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The significance of ant-hills in depressed areas of the Great Chaco

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Abstract. Ant-hills of *Camponotus punctulatus* (Mayr.) are common in Chaquenian depressed areas. We studied density, spatial distribution, shape and size of ant-hills in the Submeridional Lowlands of the Chaco. As an average there are 500 ant-hills/Ha that are conical mounds 0.62 m high covered with vegetation. Their density increases in relatively high soils, they are taller the lowest the soil, and tend to be uniformly distributed. They seem to be a flood escape mechanism of the ant colony, and are a major disturbance that has an effect on vegetation pattern and floristic richness.

Key words: ant-hills, *Camponotus punctulatus,* Chaco, disturbance, microsites.

The Chaco is a large area of the Neotropical region that spreads over W. Paraguay, E. Bolivia, N. Argentina and parts of S. Brazil (Cabrera & Willink 1973). The Submeridional Lowlands are in the S. Chaco between 28° S to 30° S and 60° W to 61° 30' W (Lewis & Pire 1981) and they are the most important depressed area of the Chaco, with a NW-SE general slope of very low energy (1.10 o/ooo). Climate is warm-temperate, humid or subhumid, and as a result of local rainfalls, overflows from neighbour areas and slow runoff, the area is often flooded at the end of summer. Soils are halo-hydromorphic with heavy texture. Like in other periodically flooded areas of E. Chaco (Morello & Adámoli 1974), *Camponotus punctulatus* (Mayr.) ant-hills are very common in this area (Fig. 1a,b). *C. punctulatus* is a widespread and polymorphyc Brazilio-argentinian ant (Kuznezov 1951) that builds mounds locally known as "tacurúes", in often flooded areas, while elsewhere their nests have different architecture. The individual mounds structure was described by Bonetto, Manzi & Pignalberi (1961). In this paper we analyse the characteristics and spatial distribution of *C. punctulatus* ant-hills in the Submeridional Lowlands and discuss their significance in site pedoturbation and heterogeneity.

MATERIAL AND METHODS

Nine sites representing different environments were chosen. Their order along the elevation gradient from the lowest to the highest is: 1, 4, 7, 3, 6, 2, 5, 9 and 8 as shown in Fig. 2. *Spartina argentinensis* grasslands with hygrophytes and rush (*Scirpus californicus* (Mey.) Steudel) patches are in low soils, and in relatively higher soils there are savannas. Site 8 is in the highest soil but it has been cultivated and abandoned for four years. Ant-hills were counted in five 225 to 2,500 m^2 quadrats laid at random in each site. In three out of the five quadrats (only one in site 8 and two in site 9) size and distance of each mound to its three nearest neighbours were measured. Site characteristics, ant-colony activity and mounds conservation state were recorded. As data were not normally distributed, non-parametric methods were used. Ant-hills density in different sites was compared with Friedman's (1937) method. Ant-hill sizes within each site were analysed with Kruskal-Wallis and Mann-Witney tests, and as in some cases ant-hill sizes within the site were statistically different, all quadrats were analysed together independently of sites with Kruskal-Wallis test and then they were compared with Dunn's test (Hollander & Wolfe 1973). As in

Fig. 1a: Ant-hill of *Camponotus punctulatus*.

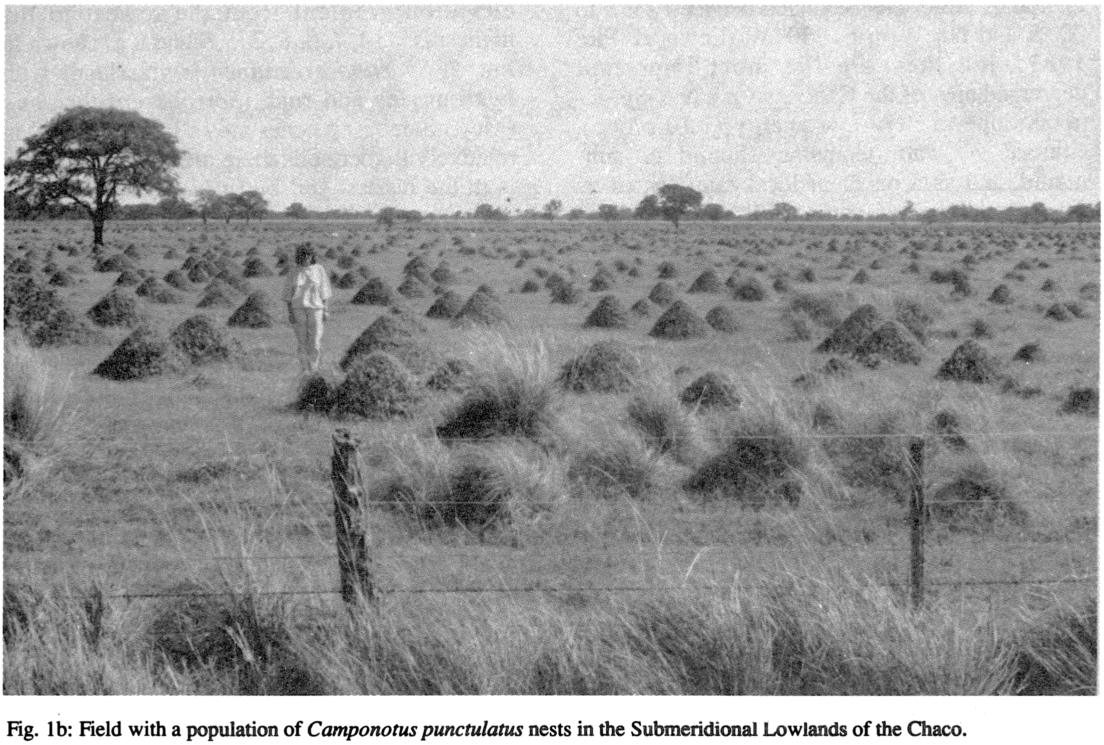

Fig. 1b: Field with a population of *Camponotus punctulatus* nests in the Submeridional Lowlands of the Chaco.

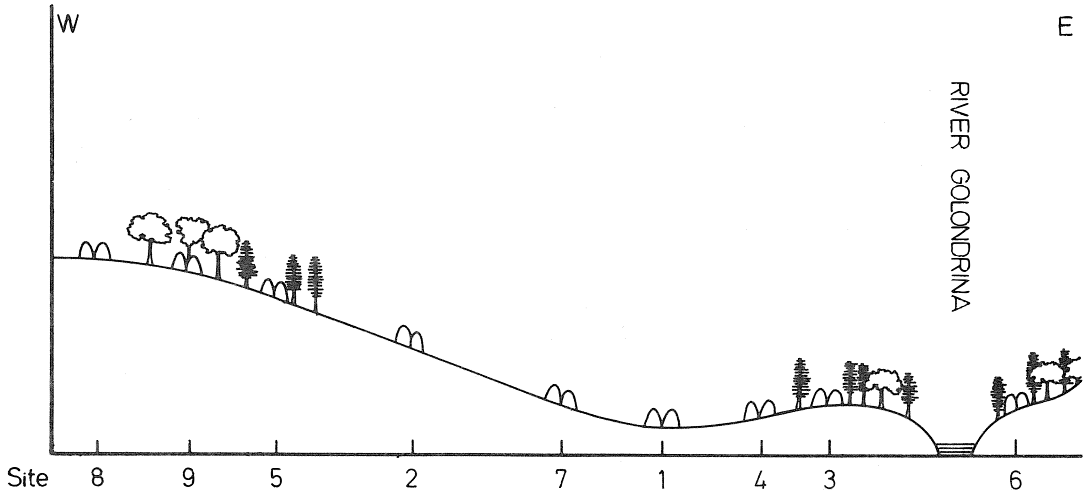

Fig. 2: Relative position of sites on an idealized profile of the region.

Dunn's test is subjective, data were iteratively analyzed with α=0.05 increments until in two succesive levels did not appear significant differences. Spatial distribution was analysed with the n-nearest neighbour method (Clark & Evans 1954, Thomson 1955).

TABLE 1

Density of ant-hills in the nine sites (N/Ha) and the significance of differences between sites

Site	1	4	7	3	6	2	5	9	8
$\bar{x}$	244.0	313.6	323.2	409.6	571.8	614.0	789.0	798.0	440.0
σ	48.6	70.3	52.7	24.2	62.6	137.5	189.1	---	
1	-				*	*	*	*	
4		-				Θ	*	Π	
7			-			Θ	*	Θ	
3				-			Π		
6					-				
2						-			
5							-		
9								-	
8									

* p= 0.05   p= 0.1   Θp=0.2   Π p= less than 0.2

RESULTS

Density varies from 212 to 1,152 ant-hills per hectare with a grand mean of 500.43 (Table 1). These densities are lower than those estimated by Bonetto, Manzi & Pignalberi (1961). Density increases in relatively higher soils and is significantly larger in savannas than in depressions. Cultivation also depressed density as it is shown by site 8. Neighbour ant-hills mean distance is 2.75m and ranges from 1.7 to 4.2m. Clark and Evans (1954) aggregation indices are in Table 2; they show that in 59.72% cases ant-hills spatial distribution is uniform, in 31.94% random and only in 8.33% grouped. Similar results (55.56% U, 34.71% R, 9.72% G) were obtained with Thomson's (1955) method. It seems that spatial distribution is slightly more uniform in harsh environments as well as in recently cultivated fields, than in higher soils where there is more aggregation. Aggregation increases from first to third neighbour's level, but it is always low.

Ant-hills are conical with an oval base. The mean basal major diameter is 1.17 m with an absolute maximum of 2.60 m and the mean minor diameter is 0.99 m with an absolute minimum of 0.15 m. Ant-hill heights are shown in Table 3; the grand mean is 0.62m with an absolute maximum of 1.85m and we considered 0.15m as the minimum height, though we observed ant-hills that were begining to be built with even lower heights. In most cases there is no significant difference between ant-hills heights from different quadrats or sites. However, ant-hills heights of five quadrats (3, 4, 11, 19, 21) were significantly different from those of other quadrats, even on the same site (Fig. 3). There is a group of quadrats (3, 11, 4) which have the highest ant-hills, quadrats 3 and 11 are in sites 1 and 4 which are in the lowest soils and other site 1 ant-hills are relatively tall

TABLE 2

Aggregation indices between 1st., 2nd. and 3rd. neighbours (Clark & Evans, 1954)

Sites / Quadrats		1	4	7	3	6	2	5	9	8
1	1st N	1.31 U	1.12 U	1.09 R	0.93 R	1.16 U	1.10 U	1.59 U	0.97 R	1.75 U
	2nd N	1.17 U	1.05 R	1.34 U	1.07 R	1.09 R	1.06 R	1.29 U	0.92 R	1.28 U
	3rd N	1.24 U	1.05 R	1.08 R	1.10 U	1.03 R	1.04 R	1.32 U	0.88 G	1.31 U
2	1st N	1.23 U	1.42 U	1.08 R	1.22 U	1.30 U	0.91 R	1.19 U	0.79 G	
	2nd N	1.22 U	1.16 U	1.02 R	1.16 U	1.16 U	0.93 R	1.09 U	0.76 G	
	3rd N	1.10 U	1.14 U	0.98 R	1.23 U	1.09 R	0.93 R	1.15 U	0.78 G	
3	1st N	1.30 U	1.22 U	1.37 U	1.09 R	1.36 U	0.90 R	1.43 U		
	2nd N	1.15 U	1.17 U	1.27 U	1.15 U	1.17 U	0.87 G	1.23 U		
	3rd N	1.07 R	1.27 U	1.25 U	1.25 U	1.14 U	0.86 G	1.25 U		

Spatial distribution: Grouped < 0.9; Random 0.9-1.10; Uniform >1.1

TABLE 3

Ant-hill heights (m)

Quadrats	1		2		3	
Sites	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ
1	0.69	0.23	0.73	0.27	0.87	0.18
2	0.78	0.25	0.62	0.22	0.64	0.18
3	0.58	0.19	0.63	0.17	0.59	0.14
4	0.57	0.11	0.86	0.29	0.62	0.18
5	0.64	0.24	0.56	0.10	0.68	0.71
6	0.68	0.27	0.71	0.40	0.72	0.24
7	0.33	0.19	0.48	0.12	0.42	0.11
8	0.51	0.06	---	---	---	---
9	0.56	0.19	0.61	0.11	----	---

as well, so it seems that mounds tend to be higher the lower the soil, but this is not the case of other ant-hills in site 4. However, the lowest ant-hills are in quadrats 19 and 21 which are in site 7 that is next to site 4 in the elevation gradient, but these ant-hills were eroded and the site had strong disturbance signs.

DISCUSSION

As some species of ant-hills are especially oriented and exposed to the sun, it has been suggested that mound building is a thermal absorption and thermo-regulation adaptative mechanism (Galle 1973, Hubbard & Cunningham 1977, Castello & Arias-de-Reyna 1982). *C. punctulatus* builds mounds only in depressed areas; the mounds are not especially oriented and they are shaded by vegetation, therefore there is little support for the thermo-regulation hypothesis. Unless mounds are eroded, they tend to be higher the lower the soil, and they are taller in rushes (which are flooded almost the whole year), than in the savannas that are on fairly well drained soils and are very seldom flooded. Therefore, this suggests that mound building is a flood escape mechanism.

Ant-hill regional significance is far greater as a major pedoturbation and landscape feature. There is an average earth movement of 92m3/Ha that in some cases can be as large as 385m3/Ha; soil is brought up from lower horizons, changing its texture, structure and most physico-chemical properties (Bonetto, Manzi & Pignalberi 1961, Baxter & Hole 1967, Bucher 1980). Also in these flat areas with low energy relief, ant-hills of this size are among the major topographic accidents.

Vegetation pattern and species diversity may be correlated among other things to environmental heterogeneity (Bazzaz 1975, Grieg-Smith 1979, Shmida & Wilson 1985). Site heterogeneity may be the result of topography and microrelief, hence, if ant-hills are major topographic accidents they should have an effect on floristic richness. This fact has usually been overlooked, though Thomas (1962) noticed that species growing on ant-hills were quite different from those on the surroundings. The effect of ant-hills of *Lasius flavus* on the vegetation was reported by Grubb, Green & Merrifield (1969), Woodell (1974), Wells *et al.* (1976) and King

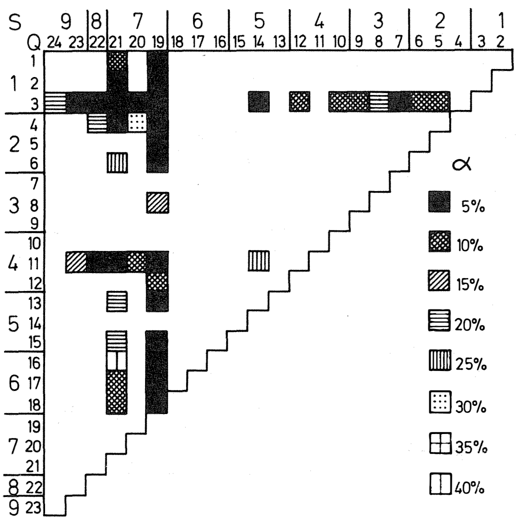

Fig. 3: Significant levels of height differences between ant-hills from all quadrats.

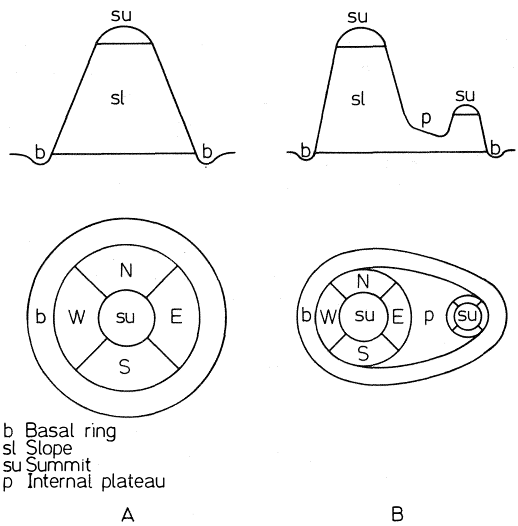

Fig. 4: Ant-hills microsites. A: Normal ant-hill, B: Eroded and recolonized ant-hill.

(1977a,b,c). It was also suggested that ant-hills of *C. punctulatus* were an important factor in the development of floristic richness (Lewis *e t al.* 1990, Lewis, Stofella & Franceschi 1990).

The building of ant-hills contribute to the creation of microsites where certain species can thrive. The microsites created by their presence is illustrated in Fig. 4. The soil around the ant-hill subsides creating the basal ring, then the slope according to exposition has different microsites and the summit is another one. If the mound is eroded and recolonized, there may be an internal plateau with a different environment and one or more new cones. As a whole, the environment on the ant-hill differs from the ground environment, as follows, in order of importance: 1) the top of the ant-hill is farther off from the water table than the ground soil, thus flood and water-logging is less intense and the soil is better aerated; 2) soil is brought up from below and is likely to be less alkaline and not so heavy textured; 3) the temperature regime is more extreme, hotter during the day in the summit and N slope and cooler on the S slope; all these characteristics are more favorable for less harsh tolerant species. But also: 1) soil is continually being brought up in live hills so that the plants are smothered; this is especially so with *S. argentinensis* tussocks; 2) plants may be harmed by root and shoot aphids raised by the ants; 3) seeds may be selectively eaten or buried too deep by ants for successful germination and 4) disturbance due to scratching and grazing, compactation by roosting birds and snakes may be greater, armadillos dig them up seeking ants for food; all these factors are or can be harmful to vegetation.

Some of these environmental factors arising from the presence of ant-hills of *C. punctulatus* are similar and others just the opposite as those arising from the presence of *Lasius flavus* ant-hills in British chalk grasslands (Grubb, Green & Merrifield 1969). However, the effect of ant-hills on floristic richness is in need of further research, and the effect of other species of ant-hills should be analysed before generalizations can be made.

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RESUMEN

Los hormigueros de *Camponotus punctulatus* (Mayr) son frecuentes en áreas deprimidas del Chaco. Estudiamos la densidad, distribución espacial, forma y tamaño de estos hormigueros en los Bajos Submeridionales del Chaco. Hay un promedio de 500 hormigueros/Ha que son

montículos cónicos de 0.62 m de altura cubiertos por vegetación. Su densidad aumenta en los suelos relativamente más altos, mientras que su altura es mayor cuanto mas bajo es el suelo, y tienden a estar uniformemente distribuídos. Aparentemente son un mecanismo de escape de las colonias de hormigas a las inundaciones. Es uno de los mayores disturbios de la región que puede tener un efecto importante en el diseño de la vegetación y en su riqueza florística.

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