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Influence of nests of leaf-cutting ants on plant species diversity in road verges of northern Patagonia

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Abstract. It has been suggested that ant nests are the most frequent small-scale disturbance that affect vegetation patterns. However, their effects on plant diversity are little studied. We document effects of nests of the leaf-cutting ant *Acromyrmex lobicornis* on physical-chemical soil properties and their influence on plant diversity near road verges in a desert steppe in NW Patagonia, Argentina. We analysed nest soils and controls for nitrogen, phosphorus, organic matter, moisture retention capacity and texture. We also analysed the vegetation on 42 nests (30 active and 12 abandoned or without life) and 42 areas without nests. Soil around nests had a greater nutrient content and capacity to retain moisture than control soils, which is mainly due to the presence of organic waste that the ants deposit on the soil surface. We found no association between the occurrence of nests and specific groups of plants, but plant diversity was higher at nest-sites than at nearby non-nest sites. This increased diversity – which is also found on abandoned nests – is mainly due to the occurrence of a larger number of native and exotic plant species on nest-sites that are uncommon elsewhere in the study area. The most abundant plant species showed similar cover values at nest and non-nest sites. This suggests that changes in diversity are associated to edaphic changes caused by nests rather than by changes in competitive balance caused by dominant species exclusion. We propose that the nests of *Acromyrmex lobicornis*, through increasing the availability of resources, generate favourable microsites that can function both as 'refuges' for less frequent native species, and as 'stepping stones' for less frequent exotic plant species.

Keywords: *Acromyrmex lobicornis*; Disturbance; Plant diversity; Soil disturbance.

Nomenclature: Correa (1969-1998).

Introduction

The occurrence of biological disturbances introduces a major source of variation to community composition. Disturbances influence the abundance and distribution of species through changes in the environment, and the spatial and temporal distribution of resources (Pickett & White 1985). Species are affected both through the modification of habitat condition and by direct impact upon individuals. Natural disturbances have been proposed to be a major factor responsible for increased diversity in terrestrial plant communities in tropical environments (e.g. Brokaw 1982; Denslow 1985) as well as in temperate (Runkle 1982; Armesto & Pickett 1985) and boreal forests (e.g. Angelstam 1998). This increased diversity is due to disturbances that facilitate persistence of plants currently less frequent in the community. Increased persistence of uncommon plant species occurs through at least two non-exclusive mechanisms: when the disturbance eliminates biomass of dominant species and therefore prevents the monopolization of some limiting resource (Grime 1979; Armesto & Pickett 1985); and/or when it increases resource availability, offering regenerative conditions different from those of the surroundings (Grubb 1977; Fox & Fox 1986).

Ant nests are recognized as one of the most important small-scale, natural disturbances that affect vegetation (Loucks et al. 1985; Woodell & King 1991). To construct and maintain their nests, the ants clear the surface of vegetation and mobilize large quantities of soil. They also concentrate organic matter of plants or insects from the surrounding area in or near the nest. The organic wastes produced by the colony are deposited in subterranean chambers or on the surface of the soil. As a consequence of these activities, the dominant species of the vegetation can become less frequent near the nest, and ant nest soils can differ in their physical-chemical properties from adjacent soils (Salem & Hole 1968; Petal 1978; Mandel & Sorenson 1982; Beattie & Culver 1983; Culver & Beattie 1983; Gotwald 1986; Laundré 1990; Pire et al. 1991; Lesica & Kannowski 1998). Ample evidence exists suggesting that, due to these modifications, the composition and abundance of vegetation near ant nests generally differ from adjacent areas (Beattie & Culver 1977, 1981; King 1977; Horvitz & Schemske 1986; Woodell & King 1991; Lessica & Kannowski 1998). However, effects on plant diversity are contradictory: while some studies find an increase in diversity near the nests (Beattie & Culver 1977; Lewis et al. 1991), others indicate a decrease (Culver & Beattie 1983; King 1977).

Leaf cutting ants (*Atta* and *Acromyrmex* spp.) greatly modify the environment surrounding their nests, offering an excellent opportunity to study the effects of natural, small-scale disturbances on vegetation. Their large nests can house hundreds of thousands of ants, remain active from 10 to 20 yr, modify the soil at a depth of up to 7 m, and affect up to 100 m^2 of surface area (Weber 1982; Cherrett 1989). Additionally, by cutting large quantities of plant material (which they use to cultivate fungus, food for the majority of the colony), leaf-cutting ants can modify the cover of certain species of plants near the nest (Cherrett 1989). In tropical and subtropical environments the way in which these nests modify the physical-chemical structure of the soil and affect vegetation is well documented (Haines 1975, 1978; Jonkman 1978; Alvarado et al. 1981; Farji-Brener & Silva 1995a, b, 1996). However, almost no information exists concerning the effects of ant nests in temperate environments, in spite of the fact that leaf-cutters can be abundant and ecologically important in those systems (Weber 1966; Farji-Brener 2000).

Acromyrmex lobicornis is the leaf-cutting ant species with the widest latitudinal range in temperate environments, reaching from ca. 23° S to 44° S (Farji-Brener & Ruggiero 1994). This ant species is very abundant in Patagonia, especially in highly disturbed steppe areas such as road verges (up to 43 nests/ha; Farji-Brener 2000). In this study we document modifications that the leaf-cutting ant *Acromyrmex lobicornis* creates in its environment, and determine the existence of vegetation changes associated with these modifications. In particular, we ask the following questions: Do nests modify surrounding soil characteristics? Is the nearby vegetation of *Acromyrmex lobicornis* nests different from sites without nests in terms of composition or diversity? Do these changes remain when the colony abandons the nest or dies?

Methods

Study area, plant community and leaf-cutting ant species

We conducted the study on the eastern border of Nahuel Huapi National Park in NW Patagonia, Argentina (41°S, 71°W). The mean annual temperature is 8 °C and the mean annual precipitation ca. 600 mm. We conducted surveys near road verges covered by herbaceous/shrub steppe vegetation. The study area was selected following an initial study in Patagonia which showed that *Acromyrmex lobicornis* is only present near road verges whereas this ant species is almost absent in areas distant from roads (Farji-Brener 1996, 2000). Given the degree of disturbance in the study area, the dominant vegetation is a mixture of native species typical of Patagonian steppes such as *Stipa speciosa*, *Mulinum spinosum*, *Imperata condensata*, *Plagiobothrys tinctoreus* and *Baccharis pingraea*, and exotics such as *Bromus tectorum*, *Onopordon acanthium*, *Carduus nutans* and *Verbascum thapsus* (Correa 1969-1998; Roig 1998).

A. lobicornis is the only leaf-cutting ant inhabiting NW Patagonia (Farji-Brener & Ruggiero 1994), and their nests are conspicuous components of the habitat. *A. lobicornis* nests reach depths of ca. 1 m, and on the soil surface the ants construct a mound of twigs, soil and dry plant material, which may reach a height and width of up to 1 m. Inside this mound, the ants grow the fungus on which they feed. Refuse, i.e. ant organic waste – such as organic material from the fungus culture, dead ants and debris – are removed from the internal fungus garden to the soil surface. The refuse is deposited in a few conspicuous and large piles on the soil surface near the mound, which makes it accessible to nearby plants (Fig. 1). These nests can be constructed on bare ground or at the base of certain plant species, which may be partially eliminated by the ants by being cut or buried. The area most affected by the nest presence can range between 10-30 m^2.

Sampling

To study vegetation associated with nests we measured cover of all vascular plant species around 30 active nests, 12 abandoned nests, and at 42 sites without nests. We collected the data towards the end of the spring of 1996, when annual plant species were present. Nest-sites were randomly selected from six survey areas of 20 m × 100 m located nearby road verges. Selected nest-mounds ranged between 70-100 cm in diameter and 50 - 80 cm in height, with a low coefficient of variation among selected mounds (CV = 16% and 12%, for diameter and height, respectively). Sites without nests (controls) were chosen from each nest-mound by selecting random angle measurements from 0-360° and random distances between 5-10 m using the algorithm proposed by Skalski (1987). We used the range of 5-10 m in order to locate the control sites away from the influence of the focal nest and their nearest neighbour nest. The abandoned nests were easily distinguished from active nests by a partially or completely broken mound, absence of ants during the entire sampling period, and little or no presence of refuse dump on the soil surface. Whit this sample design, each site without a nest (control) was paired with a site in which either abandoned or active nests were present. Thus, plant cover associated with abandoned and active nests (12 and 30 nests, respectively) were compared with their controls separately. For each site (active nests, abandoned nests and their respective controls), we measured vegetation cover within a circular plot of 2-

m radius (12.5 m^2) using the point-intercept method (Mueller-Dombois & Ellenberg 1974). This method gives an estimate of percent cover for the species that are intercepted by pins spaced at regular intervals along a transect. In each circular plot we established in a radial arrangement six transects of 2 m each with one pin/10 cm (total = 120 pins). Relative cover was expressed for each species by dividing its number of touches by 120. For the nests sites (active and abandoned) we chose the mound as the centre of the circular plot. This allowed us to include most of the area influenced by the nest, including the mound, surrounding soil and most of the external organic refuses. With these data we calculated the number of plant species (S), the plant species diversity using the Shannon Index (H'), and the evenness ($E = H'/H_{\max}$). We also calculated similarity coefficients between the vegetation of active nests, abandoned nests and control sites with the formula $S = (S_{ij}/S_i + S_j - S_{ij})$, where S_{ij} are the species present in both units, and S_i and S_j the total number of species of each compared pair (Krebs 1989).

To determine if the active nests, abandoned nests and controls differed in plant species composition, we performed a principal component analysis (PCA). To compare richness and cover values we used paired t-tests, and to compare the H' values we used a specific test for the comparison of diversity (Zar 1984).

To analyse soil modifications in relation to the nests, we collected soil samples from the base of the mounds of 10 active nests (hereafter referred to as 'nest-soils'), and refuse samples from 10 external refuse piles. We also collected soil samples from 10 of the 42 non-nest sites (controls) sampled for vegetation cover. Each soil sample or refuse sample was a compound sample product of four subsamples of refuse cores or soil cores of 10-cm diameter and 15-cm depth. The samples were dried in a stove to constant weight. Extractable phosphorus, total nitrogen, organic matter content, pH, texture, density and moisture retention capacity were measured for soil and refuse samples. Organic matter was determined by the Walkey-Black method, total N by the Kjeldahl method, total P by the Truog method (see Jackson 1982), and pH in aqueous solution (relation 1:2.5). Soil and refuse density was estimated by weighing 20 samples of a known volume (150 cm^3). To determine the rate of moisture retention we watered soils from 10 nest samples and refuse samples. We dried the samples at 50 °C and weighted them every 24 hours during 7 days. We report moisture retention capacity, which is the difference between initial and final field capacity weight, as a percentage. To compare the measured variables between nest, refuse and control soils we used one-way ANOVA and Tukey tests.

Fig. 1. Nest-mound and external refuse of the leaf-cutting ant *Acromyrmex lobicornis* in NW Patagonia. Photos by A.G. Farji-Brener.

Results

Soils

Edaphic characteristics around the nests differed significantly from the non-nest sites mainly due to the presence of refuse dumps (Table 1). While nest-soils were similar to control soils in all measured variables, refuse dumps were significantly richer in organic matter, nitrogen content and extractable phosphorus. Different texture, lower density, and greater moisture retention capacity also characterized refuse dumps. While the moisture retention capacity in soils without refuse was 18.1% and reached a constant weight at 24 h, the refuse samples could retain up to 46.4% their weight in water, which stabilized at 48 h. On the other hand, the pH and some physical properties were similar for nests, refuse dumps and controls alike. Although not quantified, nest sites showed greater micro-topographic heterogeneity than sites without nests. This was mainly due to the presence of the mound and the foraging trails, which generate slopes with differing levels of sun exposure and degrees of unevenness, respectively.

Vegetation

In the 84 survey sites we found 52 plant species, of which ca. 50% had a frequency of less than 10%. The most frequent species (>50%) were the exotics *Bromus tectorum*, *Onopordon acanthium*, *Carduus nutans* and *Verbascum thapsus*, and the natives *Stipa speciosa*, *Mulinum spinosum*, *Plagiobothrys tinctoreus* and *Imperata condensata* (Table 2a, b). Dominant species did not differ significantly in mean cover between nest and non-nest sites (Table 3). Additionally, sites with and without nests (both active and abandoned) showed a similar proportion of bare soil (20%). The multivariate analysis (PCA) showed that the sites did not differ floristically, suggesting the absence of a different plant assemblage associated with the nests (Fig. 2). In fact, the first two axes explained only 18% of the variation in plant species composition among samples. Sites with active nests form a more heterogeneous floristic group than the sites with abandoned nests, and the sites with nests (both abandoned and active), a more heterogeneous floristic group than control sites without (note the groups demarcated by 95% confidence level in Fig. 2). This suggests that, in spite of the loss of species that a nest suffers when it is abandoned or the colony dies, nest sites are always more heterogeneous in plant species composition than sites without nests. In agreement with this hypothesis, the average number of species and species diversity is greater at sites with nests than at sites without nests (Table 4). Evenness values between sites with and without nests were similar. The diversity increase in nests was due mainly to an increase in species number, mainly for rare or less frequent species (< 10%). While 12 out of 48 plant species appeared exclusively near active nests, only two of 38 did so at control sites (χ^2= 4.7; P=0.03). For abandoned nests, while 13 of 33 species appeared exclusively at nest sites, only two of 22 appeared only at sites without nests (χ^2= 4.68, P = 0.03). The similarity between active nest-sites and their control sites (0.72) was greater than the similarity between abandoned nests and their control sites (0.53). On the other hand, 90% of the species that appeared at abandoned nests (30 out of 33) were also present at active nests.

Table 1. Means (± 1 S.E.) of soil variables from *Acromyrmex lobicornis* nests with and without refuse, and control sites (n = 10). Differences were tested with an ANOVA one-way test. Means with different letters in each row are significantly different ($P <$ 0.05). OM = organic matter.

Soil variables	Soil nest + refuse	Soil nest	Control soil
OM (%)	13.8 ± 2.5^a	3.2 ± 0.3^b	2.5 ± 1.0^b
N (%)	0.76 ± 0.09^a	0.14 ± 0.02^b	0.13 ± 0.01^b
P (ppm)	597.4 ± 61.4^a	80.3 ± 19.3^b	56.5 ± 4.5^b
pH	6.9 ± 0.2	6.7 ± 0.06	6.8 ± 0.11
Clay (%)	9.7 ± 1.6	7.7 ± 0.7	7.7 ± 0.5
Fine slime (%)	18.4 ± 2.8	16.3 ± 1.5	16.9 ± 1
Bulk slime (%)	4.1 ± 1.5^a	8.5 ± 0.7^b	10.1 ± 0.5^b
Sand (%)	67.7 ± 3.7	67.3 ± 2	65.3 ± 1.8
Density (mg/cm^3)	0.44 ± 0.02^a	1.42 ± 0.02^b	1.41 ± 0.02^b

Table 2. Frequency of plant species in *Acromyrmex lobicornis* nest and non-nest sites. Origin: N = native, E = exotic species. Life form: A = annual, B = biennial, P = perennial, H = herb, G = grass, S = shrub. **a.** Active nests. Frequency gives the number of samples occupied, out of 30 (30 = 100%); **b.** Dead or abandoned nests. Frequency gives the number of samples occupied, out of 12 (12 = 100%)

Table 2a. Plant species	Nest site	Non-nest site	Origin	Life form
Brassica spec.	4	3	E?	BH
Bromus tectorum	30	30	E	PG
Carduus nutans	18	13	E	BH
Erodium cicutarium	2	3	E	AH
Erophila verna	1	3	E	AH
Hordeum comosum	11	5	N	PG
Imperata condensata	11	12	N	PG
Madia sativa	7	2	N	AH
Marrubium vulgare	8	6	E	PH
Mulinum spinosum	6	2	N	S
Onopordum acanthium	14	1	E	BH
Plagiobothrys tinctoreus	17	18	N	AH
Poa spec.	3	2	N?	PG
Senecio filaginoides	4	4	N	S
Stipa speciosa	19	17	N	PG
Verbascum thapsus	17	23	E	BH
Vulpia spec.	6	7	?	AG

Plant species with frequency < 3 present solely in nest sites:
Achillea millefolium (E, PH)
Berberis heterofilia (N, S)
Holosteum umbellatum (E, AH)
Plantago lanceolata (E, PH)
Taraxacum officinale (E, PH)
Bacharis salicifolia (N, S)
Chenopodium album (E, AH)
Mutisia spinosa (N, vine)
Sonchus asper (E, AH)
Unknown species 1.

Plant species with frequency < 3 present solely in non-nest sites:
Rodophiala elwesii (N, PH)
Unknown 2.

Table 2b. Plant species	Nest site	Non-nest site	Origin	Life form
Bromus tectorum	12	12	E	PG
Carduus nutans	7	6	E	BH
Hordeum comosum	9	1	N	PG
Imperata condensata	5	4	N	PG
Onopordon acanthium	9	4	E	BH
Plagyobotris tinctoreus	9	8	N	AH
Stipa speciosa	7	11	N	PG
Verbascum thapsus	8	8	E	BH
Vulpia spec.	4	3	?	AG

Plant species with frequency < 3 present solely in abandoned or dead nest sites:
Bacharis salicifolia (N, S)
Collomia biflora (N, AH)
Leguminosae 1
Matricaria matricarioides (E, AH)
Plantago lanceolata (E, PH)
Rodophiala elwesii (N, PH)
Unknown species: 4.
Unknown species: 3
Hypochoeris condensata (N, PH)
Madia sativa (N, AH)
Rosa eglanteria (E, S
Poa spec. (N?, PG)
Sanguisorba minor (E, AH)

Plant species with frequency < 3 present solely in non-nest sites:
Erophila verna (E, AH)
Unknown species: 2.

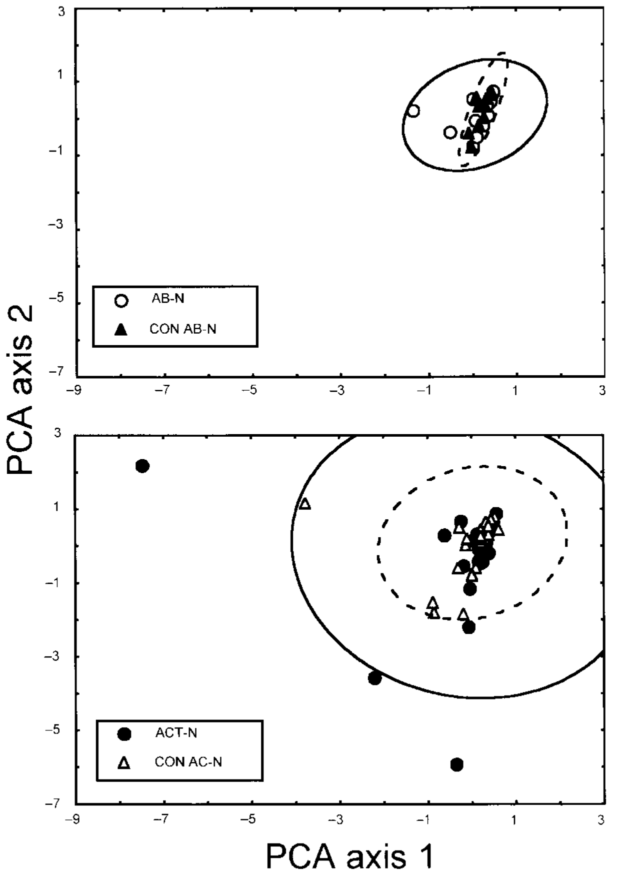

Fig. 2. Plots of the factor scores of the 84 samples according to PCA of the 52 plant species. Different symbols represent samples from active nests (ACT-N), abandon/dead nests (AB-N), and their controls. Lines represent 95% confidence interval, continuous for nest-sites and dashed for controls. Two subfigures are shown to show the pattern more clearly.

Table 3. Mean cover (± 1 S.E.) of the principal dominant plant species in *Acromyrmex lobicornis* nest (active or inactive) and non-nest sites. Means in each row are not significantly different ($P > 0.05$).

Plant species	Active nest	Abandoned or 'dead' nest	Non-nest sites
Bromus tectorum	39.2 ± 2.3	32.7 ± 3.8	39.4 ± 2.5
Imperata condensata	10.5 ± 2.8	8.0 ± 1.0	13.2 ± 3.6
Plagiobothrys tinctoreus	2.5 ± 0.6	2.4 ± 0.8	2.5 ± 0.6
Stipa speciosa	7.2 ± 1.6	17.1 ± 4.4	9.3 ± 2.1
Verbascum thapsus	3.5 ± 0.9	5.9 ± 2.2	5.4 ± 1.1
Mulinum spinosum	4.5 ± 1.6	3.8 ± 1.6	2.4 ± 2

Discussion

This study shows that *Acromyrmex lobicornis* nests modify resource availability in the soil, that higher plant diversity is associated with nests, and that the increase in diversity is maintained even when nests die or are abandoned.

The physical and chemical soil characteristics near *Acromyrmex lobicornis* nests were very different than control soils, revealing that nests are a source of edaphic heterogeneity in the study area. Soils near nests showed higher nutrient content, greater moisture retention capacity, greater micro-topographic variation, and different texture from that of soils located only 5 m away from the nests. Contrary to other studies that found nest-soils to be richer in nutrients than adjacent soils (Culver & Beattie 1983; Farji-Brener & Silva 1995a), this study found that the main cause of the higher resource concentration near nests is the refuse dumps that *Acromyrmex lobicornis* deposits on the soil surface. While nest-soils and control soils did not differ in the majority of their characteristics, the refuse dumps had between 2 to 8 × higher nutrient concentration, and a better water holding capacity (Table 1). Enrichment of nest surroundings by deposition of external refuse is a biologically important, common phenomenon in various ant species, but its effects on soil and biota has been rarely documented. For example, Haines (1978) demonstrated that external refuse presence for *Atta colombica* increased fine root concentration in the soil and accelerated nutrient flow up to 200% in tropical Panamanian forests. Wagner et al. (1997) found that, in semi-arid pastures of the United States, the external refuse dumps of *Pogonomyrmex barbatus* had up to 30 × greater density of micro-arthropods, 5 × more protozoans and a nutrient concentration up to 15 × greater than neighbouring soils. We found that refuse dumps of *Acromyrmex lobicornis* increased soil moisture retention capacity, N, P and organic matter availability, all of which are limiting factors for plant growth in semi-arid environments (Whitford 1988). Different from other ant species (which locate their refuse in subterranean chambers) the deposition of refuse at the surface by *Acromyrmex lobicornis* allows refuses to be more accessible for the herbaceous/shrub

Table 4. Plant species richness *S*, diversity *H'*, evenness *E* in *Acromyrmex lobicornis* nest sites and control non-nest sites. Values of richness are means ± 1 SE. *N* = sample size. * = $P < 0.05$.

	Active nests	Control	Abandoned /dead nests	Control
Sample size	30	30	12	12
Species richness	8.4 ± 0.4	7.1 ± 0.4 *	8.9 ± 0.7	6.7 ± 0.4 *
S	48	38	33	22
H'	1.07	0.97 *	1.00	0.86 *
E	0.64	0.61	0.66	0.64
Similarity	0.72		0.53	

vegetation typical of the steppe. Additionally, accumulation of organic refuse is a continual activity during the life of the colony, and its location in the nest surroundings can change several times, increasing spatial variation of this resource. Changes in soil characteristics by *Acromyrmex lobicornis* are accompanied by increased plant diversity near the nest (Table 4). Given that the cover of none of the dominant species decreases near the nests (Table 3) and that the percentage of bare soil was similar for sites with and without nests, the increase in species diversity seems to relate more to increased availability of resources that ant nests generate rather than to an elimination of dominant species biomass. This suggests that the modifications that ant nests create in their surroundings generate favourable microsites for several plant species. Factors shown to be modified by *Acromyrmex lobicornis* nests (nutrients, moisture and soil micro-topography) in this study are known to favour plant diversity at ant nests in both semi-arid subtropical (Hobbs 1985; Coffin & Laurenroth 1990; Lewis et al. 1991; Pire et al. 1991) and temperate environments (Beattie & Culver 1977; Nowak et al. 1990; Umbanhowar 1990; Woodell & King 1991).

Greater plant diversity at *Acromyrmex lobicornis* nests than at non-nest sites is not due to the existence of a compact group of restricted or exclusive species (i.e. species that only grow at nests), but to the presence of native and exotic rare species in the study area (Table 2a, b; see also Margutti et al. 1996). These species do not depend exclusively on nests for their existence, because despite their low frequency they can be found in areas without nests (pers. obs.). However, these rare plant species were significantly more frequent near active and abandoned nests (25% and 40%) in comparison to their controls (5% and 9% respectively).

What role could ant nests play for these subordinate plant species? In the study area *Acromyrmex lobicornis* nests are located near road verges where pioneer, ruderal and exotic species are dominant (Frenkel 1970). However, one subset of rare plant species found around nest-sites are native, non-pioneer species such as *Baccharis salicifolia*, *Rhodophiala elwesii*, *Berberis heterophylla* and *Mutisia spinosa* (Table 2a, b). The other subset of rare plant species found in nest-sites are exotics such as *Rosa eglanteria*, *Matricaria matricarioides*, *Sanguisorba minor* and *Achillea millefolium*. Consequently, we believe that ant nests can play a double role for rare plant species of the community studied, acting as 'refuges' by favouring the establishment and perpetuation of native subordinate species (Grubb 1977), and as 'stepping stones' by favouring the establishment and dispersion of rare, exotic plants species. Other studies have shown how modifications created by ant nests in their surroundings favour the regeneration and/or establishment of both exotic and native infrequent plant species (King 1977; Coutinho 1982; Culver & Beattie 1983). For example, Lewis et al. (1991) found that in the Chaco area of South America the greater richness of plants on *Camponotus punctulatus* nests was due mainly to the presence of native plant species with less than 20% frequency in the community. In the Brazilian savannas, the exotic grass *Melinis minutiflora* mainly colonizes the open spaces provided by *Atta laevigata* nests (Coutinho 1982).

Higher plant diversity at *Acromyrmex lobicornis* nests continues after the colony dies or the nest is abandoned (Table 4). This evidence supports the hypothesis that higher plant diversity is associated more with the soil modifications caused by nests than with ant activity *per se*. While ant activities such as differential defoliation or seed movement can affect vegetation patterns, such activities cease to have effect when nests die or are abandoned (Buckley 1982; Novak et al. 1990). However, physical and chemical modifications can remain for a long time after the disappearance of the colony (Bucher 1982; Cherrett 1989). 91 % of the plant species present at abandoned or dead nests are also found at active nests, suggesting that the majority of these were already established when the colony was still active. On the other hand, not all established species at active nests remain there after the colony dies or disappears, suggesting the existence of plant species more sensitive to the ant-colony's death. Given that *A. lobicornis* nests show high densities in the study area (43/ha) and high mortality or abandonment annual rates (50%), their influence on plant diversity is very frequent and dynamic through time.

One alternative hypothesis is that *A. lobicornis* ants select sites of high plant diversity for nest construction. At least three lines of evidence suggest that the ants are indirectly responsible, via nest-caused modifications, for the plant diversity changes. First, *A. lobicornis* queens do not select more diverse habitats at the moment of colony foundation (Farji-Brener unpubl.). Second, modifications of plant species distribution caused by ant nests have been documented in different ant species (Beattie & Culver 1977; King 1977; Woodell & King 1991; Lewis et al. 1991; Farji-Brener & Silva 1995b; Wagner et al. 1997; Lesica & Kannowski 1998). Third, modifications of plant species associated with ant nests are more common in ant species that construct large and long-lived nests than in species that build small, frequently relocated nests (Woodell & King 1991; Farji-Brener 1992).

Shrubs are a well-known source of heterogeneity in semi-arid environments, since their presence influences the composition and diversity of other plants in the community (Vetaas 1992). For example, in Patagonia they play an important role in determining community structure by structuring characteristic vegetation patches in the steppe (Aguiar & Sala 1994; Soriano et al. 1994). The results of this study show that, in NW Patagonia, *Acromyrmex lobicornis* nests can be an additional source of heterogeneity within steppe soils near road verges, and suggest that such modifications favour the presence of uncommon plant species. Although each nest has only one plant species on average more than control sites, when we consider the entire study area, species richness associated with nests increases 30-50% (Table 4).

We propose that the nests of *Acromyrmex lobicornis* generate favourable microsites that function both as 'refuges' for less frequent native species and as 'stepping stones' for less frequent exotic plant species, showing the complexity of the role of small-scale disturbances in the composition of plant communities in previously disturbed habitats.

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References

Aguiar, M. & Sala, O. 1994. Competition, facilitation, seed distribution and the origin of patches in a Patagonian steppe. *Oikos* 70: 26-34.

Alvarado, A., Berish, C. & Peralta, F. 1981. Leaf-cutter ant (*Atta cephalotes*) influence on the morphology of andepts in Costa Rica. *Soil Sci. Soc. Am.* 45: 790-794.

Angelstam, P.K. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *J. Veg. Sci.* 9: 593-602.

Armesto, J. & Pickett, S. 1985. Experiments on disturbance in old-field plant communities: impact on species richness and abundance. *Ecology* 66: 230-240.

Beattie, A. & Culver, D. 1977. Effects of the mound of the ant *Formica obscuripes* on the surrounding soil. *Am. Midl. Nat.* 97: 390-399.

Beattie, A. & Culver, D. 1981. The guild of myrmecochores in the herbaceous flora of West Virginia forest. *Ecology* 62: 107-115.

Beattie, A. & Culver, D. 1983. The nest chemistry of two seed-dispersing ant species. *Oecologia (Berl.)* 56: 99-103.

Brokaw, N. 1982. The definition of treefall gap and its effect of forest dynamics. *Biotropica* 14: 158-160.

Bucher, E. 1982. Chaco and Caatinga-South American arid savannas, woodlands and thickets. In: Huntley, B. & Walker, B. (eds.) *Ecology of tropical savannas*, pp. 48-59. Springer-Verlag, Berlin.

Buckley, R. 1982. *Ant-plant interactions in Australia.* Geobotany 4. Dr. W. Junk Publishers, The Hague.

Cherrett, J. 1989. Leaf-cutting ants, biogeographical and ecological studies. In: Lieth, H. & Werger, M. (eds.) *Ecosystems of the World 14b, Tropical rain forest ecosystems*, pp. 473-488. Elsevier, Amsterdam.

Correa, M.N. 1969-1998. *Flora Patagónica. 7 Vols.* Instituo Nacional de Tecnología Agropecuaria, Buenos Aires.

Coffin, D. & Laurenroth, W. 1990. Vegetation associated with nest sites of western harvester ants *Pogonomyrmex occidentalis* Cresson in a semi arid grassland. *Am. Midl. Nat.* 123: 226-235.

Coutinho, L. M. 1982. Aspectos ecologicos de sauva no cerrado. Os murundus de terra, as características psamofíticas das especies de sua vegetaçao e sua invasao pelo Capim Gordura. *Rev. Brasil. Biol.* 42: 147-153.

Culver, D. & Beattie, A. 1983. Effects of ant mounds on soil chemistry and vegetation patterns in a Colorado montane meadow. *Ecology* 64: 485-492.

Denslow, J. 1985. Disturbance-mediated coexistence of species. In: Pickett, S.T.A. & White, P.S. (eds.) *The ecology of natural disturbance and patch dynamics*, pp. 307-321. Academic Press, New York, NY.

Farji-Brener, A.G. 1992. Modificaciones al suelo realizadas por nidos de hormigas cortadoras de hojas (Formicidae. Attini): una revisión de sus efectos sobre la vegetación. *Ecol. Austr.* 2: 87-94.

Farji-Brener, A.G. 1996. Posibles vías de expansión de la hormiga cortadora *Acromyrmex lobicornis* hacia la Patagonia húmeda. *Ecol. Austr.* 6: 144-150.

Farji-Brener, A.G. In press. Leaf-cutting ant nests in temperate environments: mounds, mounds disturbances, and mortality rate in *Acromyrmex lobicornis*. *Stud. Neotrop. Faun. Environ.* 35.

Farji-Brener, A.G. & Ruggiero, A. 1994. Leaf-cutting ants (*Atta* and *Acromyrmex*) inhabiting Argentina: patterns in species richness and geographical range sizes. *J. Biogeogr.* 21: 391-399.

Farji-Brener, A.G. & Silva, J. 1995a. Leaf-cutting ant nests and soil fertility in a well-drained savanna in western Venezuela. *Biotropica* 27: 250-253.

Farji-Brener, A.G. & Silva, J. 1995b. Leaf-cutting ants and forest groves in a tropical parkland savanna of Venezuela: facilitated succession? *J. Trop. Ecol.* 11: 651-669.

Farji-Brener, A.G. & Silva, J. 1996. Leaf-cutting ant *Atta laevigata* aid to the establishment success of *Tapirira velutinifolia* (Anacardiaceae) seedlings in a parkland savanna. *J. Trop. Ecol.* 12: 163-168.

Fox, M. & Fox, B. 1986. The susceptibility of natural communities to invasion. In: Groves. R. & Burdon. J. (eds.) *Ecology of biological invasions*. pp. 57-76. Cambridge University Press, New York. NY.

Frenkel, R.E. 1970. *Ruderal vegetation along some California roadsides*. University of California Press. Berkeley. CA.

Gotwald, W. 1986. The beneficial economic role of ants. In: Vinson, S. (ed.) *Economic impact and control of social insects.* Praeger Special Studies. New York. NY.

Grime, J. 1979. *Plant strategies and vegetation processes*. J. Wiley, New York, NY.

Grubb, P. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev. Cambr. Phil. Soc.* 52: 107-145.

Haines, B. 1975. Impact of leaf-cutting ants on vegetation development at Barro Colorado Island. In: Goley, F. & Medina, E. (eds.) *Tropical ecological systems, trends in terrestrial and aquatic research*, pp. 99-111. Springer-Verlag, New York, NY.

Haines, B. 1978. Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica*, in Panama. *Biotropica* 10: 270-277.

Hoobs, R. 1985. Harvester ant foraging and plant species distribution in annual grassland. *Oecologia (Berl.)* 67: 519-523.

Horvitz, C. & Schemske, W. 1986. Ant-nest soil and seedling growth in a neotropical ant-dispersed herb. *Oecologia (Berl.)* 92: 288-290.

Jackson, M. 1982. *Soil chemical analysis*. Constable, London.

Jonkman, J. 1978. Nests of the leaf-cutting ant *Atta vollenweideri* as accelerators of succession in pastures. *Z. Angew. Entomol.* 86: 25-34.

King, T. 1977. The plant ecology of ant-hills in calcareous grasslands. I. Patterns of species in relation to ant-hills in southern England. *J. Ecol.* 65: 235-256.

Krebs, Ch. J. 1989. *Ecological methodology*. Harper & Row, New York, NY.

Laundré, J. 1990. Soil moisture patterns below mounds of harvester ants. *J. Range Manage.* 43: 10-12.

Lessica, P. & Kannowski, P. 1998. Ants create hummocks and alter structure and vegetation of a montan fen. *Am. Midl. Nat.* 139: 58-68.

Lewis, J., Franceschi, A. & Stofella, S. 1991. Effect of ant-hills on the floristic richness of plant communities of a large depression in the Great Chaco. *Rev. Biol. Trop.* 39: 31-39.

Loucks, O., Plumb-Mentjes, M. & Rogers, D. 1985. Gap processes and large-scale disturbance in sand prairies. In: Pickett, S.T.A. & White, P.S. (eds.) *The ecology of natural disturbance and patch dynamics*, pp. 72-82. Academic Press, New York, NY.

Mandel, R. & Sorenson, C. 1982. The role of harvester ants (*Pogonomyrmex occidentalis*) in soil formation. *Soil Sci. Soc. Am. J.* 46: 785-788.

Margutti, L, Ghermandi, L. & Rapoport, E. 1996. Seed bank and vegetation in a Patagonian roadside. *Int. J. Ecol. Environ. Sci.* 22: 159-175.

Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. John Wiley & Sons, New York, NY.

Nowak, R., Nowak, C., De Rocher, T., Cole, N. & Jones, M. 1990. Prevalence of *Oryzopsis hymenoides* near harvester ant mounds: indirect facilitation by ants. *Oikos* 58: 190-198.

Petal, J. 1978. The role of ants in ecosystems. In: Brian, M. (ed.) *Production ecology of ants and termites*, pp. 293-325. Cambridge University Press, London.

Pickett, S.T.A. & P.S. White. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, NY.

Pire, E., Torres, P., Romagnoli, O. & Lewis, P. 1991. The significance of anthills in depressed areas of the Great Chaco. *Rev. Biol. Trop.* 39: 71-76.

Roig, F.A. 1998. La vegetación de la Patagonia. In: Correa, M. (ed.) *Flora patagónica, Tomo VIII*, pp. 48-166. . INTA, Buenos Aires.

Runkle, J. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63: 1533-1546.

Salem, M. & Hole, F. 1968. Ant (*Formica exectoides*) pedoturbacion in a forest soil. *Soil Sci. Soc. Am.* 32: 563-567.

Skalski, J. 1987. Selecting a random sample of points in circular field plots. *Ecology* 68: 749.

Soriano, A., Sala, O. & Perelman, S. 1994. Patch structure and dynamics in patagonian arid steppe. *Vegetatio* 111: 127-135.

Umbanhowar, C. 1992. Abundance of vegetation and environment of four patch types in a northern mixed prairie. *Can. J. Bot.* 70: 277-284.

Vetaas, O.R. 1992. Micro-site effects of trees and shrubs in dry savannas. *J. Veg. Sci.* 3: 337-344.

Wagner, D., Brown, M. & Gordon, D. 1997. Harvester ant nests, soil biota and soil chemistry. *Oecologia (Berl.)* 112: 232-236.

Weber, N. 1966. Fungus-growing ants and soil nutrition. In: Rapoport, E. (ed.) *Progresos en biologia del suelo. Actas del primer Congreso Latinoamericano de Biología del Suelo, Bahia Blanca*, pp. 221-256. Unesco, Paris.

Weber, N. 1982. Fungus ants. In: Hermann, H. (ed.) *Social insects, Vol. 4*, pp. 255-363. Academic Press, New York, NY.

Whitford, W. 1988. Effects of harvester ant (*Pogonomyrmex rugosus*) nests on soils and a spring annual, *Erodium texanum*. *Southwest. Nat.* 33: 482-485.

Woodell, S. & King, T. 1991. The influence of tumulo-building ants on British lowland vegetation. In: Huxley, C. & Cutler, D. (eds.) *Ant-plant interactions*, pp. 521-535. Oxford University Press, Oxford.

Zar, J. 1984. *Biostatistical analysis*. 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.

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