

## DEGRADATION AND RECOVERY PROCESSES IN SEMI-ARID PATCHY RANGELANDS OF NORTHERN PATAGONIA, ARGENTINA

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### ABSTRACT

Vegetation in many arid and semi-arid shrublands frequently occurs in patches with high plant cover (shrub patches) interspersed in a low-cover herbaceous matrix (inter-shrub areas). We hypothesized that (a) livestock grazing is an important determinant of such spatial patterns of vegetation, and (b) redistribution of soil resources associated with shrub patches helps in the recovery of vegetation in inter-shrub areas. To test these hypotheses, we (a) used line transects to compare spatial variations in vegetation, soil microtopography, and soil physicochemical properties in grazed areas and areas protected from grazing since 1970, (b) added sediment and seeds to inter-shrub areas, and (c) measured resource redistribution after a wildfire. Results were consistent with the hypotheses. They indicated greater spatial heterogeneity in vegetation, soil microtopography and soil physicochemical properties in grazed areas than in protected areas, and that addition of sediment and seeds or redistribution of soil resources from shrub patches after a wildfire enhanced re-establishment of vegetation in degraded inter-shrub areas. As a synthesis, a conceptual model of degradation and recovery processes in semi-arid shrublands of Northern Patagonia is presented. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS: semi-arid shrublands; vegetation spatial pattern; soil spatial pattern; livestock grazing; land degradation; vegetation recovery; Patagonia

### INTRODUCTION

Vegetation in arid and semi-arid shrublands commonly occurs in patches with high plant-cover (shrub patches) interspersed in a low-cover matrix (inter-shrub areas) (Noy-Meir, 1985; Aguiar and Sala, 1999). Biomass productivity and species diversity reach their maximum expression in shrub patches, mainly because of the accumulation of resources (water, nutrients, seeds) that promote biological activity under the shrubs (West, 1989; Stavi *et al.*, 2009). Patchiness can be the result of insufficient water to support a broadly continuous distribution of vascular plants (Tongway and Ludwig, 1994), or the consequence of grazing by domestic livestock (Schlesinger *et al.*, 1990). When water is not sufficient to support a continuous distribution of vascular plants, the ratio between runoff sources (inter-shrub areas) and sinks (shrub patches) is critical to prevent water, soil, and nutrient leakage from the ecosystem (Shachak *et al.*, 1998). Conversely, when water is sufficient to support continuous distribution of vascular plants, shrub encroachment induced

by grazing represents desertification and is accompanied by increased bare ground and accelerated rates of water and wind erosion in inter-shrub areas (Archer, 2010). In these systems, restoration efforts are often aimed at reducing shrub cover.

In the semi-arid shrublands of northern Patagonia, Argentina, vegetation is arranged in discrete shrub patches embedded within a matrix of bare ground and herbaceous vegetation (Bisigato and Bertiller, 1997; Bertiller *et al.*, 2004; Kröpfl *et al.*, 2007). Shrub patches are characterized by soil elevated relative to inter-shrub areas and a diverse understory of herbaceous plants and cryptogams, whereas inter-shrub areas are characterized by scarce vegetation, low species diversity and soil degradation (wind and water erosion, compaction, physical crusting, reduced water infiltration, reduced organic matter) (Rostagno and del Valle, 1988; Rostagno, 1989; Chartier and Rostagno, 2006). Circumstantial evidence from long-term grazing exclosures and burned areas, experimental evidence (Bisigato *et al.*, 2008), and models (Bisigato *et al.*, 2002) suggest (1) grazing is an important determinant of the spatial pattern of vegetation and soil, and (2) redistribution of resources (soil, seeds, organic matter) from shrub patches facilitate recovery of vegetation in inter-shrub areas. To test these hypotheses, we (a) compared spatial heterogeneity of vegetation, soil micro-

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topography and soil physicochemical properties in areas protected from livestock grazing since 1970 with that in long-term grazed areas, (b) determined if redistribution of sediments and seeds from shrub patches was affecting inter-shrub areas, and (c) if this redistribution would promote revegetation after a wildfire. Based on our results and existing evidence, we then developed a conceptual model of degradation and recovery processes and suggest management guidelines for the sustainable use of semi-arid shrublands.

## MATERIALS AND METHODS

### Study Area

The study was conducted in the south-eastern Monte Phyto-geographical Province (Cabrera, 1976), in the north-eastern of Río Negro province, Argentina (40° 40'S, 64° 10'W). The exclusive use of private lands in the area is commercial ranching of cattle and sheep.

The climate of the region is temperate and semi-arid. Mean monthly air temperatures range from 7 °C in July to 24 °C in January, with an annual mean of 14 °C. Mean annual rainfall is 270 mm (C.V. 40 per cent), with peaks in autumn and spring. Mean annual potential evapotranspiration is 800 mm. Dominant soils are classified as Haplargids and Haplocalcids.

The vegetation is shrubland steppe dominated by the evergreen shrubs *Chuquiraga erinacea* and *Condalia microphylla*. Shrubs are arranged in patches of one or more individuals, and we use the expression "shrub patch" to refer the area immediately surrounding (and including) the shrub (s). The understory in shrub patches is occupied by cool-season C<sub>3</sub> perennial grasses, annual grasses, forbs and cryptogams. The same species groups are present in inter-shrub areas but are more poorly represented than in shrub patches. Perennial grasses are mainly represented by *Stipa tenuis* (Syn. *Nasella tenuis*; Barkworth, 1990) and to a lesser extent by *Poa ligularis*, *Piptochaetium napostaense*, *S. papposa*, *S. speciosa* (Syn. *Pappostipa speciosa*; Romaschenko *et al.*, 2008), and *S. clarazii*. Annual grasses are mainly represented by *Bromus mollis* and *Schismus barbatus*, and forbs by the annual species *Erodium cicutarium*. The cryptogamic crust is dominated by the mosses *Syntrichia princeps* and *Ceratodon purpureus*. See Godagnone and Bran (2009) for more details on climate, vegetation, and soils.

### Spatial Heterogeneity in Vegetation and Soil

For the purpose of the present study, we defined spatial heterogeneity in terms of spatial variability in vegetation cover, soil elevation, and soil physicochemical properties. We determined the extent to which they differ between shrub patches and inter-shrub areas in grazed and protected sites.

Spatial variation in vegetation, soil microtopography, and soil physicochemical properties were measured in grazed (GC) and ungrazed conditions (UGC). The area has had heavy, year-long grazing by sheep (~1.5 ha sheep<sup>-1</sup>) since the introduction of domestic livestock at the beginning of the 20th century. The UGC area (100 ha) has been excluded from livestock grazing since 1970, whereas the adjacent GC area (380 ha) has been subjected to normal grazing. Both sites were generally similar with respect to soils and topography, and are qualitatively representative of the region. However, we opted to confine transects to 1 ha areas at both sites to standardize for topography, soil, and plant community.

The line intercept method (Canfield, 1941) was used to quantify shrub and inter-shrub patch length and the per cent cover of shrubs, perennial grasses (basal cover), cryptogams, and gravel (rock fragments with diameters in the range 5–20 mm) within and between patches. The criterion to delimitate shrub patches was the presence of soil mound, because mound development is related to shrub establishment (Rostagno and del Valle, 1988). Soil mounds are of common occurrence in arid and semi-arid ecosystems, and are termed phytogenic hillocks or **nebkhas** because they are composed of wind-borne sediments that accumulate within or around the canopies of plants (El-Bana *et al.*, 2003). Line transects ( $n=5$ ) were 20 m long and placed randomly within a representative area (1 ha) in the UGC and GC sites. In GC, the sampling area was located ~1300 m from the source of water. Elevation along transects was recorded at 0.5 m intervals using an optical level, (Geomaster GM 24,  $\pm 2.5$  mm precision) to determine average soil elevation in shrub patches relative to inter-shrub areas (Ares and León, 1972). Prior to statistical analysis, cover (per cent) data were transformed (arcsin transformation) to meet normality requirements. Shrub canopy cover, shrub and inter-shrub patch length, and soil elevation data were analyzed by *t*-tests. Perennial grass basal cover and cryptogam and gravel cover were analyzed using multi-factor (grazing condition-UGC or GC, and site-shrub patch or inter-shrub area) ANOVA and LSD tests for mean comparisons.

Soil cores (10 cm diameter; 20 cm depth) were collected between plants in the center of shrub patches ( $n=30$ ) and from bare spots in the center of inter-shrub areas ( $n=30$ ) on UGC and GC sites. Samples were sieved (2 mm mesh) to eliminate plant fragments and gravel, and then analyzed for sand, silt and clay content (pipette method; Green, 1981), organic carbon content (dry combustion after carbonate removal; Nelson and Sommers, 1982), and total nitrogen content (semimicro Kjeldahl technique; Bremner and Keeney, 1965). Data were analyzed using a multi-factor (grazing condition-UGC or GC, and site-shrub patch or inter-shrub area) ANOVA and LSD tests for mean comparisons. All statistics were computed in INFOSTAT<sup>®</sup>, ver. 1.1 (Infostat Systems, Inc., Sacramento, CA, USA).

### Revegetation of Inter-Shrub Areas

To examine whether resource redistribution from shrub patches facilitates revegetation of inter-shrub areas, we conducted a manipulative experiment and made observations after a 2001 wildfire. The manipulative experiment was carried out in the GC in 2005 and 2006, when annual precipitation totalled 297 mm and 319 mm, respectively. The experimental area was located approximately 500 m from the transect sampling sites. Three treatments were applied within 30 × 30 cm plots situated in inter-shrub areas: addition of sediments (S), addition of sediments and seeds (SS) and control (C). Sediments were collected from shrub patches, sieved (2 mm mesh) to separate plant material and soil fragments, dry-heat sterilized at 105 °C for 24 h to get rid of seeds and added to plots up to 1 cm in thickness. Sterilization temperature would have likely volatilized some of the nitrogen in the soil, although we do not expect this may have influenced the results because seedling roots would rapidly reach the nutrients in the soil underlying the sediments. For the SS treatment, we added 100 seeds (98 per cent germination) and 10 seeds (95 per cent germination) of the native annual grass *Schismus barbatus* and the native perennial grass *Stipa tenuis*, respectively, to each plot in March 2005 (beginning of the annual growing cycle). The difference in seed number between species was due to seed availability. Treatments were applied in the GC area in presence or absence of livestock. Each treatment was replicated in 30 inter-shrub areas, half exposed to livestock and half protected from livestock by a wire mesh fence. Seedlings per plot were counted at the end (November) of both growing cycles (2005 and 2006), sorting by species or species group. The response variable was the cumulative seedling abundance per plot at the end of the experiment. Data were square root transformed to meet normality requirements, and analyzed using a multi-factor (treatment—S, SS or C, and presence or absence of livestock) ANOVA and LSD tests for mean comparisons.

After a summer (February 2001) wildfire in the study area, we randomly selected five shrub patches averaging ~1.5 m<sup>2</sup> in size and surrounded by large areas of bare soil (inter-shrub areas). Transects (1.2-m long) originating at the shrub patch perimeter and oriented in the four cardinal directions were established and metal rods were inserted at 10-cm-intervals. The top of the rods were 10 cm above the soil surface. The following winter (July 2001), we re-measured the height of the rods and used the difference as an indication of sediment accumulation. In the spring (November) of the same year, we quantified herbaceous seedling cover and density in 10 × 10-cm plots placed at 10-cm intervals along each transect to derived the 'frequency of plots with seedlings' for each distance from the shrub patch border. A shortcoming of this part of the observational study after the 2001 wildfire was the lack

of control for the data collected on the wildfire site, which is dealt with in the Discussion section. In the spring following the summer wildfire, we also measured perennial grass basal cover and aerial cover of annual plants on 20 × 50-cm plots randomly placed in burned ( $N=40$ ) and unburned ( $N=40$ ) shrub patches, to determine the effect of fire and sediment loss on vegetation in shrub patches. During the year of the study (2001) precipitation totalled 400 mm. There was no livestock grazing in the area during the study period. Regression analysis was performed to determine the relationship between sediment thickness (as a measure of sediment accumulation) and distance from shrub patch border, and between sediment thickness and herbaceous plant cover and density. Differences in perennial grasses and annual plants cover between burned and unburned shrub patches were assessed by *t*-tests.

## RESULTS

### *Spatial Heterogeneity in Vegetation and Soil*

Shrub cover, length of shrub patches, and distance between shrub patches were similar between GC and UGC sites, whereas the difference in elevation between shrub and inter-shrub patches were greater ( $p < 0.05$ ) in GC relative to UGC (Table I). Perennial grass basal cover was higher in inter-shrub areas than in shrub patches in UGC, but similar on the GC site (Table II). Cryptogam cover was higher in inter-shrub areas than in shrub patches in UGC, whereas the reverse was observed in GC (Table II). Perennial grass and cryptogam cover in inter-shrub areas were higher in UGC than in GC. Gravel cover was higher in inter-shrub areas than in shrub patches in GC, and similar between both sites in UGC (Table II).

Per cent total nitrogen, organic matter and sand were higher, whereas per cent silt and clay were lower, in shrub patches than in inter-shrub areas in GC (Table III). With the exception of per cent sand and silt, no differences were observed in soil properties between shrub patches and inter-shrub areas in UGC.

Table I. Mean ( $\pm 1SE$ ;  $n=5$  line transects) shrub cover, patch length, and difference in soil elevation on grazed (GC) and protected (UGC) sites

Grazing condition	Shrub canopy cover (per cent)	Shrub patch length (cm)	Inter-shrub patch length (cm)	Difference in soil elevation between shrub and inter-shrub patches (cm)
GC	63 ± 8 <sup>a</sup>	111 ± 11 <sup>a</sup>	157 ± 11 <sup>a</sup>	49 ± 4 <sup>a</sup>
UGC	42 ± 10 <sup>a</sup>	124 ± 12 <sup>a</sup>	201 ± 11 <sup>a</sup>	33 ± 4 <sup>b</sup>

Shrub and inter-shrub patch length and soil elevation in both type of patches were averaged within transect. For each variable, values followed by the same letter were statistically comparable ( $p > 0.05$ ).

Table II. Mean ( $\pm 1$ SE;  $n = 5$  line transects) cover of perennial grasses, cryptogams, and gravel in shrub patches and inter-shrub areas on grazed (GC) and protected (UGC) sites

Grazing condition	Cover (per cent)					
	Perennial grass		Cryptogam		Gravel	
	Shrub	Inter-shrub	Shrub	Inter-shrub	Shrub	Inter-shrub
GC	9.7 $\pm$ 1.7 <sup>b</sup>	6.7 $\pm$ 1.6 <sup>b</sup>	27.7 $\pm$ 4.4 <sup>a</sup>	11.8 $\pm$ 3.4 <sup>b</sup>	2.9 $\pm$ 1.0 <sup>b</sup>	22.5 $\pm$ 3.3 <sup>a</sup>
UGC	16.0 $\pm$ 3.2 <sup>b</sup>	27.1 $\pm$ 3.3 <sup>a</sup>	19.0 $\pm$ 5.5 <sup>b</sup>	34.6 $\pm$ 5.6 <sup>a</sup>	1.1 $\pm$ 0.5 <sup>b</sup>	3.2 $\pm$ 1.0 <sup>b</sup>

For each variable, values followed by the same letter were statistically comparable ( $p > 0.05$ ).

### Revegetation of Inter-Shrub Areas

There was no difference in cumulative seedling abundance between plots exposed to or protected from livestock grazing, so the data were pooled. Cumulative seedling abundance was highest when there was addition of SS, intermediate when there was addition of S only, and lowest when there was no addition of sediment or seed (Figure 1). The addition of sediment and seed enhanced recruitment of the seeded species (*Schimus barbatus* and *Stipa tenuis*) as well as that of dicot species.

In the winter following the 2001 summer wildfire, sediment thickness in inter-shrub areas decreased exponentially with the distance from the border of the shrub patch (Figure 2). The differences between cardinal directions were not significant ( $p > 0.05$ ). On the other hand, seedling frequency, cover and density increased with sediment thickness (Figure 3). Burning did not affect ( $p > 0.05$ ) either mean ( $\pm 1$ SE) perennial grass basal cover (burned shrub patches 12.1  $\pm$  1.4 per cent vs. 16.9  $\pm$  2.5 per cent in unburned patches) or annual species aerial cover (19.7  $\pm$  2.7 per cent vs. 17.6  $\pm$  2.0 per cent).

## DISCUSSION

Our results showed that protection from grazing reduced spatial heterogeneity in vegetation and soil in semi-arid shrublands of northern Patagonia. Total vegetation coverage was more spatially uniform in UGC than in GC because of the fact that inter-shrub areas were more vegetated by perennial grasses and cryptogams in the UGC (Table I). Similarly, spatial differences in soil elevation (Table I) and soil physicochemical properties (Table III) were more marked in GC than in UGC.

Grazing may induce shrub encroachment (Archer, 1994) as well as shrub patch fragmentation (Bisigato and Bertiller, 1997), which may explain higher shrub canopy cover and smaller shrub patches in GC than in UGC. Inter-shrub areas in GC were characterized by low vegetation cover, high gravel cover and high clay content in the soil. In shrubby

ecosystems, the concentration of grazing in between shrubs leads to reduced vegetation cover and soil degradation in inter-shrub areas (Schlesinger *et al.*, 1990; Bisigato *et al.*, 2005). Denuded soil is exposed to erosion agents, leading to losses of soil components from inter-shrub patches. The same erosion processes promote fertility and contribute to the formation of soil mounds (Ridolfi *et al.*, 2008). In the present study, the soil mounds were taller in GC than in UGC, and were characterized by higher concentrations of total nitrogen and organic matter. The reverse translocation of sediments (i.e., from shrub patch mounds to inter-shrub areas surrounding shrub patches) is expected to happen because of post-fire soil erosion (Figure 2, argued below).

Reversals of desertification following long-term livestock removal have been reported recently (Allington and Valone, 2010); however, our results suggest that recovery processes may be promoted by the redistribution of soil resources from shrub patches to degraded inter-shrub areas. Both artificial and natural (post-wildfire) redistribution of soil resources from shrub patches favored re-establishment of vegetation in inter-shrub areas. Seedling abundance in the treatment with addition of sediments only may have been limited by the lack of synchrony between seed rain in the study system (December) and the addition of sediments (March of the following year). A seed-capture study (Kröpfl AI, Universidad del Comahue-Argentina, unpublished) has shown that the seed rain is similar between shrub patches and inter-shrub areas. On the other hand, enhancement of seedling recruitment with addition of sediments and seeds may have resulted from an improvement in environmental conditions favoring seed anchoring and germination (Bisigato and Bertiller, 2004). Improvement in seed anchoring and in germination conditions may also explain enhanced re-establishment of dicot species with the addition of sediments and seeds.

Given the spatial extent of livestock grazing in drylands—and related rehabilitation costs, the redistribution of soil resources to inter-shrub areas induced by the summer wildfire, and the observed re-establishment of vegetation, is particularly relevant. Moreover, in the present study, we did not observe negative effects on shrub patch vegetation

Table III. Mean ( $\pm$  ISE;  $n = 30$ ) values for properties of soils in shrub patches and inter-shrub areas on grazed (GC) and protected (UGC) sites

Grazing condition	Total nitrogen (per cent)		Organic matter (per cent)		Sand (per cent)		Silt (per cent)		Clay (per cent)	
	Shrub	Inter-shrub	Shrub	Inter-shrub	Shrub	Inter-shrub	Shrub	Inter-shrub	Shrub	Inter-shrub
GC	0.14 $\pm$ 0.010 <sup>a</sup>	0.08 $\pm$ 0.004 <sup>b</sup>	2.4 $\pm$ 0.14 <sup>a</sup>	1.5 $\pm$ 0.06 <sup>c</sup>	88.0 $\pm$ 0.34 <sup>a</sup>	77.4 $\pm$ 0.58 <sup>c</sup>	3.5 $\pm$ 0.15 <sup>b</sup>	5.0 $\pm$ 0.23 <sup>a</sup>	8.5 $\pm$ 0.29 <sup>b</sup>	17.6 $\pm$ 0.56 <sup>a</sup>
UGC	0.09 $\pm$ 0.004 <sup>b</sup>	0.09 $\pm$ 0.004 <sup>b</sup>	1.8 $\pm$ 0.07 <sup>b</sup>	1.6 $\pm$ 0.05 <sup>bc</sup>	88.0 $\pm$ 0.35 <sup>a</sup>	85.3 $\pm$ 0.57 <sup>b</sup>	3.7 $\pm$ 0.21 <sup>b</sup>	5.7 $\pm$ 0.22 <sup>a</sup>	8.2 $\pm$ 0.22 <sup>b</sup>	9.1 $\pm$ 0.46 <sup>b</sup>

For each soil property, values followed by the same letter were statistically comparable ( $p > 0.05$ ).

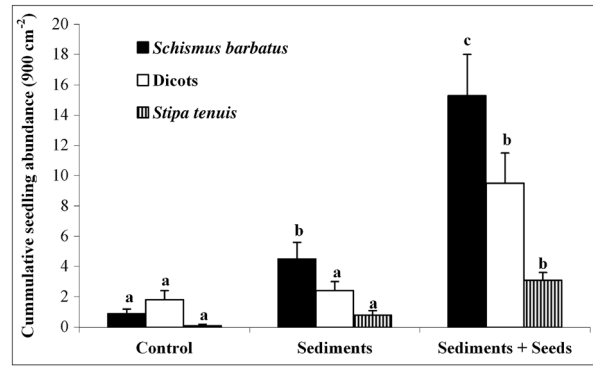


Figure 1. Mean ( $\pm$  ISE;  $n = 30$ ) cumulative seedling abundance in inter-shrub areas with or without the addition of seeds and/or sediments pooled over the 2005 and 2006 growing cycles. Means of the same species or species group with the same letter are not different ( $p > 0.05$ ).

associated with post-fire loss of sediments from soil mounds. We are aware that the lack of 'control' for the data collected on the wildfire site represents a shortcoming in the present study; however, both circumstantial and experimental evidence suggest that sediment redistribution occurs following disturbances like fire. Post-fire sandstorms are of common occurrence in the study area. Also, in similar semi-arid shrublands of north-eastern Patagonia (Rostagno 1999) and from other part of the world (Ravi *et al.*, 2009), it has been shown that erosion of burned shrub patches redistributes resources accumulated under shrubs, leading to more homogeneous spatial distribution of soil resources. Enhanced soil erodability, mainly eolian, in burned shrub patches was attributed to the soil water repellency induced by burning (Ravi *et al.*, 2006, 2007). It is unknown whether the same mechanism is operating in our study system. Using spatially explicit cellular automata model, Ravi and D'Odorico (2009) showed that

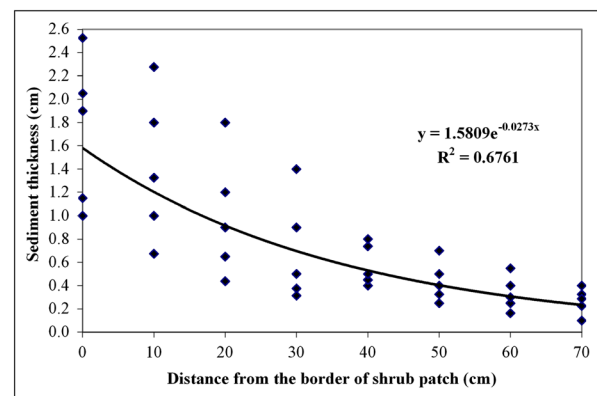


Figure 2. Accumulation of sediments in inter-shrub areas in the winter (July) following a summer (February 2001) wildfire as a function of distance from the border of shrub patch. At each distance, points represent each of the five measured shrub patches and average of the four cardinal directions. There was no unburned control for these data. This figure is available in colour online at [wileyonlinelibrary.com/journal/ldr](http://wileyonlinelibrary.com/journal/ldr)

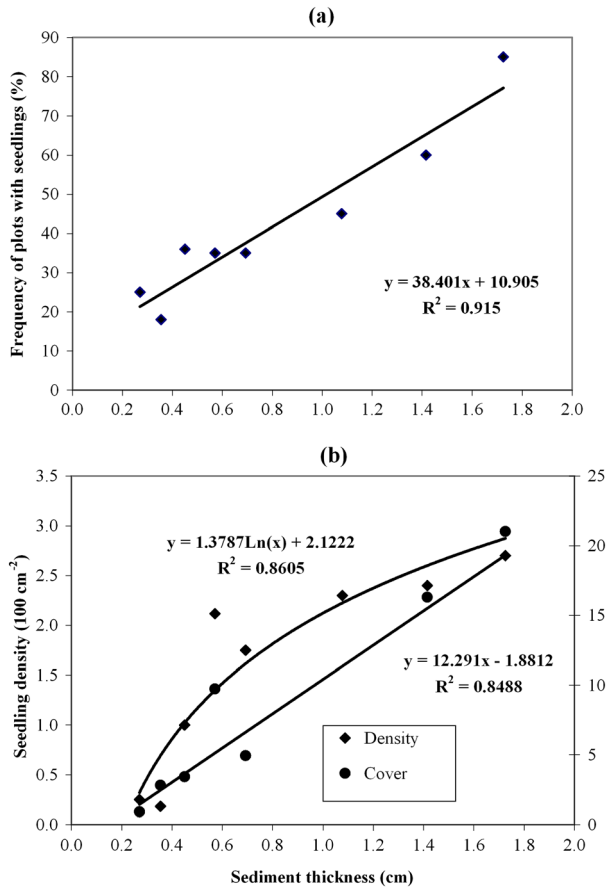


Figure 3. Frequency of plots with seedlings (a) and seedling density and cover (b) as a function of sediment accumulation. Each point was calculated from a total of 20 observations (five shrub patches and four cardinal directions). This figure is available in colour online at [wileyonlinelibrary.com/journal/ldr](http://wileyonlinelibrary.com/journal/ldr)

feedbacks between fire and soil erosion processes may play a major role in the re-establishment of vegetation in inter-shrub patches in semi-arid shrublands. Post-fire transitions from shrub steppe to grass steppe have been observed in rangelands of north-eastern Patagonia (Rostagno *et al.*, 2006).

In synthesis, we propose a model of degradation and recovery of semi-arid patchy rangelands utilized for livestock grazing, such as that of northern Patagonia, as follows. A grassland with scattered shrubs is suggested by historical accounts, long-term grazing exclosures, data from lightly grazed areas far from watering points (Kröpfl, 1999) and models (Bisigato *et al.*, 2002). Grass competition (de Villalobos *et al.*, 2005a) and fire (Bóo *et al.*, 1997) prevented shrubs from increasing in density and cover (Scholes and Archer, 1997). Heavy, continuous grazing subsequently reduced grass competition (Moretto and Distel, 1999; de Villalobos *et al.*, 2005b) and fire frequency (Bóo *et al.*, 1996), moving the system to a shrubland domain (Archer and Smeins, 1991). The concentration of grazing in remaining inter-shrub areas further

reduces herbaceous vegetation cover and promoted soil degradation (Schlesinger *et al.*, 1990; Bisigato and Bertiller, 1997). Soil compaction and physical crusting may have reduced infiltration and increased runoff precipitation and promoted resource leakage from the ecosystem (Ludwig *et al.*, 2005; Turnbull *et al.*, 2008). Alternatively, in flat landscape, mound development in shrub patches that shelter the underlying soil (Rostagno and del Valle, 1988) and reduced connectivity of bare soil patches can lead to flooding of inter-shrub areas (self-evident during rain storms in the study region) causing rain water in part be lost through evaporation (Bisigato and Lopez Laphitz, 2009). Wind and water erosion redistribute soil resources from inter-shrub patches to shrub patches leading to the development of “fertility island” (Ridolfi *et al.*, 2008). This pattern of degradation leads to the creation of a stable two-phase mosaic structure of shrub patches with high biological activity and inter-shrub areas with low biological activity. Restoration of these two-phase mosaics requires a disturbance such as prescribed fire to reduce shrub abundance and concurrent relaxation of grazing pressure to promote herbaceous species recruitment in inter-shrub areas.

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