

The Importance of Where to Dump the Refuse: Seed Banks and Fine Roots in Nests of the Leaf-Cutting Ants *Atta cephalotes* and *A. colombica*¹

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ABSTRACT

The location of the nutrient-rich organic refuse produced by a leaf-cutting ant colony varies among ant species. *Atta cephalotes* locate their organic refuse in subterranean chambers, whereas *A. colombica* place their organic refuse on the soil surface near the nest. We studied the effect of the absence or presence of external organic refuse on the abundance of fine roots and seed bank composition in the superficial horizons of ant nests. We sampled soils from ant nests or dumps and adjacent areas of 15 adult nests of *A. cephalotes* at La Selva (LS), Costa Rica, and of 15 of *A. colombica* nests on Barro Colorado Island (BCI), Panama. Soils from *A. cephalotes* nests did not differ from adjacent soils in abundance of fine-root and seed diversity. In contrast, organic refuse from *A. colombica* nests was less diverse in seed composition (due to the great abundance of *Miconia argentea*) and had a greater abundance of fine roots than adjacent areas. Thus the external location of the ant-nest organic refuse is potentially important in determining the different types of plant recolonization in abandoned or dead ant nests. The relative abundance of these *Atta* species may influence the structure and/or composition of tropical forests.

RESUMEN

En las hormigas cortadoras de hojas, la ubicación de los desechos orgánicos ricos en nutrientes producidos por el hongo que cultivan varía según la especie. Mientras *Atta cephalotes* ubica sus desechos orgánicos en cámaras subterráneas, *A. colombica* los coloca sobre la superficie del suelo cerca del nido. Nosotros estudiamos el efecto de la presencia o ausencia de desechos orgánicos externos sobre la abundancia de raíces finas y la composición del banco de semillas en los suelos superficiales cerca de los hormigueros. Para ello sacamos muestras de basureros o suelo superficial en 15 nidos y áreas adyacentes de *A. cephalotes* en La Selva (LS), Costa Rica, y en 15 nidos de *A. colombica* ubicados en Barro Colorado (BCI), Panamá. Los suelos de *A. cephalotes* no difirieron de los suelos adyacentes en abundancia de raíces finas ni en la diversidad de semillas. Por el contrario, los desechos orgánicos externos en nidos de *A. colombica* fueron menos diversos en composición de semillas (debido principalmente a la gran dominancia de *Miconia argentea*) y tuvieron una mayor concentración de raíces finas que los suelos adyacentes. La ubicación de los desechos es potencialmente importante en determinar los diferentes tipos de plantas que pueden recolonizar los nidos abandonados o muertos. Por lo tanto, la abundancia relativa de estas especies de *Atta* pueden influir en la estructura y/composición de los bosques tropicales.

Key words: ant nest; *Atta cephalotes*; *Atta colombica*; *Costa Rica*; organic refuse; *Panama*; seed bank; tropical rain forest.

SMALL-SCALE DISTURBANCES OFTEN INFLUENCE LOCAL PATTERNS OF VEGETATION. In tropical rain forests, studies of small-scale disturbances have concentrated on gaps caused by tree- or branch-falls (Denslow 1980, Brokaw 1985). In spite of the fact that animals can change resource availability significantly,

their modifications of the physical environment have not been well studied in this system (Clark 1990). A common animal disturbance that clearly modifies the environment and affects vegetation patterns in tropical rain forests is the nest of the leaf-cutting ant (*Atta* spp.). In the nest area (ca 50 m²), the ants clear vegetation and cover leaf litter with soil from their underground excavations. They collect leaves, fruits, and flowers from a large area, carry these materials to the nest, and thereby con-

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concentrate nutrients in the soil at specific sites (Haines 1978, Cherrett 1989, Farji-Brener & Silva 1995). Also, physical soil properties such as drainage and aeration are modified locally by the nest (Alvarado *et al.* 1981). By creating this dynamic mosaic of soil microhabitats, leaf-cutting ants may play an important role in structuring the understory plant community (Alvarado *et al.* 1981, Perfecto & Vandermeer 1993); however, little is known about the effect of the differential location of the organic, nutrient-rich refuse on resource availability to plants and on plant communities.

The plant materials that leaf-cutting ants harvest are transported to underground fungus gardens. Refuse such as organic materials from the fungus culture, dead ants, soil particles, and debris are removed from the fungus gardens to disposal areas. This refuse, rich in organic carbon and nutrients, is placed at a specific point, and its location (in subterranean chambers or on the soil surface) varies among leaf-cutting ant species (Haines 1978). The two more common leaf-cutting ant species in the tropical rain forests of Central America, *Atta cephalotes* and *A. colombica*, have different refuse locations. While *A. colombica* locates the organic refuse on the soil surface in the nest area, *A. cephalotes* disposes of organic refuse in underground chambers specially excavated for this purpose (Stahel & Geijskes 1939).

It is possible that the particular conditions of abandoned *Atta* nests have an important effect on forest recolonization as regeneration sites for many plants. There are at least two ways that plants recolonize abandoned ant nests: by vegetative extension of nearby plants, or by colonization from the existing seed bank. In both cases, the location of refuse could play an important role in determining the composition of the plants involved. For example, the refuse located in subterranean chambers is only within reach of nearby large trees that can utilize the nutrients located at great depths by absorbing them through their deep roots (Stahel & Geijskes 1939). In contrast, an external location of the refuse also favors nearby herbs or shrubs that can directly increase fine-root density in the refuse (Haines 1975, 1978).

The location of the refuse may also influence the composition and successful establishment from the seed bank. Often, leaf cutters collect fruit and dump unused seeds (Leal & Oliveira 1998). Although some *Atta* species with underground dumps leave seeds on the soil surface (Farji-Brener & Silva 1996, Leal & Oliveira 1998), this phenomenon is unusual; generally, discarded seeds are deposited with the refuse in

subterranean chambers at a depth of several meters. It is improbable that these seeds can serve as a viable source of recolonization. If the refuse is deposited on the soil surface, however, the seeds in the refuse have a greater chance of becoming a future source of recolonization. Additionally, the higher nutritive quality of the refuse can increase their possibilities of establishment and growth (Haines 1975). Therefore, the presence of external refuse could have an important effect on the recolonization pattern of abandoned nests.

The objective of this study was to determine the effect of the presence or absence of external refuse on two characteristics potentially important to nest recolonization by plants: the abundance of fine roots and seed bank composition in the superficial soil horizons near ant nests. If the presence of external refuse plays a role in the recolonization process of abandoned nests, we expected differences in the seed bank and fine-root density between nest areas and adjacent forest only in the case of *A. colombica*.

METHODS

Fieldwork was conducted in September and October 1996 at La Selva Biological Station (LS) in the Caribbean lowlands of Costa Rica (10°26'N, 83°59'W) at which *A. cephalotes* is the most common leaf-cutting ant species, and at Barro Colorado Island (BCI) in Panama (9°10'N, 79°51'W) on which *A. colombica* is the most common species. LS is a field station operated by the Organization for Tropical Studies (OTS) and receives *ca* 4000 mm of rain annually. The main dry season lasts from January to March, with a shorter, less-pronounced dry season in September or October. A complete description of this site is available in McDade *et al.* (1994). BCI, a field station of the Smithsonian Tropical Research Institute (STRI), receives *ca* 2600 mm of rain annually (Leigh *et al.* 1982; for flora and site description, see Croat 1978). Both forests are classified as tropical moist forests following Holdridge's (1967) life zones.

To compare the effects of the absence or presence of external refuse in nest areas on the seed bank and fine roots in the superficial soil horizons, we sampled 15 nest areas and adjacent forests for each ant species. From *A. colombica* nests, we sampled external dumps, and from *A. cephalotes* nests, we sampled soils of nest areas. Since we believed that subterranean refuse of *A. cephalotes* did not influence recolonization of abandoned nests by plants and because we wanted to focus on the effect of the external dump, the refuse of *A. cephalotes*

was not sampled. Therefore, we used this species as a reference to the effect of an external refuse in the nest area.

In both forests (BCI and LS), the sampling procedure was the same. We took six soil cores of 196 cm³ (10-cm depth × 5-cm diam.) at different random positions from the external refuse of *A. colombica*, and from the nest soil of *A. cephalotes*. In each nest area, three of the six soil core samples were pooled to analyze seed bank composition and the other three were pooled to determine fine-root densities. For each ant nest, a paired understory site was selected 10–20 m away in a random compass direction, at which we followed the same routine.

Organic refuse, soils from the nests, and paired forest soils were placed under plastic in a screened shade house (20% full sun) and watered daily. We checked for germinating seedlings on a weekly basis, scoring the number and identity (when known) of each seedling until January 1997 (16 wk). In many cases, plant identification was only possible to genus or family level, and thus, species number as used here is conservative.

To analyze seed bank composition among organic refuse, ant-nest soils, and forest soils, we made Whittaker plots of log abundance on plant species rank (Krebs 1989). We also estimated the Shannon diversity index (H) and evenness (J) for each nest area and control forest on BCI and at LS. The diversity indices of the dumps (or nest soils in the case of *A. cephalotes*) and adjacent forest soils were compared using the t -test proposed by Hutcheson (1970; cited in Zar 1984). We also compared the mean number of species and individuals between nest and adjacent forest areas on BCI and at LS using a one-way ANOVA in block design. A block was considered as the nest and the paired forest area (hereafter referred to as site).

Roots were washed from cores, sorted into one diameter class (<1.5 mm), dried to constant weight at 100°C, and the weights subjected to analysis using a one-way ANOVA in block (sites) design. We only selected the smallest roots to analyze because they are presumably the most active in nutrient uptake (Haines 1978, Sanford & Cuevas 1996). We tested for normality of dependent variables using the Wilks-Shapiro test (Sokal & Rohlf 1981). When necessary, we natural log-transformed dependent variables to meet assumptions of normality for ANOVA.

RESULTS

The nest area of each leaf-cutting ant species was ca 50 m² and was clear of vegetation and leaf litter.

All *A. colombica* nests had very obvious external refuse dumps, generally located nearer to the periphery than to the central part of the nest area. The external refuse in some nests formed one large mound, or in other cases, two or three organic mounds separated by a few meters. In some nests, we observed roots of nearby seedlings, shrubs, or vines proliferating in the organic refuse dump, and in many cases, undetermined seedlings growing on the refuse itself. In a few other nests, we observed the refuse located near stream borders, and part of the organic material dump directly in the water. None of the *A. cephalotes* nests sampled showed signs of external refuse or accumulations of discarded seeds near nest holes.

A total of 765 seedlings of ca 60 plant species were recorded from the soil and dump samples in this study; 50 seedlings were not identified to any plant family. Between 65 and 85 percent of all the seeds on BCI and at LS were bird-dispersed plant species, and ca 90 percent of the seeds were ≤5 mm, a size that enabled them to be carried by leaf-cutting ants.

Within both BCI and LS, a comparison of the sites (blocks in the ANOVA analysis) did not show significant differences in fine-root density, number of seed species, and number of seeds ($P > 0.10$ in all cases). These variables, however, varied between nest areas and adjacent forest in relation of the presence or absence of external refuse. In comparison to adjacent forest, refuse piles of *A. colombica* nests had a greater density of fine roots and a higher mean number of seeds, but showed no difference in mean number of seed species (Table 1). The higher number of seeds in the refuse was due principally to the presence of *Miconia argentea* (454 seeds in total, which represents 86% of all seeds), when compared to the number of seeds from the same species in adjacent forest soils (18 seeds in total, which represents 22.2% of all seeds). Due to this evident dominance of *M. argentea* in the refuse areas, the diversity of seeds was significantly lower in the refuse than in adjacent forest areas ($H = 0.32$ and 0.82 , respectively; $t = 11.4$, $df = 210$, $P < 0.001$; Fig. 1B). In contrast, comparisons of *A. cephalotes* nest soils to adjacent forest showed no difference in fine-root densities and mean number of seeds, but showed a significantly lower mean number of seed species (Table 1). Also, the diversity of the seed bank was not different between the *A. cephalotes* nest soils and adjacent forest soils ($H = 1.26$ and 1.35 , respectively; $t = 1.87$, $df = 155$, $P > 0.05$; Fig. 1A).

TABLE 1. *Fine root density (<1.5-mm diam.) and seed species number, density, diversity (H), and evenness (J) in control soils and dump (Atta colombica, BCI) or nest soil (Atta cephalotes, LS). N = 15 nests for each ant species. Values are mean ± SE; * = P < 0.05. Seed number and species were calculated from counting and identifying seedlings that germinated from soil samples of 588 cm³ spread on a flat surface.*

	<i>Atta cephalotes</i> (LS)		<i>Atta colombica</i> (BCI)	
	Nest soil	Control soil	Dump	Control soil
Fine roots (mg/588 cm ³)	0.24 ± 0.03	0.31 ± 0.05	1.45 ± 0.26	0.30 ± 0.04*
Seeds/588 cm ³	4.4 ± 0.85	5.9 ± 0.98	35.3 ± 15.3	5.4 ± 0.70*
(Total)	(66)	(89)	(529)	(81)
Seed species/588 cm ³	2.5 ± 0.39	3.8 ± 0.63*	2.9 ± 1.4	2.6 ± 0.29
(Total)	(22)	(25)	(18)	(15)
H	1.26	1.35	0.32	0.82*
J	0.94	0.96	0.12	0.70*

DISCUSSION

Recently abandoned *Atta* nests are like new islands in the forest ocean for shipwrecked plants. The absence of potential competitors, the presence of high light levels on the ground, and the increased nutrient status of the soil make these new islands a

good landing area for plants. Our results suggest that the presence of external refuse on a new island enhances nutrient availability for some nearby plants by concentrating nutrients at the surface, and selects the identity of the plants by accumulating discarded seeds of certain species in the refuse piles.

In general, soils from *Atta* nests can be more rich in nutrients than the surrounding soils (Farji-Brener & Silva 1995), but we only found an increase in fine-root density (which represents an increased absorptive root surface) in the *A. colombica* nest areas that included external refuse. This gain in fine-root density (>400% compared to *A. cephalotes* ant-nest soils and adjacent forest soils) suggests that the surrounding plants can access these nutrients via root growth. Thus, some of the nutrients funneled through the colony were recycled to the surrounding vegetation rather than lost via leaching through the dump into the groundwater. The incorporation of these nutrients could have direct effects on the fitness of the surrounding plants, like an increase in their production of fruits or seeds (Rissing 1986, Hanzawa *et al.* 1988) and in their vegetative growth (Haines 1975).

The seed bank of nest areas also showed differences in relation to the presence or absence of an external refuse dump. Because the ants clear the nest area of plants and the underground location of the refuse, it is not surprising that there were lower mean numbers of seed species in active *A. cephalotes* nest areas than in the adjacent forest soils. This effect in decreased seed species number probably was compensated in *A. colombica* nest areas by the ants' seed-dumping activity in above-ground refuse.

In comparison to the adjacent forest, *A. cephalotes* nest areas did not show differences in seed number and seed diversity, but *A. colombica* nest

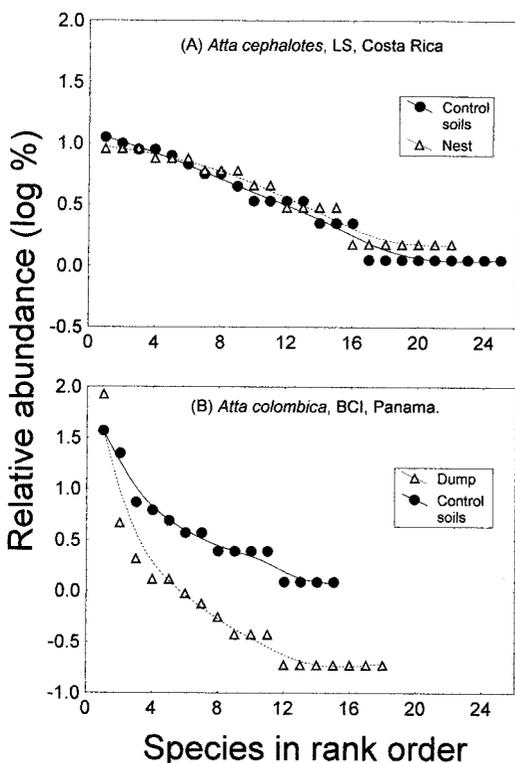


FIGURE 1. (A) Seedling species abundance in nest and control soils for *Atta cephalotes* at LS, Costa Rica. (B) Seedling species abundance in dump and control soils for *Atta colombica* at BCI, Panama.

areas showed higher numbers of seeds and lower seed diversity (Table 1; Fig. 1). It is clear that these differences exist principally because *A. colombica* ants actively harvested *M. argentea* fruits and located their seeds in the aboveground organic refuse. In other work, J. Dalling and R. Wirth (1999) found that on BCI, *A. colombica* is one of the principal seed dispersal agents of *M. argentea*, and the external refuse had a mean of a 330 *Miconia* seeds/g fresh-weight refuse. Given that *M. argentea* fruits between May and June, the seeds that germinated in our refuse samples were in the dump for at least three months. This implies that the seeds do not lose their viability by remaining in the refuse. This high concentration of seeds, the high germination rate of seeds from the refuse (73%; Jim Dalling, pers. comm.), and the fact that an *Atta* nest is a large area clear of understory vegetation suggest that abandoned *A. colombica* nests may be an important source of regeneration for the small-gap specialist *M. argentea* (Brokaw 1987). Yet it remains unclear if adults really are recruited disproportionately from these highly aggregated seed distribution patterns. For example, in a one-year study, Haines (1975) found a high mortality rate in seedlings on refuse dumps during the dry season. Intraspecific competition could be an important limiting factor because high concentrations of fine roots from the largest trees and/or small plants in the refuse dump could impact seedlings negatively by decreasing the amount of water available. The seeds in the refuse, however, can be dispersed away from these negative impacts. Some seeds may be removed by other ant species, or may be displaced by vertebrates digging for insects associated with abandoned dumps (Cherrett 1989). Also, refuse material from *A. colombica* nests is typically deposited along a slope and much of this refuse can be redeposited over a wide area following heavy rain (R. Wirth, pers. comm.).

As Levey and Byrne (1993) have pointed out, the interaction between *Miconia* seeds and leaf-cutting ants provides an alternative hypothesis for the nonrandom distribution of *Miconia* seedlings among different zones or sizes of tropical treefall gaps (Ellison *et al.* 1993). The most commonly cited hypothesis assumes that seed dispersal is not directed and posits that microhabitat differences and interspecific competition select for specialization of establishment in different zones or sizes of gaps (Denslow 1980, Brokaw 1985). Because leaf-cutting ants differ in their fruit or seed preferences (Roberts & Heithaus 1986, Kaspari 1993, Farji-Brener & Silva 1996) and microhabitat nesting

preferences (Jaffé & Vilela 1989, Vasconcelos 1990), seeds of different species may be carried non-randomly to different microhabitats. In the case of *A. colombica*, the majority of these seeds were located in the organic, nutrient-rich refuse. Thus, we hypothesize that habitat-specific differences in seedling emergence and survival among some treefall gap-colonizing species preferred by the leaf cutters for their fruits (*e.g.*, *M. argentea*) may be the partial result of differential seed location generated by leaf-cutting ant dispersal. It is interesting to speculate that there may be some plant species that preferentially germinate and survive the seedling stages on abandoned *Atta* nests, and to discuss the role of the presence of external refuse as a selective force in that process.

Since our data arise from a short-term study, it is very probable that *A. colombica* harvest fruits and locate seeds in the aboveground refuse from other plant species during the year. For example, on BCI we observed leaf cutters collecting fruits and seeds from *Annona spraguei*, one common gap-specialist plant species. Other studies have shown that leaf cutters occasionally collect seeds or fruit parts of tropical forest trees (Roberts & Heithaus 1986, Alvarez-Buylla & Martinez-Ramos 1990, Kaspari 1993, Farji-Brener & Silva 1996, Leal & Oliveira 1998). Therefore, abandoned *A. colombica* nests may serve as regeneration sites for small-seeded, reserve-limited plants that need high light levels immediately after germination and may not survive beneath a layer of leaf litter.

While falling trees or branches create gaps into which forest trees must regenerate (top down gaps), *Atta* nests also create mini-gaps that are relatively free of understory vegetation (bottom up gaps). From a seedling's point of view, *Atta* nests may be equivalent to treefall gaps in some aspects, but very different in others. Since canopy cover usually is unaffected by *Atta* activity, light level above ground level may be considerably lower than in gaps; however, light just above the soil surface where germinating seedlings are potentially could be greater than at ground level in gaps, since 100 percent defoliation of the understory is commonplace at *Atta* nests. Even though seedlings on recently abandoned nests may compete with roots of well established trees, they do not have to compete with fast growing, previously established plants in the high light environment of treefall gaps. Differences in soil structure and chemistry between gaps and *Atta* nests also may contribute to differences in plant regeneration between the two habitats; however, one of the key issues for evaluating the importance

of *Atta* nests in forest dynamics is the rate of appearance of the "new islands" (abandoned or dead *Atta* nests) in the tropical "forest ocean." Perfecto and Vandermeer (1993) found a significant turnover of *A. cephalotes* nests at LS during a two-year period, and on BCI, *A. colombica* moved ca 10 percent of their nests in a one-year period (H. Herz, pers. comm.). Given the speed with which the nests appear to turn over, understory plants and tree seedlings may be as affected by the *Atta* colonies as they are by falling trees. Indeed, it could be that for many understory plants and tree seedlings, the presence of *Atta* is a more important force driving plant community dynamics than gap-phase dynamics (Perfecto & Vandermeer 1993).

We have shown that the presence of external refuse enhances nutrient availability and decreases seed bank diversity in the superficial horizons. These effects permit us to generate some predictions about the plant composition and recolonization rate of abandoned nests from different *Atta* species. For example, due to the location of selectively harvested seeds in the nutrient-rich external refuse, we would expect a fast recolonization process by a few dominant plant species in abandoned *A. colombica* nests. In contrast, the recolonization

process in *A. cephalotes* abandoned nests would be relatively slower and more dependent on seed rain than in the case of *A. colombica*. Thus, the role of *Atta* nests in influencing forest structure is wide open to further investigation. A more detailed examination of the effect of external refuse on forest regeneration should follow the vegetation changes in nest areas with and without external refuse after abandonment, while comparing them to a nearby forest. An experimental approach combining seed and nutrient addition experiments, and survival trials at nest and non-nest areas in both situations is necessary to gain an understanding of how different *Atta* species influence plant regeneration in tropical forests.

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