Desert biome of Argentina, Ñacuñán Man and the Biosphere Reserve area (34° 20' S, 67° 58' W) and surrounding cattle-grazed ranches.

Methods: We compared seedling emergence and survival, the spatial distribution of seedlings and saplings, and the population stage-based structure of *P. flexuosa* between paired sites inside and outside the Reserve of Ñacuñán (Argentina), which has been fenced to exclude domestic cattle for ca. 40 yr.

Results: Reserve sites had lower tree recruitment and seedling emergence, in spite of having greater seed production and seedling survival. Outside the reserve, survival was higher for seedlings in high-density clumps than for isolated seedlings. Seedling clumps occurred mostly near adult individuals, where cattle dung was abundant, suggesting an effect of cattle on seed dispersal. The balance between the effects of cattle exclusion on seedling emergence and on seedling survival was reflected in the stage structure of *P. flexuosa* woodlands, as populations at fenced sites were dominated by adult individuals, whereas those at cattle-grazed areas presented greater proportions of seedlings and saplings.

Conclusion: Fencing is a common practice used worldwide to exclude conservation areas from human disturbance. For example, it is assumed that disturbed woodlands may recover after fencing, thanks to increased tree recruitment after the exclusion of large herbivores. However, the actual effectiveness of fencing as a tool for forest conservation in overgrazed environments could be controversial because sequential effects of herbivores during the tree regeneration cycle may hamper predictions of the overall balance of the recruitment process. Our results suggest that dispersal by cattle influences the regeneration of *P. flexuosa* woodlands, and that the positive effects of cattle on seedling emergence compensate for the negative effects on seed production and seedling and sapling survival. Future management of *P. flexuosa* woodlands in the Central Monte Desert should consider that tree recruitment is closely related to land use, and that cattle exclusion does not necessarily guarantee woodland recovery in the long term.

used extensively for the protection of certain species or communities (Spooner & Briggs 2008; Hayward & Kerley 2009). Fencing practices in woodland management rely on the assumption that large herbivores negatively affect tree regeneration, which can in turn result from the direct and indirect pre-dispersal effects of large domestic herbivores on seed production (Vázquez & Simberloff 2004; Gómez

2005) and the post-dispersal limitation to regeneration caused by trampling and browsing on tree seedlings and saplings (Dufour-Dror 2007). Evidence on detrimental effects of large domestic herbivores on tree populations have been found in different vegetation types worldwide, such as *Polylepis* woodlands in central Argentina (Teich et al. 2005), *Quercus* forests in the Mediterranean region (Debussche et al. 2001) and *Juniperus-Olea* forests in Ethiopia (Wassie et al. 2009). Therefore, conservation of many woodlands seems to be linked to the protection of seedlings against large herbivores to promote recruitment and growth of dominant tree species.

In contrast to the above detrimental effects, some studies have found positive effects of large herbivores on tree recruitment. For example, large herbivores can increase seed input into tree populations by acting as seed dispersers (Reid & Ellis 1995; Rohner & Ward 1999) and promote seedling establishment by modifying micro-environmental conditions (Zimmermann et al. 2009). Thus, due to the contrasting effects on the different processes involved in the plant regeneration cycle, predicting the overall response of plant recruitment to herbivore exclusion by fencing is a difficult task (e.g. Pulido & Díaz 2005). In this sense, rather than looking only to post-dispersal effects on seedlings and saplings, we need a multi-stage approach considering how herbivores modify both the net quantity of propagules entering tree populations and the per-capita survival probability of propagules across stages (Schupp 1993; Clark et al. 1999).

By depositing seeds in their dung, large herbivores can have different quantitative and qualitative roles in tree recruitment (Janzen 1981; Reid & Ellis 1995). Quantitative effects may involve increases in the number of germinated seedlings (Lieberman & Lieberman 1986), especially when seeds need some kind of scarification to germinate. Qualitative effects may concern changes in the micro-habitat where seeds are deposited and germinated. At small spatial scales, deposition of dung by large herbivores modulates seedling emergence and growth by imposing a specific micro-habitat for seedling establishment (Malo & Suárez 1995; Fragoso & Huffman 2000; Malo et al. 2000). However, the increased density of seeds and seedlings derived from clumping on dung could decrease survival due to increased pressures from predators and pathogens (Janzen 1970; Connell 1971; Howe & Smallwood 1982; Clark & Clark 1985; Peters 2003). In any case, dung deposition imposes a template of seed distribution in space, which may be further affected by fine-scale factors driving seedling emergence and survival (García & Houle 2005). In this sense, the spatial distribution of seedlings may be informative of the ecological drivers of recruitment processes (Barot et al. 1999). For example, it is assumed that dispersal matters for a species' demography when the

spatial distribution of seedlings and saplings mirrors that of propagules at the dispersal stage (Wang & Smith 2002; Howe & Miriti 2004). Conversely, the relevance of post-dispersal processes, such as density-dependent seedling mortality by predators and pathogens, may be inferred from the discordance between the spatial distributions of seed dispersal and seedling establishment (Jordano & Herrera 1995; Schupp & Fuentes 1995; García et al. 2005).

The UNESCO Man and the Biosphere (MAB) Reserve of Ñacuñán (Mendoza, Argentina) represents a good experimental framework to evaluate the effectiveness of long-term fencing on woodland conservation. The reserve was established to protect algarrobo (*Prosopis flexuosa*) woodlands, a dominant vegetation type in the Monte Desert, and fenced in 1972 to mitigate impacts of tree cutting and extensive cattle grazing, the main land-use type in the region (Abraham 2001). This conservation measure was set up with no knowledge of the actual effect of large herbivores in *P. flexuosa* regeneration potential. In fact, it is now known whether the germination probability is almost null when the endocarp remains intact and seeds are not scarified in *P. flexuosa* (Villagra et al. 2002a). Native large mammals, such as guanacos (*Lama guanicoe*), which are known to disperse *Prosopis* seeds in other regions (Fuentes et al. 1989; Campos et al. 2008), are likely to have been present in Ñacuñán in the past (Ojeda et al. 1998) but are now locally extinct. Campos & Ojeda (1997) showed that cattle and Patagonian hares (*Dolichotis patagonum*) are the most effective herbivores in increasing germination of *P. flexuosa* seeds compared to other potential herbivores in the Ñacuñán area. Moreover, *D. patagonum* activity is less abundant inside the reserve than in the cattle-grazed sites, apparently because it prefers open microhabitats with decreased low vegetation layers (grasses and herbs) and increased bare soil, which are more abundant outside the reserve (Kufner & Chambouleyron 1991; Tabeni & Ojeda 2003; Villagra et al. 2009). In any event, even though fencing does not completely exclude the activity of Patagonian hares, as it does with cattle, cattle grazing is the most common activity in this region (Guevara et al. 2009); thus we assume that most of the fencing effect on tree recruitment results from direct and indirect effects of cattle exclusion. Cattle are expected to affect demography of *Prosopis* spp. in multiple ways. First, cattle may cause pre-dispersive losses of seeds, due to decreased reproductive potential at seed set stage, as suggested by the higher seed production found in trees inside the fenced reserve relative to that in the surrounding grazed ranches (Aschero & Vázquez 2009). Second, cattle may positively affect recruitment by facilitating seed dispersal (Campos & Ojeda 1997; De Villalobos et al. 2005). Finally, negative post-dispersal effects on survival are also expected, as cattle forage on saplings and young trees when grass resources are scarce (Guevara et al. 1996).

In this study we evaluate how fencing at the MAB Reserve of Ñacuñán affected the regeneration of *P. flexuosa* and, hence, the potential for conservation in the central Monte Desert woodlands. To this end, we applied a multi-stage approach to compare the magnitude of recruitment and the population structure of *P. flexuosa* under contrasting land management regimes, inside and outside the protected area. We assumed that the long-term effects of fencing on recruitment should be reflected in the population structure, with large proportions of early stages (seedlings, saplings and young trees) relative to adult trees indicating successful and active regeneration. In cattle-grazed sites, we expected to find (1) higher seedling emergence, derived from enhanced germination following seed scarification after endozoochory by cattle; (2) lower seedling survival, due to trampling and browsing by cattle; (3) a positive relationship between seedling density and survival, due to favourable conditions in mammal dung clumps; (4) stronger clumping of seedlings and saplings, due to seed deposition in cow dung; (5) a spatial association between recruits and adult trees, because cattle commonly use big trees for shade and drop dung mostly under tree canopies; and (6) stage-based population structures characterized by higher proportions of early recruitment stages relative to adults, because of the global long-term effect of domestic cattle.

Methods

Study area, land use and species

The study area was in the Ñacuñán MAB Reserve area (Mendoza Province, Argentina; 34° 20' S, 67° 58' W; 13,200 ha) and surrounding ranches under cattle grazing, which lies within the central Monte Desert biome of Argentina (Cabrera 1971). The climate is semi-arid and most rainfall occurs in spring and summer (Oct–Mar); average annual rainfall in the region is 302.87 mm (1919–2004, CV = 38%). The ‘algarrobo’ open forest is a dominant woodland plant community in the Monte Desert, where *Prosopis flexuosa* is accompanied by the small tree *Geoffrea decorticans*, the shrubs *Larrea divaricata*, *Condalia microphyla*, *Capparis atamisquea*, *Lycium* spp. and the grasses *Pappophorum* spp., *Trichloris crinita* and *Digitaria californica*.

Degradation of *P. flexuosa* woodlands in the Central Monte started at the beginning of the 20th century, tree logging being primarily associated with charcoal and gas production, then to wood provision for the wine and furniture industries (Abraham & Prieto 1999). The extraction of woodland products by clear-cutting affected the tree cover of Ñacuñán region, both within the limits of the current protected area and in the surrounding cattle ranches; the presence of multi-stemmed trees at Ñacuñán reflects the vigorous stump resprouting after logging over the first dec-

ades of the 20th century (Abraham & Prieto 1999; Villagra et al. 2005). The period of maximum wood extraction in the past at the study area coincided with development of the railway. Cattle raising increased after 1916, when clear cutting of woodlands favoured the growth of heliophytic grasses (Roig 1971; Abraham 2001). Since then, cattle raising has progressively increased, parallel to decreasing wood exploitation, and rangeland for calf raising is now the dominant production system in the region (Abraham 2001; Guevara et al. 2009). The history of grazing intensity in the region is not well known, but it is suggested that at the beginning of 20th century, cattle stocking rate was 11 ha·AU⁻¹ (Guevara et al. 2002) and 22 ha·AU⁻¹ by the end of the 1970s (Guevara et al. 1981). The Ñacuñán protected area was created in 1961, but cattle ranching was allowed in the site until 1972, when the perimeter fence was established (Roig 1971). In summary, the MAB Reserve of Ñacuñán and the neighbouring ranches share a common recent past of logging and grazing, and there are no reasons to suspect strong differences in land-use intensity between the reserve and the adjacent lands before fencing.

Prosopis spp. (‘mesquites’ in North America, or ‘algarrobos’ in South America) are thorny legume shrubs/trees with many ecologically and culturally important functions in semi-arid and arid lands of the Americas. In their native range in the United States, Mexico, Peru, Chile, Argentina and Brazil, different species of this genus are a source of multi-purpose valuable products and an important focal species for biodiversity conservation (Felker 1998; Galera 2000). They also play an important ecological role because of their multiple interactions with native and exotic animals. *P. flexuosa* trees are a crucial natural resource, providing shade, fuel, wood for fencing and pods for human and cattle feeding in the Monte Desert ecosystem (Ladio & Lozada 2009).

Prosopis flexuosa (algarrobo dulce) is an arboreal Fabaceae (Mimosoideae) that grows in the central and northern arid and semi-arid regions of Argentina (Álvarez & Villagra 2009). The regeneration cycle of *P. flexuosa* needs an interaction with animals in two important steps for reproduction, pollination and dispersal. Flowers are produced in elongated spikes and require pollination by insects to set fruits and seeds (Aschero & Vázquez 2009). The indehiscent bean-like pods have a hard leathery endocarp and a hard seed coat protects the embryo. Germination depends on seed scarification that can take place by the passage of seeds through the digestive tract of animals (Campos & Ojeda 1997). Fruits fall fairly synchronously from the plant and are spread under the tree canopy in summer when ripe (Dec–Feb). Pod production is highly variable between years (32–100 kg·ha⁻¹; Dalmaso & Anconetani 1993). Each pod can contain, on average, 11.4 ± 8.5 (SD) seeds

($N = 148$, data from 2005; V. Aschero personal observation). The main dispersers of seeds of *P. flexuosa* are native and exotic mammals, such as Patagonian hares (*Dolichotis patagonum*), grey foxes (*Pseudalopex griseus*), guanacos (*Lama guanicoe*), wild boars (*Sus scrofa*), cattle and horses (Campos & Ojeda 1997; Campos et al. 2008). Birds, small rodents, reptiles and ants also feed on *Prosopis* fruits and are potential, but probably minor, agents of dispersal compared to large herbivores.

Sampling design

For this research, the study design consisted of five pairs of 0.25-ha plots at and around the MAB Reserve of Ñacuñán. The locations of plots were arbitrarily chosen to represent distant sampling locations along three of the four sides of the reserve, but also contrasting situations regarding fencing in the same vegetation type, the 'algarrobo' open forest (i.e. we avoided creosote, *Larrea canneifolia*, shrublands and sand dunes). Differences in physical features (soil type, slope, aspect) between plots were negligible. Each pair of plots consisted of a reserve plot located inside the reserve 1 km from the fenced edge (hereafter 'reserve plot'), and a second plot located 1 km from the fenced edge outside the reserve in the surrounding ranches (hereafter 'cattle-grazed plot'). Pairs of sites were located at least 3.5 km away from other pairs. Cattle-grazed plots were in ranches that belonged to three different landowners, and were always distant (>3 km) from artificial watering sources (where grazing is usually higher). Three of the five cattle-grazed plots were within the same ranch, along the eastern and southern limits of the reserve. Plots were set up after the *P. flexuosa* fructification period (late Dec–Jan) between May and Jun 2007. Within each plot, all *P. flexuosa* individuals were located in intensive surveys, mapped, tagged and their diameter measured at the base of the trunk (DAB). In multi-trunk individuals, DAB was calculated as follows:

$$DAB = 2 \sqrt{\frac{\{\pi(dab_1/2)^2 + \pi(dab_2/2)^2 + \pi(dab_3/2)^2 + \dots + \pi(dab_n/2)^2\}}{\pi}}$$

where $dab_1, dab_2, \dots, dab_n$ are the basal diameters for each of n trunks (Álvarez et al. 2006). DAB was used as a surrogate of age in order to compare the regeneration process in reserve and cattle-grazed areas (e.g. García et al. 1999). Trees were classified in stage-size classes as seedlings (with $DAB < 0.2$ cm and remaining cotyledons), saplings (0.2 cm $< DAB < 1.0$ cm), juveniles (1.01 cm $< DAB < 5.0$ cm) and adults ($DAB > 5.0$ cm).

To estimate seed production at each plot, ten adult trees were randomly selected at the beginning of the flowering season (Oct 2007). Three branches of each tree were

tagged, and the number of inflorescences between the tag and the tip of the branch was recorded. Once the fruits had developed sufficiently to allow distinguishing between viable and aborted seeds, the number of seeds produced in the marked branches was counted. Data from the three tagged branches were averaged for each tree. With these data, we estimated the mean number of seeds per inflorescence produced at each plot.

To estimate seedling abundance and distribution, we surveyed each plot twice at the end of the rainy period (Feb–Mar 2008), when germination commonly occurs. In each survey, three observers searched systematically for seedlings over 4 h. Although the herbaceous layer is usually denser within the fenced area, herb density differences did not lead to decreases in seedling detectability in cattle-grazed plots. Moreover, *P. flexuosa* seedlings were conspicuous and easily distinguishable from the soil or herb layer background. Reserve and cattle-grazed plots of the same pair were sampled on the same day. All seedlings were mapped and tagged by inserting a numbered plastic tooth needle near each seedling. Seedlings were monitored again in the dry season (end of Jun 2008) to record survival. Seedlings that survived more than 3 mo during the dry season were considered as recruited individuals. We mapped and counted all cow dung found at three cattle-grazed plots to analyse whether they were spatially associated with new seedlings and saplings.

Data analysis

Differences in seedling emergence between reserve and cattle-grazed plots were analysed using a general linear model with a Poisson distribution of error. We calculated seedling emergence potential (seedlings/seeds per inflorescence) as the ratio between the number of early-emerged seedlings counted and the average seed set per inflorescence for each plot. The effect of fencing on seed production was tested using a generalized linear mixed model (GLMM), considering the plot type (reserve vs cattle-grazed) as a fixed factor and site as a random factor, assuming a Poisson distribution of residuals. Response variables were rounded because the average count between samples was used to perform the analysis with Poisson generalized linear models. To test whether seedling mortality was affected by fencing, we used a contingency table and a Chi-square test. To fit these models used R statistical software (R Development Core Team 2010, Vienna, Austria).

To analyse whether seedling survival was correlated with seedling density, we selected a number of focal seedlings ($N = 45$) in which survival was surveyed, and whose spatial position was referenced in a map of all seedlings in the plot. We established a 2.5-m radius neighbourhood around each focal seedling, counting the number of

conspecific seedlings within this neighbourhood. Focal seedlings were selected so as to avoid overlaps greater than 25% of the neighbourhood sampling area (Fig. 1). We related the survival of focal seedlings to the density of conspecific seedlings in the neighbourhood by means of a spatial logistic regression, which incorporated the spatial position of focal seedlings and controlled for spatial autocorrelation biases. This analysis was performed considering only the data from one of the cattle-grazed plots, in which the density of early-emerged seedlings was high enough for analytical purposes. Spatial logistic regression was performed with SAM software (Spatial Analysis in Macroecology; Rangel et al. 2006).

To compare the spatial structure of recruitment between reserve and cattle-grazed plots, we subdivided each 0.25-ha plot into 5 m × 5 m quadrats and counted the number of items (individuals by class or cow dung) inside one. For spatial analyses, seedlings and saplings were summed and considered together within a single category. We used this classification because seedlings were very scarce in the reserve plots, and we considered that the degree of aggregation in seedlings plus saplings resulted from the cumulative effect of all spatial processes occurring during early recruitment stages. The degree of spatial clumping of seedlings and saplings, and the similarity of

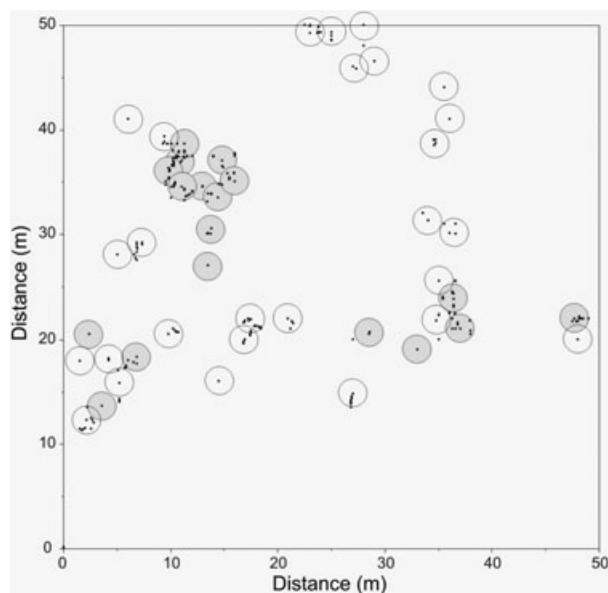


Fig. 1. Map of spatial position of *Prosopis flexuosa* seedlings (dots) in the 0.25-ha plot at site 2 outside the reserve. A 2.5-m radius neighbourhood (circles) was considered around a given number of focal seedlings to estimate the number of neighbouring seedlings. Focal seedlings were selected so as to avoid overlaps greater than 25% of neighbourhood areas. Grey circles indicate neighbourhoods around surviving seedlings and white circles indicate neighbourhoods around dead seedlings after 3–4 mo of monitoring.

this spatial clumping with cow faeces and adult trees, was evaluated using spatial analysis by distance indices (SADIE; Perry et al. 1999; see also Hampe et al. 2008). SADIE provides an aggregation index (Ia) to measure the degree of spatial clumping of a given ecological variable, represented by count data. Ia represents random ($Ia = 1$), regular ($Ia < 1$) or aggregated ($Ia > 1$) distribution patterns, and its degree of significance is assessed by means of a randomization procedure based on rearrangements of the observed counts amongst the sample units. SADIE also provides an association index, Xp (Winder et al. 2001), that measures the degree of spatial association/dissociation between two variables sampled in the same points. The index Xp ranges between +1 (complete spatial association) and -1 (complete dissociation), with 0 indicating spatial independence. The statistical significance of Xp is quantified using the Dutilleul method (Dutilleul et al. 1993), which corrects the amount of degrees of freedom in the presence of spatial autocorrelation. SADIE analyses were conducted with the software SadieShell v1.2.2 (IACR-Rothamsted, UK).

To compare the population stage structure, we used a nominal logistic model, considering proportion of individuals in each class as response variable and habitat type (reserve/cattle grazed) and site as explanatory variables. We also test for differences in the abundance of individuals with a generalized linear model assuming a Poisson distribution of error, with land use (reserve/cattle) and stage class as fixed effects and paired site as random effect.

Results

Seed production, seedling emergence and density effects on survival

Seed production was higher in the reserve plots compared to cattle-grazed plots (Fig. 2). Despite a greater seed production in the reserve plots, seedling emergence was lower there than in cattle-grazed plots (Fig. 3). In total 452 seedlings emerged in the five cattle-grazed plots and 134 seedlings in the five reserve plots. Mortality of seedlings was found to be higher in cattle-grazed plots ($\chi^2 = 23.97$, $P < 0.001$). Moreover, survival probability of seedlings was 0.35 in cattle-grazed plots and 0.58 in the reserve plots. Seedling survival was positively correlated with seedling density, and this relationship was independent of the spatial position where seedlings emerged (McFadden $R^2 = 0.13$, $\chi^2 = 8.56$, $P = 0.045$).

Spatial arrangement of seedlings, cow dung and adult trees

The values of the SADIE index of aggregation, Ia , suggested that seedlings and saplings tended to be more clumped in the cattle-grazed plots, with three out of five sites showing

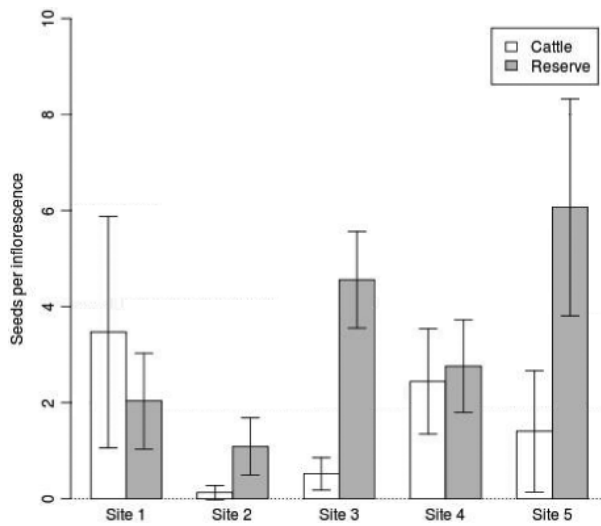


Fig. 2. Seed production (mean \pm SE) at cattle-grazed and reserve sites during the 2007–2008 reproductive period (generalized linear mixed model: $z = 1.95$, $P = 0.053$).

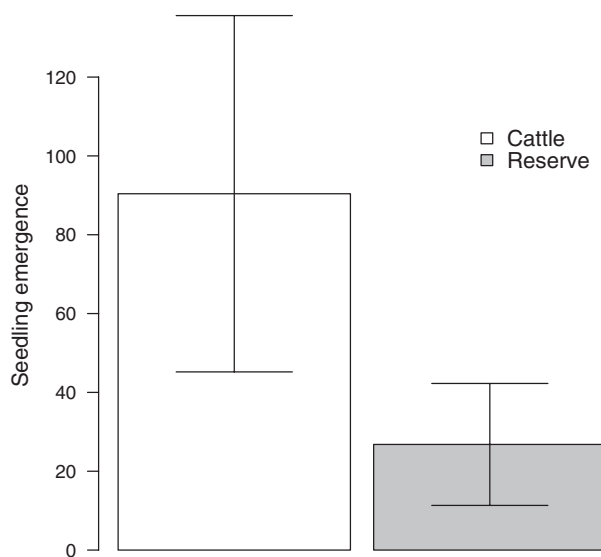


Fig. 3. Seedling emergence (seedlings/seeds per inflorescence; mean \pm SE) at cattle-grazed and reserve sites during the 2008 germination period (generalized linear model: $z = -18.21$, $P < 0.001$).

significant spatial aggregation. However, the spatial distribution of seedlings and saplings was significantly aggregated in only one reserve plot (Table 1). As judged by the SADIE indices of association, X_p , the spatial match between the distributions of seedlings and saplings and that of adult trees was also more common in cattle-grazed than in reserve plots (Table 1). In the three cattle-grazed plots where cow dung was mapped, seedling and sapling distribution was spatially associated with that of cow dung,

and dung clumps mostly occurred close to adult trees (Table 2).

Population stage structure

Reserve plots presented lower average abundance of seedlings, saplings and juvenile trees than cattle-grazed plots. Differences in abundance between plot types decreased along the gradient of stage classes: reserve plots showed eight-fold fewer seedlings, three-fold fewer saplings and twofold fewer juvenile trees than cattle-grazed plots, and virtually no difference for adult trees (Table 3). Population structure differed between reserve and cattle-grazed plots (Table 4). The average percentage of individuals in the different stage classes was significantly different between plot types and sites (Fig. 4), as cattle-grazed plots showed significantly greater proportions of seedlings and saplings than reserve plots, where juveniles and, especially, adults dominated the populations.

Discussion

Our results revealed two positive effects of fencing on the natural regeneration of *P. flexuosa*. First, there was higher seed production of trees inside the reserve. Second, a higher survival probability of seedlings was detected inside the reserve. The effect of fencing on seed production could be explained due to amelioration in pollination services. In a previous study, seed production was found to be limited by the quality of pollen deposited over the stigmas, with higher reproductive success after cross-pollination and no

Table 1. SADIE aggregation and association indices for the abundance of *Prosopis flexuosa* seedlings plus saplings (la).

Index	Site	Cattle	Reserve
Aggregation index (la)	1	1.26 ^{MS}	1.46*
	2	1.29*	1.08 ^{NS}
	3	1.14 ^{NS}	—
	4	1.35**	—
	5	1.55***	1.27 ^{MS}
Association index (ci)	1	0.45***	0.56***
	2	0.42*	0.16 ^{NS}
	3	0.38***	—
	4	0.16 ^{MS}	—
	5	0.07 ^{NS}	0.46 ^{MS}

$la > 1$ indicates an aggregated spatial pattern. Analysis was not performed in sites 3 and 4 inside the reserve, given the low number of saplings founded ($n < 7$).

Level of significance is indicated next to each la or ci value

^{NS} $P < 0.1$;

^{MS} $0.1 < P < 0.05$;

* $P < 0.05$;

** $P < 0.01$;

*** $P < 0.001$.

Table 2. SADIE association index (ci) and corresponding level of significance of the permutation test for the spatial relationship between cow dung and saplings, and cow dung and adult trees. Dung location was recorded only in three cattle-grazed plots. Asterisks indicate statistical significance of ci values, as described in Table 1.

Site	Cow dung saplings	Cow dung adults
1	0.22**	0.36***
2	0.44***	0.31***
3	0.57***	0.31***

Table 3. Average abundance of individuals in stage classes (mean \pm SE) in five paired 0.25-ha plots with contrasting habitat management. There were differences in the abundance of adult individuals at cattle-grazed and reserve plots (generalized linear mixed model, $z = 35.96$, $P < 0.001$).

Class	Cattle	Reserve
Seedling	47.8 \pm 15.42	5.8 \pm 1.5
Sapling	86.2 \pm 44.21	25.4 \pm 15.55
Juvenile	24 \pm 4.23	12.6 \pm 2.33
Adult	16 \pm 3.11	16 \pm 1.52

Table 4. Results of nominal logistic model, with proportion of *Prosopis flexuosa* individuals per stage class as response variable, and type of management (reserve or cattle grazed) and identity of paired site as predictors.

	df	Wald χ^2	P
Habitat	3	65	<0.001
Site	12	79	<0.001
Habitat \times site	12	88	<0.001
Model	27	465.69	<0.001

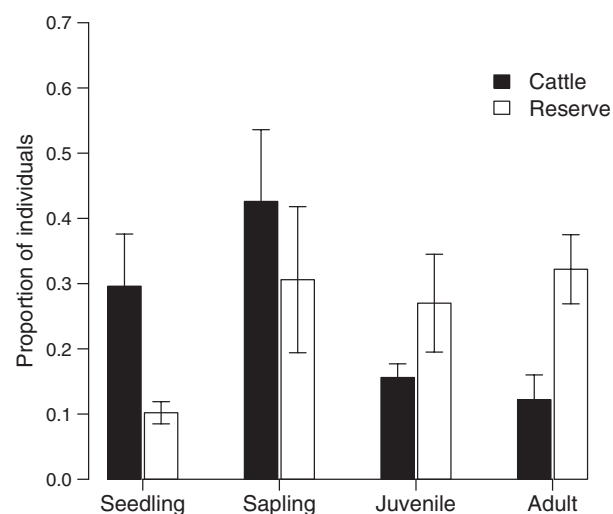


Fig. 4. Comparison of the population structure of *Prosopis flexuosa* in the MAB Reserve of Ñacuñán in reserve plots and in cattle ranch plots. Population structure is represented as the percentage of individuals (mean \pm SE) in each stage classes across the five 0.25-ha plots censused under each habitat management regime.

seed production after pollinator exclusion, indicating self-incompatibility and a dependence of biotic vectors for pollination (Aschero & Vázquez 2009). Frequency of pollinator visitation to the inflorescences of *P. flexuosa* was previously found to be higher in trees inside the MAB Reserve than in trees on the surrounding cattle ranches (Aschero & Vázquez 2009), which can help to explain the difference in seed set between land uses reported in this study. Differences in seedling mortality in the reserve and cattle-grazed areas could be associated with trampling by cattle, as judged by the fact that plastic markers and seedling shoots were frequently broken and cow hoof prints frequently occurred close to seedlings (V. Aschero, personal observation). Thus, fencing and cattle exclusion can limit trampling and browsing by large herbivores, which is known to negatively affect the survival of seedlings (Stave et al. 2006).

Despite the above positive effects of cattle exclusion by fencing, there were many more seedlings and saplings in cattle-grazed woodlands than within the reserve. Almost 50% fewer seedlings were alive by the end of the study in the reserve plots than in cattle-grazed plots (159 vs 79 seedlings, respectively, for the five 0.25-ha plots combined). We argue that this difference derived from the higher activity of both exotic (cattle and horses) and native (mainly Patagonian hares) mammals eating *P. flexuosa* fruits outside the reserve, leading to more scarified seeds available for germination and, consequently, a higher number of seedlings establishing in cattle ranches. Although the fence around the reserve's perimeter is not such a barrier for Patagonian hares as it is for cattle, it is known that the abundance of the former species is lower inside the reserve than in the surrounding cattle ranches (Ojeda et al. 1998; Tabeni & Ojeda 2003). Presumably, this medium-sized native herbivore prefers to forage in patches of low cover of herbaceous plants (Kufner & Chambouleyron 1991), a microhabitat less frequent inside the reserve but common in the surrounding cattle ranches (Villagra et al. 2009). Grey foxes (*Pseudalopex griseus*) have been described as another potential native disperser of *P. flexuosa* currently present in the area (Campos & Ojeda 1997; Villagra et al. 2002a); however, the role of grey foxes in the differences in recruitment between reserve and cattle-grazed plots is likely to be negligible, as the germination potential of *P. flexuosa* seeds is unaffected after consumption and defecation by this seed disperser (Campos & Ojeda 1997). The majority (63%) of the seedlings monitored in the reserve occurred in the same plot and were apparently associated with nests of the leafcutter ant *Acromyrmex lobicornis*, suggesting that the role of ants in seed dispersal (Milesi & López de Casenave 2004) may be ecologically important if mammalian dispersal is scarce. Cattle are the major dispersal agent that enhances the germination capacity of *P. flexuosa* (Campos & Ojeda 1997), as found for other *Prosopis*

species in other regions (e.g. Brown & Archer 1988, 1989; De Villalobos et al. 2005); thus, the dispersal activity of cattle accounts for most of the differences in recruitment recorded between the reserve and the surrounding ranches.

The importance of dispersal agents in decreasing density-dependent seed and seedling mortality (Janzen 1970; Connell 1971) was not evident in this study. Instead, higher seedling survival was recorded in denser clumps. Even though the relationship was not strong, density explained only 13% of the survival process and occurred in the plot with higher seedling emergence in a cattle-grazed area. This result may be related to the occurrence of denser seedling clumps in dung micro-habitats, where greater seed deposition and a beneficial environment for germination are expected. Cattle dung is known to improve micro-environmental conditions and nutrient availability for seedlings (Malo & Suárez 1995). Similarly, Anderson (2009) recorded positive density dependence in seedling survival in two Neotropical trees, suggesting that it could be produced by: (1) environmental factors that increase both density and survivorship or (2) heterospecific facilitation. Conspecific facilitation between seedlings could be an alternative explanation for the recorded positive density dependence found here. For example, facilitation among seedlings may occur by sharing rhizobia infection for root nodulation (Zitzer et al. 1996). Nevertheless, it is likely that the relationship between seedling clumping and survival changes from positive to negative as seedlings grow, due to resource competition, especially during periods of higher abiotic stress, such as droughts (Fowler 1986).

Clumping of seedlings and saplings was detected in fenced and cattle-grazed sites. Stronger clumping outside the reserve, as well as the spatial association between recruits (seedlings and saplings) and cow faeces in cattle ranches, are also patterns that suggest the role of cattle as dispersal vectors. In fact, endozoochorous seed dispersal is known to be responsible for plant spatial aggregation at multiple scales (Fragoso & Huffman 2000; Fragoso et al. 2003; García et al. 2005).

The spatial association between cattle dung, recruits and adult trees suggests that cattle are depositing many seeds under the adult tree canopies. This pattern of seed rain may lead to a reduced ability to colonize open, unoccupied habitats (Howe & Miriti 2004), as well as seed–sapling conflicts (Schupp 1995). In this sense, the micro-habitat under adult canopies might not be the best situation for sapling growth and survival, because of resource competition with adults and a greater probability of trampling when cattle search for shade. The influence of different microhabitats on the fate of *P. flexuosa* saplings should be carefully considered in future studies, given that sapling survival contrib-

utes substantially to population growth rate in woody plants (Silvertown et al. 1993).

The stage-based structure of *P. flexuosa* populations was different between reserve and cattle-grazed sites. Fenced habitats had lower juvenile densities relative to surrounding cattle ranches. We interpret this pattern as a static snapshot showing the cumulative balance of quantitative and qualitative effects of fencing on seed dispersal and seedling establishment during almost four decades. Inside the reserve, adult trees dominated the populations and early stages are proportionally scarce, suggesting long-term recruitment failure (Foster et al. 1996). The slow growth rate of this species can explain the similar number of adult trees inside and outside the protected area. Moreover, Villagra et al. (2002b) used dendrochronological techniques to determine that *P. flexuosa* radial growth is around 2 mm-yr^{-1} in the Ñacuñán region. Furthermore, trees can live for up to 500 yr (Villagra et al. 2002b). Assuming that trees with DAB > 5 cm were adults, we presume that those individuals that established after habitat fencing had not yet reached the adult stage, and thus adult densities were derived exclusively from individuals established before fencing. Our results represent a coarse quantitative assessment of the current demographic status and the potential regeneration of the species in contrasting land-use types: woodland protection by fencing vs cattle ranching. However, before drawing strong conclusions about population trends inside the reserve, careful consideration of integrative information would be necessary, including data on survival and growth rate of all demographic stages and a population projection model (Maron & Crone 2006). Long-term population-level studies would be needed to determine if the fecundity, germination probability and survival changes that we recorded with and without habitat fencing translate into different population growth and dynamics of *P. flexuosa* populations.

Conclusions

We show here that *P. flexuosa* regeneration was more constrained inside the MAB Reserve of Ñacuñán, which has had large herbivores excluded for almost four decades, than in the neighbouring cattle-grazed sites. Fencing promoted greater seed production per tree and more seedling survival. However, these effects did not compensate the lower seedling emergence observed in the reserve. The integration of cattle exclusion effects across seedling emergence and seedling survival was reflected in the long-term stage structure of *P. flexuosa* woodlands, with fenced sites dominated by adult individuals and grazed areas dominated by seedlings and saplings.

This study suggests that cattle are pivotal agents of seed dispersal for *P. flexuosa*, able to drive its recruitment

dynamics. Seed-to-seedling transitions may have pervasive demographic impacts, particularly when dispersal agents are lost (Howe & Miriti 2004). For other leguminous trees that dominate arid and semi-arid ecosystems, dispersal limitation due to the absence of mammalian vectors has been proposed as an important factor regulating recruitment (Janzen 1981; Janzen & Martin 1982; Ward & Rohner 1997; Rohner & Ward 1999). Thus, we argue that any attempt to preserve and manage arid woodlands of the Argentinean Central Monte Desert should consider the mechanistic role of seed dispersal at larger spatial and temporal scales, as suggested for Mediterranean-type ecosystems (Méndez et al. 2008). This proposal contrasts with the so-called 'establishment limitation paradigm', which assumes that post-dispersal constraints and micro-site availability are the main drivers of recruitment in woody plants (Méndez et al. 2008).

The suggestion that the fencing paradigm may be of limited use when endozoochory by mammals affects the long-term recruitment of trees should be incorporated into the preservation and restoration guidelines of *P. flexuosa* woodlands. In this sense, increasing the activity of medium and large native herbivores, acting as dispersal vectors inside the fenced reserve, may be a useful strategy to increase recruitment of *P. flexuosa* trees. Alternatively, seasonal cattle ranging after the period of pod maturation, and subsequent herd removal in spring, could also promote seed dispersal and germination and, at the same time, avoid the negative impact of trampling and browsing on establishing seedlings. In summary, conservation strategies for leguminous trees in arid woodlands should consider the natural history and the whole regeneration cycle of the species to be preserved over the long term.

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