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Effect of ant-hills on the floristic richness of plant communities of a large depression in the Great Chaco

Juan P. Lewis, Eduardo A. Franceschi and Susana L. Stofella
Universidad Nacional de Rosario, Facultad de Ciencias Agrarias, Santa Fe 2051, 2000 Rosario, Argentina.

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Abstract: The effect of ant-hills of *Camponotus punctulatus* (Mayr.) on the floristic richness of plant communities in the southern Chaco is analized. The ant-hills are conical mounds with an average height of 0.6 m and a diameter of 1.0 m. Ant-hills produce an increase in quadrat floristic richness, but in any given community a low percentage of species grow exclusively or preferentially on the ant-hill. Therefore the effect of ant-hills over the floristic richness of the community is less marked than over the quadrat floristic richness. Ant-hill exclusives or preferential species are rarities, *i.e.* with less than 20 % constancy, in any community. Ant-hills provide refugia for species to grow in environments otherwise unsuitable for them.

Key words: ant-hills, Chaco, disturbance, depressed areas, floristic richness.

In most plant communities there are a few abundant and constant species that make up the matrix of the community and a relatively large amount of sparsely distributed species (Grubb 1986, Grubb, Kelly & Mitchely 1982). This amount is correlated, among other factors, with the availability of microsites which are safe for establishment or regeneration (Harper 1977, Grubb 1977). Microsites are the result of microrelief and the development of the community matrix or are created by disturbance.

Ants interact with vegetation by harvesting plants for food or substrate for fungi cultures, dispersing seeds, dispersing aphids and other insects, moving soils from lower horizons to the surface and modifying soil porosity, and by building nests, thus modifying microrelief.

Mounds built by ants have different environmental characteristics from the soil where they have been built, thereby providing microsites for the establishment of plants which may not grow on the soil around (Pire *et al.* 1990). However, the effects of ant-nests on vegetation has generally been overlooked, though Thomas (1962) pointed out that plants growing on ant-hills were quite different from those on the surrounding grassland. The effect of *Lasius flavus* ant-hills on vegetation in Britain was observed by Grubb, Green & Merrifield (1969), Woodell (1974), Wells *et al.* (1976) and King (1977 a,b,c). Coffin & Lauenroth (1988) examined the effect of mounds of *Pogonomyrex occidentalis* on prairies of *Bouteloua gracilis*.

In lowlands of Tropical and Subtropical South America, *Camponotus punctulatus* (Mayr.) builds huge conical nests (Morello & Adámoli 1974, Bucher 1980, Lewis *et al.* 1990a) and it was suggested that they were an important factor in the development of floristic richness (Lewis *et al.* 1990b).

The object of this paper is to analyze the effect of ant-hills of *C. punctulatus* on the floristic richness of several plant communities growing on a large chaquenian depression. Our hypotheses are: 1) ant-hills increase the quadrat floristic richness, 2) ant-hills increase the community floristic richness, 3) there are species that grow exclusively or preferentially on the ant-hills in any community, 4) ant-hill exclusive or preferential species are rarities, *i. e.* with low constancy in the community.

MATERIAL AND METHODS

The study area. This work was done in the Submeridional Lowlands, a large depression covering more than 20.000 km² in the central portion of the Santafesinian Chaco (Argentina) between 28°S to 30°S and 60°W to 61°30'W (Lewis & Pire 1981). Climate is warm temperate, humid or subhumid towards the west. The area is often flooded at the end of summer followed by a winter drought of variable length. Soils are halo-hydromorphic and heavy textured. The vegetation of the region was described by Lewis *et al.* (1990a). The most important plant communities are *Elyonurus muticus* savannas, *Spartina argentinensis* tall grasslands and several hygrophilous communities distributed in this order along a topographic elevation gradient (Lewis *et al.* 1990b).

The ant species and their nests. C. punctula*tus* is a Brazilio-Argentinian ant, and it is the most widespread and polymorphic species of the genus in Argentina (Kuznezov 1951). In depressed areas their nests are conical mounds averaging 0.6 m in height and about 1.0 m in diameter (Fig. 1). The structure of the nests was described by Bonetto, Manzi & Pignalberi (1961). Their characteristics and distribution in relation to environment, were analized by Pire *et al.* (1990).

Vegetation and ant-hill analysis. Field data were collected together with the data needed for a phytosociological analysis of the region (Lewis *et al.* 1990a). 671 quadrats were analyzed in spring 1981 and autumn 1982. In each quadrat we recorded presence or absence of ant-hills in the whole stand, independent of their actual presence inside the quadrat. Ant-hill frequency in any given community is the percentage of stands in that community with ant-hills. All species in the quadrat were recorded and whether they grew on the ant-hill or on the surrounding ground or in both places was noted. Floristic richness is the amount of species in each quadrat, and it was divided in the ant-hill component, composed by species which appear on the ant-hills, and the ground component, composed by all the species that grow on the surrounding soil.

Fig. 1: Ant-hills of *Camponotus punctulatus* near Fortín Charrúa, Province of Santa Fe, Argentina.

The effect of ant-hills on floristic richness was calculated, taking into account only quadrats which actually had an ant-hill. The increase in floristic richness due to ant-hills is just the difference between the quadrat floristic richness and its ground component. The significance of differences was tested with Student's test at $p=0.1$ and $p=0.05$.

Within each community species were classified in nine classes according to their relative presence in each component of the quadrat floristic richness (Table 1). Plant communities will be named after the dominant species and / or physiognomy. Nomenclature follows Cabrera (1963, 1965a, 1965b, 1967, 1968, 1970) and Burkart (1969, 1974, 1979).

TABLE 1

Species degree of preference to the two components of the quadrat floristic richness based on the relative presence in each component

Class	Degree of preference	Presence in ground component (%)	Presence in ant-hill component (%)
9	Ground exclusive	100.0 - 90.5	0.0 - 9.5
8	Ground preferent	90.4 - 80.5	9.6 - 19.5
7	Ground preferent	80.4 - 70.5	19.6 - 29.5
6	Ground preferent	70.4 - 60.5	29.6 - 39.5
5	Indiferent	60.4 - 40.5	39.6 - 59.5
4	Ant-hill preferent	40.4 - 30.5	59.6 - 69.5
3	Ant-hill preferent	30.4 - 20.5	69.6 - 79.5
2	Ant-hill preferent	20.4 - 10.5	79.6 - 89.5
1	Ant-hill exclusive	10.4 - 0.0	89.6 - 100.0

RESULTS

Neither all the communities nor all the stands of any given community have *C. punctulatus* ant-hills. In Table 2 the absolute frequency of stands with ant-hills of different communities are given. Communities without ant-hills or with less than 6 quadrats are not in the table. *S. argentinensis* tall grassland has the highest percentage of stands with ant-hills. On better drained soils like *E. muticus* savannas, and lower and more often flooded soils, stands with ant-hills are less frequent. Communities like *Cynodon dactylon* turfs and *Tessaria dodoneaefolia* shrublands, which seem to be the result of soil disturbance, also have relatively low percentage of stands with ant-hills. The only important communities of the region with no ant-hills are the *Ludwigia peploides* meadows, the succulent halophyte community and the "mogotes" of *Cyclolepis genistoides*.

TABLE 2

Absolute frequency of stands with ant-hills of the Submeridional Lowlands' communities

Communities	Total number of stands	Stands with ant-hills	Absolute frequency of ant-hills
Spartina argentinensis	213	198	92.96
Cortaderia selloana	7	6	85.71
Geoffroea decorticans	7	6	85.71
Elyonurus muticus-Spartina argentinensis	21	18	85.71
Distichlis spicata	12	10	83.33
Elyonurus muticus	40	30	75.00
Paspalum intermedium	7	4	57.14
Paspalidium paludivagum	12	6	50.00
Cynodon dactylon	27	13	48.15
Paspalum lividum	21	10	47.62
Tessaria dodoneaefolia	17	8	47.06
Scirpus californicus	72	27	37.50
Typha domingensis	10	3	33.33
Echinochloa helodes	29	8	27.59
Paspalum vaginatum	45	12	26.66
Paspalum distichum	23	6	26.09

The mere presence of ant-hills produces an increase in floristic richness of any quadrat (Table 3). However, the effect of ant-hills on quadrat floristic richness, varies among communities and seasons. The ant-hills in any season produce a highly significant increase of quadrat floristic richness in the *S. argentinensis* tall grasslands. The effect is less marked in plant communities which thrive on higher and better drained soils like *T. dodoneaefolia* shrublands, *E. muticus* savannas and *E. muticus-S. argentinensis* transition

TABLE 3

Increase in quadrat floristic richness due to ant-hill presence for Spring and Autumn in the Submeridional Lowlands' communities.

	Spring				Autumn			
	Average quadrat floristic richness	Average ground component	Increment	Increment in percent	Average quadrat floristic richness	Average ground component	Increment	Increment in percent
Typha domingensis	8.50± 0.71	4.99± 0.01	3.50±0.70	70.0 **	6.50±4.95	4.00± 2.83	2.50±2.12	62.50
Paspalum vaginatum	7.75± 2.87	5.00± 2.45	2.75±1.50	55.0 *	7.25±0.96	4.50±2.08	2.75±2.22	61.10 **
Scirpus californicus	8.87± 2.29	5.73± 1.71	3.13±2.29	54.6 **	10.00±3.57	7.35±3.30	2.65±1.73	36.00 **
Echinochloa helodes	6.00± 2.45	4.00± 1.15	2.00±1.41	50.0 *	5.00±1.41	3.50±2.12	1.50±0.71	42.90
Distichlis spicata	10.57± 6.99	8.00± 5.26	2.57 ±2.15	32.1 *	9.83±5,67	8.66±5.46	1.17± 0.75	13.50
Cortaderia selloana	16.66± 2.89	12.66± 4.16	4.00±3.00	31.6 *	12.25±2.50	13.50±3.32	2.75±1.26	20.40 **
Paspalum lividum	13.40± 4.28	10.40± 4.61	3.00±2.83	28.8 *	10.86±2.54	7.71±2.93	3.14±1.77	40.73 **
Spartina argentinensis	15.28± 6.58	11.91± 6.36	3.38±2.66	28.4 **	14.16±4.56	11.29±4.73	2.86±2.08	25.30 **
Cynodon dactylon	15.50± 5.69	12.25± 3.09	3.25±2.87	26.5 *	14.33±4.23	12.66±3.83	1.66±0.82	13.11 *
Paspalum intermedium	18.00± 3.00	14.33± 4.16	3.66±1.53	25.5 **	17.00±1.41	16.00±1.41	1.00±0.00	6.25
Paspalidium paludivagum	9.75± 3.30	8.25± 2.99	1.50±1.00	18.2	10.00±1.00	8.33±1.15	1.66±0.58	19.90
Tessaria dodoneaefolia	18.75± 4.50	17.00± 5.29	1.75±0.96	10.3	23.00±1.73	21.66±2.08	1.33±0.58	6.10
*Paspalum distichum*Φ	0.00± 0.00	0.00± 0.00	0.00±0.00	0.0	10.66±2.08	9.00±2.00	1.66±0.58	18.40
Elyonurus muticus	24.50± 6.23	22.42± 5.85	2.08±1.44	9.3	19.20±6.06	17.80±6.06	3.40±4.83	19.10
E. muticus-S.argentinensis	23.27± 0.99	21.54± 1.07	1.73±1.79	8.0	18.82±5.91	15.82±6.08	3.00±3.19	19.00 **
Geoffroea decorticans	24.25± 6.99	22.50± 6.14	1.75±1.50	7.8	17.00±1.41	16.00±1.41	1.00±0.00	6.20

** Level of significance at $P < 0.05$.
* Level of significance at $P < 0.1$
Φ Only one relevé with ant-hills in spring.

TABLE 4

Percentage of species for each preference class in the Submeridional Lowlands' communities.

Communities	Season	Total species	Ground component (%) 9	8	7	6	Indiferent 5	Ant-hill component (%) 4	3	2	1 *
Typha domingensis	S	25	72.00				12.00				16.0
	A	30	86.67	6.67			6.67				
Paspalum vaginatum	S	66	87.88	6.06			1.52				4.55
	A	71	90.14	4.22	2.82	1.41	1.41				
Scirpus californicus	S	81	69.14	6.17	6.17	1.23	6.17			1.23	9.88
	A	91	80.22	3.30	1.10	2.20	4.39	2.2			6.59
Echinochloa helodes	S	47	87.23	2.13			6.38				4.26
	A	48	95.83		4.17						
Distichlis spicata	S	56	69.64	1.79	7.14	7.14	1.79			1.79	10.71
	A	42	83.33	2.38	2.38	2.38	2.38			2.38	4.76
Cortaderia selloana	S	75	86.67	1.33	1.33		4.00	2.67			4.00
	A	78	78.00	4.00	4.00		8.00	2.00			4.00
Paspalum lividum	S	62	69.35	1.61	6.45		9.68	1.61			11.29
	A	54	66.67		7.41	5.55	1.85				18.52
Spartina argentinensis	S	213	51.17	11.27	9.86	6.57	7.98	2.82		1.41	8.92
	A	193	59.07	14.51	7.77	5.70	5.70				7.25
Cynodon dactylon	S	93	81.72	5.38	3.23		5.38				4.30
	A	94	87.23	3.19	2.13	4.26	1.06				2.13
Paspalum intermedium	S	60	83.33		1.67	3.33	1.67	1.67			8.33
	A	56	96.40				3.60				
Paspalidium paludivagum	S	44	88.64				4.55	2.27			4.55
	A	33	90.91	3.03					3.03		3.03
Tessaria dodoneaefolia	S	104	90.38	1.92	1.92	1.92					3.85
	A	106	94.34	2.83	0.94						1.89
Paspalum distichum	S	42	97.62		2.38						
	A	50	92.00	4.00		2.00					2.00
Elyonurus muticus	S	171	87.72	7.02	1.75	1.17	0.58				1.75
	A	155	97.42	0.64	0.64		0.64				0.64
Elyonurus muticus-Spartina argentinensis	S	118	82.20	5.93	5.08	1.69	0.85				4.24
	A	97	78.35	5.15	6.19	1.03	4.12	1.03			4.12
Geoffroea decorticans	S	72	86.11	2.78	1.39	6.94	2.78				
	A	70	82.86	2.86	7.14	2.86	1.43				2.86

S: Spring
A: Autumn

* Classes as shown in Table 1

community, where the increase in quadrat floristic richness may be insignificant. In communities that are in lower and more often flooded soils like the Typha domingensis community, *Paspalum vaginatun* turfs, *Scirpus californicus* rushes and *Echinochloa helodes* prairies, the effect on quadrat floristic richness is more marked, with the exception of *Paspalidium paludivagum* meadows. The effect of ant-hills on quadrat floristic richness, although there are exceptions, is less marked in autumn than in spring.

In all communities most species are exclusively or preferentially in the ground component and very few are restricted or preferential to the ant-hills (Table 4). Although there is not clear cut evidence, communities in frequently flooded soil, such as the *T. domingensis* community, rushes or *Paspalum lividum* prairies, have a higher percentage of ant-hill exclusives than communities on better drained soils like the *E. muticus* savannas, *T. dodoneaefolia* shrublands, *Geoffroea decorticans* islets or *C . dactylon* turfs; even the *E. muticus-S. argentinensis* transition community has fewer ant-hill exclusives than the pure *S. argentinensis* grassland, and the former is in better drained soils than the latter.

The ant-hill exclusive and preferential species of all communities in spring and autumn, together with their behaviour in other

TABLE 5

Species degree of preference for each Submeridional Lowlands' community in Spring. *

	Typha domingensis	*Scirpus californicus*	*Echinochloa helodes*	*Paspalidium paludivagum*	*Paspalum lividum*	*Paspalum vaginatum*	*Paspalum distichum*	*Paspalum intermedium*	*Distichlis spicata*	*Cortaderia selloana*	*Spartina argentinensis*	*Geoffroea decorticans*	*Cynodon dactylon*	*Tessaria dodoneaefolia*	*E. muticus-S. argentinensis*	*Elyonurus muticus*	*Constancy* * *			
Eupatorium candolleanum	1	9	9					4		9	8		9	9	9	9	I			
Ludwigia longifolia	1										9						I			
Stemodia lanceolata	1	5						9		9	6		9	9	9	8	I			
Baccharis pingraea		1									6	9		9	9	9	I			
Oxalis sp.		1			4			9			9	9					I			
Teucrium cubense		1						8									I			
Mikania periplocifolia	9	8	5	5	8	1	9		9	8	6	9	9	9	8	9	I			
Conyza bonariensis	5	5			1				6	9	7	6	9	9	9	9	I			
Apium leptophyllum					1				9	9	6	7	5	9	9	9	I			
Heimia salicifolia					1			5		9	6			9	7	9	I			
Rumex crispus		9	9	9	1			9		9	9		9	9	9	9	I			
Verbena gracilescens					1			9		9	8		9		9	9	I			
Euphorbia serpens		9	9	9	9	9	9	9	1	9	8	9	9	9	8	8	I			
Gamochaeta subfalcata					9				1	9	8	9	9	9	9	9	I			
Plantago myosurus		7		9	9	9	7	6	1	9	8	9	7	9	9	9	I			
Cuscuta sp.						9				1	9		9				I			
Morrenia odorata								1				9					I			
Undetermined *Gramineae*								1		9	9					9	I			
Amaranthus muricatus											1						I			
Tweedia brunonis											1	9		9			I			
Baccharis coridifolia											1					9	I			
Baccharis sp.											1						I			
Bothriochloa edwarsiana											1						I			
Chloris halofila											1	9		9			I			
Undeterm. *Convolvulaceae*											1					6	I			
Euphorbia sp. (UNR 3675)											1		9				I			
Holmbergia tweedei											1			9	9	9	I			
Indigofera asperifolia											1					9	I			
Maytenus vitis-idaea											1			9	9		I			
Porophyllum ruderale											1			9			I			
Salpichroa origanifolia											1						I			
Sida rhombifolia		9									1						I			
Vernonia rubricaulis											1				9	9	I			
Wedelia brachycarpa											1						I			
Elyonurus muticus										5	5	9	1	8	6	8	I			
Bothriochloa hassleri										9	4		1	6		7	I			
Schizachyrium sp.										9			1	9	9	5	I			
Commelina sp.														1	9		I			
Rhynchosia senna											6			1	9	8	I			
Cortaderia selloana								9		5	4				1		I			
Nierembergia stricta																1	I			
Solidago chilensis			1		9			1		5	4	9		9		9	I	I		
Apium sellowianum	1	2					9		9		5		5	9	9	1	I	I		
Chaetotropis chilensis	5	1		9	5	1			7	9	7	9	9	9	9	9	I	I		
Nierembergia sp. *(UNR 3393)*		1				1				9	9					9	I	I		
Sphaeralcea chenopodifolia		1	1														I	I		
Vernonia sp.		1						9			6		9		9	1	I	I		
Neptunia pubescens		9		1				6		6	5		1	9	7	8	I	II		
Cirsium vulgare									1	9	4				1	9	I	I		
Ruellia tweediana					7			9	1	1	6	9	9	9	9	9	I	I		
Asclepias mellodora											1				1	9	I	I		
Modiolastrum gilliesii											1				1	9	I	I		
Stipa neesiana									9		1	9		1		9	I	I		
Bothriochloa laguroides				1	1			1		9	5			9	9	9	I	I	I	
Phyla canescens		6		9	1	8	9	1	1	9	7	6	9	9	8	9	I	I	I	
Desmanthus chacoensis		1			9					1	7			1	1	9	I	IV	I	II
Bothriochloa saccharoides											2				7	9	I			
Galactia sp.											2						I			
Senecio argentinus											2						I			
Spartina argentinensis	5	5	5	4	5	8	9	7	7	7	8	9	9	9	9	9	II			
Heliotropium curassavicum	9	8		9		9	9		4	9	7	8	8	9	7	9	IV			
Leptochloa chloridiformis											4	9	5	9	8	9	I			
Pappophorum pappiferum											4			9	5	9	I			

* Numbers correspond to classes in Table 1.

** Constancy classes for each species in the community where it appears as ant-hill exclusive or it has the highest ant-hill degree of preference. I: 0-20%, II: 21-40%, III: 41-60%, IV: 61-80%, V: 81-100%. Species indiferent, preferential or exclusive of the ground component for all communities were eliminated from this table.

TABLE 6

Species degree of preference for each Submeridional Lowlands' community in Autumn. *

	Typha domingensis	*Scirpus californicus*	*Echinochloa helodes*	*Paspalidium paludivagum*	*Paspalum lividum*	*Paspalum vaginatum*	*Paspalum distichum*	*Paspalum intermedium*	*Distichlis spicata*	*Cortaderia selloana*	*Spartina argentinensis*	*Geoffroea decorticans*	*Cynodon dactylon*	*Tessaria dodoneaefolia*	*E. muticus-S. argentinensis*	*Elyonurus muticus*	*Constancy* * *			
Chaetotropis chilensis		1		9					9		9						I			
Apium sellowianum		1									6		9	9			I			
Vernonia sp.		1						5		9	8		9		9	9	I			
Eryngium ebracteatum	9	1			9					9	8			9	9	9	I			
Melilotus sp.				9	1	9					9			9			I			
Verbena gracilescens		9			1					9	9		9			9	I			
Stemodia lanceolata				9	1				9	9	6			9	6	7	I			
Ruellia tweediana		9	9		1		9			5	8	9	9	9	8	9	I			
Conyza bonariensis	5	6			1			9	9	9	8	9	7	9	9	9	I			
Euphorbia serpens	9			9	1	8	9		9	9		9	9	9	9	9	I			
Conyza chilensis									1		9			9	9	9	I			
Bothriochloa hassleri									1	9	5		5	7	7	9	I			
Plucchea sagittalis		9				9		9		1	7	7	9	9	9	9	I			
Bothriochloa edwardsiana											1						I			
Undetermined Gramineae											1						I			
Solanum amygdalifolium											1						I			
Wedelia glauca											1						I	I		
Abobra tenuifolia											1			9			I			
Asclepias mellodora											1					9	I			
Opuntia sp.											1					9	I			
Verbena sp.											1					9	I			
Schkuria pinnata						9					1						I			
Maitenus vitis-idaea											1			9	9		I			
Pappophorum pappiferum											1			9	5		I			
Modiolastrum gilliesii		9									1					9	I			
Holmbergia tweediei											1	9		9	9	9	I			
Amaranthus viridens												1					I			
Neptunia pubescens		9	9			9	9	9	9	9	8	1	9		8	9	I			
Verbena intermedia								9			9		1	9		9	I			
Phyla canescens		7			9	6	9			9	8	7	9	1	6	9	IV			
Undetermined Asclepiadaceae											9	9			1		I			
Polygonum sp.											9		9		1		I			
Hyptis tetragona																1	I	I		
Elyonurus muticus		1					1		9	5	6	9	9	8	7	9	I	I		
Bothriochloa laguroides		2		1	1			9		9	5	6		9	5	9	I	I		
Sorgastrum agrostoides			9		1			9		1	8				9	9	I	I		
Apium leptophyllum		9	9		1				9	9	8	9	1	9	9	9	I	I		
Solidago chilensis	9	4	9		1			5		2	3	9	9	1	2	9	I	I	I	I
Physalis viscosa		1									1				1	1	I	I		
Bothriochloa saccharoides											2				7	9	I			
Desmanthus chacoensis		2	9		5	9	9	9		9	7	9	9	9	8	9	I			
Senecio argentinus											3						I			
Spartina argentinensis	5	5	7	3	7	8		9	7	8	8	9	8	9	9	9	II			
Heliothropium curassavicum		9				9	9		4		5	9	6			9	II			

*, **: as in Table 5.

communities, are shown in Tables 5 and 6. Ant-hill exclusives in one community may be ground exclusives in other communities, but very seldom is a species an ant-hill exclusive in several communities; the most exceptional ones are *Desmanthus chacoensis* in spring, and *Physalis viscosa* in autumn.

Ant-hill exclusives very seldom are constant species of the communities; their constancy is almost always less than 20 %, that is, they are rarities of the communities. The only exceptions are: *D. chacoensis* in two communities and *Ruellia tweediana*, *Phyla canescens* and *Neptunia pubescens* only in one community each. Ant-hill preferentials are also rarities of their communities, the exeptions being *Heliotropium curassavicum* in *Distichlis spicata* turfs and *S. argentinensis* in *P. paludivagum* meadows.

DISCUSSION

The nests of *C. punctulatus* are mounds only in lowlands, elsewhere their architecture is different (Kuznezov 1951) and it has been suggested that they are a flood escape strategy of the ant colony (Pire *et al.* 1990). Therefore it should be expected that the higher the soil of a community the lower the frequency of ant-hills. This explains why the percentage of stands of *E. muticus* savannas with ant-hills is lower than in the *S. argentinensis* grasslands; however though the frequency of *E. muticus* stands with ant-hills is lower than the *S. argentinensis* ones, the actual density of ant-hills in those stands may be significantly higher (Pire *et al.* 1990). On the other hand there seems to be a water level where these ants can not build their nests; so on stands permanently flooded, or flooded during very long periods, there are no ant-hills, which explains why the percentage of hygrophilous communities stands with ant-hills is lower than in the *S. argentinensis* grasslands which thrive in relatively higher soils, and also the actual density of ant-hills in hygrophilous stands is lower than in higher soils (Pire *et al.* 1990). Meadows of *L. peploides* are in small size ponds which are almost always flooded, surrounded by comparatively higher soils that offer a relatively better substrate for mound building, explaining why there are no ant-hills in these stands. The problem of succulent halophytes communities may be different; they are on the overflow of rivers covered by a salt layer when dry and with very low plant coverage (Lewis *et al.* 1990a), apparently an unsuitable environment for *C. punctulatus*. When a stand is ploughed, the ant-hills are destroyed, so any community affected by this type of disturbance, like the *C. dactylon* turfs, is likely to have relatively few stands with ant-hills, unless a rather long time has elapsed since it was last ploughed.

The ant-hill environment differs from the ground environment in soil texture, structure and chemical composition (Bonetto, Manzi & Pignalberi 1961), and the water level is different in both sites. However, in hygrophilous communities the difference is more marked than in communities which thrive in better drained soils, even if it is only a matter of water table. In a rush, the water table may be from 10 to 30 cm above ground level, while the ant-hill summit is well above 30 cm from the water table. In an *E. muticus* savanna the ground is seldom flooded, so that the moisture of both sites (ground and ant-hill) can be expected to be similar, or at least not very different. Moreover, in lower soils, ant-hills tend to be higher (Pire *et al.* 1990). These facts may account for the marked difference of the effect of ant-hills on the quadrat floristic richness between such pond communities like *T. domingensis* and *S. californicus* communities, and relatively high soil communities such as *T. dodoneaefolia* shrublands and *E. muticus* savannas. Seasonal difference in the effect of ant-hills on quadrat floristic richness are not easy to explain, and may be correlated to species growth forms or phenology, but the problem needs further clarification.

There are not any characteristic species of ant-hill, that is, species that in any community, or whenever they are present, grow only on the ant-hill, while there are many species that are exclusive of the ground component throughout. *D. chacoensis* is an ant-hill exclusive in four communities in spring, but it is a ground exclusive in *E. muticus* savannas, *S. argentinensis* grasslands and *P. lividum* prairies and in autumn thrives in the ground as well in several communities, and *P. viscosa* which is an ant-hill species in four communities in autumn is an extreme rarity within the region.

Data presented here give strong support to the hypothesis that ant-hills increase quadrat floristic richness and that in each community there are species that grow exclusively or preferentially on the ant-hills. But as ant-hill exclusives and preferentials are only a low percentage of the total amount of species of most communities the effect of the ant-hills on the floristical richness of the communities is not as strong as in the case of quadrats. There is also a strong support to the hypothesis that ant-hill exclusives and preferentials are rarities within the communities as very few of them have constancy values above 20 %. As most ant-hill species are rarities within the communities where they appear as such, the most conclussive evidence is that ant-hills are refugia for these species and provide a suitable microsite in an environmental otherwise unsuitable for them.

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RESUMEN

En este trabajo se analiza el efecto de los hormigueros de *Camponotus punctulatus* (Mayr) sobre la riqueza florística de las comunidades de una extensa área deprimida en el Chaco austral. Los hormigueros son montículos cónicos de 0.60 m de altura promedio y alrededor de 1.0 m de diámetro, los cuales producen un incremento de la riqueza florística de la muestra. El porcentaje de especies que crecen exclusiva o preferentemente sobre los hormigueros es bajo; por lo tanto el efecto de los hormigueros sobre la riqueza florística de la comunidad es menor que el efecto que producen sobre aquella de las muestras. Las especies exclusivas o preferentes del hormiguero son raras, esto es, tienen menos de 20 % de constancia en todas las comunidades. Los hormigueros son refugio que permiten que crezcan especies en un ambiente de otro modo inapropiado para ellas.

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