Habitat protection, cattle grazing and density-dependent reproduction in a desert tree

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Abstract Anthropogenic activities usually trigger changes in the population density of plants. Thus, land management practices can influence density-dependent demographic parameters and species interactions. We investigated plant-pollinator interactions and reproduction in Prosopis flexuosa, the largest tree species in the Central Monte desert of Argentina, an important economic and cultural resource for humans and a functionally prominent species. We hypothesized that reproductive output of P. flexuosa would be limited at low densities, and that exclusion of cattle grazing would enhance population density and consequently interaction frequency with pollinators and reproductive success. The study was conducted in and around Ñacuñán Biosphere Reserve (Mendoza, Argentina), where cattle grazing has been excluded for over 35 years. Working in five pairs of protected and cattle grazed 1-ha plots, we recorded density of adult trees, pollinator visitation frequency to inflorescences and seeds per inflorescence in focal trees. Adult tree density was higher in protected plots than in cattle grazed plots. Density of reproductive trees was positively correlated with seed production, suggesting positive density dependence for reproduction (Allee effect). Pollinator visitation to inflorescences and seed production was higher in protected plots compared with plots under cattle grazing. Suppression of anthropogenic degradation has resulted in higher adult tree density in protected plots, indirectly higher pollinator visitation to inflorescences and higher reproductive success of trees. Increased frequency of plant-pollinator interactions and tree reproduction suggest success of management practices aimed at protecting P. flexuosa woodlands.

Key words: Allee effect, Monte Desert, pollination, Prosopis flexuosa, seed production.

INTRODUCTION

Conservation efforts may require focusing on particular species, especially if they contribute disproportionately to community organization and functioning and are strong interactors. Most studies evaluating success of conservation and restoration programmes have focused on diversity and vegetation (Ruiz Jaén & Aide 2005), but important community processes such as trophic interactions, pollination or seed dispersal are not necessarily assured when diversity and vegetation physiognomy are restored. Assessment of species interactions with potential effects on the fitness of a target species may be important when conservation programmes are applied to mitigate human degradation. The study of plant-animal interactions should provide an important framework to monitor natural protected areas aimed at preserving not only the species but also the way they affect and relate to each other (Thompson 1997; Vázquez & Simberloff 2003; Forup & Memmott 2005). Because plants are rooted in the ground and cannot move to mate, many species rely on insect vectors to transport pollen between individuals. An inadequate quantity or quality of pollen deposition can reduce reproductive success in plants (Ashman et al. 2004). Thus, the study of plant-pollinator interactions may be critical for evaluating management practices to preserve target species.

Many species experience improved vital rates with increasing population density when rare (the Allee effect; Allee 1949; Courchamp et al. 1999). Individuals occurring at low densities may suffer pollen limitation and lower reproductive success through changes in pollinator visitation frequency or quality of pollen (Kunin 1992, 1993, 1997; Lamont et al. 1993; Hackney & McGraw 2001). The detrimental effect of low population density on reproduction may be especially important in self-incompatible species that rely on biotic agents for cross pollination (Murawski & Hamrick 1991). Human activities can decrease plant population density and induce an Allee effect in plant reproductive success, affecting population viability (Lamont et al. 1993; Groom 1998). For example, Ghazoul et al. (1998) found that harvesting reduced the reproductive success of the tree Shorea siamensis.

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because of changes in pollinator behaviour, particularly reduced frequency of inter-tree flights, leading to a lower outcrossing rate.

One of the main causes of anthropogenic degradation of vegetation in arid ecosystems is grazing by exotic ungulates (Milchunas et al. 1988; Tadey 2006). Browsing, trampling and consumption of vegetative and reproductive structures by cattle can directly affect demographic rates and density of plant species. Alternatively, if reproductive success is limited at low densities, cattle can affect plant reproductive success indirectly if they decrease population density (Vázquez 2007). Cattle can also indirectly affect reproductive success of plants through changes in the pollinator community because of alterations of floral and nesting resources (Thomson 1981; Gess & Gess 1993; Kruess & Tscharntke 2002; Samejima et al. 2004).

Here we report results of a study evaluating the effects of 35 years of exclusion of cattle grazing on the reproductive success of Prosopis flexuosa, the dominant tree species in the Central Monte desert of Argentina. Prosopis flexuosa plays a key role in ecosystem organization and functioning in the Monte desert: it acts as a nurse plant for the establishment of certain grass and shrubs (Rossi & Villagrá 2003), provides fruits and seeds as food for animals (Campos & Ojeda 1997; Milesi & López de Casenave 2004) and nesting sites for carpenter insects (G. Debandi 2005, pers. comm.), and contributes to soil fertilization, being capable of nitrogen fixing. It also represents an important resource for humans, providing shade for domestic animals and wood for heating, cooking and fence construction; its pods are a rich food source for humans and cattle. Because its wood has greater density and caloric value than other species present in the area, it was heavily logged for charcoal production and for use in the wine industry in the past century (Abraham & Tscharntke 2005, pers. comm.).

Here we ask whether exclusion of cattle grazing has a positive effect on the density of P. flexuosa and consequently on pollinator visitation frequency and reproductive success.

METHODS

Study sites and species

We worked in Ñacuñán Biosphere Reserve (34°02’S, 67°58’W) and surrounding areas under cattle grazing. The study area lies within the central Monte desert of Argentina (Cabrera 1971). The climate is semi-arid and most rainfall occurs in spring and summer (October–March); average rainfall in the study region is 280 mm. Grazing has been excluded from the reserve since 1972. The algarrobo woodland is one of the typical plant communities in the Monte, where P. flexuosa is accompanied by the small tree Geoffrea decorticans and several shrub (Larrea divaricata, Condalia microphylla, Capparis atamisquea, Lycium spp.) and grass species (Pappophorum spp., Trichloris crinita, Digitaria californica).

Prosopis flexuosa D.C. (algarrobo dulce) is an arboREAL Fabaceae (Mimosoideae) that grows in arid and semiarid temperate regions of Argentina. Flowers are bisexual and grow in inflorescences of 220–240 flowers (Solbrig & Cantino 1975). Inflorescences are spiciform, densiflorous racemes, 5–7 cm long; flowers are small, actinomorphic, greenish-white to yellowish; the corolla is inconspicuous and lacks morphological structures to prevent access to flower resources. Although the style protrudes early during flower development, flowers are not considered protogynous because the stigmatic surface stays dry and there is no nectar and no insect visitation during this early phase (Genise et al. 1990). Flowering occurs in mid-spring (October–November) and fruits are ripe in mid-summer (January–February). Prosopis species are insect-pollinated, with bees and wasps as the main flower visitors (Keys et al. 1995; Chiappa et al. 1997; Toro 2002). Flowers offer pollen, nectar and mating sites for pollinators (Simpson 1977; Chiappa et al. 1997). Prosopis flexuosa is considered self-incompatible, with high outcrossing rates (near 88%) (Masuelli & Balboa 1989; Bessega et al. 2000).

We worked in five sites at protected and cattle grazed habitat, each site consisting of a pair of 1-ha plots, one inside and one outside the reserve, both located at least at approx. 1 km away from the fenced reserve limit. Sites were located at least 5 km away from each other at the eastern, western and southern ends of the study area. The protected plot at one site (number 5) had to be relocated in 2006 because we found trails used by horses, cattle and humans inside the original plot. Surveys of insects visiting flowers were performed in the 2005–2006 flowering season. Seeds produced by inflorescence and tree density were estimated during the 2005–2006 and 2006–2007 seasons. The experiments on the effect of different pollination treatments on seeds per inflorescence were conducted in 2006–2007.

Density of adult trees

In each plot we established 4 parallel transects 10 m wide and 100 m long. In each transect, we counted the number of individuals of P. flexuosa at least 1.50 m in height and 5 cm in diameter at the base. We used this size-based criterion to define adult trees because we could not estimate density during the flowering period of trees; smaller individuals usually do not produce flowers (V. Aschero and D. P. Vázquez 2005, pers. comm.)

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Plant-pollinator interactions

We quantified pollinator visitation frequency by observing focal trees. Focal trees were selected randomly within each plot to sample as many flowering individuals as possible in different locations within the study plot, so as to minimize spatial autocorrelation among samples. Pollinator visitation was recorded on four occasions separated by 15–20 days throughout the flowering of *P. flexuosa* (late October–mid December). An unbalanced number of individuals was observed at each plot because the number of flowering individuals varied throughout the flowering season. Paired sites were sampled simultaneously by different observers in the morning (10:00–13:00 h) and the afternoon (15:00–18:00 h). Observers were switched between sites in each sampling period to avoid observer bias. At each focal tree, we recorded the frequency of insect visitation to 15–30 inflorescences in 5-min periods of direct observation. A total of 129 sampling periods of insect visitation to inflorescences were performed at cattle grazed plots and 117 at protected plots. Insects visiting flowers were considered pollinators only if they landed on the inflorescences and searched for pollen or nectar inside the flowers.

Tree reproduction

Reproductive success was defined as production of seeds per inflorescence. Ten individuals of *P. flexuosa* were haphazardly selected in each plot to estimate seeds per inflorescence. Branches (1 or 2 in 2005–2006 and 5 in 2006–2007) of the selected tree were tagged and the number of inflorescences between the tag and the branch tip were recorded. The number of fruits and seeds per fruit in marked branches were counted once the fruits had developed enough to allow distinguishing between viable and aborted seeds, but before maturity to avoid fruit fall and predispersal predation. The average number of seeds per fruit was multiplied by the number of fruits produced per inflorescence to estimate seeds per inflorescence.

To assess pollen limitation of reproduction, at the beginning of the flowering season we tagged nine branches in 10 trees inside and 10 trees outside the reserve. We counted the number of inflorescences on each branch and once flowering had started we randomly assigned branches to one of the following treatments (three branches per treatment per focal plant): (i) control or open pollination (i.e. flowers exposed to pollinators); (ii) exclusion from pollinators; and (iii) hand cross pollination. Pollen supplementation in treatment (iii) was achieved by rubbing inflorescences with fresh flowers on the stigma of open flowers in the selected branch that were initially bagged. Inflorescences used for hand cross pollination were collected from three conspecific trees located at least 50 m away from the focal tree. As before, we estimated number of seeds per inflorescence under each treatment.

Statistical analyses

Analyses were conducted with R statistical software version 2.4 (http://www.r-project.org/). Adult density was compared between protected and cattle grazed sites with a paired *t*-test. To evaluate whether seed production was explained by adult tree density at each plot, we fitted a linear model with the lm function of R. In this model the response variable (seeds per inflorescence) was a linear function of adult density, with grazing regime (protected and grazed) included as an additional categorical variable, which allows the slope of relationship between density and seeds per inflorescence to vary between treatments. This same model was used to evaluate the relationship between mean visitation frequency and reproduction and between mean visitation frequency and adult density.

To evaluate whether seeds per inflorescence differed between treatments we fitted a generalized linear model (GLM) with R’s glm function, using a Poisson distribution of residuals and a log link function. In the GLM approach, the intercept of the linear model is the mean of the first factor level (control in our case), using it as the reference level and defining the remaining parameters as the difference with the reference level.

The effect of habitat protection on frequency of pollinator visits and seeds per inflorescence was analysed with generalized linear mixed models, assuming a Poisson distribution of residuals and a log link function, using the lmer function of R’s lme4 package. Mixed models allow simultaneous evaluation of the effects of fixed and random factors on a numerical variable. We used ‘protection’ as a fixed factor with 2 levels and ‘site’ as a random factor with 5 levels. For the analysis of seeds per inflorescence we incorporated ‘year’ as a random factor with 2 levels.

RESULTS

Adult density of *P. flexuosa* was greater in the protected plots compared with plots currently under cattle grazing (reserve plots: 61.6 ± 5.8 trees per 4000 m²; grazed plots: 32.4 ± 6.25 trees per 4000 m²; *t* = 3.75; *P* = 0.002). Average pollinator visitation frequency
per plot was not correlated with adult tree density ($r = 0.02, P = 0.42$) or with average seed production per plot ($r = 0.05, P = 0.44$). Average seed per inflorescence per plot was positively associated with density of reproductive trees independently of site protection (Fig. 1a,b). This relationship was statistically significant for 2005–2006 (Fig. 1a) but not for 2006–2007, probably because of the influence of site four, where reproductive success was extremely low that year (Fig. 1b).

![Graph showing relationship between seeds per inflorescence and density of reproductive trees](image1)

**Fig. 1.** Relationship between seeds per inflorescence and density of adult trees (number of trees in 4000 m$^2$) at each study plot. White symbols indicate cattle grazed plots, grey symbols reserve plots. The plot relocated in 2006 is labeled with a grey circle. Linear model fit: (i) 2005–2006: $r = 0.59, P = 0.03$; and (ii) 2006–2007: $r = 0.20, P = 0.24$.

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Despite variation in pollinator visitation frequency between sites, pollinator visitation to inflorescences was significantly higher in protected plots than in cattle grazed plots (Fig. 2). We identified 30 morphospecies of flower visitors, which in descending order of importance belonged to the Hymenoptera, Coleoptera, Diptera and Leidoptera. A total of 60% of the recorded flower visitors were bees and wasps. *Colletes* sp., *Apis mellifera*, *Psaenithia* sp. and *Dialictus* sp. were the most common bees observed in the pollinator surveys.

Reproductive success was also higher in protected plots compared with grazed plots (Fig. 3a,b). Although seeds per inflorescence varied among sites and between years, the direction of the effect of the fixed factor was the same at most sites and in both years.

Reproductive sucess of *P. flexuosa* was affected by the pollination treatment (GLM deviance analysis: deviance residual = 94.8, d.f. = 55, $P < 0.001$). Seeds per inflorescence under hand cross pollination was higher than in the other pollination treatments (Fig. 4), and there was no seed production when pollinators were excluded from flowers. The difference in seeds per inflorescence between cross-pollinated and control flowers ($S$) was lower in the absence than in the presence of cattle grazing (without cattle: $S = 0.08$; with cattle: $S = 3.29$).

![Graph showing pollinator visitation frequency](image2)

**Fig. 2.** Comparisons of pollinator visitation frequency (number of visits in 5 min) at each pair of protected and grazed plots. Pollinator visitation to inflorescences increased in protected sites ($z = 3.54, P = 0.001$). Box plots show the median (middle line in boxes), 1st and 3rd quartiles (box upper and lower limits), mean (black circle), data point at least at 1.5 times the interquartile range (whisker limits) and outliers beyond whisker limits (circles). White boxes correspond to cattle grazed plots, grey boxes to protected plots.

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DISCUSSION

Our results indicate that habitat protection through fencing and exclusion of cattle implemented at Ñacuñán Biosphere Reserve resulted in greater density, pollinator visitation frequency to inflorescences and seed production in *P. flexuosa*. Moreover, we found that adult tree density had a positive effect on reproductive success, suggesting positive density dependence of reproduction for this species (Allee effect).

Adult tree density was twice as high at protected plots than at cattle grazed plots, suggesting positive effects of habitat protection and cattle exclusion. Although cattle are effective dispersers of seeds of *P. flexuosa* (Campos & Ojeda 1997), they also consume its seedlings and saplings during the dry season, when grass abundance is low (Guevara *et al.* 1996). Consequently, cattle may enhance seed dispersal while simultaneously hampering seedling survival and growth; thus, if the latter effect on juvenile survival were stronger than the former effect on seedling emergence, the net demographic effect of cattle would be negative. This net demographic effect of cattle is likely to depend on the intensity of grazing, which may influence the balance between the positive effect of dispersal, the potential negative effect in seedling growth and the negative effect we recorded on tree density and reproduction.

It is noteworthy that, in contrast to our findings, woody vegetation encroachment has been reported at cattle grazed sites in the Ñacuñán region (Asner *et al.* 2003). However, the spatial pattern of encroachment reported by Asner *et al.* (2003) was localized and variable, and their spectroscopic methods did not allow them to distinguish between *P. flexuosa* and other woody species. Furthermore, because our study was conducted at paired sites randomly located at different points along the edge of the reserve, and because we purposely avoided highly disturbed areas such as ranch centres and water sources (where most of the *P. flexuosa* detected by Asner *et al.* were located), we believe our results are more representative of the general effects of cattle grazing over the region.

Across the 10 study plots seed production tended to decrease with decreasing adult tree density, suggesting that the observed effect of habitat protection on reproductive success could have resulted from positive density dependence of seed production (Allee effect) at low population density. Our pollinator exclusion-pollen supplementation experiment support this conclusion: results indicate that *P. flexuosa* depends on pollinators for reproduction, that it is pollen-limited, and that such limitation is greater in grazed than in reserve sites. Taken together, our results suggested that seed production of *P. flexuosa* is enhanced by the presence of conspecifics at a local scale, and that extensive cattle grazing could lead to lower tree density and consequently lower seed set than in protected habitats.

Our conjecture that an Allee effect is responsible for the reproductive effect of habitat protection rests on the crucial assumption that pollinator visitation is the link between density and reproductive success. Thus, we expected that adult density of *P. flexuosa* would be positively correlated with pollinator visitation frequency, and that pollinator visitation frequency would be positively correlated with reproductive success. None of these assumptions were supported by the data. How can we explain these conflicting results? We can think in at least two explanations. First, the high
spatio-temporal variability inherent in plant-pollinator interactions (Herrera 1988; Pettersson 1991) could blur the relationship between density or reproductive success and pollinator visitation frequency. Second, because *P. flexuosa* is self-incompatible (Masuelli & Balboa 1989), not only pollen quantity but also pollen quality limitation could represent an important influence on reproductive success (Aizen & Harder 2007); quality limitation does not require a positive correlation between pollinator visitation frequency and reproductive success. Regrettably, logistic constraints prevented us from obtaining data on pollination quantity and quality.

Our finding of higher seed production in protected plots also provides valuable information about the consequences of land management practices on the fecundity of *P. flexuosa*. For example, cattle management could help the conservation of the algarrobo woodland ecosystem. In addition, the finding of positive density dependence in seed production of *P. flexuosa* could be useful for regeneration practices and sustainable harvesting. However, it is important to bear in mind that the observed reproductive effect is not necessarily demographically important. Seed availability is usually less important for population dynamics than seedling survival for trees and other long-lived species (Silvertown *et al.* 1993). Further research on the relative importance of demographic variables (e.g., fertility, seedling survival) for *P. flexuosa* could answer this question.

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