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Patch structure and dynamics in a Patagonian arid steppe

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Abstract

Two patch types were recognized in the Occidental District of the Patagonian arid steppe: i) shrubs encircled by a ring of tussock grasses, and ii) tracts of scattered tussocks. Completeness of the ring of grasses around the three dominant shrubs was a function of shrub size. Average completeness was 62, 71 and 83%, respectively for the three dominant shrubs (*Senecio filaginoides*, *Mulinum spinosum* and *Adesmia campestris*). A model for the cyclic dynamics of the two patch types was proposed. It includes a building phase (grass ring construction), a mature phase (maximum ring completeness) and a degenerate phase. In this last phase, triggered by shrub death, completeness of the ring progressively decreases until remnant grasses become undistinguishable from the scattered tussocks patch type. Ring formation occurred independently of shrub species. Grass species were differentially associated to the two patch types and to rings of different shrub species. Cyclical patch dynamics influenced the pattern of resource utilization, since the shrub-ring patch, with a share of only 18% of cover, contributed 44% of the total primary productivity.

Abbreviations: Shrub-ring patch (ST), M = asymptote, maximum completeness, D = parameter related to the initial lag, B = rate of increase in ring completeness, z = shape parameter, r = radius.

Nomenclature: The taxa names are given according to Correa, M.N., 1971–1984. Flora Patagónica. Colección Científica del I.N.T.A., Buenos Aires. *Adesmia campestris* (Rendle) Skottsb., *Berberis heterophylla* Juss., *Mulinum spinosum* (Cav.) Pers., *Poa lanuginosa* Pir., *Poa ligularis* Nees apud Steudel, *Senecio filaginoides* De Cand., *Stipa speciosa* Trin. et Rupr., *Stipa humilis* Vahl.

Introduction

The pattern and dynamics of patches represent fundamental attributes of vegetation. Several authors have emphasized the importance of patch structure as a determinant of ecosystem function (Pickett & White 1985; Fahrig & Paloheimo 1988). A patchy community structure frequently results in differences in survival, reproduction and migration of individual species, life-forms or guilds (Fowler 1984; Gibson 1988a & b). This heterogeneity is not only the result of changes in the abiotic environmental components, but it is also originated (passively and actively) by the organisms themselves (Kareiva 1986).

In one of the dominant plant communities of the Patagonian arid steppe, adult shrubs appear encircled by a ring of grasses, spotting a matrix of loosely scattered grass tussocks. This general structure of the community may be characterized as a combination of two patch types: (i) shrubs encircled by a ring of grasses (SR) and (ii) scattered tussocks (ST). The shrub-ring type appears as relatively small and dense patches. The scattered tussocks type, instead, forms larger patches with a high proportion of bare soil.

Three aspects of the patch types stand out from general observation: a) different degrees of grass-ring completeness are apparent, b) complete grass rings occur around debris of dead shrubs, and c) the same grass species are present in the two patch types and in rings around the three dominant shrub species. Taking into account these aspects, we hypothesized that: (i) the structure of the steppe is the spatial manifestation of different phases of a cyclical succession (Watt 1947), and (ii) these processes are more dependent on life forms – shrubs or grasses – than on species.

In relation to these general hypotheses the following specific predictions were tested: (i) The completeness of rings is related to the size of shrubs; (ii) a high degree of non-specificity is exhibited both by ring formation of different shrub species and by patch affiliation of the three main grasses. To describe and interpret the present state of the patch structure of the community, the relative cover of each patch type and of its components (shrubs, grasses and bare soil) was estimated.

Methods

Study area

The Patagonian arid steppe in South West Chubut Province, Argentina, is dominated by tussock grasses and by shrubs not generally exceeding 1 m in height. Average annual precipitation, for 40 years with complete records, from 1940 until 1991 was 142 mm. Mean monthly temperature was 1 °C in July and 15 °C in January. Climatic aridity index (UNESCO 1977) is 0.12. Strong winds blow, predominantly from west to east. Soils are of coarse texture; different sizes of gravel and pebbles are found in the soil profile. Sheep production, mainly for the wool industry, is the way in which vegetation is utilized in this region, as has been done since the beginning of the century (Soriano *et al.* 1983). The major plant community in the area is characterized by *Stipa speciosa*, *Stipa humilis*, *Adesmia campestris*, *Berberis heterophylla* and *Poa lanuginosa* (Golluscio *et al.* 1982).

The three major species of shrubs in this comunity are: *Adesmia camprestris*, *Mulinum spinosum* and *Senecio filaginoides*. The three species differ both in architecture and phenology. The shape of *M. spinosum* and *S. filaginoides* is approximately hemispherical, while *A. campestris* is similar to an inverted cone, its branches diverging from a central area at the base of the plant. *A. campestris* is a deciduous species, bearing leaves from September to February. *M. spinosum* keeps dead and spiny leaves, corresponding to five or more growth periods, and branches are devoid of them only at their base. *S. filaginoides* is an evergreen shrub which keeps its green and leafy appearance throughout the year.

The three dominant grasses (*S. speciosa*, *S. humilis* and *P. ligularis*) are bunch grasses approximately 30 cm in height with linear, plicate leaves. Tussocks of these three species keep old dead leaves as a high proportion of standing biomass. Live tillers show expanding leaves during the four seasons in all three cases. Thus, no definite dormant period is shown by these bunch grasses (Soriano & Sala 1983).

Sampling methods and data analysis

We used 15 transects, each 30 m long, randomly located in a 4 Ha exclosure, fenced against sheep and small mammals since 1972. Along these transects we quantified: 1) The relationship between shrub size and completeness of the ring of grasses; 2) the relative abundance of each grass species in the two patch types and the association of those grasses with patch types and shrub species; and 3) the proportion in which the different components contribute to the structure of the community. Along transects, interceptions at ground level of the following attributes were recorded: a) bare soil (including litter), b) *S. speciosa*, c) *S. humilis*, d) *P. ligularis*, e) other herbaceous species, g) *M. spinosum*, h) *S. filaginoides*, i) *A. campestris*. Interception length was recorded in each case. Of every shrub and tussock intercepted, the major diameter was measured. Whenever the intercepted tussock was part of a shrub-ring patch, the following traits were recorded: external (R ext) and internal (r) radii of the ring; number of gaps in the ring and total length of gaps measured at their external border (β). Space between two contiguous tussocks was considered a gap when it was larger than their average diameter.

Grass-ring completeness was calculated according to:

$$\text{Completeness} = (2\pi * \text{R ext} - \beta)/2\pi * \text{R ext} \quad (1)$$

The relationship between shrub size and ring completeness was studied by fitting the Richards (1959) function to data for the whole shrub population. Accordingly,

$$\text{Completeness} = \text{M} * [1 - \exp(\text{D} - \text{B} * \text{r})]^{\text{z}} \quad (2)$$

where M = asymptote, maximum completeness, D = parameter related to the initial lag, B = rate of increase in ring completeness, z = shape parameter, r = radius. The model presents 3 regions. The extent of the first one is related to parameter D. In the second region, completeness grows exponentially with a slope related to parameter B. The third region is asymptotic to a maximum value of completeness given by parameter M.

For each individual shrub species the Gompertz function, which is a special case of Richards function, was fitted. In this case,

$$\text{Completeness} = \text{M} * \exp[-\exp(\text{D} - \text{B} * \text{r})]^{\text{z}} \quad (3)$$

The minimization method used was the derivative-free quasi-Newton one, included in the NONLIN module of SYSTAT package (Wilkinson 1986).

Proportion of shrub and grass cover in each patch type as well as their contribution to total cover were estimated from interception lengths in the transects. Association of grass species to each one of the two patch types was tested using Chi square, and one-way ANOVA, for presence, and cover data, respectively (Legendre & Legendre 1983). The association between species of grasses and shrubs in SR was tested using Chi square statistics. The expected occurrence of each grass species was calculated as the total number of rings with that grass species (row total), multiplied by the proportion of shrub rings of a particular shrub species out of the total shrub-ring population (Greig-Smith 1983).

Results

Ring completeness increased as shrub radius augmented (Fig. 1A, B, C, D). The maximum of the second derivative of the general model, which was located at a radius of 13 cm (completeness 5%), was taken as the minimum size for shrubs to be included in the shrub-ring patch type. Shrubs smaller than 13 cm in radius were included in ST.

Average ring completeness around the shrub species *S. filaginoides*, *M. spinosum*, and *A. campestris*, was 62, 71 and 82%, respectively. *A. campestris* showed a shorter initial lag in the increase of completeness, a lower rate of increase of completeness and a greater maximum completeness than the other two shrub species (Fig. 1D).

The analysis of presence data indicated that *S. speciosa* occurred more frequently in the scattered tussocks than in the shrub-ring patch type (Table 1). Conversely, *S. humilis* occurred more frequently in the shrub-ring patches. *Poa ligularis* showed no significant difference in presence between the two patch types. Cover data were not as sensitive as presence data. No significative differences on cover were observed between the two patch types for any grass species. The major grass species, *S. speciosa* and *Poa ligularis*, which ac-

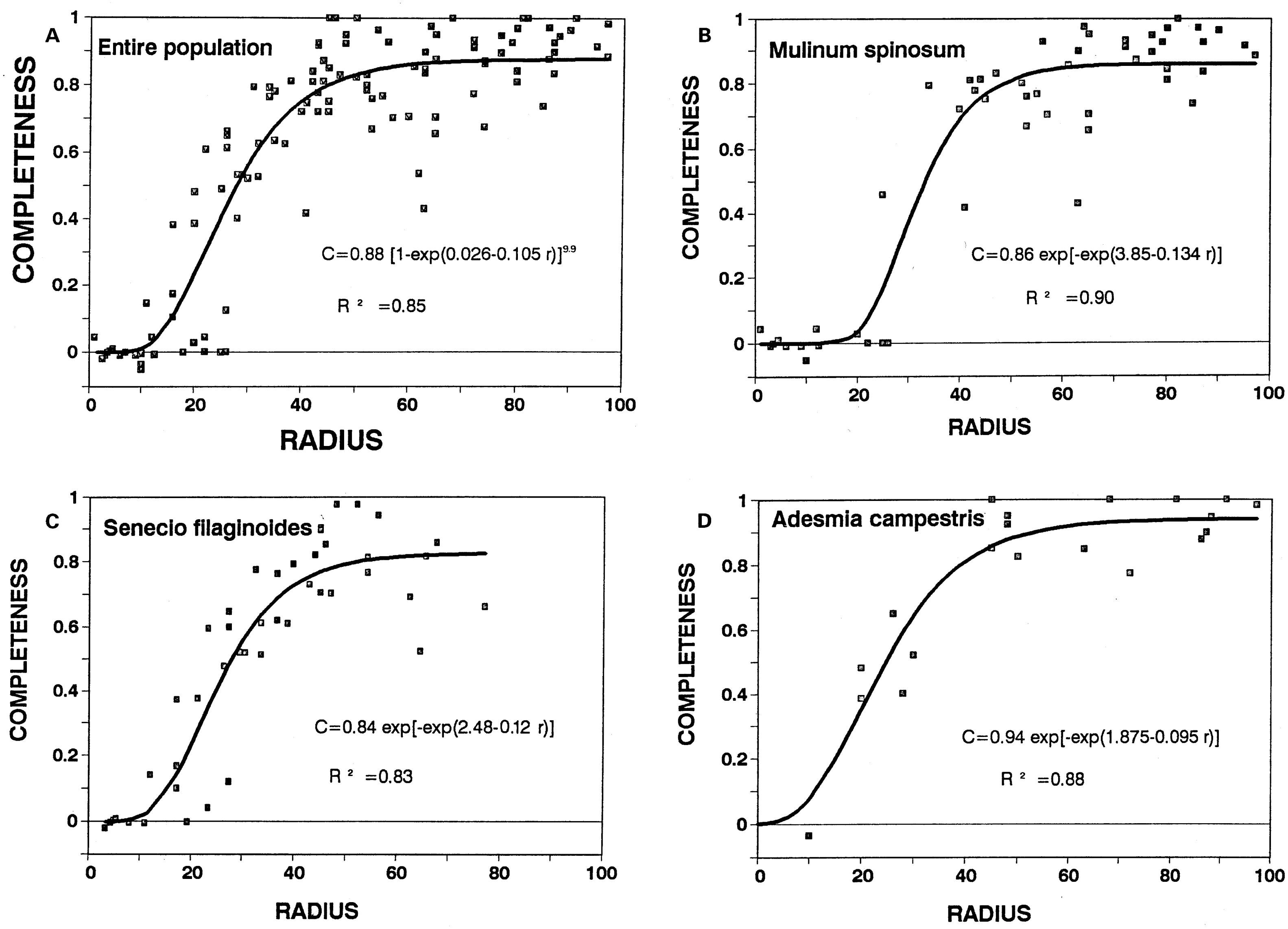

Fig. 1. Relationships between shrub radii and ring completeness. A. Entire shrub population; B. *Mulinum spinosum* (n = 54; SD for parameters M, B and D: 0.031; 0.041 and 1.16 respectively); C. *Senecio filaginoides* (n = 44; SD for parameters M, B and D: 0.43, 0.027 and 0.61 respectively); D. *Adesmia campestris* (n = 20; SD for parameters M, B and D: 0.034; 0.027 and 0.62 respectively) (c = shrub ring completeness; r = radius).

Table 1. Grass species presence and cover in the two patch types. ST: Scattered tussocks; SR: Shrub-ring. (SD values for cover estimates in parenthesis) (* P≤0.05; ** P≤0.01).

Patch type	Presence		Chi square	% Cover	
	ST	SR		ST	SR
Stipa speciosa	48	30	4.154*	9.4 (3.1)	8.4 (6.6)
Stipa humilis	7	22	7.759**	1.7 (1.5)	6.4 (6.0)
Poa ligularis	48	41	0.551	11.7 (3.1)	9.4 (7.4)
Other species	28	20	1.333	3.5 (1.8)	5.4 (5.6)

counted for 76% of total grass cover, were not associated with any particular shrub species when forming the rings. On the contrary, *S. humilis* was positively associated with *A. campestris*, and negatively associated with *S. filaginoides* ($P \leq 0.05$) (Table 2).

In the overall community, cover of the patch type SR was 17.5% (SD = 6.8%), whereas the ST patch type covered 82.5% (SD = 6.8%). In SR, average cover for shrubs was 65.8% (SD = 10.3%), for grasses 32.2% (SD = 11.2%), and for bare soil 13.5% (SD = 3.7%). The grass cover of the ring was 70.5%, which is similar to the average completeness (70.4%). In ST, grass cover amounted to 25.9% (SD = 3.4%), small shrubs (< 13 cm diam.) to 0.5% (SD = 0.8%), and bare soil to 74.0% (SD = 3.7%).

Table 2. Grass species presence in rings around different shrub species in shrub-ring patch. O: Observed number; E: Expected number (* P≤0.05).

Shrubs Grasses		Mulinum spinosum n = 46	Senecio filaginoides n = 38	Adesmia campestris n = 22	Chi square
Stipa speciosa	O	15	9	6	0.596
	E	13.02	10.75	6.25	
Stipa humilis	O	8	4	10	8.633*
	E	10.55	7.89	5.57	
Poa ligularis	O	17	14	10	0.330
	E	17.79	15.7	8.51	
Other species	O	10	7	3	0.524
	E	8.78	7.17	4.15	

No significant difference was found between grass cover in the two patch types, and the difference between bare soil proportions was very significant ($P \leq 0.001$). Taking into account the entire community, total cover was 27.0% for grasses, 11.5% for shrubs, and 61.5% for bare soil.

Discussion

Our results support the first proposed specific hypothesis. Ring completeness increases with shrub size according to Richards model. This is true both for the whole shrub population and for each one of the shrub species (Fig. 1A, B, C & D).

Our model for the dynamics of this patchy structure conceives the ring construction as the building phase of a succession cycle (Watt 1947; Connell & Slatyer 1977; Gimingham 1988). The mature phase is represented by the shrubs belonging to large size classes, encircled by nearly complete grass rings (Fig. 2). The degenerate phase is manifested, at least partially, by the presence of discernible rings around dead shrubs in different stages of fragmentation (Fig. 3).

As grass recruitment around shrubs occurs during most of the shrub life-span, a range of tussock ages must be represented in each ring. Therefore, differential death of tussocks after shrub death is expected. Our model suggests that after shrub debris is completely decomposed, the remaining fragments of the ring become undistinguishable from scattered tussocks. Each shrub establishing amidst the scattered tussocks starts a new shrub-ring patch (Fig. 4). A rather similar phenomenon has been described in Sri Lanka, where dynamics of *Cynodon dactylon* has been shown to be associated to age of the shrub *Arthrocnemum indicum* (Pemadasa 1981).

The construction of the grass ring during the building phase is the result of the facilitation effect of shrubs. In the same study site, wind velocity leeward of the shrub was 15% of the value registered in a fully exposed location, and evaporation was 36% of the maximum (Soriano & Sala 1986). A different set of evaporation data in re-

Fig. 2. Shrub ring patch at its mature phase. The shrub is *Adesmia campestris*. In upper right angle, a view of a scattered tussock patch.

lation to distance to shrubs showed that it steadily increased, both in spring and summer, from the border of the shrub to a distance of 1 m (Aguiar 1991).

In the mature phase, as completeness becomes high enough, shrub facilitation fails to show its effects because grasses already established exert a strong competition for soil water (Soriano & Sala 1986; Aguiar *et al.* 1992). The major role of grass competition was emphasized by a manipulative experiment which demonstrated that adult shrubs compete minimally with adult grasses in the Patagonian steppe (Sala *et al.* 1989). Soil water potential values determined with soil psychrometers at a depth of 12.5 cm in November (a critical month for seedling establishment), at different distances from the border of SR patches, increased from − 1.35 MPa at 2.5 cm, to − 0.10 MPa at 97.5 cm (Aguiar 1991). We suggest that during the degenerative phase facilitation disappears and competition becomes dominant in the ring, increasing the death rate of grasses. Since no grass rings have been found in which all their individual components were dead, neither a high number of complete rings lacking a shrub at its center are apparent, we postulate a process of ring fragmentation as a result of progressive tussock death.

In partial agreement with our second hypothesis, the process of grass ring formation appeared independent from plant species. The three shrubs formed grass rings reaching a high degree of completeness and the three grasses appeared in their rings (Fig. 1B, C & D; Table 2). On the contrary, grass species composition in the two patch types and in rings of different shrub species showed some examples of differential preference. *S. speciosa* was present more frequently in ST than in SR ($P \leq 0.05$) and a reversed and stronger preference was shown by *S. humilis* ($P \leq 0.01$) (Table 1). The latter was more frequently associated to *A. campestris* ($P \leq 0.05$) and less to *S. filaginoides* than expected by chance (Table 2). This can be interpreted on the basis of the different phenology (Soriano & Sala 1983) and root patterns of shrubs (Fernández Alduncin & Paruelo 1988). The deep rooted and deciduous *A. campestris* may compete less than the other two shrubs with the evergreen and shallow rooted *S. humilis*. On the contrary, *S. filaginoides* is the

Fig. 3. A ring in its destructive phase. Debris of a *Mulinum spinosum* shrub at its center.

only evergreen shrub of the community and the one which possesses a relatively shallow root system. We ignore why *S. humilis* was the only grass species that responded to these differences among shrubs.

The existence of some sort of association between shrubs and herbs in arid and semi-arid environments has been the object of analysis by several authors (Noy-Meir 1979/80; Jaksic & Fuentes 1980). Protection from winds, accumulation of sand, silt and organic debris, and production of litter might all be factors that enhance seedling establishment and plant growth around the shrubs because of their influence on water

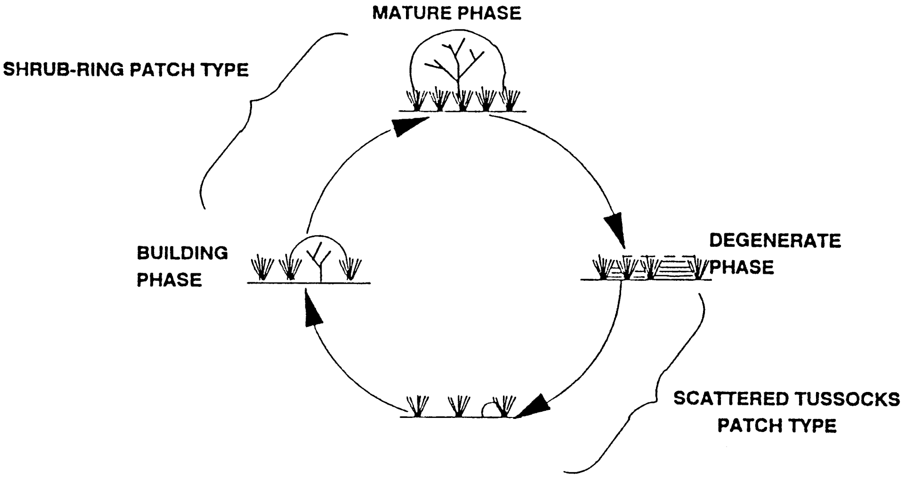

Fig. 4. Diagram of the cyclical dynamics of the patch structure in the Patagonian steppe.

dynamics and heat flux (Charley & West 1975, 1977; West & Goodall 1980).

The mature SR patch contributes more than proportionally to the average productivity of the community. The five year average of aboveground net primary productivity for the community was 60 g m^{-2} y^{-1} (Fernández Alduncin *et al.* 1991). Using their data, we calculated that 44% of productivity corresponds to the shrub-ring patch, which only represents 18% of the entire community cover. ST, with a cover of 82% in the community, contributes 56% of the total aboveground productivity. An interpretation may be that during its building phase, the SR assemblage increasingly makes use, through ring completion, of water available in the upper soil in bare soil pockets (Soriano & Sala 1986; Soriano *et al.* 1987), and through growth and branching of shrub roots, of water in deeper soil layers (Fernández Alduncin & Paruelo 1988; Sala *et al.* 1989).

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