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**Authors: C.A. Busso · G.L. Bonvissuto**

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2 **Structure of vegetation patches in northwestern**  
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4 C. A. Busso · G. L. Bonvissuto

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24 *lampa* contributed more than 84% of the total patch standing crop ( $5,777 \pm 435$  g).  
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29 **Keywords** Arid and semiarid lands · Perennial grasses and shrubs ·  
30 Qualitative and quantitative analytical plant characteristics · Regression analysis

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## Introduction

The occurrence of patches of vegetation alternating with patches of (almost) bare soil is a common feature in arid and semiarid grazing systems throughout the world (Ludwig et al. 2004; Erickson et al. 2005). These systems cover nearly 30% of the earth's land surface. Vegetation patches vary in form, from irregular mosaics to regular stands, and size, from one to several hundred meters (Montaña 1992; Haase et al. 1996).

In environmentally harsh sites and in sites where levels of resources are chronically low, such as in Monte Austral Neuquino (Patagonia, Argentina), conditions suitable for rapid plant growth may occur infrequently. Natural selection under these conditions would favor adaptations conferring tolerance to prevailing forms of abiotic stress and the ability to conserve resources that have been acquired (Pyke and Archer 1991). Shrubs encompass an array of morphological and physiological traits that can contribute to vertical stratification of resources with grasses and forbs. These lifeforms are often considered undesirable on rangelands because they are presumed to reduce herbaceous production or because their presence increases the difficulty of livestock manipulation. Yet, in many regions or landscapes within a region, woody plants are well adapted to prevailing biotic and abiotic conditions, and can provide several ecological benefits. They play a key role in primary production and nutrient cycling while stabilizing soils; creating patches of fertility in bare, soil and vegetation degraded areas; allowing the presence of palatable, preferred grasses to domestic livestock in the plant community; providing essential temporary habitat for maintaining an animal metapopulation or for dispersing animals (Longland and Bateman 2002; Bonvissuto and Busso 2006, 2007a).

Quantifying vegetation structure is crucial to identifying wildlife habitat (Schulte and Niemi 1998; Sutter and Brigham 1998) and to characterize the spatial vegetation aggregation on the landscape (Schenk et al. 2003; Erickson et al. 2005). Many measures of vegetation structure have also been developed on rangelands as an index of plant species diversity (Connell 1978; Bates et al. 2000). Research to determine the floristic composition, quantitative plant measures and spatial arrangement of the vegetation patches in the Monte Austral Neuquino is then essential.

Vegetation patches are likely to enhance local biological diversity of plants and animals, because they harbor species that are lacking in disturbed areas, and because abrupt structural changes from disturbed to undisturbed vegetation provide a habitat mosaic that facilitates high levels of species turnover. Vegetation patches also provide more evenly dispersed seed sources for re-establishment of decimated vegetation within disturbed areas, and they may harbor animal species that provide seed dispersal services (Longland and Bateman 2002). Selective inclusion of woody plants in restoration plans offers several potential advantages including enhanced herbaceous production, reduced grazing pressure on grasses by providing a refuge for heavily utilized herbaceous species, enhanced soil nutrient status, mineralization and water infiltration (Pyke and Archer 1991).

Longland and Bateman (2002) reported that there are several species that are obligate associates of the shrub species that dominate undisturbed rangelands. These results are similar to those found by Morello (1956), Yeaton (1978) and West (1989), and include understory plant species that either utilize shrubs as nurse plants or are parasitic on them. Aarssen and Turkington (1985) demonstrated that niche differentiation and differential competitive abilities combine to establish distinct positive and negative associations between species as revegetated rangelands develop through time. For example, Schenk et al. (2003) found that negative effects of *Larrea tridentata* (Ses. et Moc ex DC.) Felger & Lowe on roots of *Ambrosia dumosa* (A. Gray ex Torr.) Payne kept plants of the latter

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80 species segregated to a 3 m distance from those of *L. tridentata*. Research on associations  
81 between plant species are then important in the vegetation patches at the Monte Austral  
82 Neuquino.

83 Studies have demonstrated that succession toward woody species at the final stage, and  
84 community disturbance, can reduce plant species diversity. In central and eastern Oregon,  
85 northeastern California, and southwestern Idaho, succession to *Juniperus occidentalis*  
86 spp. *occidentalis* Hook. dominated communities has been accompanied by reductions  
87 in understory species diversity (Burkhardt and Tisdale 1969). Bates et al. (2000) also  
88 demonstrated that dominance by juniper in southeastern Oregon reduced understory  
89 diversity. They attributed this response to the high belowground interference for soil water  
90 and nitrogen conducted by juniper trees. Anyhow, these authors agree that it may take  
91 many years of woodland dominance before understory species are effectively removed  
92 from a site. Connell (1978) pointed out that plant species diversity begins to decline at  
93 some point following disturbance because either the most competitive plants eliminate the  
94 rest or the plants most resistant to damage by physical extremes or natural enemies  
95 eventually occupy most of the space.

96 Vegetation patches present a high both horizontal and vertical heterogeneity in the  
97 shrubby steppe of the Monte Austral of Chubut, Argentina. This is because of the large  
98 architectural diversity that there exists among its plant species (Bertiller et al. 2004). Biotic  
99 and abiotic characteristics have been described by Soriano et al. (1994) for vegetation  
100 patches in the Patagonian steppe. Similarly to that described for the Patagonian steppe,  
101 vegetation also has a patchy distribution in the shrubby steppe of the Monte Austral  
102 Neuquino, within the Province of Neuquén, Argentina. However, the structural charac-  
103 teristics of the dominant species in this ecological region have ever been studied, and are  
104 different from those reported for the Patagonian steppe.

105 Rangelands in the shrubby steppe of the Monte Austral Neuquino, surrounding the town  
106 of Picún Leufú (39°53'S, 69°25'W), have been exposed to continuous, uncontrolled  
107 grazing by goats, sheep and cattle since the early 1900s (Bonvissuto 2006). Forage pro-  
108 duction of these rangelands is often limited partially due to the scarce precipitation in these  
109 areas [long-term mean annual precipitation: 137.2 mm (1928–1950) (Bonvissuto 2006)].  
110 Thus, these rangelands have been exposed to similar biotic and abiotic conditions for many  
111 decades (Bonvissuto 2006). It is then expected a similar structure and spatial arrangement  
112 of the vegetation in the study region, leaving plant-uncovered interspaces among vegeta-  
113 tion patches which need immediate restoration efforts.

114 The shrubby steppe in the Monte Austral expands 3,816,025 ha. It is within the Phyto-  
115 geographical Province of the Monte (Cabrera 1971). The main economical activity in this  
116 area is grazing by cattle, sheep and goats on natural vegetation. More than 90% of farmers  
117 live in their ranches, and for most of them, rangeland utilization represents their unique  
118 income. Eighty-six percent of the ranches have an economy just for subsistence. Seventy-  
119 eight percent of the farmers occupy federal lands, and just a few have a wire fence all around  
120 their ranch. The level of desertification in this highly disturbed system is from partial severe  
121 to severe (INTA-GTZ 1996). This urgent need for land reclamation and range improvement  
122 in the vegetation-uncovered areas has also been a concern in other rangelands of the world  
123 (Thorsteinsson et al. 1971). This paper will shed light on the structural characteristics and  
124 spatial arrangement, and relationships among species, of the vegetation patches in the Monte  
125 Austral Neuquino. It will also deal with some management and conservation issues to help  
126 preventing further vegetation and soil degradation of this ecological system.

127 Three hypotheses were tested in this research: (1) structural characteristics of the  
128 vegetation patches dominated by *Larrea divaricata* Cav. and *Atriplex lampa* (Moq.)

129 D. Dietr. are similar within the whole study site ( $15 \times 15$  km), leaving extensive bare,  
130 eroded areas among vegetation patches, (2) within each patch, some species are associated  
131 with one another, but not with others. Even more, species associations are in some cases  
132 positive and in others negative, and (3) as size of the dominant shrubs (expressed as aerial  
133 standing crop) increases, plant species diversity decreases. To test these hypotheses, we  
134 determined several qualitative and quantitative analytical characteristics of one sub-group  
135 of the vegetation patches in the shrubby steppe of the Monte Austral Neuquino, and  
136 investigated relationships between them.

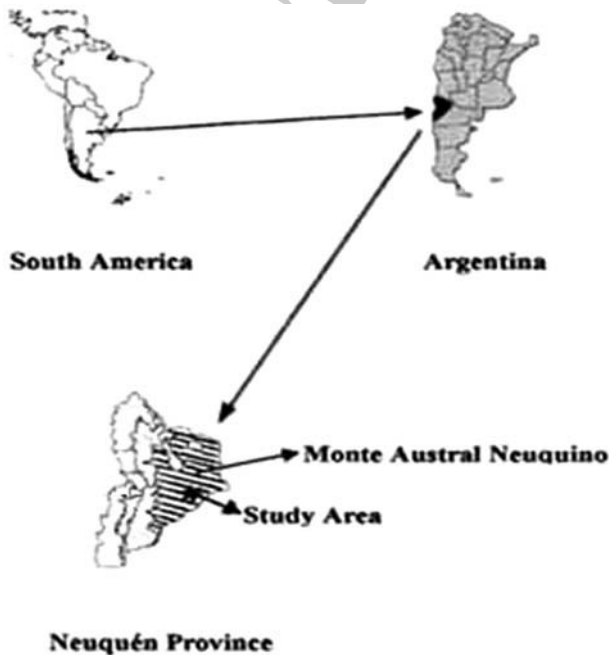
## 137 Methodology

### 138 Study site

139 This research was conducted in the shrubby steppe of *Larrea divaricata* and *Atriplex*  
140 *lampa*, nearby the town of Picún Leufú, within the Monte Austral Neuquino (Fig. 1).  
141 Initially vegetation patches were sampled within a  $15 \times 15$  km area ( $39^{\circ}20'32''S$ ;  $69^{\circ}19'$   
142  $30''W$ ). Further, more detailed studies were conducted at two sites, distant 1.5 km straight  
143 line from one another.

### 144 Climate

145 In Picún Leufú, long-term (1928–1950) average annual precipitation is 137.2 mm (Ital-  
146 consult Argentina 1966), and average annual precipitation during 1999–2005 was 200 mm.



**Fig. 1** Location of the study area in the Monte Austral Neuquino region and its relation to South America and Argentina



147 Extreme values of precipitation during 1928–1950 have been 62.7 and 245.3 mm (Morello  
148 1958). No precipitation data are available at this site between 1950 and 1999. Maximum  
149 and minimum precipitations occur during winter and spring, and summer, respectively.  
150 Monthly average values for diurnal and nocturnal temperatures are 28 and 15°C in January,  
151 respectively, and 7 and 2°C in July, respectively. Mean annual wind speed is 13 km h<sup>-1</sup>  
152 (Servicio Meteorológico Nacional 1958). November, December and January (mid-spring  
153 to early summer) have the greatest wind speeds, with a mean of 17 km h<sup>-1</sup> at 2 m height  
154 from the soil level.

## 155 Vegetation

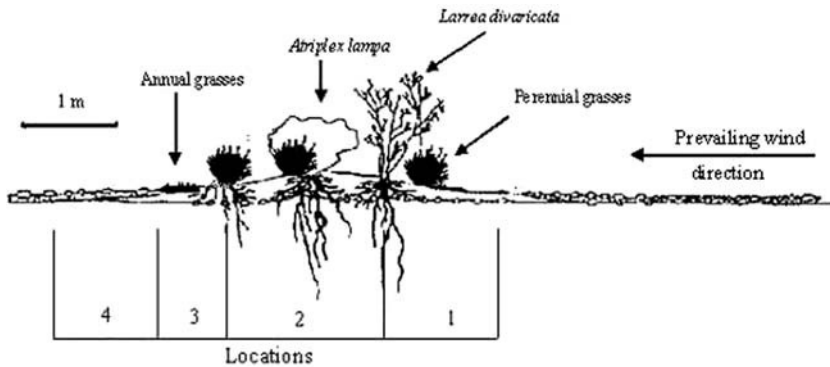
156 The shrubby steppe of the dominant *Larrea divaricata* and the co-dominant *Atriplex lampa*  
157 occupies ~1,080,000 ha in the Monte austral neuquino. The average height of this steppe is  
158 1.20 m. It is usually present either in plain areas or in those with very little slope (<5%)  
159 (Movia et al. 1982). Three strata can be found in this steppe (Movia et al. 1982): (1) *Larrea*  
160 *divaricata*, *Bougainvillea spinosa* (Cav.) Heimerl, *Monttea aphylla* (Miers) Bentham et  
161 Hooker and *Larrea cuneifolia* Cav. are present with a mean height of 1.50 m, but which can  
162 be reduced to 0.80 m on stony or fine-textured soils, (2) the second stratum varies between  
163 0.70 and 1.00 m and is characterized by the presence of *Atriplex lampa* (0.5–0.8 m height).  
164 This species is present either on sandy mounds together with *Prosopis alpataco* Philippi,  
165 *Schinus polygamus* (Cav.) Cabr., *Lycium chilense* Miers (ex Bertero), *Chuquiraga erinacea*  
166 D. Don and *Fabiana peckii* Niederlein or alone in the interspaces, (3) small shrubs form the  
167 third stratum, which is 0.05–0.60 m height [*Acantholippia seriphioides* (A. Gray) Moldenke,  
168 *Gutierrezia solbrigii* Cabr., *Verbena seriphioides* Gilles & Hook, *Senecio aff. filaginoides*  
169 DC., *Cassia aphylla* Cav. and *Grindelia chilensis* (Corn.) Cabr.] and perennial grasses  
170 [*Stipa naeii* (Nees ex Steudel), *Poa lanuginosa* (Poiret ap. Lamarck), *Poa ligularis* (Nees ap.  
171 Steudel), *Stipa speciosa* (Trinius et Ruprecht), and *Elymus erianthus* Philippi]. There are  
172 ephemeral species (*Schismus barbatus* Thellung and *Plantago patagonica* Jacquin) 0.05 m  
173 height which do not have a plant cover greater than 15%.

## 174 Soil

175 Aridisols dominate the area. There are mostly old structural plains. Landscape is controlled  
176 for the horizontal disposition of the subjacent mantle. It includes Typic Paleortids,  
177 Petrocalcic Calcicortids, Petrocalcic Paleargids and Typic Torriorthents, with shallow and  
178 saline phases (Ferrer and Irisarri 1989). According to the soil classification (Soil Survey  
179 Staff 1975) no water is available during long periods. A light tendency to the Mediter-  
180 ranean type can be observed, with greater humidity during the winter (Morello 1958).  
181 When temperature is sufficient for plant growth, soil water potentials are ≤−1.5 MPa most  
182 of the time. During the warm season, a continuous period of three of more months with  
183 available moisture does not exist (Soil Survey Staff 1975). In addition, the scarce rain has a  
184 low infiltration, especially in the corridors between vegetation patches, and most of it is  
185 loss by runoff (Bonvissuto, personal observation, EEA INTA Bariloche, Argentina).

## 186 Soil profile measurements

187 In each of the two study sites, a vegetation patch was selected to (a) analyze the soil profile  
188 and (b) to determine soil physico-chemical characteristics below plants of *Larrea divari-*  
189 *cata*. There were four different locations within each patch: (1) windward, (2) below



**Fig. 2** Vegetation patch description. The position of annual and perennial grasses, *Larrea divaricata* and *Atriplex lampa* is indicated in the patch. The prevailing wind direction comes from the side nearby location 1

190 *Larrea divaricata*, (3) under the lee, and (4) in the bare corridors among vegetation patches  
191 (Fig. 2). These four study locations have a wind-related ontogeny.

192 The soil profile and physico-chemical characteristics were described determining the  
193 following parameters: (1) texture [pipette method (INTA EEA Pergamino 1998) and the  
194 Soil Survey Staff (1975) classification was applied]; structure and hydric constants (Black  
195 et al. 1965); (2) bulk density (INTA EEA Pergamino 1998); (3) organic matter (Walkley  
196 and Black 1934); (4) infiltration (Lyford and Qashu 1969); (5) C/N ratio; (6) total nitrogen  
197 (Kjeldahl method: Carter 1993); (7) extractable K using a spectrophotometer of atomic  
198 absorption by flame emission (Carter 1993); (8) soluble P in sodium bicarbonate (Olsen  
199 and Sommers 1982) and (9) pH in water (in suspension with a relationship 1:2.5: SSSA  
200 1996). In the same suspension (1:2.5) the following were evaluated; (10) electric con-  
201 ductivity using a conductimeter Schott Gerate; (11) percentage of interchangeable sodium  
202 (USDA 1954); (12) carbonates (gasovolumetric method); and (13) initial soil moisture  
203 content (Lascano and Landivar 1997). Infiltration versus initial moisture content mea-  
204 surements were conducted on 6 October and 7 November 2000, and 7 February 2001.

205 Soil profile and physico-chemical characteristics at sites 1 and 2 are summarized in  
206 Table 1. At site 1, shallow horizons were generally clear and had a soft consistency  
207 when they were dry. A high stoniness was observed in the shallower horizons in the soil  
208 profile. The regime of soil moisture was aridic and that of temperature was mesic. The  
209 whole profile reacted to HCl indicating carbonate presence. A layer of broken sand with  
210 abundant fissures was observed in the R horizon. It was a water-insoluble material,  
211 covered in part with gypsum salts that, when submerged in water, presented a greater  
212 solubility.

213 In the first 5 cm of the soil profile, soil moisture retained at  $-1.5$  MPa was  
214  $5.46 \pm 0.18\%$  (mean  $\pm 1$  SE) on average (4 vegetation patches  $\times$  4 locations within each  
215 vegetation patch,  $n = 16$ ). Soil moisture ranged from  $0.8 \pm 0.1$  (March 1999; locations 1,  
216 3 and 4) to  $14.6 \pm 0.3\%$  (June 2000; location 2).

## 217 Vegetation patches

218 Eight transects of variable length (Fig. 3; Canfield 1941) were randomly located in  
219 the  $15 \times 15$  km research site, within which the two study sites were later selected.

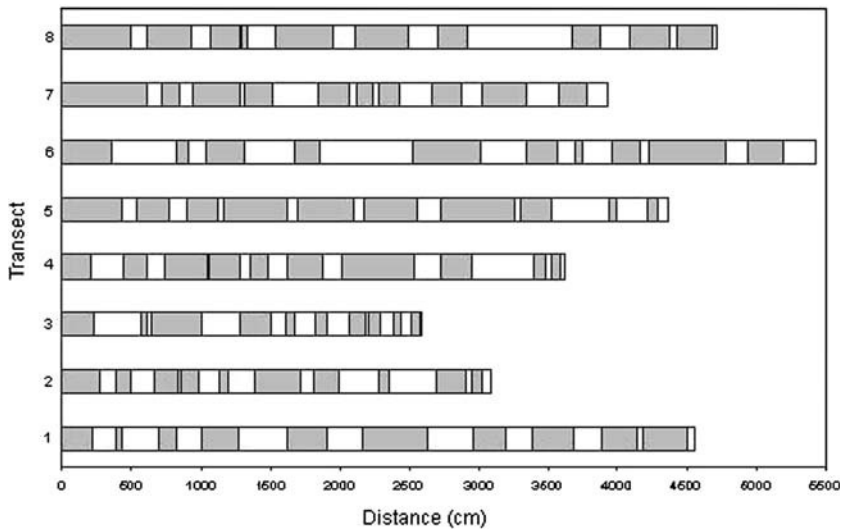


**Table 1** Soil physico-chemical properties at sites 1 and 2 in the study area

Soil physicochemical properties	Site 1	Site 2			
Horizon characteristics with increasing soil depth	4-10 cm = eolic accumulation 25-30 cm = A <sub>1</sub> /AC horizon 30-35 cm = Cca (calcic horizon) 35-70 cm = R horizon (very dense, consolidated material)				
Texture (0-5 cm soil depth)	84.5% coarse material 15.5% silty material				
Bulk density (g/cm <sup>3</sup> )	1.16±0.04*				
Organic matter (%)	Surface soil = 1.00 30 cm soil depth = 0.75		Surface soil = 1.40 30 cm soil depth = 1.20		
Infiltration** (0-5 cm soil depth)	Date	Location			
		1	2	3	4
	6 Oct 2000				
	Infiltration rate (mm/h)	158	214	41	13
	Initial soil moisture content (%)	8.5	9.8	12.4	15.4
	7 Nov 2000				
	Infiltration rate (mm/h)	631	641	288	28
	Initial soil moisture content (%)	1.8	2.3	3.4	5.5
7 Feb 2001					
Infiltration rate (mm/h)	843	797	164	23	
Initial soil moisture content (%)	1.3	1.2	1.2	2.6	
C/N ratio (surface soil)	14		11/12		
Total N (%) (surface soil)	0.04		0.07		
Extractable K (ppm) (0-5 cm soil depth)	389.7 ± 17.5***				
Soluble P (ppm) (0-5 cm soil depth)	10.8 ± 1.3***				
pH	Surface soil = 7.8 A <sub>1</sub> /AC horizon = 8.3		Surface soil = 7.7 30 cm soil depth = 8.9		
Electric conductivity (mmho/cm)	Mostly 0.2-0.4 Calcic horizon = 4.1		0.2-0.3 in the whole profile		
Percentage interchangeable Na (me/100 g soil)	Above the R horizon = 3 Below the R horizon = 44		Above the R horizon = 3 Below the R horizon = 39		
Carbonate equivalents (%)	Surface soil = 1.9 30 cm soil depth = 3.3 Below the R horizon = 13.6		Surface soil = 5.0 30 cm soil depth = 2.5 Below the R horizon = 6.9		
Cation exchange capacity (me/100 g soil)	11-13		12		

\* Mean ± 1 SE, n = 10; \*\* infiltration and soil moisture content were only evaluated at site 1; \*\*\* mean ± 1 SE, n = 6

220 Each transect intercepted ten vegetation patches (8 transects × 10 vegetation patches/  
 221 transect = 80 vegetation patches) to characterize these patches throughout their species at  
 222 the end of winter 1998. Transects were of different length because the distance between  
 223 any two vegetation patches was unequal (Fig. 3). As many quantitative and qualitative  
 224 variables as possible were measured to determine patch structure. Observations included:



**Fig. 3** Vegetation patch (*shaded areas*) distribution along each of eight transects (*horizontal bars, shaded + white areas*). Transects were of variable length (centimeters, *X axis*) as to include ten vegetation patches each. *White areas* represent bare, uncovered zones among vegetation patches

225 (a) patch diagram where the interception within the transect was detailed, and orientation  
226 of the greatest patch diameter; (b) greatest and lowest mound diameter (mound refers to the  
227 rounded area of topographically higher elevation on any vegetation patch); (c) inter-  
228 ception length of the vegetation patch with the transect; (d) mound height (height  
229 difference between the tallest part of the mound and the plant-uncovered corridors  
230 among mounds); (e) maximum vegetation height from the soil surface and name of the  
231 tallest species; (f) floristic composition of the species intercepted by the transect; (g)  
232 determination of lineal cover per species following Frangi (1978); and (h) distance to the  
233 next vegetation patch.

234 The relationship between plant species was studied to determine either positive or  
235 negative associations between them (Silvertown and Wilson 1994). Similarity between  
236 vegetation patches was also evaluated (Russell and Rao 1940).

237 Because structural variables measured in the vegetation patches were similar ( $P > 0.05$ )  
238 among the eight transects, it was decided to work with a smaller number of sites ( $n = 2$ )  
239 and various vegetation patches within each site ( $n = 8$ ). Vegetation patches used for this  
240 research were excluded from domestic herbivory during the duration of this investigation,  
241 since the experimental study area was under grazing at that time. Herbivory exclusion was  
242 performed using 1.5 m height iron fences made of  $15 \times 15$  cm quadrats. At the end of the  
243 study, the eight vegetation patches were harvested within each site (total  $n = 16$  vegetation  
244 patches) to determine patch aerial standing crop. With this purpose, entire plants of each  
245 species were harvested at the soil surface level, dried in a forced oven at  $60^\circ\text{C}$  until  
246 constant weight, and weighed. Since the greatest and smallest diameters were measured  
247 within each of the sixteen vegetation patches, standing crop could be expressed per unit  
248 surface area.

249 Species diversity was calculated from the patch floristic composition data using the  
250 Shannon (1948) index:  $H' = -\sum p_i \ln p_i$ , where  $H'$  is the diversity index,  $p$  is the



251 proportional abundance of  $i$  species which is the number of individuals of  $i$  species divided  
252 by the total number of individuals in the community.

## 253 Statistical analysis

254 When eight transects involving ten vegetation patches each were studied, frequency his-  
255 tograms were made for longest and shortest diameters, relationship between them, mound  
256 height, maximum plant height and distance to the next vegetation patch. Correlations  
257 between these variables were calculated. An analysis of species grouping (Sorensen) was  
258 realized, and results were represented using a dendrogram. A one-way ANOVA was  
259 conducted in blocks [13 treatments (species)  $\times$  8 blocks (transects)] to analyse the relative  
260 frequency of species occurrence in the vegetation patches. Simultaneous frequency was  
261 analysed following Pielou (1977).

262 The Phi-Pearson index, utilized to determine either positive or negative associations  
263 between plant species, measures departure from independence (is the correlation coeffi-  
264 cient for binary data). The greater the index value, the greater the association between  
265 species. This allowed to interpret if the existence of any given species (i.e., perennial  
266 grasses) was associated, at least in part, to the conditions which can provide other species  
267 (i.e., shrubs). Absence between any two species pairs was considered in the analysis;  
268 otherwise all correlations would be negative. It is true that an exaggerated double absence  
269 between any species pairs could determine high, spurious correlations. Because of this, all  
270 species with low frequency (<12.5%) were discarded to calculate the Phi-Pearson corre-  
271 lation index. The level of similarity at which the stems were cut in the dendrogram was  
272 0.45 (close to half of the maximum possible association).

273 When 16 vegetation patches (8 patches  $\times$  2 sites) were harvested at the end of the  
274 study, a one-way ANOVA was conducted for the variables obtained at the two sites: total  
275 standing crop per patch, greatest diameter, lowest diameter, patch surface, standing crop  
276 per unit surface area and species diversity. Regression analysis was developed between  
277 species diversity and size of the dominant shrub/s (expressed as aerial standing crop)  
278 within each vegetation patch.

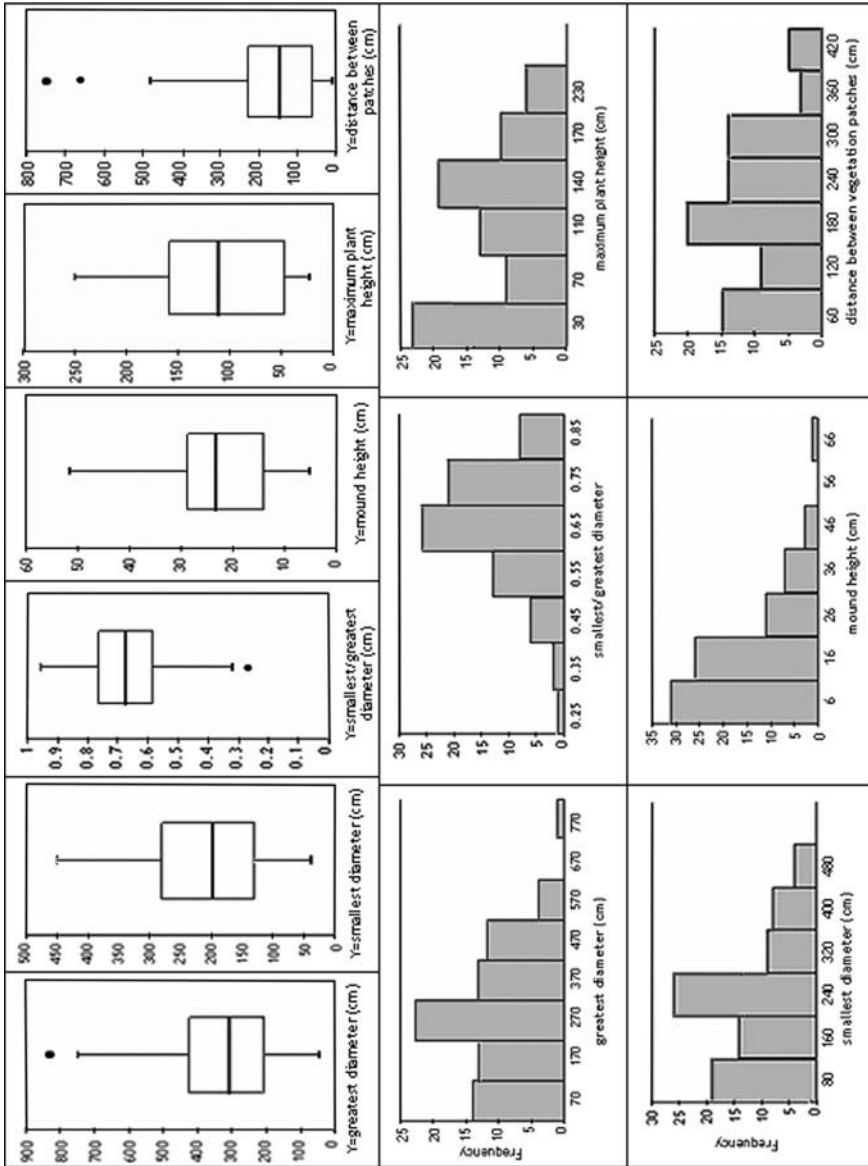
## 279 Results

### 280 Patch structure

281 This plant community was quite homogeneous. Structural characteristics of the vegetation  
282 patches were similar ( $P > 0.05$ ) among transects in the whole study area (15  $\times$  15 km).  
283 There was lower heterogeneity between than within transects. About 90% variability  
284 occurred within transects. When variation components were detected between sites, these  
285 were much lower than variation components between vegetation patches within each site.  
286 This justified a greater labour effort within each site.

287 The greatest and smallest diameter of the vegetation patches were  $315 \pm 25$  and  
288  $207 \pm 16$  cm (Fig. 4; mean  $\pm$  1 SE,  $n = 8$  transects of ten vegetation patches each:  
289 Fig. 3). Sixty-one out of the 80 vegetation patches had a greatest diameter between 140 and  
290 540 cm, and 57 of these had a smallest diameter between 90 and 330 cm.

291 Shape of the vegetation patches, defined as the relationship between the smallest and the  
292 greatest diameters, was  $66.8 \pm 13.5$  (Fig. 4). This relationship was between 0.5 and 0.9 in  
293 68 of the vegetation patches (Fig. 4).



**Fig. 4** Upper panel set: Diagram of boxes and arms for the greatest diameter, smallest diameter, the relationship smallest/greatest diameter, mound height, maximum plant height and distance to the next vegetation patch. The X axis was not drawn because there are no divisions on it. Within each panel, the Y variable is depicted at the panel's bottom. The solid line within each box represents the median. Horizontal hyphens at the top and bottom of vertical lines represent the maximum and minimum values, respectively. The lower Q1 and the upper Q3 quartiles are represented at the bottom and top horizontal lines within each box. This is where 50% of observations are found (25% between Q1 and the median and 25% between the median and Q3). Vertical bars indicate the distance between the minimum and maximum values. A point located outside this range represents an outlier. Lower panel set: Absolute frequency distribution of the greatest diameter, smallest diameter, the relationship smallest/greatest diameter, mound height, maximum plant height and distance to the next vegetation patch of vegetation patches ( $n = 8$ ) in the Monte Austral Neuquino



294 Mound height was  $23 \pm 2$  cm (Fig. 4). Height was between 0 and 36 cm in 68 out of  
295 the 80 mounds (Fig. 4). Maximum vegetation height was  $113 \pm 12$  cm (Fig. 4), being the  
296 shrub *Larrea divaricata* the tallest species. Sixty-four of the vegetation patches had plants  
297 with a maximum height of up to 170 cm (Fig. 4). Distance to the next vegetation patch  
298 within a transect was  $170 \pm 18$  cm (Fig. 4). Distance between vegetation patches was less  
299 than 310 cm in 68 of the patches (Fig. 4).

300 Vegetation patches covered  $57.73 \pm 2.34\%$  of the transects ( $n = 8$ ). *Larrea divaricata*  
301 showed the greatest percentage cover ( $19.06 \pm 1.76\%$ ) in these transects. At the same  
302 time, percentage cover of the remaining species was less than 5%.

303 Correlations between variables (greatest and smallest diameters, mound height, maxi-  
304 mum plant height, and distance to the next, closest vegetation patch) measured in the  
305 vegetation patches were all significant at  $P < 0.01$ . Greatest correlations were observed  
306 between (1) the smallest patch diameter and maximum plant height ( $r = 0.9515$ ), (2)  
307 greatest and smallest patch diameters ( $r = 0.8584$ ), (3) mound height and greatest vege-  
308 tation patch diameter ( $r = 0.8278$ ), and (4) mound height and distance to the next, closest  
309 vegetation patch ( $r = 0.8242$ ).

310 In all vegetation patches, the greatest and lowest frequencies were found for *Stipa* spp.  
311 (71.2%) and *Grindelia chiloensis* (12.5%). *Stipa* spp. and *Atriplex lampa* showed the  
312 highest simultaneous frequency (50%). Simultaneous frequencies for *Atriplex lampa* and  
313 *Larrea divaricata*; *Stipa* spp. and *Larrea divaricata*; *Poa* spp. and *Atriplex lampa*; *Lycium*  
314 *chilense* and *Atriplex lampa*; and *Poa* spp. and *Stipa* spp. were between 32 and 37%. All  
315 other copresence of each species pair was  $\leq 30\%$  and, in 42 out of 78 comparisons, it was  
316  $\leq 10\%$ .

317 Some species showed association among themselves, but not with others. Two major  
318 species groups can be observed in the dendrogram (Fig. 5). One group has a reasonable  
319 association among species ( $>45\%$ ; *Stipa* spp., *Atriplex lampa*, *Larrea divaricata*, *Lycium*  
320 *chilense*, and *Junellia ligustrina* (Lag.) Moldenke). The other group is rather diffuse and  
321 constituted by associations of two species (*Poa* spp. and *Acantholippia seriphioides*;  
322 *Grindelia chiloensis* and *Senecio aff. filaginoides*; and *Chuquiraga erinacea* and *Gut-*  
323 *ierrezia* spp.) or isolated species (*Cassia aphylla* and *Panicum urvilleanum* Kunth). In  
324 addition, there were positive and negative associations among species. The greatest  
325 ( $P = 0.0001$ ) positive association was between *Senecio* spp. and *Grindelia chiloensis*  
326 (44.8%) using the Phi-Pearson's index (Table 2).

### 327 Relationship between parameters evaluated in the vegetation patches ( $n = 16$ )

328 There were no statistical differences ( $P > 0.05$ ) between sites 1 and 2 regarding the  
329 variables standing crop ( $\text{g patch}^{-1}$  or  $\text{g m}^{-2}$ ), greatest and smallest vegetation patch  
330 diameters (m), patch surface area ( $\text{m}^2$ ), and plant species diversity. Because of this, values  
331 were grouped for both sites.

332 *Larrea divaricata* and *Atriplex lampa* contributed more than 84% of the total patch  
333 standing crop ( $5,776.8 \pm 435.0$ , Table 3). On a unit surface area measurement, patch  
334 standing crop was  $961.8 \pm 72.9 \text{ g m}^{-2}$  (Table 3). *Acantholippia seriphioides* and *Stipa*  
335 *neaei* determined an important standing crop contribution (3.67 and 2.79%, respectively),  
336 comparatively to the remaining species in the patch (Table 3).

337 Average patch size and specific diversity were  $5.93 \pm 0.33 \text{ m}^2$  and  $1.31 \pm 0.11$ ,  
338 respectively. Aboveground standing crop of the two dominant shrubs (*Larrea divaricata*  
339 and *Atriplex lampa*) decreased as plant species diversity increased ( $P < 0.05$ , Fig. 6).

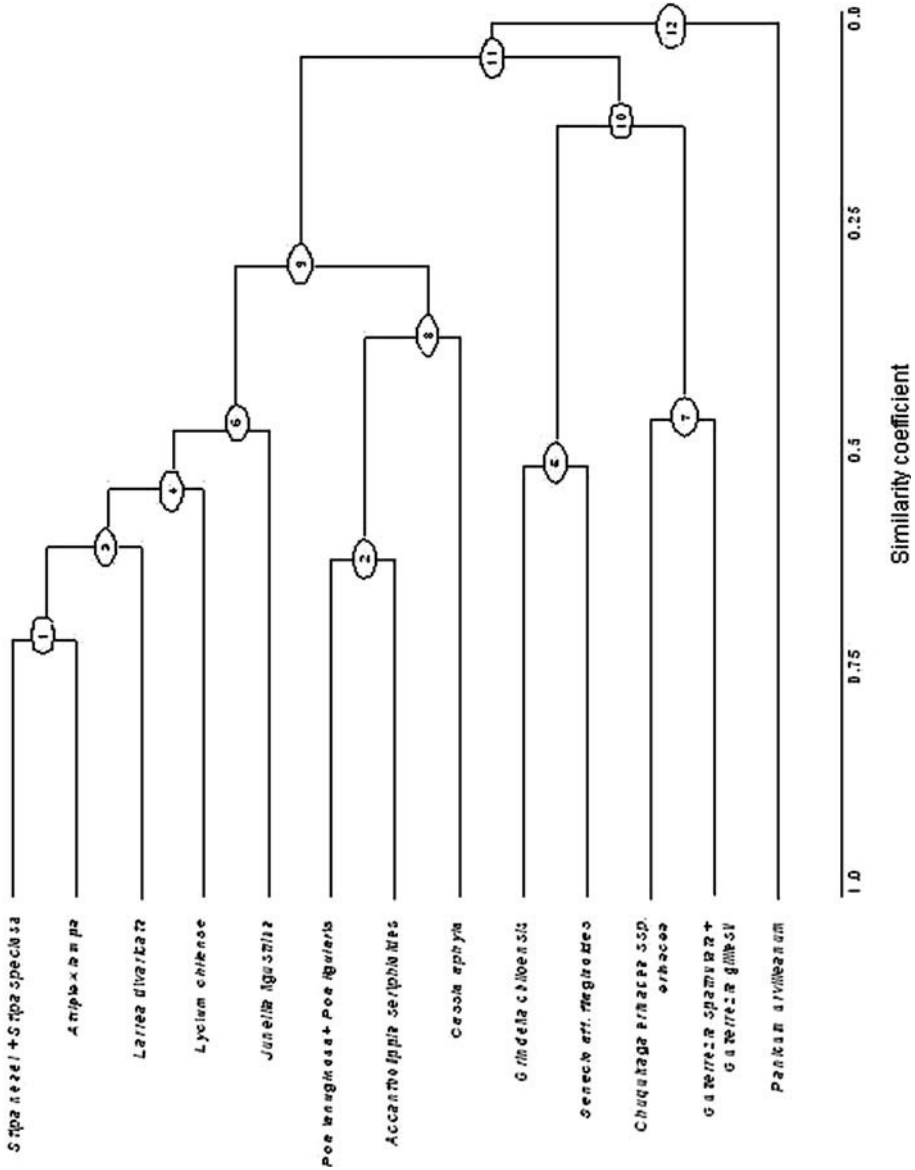


Fig. 5 Dendrogram derived from a grouping analysis (Sorensen) applied to vegetation data

340 **Discussion**

341 Patch structure

342 Differences in rangeland age and use history, among other factors, may influence com-  
 343 parison of our results with those obtained in other ecological systems. As stated in  
 344 hypthesis 1, vegetation patch structural characteristics were similar within the whole

**Table 2** Phi-Pearson's indexes to show association between species

	<i>Larrea divaricata</i>	<i>Atriplex lampa</i>	<i>Lycium chilense</i>	<i>Senecio aff. flaginoides</i>	<i>Acantholippia seriphoides</i>	<i>Junellia ligustrina</i>	<i>Gutierrezia spathulata + Gutierrezia gilliesii</i>
<i>Larrea divaricata</i>	1.000						
<i>Atriplex lampa</i>	0.184	1.000					
<i>Lycium chilense</i>	<b>0.239</b>	<b>0.296</b>	1.000				
<i>Senecio aff. flaginoides</i>	-0.068	0.027	0.066	1.000			
<i>Acantholippia seriphoides</i>	-0.054	-0.069	0.105	0.128	1.000		
<i>Junellia ligustrina</i>	0.185	<b>0.253</b>	<b>0.238</b>	0.214	<b>0.223</b>	1.000	
<i>Gutierrezia spathulata + Gutierrezia gilliesii</i>	-0.169	<b>-0.225</b>	-0.184	-0.066	-0.163	-0.029	1.000
<i>Chauquiraga erinacea</i> ssp. <i>Erinacea</i>	<b>-0.274</b>	-0.209	-0.145	0.038	-0.181	-0.173	<b>0.412</b>
<i>Cassia aphylla</i>	0.008	0.112	<b>0.276</b>	0.102	0.161	<b>0.309</b>	0.126
<i>Grindelia chiloensis</i>	-0.199	-0.050	0.009	<b>0.448</b>	<b>0.221</b>	0.152	-0.082
<i>Stipa neaei + Stipa speciosa</i>	0.201	0.130	0.108	-0.019	-0.207	0.130	-0.126
<i>Panicum urvilleanum</i>	<b>0.298</b>	0.050	-0.028	-0.202	<b>-0.249</b>	-0.168	-0.086
<i>Poa lanuginosa + Poa ligularis</i>	-0.098	0.044	0.057	<b>0.294</b>	<b>0.409</b>	<b>0.387</b>	0.092
<i>Chauquiraga erinacea</i> ssp. <i>Erinacea</i>			<i>Cassia aphylla</i>	<i>Grindelia chiloensis</i>	<i>Stipa neaei + Stipa speciosa</i>	<i>Panicum urvilleanum</i>	<i>Poa lanuginosa + Poa ligularis</i>
<i>Larrea divaricata</i>							
<i>Atriplex lampa</i>							
<i>Lycium chilense</i>							
<i>Senecio aff. flaginoides</i>							
<i>Acantholippia seriphoides</i>							
<i>Junellia ligustrina</i>							



Table 2 continued

	Chuiriraga erinacea ssp. Erinacea	Cassia aphylla	Grindelia chiloensis	Stipa neaei + Stipa speciosa	Panicum urvilleanum	Poa lanuginosa + Poa ligularis
<i>Gutierrezia spathulata</i> + <i>Gutierrezia gilliesii</i>	1.000					
<i>Chuiriraga erinacea</i> ssp. <i>Erinacea</i>	-0.011	1.000				
<i>Cassia aphylla</i>	0.200	0.080	1.000			
<i>Grindelia chiloensis</i>	0.073	0.059	0.073	1.000		
<i>Stipa neaei</i> + <i>Stipa speciosa</i>	-0.174	<b>-0.239</b>	-0.174	<b>0.219</b>	1.000	
<i>Panicum urvilleanum</i>	-0.009	<b>0.262</b>	<b>0.368</b>	-0.177	<b>-0.406</b>	1.000
<i>Poa lanuginosa</i> + <i>Poa ligularis</i>						

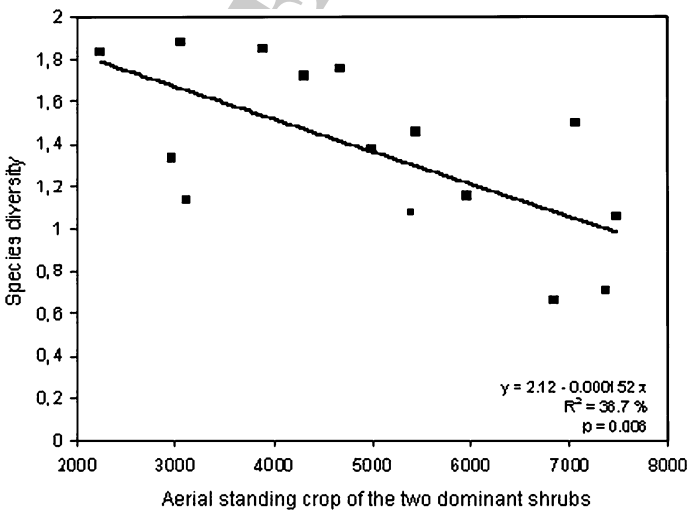
The sign of the index indicates if the association is either positive or negative  
 Values in bold are significant at  $P < 0.05$



**Table 3** Aboveground standing crop ( $\text{g patch}^{-1}$  and  $\text{g m}^{-2}$ ) and percentage contribution to total plant standing crop of each of the species present in the patch

Species	Standing crop ( $\text{g patch}^{-1}$ )	Standing crop ( $\text{g m}^{-2}$ )	Contribution (%)
<b>Dicotyledoneous shrubs</b>			
<i>Atriplex lampa</i>	900.02 $\pm$ 173.57	145.70 $\pm$ 27.37	17.34 $\pm$ 3.77
<i>Larrea divaricata</i>	4,026.38 $\pm$ 444.41	670.92 $\pm$ 76.39	67.41 $\pm$ 3.73
<i>Lycium chilense</i>	72.65 $\pm$ 34.52	11.35 $\pm$ 5.43	1.29 $\pm$ 0.60
<i>Gutierrezia spathulata</i>	107.23 $\pm$ 21.24	18.75 $\pm$ 3.75	2.15 $\pm$ 0.52
<i>Acantholippia seriphioides</i>	201.31 $\pm$ 75.70	36.55 $\pm$ 15.53	3.67 $\pm$ 1.45
<i>Cassia aphylla</i>	39.38 $\pm$ 39.38	6.17 $\pm$ 6.17	0.47 $\pm$ 0.47
<i>Junellia</i> spp.	150.06 $\pm$ 94.72	26.04 $\pm$ 17.49	2.36 $\pm$ 1.41
<i>Senecio aff. filaginoides</i>	1.37 $\pm$ 1.05	0.22 $\pm$ 0.17	0.02 $\pm$ 0.01
<i>Tetraglochin caespitosum</i>	33.95 $\pm$ 12.66	5.59 $\pm$ 2.08	0.56 $\pm$ 0.18
<b>Herbaceous dicots</b>			
<i>Boopis anthemoides</i>	1.11 $\pm$ 0.93	0.18 $\pm$ 0.16	0.02 $\pm$ 0.02
<i>Hoffmannseggia erecta</i>	23.05 $\pm$ 6.30	3.87 $\pm$ 1.16	0.49 $\pm$ 0.18
<i>Senecio goldsakaii</i>	10.69 $\pm$ 3.00	2.25 $\pm$ 0.53	0.26 $\pm$ 0.07
<i>Tarasa</i> sp.	3.96 $\pm$ 2.52	0.76 $\pm$ 0.48	0.12 $\pm$ 0.08
<b>Grasses</b>			
<i>Elymus erianthus</i>	7.38 $\pm$ 7.38	0.89 $\pm$ 0.89	0.13 $\pm$ 0.13
<i>Poa ligularis</i>	32.46 $\pm$ 14.65	5.87 $\pm$ 2.55	0.43 $\pm$ 0.21
<i>Poa lanuginose</i>	0.04 $\pm$ 0.03	0.01 $\pm$ 0.01	0.0 $\pm$ 0.0
<i>Stipa neaei</i>	149.63 $\pm$ 29.95	23.98 $\pm$ 4.66	2.79 $\pm$ 0.61
<i>Stipa speciosa</i>	15.28 $\pm$ 7.24	2.68 $\pm$ 1.25	0.33 $\pm$ 0.16

Each value is the mean  $\pm$  1 SE of  $n = 16$



**Fig. 6** Relationship between aerial standing crop of the two dominant shrubs (*Larrea divaricata* and *Atriplex lampa*) in any vegetation patch and species diversity. Each symbol comes from  $n = 1$



Author Proof

345 study area (15 × 15 km) leaving eroded, bare areas among vegetation patches. This is an  
346 indication of a broadly disturbed ecological system. Our values for average patch size  
347 (mean = 5.93 m<sup>2</sup>) were intermediate than those reported by other authors. For example,  
348 Erickson et al. (2005) found minimum-size patches of 3 m<sup>2</sup> in low-stature shrub  
349 communities dominated by *Ceanothus cordulatus* Kellogg in the central California Sierras. In  
350 the 'Monte' of Río Negro, Cecchi (2000) found that the vegetation patch size (26 m<sup>2</sup>) was  
351 greater than ours. These patches were composed by *Prosopis alpataco*, *Atriplex lampa* and  
352 *Larrea divaricata*, with an herbaceous layer dominated by *Schismus barbatus*.

353 Similar to our results, Rostagno and del Valle (1988) reported that the greatest and  
354 smallest patch average diameters were 355 and 266 cm, respectively, in a shrub-dominated  
355 community nearby Puerto Madryn-Chubut, Argentina. In other vegetation patches of the  
356 'Monte' in the Province of Río Negro, Argentina, the mean reported diameter has been  
357 580 cm (Cecchi 2000). Rostagno and del Valle (1988) found that the vegetation patch  
358 shape, defined as the relationship between the smallest to the greatest diameter, was 74.9%,  
359 a little higher value than the one we found (66.8%). These authors reported 41 cm as the  
360 average mound height in their system, which is superior to our value (23 cm). In an  
361 environment similar to that studied by Rostagno and del Valle (1988), Gile et al. (1998)  
362 described mounds of 4 cm height under plants of *Larrea tridentata* (Sessé & Moc. ex DC.)  
363 Coville at the south of New Mexico.

364 Rostagno and del Valle (1988) reported that height of shrubby vegetation, dominated by  
365 *Larrea divaricata*, ranged from 80 to 200 cm. In their study, Schenk et al. (2003) showed  
366 that *L. tridentata* reached heights over 200 cm, Gile et al. (1998), however, found indi-  
367 viduals of this species of 90–120 cm height. These values are within the range we found  
368 for *Larrea divaricata* in our study.

369 *Larrea tridentata* and *Ambrosia* have been shown to be spaced between 60 and 260 cm  
370 on sandy soil, and between 100 and 260 cm over alluvial material (Schenk et al. 2003).  
371 Lateral dispersion of *Larrea's* roots, which can average 300 cm, occurred in the inter-  
372 spaces (Brisson and Reynolds 1994).

373 Despite working in a similar ecological system, the vegetation studied by Rostagno and  
374 del Valle (1988) was lightly different from that found in our study. They reported *Larrea*  
375 *divaricata*, *Chuquiraga avellanadae* Lorentz, *Prosopidastrum globosum* Gill. ex Hook et  
376 Arn., *Schinus polygamus* and *Ephedra ochreatea* Miers as the most prominent shrub spe-  
377 cies, and *Stipa speciosa*, *S. tenuis* Philippi and *S. humilis* Cav. as the major perennial  
378 grasses.

379 Plant cover is an important factor to control partitioning of precipitation and sediment  
380 transport. Its dynamics has been recently incorporated into erosion models. In the Monte  
381 Austral Neuquino, vegetation patches cover 58% of the soil; the remaining soil stays  
382 uncovered between them. Natural vegetation often shows some kind of spatial aggregation  
383 which determines the occurrence of the four study locations shown in Fig. 2. Existence of  
384 these locations has a wind-related ontogeny. In other arid and semiarid ecosystems, wind  
385 has been much stronger winward than under the lee (Wilson and Briske 1978; Mack and  
386 Pyke 1984). This had a desiccation effect on the exposed superficial soil layers. Seedlings  
387 growing in windy environments can also be particularly vulnerable to abrasive damage by  
388 wind-born soil particles (Fryrear et al. 1973). Mounds, which are the result of eolic  
389 material accumulation under the shrub canopies, are then always associated to shrubs, and  
390 they are apart from each other by bare, vegetation-uncovered areas. Wind velocity is low  
391 nearby and below shrubs in the patagonian steppe (Bustos 1995). However, wind is an  
392 important factor for propagule dispersal at the study site (Bonvissuto 2006). Vegetation can  
393 trap seeds during secondary dispersal (Aguar and Sala 1997). In the patagonian steppe



394 grazing has reduced plant cover enhancing the occurrence of nude soil areas where mostly  
395 wind removes litter, plant propagules and in some cases the superficial soil layer (Soriano  
396 1956; Ares et al. 1990). Recuperation of native vegetation in these locations uses to be  
397 insignificant (Defossé et al. 1997). Seeds reaching the bare interspaces among vegetation  
398 patches can be lost due to wind effects (Chambers and McMahon 1994).

399 Vegetation patches produce areas of vegetated mounds with higher fertility levels and  
400 water retention capacity, and uncovered areas with different erosion rates in arid and  
401 semiarid regions (Sánchez and Puigdefabregas 1994). Rostagno and del Valle (1988)  
402 estimated that mounds under *Larrea divaricata* and *C. avellanadae* were 40% vegetated in  
403 soils of northeast Patagonia, Argentina.

404 *Larrea divaricata* (~20% cover) and *Atriplex lampa* (around 5% cover) appeared as the  
405 dominant shrubs in the transects. These species, together with other shrub and subshrub  
406 species, covered 30.4% of transects. Cover of perennial grass species did not exceed 2%.  
407 Bisigato and Bertiller (1997) observed that vegetation cover was 40–60% in a ‘Monte’ of  
408 eastern Chubut, with an annual average precipitation (188 mm) a little lower than ours  
409 during the study (200 mm). In their investigation, cover of *L. tridentata* and *Atriplex*  
410 *lampa*, together with that of the remaining shrub and subshrub species, almost reached 22%  
411 (to a distance of 600 m from a water source for domestic animals). At the same time, cover  
412 of individual grass species was less than 2%, except *Stipa speciosa* (3.5% at 3,000 m from  
413 that water source).

#### 414 Relationship between parameters evaluated in the vegetation patches

415 Study of correlations between the variables measured at each vegetation patch allowed to  
416 learn that (1) the higher the plant, the thinner the vegetation patch, (2) the relationship  
417 between the greatest and smallest diameters was relatively constant, and (3) the higher the  
418 mound, the greater the distance to the next, closest vegetation patch.

419 In this study, and in agreement with hypothesis 2, some species were found associated  
420 among themselves, but not with others. We obtained two groups of species. The first major  
421 group was composed by *Atriplex lampa*, *Larrea divaricata*, *Lycium chilense* and *Junellia*  
422 *ligustrina* which appear to foster growth of the perennial grasses *Stipa* spp. and *Poa* spp.  
423 This group is composed by species characteristic of the vegetation patches found in fields  
424 best appropriate for utilization with grazing animals, with greater forage production. The  
425 second species group was rather diffuse and composed by the species pairs *Grindelia*  
426 *chiloensis* and *Senecio aff. filaginoides*, *Acantholippia seriphioides* and *Poa* spp., and  
427 *Gutierrezia* spp. and *Chuquiraga erinacea*. The latest four species can be found in highly  
428 deteriorated, rangeland areas (Bonvissuto, personal observation, INTA EEA Bariloche,  
429 Argentina). *Cassia aphylla* and *Panicum urvilleanum* did not associate with other species.  
430 *Panicum urvilleanum* grows in more sandy soils, outside the vegetation patches.

431 Most of the species forming the vegetation patches showed positive associations  
432 between them. However, species which were out of the vegetation patches demonstrated  
433 negative associations with respect to those present in them. These findings also agree with  
434 hypothesis 2. For example, positive associations were proved between *Larrea divaricata*  
435 and (a) *Lycium chilense* (0.239), (b) *Atriplex lampa* (0.184), and (c) *Stipa* spp. (0.201).  
436 Morello (1956) observed that *Larrea divaricata* lives associated to *Atriplex lampa* in places  
437 where the water table is between 10 and 30 m depth. Schenk (2004) emphasizes that a few  
438 species can access the total soil water availability (shallow depths: <0.4 m; medium  
439 depths: 0.4–1.2 m; deep soil: >1.2 m, and water table). This could explain dominance of  
440 these species over large areas in desertic zones. It is possible that this may occur with



441 *Larrea divaricata*, if its root system is similar to that of *L. tridentata*. Gile et al. (1998)  
442 found that roots of *L. tridentata* reached 5 m depth with a horizontal extension of more  
443 than 4 m. *Atriplex*, which is a C<sub>4</sub> shrub with roots distributed close to the soil surface  
444 and up to 2 m depth (Lee and Lauenroth 1994), appears to utilize as much the water  
445 stored deep in the soil profile (as a result of the snow melt in spring) as the water coming  
446 from summer rains (when spring precipitations are scarce and soil water recharge is  
447 poor).

448 Negative associations involved *Gutierrezia* spp. and *Chuquiraga erinacea* with most of  
449 the species that associate between them to form the vegetation patches. In the Mojave  
450 Desert, plants of *Ambrosia dumosa* (A. Gray) Payne are spatially segregated to a 3 m  
451 distance from those of *L. tridentata*. This is because of negative root effects of *Larrea* on  
452 roots of *Ambrosia* (Schenk et al. 2003).

453 The mechanisms which foster development of these either positive or negative asso-  
454 ciations are the subject of future research. Some species, for e.g., may need the  
455 microenvironment generated by shrubs, such as *L. tridentata* and *Atriplex lampa*, for a  
456 successful germination, emergence and seedling establishment. *Larrea divaricata* and  
457 *Atriplex lampa* contributed 4,026 and 900 g dry weight, respectively, per vegetation patch.  
458 In this manner, they could be acting as nurse plants. West (1989) reported that shrubs can  
459 serve as the nucleus of the successional change and ecosystem development. He empha-  
460 sized that shrubs can serve as nurse plants because, for e.g., most of the seedlings of *Pinus*  
461 and *Juniperus* were under the canopy of *Artemisia* and other associated shrubs. Yeaton  
462 (1978) demonstrated that *L. tridentata* served as a nurse plant for *Opuntia leptocaulis* DC.  
463 in the Chihuahua desert.

464 *Larrea tridentata*, in turn, has used *Ambrosia dumosa* (shrub of the Asteraceae family)  
465 as nurse plant. Eighty-five percent of all young plants of *Larrea* were rooted under the canopy  
466 of *Ambrosia dumosa*. Most of the establishment of *Larrea* occurred close to the live indi-  
467 viduals of *Ambrosia dumosa* ([www.fs.fed.us/database/feis/plants.nical\\_and\\_ecological\\_](http://www.fs.fed.us/database/feis/plants.nical_and_ecological_characteristics.html)  
468 [characteristics.html](http://www.fs.fed.us/database/feis/plants.nical_and_ecological_characteristics.html)).

469 Shrub contribution to average total standing crop in the vegetation patch was a little  
470 more than 900 g m<sup>-2</sup>. This is about half the contribution of *L. tridentata* (2,000–  
471 2,057 g m<sup>-2</sup>) in the area of Sevilleta (Gosz and Milne 2005).

472 Northrup et al. (1995) found that as size of the vegetation patch increased, its structural  
473 development also increased. In our study, high correlations were established between the  
474 (1) smallest mound diameter and the maximum plant height, (2) smallest and largest  
475 diameter of the patch, (3) mound height and greatest patch diameter, and (4) mound height  
476 and distance to the next, closest vegetation patch.

477 Average diversity of the vegetation patch was 1.31 in our research. In ten shrubby  
478 communities of northwestern Spain, Basanta et al. (1989) found diversity values from 0.8  
479 to 2.0, with an average of 1.58. Standing crop of the two dominant shrubs (*Larrea di-*  
480 *varicata* and *Atriplex lampa*) and species diversity were negatively correlated in our study,  
481 which agrees with hypothesis 3. These results agree with those of Burkhardt and Tisdale  
482 (1969), who found that succession to juniper-dominated communities in central and eastern  
483 Oregon, northeastern California, and southwestern Idaho, was accompanied by reductions  
484 in understory species diversity. Understory species diversity was also reduced by juniper  
485 dominance in southeastern Oregon (Bates et al. 2000). This response was attributed to the  
486 high juniper belowground interference for soil water and nitrogen. Plant species diversity  
487 begins to decline at some point following disturbance because either the most competitive  
488 plants eliminate the rest or the plants most resistant to damage by physical extremes or  
489 natural enemies eventually occupy most of the space (Connell 1978).



490 Management and conservation implications

491 Forty-two percent of the soil surface were bare, uncovered areas among vegetation patches in  
492 our study, and mounds under the shrubs were only 40% vegetated in soils of northeast  
493 Patagonia (Rostagno and del Valle 1988). The Soil Conservation Service in Iceland has been  
494 very concerned with protection and reclamation of denuded range areas (Thorsteinsson et al.  
495 1971). In these areas, for e.g., they have re-seeded grasses for haymaking and grazing. They  
496 have also worked with livestock management. Different means for improving distribution of  
497 the livestock, such as increased fencing, distribution of salt on the range, herding, etc., are  
498 being used in some areas. This livestock management approach should also be taken in the  
499 Monte Austral Neuquino to avoid further degradation of the ecological system.

500 Rupture of the superficial soil layers in the interpatch spaces together with seeding of  
501 shrub species like *Larrea divaricata*, *Atriplex lampa* and *Gutierrezia* sp. could also be  
502 beneficial for vegetating the interspaces in years with above-average precipitation. It is  
503 recommended to wash the seeds of *Atriplex lampa* before seeding because of the presence  
504 of chemical inhibitors in its bracts (Bustos, unpublished data, EEA INTA Bariloche,  
505 Argentina). Germination of *L. tridentata* is also related to precipitation since a minimum of  
506 at least 25 mm appears necessary to induce its germination (Marshall 1995). Raven et al.  
507 (1986) also suggest that some seeds will not germinate after having some abrasion treat-  
508 ment such as that provided from the soil. Scarification of *Larrea divaricata* seeds is  
509 recommended before conducting germination trials with this species (Zappe, personal  
510 communication, EEA INTA Bariloche, Argentina). When seed germination of *Larrea*  
511 *divaricata* was conducted under controlled moisture and temperature, and its seeds were  
512 scarified, germination percentages of up to 25% were obtained (Bonvissuto and Busso  
513 2007b). Norton and Bermant (1977) have demonstrated that *Larrea divaricata* seeds  
514 occasionally germinate in the infertile, bare vegetation interspaces.

515 Overgrazing by cattle in certain arid and semiarid landscapes has resulted in severe soil  
516 compaction and manipulations such as heavy discing are required to promote infiltration of  
517 water and reestablish herbaceous vegetation in the interspaces among vegetation patches  
518 (Fulbright 1991). Forb species richness was greater during the first year after discing than  
519 on untreated areas in southern Texas (Bozzo et al. 1992). Because herbaceous species  
520 diversity may temporarily increase, treatments such as discing and roller chopping may  
521 result in posttreatment plant communities that are temporarily greater in species diversity  
522 than nontreated communities (Fulbright 1996).

523 Under conditions of severe stress, where establishment of an independent propagule can  
524 be a long and risky process, vegetative reproduction present advantages which derives of  
525 its capacity to sustain the offspring (Grime 1981). It is very likely that the vegetation  
526 establishment in the corridors among vegetation patches (location 4) is dependent upon  
527 colonization of rhizomatous species such as *Poa ligularis* and *Stipa neaei*. These species  
528 could be occupying the empty places until generation of an adequate environment for the  
529 successful germination and seedling establishment of good forage, non-rhizomatous spe-  
530 cies such as *L. erianthus* and *Poa ligularis*. The increase in herbaceous cover in the  
531 interspaces is important from a hydrologic standpoint. Erosion rates in semiarid systems  
532 are greatest in interspace zones (Wilcox and Breshears 1994). Also, research in New  
533 Mexico suggests that herbaceous ground cover is more effective at reducing erosion rates  
534 than is cover of woody vegetation (Wilcox and Breshears 1994). Clonal propagation is  
535 ecologically important because (1) it enables plants in harsh environments to persist until  
536 suitable conditions for viable seed production or seedling establishment are encountered,  
537 (2) it enables plants to survive shoot damage resulting from grazing, fire, freezing, or



538 drought stress, and (3) the mode of vegetative growth determines how plants exploit space  
539 and resource heterogeneity (Jackson et al. 1985).

540 Colonization of empty places might also depend of shrub species highly resistant to  
541 severe stress like *Gutierrezia* sp. It appears that its ability to colonize a site depends mainly  
542 of its reproductive potential and possible early establishment, which was reported by  
543 Osman and Pieper (1988) in New Mexico where vegetation was dominated by *Gutierrezia*  
544 *sarothrae* (Pursh.) Britt. and Rusby, and annual precipitation was 220 mm. This latter  
545 species produces a large seed amount and present a rapid seedling establishment, which  
546 makes it an increasing species in the community (Osman and Pieper 1988). Its root system  
547 is quite superficial and provides stability to the soil against wind and hydric erosion  
548 (Tirmenstein 1999). Superficial root systems can take advantage of short-term rainfall  
549 events (lower than 5 mm) which are very common at the study site (Busso 1997). Rains of  
550 this magnitude have rapidly stimulated physiological processes in perennial grasses  
551 (Sala and Lahuenroth 1982) and might be good used by the superficial root system of  
552 *Gutierrezia*. Advance of *Gutierrezia* sp., possibly through seedling establishment from a  
553 large seed pool (e.g., Ladyman 2003 for *G. sarothrae*), and of *Poa lanuginosa* and *Stipa*  
554 *neaei* (both rhizomatous perennial grasses) to bare, unvegetated sites, was reported after  
555 3 years (1999–2001) with precipitations 50% above the historical mean. This was observed  
556 by Bonvissuto (personal observation, EEA INTA Bariloche, Argentina) in enclosures to  
557 domestic livestock in the Monte Austral Neuquino.

558 During the summer 2002/2003, with precipitation values close to the historical mean in  
559 2002, it was observed that the plant cover had diminished in the corridors. This was  
560 because the aboveground portion of the rhizomatous grasses did not prosper in the less  
561 favourable year (Bonvissuto, personal observation, EEA INTA Bariloche, Argentina). It is  
562 possible that in such rigorous areas as the Monte Austral Neuquino, vegetation can not  
563 definitively cover the corridors among vegetation patches because of stressful ecological  
564 conditions. However, it appears that in favourable years perennial vegetation has a greater  
565 cover among vegetation patches. As a result, it can be thought that recuperation of these  
566 environments would be based in improving the structure and diversity of the already  
567 existent vegetation patches. This could be achieved by implementing strategic resting  
568 periods which avoid vegetation grazing such as plants can recuperate its vigour. This  
569 would be highly favoured if these periods were coincident with precipitation years above  
570 the historical mean.

571 We supposed at the beginning of this work that formation of new vegetation patches  
572 would start from germination and subsequent establishment of *Larrea divaricata* and  
573 *Atriplex lampa*. Shrubs like *L. tridentata* are plants which present clonal subdivisions  
574 which can facilitate dispersion of the plant canopy and facilitate the formation of large  
575 clonal patches (Schenk 1999). Lateral branches of *Larrea* can be covered by sand, and they  
576 can root close to the point where they show up from the mound (Barbour 1969). Thus,  
577 shrub groups do not develop from seedlings which grow in closed association. Formation  
578 of vegetation patches could also start from seeds of shrubs species colonizing empty areas  
579 such as *Gutierrezia* spp. This species will later generate an environment adequate for  
580 establishment of other species.

581 Mismanagement of vegetation patches for domestic herbivory will eventually lead to  
582 reduce species richness, leaving only inedible plant species (mostly shrubs) in the com-  
583 munity. This is because of the selective nature of grazing animals on the most palatable  
584 species. However, the magnitude of this impact on structure and function of a community  
585 can be minimised by managing the timing and intensity of paddock use (Ludwig et al.  
586 1999).



587 One particularly important interaction between ecological and hydrological processes in  
588 patchy semiarid lands is how vegetation patches serve to obstruct runoff, and then how this  
589 retained water increases patch growth that, in turn, provides feedbacks to the system  
590 (Ludwig et al. 2004). Such ecohydrological interactions have been mostly demonstrated for  
591 semiarid landscapes with distinctly banded vegetation patterns. Their findings do support  
592 the conclusion that vegetation patches and runoff-erosion processes do strongly interact in  
593 many semiarid landscapes across the globe. For example, Ludwig and Tongway (1995)  
594 emphasized the importance of mounds in the vegetation patches because they collect water  
595 from rainfall and air-borne particulate matter from wind. Mounds create microhabitats  
596 where soil aeration and infiltration are improved due to microfauna and microflora  
597 (Tongway and Ludwig 1989). These patches of grass clumps and debris bridges act as  
598 filters allowing large water flows to pass through without damaging the patch (Ludwig and  
599 Tongway 1995). They capture and retain scarce resources within the landscape system  
600 rather than being carried out of the system. Loss of these patches alters the whole system of  
601 erosion and deposition. Each runoff volume increases with loss of patches, thereby  
602 transporting larger quantities of eroded materials. The interception zone may not be able to  
603 handle larger volumes of runoff, which may lead to a reduced infiltration rate. This will  
604 lead to degradation of soil quality, which could decrease to levels below what is necessary  
605 to support the microhabitat. HilleRisLambers et al. (2001) also reported that pattern for-  
606 mation can occur in semiarid areas given only the positive feedback between plant density  
607 and local water infiltration coupled with the spatial redistribution of runoff water.

608 Conservation of vegetation patches is then crucial to prevent increased soil erosion and  
609 desertification in those ecological systems. This is especially true when we look at the  
610 findings of Bonvissuto (2006), who studied the vegetation patches and the surrounding bare  
611 areas in northwestern Patagonia, Argentina. Research of Bonvissuto (2006) was conducted  
612 in a study site with a rough soil surface area which will tend to slow down run-off, hence  
613 increasing the time for water infiltration and soil water storage. She found that emergence  
614 and seedling survival of two perennial grass species, *Stipa neaei* and *Elymus erianthus*,  
615 were greater underneath the shrubs in the vegetation patches than in the interpatch, plant-  
616 uncovered interspaces. This was determined, at least in part, by lower apparent soil density,  
617 wind speeds and temperature amplitudes, and greater water infiltration rates, and gravi-  
618 metric soil water and nutrient contents in the mounds below the shrubs than in the bare,  
619 surrounding areas. Experimental plots underneath the shrubs in her studies were covered  
620 by *Stipa neaei* and *Poa lanuginosa* through vegetative reproduction, after germination took  
621 place from the soil seed bank. An important seed rain reached the interspaces, but no  
622 individuals survived the high summer temperatures which used to reach 50°C. Her results  
623 leave no doubts that appropriate rangeland management is essential for maintaining the  
624 vegetation patches, and thus some vegetation cover and soil erosion control in that eco-  
625 logical system.

626 Tongway and Ludwig (1996) reported that several attempts to re-seed bare areas of the  
627 landscape using mainly grass species failed due to the poor match between introduced  
628 species and soil type. Also, re-seeding along with various mechanical soil reclamation  
629 treatments were also attempted with minimal success (Tongway and Ludwig 1996). Nelson  
630 (1999) recognized the need to take a more comprehensive approach. This entails under-  
631 standing the natural vegetation patterning and nutrient cycling of a landscape. If the  
632 nutrient cycling of a soil system is understood, it is more likely that a reasonable strategy  
633 for restoration and conservation of the soil will be developed. Once the soil is restored in  
634 the interpatch areas, re-establishment of vegetation is more feasible, thereby making the  
635 re-establishment of vegetation patterns and the effective restoration of the landscape



636 possible. Tongway and Ludwig (1990) studied the patterning of the semiarid mulga lands  
637 of eastern Australia to determine the processes that make the existing natural vegetation  
638 patches fertile. The landscape was considered as a whole, instead of only concentrating in  
639 the bare patches. Once the landscape patterning was determined, it was possible to develop  
640 a strategy to restore the soil's characteristics and nutrients, increasing the likelihood of  
641 successfully reestablishing vegetation. Later on, Tongway and Ludwig (1996) treated bare  
642 soil areas with branches. Accumulated soil was a result of both fluvial and aeolian pro-  
643 cesses. The branches caught debris by the wind from as far as 100 m away. Once the  
644 branches caught the debris, it was dropped onto the soil, and was not easily re-suspended.  
645 Water also brought leaf litter from the surrounding areas. These authors stated that the only  
646 treatment to consistently rehabilitate bare sites, alone or in combination with fertilizer and  
647 litter treatments, was the application of branches. This restoration effort was successful in  
648 proving that a simple, inexpensive technique can be used to re-establish the landscape to  
649 pre-grazing conditions. This technique demonstrates a way to amend the nutrient cycling in  
650 the soil, improve water filtration and create a microhabitat for organisms. This is a very  
651 important aspect since, as in any arid or semiarid environment, the climate has unpre-  
652 dictable rainfall events. The restoration effort also shows the importance of understanding  
653 the natural patterning of the landscape. Previous restoration efforts had failed because the  
654 important landscape processes had been ignored (Nelson 1999).

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