Revista Chilena de Historia Natural
68: 361-371, 1995

Short-term effects of removing the most abundant species on plant species co-occurrence at a spatial microscale

Efectos a corto plazo de la remoción de la especie más abundante sobre la co-ocurrencia de especies de plantas a microescala espacial

ESTELA RAFFAELE and ADRIANA RUGGIERO

Departamento de Ecología, Centro Regional Universitario Bariloche
Universidad Nacional del Comahue, Casilla de correo 1336
(8400) Bariloche, Argentina

ABSTRACT

The effect of removing the above ground parts of the most abundant species (*Juncus bufonius* L.) in an inundated mountain meadow known as "mallín" in Patagonia was analyzed. It was hypothesized that the removal of this species should cause changes in the pattern of plant species co-occurrence in a spatial microscale (i.e., within cells of a few cm^2). Two predictions were tested: (1) the removal of the most abundant species would modify the frequency distribution of the pre-existing types of co-occurrences; (2) the open space created by the removal of *J. bufonius* could be occupied by other species, resulting in co-occurrences different from the pre-existing ones. A grid composed of 625 cells of 2 x 2 cm was overlaid on 10 random plots of 50 x 50 cm. *J. bufonius* was removed from five plots and the other five were used as controls. Presence/absence of each species in each one of the 6250 cells were recorded before and after removal of the dominant species. One hundred and twenty eight types of species co-occurrences were coded, with those composed of two species being the most frequent ones. We did not find a change in the frequency distribution pattern of co-occurrences, or replacement of *J. bufonius* by the subdominant species due to removal effect at the 2 x 2 cm microscale. The restoration of the original species assemblage was observed at the beginning of the following growing season, and *J. bufonius* regained its dominance within the community, probably because its early vegetative growth. The number of rare types of co-occurrences was also maintained, although the number of cells occupied by them decreased. The latter indicated a change in the frequency of encounter between rare and abundant species. Both predictions were not supported by the data and, thus, the removal of the most abundant species represents a small disturbance to the mallin community, in terms of the patterns of species co-occurrence at a small scale. This could be a common feature of plant communities dominated by species with active vegetative reproduction.

Key words: experimental manipulation, mallín, microscale, species co-occurrence, *J. bufonius* L.

RESUMEN

Se analizó el efecto de la remoción de la biomasa aérea de la especie más abundante (*Juncus bufonius* L.) en un tipo de pradera inundada de montaña conocida como "mallín" en Patagonia. Se postuló la hipótesis de que la remoción de esta especie causa cambios en los patrones de co-ocurrencia de especies a microescala espacial (i.e., dentro de celdas que cubren pocos cm^2). Se probaron dos predicciones: (1) la remoción de la especie más abundante modificaría la distribución de frecuencias de los diferentes tipos de co-ocurrencias preexistentes; (2) el espacio abierto creado por la remoción de *J. bufonius* podría ser ocupado por otras especies, dando lugar a co-ocurrencias diferentes de las preexistentes. Una grilla compuesta de 625 celdas de 2 x 2 cm fue superpuesta sobre 10 parcelas de 50 x 50 cm dispuestas al azar. *J. bufonius* fue removido en cinco parcelas y las otras cinco se usaron como parcelas testigo. Se registró la presencia/ausencia de cada especie en cada una de las 6250 celdas, antes y después de la remoción de la especie más abundante. Se codificaron 128 tipos de co-occurrencias, siendo aquéllas compuestas por dos especies las más frecuentes. No se observaron cambios en el patrón de distribución de frecuencias de co-ocurrencias, ni tampoco un reemplazo de *J. bufonius* por las especies subdominantes debido al efecto de la remoción en la microescala de 2 x 2 cm. Se observó la restauración del ensamble original de especies al comienzo de la siguiente estación de crecimiento, y *J. bufonius* recuperó su dominancia dentro de la comunidad, probablemente debido a su temprano crecimiento vegetativo. Se mantuvo el número de co-ocurrencias raras, aunque el número de celdas ocupadas por ellas decreció. Esto último puede indicar un cambio en la frecuencia de encuentros entre especies raras y abundantes. Las dos predicciones no fueron sustentadas por los datos y, por esto, se concluyó que la remoción de la especie más abundante representa una perturbación pequeña para la comunidad del mallín, en términos de los patrones de co-occurrencias de especies a una escala pequeña. Esto podría ser una característica de comunidades de plantas dominadas por especies con una reproducción vegetativa activa.

Palabras clave: manipulación experimental, mallín, microescala, co-ocurrencia de especies, *J. bufonius* L.

(Received 3 august 1993; accepted 20 march 1995)

INTRODUCTION

The effect of the removal of one species on the competitive relations among the remaining species of a plant community has been the focus of several studies (e.g., Dayton 1975, Allen & Forman 1976, Lubchenco 1978, Fowler & Antonovics 1981, Gurevitch & Unasch 1989). They have analyzed the individual responses of the remaining species, the changes in species diversity in the community, and the interactions between pairs of species. However, the effect of species removal on species co-occurrence at a spatial microscale (i.e., in an area of few cm^2) has not been examined. Several studies have addressed the importance of microsite characteristics in determining local and microscale patterns of species coexistence in plant communities (Fowler & Antonovics 1981, Fowler 1988, Davis, Borchert and Odion 1989). The relationships between species at a very small spatial scale may be important for understanding species distributions and community structure (Stowe & Wade 1979, Silander & Antonovics 1982). It can be hypothesized that changes in community structure brought about by the removal of a species could reflect changes in the abundance and distribution of available microsites. The environmental variables that operate at this spatial scale determine effects on seedlings that may affect population dynamics and the floristic composition of the plant community (Fowler 1988). Even though the number of species may not change after the experimental removal of one species, it is possible that spatial relations among species will be altered and thus species co-occurrence patterns will be modified.

Here, we study the effects of the removal of the dominant species upon the spatial co-occurrence of subordinate species in a flooded Andean meadow, which is usually called "mallín", in nothern Patagonia. These simple communities, with plants no more of 15 cm height, are suitable for experimental manipulation and for analyzing structural changes in a spatial microscale (i.e., in plot cells of a few square cm^2 in area). Two or more species were considered neighbors (and the group was defined as "species co-occurrence") if their areal parts were recorded within a 2 x 2 cm cell. We hypothesized that the removal of the most abundant species of the assemblage would produce changes in plant species co-occurrence pattern at this spatial scale.

Two predictions were tested: (1) The removal of the most abundant species *Juncus bufonius* L. would modify the frequency distribution of the different types of co-occurrences. (2) The space opened by the removal of *J. bufonius* could be occupied by other species, resulting in new co-occurrences, that differed from those defined before the removal.

METHODS

Study area

The study was performed in a flooded mountain meadow, known as "mallín", in Patagonia. Mallines usually have a dense herbaceous cover dominated by short graminoids growing on soils with a high accumulation of organic matter.

The study site is located on the eastern slope of Cerro Blanco (41°16'S, 71°20'W) at 1500 m elevation, 17 km from San Carlos de Bariloche, Province of Río Negro, Argentina (Fig. 1). The "mallín" is surrounded by *Nothofagus pumilio* forest, and has a gentle slope which allows permanent water drainage. Most of the area is flooded during the growing season, i.e., from late November to early April (Table 1). Flooding prevents the mallín from being grazed by herbivores (mainly cattle and European hares). Two streams divide the mallín area forming permanent and semi-permanent internal water courses. Accumulation of organic material in the soil is nearly 15 cm deep. Soil pH is very acidic (3.8) and conditions are often highly anaerobic.

The climate of the region is characterized by cool winters (3° C, mean temperature in July) with occasional snow falls from June to September. Summer climate is dry (32 mm, mean precipitation and 14.2°C mean temperature in January) (Muñoz & Garay 1985). Due to the elevation of the site, the snow usually covers the mallín for approximately seven months (Table 1).

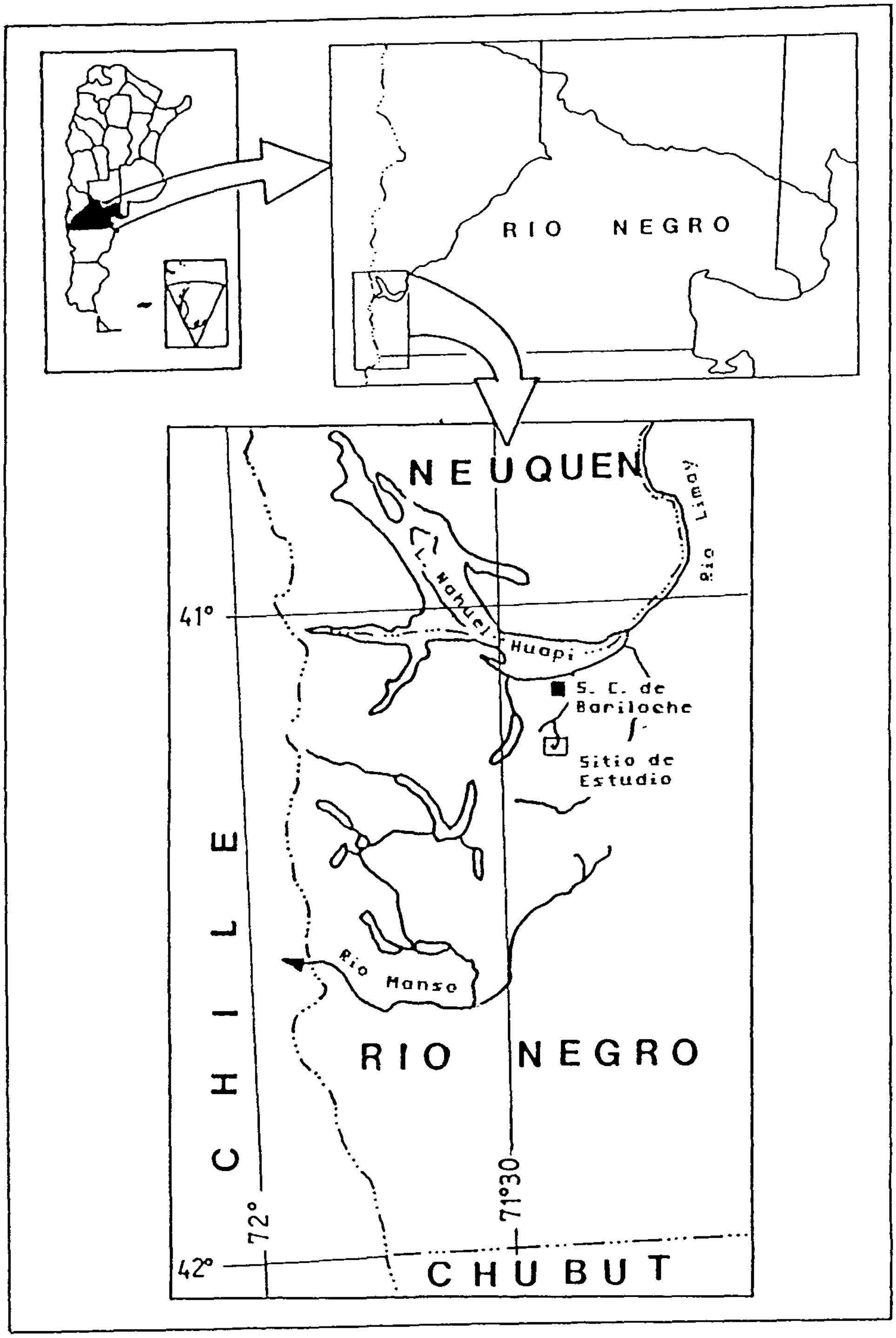

Fig. 1: Geographical location of the study site.
Localización geográfica del sitio de estudio.

The majority of plant species in the mallín are hemicriptophytes, a few rare species are annuals. The vascular flora is composed of 52 species, the three most abundant species are *Juncus bufonius* L., *Caltha sagittata* Cars., and *Carex subantarctica* Speg. (Table 2).

Sampling

Ten 50 x 50 cm plots were randomly placed in a vegetationally homogeneous section of the mallín. In five of these plots the most abundant species, *Juncus bufonius*, was

TABLE 1

Average environmental conditions recorded in a north Patagonian mallín over the course of one year. The timing of removal of *Juncus bufonius* (R) and of post-removal census (C) are indicated. Dots indicate variable conditions

Condiciones ambientales promedio registradas en un mallín del norte de la Patagonia durante el curso de un año. Se indica el momento de la remoción de *Juncus bufonius* (R) y del censo postremoción (C). Los puntos indican condiciones variables

Phenology	Months											
	J	F	M	A	M	J	J	A	S	O	N	D
Flooded soil	..										——	——
Not flooded soil	——	——	...									
Snow covered			——	——	——	——	——	——	——			
Growing season	——	——								..	——	——
Experiment			R								C	

TABLE 2

Absolute mean percent cover (%) and one standard deviation of the mean (SD) for abundant species recorded in the study site. Rare species having absolute mean cover values < 2 % are indicated in the footnote

Porcentaje de cobertura media absoluta (%) y una desviación estándar de la media (SD) para las especies más abundantes registradas en el sitio de estudio. Las especies raras que tienen una cobertura media absoluta < 2 % se indican en la nota a pie de página

	Mean Cover	
Plant species	%	SD
Juncus bufonius	78.76	9.72
Caltha sagittata	63.31	22.43
Carex subantarctica	55.45	11.60
Juncus chilensis	8.84	12.09
Trisetum spicatum	8.23	7.26
Aster valhii	4.2	11.3
Gunnera magellanica	4.1	4

[1] *Acaena antarctica, Cardamine valdiviana, Carex atropicta, Carex fuscula, Carex goodenoughii, Carex magellanica, Chlorea chica, Cortaderia pilosa, Deschampsia caespitosa, Euphrasia meiantha, Festuca purpurascens, Gentianella magellanica, Geranium sessiliflorum, Geum magellanicum, Lathyrus multiceps, Mimulus parviflorus, Poa annua, Poa borchesii, Phleum alpinum, Sagina procumbes, Scirpus inundatus, Senecio gilliesii, Silene andicola Taraxacum officinale, Trifolium repens, Valeriana* sp.

harvested at soil level (i.e., by hand weeding), while the remaining five plots were used as controls. *J. bufonius* was also removed 10 cm around all the plots so as to prevent edge effects. A grid composed of 625 (2 x 2 cm) cells was overlaid in each plot and the presence/absence of every species or group of species was recorded (local frequencies: Mueller-Dombois & Ellenberg 1974) before and after the removal of *Juncus bufonius*. The pre-treatment census was performed in early March 1988. *J. bufonius* was removed in late March 1988. Because snow covered the plots during winter, post-treatment census was done in December 1988, after the snow melted.

Species richness and species co-occurrences were determined in each one of the 625 cells per plot (N = 6250). To test our first prediction, the relative frequencies of the different types of co-occurrences were determined by analyzing the observed frequency distribution of the co-occurrences at 2 x 2 cm scale.

To test our second prediction, co-occurrence transition matrices were constructed for each plot. The transition probability (for each co-occurrence) is $p_{ij} = n_{ij}/\Sigma n_{ij}$, where n_{ij} is the number of transitions (number of cells) that change their state from March 1988 (i), to December 1988 (j). We analyzed the removal effects on relations between neighboring plants by comparing the mean transition probabilities (March-December 1988) exclusively for each one of the seven co-occurrences that simultaneously include *Juncus bufonius* and the subdominant species, *Caltha sagittata and Carex subantarctica*. A 'replacement' of *J. bufonius* would be detected, if a cell where only *Juncus bufonius* was recorded before removal, changed to any of the following states: (a) *Juncus bufonius* + a subdominant species, (b) a subdominant species alone, or (c) a group of subdominant species (without *Juncus*). Similarly, if cells occupied by co-occurrences composed of *Juncus bufonius* + a subdominant species changed their state, so as to be occupied by a subdominant species alone, this would also indicate a replacement of *Juncus bufonius*. A 'restoration' of co-occurrences was defined if a cell did not change its state after the removal.

RESULTS

One hundred and twenty eight types of species co-occurrences were coded (Appendix 1). The number of species per cell varied from 0 to 6. At the 2 x 2 cm scale (Fig. 2), two-species co-occurrences were the most frequent ones. Three-species co-occurrences were as frequent as a single species. The frequency distribution of co-occurrences did not differ between treatment and control plots (Kolmogorov-Smirnov test; $P > 0.05$).

The frequency of the most abundant of the 128 types of co-occurrences, i.e., those with > 5 % frequency for the 6250 cells were compared before and after the removal of *Juncus bufonius*, (Table 3). The frequency of all two-species co-occurrences increased in the manipulated plots, except for *Juncus bufonius-Caltha sagittata*, and the frequency of co-occurrence of *Juncus bufonius-Carex subantarctica-Caltha sagittata* increased in the control plots. A significant, although expected, decrease in the number of cells occupied only by *J. bufonius* occurred in the manipulated plots (Table 3).

Transition probabilities (March-December 1988) were used to detect the replacement of *Juncus bufonius* by other species or groups of species, and to test the effect of removal on 3-species co-occurrences by *Juncus bufonius*, *Caltha sagittata*, and *Carex subantarctica* (Table 4). On one hand, the open space created by the removal of *Juncus bufonius* was not occupied by any other species, except by *Juncus bufonius* itself. This means that vegetative growth occurred under the snow cover. On the other hand, the removal of *Juncus bufonius* did not alter the probability of persistence of pre-removal co-occurrences (i.e., restoration). This effect was strengthened by the fact that the probability of replacement of *Juncus bufonius* by other species was much lower than the probability of restoring the original assemblage, composed of *Juncus bufonius* and the subdominant species (Table 4).

Rare co-occurrences

The co-occurrences composed of at least one rare species (i.e., a species with < 2 % coverage, see Table 1) and hereafter simply called "rare species co-occurrences", showed a frequency of < 1 % of the 6250 cells. The absolute number of types of rare species co-occurrences did not change after removal of *Juncus bufonius*. However, a decrease in the number of cells occupied by rare species

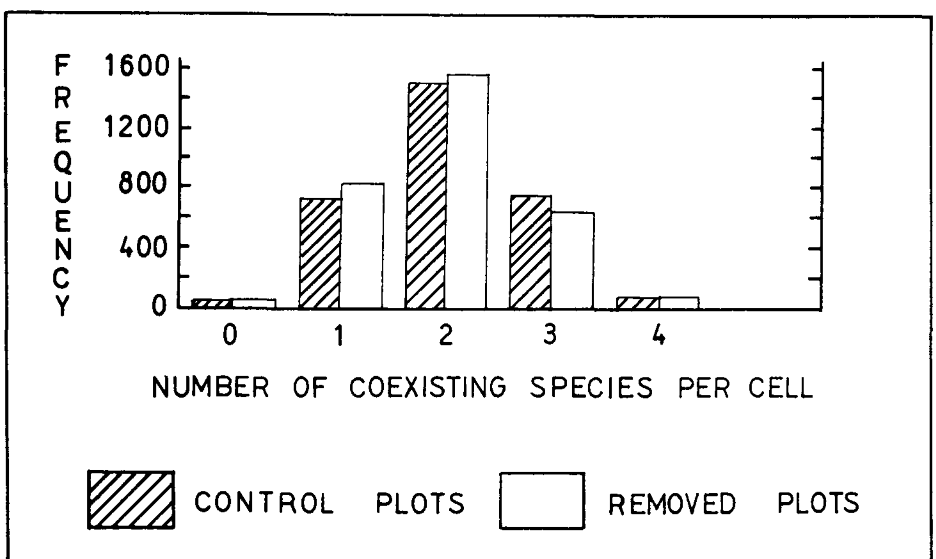

Fig. 2: Frequency distribution of plant species co-occurrences recorded at the 2 x 2 cm spatial scale experimental (dominant species removed) and control plots.

Distribución de frecuencia de co-ocurrencias de especies de plantas, en escala espacial de 2 x 2 cm, en parcelas experimentales (especie dominante removida) y testigos.

TABLA 3

Frequencies of species co-occurrence in experimental and control plots (2 x 2 cm), before (B) and after (A) removal *Juncus bufonius*

Frecuencias de co-ocurrencia de especies en las parcelas experimentales y testigos (2 x 2 cm), antes (B) y después (A) de la remoción de *Juncus bufonius*

Co-ocurrences		Experimental plot						Control plots					
		Co-ocurrence frequence					Statistical difference B vs. A (1)	Co-ocurrence frequency					Statistical difference B vs. A
	Plots	1	2	3	4	5		1	2	3	4	5	
J. bufonius-	B	69	96	143	217	107		155	35	60	51	123	
C. sagittata	A	80	113	134	247	94	NS	187	51	43	59	160	NS
J. bufonius-	B	95	83	79	50	64		105	76	109	96	121	
C. subantarctica	A	134	109	131	61	66	(+)*	24	220	212	221	106	NS
J. bufonius-													
C. subantarctica	B	45	40	48	63	100		67	14	64	23	62	
C. sagittata	A	80	58	80	88	57	NS	134	72	111	64	166	(+)*
C. sagittata-	B	22	16	15	16	18		24	9	47	18	40	
C. subantarctica	A	42	50	28	22	32	(+)*	22	10	18	9	45	NS
C. sagittata-	B	37	46	29	57	50		49	26	87	34	103	
C. sagittata	A	51	57	40	71	70	(+)*	64	7	19	22	64	NS
C. subantarctica	B	18	5	6	2	11	6	35	24	17	23		
C. subantarctica	A	56	32	20	6	11	(+)*	0	13	39	5	14	NS
J. bufonius-	B	70	172	171	152	45		134	131	81	138	96	
J. bufonius	A	65	87	96	100	43	(-)*	44	107	118	137	59	NS

(1) (+) indicate that a significative post-removal increase in the frequency of a species co-occurrence was recorded the majority of plots (results from the Sign test; *P < 0.05).
(-) indicates that a significative post-removal decrease in the frequency of a species co-occurrence was recorded in the majority of plots (results from the Sign test; * P < 0.05).
NS = no significant change.

co-occurrences was observed in the experimental plots (Table 5). The frequency of encounters of a rare species with an abundant species increased after removal (Table 6).

DISCUSSION

Small scale community pattern is often referred to as "noise" in large scale studies. However, the association of community patches with physical or biological discontinuities in the environment suggests such pattern is an element of structure that should be included in any thorough community study (Belsky 1983). The analysis of plant species co-occurrences at a small spatial scale (a few cm^2) provides an insight into spatial relations among species, and reveals how the available space is redistributed among species within a community after disturbance. Even if disturbances are small, the study of species co-occurrence patterns allows the quantification of subtle changes that otherwise would remain unnoticed when the individual species responses or overall changes in the community are analyzed. For instance, a significant increase in the frequency of 2-species co-occurrences, composed of *Juncus bufonius* and the subdominant species, *Carex subantarctica*, or composed of the subordinate species (without *J. bufonius*), was observed in disturbed plots (Table 3).

In the present study, the removal of *Juncus bufonius*, the dominant species, did not modify the frequency distribution of the different types of co-occurrences. This species was not replaced by co-occurrences composed by subdominant species *(Caltha sagittata* and *Carex subantarctica)* at 2 x 2 cm scale.

Juncus bufonius regained its dominance within the community after its removal and patterns of coexistence among species did not change, therefore, the original assem-

TABLE 4

Effect of removing *Juncus bufonius* on co-occurrences of *J. bufonius* and subdominant species

Efecto de la remoción de *Juncus bufonius* sobre las co-ocurrencias de *J. bufonius* y las especies subdominantes

Species transitions		Mean transition probabilities ± SD between march and december 1988		
From co-ocurrence	To co-ocurrence	Removal plots (N = 5)	Control plots (N = 5)	
J. bufonius- C. sagittataì	*J. bufonius*- C. sagittata	0.25 ± 0.13	0.18 ± 0.07	NS (a)
J. bufonius- *C. subantarctic*	*J. bufonius*- *C. subantarctica*	0.25 ± 0.06	0.26 ± 0.17	NS
J. bufonius- *J. bufoniu*	*J. bufonius*- *J. bufonius*	0.18 ± 0.06	0.15 ± 0.07	NS
J. bufonius- *J. bufonius*	*J. bufonius*- *C. subantarctica*	0.16 ± 0.08	0.26 ± 0.13	NS
J. bufonius- *J. bufonius*	*J. bufonius*- *C. sagittata*	0.22 ± 0.12	0.17 ± 0.13	NS
J. bufonius- *J. bufonius*	*J. bufonius*- *C. subantarctica* *C. sagittata*	0.10 ± 0.01	0.16 ± 0.09	NS
J. bufonius- *J. bufonius*	*C. sagittata*- *C. subantarctica*	0.05 ± 0.03	0.03 ± 0.01	NS
J. bufonius *J. bufoniu*	*C. sagittata* *C. sagittata*	0.07 ± 0.02	0.04 ± 0.03	NS
J. bufonius *J. bufonius*	*C. subantarctica*- *C. subantarctica*	0.02 ± 0.03	0.03 ± 0.03	NS
J. bufonius– *C. sagittata*	*C. sagittata*- *C. sagittata*	0.11 ± 0.03	0.08 ± 0.06	NS

(a) Results from Mann-Whitney test, NS: P > 0.05.

TABLE 5

Number of types of rare species co-occurrences and their abundance after removal of the dominant species

Número de tipos de co-ocurrencias de especies raras y su abundancia después de la remoción de la especie dominante

Feature	Treatment plots	Control plots
Number of types of rare species co-occurrences (a)	25 (0.20)(b)	31 (0.24)
Number of cells occupied by rare species co-ocurrences (b)	63 (0.01)	133 (0.02)

(a) Number of type of species co-occurrences with at least one rare species. The proportion of the total number of co-occurrences types (N = 128) is given in parenthesis.

(b) The proportion of the total of 6250 cells is given in parenthesis.

blage of species was restored. Apparently *Juncus bufonius* underwent vegetative growth under the snow. We did not expect this species to regenerate during winter but, as soon as the snow melted, post-removal census revealed that *Juncus bufonius* was the

TABLE 6

Absolute frequencies of all types of co-occurrence with at least one rare species

Frecuencias absolutas de todos los tipos de co-ocurrencia con al menos una especie rara

Observations	Treatment plots	Control plots
Encounters between two rare species (R-R)	1	0
Encounters between a rare and an abundant species (R-A)	17	15
Encounters between a rare and an intermediate abundance species (R-I)	0	1
Mixed encounters (R-A-I)	7	14

Rare species (R) = Total percent cover < 2 %.

Intermediate species (I) = Total percent cover < between 2 % and 10%.

Abundant specie (A) = Total percent cover higher than 10%.

most abundant species, although it was completely removed at ground level a few months ago.

The number of types of rare species co-occurrences was maintained, although the absolute number of cells occupied by them decreased in the manipulated plots. The decrease may be due to two processes: (i) a simplification of the system structure or (ii) a change in the frequency of encounters between rare and abundant species recorded within the 2 x 2 cm cells. These results confirm that changes in rare species distribution and abundance is determined by the interaction with abundant species (Grubb 1986).

Given that the hierarchy of species importance is maintained and that species co-occurrence types persist, the removal of the most abundant species as performed in this experiment can be described as an example of a small disturbance (Pickett & White 1985). Its reduced impact on the community is probably due to the pre-existing vegetative structure (rhizomes) which forms a dominant species matrix (Grubb 1986).

A final consideration on the quadrat method used here is necessary. Several authors have previously pointed to the importance of studying neighborhood relations among plant species, by analyzing contacts among individuals using plotless methods (e.g., Turkington & Harper 1979, Bouxin 1983, Whittaker 1991). They correctly noticed that their methodology eliminates the problem of arbitrary selection of plot size. However, such methods are difficult to deal with when a clear identification of individuals is not possible. The community we studied here is an assemblage of small herbaceous rhizomatous plants that are difficult to sample individually, thus we were constrainted to use a quadrat method to investigate species coexistence at small scale. Even though results are scale-dependent (e.g., Greig-Smith 1983, Kershaw 1975), we still could test for changes in species neighborhood relations.

ACKNOWLEDGMENTS

Thomas Kitzberger participated in the initial stages of this work. We deeply thank his valuable effort and encouragement. We also thank M. A. Aizen, E. Balseiro, J. Frangi, J.P. Lewis, B. Modenutti and E.H. Rapoport for the critical review of different versions of the manuscript. B. Drausal translated the manuscript into english, F. H. Planas kindly drew the figures and C. Brion identified the plant species. Thanks also to JoAnne Smith-Flueck for revising the final english version of the manuscript. Financial and logistic support for this work was provided by Universidad Nacional del Comahue and CONICET.

LITERATURE CITED

ALLEN E & R FORMAN (1976) Plant species removals and old field community structure and stability. Ecology 57: 1233-1243.

BELSKY A (1983) Small-scaled pattern in grassland communities in the Serengeti National Park, Tanzania. Vegetatio 55: 41-151.

BOUXIN G (1983) Multi-scaled pattern analysis: an example with savanna vegetation and a proposal for sampling design. Vegetatio 52: 161-169.

DAVIS F, M BORCHERT & DC ODION (1989) Establishment of microscale vegetation pattern in maritime chaparral after fire. Vegetatio 84: 53-67.

DAYTON PK (1975) Experimental evaluation of ecological dominant in a rocky intertidal algal community. Ecological Monographs 45: 137-159.

FOWLER N & J ANTONOVICS (1981) Competition and coexistence in a North Carolina grassland. I. Patterns in undisturbed vegetation. Journal of Ecology 69: 825-841.

FOWLER N (1988) What is a safe site?: neighbor, litter, germination date and patch effects. Ecology 69: 947-961.

GREIG-SMITH P (1983) Quantitative Plant Ecology. 3rd. edition, Blackwell Scientific Publications, Oxford.

GRUBB PJ (1986) Problems posed by sparse and patchily distributed species in species-rich plant communities. In: Diamond TJ & TJ Case (eds) Community Ecology: 207-224. Harper & Row, N. Y.

GUREVITCH J & RS UNNASCH (1988) Experimental removal of a dominant species at two levels of soil fertility. Journal of Botany 67: 3470-3477.

KERSHAW KA (1985) Quantitative and Dynamic Plant Ecology. New York, Elsevier.

LUBCHENCO J (1978) Plant diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. American Naturalist 112: 23-39.

MUELLER-DOMBOIS D & H ELLENBERG (1974) Aims and methods of vegetation ecology. John Wiley and Sons, Inc.

MUÑOZ EM & AF GARAY (1985) Caracterización climática de la Provincia de Río Negro. Inta Bariloche.

PICKETT STA & PS WHITE (1985) The ecology of natural disturbance and patch dynamics. Academic Press. New York.

SILANDER JA & J ANTONOVICS (1982) Analysis of interspecific interactions in a coastal plant community. A perturbation approach. Nature 298: 557-560.

STOWE LG & MJ WADE (1979) The detection of small-scale pattern in vegetation. Journal of Ecology 67: 1047-1064.

TURKINGTON R & JL HARPER (1979) The growth, distribution and neighbor relationship of Trifolium repens in a permanent pasture. I. Ordination, pattern and contact. Journal of Ecology 67: 201-218.

WHITTAKER RJ (1991) Small-scale pattern: an evaluation of techniques with an application to salt marsh vegetation. Vegetatio 94: 81-94.

APPENDIX 1

Detail of types of species co-occurrences in a mallín plant community. The number of cells (N) and the percentage (%) of the total of 3,125 cells of each type of co-occurrences in experimental and control plots are given. B = before, A = after removal of the dominant species

Detalle de los tipos de co-ocurrencias en una comunidad de plantas de mallín. El número de celdas (N) y el porcentaje (%) del total de 3.125 celdas de cada tipo de co-ocurrencia en parcelas experimentales y de control se indica en cada caso. B = antes, A = después de la remoción de la especie dominante

	Control plots				Experimental plots			
	B		A		B		A	
Co-occurrence	N	%	N	%	N	%	N	%
Bare soil	84	2.68	48	1.54	4	1.4	47	1.5
C. sagittata-C. subantarctica-Gunnera magellanica	14	0.44	19	0.61	26	0.83	18	0.58
C. sagittata-C. subantarctica-J. bufonius	230	7.36	517	16.54	296	9.47	363	11.6
C. sagittata-C. subantarctica-G. magellanica	10	0.32	4	0.13	8	0.25	14	0.45
C. subantarctica-J. bufonius-G. magellanica	15	0.48	22	0.7	24	0.76	35	1.12
C. sagittata-J. bufonius-G. magellanica	32	1.02	35	1.12	58	1.85	53	1.70
C. subantarctica-J. bufonius	507	16.22	783	25.06	371	11.87	501	16.0
C. sagittata-J. bufonius	424	13.56	500	16.	632	20.22	636	20.35
C. subantarctica-G. magellanica	6	0.19	0	0	4	0.12	8	0.26
C. sagittata-G. magellanica	23	0.73	12	0.38	28	0.89	32	1.03
J. bufonius-G. magellanica	14	0.44	22	0.70	54	1.72	34	1.09
C. sagittata-C. subantarctica	138	4.41	104	3.33	87	2.78	174	5.57
J. bufonius	580	18.56	358	11.46	610	19.52	392	12.54
G. magellanica	2	0.06	7	0.22	11	0.35	6	0.19
C. magellanica	105	3.36	71	2.27	42	1.34	125	4.
C. sagittata	299	9.56	176	5.63	220	7.04	288	9.22
Trisetum spicatum	27	0.86	1	0.03	7	0.22	3	0.1
C. sagittata-C. subantarctica-J. bufonius-G. magellanica	1	0.03	2	0.06	4	0.12	0	0
C. sagittata-C. subantarctica-T. spicatum-J. bufonius	9	0.28	36	1.15	18	0.57	12	0.38
T. spicatum-J. bufonius-G. magellanica	1	0.03	1	0.03	1	0.03	0	0
C. sagittata-C. subantarctica-Juncus chilensis-J. bufonius	14	0.44	8	0.26	36	1.15	7	0.22
C. sagittata-J. chilensis-J. bufonius	39	1.24	5	0.16	40	1.28	3	0.1
C. subantarctica-J. chilensis-J. bufonius	83	2.65	40	1.28	65	2.08	4	0.13
C. sagittata-T. spicatum-J. bufonius	24	0.76	23	0.74	32	1.02	16	0.51
C. sagittata-J. chilensis	5	0.16	1	0.03	5	0.16	0	0
T. spicatum-J. chilensis-J. bufonius	5	0.16	1	0.03	15	0.48	0	0
C. sagittata-T. spicatum-J. chilensis-J. bufonius	3	0.09	0	0	1	0.03	0	0
C. subantarctica-T. spicatum-J. bufonius	46	1.47	48	1.54	48	1.53	58	1.86
T. spicatum-J. bufonius	41	1.31	19	0.61	56	1.79	16	0.51
J. chilensis-J. bufonius	110	3.52	26	0.83	116	3.71	6	0.19
C. sagittata-T. spicatum	19	0.60	10	0.32	13	0.41	8	0.26
J. bufonius-T. repens	1	0.03	0	0	0	0	0	0
C. subantarctica-T. spicatum	45	1.44	10	0.32	13	0.41	7	0.22
C. subantarctica-J. bufonius-Trifolium repens	4	0.12	0	0	0	0	0	0
C. sagittata-C. subantarctica-T. spicatum	16	0.51	6	0.19	4	0.12	8	0.26
C. sagittata-J. chilensis-J. bufonius-G. magellanica	0	0	0	3	0.09	0	0	0
J. chilensis	3	0.09	0	0	0	0	0	0
C. subantarctica-T. spicatum-J. chilensis-J. bufonius	10	0.32	4	0.13	5	0.17	0	0
C. sagittata-C. subantarctica-J. chilensis	1	0.03	1	0.03	0	0	0	0
C. subantarctica-T. spicatum-J. chilensis-J. bufonius-G. magellanica	1	0.03	0	0	1	0.03	0	0
C. subantarctica-T. spicatum-J. bufonius-G. magellanica	2	0.06	1	0.03	0	0	6	0.19
C. subantarctica-J. chilensis	7	0.22	0	0	0	0	0	0
J. bufonius-Euphrasia meiantha	25	0.8	0	0	0	0	0	0

	Control plots				Experimental plots			
	B		A		B		A	
Co-occurrence	N	%	N	%	N	%	N	%
C. sagittata-C. subantarctica-J. bufonius-E. meiantha	3	0.09	0	0	0	0	0	0
J. chilensis- J. bufonius- E. meiantha	3	0.09	0	0	0	0	0	0
J. chilensis-E. meiantha	1	0.03	0	0	0	0	0	0
C. subantarctica-J. chilensis-J. bufonius- E. meiantha	3	0.09	0	0	0	0	0	0
T. spicatum-J. bufonius-E. meiantha	1	0.03	0	0	0	0	0	0
C. subantarctica-T. spicatum- E. meiantha	2	0.06	0	0	0	0	0	0
J. bufonius-E. meiantha-G. magellanica	1	0.03	0	0	1	0.03	0	0
J. chilensis-J. bufonius-G. magellanica	2	0.06	0	0	3	0.09	0	0
C. subantarctica-J. bufonius-E. meiantha	14	0.44	0	0	0	0	0	0
C. subantarctica-E. meiantha	6	0.19	0	0	7	0.22	0	0
C. subantarctica-J. chilensis-J. bufonius-G. magellanica	1	0.03	0	0	3	0.09	1	0.03
C. sagittata-J. bufonius-E. meiantha	5	0.16	0	0	0	0	0	0
E. meiantha	6	0.19	0	0	0	0	0	0
C. sagittata-C. subantarctica-T. spicatum-G. magellanica	2	0.06	1	0.03	0	0	0	0
C. sagittata-C. subantarctica-T. spicatum-J. chilensis-J. bufonius-G. magellanica	2	0.06	0	0	0	0	0	0
J. chilensis-G. magellanica	1	0.03	0	0	0	0	0	0
C. sagittata-C. subantarctica-J. bufonius-G. magellanica	1	0.03	0	0	0	0	0	0
C. sagittata-C. subantarctica-E. meiantha	1	0.03	0	0	0	0	0	0
C. sagittata-C. subantarctica-T. spicatum-J. chilensis- J. bufonius	2	0.06	1	0.03	0	0	0	0
C. sagittata-T. spicatum-J. bufonius - G. magellanica	1	0.03	0	0	0	0	4	0.13
C. sagittata-T. spicatum-G. magellanica	4	0.12	1	0.03	5	0.16	0	0
J. bufonius- Aster valhii	1	0.03	14	0.14	6	0.19	0	0
C. sagittata-J. chilensis-G. magellanica	0	0	0	0	2	0.06	0	0
J. bufonius-G. magellanica-A. valhii	1	0.03	0	0	0	0	0	0
C. subantarctica-J. bufonius-E. meiantha	0	0	0	0	1	0.03	0	0
C. sagittata-C. subantarctica-J. bufonius-J. chilensis-G. magellanica	0	0	0	0	2	0.06	0	0
C. sagittata-J. bufonius-G. magellanica-A. valhii	1	0.03	0	0	0	0	0	0
C. sagittata- E. meiantha	1	0.03	0	0	0	0	0	0
T. spicatum-G. magellanica	2	0.06	0	0	0	0	0	0
C. sagittata-J. bufonius-Deschampsia caespitosa	0	0	0	0	1	0.03	0	0
C. sagittata-D. caespitosa	0	0	0	0	1	0.03	0	0
C. sagittata-C. subantarctica-T. spicatum-D. caespitosa	0	0	0	0	1	0.03	0	0
C. subantarctica-T. spicatum-D. caespitosa	0	0	0	0	1	0.03	0	0
C. sagittata-T. spicatum-J. chilensis-J. bufonius-G. magellanica	0	0	0	0	2	0.06	0	0
C. subantarctica-J. bufonius-A. valhii	0	0	28	0.9	0	0	0	0
C. sagittata-C. subantarctica-J. bufonius-A. valhii	0	0	8	0.26	1	0.03	0	0
C. sagittata-A. valhii	0	0	1	0.03	0	0	0	0
C. subantarctica-T. spicatum-J. bufonius-G. magellanica-A. valhii	0	0	1	0.03	0	0	0	0
T. spicatum-J. bufonius-A. valhii	0	0	1	0.03	0	0	0	0
C. sagittata-C. subantarctica-T. spicatum-J. bufonius-A. valhii	0	0	1	0.03	0	0	0	0
C. subantarctica-T. spicatum-J. bufonius-A. valhii	0	0	1	0.03	0	0	1	0.03
C. sagittata-T. spicatum-A. valhii	0	0	1	0.03	0	0	0	0
C. subantarctica-J. bufonius-G. magellanica-A. valhii	0	0	1	0.03	0	0	0	0
C. subantarctica-T. spicatum-G. magellanica	0	0	1	0.03	0	0	3	0.1
C. subantarctica-G. magellanica-A. valhii	0	0	1	0.03	1	0.03	0	0
A. valhii	0	0	1	0.03	0	0	0	0
C. sagittata-G. magellanica-A. valhii	0	0	1	0.03	0	0	1	0.03
T. spicatum-A. valhii	0	0	1	0.03	0	0	0	0
C. subantarctica-A. valhii	0	0	1	0.03	0	0	0	0
C. subantarctica-Carex magellanica	0	0	0	0	1	0.03	1	0.03
C. magellanica	0	0	0	0	0	0	1	0.03

Co-occurrence	Control plots				Experimental plots			
	B		A		B		A	
	N	%	N	%	N	%	N	%
C. subantarctica-J. bufonius-C. magellanica	0	0	0	0	0	0	1	0.03
C. sagittata-J. bufonius-C. magellanica	0	0	1	0.03	0	0	0	0
C. sagittata-C. subantarctica-J. bufonius-C. magellanica	0	0	3	0.1	0	0	0	0
C. sagittata-J. bufonius-Carex goodenouhii	0	0	0	0	0	0	1	0.03
C. sagittata-C. subantarctica-C. goodenouhii	0	0	0	0	0	0	1	0.03
C. sagittata-C. goodenouhii	0	0	0	0	0	0	1	0.03
C. sagittata-C. subantarctica-C. magellanica	0	0	0	0	0	0	1	0.03
C. sagittata-C. magellanica	0	0	1	0.03	0	0	0	0
C. sagittata-J. bufonius-G. magellanica-C. magellanica	0	0	3	0.1	0	0	0	0
J. bufonius-G. magellanica-C. magellanica	0	0	0	0	0	0	1	0.03
C. subantarctica-J. bufonius-C. goodenouhii	0	0	0	0	0	0	1	0.03
C. sagittata-C. subantarctica-T. spicatum-G. magellanica-A. valhii	0	0	0	0	0	0	1	0.03
J. bufonius-C. magellanica	0	·0	0	0	0	0	1	0.03
C. subantarctica-J. chilensis-G. magellanica	0	0	0	0	1	0.03	0	0
C. sagittata-J. bufonius-A. valhii	1	0.03	1	0.03	0	0	0	0
C. subantarctica-T. spicatum-J. bufonius-C. magellanica	0	0	1	0.03	0	0	0	0