Ecology Letters, (2000) **3**: 219–227

REPORT

Do leaf-cutting ant nests make "bottom–up" gaps in neotropical rain forests?: a critical review of the evidence

Alejandro G. Farji-Brener[1] **and Anya. E. Illes**[2]
[1]*Lab. Ecotono, CRUB, Universidad del Comahue, Unidad Postal UNC (8400) Bariloche, Argentina. E-mail: ecotono@cab.cnea.gov.ar; alefarji@yahoo.com*
[2]*1291 Regency Dr, San Jose, CA 95129, USA.*

Abstract

We discuss the role of leaf cutting ant nests (*Atta* sp.) on the formation of understory "bottom–up" gaps in tropical rain forests. We (i) describe the characteristics of *Atta* nests that qualify them as promoters of understory gaps; (ii) review the effects of *Atta* nests on the dynamics of systems other than tropical forests; and (iii) discuss the hypotheses that in neotropical rain forests *Atta* nests affect plant productivity, and also influence distribution and community composition of the flora. Finally, we discuss the importance of *Atta* nests in the dynamics of forests and compare their effects with the better-known effects of treefall gaps. *Atta* nests modify soil structure, soil nutrient content, light intensity at ground level, seed bank composition and understory structure. The presence of the nest and associated refuse also accelerates the soil nutrient cycles. The size, high frequency, turnover rate and duration of these nests could make them a good substrate for particular species of plants. In spite of their potential importance, little information exists on the effects of *Atta* nests on plant productivity and/or plant composition in neotropical rain forests.

Keywords

Atta spp., disturbances, gaps, leaf-cutting ant nests, tropical rain forests.

Ecology Letters (2000) 3: 219–227

> "...Sometimes things are ahead and sometimes they are behind, sometimes one is up and sometimes down..."
> Lao tsu, "Tao Te Ching"

In neotropical rain forests, treefalls are dominant examples of gaps, and the most studied. However, there are gaps made by small-scale disturbances other than treefalls that can be important in these systems. We believe that leaf-cutting ant nests are an under-appreciated source of such gaps in neotropical forests.

A gap is created when a disturbance clears space and promotes changes in resource availability. If different agents cause different types of gaps, it would follow that not all gaps are alike, and so their possible effects on neotropical forest dynamics would differ. Gap openings may originate at and reach different levels of the forest, affecting the type and intensity of resource modification. If we were to imagine a vertical section of the forest, our traditional concept of gap results in a disturbance that arises from the upper layer and reaches understory levels (Fig. 1a). For example, treefalls create canopy gaps and thereby bring light down toward the forest floor (Chazdon & Fetcher 1984). Many studies show how these "top–down" gaps affect forest structure, composition and dynamics (Denslow 1980; Hartshorn 1980; Brokaw 1982, 1985; Sanford *et al.* 1986; Young & Hubbell 1991), and give gaps definitions such as "a hole in the forest extending through all levels down to an average height of two meters above ground" (Brokaw 1982). But what about an opening that originates in the understory and has its most important effects below those two meters, or a "bottom–up" gap (Fig. 1b)? Many neotropical animals cause "bottom–up" gaps through soil disturbance, including agoutis (*Dasyprocta agouti*), pacas (*Agouti paca*), wild pigs (*Tayassu*), armadillos (*Dasypus novemcinctus*), termites and leaf-cutting ants (Clark 1990; Dangerfield *et al.* 1998). Of all of the above, leaf-cutting ants (mainly *Atta* spp.) create important soil disturbances, acting as ecosystems engineers (*sensu* Jones *et al.* 1997). When *Atta* ants construct and maintain their nests, they create understory gaps by covering the forest floor with large quantities of excavated soil, clearing the area of understory vegetation and modifying the availability of resources (Haines 1978; Alvarado *et al.* 1981; Cherrett 1989). When an *Atta* colony dies or abandons a nest, the area is no longer

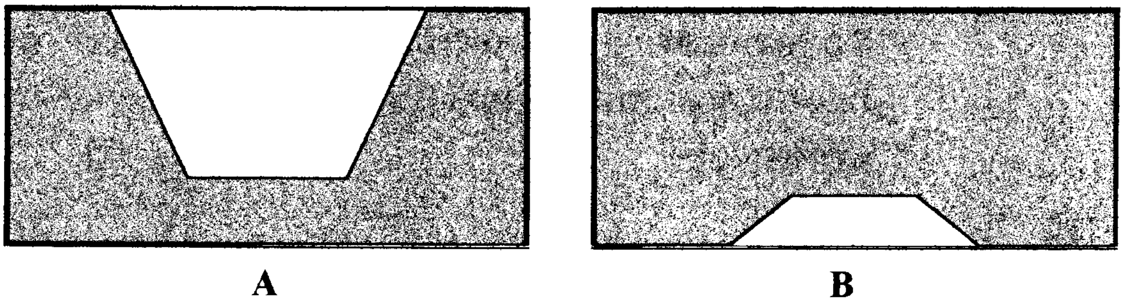

Figure 1 Schematic representation of "top–down" gaps (A) and "bottom–up" gaps (B) in a vertical cross-section of forest. Possible examples are (A) treefall and (B) abandoned or dead *Atta* ant nest. Light areas represent area of gap, dark areas represent forest.

maintained free of plants, and thus becomes an important site for recolonization.

A major question that remains unanswered is exactly how do *Atta* nests affect forest structure, composition and dynamics. Despite the fact that *Atta* nests, like treefall gaps, are common and conspicuous structural components of neotropical rain forests, data do not currently exist to answer this question. We begin to fill in this information gap from the bottom up by (i) summarizing the existing knowledge of *Atta* nests that demonstrates their role as understory gaps; (ii) reviewing the effects of *Atta* nests on the dynamics of tropical systems other than tropical rain forests; (iii) discussing the possible effects of *Atta* nest disturbances on neotropical rain forest dynamics, and (iv) comparing their effects on neotropical rain forest dynamics with the better-known effects of treefalls. We believe that, like treefalls, dead or abandoned *Atta* nests have an important influence on tropical rain forest dynamics and composition.

LEAF-CUTTING ANT NESTS AS DISTURBANCES THAT CREATE GAPS IN FOREST HABITATS

Size, intensity and frequency are characteristics of disturbances that are relevant to plant responses (Bazzaz 1983). If leaf-cutting ant nests are disturbances, then nest characteristics such as dimension, number per ha, demography and type of environmental modifications could likewise affect plant response.

Ant activities and nest characteristics

Atta nests are formidable structures that may house millions of ants and their fungus colonies for 10–20 years (Weber 1982; Cherrett 1989). During the construction, expansion and lifetimes of *Atta* nests, there are at least three colony activities that are relevant to our discussion. First, leaf-cutting ants maintain an open area free of plants and debris. *Atta cephalotes*, *A. colombica*, *A. laevigata* and *A. sexdens* (the principal tropical *Atta* species), can maintain an open area of 50–160 m^2 (Alvarado *et al.* 1981; Weber 1982; Cherrett 1989; Farji-Brener & Silva 1995a, b; personal observations). Secondly, leaf-cutting ants construct deep underground chambers and move large quantities of soil to the nest surface. An adult nest can contain 300–7800 chambers from near the surface to 7 m depth (Stahel & Geijskes 1939; Jonkman 1979; Moreira *et al.* 1995; Forti & Moreira 1997). To construct this underground network, ants may move up to 23 m^3 of soil (Autori 1942). Finally, ants cut plant material from many plant species and process it in the nest for the cultivation of their fungus. The organic wastes produced by the ants and fungus are deposited either in underground chambers or in above-ground dumps. Autori (1942) found 296 refuse chambers with organic material at 1–6 m depth in a nest of *Atta sexdens*. In an *Atta laevigata* nest, Coutinho (1984) found a large cavity containing organic matter 6 m below the surface, and in a nest of *Atta capiguara*, Amante (1964, 1967) discovered a chamber containing 500 kg of organic waste. Haines (1975, 1978) found that, unlike the above *Atta* spp., *Atta colombica* places its wastes in dumps on the surface.

Environmental modifications

Colony activities described in the preceding paragraph produce physical and chemical modifications in the nest area; such modifications may influence forest regeneration when the colony dies or the nest is abandoned (Jonkman 1978; Bucher 1982; Weber 1982; Cherrett 1989). For example, by maintaining an open area, the ants can change light incidence at ground level and increase the availability of "unoccupied" space (see Appendix 1 and 2). Ant activities also result in changes in the physical properties of the soil (i.e. profile composition), and can promote an increment in soil porosity and density. In Costa Rican rain forests, Alvarado *et al.* (1981) found that *Atta cephalotes* modified 85% of 27 soil profiles sampled in a 2.5 ha area.

Chemically, the ants modify the environment by concentrating nutrients and accelerating nutrient cycles in the nest area. In tropical parkland savannas, soils from *Atta* laevigata nests were 30%–60% higher in N, Mg, Ca and organic carbon than adjacent soils (Farji-Brener & Silva 1995a, b). In tropical rain forests, samples from *Atta* colombica surface refuse were 40%–120% richer in N, P, K and S than leaf litter (Haines 1978) and 1.3–80 times richer in N, P, K, Mg and Ca than forest soil (Haines 1975). Additionally, for external refuse of *Atta* colombica, nutrient flow is 16–98 times faster than for leaf litter controls (Haines 1978). With the return of organic matter back to the forest in the form of refuse, *A. colombica* has a net positive effect on forest energy balance (Lugo *et al.* 1973).

Nest distribution and demography

The importance of the physical and chemical modifications created by a disturbance is directly related to the disturbance's intensity and frequency, which, in the case of *Atta* nests, can be equated to nest density and demography. Nest density varies with habitat characteristics and with *Atta* species (0.04–16 nests ha^{-1}). Generally, nest density is higher in second-growth forests and disturbed areas than in old-growth forests or undisturbed areas (Haines 1978; Fowler *et al.* 1986; Cherrett 1989; Jaffe & Vilela 1989; Vasconcelos & Cherrett 1995). For example, in primary forests of Amazonia, densities of *Atta cephalotes* nests are only 0.05 ha^{-1} (Jaffe & Vilela 1989). In secondary forests of the Brazilian Amazon, *Atta laevigata*, *A. cephalotes* and *A. sexdens* can have nest densities 30 times higher than in primary forests (Vasconçelos & Cherrett 1995). While *Atta cephalotes* nest densities reach 3 ha^{-1} in Costa Rican old-growth rain forest, they reach 16 nests ha^{-1} in 10-year second-growth forest, and 7 nests ha^{-1} in disturbed forest areas along trails (Perfecto & Vandermeer 1993; Bianchi 1998). Similarly, on Barro Colorado Island in Panama, *Atta colombica* nest density is around five times higher in disturbed areas near the laboratories than in less disturbed areas farther away (Farji-Brener, unpublished data).

Mortality and natality rates for adult nests are not well documented. The only study from tropical rain forest areas showed that 33 of 74 adult *Atta cephalotes* nests died and 66 new nests appeared over a 2 year period in a 15 ha area (Perfecto & Vandermeer 1993). Additionally, abandonment rates can be high. On Barro Colorado Island, 10% of *Atta colombica* colonies (four out of 40) abandoned their nests and built new ones during a 1-year period (H. Herz, personal communication).

LEAF-CUTTING ANT NESTS AFFECT VEGETATION DYNAMICS OF OTHER SYSTEMS

Many studies in nontropical rain forest ecosystems have shown that *Atta* nests can favour a set of plants different from that of the dominant vegetation. In Paraguayan savannas and Argentinean open woodlands, abandoned or dead *Atta vollenweideri* nests are colonized largely by woody *Prosopis* spp. The ant nest is a favourable environment for these seedlings because it is free of competing grasses, rich in nutrients and higher in water content than the surrounding environment (Jonkman 1979; Bucher 1982). In Venezuelan tropical savannas, *Atta laevigata* favours the germination and establishment of the tree *Tapirira velutinifolia* in their nest area by accumulating seeds in the nutrient rich soil of the nest, and by removing the pulp from the seeds, which prevents their infection by pathogens (Farji-Brener & Silva 1996). In the Brazilian savannas, the exotic grass *Melinis minutiflora* mainly colonizes the open spaces provided by the *Atta laevigata* nests (Coutinho 1982).

Ant nest-plant relationships can have repercussions at the landscape level. Abandoned or dead nests of *Atta vollenweideri* become "woody nuclei", accelerating the invasion of woody plants into the Paraguayan savannas and transforming them into open woodlands (Jonkman 1978). Living *Atta laevigata* nests and some tree species have a synergistic relationship in Venezuelan parkland savannas, encouraging the presence of forest groves in a herbaceous matrix (Farji-Brener & Silva 1995a).

EFFECTS OF LEAF-CUTTING ANT NESTS ON NEOTROPICAL RAIN FOREST DYNAMICS

In neotropical forests, abandoned or dead *Atta* nests appear frequently and present a set of conditions favourable for plant establishment and growth that are uncommon in the forest understory: large free space, higher light incidence at ground level and greater nutrient concentrations. Given observations of the impact of *Atta* nests on other tropical or subtropical systems, we hypothesize that *Atta* nests can affect plant productivity, and species distribution and/or composition. We present preliminary evidence that supports these two nonexclusive hypotheses and we propose easily verified predictions. Finally, we discuss the possible ecological or evolutionary importance of *Atta* nests in tropical forest dynamics.

Hypothesis 1: *Atta* nests increase plant productivity

There is some preliminary evidence that abandoned or dead *Atta* nests affect plant productivity. As discussed earlier, *Atta* nest soils and/or external refuse dumps can be 1.3–80.0 times higher in nutrients than adjacent soils, an effect that remains after the colony dies or the nest is abandoned. Given that in forest soils of tropical America nutrients can limit plant growth (Vitousek 1984; Sollins 1998), the increased concentration caused by the ant nests should have an important effect on plants.

Studies have demonstrated that plants can access the increased nutrients in the nest area. Density of fine roots is 4-fold higher in the external refuse dumps of *Atta* colombica than in control soils (Haines 1978; Farji-Brener & Medina 2000). Tree roots were also found in subterranean refuse chambers of *Atta cephalotes* and *A. sexdens* 3–6 m below ground (Stahel & Geijskes 1939). Presence of roots in refuse dumps may increase soil nutrient transfer to the plant. Some studies of other non-*Atta* ant species show that plants growing in nutrient-rich nest areas increase their production of fruits and/or seeds (Rissing 1986; Hanzawa *et al.* 1988).

Although ant nests enrich the soil, and plants can access these nutrients, does this result in an increase of the growth, survival and/or reproduction of plants that recolonize the nest area? Data do not currently exist to answer this question. If the answer is yes, we would expect plants on abandoned or dead nests to (i) grow faster, (ii) accumulate greater biomass, and/or (iii) produce more flowers/fruits and flowers/fruits for longer periods of time than plants in forest areas away from *Atta* nests. To test these predictions, field and greenhouse experiments measuring growth rates, total biomass and fitness for plants in nest soils and control soils would complement comparative field measurements.

Hypothesis 2: *Atta* nests affect plant species composition and/or distribution

The environmental conditions that *Atta* nests modify may be more important for some plant species or species assemblages than others. For example, the higher light intensity at ground level would especially favour species requiring more light for establishment and initial growth, such as small-seeded plants with few energy reserves. The litter layer may act as inhibitory light filter (Vazquez-Yanes *et al.* 1990), and thus the diminished leaf litter barrier in nest areas could favour certain species that need cleared soil for germination and/or establishment. Many seeds of tropical plant species were capable of germinating in response to disruption of the overlying litter layer and disturbance of the soil without simultaneous opening of the canopy (Metcalfe & Turner 1998). The modified structure of the soil and the higher level of nutrients in the nest area could also affect species composition.

Possibly more important, *Atta* species can selectively collect fruits and seeds of tropical trees and carry them to their nests, thereby concentrating potential colonizers of specific plant species in the nutrient-rich nest area (Roberts & Heithaus 1986; Kaspari 1993). The fate of these seeds, however, may vary with *Atta* species, because different species may dump seeds in different locations above or below ground. For example, in Panamanian forests, *Atta colombica* is one of the main dispersers of *Miconia argentea* because it actively harvests fruits and dumps their seeds in above-ground refuse piles (Dalling & Wirth 1998). *Miconia argentea* also composed 86% of the total seed number found in refuse samples, making the nest area much less diverse than forest control soils in terms of seed-rain species. Greenhouse experiments showed that these seeds germinate in the refuse, suggesting that they are viable recolonizers of dead or abandoned *Atta* nests (Farji-Brener & Medina 2000). In parkland savannas of Venezuela, *Atta laevigata* ants harvest fruits of *Tapirira velutinifolia* trees and carry them to the nest, where they strip the seeds of pulp. Stripped seeds, which germinate better than control seeds in laboratory experiments, are left on the nutrient-rich nest surface and pulp is carried below ground. The consequence of this ant's activity is that forest groves with *Atta laevigata* nests have higher densities of *Tapirira velutinifolia* trees than forest groves without *A. laevigata* nests (Farji-Brener & Silva 1996). However, some *Atta* species accumulate seeds together with other organic refuse in subterranean chambers, where it is less probable that the seeds germinate and colonize the abandoned nest area (but see Leal & Oliveira 1998). *Atta* nests can also affect the abundance and diversity of small understory plants <10 cm in height. Garrettson *et al.* (1998) found that while active nests of *Atta cephalotes* in Costa Rica have lower morphospecies richness and abundance of small understory plants relative to nearby forest, abandoned nests show 58% higher morphospecies richness and 73% greater abundance than adjacent forest.

Thus, *Atta* nests affect environmental conditions in forest understory, and ants can concentrate viable seeds of certain species in the nutrient-rich nest area. This can result in a change in species abundance and richness of small understory plants. Yet, does this significantly affect the plant species composition and/or distribution in neotropical rain forests? Again, data do not currently exist to answer this question. If the answer is yes, then we would expect to find different plant species or species assemblages on dead or abandoned nests than in adjacent forest areas. To test these predictions, field and greenhouse experiments measuring germination, establishment and growth of different plant species or mixed species assemblages in nest and non-nest conditions would complement comparative field measurements. In this sense, the descriptive results discussed above from Garrettson *et al.* (1998) are a good start.

IMPORTANCE OF LEAF-CUTTING ANT NESTS FOR NEOTROPICAL RAIN FOREST DYNAMICS: LITTLE EVIDENCE, BIG INFLUENCE?

The importance of *Atta* nests can be better understood if compared with the well-known effects of treefall gaps.

The purpose of utilizing treefall gaps as a reference is not to determine which type of disturbance is more important, rather it is to help to understand what classes of plants the nests could affect, and therefore how *Atta* nests affect neotropical rain forests. Compared to treefall gaps, a dead or abandoned *Atta* nest offers plants more space clearly of understory vegetation, higher nutrient concentrations and–in some circumstances–similar light levels at ground level (Table 1, Appendix 1 and 2). For example, mean irradiance (and ranges) was 3–8 μmol m^{-2} s^{-1} for intact forest (0.5–22), 6–13 μmol m^{-2} s^{-1} for *Atta* nests (0.5–40), and 6–21 μmol m^{-2} s^{-1} (0.1–100) for treefall gaps, suggesting that irradiance in a recently abandoned or dead *Atta* nest can be as high as in some treefall gaps (Appendix 1, see also Chazdon & Fetcher 1984). Light intensity at ground level in a treefall gap may not necessarily be greater than in abandoned or dead *Atta* nests because the fallen tree and debris that it carries with it may cover the ground much more completely than a more diffuse undisturbed canopy. It is true that the light intensity above the gap may be much greater, but at ground level the treefall debris can block much of this light. However, in between the pieces of debris, there are also spots that receive almost full light. Therefore, treefall gaps promote a heterogeneous and (by mean) higher light level on the ground, while the top of an *Atta* nest offer a spatially more homogeneous high-intermediate light level. In addition, light levels in recently abandoned or dead *Atta* nest are among those levels at which pioneers tropical trees regenerate (Vazquez-Yanes *et al.* 1990; Veneklaas *et al.* 1998; Agyeman *et al.* 1999; Kyereh *et al.* 1999). Pioneer species are likely to remain dormant in the forest understory when the light is low, but can germinate in even small gaps with only 5 μmol m^{-2} s^{-1} (Kyereh *et al.* 1999). This irradiance level is rarely found on the forest floor but is common at the surface of *Atta* nests (Appendix 1). The

Table 1 Comparison between recently dead or abandoned *Atta* nests (bottom–up gaps) and treefalls (top–down gaps)

Variable	Tree fall gap	Abandoned *Atta* nest	Source
Size	mean ≈110–160 m^2 range = 40–780 m^2	mean ≈70–100 m^2 range = 30–160 m^2	1, 2, 3, 4, 5, 6, 7, 8
Shape	irregular	mainly circular	2, 6, 9, 10, 12
Light (ground level)	⩽ or > than adj. forest	> than adj. forest	34
Light (⩾70cm height)	> than adj. forest	≈than adj. forest	34, 35
Soil surface	with debris	clear of plants debris	3, 8, 12, 13, 26, 34
Nutrient level	⩽than adjacent forest	⩾than adjacent forest	10, 11, 13, 14, 15
Nutrient location	treefall crown (soil surface)	refuse dumps (soil surface or below ground)	4, 13, 16, 17 18, 19, 20
Turnover rate	75–150 years	200–300 years	6, 7, 21, 22
Seedling density	742 m^{-2}in forest soil	733 m^{-2} in nest soil 5878 m^{-2} in ext. dump	23, 24
Seedling type	>% wind dispersed <% animal dispersed	<% wind dispersed >% animal dispersed	25, 24
Understory plant richness and abundance	?	>than adj. forest	26
Occurrence time in succession	mainly late	mainly early	3, 13, 27, 28, 29, 30
Plant type that could benefit	shade intolerant for long-term growth	small seeded, nutrient-limited, litter-gap demanders, shade intolerant for initial growth	12, 24, 36
Associated animals	birds, insects, reptiles?	reptiles, arthropods	3, 31, 32, 33

Source: (1) Stahel & Geijskes 1939; (2) Weber 1982; (3) Cherrett 1989; (4) Alvarado *et al.* 1981; (5) Forti & Moreira 1997; (6) Sanford *et al.* 1986; (7) Hartshorn; (1976); (8) Clark 1990; (9) Farji-Brener & Sierra; (1993); (10) Farji-Brener & Silva 1995a; (11) Farji-Brener & Silva 1995b; (12) Brokaw 1985; (13) Haines 1978; (14) Vitousek & Denslow; (1986); (15) Uhl *et al.*; (1988); (16) Haines 1975; (17) Orians; (1982); (18) Amante 1964; (19) Amante 1967; (20) Countinho 1984; (21) Hartshorn 1980; (22) Perfecto & Vandeermer 1993; (23) Putz; (1983); (24) Farji-Brener & Medina 2000; (25) Schupp *et al.*; (1989); (26) Garrettson *et al.* 1998; (27); Putz & Milton; (1983); (28) Brokaw 1982; (29) Jaffe & Vilela 1989; (30) Vasconcelos & Cherrett 1995; (31) Levey; (1988); (32) Della Lucia *et al.* 1993; (33) Azevedo-Ramos & Moutinho 1994; (34) Appendix 1 and 2; (35) Chazdon & Fetcher 1984; (36) Metcalfe & Turner 1998.

unique characteristics of *Atta* nests (space without a litter layer, higher nutrient concentrations and higher light levels at ground level) could be important for those plant species groups whose growth and development are strongly limited by the above-mentioned factors. For example, just as treefall gaps aid the long-term growth of seedlings of shade-intolerant species, it could be that *Atta* nests favour the germination and initial growth of intermediate shade-intolerant plant species, nutrient-limited species and/or litter-gap demanders (*sensu* Metcalfe & Turner 1998). Moreover, the turnover rates of *Atta* nests are relatively similar to those of treefall gaps (Table 1), suggesting that *Atta* nests would likewise affect forest dynamics and/or composition. However, since *Atta* nests and the larger, older trees likely to cause gaps are most numerous in forests at different successional stages, they each may have their greatest influence at different times during the development of a forest. So the present hypothesis about abandoned nests of *Atta* ants as an important type of understory gaps would apply principally for secondary forests and/or at sites of earlier disturbances.

While it is generally agreed that the effects of treefall gaps are important at an ecological scale, it is debatable whether they are important at an evolutionary scale (Denslow 1980; Whitmore 1989). We believe that *Atta* nests raise the same controversy: are *Atta* nests important agents for natural selection for some plant species, or are the previously discussed effects important only at an ecological scale? The first step toward understanding this would be to determine if the modifications generated by the nests are taken advantage of by a random selection of plant species from the surrounding matrix or by a consistently repeating set of species. If *Atta* nests are an important selective force, then certain plant species or phenotypes of a species should (i) depend disproportionately on the conditions generated by the nests for survival or improvement of fitness, or (ii) be selectively harvested by the ants for their seeds, which could increase the seeds' viability and deposit them in sites that favour or improve their germination, establishment and survival rates, and (iii) possess dependent or beneficiary relationships with the ant nest sufficiently prolonged and consistent to allow for the action of natural selection.

Independent of the existence of effects at an evolutionary scale, *Atta* nests are involved in various ecological processes that could affect the productivity and composition of neotropical forests. Parts 2 and 3 above provide many examples of ecological importance. In addition, by increasing spatial heterogeneity, *Atta* nests can positively influence the species richness of plants and animals in an area (Cherrett 1989; Garrettson *et al.* 1998). Although not described here, *Atta* nests can act as feeding, nesting and/or reproductive areas for certain animal species. For example, at least 111 animal species are found associated with *Atta* nests, and at least 30% have narrow associations with them (Weber 1982; Cherrett 1989; Della Lucia *et al.* 1993). Furthermore, various species of reptiles use *Atta* nests as egg-laying sites (Azevedo-Ramos & Mountinho 1994).

STIMULATING REMARKS

Various characteristics of *Atta* nests could make them important influences on neotropical rain forest dynamics: (i) unlike other "bottom–up" gaps (but like treefall gaps), the size of the disturbance is large enough to stimulate plant response; (ii) they are a common component of neotropical rain forests; (iii) the nests die or are abandoned frequently (high turnover rate); and (iv) their effects on the soil are important for plants and remain after the colony dies or abandons them. The scale of these characteristics makes the abandoned or dead nests spatially, temporally and qualitatively a good "landing" for plants. We hope that the information presented in this work will stimulate future research on how beneficial this "landing" actually is.

ACKNOWLEDGEMENTS

To B. Loiselle, D.A. Clark, R. Montgomery, M. Aizen and J.P. Groover for important comments that improved the manuscript considerably. C. Chavez, F. Duran, E. Toral and N. Velazquez helped with the light and litter measurements in Costa Rica. We also thanks the Organization for Tropical Studies for the use of the facilities of La Selva Biological Station.

APPENDIX 1

Light level (Mean ± 1 SD, in μmol m^{-2} s^{-1}) at ground level on *Atta cephalotes* nests, treefall gaps and adjacent forests (*n* = 3 in each case) measured in a cloudy day in an old-growth tropical rain forest at La Selva Biological Station, Costa Rica.

Light measurements were taken simultaneously in each time lapse on nests, treefalls and adjacent forest with light meters Extech à model 401025. Lux units were converted to μmol m^{-2} s^{-1} using the conversion factor proposed by Young *et al.* (1987). In each case, the mean value originate from 10 random points measured at 0 cm (ground level). Values between parentheses are the average coefficients of variation (%), and can be considered as an index of the spatial variation of the light level (higher values, higher spatial variation). Treefall gaps were less than 6-month-old (O. Vargas, personal communication). We used active leaf-cutting ant nests because they were clearly of understory vegetation, a similar situation that will

	8 a.m. (+)	9.30 a.m. (*, +)	11 a.m. (*)	1.30 p.m. (*, +)	3 p.m. (+)
Treefall gap	6.6 ± 5.1 (91)^{a}	17.4 ± 2.7^{a} (102)^{a}	20.4 ± 23.8^{a} (100)	21.7 ± 12.9^{a} (81)^{a}	6.4 ± 3.3 (98)^{a}
Atta nest	6.7 ± 8.0 (43)^{b}	9.8 ± 7.1^{b} (47)^{b}	11.6 ± 9.3^{a} (65)	13.3 ± 9.7^{a} (37)^{b}	5.5 ± 2.9 (43)^{b}
Adjacent forest	3.6 ± 1.8 (44)^{b}	8.3 ± 3.4^{b} (41)^{b}	3.3 ± 1.4^{c} (62)	6.2 ± 2.0^{b} (34)^{b}	3.1 ± 2.0 (37)^{b}

characterize the top of a recently abandoned or dead *Atta* colony. In each column (separately for light levels and coefficient of variation), means which different superscripts are significantly different. $*P < 0.10$ for light level and $+P < 0.10$ for coefficient of variation (Kruskal–Wallis tests). The minimum–maximum daily values of light levels were 0.1–100, 0.5–40 and 0.5–22 µmol m^{-2} s^{-1} for tree-fall gaps, *Atta* nests and old-growth forest ground, respectively.

APPENDIX 2

Litter cover and litter biomass (mean ± 1 SD) at ground level on *Atta cephalotes* nests, treefall gaps and adjacent forests ($n = 3$ in each case) in an old-growth tropical rain forest at La Selva Biological Station, Costa Rica.

	Atta nest	Adjacent forest	Treefall gap
Litter cover (%)	50 ± 2.1^{a}	84.1 ± 8.1^{b}	89.8 ± 8.6^{b} (**)
Litter biomass (dry g 0.25 cm^{-2})	9.8 ± 6.7^{a}	21.2 ± 1.3^{b}	39.2 ± 16.1^{c} (**)

Litter cover were measured in each nest, treefall gap and adjacent forest with three 1-m^{2} plots subdivided in 16 squares. In each plot we randomly choose four random subplots to measure litter biomass. In each row, values with different superscripts are significantly different. $**P < 0.01$, Kruskal–Wallis test.

REFERENCES

Agyeman, V., Swaine, M. & Thompson, J. (1999). Responses of tropical tree seedlings to irradiance and the derivation of a light response index. *J. Ecol.*, 87, 815–827.

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. J.*, 45, 790–794.

Amante, E. (1964). Nota previa sobre a estrutura do ninho de una nova formiga sauva (*Atta* sp) (Hymenop., Formicidae). *Biológico*, 30, 96–97.

Amante, E. (1967). Prejuizios causados pela formiga sauva en plantacoes de Eucalyptos e Pinus no estado de Sao Pablo. *Silvicultura Em Sao Pablo*, 6, 355–363.

Autori, M. (1942). Contribucao para o conocimento da sauva (*Atta* spp) 3. *Excavacao de un Sauverio. (Atta Sexdens). Archivos Do Instituo Biologico Do Sao Pablo*, 13, 137–148.

Azevedo-Ramos, C. & Mountinho, C. (1994). Amphisbaenians (Reptilia: amphisbaenidae) in nest of *Atta sexdens* in eastern Amazonia. *Brazil. Entomol. News*, 18, 3–4.

Bazzaz, F.A. (1983). Characteristics of populations in relation to disturbance in natural and man-modified ecosystems. In: *Disturbance and Ecosystems* (eds Mooney, H. & Godron, M.). Springer-Verlag, New York, pp. 259–274.

Bianchi, G. (1998). Densidad poblacional de hormigas cortadoras (*Atta cephalotes*) en la reserva biológica La Selva, Costa Rica. In: *Ecología tropical y conservación, 98–2. O.T.S. Course Book* (eds Farji-Brener A.G. and Chinchilla F.). San José, Costa Rica, pp. 289–291.

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

Brokaw, N. (1985). Treefalls, regrowth, and community structure in tropical forests. In: *The Ecology of Natural Disturbance and Patch Dynamics* (eds Picket S. & White P.). Academic Press, San Diego, pp. 53–69.

Bucher, E. (1982). Chaco and Caatinga-South American arid savannas, woodlands and thickets. In: *Ecology of Tropical Savannas* (eds Huntley, B. & Walker, B.). Springer-Verlag, Berlin, pp. 48–79.

Chazdon, R. & Fetcher, N. (1984). Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *J. Ecol.*, 72, 553–564.

Cherrett, J.M. (1986). Leaf-cutting ants, biogeographical and ecological studies. In: *Ecosystem of the World 14b, Tropical Rain Forest Ecosystem* (eds Lieth, H. & Werger, M.). Elsevier, New York, pp. 473–488.

Clark, D. (1990). The role of disturbance in the regeneration of neotropical moist forests. In: *Reproductive Ecology of Tropical Forest Plants. Man and the Biosphere Series.* 7 (eds Bawa, K. & Hadley, M.). Unesco, Paris, 291–315.

Coutinho, L. (1982). Aspectos ecologicos da saúva no cerrado. Os murundus de tierra, as caracteristicas psamofiticas das especies de sua vegetacao e a sua invasao pelo Capim Gordura. *Revista Brasilera de Biologia*, 42, 147–153.

Coutinho, L. (1984). Aspectos ecológicos da sauva no cerrado. A saúva, as queimadas e sua possivel relacao na ciclagem de nutrientes minerais. *Boletim Zoologico de la Universidad de Sao Paulo*, 8, 1–9.

Dalling, J. & Wirth, R. (1998). Dispersal of *Miconia argentea* seeds by the leaf-cutting ant *Atta colombica*. *J. Trop. Ecology*, 14, 705–710.

Dangerfield, J., McCarthy, T. & Ellery, W. (1998). The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *J. Trop. Ecology*, 14, 507–520.

Della Lucia, T., Moreira, D. & Oliveira, M. (1993). Inimigos naturais e organismos associados aos ninhos. In: *As Formigas Cortadeiras*, (eds Della Lucia, T.). Vicosa, Brazil, pp. 131–150.

Denslow, J.S. (1980). Gap partitioning among tropical rainforest trees. *Biotropica Suppl.*, 12, 47–55.

Farji-Brener, A.G. & Sierra, C. (1993). Distribution of attacked plants along trails in leaf-cutting ants: consequences in territorial strategies. *Revista Biología Tropical*, 41, 891–896.

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

Farji-Brener, A.G. & Silva, J. (1995b). 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. (1996). Leaf-cutting ant *Atta laevigata* aid to the establishment success of *Tapirira velutinifolia* (Anacardiaceae) seedlings in a parkland savanna. *J. Trop. Ecology*, 12, 163–168.

Farji-Brener, A.G. & Medina, C. (2000). The importance of where to dump the refuse: seed banks and fine roots in nests of the leaf-cutting ants *Atta cephalotes* and *Atta colombica*. *Biotropica*, 32(1), 120–126.

Forti, L. & Moreira, A. (1997). Architecture of Atta nests. In: *Mirmecologia Neotropical. Anais Do VI International Pest Ant Symposium* (eds Delabie, J., Campiolo, S., Do Nascimiento, I. & Ferreira, C.). Ilheus, Brazil, pp. 91.

Fowler, H., Da-Silva, L., Forti, C. & Saes, N. (1986). Population dynamics of leaf-cutting ants. In: *Fire and Leaf-Cutting Ants: Biology and Management* (eds Logfren, S. & Vander Meer, R.). Westview Press, Boulder, CO, pp. 123–145.

Garrettson, M., Stetzel, J., Halpern, B., Hearn, J., Lucey, B. & Mckone, M. (1998). Diversity and abundance of understory plants on active and abandoned nest of leaf-cutting ants (*Atta cephalotes*) in Costa Rica rain forest. *J. Trop. Ecology*, 14, 17–26.

Haines, B. (1975). Impact of leaf-cutting ants on vegetation development at Barro Colorado Island. In: *Tropical Ecological Systems, Trends in Terrestrial and Aquatic Research* (eds Goley, F. & Medina, E.). Springer-Verlag, New York, pp. 99–111.

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

Hanzawa, F., Beattie, A. & Culver, D. (1988). Directed dispersal: demographic analysis of an ant-dispersed mutualism. *Am. Naturalist*, 131, 1–13.

Hartshorn, G. (1976). Tree falls and tropical forest dynamics. In: *Tropical Trees as Living Systems* (eds Tomlison, P. & Zimmerman, M.). Cambridge University of Press, New York, pp. 617–630.

Hartshorn, G. (1980). Neotropical forest dynamics. *Biotropica Suppl.*, 12, 23–30.

Jaffe, K. & Vilela, E. (1989). On nest densities of the leaf-cutting ant *Atta cepahlotes* in tropical primary forest. *Biotropica*, 21, 234–236.

Jones, C., Lawton, J. & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, 78, 1946–1957.

Jonkman, J. (1978). Nests of the leaf-cutting ant *Atta vollenweideri* as accelerators of succession in pastures. *Z Angewandte Entomologie*, 86, 25–34.

Jonkman, J. (1979). Distribution and densities of nest of the leaf-cutting ant *Atta vollenweideri* Forel in Paraguay. *Z Angewandte Entomologie*, 88, 27–43.

Kaspari, M. (1993). Removal of seeds from Neotropical frugivore droppings. Ants response to seed number. *Oecologia*, 95, 81–88.

Kyereh, B., Swaine, M. & Thompson, J. (1999). Effect of light on the germination of forest trees in Ghana. *J. Ecol.*, 87, 772–783.

Leal, I. & Oliveira, P. (1998). Interactions between fungus-growing ants (Attini), fruits and seeds in cerrado vegetation in southeast Brazil. *Biotropica*, 30, 170–178.

Levey, D.J. (1988). Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology*, 69, 1076–1089.

Lugo, A., Farnworth, E., Pool, D., Jerez, P. & Kaufman, G. (1973). The impact of the leaf cutter ant *Atta colombica* on the energy flow of a tropical wet forest. *Ecology*, 54, 1292–1301.

Metcalfer, D. & Turner, I. (1998). Soil seed bank from lowland rain forest in Singapure: canopy-gap and litter-gap demanders. *J. Trop Ecology*, 14, 103–108.

Moreira, A., Vitorio, A. & Forti, L. (1995). Arquitetura da colonia da sauva *Atta laevigata* (Hymen., Form.). In: *Anais XII Encontro de Mirmecologia*. Brazil, pp. 67.

Orians, G. (1982). The influence of tree-falls on tropical forests species richness. *Trop. Ecol.*, 23, 255–279.

Vazquez-Yanes, C., Orozco-Segovia, A., Rincon, E., Sanchez-Coronado, M., Huarte, P., Toledo, J. & Barradas, V. (1990). Light beneath the litter in a tropical forest: effect on seed germination. *Ecology*, 71, 1952–1958.

Perfecto, I. & Vandermeer, J. (1993). Distribution and turnover rate of a population of *Atta cephalotes* in a tropical rain forest in Costa Rica. *Biotropica*, 25, 316–332.

Putz, F. (1983). Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology*, 64, 1069–1074.

Putz, F. & Milton, K. (1983). Tree mortality rates on Barro Colorado Island. In: *The Ecology of Tropical Forest: Seasonal Rhythms and Long-Term Changes* (eds Leigh, E., Rand, S. & Windsor, D.). Smithsonian Institution Press, Washington, D.C., pp. 95–100.

Rissing, S. (1986). Indirect effect of granivory by harvester ants: plants species composition and reproductive increase near ant nest. *Oecologia*, 68, 231–234.

Roberts, J. & Heithaus, J. (1986). Ants rearrange the vertebrate-generated seed shadow of neotropical fig tree. *Ecology*, 67, 1046–1051.

Sanford, R.L., Braker, E. & Hartshorn, G. (1986). Canopy openings in a primary neotropical lowland forest. *J. Trop. Ecology*, 2, 277–282.

Schupp, E., Howe, H., Augspurger, C. & Levey, D. (1989). Arrival and survival in tropical treefall gaps. *Ecology*, 70, 562–564.

Sollins, P. (1998). Factors influencing species composition in tropical lowland rain forest: does soil matter? *Ecology*, 79, 23–30.

Stahel, G. & Geijskes, D. (1939). Ueber den bau der nester von *Atta cephalotes* L. & *A. sexdens* L. (Hymenop., Formicidae). *Revista Entomologia*, 10, 27–78.

Uhl, C., Clark, H., Dezzeo, N. & Maquirrino, P. (1988). Vegetation dynamics in Amazonian trefall gaps. *Ecology*, 69, 751–763.

Vasconçelos, H. & Cherrett, M. (1995). Changes in leaf-cutting ant populations (Formicidae; Attini) after the clearing of mature forest in Brazilian Amazonia. *Studies Neotrop Fauna Environ.*, 30, 107–113.

Veneklaas, E. & Poorter, L. (1998). Growth and carbon partitioning of tropical seedlings in contrasting light environments. In: *Physiological Mechanisms and Ecological Consequences* (eds Lambers, H., Poorter, H. and Van Vuuren, M.). Bakhuys Publishers, the Netherlands, pp. 337–361.

Vitousek, P. (1984). Litterfall, nutrient cycling and nutrient limitation in tropical forests. *Ecology*, 65, 285–298.

Vitousek, P. & Denslow, J. (1986). Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *J. Ecol.*, 74, 1167–1178.

Weber, A. (1982). Fungus ants. In: *Social Insects*, Vol. 4 (ed. Hermann, H.). Academic Press, London, pp. 255–363.

Whitmore, T. (1989). Canopy gaps and the two major groups of trees. *Ecology*, 70, 536–538.

Young, S., David, C.T. & Gibson, G. (1987). Light measurement for entomology in the field and laboratory. *Physiol. Entomol.*, 12, 373–379.

Young, T. & Hubbell, S. (1991). Crown asymmetry, treefalls, and the repeat disturbance of broad-leaved forest gaps. *Ecology*, 72, 1464–1471.

BIOSKETCH

Alejandro G. Farji-Brener's research interests include insect–plant interactions, ant ecology and leaf-cutting ants' effects on tropical and temperate habitats.

Editor, J.P. Grover
Manuscript received 30 September 1999
First decision made 30 November 1999
Manuscript accepted 1 February 2000